

# Population dynamics of black spruce and white spruce near the arctic tree line in the southern Brooks Range, Alaska<sup>1</sup>

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**Abstract:** Black spruce (*Picea mariana* (Mill.) BSP) is the dominant species in interior Alaska but it is largely absent from the arctic tree line. To evaluate the importance of climate and fire as controls over the species distribution, we re-constructed stand history at three sites near its northern limit in Alaska, where it grows with white spruce (*Picea glauca* (Moench) Voss). We developed a matrix model to explore black spruce population dynamics and response to varying fire intervals. All sites burned in the early 1900s. High recruitment of black spruce occurred for <30 years following the fire, but most current black spruce recruitment is clonal and seed viability is low. White spruce recruitment has been consistently high since the fire, and the majority of seedlings in the stands are white spruce. Despite low recruitment, the matrix model suggests that black spruce populations are nearly stable, largely because of low adult mortality rates. Although black spruce recruitment is stimulated by fire, the model indicates that fire intervals <350 years would destabilize the population, primarily because of slow growth and low seed production. Population dynamics of black spruce at its northern limit in Alaska thus appear to reflect an interaction between fire, which determines the temporal pattern of tree recruitment, and climate, which limits tree growth and, presumably, viable seed production.

**Résumé :** L'épinette noire (*Picea mariana* (Mill.) BSP) est l'espèce dominante dans la région intérieure de l'Alaska mais elle est presque absente à la limite des arbres dans l'Arctique. Pour évaluer l'importance du climat et du feu en tant que facteurs déterminants pour la répartition géographique de cette espèce, les auteurs ont reconstitué l'historique du peuplement à trois endroits situés près de sa limite nord en Alaska, où elle croît avec l'épinette blanche (*Picea glauca* (Moench) Voss). Ils ont développé un modèle matriciel pour étudier la dynamique de population de l'épinette noire et sa réaction à différents intervalles entre les feux. Tous les sites ont brûlé au début des années 1900. Le recrutement d'épinettes noires a été élevé pendant moins de 30 ans après le feu mais la plupart des recrûs actuels d'épinette noire sont des clones et la viabilité des graines est faible. Le recrutement d'épinettes blanches est demeuré constamment élevé depuis le feu et la majorité des semis présents dans les peuplements sont des épinettes blanches. Malgré un faible recrutement, le modèle matriciel indique que les populations d'épinette noire sont presque stables, en grande partie à cause du faible taux de mortalité chez les adultes. Bien que le feu stimule le recrutement de l'épinette noire, le modèle indique que des intervalles entre les feux plus courts que 350 ans déstabiliseraient la population, principalement à cause du faible taux de croissance et de la faible production de graines. La dynamique de population de l'épinette noire à sa limite nord en Alaska semble donc refléter une interaction entre le feu, qui détermine le patron temporel de recrutement des arbres, et le climat, qui limite la croissance des arbres et, vraisemblablement, la production de graines viables.

[Traduit par la Rédaction]

## Introduction

Future warming in high northern latitudes is likely to change the distribution and relative abundance of forest types. In Alaska and Siberia, warming during the last century has been associated with an expansion of tree-line white spruce (*Picea glauca* (Moench) Voss) forests into arctic and alpine

tundra ecosystems (Lloyd et al. 2002; Lloyd and Fastie 2003; Esper and Schweingruber 2004). Further expansion of white spruce forests into tundra communities is likely as the climate continues to warm. Changes in the distribution of other non-tree-line forest types may occur in the future and are in general less well studied than changes in tree-line forests, despite the potential for such changes in other forest types to generate feedbacks on regional climate as a result of changes in albedo, ecosystem carbon storage, and disturbance regime. The expansion of black spruce forests in Alaska 5000 years ago, for example, was associated with large increases in fire frequency (Lynch et al. 2002; Lloyd et al. in press). The positive relationship between black spruce abundance and fire frequency persists on the modern landscape, where black spruce forests are consistently associated with higher fire frequency (Larsen 1997; Parisien and Sirois 2003). The expansion of black spruce forests into areas currently occupied by white spruce thus has important implications for regional

Received 30 November 2004. Accepted 25 May 2005.  
Published on the NRC Research Press Web site at  
<http://cjfr.nrc.ca> on 14 October 2005.

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<sup>1</sup>This article is one of a selection of papers published in the  
Special Issue on Climate–Disturbance Interactions in Boreal  
Forest Ecosystems.

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disturbance regimes and possibly climate. The degree to which climate change is likely to alter the distribution and (or) areal extent of other forest types in the boreal forest, however, remains poorly understood.

Although climate is clearly implicated as a control over the distribution of tree-line forests, its importance in limiting the distribution of non-tree-line forests is less clear. For example, black spruce (*Picea mariana* (Mill.) BSP) is the dominant species in the boreal forests of interior Alaska. In the interior, it commonly occurs on poorly drained north-facing slopes underlain by shallow permafrost. White spruce, in contrast, occupies productive river floodplains and drier upland sites (Yarie 1983). Despite the common occurrence of black spruce at very cold sites within the center of its range, it is uncommon at tree line in Alaska (Viereck 1979), and it is absent from the arctic tree line entirely. This pattern suggests temperature limitation of black spruce distribution and thus the potential for black spruce to expand northward as climate warms. However, black spruce is a dominant species at tree line from eastern Canada to the Northwest Territories (Black and Bliss 1980; Payette and Gagnon 1985; Sirois and Payette 1991; Laberge et al. 2001). This contrast between its distribution in eastern and western North America suggests that factors other than climate are probably important in limiting black spruce distribution in at least part of its range. Similarly contrasting east–west distributions of jack pine (*Pinus banksiana* Lamb.), which reaches tree line in central Canada but not eastern Canada, have been attributed to low fire frequencies in eastern Canada (Asselin et al. 2003). If the distributional limit of black spruce in the western portion of its range is controlled by fire or some other nonclimatic factor, the sensitivity of black spruce forests to future warming is likely to be lower than in the eastern portion of its range, where climatic limits seem to be more important.

