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Recovery of Aboveground Plant Biomass and Productivity After Fire in Mesic and Dry Black Spruce Forests of Interior Alaska

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ABSTRACT

Plant biomass accumulation and productivity are important determinants of ecosystem carbon (C) balance during post-fire succession. In boreal black spruce (*Picea mariana*) forests near Delta Junction, Alaska, we quantified aboveground plant biomass and net primary productivity (ANPP) for 4 years after a 1999 wildfire in a well-drained (dry) site, and also across a dry and a moderately well-drained (mesic) chronosequence of sites that varied in time since fire (2 to ~116 years). Four years after fire, total biomass at the 1999 burn site had increased exponentially to 160 ± 21 g m^{-2} (mean ± 1SE) and vascular ANPP had recovered to 138 ± 32 g m^{-2} y^{-1}, which was not different than that of a nearby unburned stand (160 ± 48 g m^{-2} y^{-1}) that had similar pre-fire stand structure and understory composition. Production in the young site was dominated by re-sprouting graminoids, whereas production in the unburned site was dominated by black spruce. On the dry and mesic chrono-sequences, total biomass pools, including overstory and understory vascular and non-vascular plants, and lichens, increased logarithmically (dry) or linearly (mesic) with increasing site age, reaching a maximum of 2469 ± 180 (dry) and 4008 ± 233 g m^{-2} (mesic) in mature stands. Biomass differences were primarily due to higher tree density in the mesic sites because mass per tree was similar between sites. ANPP of vascular and non-vascular plants increased linearly over time in the mesic chronosequence to 335 ± 68 g m^{-2} y^{-1} in the mature site, but in the dry chronosequence it peaked at 410 ± 43 g m^{-2} y^{-1} in a 15-year-old stand dominated by deciduous trees and shrubs. Key factors regulating biomass accumulation and production in these ecosystems appear to be the abundance and composition of re-sprouting species early in succession, the abundance of deciduous trees and shrubs in intermediate aged stands, and the density of black spruce across all stand ages. A better understanding of the controls over these factors will help predict how changes in climate and fire regime will affect the carbon balance of Interior Alaska.

INTRODUCTION

Fire is part of the natural disturbance regime of many boreal regions, although recent evidence suggests that anthropogenically induced climate change may be increasing the burned area in North American (Kasischke and others 1995; Kurz and Apps 1995, 1999; Kasischke 2000; Stocks and others 2003; Kasischke and others 2006) and Eurasian forests (Dixon and Krankina 1993; Conard and I-vanova 1997; Stocks and others 1998; Zimov and others 1999; Vlassova 2002). Because high-latitude ecosystems store approximately 40% of global carbon (C) stocks in biomass and soils (Dixon and others 1994), an amount equal to the atmospheric C pool, there has been considerable interest in understanding how these systems will respond to climate warming. Combustion of vegetation and forest floor transfers C directly from terrestrial ecosystems to the atmosphere, so increased burned area or fire intensity in the boreal biome could be a strong, positive feedback to atmospheric CO_2 concentrations (Kasischke and others 1995; Kurz and Apps 1995), at least in the early years after fire (Randerson and others 2006). At a regional scale, the effect of fire on species composition, soil drainage, and stand age distribution will ultimately regulate whether the CO_2 feedback is positive or negative. The response of this long-term signal to the combination of climate change and altered fire regime is largely unknown for the boreal biome. Patterns of plant species composition, biomass accumulation, and productivity across post-fire succession are important determinants of the amount (Chen and others 2002; Litvak and others 2003; Bond-Lamberty and others 2004), structure (Bhatti and others 2002; Bond-Lamberty and others 2002b; Wang and others 2003), residence time (Harden and others 2000), and decomposability of C inputs (Hobbie and others 2000) to these systems.

In Interior Alaska, black spruce ((*Picea mariana* (Mill.) BSP) stands cover approximately 70% of the forested area (Viereck and others 1986; Chapin and others 2006b) and occupy landscape positions that range from permafrost-free well-drained soils to permafrost dominated and poorly drained soils (Viereck and others 1983; Chapin and others 2006a). These forests are highly flammable due to their architecture and resin production as well as the thick moss layer on the forest floor (Dyrness and others 1986), and fire return intervals range from 70 to 100 years (Yarie 1981; Viereck and others 1986; Kasischke and others 1995). Wildfires tend to be large and high-intensity (Viereck and others 1983) and while few boreal overstory species survive fire, many understory species re-sprout after fire from buried or protected meristems (Dyrness and others 1986; Mann and Plug 1999). Black spruce are semi-seritonous and release seed after fire, with the majority of trees recruiting in the first 5 years after fire (Zasada and others 1992). Stands may or may not go through a deciduous phase where trembling aspen (*Populous tremuloides*) and tall shrubs (mainly *Salix* spp.), which may re-sprout after fire (Johnstone 2006), dominate over the 15–50 years prior to closure of the black spruce canopy (Chapin and others 2006b). Moss and lichen expansion across the forest floor follows similar timing, with moss cover reaching its maximum between 30 and 50 years (Chapin and others 2006b; Harden and others In Review), concurrent with canopy closure by black spruce and a reduction in deciduous litter. The deciduous phase appears to be related to interactive effects of fire severity and site drainage as evidenced by the fact that sites that burn severely (O'Neill and others 2003), or at a high frequency (Johnstone 2006) have the highest abundance of aspen and willow species. At the landscape level, both the severity and frequency of fire appear to be related to soil drainage (Viereck and others 1983; Harden and others 2000).

Although patterns of species dominance over post-fire succession have been described for Alaskan black spruce stands, there are few published measurements of productivity and biomass after fire. In conjunction with a chronosequence study of soil C dynamics, O'Neill and others (2003) used a mass balance model to conclude that C inputs balanced C losses 7–15 years after fire. Yarie and Billings (2002) used forest inventory data from stands across Alaska (including maritime regions) to estimate generalized biomass accumulation curves for black spruce green timber. They show that biomass accumulation peaked between 75 and 150 years. Simulation modeling of ecosystem C dynamics over post-fire succession (Zhuang and others 2003) suggests that C balance is most sen-

Table 1. Forest Characteristics of Black Spruce Chronosequence Sites Near Delta Junction, Alaska

Drainage[1]	Year burned	Stand dominant (pre-fire)	Ground cover dominants	Organic layer depth (mean, cm ± 1SE)
Well-drained (Dry)	1999	(*Picea mariana*)	*Ceratodon purpureus, Polytrichum* spp.	4.2 (6.8)
	1987	*Populous tremuloides* (*P. mariana*)	*C. purpureus, Polytrichum* spp.	7.8 (12.5)
	~1921	*P. mariana*	Feather moss[2] and lichen[3]	11.9 (15.0)
Moderately well-drained (Mesic)	1999	(*P. mariana*)	*C. purpureus, Polytrichum* spp.	12.3 (12.3)
	1994	*P. tremuloides* (*P. mariana*)	*C. purpureus, Polytrichum* spp.	8.7 (12.6)
	1956	*P. mariana*	Feather moss[2]	8.2 (8.7)
	~1886	*P. mariana*	Feather moss[2]	23.1 (19.9)

[1] *From Manies and others 2004.*
[2] *Dominant species of feather moss: Hylocomium splendens, Pleurozium schreberi, and Aulacomnium spp.*
[3] *Dominant lichen genera are Cetraria, Cladonia, Cladina, and Peltigera.*

sitive to N fixation, moss accumulation, organic layer depth, soil drainage, and fire severity. Finally, there are several comprehensive studies of post-fire succession in Central and Eastern Canada (Black and Bliss 1978; Foster and others 1985; Litvak and others 2003; Wang and others 2003; Bond-Lamberty and others 2004; Harper and others 2005; Lecomte and others 2006), but the trees in these sites inhabit different soil drainage and temperature regimes than their Alaskan relatives, potentially resulting in different rates of ecosystem C dynamics (Vogel and others 2005).

