

## AGE AND STRUCTURE OF A *PICEA MARIANA* STAND AT THE SOUTHERNMOST EXTENT OF ITS RANGE IN SOUTHERN MICHIGAN

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### ABSTRACT

Climate change has begun to cause shifts in the distributions of tree species, particularly those in northern latitudes. Because such shifts have largely consisted of contractions at the southern limits of the range of a species, understanding the structure and development of forests at the southernmost extent of a species' distribution is important for identifying the impacts of climate change. We studied stand structure, stand history, and current regeneration of a small stand dominated by *Picea mariana* (Mill.) Britton, Sterns & Poggenb. (black spruce) in southeastern Michigan. The composition and structure of the overstory, understory, and ground cover layers were recorded, and the diameter, height, and age of selected individuals of *P. mariana* were measured. The stand was nearly monotypic, dominated by *P. mariana* in all layers but the ground cover. We estimate the stand to be even-aged, approximately 70 years old, and likely to have been established after a stand-replacing fire in the early 1940s. The stand lacked the significant regeneration that has been documented for *P. mariana*-dominated forests at higher latitudes, either by seed or by layering; we speculate that most tree establishment occurred in the first two decades following the fire until an unfavorable seedbed of *Sphagnum* moss developed that limited further recruitment of tree seedlings. We expect that in the absence of fire the stand will not transition from an even- to an uneven-aged stand, as is typical for *P. mariana* in the boreal forest, and its successional trajectory remains unclear. Understanding how forest development varies for species at their southernmost extent is critical for differentiating the future effects of climate change, and further study is therefore needed to document the forest dynamics of *P. mariana* in such locations.

KEYWORDS: Mud Lake bog, black spruce, peatland forests, forest dynamics

### INTRODUCTION

One of the most prominent topics of interest to ecologists today is the potential impact of climate change on the distribution of species. Researchers have documented significant shifts in the range of tree species in several regions of the United States where increases in mean annual temperature have been most substantial, such as the Northeast and the Upper Midwest (e.g., Zhu et al. 2011). The process of the change in distribution remains unclear, however. Iverson et al. (2004) predicted that the centroid of suitable habitat of 134 tree species in the eastern US could migrate as much as 800 km, and Woodall et al. (2009) documented a northward shift for many northern species. Zhu et al. (2011) found lit-

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tle evidence for northward migration of tree species, but their data suggested that the ranges of tree species tend to contract with climate change, particularly at the southern border. Other studies have also suggested that the ranges of eastern tree species in the United States tend to contract from the south without expanding to the north as climate change progresses (e.g., Murphy et al. 2010). Understanding the dynamics of forest stands dominated by species at the southern extent of their range is therefore important for predicting the persistence of such species and their potential for range contraction.

*Picea mariana* (Mill.) Britton, Sterns & Poggenb. (black spruce) is widespread in the North American boreal forest, where it often dominates forests on cool and nutrient-poor soils (Rowe 1972; Van Cleve and Viereck 1981). It reaches the southern extent of its distribution in North America in southern Michigan and Wisconsin, Pennsylvania, and New Jersey (Little 1971), where it is typically limited to low-lying, cold, wet ecosystems on organic soils such as bogs and other peatlands (Cohen and Kost 2008). Forests dominated by *Picea mariana* often originate from stand-replacing fires, which kill previously established trees and release seeds from semi-serotinous cones, resulting in even-aged postfire stands (Greene et al. 1999; Charron and Greene 2002; Bouchard et al. 2008; Rossi et al. 2009).

