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Implications of increased deciduous cover on stand structure and aboveground carbon pools of Alaskan boreal forests

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Abstract. Fire activity in boreal forests has increased recently with climate warming, altering stand structure and composition in many areas. Changes in stand dynamics have the potential to alter C cycling and biophysical processes, with feedbacks to global and regional climate. Here, we assess the interactions between fire, stand structure, and aboveground C accumulation and storage within boreal forests of interior Alaska, where increased fire severity is predicted to shift forest composition from predominantly black spruce (*Picea mariana*) to greater deciduous cover. We measured aboveground biomass and net primary productivity (ANPP) of trees and large shrubs, snags, and downed woody debris across 44 mid-successional (20–59 years since fire) stands of varying deciduous importance value (IV), determined by relative density, basal area, and frequency of deciduous trees and large shrubs within each stand. Aboveground biomass, ANPP, and deciduous snag biomass increased significantly with increased deciduous IV and years since fire. Deciduous IV had little influence on evergreen snag biomass and downed woody debris, but both C pools decreased with years since fire. Forest type also affected stand structure and C pools. Black spruce stands had shorter trees with less basal area and aboveground biomass and slower rates of biomass accumulation and ANPP compared to those dominated by trembling aspen (*Populus tremuloides*) or Alaska birch (*Betula neoalaskana*). These parameters in black spruce stands were similar to mixed stands of black spruce and aspen but were often lower than mixed stands of black spruce and Alaska birch. Much of the biomass accumulation in deciduous stands was attributed to higher tree-level ANPP, allowing individual stems of deciduous species to accumulate more stemwood/bark faster than black spruce trees. If increased fire activity shifts stand composition from black spruce to increased deciduous cover, ANPP, aboveground tree/large shrub biomass, and deciduous snag biomass will increase, leading to increased aboveground C pools in mid-successional forest stands of interior Alaska. While species dominance shifts like these will impact aboveground patterns of landscape-level C cycling in boreal forests, variations in soil C pools and forest properties like albedo must also be assessed to accurately determine implications for global and regional climate.

Key words: aboveground net primary production (ANPP); Alaska, USA; biomass; boreal forest; carbon; climate change; deciduous; fire; *Picea mariana*; snag; succession; woody debris.

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Introduction

Wildfire is the primary disturbance in the boreal forest biome (Johnson 1992, Payette 1992, Goldammer and Furyaev 1996) and is a fundamental driver of ecosystem processes, including forest stand development (Van Cleve et al. 1983*a*), biogeochemical cycles (Amiro et al. 2009), and energy and water balance (McGuire et al. 2006, Randerson et al. 2006). Over the last three decades, fire frequency, extent, and severity have increased in many areas of the boreal forest, probably due to climate warming and drying (Kasischke and Turetsky 2006, Soja et al. 2007), and global climate change models predict a further intensifying fire regime as atmospheric temperatures increase (Stocks et al. 1998, Tchebakova et al. 2009). Because boreal forests contain a large proportion of global terrestrial carbon (C) stocks (Kasischke and Stocks 2000), there has been great interest in understanding the effects of an altered fire regime on these ecosystems and potential feedbacks to climate warming (e.g., Randerson et al. 2006, Bond-Lamberty et al. 2007, Johnstone et al. 2010*a*, Beck et al. 2011). Directly, increased fire activity can reduce C stored in vegetation and organic soils and increase atmospheric CO_2 concentrations (Balshi et al. 2009), creating a positive feedback to climate warming (Kasischke et al. 1995, Kurz et al. 2008). Fires can also initiate an array of indirect effects on forest regrowth and stand dynamics that influence C accumulation patterns (Kasischke et al. 2000) and surface energy fluxes (Randerson et al. 2006) and ultimately determine whether an altered fire regime will lead to a positive or negative feedback to climate warming (Goetz et al. 2007).

One of the most important ways an intensifying fire regime may indirectly impact boreal forest stand dynamics and C pools is by altering demographic processes and creating a pattern of forest regrowth that differs from the pre-fire stand. Across the boreal forest, post-fire recruitment of trees and large shrubs is largely controlled by the depth of the soil organic layer (SOL) because this determines the distance a seedling's root must grow before reaching the mineral soil, which provides a more stable moisture environment than the SOL (Johnstone and Chapin 2006, Greene et al. 2007). With increasing fire severity, SOL consumption increases, decreasing SOL depth and increasing mineral soil exposure (Kasischke and Johnstone 2005, Turetsky et al. 2010). These post-fire changes in SOL depth and soil characteristics can strongly influence successional trajectories of dominant plant species (Kasischke et al. 2000) because of variable plant recruitment strategies exhibited by potential colonizers (Johnstone and Chapin 2006) and the tendency for post-fire recruitment patterns to predict future stand dynamics (Johnstone et al. 2004, Johnstone et al. 2010*b*, Johnstone et al. 2010*c*). Differences in dominant vegetation among successional trajectories can, in turn, alter stand attributes and C storage because of differences in vegetation longevity, productivity, growth habit, litter quality, and flammability. Thus, understanding how post-fire stand dynamics and C pools vary with shifts in dominant vegetation is essential for predicting how boreal forests will influence future patterns of land-atmosphere C exchange and scaling up stand-level C budgets to the landscape. Yet, despite the importance of post-fire stand dynamics and C accumulation patterns within boreal forests to climate feedbacks, our current knowledge of how these parameters vary with an intensifying fire regime remains limited.

To address this limitation, we quantified aboveground tree and large shrub biomass, net primary productivity (ANPP), snag biomass, and downed woody debris within boreal forests of interior Alaska, where many areas previously dominated by the evergreen conifer black spruce (*Picea mariana* (Mill.) B.S.P.) are predicted to shift to stands with greater cover of deciduous species such as Alaska birch (*Betula neoalaskana* Sarg.) and trembling aspen (*Populus tremuloides* Michx.) (Rupp et al. 2002, Chapin et al. 2004, Johnstone et al. 2010*b*). This shift is expected because recent increases in burn area and severity have favored the establishment and growth of light-seeded deciduous species, which readily germinate on high moisture mineral seedbeds (Johnstone and Kasischke 2005, Johnstone and Chapin 2006, Johnstone et al. 2010*b*). In contrast, post-fire recruitment of black spruce occurs via a large aerial seedbank contained within semi-serotinous cones (Viereck 1973). Large inputs of relatively heavy seeds occurring soon after the fire disturbance maximizes black spruce establishment following low-severity fires (Johnstone and Chapin 2006). This has facilitated a historical pattern of successional self-replacement following fire (Kurkowski et al. 2008) and continued dominance of these stands across the landscape (Chapin et al. 2004).

We expected a fire-induced shift in dominant vegetation to have important implications for stand dynamics and aboveground C balance during post-fire succession because of fundamental differences between evergreen and deciduous functional types. Black spruce's evergreen growth form and dense, dark foliage create cold, moist understory conditions. These conditions, combined with recalcitrant leaf litter, limit decomposition and nutrient availability and promote a thick organic horizon and permafrost development (Flanagan and Van Cleve 1983), which can lower tree productivity and standing biomass (Van Cleve et al. 1983*b*). Thus, the proportion of C stored in black spruce stands may be higher in SOL compared to aboveground tree components. In contrast, deciduous trees and large shrubs lose their foliage annually, creating a regular supply of organic material to the forest floor. This litter is more easily decomposed because of its higher quality and the more favorable (warmer/drier) understory conditions, leading to faster rates of soil nutrient turnover and increased nutrient availability (Van Cleve et al. 1983*a*). Leaf litter inputs also minimize moss growth, restricting permafrost development, increasing nutrient uptake ability (Van Cleve et al. 1983*a*). All of these conditions tend to promote low high rates of productivity and large amounts of standing biomass within deciduous stands and a thin SOL (Van Cleve et al. 1983*b*).

To evaluate the effects of increasing deciduous dominance on stand dynamics and aboveground C pools within boreal forests of interior Alaska, we sampled 44 mid-successional (20–59 years since fire) forest stands varying in composition from predominantly black spruce to predominantly deciduous trees and large shrubs. Our primary objective was to understand the influence of increasing deciduous dominance on aboveground C pools across a diverse landscape, independent of deciduous species composition. We were interested in 'deciduousness' from a broad perspective for several reasons: (1) most deciduous trees and large shrubs (e.g., willows) are light-seeded and wind-dispersed (Walker et al. 1986), characteristics usually associated with increased abundance following high-severity fires (e.g., Johnstone and Chapin 2006), (2) all deciduous trees and large shrubs represent a source of competition with black spruce (Imo and Timmer 1999), (3) attempts to scale C pools to the landscape are often based on satellite imagery and tend to use the lighter-colored foliage of deciduous species as a whole but do not distinguish between different deciduous species (e.g., Beck et al. 2011), and (4) the amount of biomass contained in deciduous species is important for understanding surface energy fluxes and water balance (Amiro et al. 2006, Liu and Randerson 2008). We focused on mid-successional C dynamics because this stage may become more prevalent with an increase in fire frequency, burn area, and fire season, and most previous C budgets and models utilize data from mature stands (e.g., Gower et al. 2001), while the pervasiveness of fire across the landscape clearly leads to a mosaic of different-aged stands. We also provide estimates of downed woody debris and snag biomass because these are important yet understudied C pools in boreal forests (Harden et al. 2000, Bond-Lamberty et al. 2002*b*) and because we expected fire severity to influence not only demographic processes but to also determine whether fire-killed trees entered the snag or woody debris C pool. Whether dead trees are in contact with the forest floor could affect C dynamics throughout the successional cycle by influencing the susceptibility of these C pools to decomposition (Bond-Lamberty et al. 2002*b*) and/or soil burial (Hagemann et al. 2010). In addition, because our sampling encompassed stands of varying species composition, our data provided a unique opportunity to assess the effects of forest type on mid-successional C pools.

