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Relative importance of different secondary successional pathways in an Alaskan boreal forest

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Abstract: Postfire succession in the Alaskan boreal forest follows several different pathways, the most common being self-replacement and species-dominance relay. In self-replacement, canopy-dominant tree species replace themselves as the postfire dominants. It implies a relatively unchanging forest composition through time maintained by trees segregated within their respective, ecophysiological niches on an environmentally complex landscape. In contrast, species-dominance relay involves the simultaneous, postfire establishment of multiple tree species, followed by later shifts in canopy dominance. It implies that stand compositions vary with time since last fire. The relative frequencies of these and other successional pathways are poorly understood, despite their importance in determining the species mosaic of the present forest and their varying, potential responses to climate changes. Here we assess the relative frequencies of different successional pathways by modeling the relationship between stand type, solar insolation, and altitude; by describing how stand age relates to species composition; and by inferring successional trajectories from stand understories. Results suggest that >70% of the study forest is the product of self-replacement, and tree distributions are controlled mainly by the spatial distribution of solar insolation and altitude, not by time since last fire. As climate warms over the coming decades, deciduous trees will invade cold sites formerly dominated by black spruce, and increased fire frequency will make species-dominance relay even rarer.

Resume: La succession apres feu dans la foret boreale de I' Alaska adopte differents modes, les plus communs etant Ie retour des memes especes et la dominance successive de differentes especes. Dans Ie cas du retour des memes especes, les especes d'arbres qui dominent la canopee sont remplacees par les memes especes qui deviennent dominantes apres un feu. Cela implique que la composition de la foret qui demeure relativement stable dans Ie temps soit maintenue par des arbres qui sont restreints a leur niche ecclogique respective dans un pays age complexe du point de vue environnemental. Au contraire, la dominance successive de differentes especes suppose l'erablissement apres feu de plusieurs especes d'arbres suivi par des changements ulterieurs de dominance dans la canopee. Cela signifie que la composition du peuplement change avec Ie temps apres un feu. Les frequences relatives de ces modes de succession et d'autres sont peu connues rnalgre leur importance dans la determination de la mosaique d'especes de la foret actuelle et de leurs differentes reactions potentielles aux changements climatiques. Dans cet article, nous evaluons la frequence relative de differents modes de succession en modelisant la relation entre Ie type de peuplement, I'ensoleillement et l'altitude: en decrivant comment la composition en especes est reliee a l'age du peuplement et en deduisant Ie mode de succession a partir du sous-etage d'un peuplement. Les resultats indiquent que plus de 70 % de la foret etudiee est Ie resultat du retour des memes especes et que la distribution des arbres est regie principalement par la distribution spatiale de l'ensoleillement et l'altitude, non par Ie temps ecoule depuis Ie dernier feu. A mesure que Ie climat se rechauffera au CoUl'S des prochaines decennies, les especes decidues vont envahir les stations froides autrefois dominoes par l'epinette noire et I'augmentation de la frequence des feux va faire en sorte que la dominance successive de differentes especes sera encore plus rare.

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Introduction

Understanding postfire succession is of basic importance for understanding boreal forest dynamics. The primary, natural disturbance factor in this biome is fire (Johnson 1992), and most parts of the forest mosaic on upland landscapes in Interior Alaska are embarked on some pathway of postfire succession (Chapin et al. *2006a).* Four different pathways possibly occur after fires in Interior Alaska (Table I), and their relative importance in determining the present forest mosaic is poorly understood.

"Self-replacement" occurs when the same tree species

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Table 1. Inferred successional pathways under different scenarios of tree recruitment and fire frequency.

	Prefire dominant	Postfire recruits	Canopy dominant at time of next fire	Successional pathway
1	Spruce	Spruce only	Spruce	Self-replacement
2	Birch	Birch only	Birch	Self-replacement
3	Aspen	Aspen only	Aspen	Self-replacement
4	Birch	Birch and spruce	Birch (short fire interval)	Self-replacement
5	Aspen	Aspen and spruce	Aspen (short fire interval)	Self-replacement
6	Spruce	Birch and spruce	Spruce (long fire interval)	Species-dominance relay
7	Spruce	Aspen and spruce	Spruce (long fire interval)	Species-dominance relay
8	Spruce	Birch and spruce	Birch (short fire interval)	Species replacement
9	Spruce	Aspen and spruce	Aspen (short fire interval)	Species replacement

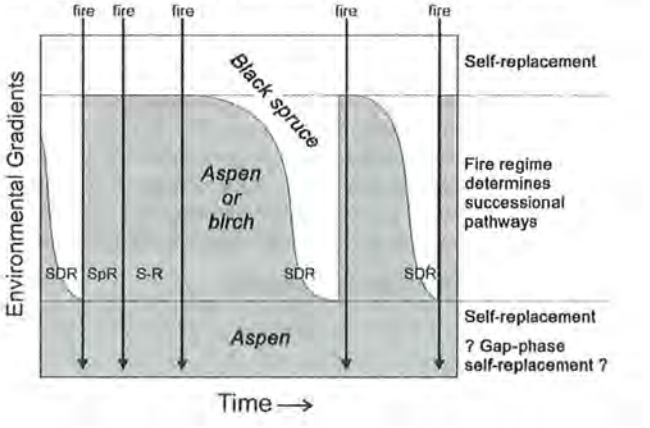
that dominated the pretire canopy Immediately re-establishes itself after a fire and continues as canopy dominant. This pathway is well documented in stands of black spruce *(Picea mariana* (Mill.) BSP) (Johnstone and Chapin *2006a),* where seeds that are stored in semiserotinous cones enable rapid re-establishment after fires (Zasada et al. 1992). Self-replacement also occurs commonly in stands of aspen *(Populus tremuloides* Michx.) and birch *(Betula papyrifera* Marsh.), where fires recur before slowly invading spruce trees can gain canopy dominance (Youngblood 1995). Self-replacement in aspen stands occurs by root suckering (Johnstone and Chapin *2006a)* and in birch stands by stump sprouting (Lutz 1956).

"Species-dominance relay" occurs when different tree species successively assume canopy dominance after a fire. In concept, this pathway is closely related to "relay floristics" and "initial floristic composition" (Finegan 1984). Within the first decade after fires in Interior Alaska, seedlings of both deciduous and coniferous trees are established, and within 50 years, birch and aspen overtop the herbs and willow shrubs (Johnstone et al. 2004). Spruce trees *(P. mariana* and (or) *Picea glauca* (Moench) Voss) usurp the canopy some time later, though estimates vary about the time required for spruce to take over (Van Cleve and Viereck 1983), probably because of variations in local growing conditions (Youngblood 1995). Spruce trees maintain their dominance until the next fire, when the relay begins again (Table 1).

The third pathway, "species replacement," can occur in at least two different ways. A particularly intense fire can extirpate the prefire stand entirely, allowing different species to take over after the fire. The same thing can happen if the interval between fires shortens enough to interrupt species-dominance relay at an early stage (Johnstone and Chapin *2006b).* The size and severity of fires are well known to influence tree regeneration in recent burns (Johnstone and Kasischke 2005). Typically, the success of postfire seedling establishment by aspen, birch, and black spruce increases with the amount of organic matter burned off the soil surface (Charron and Greene 2002). This effect is most pronounced for aspen and birch, which have relatively small seeds with only limited energy reserves (Johnstone and Chapin *2006a).*

A fourth, possible pathway is "gap-phase self-replacement," which occurs when canopy trees self-replace in gaps opened by tree deaths from causes other than fire. This pathway exists in aspen stands in western Canada (Cumming et al. 2000), but has not yet been documented in Alaska.