The growth form of *Picea mariana*, characterized by low branches that act as “ladder fuels” between the ground and the canopy, facilitates stand-replacing crown fires (Johnson 1992), and the species depends on the recruitment of post-fire seedlings to dominate stands over long time periods. Most seedlings establish in the first 5–10 years after a fire (Johnson and Fryer 1989); post-fire recruitment and subsequent succession depend strongly on the availability of seeds and the quality of the seed bed (Greene et al. 1999; Johnstone and Chapin 2006), because seedling establishment is often limited by the presence of *Sphagnum* moss on the soil surface. In the absence of additional stand-replacing fires, or where the interval between such fires exceeds the lifespan of the trees, canopy gaps develop after perhaps 120 years (Johnson 1992; Harper et al. 2004; Pham et al. 2004; Rossi et al. 2009), and the stand becomes multi-aged as new cohorts develop in the gaps. Multi-aged *P. mariana* stands are common in northeastern North America (Boucher et al. 2003).

We examined a small stand dominated by *Picea mariana* in southeastern Michigan with the objectives of determining stand history, describing current stand structure and growth, documenting current regeneration, and predicting the future development of the stand. *Picea mariana* stands have been extensively studied in northern latitudes closer to the center and northern extent of their distribution (e.g., Black and Bliss 1980; Bonan and Sirois 1992; Rossi et al. 2009; Tremblay et al. 2011), but fewer data exist that describes *P. mariana* stand structure and development following fire at its southern limit (but see Bonan and Sirois 1992; Locky et al. 2005), and none for southern Michigan. Regional studies of plant and forest communities in peatlands are needed because of the wide variability evident in this wetland type across North America (Jeglum 1991; Locky et al. 2005). Although early descriptions of *P. mariana* stands in southern Michigan exist (Pennington 1906), rapid climate change in the 20th century has necessitated re-analysis of forest types at their southern limits for the purposes of

assessing local conservation efforts as well as of further contributing to our understanding of climate change impacts on these populations of forest tree species.

#### METHODS AND MATERIALS

##### *Study Area*

The *Picea mariana* stand encompasses approximately 0.7 ha directly northeast of Mud Lake in Livingston County in southeastern Michigan (42°24'56" N, 83°47'30" W). Mud Lake is a glacial kettle lake, lying low in the landscape and subjected to cooler temperatures than the surrounding uplands, and is likely a former arm of nearby Independence Lake that has been isolated by extensive peat deposition (Pennington 1906; Cohen and Kost 2008). Other small, isolated populations of *P. mariana* are scattered around the region, but the stand at Mud Lake is likely to be the largest in the area where *P. mariana* is the dominant overstory species. The stand is located on thick, acidic, organic (peat) soils and lies approximately 75 m from a floating *Sphagnum* mat that surrounds Mud Lake. The forest floor in the stand itself is dominated by *Sphagnum* mosses and exhibits significant microtopography as hummocks and hollows (Figure 1; Heinselman 1963; Halsey and Vitt 2000). *Sphagnum* mosses sustain wet, cold, acidic, low-nutrient conditions that slow decomposition and facilitate the further development of peat (Halsey and Vitt 2000; Cohen and Kost 2008). The bog mat directly south of the stand supports ericaceous shrubs, including *Vaccinium corymbosum* L. (high-bush blueberry), *Chamaedaphne calyculata* (L.) Moench (leatherleaf), and *V. oxycoccos* L. (small cranberry), as well as *Typha* spp. (cattail), and has little or no tree canopy cover. The forest otherwise



FIGURE 1. Interior of the *Picea mariana* stand near Mud Lake, Livingston County, southeastern Michigan, exhibiting heavy dominance by *P. mariana* and a *Sphagnum*-covered forest floor. Photograph by Dan Kashian, September 28, 2010.

surrounding the stand is dominated by *Larix laricina* (Du Roi) K. Koch (tamarack) and hardwoods including *Betula alleghaniensis* Britt. (yellow birch), *Acer rubrum* L. (red maple), and *Ulmus americana* L. (American elm); *L. laricina* is most common to the west of the stand. Pennington (1906) reported that the entire area around Mud Lake was subject to the removal of individual trees for Christmas trees and fenceposts at the turn of the 20th century and was burned by large, severe fires in 1856 and 1888.