The goals of this study were to describe the changes in community structure and aboveground net primary productivity (ANPP) and biomass that occur over post-fire succession in the upland black spruce forests of Interior Alaska. We present measurements that span two different time scales: recovery 1–4 years after fire and recovery over the entire successional cycle. For the former, we followed vegetation recovery for 4 years after the 1999 Donnelly Flats fire near Delta Junction, Alaska. We used a chronosequence approach for the latter by selecting two sequences of sites in the region that varied primarily in time since fire: a mesic sequence on moderately well-drained soil with permafrost and a dry sequence located on well-drained soils without permafrost (Manies and others 2004). These sequences represent transitions in environmental factors that might occur with climate warming, including loss of permafrost and subsequent increases in soil drainage (Harden 2006).

MATERIALS AND METHODS

Study Sites

This study was conducted in the Donnelly Flats (65°55'N, 145°44'W) area located near Delta

Junction in Interior Alaska, in seven upland sites that were previously dominated by black spruce (*Picea mariana*; Manies and others 2004; O'Neill and others 2002, 2003). All sites were located within a 100-km^2 area on gently sloped alluvial flats that range from moderately well-drained soils dominated by permafrost to well-drained soils where permafrost was largely absent. Soil drainage was based on depth to water table and hydraulic conductivity (Manies and others 2004). Our study (Table 1) include three sites on well-drained soils that burned in stand-killing wildfires in 1999, 1987, and approximately 1921 (Treseder and others 2004, 2007), hereafter the dry chronosequence, and four sites on moderately well-drained soils that burned in 1999, 1994, 1956, and approximately 1886 (Manies and others 2004; Harden 2006), hereafter the mesic chronosequence. Time since last fire was determined by historical record in the younger sites and by tree ring analyses in the older sites. Some or all of these sites have been used to assess the effects of fire on soil C storage and emissions (O'Neill and others 2002, 2003; Zhuang and others 2003; Harden 2006), soil chemistry (Neff and others 2005), hydrogen fluxes (Rahn and others 2002), fungal community composition and dynamics (Treseder and others 2004, 2007), seasonal CO_2 and $^{18}O–CO_2$ fluxes (Welp and others 2006) and energy exchange (Chambers and Chapin 2003; Liu and others 2005; Randerson and others 2006).

Within each chronosequence, sites were chosen to have similar state factors (that is, climate, potential biota, relief, parent material) other than time (Jenny 1941; Amundson and Jenny 1997). *Climate*: Micrometerological data collected in the 1999, 1987, and 1921 dry sites (Liu and others 2005; Randerson and others 2006; Welp and others 2006, 2007) and the 1994 (Chambers and Chapin

2003), 1999 and 1886 mesic sites (Harden and others 2006) support the idea that sites in both chronosequences experienced a similar climatic regime. The regional climate is cold and dry with an annual mean surface air temperature of −2.1°C during the 1970–2000 period (Western Regional Climate Center 2001). Over this same period, mean temperatures in January and July were −20°C and 16.0°C, respectively, and mean annual precipitation (MAP) was 290 mm. Approximately 65% of precipitation fell during June, July, and August. *Potential biota*: Although all stands were currently or historically dominated by black spruce and were in a close enough proximity that they belong to the same regional pool of potentially colonizing organisms, the understory vegetation and ground cover varied with soil drainage and stand age (Table 1). The oldest dry stand was a lichen woodland (Viereck and others 1983), with groundcover dominance split between feathermoss and lichens. *Vaccinium uliginosum* and *V. vitis-idaea* were the most abundant understory species, with deciduous shrubs and trees, forbs and graminoids present but at low abundance. Many of the same species re-sprouted or recruited after fire in the 1999 dry site and dominated the understory in the 1987 dry site. Species characteristic of well-drained ecosystems that were present in all dry chronosequence sites and absent from the mesic sites were the grass *Festuca altaica* and the evergreen shrub *Arctostaphylos uva-ursi*. These species were present, however, on trails and roadsides around the mesic sites. The oldest mesic stand had continuous feathermoss ground cover and a high abundance of *Vaccinium* spp. Feathermoss occupied almost the entire ground surface in the 1956 and 1886 mesic sites. In the 1994 mesic site it persisted in patches that appeared to have escaped burning. Vascular nomenclature follows Hultén (1968) and non-vascular nomenclature follows Vitt and others (1988). *Relief*: Sites in both chronosequences were within a 100-km^2 area with little variation in slope or topography (Manies and others 2004; O'Neill and others 2002). *Parent material*: Soils along both chronosequences were mainly derived from the Donnelly moraine and wind blown loess and have been described in detail elsewhere (O'Neill and others 2002; Manies and others 2004 and http://www.pubs.usgs.gov/of/2004/1271/; Harden and others 2006). Differences in drainage between the chronosequences are thought to be related to differences in water table depth and texture (Manies and others 2004).

Although great care was taken to control state factors within and between chronosequences, it was difficult to fully constrain the effects of past fires on productivity or biomass pools. In the 1999, 1994, and 1987 sites, fires were stand replacing (M. C. Mack, personal observation). In the 1957 mesic site, the relatively small range of tree sizes suggests a single cohort of black spruce. In the mature 1886 mesic and 1921 dry sites where tree sizes are quite variable, however, the number of trees sampled for age was not large enough to determine whether stands are comprised of a single cohort (J. G. Vogel, personal communication). At the landscape-scale, the severity and frequency of fire are likely to be related to soil drainage (Viereck and others 1983; Harden and others 2000). At the site level, however, stochastic factors such as weather conditions, time since last fire, and neighboring vegetation can also affect fire severity. Post-fire vegetation recovery is similarly affected by stochastic processes such as timing of fire in relation to both vegetative and reproductive phenology, proximity of seed source, and/or the effects of past and present climate conditions on demographic processes. Finally, we caution the reader to keep in mind at all times that this is an observational study; we depend on the assumptions of the chronosequence approach to make inferences about time.

Tree Biomass and Primary Production

We used a combination of inventory and allometric methods to estimate aboveground live tree biomass and production in the sites with trees greater than 1.37 m in height, including the 1987 and 1921 dry sites, and the 1956 and 1886 mesic sites. Sixteen 100 m^2 plots were established in the dry sites in four blocks with greater than 100 m between blocks, and six 100 m^2 plots were established at greater than 100 m from each other in the 120-year-old mesic site ($n = 6$). The diameter at breast height (DBH; 1.37 m) was measured on all trees in these plots. In the 1956 mesic site, tree density and DBH were estimated with a modified point-center-quarter method (Manies and others 2004). When applied in the same site (1886 mesic), these methods produced statistically indistinguishable estimates of tree density (plot method = 4933 ± 415, mean ± 1 standard error trees/ha; point-center-quarter method = 4192 ± 900 trees/ha: $t_5 = 0.373$, $P = 0.54$).

