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

by

Alicia Lew
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Supervisory Committee

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Abstract

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Lodgepole pine (*Pinus contorta* Douglas ex Louden) is the most widespread pine in North America and the single most abundant tree species in British Columbia (BC). Its vast distribution, diversity and economic value make it an important species for timber harvest and subsequent reforestation. Climate change raises serious concerns over the adaptability and effective management of BC's future forests. The majority of lodgepole pine seedlings requested for replanting are produced from seed obtained from wild stands, but the relationship between climate variation and the seed production of natural populations 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.

Historical cone collection data were obtained from archived records of 1948 seedlots in 22 different natural stand seed planning zones (SPZs) of BC. Collections were made between 1963 and 2013 and seed yield (kg fresh seed/hL cone) was determined for each seedlot. First, natural variation in seed production of lodgepole pine was examined in 18 different SPZs. The Nass Skeena Transition (NST) represents a unique intersection between continental and maritime ecosystems and was found to have a significantly higher mean seed yield compared to all other zones, with the exception of Hudson Hope (HH). However, variance in seed yield for NST was found to be an order of magnitude higher than that of other SPZs, indicating that seed production in this region is exceptionally variable. These findings provide a valuable geographic baseline for the reproductive fitness of lodgepole pine, suggesting that climate adaptation and mitigation strategies for some areas of the province may need to be region-specific.

In addition, the relationship between climate variation and the seed production of *P. contorta* in BC was evaluated. The climate of each region was described using dynamically-downscaled Global Circulation Model (GCM) and reanalysis climate output from the Canadian Regional Climate Model (CRCM). Annual, winter, and summer means were explored for each of the climate variables of interest: total precipitation (mm) and surface air temperature (°C). Temporal correlations between the mean annual seed yield anomaly and the anomaly of both climate variables were significant under a variety of climate schemes in a number of SPZs. Significant overall trends in climate variables were also captured using GCM-driven CRCM output. While these two analyses independently highlighted significant relationships between seed yield and climate, their joint implications were unclear. Shifts in the CRCM boundary conditions revealed that the results lacked robustness during the historical period, inhibiting the investigation of future projections. Ambiguous age ranges for each cone collection and temporal restrictions of the seed collection data may be partially responsible for these inconclusive results. Results from the first half of this thesis suggest that, with few exceptions, seed production is relatively stable across SPZs spanning a wide range of climate regimes. Thus, the investigation of the relationship between reproductive fitness and climate may be complicated by the extraordinary adaptability of lodgepole pine and the high genetic variation in natural populations.

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CHAPTER 1: INTRODUCTION

Lodgepole pine (*Pinus contorta* Douglas ex Louden) is the most abundant and extensively harvested tree in British Columbia (BC), making it a critical source of timber products and pulp and paper (Owens 2006). The commercial importance of Interior lodgepole pine (*P. contorta* var. *latifolia*) in BC has heightened interest in its environmental 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 in BC (Ying and Yanchuk 2006).

Lodgepole pine has been the primary reforestation species in the province since the 1960s (Illingworth 1966) and typically accounts for half of the seedlings requested annually for replantation (Anonymous 2013b). To help 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 are unable to meet the current seed demand and the majority of lodgepole pine seedlings requested for replanting are still produced from seed obtained from wild stands (Hadley et al. 2001).

Climate change raises serious concerns regarding the adaptability and effective management of BC's future forests and will likely have severe implications for both native and plantation lodgepole pine populations (Rehfeldt et al. 1999). However, the effect of climate on variation in seed production of natural populations has yet to be assessed.

Lodgepole Pine Reproduction

Similar to other pine species, the twenty-six month reproductive cycle of lodgepole pine is longer than that of many other conifers (Owens and Blake 1985). Pollen-cone and seed-cone bud initiation occurs in the first summer. The reproductive structures then become dormant and over-winter, with the seed-cone buds and pollen completing development the following spring. Female cones are pollinated in late May or June of the same year and the growth of female tissues occurs for a brief period before the seed-cones return to a dormant state late in the summer. The cycle then resumes the following spring, with fertilization occurring around June and the development of the embryo, seed, and cones concluding by the end of the summer (Philipson 1997; Owens 2006). Reproduction is one of the most biologically expensive investments for any organism, and coniferous trees are no exception. In *Pinus sylvestris*, for example, reproductive effort is estimated to vary between 2 and 6% of total annual photosynthesis (Ovington 1961). Since resources are limited, the allocation of energy towards reproduction may limit other biological processes (Cody 1966). Climate is thought to have the most important influence on the temporal variation of the trade-off between reproduction and growth in pines (Lee 1979; Despland and Houle 1997).

Serotiny of Lodgepole Pine

In areas with a frequent forest fire regime, *P. contorta* regeneration has adapted through the development of closed, or serotinous, cones (Elfving et al. 2001). The serotinous cones do not open upon maturity and remain sealed until they are subjected to an appropriate environmental trigger: sufficiently high temperatures of 45-65°C (Lotan 1970; Perry and Lotan 1977). Any given natural stand may include a combination of serotinous trees and trees with cones that open at maturity (Tinker et al. 1994), with both types of lodgepole pine cones requiring the same time to develop. However, serotiny can complicate assessments of cone age, as closed cones—containing viable seed—may be retained on the trees for several years (Lotan 1970).

Climate Change in British Columbia

The El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) are the two most important modes of ocean-atmosphere variability influencing the climate of British Columbia (BC) (Stahl et al. 2006). These two patterns of climate variability occur naturally and are associated with changes in the surface temperature of the Pacific Ocean, which affects temperature and precipitation throughout the Pacific region (Wu et al. 1993; Mantua and Hare 2002). During warm ENSO events, better known as 'El Niño', conditions in BC tend to be warmer and drier. Anomalously low temperatures and high precipitation for the province typically characterize the cool phase of ENSO, or 'La Niña' (Fleming and Whitfield 2010). ENSO operates on a timescale of 3-7 years (Wolter and Timlin 1998), while PDO occurs on much longer decadal timescales (Mantua and Hare 2002). Similar to ENSO, the negative PDO phases are typically associated with cooler and wetter conditions for BC (Shabbar et al. 1997). The positive or warm phase of PDO tends to have variable effects on precipitation and leads to slightly warmer spring and winter temperatures in BC (Stahl et al. 2006). In addition, the PDO can amplify or dampen the effects of ENSO depending on the alignment of their phases (Gershunov and Barnett 1998; Biondi et al. 2001). As global climate begins to change, these Pacific climate patterns seem to be changing in their frequency and intensity (Trenberth and Hurrell 1994; Timmermann 1999), which has major implications for ecosystems throughout BC. Future summers are expected to be warmer and drier, while winters will likely be warmer and wetter than present; the changes in climate are not expected to be uniform throughout 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).

The Mountain Pine Beetle Epidemic

Increase in the occurrence of pests is one of many future impacts that climate change is predicted to have in BC (Bentz et al. 2010). The current mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak is the most devastating forest health epidemic in the history of the province (Axelson et al. 2009). Warmer winters and drier summers are suspected to be facilitating the infestation, since mortality of the beetle depends on cold winter temperatures (Amman and Cole 1983) and the incidence of drought tends to inhibit the defense capabilities of lodgepole pine (Safranyik et al. 1975). Between 1998 and 2012, the mountain pine beetle destroyed over 18 million hectares of BC pine forest, totalling more than half of the province's commercial pine population (Anonymous 2013a). The catastrophic extent of the damage sustained by BC forests has led to a massive increase in the rate of timber harvest, since the trees must be utilized relatively quickly in order to retain their value (Safranyik and Wilson 2007). Since 2005, lodgepole pine has represented in excess of 60% of the annual allowable cut from the beetle-infested region (Peter and Bogdanski 2011). The forestry industry has dramatically intensified planting in order to compensate for these losses.

Future Concerns

Concerns surrounding the adaptability of lodgepole pine to climate change have inspired the development of extensive models relating local climate to growth characteristics, pest hazard, and survival (Rehfeldt et al. 1999; Wu et al. 2005; Wang et al. 2006). However, research on the effect of climate on variation in reproductive characteristics of *Pinus contorta* is in its infancy (Berland 2013), even though it is essential to the production of sufficient seed for reforestation. Furthermore, it is not completely understood how the seed production of natural stand lodgepole pine typically varies in response to climate –information that is especially vital in the face of changing climate. It is not possible to effectively predict how climate will impact the reproductive capacity of *P. contorta* in the future unless we can properly quantify the relationship based on historical climate trends.

