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An assessment of *Pinus contorta* seed production in British Columbia: Geographic variation and dynamically-downscaled climate correlates from the Canadian Regional Climate Model

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ABSTRACT

The ecological and economic importance of lodgepole pine (*Pinus contorta* Douglas ex Louden) in British Columbia (BC) has heightened interest in the adaptability and effective management of the species, especially as climate changes. The relationship between climate and the seed production of natural populations is a key management issue that has yet to be assessed. The purpose of this study is to determine if variation in *P. contorta* seed yield is related to the climate of BC.

Regional differences in the seed production of lodgepole pine were examined using 1924 archived seedlot collections across 18 different natural stand seed planning zones (SPZs) in BC. The relationship between climate variation and the seed production of *P. contorta* was then evaluated using dynamically-downscaled output from the Canadian Regional Climate Model (CRCM).

Seed production is relatively consistent across SPZs spanning a wide range of climate regimes, with the exception of Nass Skeena Transition (NST) where seed yield is an order of magnitude higher than elsewhere. Significant temporal correlations between overall trends in seed production and both temperature and precipitation were found using the CRCM output. However, only three of the 18 SPZs showed a significant overall trend in mean annual seed yield based on cone collections made between 1963 and 2013, suggesting that the reproductive capacity of natural populations is well adapted to decadal-scale climate change. Tolerance to significant variation in climate likely plays an important role in explaining the ability of this species to thrive well outside its natural range.

1. Introduction

Lodgepole pine (*Pinus contorta* Douglas ex Louden), known for its exceptional latitudinal range from 31°N in Baja California to 64°N in Yukon (Koch, 1996), has the ability to grow in a wide range of ecosystems (Richardson, 2000). Three different varieties—*P. contorta* var. *latifolia* Engelm., *P. contorta* var. *contorta* Doug. ex Loud., and *P. contorta* var. *murrayana* (Balf.) Engelm. (Kral, 1993)—occupy a broad elevational range from 0 to 3900 m (Wheeler and Critchfield, 1985) and are adapted to maritime, continental, and subalpine conditions (Rehfeldt et al., 1999; Richardson, 2000).

In areas with frequent forest fires, *P. contorta* regeneration has further adapted through the development of closed, or serotinous, cones (Elfving et al., 2001), which do not open upon maturity, but remain sealed until they are subjected to sufficiently high temperatures. Consequently, lodgepole pine plays an important role in colonizing post-fire landscapes (Lotan, 1970; Perry and Lotan, 1977). The pioneer characteristics of the species, along with its edaphic and climatic tolerance, give the prerequisites for a wide ecologic amplitude (Case and Peterson, 2007; Richardson, 2000).

The commercial importance of interior lodgepole pine (*P. contorta* var. *latifolia*) in BC has resulted in heightened interest in its adaptations and growth potential under various environmental conditions (Wang et al., 2004). Extensive reforestation and tree improvement programs have been developed to ensure sustainable forestry practices for the species (Ying and Yanchuk, 2006). To help

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Abbreviations: CRCM, Canadian Regional Climate Model; GCM, General Circulation Model; NST, Nass Skeena Transition; SPZ, seed planning zone.

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meet the increasing reforestation demands of the province, seed orchards have been established to provide high quality, genetically selected seed (Owens et al., 2005); however, these orchards continue to be unable to meet the high reforestation demands (Anon., 2015). The majority of lodgepole pine seedlings are produced from seed obtained from wild stands (Hadley et al., 2001).

Despite its importance to reforestation in BC, geographic variation in the seed production of natural lodgepole pine populations is not fully understood. Earlier research on cone production and seed yield in natural stands indicated that seed production could vary considerably between regions and years (Critchfield, 1980). Bates (1930) reported an annual mean of 180,000 germinable seeds per hectare for a southern Wyoming stand. Over a 10-year period of collections, seed production ranged between 0 and 336,000 seed per hectare. During the same decade, the annual mean seed production for a Colorado stand was reported as 790,000 germinable seeds per hectare, with a range of 74,000 to 2,042,000 (Bates, 1930). Despite these apparent differences, more extensive research on the spatial variation in wildstand lodgepole pine reproduction has been problematic due to this species' wide distribution, long lifespan, and relatively slow reproductive turnover (Mátyás, 1996). Understanding how reproduction may vary geographically in natural stands provides a valuable baseline to potentially improve reforestation stock and practices, particularly when faced with future environmental challenges.

Climate change will likely have severe implications for both native and plantation populations. For BC, future summers are generally expected to be warmer and drier, while winters will likely be warmer and wetter than present; however, the changes in climate are expected to vary across the province (Werner, 2011). In addition, climate change is expected to increase the severity of forest fires in BC (Flannigan et al., 2005) as well as the incidence of foliar disease (Woods et al., 2005) and pests (Bentz et al., 2010). Information about how forests respond to climatic variability will allow managers to better anticipate and plan for future changes to ecosystem dynamics. Although it is possible for vegetation to naturally remain out of balance with climate for hundreds or even thousands of years, it is not clear how forests will respond to the accelerated pace of anthropogenic climate change (Adams, 2007). In BC, concerns over the maladaptation of forest species based on their current distributions and slow reproductive turnover has inspired research on more active forestry responses, including human intervention through assisted migration (O'Neill et al., 2008b; Leech et al., 2011).

Much of the research to date has focused on climate responses pertaining to growth. The growth and survival of individual trees appears to be related to the climatic conditions of the local environment (Rehfeldt et al., 1999; Wu et al., 2005; O'Neill et al., 2008a). Using test sites from the Illingworth provenance trials (Illingworth, 1978), Berland (2013) found the mean number of seeds per cone appeared to be relatively stable across climate regimes, in contrast to tree growth and survival, which varied widely across these same regimes. Further research from natural stands is needed to understand the challenges that forests might face in a changing climate. Understanding historical climate trends is essential in order to put future projections in context. Global Circulation Models (GCMs) are capable of simulating historical and future changes in climate regimes, typically on scales of hundreds of kilometers. However, these analyses are often of little use to decision makers, who require information on smaller scales to evaluate risks and develop adaptation strategies (Mearns et al., 2003). The issue of model scale can be addressed by downscaling information using either a statistical or dynamical technique. To date, studies examining population-scale responses of *P. contorta* to climate have been primarily conducted using statistically-downscaled climate output from ClimateWNA (Rehfeldt et al., 1999; Wang et al., 2006; Berland, 2013). Although there are some advantages to this technique, the methodological constraints of statistical downscaling cannot account for changes in climate variability over time (Fowler et al., 2007). An alternative technique, which provides similar outcomes, utilizes dynamically-downscaled climate output generated by Regional Climate Models (RCMs).

Here, we characterize the spatial and temporal pattern of seed yield in 18 natural stand seed planning zones in BC, in order to establish a baseline estimate of how the reproductive capabilities of *P. contorta* may vary geographically. Then, dynamically-downscaled output from the Canadian Regional Climate Model (CRCM) version 4.2.4 (Sushama et al., 2010) is used to examine the relationship between climate variation and natural stand *P. contorta* seed production in BC.

2. Materials and methods

2.1. Seed yield of natural stands

Historical cone collection data were obtained from archived records of 1948 seedlots in 22 different natural stand seed planning zones (SPZs): Big Bar (BB), Bulkley (BLK), Bush (BSH), Chilcotin (CHL), Central Plateau (CP), Cariboo Transition (CT), Dease Klappan (DK), East Kootenay (EK), Finlay (FIN), Fort Nelson (FN), Hudson Hope (HH), McGregor (MGR), Mica (MIC), Mt. Robson (MRB), Nechako (NCH), Nass Skeena Transition (NST), Quesnel Lakes (QL), Shuswap Adams (SA), Submaritime (SM), Thompson Okanagan Arid (TOA), Thompson Okanagan Dry (TOD) and West Kootenay (WK) (Fig. 1). These 22 natural stand SPZs were established by the BC Ministry of Forests based on provenance performance in field tests (Anon., 1987). SPZs in use in BC were originally created by overlaying clinal adaptive genetic variation determined from these field tests onto an ecological classification of forest lands (Ying and Yanchuk, 2006). The boundaries of these natural stand SPZs correspond to biogeoclimatic subzones (Anon., 1987) and represent regions that are more or less environmentally uniform (Ying and Yanchuk, 2006). All natural stand lodgepole pine SPZs used in this study, with the exception of the coastal Submaritime zone, are categorized as interior regions.

Cones were collected according to guidelines by Lavender et al. (1990). Samples were processed in the year of collection; standardized methods for handling cones and extracting seed were used (Kolotelo et al., 2001). Seedlots were collected for each SPZ between 1963 and 2013 and a minimum cone collection from 10 trees was required for each seedlot. Each of the 1948 seedlots was collected on a single occasion. The fresh weight of the seeds (in kilograms, kg), along with the volume of cones (in hectolitres, hL), was determined for each seedlot collection. Fresh seed masses were standardized to a common moisture content of 7% in order to minimize variation associated with the drying process. Seed yield (kg fresh seed/hL cone) for each seedlot was then determined by dividing the standardized weight of fresh seed by the volume of cones collected. Seedlots were arranged into their respective SPZ and updates from the BC Ministry of Forests SEEDMAP GIS software ensured that all seedlots received the appropriate SPZ designation based on their geographic coordinates.

