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ARTICLE

Nonlinear responses of white spruce growth to climate variability in interior Alaska

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Abstract: Ongoing warming at high latitudes is expected to lead to large changes in the structure and function of boreal forests. Our objective in this research is to determine the climatic controls over the growth of white spruce (*Picea glauca* (Moench) Voss) at the warmest driest margins of its range in interior Alaska. We then use those relationships to determine the climate variables most likely to limit future growth. We collected tree cores from white spruce trees growing on steep, south-facing river bluffs at five sites in interior Alaska, and analyzed the relationship between ring widths and climate using boosted regression trees. Precipitation and temperature of the previous growing season are important controls over growth at most sites: trees grow best in the coolest, wettest years. We identify clear thresholds in growth response to a number of variables, including both temperature and precipitation variables. General circulation model (GCM) projections of future climate in this region suggest that optimum climatic conditions for white spruce growth will become increasingly rare in the future. This is likely to cause short-term declines in productivity and, over the longer term, probably lead to a contraction of white spruce to the cooler, moister parts of its range in Alaska.

Résumé : Le réchauffement en cours aux latitudes élevées devrait entraîner d'importants changements dans la structure et la fonction des forêts boréales. Cette recherche avait pour but d'identifier les facteurs climatiques qui régissent la croissance de l'épicéa blanc (*Picea glauca* (Moench) Voss) présent aux extrémités les plus sèches et les plus chaudes de son aire de répartition à l'intérieur de l'Alaska. Nous avons ensuite utilisé ces relations pour déterminer quelles variables climatiques sont les plus susceptibles de limiter sa croissance future. Nous avons collecté des carottes dans cinq stations sur des épicéas blancs croissant sur des falaises abruptes exposées au sud, en bordure de rivière, à l'intérieur de l'Alaska et nous avons analysé la relation entre la largeur des cernes et le climat à l'aide d'arbres de régression amplifiés. La précipitation et la température de la saison de croissance précédente ont un effet déterminant sur la croissance dans la plupart des stations : les arbres croissent le mieux lors des années les plus fraîches et les plus humides. Nous avons identifié des seuils précis de la réaction de croissance à plusieurs variables, incluant des variables associées à la température et aux précipitations. Les prédictions du modèle de circulation générale au sujet du climat futur dans cette région indiquent que les conditions climatiques optimales pour la croissance de l'épicéa blanc deviendront de plus en plus rares dans l'avenir. Cela est susceptible de causer le déclin à court terme de la productivité et probablement de provoquer à plus long terme le recul de l'épicéa blanc et son confinement dans les parties les plus fraîches et les plus humides de son aire de répartition en Alaska. [Traduit par la Rédaction]

Introduction

Boreal forests cover much of northern Eurasia and North America; of the terrestrial carbon contained in forest ecosystems, roughly half is in the biomass and soils of boreal forests (Dixon et al. 1994). Climate is now changing rapidly in many boreal regions, and significant potential exists for strong biotic feedbacks on the climate system as ecosystems respond to climate change (Chapin et al. 2000). In interior Alaska, the largely forested region between the Alaska and Brooks Ranges, mean annual temperature has risen 1.4 °C (Wendler and Shulski, 2009) and growing season length has increased by three days per decade since 1970 (Euskirchen et al. 2010). Climate warming is likely to cause changes in tree growth, fire regimes, and the geographic ranges of tree species. These changes may in turn give rise to strong feedbacks on the climate system as boreal carbon cycles and land-surface energy budgets change (Chapin et al. 2000, 2005; Hinzman et al. 2005). Understanding how boreal tree species respond to climate warming is thus critical to predicting the future state of ecosystems at regional and global scales.

Predicting the effects of changes in climate on tree growth in a climatically extreme region like the boreal zone would appear, at first glance, to be a relatively simple proposition. In a region where the growing season is often less than 4 months long, warming could be expected to lead to consistent increases in tree growth. However, previous studies of white spruce (*Picea glauca* (Moench) Voss) responses to climate change in Alaska and northern Canada have revealed a remarkably complex response to climate (Briffa et al. 1998; Lloyd and Fastie 2002; Wilmking et al. 2004, 2005; Driscoll et al. 2005; Lapenis et al. 2005; McGuire et al. 2010; Andreu-Hayles et al. 2011; Porter and Pisaric 2011; Ohse et al. 2012). Indeed, climatic controls over tree growth in the boreal forest vary significantly in space and time (Lloyd et al. 2011) and would seem to be characteristically nonlinear (D'Arrigo et al. 2004; Wilmking et al. 2005). Growth responses to climate can vary significantly between individual trees in the same stand (Wilmking et al. 2004), as well as varying within any given individual tree over time (Driscoll et al. 2005; Lloyd and Bunn 2007; Ohse et al. 2012).

Two different explanations have been proposed for the observed temporal variability in the climate response of boreal

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Table 1. Location of study sites in interior Alaska.

Site	Lat.	Long.	Earliest year sampled	No. of trees	Avg. correlation between trees
Alces Bluff	63°49′19.30″N	144°48′26.90″W	1835	29	0.394
Eagle Bluff	64°47′57.64″N	141°11′26.81″W	1854	30	0.466
Nenana Bluff	64°10′13.26″N	149°17′58.62″W	1827	30	0.415
Salcha Bluff	64°28′34.92″N	146°58′28.76″W	1847	20	0.577
Tanana Bluff	63°43′13.00″N	144°08′7.90″W	1751	20	0.384

Note: The earliest year sampled is the inner ring date of the oldest tree sampled, uncorrected for missed pith or core height.

trees: changes in the nature of limiting factors — in particular the increased importance of nonclimatic limiting factors (D'Arrigo et al. 2008) — and nonlinearities or thresholds in growth response to climate (Wilmking et al. 2004). To date the most important threshold effects involve growing season temperature. For instance, for white spruce in northern Alaska, Wilmking et al. (2004) infer that a 12 °C mean July temperature is the critical threshold above which water stress becomes an important constraint and growth declines rapidly. Across the entire region from western tree line along the Bering Sea coast to the continental interior of Alaska, Beck et al. (2011) observe that white spruce ring widths increase as May–July temperatures warm, but only up to 11–12 °C; above that temperature they decline. Although the presence of such thresholds in tree growth can be inferred from analyses of how trees' responses to climate change over time (Wilmking et al. 2004) or space (Beck et al. 2011), new statistical methods are needed to thoroughly explore these threshold responses, and that is what we do here.

In addition to the complications of nonlinearities, boreal forest responses to changing climate are further complicated by the synergistic effects of climate drivers on tree growth, with different combinations of climate and weather causing different growth patterns. A good example of this is the different role that summer precipitation plays in white spruce growth in two topographic settings in Alaska. The growth of upland white spruce is controlled mainly by drought stress resulting from interactions between high summer temperature and low winter precipitation, but with no effect from variations in summer precipitation (Barber et al. 2000, McGuire et al. 2010). In contrast, white spruce growing on floodplains nearby, where groundwater is present at shallow depths and where rooting depths may be correspondingly shallow, respond negatively to summer temperature in a pattern that is presumably also a result of drought stress. Unlike white spruce in the uplands, the floodplain trees are also sensitive to summertime precipitation (Juday and Alix 2012). This floodplain–upland comparison illustrates two important features of white spruce response to climate: tree response to warming can be modified by changes in precipitation, and the expression of this synergy varies according to landscape position. In this study, we describe how white spruce growing at the warmest, driest sites in the Alaskan interior have responded to climate change over the last century. Using a novel application of statistical methods designed for the analysis of nonlinear and lagged relationships among multiple interacting variables, we describe the climatic controls of white spruce at the driest, warmest parts of their subarctic range. We then use these relationships as a basis for predicting how these trees may respond to a warming climate over the next 100 years. Specifically, we address three questions. (1) What are the important climatic controls over white spruce growth at the warmest, driest margins of its range in interior Alaska? (2) What are the thresholds, if any, in growth response to climate? (3) Based on those relationships, how is warming over the next 100 years likely to affect white spruce forests now growing near their physiological limit?

