



Gap regeneration within mature deciduous forests of Interior Alaska: Implications for future forest change



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ABSTRACT

Increased fire severity in boreal forests of Interior Alaska is shifting forest canopy composition from black spruce (*Picea mariana*) to deciduous species, including trembling aspen (*Populus tremuloides*) and Alaska paper birch (*Betula neoalaskana*). Because deciduous trees are less flammable than black spruce, the dominant disturbance regime in deciduous forests could move away from fire to one of gap disturbances. In this study, we quantified forest gap characteristics and vegetation within eight mature (62–119-yr-old) deciduous stands in Interior Alaska. Canopy gaps were generally small (true gap area <50 m²), formed by the mortality of 4–16 gap makers (which were always deciduous trees), and occupied ~17–29% of the forest except in the oldest stand, where gap fraction exceeded 45%, and in one anomalous 84-yr old stand, where gaps were absent. Canopy openness increased linearly with gap area, but density of both deciduous and evergreen tree recruits was generally low and insufficient to create future stands with densities similar to those currently found in mature stands across the landscape. Canopy openness was instead correlated with decreased leaf litter cover and increased cover of moss, lichen, and evergreen shrubs. Given the low recruitment of trees with canopy gaps and the decreased probability of fire, deciduous stands will likely transition to non-forested areas or low density stands once overstory trees reach maturity and die. This could have numerous implications for ecosystem function, including carbon (C), water, and energy balance, and potential feedbacks to future fire occurrence and regional climate.

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1. Introduction

Across boreal forests of Interior Alaska, annual burned area and fire severity have increased in conjunction with climate warming and drying (Kasischke et al., 2010; Turetsky et al., 2011). Because fire severity in boreal Alaska is mostly related to fire combustion of the soil organic layer (SOL) (Boby et al., 2010), and the residual SOL provides the seedbed for future tree establishment, increased fire severity has numerous potential consequences for forest regrowth (Johnstone et al., 2010; Johnstone and Chapin III, 2006; Johnstone and Kasischke, 2005). Black spruce (*Picea mariana* (Mill.) BSP), which covers much of Interior Alaska, typically self-replaces following low-severity fires that leave behind much of the SOL (Fig. 1A) (Kurkowski et al., 2008; Van Cleve et al., 1991; Van Cleve and Viereck, 1981). Light-seeded deciduous species (e.g., *Populus tremuloides* Michx. and *Betula neoalaskana* Sarg.), however, prefer high-quality mineral soil seedbeds left behind by high-severity fires and tend to out-compete heavier-seeded black

spruce on these sites (Johnstone et al., 2010). Because initial regeneration dynamics following crown-replacing boreal fires persist as stands age (Johnstone et al., 2004), increased fire severity can lead to a shift in successional trajectories away from black spruce self-replacement to one with a dominant deciduous phase (Fig. 1B) (Bernhardt et al., 2011; Hollingsworth et al., 2013; Johnstone et al., 2010; Johnstone and Chapin III, 2006; Kurkowski et al., 2008).

This shift in forest composition has numerous ecological consequences because of inherent differences between evergreen and deciduous tree functional types. Deciduous trees have greater aboveground net primary productivity (ANPP) and accumulate and store more carbon (C) and nitrogen (N) in tree biomass and snags than black spruce (Alexander et al., 2012; Alexander and Mack, 2016). Deciduous trees have higher latent heat fluxes (evapotranspiration) during summer compared to coniferous stands and higher albedo during both summer and winter (Amiro et al., 2006; Liu and Randerson, 2008). Thus, these differences between deciduous and coniferous forests can alter carbon, energy, and water cycling, with potential implication for regional climate (Beck et al., 2011).

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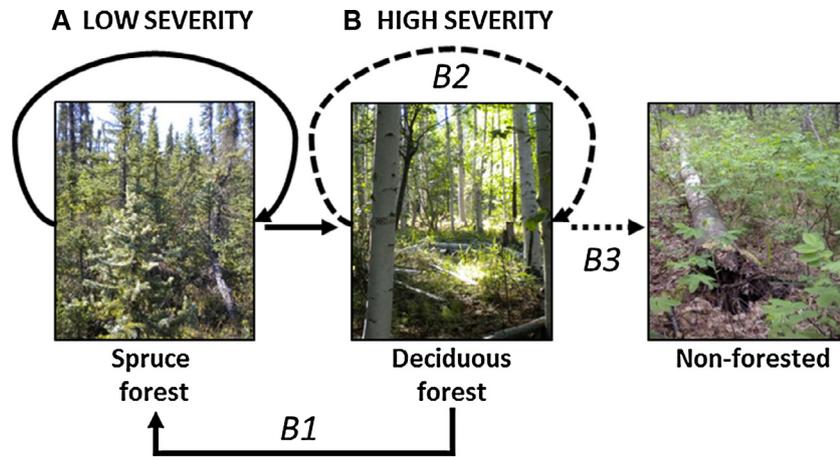


Fig. 1. Hypothetical forest successional trajectories under (A) low and (B) high fire severity within Interior Alaska. Black spruce typically self-replaces following low-severity fires, but if stands transition from black spruce to deciduous forests following high severity fire, they may undergo further successional changes, including (B1) reversion back to black (or white) spruce, (B2) self-replacement as deciduous forests, or (B3) conversion to a non-forested state.

