Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains

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Summary

1. Seed production by *Picea engelmannii* was monitored at 13 sites distributed across a ~670 m elevation gradient for 40 years. Time series of annual seed output was investigated for evidence of masting behaviour and trends in seed abundance over time.

2. We used regression models in a likelihood framework to examine climate effects on seed production for critical periods in the species' reproductive cycle.

3. We rigorously evaluated the performance of two gridded climate data sets, PRISM and TopoWx, before using associated variables as predictors in the seed models.

4. Seed production at these sites does not strictly conform to the classic masting concept. Seed abundance was highly variable over time and strongly synchronized among sites, but mast years could not be objectively identified due to intermediate levels of seed output.

5. Model results indicate that climate conditions across multiple years cumulatively determine reproductive output. High seed rain is associated with elevated summer temperatures in the year that seeds are dispersed, low spring snowfall in the year preceding seed dispersal when buds are initiated, and reduced spring snowfall in a so-called priming year two years prior to seed dispersal. Low spring precipitation putatively increases growing season length and resource accumulation in seed trees.

6. Linear models identified significant positive trends in seed output over time. Anomalous aridity and summer warmth in the latter half of the study period were highly favourable for seed production and were associated with increases in seed abundance.

7. *Synthesis.* The increases in seed output observed in this study may promote population fitness of *P. engelmannii* in the face of changing climate regimes and increasing frequencies of fire- and insect-related tree mortality in the Rocky Mountains. Since this species lacks a persistent seed bank, re-colonization of disturbed areas or dispersal to shifting habitats depends on adequate production of seed by surviving trees, which according to these analyses may be moderately enhanced by current climate trends. However, some evidence also indicates that increases in seed output will ultimately be constrained by threshold high temperatures in the seed maturation year.

Key-words: climate change, life-history trade-offs, masting, maximum likelihood, PRISM, reproductive ecology, TopoWx

Introduction

Historical reconstructions of climate suggest that modern rates of climate warming may be unprecedented in the context of the past 1000 years (Mann, Bradley & Hughes 1999), and evidence is accumulating that forests are becoming increasingly vulnerable to these climate trends. Temperature stress and drought have been implicated in elevated rates of canopy tree mortality for multiple tree species world-wide (Van Mantgem *et al.* 2009; Allen *et al.* 2010). Rising temperatures have also been associated with more frequent wildfire (Littell *et al.* 2009) and severe insect outbreaks (Raffa *et al.* 2008), compounding the effects of heat stress on forest dynamics. As an example, an extreme drought event in the

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American south-west during the 1950s caused widespread mortality and range contraction of *Pinus ponderosa* and *Pinus edulis* (Allen & Breshears 1998; Macalady & Bugmann 2014). The facility of trees to recolonize sites after disturbance or disperse seed to shifting habitats depends, in part, on their inherent reproductive capacity (Angert *et al.* 2011). Warming temperatures have been associated with depressed seed output in some species (Redmond, Forcella & Barger 2012), suggesting that climate change may effect not only rates of disturbance and tree mortality, but also life-history processes that determine the potential of an affected population to recover from disturbance.

The phenology of flowering and seed production has been widely studied for a range of plant species across multiple scales, from the stand level to the level of individual flower (Fenner 1998). Two noteworthy patterns emerge from previous studies that may have significant implications for seedling recruitment following disturbance and adult mortality; seed production is often highly variable from year to year, and individuals of a species are highly synchronized over space and time (Silvertown 1980; Kelly & Sork 2002). Synchronization appears to be a ubiquitous characteristic of the reproductive biology of plant taxa globally (Koenig & Knops 2000), and this synchronization may encompass large geographic areas for some tree species (Koenig & Knops 1998; Schauber *et al.* 2002; Liebhold, Koenig & Bjørnstad 2004). Reproductive processes that are synchronized and additionally periodic, so that well-defined intervals separate seed crops, are commonly classified as masting or mast seeding processes (Janzen 1976; Kelly 1994; Herrera *et al.* 1998).

The physiological mechanisms determining both variability and synchronization of seed output remain poorly understood (Piovesan & Adams 2001; Rees, Kelly & Bjørnstad 2002; Smaill *et al.* 2011; Koenig & Knops 2014; Pearse, Koenig & Knops 2014). Spatial synchronization of seed production across large areas suggests that climate may be an important driver of seed production via the so-called Moran effect (Hudson & Cattadori 1999). Indeed, high temperatures and/or drought conditions during the period of reproductive bud initiation have frequently been correlated with elevated seed output (Daubenmire 1960; Woodward *et al.* 1994; Houle 1999; Piovesan & Adams 2001; Selås *et al.* 2002; Schauber *et al.* 2002; Roland, Schmidt & Johnstone 2014). Experimental treatments in nursery settings have also demonstrated enhanced reproductive response to drought or heat stress in some species (Holmsgaard & Olsen 1966; Ross 1985). Duff & Nolan (1958) hypothesized that stress-induced seed production may be related to within-plant competition for finite resources. Specifically, environmental conditions that depress vegetative growth early in the growing season result in enhanced initiation and development of ovulate cone structures in late summer. This hypothesis is supported by observations that large seed crops are dependent on the successful initiation of reproductive buds and that high failure rates in the initiation of bud primordia are common (Forcella 1981; Harrison & Owens 1983; Owens 1995).

An alternate hypothesis gaining empirical support involves history and antecedent processes. Previous studies have identified relationships between climate variation in years preceding reproductive bud initiation and subsequent levels of seed output (Woodward *et al.* 1994; Piovesan & Adams 2001; Richardson *et al.* 2005; Roland, Schmidt & Johnstone 2014). Climate may affect external resource supplies that are essential for the synthesis of reproductive tissue. For example, Smaill *et al.* (2011) identified correlations between seed abundance and climate factors in years preceding reproductive bud initiation that putatively increase rates of nitrogen mineralization in soils.

The objective of this study is to explore long-term relationships between climate and the reproductive biology of *Picea engelmannii* Parry ex Engelm. (Engelmann spruce) in subalpine forests of the Rocky Mountains in North America. These forests provide critical ecosystem services and are likely to experience rapid ecological changes due to accelerated warming rates relative to lower elevation regions (Pepin *et al.* 2015). We examined a 40-year record of seed abundance from a subalpine forest in central Colorado for the evidence of masting behaviour, trends in seed production over time and potential trade-offs between tree growth and reproductive effort. The reproductive cycle in *P. engelmannii* is a complex process that spans multiple years (Owens & Blake 1985). Seeds that mature and are dispersed in a given (current) year are initiated in late summer of the preceding year. Nonlinear regression models were constructed to quantify the importance of climate factors on seed production across all phases of this reproductive cycle. Model selection and information theory were used to evaluate two main hypotheses: (i) reproductive bud development is stress induced, following Duff & Nolan (1958); (ii) seed production depends on internal plant resources, such as carbohydrate or nutrient reserves, acquired in years preceding seed bud initiation or seed maturation. These hypotheses are not strictly independent as environmental stress during the spring season of the bud initiation year could influence seed production through either of these pathways.

