Carbon Accumulation Patterns During Post-Fire Succession in Cajander Larch (*Larix cajanderi*) Forests of Siberia

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ABSTRACT

Increased fire activity within boreal forests could affect global terrestrial carbon (C) stocks by decreasing stand age or altering tree recruitment, leading to patterns of forest regrowth that differ from those of pre-fire stands. To improve our understanding of post-fire C accumulation patterns within boreal forests, we evaluated above- and belowground C pools within 17 Cajander larch (*Larix cajanderi*) stands of northeastern Siberia that varied in both years since fire and stand density. Early-successional stands (<20-year old) exhibited low larch recruitment, and consequently, low density, aboveground larch biomass, and aboveground net primary productivity ($ANPP_{tree}$). Mid-successional stands (21- to 70-year old) were even-aged with considerable variability in stand density. High-density mid-successional stands had 21 times faster rates of $ANPP_{tree}$ than low-density stands (252 vs. 12 g C m^{-2} y^{-1}) and 26 times more C in aboveground larch biomass (2,186 vs. 85 g C m^{-2}). Density had little effect on total soil C pools. During late-succession (>70-year old), aboveground larch biomass, $ANPP_{tree}$, and soil organic layer C pools increased with stand age. These stands were low density and multi-aged, containing both mature trees and new recruits. The rapid accumulation of aboveground larch biomass in high-density, mid-successional stands allowed them to obtain C stocks similar to those in much older low-density stands (~8,000 g C m^{-2}). If fire frequency increases without altering stand density, landscape-level C storage could decline, but if larch density also increases, large aboveground C pools within high-density stands could compensate for a shorter successional cycle.

Key words: larch; Siberia; carbon; fire; succession; stand age; density; climate warming.

INTRODUCTION

Global change models predict high-latitude boreal forests will become increasingly susceptible to fire activity as climate warms and dries (Flannigan and others 2005; Wotton and others 2010). Because boreal forests sequester a large proportion of global terrestrial carbon (C) stocks (Kasischke 2000), climate-induced alterations to boreal fire regimes could alter global C cycling (Harden and others 2000; Bond-Lamberty and others 2007; Turetsky and others 2011) and future climate (Randerson and others 2006). As fire frequency and severity increase, aboveground and surface soil C stocks will initially decrease due to transfer of C to the atmosphere, potentially creating a positive feedback to climate warming (Amiro and others 2009). However, increased fire activity may also alter forest regrowth, with variable effects on net ecosystem C balance (NECB; Kasischke and others 2000) and surface energy fluxes such as albedo and evapotranspiration (Amiro and others 2006; Randerson and others 2006). The net effect of these changes can lead to an array of climate system feedbacks (Beck and others 2011).

Two important ways increased fire activity may alter forest regrowth and NECB is by decreasing stand age and/or altering tree recruitment. As the frequency of stand-replacing fires increases, stand age decreases (Kasischke and others 1995; Weir and others 2000; Kashian and others 2006). If stands fail to develop to their pre-burn stature before re-burning, increased fire frequency will lead to a decline in ecosystem C pools (Thornley and Cannell 2004). Increased fire activity may also change stand density and composition by altering seed availability and suitability of germination microsites (Schoennagel and others 2003; Johnstone and others 2010a, b). For example, in lodgepole pine forests of Yellowstone National Park, increased frequency of stand-replacing fires leads to higher cone serotiny and higher density stands (Kashian and others 2004) with greater ANPP (Turner and others 2004) and standing biomass (Kashian and others 2006). In boreal Alaska, increased fire severity in mature black spruce stands of intermediate site quality reduces the soil organic layer (SOL) depth (Kasischke and Johnstone 2005; Kane and others 2007), favoring germination of small-seeded deciduous trees and shifting forest successional trajectories away from black spruce self-replacement to pathways with greater deciduous dominance (Johnstone and Kasischke 2005; Johnstone 2006; Johnstone and

others 2010a, b). This shift leads to greater above-ground C storage because deciduous stands accumulate more C in live and dead trees than black spruce stands (Alexander and others 2012). Because fire can influence C dynamics in many ways, understanding the magnitude of post-fire C changes across an array of boreal forest landscapes is essential for predicting future fire–vegetation–climate interactions.

The primary objectives of this study were to (1) evaluate above- and belowground C pools within Cajander larch (*Larix cajanderi*) stands of northeastern Siberia that vary in both stand age and density and (2) discuss the potential implications of these variations in stand structure on future C pools under a warming climate with increased fire activity. Siberian larch forests are distinct from other boreal forests in that they are comprised of a single coniferous tree genus with a deciduous growth habit and can grow on continuous permafrost (Osawa and Zyryanova 2010). Larch forests are also critically important to the global C cycle. They comprise 20% of the world's boreal forests (Osawa and Zyryanova 2010), represent one of the largest remnant natural forests in the world (Sanderson and others 2002), overlay C-rich ''yedoma'' permafrost ($\sim$500 Pg for Siberia; Zimov and others 2006), and occupy watersheds from which most freshwater entering the Arctic Ocean originates (Peterson and others 2002). Despite their uniqueness and importance, our current knowledge of Siberian larch forest ecology and potential susceptibility to climate change remains limited because of logistical constraints associated with conducting research in Siberia and minimal translations of Russian scientific efforts into English. The few published studies detailing C pools in Siberian larch forests have focused on central Siberia and often encompass only young and mature stands (for example, Kajimoto and others 1999, 2006, 2010; Usoltsev and others 2002), with limited emphasis on mid-succession, although stands of this age are likely to become more prevalent if climate change increases fire frequency. As such, uncertainties regarding current C pools in Siberian boreal forests significantly limit our ability to predict climate-induced changes to the global C cycle (Ito 2005).

We expected Cajander larch stands to be developing along a variety of successional trajectories depending on the severity of the last fire and stand regeneration capacity (Figure 1). Because fires are often stand-replacing (Valendik and Ivanova 2001), we predicted most stands would be proceeding
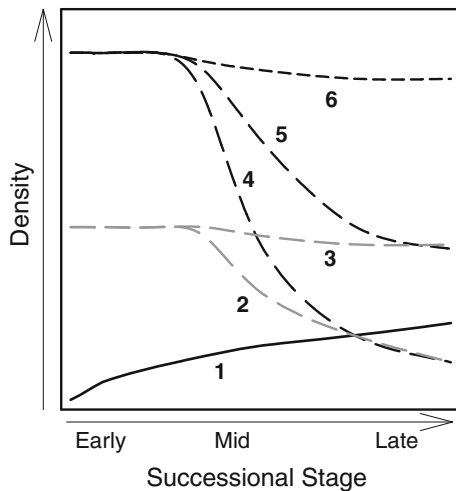
Figure 1. Hypothesized density trajectories during post-fire succession within Cajander larch forests of northeastern Siberia (see "Introduction" for description).

along even-aged trajectories where most recruitment occurs within a few decades following fire (Shorohova and others 2009). However, we anticipated post-fire stand density to vary depending on fire characteristics that influence seed availability and/or favorability of germination microsites. For instance, because larch recruitment depends upon annual release of wind-dispersed seeds, a large fire could increase the distance to seed sources, leading to stands of low density that exhibit a slow increase in density over time due to the gradual recruitment of trees as the stand ages (trajectory 1) (Foster 1985). These stands would have an even-aged structure in early-succession but become multi-aged as they mature. Recruitment beyond early-succession might be facilitated by sporadic events, such as tree mortality and creation of "tip-up mounds" that expose mineral soils and promote germination and establishment. If these stands remained at low density, there would be no self-thinning because resource competition would be low. In contrast, severe fires could reduce SOL depth and increase tree recruitment (Johnstone 2006). In these instances, stands could recruit at medium (trajectories 2 and 3) to high (trajectories 4, 5, or 6) densities. Trees would likely grow larger as they matured, but stand density would remain near its initial level until mid-succession when competition for resources led to self-thinning (trajectories 2, 4, and 5). Alternatively, stands could stagnate with little changes in growth or density even in the mature forest (trajectories 3 and 6) (White 1980).