Research Objectives

In the first half of this thesis I will 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. This historical standard will be a valuable reference point for comparison with future periods.

The overarching purpose of the second half of my thesis is to contribute to the understanding of how climate influences the reproductive fitness of natural stands of *P. contorta* in BC. This information will have important implications for reforestation and breeding programs, especially as climate changes in the future. However, consistently quantifying the relationship between climate and seed yield in natural stands based on historical climate is essential before future projections of impacts can be made. This study is intended to expand on the current knowledge of population-scale responses of lodgepole pine to climate using climate output that is dynamically downscaled by the Canadian Regional Climate Model (CRCM).

Thesis Format

The outline of this thesis is as follows: Chapter 2 contains the analysis of regional variation in *P. contorta* seed production for natural stands in BC. Chapter 3 investigates the relationship between mean annual seed yield for the same natural stands of *P. contorta* and climate output from CRCM version 4.2.4. Chapter 4 concludes this thesis with a summary of major findings and suggestions for future research.

CHAPTER 2: EVIDENCE OF REGIONAL VARIATION IN *PINUS CONTORTA* SEED PRODUCTION IN BRITISH COLUMBIA

Introduction

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

Since the 1960s, lodgepole pine has been the primary reforestation species in BC (Illingworth 1966) and typically accounts for half of the seedlings requested annually for replantation (Anonymous 2013b). Research to date has primarily focused on improving seed yield in lodgepole pine seed orchards (Owens et al. 2005) and clonal grafts (Ying et al. 1985; Stoehr et al. 1995), in the interests of expanding reforestation programs. However, the majority of seedlings requested for replanting stock are produced from seed obtained from wild stands of lodgepole pine (Hadley et al. 2001). Recent disturbances related to climate change, such as the mountain pine epidemic (Bentz et al. 2010), have significantly increased reforestation demand throughout the province.

A review of earlier research on cone production and seed yield in natural stands indicates that seed production can vary considerably between regions and years (Critchfield 1980). Bates (1930), for instance, reported an annual average of 180 000 germinable seeds per hectare for a southern Wyoming stand, with a range of 0 to 336 000 over a 10-year period of collections. During the same decade, the annual average 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 of the geographic variation in wildstand lodgepole pine reproduction has been problematic, presumably due to the vast distribution, long lifespan, and relatively slow reproductive turnover of the species (Mátyás 1996).

The current study examined differences in *P. contorta* seed production between 18 natural stand seed planning zones (SPZs) from the interior of BC. For an economically and ecologically valuable species such as lodgepole pine, 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.

Materials and Methods

Seed Yield of Natural Stands

Historical cone collection data were obtained from archived records of 1948 seedlots in 22 different natural stand 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) (Figure 2.1). These 22 natural stand SPZs were established by the BC Ministry of Forests based on provenance performance in field tests (Anonymous 1987). The clinal adaptive genetic variation determined from these tests overlay an ecological classification of forest lands, thereby delineating the SPZs (Ying and Yanchuk 2006). The boundaries of these natural stand SPZs correspond comparatively to biogeoclimatic subzones (Anonymous 1987) and represent regions that are relatively environmentally uniform (Ying and Yanchuk 2006). The delineation of these seed zones, or any other biogeoclimatic division of the province, is continuously adjusted as seed transfer guidelines evolve and ecological classification improves (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. Standardized procedures for cone collection (Lavender et al. 1990) and post-collection cone handling and seed extraction (Kolotelo et al. 2001) were used. 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.

Data Analysis

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.

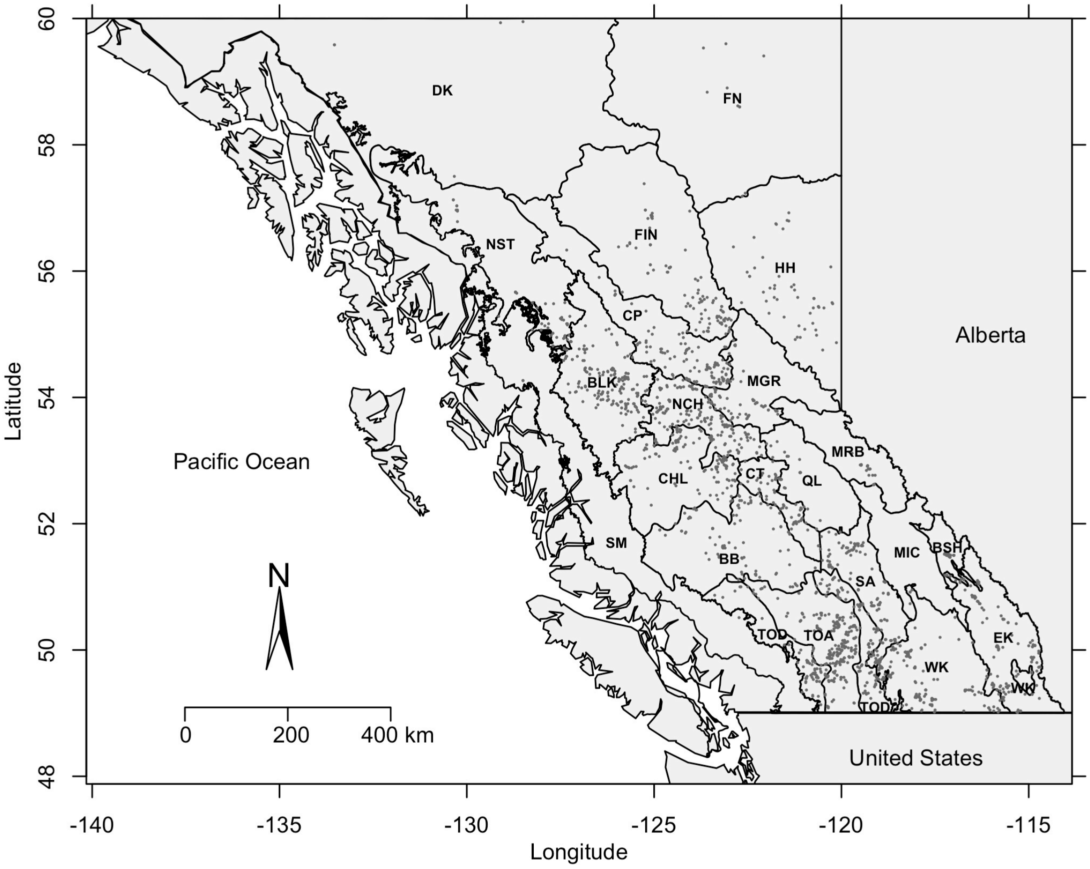

Figure 2.1: Natural stand lodgepole pine (*Pinus contorta* Douglas ex Louden) seed planning zones in British Columbia and the locations of 1948 seedlots sampled between 1963 and 2013. SM, DK, MIC and FN were excluded from subsequent statistical analyses due to their small sample size.

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.

Seed planning zones with fewer than 10 total seedlot collections—SM, DK, MIC and FN—were excluded from the statistical analyses due to their small sample size and insufficient temporal coverage. Consequently, the final sample size was 1924 seedlots. Boxplots and scatterplots of the seed yield were generated for the remaining 18 SPZs (Figures 2.2 and 2.3) and yield data were log-transformed to normalize the data and reduce skew. The Brown-Forsythe test ($\alpha = 0.05$), 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 used on the transformed data to test for differences between the mean seed yield of each zone. All statistical analyses for this study were carried out in R version 3.1.0 (R Core Team 2014).

Results

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 NST was found to be an order of magnitude higher than that of other SPZs (Table 2.1) and was illustrated by probability density functions (Figure 2.4).