MATERIALS AND METHODS

Study area

This study took place across a ~800 km^2 area of upland boreal forests of interior Alaska (Fig. 1). Climate is continental, with long, cold winters and warm, dry summers. Average monthly surface air temperature in Fairbanks, AK from 1971–2001 ranged from −23°C in January to 17°C in July (Alaska Climate Research Center 2012).

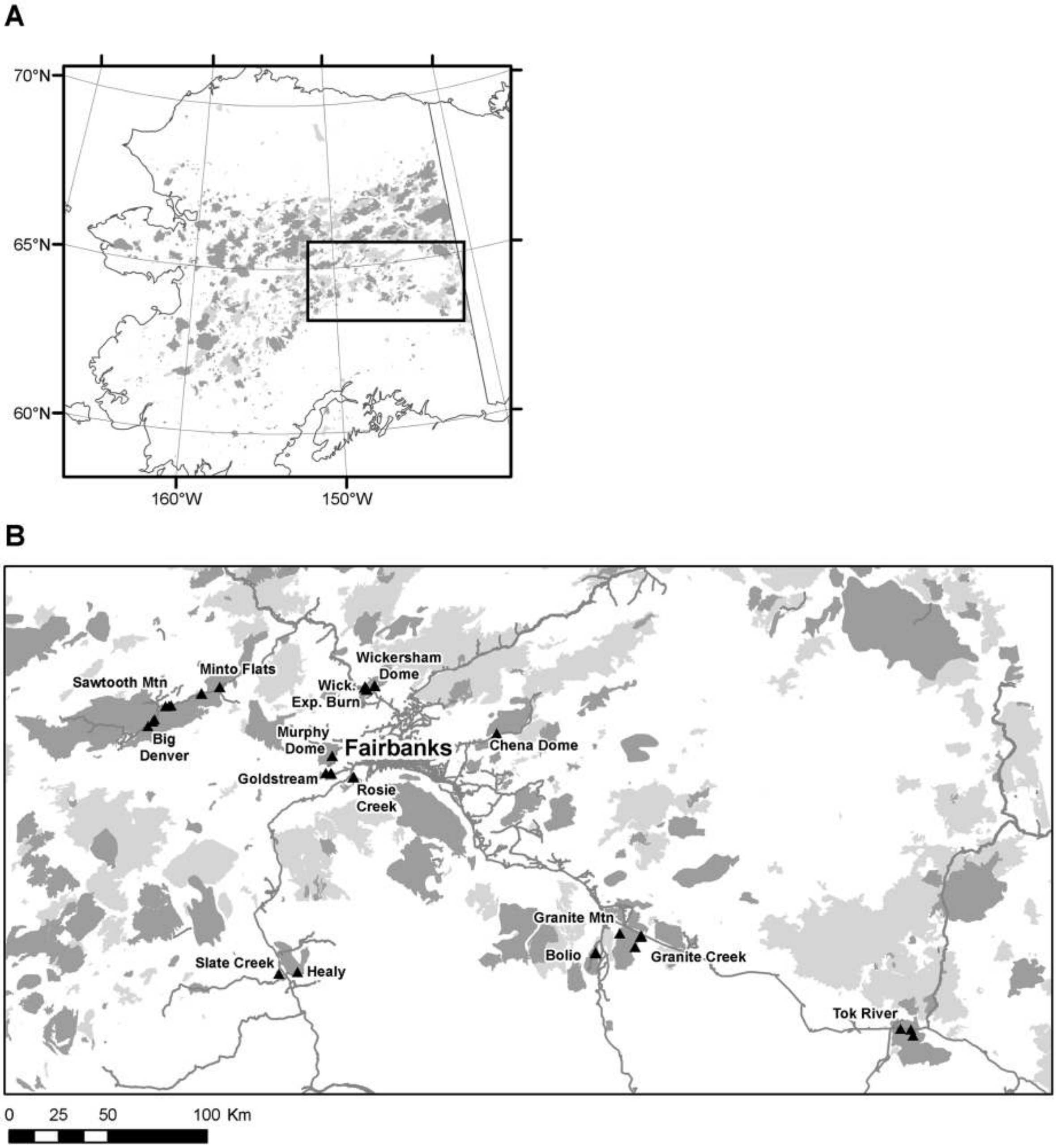

Fig. 1. (A) Study area in Alaska with (B) sampled fire scars labeled and sampling sites represented by solid triangles. All fire scars of intermediate age (20–59 years since fire) at the time of sampling are shown in dark grey. Younger fire scars are shown in light grey.

Nearly half (47%) of annual precipitation (260 mm) occurs during the growing season (June–August). Climate is highly influenced by geographic bounding by the Brooks Range to the north, the Alaskan Range to the south, and the Mackenzie Range to the east, which limits the influence of polar air masses from the north and oceanic air masses from the south. Permafrost is discontinuous in this area (Péwé 1975), and soils range from poorly-drained Gelisols to well-drained, permafrost-free Inceptisols (Dyrness and Viereck 1982). The continental climate also proves conducive to frequent wildfires. Fire return intervals in boreal forests of western North America range from 50–150 years (Payette 1992).

Site selection

To assess the effects of increasing deciduous dominance on aboveground C pools, we surveyed road-accessible, mid-successional fire scars (20–59 years after fire) within interior Alaska during summers 2008–2010 (Fig. 1). Fire scars were mapped by the Alaska Fire Service and their locations acquired from the Alaska Geospatial Data Clearinghouse (U.S. Department of the Interior Bureau of Land Management 2012). Within each fire scar, we located forest stands of varying deciduous dominance using a combination of satellite imagery depicting deciduous versus evergreen cover (Beck et al. 2011) and ground observations. Our goal was to find at least three stands per fire scar ranging from predominantly coniferous to predominantly deciduous canopy composition that could have originated following fire within a stand previously dominated by black spruce. However, this was not always possible, and some fire scars have only one stand or two or more stands with similar canopy composition. We assessed the possibility of black spruce origination by looking for fire-killed stems, stumps, and logs of black spruce, regenerating black spruce in the understory, and by avoiding southeast facing slopes, where black spruce typically does not grow. Fire-killed black spruce were differentiated from white spruce (*P. glauca*) based on size, location of cones, and twig morphology. We also avoided sampling poorly-drained black spruce stands, which have a longer burn return interval and rarely transition to other tree species.

In total, we sampled 53 stands within 16 fire scars. Four stands were removed after determining that actual tree ages were substantially older than the fire age, suggesting these stands did not burn, or had low-severity fires, despite their location within a known fire scar. Four additional stands were removed because of known pre-sampling characteristics that rendered them different from all other sampled stands: two were riparian with substantial white spruce dominance and two were a low-lying, moist black spruce stands. An additional stand that consistently produced outlying data, likely due to its location along a hillside with considerable drainage, was also removed. This left 44 stands for our analyses.

Aboveground biomass and net primary productivity (ANPP) of trees and large shrubs

Stand inventories and allometric equations were used to estimate aboveground biomass of trees and large shrubs (*Salix* and *Alnus* spp.). Within each stand, we established a 100-m long transect subdivided into five 20-m long subsections. Along a 10-m portion of each 20-m subsection (note: a few stands in 2008 were measured along a 5-m long section), we measured diameter at breast height (DBH; 1.4 m tall) or basal diameter (BD; for stems $<$1.4 m tall) of living and dead trees and large shrubs falling within 1 m to either side of the transect. This generated five replicate sub-plots within each stand.

Stand inventories were converted to live and dead biomass using allometric equations. For most species, we derived allometric equations (Appendix A) from raw harvest data (Bonanza Creek Long Term Ecological Research Site 2009; see Yarie et al. 2007 for details of trees sampled). The best-fit power equations ($y = ax^b$; $x =$ BD or DBH; $y =$ dry mass) relating BD and DBH to each tree component and aboveground total biomass were generated by log transforming the data and fitting a best-fit line to determine the value of a and to test significance of the fit (SigmaPlot version 11). The y-intercept of the linear equation generated from the log-transformed data was then back-transformed to determine the value of b. Power equations were confirmed using the power regression function in Microsoft Excel. For *Larix laricina* (Du Roi) K. Koch (only 5 individuals sampled) and *Salix* spp., published equations were used (Bond-Lamberty et al. 2002*a*). For alder (*Alnus* spp.), equations were produced from raw harvest data previously acquired in interior Alaska (F. S. Chapin III, *unpublished data*). Standing dead biomass for alder was estimated directly from harvest data; for all other species, it was estimated as the difference between total live biomass and live crown biomass. Leaf area index (LAI) was measured at 20-m intervals along each transect using a LAI-2000 Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, Nebraska, USA).