In this study we investigated the hypothesis that black spruce is not at its climatic limit in northern Alaska and that its distribution is instead a function of latitudinal gradients in fire regime and (or) competitive interactions with white spruce. We addressed the following specific questions: (i) Is recruitment in the northernmost populations of black spruce limited to postfire conditions, as in more southerly populations? (ii) In the absence of fire, what is the comparative regeneration success of black spruce and white spruce growing in mixed stands at the northern limit of black spruce? (iii) How sensitive are black spruce population dynamics to changes in fire frequency? (iv) Is there any evidence for climatic limitations on the growth of black spruce at its northern limit?

## Materials and methods

### Field methods

To locate the northern limit of black spruce near the arctic tree line in the Brooks Range, Alaska, we surveyed forest composition at 5- to 8-km intervals on a 50 km long north–south transect parallel to the Dalton Highway, identifying a minimum of 100 trees at each sampling location. We did not sample unforested sites. Three permanent study sites (67°32'33"N, 67°33'13"N, and 67°34'16"N) were chosen at the location identified from this survey as that of the northernmost mixed populations of black and white spruce. All plots were at

least 200 m from the road edge. The study sites were systematically located approximately 1.5 km apart near the base of Sukakpak Mountain, a marble graphite, dolomite, and limestone formation. The elevation of the sites ranged from 443 to 470 m, and all were west facing (297°–280° aspect). Permafrost is widespread in this area (Brown and Kreig 1983), and midsummer thaw depth at our sites was <0.5 m. Vegetation consisted of tussock tundra and patchy stands of black and white spruce. As is typical of forest–tundra transition zones, understory vegetation included a variety of lichens and low shrubs (e.g., *Salix* spp., *Betula glandulosa*, *Vaccinium* spp., and *Ledum groenlandicum*).

We established three randomly located plots, each 15 m × 15 m, at each site. In each study plot, every live tree was permanently tagged and an increment core was obtained that included the pith as close to the root crown as possible. Trees too small to core (<1.3 m tall and <2 cm in basal diameter) were classified as seedlings. Seedling age was estimated by counting annual stem internodes. Black spruce seedlings can establish either from seeds or by layering, when branches that contact the ground root adventitiously. We excavated the base of each seedling, sapling, and small adult black spruce to examine the root structure for signs of clonal origin in the form of a current or prior connection to a parent tree.

The number of cones on each live tree was estimated according to five categories: 0, 1–20, 20–50, 50–75, and 75–100 cones per tree. To estimate the production of viable seeds by black spruce, we removed all 2001 cones (the most recent mature cones) and a large subset of pre-2001 cones from each of six black spruce at each site. Cone age-classes were kept separate. In total, 3030 cones were collected from the 18 trees. All cones were stored in paper bags until further processing. White spruce cones were not mature at the time of sampling, so no white spruce cones were collected.

Cross sections were collected from all dead trees and seedlings in the plots. We identified fire-killed trees by the presence of charred branch stubs and an absence of bark. Cross sections were collected from fire-scarred trees outside the study plots.

### Laboratory methods

Tree cores were mounted on wooden strips and sanded. Ring width was measured to a precision of 0.002 mm on a Velmex sliding-stage micrometer (Velmex, Inc., Bloomfield, New York). Ring-width series were cross-dated using both statistical (Holmes 2000) and visual (Stokes and Smiley 1968) cross-dating methods. Germination dates were estimated from cross-dated inner-ring dates after correction for missed pith and time to grow to core height. In cores that lacked the pith, number of years to the pith was calculated by estimating the distance to the pith from the curvature of the inner rings and calculating the number of rings in that distance from the growth rate of the innermost 20 rings in the core. Inner-ring dates were corrected for the time to grow to core height from a linear regression of seedling age on seedling height. The relationship was estimated separately for each species. Death dates were established for dead trees using a combination of visual and statistical cross-dating. No attempt was made to correct death dates for erosion of wood

**Table 1.** Transition probabilities in matrix **A** describing the population dynamics of black spruce at the species' northern limit.

Size class	$n_t$	Seed	Germinant	Seedling	Sapling	Small adult	Medium adult	Large adult
Seed	119 627	0.493				479	479	479
Germinant	7	0.023	0.029					
Seedling	195		0.003	0.918				
Sapling	77			0.010	0.964			
Small adult	88				0.026	0.958		
Medium adult	69					0.032	0.950	
Large adult	19						0.040	0.991

**Note:** Germinants are seedlings <12 cm tall. Seedlings are individuals between 12 and 130 cm tall. Saplings are >1.3 cm tall with DBH <2 cm. Adult size classes are based on DBH (small: 2–5 cm; medium: 5–8 cm; large: >8 cm).  $n_t$  values show the observed size structure of the population at the time of sampling. The probability of growing to the next size class is shown in the subdiagonal (e.g., the probability of growth from seedling to sapling is 0.01) and the probability of remaining alive in the same class is shown along the diagonal (e.g., the probability of remaining a seedling is 0.918). The probability of clonal reproduction as a transition from the small, medium, and adult size classes to the seedling size class is 0.002. Total fecundity, the number of seeds per year produced by individuals, was 479 seeds/year for the small, medium, and large adults. Only nonzero probabilities or fecundities are shown.

from the outer surface, so mortality dates should be interpreted as a minimum estimate of the year of death.