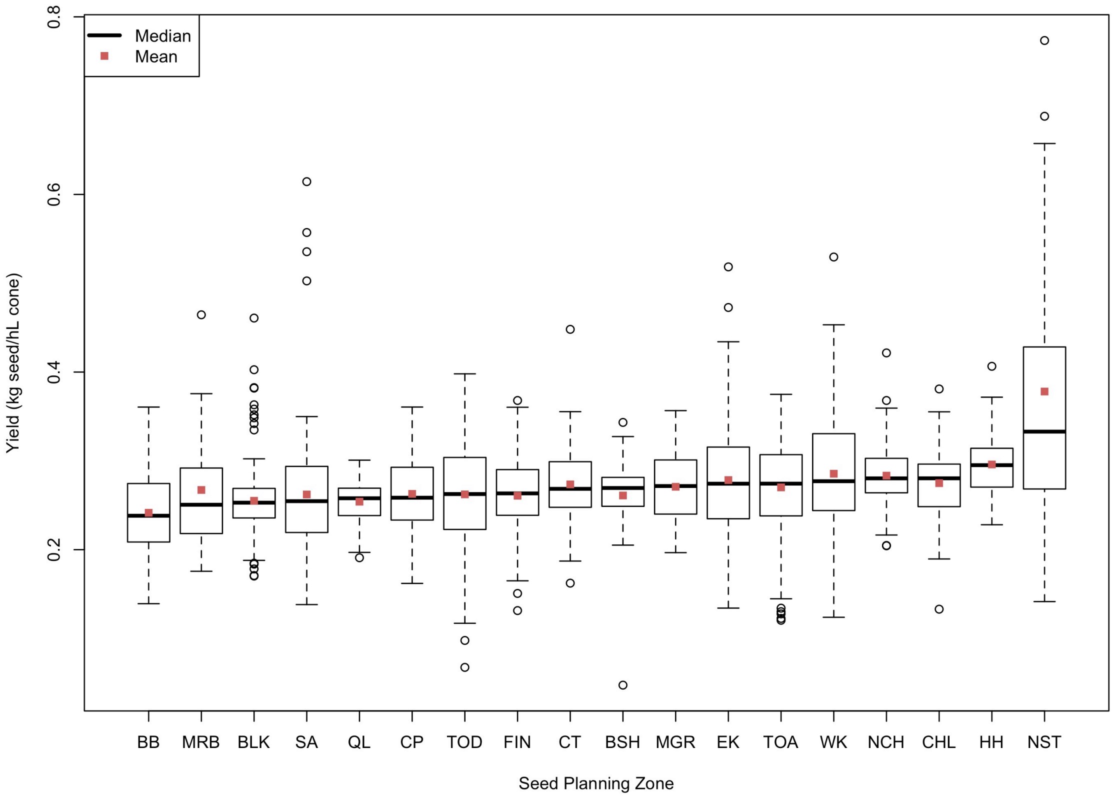

Figure 2.2: Boxplots of natural stand lodgepole pine (*Pinus contorta* Douglas ex Louden) seed yield (kg seed/hL cone) for 18 seed planning zones in British Columbia, Canada, organized by increasing median value. Outliers (open circles) fall more than 1.5 times the interquartile range away from the 1st and 3rd quartiles.

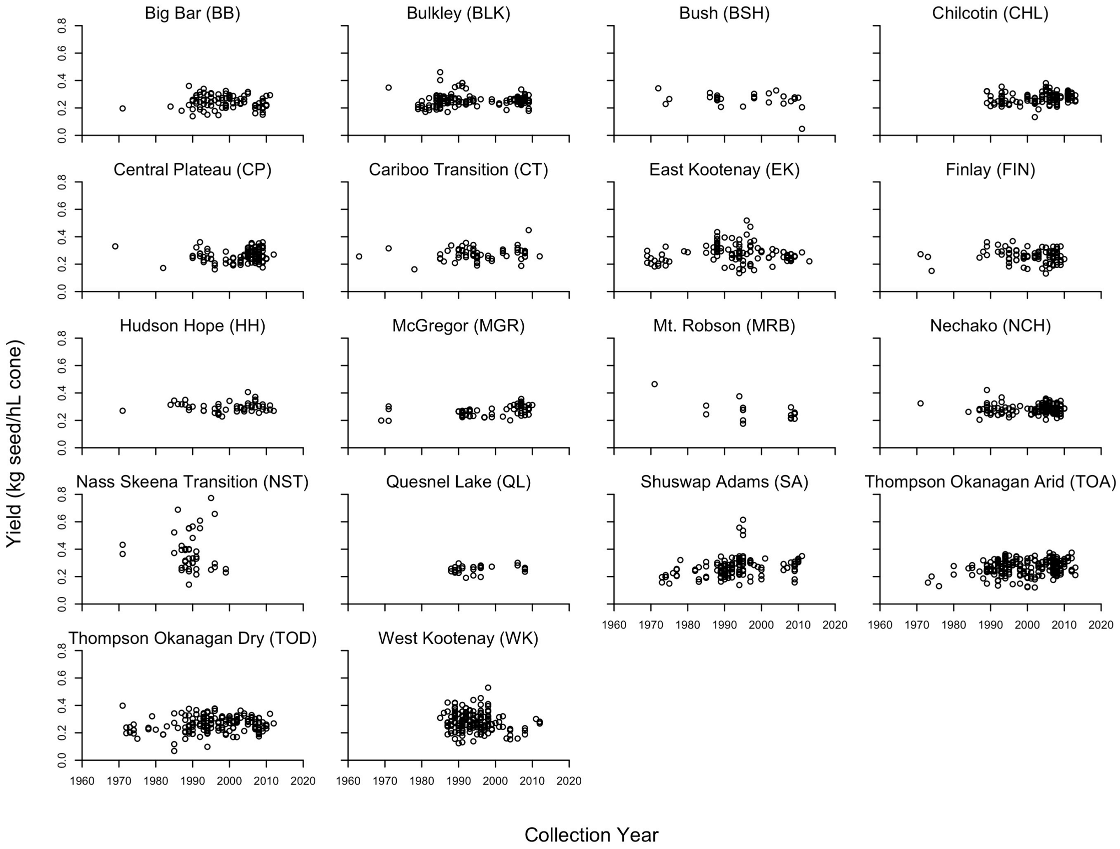

Figure 2.3: Natural stand lodgepole pine (*Pinus contorta* Douglas ex Louden) seed yield (kg seed/hL cone) for 18 seed planning zones in British Columbia, Canada, with collections between 1963 and 2013.

Table 2.1: Summary of the number of seedlots sampled and descriptive statistics (mean and variance) 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.