Fig. 1. Conceptual model of a forested, hilly landscape in Interior Alaska showing how different pathways of secondary forest succession relate to environmental gradients (altitude, solar insolation) and to the interval between fires. "S-R" is self-replacement, "SDR" is species-dominance relay, and "SpR" is species replacement. At sites where all the tree species can grow, the pathway taken (as judged at the time of a stand-replacing fire) is controlled by fire frequency. If fire is absent long enough (>100 years), species-dominance relay will occur. More frequent fires will interrupt species-dominance relay (for instance, black spruce growing in the understory of birch or aspen) and cause the canopy (aspen or birch) to replace itself. At the two extremes of the environmental gradient, black spruce and aspen occupy sites where only they are physiologically able to grow. At these sites, only self-replacement is possible after fires. Our research questions are the following: What proportion of stands in the study area originated via self-replacement versus species-dominance relay? and what successional pathways will these stands take in the future in the absence of fire? The natural history this diagram is based on is described in the Introduction section.



Which successional pathway is taken is strongly influenced by the combined effects of tire frequency and where on the landscape different tree species can grow. The duration of fire-free intervals determines how long succession can proceed before being restarted (Fig. 1). Where a tree can grow is determined by how its ecophysiological tolerances map onto the environmentally heterogeneous landscape. If these site effects mean that only one tree species can grow at a particular site, then only the self-replacement pathways are possible. If multiple species can grow there, then the species-dominance relay and species-replacement pathways are possible. The fire frequency is critical for both of these

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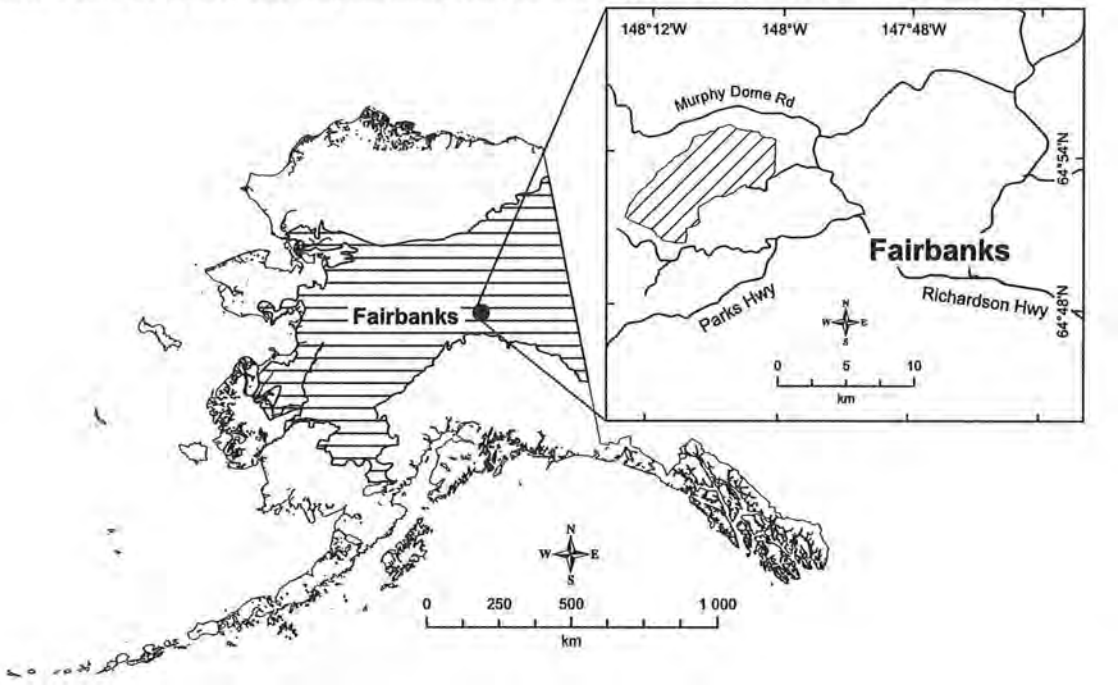
Fig. 2. Location of Ester Dome study area (diagonal lines) within the Interior Alaskan boreal forest (horizontal lines).



pathways because the canopy-dominant species is determined by time since last fire (Table 1). Together, the criteria of suitable site and sufficient time determine where on the landscape different successional pathways can occur. Our research questions are the following: What proportion of a forested landscape in Interior Alaska is presently developing along which successional pathway? and what are the rules involving time since last fire and site effects that control the pathway taken?

Study area

We worked in a 50 km^2 area on the northwest side of Ester Dome, a massif of complex and steep topography 20 km northwest of Fairbanks, Alaska (Fig. 2). Bedrock consists of schist overlain by loess and gravel of varying thickness depending on slope position. Altitudes range from 140 m a.s.l. in valleys to 770 m a.s.l. on the ridge tops, which lie below the regional treeline. Much of Interior Alaska is made up of similarly hilly terrain lying below treeline, and the study area is representative of the north-facing portions of this regional landscape.

The tree flora of our study area is dominated by just three species: black spruce, aspen, and birch. White spruce is uncommon both in the study area and on similar upland landscapes in Interior Alaska. Descriptions of the general vegetation types found in our study area are found in Viereck et at. (1992) and Hollingsworth et al. (2006). Aspen usually grow in the study area in pure stands with sparse understories containing aspen root suckers, senescent clumps of alder *(Alnus sinuata* (Regel) Rydb. and *Alnus tenuifolia* Nutt.) and willow *(Salix* spp.), along with varying densities of black spruce seedlings and saplings. Birch also typically grows in pure stands with few understory species other than senescent alder and willow and varying densities of black spruce seedlings and saplings. Several distinct types of black spruce communities occur in the study area including both dry acidic, wet acidic, and nonacidic subtypes (Hollingsworth et al. 2006). Wet acidic black spruce communities are relatively common in the study area where they grow on peat deposits on steep, north-facing slopes and have shallow active layers under mats of *Sphagnum* moss.

The four tree species common at upland sites in Interior Alaska display strong differences in site preferences. Aspen is largely restricted to sites with thick (> 1 m) active layers (Chapin et al. *2006a),* which are usually found on south-facing slopes that receive abundant solar radiation. Black spruce out-competes other tree species on cold, wet sites underlain by permafrost, because of its tolerance for waterlogging (Islam et al. 2003) and its ability to conserve nutrients (Chapin et at. *2006b).* Birch grows best on east- and west-facing slopes with deep active layers but that are cooler and wetter than aspen-dominated sites (Neiland and Viereck 1977). White spruce has site tolerances broadly similar to those of birch (Nienstaedt and Zasada 1990).

Interior Alaska, the region between the Alaska and Brooks Ranges, experiences a subarctic continental climate (Haugen et at. 1982) associated with large seasonal fluctuations in temperature (Slaughter and Viereck 1986). There are 18-21 h of sunlight during the main growing-season months of June and July; and daily highs reach the mid-20s (^{o}C) with extremes above 30 °C. In contrast, December, January, and February have only 3-6 h of sunlight, and daily highs can stay below -30°C for weeks at a time (Alaska Climate Research Center 2005). Mean annual temperature is below freezing, which allows discontinuous permafrost to form in the area.