Ring widths were measured on all live trees. Individual ring-width series were cross-dated and subjected to conservative detrending using either a horizontal line, a line of negative slope, or a negative exponential curve. A ring-width chronology representing the mean of the individual ring-width series was developed for each species at each site. Each chronology consisted of a minimum of 10 trees that established prior to 1930. The response of tree growth to climate was analyzed by comparing ring-width chronologies with climate data from the climate station at Bettles, Alaska. Monthly climate data from 1953 to 2001 were obtained from the National Climatic Data Center. A 12-month window, from the September prior to the current growing season through the August of the current growing season, was used in the analyses. In addition to total monthly precipitation and mean monthly temperature, we calculated total winter precipitation and mean winter temperature (November–March) and total summer precipitation and mean summer temperature (June–August). We used stepwise linear regression analysis to select the subset of climate parameters to which ring widths were significantly related at each site and to estimate the amount of variance in growth that was explained by climate.

Germination rates were estimated under controlled conditions in the Middlebury College greenhouse. Cones were air-dried for 6 months in paper bags. Four cones from each of the two age-classes (2001 and pre-2001) were randomly selected for each tree. Black spruce cones are semiserotinous, so cones were opened by heating in a drying oven at 60 °C for 8 h to facilitate opening and seed release (Greene and Johnson 1994). All seeds were extracted from the cones, seed numbers recorded, and the seeds placed on moistened filter paper in plastic petri dishes. Seeds were watered as necessary. Seeds were observed for a period of 30 days, during which germination was recorded daily. Germination was defined as the time when the radicle broke the seed coat.

### Development of the matrix model

We constructed a size-based matrix model (Lefkovich 1965) to describe black spruce population dynamics. The basic matrix model is given by eq. 1.

$$[1] \quad \mathbf{n}_{(t+1)} = \mathbf{A}\mathbf{n}_{(t)}$$

The vector  $\mathbf{n}_{(t)}$  gives the abundance in each size class at time  $t$  and is derived from the observed size structure. The population projection matrix, **A** (Table 1), contains probabilities of growth, survivorship, fecundity, and mortality for the individuals in each size class. The projection interval from  $t$  to  $t + 1$  represents a time period of 1 year. The matrix analysis produces an estimate of the asymptotic growth rate, lambda ( $\lambda$ ), which is calculated as the dominant eigenvalue of **A**. Lambda is the finite rate at which the population would grow if the conditions necessary to produce **A** remained constant through time (Caswell 2001; Caswell and Kaye 2001).

Our model divided the population into seven distinct size classes (Table 1). The large-adult category was assumed to be an absorbing state until the time of death. Trees and seedlings encounter three possibilities during each time step of the model: they can grow into the next size class, remain in the current size class, or die. The probability of growth into the next size class ( $G$ ) for seedlings, saplings, and adult trees was based on measured ring widths (for saplings and adults) or height growth rates (for seedlings; calculated by dividing seedling height by seedling age). From these growth rates, the time required to grow through a particular size class could be estimated, and the annual probability of growing out of a size class was then calculated as the inverse of the time required to grow through the current class.

The probability of death ( $M$ ) was calculated from the observed frequency of dead trees and seedlings. The low frequency of dead trees prevented us from calculating size-specific mortality rates, so we assumed that mortality was constant for all size classes of adult trees. The number of non-fire-killed trees that died in each decade was divided by the total number of adult trees that were alive during that decade. The adult mortality rate was then calculated as the mean of the decadal estimates; the model thus assumes that mortality does not vary among years in nonfire conditions. Seedling mortality was calculated as the number of dead seedlings in the plot at the time of sampling divided by the number of live seedlings in the plot at the time of sampling. This approach assumes that the dead seedlings were members of the same cohort as the current live seedlings. Because the three probabilities ( $G$ ,  $M$ , and remaining ( $R$ )) must

sum to 1, the probability of remaining ( $R$ ) in the size class could be calculated from the probability of growth ( $G$ ) and mortality ( $M$ ).

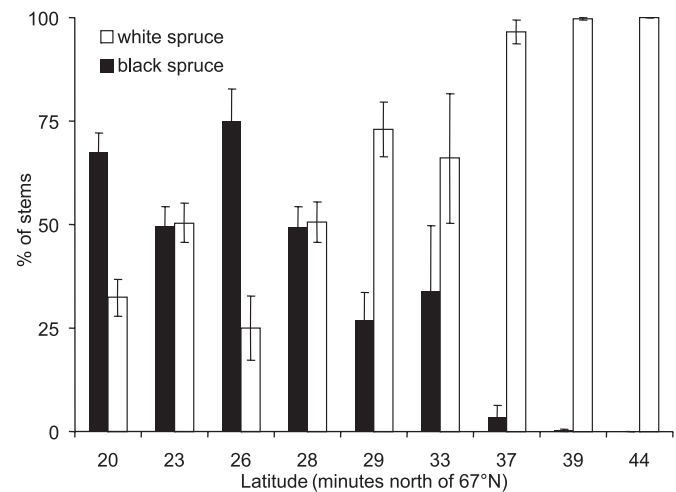
Individuals in the seed size class experience one of two fates: they can successfully germinate and move into the germinant size class, or, because black spruce has semi-serotinous cones, they can remain a seed. Germination rate, the transition from seed to germinant size classes, was calculated in two steps. First, the potential number of germinants produced per year was calculated from the greenhouse germination rate and counts of cone production in the field. Second, to obtain an estimate of actual germinants produced per year, this value was modified to incorporate very early mortality (i.e., seeds that germinate but immediately die), which was not observed in the field. This early-mortality rate was estimated as the ratio of observed germinants in the population to potential germinants (i.e., the number of germinants expected on the basis of calculations of seed viability and total population of seeds). The probability that a seed would fail to disperse (i.e., remain a seed) was estimated as the ratio of seeds remaining in open cones to seeds present in sealed cones. We assumed that seed viability did not differ between seeds that do and do not disperse.