Site-specific allometric equations were developed for black spruce in the 1921 dry site and in the 1956 and 1886 mesic sites. An aspen (*Populous tremuloides*) equation was developed for the 1987 dry site; it was also used to estimate aspen biomass in the 1956 mesic site, where aspen comprised 26% of

Table 2. Site-Specific Tree Allometric Equations and Statistics Used to Calculate Tree Biomass (g tree^{-1}) in Black Spruce Stands Near Delta Junction, Alaska

Site (species)	Biomass pool (g tree^{-1})	Slope	Intercept	R^2	df	MSE	P
1886 mesic (*Picea mariana*)	Stem	125.1	−350.0	0.97	1,8	788,578	<0.001
	Coarse old branches	20.9	−37.5	0.44	1,8	867,493	0.04
	Fine old branches	21.0	83.1	0.90	1,8	72,283	<0.001
	Cones	5.0	−55.0	0.48	1,8	41,999	0.03
	Old leaves	32.3	37.4	0.87	1,8	243,995	<0.001
	New branches	1.0	−0.6	0.96	1,8	70.7	<0.001
	New leaves	4.3	13.3	0.87	1,8	4252	<0.001
	Total	130.9	19.0	0.97	1,8	801,820	<0.001
1921 dry (*P. mariana*)	Stem	112.9	30.0	0.90	1,11	1,279,090	<0.001
	Coarse old branches	8.4	−7.6	0.75	1,11	21,844	<0.001
	Fine old branches	7.7	16.6	0.85	1,11	9310	<0.001
	Cones	28.8	−264.5	0.71	1,11	309,415	<0.001
	Old leaves[1]	225.6	−39.9	0.65	1,10	11,170	0.002
	New branches	0.36	2.27	0.68	1,11	55.48	<0.001
	New leaves	1.84	9.01	0.87	1,11	472.2	<0.001
	Total	168.4	248.2	0.90	1,11	3,128,560	<0.001
1956 mesic (*P. mariana*)	Stem	100.9	−30.6	0.97	1,7	97,438	<0.001
	Fine old branches	3.1	29.5	0.93	1,7	201.61	<0.001
	Cones	15.2	−40.7	0.90	1,7	5185	<0.001
	Old leaves	5.1	49.8	0.93	1,7	588.65	<0.001
	New branches	0.1	0.7	0.81	1,8	0.53221	<0.001
	New leaves	0.5	3.1	0.88	1,7	11.5305	<0.001
	Total	119.1	59.5	0.99	1,7	57,953	<0.001
1987 dry (*Populous tremuloides*)	Stem	160.8	−331.1	0.97	1,11	620,226	<0.001
	Old branches	14.0	25.9	0.95	1,11	8865	<0.001
	New branches	3.5	−1.7	0.84	1,10	1036.85	<0.001
	New leaves	13.7	5.1	0.97	1,11	5361.5	<0.001
	Total biomass	190.7	−290.0	0.99	1,11	467,578	<0.001

Independent variable is DBH ^{2} unless otherwise noted.
[1] *Independent variable is ln(DBH).*

the total basal area. In each site, 10–13 trees were selected in a semi-random manner, where initial selection was stratified to span 90% of the stand DBH range as determined by the inventories described above. All trees were harvested in August 2001. Diameter at breast height, basal diameter at moss level, and height were measured. Each tree was felled at ground level, returned to the lab and separated into dead material, stem, coarse old branches (without attached leaves), fine old branches (with attached leaves), cones, dead branches, old leaves, and the current year's leaves and stems. Aspen were separated into dead material, stem, old branches, and the current year's branches and leaves. These components were weighed wet and chopped into small pieces. Subsamples were weighed, dried at 60°C until they reached a constant mass and reweighed to determine dry weight ratio.

For each site, the best-fit linear equation relating the square of DBH (DBH^2; with units of cm^2) to each biomass pool (g biomass m^{-2}) except for old leaves, which was best fit by lnDBH. In all cases, DBH^2 or lnDBH was a better predictor of biomass than was aDBH[b] (data not shown). Data were log-transformed if necessary to meet the assumptions of linear regression. All allometry regression analyses were carried out with Systat version 10.2 (Systat Software Inc. 2002). Allometric equations (Table 2) were combined with plot-level inventory data to estimate biomass on a per unit area basis. Approximately 10% of the trees greater than 1.37 m in height at each site were smaller than the minimum DBH included in our equations (Table 3) and for these trees, we used regression equations forced through the origin (data not shown).

To estimate annual diameter increment increase, we analyzed tree ring width on a subset of allometry trees from each site (*n* = 3–9) with a microscope and micrometer. Power analysis from a larger set of black spruce tree ring increments from three stands in Interior Alaska (*n* = 42, J. G. Vogel,

Table 3. Maximum, Minimum, and Mean Diameter (cm) at Breast Height (1.37 m) and Height (m) for Trees Used in Allometric Equations

Year burned	Species	DBH (cm)					Height (m)		
		n	Max.	Min.	Mean	SE	Max.	Mean	SE
1987	*Populous tremuloides*	13	9.2	0.4	3.4	0.9	10.0	5.5	0.9
1956	*Picea mariana*	10	6.5	0.5	3.5	0.7	5.0	3.2	0.4
1921	*P. mariana*	13	9.6	2.0	4.3	0.7	6.4	3.0	0.4
1886	*P. mariana*	10	10.6	2.3	6.0	0.9	7.4	4.4	0.6

Minimum tree height for equations reported was 1.37 m in all sites.

unpublished data), indicated that as few as four tree ring widths could be used to estimate site ANPP within a 95% confidence interval. Such a low sampling intensity for tree rings may be a reflection of the even-aged, structurally simple nature of black spruce forests. The mean of the average annual ring width for the last 10 years was used with the stem allometry equation to calculate secondary growth for each tree measured in the inventory. Stand biomass was also calculated with our inventory but regional Alaskan (Yarie and others 2007) or Canadian equations (Singh 1986), and these values were compared to estimates derived from the local equations.

Understory Biomass and Primary Production

Aboveground biomass of vascular plants, mosses and lichens was measured across all sites by destructive harvest in July 2001 at approximately peak biomass. To more closely examine the dynamics of regrowth in the first several years after fire, biomass was also measured in the 1999 dry site 2 months after the fire as well as mid-summer in 2000–2002; it was also measured in 2000, 2001, and 2002 in the mature (1921) dry site for comparison. Trees less than 1.37 m in height that were excluded from the inventory described above were included in these harvests. In harvests of the 1999 dry site, we determined whether each species was a re-sprouter by assessing the presence of charred stems or large rhizomes. We also monitored species or generic richness on an annual basis in these sites by recording the presence of all species within a 144-m^2 plot surrounding the 1 m^2 harvest blocks. We did not survey species richness in the other sites.

In each site, aboveground biomass was clipped from either 6 or 12 randomly located 1 m^2 quadrats. Organic depth was measured at the four corners of each quadrat and averaged. In the mesic chronosequence sites and the 1987 dry site, aboveground biomass of vascular species was clipped from six 1 m^2 quadrats randomly located along two 100 m long permanent transects (Manies and others 2004). Mosses and lichens were collected from a 400-cm^2 organic soil plug sawed from a randomly selected corner of the 1 m^2 quadrat following vascular plant clipping. In the 1987 dry site and the 1994 mesic site, we also harvested tall shrubs in a 4-m^2 quadrat surrounding the 1-m^2 quadrat to account for their larger stature. Vegetation was harvested similarly in the 1999 and 1921 dry sites, except that 12 quadrats were harvested.

