Oecologia (2014) 174:665–677
DOI 10.1007/s00442-013-2821-6

PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Climate sensitivity of reproduction in a mast-seeding boreal conifer across its distributional range from lowland to treeline forests

Carl A. Roland · Joshua H. Schmidt · Jill F. Johnstone

Received: 20 August 2013 / Accepted: 28 October 2013 / Published online: 10 November 2013

Abstract Mast-seeding conifers such as *Picea glauca* exhibit synchronous production of large seed crops over wide areas, suggesting climate factors as possible triggers for episodic high seed production. Rapidly changing climatic conditions may thus alter the tempo and spatial pattern of masting of dominant species with potentially far-reaching ecological consequences. Understanding the future reproductive dynamics of ecosystems including boreal forests, which may be dominated by mast-seeding species, requires identifying the specific cues that drive variation in reproductive output across landscape gradients and among years. Here we used annual data collected at three sites spanning an elevation gradient in interior Alaska, USA between 1986 and 2011 to produce the first quantitative models for climate controls over both seedfall and seed viability in *P. glauca*, a dominant boreal conifer. We identified positive associations between seedfall and increased summer precipitation and decreased summer warmth in all years except for the year prior to seedfall. Seed viability showed a contrasting response, with positive correlations to summer warmth in all years analyzed except for one, and an especially positive response to warm and wet conditions in the seedfall year. Finally, we found substantial reductions in reproductive potential of *P. glauca* at high elevation due to significantly reduced seed viability there. Our results indicate that major variation in the reproductive potential of this species may occur in different landscape positions in response to warming, with decreasing reproductive success in areas prone to drought stress contrasted with increasing success in higher elevation areas currently limited by cool summer temperatures.

Keywords Alaska · Bayesian models · Denali · *Picea glauca* · Reproductive ecology

Introduction

Patterns of plant reproduction, particularly those that are sensitive to changing climate conditions, are likely to be a key factor determining the response of species' and biome distributions to environmental change (Morin et al. 2008). We know that reproductive constraints have played an important role in mediating the migration of temperate and boreal tree species in response to climate change in the past (Svenning and Skov 2007), but we still have very limited knowledge from which to predict future responses (Bykova et al. 2012). The challenge of predicting future reproductive constraints is particularly difficult for mast-seeding species, which typically exhibit a high temporal variation in seed production (e.g., Janzen 1976; Kelly 1994) and thus require large datasets to adequately characterize reproductive dynamics (e.g., Crone et al. 2011; Mooney et al. 2011). However, mast-seeding species are also characterized by

---

Communicated by Tim Seastedt.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-013-2821-6) contains supplementary material, which is available to authorized users.

C. A. Roland (✉) · J. H. Schmidt
National Park Service, Central Alaska Network, 4175 Geist Road, Fairbanks, AK 99709, USA
e-mail: carl_roland@nps.gov

C. A. Roland
Denali National Park and Preserve, P. O. Box 9, Denali Park, AK 99755, USA

J. F. Johnstone
Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK S7N 5E2, Canada

synchronous production of large seed crops over large geographic areas (Kelly 1994; Koenig and Knops 1998), suggesting a high sensitivity to climate factors as triggers for episodic seed production. Understanding the future reproductive dynamics of systems dominated by mast-seeding species thus requires an improved understanding of the climate conditions that may drive variability in reproductive output.

Broad patterns of spatial synchrony are characteristic of many mast-seeding species (Kelly 1994; Koenig and Knops 1998); however, this broad synchrony contrasts with evidence from individual species of shifting controls over seed production across environmental gradients (e.g., Mencuccini et al. 1995; Allen et al. 2012). Plasticity in masting behavior and changes in environmental controls over seed production are important elements of understanding the reproductive dynamics of mast-seeding species across real landscapes (Crone et al. 2011). In particular, patterns of seed availability and quality close to ecosystem boundaries or species range limits may play a critical role in determining species distribution limits (e.g., Tremblay et al. 2002).

The boreal conifer, *Picea glauca* (Moench) Voss (white spruce), is a well-recognized mast-seeding species that is distributed across large gradients in climate, from the southern boreal forest to its northern margins at latitudinal and alpine treelines. Given the widespread dominance of this species, it is likely that patterns of *P. glauca* viable seed production have important influences on the patterns of species distribution, forest stand dynamics, and the position of the boreal forest biome. These characteristics make *P. glauca* a good study species for investigation of the factors influencing the dynamics of mast seed production across environmental gradients. Seed production in *P. glauca* is a 2-year process, with reproductive buds initiated upon cessation of shoot growth in the year prior to flowering (Nienstaedt and Zasada 1990). *P. glauca* flowering occurs in the spring of the following year with mature seeds generally formed by late summer, and seedfall from ripened cones commencing in late summer or early fall (Nienstaedt and Zasada 1990). At each stage of the seed production process of *P. glauca*, climatic factors, particularly temperature, have been implicated as important influences on the reproductive process (e.g., Nienstaedt and Zasada 1990; Juday et al. 2003; Gaertner et al. 2011; Krebs et al. 2012).

We used long-term datasets (1986–2011) of seedfall and viability of *P. glauca* in Alaska, USA to test and quantify climate cues that influence *P. glauca* reproduction and to examine how seed production and viability vary along landscape gradients of elevation. In particular, we tested the hypothesis that variations in climate across multiple lag years were significantly associated with patterns of reproductive performance in a given year. We used data from sites spanning productive lowland forest to high-elevation forest to assess whether climatic controls varied across this dominant landscape gradient. Additionally, we used seed viability data from a fine-scale elevational gradient collected during two high-cone-production years (1998 and 2008) to determine whether there were thresholds in seed quality that imply important environmental controls over reproductive potential near the species' elevational limits. Our approach used a conceptual model of the critical climatic cues governing cone and seed production for *P. glauca* in Alaska (Juday et al. 2003) as a point of departure and employed Bayesian regression modeling to quantify the effects of climate and other covariates on seedfall and viability. These analyses yield the first set of quantitative models describing the associations between climate factors and the synchronous, episodic seedfall and viability of this dominant boreal forest tree, and new insights into how the reproductive process is modified across elevational gradients.

Materials and methods

Study area

We collected data at three separate sites located within two long-term monitoring stations in interior Alaska: two sites in Denali National Park (approximately 63.73°N, −148.99°W) and a third at the Bonanza Creek (BNZ) Long-Term Ecological Research (LTER) site, approximately 118 km northeast of Denali and 29 km southwest of Fairbanks (approximately 64.70°N, −148.25°W; Online Resource 1; Fig. S1; Tables S1, S2). We used climate data for the Denali sites from the Denali headquarters climate station (63°43′N, 148°58′W; 628-m elevation) and corresponding data for the BNZ site from the Fairbanks International Airport weather station (Online Resource 1; Fig. S1). Both study sites have a continental climate characterized by long, cold, dry winters with short, relatively warm summers (Shulski and Wendler 2007). Most of the precipitation falls during the warm months in interior Alaska. Denali, located in the mountains, has cooler summers, warmer winters, higher annual precipitation, and greater snowfall than BNZ (Shulski and Wendler 2007).

Plot locations and descriptions

We collected seedfall and viability data from 1992 to 2011 in the Denali sites (Online Resource 1; Figs. S1 S2; Table S1) which included: (1) the Denali forest site (Forest) containing three plots in mature *P. glauca* forest in Rock Creek at 740 m mean elevation; and (2) the Denali treeline site (Treeline) containing three plots in open *P. glauca*-dwarf birch treeline vegetation at 977 m mean elevation. We measured air and soil temperatures at 10 cm depth in the Denali plots during the growing seasons of 2010 up to and including 2012 with Tid-Bit sealed mini-dataloggers (Online Resource 1; Fig. S4).