The matrix model included both seed and clonal reproduction. Reproduction from seed, or fecundity ( $F$ ), was calculated from the average number of cones per tree at the study sites and the counts of seeds in harvested cones. We lacked sufficient replication to estimate size-specific fecundity and so we applied the same value to all adult size classes. Clonal reproduction ( $C$ ) is represented in the matrix as the probability of moving directly from an adult size class to that of a seedling. The annual probability of clonal reproduction was estimated as the proportion of trees in the population with clonal offspring divided by the age of the oldest known clone.

The matrix component of Microsoft Excel Poptools (Hood 2003) was used to perform elasticity analyses on the projection matrix (Valverde and Silvertown 1998; Caswell 2001). Elasticity analysis measures the proportional contribution of each matrix element to  $\lambda$ . Because reproduction and mortality rates of small size classes are relatively poorly known, we conducted a sensitivity analysis by running the model with a range of estimates of fecundity, clonal reproduction, and mortality. The range of values was obtained from the data and represents the minimum, mean, and maximum values possible based on the error in our data.

A second matrix,  $\mathbf{B}$ , was used to simulate the effect of varying fire intervals on  $\lambda$ . Matrix  $\mathbf{B}$  simulated the population structure after a stand-killing fire. We ran the analysis using two assumptions about fire: (1) it kills all trees and leaves only potentially viable seeds and (2) it leaves 11% of the adult population. The second scenario was based on our age-structure data, which indicated that approximately 11% of the adults in the population predated the last fire. Postfire germination rates have been reported to be four times higher than in a nonfire year (Sirois et al. 1994), so for scenario 1 (100% mortality of trees) the new matrix was composed of all zero entries except for a new germination probability of 0.092 (four times the nonfire germination rate). Scenario 2 used a matrix that was composed of all zero entries except for the germination probability of 0.092 and an adult survival

**Fig. 1.** Relative abundances of black and white spruce along a north–south transect parallel to the Dalton Highway in the Brooks Range, Alaska. Values are given as the mean  $\pm$  1 standard error.



probability of 0.11. We also made the simplifying assumption that the postfire increase in germination persists for only one time step, thus this analysis should be interpreted as providing insight into the relative effects of a changing fire regime and not for absolute values of  $\lambda$ , as it is likely that our approach will underestimate  $\lambda$ . Using Matlab-PC software (The Mathworks, Inc., Natick, Massachusetts), the unburned matrix,  $\mathbf{A}$ , was multiplied by the burn matrix,  $\mathbf{B}$ , at varying time intervals to simulate the effect of a variable fire frequency. A new matrix,  $\mathbf{C}$ , was defined as shown in eq. 2.

$$[2] \quad \mathbf{C} = [\mathbf{A}]^{i-1} \times [\mathbf{B}]$$

where  $i$  is the time elapsed before the onset of the fire conditions, which are described by matrix  $\mathbf{B}$ . New  $\lambda$  values were then calculated for the resulting populations experiencing periodic fire-return intervals from 0 to 500 years. Lambda values were annualized using eq. 3, in which  $\text{eig}(\mathbf{C})$  is the dominant eigenvalue of matrix  $\mathbf{C}$ , and other variables are as previously defined.