Samples were returned to the lab and sorted into species and tissues within 1 day of harvest. Each vascular species was separated into several tissue categories including current year and previous year leaves, current year and previous year stems, and fruits or inflorescences following methods modified from Shaver and Chapin (1991) and Chapin and others (1995). Mosses were separated to species and lichens to genera. We included all structurally intact moss and lichen tissue in the live biomass category. This was determined by tugging gently on the brown part of the moss or lichen ramet; the part that broke off was determined to be litter. Large samples were chopped into small pieces, mixed, and then subsampled for fresh and dry weights. Tissues were then dried at 60°C for 48 h or more before weighing.

Aboveground vascular net primary production (ANPP) was estimated as the sum of the current year's apical growth, including leaves and stems. We did not measure secondary growth for understory plants and thus our ANPP values represent an underestimate for shrubs where secondary growth is likely important, mainly *Salix* spp. and trees less than 1.37 m tall. Apical growth was defined as that produced from apical or intercalary meristems during the current growing season; it was calcu-

lated by summing the masses of all current year's leaf, stem, and reproductive tissues in the quadrat harvested.

Harden and others (In Review) measured moss production in these sites by measuring the apical growth of individual species and then scaling growth to the plot level with digital mapping. At each site, an average of ten 60×60 cm^2 moss plots were arranged along greater than 100 m transects with plots spaced every 20–40 m. Percent cover values for up to five dominant moss species within each plot were recorded in fall 2001 via digital photos, extensive field notation, and digitization with Arcview 8.0 software (ESRI Software 2001). Apical growth for each species within each plot was based on growth between June and September of 2001. Within each plot, 10 cm^2 dense, generally single-species patches of moss were dyed with a fluorescent brightener (no. 28, Sigma Scientific, F 3543-56) in early June. Sprayed moss samples were harvested in late September using a coring device of known area and refrigerated until measurement. Apical growth of each ramet was measured individually under a black light using calipers and new growth was harvested, dried, and weighed to estimate per ramet production. The density of stems per m^2 was determined from the % cover plots described above. Moss NPP per species was then estimated on a per plot basis as the mass of apical growth per ramet times the ramet density per unit area times the areal coverage. To validate this method of estimating moss NPP, Harden and others (In Review) compared estimates of *H. splendens* productivity to estimates based on a morphological growth marker (Russell 1988). They found that the fluorescent dye method underestimated *H. splendens* production relative to the morphological method, possibly due to an offset in the timing of harvest of the two methods. We have chosen to report the fluorescent dye methods here because these estimates likely represent the most conservative estimate of moss NPP.

Statistics

To understand whether differences in biomass pools were due to site-specific allometric differences, we used ANOVA to test for differences among sites in the ratio of DBH to height, or mass of leaves, stem, new growth or branches. We used ANCOVA to compare the slopes and intercepts of allometric relationships between DBH and height, or mass of leaves, stem, new growth or branches between our Alaskan stands and stands from Northern Manitoba (Bond-Lamberty and others

2002a). We used general linear models to compare biomass and ANPP means among sites within chronosequences and Bonferroni post hoc comparisons to differentiate between means. Data were natural log-transformed when necessary to meet the assumptions of ANOVA. Most analyses were done with Systat version 10.2 (Systat Software Inc. 2002). However, we used a curve-fit module in DeltaGraph version 5.6.2 (SPSS Inc. and Redrock Software 2006) to describe how biomass or ANPP changed across time within a chronosequence. Note that we did not force regression equations through zero because we felt that the relationship should not be interpreted beyond the range of values sampled.

RESULTS

Black Spruce Allometry

Both local and regional variation in black spruce allometry had significant effects on estimates of ecosystem biomass. Within our Alaskan sites, black spruce in the 1921 dry site had less leaf mass per unit DBH (64 ± 11 g cm^{-1}, mean $\pm$ 1SE; $F_{2,28} =$ 16.39, $P < 0.001$) than trees in the 1886 (151 ± 19 g cm^{-1}) or 1956 (332 ± 63 g cm^{-1}) mesic sites. Stem mass per unit DBH was highest in the 1886 mesic site (715 ± 138 g cm^{-1}, mean $\pm$ 1SE; $F_{2,27} = 4.09$, $P = 0.03$) and lowest (and not differentiable) in the 1921 dry and 1956 mesic sites (455 ± 57 and 356 ± 60 g cm^{-1}, respectively). These and other differences in allometry would have caused a greater than 50% overestimate of biomass pools if mesic equations were used to estimate dry site biomass.

Black spruce biomass pools generated with our site inventories and either (1) a generalized Canadian black spruce equation (Singh 1986) or (2) a generalized Alaskan equation (Yarie and others 2007) overestimated biomass in the mature dry stand relative to the site-specific equations (90 and 42% greater than site-specific values for Canadian and Alaskan models, respectively), slightly overestimated biomass in the mature mesic stand (35 and 7% greater than site-specific values), and slightly underestimated biomass in the 1956 mesic site (10 and 13% less than site-specific values; Figure 1).

When compared to direct measurements of black spruce trees from Northern Manitoba (Bond-Lamberty and others 2002a), our Alaskan trees increased less in height (ANCOVA Region $\times$ DBH $F_{1,67} = 4.66$, $P = 0.03$) and stem mass (ANCOVA Region $\times$ DBH $F_{1,67} = 7.01$, $P = 0.01$) per unit increase in DBH than the Canadian trees (Figure 2),
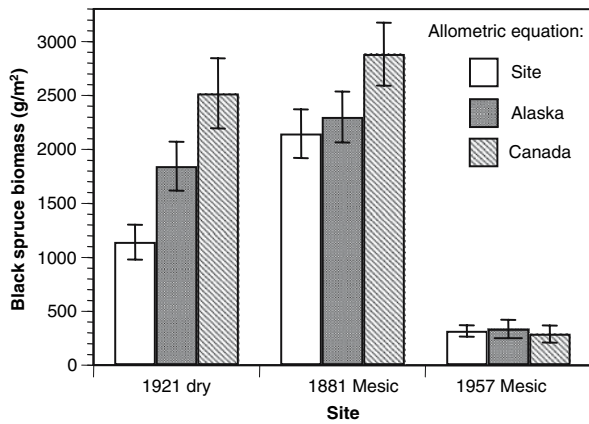
Figure 1. Black spruce biomass pools across three sites near Delta Junction, Alaska, calculated using allometric equations that were site specific (this study), regional-Alaska (Yarie and others 2007), or regional-Canada (Singh and others 1986). Values are means (±1 standard error (SE)).

but were similar in other aspects. For example, the slopes of the relationships between DBH and total biomass, total new growth, total leaves or total branches were not different between Alaskan and Canadian trees (data not shown).

Biomass and ANPP Recovery Immediately After Fire in the 1999 Dry Site

Although biomass in the 1999 dry site was less than 6% of the mature 1921 dry stand 3 years after fire, ANPP did not differ between these sites (Figure 3). Re-sprouters, including *Festuca altaica, Salix* spp., *Ledum palustre, Vaccinium uliginosum* and *V. vitis-ideae*, contributed 55% of biomass and 70% of ANPP at the burned site, showing that the rapid growth recovery was dominated by individuals who survived the fire, not new recruits.