We used seedfall and viability data from 1986 to 2011 from the BNZ site, which included two plots (FP4A and UP3A) in mature *P. glauca* forest at BNZ near the Tanana River south of Fairbanks at 258 m mean elevation (Online Resource 1; Table S1; Figs. S1 S2). Although seedfall has also been monitored at other sites at BNZ, we used data from FP4A and UP3A because they had consistent and complete seedfall data across the observation period and were directly comparable in terms of *P. glauca* basal area to the Denali Forest site (Online Resource 1; Table S1; Fig. S2). Mean *P. glauca* basal area and mean diameter at breast height (DBH = 1.3 m above ground) of *P. glauca* stems were highest in BNZ, intermediate in the Forest site and lowest in the Treeline site, whereas mean *P. glauca* stem density was highest in the Forest site, and lowest at BNZ (Online Resource 1; Fig. S2; Table S3).

Seedfall

We define seedfall as the number of seeds deposited on the ground per square meter (i.e., seed density). Seedfall was measured using six 0.25-m^2 seed trays placed on the forest floor in each of the three plots in the Forest and Treeline sites from 1992 to 2011 and in the two plots in BNZ site from 1986 to 2011. Seed trays were square wooden frames with interior dimensions of 50 cm × 50 cm, which were lined with fabric and covered with coarse-mesh galvanized hardware cloth to exclude animals. Seed trays were deployed in the fall prior to seedfall and retrieved after snowmelt, usually in May. The contents of each tray were sorted, and *P. glauca* seeds were removed and counted. *P. glauca* seeds were stored in a freezer awaiting germination trials.

Seed viability

We measured seed viability as the proportion of seeds that germinated from a given sample. Seeds were placed in petri dishes lined with filter paper, wetted with distilled water. Following natural cold scarification in the field (BNZ and Denali) and an additional cold scarification in the lab (Denali), seeds were placed in sealed petri dishes. The dishes were placed in a growth chamber at 20 °C with photoperiod of 16 h light and 8 h darkness for 10 days whereupon we tallied the number of seeds that germinated (radicle emergence). In high seedfall years at the BNZ site, a random subsample of seeds from each tray was used in the germination trials ($\geq$100 seeds per tray).

Cone harvests on elevation transects

We harvested *P. glauca* cones at nine sites arrayed on an elevation gradient near the east end of the Denali Park Road in both 1998 and 2008 (Online Resource 1; Fig. S1; Table S2). Four of these sites were visited in both years, including sites in the vicinities of the Forest and Treeline long-term sites and the park headquarters vicinity. We harvested a branch with a southeast growing orientation at random from the upper 2 m of the crown from each of the selected trees and assigned each cone from each branch a unique identifier. Cones were air dried and placed in a freezer prior to processing then measured for length, after which all seeds were extracted from a random subsample of the cones, counted and weighed. Seeds were stored frozen awaiting germination trials for viability which followed the same procedure used for the Denali sites described above.

Model covariates

We considered 12 different climate variables (Table 1) as covariates to explain variation in *P. glauca* seedfall and viability. To investigate the timing and quantity of precipitation and the accumulation of growing degree days (GDD; base temperature 5° C) during the spring and summer periods, we summed these values over different periods representing early and late spring, as well as the entire period from April to August. We retrieved raw climate data from the Western Region Climate Center for McKinley Park (Denali; http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ak5778, accessed 25 April 2013) and Fairbanks (BNZ; http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ak2968, accessed 25 April 2013). We also considered 1- to 3-year lags in these measures to represent prior years' effects on tree condition. We considered the mean minimum temperature observed at each weather station during the period from mid-May to mid-June to represent the effects of cold weather events on reproduction, as well as the number of days with precipitation recorded during the normal pollination period for *P. glauca* (15 May–30 June) to identify possible influences on pollination success. In addition, the effects of mean snow depth and cumulative snowfall at each site were considered based on the hypotheses that heavy snow can mechanically damage incipient cones during the winter prior to flowering (e.g., Juday et al. 2003). The mean basal area within each plot was included in the seedfall models to account for higher abundance of *P. glauca* trees in some plots.

Table 1 Covariates used to model the influence of climate on *Picea glauca* reproductive output from the long-term climate stations at Fairbanks International Airport [for Bonanza Creek Long-Term Ecological Research site (BNZ)] and Denali National Park headquarters area

Variable name	Description (units)	Denali	Fairbanks
PPT April–June	Sum of PPT April–June (cm)	8.41 (±3.73)	5.71 (±2.61)
PPT May and June	Sum of PPT May and June (cm)	7.45 (±3.16)	4.97 (±2.20)
PPT May–July	Sum of PPT May–July (cm)	15.73 (±4.08)	10.47 (±4.12)
PPT April–August	Sum of PPT May–August (cm)	23.63 (±6.29)	15.90 (±5.32)
GDD April–June	Cumulative GDD April–June[a]	269.7 (±51.9)	509.3 (±68.38)
GDD May and June	Cumulative GDD May–June[a]	267.0 (±51.0)	493.09 (±61.87)
GDD May–July	Cumulative GDD May–July[a]	522.4 (±74.6)	872.45 (±82.12)
GDD April–August	Cumulative GDD May–August[a]	695.7 (±110.7)	1,159.61 (±121.63)
MMT early	MMT for mid-May to mid-June	2.82 (±1.03)	7.59 (±1.26)
Snow depth	Mean snow depth on ground 15 October–1 April	36.7 (±19.7)	36.8 (±15.6)
Snowfall	Cumulative snowfall 15 October–1 April	150.1 (±78.3)	146.7 (±69.4)
No. PPT days early	Number of days with measurable PPT 15 May–30 June	17.6 (±3.8)	14.7 (±5.5)
Sum of PPT early	Sum of PPT 15 May–30 June (cm)	6.81 (±3.19)	4.30 (±2.05)

Mean (±SD) values for 1984–2011 are given

PPT precipitation, *MMT* mean minimum temperature

[a] Growing degree days (*GDD*) calculated from base daily mean temperature of 5° C

Statistical analysis

General approach

We conducted the analysis of each reproductive component across all three sites simultaneously. We used Akaike information criterion (AIC) (Burnham and Anderson 2002) to select among competing generalized linear models that contained various combinations of fixed-effects covariates. Due to the large computational burden associated with model fitting and selection in a fully Bayesian framework, model comparison and selection followed a hierarchical process similar to that used by Roland et al. (2013), using a frequentist approach for the model selection process and a Bayesian approach for final model fitting and inference. There was no theoretical reason to suggest that this approach would bias our results; in contrast, it allowed us to both select among large numbers of potential models and accommodate additional sources of unmeasured variation through the addition of random effects. Using the strengths of both frequentist and Bayesian methods helped us to arrive at a more parsimonious model with appropriate measures of precision than would have been logistically possible otherwise.