2.2. Analysis of regional variation in Pinus contorta seed production

Seed planning zones with fewer than 10 total seedlot collections over the five decades—SM, DK, MIC and FN—were excluded from statistical analyses due to their small sample size and insufficient temporal coverage. Consequently, the final sample size was 1924 seedlots. The Brown-Forsythe test (α significance level = 0.05),

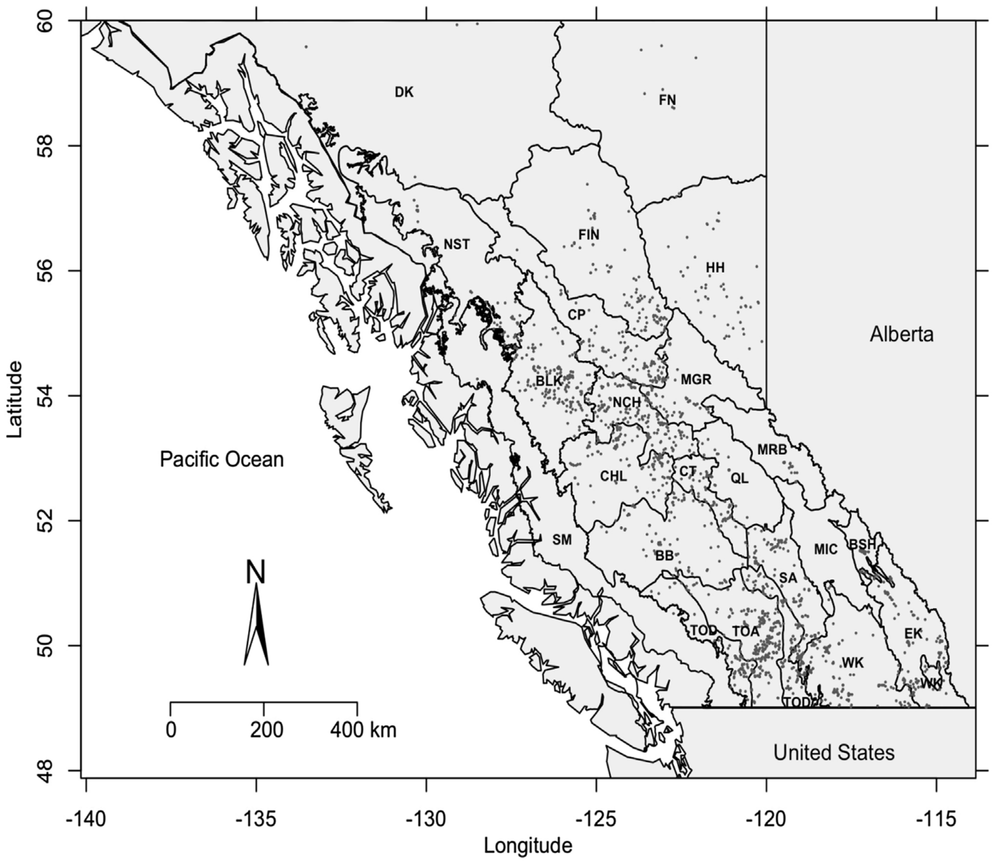

Fig. 1. Natural stand lodgepole pine (*Pinus contorta* Douglas ex Louden) seed planning zones in British Columbia and the locations of 1948 seedlots sampled between 1963 and 2013. SM, DK, MIC and FN were excluded from subsequent statistical analyses due to small sample sizes.

based on absolute deviations from the median, was performed on untransformed data to test for homogeneity of variance. In order to account for heterogeneity of variance and unequal sample size, Welch's analysis of variance (ANOVA) and post-hoc Games-Howell tests ($\alpha = 0.05$) were conducted on log-transformed seed yields to test for differences between the mean seed yield of each zone. Log transformation was used to normalize the data and reduce skew. All statistical analyses were carried out in R version 3.1.0 (R Core Team, 2015).

2.3. Climate output

Regional Climate Model output is quite temporally realitistic when reanalyses are input as the boundary conditions, primarily because reanalysis integrates meteorological observations (Kalnay et al., 1996). However, the limited availability of these reanalyses restricts the number of realizations of the RCM that can be generated. When implemented as boundary conditions, GCMs allow for many more realizations using the RCM (Pierce et al., 2009), but introduce temporal ambiguity to the output (Kendon et al., 2010). Model output from CRCM version 4.2.4 (Sushama et al., 2010) served as the climate information for this study. Output was utilized from two runs with NCEP-DOE Reanalysis 2 boundary forcing at both a 15 km (CRCM15-NREA) and 45 km (CRCM45-NREA) resolution and from eight 45 km resolution runs with GCM boundary forcing. Boundary forcing for the GCM-driven runs were provided by three realizations of the ECHAM5 coupled GCM (Roeckner et al., 2003) and five realizations of the CGCM3 coupled GCM (McFarlane et al., 2005). These eight ensemble member simulations are subsequently referred to as CRCM45-GCM. The reanalysis-driven runs of CRCM extended from 1979 to 2004, while the GCM-driven runs were analyzed from 1958 to 2000. The GCM-driven CRCM realizations were truncated at the year 2000, because that date represents the end of the model's historical emissions scenario. The two climate variables of interest were 2-m surface air temperature (°C) and total precipitation (rain & snow, mm), henceforth referred to as surface temperature and precipitation, respectively. Mean annual, winter (December–February), and summer (June–August) temperature and precipitation were calculated using each model simulation.

The reason why RCM model output was used rather than a gridded observation product, like Climate WNA, was because the high resolution of this historical output is achieved through use of PRISM (Daly et al., 2002), which employs a climate-elevation interpolation scheme. As such, there is no a priori requirement for dynamic and thermodynamic consistency of the downscaled product. In addition, our goal was to eventually explore the potential effects of future climate change on lodgepole pine seed production. As such, it was important that we retained the same modelling framework throughout our analysis

2.4. Lodgepole pine serotiny

Any given natural stand may include both serotinous trees and trees with cones that open at maturity (Tinker et al., 1994). However, serotiny can complicate assessments of cone age, as three years are typically required for cones to reach maturity, and closed cones and viable seeds may remain on the trees for several years following maturation (Lotan, 1970). In the present study, the age range of cones represented in each seedlot collection was unclear. Thus, the climate corresponding to each collection had to be assigned more conservatively using a mean value. A moving window, or trailing-mean, of 3, 5 and 10 years was calculated for each climate variable using each CRCM simulation in order to account for the serotiny of lodgepole pine. In the case of annual means, the previous 3, 5 or 10 years of output were averaged and assigned to the final year of the window. For the winter (summer) mean, the previous 3, 5 or 10 winter (summer) means were averaged and assigned to the final winter (summer) of the window. We refer to each unique combination of model output, trailing-mean and seasonal or annual average as a climate scheme.

2.5. *Climate analyses*

For each climate scheme, the 1924 seedlots were individually assigned an appropriate value of each climate variable based on two criteria: the year of collection and the SPZ. First, the collection year isolated the correct time slice of the climate output for that seedlot. Next, the applicable SPZ designation for that seedlot further isolated grid cells of a particular longitude and latitude. These gridcells were then weighted with respect to their area coverage and the spatially-weighted mean of the climate variable was assigned to the seedlot of interest. This procedure was repeated for each seedlot under each climate scheme.

Once the appropriate climate variable values were assigned to each seedlot, the seedlots were grouped by SPZ. The seed yields of seedlots collected in the same SPZ during the same year were averaged to determine a mean annual seed yield for that region. Within individual SPZs, the anomaly from the mean was then calculated for both the mean annual seed yield and the climate variable of interest using each set of climate output. Climate anomalies calculated from reanalysis-driven CRCM output were represented under each of the three trailing-means, i.e. 3, 5 and 10 years. Anomalies of climate model output were independently calculated for each of the eight CRCM45-GCM ensemble members before averaging them together to give a multi-model ensemble mean anomaly and a ± 2 standard deviation envelope based on the ensemble spread. The CRCM45-GCM output was also represented under each of the three trailing-means.

Climate variable anomalies calculated from CRCM45-NREA output were investigated first. The temporal correlation between each climate variable anomaly and the mean annual seed yield anomaly in each SPZ was calculated using Spearman's rank correlation, primarily due to concerns surrounding both small sample sizes and non-normality. Correlation coefficients (r_s) and p-values ($\alpha = 0.05$) from independent tests for each SPZ were compared geographically using maps for each climate variable. SPZs with fewer than 10 discrete years of seed yield data for the affiliated climate scheme were excluded from the statistical analysis due to their small sample size and insufficient temporal coverage. Global hypotheses of significant correlation ($\alpha_{global} = 0.05$) were tested using the Monte Carlo approach developed by Livezey and Chen (1983). This approach accounts for the possibility that SPZs in close spatial proximity to each other may be correlated. Specifically, it allows one to assess the minimum fractional area of the domain over which local statistical significance at a given level, say 95%, needs to be achieved in order that the set of locally significant correlations not be due to chance alone.

Climate variable anomalies calculated from CRCM45-GCM simulations were then analyzed. Instead of temporal correlations, overall trends in climate variables were determined in each SPZ as a means of dealing with the asynchronous nature of these realizations. SPZs with fewer than 10 discrete years of seed yield data for the affiliated climate scheme were once again excluded from the analysis due to their small sample size. The trend was determined by fitting a linear regression to each climate variable anomaly. The slope (β) of the ensemble mean anomaly was of primary interest in each SPZ, but the slopes of individual ensemble member anomalies were also calculated as a way of gauging the variability in slopes. For comparison, a linear regression was also fit to the mean annual seed yield anomaly over the same interval. Each slope was then tested to see if it was significantly different from zero at the 5% level. Multi-model agreement was declared if five or more individual ensemble members showed a significant trend that agreed with the sign of the significant ensemble mean trend (Tebaldi et al., 2011). The sign and significance of the ensemble mean and mean annual seed yield linear regressions were compared geographically between zones using maps for each climate scheme. In SPZs where the majority of GCM-driven ensemble members showed a significant trend and, additionally, a significant temporal correlation was previously found with CRCM45-NREA output, linear regressions were fit and tested for CRCM45-NREA output over the same time period as CRCM45-GCM.

Table 1
Summary of the number of seedlots and descriptive statistics (mean, standard error and variance) of natural stand lodgepole pine (*Pinus contorta* Douglas ex Louden) seed yield (kg seed/hL cone) for 18 seed planning zones (SPZ) in British Columbia, Canada.

SPZ	Number of Seedlots	Mean Seed Yield (kg/hL) ± S.E.	Variance
NST	43	0.378 ± 0.0030	0.0199
HH	51	0.296 ± 0.0002	0.0012
WK	184	0.285 ± 0.0003	0.0045
NCH	160	0.283 ± 0.0001	0.0011
EK	117	0.278 ± 0.0004	0.0044
CHL	128	0.275 ± 0.0001	0.0014
CT	62	0.274 ± 0.0003	0.0021
MGR	62	0.271 ± 0.0002	0.0014
TOA	250	0.270 ± 0.0002	0.0026
MRB	17	0.267 ± 0.0012	0.0048
CP	115	0.263 ± 0.0002	0.0019
SA	148	0.262 ± 0.0004	0.0047
TOD	170	0.262 ± 0.0002	0.0031
BSH	30	0.261 ± 0.0005	0.0027
FIN	99	0.261 ± 0.0002	0.0022
BLK	163	0.255 ± 0.0001	0.0017
QL	29	0.254 ± 0.0001	0.0007
BB	96	0.242 ± 0.0002	0.0021

3. Results and discussion

3.1. *Regional variation in* Pinus contorta *seed production*

The Brown-Forsythe test indicated unequal variances ($F_{(17,1906)} = 16.61$, $p < 0.0001$) between the seed yields of the 18 SPZs included in the statistical analysis. In particular, the variance in seed yield for Nass Skeena Transition (NST) was an order of magnitude higher than that of other SPZs (Table 1; Fig. 2). In addition, the mean seed yield of NST (0.378 kg seed/hL cone) was considerably higher than the mean seed yield of the 17 other zones (0.268 kg seed/hL cone) (Table 1). Welch's ANOVA indicated significant differences in mean seed yield between seed planning zones ($F_{(17,398)} = 11.2$, $p < 0.0001$). Post-hoc analyses using pairwise Games-Howell tests revealed that mean seed yield was significantly higher in NST compared to all other zones (Table 2) except HH ($t_{(49)} = 3.3$, $p = 0.1260$). When the same analysis was performed on the untransformed data, NST seed yield was significantly higher than all other zones ($F_{(17,398)} = 10.2$, $p < 0.0001$), including HH, though the difference between NST and HH was barely significant ($t_{(46)} = 3.7$, $p = 0.0461$). Since NST is near the coast and HH is in the BC Interior, these regions represent very different conditions.