### Field Sampling and Analysis

The *Picea mariana* stand was sampled using six contiguous 10 × 20 m (200 m<sup>2</sup>) plots; the plots were located at least 20 m from the edges of the stand. Within each plot, all live and dead overstory trees ≥ 1.5 cm diameter at breast height (DBH; breast height = 1.4 m) were identified to species, counted, and measured for DBH. Live trees and shrubs measuring 1.5–9.0 cm DBH were classified as understory, and those ≥ 9.1 cm were classified as overstory. All live woody groundcover species (< 1.5 cm DBH and those < 1.4 m tall, regardless of DBH) were tallied by species within four 0.5 × 8 m belt transects (16 m<sup>2</sup> total) in each plot, extending from each corner of the plot along the long axis of the plot boundary. Other than *Sphagnum*, herbaceous vegetation was virtually absent in the stand and was not sampled. The stem density of all three forest strata was determined by converting stem counts in each plot to stems/ha. Relative density (number of stems of a species / number of stems of all species) was calculated for overstory, understory, and ground cover species. Relative dominance (basal area of a species / basal area of all species) was calculated for overstory trees.

Tree height was determined with a clinometer for five randomly selected *Picea mariana* trees in each plot (n = 30 trees), estimated to the nearest 0.25 m. The abundance of coarse woody debris (fallen dead wood) was estimated using the planar intercept method along 5 non-overlapping 15.2 m transects (76 m total transect length for the stand), as described by Brown (1974). The age of each *P. mariana* overstory tree that stood within four meters of each plot corner and the 10 m mark of the long axis of each plot (n = 156 trees) was determined using an increment core extracted 30 cm from the ground. Prior to determining the age, the cores were mounted and sanded using standard techniques (Speer 2010), and annual rings were measured to the nearest 0.01 mm using a sliding bench micrometer. The relationship between tree age and diameter was modeled using the Michaelis-Menten function ( $y = a*x/b+x$ ), where y = age, x = diameter, and a and b are parameters. The Michaelis-Menten function is most appropriate for ecological data that increase to an asymptote from the origin (Cardinale et al. 2006). The site index of the stand was calculated using overstory tree height and age plotted on site index curves developed for *P. mariana* in northeastern Minnesota (Carmean et al. 1989) and on peatlands in northern Ontario (Payandeh 1978).

## RESULTS

*Picea mariana* represented 99.2% of the overstory trees in the stand; other overstory species included three stems of *Larix laricina* (0.5%) and a single stem of *Betula alleghaniensis* (0.3%). *Picea mariana* was the only overstory tree in four of the six plots, where its density ranged from 1350 to 2050 stems/ha (1775 stems/ha for the stand). The total basal area for the stand was 28.22 m<sup>2</sup>/ha, 97.8% of which was attributable to *P. mariana*, 1.4% to *L. laricina*, and 0.8% to *B. alleghaniensis*. *Picea mariana* was less dominant in the understory, but still composed 72.1 % of that layer at a density of 792 stems/ha; *L. laricina* (17.1%), *B. alleghaniensis* (10.1%), and *Quercus rubra* L. (red oak; 0.6%) were the other species present. The understory overall was quite sparse, with a density of 1150 stems/ha for all species combined. The woody groundcover was also sparse and was dominated by *Vaccinium corymbosum* (79.6%), especially in the southern portion of the stand closest to Mud Lake. *Acer rubrum* and *B. alleghaniensis* were also present in the ground cover, but represented less than 10% of the

TABLE 1. Density (stems/ha) of overstory, understory, and ground cover in each of six plots and in the stand as a whole near Mud Lake, Livingston County, Michigan. Values in parentheses are relative density (%) for the species.