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

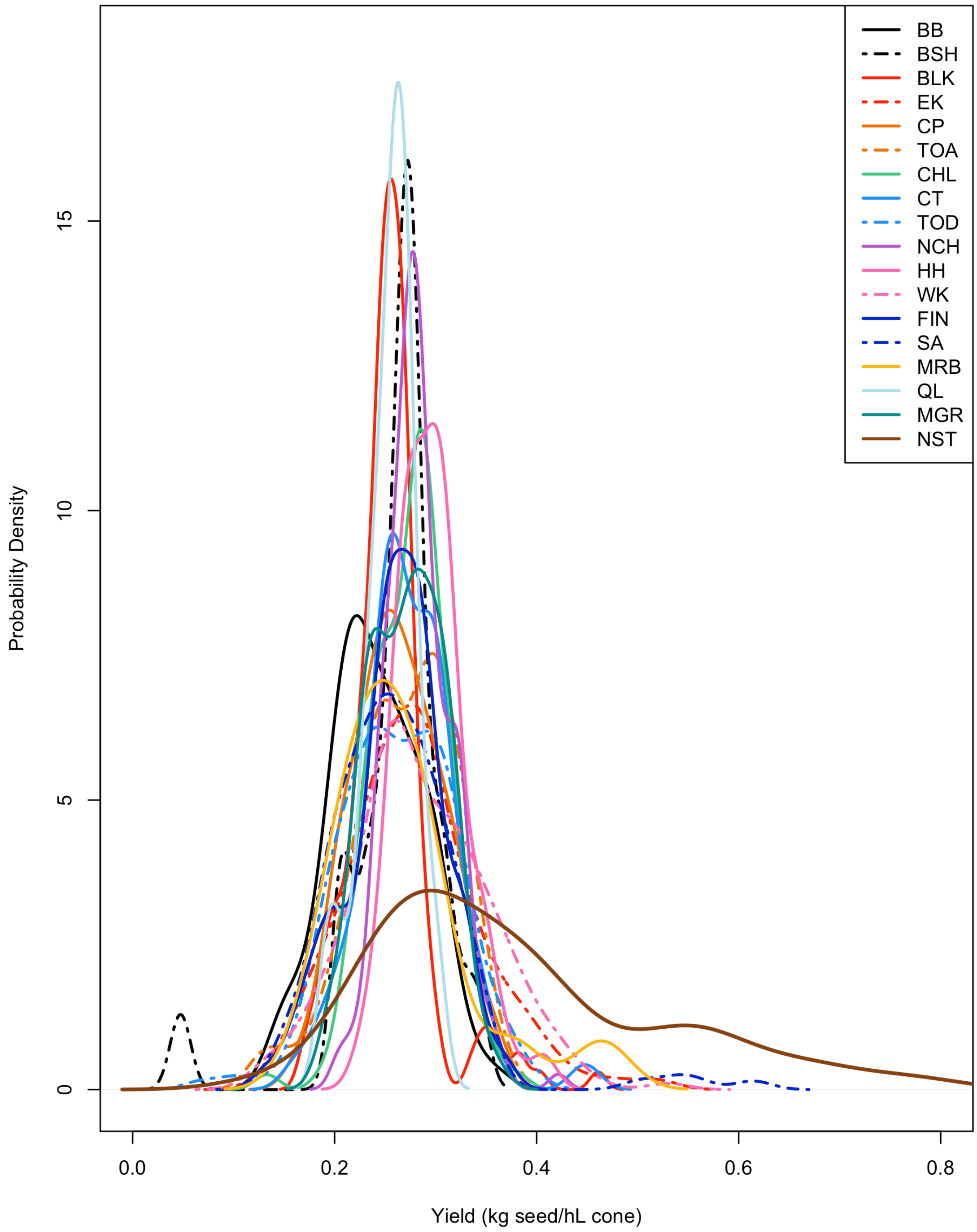

Figure 2.4: Probability density functions of natural stand lodgepole pine (*Pinus contorta* Douglas ex Louden) seed yield (kg seed/hL cone) for 18 seed planning zones in British Columbia, Canada.

The mean seed yield of NST (0.378 kg seed/hL cone) was found to be considerably higher than the mean seed yield of the 17 other zones (0.268 kg seed/hL cone) (Table 2.1). Furthermore, 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 than in all other zones except HH (Table 2.2). 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 ($t_{(46)} = 3.7$, $p = 0.0461$).

Discussion

The Nass Skeena Transition SPZ is situated in northwestern BC (Figure 2.1) and spans the intersection between the Coastal Mountains to the west, the Skeena Mountains to the southeast and the Stikine Plateau to the northeast. As a result of its unique geography, this zone represents a heterogeneous, transitional climate with both maritime and continental characteristics (Bennuah et al. 2004). Consequently, its steep environmental gradient makes NST a well-known hotspot for interspecific hybridization and introgression between coastal and interior coniferous species (Hamilton et al. 2013). Introgression theoretically arises when hybridization and back-crossing occur over many generations, resulting in individuals with varying proportions of genetic material from each parental species (Arnold 1997). 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) and presumably higher tolerance of environmental

Table 2.2: Results of post-hoc Games-Howell tests for differences in mean seed yield of natural stand lodgepole pine (*Pinus contorta* Douglas ex Louden), with emphasis on pair-wise comparisons between Nass Skeena Transition (NST) and 17 other seed planning zones in British Columbia, Canada.

	t-value	**df**	**P-value**
QL:NST	5.8	53	< 0.0001
BB:NST	6.9	54	< 0.0001
BLK:NST	6.1	46	< 0.0001
FIN:NST	5.6	53	0.0001
SA:NST	5.7	53	0.0001
TOD:NST	5.7	52	0.0001
CP:NST	5.5	49	0.0002
TOA:NST	5.2	47	0.0005
MGR:NST	4.9	51	0.0014
CT:NST	4.7	55	0.0024
CHL:NST	4.7	47	0.0025
EK:NST	4.6	56	0.0030
WK:NST	4.3	52	0.0087
BSH:NST	4.2	65	0.0100
NCH:NST	4.2	44	0.0137
MRB:NST	3.9	44	0.0268
HH:NST	3.3	49	0.1260

stresses (Fan et al. 1997). For instance, increased white pine weevil (*Pissodes strobi* Peck) resistance has been observed in some natural spruce hybrids in the Nass and Skeena watersheds (Ying 1991), making it one of only three isolated locations in BC known to possess this heritable ecological adaptation (King and Alfaro 2009).

Though less well-studied, lodgepole pine also shows unique characteristics in NST, where it has been a considerable seral component of the forests for at least the past 10 000 years (Strong and Hills 2013). Two varieties of lodgepole pine are relevant to this region: 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). Levels of foliar secondary metabolites, which play a role in relieving 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 (e.g., drought), thereby allowing the trees to allocate additional resources to secondary metabolism and reproduction (Herms and Mattson 1992).

Previous research indicates that lodgepole pine growing at low to middle elevations, similar to those found in NST, responds positively to higher precipitation (Case and Peterson 2007). Since native populations of *P. contorta* var. *latifolia* tend to be found in environments that are cooler than their optimum for growth and drier than their optimum for survival (Rehfeldt et al. 1999), it is possible that the more maritime climate of NST is advantageous for lodgepole pine (Wallis et al. 2011). However, conditions in this area may also be favorable for biological stresses, such as pest development, which would impose selective pressures on the trees to produce more defense-related chemicals (Wallis et al. 2010). In recent years, Dothistroma needle blight (*Dothistroma pini* Hulbary) has caused severe and widespread damage to lodgepole pine plantations in the Nass River valley (Woods et al. 2005). There have also been major pine beetle infestations in the Nass and Skeena river areas in the late 1970s and 1980s (Unger 1993).

Although NST is considered an interior natural stand seed planning zone, 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 account for the limited height attained by interior lodgepole pine trees near the coast-interior transition zone of western Canada (Xie and Ying 1995). Coastal regions are generally more productive (Parish and Thomson 1994), causing varieties like shore pine (*P. contorta* var. *contorta*) to be better adapted to deal with competition from fast-growing species like Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Roche 1962). *Pinus contorta* var. *contorta* populations are also, on average, the most genetically variable in lodgepole pine (Wheeler and Guries 1982a) and tend to exhibit higher seed yields than the interior variety (Anonymous 2010). These 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 (Figure 2.3), especially since operational limitations in the present study made varietal identification unfeasible.

While samples in our analysis were not identified based on variety, differences in serotiny, or closed-cone habit, between coastal and interior populations may also explain the differences in seed production of NST. Fire-induced serotiny is ecologically important for lodgepole pine and ensures that it remains an aggressive pioneer species (Muir 1993). While most of the interior distribution of the species has serotinous cones, the trait tends to be uncommon in coastal populations (Fowells 1965) where fire is a less prevalent environmental disturbance (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 periodic 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 in this environment.

Based on the limitations of the present study, it is unclear why NST and HH do not have significantly different mean seed yields. Future research may reveal potential climatic and geographic explanations for this similarity. However, HH is situated in an area where extensive interspecific hybridization between lodgepole pine and jack pine (*Pinus banksiana* Lamb.) is well-documented (Wheeler and Guries 1987). It is suspected that jack pine introgression may have influenced the evolution of disease and insect resistance in lodgepole pine provenances from this region (Wu et al. 1996). Although it is unclear whether this jack pine introgression zone influences lodgepole pine seed production in any way, natural hybrid zones are known to be important sources of novel genetic variation in which recombinants may become superiorly adapted (Hamilton et al. 2013). Enhanced seed production in these two zones may also be attributed to phenotypic plasticity, which is 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).

Both environmental and genetic factors may help to explain the geographic differences in lodgepole pine seed yield observed in this study. However, the overall contribution of each factor remains unclear. In a previous study, correlations between climate and growth were found to vary regionally (McLane et al. 2011). When grown in warm common test sites of the Illingworth lodgepole pine provenance trial (Illingworth 1978), populations from warm provenances or origins responded more strongly to summer aridity, whereas populations originating from cold provenances responded more to 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, Berland (2013) investigated the reproductive traits of lodgepole pine in Illingworth provenance test sites and found that the average number of seeds per cone remained relatively stable regardless of provenance or climate. In my study, a similar lack of variability in seed yield (kg seed/hL cones) was generally observed within and between natural stand SPZs (Figure 2.3 and Table 2.1). However, since the present study investigated natural stands rather than provenance trials, distinguishing between genetic and environmental effects was problematic.