The presence of permafrost and the thickness of the ground that thaws in summer have important effects on tree

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Table 2. Model covariates derived from elevation models.

Covariate	Min.	Max.	Mean	SD
Altitude (m)	143	709	349	123
Slope gradient (°)	1	79	15	8
Slope aspect (°)	0	359	195	114
Flow accumulation (no. of cells)*	0	10 124	85	542
Solar radiation (watt hours/m^2; 1 watt hour = 3600 J)	110 621	468 459	386 684	49 396

*This measurement unit is the number of upslope grid cells that flow into each sampled grid cell.

distributions in the study area. Permafrost is perennially frozen ground. In summer the uppermost 20-100 cm of the ground thaws, only to refreeze the following winter. Plant roots are restricted to this active layer, whose thickness is controlled by aspect, altitude, topographic shading, and the presence of insulating moss layers. South-facing slopes are usually free of permafrost. Precipitation averages 270 mm, most falling as rain in late summer, and snow cover usually persists from October until April (Alaska Climate Research Center 2005).

Fire is the predominant cause of tree mortality in Interior Alaska. Fire frequency is poorly quantified but probably ranges from 75 to 150 years in many forest stands (Viereck 1973; Fastie et al. 2003). Tree throws are rare in the study area, and we saw no evidence for insect-caused mortality of trees.

Methods

Where the different tree species can grow

We assessed the potential for different tree species to grow at particular sites by examining spatial correlations between tree distributions and topographic variables. This involved first classifying the forest vegetation using satellite imagery, then verifying this classification in the field, and finally building a regression model describing the relationship between stand type and the topographic variables of solar insolation, altitude, slope gradient, slope aspect, and area drained upslope.

We manually delineated classification training areas in five stand-cover types on a 0.60 m spatial resolution, multiband Quickbird satellite image. We positioned these training areas throughout the study area to capture the widest range of spectral responses for each cover type. Black spruce, aspen, birch, alder, and bare ground had 20, 14, 14, 19, and 20 training areas, respectively. The black spruce cover type includes a few white spruce stands because of difficulty in distinguishing between the two spectrally. Later field verification showed that white spruce was a minor component in the overall spruce cover type. We used the training areas to guide the computer model in a supervised classification routine using the maximum likelihood method, 'and then conducted field verification on 54 randomly distributed points on the landscape. At each of these points, we assigned an actual cover type based on both a subjective estimate of canopy dominance and optical measurement of stem basal area.

We next estimated the total, potential insolation between May 15 and August 15 incident on each image pixel with a 20 m spatial resolution elevation grid derived from spaceborne synthetic aperture radar (SAR). The insolation model algorithms accounted for the influences of view-shed, surface orientation, elevation, and atmospheric conditions such as cloud cover (Fu and Rich 1999). We used as m spatial resolution, airborne SAR elevation grid to calculate the remaining model covariates, which included the water flow into each grid cell from all upslope cells (flow accumulation tool, ESRI), slope gradient, slope aspect, and altitude.

Finally, we determined the relationship between classified vegetation types and topographic variables using a multinomial logistic regression model (Davis and Goetz 1990; Augustine et al. 2001). We randomly selected 1000 points within the study area, eliminated any points falling in grid cells previously classified as treeless, and then used the cells containing the remaining 772 points for the logistic regression model. Our response variable contained three levels of vegetation classes, black spruce, aspen, and birch. Initial model covariates included summer potential insolation, flow accumulation, slope gradient, slope aspect, and altitude (Table 2). We then investigated potential sources of multicollinearity between variables. No automated model selection procedures were incorporated, which allowed us greater control over any multicollinearity effects. A two-stage, manual model-selection methodology was incorporated, and the saturated model included all main effects and two-way interactions. At stage one, we eliminated interaction terms with significance greater than 0.2 from the model. At stage 2, we eliminated any term with significance greater than 0.05 until all terms were significant ($\alpha = 0.05$). We chose the final model on the basis that all the variables were significant and that it had the highest predictive ability based on the classification table. We then derived probabilities of class membership from parameter estimates.

Estimating the time to relay in mixed birch - black spruce sands

Stands that are currently undergoing a relay in canopy dominance are rare in the study area. Careful search yielded only two stands where canopy-emergent black spruce are growing within a disintegrating canopy of senescent birch. Test stand 1 is east-facing, test stand 2 is southeast-facing, and both are situated at 475 m a.s.l. In each stand, we reconstructed the time of tree ascension into the canopy by determining the trees' ages at different bole heights. We felled pairs of trees, one black spruce and one paper birch, whose crowns contacted one another. Five pairs of trees were felled in test stand 1, and six pairs were felled in test stand 2. We felled the trees as close to the ground as possible and estimated the height above root collar by digging down and visually locating the root collar. We measured bole height from the level of the root collar, and took cross-sections at 1-2 m intervals. We fine-sanded the cross-sections and counted the annual rings under a dissecting microscope.

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Fig. 3. Supervised image classification of Ester Dome study area showing locations of the 34 sampled stands distributed across the study area. Vegetation classes are used as response variables with topographic covariates in a multinomial logistic regression model.

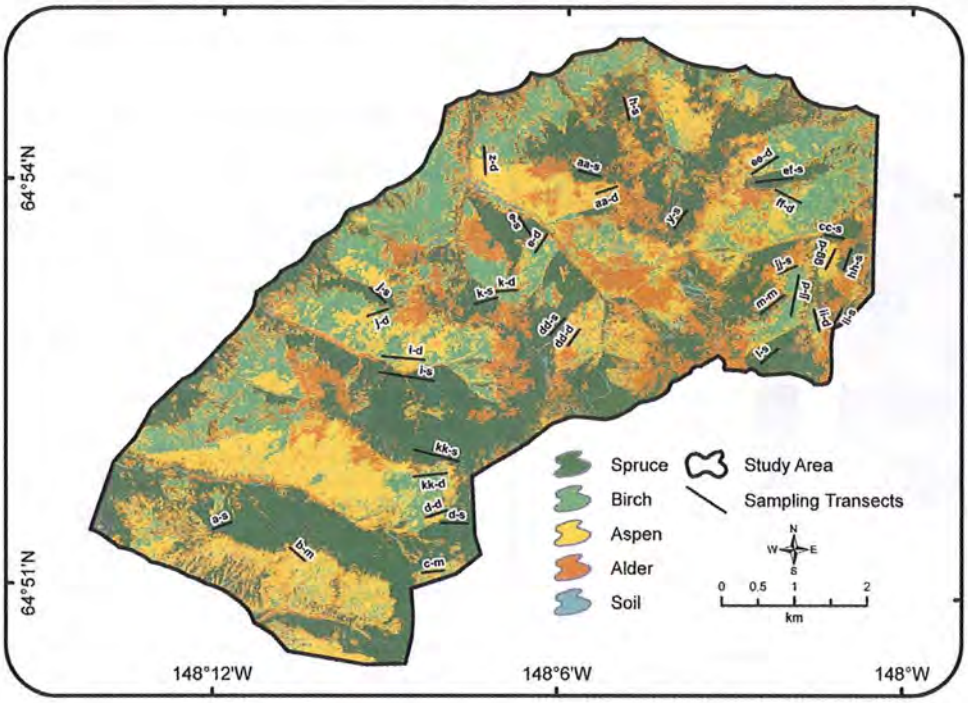

Table 3. Supervised vegetation classification error matrix.