$$[3] \quad \lambda = [\max(\text{eig}(\mathbf{C}))]^{1/(i+1)}$$

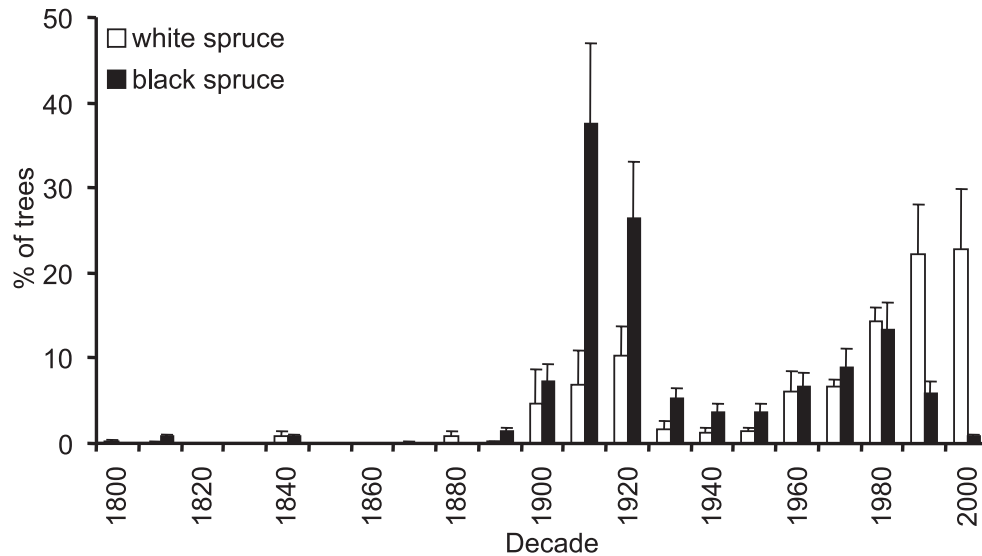
## Results

### Stand history

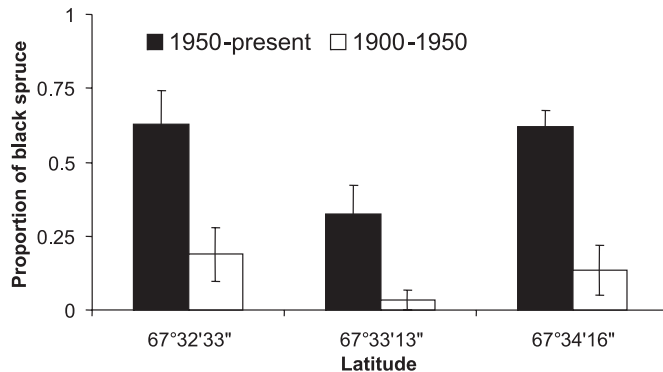
Black spruce made up >50% of trees south of 67°20'N, but abundance declined rapidly after that point and black spruce occurred only sporadically as isolated individuals north of 67°37'N (Fig. 1). White spruce, in contrast, continued to occur in relatively dense stands until tree line, approximately 40 km north of the northernmost black spruce.

We cross-dated a total of 21 fire-killed trees ( $n = 5-8$  per site). Of the outer-ring dates, 67% fell between 1896 and 1902. At the two northern sites, 92% of the outer-ring dates occurred during that time period. We successfully cross-dated two fire scars from black spruce trees, and these indicated a fire between late 1901 and early 1902. Collectively, the fire-scar and outer-ring dates point to a fire occurring in the early 1900s at all three sites.

**Fig. 2.** Recruitment history of black and white spruce in the southern Brooks Range. Because of differences in total tree density among sites, values are expressed as the mean percentage of trees at each site that established during each decade. Error bars are +1 SE ( $n = 3$  sites).



**Fig. 3.** Proportion of black spruce with clonal origin from 1900 to 1950 and from 1950 to 2002. Values are given as the mean  $\pm$  1 SE ( $n = 3$  plots/site).



The recruitment history supports the inferred fire history: almost 99% of the trees established after 1900 (Fig. 2). Both species experienced high recruitment between 1900 and 1930. But while more than 45% of black spruce established between 1900 and 1930, only 11% of white spruce established during this time period. Postfire recruitment is thus relatively more important for black than for white spruce. Relatively high rates of black spruce recruitment occurred between 1960 and 1990, but more than 50% of these recruits were of clonal origin. In contrast, only 12% of recruits originated from layering between 1900 and 1950 (Fig. 3). White spruce recruitment was very high in recent decades (Fig. 2), and although only  $41\% \pm 12\%$  (mean  $\pm$  SE;  $n = 3$  sites) of adult trees are white spruce, white spruce make up  $67\% \pm 20\%$  ( $n = 3$  sites) of seedlings. This represents a significant departure from the assumption that relative abundances should be similar in adult and seedling size classes ( $\chi^2 = 3348$ ,  $df = 2$ ,  $p < 0.05$ ).

Despite the paucity of very young (<10 years old) black spruce seedlings, seeds collected and germinated in the greenhouse were still viable. None of the 1966 seeds from the

2001 year class of cones germinated, but 79 of the 1722 pre-2001 seeds (4.59%) germinated. The overall germination rate under greenhouse conditions was therefore 2.1%.