Aboveground NPP (ANPP) for each stand was estimated as the sum of annual crown growth and secondary growth. Annual crown growth for trees was estimated using allometric equations (Appendix A) computed from raw harvest data as described above for biomass. Crown growth for large shrubs (*Salix* and *Alnus* spp.) was computed as the sum of foliage biomass (acquired from allometric equations) and new branch biomass, which was estimated as the average proportion of live branch biomass attributable to new growth. This proportion was based on previous harvests and was 10% for *Alnus* spp. (F. S. Chapin III, *unpublished data*) and 17% for *Salix* spp. (Mack et al. 2008). Stand-specific estimates of secondary tree growth were computed using annual diameter increment increases of canopy trees determined from growth ring measurements. At 20-m intervals along each 100-m transect, we randomly selected a tree of each canopy dominant and obtained a wood slab or core from the base of the tree (~20 cm above the organic soil). Wood slabs were dried at 60°C, sequentially sanded using finer and finer grits to obtain a smooth, clear surface, and scanned at 1200 dpi. Ring number and width were determined using WinDendro (Regent Instruments, Ontario). Secondary growth of tree species not sampled but present in the transect (typically <10% of total basal area) was estimated using the average growth increment of all sampled trees within a stand. The mean average annual ring width for the last 5 years was used with stemwood/bark allometry equations to calculate secondary growth. Secondary growth for *Alnus* and *Salix* spp. were estimated as 29.8% growth per year, based on estimates for *S. pulchra* Cham. (Shaver 1986). We present ANPP at the stand level, which is ANPP summed for all trees divided by the sampling area, and $\mathrm{ANPP}_{\mathrm{tree}}$ at the tree level, which is ANPP of the stand divided by stand density.

Downed woody debris

Downed woody debris was measured along each 20-m subsection of the 100-m transect line using the line intercept method (Brown 1974). Downed fine woody debris (FWD) was tallied within five size classes, and downed coarse woody debris (CWD; ≥7 cm) was recorded by species, diameter (cm), and decay class according to Manies et al. (2005). Trees were considered downed woody debris and not snags if they were at angle <45 degrees to the forest floor. Field data for FWD were converted to wood mass per unit area using multiplier values from the Northwest Territories, which take into account specific gravity, tilt, and mean squared diameter (Nalder et al. 1997). All FWD calculations were based on multiplier values for black spruce because we could not identify FWD by species. CWD field data were converted to mass per unit area using decay classes and density values derived from wood of the same or similar tree species (e.g., white birch substituted for Alaska birch, and black spruce substituted for white spruce) within Ontario, Canada (Ter Mikaelian et al. 2008). Tilt was assumed to be 1 for all CWD estimates.

Statistical analysis

A suite of uni- and multivariate regression models were fitted to the data to determine how much of the variation in C pools could be explained by deciduous importance value (IV) and two other potentially important explanatory variables, years since fire and total stem density, which have been shown in other studies to influence C pools (e.g., Mack et al. 2008). To determine the deciduous IV of each stand, we grouped tree and large shrub (*Salix* spp. and *Alnus* spp.) species by their leaf phenology (evergreen vs. deciduous) and then calculated an IV of the deciduous component of each stand based on stand inventory data, where IV = relative density + relative basal area + relative frequency. All response variables were tested for normality and homogeneity of variance prior to analyses and were transformed using logarithmic (biomass and ANPP) or square-root (snags and woody debris) transformations when they did not meet these underlying assumptions. We then generated linear models containing each of the three explanatory variables independently and every combination of these variables and their interactions using the base package in R (R Core Development Team 2010). Since our original study design was to sample several forest stands of varying deciduous dominance within the same fire scar, we also modeled our data using 'fire scar' as a random effect. However, this did not improve our models, so was left out of future analyses. We selected the 'best-fit' multivariate model for each dependent variable based on Akaike Information Criteria (AIC) values corrected for small sample sizes (AICc) and compared this model to the more parsimonious, univariate models. The AIC estimates goodness of fit for a statistical model and is computed as $2k - 2(\ln)L$, where k is the number of parameters in the statistical model, and L is the maximized value of the likelihood function for the estimated model. We specifically used AICc, which takes into account sample size and prevents overfitting of the model (Burnham and Anderson 2004). We present 'goodness-of-fit' results for each significant univariate model and the 'best-fit' multivariate model based on transformed data, but stand-level means and standard errors are presented for untransformed data.

To better understand how compositional variations among forest stands influence C pools, we subdivided stands into forest types based on the relative contribution of each species to total stand biomass. Species occurring infrequently (*L. laricina*, *P. balsamifera* L., and *P. glauca* (Moench) Voss) were grouped into a single 'other' category, and willows and alders were grouped into a 'tall shrub' category. Any species constituting at least 20% of stand biomass was considered to be a dominant stand component. For 27 of 44 stands, black spruce ($n = 14$), aspen ($n = 12$), Alaska birch ($n = 3$), or shrubs ($n = 1$) clearly dominated, having greater than 66% of stand biomass. The other stands grouped into black spruce/shrub ($n = 4$), black spruce/aspen ($n = 3$), black spruce/aspen/shrub ($n = 3$), black spruce/Alaska birch ($n = 6$), and black spruce/Alaska birch/shrub ($n = 2$). The single shrub stand was removed from our analyses, and the stands containing a mix of shrubs and trees were grouped with stands containing the same dominant tree component. This approach generated five forest types (Appendix B).

We compared stand characteristics and C pools among forest types of similar ages using an ANOVA (SAS version 9.2). To do this, we grouped forest types into two age categories: (1) 20–39 years since fire and (2) 40–59 years since fire. This grouping yielded a single Alaska birch stand in the younger age category and single aspen stand in the older age category. Thus, we present data from these stands for comparative purposes, but removed them from statistical analyses. To improve our understanding of how aboveground biomass, ANPP, and ANPP per tree vary with years since fire among forest types, we tested for an interaction effect of forest type and years since fire, and when significant, performed post-hoc multiple comparison tests to determine differences among slopes (GraphPad Prism version 5.0). Because our sample size was reduced by dividing stands into forest types, we report significance for all analyses of forest type at $\alpha = 0.10$. F-values were computed based on Type III sums of square.

RESULTS

Aboveground NPP and C pools as a function of deciduous IV, years since fire, and density

Model comparisons indicated that both deciduous IV and years since fire significantly influenced total aboveground biomass of trees and large shrubs and their aboveground productivity (ANPP) (Table 1), while stand density had no detectable effect. Aboveground biomass and ANPP exhibited a significant linear increase with increased deciduous IV and years since fire (Fig. 2; Table 1). Biomass ranged from a low of 58.0 ± 30.0 g/m^2 in a 26-year-old black spruce stand to 11,614.8 ± 1475.6 g/m^2 in a 40-year-old Alaska birch stand. ANPP varied from 8.4 ± 3.9 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in the same 26-year-old black spruce stand to 833.3 ± 128.3 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in a 51-year-old Alaska birch stand. When considered independently, deciduous IV and years since fire explained 17% and 33% of the variation in biomass and 26% and 12% of the variation in ANPP, respectively. Including both independent variables in a multivariate model substantially improved our ability to explain variations in biomass and ANPP, capturing 64% and 48% of their variability, respectively. The lack of stronger correlations among dependent and independent variables may reflect landscape heterogeneity, as stands were sampled across a vast area encompassing a range of aspects, slopes, and soil conditions. Notably, however, the trend of increasing aboveground biomass with increasing deciduous IV was detected within individual fire scars (data not shown), suggesting the impor-

Table 1. Summary of significant univariate and the 'best-fit' multivariate regression models to predict aboveground C pools within boreal forests of interior Alaska ($n = 44$).

Dependent variable	Model type	Independent variable(s)	P	adj. R^2	AIC$_c$	ΔAIC$_c$
Aboveground biomass (g/m^2)	Significant univariate	Deciduous IV (+)	0.002	0.17	60.2	35.6
		Years since fire (+)	$<$0.001	0.33	51.0	26.4
	'Best-fit' multivariate	**Deciduous IV** (+), **Years since fire** (+)	**$<$0.001**	**0.64**	**24.6**	**0.0**
ANPP (g·m^{-2}·yr^{-1})	Significant univariate	Deciduous IV (+)	0.001	0.26	276.5	13.8
		Years since fire (+)	0.015	0.12	284.5	21.8
	'Best-fit' multivariate	**Deciduous IV** (+), **Years since fire** (+)	**$<$0.001**	**0.48**	**262.7**	**0.0**
Evergreen snag biomass (g/m^2)	Significant univariate	**Years since fire** (−)	**0.011**	**0.13**	**343.7**	**0.0**
Deciduous snag biomass (g/m^2)	Significant univariate	Deciduous IV (+)	0.013	0.12	326.9	21.1
		Years since fire (+)	0.001	0.24	320.4	14.6
	'Best-fit' multivariate	**Deciduous IV** (+), **Years since fire** (+), **Deciduous IV × Years since fire** (+)	**$<$0.001**	**0.49**	**305.8**	**0.0**
Downed woody debris (g/m^2)	Significant univariate	Deciduous IV (+)	0.046	0.07	257.5	9.2
		Years since fire (−)	0.001	0.23	249.0	0.7
		Density (+)	0.015	0.11	255.6	7.3
	'Best-fit' multivariate	**Deciduous IV** (+), **Years since fire** (−), **Density** (+)	**0.001**	**0.29**	**248.3**	**0.0**

Notes: Candidate univariate models included deciduous importance value (IV), years since fire, and total stem density. Multivariate models included all combinations of these variables. Only the best fit multivariate model with the lowest AIC$_c$ (Akaike Information Criteria corrected for small sample sizes) is presented, while all univariate models exhibiting a significant effect are shown. ΔAIC$_c$ indicates the difference between AIC$_c$ values for the best fit model among uni- and multivariate models. A plus or negative sign indicates the direction of the effect of the independent variable on the dependent variable.

tance of this explanatory variable regardless of other factors such as stand age or landscape variability.