Material and methods

Study area

Interior Alaska is the mostly forested region between the Alaska and Brooks Range. The regional topography consists of broad tectonic basins separated by low mountain ranges and interconnected by rivers. The combination of a diverse topography with low sun angles in summer sets up a complex mosaic of radiative microclimates (Kurkowski et al. 2008), which give rise to a corresponding mosaic of soil microclimates. These soil microclimates influence both the distribution of permafrost and the thickness of the active layer, the upper portion of the ground that freezes and thaws every year. Soil temperature strongly influences vegetation distribution, decomposition rates, and soil – organic horizon thickness (Harden et al. 2006). Interior Alaska lies within the zone of discontinuous permafrost (Osterkamp and Romanovsky 1999), and stand-replacing fires are the most frequent forest disturbance (Viereck et al, 1983). The most abundant tree species in the region is black spruce (*Picea mariana* Mill.), which usually grows on the coldest, wettest soils with the thickest organic horizons. Aspen occupies the warmest, driest sites where the organic mat is thin or absent. White spruce and birch (*Betula neoalaskana* Sarg.) occupy sites that have microclimates and soil characteristics intermediate between black spruce and aspen.

The upper Tanana valley experiences some of the warmest summer temperatures (around 16.6 °C) and lowest annual precipitation <280 mm) in the state (Wendler and Shulski 2009). The climate in this part of Alaska is classified as semiarid based on evapotranspiration estimates (Patric and Black 1968), and this region is the warmest, driest part of white spruce's geographical range in Alaska. The very driest sites for tree growth within the Tanana valley are steep (20°–50°), south-facing hillslopes that owe their existence to erosion by large rivers. They typically rise 50–300 m from floodplains to forested hilltops. Vegetation on these steep slopes typically consists of relatively open forests of white spruce and aspen, interspersed with sagebrush (*Artemisia frigida*) and various graminoids (*Calamagrostis canadensis, Festuca* spp.).

Field methods

We cored 20–30 trees at each of five south-facing river bluffs (Table 1). We systematically chose the largest trees to core, to maximize the temporal extent of the ring-width records. In most cases, our sample represents a complete survey of trees growing on the bluff face, with additional trees cored at the top and bottom of each bluff. There were no significant differences in growth or climate response for trees growing on the bluff face compared to those on the top or bottom, so we pooled all of the trees from each bluff for subsequent analysis.

Tree-ring analysis

Tree cores were mounted, sanded, and measured to the nearest 0.001 mm using a winDendro Image Analysis system (Regent Instruments, Inc.). Tree-ring analysis was completed in R (R Development Core Team 2011), using the package dplR (Bunn 2008). Cross-dated ring-width series were standardized to remove differences in growth rate among individuals, but the series were not detrended. We avoided detrending for three reasons. First, the

Fig. 1. Standardized ring-width indices (solid line) of white spruce trees at five sites in interior Alaska. The running expressed population signal (eps; 50-year window) is shown by the broken line.

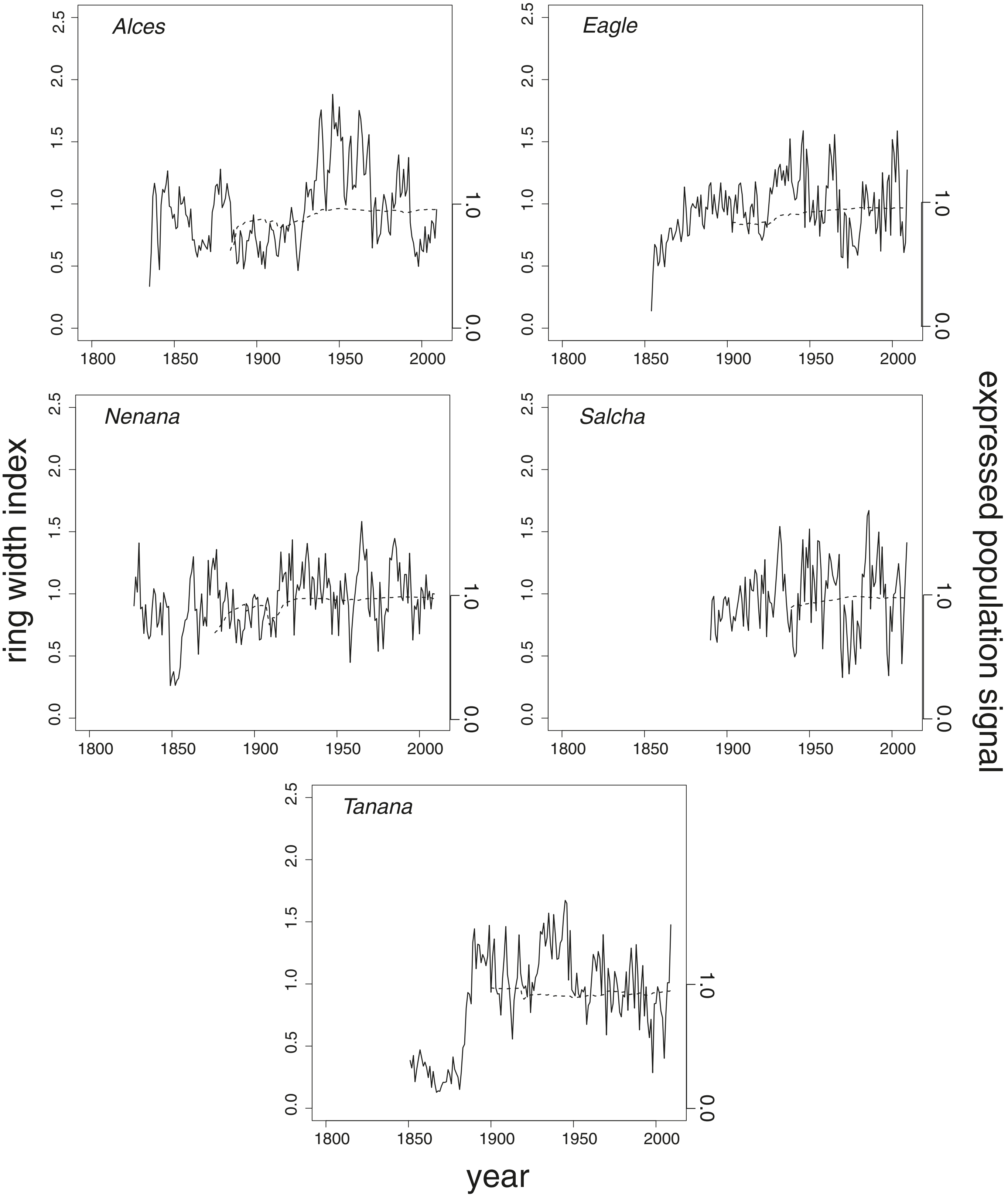


Table 2. Metaparameter values used in the sensitivity analysis.