Three years after the 1999 fire, there were large differences in composition between the youngest and oldest site on the dry chronosequence (Figure 4). In the 1999 dry site, graminoids (mostly *F. altaica*) comprised 37% of biomass and 41% of ANPP. Production efficiency was substantially higher in the burned site than in the unburned site. Aboveground NPP in 2002 was 63% of biomass, with 47% of biomass turning over in litterfall (senesced stems, inflorescences and leaves) largely due to the herbaceous perennial growth form of these graminoids. In the unburned site, ANPP was less than 10% of biomass. Graminoids were less than 1% of the biomass in the unburned stand (Appendix 1, http://www.springerlink.com), but
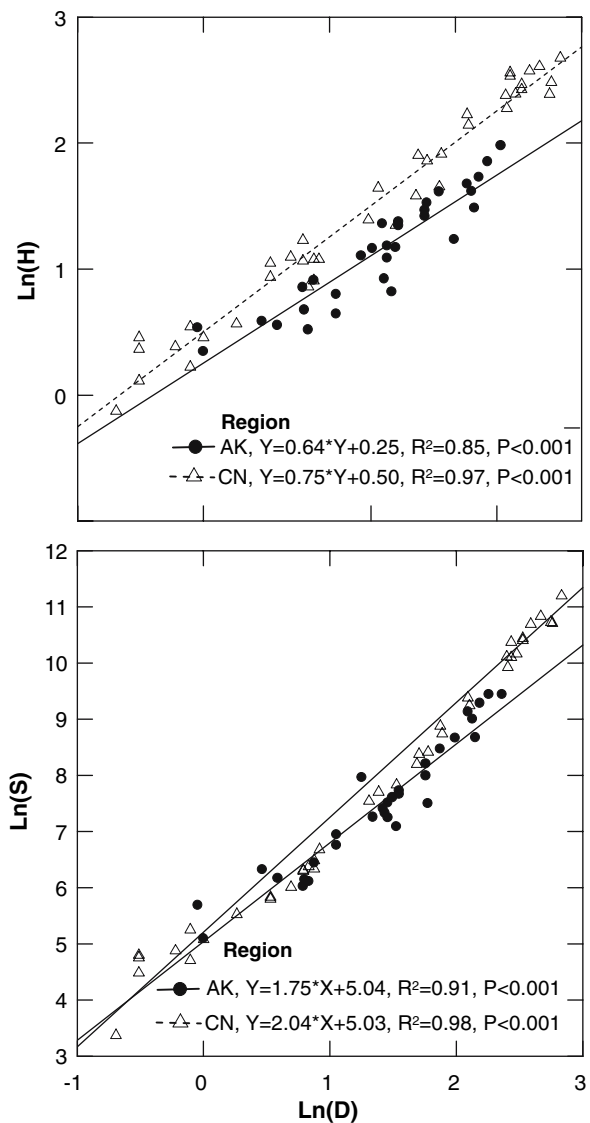

Figure 2. Black spruce stem diameter at breast height (*D*, cm) versus height (*H*, m) or stem mass (*S*, g) for trees from this study of sites near Delta Junction, Alaska (AK), or from Manitoba, Canada (CN) (redrawn from Bond-Lamberty and others 2002).

were present in each sampled plot. Blueberries (*V. uliginosum*) and cranberries (*V. vitis-ideae*) dominated understory vascular biomass and ANPP in the unburned stand but were reduced to a very small biomass after fire (Appendices 1 and 2, http://www.springerlink.com).

Fire did not cause a net change in vascular plant species richness (30 species), but altered composition and dramatically decreased moss and lichen richness from 16 to 3 genera (Appendix 3, http://www.springerlink.com). Absent from the burned site were: tall deciduous shrubs *Spirea beauverdiana* and *Rosa acicularis*, the evergreen shrub *Empetrum*
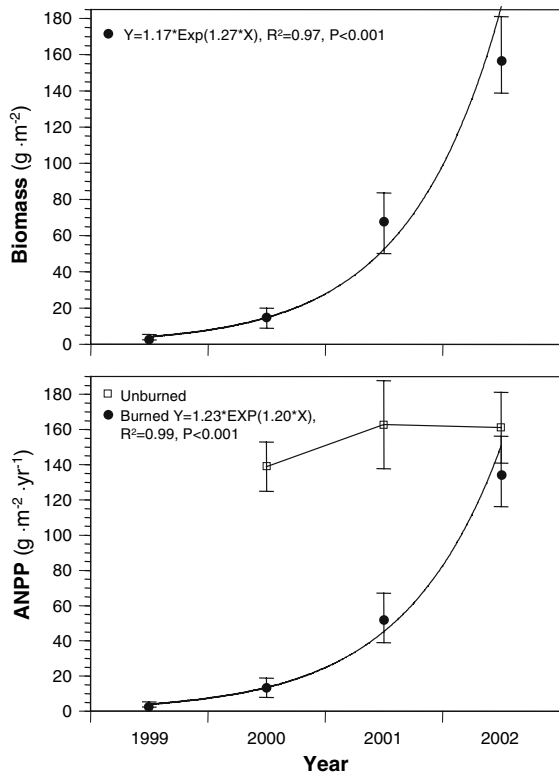
Figure 3. Post-fire recovery of aboveground biomass and net primary productivity (ANPP) over time in the 1999 dry site, and ANPP in the 1921 dry site near Delta Junction, Alaska. Values are means (±1SE). The SE for ANPP in the 1921 dry site was propagated according to Bevington (1969) so that it was weighted by the proportional contribution of each sampling group (that is, trees and understory plants in the 1921 site and understory vascular plants and mosses in the 1999 site).

nigrum, forbs *Delphinium brachycentrum*, *Equisetum scirpoides*, *Geocaulon lividum*, and *Pedicularis labradorica*, although all of these species were collected within the greater burned area (M. C. Mack, unpublished data). Species present in the burned site but absent from the unburned site were species that presumably recruited from seed, including forbs *Anemone parviflora*, *Corydalis sempervirens*, *Dracocephalum parviflorum*, and *Solidago multiradiata*, and graminoids *Carex praticola*, *Hierochloe alpina*, and *Luzula multiflora*. Black spruce seedlings were observed in the burned site by 2002. *Politrichum juniperum*, which has stems that reach mineral soil (Vitt and others 1988), was the only non-vascular species to re-sprout after fire, and a fire-following moss, *Ceratodon purpureum*, and liverwort, *Marchantia polymorpha*, were the only species that presumably recruited from spores after fire.