In this work, assessments of seed yield may have been complicated by the serotiny of lodgepole pine. Cones and viable seeds may be retained on the tree for multiple years before they are released, obscuring the age-range of cones represented in each seedlot collection. Although guidelines for cone collectors specify that collections should be made of healthy cones and must exclude unhealthy-looking cones, any single seedlot collection may contain cones from a number of indistinguishable years. Consequently, this may average out the seed yields, and, therefore, potentially contribute to the relative stability of seed yield observed within and across the majority of SPZs. Another complication arises from the one-off nature of the cone collections. Collections were made singly and not repeatedly from each seedlot. Thus, the seed yield results from combined seedlots in each SPZ may be confounded by temporal and spatial differences between the seedlots themselves. Since seedlot collections were not temporally consistent between zones (Figure 2.3), it is also difficult to make inferences about the differences between seed planning zones from this study alone, especially when regional and global climate may have had variable impacts over the 50-year timespan of the collections.

Conclusion

Overall, my analysis demonstrates that lodgepole pine in NST have a significantly higher mean seed production compared to trees found in other interior seed planning zones, suggesting that the distinctive geography and heterogeneity of this region may be conferring a reproductive advantage (Herms and Mattson 1992). Although mean seed production in NST was not significantly different from that in HH, it is noteworthy that HH is a region where jack pine introgression is well known (Wu et al. 1996). Brown-Forsythe’s test showed unequal variances between the seed yields of the 18 zones and the variance in seed yield for NST was found to be an order of magnitude higher than that of other SPZs (Table 2.1), indicating that the region also exhibits extraordinarily variable seed production. This geographic variation in reproductive fitness suggests that climate adaptation and mitigation strategies for some areas of the province may need to be region-specific. Although this study cannot directly attribute reproductive differences to specific environmental or genetic factors, the unique seed production in NST documented here is certainly worthy of further investigation. Transitional ecosystems offer an exceptional opportunity to understand how environmental variability and selection pressure may lead to adaptive evolution (Hamilton et al. 2013), which is particularly important for managing this economically important tree species in a changing climate.

CHAPTER 3: CLIMATIC CORRELATES OF *PINUS CONTORTA* SEED PRODUCTION IN BRITISH COLUMBIA

Introduction

Information about how forests respond to climatic variability will allow managers to better anticipate and plan for future changes to ecosystem dynamics. It is expected that most forest tree species will be left growing in temperatures far too warm for them (Adams 2007). Although past events suggest that 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). For a wide-ranging and incredibly variable species such as lodgepole pine, these types of assessments require a particularly thorough understanding of how climate impacts all aspects of the organism.

As a result of the economic and ecological value of lodgepole pine, much of the research to date has focused on climate responses pertaining to growth. The growth and survival of individual trees seems to be related to the climatic conditions of the local environment (Wu et al. 2005). In the North Cascades National Park, for example, climatic variability at annual and decadal timescales is thought to be the primary driver of growth variation in *Pinus contorta* var. *latifolia* (Case and Peterson 2007). It is also hypothesized that young lodgepole pine plantations in the sub-boreal zone of BC may benefit temporarily from the longer growing seasons predicted as climate changes (Cortini et al. 2011).

Growth and survival are certainly essential components of biological fitness—the ability to survive, reproduce and propagate genes in an environment—but so is reproduction. Research on the effects of climate variation on the reproductive characteristics of lodgepole pine has only recently begun. Berland (2013) utilized multiple analysis of variance and univariate linear modelling to develop a best-fit model for predicting the number of lodgepole pine seeds per cone. The model included a single principal component that was most closely aligned with variables related to temperature, the number of frost-free days, and degree-days above 5 °C or below 0 °C. It was determined that climate may not be the most important factor in predicting the number of seeds per cone, since the best-fit model only explained 4.1 % of the variation in the data (Berland 2013). Furthermore, the average number of seeds per cone was relatively stable across climate regimes, which is fascinating considering that growth and survival tend to vary widely across these same regimes (Rehfeldt et al. 1999; Wu et al. 2005; O'Neill et al. 2008a). These findings undoubtedly necessitate support from further research in order to ensure that reforestation seed sources are effectively managed in a changing climate.

Understanding the historical trends in temperature and precipitation is essential in order to put future climate projections in context. Overall, historical climate records indicate a rise in annual surface air temperature for BC during the 20th century (Zhang et al. 2000; Whitfield et al. 2002), with the most pronounced warming occurring in the winter and in more northern regions (Rodenhuis et al. 2007). Spatial and temporal patterns in annual precipitation tend to be much more variable; mean annual precipitation has generally increased across BC over the past 100 years (Zhang et al. 2000), but has decreased locally in the south coastal region, Columbia River basin, and Peace watershed during winter over the past 50 years (Rodenhuis et al. 2007). In BC, long-term assessments using observational data are possible due to an extensive inventory of instrumental climate records extending back to around 1950 (Walker and Sydneysmith 2008). Although the network of climate stations has expanded considerably since then, it still lacks sufficient spatial coverage to accurately reflect the extremely diverse climate of the province (Miles and Associates 2003). Climate modelling offers a unique solution to this issue: the dynamics of the climate system may be understood and future projections can be made over large areas using mathematical simulations.

Global Circulation Models (GCMs) are capable of simulating historical and future changes in the climate regime, 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. Statistical downscaling approaches utilize complex equations in order to interpolate output to a higher resolution (Wilby and Wigley 1997). These techniques can be restricting, as they often require temporally extensive datasets of climate variables in order for statistical relationships to be properly calculated (Fowler et al. 2007). In addition, the location of the observation stations dictates where the statistical technique can be applied (Fowler et al. 2007). However, statistical downscaling is also much less computationally expensive than its dynamical counterpart (Newman et al. 2011).

Dynamical downscaling is a nested modelling technique whereby output generated from a lower-resolution model is fed into a higher-resolution Regional Climate Model (RCM) as its initial and boundary conditions (IPCC 2007). While the lower-resolution model output is often from a GCM, it can also be from meteorological reanalysis (IPCC 2007). Reanalyses are created using a fixed data assimilation scheme and models that utilize a varying availability of raw historical data for given time periods (Kalnay et al. 1996). These global data sources represent a reasonably accurate simulation of the actual climate (Gibson et al. 1997) on large scales (similar to that of GCMs) and are a combination of models and observations.

RCM output tends to reflect a reasonable degree of temporal reality when reanalyses are input as the boundary conditions, primarily because reanalysis integrates meteorological observations (Kalnay et al. 1996). However, since reanalyses are confined to the historical period, this limits the number of realizations of the RCM that can be generated. Smoothing climate variability using a multitude of realizations is essential if there is any hope of isolating signals, particularly over relatively short timescales (Pierce et al. 2009). GCMs can be extended into the future and, when implemented as boundary conditions, provide an opportunity for many more realizations using the RCM (Pierce et al. 2009). Physically reasonable, but not necessarily observed, initial conditions for the 3D state of the atmosphere, ocean and land surface are used to integrate the system of governing nonlinear equations in a GCM forward in time, with no further observational input (Satoh 2013). An ensemble of simulations can be generated using slightly perturbed versions of these initial states. The atmospheric dynamical equations are sufficiently nonlinear as to produce a stochastic component that, after a few years, removes any sensitivity of subsequent states to the initial conditions (Palmer and Williams 2008; Satoh 2013). Consequently, there is no expectation of temporal synchronicity between individual GCM runs, or ensemble members (Déqué et al. 2007). As a result, GCMs are also unable to pinpoint short-term variability in the climate system, such as El Niños, with a high degree of certainty (Schneider et al. 2003; IPCC 2007). Despite these limitations, the mean of multiple ensemble members can reasonably reflect long-term trends (i.e., decadal and longer) in climate, which is still valuable information on a regional scale. It is important to recognize, however, that RCMs fed with GCM boundary conditions retain this temporal ambiguity in their own output (Kendon et al. 2010).

In general, dynamical downscaling systematically links models of different scales so that an increasingly detailed representation of a region can be generated without losing the dynamic characteristics of each individual gridcell (IPCC 2007). Unlike statistical techniques, RCMs are capable of representing all climate variables present in the model and are not limited to variables with long observational records. Furthermore, RCMs generate output over the entire region of interest, regardless of where the historical climate observations were made (Fowler et al. 2007).