Evergreen snag biomass decreased linearly with years since fire, while deciduous snag biomass increased (Table 1, Fig. 2). Deciduous snag biomass also exhibited a significant linear increase with increased deciduous IV. Density had no effect on either dependent variable. Evergreen snag biomass declined from 2472.4 ± 912.0 g/m^2 in a 20-year-old stand to no biomass in numerous stands of various ages. Although years since fire was a significant explanatory variable of evergreen snag biomass, it explained only 13% of the variability. Model comparisons indicated that no multivariate model predicted evergreen snag biomass better than a univariate model based on years since fire. When considered independently, years since fire and deciduous IV explained 12% and 24% of the variability in deciduous snag biomass, respectively, which increased from no biomass in several black spruce stands to 1600.2 ± 557.6 g/m^2 in a 51-year-old Alaska birch stand. Including both explanatory variables and their interaction in a multivariate model explained 49% of the variability in deciduous snag biomass.

Downed woody debris biomass exhibited a more complicated trend, with all three modeled independent variables significantly explaining variation in this parameter (Table 1, Fig. 2). Downed woody debris exhibited only a modest increase with increasing deciduous IV and stand density, but declined with increasing years since fire, ranging from 157.0 ± 43.4 g/m^2 in a 50-year-old black spruce stand with 6.2 trees m^{-2} to 4162.8 ± 1558.9 g/m^2 in a 39-year-old black spruce stand with 5.7 tree/m^2. Deciduous IV and density explained only 7% and 11% of the variation in downed woody debris, while years since fire explained 23%. The 'best-fit' multivariate model included all three explanatory variables, capturing 29% of the variability in downed woody debris. However, model comparisons indicate that this model was only 0.7 AICc units different from the univariate model with only years since fire as an explanatory variable, suggesting that the more complex model is no better at explaining variations in downed woody debris than the more parsimonious univariate model.

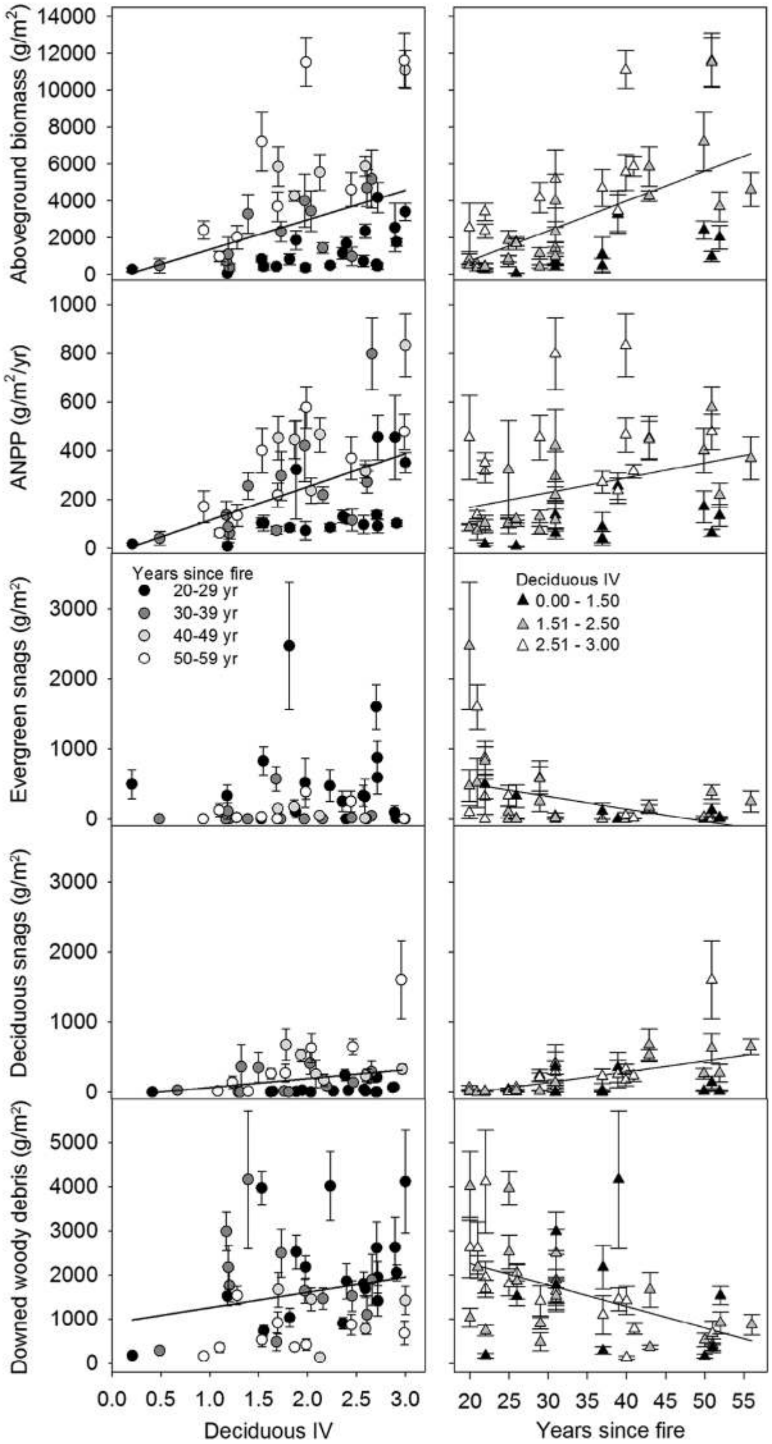

Fig. 2. Variations in aboveground C pools as a function of deciduous importance value (IV) and years since fire across 44 mid-successional boreal forest stands within interior Alaska.

Table 2. Mean stand characteristics and aboveground C pools for 20–39-year-old stands distributed across boreal forest types within interior Alaska.

	Forest type							
Parameter	Black spruce ($n = 10$)	Black spruce + Alaska birch ($n = 4$)	Black spruce + Aspen ($n = 4$)	Aspen ($n = 11$)	Alaska birch ($n = 1$)†	df	F	P
Stand characteristic								
Density (trees/m^2)	4.9 (4.4)	3.0 (0.9)	7.1 (8.0)	3.7 (5.3)	2.6	3, 25	0.59	0.63
Tree diameter (cm)	1.1^A (0.3)	1.4^A (0.4)	1.4^A (0.5)	2.0^B (0.8)	2.8	3, 25	4.94	<0.01
Basal area (cm^2/m^2)	6.2^A (4.7)	7.1^A (4.9)	9.4^{AB} (5.7)	12.2^B (5.2)	20.2	3, 25	2.66	0.07
Height (m)	2.2^A (1.3)	3.3^A (1.3)	3.3^A (2.4)	6.4^B (2.0)	7.1	3, 25	10.70	<0.001
Leaf area index (m^2/m^2)	0.5^A (0.5)	0.5^A (0.2)	0.5^A (0.3)	1.1^B (0.6)	0.2	3, 24	2.93	0.06
Aboveground biomass (g/m^2)‡								
Foliage	92.0 (58.1)	98.5 (67.7)	162.3 (153.9)	145.1 (62.9)	179.1	3, 25	1.27	0.31
Live branches	145.4^A (188.3)	194.4^A (171.7)	254.9^{AB} (155.2)	386.7^B (187.9)	481.4	3, 25	3.25	0.04
Stemwood/bark	355.3^A (278.1)	812.6^A (493.6)	771.6^A (802.7)	1910.5^B (1021.2)	4338.1	3, 25	8.16	<0.001
Total	675.0^A (493.1)	1219.6^A (799.9)	1409.8^A (1342.8)	2705.8^B (1354.2)	5180.9	3, 25	6.90	0.017
ANPP (g·m^{-2}·yr^{-1})								
Crown growth	44.3^A (45.4)	57.5^A (37.2)	75.9^{AB} (40.7)	111.7^B (54.0)	191.5	3, 25	3.74	0.02
Secondary growth	50.2^A (44.7)	93.0^A (64.3)	82.0^A (52.8)	156.1^B (96.7)	606.8	3, 25	3.83	0.02
Total	94.5^A (89.4)	150.4^A (98.2)	157.9^{AB} (92.5)	267.8^B (142.5)	798.3	3, 25	4.12	0.02
Per tree	25.6^A (18.2)	56.6^A (39.0)	61.1^A (49.2)	122.4^B (72.0)	330.6	3, 25	6.35	<0.01
Snags (g/m^2)								
Evergreen	430.4 (749.9)	238.2 (395.3)	248.0 (286.2)	274.6 (351.9)	43.8	3, 25	0.23	0.88
Deciduous	46.4 (111.1)	36.3 (66.3)	109.4 (163.2)	259.0 (382.8)	289.6	3, 25	1.44	0.25
Total	476.7 (733.8)	965.3 (1244.5)	357.4 (200.3)	533.6 (445.1)	333.4	3, 25	0.64	0.59
Downed wood debris (g/m^2)								
Fine woody debris (FWD)	1051.6 (626.4)	1018.2 (247.8)	1823.5 (792.4)	1238.3 (532.4)	567.0	3, 25	1.88	0.16
Coarse woody debris (CWD)	600.0 (683.7)	714.9 (592.8)	1131.7 (794.9)	735.8 (878.0)	1323.4	3, 25	0.45	0.72
Total	1651.6 (1237.8)	1733.1 (777.3)	2955.2 (1343.3)	1974.1 (896.7)	1890.3	3, 25	1.47	0.25

Notes: Values are means (±1 SD). Different superscript letters indicate significant differences among forest types for a given forest parameter.