Metaparameter	Bag fraction	cv folds	Interaction depth	Min. obs. per node
Values considered	0.25, 0.5, 0.75, 1.0	5, 10, 15, 20, 25	1, 2	1, 3, 5, 10
Final value	**0.5**	**15**	**2**	**1**

majority of the ring-width series did not display a significant series-length growth trend, and would have been detrended with a horizontal line. Second, in a handful of cores, detrending with a negative exponential or negative line introduced serious end effects in the most recent decades of the series. Finally, we were interested in preserving as much low-frequency variation as possible. To assess the effects of detrending the data, we analyzed the data on nondetrended (but standardized) series and on detrended series, and found no differences in the outcome of the analysis (data not shown). The uniformity of the tree-ring signal within each site was assessed with the expressed population signal (EPS), using a threshold value of 0.85 (Wigley et al. 1984). We calculated a running EPS for a 50-year moving window (Fig. 1). EPS value for all sites exceeded the threshold of 0.85 during the period for which climate analyses were conducted.

Statistical analysis

The generalized boosting model (GBM) framework was used to construct boosted regression trees (BRT) to quantify the impact of seasonal temperature and precipitation signals on annual tree-ring growth. Elith et al. (2008) and De'ath, (2007) provide a detailed description of the application of these methods to ecological data. A description of the theoretical basis for the GBM framework and algorithms is provided by Friedman (2001). Models were fit using the gbm package (Ridgeway 2010) in the R statistical computing language (R Development Core Team 2011). The climate data were assembled using a 1-km spatial resolution PRISM downscaled version of the Climatic Research Unit 3.1 gridded monthly temperature and precipitation data (Mitchell and Jones 2005; Simpson et al. 2005). These downscaled data and documentation for the downscaling procedure are available at http://www.snap.uaf.edu/data.php. The pixel from this downscaled data set that contained the location for a given site was used as the source for the monthly temperature and precipitation data for each of the five sites. The CRU 3.1 data set has a temporal coverage of 1901–2009; because it was of interest to assess the potential for the previous summer to influence the tree-ring growth for the current year, our analysis began in 1902.

Because of its high latitude and continental-interior location, interior Alaska's climate does not correspond to the typical seasonal cycle of the temperate zone (Olsson et al. 2003). For this reason, we partitioned the annual cycle into ecological seasons based on the natural history of weather and tree growth in interior Alaska. "Summer" is considered to be the months of June, July, and August. It was also of interest to be able to assess the importance of the beginning and end of the growing season; hence, May and September were considered as individual "shoulder" seasons. Based on Olsson et al. (2003), we divided winter into two parts, early and late winter based on precipitation rates and air temperatures. Precipitation in the form of snowfall declines monotonically from October to March when measured by average (across the period of record) monthly total. Temperatures decline between October and January and reach minima in January through March (Olsson et al. 2003). We define October through January as "early" winter and February through March as "late" winter.

Each BRT model was fit with a total of 12 explanatory climate variables. Custom metaparameter settings were used in the construction of the BRT models. The specific metaparameter settings were determined using a simple sensitivity analysis. The goal of the sensitivity analysis was twofold: (*i*) identify the set of metaparameters that maximized the correlation between the observed tree-ring indices and the estimated values generated by the BRT model and (*ii*) define models that are robust with respect to the stochastic component of the BRT. The stochastic component of the BRT models comes from both the random component of the cross-validation and bag fraction values <1 (Friedman 2001; De'ath 2007; Elith et al. 2008).

For continuous data, the choices for the distribution in the BRT model are laplace (absolute error) and Gaussian (squared error), with the latter providing better correlation between the observed data and GBM-based model estimates. The next two values to be considered are the shrinkage (learning rate) and the number of trees. Generally speaking, lower values of the shrinkage result in model estimates with higher correlation to the observed data. There is a point of diminishing returns where lower shrinkage rates result in negligible increases in model performance. We found that a shrinkage value to 0.001 approximated this point of diminishing returns. The shrinkage is also related to the number of trees. The optimal number of trees can be determined by several methods, and we chose the cross-validation method. The word "optimal" is used in the sense of minimizing the predictive deviance. A 15-fold cross-validation (Elith et al. 2008) was used to estimate the optimal number of trees. The maximum number of trees fit was set to 30 000 and the optimal was always less than this value but typically greater than 10 000. While the estimate of the optimal number of trees varied among sites and the BRT model for a given site, the metaparameter settings used for the final models presented here result in analyses that are robust with respect to this stochasticity.

The range of values considered in the sensitivity analysis and the final metaparameter values used in this analysis are presented in Table 2. The correlation between the observed and fitted values was relatively robust to slight changes in the metaparameters; hence, the model for each site was fit using the final metaparameters shown in Table 2. We set the maximum order of interaction considered to be 2 to facilitate ease of interpretation of results and minimize the potential for overfitting not accounted for with the computation of the optimal number of trees. The R-squared values for the site-specific models ranged from 49.7%–68.3% (Table 3).

In addition to its facility in dealing with multiple interacting variables, GBM modeling (including boosted regression trees) allows for the characterization of partial dependence, which quantifies potentially nonlinear and nonmonotonic changes in the response of interest as a function of the explanatory variables. The ability to characterize nonlinear changes in this manner is one of the strengths of the GBM approach. In the present application, the partial dependence plots quantify the changes in the tree-growth index as a function of each of the seasonal climate signals considered. We have also included importance values (Table 4), which show the relative influences of the explanatory variables within the model. The univariate partial dependence plots use a weighted tree traversal method (Friedman 2001) to integrate across the influence of other explanatory variables in the model. Hence, the univariate partial dependence plots show the average change of the response as a function of the explanatory variable of interest.

To assess the potential impact of future climate changes on tree growth, we defined for each month and season the range of temperature or precipitation values at which tree growth was optimum.

Table 3. R^2 values for observed versus predicted values for generalized boosting models (GBMs).

	Site				
	Alces	Eagle	Nenana	Salcha	Tanana
R^2	0.641	0.497	0.637	0.609	0.683

Table 4. Relative influence of 12 climate variables on tree growth.

	Site				
Variable	Alces	Eagle	Nenana	Salcha	Tanana
Prior June–August precipitation	**13.5**	11.0	**13.5**	**24.5**	11.2
Prior June–August temperature	1.8	**14.1**	7.5	7.8	**20.5**
September precipitation	8.0	7.4	9.0	6.7	**12.2**
September temperature	8.3	5.6	8.4	4.6	2.0
October–January precipitation	4.8	8.8	3.3	2.6	7.5
October–January temperature	8.8	**13.2**	8.1	4.2	4.3
February–April precipitation	**11.3**	**12.7**	5.5	2.5	**14.4**
February–April temperature	9.0	4.3	9.2	**17.6**	5.2
May precipitation	**17.0**	5.2	5.8	6.0	2.9
May temperature	8.8	5.0	**19.2**	**13.9**	5.7
June–August precipitation	6.4	6.6	3.0	5.6	4.9
June–August temperature	2.3	6.3	7.5	4.0	9.3

Note: Influences were derived from the generalized boosting models (GBMs). The three most important variables at each site are in boldface text.