To date, extensive studies examining population-scale responses of *P. contorta* to climate have been primarily conducted using statistically-downscaled climate output (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). By comparison, climate output generated by RCMs through dynamical downscaling retains information describing physically consistent processes in the climate system (Fowler et al. 2007). As a result, RCMs are predicted to provide more realistic outcomes for highly complex terrain (Giorgi et al. 2001), such as that in BC. However, no suitable RCM was previously available for the province. While neither downscaling technique has been found to be consistently superior (Newman et al. 2011), research using RCMs is necessary to expand on the breadth of knowledge founded by studies using statistically-downscaled climate outputs.

The current study utilized output from the Canadian Regional Climate Model (CRCM) in order to examine the relationship between climate variation and natural stand *P. contorta* seed production in BC. Understanding how the reproductive capacity of lodgepole pine responds to variations in climate will be vital information for managing future climate-related alterations to reforestation seed sources and other forestry practices in the province.

Materials and Methods

Seed Yield of Natural Stands

Historical cone collection data were obtained from archived records of 1948 seedlots in 22 different natural stand SPZs (see Chapter 2 Figure 2.1) established by the BC Ministry of Forests (Anonymous 1987). SPZ labels are henceforth excluded from figures to minimize clutter. Refer to Chapter 2 Materials and Methods for more information.

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.

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. The seed yields of seedlots collected in the same SPZ during the same year were averaged together to determine a mean annual seed yield for that region.

Climate Output

Model output from CRCM version 4.2.4 served as the climate information for this study. Output was utilized from two runs with NCEP-DOE Reanalysis 2 boundary forcing at both a high (15 km x 15 km) and low (45 km x 45 km) resolution and from 8 low-resolution (45 km x 45 km) runs with GCM boundary forcing (Table 3.1). The reanalysis-driven runs of CRCM extended from 1979-2004, while the GCM-driven runs were analyzed from 1958-2000 in order to remain consistent with the historical emissions scenario incorporated in the model. The two climate variables of interest were 2-metre surface air temperature (°C) and total precipitation (rain & snow) (mm), henceforth referred to as surface temperature and precipitation, respectively. The annual, winter (December-February, DJF), and summer (June-August, JJA) mean of each climate variable was also calculated using each model output. Model output from the 15 km x 15 km resolution CRCM output with reanalysis boundary forcing was also averaged from 1979 to 2004 and mapped for each climate variable in order to geographically compare the climatic differences between zones.

Table 3.1: Model output from the Canadian Regional Climate Model (CRCM) version 4.2.4 utilized in this study.

Run Name	Resolution	Boundary forcing (ensemble member)	Years
CRCM15-NREA	15 km x 15 km	NCEP-DOE Reanalysis 2	1979-2004
CRCM45-NREA	45 km x 45 km	NCEP-DOE Reanalysis 2	1979-2004
CRCM45-EGCM1	45 km x 45 km	ECHAM5 coupled GCM (#1)	1958-2000
CRCM45-EGCM2	45 km x 45 km	ECHAM5 coupled GCM (#2)	1958-2000
CRCM45-EGCM3	45 km x 45 km	ECHAM5 coupled GCM (#3)	1958-2000
CRCM45-CGCM1	45 km x 45 km	CGCM3 coupled GCM (#1)	1958-2000
CRCM45-CGCM2	45 km x 45 km	CGCM3 coupled GCM (#2)	1958-2000
CRCM45-CGCM3	45 km x 45 km	CGCM3 coupled GCM (#3)	1958-2000
CRCM45-CGCM4	45 km x 45 km	CGCM3 coupled GCM (#4)	1958-2000
CRCM45-CGCM5	45 km x 45 km	CGCM3 coupled GCM (#5)	1958-2000

Accounting for Serotiny

A moving window, or trailing-mean, of 3, 5 and 10 years was calculated for each climate variable using each CRCM model output in order to account for the serotiny of lodgepole pine. Since fully-developed cones and viable seeds may be retained on the tree for multiple years, the age-range of cones from each seedlot was highly ambiguous. Thus, the climate corresponding to each collection had to be assigned more conservatively using a mean value. In the case of annual means, the previous 3, 5 or 10 years of output was averaged and assigned to the final year of the window. For the winter (and summer) mean, the previous 3, 5 or 10 winter (summer) means were averaged and assigned to the final winter (summer) of the window. Each unique combination of model output, trailing-mean and seasonal or annual average is henceforth referred to as a climate scheme.

Data Analysis

For each climate scheme, the 1948 seedlots were individually assigned an appropriate value of each climate variable based on two criteria: the year of collection and the seed planning zone. First, the collection year isolated the correct time slice of the climate output for that seedlot. Next, the applicable seed planning zone designation for that seedlot further isolated gridcells of a particular longitude (λ) and latitude (*ϕ)*. These gridcells were then weighted with respect to latitude and the spatially-weighted mean ($\bar{\chi}_{weighted}$) of the climate variable (χ) was assigned to the seedlot of interest:

$$\bar{\chi}_{weighted} = \frac{\sum_i \sum_j \chi_{(\lambda_i,\phi_j)} \cos(\phi_j)_{(\lambda_i,\phi_j)}}{\sum_i \sum_j \cos(\phi_j)_{(\lambda_i,\phi_j)}}$$

(Eq. 1)

This procedure was repeated for each seedlot under each climate scheme. For any climate model, it is imperative that the output be averaged temporally and over a pre-determined area because the inherent internal variability of the model makes it inappropriate to analyze individual gridcells at individual time-steps (Hewitson 2003).

Once the appropriate climate variable values were assigned to each seedlot, the seedlots were divided based on their corresponding SPZ. 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 different set of climate output. Climate anomalies calculated from reanalysis-driven CRCM output were represented under each of the three trailing-means: 3, 5 and 10 years. Anomalies of climate model output were independently calculated for each of the 8 GCM-driven CRCM ensemble runs before averaging them together to give a multi-model ensemble mean anomaly and a ± 2 standard deviation envelope based on the ensemble spread. The GCM-driven CRCM output was also represented under each of the three trailing-means: 3, 5 and 10 years.

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 small sample sizes and bivariate 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. Despite the issue of multiplicity, global hypotheses of significant correlation ($\alpha_{global} = 0.05$) were tested using the approach developed by Livezey and Chen (1983), and the probability distribution function for the binomial distribution:

$$\Pr\{X = x\} = \binom{N}{x} p^x (1-p)^{N-x},\ x = 0, 1, \ldots, N \qquad \text{(Eq. 2)}$$

where X is the number of significant individual tests out of N tests conducted, and p is the level (0.05) of the local tests.

Climate variable anomalies calculated from GCM-driven CRCM output were then analyzed. Instead of temporal correlations, overall trends in climate variables were determined in each SPZ as a means of dealing with the nonsynchronous temporal nature of the 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 trendline to each climate variable anomaly. The slope 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 purposes, a linear trendline was also fit to the mean annual seed yield anomaly over the same interval. The slope (β) of each trendline was then tested to see if it was significantly different ($\alpha = 0.05$) from zero. 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. Despite its simplicity, this approach has been used for determining the level of multi-model agreement in future climate projections (Tebaldi et al. 2011). The sign and significance of the ensemble mean and mean annual seed yield linear trendlines 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 trendlines were subsequently fitted and tested for CRCM45-NREA output over the same time period as the GCM-driven output. All statistical analyses for this study were carried out in R version 3.1.0 (R Core Team 2014).