The long-term consequences of increased deciduous dominance, however, are largely unknown because we have little knowledge about successional processes once a stand becomes dominated by deciduous trees. Deciduous stands have low flammability due to low fuel accumulation and high leaf moisture (Chapin et al., 2008; Hély et al., 2000), so the possibility of large-scale fire disturbances resetting succession could decrease as deciduous stands become more dominant (Johnstone et al., 2011). Deciduous trees of Interior Alaska are relatively short-lived (80–150 yr; Yarie and Billings, 2002), and mortality of individual trees increases after 60 yr (Viereck et al., 1983). Thus, a long fire-free interval combined with the short lifespan of deciduous trees may allow succession to proceed following gap-phase dynamics, where regeneration occurs in canopy openings (<200 m²) created by the death of single or multiple trees (McCarthy, 2001). However, because of the landscape dominance and obvious large-scale consequences of stand-initiating wildfire disturbances on forest successional dynamics, there has been little attention given to the role of gap disturbances on tree recruitment in boreal forests (McCarthy, 2001), and we know of no studies investigating gap processes in mature deciduous forests of Interior Alaska.

Gap dynamics within mature deciduous forests may follow different paths depending on individual species' abilities to establish within and/or utilize the newly-opened growing space (Fig. 1B1–3). Black or white (*P. glauca* (Moench) Voss) spruce that recruited with deciduous trees relatively soon after fire could emerge from understory suppression following mortality of the deciduous canopy (Fig. 1B1), following relay succession (Kurkowski et al., 2008). Spruce could also recruit into new gaps from nearby seed sources, especially during episodic mast years of the wind-dispersed white spruce but also from relict (fire-surviving) trees of either spruce species (Fig. 1B1). Deciduous stands could self-replace from new recruits or advanced regeneration via gap dynamics (Fig. 1B2), allowing deciduous stands to persist (Cumming et al., 2000; Fastie et al., 2002). Alternatively, tree regeneration within gaps could be minimal due to low light or a poor seedbed, and grasses, shrubs, and other understory vegetation could become the dominant cover, leading to conversion to a non-forested state (Fig. 1B3). Thus, while increased fire severity may lead to successional trajectories punctuated by a deciduous phase, long-term implications for C, water, or energy balance will ultimately depend on the length of this phase and the successional pathway following deciduous dominance.

The primary objective of this study was to gain a better understanding of the potential for tree recruitment within deciduous forests of Interior Alaska as they mature and overstory trees die, creating canopy gaps. To address this objective, we asked the following questions about mature deciduous stands of Interior Alaska: (1) What is the frequency and size distribution of canopy gaps? (2) What type of tree mortality forms canopy gaps? (3) How does gap size affect canopy openness? (4) Do vegetation regeneration patterns vary with gap size and canopy openness? and (5) Are gaps filled by deciduous or spruce trees, or are they occupied by other vegetation types? We hypothesized that (1) canopy gaps would be common in mature deciduous stands of Interior Alaska due to mortality of the deciduous overstory, and (2) tree recruitment within gaps would be dominated by deciduous species and increase with increased gap area due to increased canopy openness. Because deciduous stands will likely become more dominant across the landscape with increased fire severity, there is a clear need to understand successional dynamics as these stands age.

2. Methods

2.1. Study area

This study took place within an 800-km² area of Interior Alaska. This region is bounded to the north by the Brooks Range and altitudinal treeline (67°N), to the south by the Alaskan Range (63°N), to the west by the Dalton Highway (150°W), and to the east by the Alaska/Canadian border (142°W), and includes the Yukon, Tanana, and Kuskokwim River valleys (Hulten, 1968). Climate is continental, with long, cold winters (−23 °C in January) and warm, dry summers (17 °C in July) (Alaska Climate Research Center, <http://climate.gi.alaska.edu/>). Nearly half (47%) of annual precipitation (286 mm) occurs during the growing season (June–August) and about 35% falls as snow (Hinzman et al., 2005), which covers the ground 6–9 months per year (Slaughter and Viereck, 1986). The region is underlain by discontinuous permafrost (75–80%) except along floodplains and on south-facing slopes (Osterkamp and Romanovsky, 1999). Soils range from poorly-drained Gelisols to well-drained, permafrost-free Inceptisols (Dyrness, 1982). The continental climate also proves conducive to wildfires. Fire return interval in Interior Alaska was ~196 yr from 1950 to 2000 and dropped to ~144 yr during the 2000s (Kasischke et al., 2010). The region is dominated by forests of black spruce, an evergreen,

semiserotinous conifer, intermixed with local patches of deciduous trees, including trembling aspen and Alaska paper birch. Tall shrubs, including willows (*Salix* spp.) and alder (*Alnus* spp.) occur frequently across all stand types (Alexander et al., 2012). Mosses, including feathermosses and *Sphagnum* spp., often dominate the understory of mature black spruce stands (Turetsky, 2003; Viereck et al., 1983), while heavy leaf litter tends to limit moss cover in deciduous stands (Chapin III et al., 2006).