METHODS

Study Area

Research was conducted near the Northeast Science Station (NSS) in Cherskii, Sakha Republic, Russia in northeastern Siberia (68.74°N, 161.40°E) (Figure 2), which is located on the Kolyma River, approximately 250-km north of the Arctic Circle and approximately 130-km south of the Arctic Ocean. Climate is continental, with warm summers (June average = 12°C), cold winters (January average = −33°C), and average annual temperature of −11.6°C (Cherskii Meteorological Station, S. Davydov, personal observation). Annual precipitation is low (210 mm y^{-1}; S. Zimov, unpublished data), with about half falling during summer (The Climate Reference Book of the USSR 1966). Air temperatures have been exceptionally warm during the last decade; in 2007, for example, average annual temperature was −7.6°C, and average July temperature was 16°C (S. Davydov, personal observation). The fire return interval is 50–120 years (Schepaschenko and others 2008).

Forests consist of a single larch species, *L. cajanderi*, which is adapted to growth on continuous permafrost (Abaimov 2010) and ranges in size from small trees resembling dwarf shrubs to trees near 25-m tall. Seeds are produced annually, with heavy masts every 2–3 years and dissemination beginning in early autumn (Abaimov 2010). Understory vegetation consists of deciduous shrubs (*Betula divaricata*, *B. exilis*, *Alnus fruticosa*, *Salix pulchra*, *S. alaxensis*, *S. glauca*, and other *Salix* species), evergreen shrubs (*Pinus pumila*, *Vaccinium vitis-idaea*, *Arctous alpine*, *A. erytrocarpa*, *Empetrum androgynum*, *Pyrola grandiflora*, and *Ledum decumbens*), herbs (*Carex appendiculata*, *Artemisia tilesii*, *Pedicularis lapponica*, *Luzula multiflora*, and *Epilobium angustifolium*), grasses (*Calamagrostis neglecta*), mosses [for example, *Aulacomnium turgidum* (which is dominant) and *Sphagnum* spp.], and lichens (for example, *Cetraria cuculata*, *Cladonia rangiferina*; Petrovsky and Koroleva 1979).

Prior to the field season, fire scars within approximately 100-km radius of Cherskii were identified using a combination of satellite imagery and personal knowledge of fire scars too small to be detected via satellite. Within ten accessible fire scars and adjacent mature forests, we performed an initial reconnaissance to assess variability in stand characteristics, including tree size (that is, presumably indicative of stand age) and density and identified 17 stands (14 = upland; 3 = riparian) located in flat terrain for sampling (Figure 2).
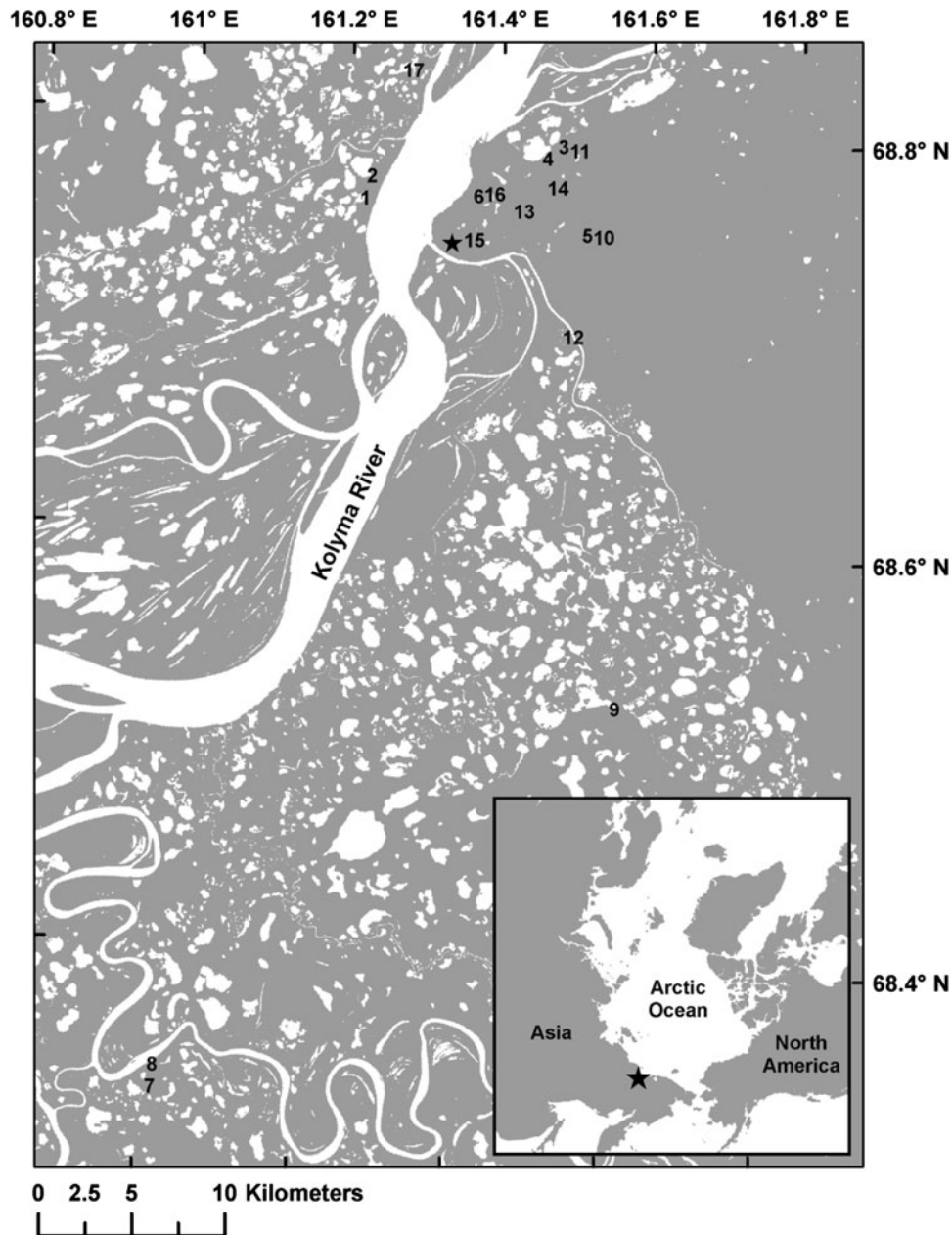
Figure 2. Locations of 17 Cajander larch forest stands sampled near the Northeast Science Station (indicated by star) in Cherskii, Russia in northeastern Siberia.

For each stand, the time elapsed since the last fire was determined based on temporal analysis of satellite images, known fire dates provided by NSS scientists, or age of the oldest tree. To determine stand age, a wood slab or core was obtained from the base (~20 cm above the organic layer) of 5–10 trees sampled randomly at 10- or 20-m intervals along a 100-m transect placed within the center of each stand. Wood samples were dried at 60°C and sanded sequentially with finer grit sizes to obtain a smooth surface. A high-resolution digital photograph was acquired for each sample using a camera attached to a leveling device and analyzed for ring count using WinDendro (Regent Instruments, Inc., Ontario) upon return to the US

Stand Characteristics, Aboveground Biomass, and ANPP$_{tree}$ of Larch Trees

Stand inventories were used to estimate larch density and size. Within each stand, we established five 10-m^2 (high-density stands) or 20-m^2 (low-density stands) plots evenly spaced along the same 100-m-long transect mentioned above for stand age determination. Plots were located 10–20 m apart along the transect and encompassed a total of

Table 1. Allometric Equations and Statistics Used to Calculate Components of Cajander Larch Biomass

Size class	Biomass	Obs	Coefficients		
			a	b	R^2
Basal diameter (BD)	Stem	30	8.00	2.56	0.97**
BD range: 0.7–39.2 cm	Branches	30	22.91	2.13	0.98**
Height Range: 0.23 - 15.32 m	Foliage	30	22.55	1.45	0.89**
	Total	30	39.46	2.26	0.99**
Diameter at Breast Height (DBH)	Stem	32	81.42	2.10	0.98**
DBH range: 0.08–29.3 cm	Branches	32	69.66	1.99	0.96**
Height range: 1.37–15.32 m	Foliage	32	40.50	1.41	0.86**
	Total	32	179.20	2.01	0.99**

Estimates are based on raw harvest data from seven trees reported by Kajimoto and others (2006) and 30 trees collected near the Northeast Science Station in Cherskii, Russia in 2002. All equations are expressed in the form of $y = ax^b$ [x = BD or DBH; y = biomass (g dry wt tree^{-1})].
**P < 0.001.