Results

Climatic differences between zones were predicted using the high resolution CRCM15-NREA output and illustrated based on the average of each climate variable from 1979-2004 (Figure 3.1). Results from the model are reasonably consistent with previous research of the spatial variability of climate in BC (Walker and Sydneysmith 2008). On average, the CRCM model output reveals, as expected, that the southern interior, central interior and northeastern zones of BC tend to be warmer annually than those in the northwest or far southeast of the province (Figure 3.1a). The model shows that northern regions, as well as those in the realm of the Rocky Mountains, tend to have lower mean winter surface temperatures than the rest of the province (Figure 3.1b), presumably due to the influx of cold Arctic air from the north and east (Walker and Sydneysmith 2008). Coastal regions are predicted to have warmer mean winter surface temperatures (Figure 3.1b). Oceans have a greater heat capacity than land, resulting in a moderating effect on surface temperatures in nearby coastal areas (Klock and Mullock 2001). In addition, regions along the BC coast are found to receive the most precipitation in all seasons (Figure 3.1d-f), which makes sense due to their proximity to the ocean and

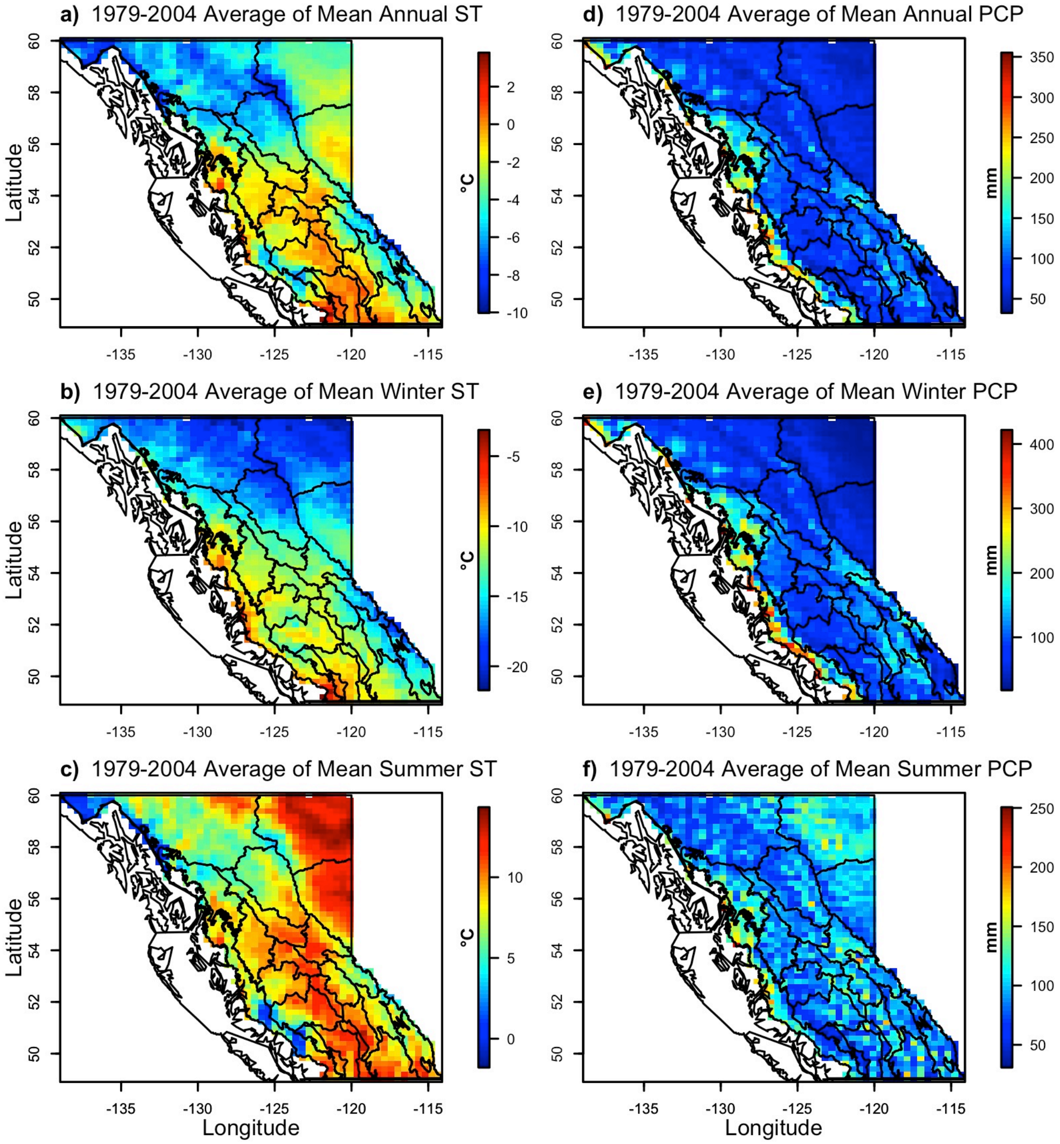

Figure 3.1: 1979-2004 average of mean annual (a), winter (b) and summer (c) surface temperature (ST); and mean annual (d), winter (e), and summer (f) precipitation (PCP) predictions for British Columbia using 15 km x 15 km Canadian Regional Climate Model version 4.2.4 output with NCEP-DOE Reanalysis 2 boundary forcing.

the uplift of moist Pacific air by dominant westerly winds interacting with the Coast Mountains (Walker and Sydneysmith 2008). In contrast, the model finds that the southwestern border of the interior plateau has a relatively dry climate during all seasons (Figure 3.1d-f), which would be expected in the rain shadow of the Coast and Cascade Mountains.

The correlation between each climate variable anomaly and the mean annual seed yield anomaly was calculated for seed planning zones meeting the sample size criteria ($n \geq 10$) using CRCM45-NREA output (Figures 3.2 and 3.3). Local correlations were significant ($\alpha = 0.05$) and reasonably strong in 24 unique combinations of climate schemes and SPZ using CRCM45-NREA output (Table 3.2). In addition, the global null hypothesis—that all local null hypotheses are true—was tested using the approach developed by Livezey and Chen (1983). Climate schemes that produced a sufficient number of statistically significant individual results to warrant the rejection of the global null hypothesis ($\alpha_{global}= 0.05$) are highlighted with red borders in Figures 3.2 and 3.3. In these scenarios, there is a probability no higher than 0.05 that an equivalent or greater number of significant local correlations would have been observed by chance. Anomalies and correlations involving 15 km x 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.

The overall trend of each climate variable anomaly and the mean annual seed yield anomaly was calculated for seed planning zones meeting the sample size criteria

Table 3.2: 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 the CRCM45-NREA run of the Canadian Regional Climate Model version 4.2.4. 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**	**Degrees of Freedom (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