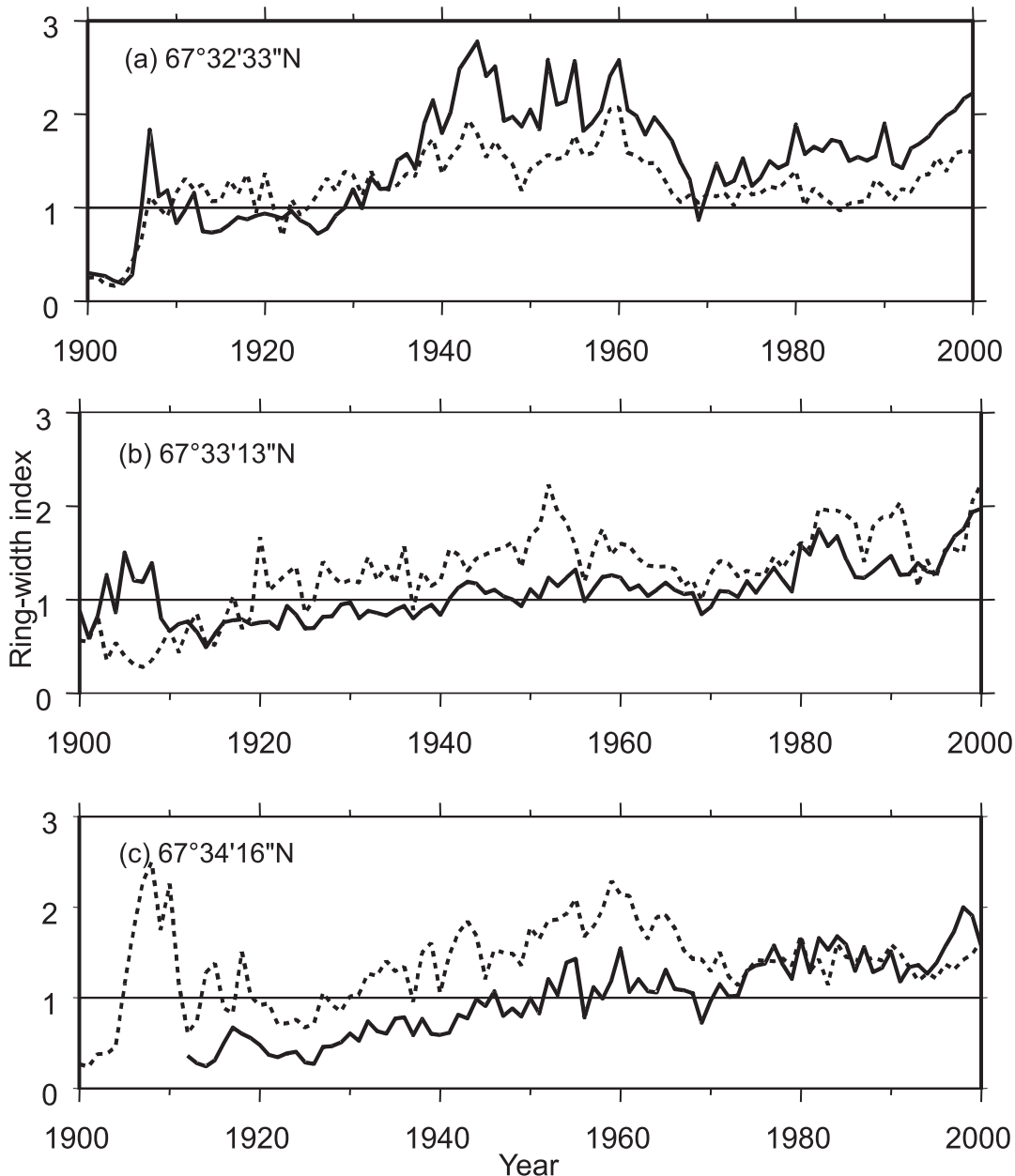
### Growth response to climate

Black spruce growth increased during the 20th century at the two northernmost sites (Figs. 4b and 4c). Black spruce at the southernmost site experienced rapid growth in the mid-1900s and slower growth in recent decades (Fig. 4a). White spruce growth rates at all three sites were highest in the mid-1900s (Figs. 4a–4c). The two species exhibited very different responses to climate (Table 2). Neither species was greatly affected by climate at the southernmost site, although white spruce growth was weakly and inversely correlated with summer temperature. At the two northern sites, black spruce growth responded positively to summer (June or July) temperature. White spruce response to climate was more variable among sites: growth was inversely related to summer temperature at the northern and southern site and positively related to summer temperature at the intermediate site.

### Population dynamics

The matrix model suggests that black spruce populations are relatively stable, although the population is projected to decline slightly through time ( $\lambda = 0.997$ ). The elasticity analyses indicated that the stability of the population was derived in large part from the low mortality rates in sapling, large, and medium adult size classes (i.e., the high probability of individuals remaining in those size classes; Table 3). The results of our sensitivity analysis indicated that our estimates of  $\lambda$  were relatively insensitive to variation in reproductive or early-mortality rates (Table 4). Large increases in seed production or germinant survivorship increased  $\lambda$  slightly to values just over the threshold of 1, but the overall range of  $\lambda$  values in the sensitivity analysis was extremely small: a model run with no seed reproduction produced the lowest  $\lambda$  value (0.9908) and a model run with the minimum net germinant mortality produced the highest (1.0088). This suggests

**Fig. 4.** Ring-width chronologies for black spruce (solid line) and white spruce (broken line) at three study sites. Ring-width measurements are standardized to a mean of 1, creating a dimensionless ring-width index. Values  $>1$  indicate years with above-average growth and values of  $<1$  indicate years with below-average growth.



that the model conclusions are likely robust to relatively large errors in estimating fecundity and early mortality.

The analyses with the fire matrix (**B**) indicated that in the absence of fire, or during periods of prolonged fire intervals, these populations remain very stable. The two scenarios differed only slightly:  $\lambda$  values were consistently lower for a particular fire interval when we assumed that no adults survived the fire than when we assumed 11% survival, but the pattern of response to changes in fire interval were identical. In both scenarios,  $\lambda$  increased rapidly as fire interval increased from 1 to  $>100$  years, but although it approached stability ( $\lambda = 1$ ), it never exceeded that threshold (Fig. 5). The highest  $\lambda$  values were observed at very long fire intervals ( $>350$  years), and the results suggest that fire intervals

$<100$  years would be associated with rapid declines in population size.