† Forest types represented by only a single stand were removed from statistical analyses.

‡ A separate allometric equation was used to estimate total aboveground biomass so the individual components do not sum to this number.

Stand characteristics, aboveground NPP, and C pools across forest types

Among younger stands (20–39 years since fire), density, height, diameter, basal area, LAI, aboveground biomass, and ANPP of black spruce stands consistently differed from aspen stands (Table 2). Black spruce stands contained trees that were three times shorter than aspen stands (2.2 ± 1.3 m vs. 6.4 ± 2.0 m) with half the basal area (6.2 ± 4.7 vs. 12.2 ± 5.2 cm^2/m^2) and LAI (0.5 ± 0.5 vs. 1.1 ± 0.6 m^2/m^2). Biomass contained within live branches and stemwood/bark was 2.7 and 5.4 times lower in black spruce stands compared to aspen stands, and total biomass was four times less in black spruce (675.0 ± 493.1 g/m^2) compared to aspen (2705.8

Table 3. Mean stand characteristics and aboveground C pools for 40–59-year-old stands distributed across boreal forest types within interior Alaska.

	Forest type							
Parameter	Black spruce ($n = 4$)	Black spruce + Alaska birch ($n = 4$)	Black spruce + Aspen ($n = 2$)	Aspen ($n = 1$†)	Alaska birch ($n = 2$)	df	F	P
Stand characteristic								
Density (trees/m^2)	4.6^{A} (2.1)	2.8^{B} (0.3)	1.8^{B} (0.8)	0.8	0.9b (0.3)	3, 8	4.10	0.05
Tree diameter (cm)	1.6^{A} (0.4)	2.8^{B} (0.3)	2.7^{B} (0.8)	5.2	6.0c (0.9)	3, 8	33.47	<0.001
Basal area (cm^2/m^2)	13.8^{A} (8.9)	27.0^{B} (4.5)	16.1^{A} (2.4)	21.6	30.8c (2.2)	3, 8	5.12	0.03
Height (m)	2.7^{A} (0.2)	7.9^{B} (3.2)	8.1^{B} (0.8)	10.6	13.8c (0.3)	3, 8	14.86	<0.01
Leaf area index (m^2/m^2)	0.7^{A} (0.6)	2.3^{B} (0.5)	1.1^{A}	1.8	2.9b (0.7)	3, 7	8.79	<0.01
Aboveground biomass (g/m^2)‡								
Foliage	282.0^{A} (116.1)	500.4^{B} (85.2)	249.6^{A} (34.9)	191.5	291.7c (4.3)	3, 8	5.71	0.02
Live branches	442.6^{A} (413.2)	889.1^{BC} (221.8)	546.8^{AB} (86.2)	574.9	1284.7c (11.3)	3, 8	4.43	0.04
Stemwood/bark	1256.7^{A} (683.3)	5273.8^{B} (2430.2)	2953.4^{A} (682.0)	4897.7	9506.5c (334.6)	3, 8	13.36	<0.01
Total	2425.2^{A} (1368.9)	7534.9^{B} (2753.4)	4152.4^{A} (644.8)	5869.4	11363.6c (355.3)	3, 8	11.51	<0.01
ANPP (g·m^{-2}·yr^{-1})								
Crown growth	94.1^{A} (78.2)	214.2^{BC} (62.1)	135.7^{AB} (39.7)	158.2	344.0c (21.5)	3, 8	7.66	<0.01
Secondary growth	109.1 (89.4)	260.1 (13.6)	158.3 (66.9)	158.1	311.7 (229.7)	3, 8	2.48	0.14
Total	203.2^{A} (167.1)	474.2^{BC} (74.4)	294.0^{AB} (106.6)	316.3	655.6c (251.2)	3, 8	4.99	0.03
Per tree	46.3^{A} (31.1)	184.6^{B} (47.7)	189.7^{B} (139.5)	480.0	720.7c (24.2)	3, 8	56.25	<0.001
Snags (g/m^2)								
Evergreen	79.8 (83.7)	152.1 (163.5)	126.3 (177.0)	8.4	0.3 (0.5)	3, 8	0.68	0.59
Deciduous	170.9 (243.9)	434.8 (254.9)	458.5 (265.7)	229.9	963.9 (899.9)	3, 8	1.78	0.23
Total	250.8 (320.2)	586.9 (391.9)	584.8 (442.7)	238.3	964.2 (900.3)	3, 8	1.06	0.42
Downed wood debris (g/m^2)								
Fine woody debris (FWD)	319.3 (176.5)	334.9 (139.0)	632.7 (125.9)	779.3	43.0 (4.6)	3, 8	2.06	0.15
Coarse woody debris (CWD)	282.3 (461.3)	348.9 (611.4)	258.6 (155.1)	177.5	62.0 (56.9)	3, 8	0.23	0.87
Total	602.2 (626.0)	683.8 (675.2)	891.3 (29.2)	896.8	104.9 (52.3)	3, 8	0.31	0.82

Notes: Values are means (± 1 SD). Different superscript letters indicate significant differences among forest types for a given forest parameter.

† Forest types represented by only a single stand were removed from statistical analyses.

‡ A separate allometric equation was used to estimate total aboveground biomass so the individual components do not sum to this number.

± 1354.2 g/m^2) stands. Crown growth, secondary growth, and total ANPP were three times less in black spruce compared to aspen stands, while ANPP expressed on a per tree basis was 5 times less. Although we only sampled a single Alaska birch stand in this age category, biomass and ANPP components of black spruce stands were also consistently lower than those in this Alaska birch stand. C stored within biomass of snags and downed woody debris did not vary among stand types.

Among older stands (40–59 years since fire), density, height, diameter, basal area, LAI, aboveground biomass, and ANPP of black spruce stands often differed from stands comprised of aspen, Alaska birch, or a mix of black spruce and

Table 4. Analysis of covariance results comparing the regression slopes of across forest types for aboveground biomass, aboveground net primary productivity (ANPP), and $\mathrm{ANPP}_{\mathrm{tree}}$.

	Aboveground biomass ($\mathrm{g/m^2}$)			ANPP ($\mathrm{g \cdot m^{-2} \cdot yr^{-1}}$)			$\mathrm{ANPP}_{\mathrm{tree}}$ ($\mathrm{g \cdot m^{-2} \cdot yr^{-1}}$)		
Source	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Forest type	5, 31	1.87	0.12	5, 31	3.35	0.02	5, 31	0.75	0.59
Years since fire	5, 31	17.29	<0.001	5, 31	0.13	0.72	5, 31	7.91	0.008
Forest type × Years since fire	5, 31	4.36	0.004	5, 31	1.99	0.10	5, 31	3.3	0.02
Contrasts									
Black spruce vs. Alaska birch/Black spruce	1, 18	22.77	<0.001	1, 18	5.1	0.04	1, 18	12.91	0.002
Black spruce vs. Aspen/Black spruce	1, 16	3.16	0.09	1, 16	0.81	0.38	1, 16	3.13	0.1
Black spruce vs. Aspen	1, 22	3.27	0.08	1, 22	0.13	0.72	1, 22	11.75	0.002
Black spruce vs. Alaska birch	1, 13	8.63	0.01	1, 13	4.33	0.06	1, 13	15.13	0.002
Alaska birch/Black spruce vs. Aspen/Black spruce	1, 10	10.51	0.009	1, 10	3.05	0.11	1, 10	0.52	0.49
Alaska birch/Black spruce vs. Aspen	1, 16	5.36	0.03	1, 16	3.72	0.07	1, 16	1.43	0.25
Alaska birch/Black spruce vs. Alaska birch	1, 7	0.05	0.84	1, 7	9.56	0.02	1, 7	2.66	0.15
Aspen/Black spruce vs. Aspen	1, 14	0.44	0.52	1, 14	0.92	0.35	1, 14	2.71	0.12
Aspen/Black spruce vs. Alaska birch	1, 5	4.78	0.08	1, 5	12.8	0.02	1, 5	2.38	0.18
Aspen vs. Alaska birch	1, 11	2.05	0.18	1, 11	2.07	0.18	1, 11	0.46	0.52

Alaska birch, but tended to be similar to mixed stands of black spruce and aspen stands (Table 3). The most pronounced differences were between black spruce and Alaska birch stands. Compared to Alaska birch, black spruce stands were five times denser (4.6 ± 2.1 vs. 0.9 ± 0.3 $\mathrm{trees/m^2}$) and comprised of shorter trees (2.7 ± 0.2 vs. 13.8 ± 0.3 m) with smaller diameters that encompassed less than half the basal area (13.8 ± 8.9 vs. 30.8 ± 2.2 $\mathrm{cm/m^2}$). Black spruce stands also had four times lower LAI values than these stands (0.7 ± 0.6 vs. 2.9 ± 0.7 $\mathrm{m^2/m^2}$). Total biomass was approximately five times lower in black spruce (2425.2 ± 1368.9 $\mathrm{g/m^2}$) compared to Alaska birch stands (11,363.6 ± 355.3 $\mathrm{g/m^2}$), due to three times lower live branch biomass and eight times lower stemwood/bark biomass. Although we only sampled a single aspen stand in this age category, biomass and ANPP components of black spruce stands were also consistently lower than those in this aspen stand. Similar to younger stands, C stored within biomass of snags and downed woody debris did not vary among stand types.