These analyses were done on a site-by-site basis, since the optimum conditions varied among sites. These ranges were defined based on the partial dependence plots generated by the GBM models. Those optimum growth ranges were then compared with the distribution of climatic values for each month and season for the time period 2001–2100, based on the average of five general circulation models (GCMs; Walsh 2008). The expected sensitivity of tree growth to changes in that variable at each site was quantified based on two parameters: the relative influence of the variable (as indicated by its importance value in the BRT models) and the vulnerability of tree growth to changes in that variable in the future. Variables whose relative influence exceeded the median importance value at each site were classified as "high importance"; those with relative influences lower than the median were classified as "low importance". Vulnerability was assessed on a categorical scale, based on a comparison of how the distribution of predicted values for that month and season in the future overlapped with the optimum growth range defined by the BRT models (Table 5). The variables most likely to contribute to significant changes in these forests, therefore, would be those that had a large effect on growth (high importance) and whose value was predicted to change in the future, relative to the optimum conditions for growth.

Results

There was relatively high interannual variability in ring width, but with the exception of Tanana Bluff, where tree growth declined since the early 1900s, there were no persistent trends in growth over the 20th century (Fig. 1). Average growth was significantly and positively correlated between all pairs of sites (all $Ps < 0.05$; data not shown). Some aspects of growth response to climate were relatively consistent across all five sites (Table 4 and Fig. 2). Total precipitation during the previous summer and late-winter seasons had a comparatively large influence on tree growth across sites (Fig. 2). Early winter and May precipitation were comparatively less important as predictors of growth, except at Alces Bluff, where May precipitation was the most important influence on growth. Tree growth was more sensitive to temperature and precipitation in the previous summer than in the current summer. Spring and summer temperatures tended to be more influential than winter temperatures: at all sites but Alces, temperature in the previous summer or in May was among the three variables with the highest relative influence. September conditions were generally unimportant, except at Tanana Bluff, where September precipitation had a comparatively large effect on growth.

Despite these similarities, there were important differences among sites in the relative influence of different climate variables. The importance of May conditions, for example, varied substantially among sites: May precipitation was the most important influence on tree growth at Alces Bluff, and was among the four least important influences at Eagle, Nenana, and Tanana Bluffs. May temperature, likewise, had a large influence on growth at Nenana and Salcha Bluffs, and a relatively minor influence at Eagle and Tanana Bluffs. The importance of winter temperature also varied among sites: late-winter temperature was the second most important control over growth at Salcha Bluff, but of low to moderate importance at the other sites.

Tree growth responses to climate tended to be highly nonlinear for most variables, characterized by asymptotic curves with relatively steep thresholds in growth response to climate (Fig. 3). For example, growth at Alces and Salcha Bluffs was relatively insensitive to increases in prior summer precipitation at low precipitation levels (<150 mm) but increased sharply at moderate levels (175–200 mm) of precipitation. Further increases in precipitation above that threshold tended to produce negligible increases in growth. Similar nonlinear responses to precipitation occurred at Alces Bluff (for May precipitation) and Tanana Bluff (for late-winter precipitation). Nonlinear responses prevailed for temperature variables as well: growth was relatively insensitive to temperature at both high and low ranges, but decreased or, in the case of tree response to early winter temperature at Eagle, increased sharply as temperature warmed across a threshold.

Optimum growth occurred at a relatively consistent range of growing season temperatures (Fig. 4). For example, at four of the five sites, growth was highest when summer temperatures in the previous year were less than 12–14 °C; growth declined as temperatures warmed above this point. This temperature range corresponds to the very coolest years of the last 100 years. At Alces Bluff, in contrast, the growth response to summer temperature was positive, with the highest growth occurring at the warmest temperatures, 14–16 °C.

At all sites, growth was maximized in years when May temperatures were below 6 °C. These temperatures correspond to the coolest values experienced during the last 100 years at most sites, and suggest that optimum conditions for growth have been relatively rare. In contrast to the relatively similar optima for spring and summer temperatures, the winter temperatures that were optimal for growth varied widely among sites, occurring at –10 to –15 °C at some sites and –20 °C or colder at others.

The range of precipitation at which growth was optimal varied substantially among sites as well, but at most sites, trees grew best in wet years (Fig. 5). Optimal growth occurred in the wettest quartile of years for almost all sites and during all months. The pattern was particularly striking for prior summer precipitation, where the highest growth occurred in the years with the wettest summer precipitation. Exceptions to this occurred at Nenana and Salcha Bluffs, where optimum growth corresponded to years with moderate early winter (October–January) precipitation, and Eagle, where optimum growth occurred during the years with the lowest May precipitation.

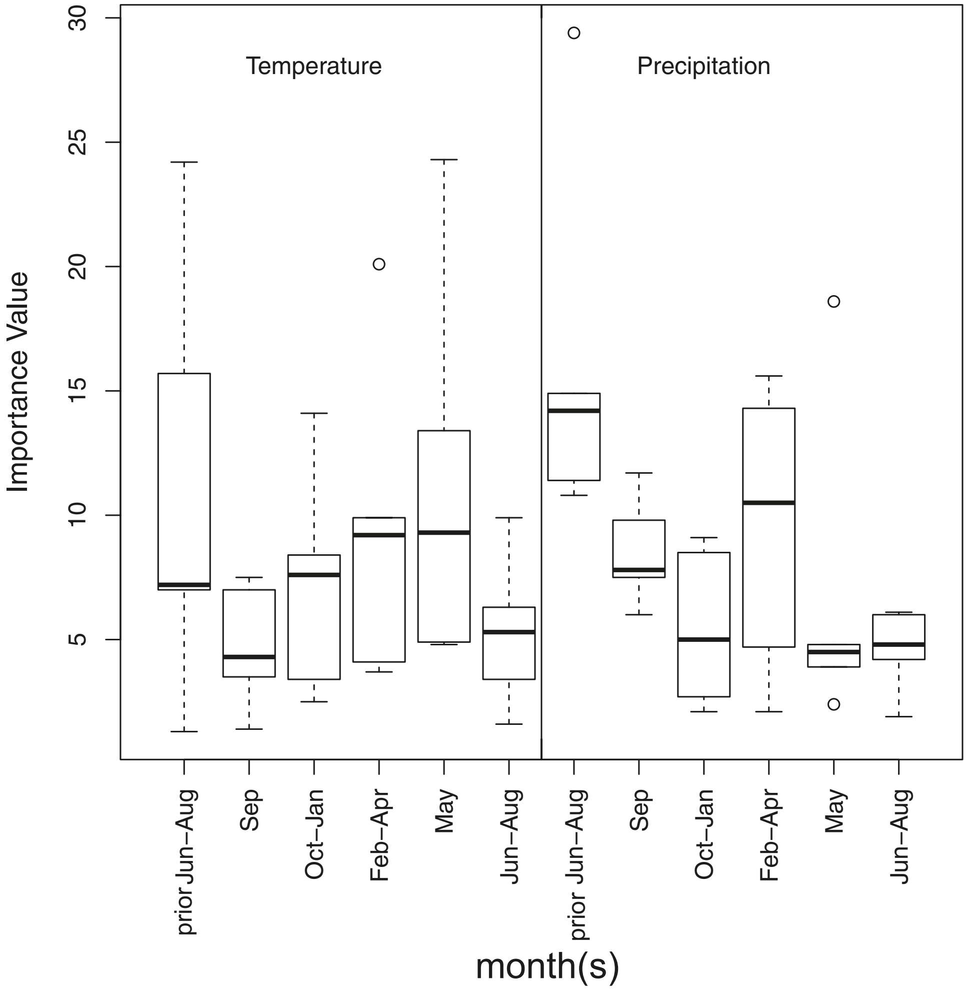
Combining each variable's relative influence (from the BRT models) with its predicted future range and variability allows us to identify the variables that are most likely to be important drivers of forest change at each site (Fig. 6). We defined these potential drivers as variables that had a large influence on growth in the past and whose range is predicted to change enough so that optimal conditions will rarely be encountered in the future. Growing season precipitation (of the previous year) was an important

Table 5. Vulnerability ranking for climate variables.