Materials and methods

STUDY SITE

The study site is located within Fraser Experimental Forest (39°51′N, 105°55′W) in the Rocky Mountains of central Colorado. Fraser is a dedicated research area managed by the United States Forest Service (Alexander & Watkins 1977). Thirteen 0.16 ha seed collection plots were established between 1968 and 1970 in closed-canopy, high-elevation forest (Alexander, Watkins & Edminster 1982). Seed plots span an elevation gradient of 670 m and are separated by horizontal distances ranging from 159 to 8420 m. The uppermost plot occurs near treeline at ~3500 m. Mature *P. engelmannii* and *Abies lasiocarpa* predominate across all sites with minor components of *Pinus contorta* var. *latifolia* occurring at lower elevations. Increment core samples indicate that tree ages range from 200 to 400 years. Climate is characterized by cold temperatures, short growing seasons and high snowfall. Mean annual temperature during the 40-year study period was ~1.6 °C. Mean annual precipitation increases with elevation,

ranging from 574 mm yr^{-1} at 2770 m to 752 mm yr^{-1} at 3230 m. Precipitation is relatively evenly distributed across seasons, but nearly two-thirds of annual total precipitation falls as snow between the months of October and May.

SEED COLLECTION AND GROWTH INCREMENT SAMPLING

Ten wire mesh seed traps (0.093 m^2 in area) were randomly located within each of the 13 plots. Trap locations have remained constant for the length of the study. Seeds were collected from traps once per year following snowmelt in the spring of the year after seed maturation and release from cones. Seed counts and viability were determined for *P. engelmannii* only. Heights and diameters of all plot trees with diameters $\geq$ 10 cm (at 1.37 m ground height) were measured at approximately 10-year intervals. Stand basal area (*BA*) in m^2 per hectare was computed for each plot and species based on diameter measurements. Tree diameters and *BA* for non-measurement years were interpolated using linear regression.

We collected tree core samples in the summer of 2011 to determine long-term variability in annual radial growth. Approximately 15 canopy trees were sampled in each of the 13 seed plots. We subjectively selected dominant canopy trees proximate to seed trap locations. A minimum of two cores were extracted from every sample tree from opposite sides of the stem, parallel to the slope contour and within 30 cm of the root crown. Cores were bonded to wooden core mounts, surfaced using progressively finer grades of sandpaper until tracheid cells were clearly visible under magnification and cross-dated using skeleton plots to ensure correct ring dates with annual resolution (Speer 2010). We then measured all ring widths in each core to a precision of 0.001 mm using a Velmex measuring system with an A40 UniSlide. Ring widths were tested for measurement or dating errors using COFECHA (Grissino-Mayer 2001). Approximately 400 cores were processed and measured.

CLIMATE ANALYSES

We analysed trends in climate based on standardized climate records acquired from two meteorological stations located at 2770 and 3230 m. These two stations were selected from among a complex of stations at Fraser because their associated climate records were essentially complete for the length of the study. We aggregated the daily time series of temperature and precipitation to monthly, seasonal and annual values after first inspecting records for missing and extreme values. Details regarding climate data processing are described in the Appendix S1 (Supporting Information). Temporal trends in climate were examined using linear regression (McGuire *et al.* 2012).

We also used available station data to evaluate and compare two gridded climate data sets, PRISM (Daly *et al.* 2008) and TopoWx (Oyler *et al.* 2014). Based on goodness-of-fit (GOF) measures, TopoWx temperature and PRISM precipitation data were used in all modelling analyses (see Appendix S1).

SEED PRODUCTION ANALYSES

Temporal and spatial trends

We first examined the 13 chronologies of seed data for long-term trends in seed production and evidence of masting behaviour, including periodicity, bimodality and spatial synchronization among plots. We first converted raw counts of total seed per trap for 10 traps in each of 13 plots to estimates of annual mean seed abundance per m^2 ground area in each plot. These density estimates of seed output were used in all analyses unless otherwise noted. We analysed long-term trends in seed abundance using general linear models with autocorrelation structures (Richardson *et al.* 2005). Linear methods were used to provide parsimonious fits to trends visually evident in scatterplots. Year and elevation were included as predictors.

We generated descriptive statistics and histograms to characterize the distributions of seed density data and identify potential periodic or bimodal behaviour related to masting processes. Autocorrelation functions (ACF) were also computed to test for serial correlation related to temporal trends or negative lagged effects related to the costs of reproduction (Kelly & Sork 2002; Knops, Koenig & Carmen 2007). Spatial synchrony in seed production among plots was evaluated using Pearson product-moment correlations and correlograms. Preliminary trend analyses suggested that the time series of seed abundance had significant temporal structure and therefore violated assumptions of a purely random processes; specifically, that observations are mutually independent and identically distributed (Chatfield 2004). The Augmented Dickey–Fuller test also revealed statistically significant correlations between the mean and variance within each series, indicating non-stationary processes. Temporal structure or common long-term trends related to broad-scale contemporaneous processes such as climate warming may cause spurious correlations among plots and obfuscate tests of spatial synchrony (Liebhold, Koenig & Bjørnstad 2004). However, data transformations and autoregressive modelling to remove trends may inadvertently dampen high-frequency chronology variance related to masting processes or reproductive variability (Bjørnstad, Ims & Lambin 1999), consequently removing part of the signal of interest. We therefore evaluated synchrony among plots using two alternate data sets: untransformed seed rain data scaled by the basal area of spruce in each plot, and detrended, white noise residuals from a first order autoregressive moving average (ARMA) model. Before detrending, seed counts from each plot were log transformed to stabilize variances (Chatfield 2004). Matrices of pairwise plot correlation coefficients were calculated for each data set, and nonparametric spline correlograms with bootstrapped confidence envelopes were computed to evaluate synchrony as a function of distance (Bjørnstad & Falck 2001).