As a result of its geography, NST has a heterogeneous, transitional climate with both maritime and continental characteristics (Bennuah et al., 2004). Consequently, its steep environmental gradients makes NST a well-known hotspot for interspecific

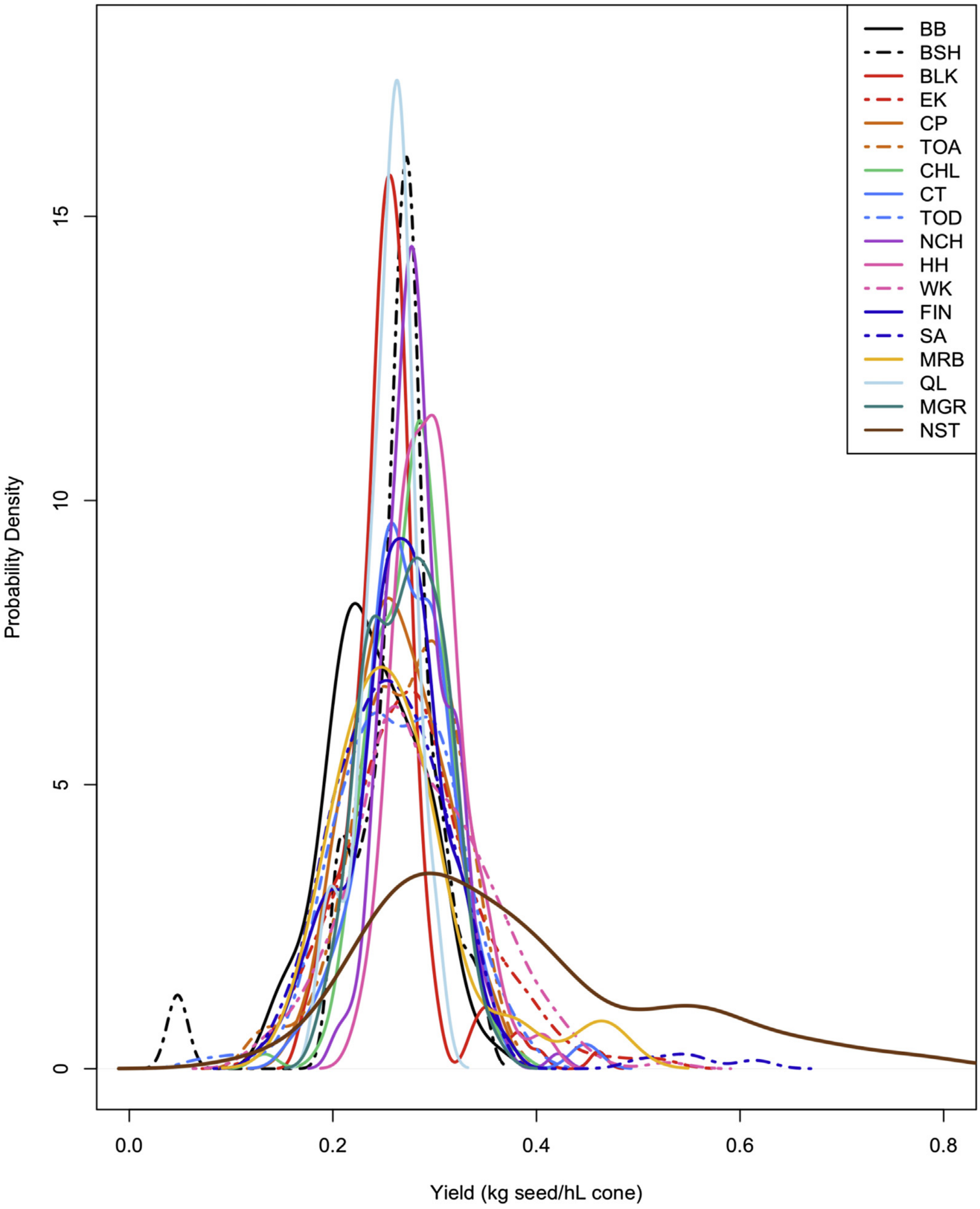

Fig. 2. Probability density functions of natural stand lodgepole pine (*Pinus contorta* Douglas ex Louden) seed yield (kg seed/hL cone) for 18 seed planning zones in British Columbia, Canada.

hybridization and introgression between coastal and interior coniferous species (Hamilton et al., 2013). In particular, introgressive hybridization is known to occur between Sitka spruce (*Picea sitchensis* Bong.) and white spruce (*Picea glauca* (Moench) Voss) in this region (Roche, 1969), resulting in increased genetic variability (Hamilton and Aitken 2013), pest resistance (Ying, 1991; King and Alfaro, 2009) and higher tolerance of environmental stress (Fan et al., 1997). Although less well-studied in NST than spruce, lodgepole pine is represented by two varieties—shore pine (*Pinus contorta* var. *contorta*) and interior lodgepole pine (*P. contorta* var. *latifolia*) (Koch, 1996). Analysis of geographical variation of lodgepole pine monoterpenes showed substantial chemical differences between coastal and interior varieties, with populations of unique intermediate character in areas such as the Skeena River region (Forrest, 1980). Concentrations of foliar secondary metabolites, known to be active in regulating abiotic and biotic stress, are also consistently higher in stands of *P. contorta* var. *latifolia* found in the Interior Cedar-Hemlock biogeoclimatic zone (Meidinger and Pojar, 1991) of NST compared to other interior stands (Wallis et al., 2011). The extended growing season provided by the mild, moist, transitional climate of this region may reduce abiotic stress such as drought, thereby allowing the trees to allocate additional resources to reproduction (Herms and Mattson, 1992).

Although NST is considered an interior natural stand SPZ, gene flow between coastal and interior varieties of lodgepole pine is assumed to occur (Koch, 1996). For instance, genetic influence from the smaller-sized coastal variety was suspected to contribute to the lower heights attained by interior lodgepole pine trees near the coast-interior transition zone in western Canada (Xie and Ying, 1995). The maritime populations of lodgepole pine are genetically more variable (Wheeler and Guries, 1982a) and tend to exhibit higher seed yields than the interior variety (Anon., 2010). These

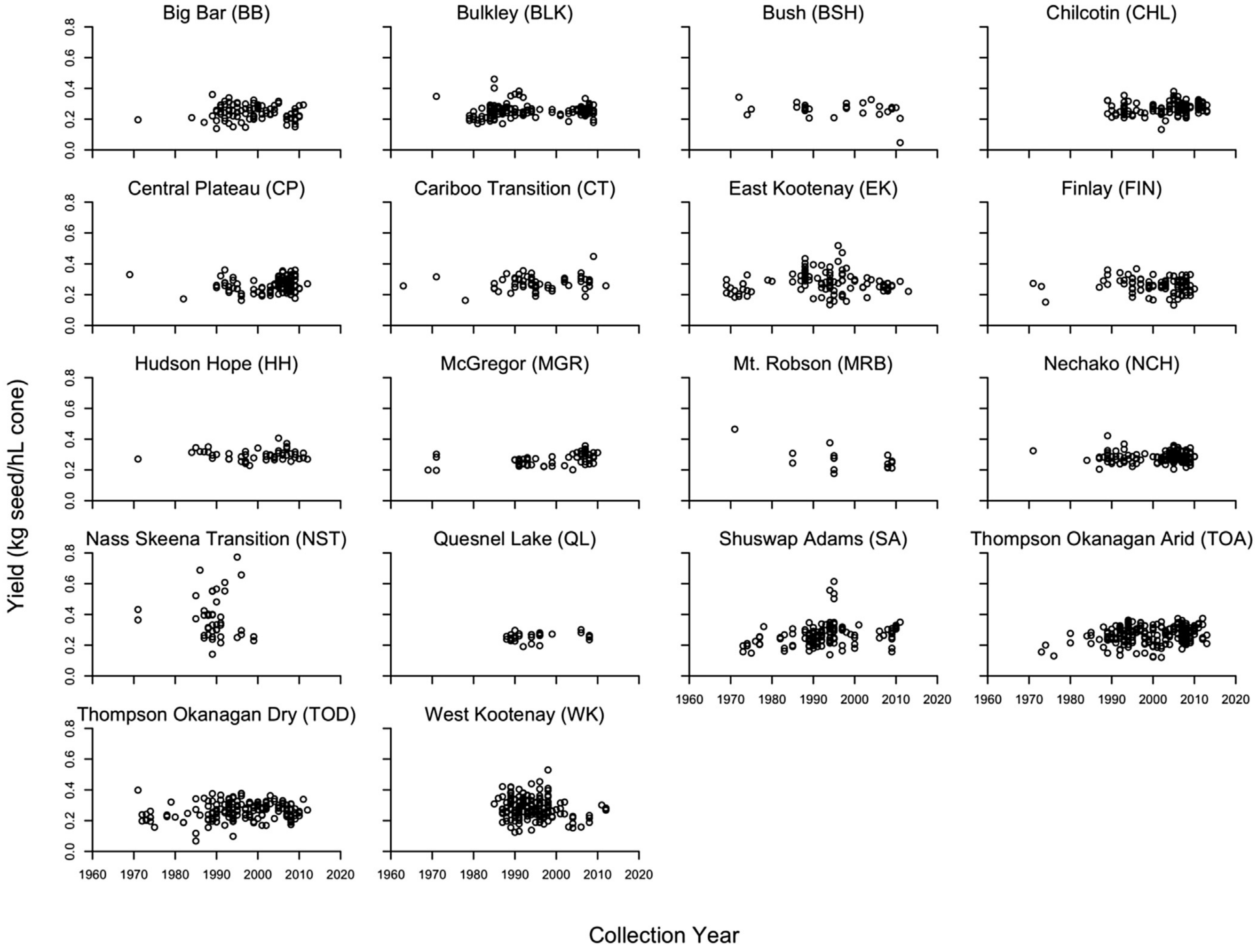

Fig. 3. Natural stand lodgepole pine (*Pinus contorta* Douglas ex Louden) seed yield (kg seed/hL cone) for 18 seed planning zones in British Columbia, Canada, with collections between 1963 and 2013.

two varieties of lodgepole pine intergrade along the coastal range of BC (Arno and Hammerly, 1978), so it is possible that influence from the coastal variety may be responsible for the exceptional seed yields in the interior NST zone (Figs. 2 and 3).