	Field validation				
Classification	Alder	Aspen	Birch	Spruce	User accuracy (%)
Alder	7	1	0	2	70
Aspen	2	4	1	0	57
Birch	0	1	12	0	92
Spruce	0	0	0	24	100
Producer accuracy (%)	78	67	92	92	87 overall

Stand ages, understory composition, and forest history

We sampled tree ages in 34 stands chosen for their canopy uniformity on high-resolution satellite imagery and for their dispersion across the study area (Fig. 3). By selecting stands with uniform canopies, we avoided ones that had experienced spatially variable fire severities the last time they burned. Of these stands, 16 were dominated by black spruce; 8 were dominated by birch; 4 were dominated by aspen; 3 were dominated by birch and aspen; 2 were dominated by black spruce and birch; and 1 was dominated by white spruce, birch, and aspen. In each of these stands, we randomly selected between 15 and 60 trees spaced roughly 5 m apart along a randomly oriented transect through the stand. We cored stems at an average height of 11 cm above the ground. Cores were mounted, dried, sanded, and the annual rings were counted under a dissecting microscope. In each stand where we cored trees, we randomly placed five, 10 m^2 quadrats and counted the number of stems <2 m in height belonging to the different tree species. In each quadrat, we used a shovel to search for charred logs, stumps, and bark fragments in the duff layer. We identified birch remains by their distinctive bark and black spruce logs and stumps by their bark, by their preserved wood, and by the distinctly tall, thin trunks of this species.

Results

Image classification

The error matrix of the supervised vegetation classification (Table 3) indicates user accuracies of 70% for alder, 57% for aspen, 92% for birch, and 100% for spruce. Producer's accuracy is 78% for alder, 67% for aspen, 92% for birch, and 92% for spruce. Overall accuracy is 87% with a kappa statistic of 81 %.

Regression modeling

The final model includes aspen, birch, and spruce as response variables and insolation and altitude (Fig. 4) as significant ($\alpha = 0.05$) covariates. We found that slope gradient, slope aspect, and upslope-now accumulation were not significant covariates. The probability of a site being dominated by black spruce declines when going from cooler, high altitude flow insolation sites to warmer, lower altitude / higher insolation sites (Fig. 5). Birch stands occupy

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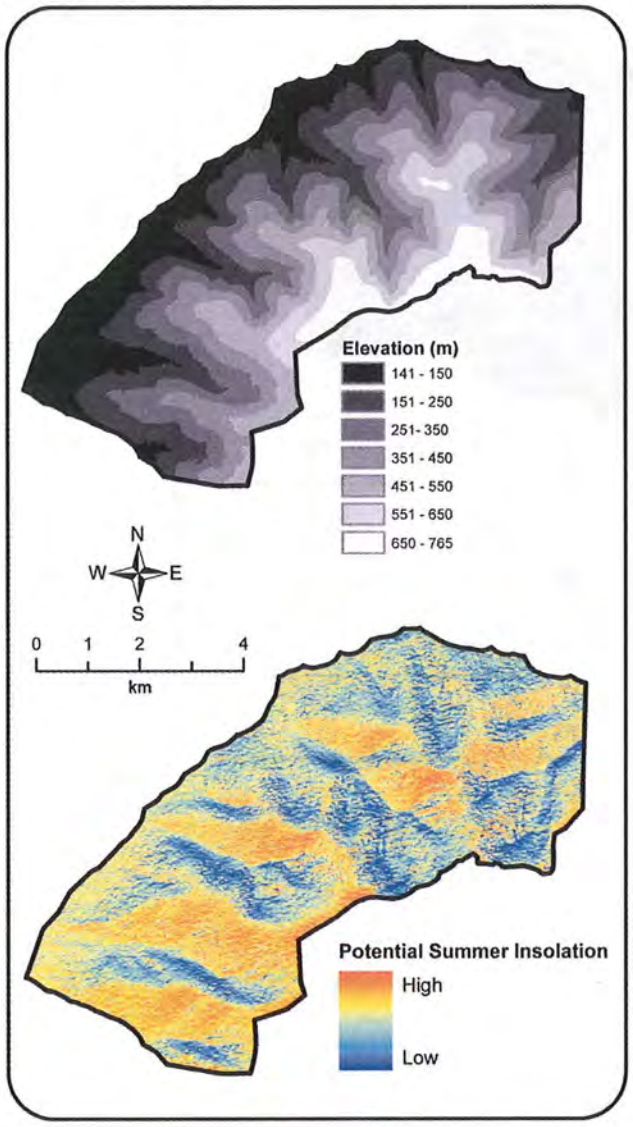
Fig. 4. Altitude and potential summer insolation were the significant ($\alpha = 0.05$) topographic variables in the final multinomial logistic regression model.



a relatively narrow range of lower altitude sites with moderately high insolation, while aspen grow at sites with the highest insolation but across a wide range of altitudes.

By combining the probability plots for black spruce growing with birch and black spruce growing with aspen, we can predict where these species are able to coexist in the study area, and therefore where the species-dominance relay and the species replacement pathways can potentially occur (Fig. 6). For reasons detailed in the Discussion section, we chose a species cohabitation probability of >35% to identify sites where two or more of the tree species can potentially coexist. The potential zone tor black spruce and birch cohabitation occurs only at sites located below 300 m altitude that have mid- to high-insolation values, while the black spruce and aspen zone of cohabitation occurs only above 350 m at the sites with the highest insolation. It turns out that the coexistence of deciduous and conifer species is unlikely across much of the altitude-insolation response surface (Fig. 6), and only about 15% of the real landscape seems able to support spruce together with either aspen or birch (Fig. 7).

Time to relay dominance in birch - black spruce stands

In test stand 1, birch and black spruce probably established themselves simultaneously after a fire that occurred ca. AD. 1790 (Fig. 8), despite their differences in basal age. Ring counts at root collar tend to underestimate the germination date of spruce more (up to 43 years) than they do deciduous species (up to 11 years) (DesRochers and Gagnon 1997; Gutsell and Johnson 2002). In test stand 1, birch trees initially grew faster and dominated the canopy for at least the first 150 years after the fire until ca. AD. 1940. Because the birch canopy is disintegrating now, it is difficult to tell if the birches were once taller than today; if they were, birch dominance could have persisted until AD. 1950 or even later. We infer that spruce assumed canopy dominance in this stand sometime between 150 and 200 years after stand establishment. In test stand 2, birch and black spruce probably established after a fire ca. A.D. 1810. Again, the birch grew faster and dominated the canopy for at least the first 120 years (Fig. 8). The transition from birch to black spruce dominance in the canopy here occurred between 120 and 170 years after stand establishment. Based on the reconstructed timing of species-dominance relay in these two stands, we estimate it typically takes 150 years for birch stands to succeed into black spruce stands in the study area. We were unable to find any stands where black spruce were invading a senescent canopy of aspen, but based on the life expectancy of aspen at other sites in Interior Alaska, aspen probably succeeds to spruce slightly faster than birch stands do, perhaps 100-120 years after a fire. In what follows, we adopt a conservative estimate of 100 years for the time required for species-dominance relay to proceed from either birch or aspen to black spruce.