Changes in aboveground biomass, ANPP, and $\mathrm{ANPP}_{\mathrm{tree}}$ as a function of years since fire varied among forest types (Tables 4 and 5; Fig. 3). Aboveground biomass exhibited a significant linear increase with years since fire in all forest types, except Alaska birch, which had low replication ($n = 3$), but the rate of biomass accumulation was 2–7 times lower in black spruce stands compared to all other forest types. ANPP expressed at the stand level did not vary with years since fire in black spruce, aspen, or Alaska birch stands, but exhibited a significant linear increase with years since fire in mixed stands. $\mathrm{ANPP}_{\mathrm{tree}}$ increased with years since fire in all forest types, but this trend was not significant in black spruce/aspen stands and Alaska birch stands. The rate of increase was slowest in black spruce stands compared to all other forest types.

Table 5. Parameter estimates, regression coefficient, and significance of linear models for each forest type and aboveground biomass, aboveground net primary productivity (ANPP), and $\mathrm{ANPP}_{\mathrm{tree}}$.

	Aboveground biomass ($\mathrm{g/m^2}$)			ANPP ($\mathrm{g \cdot m^{-2} \cdot yr^{-1}}$)			$\mathrm{ANPP}_{\mathrm{tree}}$ ($\mathrm{g \cdot m^{-2} \cdot yr^{-1}}$)		
Forest type	int	slope	R^2	int	slope	R^2	int	slope	R^2
Black spruce	−650	54.7	0.3*	37.1	2.7	0.06	−3.7	1.1	0.26
Black spruce/Alaska birch	−8804.2	345.7	0.8**	−267	15.2	0.63*	−127	6.5	0.66*
Black spruce/Aspen	−1894.8	115.1	0.95***	−33.7	6.5	0.77*	−50	4.2	0.41
Aspen	−1336.4	150.6	0.47*	263	0.31	0	−188	11.9	0.48*
Alaska birch	−3369.5	311.6	0.76	1379	16.6	0.72	−135	17.9	0.62

$^*P < 0.05$, $^{**}\ P < 0.01$, $^{***}\ P < 0.001$.

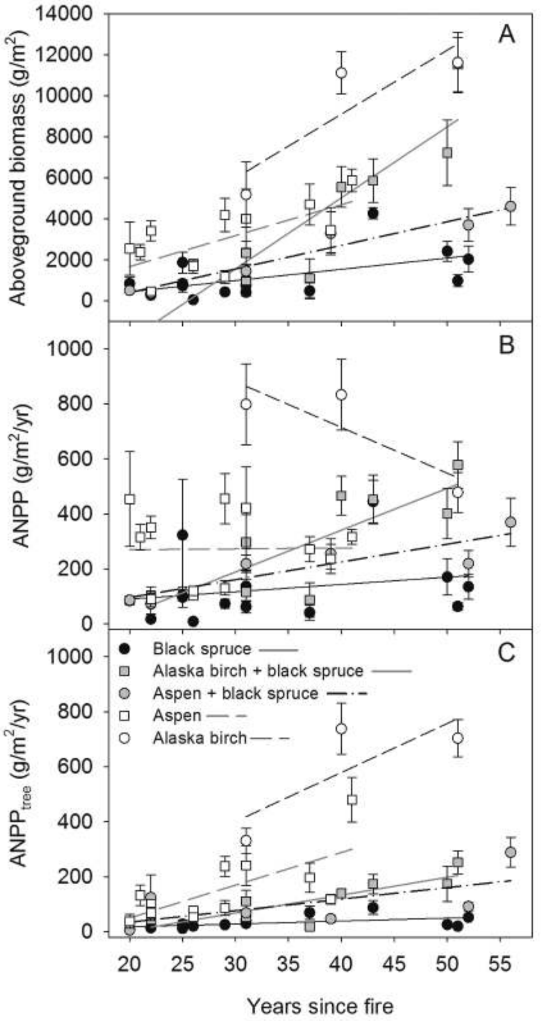

Fig. 3. (A) Aboveground biomass in trees and large shrubs, (B) aboveground net primary productivity (ANPP) of the stand, and (C) ANPP expressed on a per tree basis for mid-successional stands of five forest types located in interior Alaska.

DISCUSSION

If fire intensity continues to increase with climate warming and drying as predicted (Turetsky et al. 2010), many areas of the interior Alaskan boreal forest may experience a threshold response where stands previously undergoing repeated successional cycles of black spruce self-replacement shift to new trajectories characterized by greater deciduous dominance (Johnstone et al. 2010*a*). Beck et al. (2011) suggest that this shift is already underway, as forested areas which burned at a high severity since the 1950s currently exhibit a greater fraction of deciduous biomass than stands which burned at a low severity. This transition will likely have numerous consequences for wildlife (Chapin et al. 2008), local climate (Randerson et al. 2006), and future forest flammability (Rupp et al. 2002, Johnstone and Chapin 2006). Our findings here suggest that a trajectory shift will also alter mid-successional C dynamics, leading to increased C accumulation rates and storage in aboveground C pools.

Aboveground biomass and ANPP

Both aboveground biomass and ANPP of trees and large shrubs increased with increasing deciduous IV. These increases were inextricably linked to increases due to years since fire but were unaffected by stand density. They may also be partially associated with the type of deciduous species, as Alaska birch stands accumulated and stored more biomass than aspen stands. However, because we sampled only three Alaska birch stands, we cannot determine whether these trends hold true across the landscape or simply reflect differences in site quality between sampled aspen and Alaska birch stands. Modeled estimates of aspen vs. Alaska birch biomass across interior Alaska based on Forest Inventory Analysis (FIA) data suggest that landscape-level aboveground biomass in Alaska birch forests is often much greater than that in aspen forests, especially during mid-succession (Yarie and Billings 2002). However, previous research has clearly shown that site quality can produce substantial variations in ANPP and biomass, even among stands of similar age and composition. For instance, Viereck et al. (1983) measured two and three times higher aspen ANPP and biomass, respectively, on a 60-year-old mesic site compared to a 50-year-old dry site within interior Alaska, and Wang et al. (1995) measured approximately two times higher paper birch (*B. papyrifera* Marsh.) biomass on 'good' vs. 'poor' quality sites. Regardless of the factors contributing to high levels of Alaska birch ANPP and biomass, our data clearly demonstrate that these parameters are consistently lower in mid-successional black spruce stands compared to those dominated by aspen or Alaska birch and often lower than stands of mixed composition. Much of the biomass accumulation in deciduous stands can be attributed to higher tree-level ANPP, allowing individual stems of deciduous species to accumulate more stemwood/bark faster than black spruce trees. A similar trend of higher mid-successional biomass in mixed/deciduous stands compared to black spruce stands was also observed by Mack et al. (2008), working in interior Alaska, and Goetz and Prince (1996) in northern Minnesota.

Our estimates of aboveground biomass and ANPP for mid-successional stands vary somewhat from those reported in other studies. Both biomass and ANPP of black spruce and aspen stands were similar to those modeled by Yarie and Billings (2002) for interior Alaska, but our estimates for Alaska birch stands were 2–3 times higher than their estimates. Our data from only three stands may represent anomalously high values associated with site quality or other factors unrepresentative of the larger landscape. Our biomass estimates for mid-successional aspen stands were about three times less than those quantified across a chronosequence of aspen stands in British Columbia, Canada (Wang et al. 1995), likely reflecting regional differences in climate and length of growing season that limit height and diameter growth of individual trees, as stand density in our study was similar to or greater than that measured in the Canadian study. Compared to another study in interior Alaska, our estimate of aboveground biomass of a 40-year-old aspen stand was 12% higher than that reported for a 50-year-old aspen stand growing on a dry site but was four times lower than a 60-year-old aspen stand growing on a mesic site; our biomass estimate for two 40–59-year-old Alaska birch stands was 11% higher than a 77-year-old Alaska birch stand (Viereck et al. 1983, Van Cleve et al. 1983*b*). Our approximations of aboveground biomass and ANPP for black spruce stands were considerably lower than those estimated for 20 and 37-year-old well-drained stands in northern Manitoba, Canada (Wang et al. 2003, Bond-Lamberty et al. 2004), likely because trees in the present study were smaller with less basal area and lower LAI.

Downed woody debris and snags

We found little effect of deciduous IV on downed woody debris or evergreen snag biomass. Evergreen snags were highest in the youngest stands, likely due to a pulse of inputs following the fire disturbance, and declined with years since fire. Downed woody debris declined with years since fire and increased with stand density. A decrease with years since fire suggests decreased inputs following the initial disturbance, burial of downed woody debris by mosses and other plants, and/or incorporation into the soil C pool (Hagemann et al. 2010). Increased downed woody debris with stand density may be indicative of self-thinning leading to whole tree or branch mortality (Sturtevant et al. 1997). Or, the close proximity of trees may cause physical abrasion and transfer of branches to the forest floor.