In addition to varietal differences, the lack of serotiny in cones in NST compared to those in interior SPZs may also explain the differences in seed production. Fire-induced serotiny is ecologically important for lodgepole pine, ensuring that it remains an aggressive pioneer species (Muir, 1993). Serotiny is common in lodgepole pine in the BC Interior. In contrast, serotiny is rarely found in the maritime region (Fowells, 1965) where fire is less prevalent (Lertzman et al., 2002). Individual trees may need to produce fewer seeds in order to have the same reforestation impact in areas where serotiny is relatively ubiquitous and fire dominates the landscape. On the Pacific Northwest Coast—a region without frequent fire—lodgepole pine tends to be replaced by more shade-tolerant species such as Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Reeb and Shaw, 2015) and may require a larger seed set to remain competitive.

Hudson Hope (HH) SPZ is situated in an area in which extensive interspecific hybridization occurs between lodgepole pine and jack pine, *Pinus banksiana* Lamb. (Wheeler and Guries, 1987). Although natural hybrid zones are known to be important sources of novel genetic variation in which recombinants may become superiorly adapted (Hamilton et al., 2013), it is not known whether lodgepole pine seed production is influenced. Enhanced seed production in HH and NST may also be attributed to phenotypic plasticity, i.e. the ability of a given genotype to provide a range of physiological or morphological phenotypes in response to different environmental conditions (Voltas et al., 2008). It is difficult to distinguish between genetic adaptation and phenotypic plasticity, but both are important mechanisms by which long-lived organisms are bound more strongly to their environment (Mátyás, 1996).

Seed yields in HH and NST contrasted with those in other SPZs. Both environmental and genetic factors may help to explain the geographic differences. In a previous study, correlations between climate and growth were found to vary regionally (McLane et al., 2011). When grown in common test sites, i.e. the Illingworth lodgepole pine provenance trial, populations from warm regions were affected more strongly by summer aridity, whereas populations originating from cold regions were affected more by annual temperature. According to McLane et al. (2011), the differences in sensitivity among populations grown under similar environmental conditions provide a measure of the influence of both genetics and site climate. In contrast, a study of reproductive traits of lodgepole pine in Illingworth provenance test sites found that the mean number of seeds per cone remained relatively stable regardless of provenance or climate (Berland, 2013). In our study, a similar lack of variability in seed yield was generally observed within and between natural stand SPZs (Tables 1 and 2; Fig. A.1 in Appendix A). Comparison to Berland's study is limited, because our study investigated

Table 2

Schemes of climate variable anomalies showing a statistically significant ($\alpha = 0.05$) Spearman's rank correlation (r_s) with the mean annual *Pinus contorta* seed yield anomaly (kg/hL) of the corresponding seed planning zone (SPZ) using precipitation (PCP) and surface temperature (ST) climate output from CRCM45-NREA. Trailing-means indicate the number of preceding years, summers or winters that were averaged together for each climate output analysis.

SPZ	Climate Variable Anomaly		Trailing-mean (years)	r_s	p-value	*df*
HH	PCP	Annual	5	−0.547	0.0306	14
			10	−0.650	0.0259	10
		Summer	3	−0.638	0.0094	14
			5	−0.765	0.0009	14
			10	−0.755	0.0066	10
	ST	Summer	3	−0.600	0.0160	14
			5	−0.624	0.0116	14
			10	−0.671	0.0204	10
CP	PCP	Annual	3	0.626	0.0253	11
			5	0.790	0.0036	10
	ST	Annual	3	0.654	0.0183	11
		Summer	3	0.857	0.0003	11
		Winter	5	0.748	0.0074	10
FIN	PCP	Annual	5	0.560	0.0401	12
			10	0.560	0.0499	11
		Summer	10	−0.632	0.0237	11
		Winter	5	0.609	0.0237	12
BLK	PCP	Annual	10	−0.582	0.0403	11
		Summer	5	−0.600	0.0099	16
	ST	Summer	10	−0.599	0.0340	11
EK	ST	Winter	5	−0.511	0.0321	16
SA	PCP	Summer	5	0.579	0.0264	13
TOA	PCP	Winter	10	−0.679	0.0049	15
WK	ST	Winter	5	−0.454	0.0458	15

natural stands rather than provenance trials, and we cannot distinguish between genetic and environmental effects. Since seedlot collections were not temporally consistent between zones (Fig. 3), it is also difficult to make inferences about the differences between SPZs from this study alone, particularly given that regional and global climate may have had variable impacts over the 50-year timespan of the collections.

3.2. Seed yield-climate relations

Local correlations between each climate variable anomaly and mean annual seed yield anomaly were significant ($\alpha = 0.05$) in 24 unique combinations of climate schemes and SPZ using CRCM45-NREA output (Table 2; Fig. 4, Fig. A.2 in Appendix A). Climate schemes that produced a sufficient number of statistically significant individual results to warrant rejection of the global null hypothesis ($\alpha_{\text{global}} = 0.05$) are highlighted with red borders in Fig. 4 and Fig A.2 (in Appendix A). In these scenarios, there was a probability no higher than 0.05 that an equivalent or greater number of significant local correlations would have been observed by chance. The majority of significant local correlations found using CRCM45-NREA output were in more northern SPZs such as HH, CP, FIN and BLK (Table 2). Only four different climate schemes showed global field significance ($\alpha_{\text{global}} = 0.05$): 5-year mean annual precipitation, 10-year mean annual precipitation, 5-year mean summer precipitation (Fig. A.2 in Appendix A), and 5-year mean winter surface temperature (Fig. 4). Anomalies and correlations involving 15 km × 15 km CRCM output with NCEP-DOE Reanalysis 2 boundary forcing (i.e., CRCM15-NREA) were indistinguishable from the lower resolution analyses displayed here and are henceforth not discussed in detail.

In general, CRCM45-GCM output collectively captured a warming signal in surface temperatures throughout the province (Fig. 5). Although we calculated the overall trend of each climate variable anomaly and the mean annual seed yield anomaly was calculated using CRCM45-GCM output, only the overall trends are illustrated for surface temperature anomalies (Fig. 5) and, in the appendix, for precipitation anomalies (Fig. A.3 in Appendix A). Three of the eighteen SPZs—EK, TOA and SA (Figs. 5, A.3 in Appendix A; Table 3)—showed a trend in the mean annual seed yield anomaly that was significantly different ($\alpha = 0.05$) from zero (data for remaining 15 SPZs not shown). Across these three SPZs, 23 climate schemes showed climate anomaly trends that were significantly different from zero ($\alpha = 0.05$) amongst the ensemble members using CRCM45-GCM output (Table 3). Significant overall trends found using the ensemble mean of GCM-driven CRCM output that were supported by the majority of ensemble members were captured more often in surface temperature anomalies (Fig. 5) than in precipitation anomalies (Fig. A.3 in Appendix A).

SPZs where CRCM45-NREA output showed strong correlations with the mean annual seed yield anomaly (Table 2) were the natural starting point for further analysis. Meteorological reanalysis represented our best estimate of observed climate on large scales. CRCM dynamically downscaled these boundary conditions to produce a synchronized simulation of actual climate over BC. However, since only one realization of the reanalysis-driven CRCM was used, eight additional GCM-driven ensemble runs of CRCM were necessary to increase confidence in the overall trends of the climatic variables. Zones where the CRCM45-NREA output was significantly correlated with the mean annual seed yield anomaly and, furthermore, where the majority of ensemble members agreed with the significant trend of the ensemble mean CRCM45-GCM output, were highlighted as the best opportunities for investigating relationships between climate and seed production.

In most SPZs, significant trends in CRCM45-GCM and CRCM45-NREA output were unfortunately coupled with non-significant trends or contradictory results in the seed yield anomalies, restricting further analysis. In Hudson Hope (HH), for instance, the ensemble mean of GCM-driven output of 5-year mean summer surface temperature anomalies showed a significant positive increase ($\beta = 0.021$ °C year^{-1}, $p < 0.0001$) from 1971 to 2000 (Fig. 7a). CRCM45-NREA output of 5-year mean summer surface temperature anomalies were negatively correlated with the mean annual seed yield anomaly ($r_{s(14)} = -0.624$, $p = 0.0116$) from 1984 to 2004 (Fig. 6a). Over the period of overlap with CRCM45-NREA, i.e. 1984–2000, the result is similar: $\beta = 0.021$ °C year^{-1}, $p = 0.0003$. The trend in CRCM45-NREA 5-year mean summer surface temperature anomalies over this period was also significant and of the same sign: $\beta = 0.037$ °C year^{-1}, $p = 0.0174$. Consequently, there was no reason to suspect that the single realization of CRCM45-NREA output was unreasonably different from the CRCM45-GCM output. However, since the slope of the mean annual seed yield anomaly was not significantly different from zero during both the 1971–2000 ($\beta = -0.001$ kg hL^{-1} year^{-1}, $p = 0.4843$) and 1984–2000 ($\beta = -0.003$ kg hL^{-1} year^{-1}, $p = 0.0583$) intervals, the results for this SPZ were inconclusive.