2.2. Study sites

Mature (>60-yr old) deciduous stands (a relatively homogeneous, contiguous area of trees of similar size and structure) of trembling aspen or Alaska paper birch were inventoried during summers 2009–2011 as part of two other studies aimed at assessing C and N pools across different forest types (Alexander et al., 2012; Alexander and Mack, 2016). We located mature stands using a combination of fire perimeter maps (Alaska Geospatial Data Clearinghouse, U.S. Department of the Interior Bureau of Land Management 2012), satellite imagery depicting deciduous versus evergreen cover (Beck et al., 2011), and ground observations.

To ensure stands were >60-yr-old, stand age was determined by obtaining a wood slab or core from the base (~20 cm above the organic layer) of 5–10 canopy dominant trees sampled randomly at 10 or 20-m intervals along a 100-m transect placed within the center of each stand. Wood slabs were dried at 60 °C, sequentially sanded using finer and finer grits to obtain a smooth, clear surface, and scanned at 1200 dpi. Ring number was determined using WinDendro (Regent Instruments, Inc., Ontario). Stand age is the mean ring number of all sampled trees within the stand. Canopy height was determined for the same trees used to age the stand using a clinometer. Leaf area index (LAI) was measured at 20-m intervals along the same transect using a LAI-2000 Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, NE). Stand density and other general stand characteristics were estimated according to Alexander et al. (2012) and Alexander and Mack (2016). Trees were considered 'adults' if they were tall enough (1.4 m) to have a DBH. Stands with evidence of human activities (e.g., wood cutting, camping, etc.) were avoided.

2.3. Canopy gap distribution & area

Canopy gaps within each stand were located using the line-intercept method (Runkle, 1992). One to five 100-m long transect lines were established within a homogeneous patch of the interior of each stand. The number of transects varied depending on the frequency of canopy gaps, with stands containing many gaps having fewer transects. Gaps were defined as visibly detectable open sky areas within the main forest canopy formed by the death of one or more trees (Runkle, 1992) with the tallest stem less than f the height of the adjacent overstory canopy (Hart and Grissino-Mayer, 2009) intersecting each transect line. To be a true gap, rather than a large stand-level disturbance, the length of the longest axis of the gap (D) could not exceed the average height (H) of the canopy (i.e., $D/H < 1$) (Ott and Juday, 2002; Runkle, 1992). The true area of each gap was estimated by measuring the gap length (i.e., largest distance from gap edge to gap edge) and gap width (i.e., largest distance perpendicular to the length). The expanded gap area was measured similarly by determining the four vertices of the gap consisting of the two main canopy trees forming the length and two main trees forming the width of the gap and measuring the distance between these trees. Gap length was divided by gap width to calculate eccentricity, where values >1 indicate elliptical gaps and those closer to 1 indicate circular gaps (Battles et al., 1996). Most gaps (>95%) had eccentricity values >1; thus, gap length and width measurements were fitted to the

formula of an ellipse to determine gap area (Runkle, 1992). Gap fraction, the fraction of the stand occupied by canopy gaps, was estimated by dividing the total transect length occupied by true gaps by the total transect length.

2.4. Canopy openness & gap origin

Percent of overhead area not covered by canopy (i.e., canopy openness), a proxy for understory light (Englund et al., 2000), was estimated at the edge and center of each true and expanded gap and at the gap center using a convex spherical densiometer. Mean values represent the average of all values recorded within each gap. Gap origin was determined by noting whether the gap formed via a downed tree, snag, snapped stem, or only a stump remained (Clinton et al., 1994). Each 'gap maker' was identified to species using bark and branching characteristics, and diameter at breast height (DBH) and height were measured.

2.5. Tree and large shrub recruitment & ground layer cover

Tree recruitment within each gap was characterized by identifying each stem with a $< f$ height of adjacent overstory to the lowest possible taxonomic level and measuring the DBH or basal diameter (if $< DBH$ tall) and height of each stem within a 0.85-m belt transect running along the length and width of the expanded gap area. Ground layer percent cover (deciduous shrub, evergreen shrub, herb, moss, lichen, and leaf litter) within each true gap was visually estimated within three randomly-placed 0.25-m² quadrats.

2.6. Data analysis

Relationships between gap area and canopy openness, gap maker basal area and gap area, gap area and understory tree/large shrub recruitment, and gap openness and understory cover were explored using a linear mixed model with stand as a random factor. Gap was the experimental unit ($n = 40$). All regression analyses were performed using JMP v. 12.0.

3. Results

3.1. Stand characteristics

The mature deciduous stands in this study ranged in average age from ~62 to 119 yr old and varied in composition and structure (Table 1). Alaska paper birch dominated five of eight stands, while trembling aspen dominated three stands. Canopy height ranged from ~11 to 21 m, and LAI varied 3-fold, from a low of ~1 to a high of 3. Density ranged between 0.18 and 0.72 individuals m⁻², and total aboveground biomass ranged from ~6600 to 20,000 g m⁻². One 84-yr old Alaskan birch stand was unique in that it was comprised of small trees (mean DBH = 4.9 cm) with higher density and lower total biomass than other similarly-aged stands.