We began by assuming that our sites were unique (i.e., we used site-specific intercepts). The order of the consideration of additional variables was determined from the expected importance of each set of covariates in each time period based on a priori hypotheses laid out in the conceptual model by Juday et al. (2003). This structured approach allowed us to select the best-fitting combination of fixed effects describing variation in each component, while minimizing problems with correlation among a large number of similar covariates (weather variables across four time lags) and reducing the potential size of the model set to a manageable level. Competing fixed-effects models were fit and selected in the program R 2.14.2 (R Development Core Team 2012). We conducted final analyses in a Bayesian framework using WinBUGS 1.4.2 (Spiegelhalter et al. 2004), adding random effects terms at the appropriate levels to account for overdispersion and dependence in the data. This allowed us to readjust the precision of our parameter estimates to more accurately reflect uncertainty, thereby giving us more confidence in the magnitude and direction of the estimated effects. By including all sites together in each analysis, we were able to use information on covariate relationships across all sites to improve the precision of the estimated effects.

Seedfall

We assumed the seed counts came from a Poisson distribution and used generalized linear models with a log link to describe the effects of covariates on counts for each seed tray in the sample for each site in each year. The model selection hierarchy was informed by the conceptual model for *P. glauca* seed production (Juday et al. 2003) and began by considering combinations of precipitation and GDD variables in the year prior to flowering ($t - 1$), representing conditions during cone initiation that were expected a priori to have a large influence on seedfall observed in the current year (t). After selecting the best combination of precipitation and GDD variables for the initiation year, we considered the additional effects of snow depth and accumulation as well as the number of days with measurable precipitation in May and June. We then selected among combinations of precipitation and GDD in the current year (t), followed by combinations of precipitation and GDD in the 2 years prior to cone initiation ($t - 2$ and $t - 3$). Finally, we used site-level basal area as a covariate describing variation in seed count because seeds were attributable to individual seed collection trays, but not to a specific tree. We also considered a change point trend model which allowed the trend at each site to differ between the period prior to 2004 and 2004 and later. The reason for considering this change point was that the summers of 2004–2005 were the warmest 2-year interval in the observation period for both sites, and we sought to test the hypothesis that trends in *P. glauca* reproductive responses before and after this climatic event were different.

Model selection at each step in the hierarchy was based on a comparison of AIC values and the top model at each step was carried forward. At the end of the selection process, the best overall fixed-effects model was refit in a Bayesian framework with the addition of a site-specific, individual random effect [$\sim N(0, 1000)$] to account for overdispersion and lack of independence among repeated measures of individual trays across years within each of the three sites. All model parameters were assigned uninformed priors [$\sim N(0, 1000)$]. Continuous weather covariates were standardized to have a mean of 0 and a SD of 1 to improve model convergence. This also allowed a direct comparison of the relative importance of coefficients. Using Markov chain Monte Carlo methods, we ran two chains for 1 million iterations each to ensure convergence, discarded the first 500,000 values as burn-in, and thinned the remaining values by 25. The means of the remaining values from the posterior distributions were used as parameter estimates and the 2.5 and 97.5 % values formed the bounds of the 95 % credible intervals. When these intervals overlapped 0 for a variable included in the model, we assumed that there was inconclusive evidence of the effect size or direction and did not interpret those variables further.

Seed viability

Viability data consisted of the number of successes (germinated seeds) and failures (ungerminated seeds), rather than counts. We assumed that these data could be represented by a binomial distribution, and we used generalized linear models with the logit link function to describe the effect of covariates on the probability of seeds germinating successfully. The basic order of variable consideration and model selection followed that of the seed count analyses, with a few important differences. We assumed that snow depth and accumulation, and the basal area of the plot would not have any effect on seed viability. We considered the precipitation and GDD variables, including all lags, as possible predictors along with trends through time as described above. Final Bayesian model fitting followed the process described for the count models above.

Cone harvests on elevation gradient

We used the same basic linear regression approach and model structure for each of four analyses investigating relationships between harvested cone and seed attributes (i.e., cone length, seed number, seed weight, seed viability) and site- and tree-level covariates (i.e., year, elevation, DBH, cone length). Cone length was modeled as a function of year, elevation, and DBH, and assuming a normal distribution. Seed count was modeled as a function of year, elevation, and cone length and assuming a Poisson distribution. Seed weight was modeled as a function of year, elevation, and cone length and assuming a normal distribution. Seed viability was modeled as a function of year, elevation, and DBH assuming a binomial distribution. A random effect at the level of the individual tree was included in each analysis to control for individual tree effects not explained by the covariates. All analyses were conducted in a Bayesian framework using uninformed priors. We only considered a single model for each attribute; however, if the 95 % credible intervals for a given parameter estimate overlapped 0, the magnitude and direction of the estimate was not interpreted.

Results

Variation in climate

Annual patterns in summer temperature (i.e., GDD) and early season precipitation sums in Denali and BNZ showed broad similarities across the observation period for this study, although they clearly differed in absolute terms with Denali being consistently cooler and frequently wetter during the growing season than the Fairbanks area (Table 1; Online Resource 1; Table S4; Figs. S3, S4). Higher annual snowfall and deeper snowpacks were observed in Denali as compared to Fairbanks over the period (Table 1). Summer soil temperatures were higher at BNZ and Treeline than in the Forest site and soils warmed earlier in the spring at BNZ (Online Resource 1; Fig. S4; Table S4).

Seedfall

Seedfall summary

Mean annual seedfall (±SE) for the three sites over their respective observation periods was 428 ± 63, 338 ± 43, and 18 ± 2 seeds m^{-2} for the BNZ, Forest and Treeline sites respectively, with corresponding coefficients of variation for