Statistical models used to determine the climate drivers of seed rain

We constructed the following independent, nonlinear regression models to investigate the role of climate across all phases of the reproductive cycle of *P. engelmannii*: (i) a maturation year model tested climate effects in the year that seeds mature and are dispersed; (iii) a bud initiation model tested environmental effects during the year of reproductive bud initiation (one year prior to seed maturation); (iii) a priming year model evaluated the importance of antecedent climate conditions (two years prior to seed maturation). A full model integrated the effects of climate across all years. Implicit in these models are tests of the two alternate hypotheses discussed in the introduction; specifically, that environmental stress in the initiation year leads to trade-offs and enhanced initiation of reproductive buds (Duff & Nolan 1958), and alternately, that antecedent climate conditions influence internal plant resources available for seed development.

We tested the effects of alternate climate predictors on seed rain in each model including average temperature and total precipitation for annual and seasonal (spring and summer) periods. Seasons were defined according to 3 month intervals beginning with December of the previous year. A period of vegetative shoot elongation (April to

June; Harrison & Owens 1983) was also defined to facilitate tests of Duff & Nolan's (1958) hypothesis. We normalized or scaled individual climate variables by the corresponding overall mean of each site based on the assumption that seed production depends on relative variations in temperature and precipitation rather than absolute levels. This scaling procedure generates dimensionless indices of climate with unit means.

To explicitly evaluate the effect of tree growth on the development of reproductive buds during the bud initiation year, we used an index of growth as an additional predictor variable in the bud initiation model. Plot-specific growth indices were quantified from ring width measurements. Ring widths were first standardized using traditional dendrochronological methods, which included a power transformation to stabilize ring width variance (Cook & Peters 1997) and the computation of residuals from a fitted cubic spline function (50% cut-off frequency of 32 years) and autoregressive model to remove to remove long-term size and age related trends. Residuals were combined into chronologies or indices of radial growth for each site using a biweight robust mean, which minimizes effects of extreme values (Cook & Kairiukstis 1990). Standardization analyses were performed in ARSTAN (Cook 1985).

We used maximum-likelihood methods in the construction of the regression models. The response variable for all models was mean annual seed abundance per square metre of ground area. *BA* of *P. engelmannii* varied significantly among plots and was included as a predictor. We used a mixed model design with a random plot effect. Each analysis required the estimation of 13 site-specific intercept terms (the random effects) and the parameters for at least 3 independent variables or effects:

$$\text{Seed rain} = \text{PotSeed} \times \text{Temperature effect} \times \text{Precipitation effect} \times \text{Basal area}$$

Intercept terms (PotSeed) represent site-specific maximum potential seed abundance produced under optimum climate conditions. Multiplicative predictor variables for the effects are scalar terms constrained to range from 0 to 1 that reduce maximum potential seed rain. We used Gaussian functions to estimate both *BA* and climate effects:

$$\text{Climate (or BA) effect} = \exp\left[-0.5 \times \left(\frac{X - X_0}{X_1}\right)^2\right]$$

where X is the observed climate variable or BA for a given period, X_0 corresponds to the value of the independent variable at which maximum PotSeed occurs, and X_1 describes the variance of the term. Gaussian functions are flexible and can fit data distributions that are unimodal, monotonically increasing or monotonically decreasing.

We used simulated annealing (Goffe, Ferrier & Rogers 1994) with 40,000 iterations to solve for maximum-likelihood estimates of the regression coefficients. Simulated annealing is a global optimization algorithm that uses an iterative procedure to simultaneously search for parameter values that maximize the likelihood of observing the recorded seed trap counts. Model residuals were approximately normal, but heteroscedastic. Therefore, we used a modified normal probably density function (PDF) to estimate likelihood in which variance is a power function of the mean. The residual (ε_i) for the ith observation becomes

$$\varepsilon_i = \alpha + X_i^\beta$$

where X_i is the predicted value for the ith observation, and α and β are estimated by annealing. Tests for temporal autocorrelation confirmed that residuals were random. Bias and R^2 were used to quantify the GOF of alternate models. Bias represents the difference between the predicted response and the observed data and was quantified from the slope of the regression of observed on predicted seed abundance (Canham *et al.* 2006). Unbiased models will generate unit slopes in this regression. Consistent under-prediction or over-prediction will result in slopes greater or less than 1.0, respectively. Akaike information criterion corrected for small sample size (AIC_C) was used to select the most parsimonious models (Burnham & Anderson 2002). AIC_C provides a quantitative measure of model performance that balances model fit, as measured by log-likelihood, and model complexity, determined by the number of parameters in the model. All analyses were conducted in R (Version 3.2.3, R Core Team 2013). Likelihood models were constructed using the likelihood package version 1.6.

TREE GROWTH ANALYSES

We further explored potential trade-offs between growth and reproduction using cross-correlation functions. We used the pre-whitened residuals of both radial growth and seed abundance (methods previously described) in cross-correlation analyses to avoid spurious correlations attributed to temporal autocorrelation.

We also examined the response of tree radial growth to critical climate conditions identified by seed production models as important for the initiation of reproductive buds. We constructed regression models, again in a maximum-likelihood framework, with radial growth as the response. These regression models were fitted with raw ring width measurements rather than the pre-whitened residuals for which portions of the climate signal have potential been removed. We incorporated a tree size predictor based on reconstructed diameters to explicitly account for the effects of increasing tree size on ring width:

$$\text{Radial growth} = \text{PotGrowth} \times \text{Temperature effect} \times \text{Precipitation effect} \times \text{Size effect}$$

Regression coefficients were computed using maximum likelihood with simulated annealing per above. We tested alternative climate predictors including lagged effects to identify the most parsimonious model. We hypothesized a direct relationship between growth and climate and therefore did not normalize climate predictors as with the seed models. Residuals from growth models were approximately normal and had no autocorrelation.