50–100 m^2. Diameter at breast height (DBH; 1.4-m tall) or basal diameter (BD; <1.4-m tall) was measured for live and dead trees, and percent of overhead area covered by canopy (Lemmon 1956), a proxy for understory light (Englund and others 2000), was assessed using a convex spherical densiometer. Canopy height was determined for 5–10 trees sampled randomly at 10- or 20-m interval along the 100-m transect using a meter tape or clinometer.

Inventories were converted to aboveground biomass and net primary productivity (ANPP$_{tree}$) of larch trees using allometric equations (Table 1) developed from raw tree harvest data from a previously published study ($n = 7$; Kajimoto and others 2006) and from trees harvested from three stands (15-year-old low density, 60-year-old low density, and 60-year-old high density) near Cherskii in 2002 ($n = 30$). For the latter, DBH, BD, and height were measured prior to felling at ground level. Whole trees were separated into dead material, stemwood/bark, foliage, cones, and branches, chopped into pieces, and weighed. Subsamples were dried at 60°C to a constant weight, reweighed to determine a dry:wet ratio, and analyzed for %C using a Costech Elemental Analyzer (Costech Analytical, Los Angeles, California, USA).

The best-fit power equations ($y = ax^b$; x = BD or DBH; y = dry mass) relating BD and DBH to various biomass components were generated using nonlinear regression (SigmaPlot v. 11). Aboveground total biomass was computed as the sum of foliage, branch, and stemwood/bark biomass. Snag biomass was computed as the difference between aboveground total biomass and foliage biomass, as most snags still had coarse branches attached. ANPP$_{tree}$ was estimated as the sum of foliage biomass and secondary growth. Because we could not transport

tree slabs/cores back to the US and some digital images were of poor resolution, we estimated secondary growth using two approaches. First, all images of sufficiently high resolution were analyzed for ring width using WinDendro. For each stand, the mean average annual ring width for the last 10 years was used with stemwood/bark allometry equations to calculate secondary growth. We also calculated secondary growth using the 10-year average annual increment for trees collected in the 15- and 60-year-old high-density stands used to develop allometric equations. In this estimation, separate values were used for trees shorter than DBH height ($n = 5$) and those having a DBH ($n = 9$). These two estimates were highly correlated ($R^2 = 0.99$); here, we report ANPP$_{tree}$ based on the first approach. Mass values were converted to C pools using 46% C for foliage, 47% C for stemwood/bark, and 48% C for branches based on average values determined for allometry trees.

Downed Woody Debris

Downed woody debris C pools were estimated using the line-intercept method (Brown 1974). The 100-m transect previously established within each stand for other measurements was subdivided into five successive 20-m subsections. Classes I (0.0–0.49 cm in diameter) and II (0.5–0.99 cm) pieces of fine woody debris (FWD) were tallied along the first 5 m of each subsection, Class III (1.0–2.99 cm) along the first 10 m of each subsection, and classes IV (3.0–4.99 cm), V (5.0–6.99 cm), and downed coarse woody debris (CWD; >7-cm diameter) along the entire 20-m length. Diameter and decay class of CWD were recorded according to Manies and others (2005). Trees were considered CWD and

not snags if they were at an angle less than 45° to the forest floor. FWD was converted to wood mass per unit area using average multiplier values for softwood boreal trees from the Northwest Territories of Canada (Nalder and others 1997). CWD data were converted to mass per unit area using decay classes and density values derived for softwood boreal tree species within Ontario, Canada (Ter Mikaelian and others 2008). Mass values were converted to C pools using 47% C based on that of *L. cajanderi* boles.

Soils

To estimate soil C pools, we sampled SOL and upper mineral soil (10-cm depth) at 20-m intervals along each 100-m transect (n = 5) using a 7.5-cm-diameter metal soil corer. Following homogenization and removal of coarse materials (> 2 mm), soil subsamples (which included fine roots) were dried at 60°C (organic) or 105°C (mineral soil) for 48 h to determine bulk density and soil moisture. Organic matter (OM) content was estimated on oven-dried subsamples by loss-on-ignition (LOI) at 550°C for 4 h and converted to C content using a linear equation describing the relationship between LOI and C content developed using soil samples collected near Cherskii in 2002 (C content = 0.51 * LOI − 0.6, R^2 = 0.99, $P < 0.0001$). Total C contained within organic and mineral horizons was calculated as the product of each soil core's horizon depth, bulk density, and calculated C content plus coarse fraction (roots, charcoal, buried wood) C pool based on coarse material mass values and 50% C. Coarse material represented less than 3% of total soil C pools. More detailed measurements of SOL depth were acquired at 1-m interval along the first 5-m of each 20-m subsection of the transect using a ruler after inserting a serrated knife into the soil to view horizons.

Understory Plant Composition and Abundance

Understory composition and abundance were determined at 1-m interval along the first 5-m of each 20-m subsection of the 100-m transect using the line point-intercept method. At each sampling point, vegetation, leaf litter, and other material (wood, rocks, animal waste) touching a 0.5-cm diameter, 1.4-m-high sampling pin were identified to the lowest possible taxonomic level and contact points (that is, hits) with the pin enumerated. Data were re-classified by functional type for analyses and expressed as average number of hits per stand.

Understory and Larch Biomass Within Low- and High-Density 60-Year-Old Stands

We expected understory contribution to aboveground biomass to increase as larch density decreased, but we were unable to sample understory biomass in summer 2010. Thus, we compared understory and larch biomass within a 60-year-old low-density (0.04 trees m^{-2}) larch stand and an adjacent 60-year-old high-density (2.1 trees m^{-2}) larch stand, both sampled in 2002. Ground layer vegetation and small shrubs were harvested in 10 plots using a 0.25- and 1-m^2 frame, respectively, sorted by species, and separated into old and new leaves, branches, stems, and reproductive tissues. Samples were dried at 60°C to a constant weight. Larch biomass was determined using stand inventories within 4, 10, or 20-m^2 subplots (size and number varied with density) and site-specific allometric equations (data not shown). Biomass values were converted to C pools using %C values previously determined for each vegetation component.

Determination of Density Trajectories

We used several criteria to determine each stand's likely density trajectory. First, we evaluated tree age and size-class frequency distributions to determine whether the stand was even- or multi-aged (Appendices 1, 3). Normal and/or single-peaked distributions indicated even-aged stands (Shorohova and others 2009) undergoing trajectories where most recruitment occurred following a stand-replacing fire (Oliver and Larson 1996). Non-normal, multimodal, reverse J-shaped, or uniformly broad and flat age and size-class frequency distributions indicated multi-aged stands characterized by gradual or periodic recruitment in the absence of stand-replacing fire but likely influenced by surface fires and/or "gap dynamics" (Shorohova and others 2009). Tree age and size were highly correlated across stands (R^2 = 0.62; $P < 0.001$).

Second, we used live tree, snag, and downed woody debris density estimates to gauge whether the observed density of late-successional stands could have resulted from self-thinning of stands that had medium to high density during mid-succession (Appendices 2, 3). Stands younger than 20 years old were considered early-successional, as most larch recruitment occurs within 20 years following fire (S. Zimov, personal observation). Stands older than 70 years old were considered late-successional based on time needed for larch stands in central Siberia to return to pre-fire status

(50–90 years post-fire; Zyryanova and others 2010). Mid-successional stands were 20 to 70 years old. We assumed that all live and dead trees present in mid-succession were still present in late-succession given the slow decomposition rates in boreal environments (Jonasson and others 2001). We accounted for new recruits in late-successional stands by removing live trees shorter than DBH height from our live tree density estimates. We made several assumptions regarding the percentage of trees in the original stand that had fallen over and were now part of the downed woody debris pool. This was necessary because the line-intercept method used for downed woody debris biomass does not yield a direct estimate of downed woody debris density on a unit area basis. We assumed most mid-successional trees were still standing, and calculated downed woody debris density of mid-successional stands to be 5% of the stand's original density [live tree density + snag density + 0.05 * (live tree + snag density)]. We assumed that 33% of the original trees in late-successional stands would be present as downed woody debris. This was based on doubling the abundance estimates of downed woody debris pieces larger than 1 cm in diameter along our line-intercept transects. Because of potential errors associated with this estimation, we also calculated this parameter based on 50 and 66% of the original stand being present as downed woody debris.