Little correlation between deciduous IV and downed woody debris or evergreen snag biomass suggest that the factors influencing demographic processes and aboveground biomass of living trees/large shrubs (i.e., fire severity and soil organic layer depth) differ from those affecting snag and woody debris C pools. Alternatively, the influence of fire severity on these pools may be most pronounced in early-successional stands. For instance, a thick residual soil organic layer in young stands burned at a low severity may keep fire-killed trees standing, while consumption of the organic layer in stands burned at high severity may cause trees to fall and enter the downed woody debris pool. However, over time, as the roots of fire-killed snags decay and soils subside around the root ball, even a thick soil organic layer may be unable to keep fire-killed trees in the snag C pool.

Deciduous snag biomass increased with increasing deciduous IV, but only in the older stands. Because longevity of deciduous trees and large shrubs is shorter than black spruce trees, these individuals begin contributing to the deciduous snag pool in the later parts of mid-succession. Thus, as deciduous IV increases, there appears to be two distinct periods of tree mortality: one caused by the initial disturbance and one related to individual deciduous tree mortality as the stand ages. Although snags are more resistant to decomposition than downed woody debris (Wei and Kimmins 1998, Kasischke and Stocks 2000), the earlier mortality of deciduous trees compared to black spruce trees suggests that the C accumulated in aboveground biomass in these stands could represent a less persistent C reservoir.

Implications of increased 'deciduousness' on ecosystem C dynamics

The consequences of increased fire severity on aboveground C accumulation rates and pools will depend on the proportion of the landscape with pre-fire conditions conducive to a trajectory shift. Moderate to well-drained areas (Johnstone et al. 2010*b*) on southerly slopes and mid-elevation (Kurkowski et al. 2008) or those with flat topography (Kasischke et al. 2000) are most susceptible to fire severity impacts and successional shifts because they are drier, burn readily, and are within the physiological tolerances of both black spruce and deciduous trees (Kurkowski et al. 2008). Kurkowski et al. (2008) suggest that about 30% of black spruce stands currently on the landscape today have the potential to shift from a self-replacement trajectory to one with greater deciduous dominance.

To illustrate the potential impacts of a trajectory shift on landscape-level C pools, we used our aboveground biomass estimates to calculate changes in aboveground C pools associated with a shift from mature black spruce forests to mid-successional forests of mixed or deciduous composition. Mature (>60-year-old) black spruce forests cover ~7.3 million ha within interior Alaska, with an average aboveground biomass of 27.7 Mg/ha (Yarie and Billings 2002). Based on aboveground biomass estimates associated with the range of forest types and conditions sampled in this study, if these areas simultaneously shifted to aspen or mixed black spruce/aspen mid-successional stands, aboveground biomass stored in boreal forests of interior Alaska would remain unchanged because these mid-successional stands are able to accumulate and store biomass faster than mature black spruce stands. However, if mature black spruce stands converted to mixed black spruce/Alaska birch or Alaska birch stands, aboveground biomass would increase by 35 (58%) or 142 (235%) million Mg, respectively. The forest biomass of boreal Alaska is currently estimated at 815 million Mg (Yarie and Billings 2002); as such, a trajectory shift to Alaska birch would represent a 12% and 17% increase in total aboveground biomass during mid-succession, respectively. Most biomass in deciduous stands accumulates as stemwood/bark, which decomposes slowly (Trofymov et al. 2002), so would likely provide a long-term snag and downed woody debris C reservoir within these stands even as deciduous trees/large shrubs die (Swift 1977).

In addition to increased 'deciduousness' as a consequence of increased fire severity, compositional shifts may also occur due to direct effects of climate warming and drying, potentially amplifying the effects of shifting forest trajectories on aboveground C pools. For instance, Calef et al. (2005) used a logistic regression modeling approach to examine the effects of climate warming and drying on forest cover and found that deciduous forest stands in interior Alaska expand with increased atmospheric temperatures and decreased precipitation, and that much of this expansion occurred at the loss of white spruce. They also found that deciduous cover increased with decreased fire return interval, but fire-vegetation feedbacks may negate this effect. Although the fire return interval in interior Alaska has recently decreased from 196 to 144 years due to a prolonged fire season and increased burned area (Kasischke et al. 2010), a continued decrease may only occur as long as highly flammable black spruce stands remain dominant across the landscape (Rupp et al. 2002). A shift to greater deciduous dominance would presumably increase fire return intervals (Chapin et al. 2008) due to lower fuel accumulation in the forest floor and understory, higher leaf moisture (Johnson 1992), and lower flammability (Cumming et al. 2000, Chapin et al. 2008).

The role of successional trajectories in C balance also depends upon the fate of mixed and deciduous stands as they mature, yet stand dynamics during later successional stages are largely unknown. Deciduous trees live between 80 and 150 years (Yarie and Billings 2002), but mortality increases and ANPP declines after 60 years (Viereck et al. 1983). Deciduous tree regeneration may proceed asexually via gap dynamics (Cumming et al. 2000), but because aspen and paper birch are generally shade-intolerant (Kobe and Coates 1997), regeneration potential may be limited without wind, ice, or other disturbances to fell multiple trees and create large canopy gaps. Because conifer abundance is usually low in the deciduous understory

(Johnstone and Chapin 2006, Kurkowski et al. 2008), these stands are also unlikely to proceed along a relay successional pathway, where black spruce emerge from understory suppression following mortality of the deciduous canopy. Understory composition of mature deciduous stands is often comprised of shrubs and grasses (Viereck et al. 1983); therefore, these functional types may become the dominant cover where tree regeneration is limited. Mixed stands may eventually succeed to black spruce (i.e., relay succession) as long the fire return interval remains sufficiently long because relay succession may require up to 200 years (Schulze et al. 2005). If this occurs, black spruce stands originating via relay succession may have lower density, aboveground biomass, productivity, and soil C pools than black spruce stands originating via self-replacement because of legacy effects left behind by deciduous trees and large shrubs (Mack et al. 2008).

If increased fire severity also alters belowground biomass or soil C pools, this may either accentuate or offset the differences in aboveground C pools observed between forest stands undergoing different successional trajectories. In black spruce stands, a large soil C pool tends to accumulate due to a thick moss understory and low decomposition rates (Van Cleve et al. 1983*a*; Gower et al. 1997). Deciduous leaf litter physically impedes moss development (Oechel and Van Cleve 1986) and decomposes more rapidly (Flanagan and Van Cleve 1983), lowering mean residence times of soil C (Flanagan and Van Cleve 1983). For example, Van Cleve et al. (1983*b*) reported that the C stored within the forest floor and top 70 cm of mineral soil within mature black spruce stands (120–150-year-old) was ~8,000 and 7,000 g/m^2, respectively, compared to only ~6,000 and 5,000 g/m^2 in mature Alaska birch stands (70–130-year-old). However, aboveground tree biomass was only ~5,000 g/m^2 in these black spruce stands compared to ~12,000 g/m^2 in the Alaska birch stands. While these findings represent only one study area and extremes in species composition, they do suggest that soil C pools in black spruce stands may not always be sufficient to offset the high levels of aboveground biomass in deciduous stands and that consideration of both above- and belowground C pools are essential for estimating the effects of trajectory shifts on boreal forest C dynamics.

CONCLUSIONS

Our data suggest that a climate-driven increase in fire severity and consequent shift from black spruce self-replacement to successional trajectories with greater deciduous dominance will lead to a substantial increase in aboveground C accumulation during mid-succession. This increase will be driven by greater rates of aboveground biomass accumulation, ANPP, and deciduous snag biomass. Whether these increases are sufficient to offset C lost to the atmosphere during the initial high-severity fire disturbance is still unknown, but will ultimately depend upon the accumulation of belowground C pools, fire frequency effects on the length of the successional cycle, and the fate of C pools as stands mature. Increased deciduous dominance during mid-succession will also have regional climate implications (Randerson et al. 2006). Surface albedo will increase because deciduous species have lighter-colored foliage than black spruce, and when leafless, expose the snow-covered ground (Goetz et al. 2007, Beck et al. 2011). Surface conductance and evapotranspiration will also increase, leading to higher levels of atmospheric water vapor (Amiro et al. 2006).

Although this study focused on interior Alaska, the potential for a trajectory shift exists across the boreal forest, yet the effects on ecosystem C balance and climate will likely vary with dominant vegetation, fire frequency, and permafrost conditions. Vegetation functional type (tree vs. shrub vs. grass), growth form (deciduous vs. coniferous), regeneration strategy (seed vs. vegetative), longevity, and flammability all influence C accumulation potential. Fire frequency determines the time frame over which C can accumulate, stand age distribution, and the prevalence of bare, charred soils. Permafrost depth and distribution affect the amount of protected C and its susceptibility to atmospheric release following fire disturbances. Thus, predicting the effects of climate-driven alterations to the fire regime on long-term C balance and climate feedbacks requires the integration of multiple studies assessing C pools within various regions of the boreal forest biome differing in vegetation composition, stand age, and permafrost stability.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Allometric equations and statistics developed to calculate components of tree biomass (g/tree) and annual crown growth (g·tree^{-1}·yr^{-1}) based on basal diameter (trees <1.4 m tall) and diameter at breast height (DBH; trees ≥1.4 m tall). All equations are expressed in the form of $y = ax^b$. Equations for *Salix* spp. and *Larix laricina* were obtained from Bond-Lamberty et al. 2002*a*.