Results

CLIMATE TRENDS

Analyses of instrumental data from Fraser indicate significant positive trends in temperature over the 40-year period of seed data collection (Fig. 1). Mean annual *Tmin* and *Tmax* increased by ~1.0 °C from the first half to the latter half of the study period according to paired t tests ($P < 0.001$). Instrumental data show that annual mean temperature in the last decade of the study period exceeded the previous 30-year mean by over 1.0 SD and that six of the warmest years in the 40-year record occurred between 1999 and 2008. Warming trends are relatively consistent over the elevation range separating climate stations (~460 m). However, significant differences in temperature trends were detected across seasons (Table S1 in Supporting Information). Maximum warming
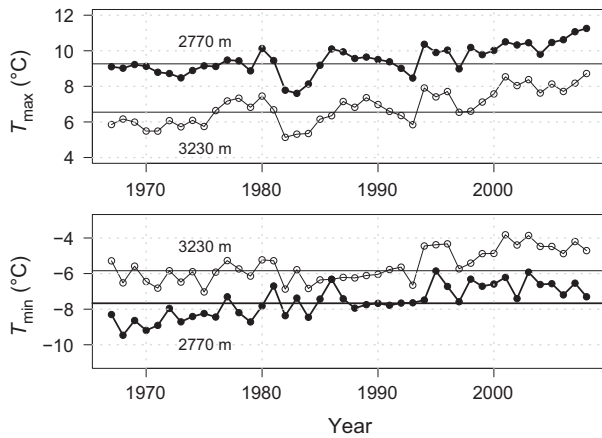
Fig. 1. Time series of mean annual *Tmax* and *Tmin* at high-elevation (3230 m) and low-elevation (2770 m) climate stations at Fraser. Horizontal lines represent year 1970 to 2000 means (normals) and highlight generally enhanced warming rates at both elevations since the mid-1990s. These instrumental data indicate ubiquitous temperature inversions caused by cold air drainage, a widespread phenomena in mountainous terrain (Nolan Doesken, Colorado State Climatologist, personal communication).

occurred in spring months for all sites, when rates of temperature change ranged from 0.6 to 1.0 °C decade^{-1}. Rates of temperature change were lowest in winter and summer months. No significant trends ($P = 0.1$) in annual or seasonal precipitation were detected.

TEMPORAL AND SPATIAL PATTERNS OF SEED PRODUCTION

Regression models revealed a significant positive trend in seed production of ~ 50 seeds m^{-2} decade^{-1} for the 40-year study period (Table 1; Fig. 2). Elevation had a weak and non-significant effect. Independent linear models for the first and latter two decades of the study period suggest that positive trends in seed production began *ca.* 1990, concurrent with trends observed in the instrumental climate data. Positive trends were driven in part by an extreme seeding event in 2006. Increasing tree age over the course of the study is an unlikely driver of observed trends in seed output since mean tree age across all plots based on core samples collected in 2010 was 239 years. Only, a few scattered individual trees

Table 1. Temporal and altitudinal effects on seed production from general linear models with autocorrelation structures (lag effect)

Time period	Variable	Effect size (seed m^{-2})
1970–1989	Year	0.95
	Elevation	0.01
	Lag effect	−0.15*
1990–2010	Year	10.69*
	Elevation	0.18
	Lag effect	−0.13*
Full period (1970–2010)	Year	5.31***
	Elevation	0.09
	Lag effect	−0.12**

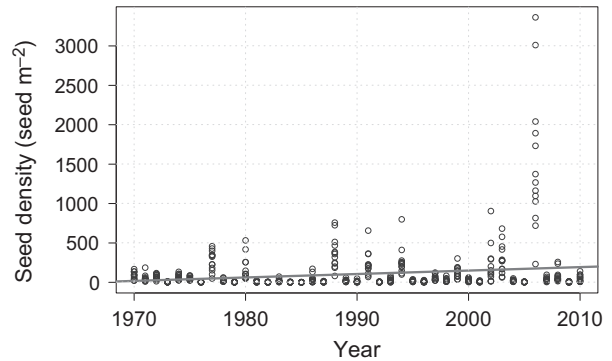Significance: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Fig. 2. Time series of seed abundance per m^2 of ground area for 13 study sites. Synchronicity among sites for high, low, and intermediate levels of seed production is evident. The slope of the fitted regression line reflects an overall positive trend in seed output over the course of the study (~ 50 seeds m^{-2} decade^{-1}).

were younger than 100 years. Forest Service stand inventory data support our age estimates (Alexander, Watkins & Edminster 1982). In addition, these closed-canopy stands were relatively stable over the study period as quantified by periodic censuses conducted by the Forest Service. Tree mortality and recruitment of reproductively mature trees into the canopy were relatively low.

Descriptive statistics (Table 2) and histograms (not shown) indicate strongly right-skewed distributions of seed abundance reflecting a prevalence of low seed years interrupted by infrequent episodes of high seed rain. Coefficients of variation (CV) ranged from 1.6 to 3.3, indicating high variability in seed production among years relative to other published data (Kelly 1994). Variability as measured by CV also increased significantly with elevation ($P < 0.001$), although mean seed abundance did not ($P = 0.7$). Time-series data similarly reveal variable and irregular seed production patterns over time with notable years of intermediate seed abundance over the 40-year study period. In addition, evidence for bimodality was not observed in histograms or detected by kurtosis estimates, which were strongly positive. Although not definitive indicators of bimodality, large negative values of kurtosis are generally associated with bimodal distributions (DeCarlo 1997). ACFs (Fig. S1 in Supporting Information) indicate the presence of consistent, positive 3rd order autocorrelation across all plots (ranging from 0.01 to 0.42). ACFs also reveal low levels of negative 1st and 2nd order autocorrelation in seed chronologies across all plots (ranging from -0.22 to -0.06; Table 2), though most coefficients were non-significant or only marginally significant according to confidence limits (not shown) computed following Salas *et al.* (1980).

An examination of the time series plot of seed production subjectively indicates strong synchrony among sites (Fig. 2). Correlation analyses were conducted to quantify the degree of synchrony among sites. As discussed, we compared levels of correlation for the untransformed seed rain data with those using white noise residuals from an autoregressive model. The resulting overall mean correlation between seed plots was 0.88 for untransformed data and 0.86 for model residuals. Nearly equivalent results could be explained by the low levels

Table 2. Statistics describing the distribution of annual seed rain (seed m^{-2}) over the 40-year study period for 13 study sites. Confidence intervals (CI) for the CV and the first order autocorrelation coefficient (ACF.1) were computed using bootstrap sampling. Sites are designated by elevation and are ordered from low to high elevation. Ranges in stand basal area (BA) for all plots were interpolated from Forest Service inventory data