Stand ages

We aged 1059 trees in 34 different stands (Fig. 9). Of the 523 black spruce trees we aged, 364 (70%) of them were <100 years old. Similarly, 11 of the 16 black spruce dominated stands we sampled had mean ages <100 years (Fig. 9). Only 1 of the 136 aspen trees we cored was older than 100 years; the majority were between 50 and 80 years old (Fig. 9). Out of the 330 trees cored and 11 felled, the only birch trees we encountered that were older than 100 years were in the two canopy-history plots, where they had followed the species-dominance relay pathway.

Tree recruitment within existing stands

The relative abundance of seedlings and saplings of different species in the understories of stands provide insights into the possible future development of stands in the absence of fire. Large numbers of black spruce are established within the understories of black spruce, mixed black spruce and birch, and birch stands (Fig. 10). In contrast, the most abundant seedlings and saplings in aspen stands and in mixed birch-aspen stands are aspen root suckers. Black spruce rep-

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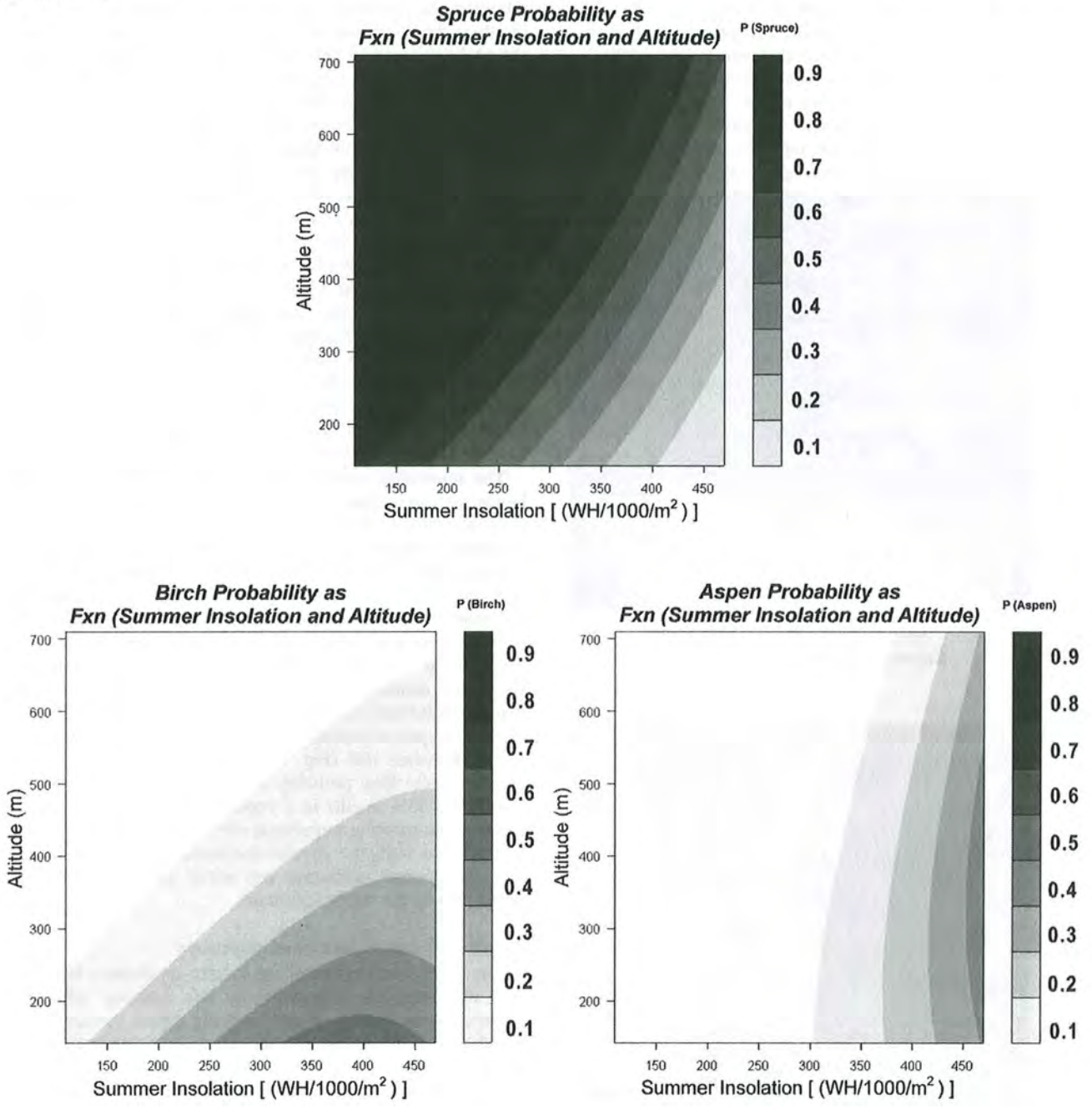
Fig. 5. Probabilities of spruce, birch, and aspen growing within a phase space defined by altitude and summer insolation. These plots were produced by transforming the multinomial logistic regression results into probabilities based on the covariates of altitude and potential summer insolation.



resents more than 50% of all stems <2 m tall in half the quadrats within birch stands and 65%-100% of the quadrats within black spruce and in mixed spruce-deciduous stands. **In** contrast, only 15%-20% of quadrats in aspen and in mixed aspen-birch stands had >50% black spruce in their seedling and sapling populations.

Insights from the forest floor

Only in birch stands did we find sufficient numbers of charred stumps, charred logs, and bark fragments to infer the composition of preceding stands. Of the 40 quadrats examined in birch stands, 39 of them contained evidence for a preceding stand composed of a mixture of birch and black spruce. We were unable to infer the exact proportions of spruce and birch because of the poorer preservation potential of birch compared with black spruce. One of the quadrats lacked any evidence of birch but contained the charred stumps and logs of black spruce.