	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Stand
<b>Overstory (&gt; 9.0 cm DBH)</b>							
<i>Picea mariana</i>	2050 (100.0)	1900 (100.0)	1800 (98.0)	1900 (100.0)	1650 (100.0)	1350 (93.6)	1775 (99.2)
<i>Larix laricina</i>						150 (7.4)	25 (0.5)
<i>Betula alleghaniensis</i>			50 (2.0)				8 (0.3)
<b>Understory (1.5–9.0 cm DBH)</b>							
<i>Picea mariana</i>	750 (93.8)	600 (85.7)	1000 (80.0)	600 (42.9)	1250 (86.2)	550 (42.3)	792 (72.1)
<i>Larix laricina</i>	50 (6.3)		200 (16.0)	750 (53.6)	100 (6.9)	250 (19.23)	225 (17.1)
<i>Betula alleghaniensis</i>		100 (14.3)	50 (4.0)	50 (3.6)	100 (6.9)	450 (34.6)	125 (10.1)
<i>Quercus rubra</i>						50 (3.9)	8 (0.6)
<b>Ground cover (&lt; 1.5 cm DBH or &lt; 1.35 m tall)</b>							
<i>Vaccinium corymbosum</i>	20750 74.4)	14350 (68.0)	16800 (92.3)	4250 (90.4)	3850 (80.2)	5400 (98.2)	10900 (79.6)
<i>Acer rubrum</i>	2700 (9.7)	4500 (21.3)	450 (2.5)	50 (1.1)	150 (3.1)	50 (0.9)	1317 (9.6)
<i>Betula alleghaniensis</i>	3500 (12.5)	2000 (9.5)	850 (4.7)	50 (1.1)	50 (1.0)		1075 (7.8)
<i>Picea mariana</i>	550 (2.0)	250 (1.1)	50 (0.2)	300 (6.4)	750 (15.6)	50 (0.9)	325 (2.4)
<i>Frangula alnus</i>	300 (1.0)						50 (0.3)
<i>Quercus rubra</i>	100 (0.3)		50 (0.2)	50 (1.1)			33 (0.2)

stems. A few stems of *Frangula alnus* Miller (glossy buckthorn) and *Q. rubra* were also found in the ground cover. *Picea mariana* was not common in the ground cover, representing only 2.4% of the stems (Table 1). We found no evidence of layering by *P. mariana* in our sampling.

The DBH of *Picea mariana* ranged from 2.0 cm to 21.2 cm (coefficient of variation = 40%) with a mean diameter of 11.05 cm, and exhibited no obvious spatial pattern of variation across the six plots (Table 2). The size distribution of *P. mariana* revealed a bell-shaped curve typical of an even-aged stand (Oliver 1981; Johnson 1992), with only a few dead trees that were found mostly in the smaller size classes (Figure 2). Most of the dead trees were *P. mariana* (64%);

TABLE 2. Mean values of diameter at breast height (DBH) ( $n = 331$ ), height ( $n = 30$ ), and age ( $n = 156$ ) of *Picea mariana* in each of six plots near Mud Lake, Livingston County, Michigan, and in the stand as a whole ( $\pm$  one standard error). The  $n$  values given above are for the stand as a whole.

	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Stand
DBH (cm)	11.54 $\pm$ 0.44	11.64 $\pm$ 0.60	10.17 $\pm$ 0.48	10.44 $\pm$ 0.58	9.64 $\pm$ 0.58	11.22 $\pm$ 0.73	11.05 $\pm$ 0.22
Height (m)	12.1 $\pm$ 0.61	11.0 $\pm$ 0.59	10.7 $\pm$ 0.92	10.6 $\pm$ 0.61	9.9 $\pm$ 1.09	10.6 $\pm$ 0.71	10.8 $\pm$ 0.32
Age (yrs)	66.2 $\pm$ 3.06	68.2 $\pm$ 4.37	66.2 $\pm$ 2.73	59.4 $\pm$ 3.36	49.8 $\pm$ 3.68	54.8 $\pm$ 2.73	56.1 $\pm$ 0.76

*Larix laricina* constituted 34% of them, and there was one dead stem of *Betula alleghaniensis* (2%). Most of the dead stems of *L. laricina* were found in the center of the stand, where 43% of all dead trees were sampled. The presence of only a few standing dead trees (constituting a basal area of 7.6 m<sup>2</sup>/ha) suggested that recent self-thinning has not occurred in the stand, at least among *P. mariana*, which represented 68% of the standing dead basal area. Moreover, fallen dead wood included only 7738 kg/ha of woody debris < 2.5 cm in diameter, and only 4688 kg/ha of woody debris > 7.6 cm in diameter.