Site elevation (m)	BA (m^2 ha^{-1})	Mean	Median	Max	Min	SD	b2*	CV	CI 95% (CV)	ACF.1	CI 95% (ACF.1)
2800	28.3, 34.2	132	34	1373	0	250	16.31	1.9	1.42, 2.66	−0.19	−0.40, 0.17
2807	37.4, 38.9	73	18	1027	0	168	26.68	2.29	1.66, 3.66	−0.13	−0.39, 0.08
2887	46.4, 54.8	34	9	232	0	56	7.26	1.63	1.29, 2.06	−0.22	−0.69, 0.14
2908	68.2, 73.3	56	17	816	0	134	26.7	2.39	1.72, 3.72	−0.12	−0.45, 0.02
2919	53.7, 61.6	187	61	1892	0	346	15.84	1.85	1.40, 2.57	−0.19	−0.61, 0.10
2964	36, 41.6	92	25	1163	0	194	23.97	2.1	1.52, 3.26	−0.12	−0.45, 0.02
2990	31.3, 35.1	129	36	1732	1	285	25.8	2.21	1.54, 3.40	−0.12	−0.45, 0.02
3038	32.4, 40.9	68	13	719	0	153	15.02	2.26	1.63, 3.01	−0.07	−0.35, 0.13
3054	35.4, 37.2	96	26	1267	0	213	23.7	2.21	1.62, 3.38	−0.13	−0.45, 0.01
3138	20.1, 26.3	70	15	1097	0	180	27.15	2.56	1.88, 4.03	−0.08	−0.36 0.09
3322	20.4, 25.7	113	18	2041	0	325	31.79	2.87	2.06, 4.79	−0.09	−0.35, 0.01
3385	38.7, 43.6	156	19	3011	0	480	32.2	3.07	2.27, 5.21	−0.06	−0.25, 0.12
3474	42.2, 49.6	160	16	3363	0	536	32.76	3.36	2.50, 5.51	−0.06	−0.22, 0.14

*Kurtosis $= \dfrac{(\sum (Xi-\bar{X})^4/n)}{(\sum (Xi-\bar{X})/n)^2}$ (DeCarlo 1997).

of temporal autocorrelation present in the original seed series, as autoregressive modelling accounted for only ~5% of the variance in the original seed series. Spatial patterns in synchrony quantified by correlograms were also comparable between the transformed and untransformed seed rain data and illustrate that interplot correlation does not decay with distance within the 8-km extent of the Fraser study area (Fig. 3). Similarly, a fitted spline function shows no significant departures from the overall mean synchrony level with distance (Fig. 3).

CLIMATE EFFECTS ON SEED RAIN

The modelling framework used in this study identifies the relative importance of climate variation on seed rain for critical
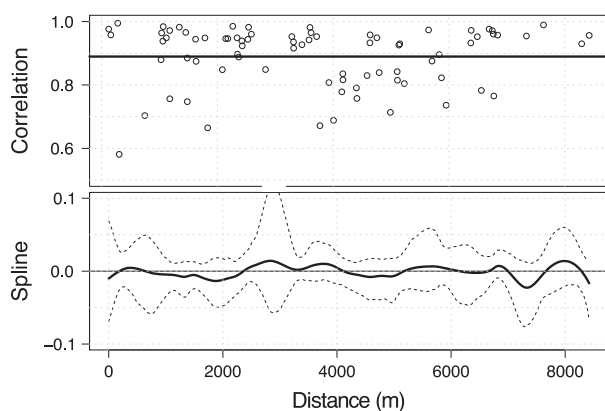

Fig. 3. Correlograms computed from untransformed seed rain data illustrating spatial patterns of synchrony in rates of seed production. Upper figure shows all pairwise plot correlations plotted as a function of separating distance. The black horizontal line indicates the overall mean correlation (0.88). The spline correlogram in the lower plot is a continuous function estimating covariance as a function of distance separating seed-fall plots with corresponding confidence limits derived from bootstrap resampling (Bjørnstad & Falck 2001). The spline correlogram is centred so that the zero reference line denotes the overall mean level of synchrony across the study area.

phases of the reproductive cycle. The best models generated predictions with low to moderate levels of bias (Table 3), ranging from 0.8 for a relatively poor fitting seed maturation model to 1.2 for the final full model. Therefore, the best full model, with a slope of 1.2, generally under-predicted observed seed abundance, though an examination of residual plots (not shown) reveals that very high seed years were consistently under-predicted and low or zero seed years were generally over-predicted.

The seed maturation model indicates that climate in the year of seed dispersal has a comparatively weak influence on seed abundance. The best seed maturation model explained approximately 14% of the variance in the seed rain data. Model selection using AIC excluded the effect of *BA* of *P. engelmannii* from the final best model. Scatterplots suggest that *BA* is only weakly correlated with seed production during years of high seed output, when large trees and/or dense stands with high biomass of *P. engelmannii* produce disproportionately more seeds (see Table 2 for ranges in plot BA over the 40-year study period). The seed maturation model shows that peak seed production only occurs when average summer temperatures in the year of seed maturation are ~10% higher than long-term means for a given site (Fig. 4). Summer temperatures only slightly colder than normal in the year of seed maturation (~5% below mean levels) lead to low or no seed production. Notably, summer temperatures only varied by ~20% above or below the overall mean of each site within the 40-year study period.

The best bud initiation model, which integrated temperature effects from the seed maturation year (Table 3), provided a stronger fit to the seed rain data compared with the seed maturation model alone; R^2 increased to ~19% for this composite model. Precipitation during the period of shoot elongation had the strongest effect on seed output. Specifically, low levels of precipitation during the period of shoot growth in the bud initiation year were associated with high seed rain in the subse-

Table 3. Goodness-of-fit and model comparison measures for models of seed rain. Models test climate effects on seed output across 3 years: the seed maturation year; the bud initiation year, one year prior to seed maturation; and the priming year, two years prior to seed maturation. Full models integrate climate effects in all 3 years. Statistics are shown for the most parsimonious models selected by AICc (corrected for small sample size)

Model	Covariates	n	NP*	AICc	R^2	Bias
Seed Maturation	*Tave*‡ summer lag0	533	17	6289.5	0.140	0.81
Bud Initiation	*Tave* summer lag0 *ppt*† shoot period lag1	533	19	6253.6	0.189	0.91
Bud Initiation + growth	*Tave* summer lag0 *ppt* shoot period lag1 Radial growth lag1	533	21	6216.9	0.191	0.88
Priming	*Tave* summer lag0 *ppt* spring lag2	533	19	6160.0	0.396	1.15
Full	*Tave* summer lag0 *ppt* shoot period lag1 *ppt* spring lag2	533	21	6114.0	0.355	1.16
Full + growth	*Tave* summer lag0 *ppt* shoot period lag1 *ppt* spring lag2 Radial growth lag1	533	23	6079.8	0.388	1.20

*Number of parameters.
†Precipitation.
‡Average temperature.