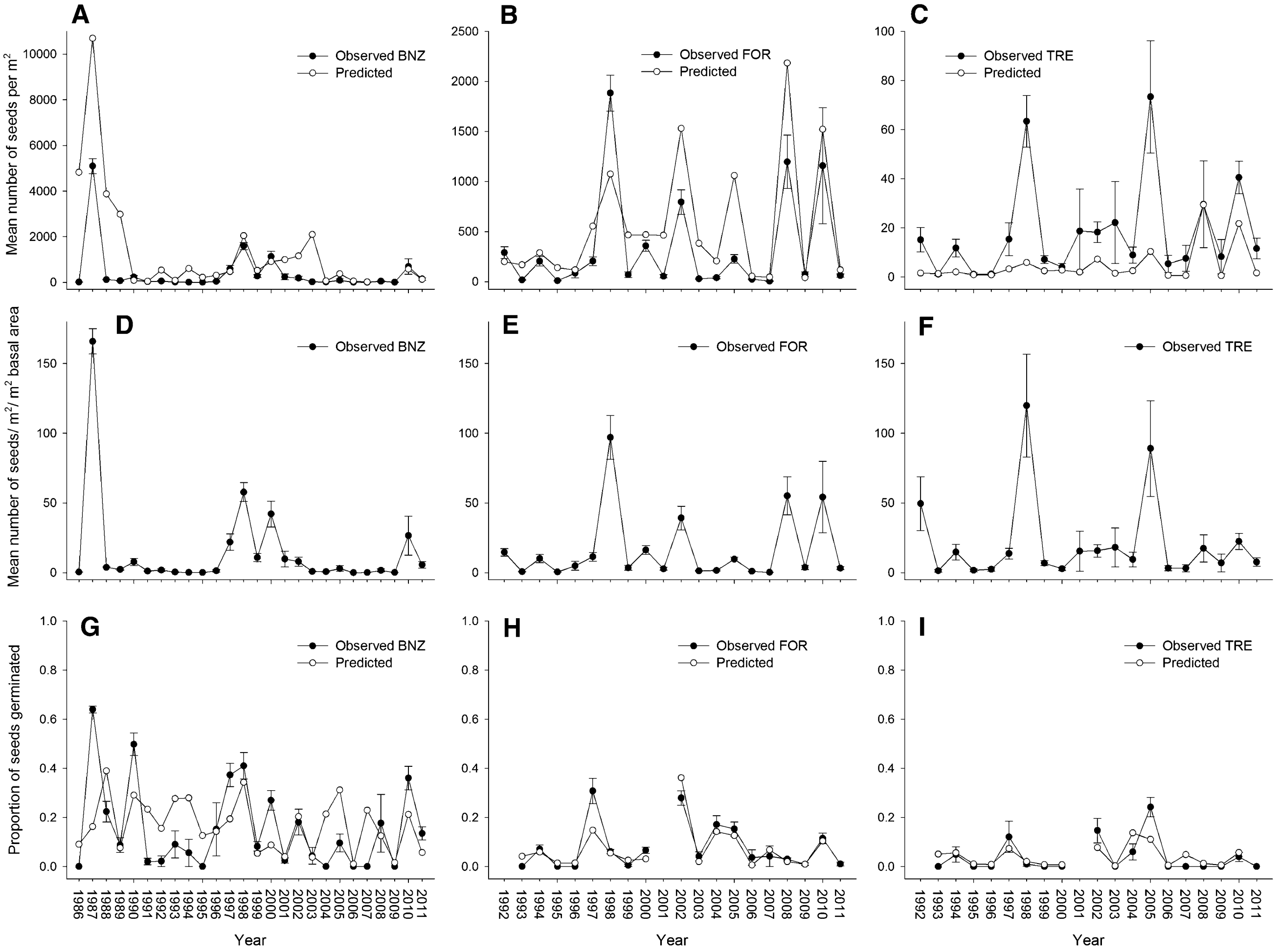

Fig. 1 Plots showing the observed (±SE) and predicted (based on generalized linear models) annual variation in mean seedfall m^{-2} (**a**–**c**), mean seedfall m^{-2} normalized by plot *Picea glauca* basal area (**d**–**f**) and seed viability (proportion of seeds germinated; **g**–**i**) for the Bonanza Creek Long-Term Ecological Research site (*BNZ*; *left column*), Forest (*For*; *middle column*) and Treeline (*TRE*; *right column*) study areas. Note: the *y*-axis scaling of the mean number of seeds m^{-2} differs among the three different sites

annual seedfall of 2.4, 1.5, and 1.1 for these sites. Mean annual seedfall for BNZ for the period 1992–2011 (corresponding to the time frame of the Denali dataset) was 258 seeds m^{-2}. When expressed as seeds m^{-2} m^{-2} *P. glauca* basal area, values were quite similar across sites: 15 seeds m^{-2} m^{-2} basal area for BNZ, 17 seeds m^{-2} m^{-2} basal area for the Forest site, and 21 seeds m^{-2} m^{-2} basal area for the Treeline site over their respective observation periods. There was high variation in mean annual seedfall both among years and among sites (Fig. 1a–f). The highest value in BNZ occurred in 1987 (5,098 seeds m^{-2}), followed by a 10-year period of very low mean annual seedfall. All three sites showed some similarities in annual patterns (Fig. 1a–f) with the strongest positive correlation between pairs of mean annual seedfall values were for the BNZ and Forest sites, followed by Forest and Treeline, and the least similarity in the seedfall values between BNZ and Treeline (Online Resource 1; Table S5).

Statistical model for seedfall

Our models indicated that higher precipitation and lower GDD sums were positively correlated with seedfall for all years (t, $t-2$, $t-3$) except for the cone initiation year ($t-1$) in which relative aridity and warmth were correlated with increasing seedfall (Table 2; Figs. 2a, 3). Annual seedfall was also negatively influenced by high total snowfall in t and $t-1$ and by increasing number of days of early season precipitation in t (Table 2; Fig. 2a). Intercepts for the BNZ and Forest sites were not different, but were both significantly higher than Treeline (Table 2). Seedfall estimates declined at similar rates through time for all sites and time periods (Online Resource 1; Table S6).

When we plotted the $t-1$ values for April–June precipitation and May–July GDD sums in Forest and BNZ for each year in the observation period, there was a clear

Table 2 β-estimates from Bayesian models of seedfall and seed viability in Denali and BNZ, Alaska

Attribute	Seedfall	Viability
Reduction in deviance†	0.72	0.70
BNZ intercept	7.17^{a}	−4.99^{a}
Forest intercept	5.08^{a}	−3.92^{a}
Treeline intercept	1.78^{b}	−1.88^{a}
Warmth in the current year (t)	GDD May–July −1.03	GDD May–July +1.83
Warmth 1 year prior ($t - 1$)	GDD May–July +0.67	GDD April–June +0.58
Warmth 2 years prior ($t - 2$)	GDD April–August −1.11	GDD April–August −0.81
Warmth 3 year prior ($t - 3$)	NS	GDD April–August +0.94
Precipitation sum in t	May–June +0.25	May–July +0.35
Precipitation sum in $t - 1$	April–June −0.47	April–June −0.48
Precipitation sum in $t - 2$	April–August +0.29	NS
Precipitation sum in $t - 3$	April–August +0.52	n.a.
No. PPT days early	−0.30	n.a.
Snowfall in winter t	Total snowfall −0.60	n.a.
Snowfall in $t - 1$	Total snowfall −0.47	n.a.
P. glauca BA in plot	NS	n.a.

Estimates are presented on the log scale for seedfall and the logit scale for viability. All covariates were standardized to have a mean = 0 and SD = 1, so the magnitudes of the coefficients are directly comparable. *Letters* identify sites with significantly different intercept estimates; sites with 95 % credible intervals that do not overlap have *different letters*

BA basal area *NS* non-significant, *n.a.* not assessed; for other abbreviaitons, see Table 1

† Reduction in deviance statistics provide the proportional reduction in deviance of the full generalized linear models regression model as compared to the intercept-only null model

clustering of the 6 highest seedfall years in BNZ corresponding to warmer and drier $t - 1$ initiation years for these high seed crops (Fig. 3). Furthermore, the $t - 1$ conditions for the 2 prior *P. glauca* mast years known for the area [1958 and 1970 (Juday et al. 2003)] also cluster with these larger seed crops from our observation period (Fig. 3). Values from Denali Forest also show a strong tendency to cluster in the lower right quadrant defined by the warm, dry early season conditions in $t - 1$, although the amount of variation in these two parameters among the top 6 seedfall years for the Forest site was larger than for BNZ (Fig. 3).

Seed viability

Viability summary

The highest long-term mean annual germination percentage over the observation period was at BNZ where there was an average of 18 % viable seeds per year (±1.5 %), followed by the Forest site with overall mean annual germination percentage of 8 % (±0.7 %) and the Treeline site with 5 % mean annual germination (±1.0 %). As with seedfall, there was dramatic inter-annual and between-site variation in seed viability, which varied from 0 to 63.9 % at BNZ and 0 to 30.7 % and 0 to 24.2 % for the Forest and Treeline sites, respectively (Fig. 1g–i). Annual estimates for seedfall and seed viability were highly positively correlated for BNZ ($r = 0.73$ over the period 1992–2011; Online Resource 1; Table S5). There was not a similarly high positive correlation in the Forest ($r = 0.18$) or Treeline ($r = 0.49$) sites (Online Resource 1; Table S5). Indeed, high seed production coincided with high seed viability in only 1 year at the Forest site (2002), and similarly occurred once at the Treeline site in the warm, dry summer of 2005 (Table 3). High annual variation in seed viability thus strongly influenced differences in effective annual viable seedfall among these sites (Table 3).

