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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 m^2), 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.

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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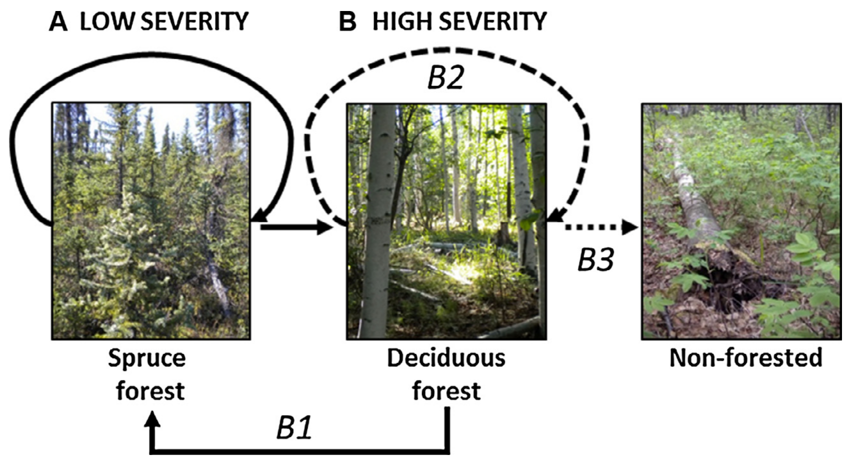

Fig. 1. Hypothetical forest successional trajectories under (A) low and (B) high fire severity within Interior Alaska. Black spruce typically self-replaces following low-severity fires, but if stands transition from black spruce to deciduous forests following high severity fire, they may undergo further 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 m^2) 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-km^2 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,