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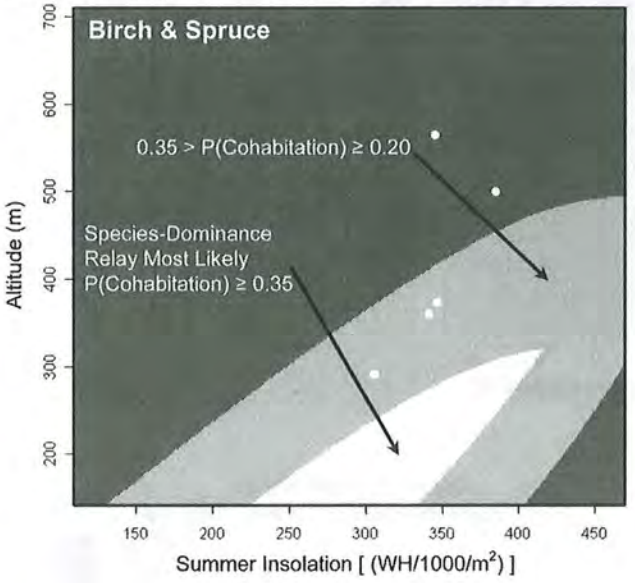
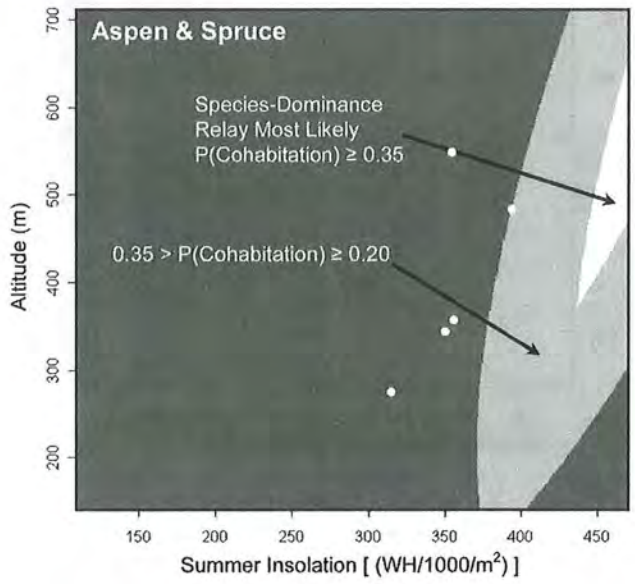
Fig. 6. Regions in which different tree species can potentially grow together and therefore species-dominance relay can occur. Plots were generated by combining the birch and spruce as well as the aspen and spruce plots from Fig. 5 for those areas having <20%, ≥20%, and ≥35% probability of supporting both birch and spruce or aspen and spruce. Unshaded regions have ≥35% probability of supporting both deciduous and spruce species and indicate where species-dominance relay is most likely to occur. Shaded regions have <35% probability of supporting both deciduous and spruce species. White dots represent the black spruce stands in the study area whose mean age is >100 years.





Discussion

Potential habitats and successional pathways

The model accurately predicts, with a probability up to 90%, where black spruce trees grow on the study landscape (Fig. 5). But when it attempts to predict the locations of birch and aspen, the probabilities drop to 50%-60%. Is this model still useful for predicting where species-dominance relay can and cannot occur? Most of the model's inaccuracy involves the locations of aspen and birch stands, and there are probably several reasons for this. First, stands of black spruce do occur that have passed through species-dominance relay, so these same sites would support aspen or birch stands if they had burned more recently. Other lines of evidence discussed below suggest that species-dominance relay is possible in roughly 30% of the study area. The second reason why our regression model has some difficulty predicting the locations of birch and aspen stands is that these two species overlap in their mutual site preferences, which makes predicting the presence of one or the other difficult on the basis of solar insolation and altitude. The primary use we make of the regression model is to estimate how much of this landscape can support both black spruce and deciduous trees and hence possibly undergo species-dominance relay in the absence of fire. Since the model accurately predicts where black spruce can and cannot grow, it is useful for inferring where species-dominance relay can and cannot occur.

The regression model suggests only ~ 15% of the study landscape can support spruce as well as either aspen or birch (Fig. 6). This 15% estimate comes from applying the relationships between tree species and altitude and summer insolation (Fig. 5) to the topography of the study area (Fig. 7) and uses $P > 35\%$ on the response surfaces as the cutoff for potential cohabitation between black spruce and either aspen or birch. Using probabilities <35% results in more deciduous trees in the study area than our vegetation classification shows are actually there. This is not an artifact of a forest that has followed the species-dominance relay pathway into a state of spruce domination. Most stands in the study area are <100 years old (Fig. 9), so if deciduous trees could grow at a site they probably would be growing there today. Using $P > 35\%$ results in a vegetation map (Fig. 7) that resembles the existing vegetation cover (Fig. 3). These results suggest that both the species-dominance relay and the species replacement pathways can occur only in a relatively small part of the study landscape.

Stand ages and successional pathways

The >100 years required for species-dominance relay further constrains the importance of this pathway within the present forest. Most of the existing black spruce stands could not have developed along the species-dominance relay pathway because they are <100 years old (Fig. 9). Only a third of the black spruce stands and 30% of the total black spruce trees we aged in the study area were >100 years old, indicating that only about a third of the black spruce in the present forest could potentially have followed a pathway of species dominance relay. Furthermore, when the five >100-year-old black spruce stands are plotted on the insolation-altitude phase space (Fig. 6), none of them fall within the >35% zone of potential cohabitation for spruce with either birch or aspen. This suggests that, in fact, somewhat <30% of black spruce stands in the study area originated via the species-dominance relay pathway.

Further support for this <30% estimate for the frequency

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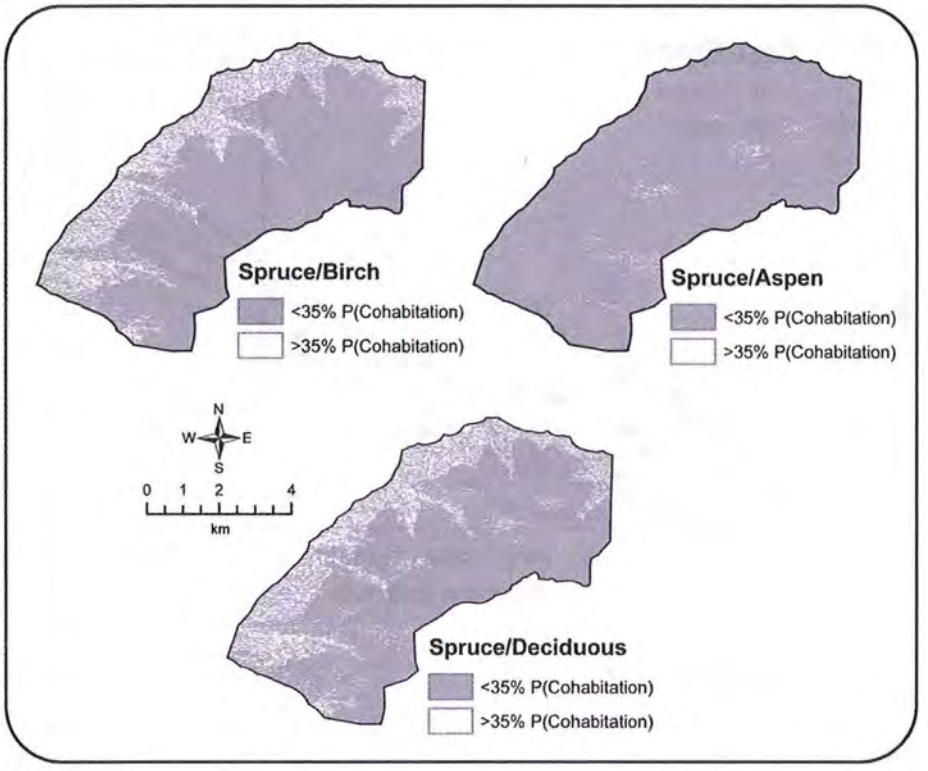
Fig. 7. Cartographic representation of Fig. 6 showing areas where species-dominance relay is possible.



of the species-dominance relay pathway comes from the two birch - black spruce stands where we reconstructed canopy history. These were the only two, birch - black spruce stands that were going through species-dominance relay that we were able to find in the study area (Fig. 8). By mapping the boundaries of these two stands on the satellite imagery, we found that together they represent only 15% ± 5% of the total study area.