3.2. Canopy gap distribution, openness, and makers

Gap frequency across the stands ranged from 0 to 6 gaps per 100 m⁻¹, with 0–45% of the forest stand occupied by true gaps and 0–88% occupied by extended gaps (Table 2). Again, the 84-yr old birch stand was an anomaly, having no gaps. Among other stands, gaps tended to be elliptical in shape (eccentricity > 1), and gap area ranged from 17 to 44 m⁻², with expanded gap area often twice as large. The oldest stand (stand 8) had the greatest true and expanded gap area and the highest canopy openness

Table 1
Location and general characteristics of eight mature deciduous stands sampled for canopy gap dynamics within Interior Alaska. nd = no data. Deciduous trees are trembling aspen (*Populus tremuloides*) and Alaska paper birch (*Betula neolaskana*); evergreen trees include white and black spruce (*Picea glauca* and *mariana*, respectively). Tall shrubs are alder (*Alnus* spp.) and willow (*Salix* spp.).

Stand	Dominant overstory	Lat (N)	Long (W)	Avg age (yr)	Age range (Min–Max)	Canopy height (m)	LAI ($m^2 m^{-2}$)	Density (individuals m^{-2})				Aboveground biomass ($g m^{-2}$)			
								Dec trees	Evg Trees	Tall shrubs	Total	Dec trees	Evg trees	Tall shrubs	Total
1	Birch	63.785	145.062	62	50–55	11.2	2.72	0.26	0.28	0.09	0.63	12,622	482	338	13,441
2	Aspen	65.426	148.892	70	62–78	17	3.00	0.17	0.12	0.12	0.41	13,456	563	1523	15,542
3	Birch	65.404	148.230	74	68–81	17.7	2.29	0.12	0.00	0.12	0.24	9389	0	74	9463
4	Birch	65.153	147.466	77	74–79	20.9	2.33	0.18	0.00	0.00	0.18	12,408	0	0	12,408
5	Aspen	63.890	145.862	84	76–90	10.9	0.96	0.22	0.09	0.00	0.31	10,392	22	0	10,413
6	Birch	65.444	148.776	84	83–85	18.5	1.82	0.72	0.00	0.00	0.72	6570	0	0	6570
7	Birch	64.902	148.275	87	81–100	17.1	nd	0.26	0.00	0.07	0.33	19,949	0	94	20,043
8	Aspen	63.368	143.534	119	111–137	15.8	1.54	0.24	0.28	0.20	0.72	12,713	42	112	12,867

Table 2
Number of gaps sampled and their average frequency, size, fraction, and canopy openness (\pm SE) within eight mature deciduous stands in Interior Alaska. ^aStand 6 had no gaps so has no data for some parameters (ND).

Stand	Gaps sampled (#)	Gap freq (gaps $100 m^{-1}$)	True gap area (m^2)	Ext gap area (m^2)	Gap fraction (%)	Eccen-tricity	Ext gap fraction (%)	Canopy openness (%)
1	7	2.33	24.6 (4.1)	62.1 (12.0)	17.9	1.6 (0.3)	28	14 (3)
2	4	2.00	16.6 (2.0)	54.6 (5.5)	17.3	1.3 (0.2)	25	13 (2)
3	5	2.00	26.3 (7.3)	82.6 (19.5)	17.0	1.7 (0.1)	24	12 (1)
4	6	3.00	14.8 (6.9)	55.4 (20.1)	26.5	1.4 (0.1)	42	12 (2)
5	6	6.00	25.9 (3.3)	50.1 (4.9)	28.5	1.5 (0.1)	43	37 (5)
6	0 ^a	0.00	0.0 (0.0)	0.0 (0.0)	0.0	ND ND	0	ND ND
7	6	3.00	26.5 (6.1)	86.1 (17.8)	21.1	1.7 (0.1)	36	26 (2)
8	6	6.00	43.6 (6.3)	88.2 (9.6)	45.3	1.7 (0.3)	62	54 (5)

(54%). Canopy openness exhibited a significant positive linear increase with true and expanded gap area ($R^2 = 0.83$, $P = 0.006$, $n = 40$ for both) (Fig. 2).

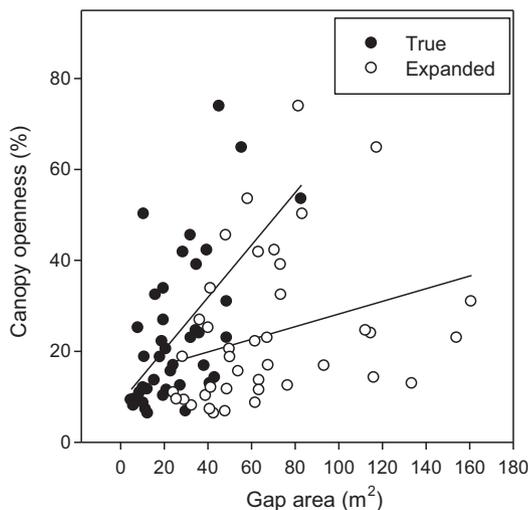


Fig. 2. Canopy openness as a function of true and expanded gap area within 40 gaps distributed across eight mature deciduous stands in Interior Alaska. Regression lines were fitted to raw data; statistical fit was determined using stand as a random factor.