Statistical model for seed viability

Our best approximating model identified current year GDD sum for the May–July period as the strongest predictor of seed viability (Table 2; Fig. 2b). Other significant predictors were GDD sums in $t - 3$ (April–August) and $t - 1$ (April–June) and May–July precipitation sum in t. We identified negative associations between seed viability and warmth in $t - 2$ (April–August GDD) and increasing early season precipitation in $t - 1$ (Table 2) indicating that *P. glauca* seed viability was highest during warm

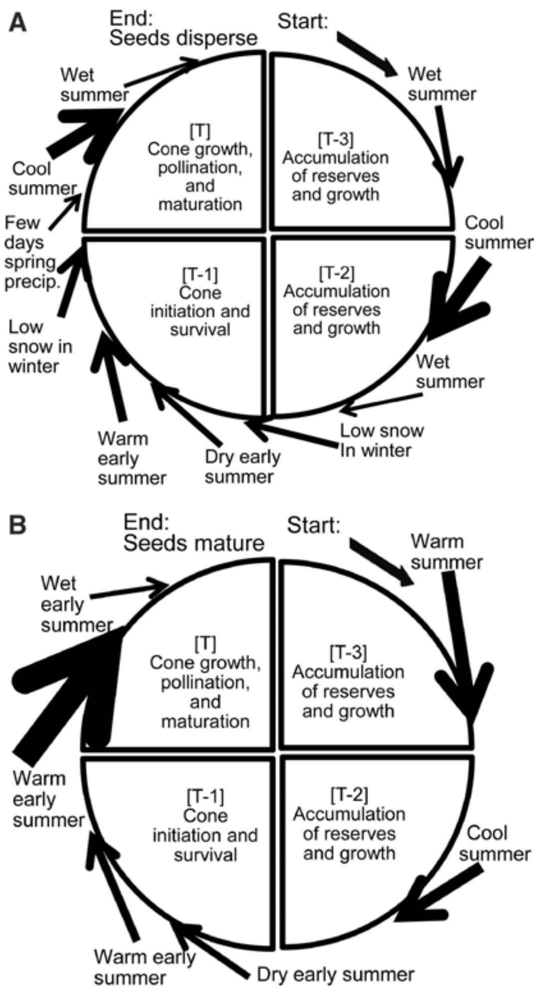

Fig. 2 Diagrams illustrating the results of statistical models predicting the influences of covariates on two facets of *P. glauca* reproduction, over a 4-year period [beginning with current year (*T*) − 3 and ending in *T*]: **a** seedfall, and **b** seed viability. Only significant covariates are included, which have been phrased as positive influences for this figure (thus if seedfall was negatively influenced by summer warmth, the positive equivalent "cool summer" is used here). Each significant covariate is indicated with an *arrow*, with *arrow thickness* indicating the magnitude of influence of the variable (standardized β-coefficients). Consult Table 2 for specific covariates and values for β-coefficients

and wet summers following a warm, dry summer (Table 2; Fig. 2b). Trends in viability were identified for the Forest site (increasing) and BNZ post 2003 (decreasing) only, with viability remaining relatively constant at both Treeline throughout the study and in BNZ prior to 2004 (see Online Resource 1; Table S6).

Cone harvests on elevation gradients

Mean annual *P. glauca* seedfall was relatively high in the adjacent Forest and Treeline plots during the years 1998 and 2008 when we performed cone harvests along elevation transects (Fig. 1). Our models indicated that *P. glauca* cone length, seed mass per cone, and germination probability all declined significantly with increasing elevation for both years (Table 4; Fig. 4). Indeed, at the highest elevations (above 900 m) seed germination was negligible for all sites in both years (Fig. 4). In addition, our results indicated that germination probability and cone length were higher in 2008 than in 1998. Tree DBH was not significantly related to any of the measured cone and seed attributes in the data set.

Discussion

Our study presents the first long-term record for *P. glauca* seed production and viability across an elevation gradient from closed low-elevation forests to treeline stands, and reveals new insights into possible future trajectories for this dominant boreal forest species based on its observed reproductive responses to climate. We identified significantly positive associations between seedfall and increased summer precipitation and decreased summer warmth in all years except for the year prior to seedfall. Interestingly, our seed viability results showed a contrasting set of responses to climate, with significantly positive correlations to summer warmth in all years except for the year prior to cone initiation, and a particularly strong positive response to warm and wet conditions in the seedfall year. Finally, we found substantial reductions in reproductive potential of *P. glauca* at high-elevation sites due to significantly reduced seed viability there. Our results thus suggest potentially diverging trends in reproductive output by stands of *P. glauca* trees in differing landscape positions based on their observed responses to climate.

We found that some of the strongest associations of climate conditions with reproductive performance occurred in the year concurrent with seed production, suggesting that climate factors act as direct constraints on the production and development of seeds while they are maturing. However, we also found significant effects of climate conditions up to 3 years prior to seedfall on both seedfall and viability in *P. glauca*, suggesting that patterns of resource accumulation over considerable time spans also play a major role in driving mast behavior (e.g., Koenig and Knops 2000). In addition, our data support the observation that the degree of interannual variability in seed production varies across the landscape for masting species, and that masting responses are plastic and modified in degree by site-specific limiting factors (e.g., Crone et al. 2011). Finally, although we observed *P. glauca* stands at high elevation producing seeds in similar amounts to lowland stands (per unit basal area), low GDD at high-elevation sites likely results in strongly diminished seed viability in treeline stands. This discrepancy