Biomass and ANPP Across Mesic and Dry Chronosequences

Total aboveground biomass in 2001 ranged from 58 ± 56 to 2469 ± 180 and 211 ± 163 to 4008 ± 233 g m^{-2} (mean $\pm$ 1SE) for the dry and mesic chronosequences, respectively (Figure 5), and varied significantly within each chronosequence (dry $F_{1,16} = 11.62$, $P = 0.04$; mesic $F_{1,22} = 25.08$, $P = 0.003$). Biomass accumulation was highly predictable with time since fire ($R^2 \geq 0.98$) despite the likely variation in past fire history across the sites (Figure 5). Biomass increased linearly across the mesic chronosequence and logarithmically across the dry chronosequence
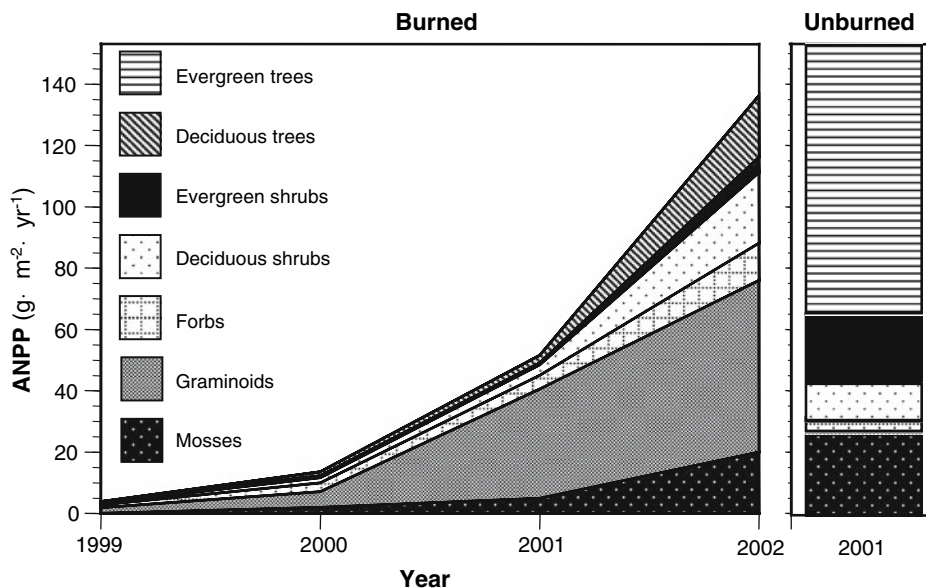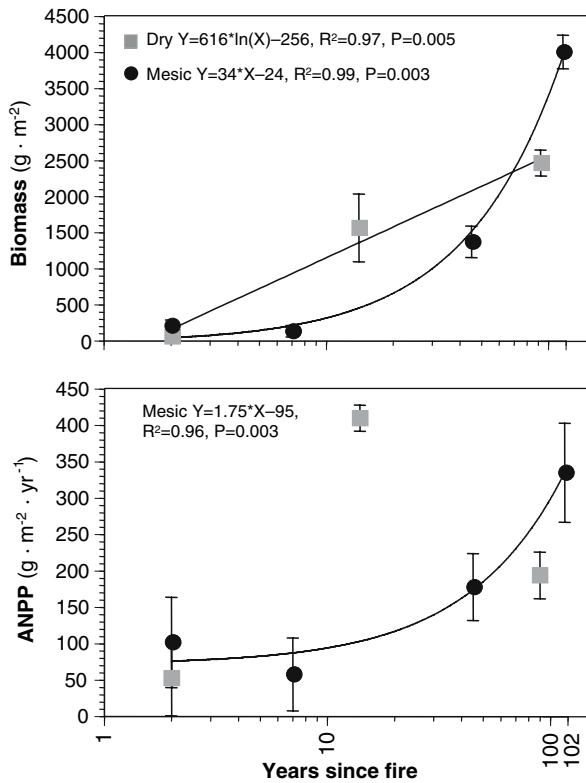

Figure 4. Percent contribution of plant functional groups to ANPP in the 1999 dry site over 4 years (1999–2002) and the 1921 burn (2002). Species contained in each functional group are identified in Table 4 (trees) and Appendices 2 (vascular understory) and 3 (mosses).

Figure 5. Biomass accumulation and ANPP across dry and mesic chronosequences of sites that vary in time since fire near Delta Junction, Alaska. Values are means (±1SE), where SE was propagated according to Bevington ([1969](#)) so that it was weighted by the proportional contribution of each sampling group (that is, trees and understory plants and lichens for biomass and trees and understory vascular plants and mosses for ANPP). Note that the *x*-axis is log-scaled to better visualize differences among younger sites. This results in linearization of the natural log curve fit across the dry chronosequence sites, and curvature of the linear fit across the mesic chronosequence sites.

primarily because of greater aspen (Table [4](#)) and willow biomass (Appendix 1, http://www.springerlink.com) accumulation in the 1987 dry site than in the intermediate-aged mesic sites ($P < 0.05$ for 1987 site versus all contrasts). Deciduous trees and willows were almost absent from mature stands, although downed aspen stems and standing dead willow stems were common (M.C. Mack, personal observation).

Total biomass was 1.4 times higher in the mesic mature stand (1886) than in the dry stand (1921; $P = 0.001$). Although we cannot determine from this selection of sites whether these mature stands represent maximum peak biomass for mesic and dry stand types, biomass trajectories make it unlikely that the mature dry stand will reach the level

of the mature mesic stand before the next fire cycle (<150 years; Figure [5](#)). Between 70 and 80% of total biomass was contributed by black spruce in the mesic and dry mature stands, respectively, with about half of this biomass in wood (Table [4](#)). Greater tree biomass in the mesic site than in the dry site was primarily due to higher tree density in the mesic site because basal area:density ratios were similar between sites (Table [4](#)). Mosses and lichens contributed 23% of biomass in the mesic stand, but only 12% in the dry stand, where moss biomass was an order of magnitude less than in the mesic stand ($P < 0.001$; Appendix 3, http://www.springerlink.com). Lichen biomass was similar between the two mature sites (Appendix 3, http://www.springerlink.com).

Total ANPP differed significantly among sites (mesic $F_{1,22} = 38.09$, $P < 0.0001$, dry $F_{1,16} = 17.08$, $P = 0.003$). Across the mesic chronosequence, ANPP increased linearly due to a linear increase in tree ANPP and a logarithmic increase in moss ANPP over secondary succession (Figure [6](#)). Understory vascular ANPP did not vary significantly across the mesic sites (Figure [6](#)). Across the dry chronosequence, by contrast, the highest rate of total ANPP was in mid-succession ($P < 0.05$ for all contrasts; Figure [5](#)) due to the contributions of deciduous species, mainly aspen (89 ± 7 g m^{-2} y^{-1}) and understory willow (246 ± 114 g m^{-2} y^{-1}; Appendix 2, http://www.springerlink.com). These species were much less abundant on the mesic chronosequence, but similarly peaked in production in the intermediate-aged sites (Appendix 2). Moss NPP increased along a linear trajectory across the mesic chronosequence, peaking in the 1886 mesic site (Figure [6](#)). Productivity in this site was similar to NPP in the 1987 and 1921 dry sites despite an order of magnitude more biomass in the mature mesic (1886) site (Appendix 3, http://www.springerlink.com).

DISCUSSION

In the 1999 dry site where we followed growth for 4 years, ANPP was surprisingly resilient to fire disturbance and returned to the level of the mature 1921 dry stand by year four despite radical changes in species composition. Treseder and others ([2007](#)) observed that root length production was not different between these two sites in 2002, suggesting that belowground production was similarly resilient. The re-sprouters that dominated post-fire productivity must have had roots and/or rhizomes buried in deep organic or mineral soil because over 70% of organic soil depth was consumed in the fire (Neff and others [2005](#)). Rhizomes and roots may

Table 4. Tree Density, Basal Area, and Aboveground Biomass Pools for all Trees over 1.37 m Height in Black Spruce Stands Near Delta Junction, Alaska

| Metric	Biomass pool	Drainage and year burned				
		Dry		Mesic		
		1987	1921	1956	1956	1886
Species		*Populous tremuloides*	*Picea mariana*	*P. mariana*	*P. tremuloides*	*P. mariana*
Density (trees ha^{-1})		3956 (370)	3744 (462)	1387 (572)	530 (232)	4933 (415)
Basal area (m^2 ha^{-1})		2.80 (0.38)	8.06 (1.0)	3.82 (1.89)	0.45 (0.18)	10.17 (0.95)
Biomass (g m^{-2})	Stem	483 (71)	1114 (142)	244 (36)	134 (54)	1447 (156)
	Coarse old branches	53 (7)	84 (10)	–	15 (5)	257 (65)
	Fine old branches	–	85 (10)	10 (1)	–	304 (30)
	Cones	–	223 (30)	28 (4)	–	44 (5)
	Old leaves	–	100 (12)	17 (2)	–	558 (52)
	New branches	5 (1)	5 (0.5)	1 (1)	3 (1)	13 (1)
	New leaves	50 (7)	22 (3)	2 (1)	14 (5)	61 (6)
	New stem	35 (4)	37 (4)	19 (7)	12 (6)	46 (4)
	Total	660 (64)	1961 (109)	319 (43)	178 (66)	2730 (91)
	New	89 (7)	89 (11)	22 (8)	29 (12)	120 (10)