## Discussion

The results of this study indicate that black spruce population dynamics at the species' northern limit in Alaska are controlled both by cool climatic conditions, which reduce growth rates and the production of viable seeds, and by fire, which creates periodic opportunities for sexual reproduction. Competitive interactions with white spruce are an additional factor that may affect the long-term stability of these marginal populations. The importance of fire in controlling population dynamics is clear from the recruitment history at the

**Table 2.** Growth responses of trees to climate at three study sites in the southern Brooks Range.

Latitude (N)	Species	Significant variable(s)	Partial correlation	$R_{adj}^2$	F	p
67°32'33"	Black spruce	None	—	—	—	—
	White spruce	July temperature	-0.297	0.067	4.154	0.048
67°33'13"	Black spruce	Winter temperature	0.460	0.231	7.594	0.002
		June temperature	0.332			
	White spruce	Previous December precipitation	-0.390			
67°34'16"	Black spruce	June temperature	0.388	0.478	9.049	<0.005
		Winter temperature	0.330			
		July precipitation	0.589			
		July temperature	0.624			
	White spruce	March precipitation	-0.398	0.281	9.586	<0.005
		Previous December precipitation	-0.362			
		May precipitation	0.347			
		July temperature	-0.452			
		April temperature	-0.389			

**Note:** Climate data were obtained from the climate station at Bettles, Alaska, and cover the time period 1953–2001.  $R_{adj}^2$  is the coefficient of determination ( $R^2$ ) adjusted for the loss of degrees of freedom. Significant variables are those that entered the stepwise regression model for that particular site.

**Table 3.** Results of elasticity analysis from the matrix analysis of black spruce population dynamics in the Brooks Range, Alaska.

	Seed	Germinant	Seedling	Sapling	Small adult	Medium adult	Large adult	Reproductive value
Seed	0.0053	0	0	0	0.001	<0.001	0.004	0
Germinant	0.0054	0.0002	0	0	0	0	0	0
Seedling	0	0.005	0.064	0	<0.001	<0.001	<0.001	0.026
Sapling	0	0	0.006	<b>0.1589</b>	0	0	0	0.201
Small adult	0	0	0	0.006	<b>0.135</b>	0	0	0.258
Medium adult	0	0	0	0	0.005	0.089	0	0.258
Large adult	0	0	0	0	0	0.004	<b>0.511</b>	0.258

**Note:** Elasticities measure the proportional contribution of each matrix element to the  $\lambda$  value. The values in boldface type are the three highest values, indicating the three transitions that contribute most to the observed  $\lambda$  value. The reproductive value integrates survivorship and fecundity and indicates the proportional contribution of each size class to the overall population reproductive rate.

**Table 4.** Sensitivity analysis of fecundity and germinant mortality.

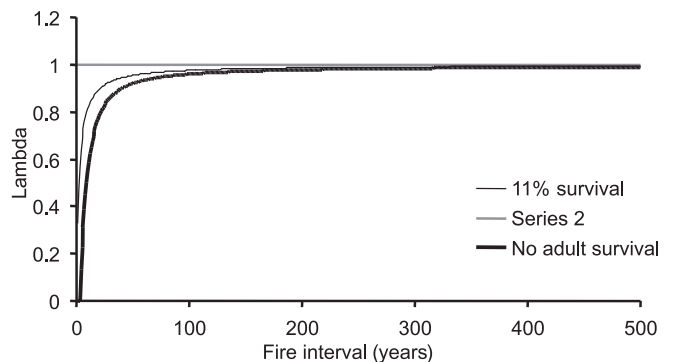
	$\lambda$
Fecundity	
Min.	0.9957 (292 <sup>a</sup> )
Mean	0.9979 (479 <sup>a</sup> )
Max.	1.0002 (693 <sup>a</sup> )
Net germinant mortality	
Min.	1.0088 (94 <sup>b</sup> )
Mean	0.9979 (96 <sup>b</sup> )
Max.	0.9960 (98 <sup>b</sup> )
No seed reproduction	0.9908
No clonal reproduction	0.9978

**Note:** Matrix analyses were run using a range of estimates of fecundity and net germinant mortality. The range was defined by the actual data and used the minimum, mean, and maximum values possible given the observed data. The matrix analysis was also run with two extreme scenarios: no seed reproduction, in which fecundity was set to zero (but clonal reproduction was at observed levels), and no clonal reproduction, in which clonal reproduction was set to zero (but seed reproduction was at observed levels).

<sup>a</sup>Fecundity was measured as the number of dispersing seeds per year.

<sup>b</sup>Net germinant mortality was measured as a percentage.

**Fig. 5.** Effect of fire interval on  $\lambda$  values. The shaded reference line indicates a  $\lambda$  value of 1, at which population size is stable. The two solid lines indicate the results of two scenarios: in the 11% survival scenario, 11% of adult trees were assumed to have survived the fire, and in the “no adult survival” scenario, only potentially viable seeds survived the fire.



three sites: in all cases, most of the sexual reproduction by black spruce was limited to the 3 decades following the most recent fire. This pattern is consistent with black spruce population dynamics elsewhere in its range, where it is com-

monly assumed to be a fire-dependent species (Yarie 1981, 1983; Lavoie and Sirois 1998; Fastie et al. 2002). However, unlike in central portions of its range, where postfire recruitment is sufficiently high that dense even-aged stands form within a few decades after fire, at its northern limit in the Brooks Range the forest canopy remains sufficiently open that recruitment continues to be possible for a century or more after a fire. However, each of the three populations sampled here exhibited a switch from predominantly sexual reproduction in the decades immediately following a fire to predominantly asexual reproduction when nonfire conditions prevailed. Dependence on asexual reproduction is common at the northern limit of black spruce, and the stability of marginal black spruce populations during periods of unfavorable conditions is often attributed to the species' ability to reproduce asexually (e.g., Payette and Gagnon 1979; Sirois 1997).