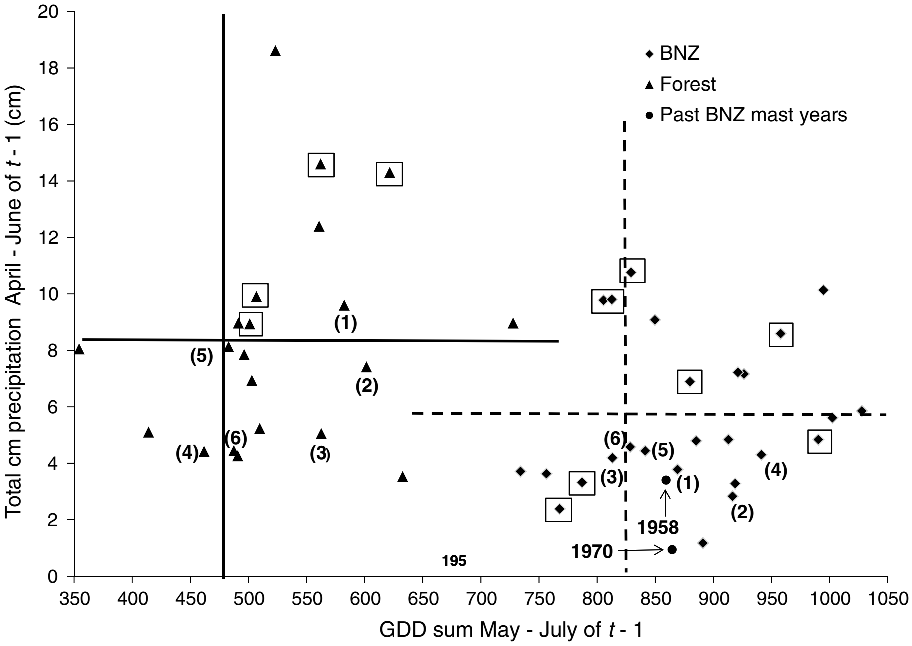

Fig. 3 Plots showing the observed climate conditions in the cone initiation year ($t - 1$) for each year that seedfall was recorded in this study (1986–2011) based upon annual values for precipitation sum in April–June and growing degree days (*GDD*) sum May–July, for the Denali Forest (*triangles*) and BNZ (*diamonds*) sites. The *intersecting lines* indicate the long-term means for each climate variable for the respective sites (1948 to present), with *dashed lines* for BNZ and *solid lines* for Denali. *Numbers in parentheses* are the rank of the mean annual seedfall for the years within the entire observation period, i.e., (*1*) for BNZ represents the $t - 1$ values of the highest mean annual seedfall (1987), and (*1*) in Denali represents $t - 1$ conditions for seed crop of 1998. In addition, the $t - 1$ conditions for the 2 previous mast seedfall years in the BNZ area [1958 and 1970 (see Juday et al. 2003)] are plotted with *circles*. *Symbols* surrounded by a *box* represent $t - 1$ conditions for years with negligible mean annual seedfall values (<25 seeds m^{-2})

Table 3 The mean annual seedfall, germination percentage, and resulting estimated mean number of *viable* seeds m^{-2} m^{-2} for the 4 highest seedfall years recorded at each of three sites examined in this study in Denali National Park and Preserve and BNZ, Alaska

Site	Year	Seeds m^{-2} (±SE)	Germination % (±SE)	Estimated no. viable seeds m^{-2}
BNZ	1987	5,098 (±10)	63.9 % (±1.4)	3,258
	1988	1592 (±7)	41.0 % (±5.4)	653
	2000	1128 (±9)	26.9 % (±4.0)	304
	2010	694 (±14)	36.0 % (±4.8)	250
Forest	1998	1884 (±15)	6.0 % (±8.5)	114
	2008	1197 (±12)	3.0 % (±0.5)	36
	2010	1158 (±24)	11.4 % (±2.1)	133
	2002	795 (±8)	27.9 % (±2.9)	222
Treeline	2005	73 (±34)	24.2 % (±4.0)	18
	1998	63 (±18)	0.0 % (±7.5)	0
	2010	41 (±13)	3.5 % (±1.9)	1
	2008	30 (±16)	0 (±0.0)	0

Table 4 Model results for the relationships between five covariates and *P. glauca* seed germination from cones harvested along elevation gradients in Denali National Park and Preserve during 1998 and 2008

Covariate	Cone length	No. seeds per cone	Total seed mass per cone	Germination probability
Elevation	−	0	−	−
1998	−	+	+	−
2008	+	−	−	+
Tree DBH	0	0	0	0
Cone length	n.a.	+	+	0

+ Indicates a significant positive association with germination probability, − indicates a significant negative association, *0* indicates no significant association with germination probability

DBH diameter at breast height

between production and viability has important implications for predicting the dynamics of this species across the landscape in the context of a warming climate, particularly if warming results in high-elevation sites consistently crossing a GDD threshold for achieving substantial seed viability. Conversely, our results suggest the possibility of a divergent trend at lower elevations, where the positive influence of precipitation on both *P. glauca* seedfall and viability, and negative influences of GDD on seedfall in t and $t - 2$, suggest that lowland stands may experience declines in reproductive potential if future warming increases the frequency of drought stress episodes.

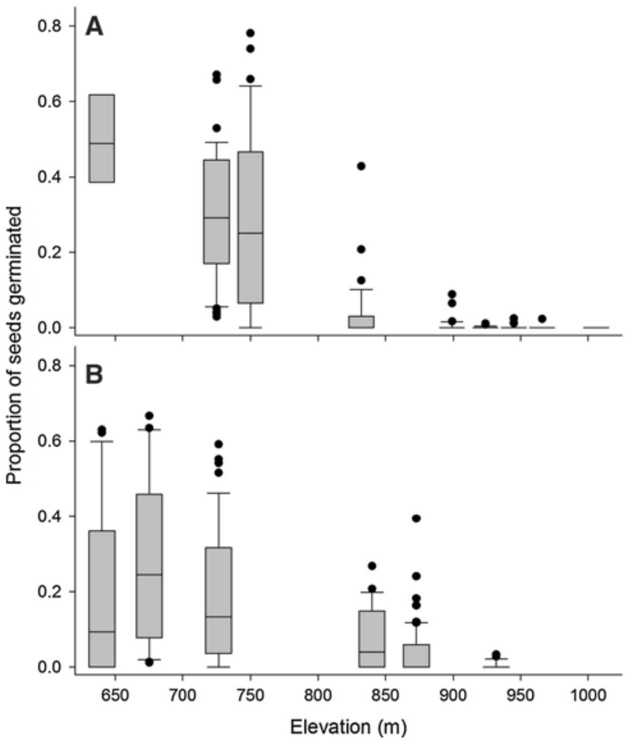

Fig. 4 Box-and-whisker plots for proportion of seeds germinated from *P. glauca* cones harvested along elevation transects in Denali National Park and Preserve, 1998 (**a**) and 2008 (**b**) showing median, quartile values and outliers for seed germination percentage by site. *Individual values* represent mean proportion of seeds germinated per cone. Note: values for sites that were separated by fewer than 20-m elevation were combined for this figure

Climate sensitivity of *P. glauca* reproduction

Climate factors in the year prior to seedfall may act as direct triggers of reproductive bud initiation, while conditions in the year concurrent with seedfall may affect the development and successful maturation of those buds. We found that early season drought and warmth in $t - 1$ were significant predictors of increased seedfall. This pattern accords with previous work suggesting that summer warmth and aridity in year $t - 1$ are important triggers of mast seed production in *Picea* (Nienstaedt and Zasada 1990; Selas et al. 2002; Juday et al. 2003; Krebs et al. 2012). However, we identified *negative* effects of year t summer warmth on seedfall (see also Krebs et al. 2012), and *positive* effects of year t summer precipitation on both seedfall and viability. Negative effects of warm summer conditions and positive effects of summer precipitation on reproductive attributes in the concurrent year may indicate that summer drought stress affects the capacity of trees to allocate resources to a rapidly growing and physiologically demanding new cone crop. Several studies have documented negative responses of *P. glauca* radial growth to summer warmth in interior Alaska (e.g., Barber et al. 2000; Wilmking et al. 2004; Juday and Alix 2012), a pattern that has been attributed to heat-induced drought stress (Barber et al. 2000). Somewhat incongruously, our analyses indicated that high numbers of days with precipitation within the May–June pollination window of year t was a negative influence on seedfall. This pattern is consistent with the hypothesis that prolonged wet weather may diminish pollination efficiency by removing pollen from the air thus reducing transmission of pollen to female cones (Juday et al. 2003).

We found evidence of significant lagged effects of climate in years $t - 2$ and $t - 3$ on reproductive output, a relationship that is considered to be indicative of within-tree patterns of resource accumulation and allocation trade-offs (e.g., Koenig and Knops 1998). Moist and/or cool conditions during the $t - 2$ and $t - 3$ growing seasons were important positive influences on *P. glauca* seedfall in year t. Cool and moist conditions in lag years may allow for the accumulation of energy or nutrient reserves through the alleviation of drought stress or by reducing cone initiation (thus reducing current year expenditures). Furthermore, our data show high seedfall years are followed by very low years in almost all cases, consistent with the hypothesis of resource depletion (Koenig and Knops 1998). Although initial hypotheses linked lagged climate effects with resource allocation of carbohydrate reserves, recent observations indicate that stored carbohydrates are not necessary for fruit and seed production in masting angiosperm trees (Hoch et al. 2013; Ichie et al. 2013). However, depletion of other limiting resources, such as nitrogen and phosphorus, has been associated with years of high seed production in mast-seeding conifers (Sala et al. 2012). Under both hypotheses, acquisition of sufficient reserves to support the production of cones and seeds appears to be the central mechanism driving responses to climate conditions in prior years.