Our sampling captured stands undergoing a variety of density trajectories (Figure 1; see "Results"), but only trajectory 1 could be assigned to stands across all successional stages. Thus, we limited our description of temporal trends to only these stands and acknowledge several limitations to minimize misinterpretations. Although impossible to determine if these stands originated from and developed under similar circumstances (Walker and others 2010), several aspects of the current sampling design reduce confounding factors and provide support that C pool trends are truly age related and not indicative of landscape variability in environmental conditions or resource availability (Bond-Lamberty and others 2004). First, larch stands have only one tree species, so alternative species trajectories are impossible. Second, alternative trajectories due to differences in initial recruitment and stand density are analyzed separately. Third, 8 of 11 stands proceeding along trajectory 1 were upland and well drained with similar geology and climate. The three riparian stands (two 5-year-old stands and one 205-year-old stand) did not produce outlying results or alter overall conclusions.

We also compared mean C pools and understory vegetation across five stand types based on successional stage and density trajectory. Raw data used to compute these means are provided in Appendices 4 and 5. Differences among these five categories were assessed using ANOVA (PROC GLM; SAS Institute Inc., 2001). F values were computed based on Type III sums of square. Significant differences among stands were compared via a post hoc Fisher's LSD test at $\alpha = 0.05$. All variables not meeting underlying assumptions of normality and homogeneity of variance were log or square-root transformed prior to analyses. We report P values from transformed data, but means and standard errors from untransformed data.

RESULTS

Successional Trajectories

Our sampling captured stands proceeding along several successional trajectories (Figure 3; Appendix 3). Of the four early-successional stands, three were even-aged and one was multi-aged due to several overstory trees that survived the most recent fire. We measured little recruitment, and larch density was low, varying from no trees in a 5-year-old stand to 0.05 ± 0.03 trees m^{-2} in a multi-aged stand within the same fire scar (Table 2). About 40% of trees within this multi-aged stand were comprised of new recruits. The low density of these stands suggests that they are likely following tra-
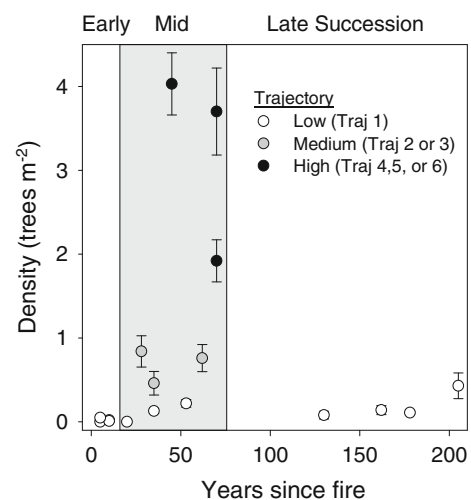

Figure 3. Likely density trajectories of 17 Cajander larch forest stands sampled near the Northeast Science Station in Cherskii, Russia in northeastern Siberia. Values are the mean of five subplots per stand ±1SE. *Note*: The increase in density observed among mid-successional stands was not significantly related to years since fire.

Table 2. Characteristics of 17 Cajander Larch Stands Sampled Near the Northeast Science Station in Cherskii, Russia in Northeastern Siberia

Years since fire	Early-successional[d]				Mid-successional								
	5	5	10	10	20	28	35	35	45	53	62	70	70
Source[a]	Sat.	Sat.	NSS	NSS	NSS	NSS	Sat.	Sat.	NSS	T.C.	T.C.	NSS	NSS
Stand	1	2	3	4	5	6	7	8	9	10	11	12	13
Habitat[b]	Rip	Rip	Upl	Upl	Upl	Upl	Upl	Upl	Upl	Upl	Upl	Upl	Upl
Elev (m)	0.3	2.7	42.4	48.2	132.9	64.6	6.7	13.4	29	139.9	22.6	11.3	38.7
Tree age (y)[c]	32–94	–	4	4–5	–	21–28	10–135	10–17	26–44	38–53	36–62	38–65	32–65
Density (trees m^{-2})	0.05 (0.03)	0.00 (0.00)	0.02 (0.02)	0.01 (0.01)	0.00 (0.0)	0.84 (0.19)	0.46 (0.14)	0.13 (0.03)	4.03 (0.37)	0.22 (0.05)	0.76 (0.16)	1.92 (0.25)	3.70 (0.52)
Diameter (cm)	3.8 (2.4)	–	0.2 (0.2)	0.1 (0.1)	–	2.2 (0.5)	4.4 (1.9)	0.8 (0.0)	2.1 (0.1)	3.6 (0.4)	4.1 (0.6)	3.3 (0.3)	1.7 (0.1)
Basal area (cm)	5.6 (3.9)	–	0.01 (0.01)	0.01 (0.01)	–	4.1 (1.3)	7.6 (2.7)	0.1 (0.0)	19.8 (1.0)	2.5 (0.6)	12.3 (1.8)	28.1 (6.3)	12.9 (2.0)
Height (m)	4.4 (1.2)	–	0.4 (0.1)	0.5 (0.1)	–	4.5 (0.3)	8.1 (0.5)	1.0 (0.1)	4.3 (0.5)	3.3 (0.4)	6.7 (0.5)	6.8 (0.7)	3.4 (0.3)
Canopy cover (%)	15.5 (1.0)	7.5 (0.6)	7.9 (1.6)	2.9 (0.9)	0.7 (0.4)	30 (10.4)	25.6 (2.6)	8.9 (2.4)	66.3 (2.4)	12.8 (2.9)	70.2 (4.4)	71.6 (3.5)	45.8 (7.4)

Years since fire	Late-successional			
	130	162	178	205
Source[a]	T.C.	T.C.	T.C.	T.C.
Stand	14	15	16	17
Habitat[b]	Upl	Upl	Upl	Rip
Elev (m)	44.2	43.3	71.6	4.9
Tree age (y)[c]	33–130	39–162	107–178	25–205
Density (trees m^{-2})	0.08 (0.05)	0.14 (0.05)	0.11 (0.02)	0.43 (0.15)
Diameter (cm)	2.6 (1.2)	7.7 (4.0)	9.9 (2.0)	4.2 (1.1)
Basal area (cm)	1.8 (1.3)	8.1 (5.1)	8.7 (2.2)	14.2 (6.0)
Height (m)	5.1 (0.4)	8.8 (1.2)	8.3 (0.7)	6.9 (1.6)
Canopy cover (%)	8.1 (2.8)	28.6 (9.1)	20.6 (4.8)	38.1 (4.3)

Values are means (±1 SE).
[a]Time since fire for each stand based on several sources: satellite imagery (Sat.), personal knowledge of Northeast Science Station scientists (NSS), and age of oldest tree in a stand determined using tree cores (T.C.).
[b]Stands were samples in riparian (Rip) and upland (Upl) areas.
[c]Aged trees included individuals originating from the previous fire; thus, ages may be older than what might be expected based on years since fire.
[d]Early = 0–19 years since fire; mid = 20–70 years since fire; late = 71–205 years since fire.
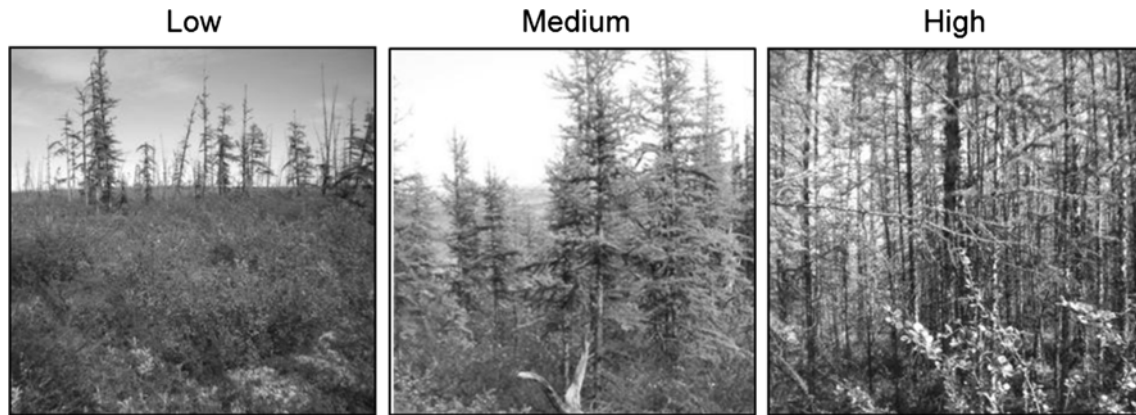
Figure 4. Variations in stand density (low, medium, high) observed within 17 Cajander larch forest stands sampled near the Northeast Science Station in Cherskii, Russia in northeastern Siberia.