In the East Kootenay (EK) SPZ, where a sound comparison between all elements of the study was possible, CRCM45-NREA output of 5-year mean winter surface temperature anomalies was negatively correlated with the mean annual seed yield anomaly ($r_{s(16)} = -0.511$, $p = 0.0321$) from 1985 to 2004 (Fig. 6b). The ensemble mean of GCM-driven output of 5-year mean winter surface temperature anomalies showed a significant positive increase ($\beta = 0.038$ °C year^{-1}, $p < 0.0001$) from 1969 to 2000 (Fig. 7b). Both the GCM and reanalysis-driven CRCM output captured significant relationships in this SPZ under this climate scheme (Tables 2 and 3). In addition, the slope of the mean annual seed yield anomaly was significantly different from zero in EK from 1969 to 2000, $\beta = 0.002$ kg hL^{-1} year^{-1}, $p = 0.0066$ (Fig. 7b). However, when the overall trends of these components were investigated by fitting linear regressions for the overlapping period from 1985 to 2000, the slopes of the ensemble mean GCM-driven climate

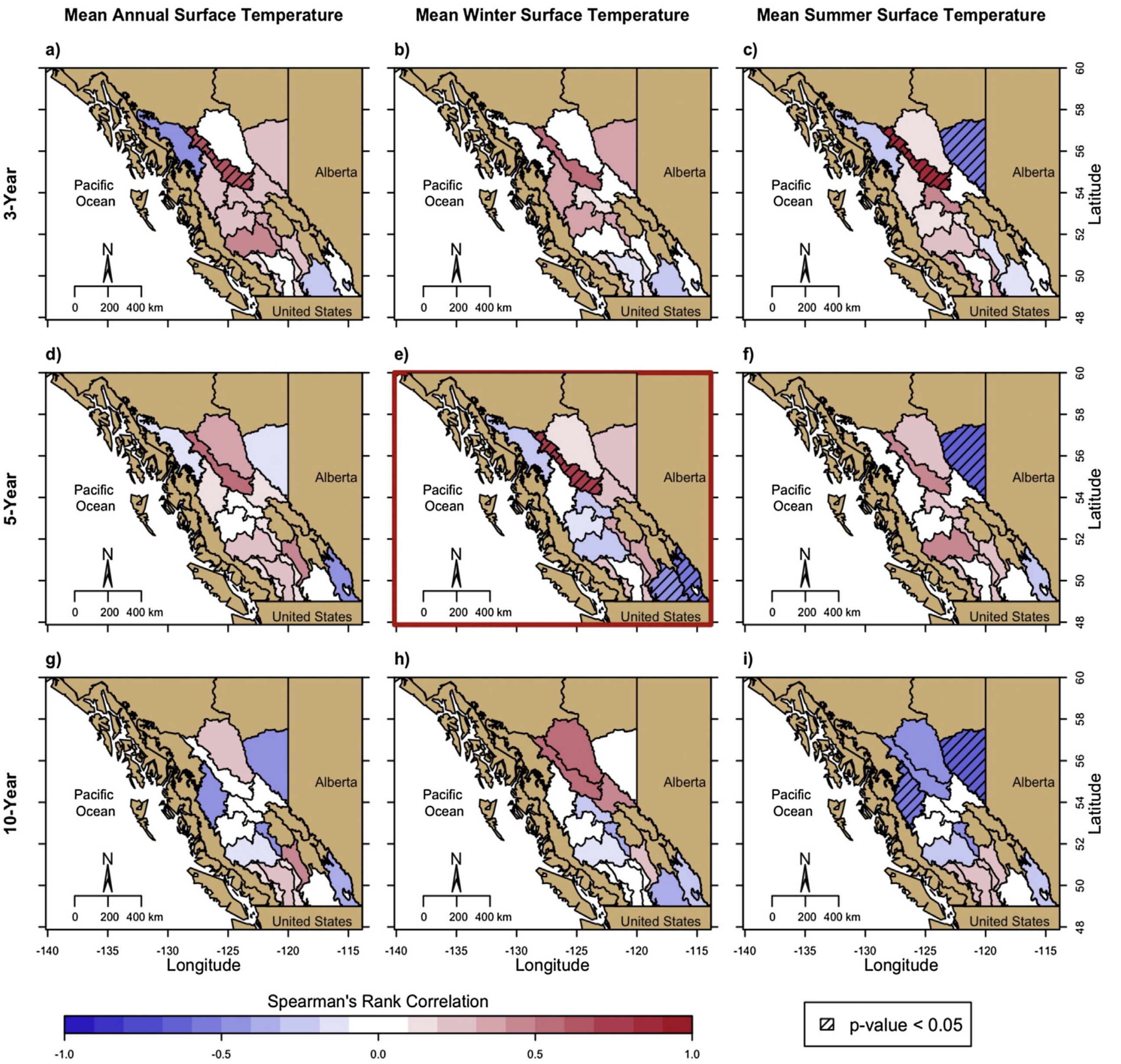

Fig. 4. Temporal correlations for surface temperature. Spearman's rank correlation (r_s) between the mean annual *Pinus contorta* seed yield anomaly (kg/hL) of the corresponding seed planning zone (SPZ) and different climate schemes using output from CRCM45-NREA: Mean annual (a), winter (b) and summer (c) surface temperature with a 3-year trailing-mean; mean annual (d), winter (e) and summer (f) surface temperature with a 5-year trailing-mean; and mean annual (g), winter (h) and summer (i) surface temperature with a 10-year trailing-mean. Local significance ($\alpha = 0.05$) is identified by hatching, and red borders around a panel indicate global field significance ($\alpha_{global} = 0.05$). SPZ with $n < 10$ discrete years of seed yield data for the affiliated climate scheme were excluded.

anomaly ($\beta = 0.014$ °C year^{-1}, $p = 0.0552$), reanalysis-driven climate anomaly ($\beta = 0.013$ °C year^{-1}, $p = 0.5219$) and seed yield anomaly ($\beta = -0.001$ kg hL^{-1} year^{-1}, $p = 0.5865$) were not significantly different from zero.

While investigations using the reanalysis and GCM-driven CRCM output independently produced significant results, the predictive skill of each analysis was hindered for different reasons. The reanalysis-based temporal correlations were calculated using a single realization of CRCM, limiting the reliability of the climate signal. In contrast, averaging eight individual CRCM45-GCM members made the climate signal much clearer, but the temporal ambiguity of this output only allowed for overall trends to be investigated. Thus, the relationship between climate and seed production could not be determined with a high degree of certainty.

The complexities of biological and climate systems makes exploring the relationship between annual seed production and climate difficult, particularly at large spatial scales. Research to date has focused on the impact of climate on tree seed production in the form of mast seeding events—periods where some species produce exceptionally large seed crops. Norton and Kelly (1988) hypothesized that variations in annual climate may cause periods of decreased biological stress and allow trees to produce more seeds. In particular, mean summer temperatures were found to have a weak—but significant—positive correlation with the annual seed production of rimu (*Dacrydium cupressinum* Lamb.) in New Zealand, but no significant correlations were found between total seed production and rainfall (Norton and Kelly, 1988). A similar relationship has been noted in Douglas-fir (*Pseudotsuga menziesii* Mirb. (Franco)) with mean temperatures in the previous June positively correlated

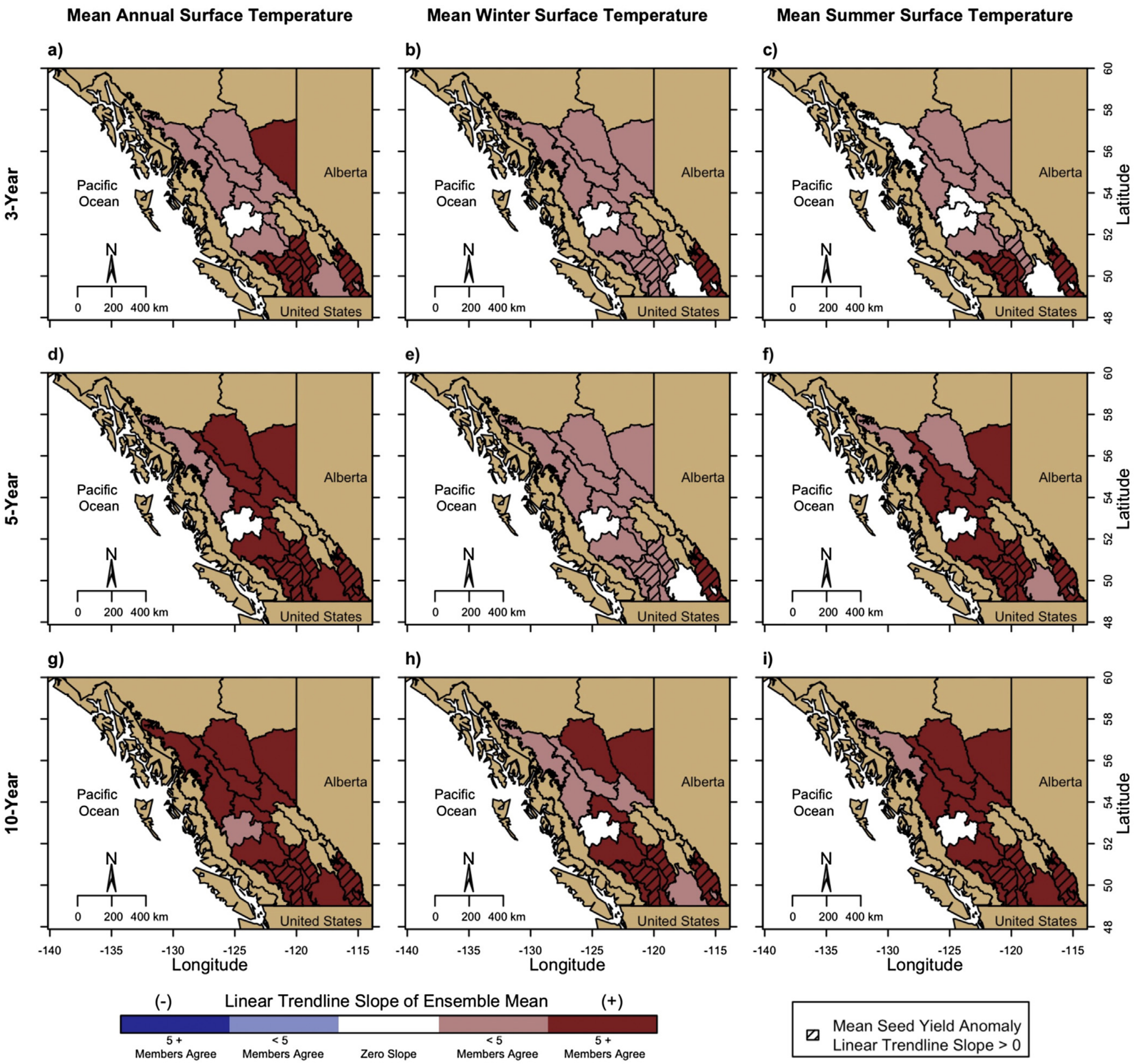

Fig. 5. Signs of significant ($\alpha = 0.05$) linear regression slopes (β) for ensemble mean surface temperature anomalies of the corresponding seed planning zone (SPZ) under different climate schemes using CRCM45-GCM output: mean annual (a), winter (b) and summer (c) surface temperature with a 3-year trailing-mean; mean annual (d), winter (e) and summer (f) surface temperature with a 5-year trailing-mean; and mean annual (g), winter (h) and summer (i) surface temperature with a 10-year trailing-mean. SPZs showing a significant positive slope for the mean annual Pinus contorta seed yield anomaly (kg hL^{-1} year^{-1}) are indicated by hatching. White SPZs indicate that the slope of the ensemble mean surface temperature anomaly (°C year^{-1}) was not significantly different from zero ($p > 0.05$). Dark red or dark blue coloration identifies SPZs where a strict majority of 5 or more individual ensemble members agree with the significant slope of the ensemble mean. SPZs with $n < 10$ discrete years of seed yield data for the affiliated climate scheme were excluded.