Tree height of *Picea mariana* averaged 10.8 m for the stand (coefficient of variation = 16%), ranging between 6.75 and 14.25 m with the tallest trees found closest to Mud Lake (Table 2). The height distribution of *P. mariana* was skewed to the right with most trees being 9 to 12 m tall (Figure 3). The mean age of *P. mariana* in the stand was 56 years ( $\pm$  0.76 yrs, c.v. = 17%), ranging from 29 to 75 years with the oldest trees occurring in the southern part of the stand nearer Mud Lake (Table 2). The age distribution of *Picea mariana* also approximates a

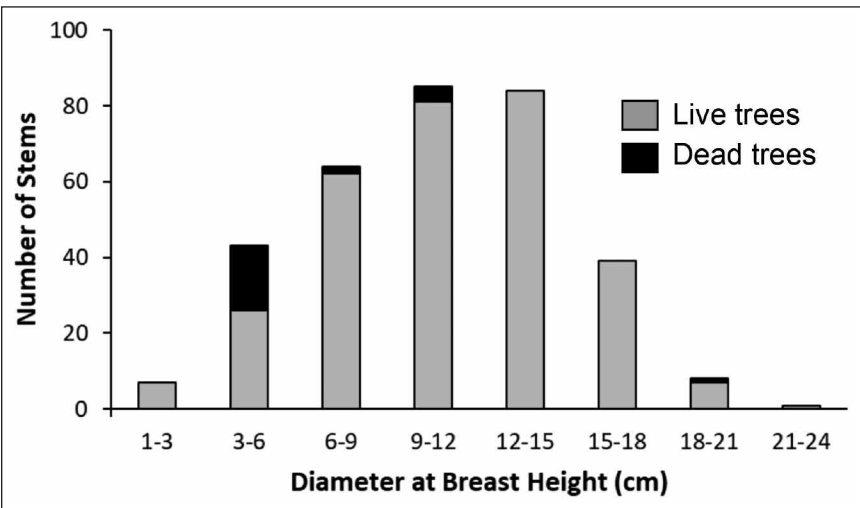


FIGURE 2. Size distribution for all *Picea mariana* trees > 1.5 cm diameter at breast height in the six plots ( $n = 331$ ). The dark portion of a bar indicates the number of standing dead trees in that size class. The bell-shaped size distribution is characteristic of an even-aged stand.

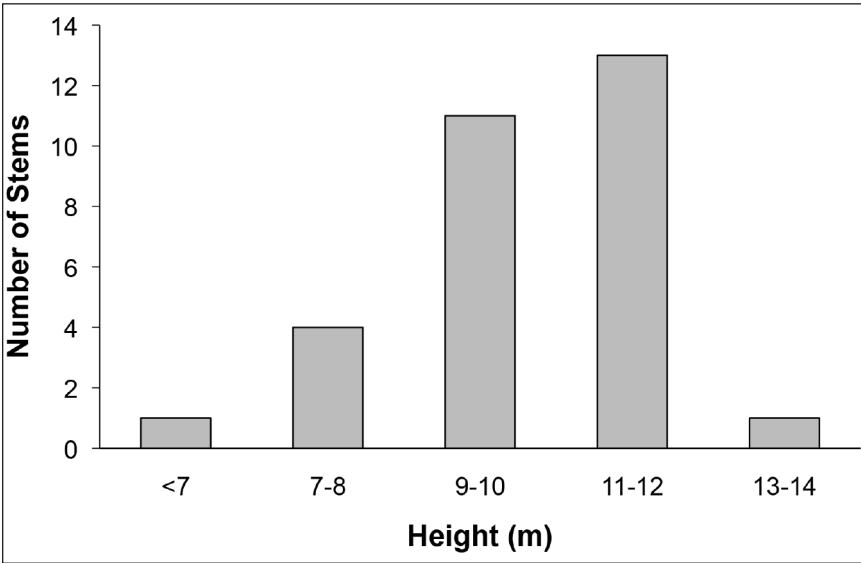


FIGURE 3. Height distribution for 30 randomly-selected *Picea mariana* trees in the six plots.