		Basal diameter				DBH			
Species	Tree component	*a*	*b*	R^2	Obs	*a*	*b*	R^2	Obs
Alnus spp.	Total biomass	32.17	2.54	0.96***	10	...	...	...	...
(Alder spp.)	Stemwood/bark	24.62	2.58	0.97***	10	...	...	...	...
	Foliage	1.30	2.37	0.65***	10	...	...	...	...
	Live branches	5.38	2.40	0.83***	10	...	...	...	...
	Live crown	6.77	2.40	0.81***	10	...	...	...	...
	Dead total biomass	22.08	2.59	0.97***	7	...	...	...	...
Betula neoalaskana	Total biomass	26.29	2.68	0.92***	25	164.18	2.29	0.98***	19
(Alaska birch)	Stemwood/bark	26.81	2.62	0.92***	25	147.96	2.25	0.98***	19
	Foliage	0.63	2.65	0.86***	25	6.39	2.10	0.89***	19
	Live crown	1.38	3.08	0.89***	7	15.15	2.49	0.94***	19
	Crown growth	3.45	2.38	0.47	6	10.47	1.92	0.88***	10
Picea glauca	Total biomass	53.74	2.45	0.96***	37	96.77	2.40	0.98***	58
(White spruce)	Stemwood/bark	39.13	2.44	0.95***	37	48.44	2.51	0.98***	58
	Foliage	2.59	2.58	0.75***	29	25.22	2.04	0.78***	49
	Live crown	3.01	2.79	0.90***	37	29.34	2.24	0.83***	58
	Crown growth	5.02	1.75	0.56***	27	7.99	1.62	0.61***	49
Picea mariana	Total biomass	37.29	2.40	0.92***	119	271.46	1.84	0.92***	78
(Black spruce)	Stemwood/bark	11.38	2.67	0.95***	119	117.91	1.99	0.95***	78
	Foliage	14.61	1.86	0.50***	98	55.40	1.47	0.50***	56
	Live crown	21.64	2.12	0.72***	120	83.52	1.80	0.72***	78
	Crown growth	1.83	1.75	0.50***	56	5.26	1.55	0.50***	56
Populus tremuloides	Total biomass	56.83	2.49	0.96***	23	134.10	2.26	0.99***	40
(Trembling aspen)	Stemwood/bark	12.55	2.98	0.99***	5	64.01	2.51	0.98***	23
	Foliage	8.73	2.00	0.93***	23	18.98	1.53	0.91***	41
	Live crown	18.16	2.43	0.98***	5	41.74	1.83	0.83***	21
	Crown growth	3.45	2.38	0.98***	5	10.24	1.76	0.91***	23
Populus balsamifera	Total biomass	58.29	2.44	0.96***	17	133.71	2.29	0.96***	17
(Balsam poplar)	Stemwood/bark	43.35	2.47	0.95***	17	98.26	2.32	0.96***	17
	Foliage	11.22	1.76	0.86***	17	22.16	1.62	0.84***	17
	Live crown	7.36	2.46	0.93***	17	17.24	2.30	0.94***	17
	Crown growth	14.73	1.72	0.86***	15	27.14	1.60	0.85***	15

*** $P < 0.001$.

APPENDIX B

Table B1. Characteristics of 44 mid-successional (20–56 year since fire) forest stands sampled across boreal forests of interior Alaska.

Fire name	Burn year	Year sampled	Since fire (yr)†	Elev (m)	Slope (°)	Aspect (°)	Dec IV‡	Tree age (yr)¶	LAI‖	Forest type††
Slate Creek	1987	2009	22	550	8	68	0.21	PM: 8–11(27)*	0.09	PM
Wickersham Dome	1971	2008	37	526	1	203	0.49	BN: 27–34; PM: 24–31(51)*	nd	PM
Chena Dome	1958	2008	50	229	3	145	0.94	PM: 32–42	0.34	PM
Murphy Dome	1958	2009	51	200	6	11	1.1	PM: 31–45	1.64	PM
Wickersham Dome Exp	1978	2009	31	509	10	108	1.17	BN: 13–22; PM: 20–28	0.14	PM
Minto Flats	1983	2009	26	428	9	103	1.18	PM: 19–22	2.36	PM
Wickersham Dome	1971	2008	37	403	11	235	1.19	BN: 24–35; PM: 23–32	nd	PM + BN
Wickersham Dome Exp	1978	2009	31	521	8	108	1.2	PM: 19–26	1.36	PM
Sawtooth Mountain	1957	2009	52	489	4	213	1.28	PM: 37–42	0.67	PM
Big Denver	1969	2008	39	125	0	234	1.39	PM: 27–34; PT: 30–35	0.62	PM + PT
Rosie Creek	1983	2008	25	210	5	128	1.53	BN: 12–22; PM: 19–22	0.52	PM
Healy	1958	2008	50	642	6	149	1.53	nd	2	PM + BN
Slate Creek	1987	2009	22	553	5	109	1.55	BN: 14–18; PM: 13–16	0.34	PM + BN
Bolio	1981	2010	29	507	2	301	1.58	PM: 11–23(39)*; PT: 27–28	1.69	PT
Sawtooth Mountain	1957	2009	52	502	4	286	1.7	PM: 31–43; PT: 36–40	1.05	PM + PT
Goldstream	1966	2009	43	144	1	38	1.7	BN: 35–37; PM 32–37	2.9	PM + BN
Wickersham Dome Exp	1978	2009	31	494	9	124	1.73	BN: 17–24; PM: 20–25	0.67	PM + BN
Tok River	1990	2010	20	504	0	Flat	1.82	PM: 14–17	0.27	PM
Goldstream	1966	2009	43	144	3	276	1.87	PM: 33–37	1.55	PM
Rosie Creek	1983	2008	25	212	10	154	1.88	BN: 14–21; PM: 22–24	1.35	PM
Wickersham Dome Exp	1978	2009	31	522	8	130	1.97	PM: 21–31; PT: 28–32	0.39	PT
Granite Creek	1987	2009	22	436	1	20	1.98	PM: 11–18	0.13	PM + PT
Murphy Dome	1958	2009	51	197	6	53	1.99	BN: 42–48 (57)*; PM: 33–47	0.12	PM + BN
Big Denver	1969	2008	39	136	0	192	2.04	PM: 25–31; PT: 30–37	0.9	PT
Big Denver	1969	2009	40	269	7	255	2.13	BN: 31–35; PM: 27–32	1.83	PM + BN
Wickersham Dome Exp	1978	2009	31	515	12	87	2.16	PM: 19–25	0.92	PM + PT
Tok River	1990	2010	20	503	0	Flat	2.23	PM: 15–18; PT: 10–17	0.33	PM + PT
Minto Flats	1983	2009	26	473	15	122	2.4	PM: 16–20; PT: 25–26	0.19	PT
Bolio	1981	2010	29	496	2	301	2.41	PM: 19–27	0.29	PM
Granite Mountain	1954	2010	56	419	0	61	2.45	PM: 27–38; PT: 51–53	nd	PM + PT
Wickersham Dome Exp	1978	2009	31	537	7	105	2.46	PM: 14–23; PT: 28–31	0.43	PM + BN
Bolio	1981	2010	29	496	1	308	2.49	PT: 24–28	0.76	PT
Rosie Creek	1983	2008	25	199	6	154	2.57	BN: 13–21; LL: 14–17; PM: 15–20	0.27	PM
Granite Creek	1987	2008	21	385	1	54	2.59	PM: 15–18; PT: 15–19	1.68	PT
Big Denver	1969	2010	41	345	5	206	2.59	PT: 39–41; PM: 26–32	1.78	PT
Wickersham Dome	1971	2008	37	483	11	176	2.61	PM: 22–29; PT: 34–36	1.27	PT
Wickersham Dome Exp	1978	2009	31	494	9	140	2.66	BN: 22–29; PM: 20–25	0.22	BN
Granite Creek	1987	2008	21	382	0	45	2.71	PM: 7–16; PT: 8–17	0.26	SA + AL
Granite Creek	1987	2008	21	383	0	45	2.72	PM: 14–17; PT: 10–15	0.22	PT
Tok River	1990	2010	20	500	1	297	2.89	PT: 15–17	1.56	PT
Minto Flats	1983	2009	26	417	11	99	2.91	PM: 16–22; PT: 25–27	2.39	PT
Murphy Dome	1958	2009	51	208	7	45	2.99	BN: 39–48	0.2	BN
Slate Creek	1987	2009	22	572	5	64	3	BN: 17–20; PT: 19–22	1.97	PT
Big Denver	1969	2009	40	221	8	160	3	BN: 29–34	3.43	BN

Notes: nd = No data. BN = Alaska birch, PG = white spruce, PM = black spruce, PT = trembling aspen, AL = alder, SA = willow. Flat = Stands were on flat ground so do not have slope or aspect.

† Years since fire based on sampling year minus year burned.

‡ Deciduous Importance Value (IV). See *Materials and Methods* for calculation.

¶ Tree age ranges for canopy species.

* Ages in parentheses exceeded years since fire. Stands with two or more trees older than age of fire scar were removed from analyses.

‖ Leaf area index (LAI).

†† Stand composition based on relative contribution of species to total standing biomass. See *Materials and Methods*.