Sites without trees greater than 1.37 m in height (1999 dry, and 1994 and 1999 mesic) are not included. Values are means (±1SE) and were calculated from stand inventories and allometric equations (Table 2).

have been lingering in mineral soil since the last burn, which is a pattern observed for grasses in black spruce/feathermoss sites (Dyrness and others 1986), as well as trembling aspen (Johnstone and Kasischke 2005) which may re-sprout from root suckers after fire (Dyrness and others 1986). Species known to root in the organic layer dominated pre-fire understory biomass, namely blueberries (*Vaccinium uliginosum*) and cranberries (*V. vitis-idaea*); these species recovered slowly after fire in the 1999 dry site. The 1999 mesic site had substantially thicker organic soil layers both before and after fire then the 1999 dry site (Harden 2006). Blueberry biomass was not different but ANPP was twice as large in the 1999 mesic site then in the mature mesic chronosequence site (1886). Cranberries, by contrast, had 93% less biomass in the 1999 than in the 1886 mesic site, which may be due to the fact that their rhizomes tend to be only 2–3 cm deep in the moss litter layer (Dyrness and others 1986), whereas blueberries tend to root in the fibric layer (M. C. Mack, personal observation). Most important in the rapid recovery of ANPP after fire appears to be the survival of key species, which may, in part, be related to whether meristems are protected in unburned layers of soil. Other factors that likely contribute to the rapid rate of ANPP recovery include increased resource availability due to release of N and P via combustion (Raison 1979), decreased competition (for example, Brewer 1999), warmer soils stimulating microbial decom-

position and mineralization of nutrients from soil organic matter (for example, Harden and others 2003), and more available moisture due to reduced evapotranspiration (Chambers and Chapin 2003).

Across all sites, ANPP was highest in the 1987 dry site where deciduous trees and shrubs dominated biomass and production. Aspen and willow re-sprouts were present in the 1999 dry site (Appendix 1, http://www.springerlink.com), and stems of dying or dead aspen and willow were visible in the dry mature site (M. C. Mack, personal observation), so it is plausible that these sites are part of a successional trajectory that includes co-dominance of black spruce with deciduous trees during mid-succession (for example, Kasischke and others 2000). In the mesic chronosequence, deciduous trees and tall shrubs were present but at low abundance in intermediate aged sites and were absent from the mature site. Therefore, in contrast to the dry chronosequence, the mesic sequence may represent self-replacement, or spruce-to-spruce successional trajectory (Chapin and others 2006b).

Fire severity, drainage and soil temperature have been identified as factors driving the abundance of aspen and tall shrubs in Interior Alaska. Aspen density was positively related to fire severity in a nearby mesic site that burned in 1994 (Johnstone and Kasischke 2005) and aspen and willow were more abundant in more frequently burned sites in the Yukon (Johnstone 2006) presumably due to the better survivorship of species with rhizomes
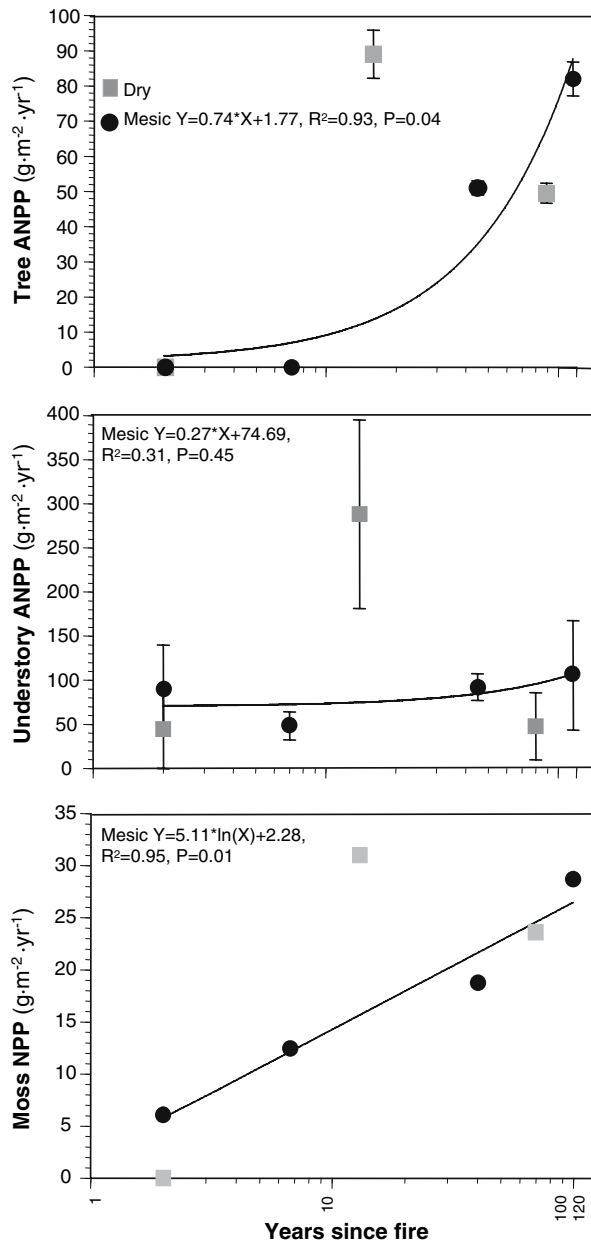
Figure 6. Tree, understory, and moss ANPP across dry and mesic chronosequences of sites near Delta Junction, Alaska, that differ in time since fire. Values are means (±1SE). Moss ANPP values are from Harden and others (In Review). Note that the x-axis is log-scaled to better visualize differences among younger sites.

and roots in the mineral soil. Across the landscape, single species stands of aspen are found in relatively warm, well-drained sites (Viereck and others 1983; Van Cleve and others 1991; Chapin and others 2006b). Severe or frequent fires can increase soil temperature though the removal of insulating moss and soil organic matter and increase drainage through thermal erosion of permafrost. Thus, the

high abundance of deciduous tree and tall shrub species in the 1987 dry site could be related to thermal effects of severe fire or alternatively, the site could just be an anomalously warm, well-drained patch of the landscape. Finally, stochastic processes such as the proximity to seed sources could play a role in the establishment of deciduous species as well and cannot be ruled out as a factor contributing to compositional differences between the chronosequences.

Black spruce density, basal area, biomass and ANPP in the mature sites were within the range reported for Interior Alaska (Viereck and others 1983; Yarie and Billings 2002; Hollingsworth and others 2006). Biomass in our mesic 1886 stand was 90% of peak black spruce biomass estimated from large-scale forest inventory measurements across the state of Alaska (Yarie and Billings 2002), suggesting that this stand may be at or near peak biomass. The mature dry (1921) stand, by contrast, accumulated 78% of biomass predicted for its age class (Yarie and Billings 2002). If the biomass accumulation curve for this chronosequence is projected to 150 years (that is, Yarie and Billings' (2002) estimate of maximum stand biomass), peak biomass would be 2,831 g m^{-2}; still substantially less than peak biomass in the mesic chronosequence.