Winter snowfall has been suggested as a driver of reproductive output in *P. glauca* (Juday et al. 2003), and we found some support linking winter precipitation to observed reproductive output. Specifically, increasing total snowfall in the winter prior to cone initiation was negatively correlated with seedfall, which suggests that a smaller snowpack may increase the early season drought experienced by trees that stimulates cone initiation, and increasing total snowfall the next year (during the winter prior to seedfall) was negatively correlated with seedfall, indicating a possible role in snowloads in affecting seed production by damaging incipient cone crop or through some other mechanism (e.g., Juday et al. 2003).

Very few studies of masting behavior have examined interannual variability in seed quality (e.g., viability) concurrently with seed production over long periods of time as we have here. We found that concurrent-year warmth had the strongest influence (by a factor of 2) on seed viability. Current-year precipitation also had a positive influence on seed viability. Thus, concurrent-year conditions appear to exert a relatively stronger influence over seed maturation and quality (viability) than they do over seedfall numbers. Notably, we found evidence of a GDD requirement for *P. glauca* to produce a viable seed crop in Alaska. Our results confirm earlier, single-year studies that found trees in sites with <670–700 GDD (Zasada 1988) or at >600-m elevation (Zasada et al. 1978) did not produce fully formed *P. glauca* embryos. The 670–700 GDD threshold suggested by Zasada (1988) is routinely exceeded at BNZ, where we observed a high correlation between mean annual seedfall and mean annual viability at BNZ ($R = 0.83$), but is frequently not met in the cooler Denali sites, were we found low correlations between seedfall and viability (Forest = 0.18 and Treeline = 0.49). Importantly, then, even when relatively large seed crops were produced at high-elevation sites, as in 1998, the effective numbers of viable seeds that resulted were quite small due to extremely low viability (6 and 0 % for Forest and Treeline sites in 1998). Our cone harvest results also showed a precipitous decline in seed viability with elevation; above approximately 900-m elevation (presumably the coolest sites due to lapse rate), seed viability was negligible in both of the high seedfall years we investigated. A major consequence of GDD limitations on seed viability is a mismatch between viability and production that occurs in cooler or higher elevation sites that has also been observed in several other conifer species (Zasada et al. 1992).

Spatial and temporal variation in reproductive output

P. glauca has long been recognized as a mast-seeding species (Kemp and Keith 1970; Juday et al. 2003; Krebs et al. 2012); however, the degree of synchrony among individuals varies with distance (Lamontagne and Boutin 2007). *P. glauca* stands in our study generally conformed to the expected episodic pattern of reproduction and showed similar concurrent timing of high and low years across the observation period, particularly in the BNZ and Forest sites. Thus the underlying causes triggering *P. glauca* mast-years likely operate on large spatial scales (Koenig and Knops 1998; Krebs et al. 2012).

Our results revealed that *P. glauca* stands growing in sites with considerable differences in summer climate and winter snowfall produced comparable mean seedfall values (especially when standardized by area and basal area). Thus, even though the values for observed climate parameters differed markedly between BNZ and Denali Forest sites, the relative response in annual seed production by the trees to climate was quite similar. Indeed, high seedfall years occurred in response to $t - 1$ climate conditions that were *relatively* warm and dry for the site in question but were nonetheless quite different (in absolute terms) among sites. Furthermore, our model for seed production broadly agrees with the relationships identified by Krebs et al. (2012) for an independent dataset of *P. glauca* cone production in the Yukon Territory (over 500 km away), in that both models identify similar and opposing effects of summer temperature in years $t - 1$ and $t - 2$.

Our analyses provide evidence that reproduction of *P. glauca* trees follows a broadly similar masting strategy across gradients from lowland to upland forests. However, variations in stand basal area and differences in the degree to which climate factors limit the different stages of reproduction means that there is likely to be considerable variation in the observed signals of masting across environmental gradients. Our data showed that stands at Treeline actually produce equal or greater numbers of seeds as trees in low-elevation forests on a per unit basal area basis. However, coefficients of variation for mean annual seedfall decreased by more than twofold from 2.4 in the lowland (BNZ) to 1.1 in Treeline. This pattern is opposite to that predicted from the hypothesis that higher elevations are subject to low resource availability and thus should show an increased potential for resource depletion and extreme reproductive variability at high elevations (see also Allen et al. 2012). In contrast, the higher interannual variability we observed in closed low-elevation forests may indicate that constraints on resource allocation to reproduction result from increased intraspecific competition in high-density stands (Rossi et al. 2012) or greater drought stress in lowland forests. Alternatively, masting behavior may be synchronized in response to the temporal and spatial dynamics of dominant seed predators, such as red squirrels (e.g., LaMontagne and Boutin 2007). Masting in *P. glauca* thus appears to be a relatively plastic response that occurs synchronously over wide geographic areas, but also varies substantially in amplitude across the landscape in response to localized limiting factors (LaMontagne and Boutin 2007; Crone et al. 2011; Allen et al. 2012).

An intriguing question posed by the apparent context-specific reproductive responses of *P. glauca* stands to climate demonstrated here is whether our results reflect a remarkable level of phenotypic plasticity that allows *P. glauca* trees to acclimatize to widely varying climate norms during their development. Or alternatively, our results may reflect ecotypic specialization in reproductive responses among the different populations of trees resulting from selection pressures acting to align tree responses with varying local climate norms across these different sites. Long-term reciprocal transplant experiments conducted across this gradient would be required to parse the relative importance of acclimatization versus local ecotypic differentiation in *P. glauca* responses to climate, which may both be at play.

We found a clear reduction in reproductive potential of *P. glauca* stands near the species elevation limits, due to substantially reduced seed viability, despite a high relative allocation to seed production by individual trees at high elevation. This pattern mirrors latitudinal gradients in seed production of similar treeline species such as *Picea mariana* (Sirois 2000). Decreases in the number or basal area of trees able to produce seeds [including potential pollen limitation (e.g., O'Connell et al. 2006)], and reduced seed viability indicates that expansion of *P. glauca* near elevational treeline may be limited. The high sensitivity of seed viability to thresholds in GDD sums, particularly at high elevations, suggests that production of viable seeds near treeline will necessarily be episodic. The rarity of years in which high seed production is likely to correspond to high seed viability at treeline sites provides a potential mechanism to explain observations of episodic tree expansion observed for *P. glauca* at Treeline (e.g., Danby and Hik 2007).