On average, 4–16 gap makers encompassing a total basal area of 508–1591 cm^2 , contributed to gap formation (Table 3). Gap makers were always deciduous trees that were standing dead (i.e., snags) or dead and down trees. Snags were most common in younger stands (stands 1–4), while down trees were more abundant in older stands (stands 5, 7–8). There was a positive linear increase in gap area as a function of basal area of gap makers (Fig. 3; true gaps: $R^2 = 0.40$; $P = 0.006$; expanded gaps: $R^2 = 0.40$; $P = 0.0005$).

3.3. Tree and large shrub recruitment

Tree recruitment within canopy gaps was relatively low, never exceeding 1 deciduous or evergreen tree m^{-2} ; tall shrub recruitment was also <0.25 shrubs m^{-2} , except at stand 5, where shrub recruitment was ~ 1.5 shrubs m^{-2} (Table 4). Most tree recruits were <2 m tall, except for a single black spruce tree of 9.24 m in stand 4 (Table 4). There was no apparent relationship between true or expanded gap area and density or height of tree or large shrub recruits (data not shown) or between canopy openness and recruit density or height (Fig. 4A and B).

In five of the seven stands with canopy gaps, mean density of deciduous tree recruits was substantially lower than density of adult trees in the current stand; density of evergreen recruits was often higher than that of adult evergreen trees in the current stand, but much lower than density of deciduous tree recruits (compare Tables 1 and 4). Relative density of deciduous vs evergreen recruits varied with overstory dominance. Stands dominated by Alaskan birch in the overstory (stands 1, 3, 4, and 7) typically had more deciduous recruits, while stands dominated by aspen

Table 3

Gap maker basal area and density (\pm SE) across 40 gaps within eight mature deciduous stands of Interior Alaska. Stand 6 not included in table because no gaps were found at this stand. All gap makers were either Alaskan birch or trembling aspen.

Stand	Down ($\text{cm}^2 \text{gap}^{-1}$)	Snag ($\text{cm}^2 \text{gap}^{-1}$)	Snap-off ($\text{cm}^2 \text{gap}^{-1}$)	Stump ($\text{cm}^2 \text{gap}^{-1}$)	Total ($\text{cm}^2 \text{gap}^{-1}$)	Den (ind gap^{-1})
1	16 (12)	245 (80)	43 (28)	9 (9)	312 (94)	5.4 (1.4)
2	60 (16)	62 (62)	0 (0)	7 (7)	128 (78)	5.8 (3.4)
3	185 (95)	215 (119)	108 (50)	0 (0)	508 (108)	3.7 (0.9)
4	267 (59)	401 (240)	94 (40)	198 (77)	960 (228)	10.8 (1.7)
5	481 (236)	392 (89)	96 (61)	28 (15)	997 (283)	9.2 (2.0)
7	742 (251)	133 (61)	324 (96)	392 (167)	1591 (335)	15.8 (3.1)
8	507 (113)	375 (105)	109 (94)	8 (8)	999 (159)	9.3 (1.7)

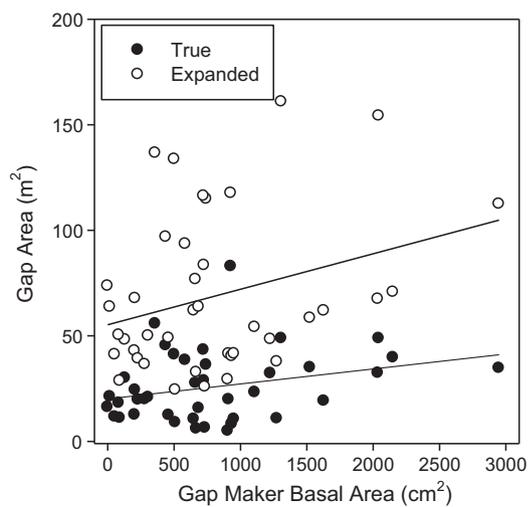


Fig. 3. Influence of gap maker basal area (trees + large shrubs) on expanded and true gap area within 40 gaps across eight mature deciduous stands in Interior Alaska. Regression lines were fitted to raw data; statistical fit was determined using stand as a random factor.

(stands 2, 5, and 8) often had more or similar amounts of evergreen recruits (Table 4). Deciduous recruits were often dominated by the same species occupying the canopy, while evergreen recruits were a mix of both black and white spruce, with neither species exhibit-

ing increased density beneath a particular deciduous species' canopy.

3.4. Understory cover

Canopy cover had variable impacts on understory cover (Fig. 5). Cover of moss ($R^2 = 0.67$, $P = 0.02$) and lichen ($R^2 = 0.64$, $P = 0.02$) exhibited significant linear increases with increased canopy openness (Fig. 5A and B, respectively). Evergreen shrub cover increased with canopy openness, but the change was not significant ($R^2 = 0.81$, $P = 0.14$, Fig. 5C). Cover of deciduous shrubs and herbaceous species were highly variable at low to moderate canopy openness but declined at high canopy openness (>50%; Fig. 5D and E, respectively). Leaf litter decreased linearly with increased openness ($R^2 = 0.91$, $P = 0.005$; Fig. 5F) and occupied much of the ground layer cover (>80%) in canopy gaps except in the oldest stand where moss cover approached 70% (Table 5).