quent year (Fig. 4). Weak evidence for a temperature effect was also detected. Seed rain appears to be maximized when temperatures during shoot elongation are slightly above long-

term means (~4% greater). However, shoot period temperature was highly correlated with corresponding precipitation ($r = -0.6$) and ultimately excluded from the final model based on AICc. The positive response to reduced spring precipitation appears, at first, to be consistent with Duff & Nolan's (1958) hypothesis, previously described in the introduction, that early spring drought stress may depress vegetative growth, thereby facilitating the enhanced initiation of reproductive buds in late summer. However, the tree growth explanatory variable used in this model shows that seed output actually increases with increasing radial increment (Fig. 4). Similarly, cross-correlation functions (Fig. 5) show positive associations between tree growth in the initiation year and subsequent seed output for most plots. Trade-offs between growth and reproduction, expected under Duff & Nolan's (1958) hypothesis, are therefore not evident in this data set. Furthermore, our models of tree growth revealed, despite a weak climate signal in the tree rings (Table S2), a positive rather than negative response in radial growth to low precipitation during the period of shoot elongation (Fig. 6). Thus, radial growth and seed output appear to covary due to a congruent positive response to reduced precipitation in spring months. These results suggest that high radial growth in the bud initiation year, associated with low spring precipitation, may reflect favourable conditions for carbon or nutrient gain that may facilitate enhanced seed development and maturation in the subsequent year.

The best priming year model, which also integrates temperature effects from the maturation year (Table 3), indicates that climate conditions two years prior to seed maturation have
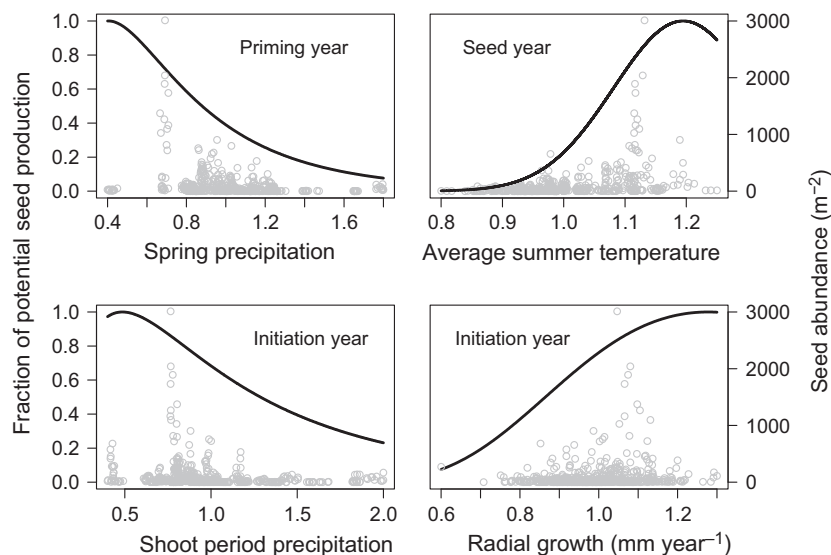

Fig. 4. Fraction of modelled potential seed production (solid curves) and observed seed abundance per square metre of ground area (open circles) as a function of the 4 main predictors from the most parsimonious full model of seed production. Maximum potential seed output occurs when predictors are at their optimum levels for seed production. Each panel independently identifies the fractional decrease in potential seed output caused by the associated effect when all other predictors are held constant. Panels are arranged from upper left to lower right to correspond with the strength of the corresponding submodel, based on AICc scores. Climate variables were normalized by the corresponding long-term mean of each site to produce dimensionless indices of climate. Climate values therefore indicate departures from the corresponding means (1.0) of each site. For example, spring precipitation values of 1.2 indicate that precipitation levels were 20% above long-term means. Standardized radial growth values derived from ring width measurements similarly have unit means (see methods in text).

strong effects on seed rain, explaining ~40% of the variance in the fitted data. Seed rain appears to be maximized when spring precipitation two years prior to seed dispersal is ~50% below long-term means. Again, it appears that reduced spring precipitation is associated with the accumulation of plant reserves that subsequently enhance seed output.

Our best full model, which integrates the previous 3 submodels, produced the strongest fit to the observational data based on AICc suggesting that conditions in all years of the reproductive cycle are cumulatively important for seed production and that favourable conditions in any one year alone are insufficient for the production of abundant seed (Table 3).
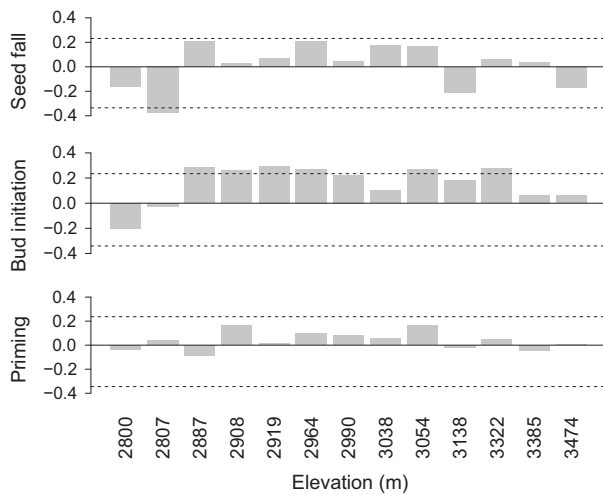

Fig. 5. Cross-correlation functions between standardized radial growth indices and pre-whitened residuals of seed abundance for three periods in the reproductive cycle. Autoregressive models were used to generate pre-whitened residuals. Dashed lines delimit 95% confidence limits.
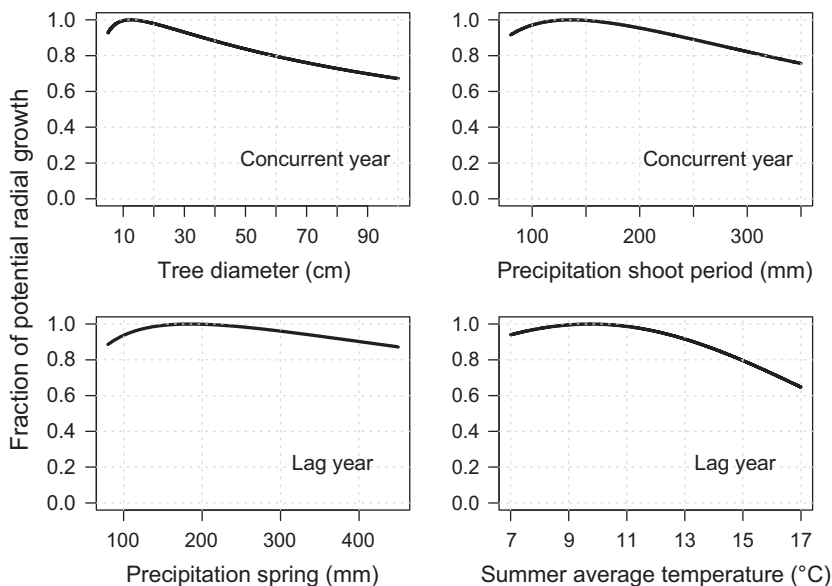
Discussion