jectory 1 (Figure 1). During mid-succession, 8 of 9 stands exhibited a narrow age range (< 25 year) and single-peaked or Gaussian age and size-class frequency distributions, suggesting most trees within these stands originated soon after the last fire. One 35-year-old stand was multi-aged due to the presence of several mature trees, but around 80% of trees within this stand were small (< 2 cm DBH), again suggesting recruitment soon after the last fire. Mid-successional stands exhibited a wide range of stand densities, even among stands of similar age (Figure 4; Table 2). Most importantly, because most trees recruited within a narrow time frame, current density of mid-successional stands likely reflects initial post-fire recruitment patterns rather than gradual recruitment. Three mid-successional stands had low density and are likely proceeding along trajectory 1. Three stands, including the multi-aged stand, had medium density and are likely following trajectory 2 or 3, whereas three stands had high density and are likely on trajectories 4, 5, or 6. All four late-successional stands were multi-aged with low density, and about 84% of trees were new recruits. Our estimates of live tree, snag, and woody debris density suggest that late-successional stands likely did not originate via self-thinning of medium or high-density mid-successional stands and that these stands are likely proceeding along trajectory 1 (Appendix 3).

Larch Aboveground Biomass and ANPP$_{tree}$

Stands proceeding along a low-density trajectory (trajectory 1) exhibited low larch recruitment in early- and mid-succession and consequently low aboveground biomass and ANPP$_{tree}$ (Figure 5A, B). Most increases in aboveground larch biomass and ANPP$_{tree}$ occurred during late-succession and were

driven by increased tree size, a pulse of new recruits, and increased stand density in the oldest stand. On average, low-density late-successional stands had 6 and 10 times higher mean aboveground larch biomass and 6 and 4 times higher ANPP$_{tree}$ than low-density, early- and mid-successional stands, respectively (Table 3).

Stands proceeding along medium- and high-density trajectories accumulated more C in larch aboveground biomass and had faster rates of ANPP$_{tree}$ compared to similarly aged stands proceeding along a low-density trajectory (Figure 5A, B; Table 3). For example, a 45-year-old stand undergoing a high-density trajectory had ten times higher aboveground larch biomass ($2{,}143 \pm 110$ g C m^{-2}) and 8 times higher ANPP$_{tree}$ (283 ± 21 g C m^{-2} y^{-1}) than a 53-year-old stand undergoing a low-density trajectory (Appendix 4). Mid-successional stands with medium- and high-density stored approximately 10 and 26 times more C, respectively, and had about 8 and 21 times faster rates of ANPP$_{tree}$ than low-density mid-successional stands (Table 3).

Because density had such a large effect on larch aboveground biomass and ANPP$_{tree}$, mid-successional stands proceeding along medium and high-density trajectories were able to store as much or more C in larch biomass as much older late-successional stands (Figure 5A, B; Table 3). Compared to low-density late-successional stands, medium-density mid-successional stands stored a similar amount of C in total aboveground biomass, whereas high-density stands stored about 2.5 times more C. Regardless of density, mid- and late-successional stands contained 50–60% of total larch biomass in stems compared to 35–40% in branches and less than 5% in foliage (Appendix 5), but foliage:stem, foliage:branch, and branch:stem biomass ratios did not vary significantly with stand type (Table 3).
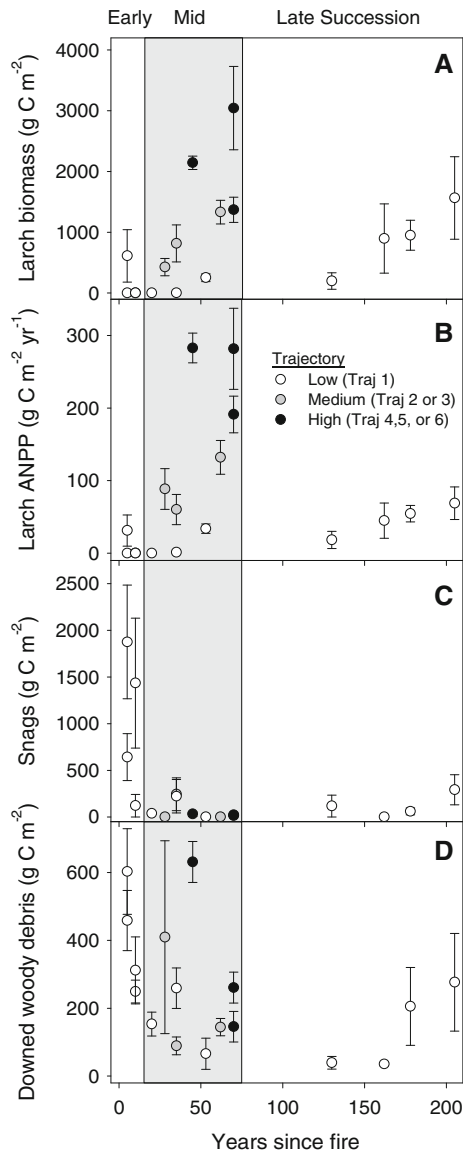
Figure 5. Total aboveground larch biomass (**A**), aboveground net primary productivity (**B**), snag biomass (**C**), total downed woody debris (**D**) of 17 Cajander larch forest stands near the Northeast Science Station in Cherskii, Russia as a function of years since fire (early, mid-, and late-successional stages) and density trajectory (low, medium, and high). Values are the mean of five subplots per stand ±1 SE.

Snags and Downed Woody Debris

Snag C pools were highly variable among low-density early-successional stands, but declined from early- to mid-succession and then remained relatively stable from mid- to late-succession independent of variations in mid-successional density (Figure 5C). Snag C pools varied between greater than 1,400 g C m^{-2} in two early-successional

stands and less than 300 g C m^{-2} in all other stands. On average, low-density early-successional stands stored 4–10 times more C in snags than all other stands (Table 3).

Downed woody debris C pools exhibited a U-shaped distribution with years since fire across stands undergoing a low-density trajectory (Figure 5D). These pools were highest 5 years following fire (459 ± 126 and 603 ± 89 g C m^{-2}), gradually declined to 36 ± 11 g C m^{-2} 162 years post-fire, and then recovered to 277 ± 144 g C m^{-2} in the oldest stand (205 years post-fire), presumably due to increased mortality of older trees. Downed woody debris C pools within one mid-successional stand proceeding along a high-density trajectory were relatively high (631 ± 60 g C m^{-2}) due to large amounts of FWD (421 ± 71 g C m^{-2}) (Appendix 4).

SOL and Upper (0–10 cm) Mineral Soils

Across the low-density trajectory, C stored within the SOL declined from early- to mid-succession and gradually increased through the early stages of late-succession (Figure 6A). This pattern led to significantly higher mean SOL C pools in low-density late-successional stands compared to those in early- and mid-succession (Table 3). Mid-successional stands proceeding along a high-density trajectory had mean SOL C pools similar to low-density late-successional stands (Table 3).