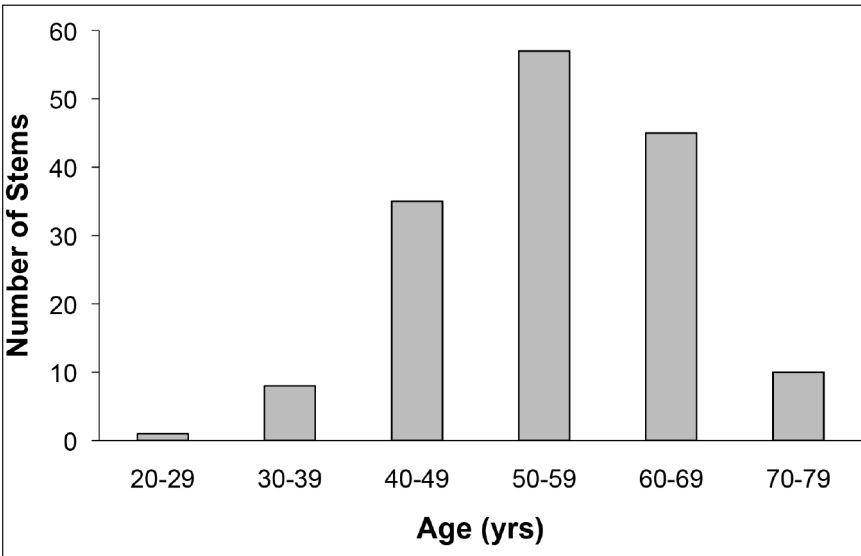


FIGURE 4. Age distribution for 156 randomly-selected *Picea mariana* trees in the six plots. Most of the trees were established in the first 30 years following the fire.



FIGURE 5. Cumulative basal area ( $\text{m}^2$ ) for an average *Picea mariana* tree in the six plots. Solid lines indicate the maximum and minimum cumulative basal area for trees at a given age; the dashed line represents the average ( $n = 156$ ). The shallow slope of the average basal area growth curve suggests that growth was extremely slow throughout the life of a given tree in the stand.

bell-shaped curve typical of an even-aged stand, with 65% of trees aged 50 to 70 years old and very few young trees in the stand (Figure 4). The site index of the stand was low but within the range of *P. mariana* at northern latitudes (Viereck and Johnston 1990), approximating  $SI = 10.75$ . The annual diameter growth of *P. mariana* was highly variable among individual trees, and this variability in growth increased with the age of the tree (Figure 5). The rate of increase of annual growth was very slow, and canopy closure was likely to have been achieved within the first decade following stand initiation. Growth of suppressed trees was nearly zero for almost 35 years after stand initiation, followed by a sudden but slight increase in growth that probably represents a minor growth release by stand age 40 (Figure 5). The Michaelis-Menten model explained only 38% of the variation in the relationship between age and diameter of *P. mariana* ( $\text{Age} = 87.635 \cdot \text{DBH} / 6.655 + \text{DBH}$ ;  $R^2 = 0.38$ ;  $p < 0.001$ ).

## DISCUSSION

The *Picea mariana* stand near Mud Lake is a near-pure, even-aged stand growing on deep organic soil with a heavily *Sphagnum*-covered forest floor that has probable ramifications for stand structure, development, and future persistence. We estimate that the stand originated in the early 1940s, probably following a stand-replacing fire that would have created the opportunity for heavy post-