4. Discussion

Canopy gaps formed by the mortality of one or more overstory trees were common within most mature (62–119 yr old) deciduous stands sampled in this study. Gaps were generally small (true gap area <50 m²) and occupied ~17–29% of the forest except in the oldest stand, where gap fraction exceeded 45%, and in one anomalous 84-yr old stand, where gaps were absent. The large difference in gap fraction between the oldest stand and other stands, which were >30 yr younger, suggests that deciduous tree canopy

Table 4

Mean density and height (\pm SE) of tree and large shrub regeneration within canopy gaps found in mature deciduous forests of Interior Alaska. Stand 6 not included in table because no gaps were found at this stand. – indicates no height because no individuals were found.

Stand	Density (indiv m^{-2})			Height (m)		
	Decid	Evg	Shrub	Decid	Evg	Shrub
1	0.93 (0.27)	0.32 (0.11)	0.00 (0.00)	0.14 (0.03)	0.72 (0.26)	–
2	0.02 (0.02)	0.20 (0.14)	0.02 (0.02)	0.51 –	0.85 (0.19)	2.93 –
3	0.13 (0.12)	0.00 (0.00)	0.22 (0.07)	1.69 (0.33)	–	1.70 (0.30)
4	0.50 (0.34)	0.01 (0.01)	0.00 (0.00)	0.33 (0.01)	9.24 –	–
5	0.13 (0.06)	0.15 (0.05)	1.48 (0.86)	0.71 (0.21)	2.19 (1.02)	0.94 (0.23)
7	0.17 (0.05)	0.02 (0.02)	0.19 (0.07)	0.69 (0.06)	0.33 –	1.86 (0.24)
8	0.20 (0.07)	0.46 (0.21)	0.06 (0.03)	0.37 (0.08)	1.79 (0.16)	1.02 (0.14)

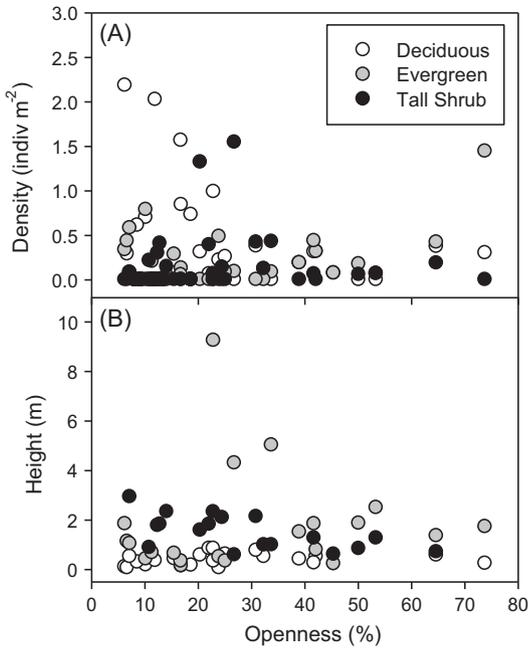


Fig. 4. Recruit (A) density and (B) height of deciduous and evergreen tree and tall shrubs in relation to canopy openness within 40 gaps distributed across eight mature deciduous forests of Interior Alaska.

mortality increases when tree age approaches 100-yr-old. The high gap fraction in the oldest stand also suggests that gaps must remain open for an extended period. The lack of canopy gaps in the 84-yr-old birch stand suggests that factors other than tree age can influence canopy mortality and gap formation. While trees in this birch-dominated stand were similarly-aged to two other birch stands (stands 4 and 7), mean individual tree diameter was only 8 cm compared to ~14 cm in these other stands. Thus, it is

possible that survival declines as DBH increases due to reduced tree vigor and/or susceptibility to disease, insects, windthrow, or drought (Yao et al., 2001). Another possible explanation for the lack of gaps in this stand is that this stand is in an earlier stage of stem exclusion, and any gaps produced are quickly filled by lateral branch extension of trees neighboring the gap (Runkle, 2013). For stands of similar age, the percentage of the forest in gaps was slightly higher than that reported for a mature (78-yr-old) aspen-dominated stand (11%) in northwestern Quebec (Kneeshaw and Bergeron, 1998) but equivalent to a 67-yr-old aspen stand (17%) in Alberta, Canada (Cumming et al., 2000). Gap fraction occupied a slightly wider range (0–45%), but similar median (20%), than that previously documented across coniferous-dominated boreal and subalpine forests (6–36%; median 21%) (McCarthy, 2001).