C stored within the upper (0–10 cm) mineral soil and total soil C exhibited similar temporal patterns across stands undergoing a low-density trajectory (Figure 6B, C; Table 3). Values were variable in early- and mid-succession and increased with years since fire in late-succession. Upper mineral soil C increased from 3,046 ± 430 g C m^{-2} in a 130-year-old stand to 5,166 ± 864 g C m^{-2} in a 205-year-old stand, and total soil C increased from 5,522 ± 158 to 7,632 ± 841 g C m^{-2} in these same stands. Mid-successional stands proceeding along medium- and high-density trajectories did not vary from similarly aged low-density stands, and mean C pools in upper mineral soils and total soil C were not significantly different among stand types.

Canopy Cover, Leaf Litter, and Understory Vegetation

Across the low-density trajectory, canopy cover varied little during early- and mid-succession then gradually rose about fivefold during late-succession, from 8.1 ± 2.8% in a 130-year-old stand to 38.1 ± 4.3% in a 205-year-old stand (Figure 7A). Mean canopy cover was around three times higher

Table 3. Distribution of C Pools, ANPP, OM Depth, Allocation Patterns, Understory Vegetation, Leaf Litter, and Canopy Cover for Each Stand Type and Results of the ANOVA Test for Treatment (Successional Stage and Density) Effect

Parameter	Successional stage-density trajectory					ANOVA test for treatment effect
	Early-low $n = 4$	Mid-Low $n = 3$	Medium $n = 3$	High $n = 3$	Late-low $n = 4$	
Aboveground biomass (g C m^{-2})						
Foliage	6.7a* (6.6)	8.0a (7.5)	64.7b (18.6)	207.5c (24.6)	39.5ab (9.6)	$F = 33.83_{4,16}$ $P < 0.001$
Branches	57.5a* (57.4)	32.9a (32.5)	329.1b (100.7)	841.0c (185.1)	337.3b (103.1)	$F = 9.10_{4,16}$ $P < 0.01$
Stem	88.7a* (88.7)	43.8a (43.6)	464.0ab (144.9)	1137.2c (278.5)	525.3b (167.3)	$F = 7.12_{4,16}$ $P < 0.01$
Total AG biomass	152.9a* (152.8)	84.7a (83.7)	857.8b (262.3)	2185.8c (483.5)	902.2b (279.7)	$F = 8.82_{4,16}$ $P < 0.01$
ANPP (g C m^{-2} y^{-1})	7.8a* (7.8)	11.6ab (11.1)	93.6c (20.9)	251.8d (30.3)	46.6bc (10.7)	$F = 35.06_{4,16}$ $P < 0.001$
Woody debris (g C m^{-2})						
FWD	198.5a (19.3)	109.5ab (36.9)	94.9ab (27.2)	247.9c (91.8)	61.7b (17.1)	$F = 3.46_{4,16}$ $P = 0.04$
CWD	207.1 (66.7)	49.9 (24.5)	119.4 (100.7)	97.9 (56.0)	77.5 (45.0)	$F = 0.99_{4,16}$ $P = 0.45$
Total woody debris	405.6 (79.1)	159.5 (55.9)	214.3 (98.9)	345.8 (146.5)	139.2 (60.5)	$F = 1.86_{4,16}$ $P = 0.18$
Snags (g C m^{-2})	1018.3a (393.4)	86.9b (68.6)	81.4b (81.2)	22.5b (5.0)	117.1b (62.8)	$F = 4.1_{4,16}$ $P = 0.03$
Soil (g C m^{-2})						
Organic layer	2191.7ab (133.0)	1459.2b (199.8)	1741.9ab (377.3)	2473.5ac (456.9)	3027.3c (365.4)	$F = 3.77_{4,16}$ $P = 0.03$
Upper mineral (0–10 cm)	3264.6 (290.5)	3868.5 (351.9)	3152.5 (510.8)	3451.7 (354.2)	3878.0 (471.6)	$F = 0.69_{4,16}$ $P = 0.61$
Total soil	5456.3 (241.0)	5327.7 (528.2)	4894.4 (854.4)	5925.4 (588.8)	6905.3 (472.5)	$F = 2.22_{4,16}$ $P = 0.13$
OM depth (cm)	4.4a (1.0)	5.8ab (1.8)	9.6bc (0.7)	8.5bc (1.8)	11.6c (1.8)	$F = 4.11_{4,16}$ $P = 0.03$
Overall total (g C m^{-2})	7033.1 (711.3)	5658.8 (612.8)	6047.9 (1027.8)	8479.4 (822.1)	8063.7 (806.6)	$F = 2.15_{4,16}$ $P = 0.14$
Allocation (g tree^{-1}/g tree^{-1})						
Foliage:Stem	4.1 (2.0)	2.3 (1.9)	1.5 (0.9)	0.7 (0.1)	0.8 (0.4)	$F = 1.52_{4,14}$ $P = 0.27$

Table 3. continued

Parameter	Successional stage-density trajectory					ANOVA test for treatment effect
	Early-low $n = 4$	Mid-Low $n = 3$	Medium $n = 3$	High $n = 3$	Late-low $n = 4$	
Foliage:Branch	1.1 (0.4)	0.8 (0.4)	0.6 (0.1)	0.5 (0.0)	0.5 (0.1)	$F = 1.35_{4,14}$ $P = 0.32$
Branch:stem	2.9 (0.8)	2.2 (1.2)	1.4 (0.4)	1.1 (0.1)	1.1 (0.3)	$F = 2.14_{4,14}$ $P = 0.15$
Canopy cover (%)	8.4a (2.6)	7.5a (3.5)	41.9b (14.2)	61.3c (7.9)	23.9b (6.4)	$F = 9.13_{4,16}$ $P < 0.01$
Leaf litter (# hits)	1.8a (0.5)	4.5bc (0.8)	6.0c (1.4)	4.5bc (0.5)	3.6b (0.2)	$F = 5.15_{4,16}$ $P = 0.01$
Understory vegetation (# hits)						
Moss	4.2 (0.7)	7.6 (3.0)	6.2 (3.1)	4.3 (3.5)	13.0 (2.4)	$F = 2.30_{4,16}$ $P = 0.12$
Lichen	0.3a (0.2)	3.1c (1.1)	1.3abc (0.7)	0.4a (0.2)	2.2bc (1.0)	$F = 3.22_{4,16}$ $P = 0.05$
Herbs	22.5a (4.3)	15.1ac (5.7)	9.0bc (3.1)	5.5bc (2.5)	5.4b (1.6)	$F = 4.42_{4,16}$ $P = 0.02$
Shrubs	7.6a (1.1)	25.0b (8.7)	18.8bc (6.1)	9.4ac (2.2)	16.4abc (1.0)	$F = 2.72_{4,16}$ $P = 0.08$
All other plants	1.5 (0.8)	1.1 (1.1)	1.3 (0.2)	2.0 (1.2)	0.5 (0.3)	$F = 0.53_{4,16}$ $P = 0.72$
Total Plants	36.0 (4.8)	51.9 (14.0)	36.6 (9.8)	21.5 (4.9)	37.4 (1.4)	$F = 1.91_{4,16}$ $P = 0.17$