REPRODUCTIVE DYNAMICS

The reproductive biology of *P. engelmannii* at Fraser does not strictly fit into the classical masting concept as defined by Kelly (1994). Seed production was highly variable across years and strongly synchronized among sites, but mast events could not be unambiguously identified. Instead of a bimodal distribution of seed abundance, seed output varied continuously over time, with notable, intermediate levels of seed abundance evident (Fig. 2). These patterns agree with results from Koenig & Knops (2000), who found minimal evidence for bimodality in a review of seed production data for a range of northern hemisphere tree species. However, we did identify evidence, based on ACFs, for a weak periodic structure, reflecting at least moderate increases in seed output over 3-year intervals. Interestingly, Woodward *et al.* (1994) also detected a 3-year cycle in the seed output of *A. lasiocarpa*, a conifer that regularly co-occurs with *P. engelmannii* in sub-alpine forests of North America.

CLIMATE EFFECTS ON SEED RAIN

A primary goal of this study was to develop parsimonious mechanistic models of seed production that could be used to parameterize fecundity in a simulation model such as SOR-TIE (Pacala *et al.* 1996). We were more interested in understanding general mechanisms using readily interpretable analyses rather than modelling seed production at Fraser with the highest degree of fidelity to the observed seed rain record. We, therefore, purposefully avoided constructing overly complex models that might improve model fit at the expense of model generality. Similarly, we minimized intensive data management, such as log-transformations, which are commonly applied to seed count data (Koenig & Knops 2000), that might improve model fit but inhibit the interpretability of

Fig. 6. Fraction of maximum potential radial growth as a function of climate and tree size predictors from the most parsimonious likelihood model. Each panel independently identifies the fractional decrease in potential radial growth caused by the associated effect when other predictors are held constant. Climate predictors were not transformed. The upper two panels represent effects in the year concurrent with tree growth, while the lower two panels indicate effects in the year preceding ring width formation. Tree diameter was included to account for the effects of size and age on radial growth rates.

model results. Nevertheless, the best models fitted with raw seed data achieved a reasonably strong fit, explaining ~40% of the variability in observed seed abundance.

Model results do not unambiguously support the stress/trade-off hypothesis of Duff & Nolan (1958). Low spring precipitation in the initiation year was found to be correlated with subsequent high seed rain a year later, as predicted by this hypothesis. However, evidence for trade-offs between growth and reproduction, a critical element of this hypothesis, was lacking. Rather, diameter growth and seed production co-varied (Figs 4 and 5), due to coincident positive responses to low spring precipitation. In addition, average summer temperatures in the initiation year had no significant effect on either seed production or diameter growth. We hypothesize, therefore, that elevated spring precipitation, which predominantly occurs as snow at Fraser, reduces growing season length, impacting both diameter growth and late summer reproductive bud initiation (Woodward *et al.* 1994). Deep, persistent snowpacks associated with high spring precipitation may persist well into the growing season at these elevations, maintaining low soil temperatures and consequently limiting plant physiological processes, even as air temperatures warm (Fritts 1976). Thus, evidence for drought or heat stress limiting growth processes and thereby facilitating the initiation and development of reproductive buds is limited.

A basic tenet of life-history theory is that internal plant resources are finite and that high reproductive effort reduces nutrient or carbon reserves at the expense of other processes (Reznick 1985). Widespread negative correlations between radial growth and reproduction in trees support this assumption (Koenig & Knops 1998). The lack of evidence for visible trade-offs in this study is not unprecedented however (Speer 2001; Knops, Koenig & Carmen 2007; Żywiec & Zielonka 2013). Our failure to identify expected trade-offs may be attributed to within-plant resource variability. Costs associated with reproductive bud development may be concentrated within branches and shoots, which we did not measure, rather than in the main stem (Hoch 2005; Sánchez-Humanes, Sork & Espelta 2011).

More evident is the influence of priming year climate on subsequent levels of seed rain. Among all phases of the reproductive cycle, climate conditions two years prior to seed fall had the strongest effects on indices of model fit. Spring precipitation that was ~50% below mean levels during the priming year correlated with high seed rain two years later. In support of these model results, negative, albeit weak, lagged autocorrelation coefficients suggest that reproductive output depends on the restoration of plant resources depleted by previous reproductive effort. We hypothesize once again that spring snowfall and snowpack depth affect growing season length, thereby limiting either nutrient acquisition from soils (Smaill *et al.* 2011) or net carbon gain through photosynthesis. Notably, Hoch *et al.* (2013) found that seed production in oak and beech was not dependent on stored carbon reserves. Similarly, Richardson *et al.* (2005) found, using model selection, that net carbon in the priming year was not an important predictor of seed output for beech trees in New Zealand.

These findings suggest that nutrient reserves, rather than carbon, may be determining reproductive dynamics in some species.

Model results also indicate that warm temperatures in the year of seed maturation are associated with high seed rain, although this is the weakest effect. The seed maturation model reveals that high seed rain is dependent on a relatively narrow range of concurrent average summer temperatures. Specifically, high seed rain is associated with summer temperatures that exceed long-term means by between ~10 and 20%. Interestingly, summer temperatures that exceed this range are correlated with decreasing seed rain. It is generally assumed that growth processes in trees at high elevations are limited by temperature rather than precipitation (Brown & Shepperd 1995; Salzer & Kipfmueller 2005). Hypotheses explaining temperature limitation in high-elevation trees include insufficient net photosynthesis or a direct thermal effect on meristematic activity (Hoch & Körner 2003). Elevated summer temperatures may, therefore, result in enhanced rates of tissue synthesis, including cone and seed development. Richardson *et al.* (2005) also found positive associations between warm temperatures, carbon availability and seed output in the maturation year. In contrast, Roland, Schmidt & Johnstone (2014) identified negative effects associated with high summer temperatures on seed output in *Picea glauca*, which they attributed to the effects of drought stress on tree physiology. We may likewise be observing a negative moisture stress effect at this site as temperatures warm beyond a threshold level.