Temperature		Precipitation	
Category	Upper (warm) limit of optimum range is	Category	Lower (dry) limit of optimum range is
6	Below the minimum of predicted temperature	6	Above the maximum predicted precipitation
5	Between the minimum and the 25th percentile of predicted temperature	5	Between the maximum and the 75th percentile of predicted precipitation
4	Between the 25th and 50th percentile of predicted temperature	4	Between the 50th and 75th percentile of predicted precipitation
3	Between the 75th and 50th percentile of predicted temperature	3	Between the 25th and 50th percentile of predicted precipitation
2	Between the 75th percentile and maximum predicted temperature	2	Between the minimum and the 25th percentile of predicted precipitation
1	Above the maximum predicted temperature	1	Below the minimum predicted precipitation

Note: Vulnerability categories were defined based on the overlap between the optimal range for growth at a site and the predicted distribution of values for the period 2001–2100. Our ranking assumes that trees that prefer cool, wet conditions will be most vulnerable as climate warms and moisture availability declines. The ranking extends from a value of 1 (least vulnerable) to 6 (most vulnerable).

Fig. 2. Median importance values of each climate variable (n = 5 sites). Upper and lower limit of boxes represent the 75th and 25th percentiles and the upper and lower whiskers represent the 10th and 90th percentiles.

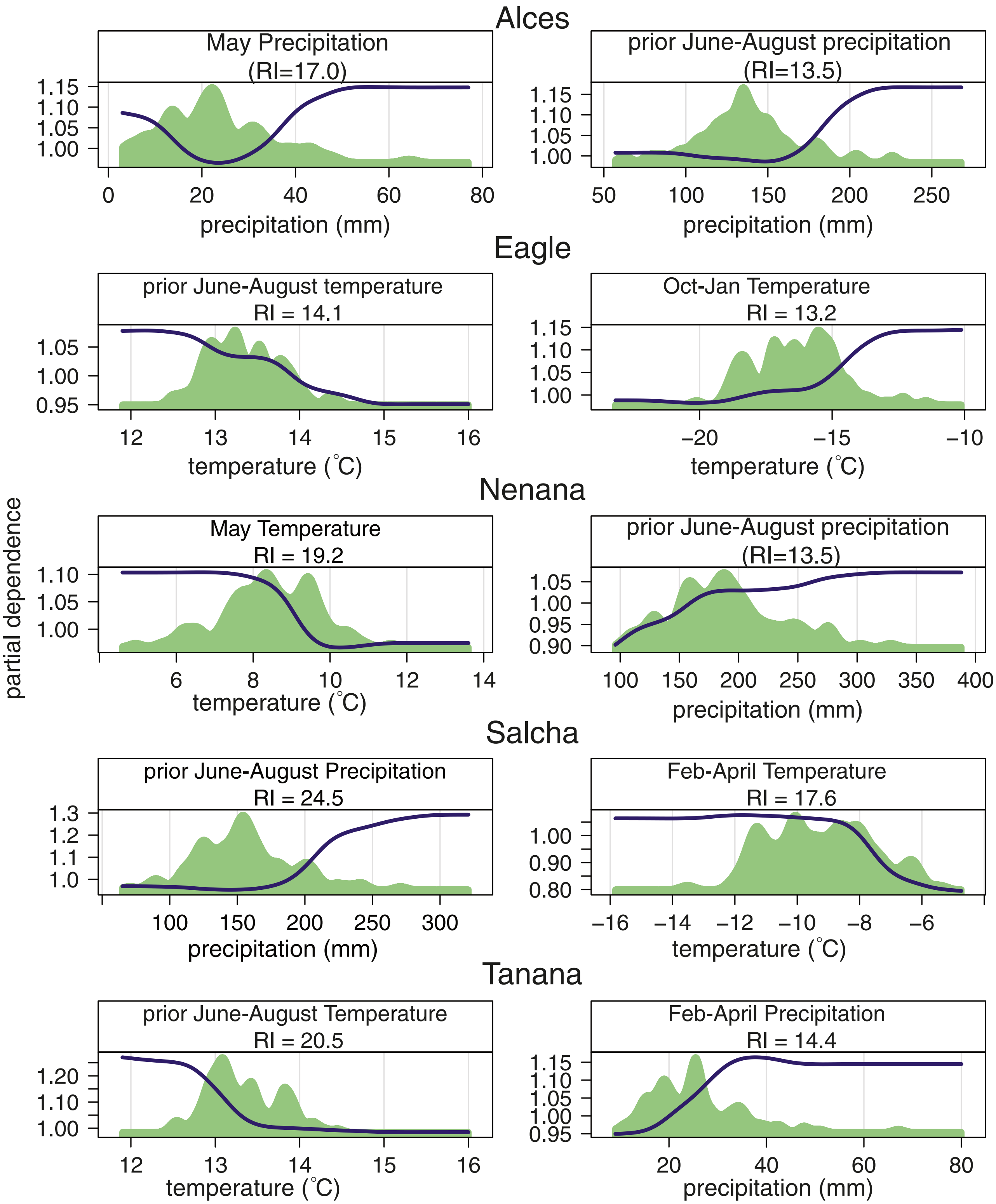


driver of change at all five sites. Temperature in the late winter (February–April) or spring (May) was an important driver of growth at three sites, and summer temperatures (of either the current or previous year) fell in the high importance quadrant at three sites.

Discussion

Our analyses confirms previous research findings that white spruce growing at warm dry sites in the Alaskan boreal forest grow best during cool wet summers (Barber et al. 2000; Wilmking et al. 2004; Beck et al. 2011; Juday and Alix 2012). Growth rates were highest in years when spring and summer were cool and when precipitation was high during the previous summer and — at some sites — during the preceding winter. Despite these common patterns of response to climate, there were differences among sites in the relative influence of different climate variables. These differences are not explained by site location or site topography, and the cause of this heterogeneity warrants further investigation.

Fig. 3. Partial dependence plots for the two variables with the highest relative influence on growth at each site. The solid line in each plot indicates how ring width (*y* axis) changes as a function of the variable in question. The green curves for each plot show the frequency distribution of the climate variable for the period 1902–2009. Early winter is the period from October through January. Late winter is the period from February through April. Summer is June through August. RI, relative influence.



Our most important finding is that, over the last 100 years, the optimal conditions for growth have represented a rare subset of climate conditions. At most of these south-facing bluff sites, optimal growth was reached when prior summer and spring temperatures were in their coolest decile, and prior summer precipitation was in its wettest decile. In most years, growth of white spruce at the warm, dry margins of its range in interior Alaska is thus limited by some combination of excessive temperatures and limited moisture.

Fig. 4. Optimum temperature range for white spruce growth. Green-shaded boxes define the optimum range of spruce growth from the generalized boosting models (GBMs). The box and whisker plots indicate the median (bold lines), the 25th and 75th percentiles (lower and upper edges of the box), and the range (whiskers) of observed or predicted climate conditions. The white box and whisker plots indicate the observed distribution of mean temperature values for each month and season from 1902 to 2009. The red box and whisker plots indicate the projected distribution of temperature values from 2002 to 2100, based on five general circulation models (GCMs; Walsh et al. 2008).