Values are means (± 1 SE). Values with different letters indicate significant differences among stand types (Fisher's LSD, $P < 0.05$).
*Aboveground biomass of larch trees and ANPP values for early-successional stands presented here include mature trees that survived the last fire. If these trees are removed, values decrease as follows: Foliage (0.2 $\pm$ 0.2 g C m^{-2}), branches (0.2 $\pm$ 0.2 g C m^{-2}), stem (0.1 $\pm$ 0.1 g C m^{-2}), total aboveground biomass (0.5 $\pm$ 0.4 g C m^{-2}), and ANPP$_{tree}$ (0.2 $\pm$ 0.2 g C m^{-2} y^{-1}). Statistical differences among stands did not change.
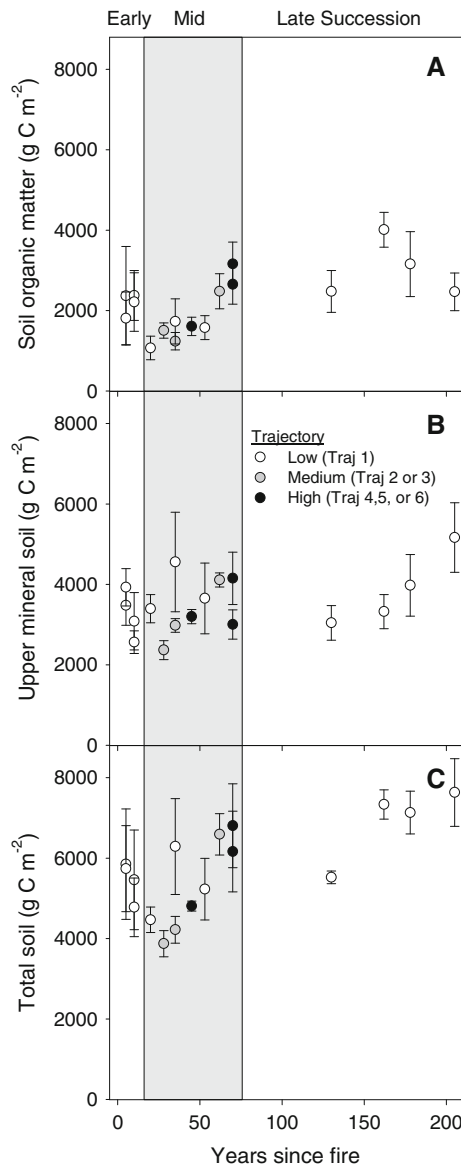
Figure 6. SOL (**A**), upper (0–10 cm) mineral soil (**B**), and total soil C (**C**) of 17 Cajander larch forest stands near the Northeast Science Station in Cherskii, Russia as a function of years since fire (early, mid-, and late-successional stages) and density trajectory (low, medium, and high). Values are the mean of five subplots per stand ±1 SE.

in low-density late-successional stands compared to low-density early- and mid-successional stands (Table 3). Stands proceeding along medium- and high-density trajectories had 6 and 8 times higher canopy cover, respectively, compared to similarly aged stands proceeding along a low-density trajectory and approximately two and three times higher canopy cover than low-density late-successional stands. Canopy cover increased with increased larch biomass across all stands ($y = 0.02x + 11.9$, $R^2 = 0.83$, $P < 0.001$; data not shown).
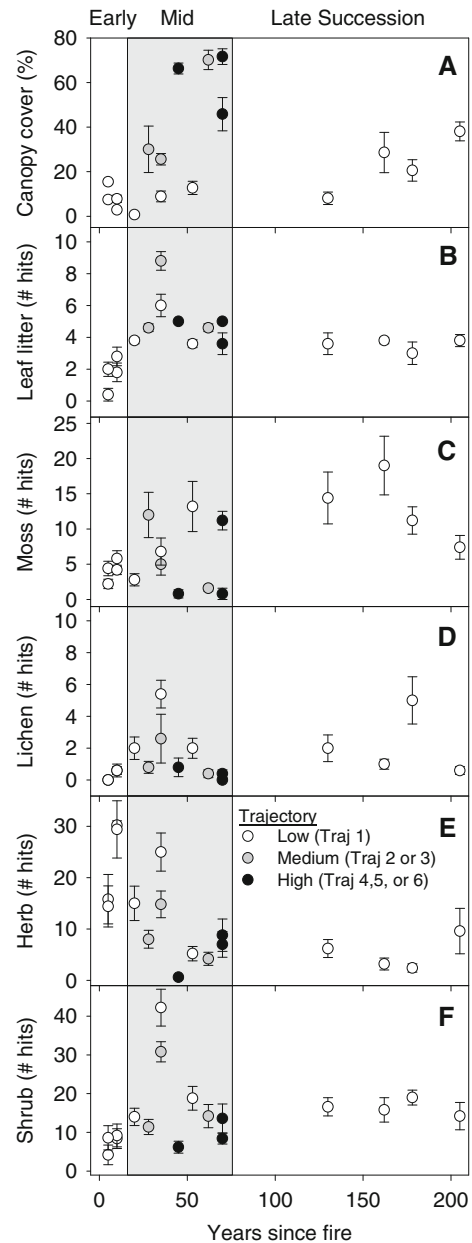

Figure 7. Canopy cover (**A**), leaf litter cover (**B**), moss cover (**C**), lichen cover (**D**), herb cover (**E**), and shrub cover (**F**) of 17 Cajander larch forest stands near the Northeast Science Station in Cherskii, Russia as a function of years since fire (early, mid-, and late-successional stages) and density trajectory (low, medium, and high). Values are the mean of five subplots per stand ±1 SE.

Across all stands, leaf litter abundance increased from early- to mid-succession and leveled off through late-succession (Figure 7B). On average, leaf litter in low-density early-successional stands was two times lower than low-density mid- and late-successional stands (Table 3). Mid-successional stands undergoing medium- and high-density

Table 4. Distribution of Total Aboveground C Pools (g C m^{-2}) Within Low (0.04 trees m^{-2}) and High (2.1 trees m^{-2}) Density 60-Year-Old Larch Stands Sampled Near the Northeast Science Station in 2002

Pool	Successional stage-density	
	Mid-low	Mid-high
Larch	24.6 (6.5)	1860.3 (316.3)
Understory		
Moss	90.4 (18.8)	16.8 (5.5)
Lichen	50.1 (6.7)	2.4 (0.7)
Forb	1.5 (0.3)	0.5 (0.1)
Grass	0.3 (0.1)	0.1 (0.1)
Sedge	0.5 (0.2)	0.0 (0.0)
Deciduous Shrub	97.3 (21.8)	41.6 (11.2)
Evergreen shrub	63.9 (16.2)	21.9 (14.3)
Total understory	304.1 (25.9)	72.1 (18.8)
Total	328.7 (32.1)	1932.4 (329.0)

Values are means (±1 SE).

trajectories had similar leaf litter abundance compared to other stand types.

Patterns of understory vegetation abundance varied with vegetation type (Figure 7C–F; Table 3). Moss abundance was highly variable and did not differ among stand types, but was often lowest in stands with high canopy cover (>60%) (compare Figure 7A, C). Herb abundance declined from early- to late-succession, decreasing 15-fold from about 30 hits in a 5-year-old stand to about 2 hits in a 178-year-old stand and then recovering to about 9 hits in the 205-year-old stand (Figure 7D). Lichen and shrub abundance were highly variable, but tended to be lowest in low-density early-successional stands and high-density mid-successional stands.

Understory Biomass as a Function of Larch Density and Biomass

There appears to be a trade-off between larch density and understory biomass (Table 4). C stored within larch biomass was 76 times higher whereas understory biomass was four times lower in the high-density 60-year-old stand compared to the same-aged low-density stand. However, total aboveground C was six times higher in the high-density compared to low-density stand.

DISCUSSION

Our findings suggest that climate-driven modifications to boreal fire regimes that alter stand age

distribution and/or tree recruitment could have important implications for C cycling. We measured a mosaic of post-fire C pools in Cajander larch forests reflecting variability in both stand age and density. Across a low-density trajectory, total C pools and ANPP$_{tree}$ increased with stand age due to increased tree size, a pulse of new recruits, and SOL development. However, the most substantial changes in C pools were associated with increased stand density. Mid-successional larch stands undergoing high-density trajectories had 21 times faster rates of ANPP$_{tree}$ and stored 26 times more C in aboveground larch biomass compared to similarly aged low-density stands. The ability of high-density stands to rapidly accumulate aboveground tree biomass allowed them to obtain C stocks equivalent to much older low-density stands. Although our data from a low- and high-density 60-year-old stand suggest a trade-off between increased larch density and decreased understory biomass, the magnitude of decrease in understory biomass was nowhere near the amount of biomass gained by increasing larch density.

C pools associated with dead material (snags, downed woody debris, and soil) were insensitive to mid-successional changes in stand density, and across the low-density trajectory, exhibited temporal trends often described in other boreal forests. Snag C pools declined rapidly post-fire suggesting a transfer of fire-killed trees to the downed woody debris pool (Boulanger and Sirois 2006). Downed woody debris C pools exhibited a U-shaped distribution, likely resulting from a gradual reduction in inputs following fire and increased inputs in late-succession as trees senesce (for example, Sturtevant and others 1997 Pedlar and others 2002). SOL C pools increased from mid- to late-succession, likely due to an accumulation of dead moss material and slow decomposition (for example, Nalder and Wein 1999; Shrestha and Chen 2010). Upper mineral soil C pools increased through late-succession, possibly due to downward transport of organic compounds to deeper soil horizons (Harden and others 2000). Because dead material tended to vary with stand age, increased fire frequency will likely have a large impact on these C pools.