fire seedling recruitment (Johnstone et al. 2009; Brown and Johnstone 2012). Pre-fire forest composition remains unclear. Pennington (1906) reported the area including the *P. mariana* stand to be a *Larix laricina*–*P. mariana* community with the two species existing in equal proportions; he also described the area to be recently burned all around Mud Lake based on burned stumps and other evidence, though not in the precise area of the current *P. mariana* stand. We presume the current stand to have originated from a stand-replacing fire with sufficient severity to release *P. mariana* seeds from semi-serotinous cones (Greene et al. 1999) and eliminate *L. laricina*, thereby allowing *P. mariana* to establish and dominate the stand. It is unclear why *P. mariana* is uncommon elsewhere near Mud Lake on organic soils that typically support the species (Harper et al. 2005). Variation in severity of a fire much larger than but including the current stand could explain the local distribution of *P. mariana* if the severity were sufficiently high to incinerate cones and eliminate the seed source (Johnstone et al. 2009), but we have no data to support this possibility.

The *Picea mariana* stand at Mud Lake exhibits many of the characteristics of a classic even-aged stand that result from a stand-replacing fire (Johnson 1992), but it appears to show several structural and developmental trends different from those studied in the boreal forest. Oliver (1981) proposed a general four-stage model for stand development that includes (1) stand initiation dominated by disturbance-created coarse woody debris and high tree establishment; (2) stem-exclusion highlighted by density-dependent mortality (self-thinning); (3) understory re-initiation caused by canopy fragmentation; and (4) old-growth forest with high structural diversity. Oliver's model is a simple representation of stand development that has been broadly applied to many forest types, both deciduous and coniferous (Oliver and Larsen 1990), but has sometimes been found to be less applicable for stands with complex structures or those found on extreme or atypical site conditions (Kimmins 2003). Harper et al. (2005) unsuccessfully applied the model to *P. mariana* on organic soils in northwestern Quebec. Rather than exhibiting four stages of development, stands of *P. mariana* in Quebec exhibited a short period of decomposition of disturbance-created dead wood and a long, continuous period of tree establishment and growth until the stands reached the old-growth stage (Harper et al. 2004; 2005). We suggest that the Mud Lake stand also fails to fit the four-stage model, in that most of the tree establishment occurred in the first 20 years after a stand-replacing fire. We speculate that tree establishment occurred prior to the formation of an unfavorable seedbed that will limit further *P. mariana* recruitment throughout the development and eventual senescence of the stand.

Most obviously, the Mud Lake stand lacks significant regeneration of *Picea mariana* (Table 1). *Picea mariana* is known to be a shade-tolerant species that can survive in the forest understory for more than 100 years (Greene et al. 1999; Rossi et al. 2009). High shade tolerance allows the formation of advanced regeneration—the presence and persistence of seedling and saplings in a stand that can recruit to the overstory to develop a subsequent cohort when gaps form in the current canopy—in part because the cones are semi-serotinous and provide a suitable seed rain once the trees reach reproductive maturity (Greene et al. 1999; Brown and Johnstone 2012). Therefore, lack of regeneration at Mud Lake prob-

ably reflects the unfavorable seedbed in the presence of *Sphagnum* moss, which has been documented to be a major limitation to tree seedling recruitment in stands dominated by *P. mariana* (Johnstone et al. 2009; Brown and Johnstone 2012). The “hummock-hollow” microtopography—present at Mud Lake and typical of mossy ground cover—exposes seedlings to extremely droughty conditions on hummocks and wet conditions in hollows where germination is unlikely (Black and Bliss 1980; Johnstone et al. 2009; Brown and Johnstone 2012; but see Aksamit and Irving 1984). The development of a mossy seedbed also decreases temperature and nutrient availability (Harper et al. 2005). As such, seedling establishment in *P. mariana* often occurs in the first few years following fires prior to the development of a mossy seedbed (Black and Bliss 1980; Greene et al. 1999; Johnstone et al. 2009), as it probably did at Mud Lake. For these reasons, Rossi et al. (2009) reported that vegetative reproduction via layering is favored over the recruitment of seedlings in the decades and centuries after fires for *P. mariana* in the boreal forest; however, layering by *P. mariana* was also absent at Mud Lake.