Although fire appears to be an important prerequisite for sexual reproduction in these populations, our modeling analyses indicated that the populations were also likely to be highly sensitive to variation in fire frequency. Very frequent fires, those occurring <100 years apart, were associated with  $\lambda$  values <1, and thus with the potential for rapid population declines. Similarly, Black and Bliss (1980) concluded that low seed production and slow maturation of trees in tree-line black spruce populations in the Northwest Territories combined to create a threshold fire interval of 80–100 years below which population density would decline.

The impact of long fire intervals on these populations is less certain. In our model,  $\lambda$  continued to increase slightly as fire intervals approached the maximum tested interval of 500 years. However, our model made two key simplifying assumptions that make it likely to overestimate  $\lambda$  values at long fire intervals. First, the model did not incorporate any change in adult mortality with tree age. In reality, older trees often become susceptible to secondary disturbances like windthrow or insect outbreaks (Harper et al. 2002), in which case the individuals with the highest fecundity might begin to be replaced by saplings and smaller adults. Fires occurring during this period of canopy turnover might reduce population density because of the low availability of viable seed at that point in stand development (Black and Bliss 1980). Second, our model did not incorporate interspecific interactions. A lengthening of the fire cycle might lead to the successional replacement of black spruce by white spruce, by virtue of the latter species' enhanced ability to germinate and establish in unburned conditions. Our data strongly suggest that in burned conditions, black spruce reproduces more effectively than white spruce, but in unburned conditions, white spruce has a clear advantage (e.g., Parisien and Sirois 2003). This would likely translate into a high probability of stand turnover from black to white spruce if fire intervals were sufficiently long.

Although fire clearly plays an important role in controlling temporal patterns of regeneration in black spruce populations at the species' northern limit, our data provide evidence that climate limits the amount of growth, as cool conditions reduce both growth rates and seed production in these marginal populations. Our results confirmed that the production of viable seeds at the northern limit of black spruce is very limited. Low viable seed production near the species north-

ern limit has been attributed to low pollen viability (Elliott 1979) and the effects of low growing-season warmth on seed development (Black and Bliss 1980; Sirois 2000). Our data also suggested that the growth of adult black spruce trees was temperature-limited. The variation in growth explained by climate increased with latitude, and black spruce growth at the two northern sites was significantly and positively correlated with summer temperatures. Cool conditions could thus reduce growth rates and exacerbate low seed production by increasing the time to reproductive maturity. Temperature constraints on black spruce regeneration are known to be an important driver of the long-term dynamics of black spruce near the edges of its range. Relict woodlands in eastern Canada, for example, reflect black spruce establishment during periods of warm conditions, but these relict populations were left beyond the limit of seed production when conditions subsequently worsened (Payette and Gagnon 1985; Payette and Morneau 1993). In the absence of sexual reproduction, such populations are very vulnerable to any disturbance, like fire, that removes the adult trees.

It is thus likely that the long-term stability of these populations reflects a delicate balance between fire, which creates optimal conditions for reproduction, and climatic conditions, which control overall reproductive output. Further study of the role of interspecific competition with white spruce as a limit is also warranted given the very different recruitment histories of the two species. Fire is clearly necessary to create conditions favorable to reproduction from seed, and thus in the absence of fire black spruce would rely increasingly on clonal reproduction. In a monospecific stand, black spruce could persist indefinitely by layering (Laberge et al. 2001). The presence of white spruce, however, raises the possibility of a shift toward increasing dominance by white spruce, which can establish by seed in high densities in the absence of fire. The likelihood of such a transition depends on the relative reproductive rates of the two species and the relative competitive ability of clonal black spruce seedlings and non-clonal white spruce seedlings. Clonal seedlings should have a competitive advantage over nonclonal seedlings because of persistent connections to the parent. However, white spruce has a clear numerical advantage over black spruce: our plots had  $90.3 \pm 41.7$  white spruce seedlings per hectare and only  $21.6 \pm 5.8$  black spruce seedlings or clones per hectare. This suggests that stands should become increasingly dominated by white spruce over time. Periodic fires would thus, in theory, be necessary to allow black spruce to maintain dominance. However, because climatic constraints limit the rate at which trees reach mature size and the frequency with which they produce viable seeds, there is likely to be a threshold fire frequency below which black spruce would be unable to successfully recolonize. Fire and climate interact in similar ways to control the population dynamics of black spruce in eastern Canada, where the combination of fires and unfavorable climatic conditions has led to the deforestation of tree-line areas (Payette and Gagnon 1979, 1985).

Although both fire and climate are clearly important in these stands, their relative importance remains unknown. For example, black spruce may be at its climatic limit and incapable of producing viable seeds north of its current location regardless of the fire regime in those areas. Alternatively, black spruce may be capable of producing viable seeds north

of its current location but cool, wet condition in the central Brooks Range may make fires sufficiently rare (e.g., Kasischke et al. 2002) that opportunities for black spruce establishment are effectively nonexistent. Nonetheless, these results suggest that unlike white spruce, which has expanded into tundra in the absence of disturbance (e.g., Lloyd and Fastie 2003), the response of the northernmost black spruce populations in Alaska to future warming is likely to depend on changes in both climate and fire intervals.

## Acknowledgements

We thank Nick Benjamin, Charlie Bettigole, and Jon Katz for assistance with the fieldwork and laboratory work on this project. Funding for this research was provided by the Bonanza Creek LTER (DEB-0080609), the Middlebury College Department of Biology, the Janet Curry Fellowship, and the Middlebury College Senior Work Fund (grants to A.E.W. in support of her senior thesis research).

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