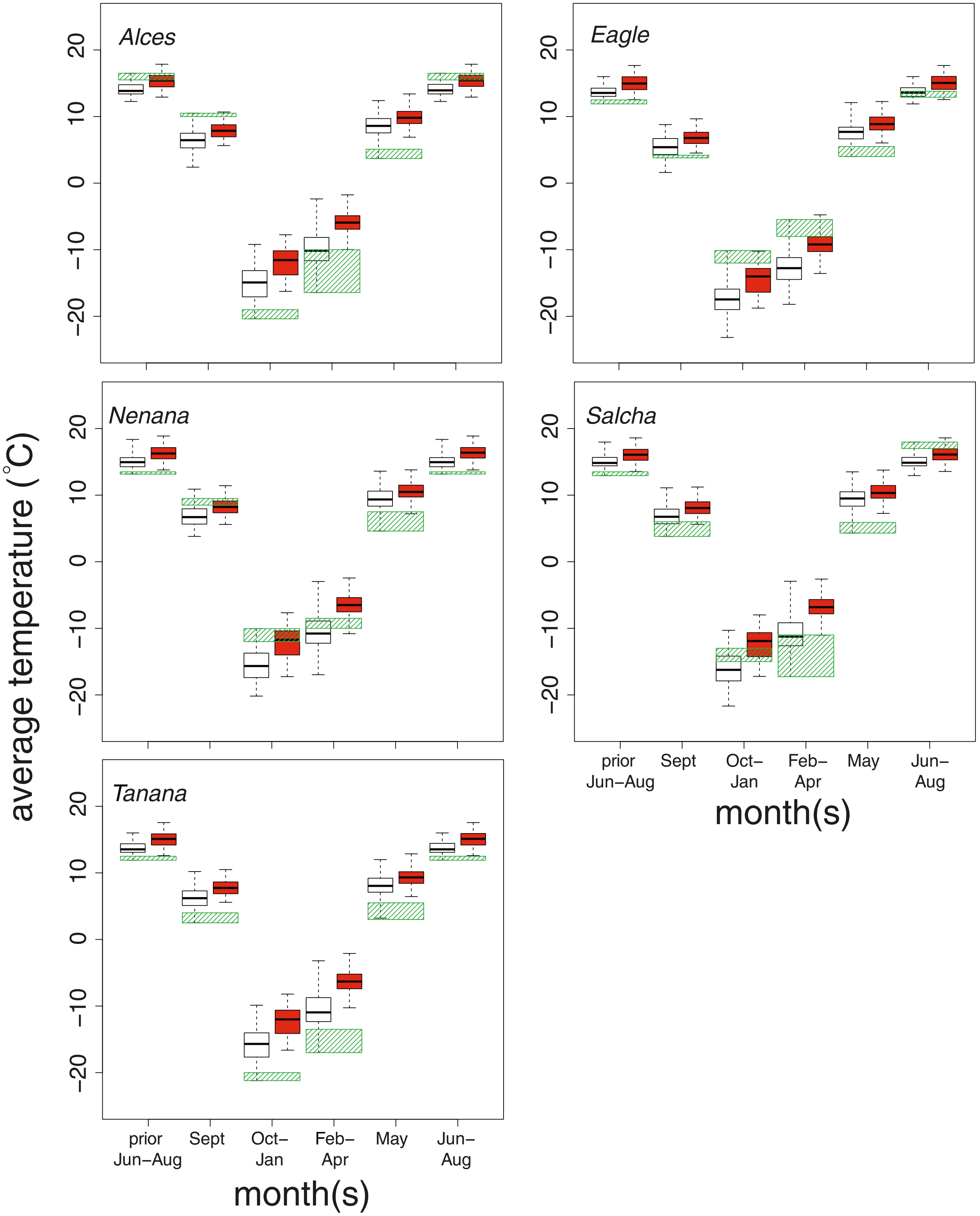


Fig. 5. Optimum precipitation range for white spruce growth. Green-shaded boxes define the optimum range of spruce growth from the generalized boosting models (GBMs). The box and whisker plots indicate the median (bold lines), the 25th and 75th percentiles (lower and upper edges of the box), and the range (whiskers). The white box and whisker plots indicate the observed distribution of total precipitation values for each month and season from 1902 to 2009. The red box and whisker plots indicate the projected distribution of precipitation values from 2002 to 2100, based on five general circulation models (GCMs; Walsh et al. 2008).