with cone production (Eis, 1973). Other research found that variability in annual seed production in various masting tree species is correlated with annual rainfall (Sork et al., 1993; Woodward et al., 1994). In contrast, analyses conducted by Koenig and Knops (2000) found that mast seeding did not correlate with patterns of variability in either annual rainfall or mean temperature. Lodgepole pine cone production varies from year-to-year, though not as much as other conifers (Elliott, 1974; Herrera et al., 1998). The present study found significant, moderate to strong correlations between the mean annual seed yield of lodgepole pine and climate variables from a reanalysis-driven run of CRCM (Table 2), as well as significant overall trends using an ensemble of GCM-driven CRCM output (Table 3).

Our study investigated the correlation between and overall trend in seed production and climate, and cannot conclusively attribute the causation of such relationships without further research. However, it is interesting to recall that lodgepole pine has exceptionally broad ecologic amplitude (Case and Peterson, 2007) and is capable of adapting to diverse, and often severe, environmental conditions (Rehfeldt et al., 1999). Yellow cedar (*Callitropsis nootkatensis* D. Don)—a generalist species—is also adapted to wide climatic gradients and, in terms of its productivity, appears to be insensitive to differences in moisture (Russell and Krakowski, 2012).

A portion of lodgepole pine's adaptability can be explained in terms of genetic variability, growth and survival. Populations

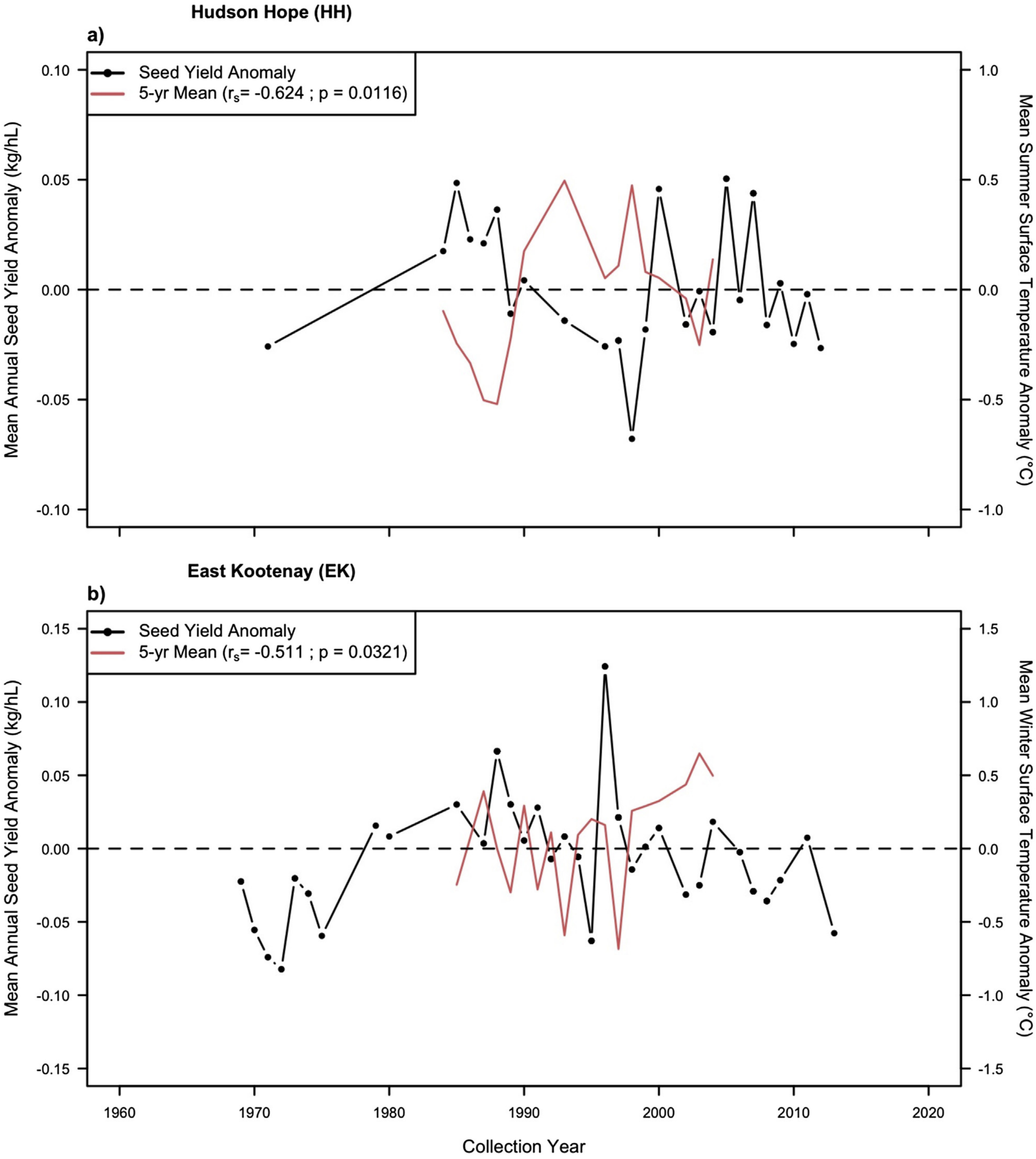

Fig. 6. Temporal variation of mean annual *Pinus contorta* seed yield anomaly (kg/hL) along with: a) 5-year mean summer surface temperature (ST) anomaly in Hudson Hope (HH), and b) 5-year mean winter ST anomaly in East Kootenay (EK) calculated using output from CRCM45-NREA.

throughout BC are significantly different from one another (Xie and Ying, 1995; Rehfeldt et al., 1999). High genetic variation in this species is maintained through long distance dispersal (Critchfield, 1980), high outcrossing rates (Liewlaksaneeyanawin, 2006), and an intolerance of natural self-fertilization (Yeh and Layton, 1979). However, Wheeler and Guries (1982b) found that the genetic variability between populations was less than that contained within populations. Berland (2013) hypothesized that this genetic variation within populations may be responsible for the relative stability of reproductive traits—namely, the mean number of seeds per cone—across climate regimes in BC. Interestingly, our work found a similar lack of variability in seed yield between 18 different seed planning zones in BC (Figs. 2 and 3), despite these regions having very different climates. In addition, only three of the 18 seed planning zones—EK, SA and TOA—showed a significant non-zero trend in their mean annual seed yield anomaly based on cone collections made over the past 50 years (Figs. 5, A.3 in Appendix A, Table 3). Despite natural year-to-year variability, the remaining SPZs seem to be maintaining a relatively constant overall reproductive output over the past few decades.

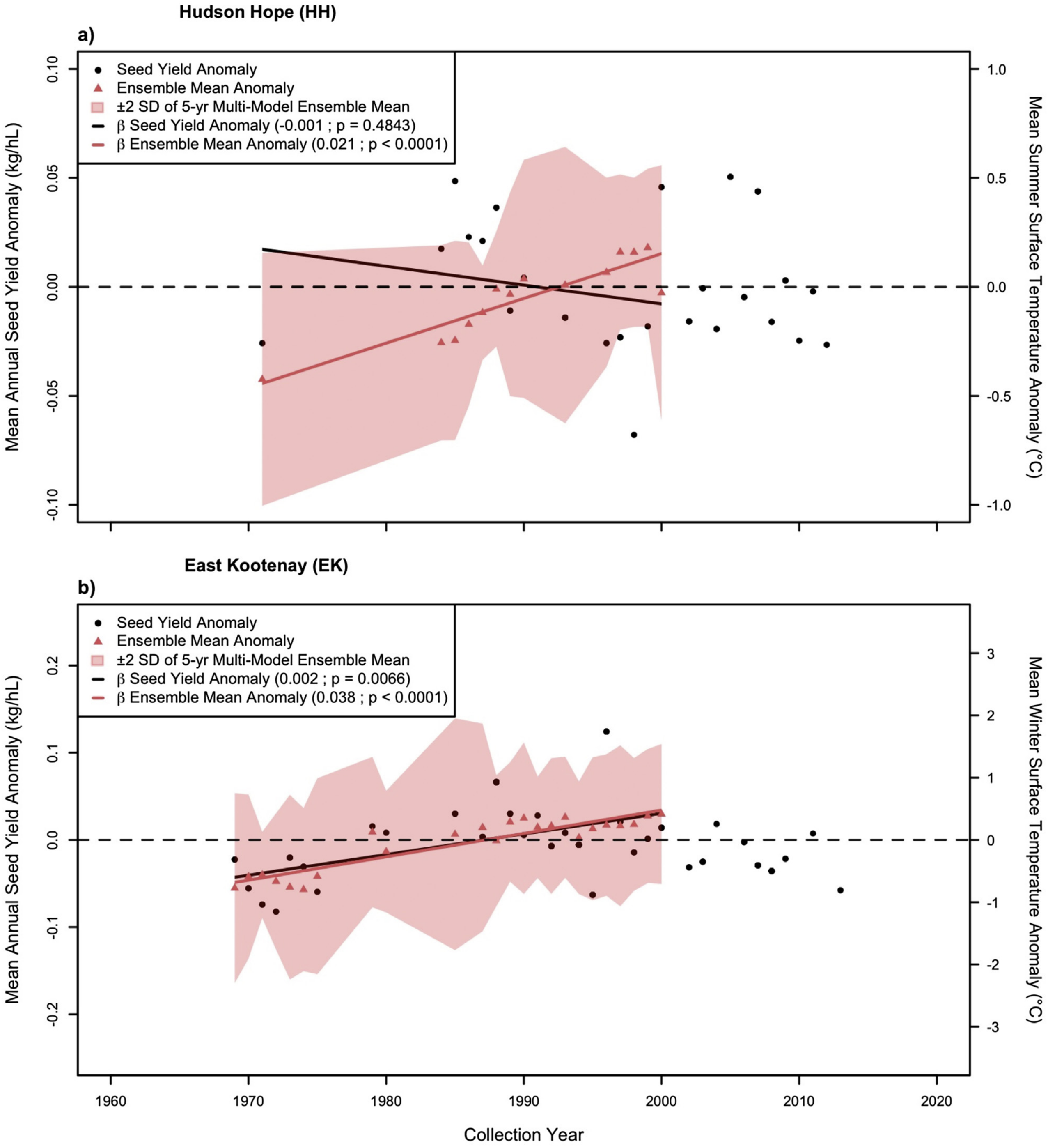

Fig. 7. Temporal variation of mean annual *Pinus contorta* seed yield anomaly (kg/hL) along with: a) Fitted linear regression of 5-year mean summer surface temperature (ST) anomaly in Hudson Hope (HH), and b) Fitted linear regression of 5-year mean winter ST anomaly in East Kootenay (EK) calculated from the eight-member ensemble mean of CRCM45-GCM output. Ensemble mean ST linear regressions have units of °C year^{-1}. The fitted linear regression for the mean annual seed yield anomaly (kg hL^{-1} year^{-1}) for each zone is indicated in solid black.