As expected, canopy openness increased linearly with increase gap area, but increased openness did not lead to increased density of either deciduous or evergreen tree recruits. Recruit density was low due to either an inability of new individuals to establish or low abundance or vigor of advance regeneration (McCarthy, 2001). Establishment of new individuals could have been impeded by an unfavorable seedbed in canopy gaps. Seeds of both deciduous and evergreen trees germinate best on high-quality mineral soil seedbeds (Johnstone and Kasischke, 2005). Despite a large proportion of gap-makers existing as down trees, this did not create a pit and mound topography and increased exposure of mineral soils (Alexander, pers. observ.). In small gaps, leaf litter cover was high (>70%), and leaf litter can reduce tree seedling establishment by crushing seedlings (Koroleff, 1954) or reducing winter insulation (DeLong et al., 1997; Simard et al., 2003). In large gaps, moss, lichen, and evergreen shrub cover was high, and these plants can suppress tree regeneration through several mechanisms. Mosses can negatively impact tree seedling establishment through competition for light and smothering of seedlings (Hörnberg et al., 1997). Ericaceous species, which include common evergreen shrubs like lowbush cranberry (*Vaccinium vitis-idaea* L.) and Labrador tea

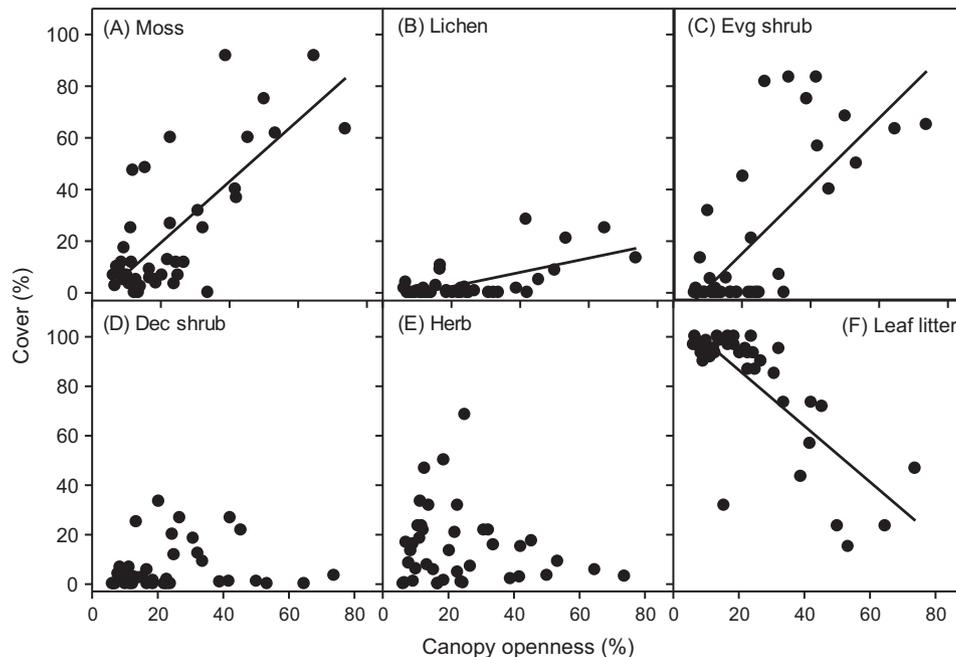


Fig. 5. Relationship between canopy openness and understory cover within canopy gaps of mature deciduous stands of Interior Alaska. (A) Moss, (B) lichen, and (C) evergreen shrub cover exhibited linear increases with canopy openness. (D) Deciduous shrub and (E) herbaceous cover were variable at low and moderate openness and declined at high openness (>50%). (F) Leaf litter cover significantly decreased with increasing openness. Regression lines were fitted to raw data; statistical fit was determined using stand as a random factor.

Table 5

Understory percent cover and biomass (\pm SE) by functional type within mature deciduous stands of Interior Alaska. Stand 6 not included in table because no gaps were found at this stand.

Stand	Understory cover (%)					
	Dec Shr	Evg Shr	Herb	Lichen	Moss	Litter
1	0.8 (0.8)	4.8 (4.5)	1.2 (0.8)	4.1 (1.6)	5.4 (0.9)	98.8 (0.6)
2	8.3 (5.8)	0.0 (0.0)	23.2 (9.2)	0.0 (0.0)	10.0 (5.4)	96.3 (1.7)
3	4.4 (1.3)	15.1 (13.7)	25.4 (5.0)	0.0 (0.0)	3.7 (1.8)	90.8 (3.6)
4	1.9 (0.8)	5.7 (3.8)	14.4 (5.0)	0.6 (0.4)	25.1 (9.3)	92.8 (1.5)
5	20.0 (4.8)	52.1 (11.9)	12.3 (2.0)	1.4 (0.8)	27.2 (10.0)	72.2 (9.0)
7	10.7 (3.4)	1.2 (1.2)	27.4 (9.2)	0.0 (0.0)	19.1 (4.1)	91.4 (1.8)
8	1.0 (0.5)	67.5 (5.7)	4.6 (4.3)	16.3 (4.2)	70.6 (8.1)	34.7 (6.7)

(*Rhododendron tomentosum* Harmaja), are strong competitors with young trees, especially on poorer, late-successional sites, and can also suppress boreal tree establishment through allelopathic effects (Jäderlund et al., 1996; Zackrisson et al., 1997). Thus, seedbed conditions within canopy gaps were likely of poor quality, contributing to low establishment of tree recruits.

Low abundance of advance regeneration in the understory of deciduous stands also could have contributed to low recruit density in gaps. Conifers can fail to accumulate beneath a deciduous overstory (Johnstone and Chapin III, 2006; Kurkowski et al., 2008) because deciduous species often outcompete conifers during early-succession (Johnstone and Chapin III, 2006) and deciduous leaf litter impedes conifer establishment (Simard et al., 1998, 2003). Deciduous advance regeneration may have been low because trembling aspen and birch are generally shade-intolerant (Kobe and Coates, 1997). Deciduous stands tend to have a high LAI and a shady understory, which could lead to high mortality of deciduous seedlings/saplings and an inability of deciduous regeneration to accumulate in the understory.