Implications of Shifting Stand Age and Density on Landscape-Level C Storage

A fire-induced shift in larch forest stand age and/or density could have several implications for landscape-level C storage. In the absence of density changes, most C accumulation within Cajander larch forests occurred during late-succession

(>100 year), a pattern observed in other Siberian larch forests (Schulze and others 1995, Kobak and others 1996; Kajimoto and others 2010). If increased fire frequency leads to increased prevalence of early- and mid-successional stands without simultaneous changes in stand density, landscape-level C storage capacity will likely decline. Larch forests cover 263 million ha (Forest Fund of Russia 1999), of which 48% is Cajander larch (Abaimov 2010). If, for example, 50% of these forests are low-density late-successional stands, and they shift to low-density mid-successional stands, total C storage (exclusive of understory vegetation) will decrease by 29%, from 5.2×10^9 to 3.7×10^9 Mg C. In contrast, low-density late-successional stands stored, on average, the same amount of C as high-density mid-successional stands. Kajimoto and others (2010) report a similar trend where Dahurian larch (*L. gmelinii*) aboveground C pools within a medium-density (1.4 trees m^{-2}) 26-year-old stand ($\sim$1,200 g C m^{-2}) were greater than those in several low-density (<0.2 trees m^{-2}) late-successional (>100-year-old) stands. These findings suggest that if increased fire activity simultaneously increases fire frequency and stand density, large aboveground C pools within high-density stands could compensate for a shorter successional cycle.

The effects of increased stand density on C pools will likely persist throughout the fire-free interval. If high-density stands self-thin and become medium- or low-density in late-succession (trajectory 4 or 5), the slow decomposition rates of highly recalcitrant woody material in boreal environments mean that aboveground C accumulated during mid-succession will continue to provide a long-term C pool. Alternatively, if high-density larch stands stagnate (trajectory 6) and show little change in height or diameter for an unidentified period (Abaimov and Sofronov 1996), soil C pools may continue to increase due to increased leaf litter inputs and low understory light, which may further lower soil temperatures and reduce decomposition (Schulze and others 1995). Our data from a 45- and a 70-year-old stand with similarly high density (>3.5 trees m^{-2}) seem to support this hypothesis. Despite a 25-year difference in stand age, total aboveground biomass and ANPP of both the stands were similar, but C pools in the SOL were two times higher in the 70-year-old stand. Thus, increased stand density may have long-term effects on C pools through direct effects on aboveground tree biomass and indirect effects on the understory environment.

The effects of increased fire activity on stand density and coincident C pools may be more pronounced in Siberian regions dominated by other larch species, as these stands often obtain post-fire densities considerably higher than those reported here. In Central Siberia, Sofronov and Volokitina (2010)report Dahurian larch densities in young stands exceeding 15 trees m^{-2}. Kajimoto and others (2010) measured equivalently high density in a 14-year-old stand (14.8 seedlings m^{-2}) and even higher density in a 10-year-old stand (39.6 seedlings m^{-2}). Unless self-thinning due to low light, a shallower active layer, and/or increased root competition (Abaimov and Sofronov 1996) occurs at a relatively young age and reduces productivity substantially, aboveground C pools could exceed those reported in this study. For instance, Sobachkin and others (2005) experimentally manipulated larch stand density (0.05–12.8 trees m^{-2}) and found that after only 18 years, basal area and stem volume were ten times higher in the highest density stands, presumably because of reduced competition from grasses and shrubs. These stands showed no signs of stagnation or thinning, suggesting that high-density stands can accumulate large aboveground C pools in relatively short periods, with potentially long-term effects on C storage.

Potential Factors Affecting Larch Density

The strong relationship between larch density, stand structure, and C storage underscore the need for understanding post-fire conditions leading to increased larch density to predict C pools under a warming climate. Based on previous studies, increased larch density should occur following fires that partially consume the SOL (Abaimov and Sofronov 1996). A thin SOL prevents drying of upper mineral soils and seed desiccation while decreasing the distance seedling roots must travel before reaching the mineral soil (Johnstone and Chapin 2006). Several studies in Central Siberia suggest a post-fire SOL depth of 2–5 cm maximizes Dahurian larch (*L. gmelinii*) regeneration (Sofronov and Volokitina 2010). Because larch do not establish seed banks, but rather produce seed crops annually (Abaimov 2010), nearby seed sources are also necessary for post-fire recruitment.

In this study, however, two early- and one mid-successional stands had little to no larch regeneration despite nearby seed sources and a shallow SOL depth (<3.5 cm), suggesting that other factors may limit larch regeneration. These stands were located in upland areas where grass cover was greater than 40%. Adjacent to one early-successional stand, we noticed small patches of larch recruitment in areas where grasses had died back, suggesting competition

with grasses as a potential biotic limitation to larch regeneration (Sobachkin and others 2005). Cherbakov (1979) and Shirota and others (2006) noted that larch recruitment was greatest on ''safe sites'', areas such as logs, the base of standing trees, or exposed mineral soils because these sites were devoid of vegetation and leaf litter that physically impede the growth of seedlings. Competition with shallow-rooted vegetation on soils with a thick permafrost layer has also been noted to decrease seed germination and seedling establishment (Abaimov and Sofronov 1996). These findings suggest that heavy larch recruitment may only follow high-severity fires that damage root systems of vegetation with resprouting capacity. In the other two early-successional stands studied here density was also low, but SOL depth was greater than 5–7 cm, and there was considerable post-fire subsidence, thermokarst formation, and pools of standing water, signifying that excessive soil moisture in addition to a deep SOL may have limited larch recruitment.

The presence of only low density late-successional larch stands near Cherskii is also worth further investigation. Our sampling occurred over only a short period, and we were limited to easily accessible stands. Thus, we likely failed to capture landscape variability in stand structure, as medium-density late-successional larch stands have been observed in other regions (Khlynovskaya and others 1988; Kajimoto and others 1999, 2010. Alternatively, something may have changed in the 1940's when our oldest high-density stands originated that caused a shift to higher density trajectories. Kharuk and others (2005) reported increased Dahurian larch diameter and stand density in the forest-tundra ecotone in Central Siberia over the last several decades and attributed these changes to increased temperature, precipitation, and increased fire activity. Thus, changing climate during the first half of the twentieth century may have produced the high-density stands found near Cherskii today. Other anthropogenic influences on the fire regime may have also been important. During the mid-1900's, Cherskii was undergoing population growth in connection with establishment of an active fishery (1941–1944), geodesy and geological surveys, and airport/sea port construction related to gold mining in Bilibino region (S. Zimov, personal observation), and establishment of a nuclear power station on the West Chukchi Peninsula (S. Davydov, personal observation). Thus, it is also possible that humans intentionally or unintentionally set fires that produced novel burn conditions that increased stand density.

CONCLUSIONS

A fire-driven shift to younger and/or denser Siberian larch stands could impact boreal forest C cycling in a variety of ways. A reduction in the fire return interval without changes in stand density could lead to a decline in landscape-level C storage. If stand density increases, however, large aboveground C pools within these stands may compensate for a shorter successional cycle. Increased stand density may also affect regional climate by lowering albedo through darker foliage in summer and reduced snow cover (due to greater bole density) in winter and spring. An increase in stand density could also feed back to the fire regime, making it more difficult to predict how density shifts will impact long-term C storage. For instance, more closely packed trees could decrease ignitability because green foliage and branches are less flammable than understory vegetation. Accurate predictions of these impacts require estimates of the current larch density distribution across Siberian boreal forests, knowledge of post-fire conditions conducive to altering larch density, quantification of the proportion of the landscape most likely to see shifts in successional characteristics, and estimations of C pools within high-density stands at various successional stages and across the landscape.

ACKNOWLEDGMENTS

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