Lower black spruce biomass and ANPP in the mature dry (1921) site than in the mature mesic (1886) site appears to be driven primarily by higher tree density in the latter site because biomass and ANPP per tree were similar between sites (Table 4). Yarie and Van Cleve (2006) similarly found black spruce production to be constant over variably drained stand ages ranging from 50 to 150 years when productivity was standardized to full stocking rate. Lower density in the mature dry than in the mature mesic site could be related to processes directly attributable to drainage, such as self thinning due to water competition (for example, Reid and others 2003), interactions with abundant deciduous tree species (Johnstone and Kasischke 2005) or feedbacks between fire and drainage (Harden and others 2006). Alternatively, differences in density could be caused by processes that are relatively independent of drainage, such as climatic extremes during the sensitive early years of spruce seedling establishment.

Our 1956 mesic site had only 25% of the tree density of the 1886 mesic site and contained only 16% of black spruce biomass predicted for its age class by Yarie and Billing's (2002) accumulation curve. Because upland black spruce stands tend to be comprised of a single cohort (Viereck and others

1986), it seems unlikely that density will quadruple in the next 50 years. These differences in density, then, may represent poor site matching in the mesic chronosequence and confound estimates of biomass accumulation and ANPP. To explore the impact of this on our biomass estimates, we multiplied per tree biomass of the 1956 mesic site (2,300 g tree^{-1}) by density of the mature mesic (1886) site (Table 4), yielding an estimate of 1,135 g m^{-2}, which is within 10% of Yarie and Billing's (2002) estimate for this age class. When this value was plotted on our chronosequence biomass accumulation curve (Figure 3), the curve is still best-fit by a linear equation ($Y = 34.5*X - 169.4$, $R^2 = 0.97$, $P = 0.01$), suggesting that the functional shape of biomass accumulation would still differ between mesic and dry chronosequences if density was held constant across the mesic chronosequence.

Our Alaskan black spruce stands had less biomass and were less productive than comparable well-drained stands in Manitoba, Canada, due to both lower tree density and lower per tree biomass and growth. Tree density was less than half of values reported for well-drained sites in Canada (8,000–16,000 stems/ha; Bond-Lamberty and others 2002a; Wang and others 2003). Per tree production (Vogel and others 2005), basal area and biomass (Wang and others 2003) were similarly less than half of values reported for well-drained sites in Canada. ANPP was about one third of values reported for stands in Manitoba (Bond-Lamberty and others 2004) and one quarter of values reported for Larch forests in Central Siberia (Kajimoto and others 1999; Schulze and others 1999) and Scots Pine forests in Finland (Helmisaari and others 2002).

Differences in growth allometry between our Alaskan stands and those from Northern Manitoba provide some evidence that the low productivity of Alaskan stands may be due to moisture stress. Regional mean annual precipitation was 30% lower in our Alaskan sites than in the Manitoba sites, indicating that available soil moisture may be lower in our sites. Our Alaskan trees were significantly shorter and had less stem mass per unit increase in DBH than their Canadian relatives. In black and white spruce stands across Canada, reduced height and shoot growth has been linked to soil moisture deficits (Wang and Klinka 1995; Peng and others 2004). In response to water stress, trees may grow more wood per unit height (Koch and others 2004), apparently to decrease the potential for embolism in xylem during periods of moisture stress (Tyree and Sperry 1989). Our observation of changes in allometry and its influence on biomass

also agrees with the observation that black spruce in Alaska may allocate more C belowground where moisture appears to be more limiting (Vogel and others 2005).

Moss biomass began to accumulate surprisingly early in succession as indicated by the large increases in *Ceratodon* spp. and *Polytrichum* spp. over the first 4 year of succession in the 1999 dry site. Composition shifted to feathermoss dominance in both the mesic (1886) and dry (1921) mature sites. Because feathermoss lack water-conducting tissues, it was surprising that its production was similar between mesic and dry sites (Figure 6) despite an order of magnitude difference in moss biomass pools (Appendix 3, http://www.springerlink.com). As a result, ANPP per unit biomass, or production efficiency, was drastically lower in the mesic site, which may indicate lower light or nutrient availability in this site where mosses are both densely packed and beneath a closed canopy. Alternatively, it may indicate that that there is more brown moss (that is, structurally intact brown material that may or may not be physiologically active) in the mesic stand. Due to cool soils and moist conditions, decomposition of senescent moss may be slower in the mesic stand than in the dry stand, resulting in more intact brown material. Our measurements of moss biomass pools in the mesic mature stand were on par with green plus brown biomass pools in a black spruce/feathermoss community in Washington Creek, AK (Oechel and Van Cleve 1986), and twice as large as estimates for a similar community in Canada where only the green biomass was sampled (O'Connell and others 2003).

Black Spruce Forests, Climate Change, and Fire

The boreal forests of Interior Alaska are experiencing a rapidly changing climate (Serreze and others 2000) that should alter site drainage as permafrost thaws and ceases to restrict water infiltration (Yoshikawa and others 2003). Precipitation has increased in Interior Alaska along with temperature over the last 30 years (Hinzman and others 2006), but higher rates of evapotranspiration due to warmer temperatures appear to outweigh increased precipitation, leading to drier soils (Oechel and others 2000). Warmer temperatures and drier surface soils may furthermore increase fire frequency and severity (Stocks and others 1998; Kasischke and others 2006), which can also have strong effects on soil drainage. Fire removes insulating moss and soil organic matter and the resultant increased heat penetration into soil can

rapidly degrade permafrost (Yoshikawa and others 2003), also leading to drying of surface soils (Hinzman and others 2006).

What will happen to productivity and biomass accumulation in upland black spruce stands as climate warms in Interior Alaska? Drier soils and more severe fires may increase the frequency of stands undergoing a mixed black spruce-deciduous successional trajectory similar to those in our dry chronosequence. The data from our chronosequences suggest that this shift in successional trajectory may lead to an increased rate of biomass accumulation early in succession, but lower biomass accumulation later in succession due to the low density of black spruce. Productivity may peak earlier when deciduous species dominate, but production in mature stands may be lower. Functional characteristics of dominant species suggest that the mixed deciduous trajectory may store less C in the forest floor and soils because plant inputs are highest when plant materials are most decomposable (during the deciduous phase) and lower when plant materials are most recalcitrant (evergreens and mosses in the mature phase). In support of this is the observation that there are larger pools of soil organic carbon in the mesic mature site than in the dry mature site (Harden 2006). Thus an increase in the frequency of mixed black spruce-deciduous stands across the landscape may lead to reduced regional carbon storage in both biomass and soils.

CONCLUSIONS

Our data provide insight into several aspects of post-fire succession in the black spruce forests of Interior Alaska and provide focus for future studies. First, ANPP was resilient to fire in the 1999 site. After 4 years, it returned to a level not different than the mature dry (1921) site primarily due to the contributions of re-sprouting species. We need to better understand the controls over fire survivorship of pre-fire vegetation to predict post-fire composition and productivity. Second, the most productive stand in our seven sites was dominated by deciduous trees and tall shrubs. Understanding of the factors that control the abundance and productivity of these species may be key to predicting peak productivity across succession. Third, black spruce allometry varied both regionally and locally, which can cause substantial variation in estimates of biomass and may be the result of varying moisture availability across sites. Finally, the observation that black spruce density at stand maturity had large effects on stand productivity and biomass warrants future exploration of the controls over

density. Future research on the mechanisms that regulate these patterns will greatly improve our ability to predict the response of fire-prone Alaskan boreal forest to a warming climate.

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