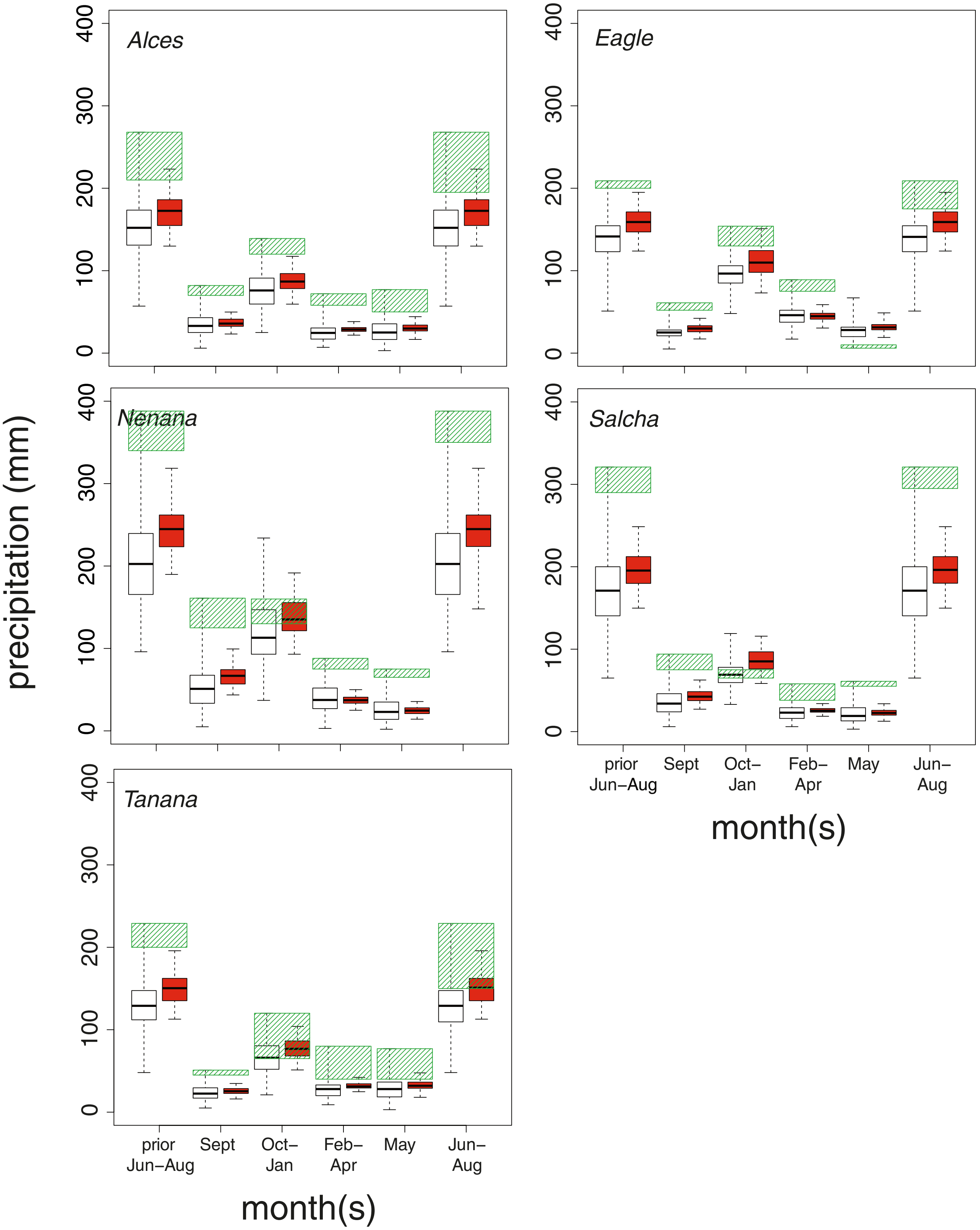
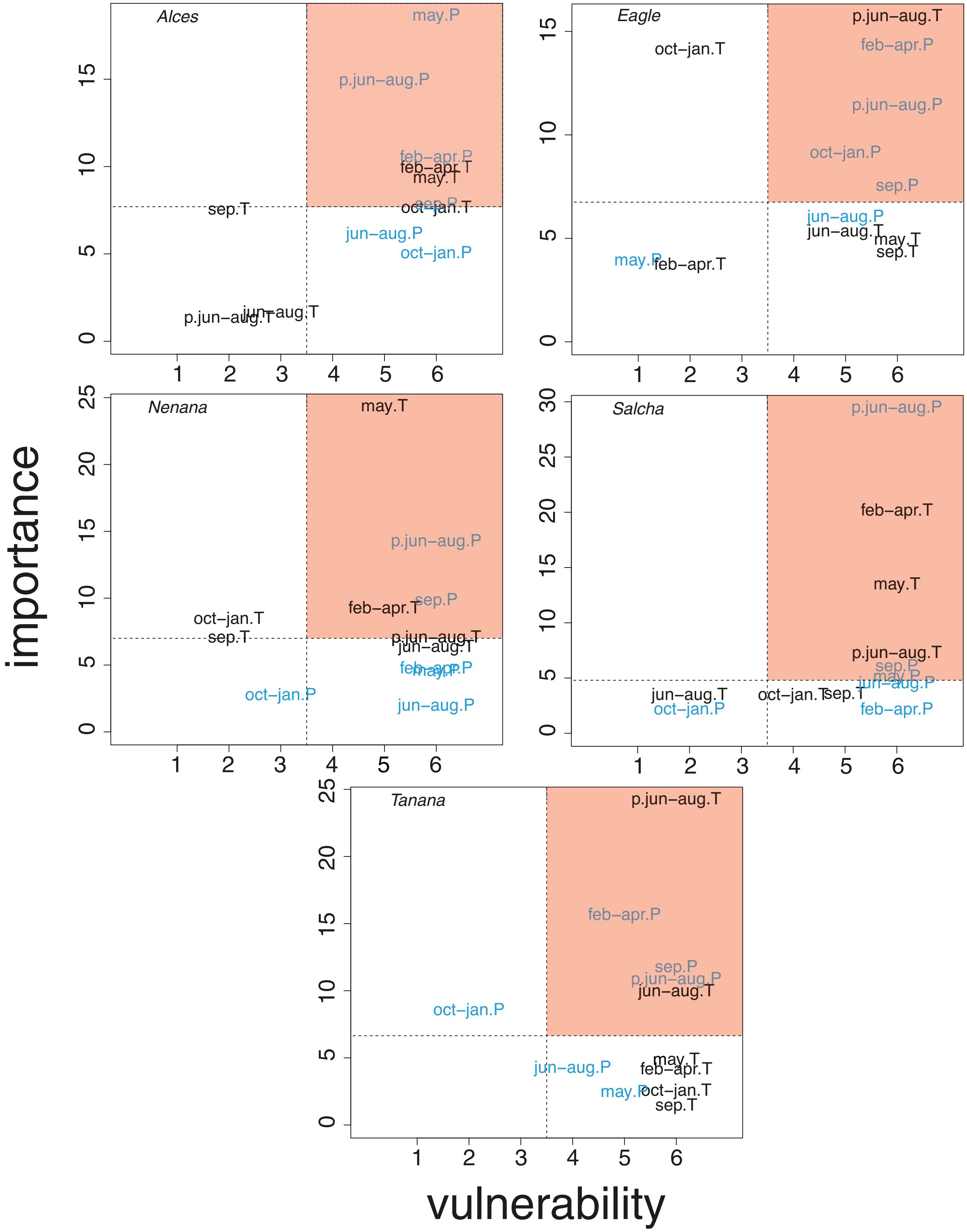


Fig. 6. Variables likely to drive changes in white spruce forests in the future. Importance value indicates the variable's relative influence on tree growth in the generalized boosting models (GBMs). Vulnerability describes the likelihood that thresholds in growth response to that variable will be crossed in the next 100 years (see Table 5 for details). The broken lines indicate the median importance value at that site, or the midpoint on the vulnerability scale. The red square highlights the area in which both relative influence and vulnerability are above the median or midpoint; these are the "high importance" variables. Variable names ending in "P" indicate total precipitation and are graphed in blue text. Those ending in "T" indicate mean temperature and are graphed in black text. Prior summer is distinguished by the prefix "p".



Climatic conditions during the current growing season — the time when cambial activity is actually occurring — were consistently less important than climatic conditions during the 12 months prior to the onset of cambial activity. These lagged responses likely reflect a combination of physiological and environmental carryover effects. In water-limited environments, soil–water recharge is one mechanism that has been long-identified as a potential reason why ring width in a particular year may reflect conditions that occurred prior to the onset of cambial activity (Fritts 1974). Physiologically controlled, lagged responses are also common in conifer species with evergreen leaves and determinate growth (e.g., Fritts (1974), D'Arrigo and Jacoby (1993), Jacoby et al. (1996), Juday and Alix (2012)). In these species, growth integrates the effects of environmental conditions over multiple years. At our sites, precipitation for the preceding year was significantly more important than precipitation during the period of cambial growth.

Although tree-ring data can provide insight into these short-term lags, the effects of longer term carryover from a tree's ontogenetic development remain unknown. For example, Way and Oren (2010) found that trees growing at high temperatures in several different biomes tend to allocate less biomass to roots. These trees may ultimately be more sensitive to drought than a comparable tree grown at low temperatures (Way and Oren 2010). Given that south-facing bluffs are among the warmest microsites in interior Alaska, "architectural" factors like this may exacerbate the drought sensitivity of these trees.

Nonlinear responses of growth to climate were prevalent among the trees we studied; this finding adds to the growing body of evidence suggesting that threshold responses to warming may be widespread (e.g., Way and Oren 2010). Boosted regression models allow us to clearly identify thresholds in growth response to climate and to develop statistical models of growth responses to climate with greater explanatory power than linear statistical models. The prevalence of nonlinear responses to climate has important implications for our understanding of how the boreal forest responds to climate variability, and our ability to identify and describe these threshold responses is crucial for developing accurate predictions of the impacts of warming on the global boreal forest.