Inferences from the understory

A third way of assessing the importance of the species-dominance relay pathway is by examining the present compositions of seedling and sapling populations in the understories of different stand types. Black spruce seedlings and saplings are abundant in stands where the current canopy dominants are either black spruce, mixed black spruce - birch, or birch (Fig. 10). In contrast, black spruce is scarce in the understories of aspen and mixed aspen-birch stands. Black spruce regeneration in the understory is spatially highly clumped, possibly because of the importance of layering in recruiting new ramets, so the number of survey quadrats where more than half of the seedlings and saplings are black spruce give a clearer picture of the potential importance of black spruce in the course of future stand development (assuming these stands do not burn). Black spruce is the most abundant understory tree species in about 70% of the area surveyed in three mixed spruce-deciduous stands, in about 50% of the area surveyed in eight birch stands, in about 20% of the area in three birch-aspen stands, and about 15% of the area in four aspen stands. Supporting evidence for the importance of the species-dominance relay pathway in birch stands comes from forest history reconstructed from stumps, logs, and bark fragments. All the birch stands we examined contained evidence for a preceding stand composition including at least some canopy-sized spruce that most likely was black spruce. Based on these results, we speculate that in the absence of fires restarting succession, black spruce would assume canopy dominance at 15% -50% of sites now dominated by birch and aspen trees.

But why are there so many old black spruce trees?

It would make sense that the oldest trees in the forest would be spruce if species-dominance relay was a commonly followed pathway of succession. So if species-dominance relay is a relatively uncommon pathway for succession to take in the study area, why are the oldest trees black spruce (Fig. 9)? The answer is that most of these old black spruce trees are growing in a particular topographic setting within a particular community type with a different fire regime from the rest of the landscapes. Most of the black spruce trees that are >100 years old grow on moist, north-facing slopes as part of wet-acidic, black spruce communities (Hollingsworth et al. 2006) that consist of open-canopied, elfin forest of black spruce growing on peat with an understory of *Sphagnum* moss. In contrast with feather mosses, which readily dry out and readily bum, *Sphagnum* mosses rarely dry out and are difficult to burn. We suspect that fires have difficulty spreading through the moist *Sphagnum* peatlands, allowing the black spruce there to reach relatively great ages.

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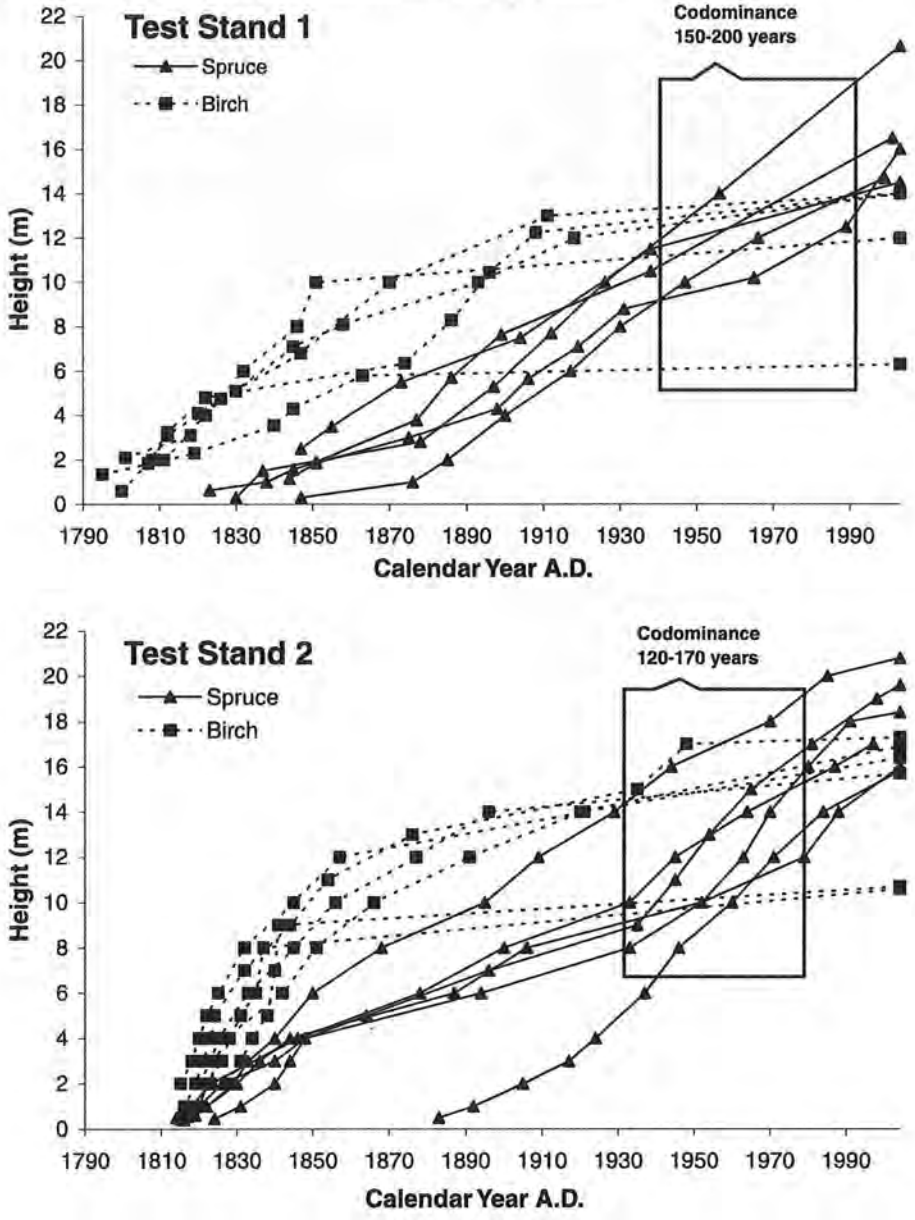
Fig. 8. Reconstructions of interactions between birch and black spruce canopies in two stands currently engaged in species-dominance relay. In these stands, it took approximately 150 years for species-dominance relay to occur.



The prevalence of self-replacement

In contrast with the time dependence of species-dominance relay, the self-replacement pathway results in a forest where most of the species mosaic remains fixed on the landscape regardless of the time since the last fire. Interactions between tree physiology and site conditions rather than time since last fire are the main controllers of stand composition. In this northwest-facing study area, potential summer insolation and altitude alone predict black spruce distribution with results up to 90% probability and predict aspen and birch distribution with probabilities up to 60%. These results are consistent with the existence of strong environmental-physiological controls over tree distribution and with the origin of many stands through self-replacement.

Gap-phase self-replacement and species **replacement**

Based on the tree-age data, there is no evidence that gap-phase self-replacement is a significant successional pathway within aspen and birch stands in the study area. Cumming et al. (2000) found that aspen stands in western Canada begin gap-phase self-replacement starting around 100 years after stand initiation. The rarity of aspen (and birch) trees older than 100 years suggests these stands have not persisted long enough for mortality agents other than fire to become important in opening gaps. It would be interesting to look in detail for evidence of gap-phase self-replacement in the wet-acidic, black spruce communities where the oldest black spruce trees survive. The small stature of these trees, the open canopies of these stands, the rarity of senescent trees,

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Fig. 9. Main graph shows the age frequency of 1059 trees cored in 34 stands. Inset graph shows the mean ages of 16 black spruce stands.