Release of suppressed advance regeneration also was not evident in gaps, as tree and large shrub height showed no change with increased canopy openness. While canopy release has been shown for aspen suckers in response to experimental (Groot et al., 1997) ($\sim 60\text{-m}^2$) and natural gap formation (Cumming et al., 2000) in more southerly forests, this was not seen here. A lack of response may be because gaps of the size documented here do not increase light as much at these more northerly latitudes or because changes in soil temperature, which can promote regeneration growth of aspen suckers (Peterson and Peterson, 1992), do not occur in conjunction with increased light at these latitudes.

Given the low recruitment of trees and large shrubs with canopy gaps and the decreased probability of fire in deciduous stands (Johnstone et al., 2011), deciduous stands may transition non-forested areas or low-density stands once overstory trees reach maturity and die. In this study, only two stands had higher density of deciduous recruits than the density of adult deciduous trees in the current stand, and even then, recruit density was low. Assuming no additional recruitment, which is likely given the poor seedbed, and the loss of only 1 recruit yr^{-1} , the youngest stand with the highest deciduous density (stand 1), would have a lower deciduous tree density than adult trees in the current stand in only 42 yr (making this stand only 104-yr-old). All other stands would be absent of deciduous tree recruits in <28 yr. Density of evergreen tree recruits was lower than that of deciduous recruits, so the likelihood of stands transitioning to black or white spruce stands is highly unlikely. Density of evergreen recruits was

<0.4 trees m^{-2} , eight times lower than black spruce density in mature coniferous stands (3.3 black spruce trees m^{-2}) (Alexander and Mack, unpub. data). In all stands except the oldest, evergreen tree density would reach zero in <20 yr in if no further recruitment and a mortality rate of one individual yr^{-1} .

A transition to non-forested areas will likely have numerous implications for ecosystem function, including carbon (C), water, and energy dynamics. Because understory plants have lower biomass than trees (Mack et al., 2008), non-forested areas will have a lower capacity to accumulate and store C. Increased moss cover in previously deciduous forests could increase depth of the insulating soil organic layer, promoting development or thickening of permafrost (Viereck et al., 1983). A decrease in available rooting volume and transition to lower quality moss litter may further limit plant productivity (Van Cleve and Viereck, 1981). Conversely, increased cover of low-growing shrubs could trap more snow, leading to higher winter insulation, warming of underlying permafrost soils, and mineralization of nutrients needed to further promote shrub productivity (Sturm et al., 2005). While deciduous forests have higher albedo than coniferous forests in both summer and winter due to more reflective foliage and higher snow exposure, respectively, they would likely have lower albedo than non-forested areas in winter because trees grow above the snow-pack. In addition, evapotranspiration rates will likely decrease with a conversion from deciduous trees to low-growing mosses and/or shrubs, which could reduce atmospheric water vapor, leading to a cooling effect (Swann et al., 2010). Finally, increased prevalence of non-forested areas dominated by mosses, lichens, and short shrubs could increase fire frequency, as these due understory communities have high flammability (Dyrness et al., 1986). Ultimately, a conversion from deciduous forests to non-forested areas could have numerous impacts on boreal ecosystem function with potential feedbacks to regional climate.

5. Conclusions

In response to climate warming and increased fire severity, boreal forests of Interior Alaska are undergoing a shift in forest dominance from the evergreen conifer, black spruce, to deciduous forests comprised trembling aspen and Alaskan birch (Johnstone et al., 2010; Mann et al., 2012). Although deciduous forests embedded in a matrix of spruce often burn, they are less flammable than coniferous stands and their likelihood of burning will likely decrease as their dominance across the landscape increases (Johnstone et al., 2011). In the absence of stand-replacing fires, deciduous stands will likely achieve old-growth status, and gap

disturbances due to single or multiple overstory tree mortality will likely become the dominant disturbance regime. In more southerly boreal forests, studies have found that gap filling by newly-established or advance regeneration of deciduous trees, and eventually, evergreen trees can maintain these areas in a forested state, which typically revert back to fire-prone coniferous state after going through a deciduous phase (Cumming et al., 2000; Kneeshaw and Bergeron, 1998). However, our findings suggest that gap conditions in Interior Alaska deciduous stands may be insufficient to foster tree recruitment, and that gap-phase processes may not maintain the forest canopy. This could lead to a conversion of deciduous forests to a non-forested state, which could persist without disturbances to the forest floor to improve seedbed conditions and tree recruitment. Thus, a conversion from deciduous forests to a non-forested state could be long-lived with numerous consequences for ecological processes including C and N accumulation and storage (Alexander et al., 2012; Alexander and Mack, 2016), albedo, and water cycling, and potential implications for future flammability and regional climate.

Author contributions

HDA: Designed study, performed research, analyzed data, and wrote manuscript; MCM: Contributed to data interpretation and critically reviewed the manuscript.

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