There are some practical implications of our work, in particular how to choose sites for seed orchards with the aim of optimizing seed yield. This is because seed yield is not always stable. Studies by Bates (1930) and Critchfield (1980) showed that in Wyoming and Colorado seed production was highly variable from one year to the next. Repeated poor seed production continues to be recorded from lodgepole pine seed orchards planted out of its natural climatic range. In these public and private seed orchards in the North Okanagan of British Columbia, cone production is good, but seed yield is very poor (Anon., 2002; Owens et al., 2005). In this region, which is part of the TOD SPZ, the orchards are planted out of the zone of operational forestry, i.e. at lower elevations where lodgepole pine does not normally occur. Although there may be many reasons for failure, including pests and diseases, a notable feature of these sites are extreme July and August temperatures. Our study would suggest that planting of future orchards *within* the natural range of lodgepole pine ought to restore seed yield to levels seen in surrounding trees. Indeed, seed orchards within range have normal seed production, e.g. Prince George Tree Improvement Station, which is planted in the transitional zone between the Prince George

Table 3
Schemes showing a linear trendline slope (β) that is significantly different from zero ($\alpha = 0.05$) for both the mean annual *Pinus contorta* seed yield anomaly (kg hL^{-1} $year^{-1}$) of the corresponding seed planning zone (SPZ) and the ensemble mean of either the CRCM45-GCM precipitation (PCP, mm $year^{-1}$) or surface temperature (ST, °C $year^{-1}$) anomalies. In all cases, 5 or more individual ensemble members agree with the slope of the ensemble mean. Trailing-means indicate the number of preceding years, summers or winters that were averaged together for each climate output analysis.

SPZ	$\beta_{SeedYieldAnomaly}$	p-value	Climate Variable Anomaly		Trailing- mean (years)	$\beta_{EnsembleMean}$	p-value	Num. of Ensemble Members in Agreement	Degrees of Freedom
EK	0.002	0.0066	ST	Annual	3	0.026	<0.0001	7	22
					5	0.025	<0.0001	6	22
					10	0.023	<0.0001	7	22
				Winter	3	0.040	<0.0001	6	22
					5	0.038	<0.0001	5	22
					10	0.030	<0.0001	6	22
				Summer	3	0.026	<0.0001	5	22
					5	0.025	<0.0001	7	22
					10	0.023	<0.0001	8	22
TOA	0.004	0.0006	PCP	Annual	10	0.092	<0.0001	6	18
			ST	Annual	3	0.025	<0.0001	5	18
					5	0.024	<0.0001	6	18
					10	0.023	<0.0001	7	18
				Winter	10	0.031	<0.0001	5	18
				Summer	3	0.023	0.0001	5	18
					5	0.024	<0.0001	5	18
					10	0.024	<0.0001	7	18
SA	0.003	0.0074	ST	Annual	3	0.021	<0.0001	5	19
					5	0.023	<0.0001	6	19

and Central Plateau SPZ (Anon., 2002). Stable seed production can also be a problem, allowing lodgepole pine planted in new environments to become invasive. Exotic plantations in New Zealand produced abundant seed, which, because of its lightweight nature spread quickly over large areas. Furthermore, the serotinous cones proved well-adapted to fire-regulated native habitats, such as tussock grass communities (Richardson et al., 1994). This has led to ecological shifts that are undesired, but difficult to prevent once the tree is established.

In Canada, lodgepole pine is undergoing range expansion at its northern distribution limits with no evidence of strong climatic restrictions on population growth, indicating that the species has yet to reach equilibrium with current climatic conditions in this region (Johnstone and Chapin, 2003). These findings suggest that lodgepole pine may have an even broader ecological amplitude than previously recognized.

4. Conclusions

We found that lodgepole pine in NST had a significantly higher mean seed yield compared to all other zones in British Columbia, with the exception of HH. The variance in seed yield for NST was an order of magnitude higher than that of other SPZs, indicating that seed production is exceptionally variable in this region. In the future, transitional ecosystems such as NST present a unique opportunity to investigate how environmental variability and selection pressure may lead to adaptive evolution.

Analyses conducted using reanalysis and GCM-driven CRCM output independently found significant correlations between climate schemes and mean annual seed yield, but in different SPZs. These differences may be attributed to ambiguous age ranges for each cone collection and temporal restrictions of the seed collection data and reanalysis-driven climate output.

With the exception of NST, seed production was found to be relatively stable across the climate gradients represented by the SPZs. Only three of the 18 SPZs showed a significantly non-zero trend in their mean annual seed yield based on cone collections made over the past 50 years—namely, EK, SA and TOA. The extraordinary adaptability of lodgepole pine and the high genetic variation in natural populations may be contributing to the constancy of these reproductive characteristics, thereby concealing any potential relationships with climate and possibly allowing this species to tolerate decadal-scale changes in climate change.

Acknowledgements

Dave Kolotelo of the BC Ministry of Forests, Lands and Natural Resource Operations is gratefully acknowledged for providing the archived cone collection data that made this work possible. We sincerely thank Greg O'Neill, Michael Carlson and Nicholas Ukrainetz for their patient and tremendously constructive discussions of this work, Ed Wiebe for technical support, and Caitie Frenkel for editorial assistance. We would also like to thank Susan Zedel, Jared Lew, Spencer Reitenbach, Markus Schnorbus and Leslie McAuley for their assistance with the acquisition and re-projection of the spatial shape files. CRCM simulations were conducted by Michel Giguère at Ouranos Consortium and at the University of Victoria as part of the Natural Sciences and Engineering Research Council of Canada's (NSERC) –CRD project, Dynamical Downscaling of Western and Eastern Canadian Hydroclimate, with infrastructure funding from the Canadian Foundation for Innovation and the British Columbia Knowledge Development Fund. The authors are grateful for funding obtained through the NSERC's CREATE Program in Interdisciplinary Climate Science, Discovery Grant Program and PGS Program.

Appendix A.

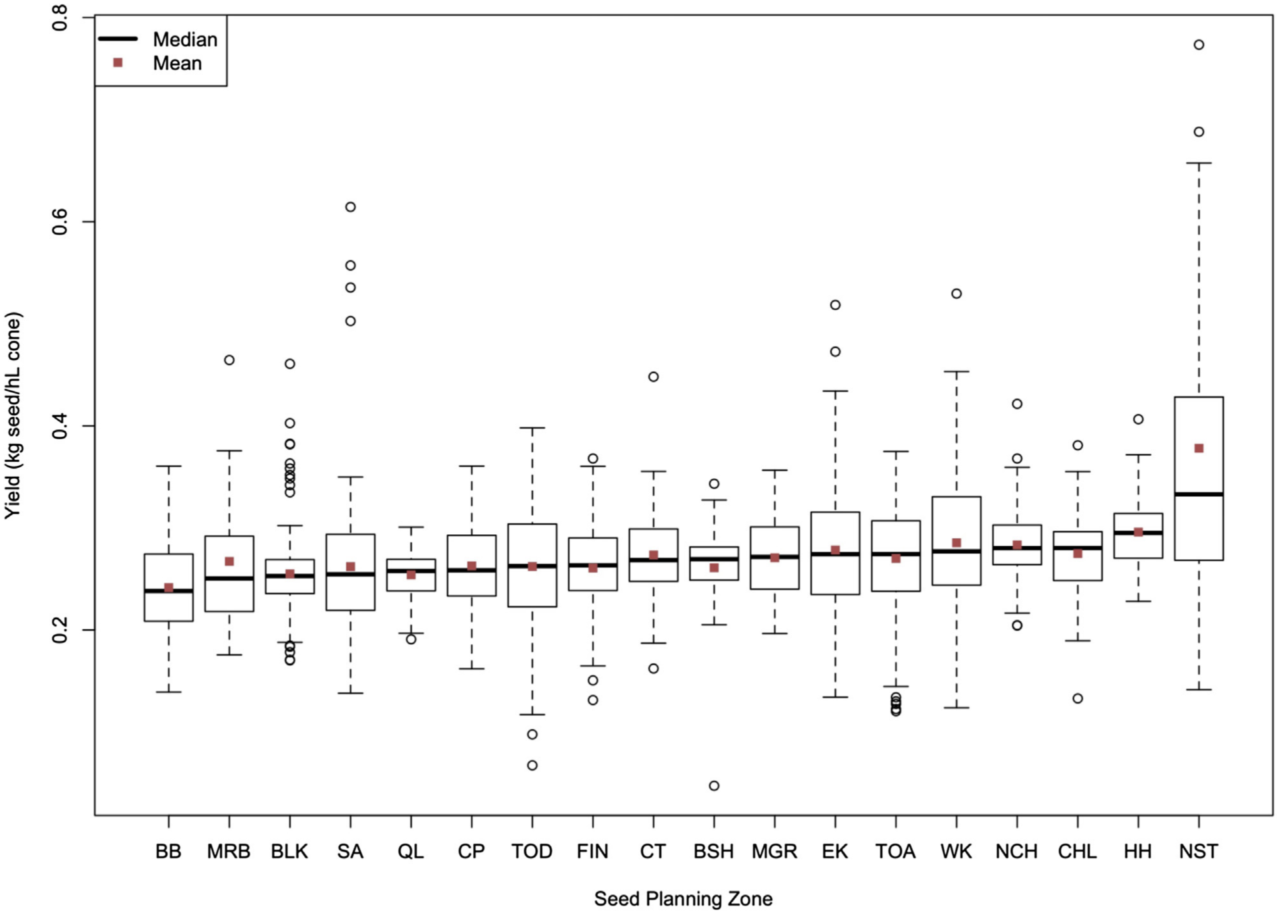

Fig. A.1. Boxplots of natural stand lodgepole pine (*Pinus contorta* Douglas ex Louden) seed yield (kg seed/hL cone) for 18 seed planning zones in British Columbia, Canada, organized by increasing median value. Outliers (open circles) fall more than 1.5 times the interquartile range away from the 1st and 3rd quartiles.