There is some evidence that *P. engelmannii* has acclimated to local climate variation among sites. The congruent Gaussian response to relative summer temperature previously discussed, with seed rain maximized by summer temperatures approximately 10% above local site means, suggests that trees at different sites may have adapted to local climate regimes. Recall that climate varies substantially across the almost 700 m elevation gradient; average annual temperature decreased by over 2°C, mean annual precipitation increased by over 120 mm (mostly as snow), and growing season length, measured by the number of days with *Tmin* greater than 5°C, declined by an average of 12 days from valley bottom to upper elevation plots. In spite of this relatively steep climate gradient, statistically significant differences in mean seed rain among sites were not observed.

TRENDS IN SEED OUTPUT

Significant temporal trends were detected for both temperature and seed production at Fraser. Analyses of instrumental data revealed significant positive trends in both *Tmin* and *Tmax*, particularly since the mid-1990s (Fig. 1). Concurrently, seed abundance has increased at Fraser over the latter half of the study period according to fitted multiple regression models (Fig. 2). Trends in both temperature and seed production were consistent across elevations, contrasting the positive elevation-dependent trends in seed production identified by Richardson *et al.* (2005) for beech. Positive trends associated with *P. engelmannii* are attributed to increases in both intermediate

and large seed years. Particularly high seed rain was observed in 2002, 2003 and 2006, approximately corresponding to a period of severe drought and high temperatures across Colorado (Pielke *et al.* 2005). Climate records from Fraser indicate that 3 of the driest springs occurred in 2002, 2004 and 2006 and that mean summer temperatures in 2002, 2003 and 2006 were among the highest in the 40-year study period. Thus, anomalous climate conditions that were favourable for seed production resulted in elevated seed abundance during the most recent decade of the study period.

A recent model that uses interannual temperature variation to quantify seed output for a range of taxa predicts that global climate change will have negligible effects on overall patterns of seed production (Kelly *et al.* 2013). Trends in seed abundance and associated climate at Fraser appear to contradict this prediction. Significant climate driven changes in reproductive effort have also been documented for other tree species (Richardson *et al.* 2005; Redmond, Forcella & Barger 2012). Increases in tree age or changes in stand densities are unlikely drivers of observed increases in seed abundance at Fraser since all plots were comprised of mature, stable, closed-canopy forests with mean stand ages of approximately 200 years at the start of the study in 1970. Previous research suggests that seed production in *P. engelmannii* peaks in mature trees between the ages of 100 and 250 years (Alexander 1974). In addition, stand basal area was excluded as a predictor from the most parsimonious models of seed production indicating that changes in tree size or possible increases in the number of reproductively mature individuals over time were not significant factors influencing trends in seed output.

No system can sustain unlimited growth, and we expect that current trends in seed output at Fraser will be constrained by inherent physiological limits or external processes. Indeed, our model results identify a potential threshold temperature level in the summer of seed maturation, above which seed output is predicted to decline (Fig. 4). Temperature increases in the most recent decade already appear to be bumping up against this threshold, which is ~20% above long-term mean summer temperature for a site. Constraining factors may include elevated respiration rates associated with higher temperatures that subsequently reduce plant carbon reserves. Alternatively, the compounding effects of reduced snowpack depth, earlier snowmelt and warmer summer temperatures may result in drought stress and an effective shortening of growing season length. In a related trend, late summer drought stress has been identified as a potential cause for the weakening of the growth response in high-elevation and northern latitude tree species to warming temperatures over recent decades (D'Arrigo *et al.* 2008).

Changes in the reproductive biology of *P. engelmannii* may have a range of impacts affecting the composition, functioning and trajectories of change in subalpine forests of the Rocky Mountains. Differential responses among tree species to climate change may alter the availability of seed propagules for regeneration by sympatric species following disturbance and thus affect the composition of future forests. For example, limited evidence exists that reproduction in *A. lasiocarpa* may

respond negatively to increasing temperatures, potentially due to a requirement for cool summer temperatures during the priming year (Woodward *et al.* 1994). Thus, reproduction in *A. lasiocarpa* and *P. engelmannii*, which commonly co-occur in this region, may have inverse responses to climate change. Changes in seed production may also effect interconnected food webs through complex, poorly understood pathways (Ostfeld, Jones & Wolff 1996). Increases in seed abundance may directly benefit seed consumers, such as pine squirrels (*Tamiasciurus hudsonicus fremonti*), insects and other small mammals (Alexander 1974). However, feedback loops are also possible. More frequent and larger seed crops may effectively smooth reproductive variability and consequently compromise any evolved benefits of predator satiation, a postulated mechanism for the regulation of seed consumer populations that depends on synchronized, irregular seed output (Silvertown 1980). Long-term population fitness in *P. engelmannii* may thereby be negatively impacted. On the other hand, elevated seed rain may enhance the resiliency of *P. engelmannii* populations in the face of increasing frequencies of fire- and insect-related tree mortality. Seeds from this species suffer high predation losses, germinate quickly under a range of conditions and have a limited period of viability after release from cones (Johnson & Fryer 1996). Thus, in the absence of a persistent, viable seed bank, the reproductive success of *P. engelmannii* may depend on the availability and dispersal of adequate seed from surviving cone-bearing trees, which, according to these analyses, may be moderately enhanced by current warming trends in climate.

Acknowledgements

Data accessibility

Time series of seed abundance and tree ring width data: USDA Forest Service Research Data Archive doi: http://dx.doi.org/10.2737/RDS-2016-0004 (Buechling *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Comparison of prism and topowx gridded temperature datasets.

Figure S1. Autocorrelation function for each seed plot, designated by elevation, showing degree of serial correlation (y axis) for 3 lag years based on the untransformed time series of seed counts.

Figure S2. GOF statistics, including mean absolute error (MAE), R^2 of the regression of observed vs. predicted temperature, and percent bias (Pbias), comparing PRISM and TopoWx estimates of seasonal *Tmax* and *Tmin* at Fraser climate stations.

Figure S3. Time series of PRISM and TopoWx estimates of annual *Tmin* and *Tmax* for summer and winter.

Table S1. Warming trends in station observations of *Tmin* and *Tmax* (°C/decade) by elevation and season derived from the slopes of the linear regression of temperature on year for the period 1970 to 2008

Table S2. Goodness of fit and model comparison measures for hierarchical models of radial growth