Our results reveal substantial variation in reproductive potential in *P. glauca* across an elevational gradient from lowland to treeline forests. One likely explanation for these patterns is the varying influence of limiting climate conditions on both seedfall and viability among years and among sites, although unmeasured biotic or abiotic variables may also have played a role in causing these patterns. Our results thus suggest that climate change may result in these differences across the landscape being magnified through time. For example, if future warming is sufficient to surmount the proposed GDD threshold on seed viability in subalpine sites on a regular basis, our models suggest that there is a potential for dramatic and immediate increase in viable seed production at high elevation relative to current levels (such as was observed in our Treeline site in 2005). At the warm and dry end of the gradient, on the other hand, we expect that increased drought stress caused by warming could greatly reduce the reproductive potential of *P. glauca* over large areas within the core of its lowland range due to decreasing seedfall if predictions of future warming are realized (Juday et al. 2005). This pattern demonstrates that although mast-seeders may respond in concert to broad interannual variations in climate, changes in reproductive potential in response to directional climate change is a context-specific process that depends on the relative importance of limiting climate factors.

Acknowledgments The authors thank the many people who have assisted with data collection over the two decades of this study. Research in the Bonanza Creek LTER study area have been supported by long-term funding from the LTER program at the National Science Foundation (current grant DEB-1026415) and the US Forest Service Pacific Northwest Research Station, and benefit from early contributions by J. Zasada, K. Van Cleve, and L. Viereck. Monitoring in Denali was supported by the National Park Service, and benefited from the early contributions of R. Densmore and J. Van Horn. Special thanks to E. F. Nicklen for running seed germination trials in Denali and assistance with preparation of figures, and to S. Stehn for leading field collection effort and assisting with database design, and to B. Charlton for leading field and laboratory work at BNZ. E. F Nicklen and S. E. Stehn, and several anonymous reviewers provided helpful comments on an earlier draft.

References

Allen RB, Norman WH, Richardson SJ, Platt KH (2012) Synchronicity, periodicity, and bimodality in inter-annual tree seed production along an elevation gradient. Oikos 121:367–376

Barber VA, Juday GP, Finney BP (2000) Reduced growth of Alaska white spruce in the twentieth century from temperature-induced drought stress. Nature 405:668–672

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Bykova O, Chuine I, Morin X, Higgins SI (2012) Temperature dependence of the reproduction niche and its relevance for plant species distributions. J Biogeogr 39(12):2191–2200

Crone EE, McIntire EJB, Brodie JF (2011) What defines mast seeding? Spatio-temporal patterns of cone production by whitebark pine. J Ecol 99(2):438–444

Danby RK, Hik DS (2007) Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. J Ecol 95:352–363

Gaertner SM, Lieffers VJ, Macdonald SE (2011) Ecology and management of natural regeneration of white spruce in the boreal forest. Environ Rev 19:461–478

Hoch G, Siegwolf RTW, Keel SG, Korner C, Han QM (2013) Fruit production in three masting tree species does not rely on stored carbon reserves. Oecologia 171(3):653–662

Ichie T, Igarashi S, Yoshida S, Kenzo T, Masaki T, Tayasu I (2013) Are stored carbohydrates necessary for seed production in temperate deciduous trees? J Ecol 101(2):525–531

Janzen DH (1976) Why bamboos wait so long to flower. Annu Rev Ecol Syst 7:347–391

Juday GP, Alix C (2012) Consistent negative temperature sensitivity and positive influence of precipitation on growth of floodplain *Picea glauca* in interior Alaska. Can J For Res 42:561–573

Juday GP, Barber V, Rupp S, Zasada JC, Wilmking M (2003) A 200-year perspective of climate variability and the response of white spruce in interior Alaska. In: Greenland D, Goodin DG, Smith RC (eds) Climate variability and ecosystem response at long-term ecological research sites. Oxford University Press, Oxford, pp 226–250

Juday GP, Barber VA, Duffy PA, Linderholm H, Rupp TS, Sparrow S, Vaganov EA, Yarie J (2005) Forests, land management, and agriculture. In: ACIA (eds) Arctic climate impact assessment. Cambridge University Press, New York

Kelly D (1994) The evolutionary ecology of mast seeding. Trends Ecol Evol 9(12):465–470

Kemp GA, Keith LB (1970) Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology 51(5):763–779

Koenig WD, Knops JMH (1998) Scale of mast-seeding and tree-ring growth. Nature 396:225–226

Koenig WD, Knops JMH (2000) Patterns of annual seed production by northern hemisphere trees: a global perspective. Am Nat 155:59–69

Krebs CJ, LaMontagne JM, Kenney AJ, Boutin S (2012) Climatic determinants of white spruce cone crops in the boreal forest of southwestern Yukon. Botany 90:113–119

LaMontagne JM, Boutin S (2007) Local-scale synchrony and variability in mast seed production patterns of Picea glauca. J Ecol 95:991–1000

Mencuccini M, Piussi P, Zanzi Sulli A (1995) Thirty years of seed production in a subalpine Norway spruce forest: patterns of temporal and spatial variation. For Ecol Manage 76:109–125

Mooney KA, Linhart YB, Snyder MA (2011) Masting in ponderosa pine: comparisons of pollen and seed over space and time. Oecologia 165:651–661

Morin X, Viner D, Chuine I (2008) Tree species range shifts at a continental scale: new predictive insights from a process-based model. J Ecol 96(4):784–794

Nienstaedt H, Zasada JC (1990) Silvics of North America. Volume 1. Conifers. Agriculture handbook 654. In: Burns RM, Honkala BH (eds) *Picea glauca*. United States Department of Agriculture and Forest Service, Washington, DC, pp 165–185

O'Connell A, Mosseller LM, Rajora OP (2006) Impacts of forest fragmentation on the reproductive success of white spruce (*Picea glauca*). Can J Bot 84:956–965

R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0. http://www.R-project.org/

Roland CA, Schmidt JH, Nicklen EF (2013) Landscape-scale patterns in tree occupancy and abundance in subarctic Alaska. Ecol Monogr 83(1):19–48

Rossi SH, Morin Laprise D, Gionest F (2012) Testing masting mechanisms of boreal forest species at different stand densities. Oikos 121:665–674

Sala A, Hopping K, McIntire EJB, Delzon S, Crone EE (2012) Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. New Phytol 196(1):189–199

Selas V, Piovesan G, Adams JM, Bernabei M (2002) Climatic factors controlling reproduction and growth of Norway spruce in southern Norway. Can J For Res 32:217–225

Shulski M, Wendler G (2007) The climate of Alaska. University of Alaska Press, Fairbanks 216 pp

Sirois L (2000) Spatiotemporal variation in black spruce cone and seed crops along a boreal forest—tree line transect. Can J For Res 30:900–909

Spiegelhalter DJ, Thomas A, Best NG, Lunn D (2004) WinBUGS Version 1.4.1. User manual. Medical Research Council Biostatistics Unit, Cambridge

Svenning JC, Skov F (2007) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? Ecol Lett 10:453–460

Tremblay MF, Bergeron Y, Lalonde D, Mauffette Y (2002) The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (*Acer rubrum* L.) populations at the northern limit of the species range. J Biogeogr 29:365–373

Wilmking M, Juday GP, Barber VA, Zald HJ (2004) Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. Glob Change Biol 10:1–13

Zasada JC (1988) Embryo growth in Alaskan white spruce seeds. Can J For Res 18:64–67

Zasada JC, Sharik TL Nguyen M (1992). The reproductive process in boreal forest trees. In: Shugart HH, Leemans R, Bonan GB (eds) A systems analysis of the global boreal forest. Cambridge University Press, Cambridge, pp 85–125

Zasada JC, Foote MJ, Deneke FJ, Parkerson RH (1978) Case history of an excellent white spruce cone and seed crop in interior Alaska: cone and seed production, germination and survival. USDA Forest Service General Technical report PNW-65. Pacific Northwest Forest and Range Experiment Station