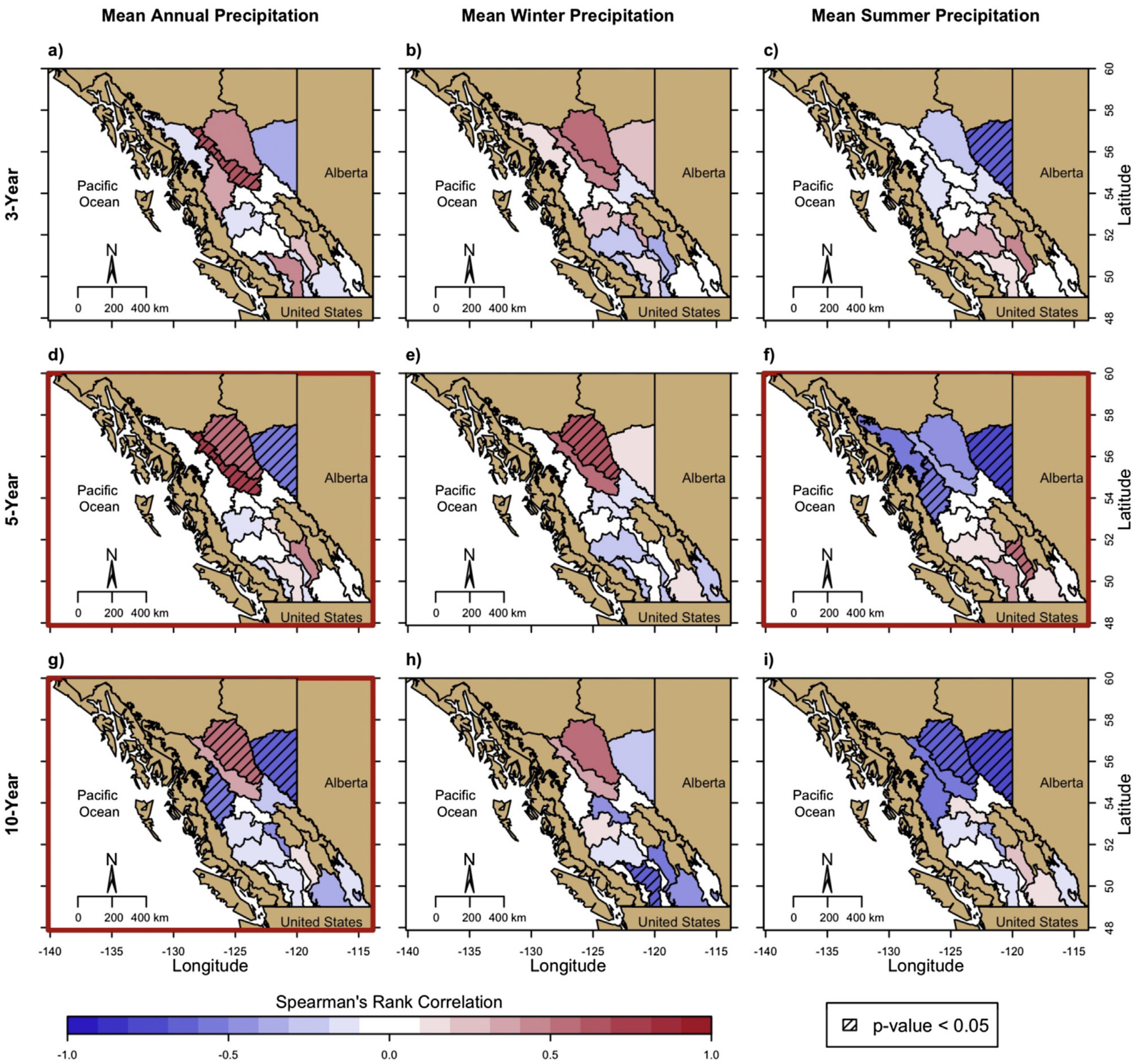

Fig. A.2. Temporal correlations for precipitation. Spearman's rank correlation (r_s) between the mean annual *Pinus contorta* seed yield anomaly (kg/hL) of the corresponding seed planning zone (SPZ) and different climate schemes using output from CRCM45-NREA: Mean annual (a), winter (b) and summer (c) precipitation with a 3-year trailing-mean; mean annual (d), winter (e) and summer (f) precipitation with a 5-year trailing-mean; and mean annual (g), winter (h) and summer (i) precipitation with a 10-year trailing-mean. Local significance ($\alpha = 0.05$) is identified by hatching, and red borders around a panel indicate global field significance ($\alpha_{global} = 0.05$). SPZ with $n < 10$ discrete years of seed yield data for the affiliated climate scheme were excluded. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

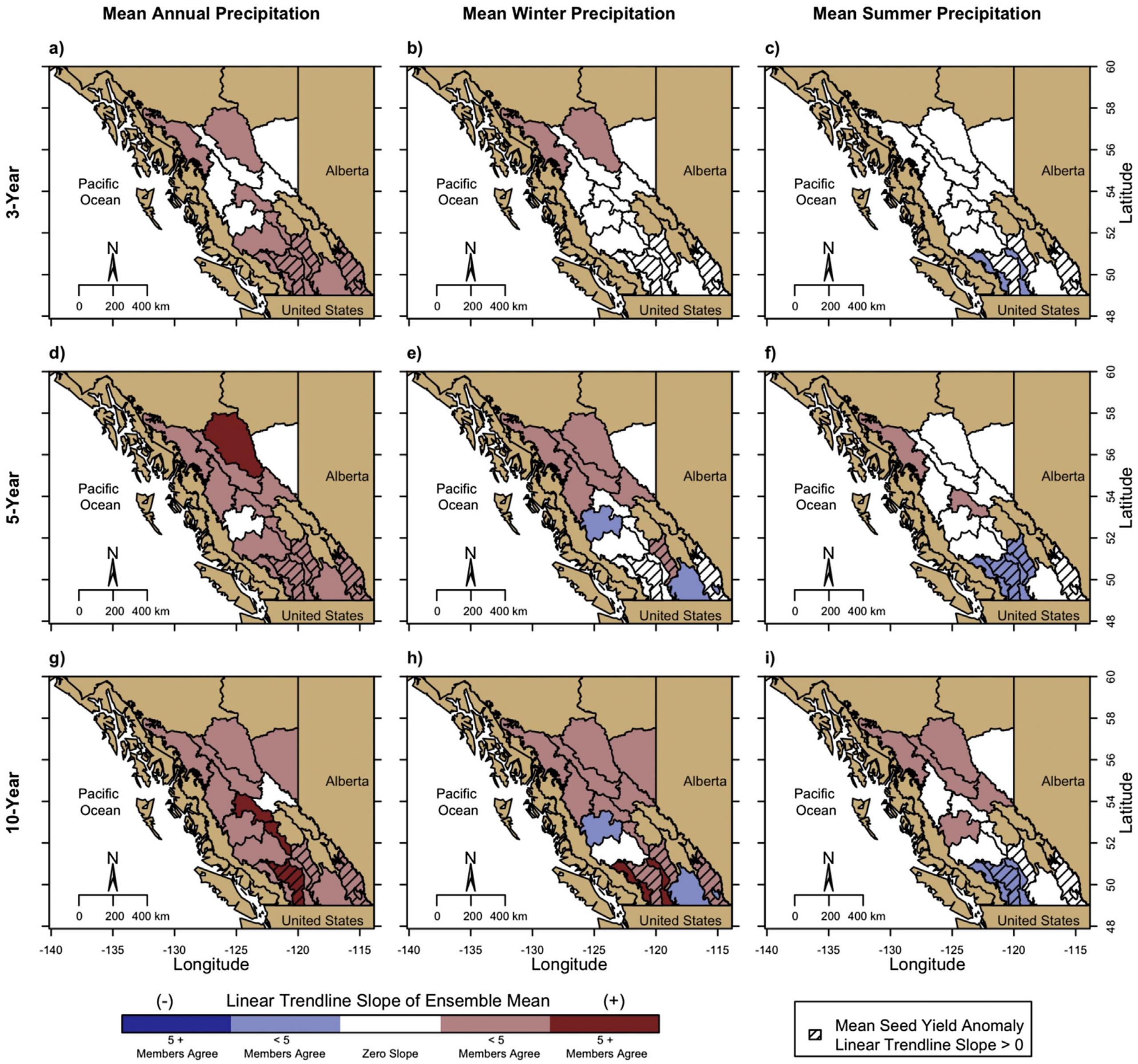

Fig. A.3. Signs of significant ($\alpha = 0.05$) linear trendline slopes (β) for ensemble mean precipitation anomalies of the corresponding seed planning zone (SPZ) under different climate schemes using CRCM45-GCM output: mean annual (a), winter (b) and summer (c) precipitation with a 3-year trailing-mean; mean annual (d), winter (e) and summer (f) precipitation with a 5-year trailing-mean; and mean annual (g), winter (h) and summer (i) precipitation with a 10-year trailing-mean. SPZs showing a significant positive slope for the mean annual *Pinus contorta* seed yield anomaly (kg hL^{-1} $year^{-1}$) are indicated by hatching. White SPZs indicate that the slope of the ensemble mean precipitation anomaly (mm $year^{-1}$) was not significantly different from zero ($p > 0.05$). Dark red or dark blue coloration identifies SPZs where a strict majority of 5 or more individual ensemble members agree with the significant slope of the ensemble mean. SPZs with $n < 10$ discrete years of seed yield data for the affiliated climate scheme were excluded. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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