The asymptotic growth responses prevalent in our data suggest that growth, while relatively insensitive to a broad range of climate conditions, is likely to increase or decrease rapidly as thresholds in climate are crossed. The form of the growth responses identified in this research are consistent with those proposed by Loehle (1998) who argued that asymptotic growth responses to climate are much more prevalent than the unimodal, or parabolic, responses inherent in most forest growth models (Loehle 1998). The widespread occurrence of thresholds in growth suggests that small changes in climate may have disproportionately large effects on tree growth in interior Alaska.

Two categories of factors may explain the nonlinearities in white spruce's physiological responses to climate: factor-discrete and synergistic climate-forcing factors. Discrete climate factors are revealed in cases where the response threshold is relatively consistent from site to site. For instance, thresholds in tree responses to summer temperature were reached at 12–14 °C at the majority of our sites, and this probably represents a real physiological threshold in growth response to temperature. Such a threshold in growth response to summer temperature is consistent with prior research. Remote sensing analyses have indicated that areas of interior Alaska with summer temperatures in excess of 18 °C have experienced trends of declining productivity (as estimated by NDVI, normalized difference vegetation index) in recent years, while areas with summer temperatures below 15 °C have experienced stable or rising productivity (Parent and Verbyla 2010). Wilmking et al. (2004), similarly, found that the growth of white spruce in the Alaska Range declined steeply when previous July temperatures were above ~12 °C. Unfortunately the relatively coarse geographic and spatial resolution of the existing climate data complicates the identification of the exact values of these thresholds. Our analyses used monthly mean climate data, but the biological basis for tree response to climate probably reflects a much more complex set of climatic parameters — the cumulative effects, for example, of elevated temperatures that persist over several weeks (and across months), or the very discrete effects of short-term excursions above some maximum threshold.

Other growth-response thresholds likely reflect complex synergistic interactions between multiple environmental variables, for instance, between soil and air temperature. At many of our sites, growth decreased abruptly as May temperatures warmed from 5 to 10 °C. Root growth of many conifers is suppressed at temperatures below that approximate threshold (Grossnickle 1988; Lopushinsky and Max 1990; Vapaavuori et al. 1992; Landhausser et al. 2002). In a warm spring (May), air temperature may rise faster than soil temperature, leading to a situation in which the canopy desiccates while roots are still too cold for optimal growth and water uptake.

A better understanding of the environmental controls on cambial activity and xylogenesis may help to elucidate the mechanisms behind the statistical relationships between ring width and climate, and to identify the precise values of both the factor-discrete and synergistic physiological thresholds (e.g., Vaganov et al. 2011). Physiological thresholds in xylogenesis are relatively well-established: xylogenesis in conifers usually commences when minimum temperature rises above 4 °C (Rossi et al. 2008). Cambial division is probably triggered in early summer by a temperature-mediated surge of cytokinin produced in the roots, coinciding with auxin production in the active shoots, which also possesses a sharp temperature threshold (Lupi et al. 2012). Complicating any straightforward linkage between environmental conditions and tree growth are the potentially important modifying effects of cellular stores of previous years' photosynthates and overall nutrient status of the tree (Jarvis and Linder 2000). Likewise, it is unclear how wood production is shut down later in the summer. A potentially important factor that could modify the phenology of xylogenesis is the overall architecture of the tree; for instance, how much of its previous growth a particular tree has invested in roots versus canopy structure. As mentioned earlier, cambial activity and xylogenesis respond to climate on a daily (or even hourly) basis (Evans et al. 2006, Vaganov et al. 2011), and this complicates interpretation of the relationship between annual ring width and more coarsely resolved climate data. Reanalysis using daily climatological data, or data compiled into other submonthly categories, would be helpful in clarifying the physiological basis of the thresholds identified in this analysis.

Together, these findings suggest that warming over the next 100 years is likely to lead to significant changes in white spruce stands now growing at the warm, dry end of the species' range in interior Alaska. Our results are consistent with other studies that have shown a northward shift in the optimal climate for boreal species in recent decades. For example, Gray and Hamann (2012) concluded that, as a result of the warming that has already occurred, suitable habitat for white spruce in the boreal forest had shifted northwards by 207 km since 1960. Our study is able to identify those key variables most likely to drive future forest change in interior Alaska. Forest change is likely to be driven by those factors — primarily summer precipitation and temperature — that are important controls over growth today and for which thresholds are likely to be crossed with increasing frequency in the future. For some seasons, the optimal temperatures for growth do not overlap at all with the GCM-predicted distribution of conditions in the next 100 years. These patterns are reflective of broader trends in white spruce growth throughout the region: combined tree-ring width and remote sensing data indicate that rapid changes in the growth patterns of white spruce are underway right now all across interior Alaska (Beck et al. 2011).

As particularly stressful conditions occur more and more frequently, tree growth is likely to decline and, eventually, a contraction of white spruce forest from these warmest, driest sites seems inevitable, barring adaptive evolutionary changes in thermal tolerance. The potential for the thermal optimum of white spruce to evolve in response to chronically stressful conditions remains unknown. Genetic diversity is relatively high both within and among white spruce populations in interior Alaska (Alden and Loopstra 1987), but given the relatively long generation time of white spruce relative to the rate of climate warming, adaptation seems unlikely to occur sufficiently rapidly to offset temperature and drought-induced stress in the coming years.

The demographic implications of increasing physiological stress inferred here for white spruce growing at dry sites in interior Alaska remain uncertain, as declining growth is not always directly reflected in population-level processes in white spruce populations. For example, tree line white spruce in interior Alaska have experienced declining growth in response to warming temperatures in recent decades (Lloyd and Fastie 2002) at the same time that recruitment has increased and population ranges have expanded in the very same sites (Lloyd and Fastie 2003). Nonetheless, it seems likely that extended periods of unfavorable climate in the future may reduce growth and lead to longer periods of chronically stressing conditions — and perhaps reduced reproduction and recruitment — without producing outright mortality of adult trees.

On the other hand, increasingly long periods of chronic stress may make these trees more susceptible to pests and pathogens, compounding the direct effects of warming on pest populations (Mattson and Haack 1987; Werner et al. 2006; Soja et al. 2007) and predisposing the forests to rapid turnover. Climate change has contributed to the dieback of trees throughout western North America by predisposing trees to insect and pathogen attack by placing trees under acute and (or) chronic physiological stress at the same time that it allows insect and pathogen ranges to expand (Logan and Powell 2001; Millar et al. 2007, 2012; Williams et al. 2010). In interior Alaska, as in many parts of the western USA, warmer, drier summers are also associated with increased fire risk (Kasischke and Turetsky 2006; Xiao and Zhuang 2008). Together, increased fire risk and greater susceptibility to pests may lead to rapid increases in mortality and population turnover at marginal sites like these south-facing bluffs. Models developed in the southern boreal forest, which project a contraction of spruce and expansion of aspen (Hogg 1994; Hogg and Hurdle 1995; Hamann and Wang 2006) may provide reasonable descriptions of likely dynamics in the interior boreal forest. Indeed, a model of interactions between climate change, fire regime, and vegetation in interior Alaska indicated that a conversion from spruce-dominated forest to deciduous-dominated vegetation is possible over the next 50 years in interior Alaska (Mann et al. 2012). In summary, as climate warms in the future, optimal conditions for white spruce growth seem likely to become increasingly rare. This will lead in the short term to declines in productivity, and over the longer term seems likely lead to a contraction of white spruce forests to the cooler, moister parts of their range.

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