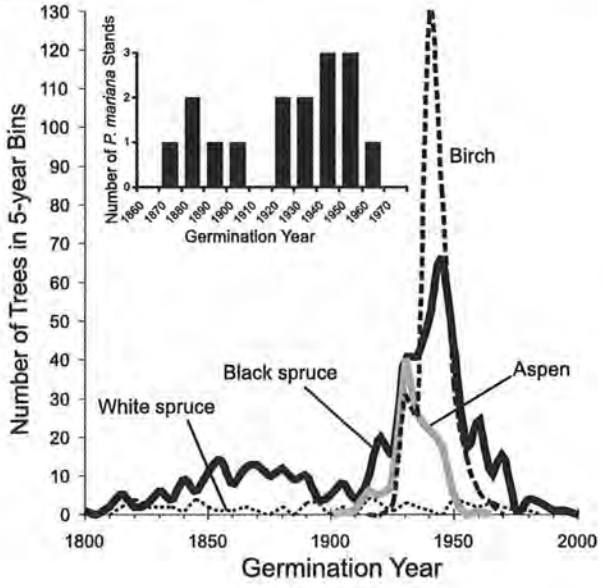
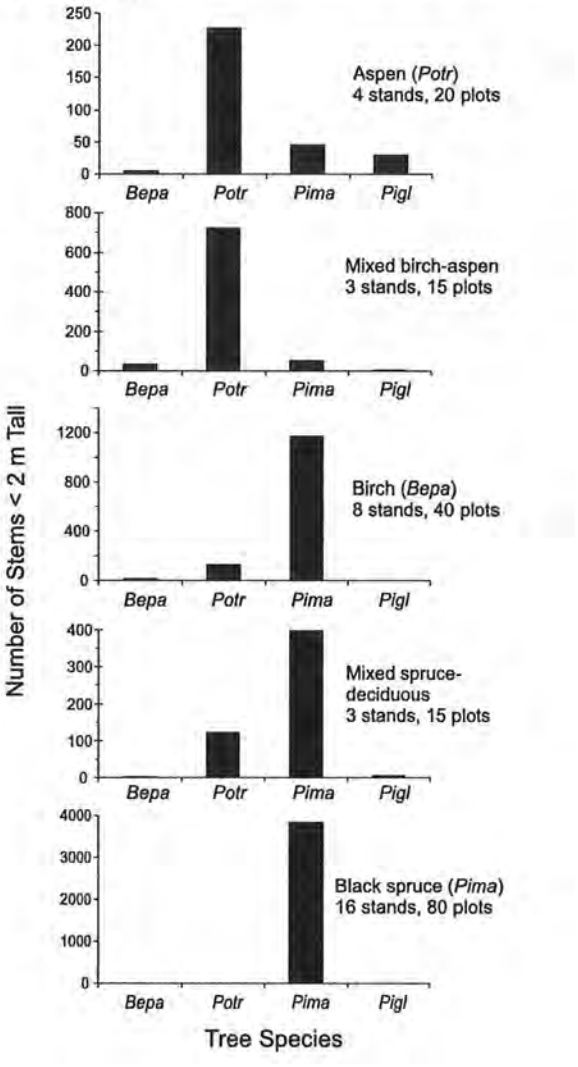


Fig. 10. Regeneration of tree species in the understories of different stand types. Bepa,birch (*Betula papyrifera*); Potr, aspen (*Populus tremuloides*); Pima, black spruce (*Picea mariana*); and Pigl, white spruce (*Picea glauca*).



and the presence of fire-scarred trees all suggest that occasional fires are more important than gap-phase dynamics in determining age structure there. Our data cannot precisely resolve the importance of the fourth successional pathway, species replacement after severe or extensive fires; however, the same arguments supporting the widespread occurrence of self-replacement make it seem unlikely that radical shifts in species composition can occur at many sites on this landscape even after the most severe fires.

How representative is the study area of the Alaskan boreal forest?

Other workers have looked for a predictive relationship between spatial patterns of solar insolation and tree distribution in Interior Alaska and failed to find one (W.S. Armbruster, personal communication 2006), probably because they were looking at south-facing slopes and at altitudes lower than our study area. The link between solar insolation and tree growth should be strongest on colder, north-facing slopes and at higher elevations. If the insolation-tree linkage is indeed weaker on lower elevation terrain with southerly aspects, the self-replacement pathway is probably not as important there as in our study area.

The other issue concerning representativeness involves fire history. There are active gold mines on the lower slopes of Ester Dome today, and mining began in the Fairbanks mining district in 1904. Mining activities in the first several decades of the last century left a distinctive mark on the forest age structure in Interior Alaska (Fastie et al. 2003; P. Duffy, personal communication 2007). Gold miners felled and burned large tracts of forest surrounding their workings, and the typical signature of mining impacts in the forest's age structure is a dearth of trees surviving the first 20-30 years of the 20th century followed by a surge in tree recruitment starting in the 1930s (when gold prices fell). The age-frequency graph of trees in our study area (Fig. 9) matches this general pattern. This suggests that the forest stands we see today, with the possible exception of steep, north-facing elfin forests of black spruce, may have more young trees than is normal for a "natural" forest in interior Alaska. Something similar is suggested by the fragmentary evidence provided by the prefire forest composition of the 40 quadrats in birch stands. The presence of both birch and black spruce in these stands at the time of the last fires suggests that fire had been absent long enough for species-dominance relay to be underway. An anthropogenically heightened fire frequency of the early 20th century could partly explain why stands that have followed a successional pathway of species-dominance relay are so rare today in our study area.

On the other hand, the concept of a "natural" fire regime is a deceptive abstraction in light of the variability of climate, even prior to the onset of anthropogenic warming. The reality is that fire frequency, natural or not, has in-

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creased over the last several decades (Flannigan et al. 2001; Duffy et al. 2005) and will probably continue to increase as climate warms (Soja et al. 2007). This combination of more frequent fires and an overall warmer landscape will probably favor self-replacement on the warmer sites where aspen and birch grow today, and, at the same time, allow aspen and birch to invade what were formerly the cooler, spruce-only sites.

Conclusions

Self-replacement has been the most frequent successional pathway in our study area over the last century at least, and this is probably for several reasons. The low sun angles typical of this high latitude region create sharp gradients in air and soil temperatures when superimposed onto steep topography. When combined with relatively high elevation and a northerly exposure, these sharp temperature gradients create a pronounced environmental mosaic, certain parts of which best suit the establishment, growth, and reproduction of certain tree species. Black spruce thrives in the highest, shadiest sites; birch grows best at lower, warmer sites; and aspen is restricted to the sunniest sites. After a fire, each of these species tends to re-establish itself at the sites within their physiological optimum. Species-dominance relay and species replacement are possible only at sites where the physiological tolerances of different tree species overlap. The main zone of overlap is the shadier, higher elevation parts of the birch zone where black spruce can establish beneath birch canopies; however, even at these sites where species-dominance relay is possible, the completion of this pathway requires that fires are absent for > 100 years, which seems to have rarely occurred in the study area during the last century and may be even less likely to occur during the next century. Gap-phase self-replacement, which is a possible but still undemonstrated successional pathway in aspen and possibly birch stands in Alaska, similarly requires a fire-free interval > 100 years and so is unlikely in the study area. Already the predominant successional pathway today, self-replacement is likely to become even more common as climate warms, fire frequency increases, and the distributions of aspen and birch expand at the expense of black spruce,

Acknowledgements

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