In addition to the lack of regeneration, the *Picea mariana* stand at Mud Lake appears to lack evidence of self-thinning that presumably would have occurred at the time of canopy closure. Most typically, dead wood in a stand is initially abundant immediately after the disturbance, then decreases but is still common as self-thinning occurs, stabilizing at low abundance, and finally increases again with older tree mortality (Harmon et al. 1986). The amount of dead wood at Mud Lake is extremely low, where 62% of the dead wood is less than 2.5 cm in diameter, and dead wood approximating that resulting from self-thinning was only 4.7 kg/ha, in contrast to *P. mariana* stands in Labrador that contained 9300 kg/ha (Hageman et al. 2009) and in northern Quebec that contained 13530 kg/ha (Boulangier and Sirois 2006). Harper et al. (2005) estimated that self-thinning occurred approximately 40 years after stand initiation in northwestern Quebec, and thus we would ordinarily expect the Mud Lake stand to have experienced stem exclusion already given its age. However, the rate of decomposition at the Mud Lake stand is far too slow to explain its lack of dead wood, even if some fallen dead wood at Mud Lake had been obscured by moss or buried and thereby missed during sampling. Annual growth rings also showed little evidence of self-thinning (Figure 5); we therefore conclude that little self-thinning has occurred in the stand since initial tree establishment.

Given the lack of regeneration and self-thinning at Mud Lake, as well as a lack of layering, we do not expect the stand to develop into a multi-cohort stand typical of the boreal forest (Boucher et al. 2003). At northern latitudes, even-aged *Picea mariana* stands transition to uneven-aged stands as secondary disturbances—typically individual tree deaths that create canopy gaps—occur at small scales and low intensities (Rossi et al. 2009; Tremblay et al. 2011). Such a transition is especially common where the interval between fires is longer than tree longevity (stand age 120–200 years in the northern portions of its distribution; Tremblay et al. 2011). It remains too early in the development of the Mud Lake stand to adequately assess its adherence to Oliver’s (1981) model, but its current closed and uniform canopy of co-dominant trees, little fallen or standing dead wood or other evidence of recent self-thinning, lack of regeneration, and a forest

floor heavily carpeted by *Sphagnum* moss suggest that a multi-aged or uneven-aged stand is unlikely to develop. Instead, we speculate that the stand experienced the majority of its tree establishment in the first 20–30 years following a stand-replacing wildfire and that regeneration is now limited by the development of an unfavorable seedbed.

Given the unusual environmental conditions apparently governing stand dynamics of the stand at Mud Lake, it remains difficult to predict the direction of forest succession. One potential successional trajectory is that in the absence of fire the stand will succeed to a deciduous forest as its canopy begins to break up. Such succession would probably be dominated by nearby species able to survive long periods in a seedbed, such as *Betula alleghaniensis* (Greene et al. 1999) and *Acer rubrum* (Lambers and Clark 2005), both of which are abundant within 50 m of the *P. mariana* stand. The likelihood that the stand succeeds to a deciduous forest is uncertain, however, because the aggressive development of *Sphagnum* on deep, acidic organic soils is likely to limit the establishment of deciduous tree species as much as it does *P. mariana*. Although occasional deciduous seedling establishment may occur in such conditions, succession from coniferous to deciduous forest in depressional peatlands is rarely documented (Crum 1992).

The structure and development of *Picea mariana* stands at their southernmost extent is poorly understood (Bonan and Sirois 1992), and our study should serve as one of several that adds to our knowledge in this area. Though the growth of *P. mariana* is considered to be optimal at its southern limit (Bonan and Sirois 1992), our study suggests that stand development may proceed very differently as compared to stands in the heart of its range. Given that southerly stands are likely to be among the earliest responders to climate change, it is important that we are able to differentiate latitudinal variation in stand structure and development from responses to a changing climate if we are to accurately predict the future of *P. mariana* and other boreal species. Replication of our work in other stands at the southernmost extent of *P. mariana* and other boreal species is clearly needed to achieve this goal.

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