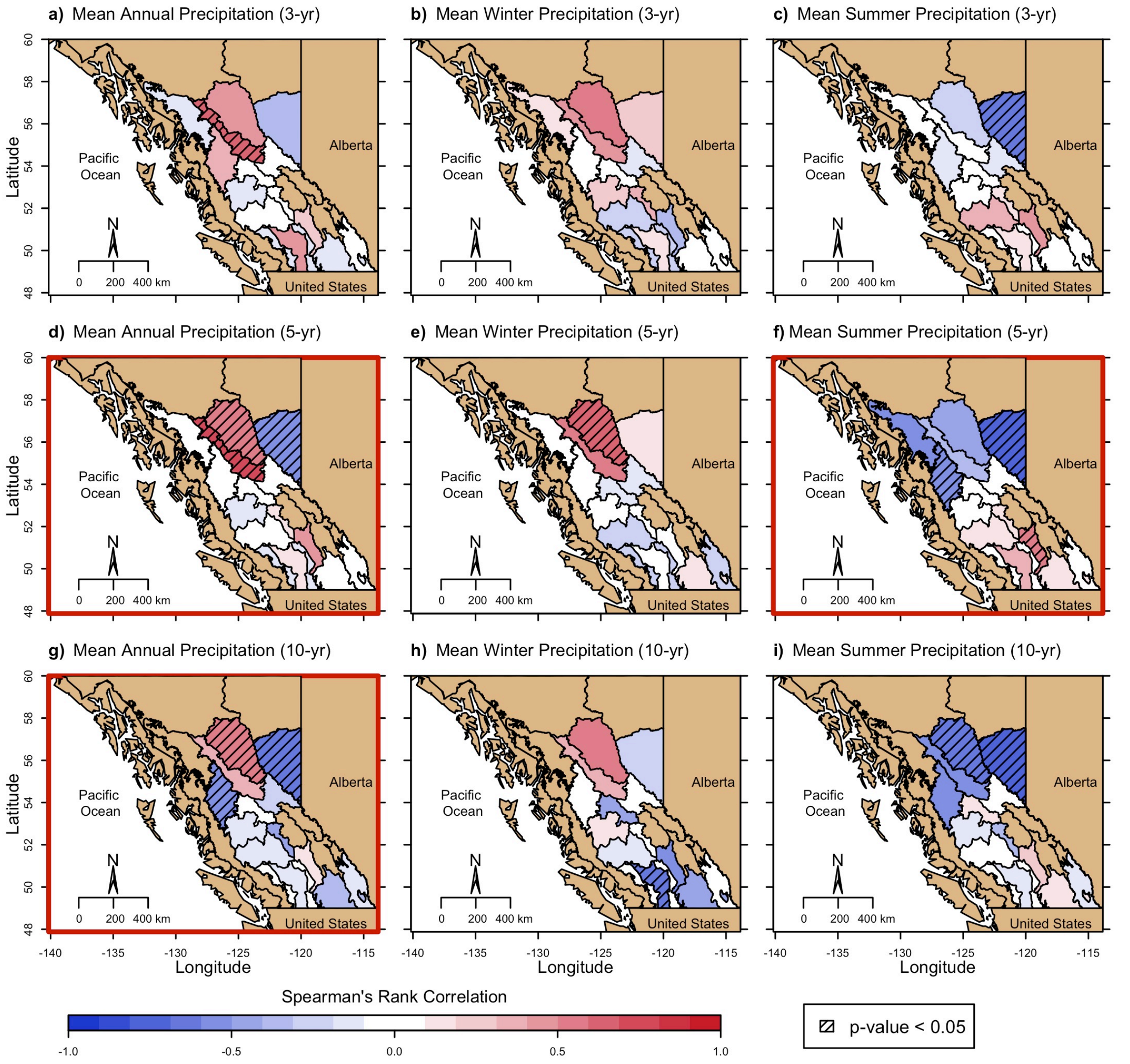

Figure 3.2: Temporal correlations for precipitation. Spearman's rank correlation (r_s) between the mean annual *Pinus contorta* seed yield anomaly (kg/hL) of the corresponding seed planning zone (SPZ) and different climate schemes using Canadian Regional Climate Model version 4.2.4 output from CRCM45-NREA: 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 (α_{global}= 0.05). SPZ with $n < 10$ discrete years of seed yield data for the affiliated climate scheme were excluded.

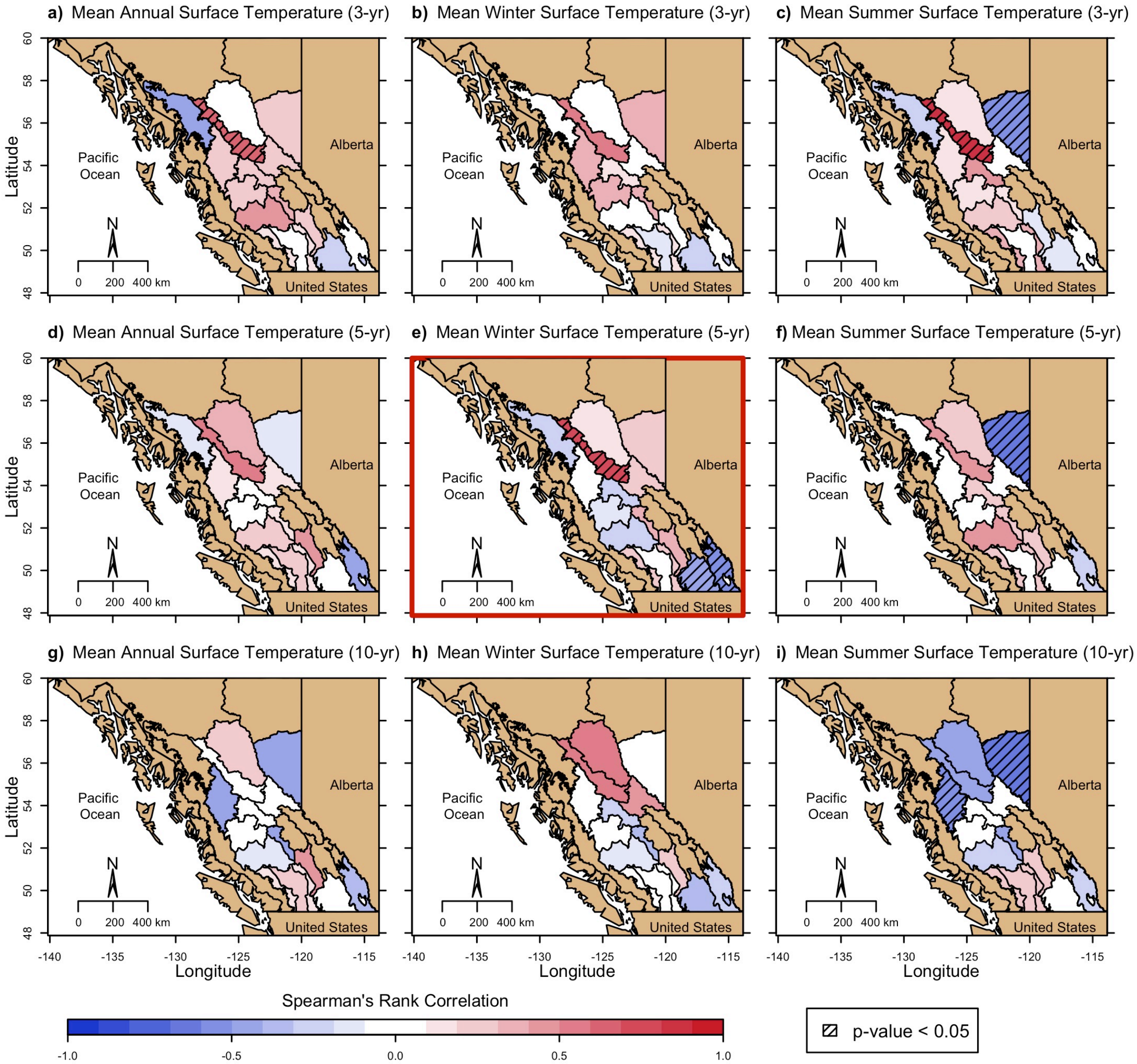

Figure 3.3: Temporal correlations for surface temperature. Spearman’s rank correlation (r_s) between the mean annual *Pinus contorta* seed yield anomaly (kg/hL) of the corresponding seed planning zone (SPZ) and different climate schemes using Canadian Regional Climate Model version 4.2.4 output from 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.

($n \geq 10$) using CRCM output with GCM boundary forcing at the 45 km x 45 km resolution (Figures 3.4 and 3.5). Only three SPZs showed a trend in the mean annual seed yield anomaly that was significantly different ($\alpha = 0.05$) from zero: EK, TOA and SA (Table 3.3). Across these SPZs, 23 climate schemes found climate anomaly trends that were significantly different from zero ($\alpha = 0.05$) amongst the majority of ensemble members using GCM-driven CRCM output (Table 3.3).

The majority of significant local correlations found using CRCM45-NREA output are in more northern SPZs such as HH, CP, FIN and BLK (Table 3.2). However, only four different climate variables showed global field significance ($\alpha_{global}= 0.05$): 5-year mean annual precipitation, 10-year mean annual precipitation, 5-year mean summer precipitation (Figure 3.2), and 5-year mean winter surface temperature (Figure 3.3). Within this group, 5-year mean summer precipitation is negatively correlated with seed production in more northern SPZs such as HH and BLK, and is only positively correlated in one southern SPZ—namely, SA (Figure 3.2f). Mean winter surface temperature averaged over a 5-year window shows the opposite relationship, with CP indicating a positive correlation and the more southern sites—EK and WK—having negative correlations (Figure 3.3e).

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 (Figure 3.5) than in precipitation anomalies (Figure 3.4). In general, GCM-fed CRCM output collectively captures a warming signal in the surface temperatures throughout the province (Figure 3.5).

Table 3.3: 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) of the corresponding seed planning zone (SPZ) and the 8-member ensemble mean of climate variable anomalies generated using 45 km x 45 km precipitation (PCP) and surface temperature (ST) climate output from the Canadian Regional Climate Model (CRCM) version 4.2.4 with Global Circulation Model (GCM) boundary forcing. 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	$\beta_{\text{Seed Yield Anomaly}}$	p-value	Climate Variable Anomaly		Trailing - mean (years)	$\beta_{\text{Ensemble Mean}}$	p-value	Num. of Ensemble Members in Agreement	df
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
					10	0.022	<0.0001	6	19
				Winter	10	0.033	<0.0001	6	19
				Summer	5	0.023	<0.0001	5	19
					10	0.022	<0.0001	7	19

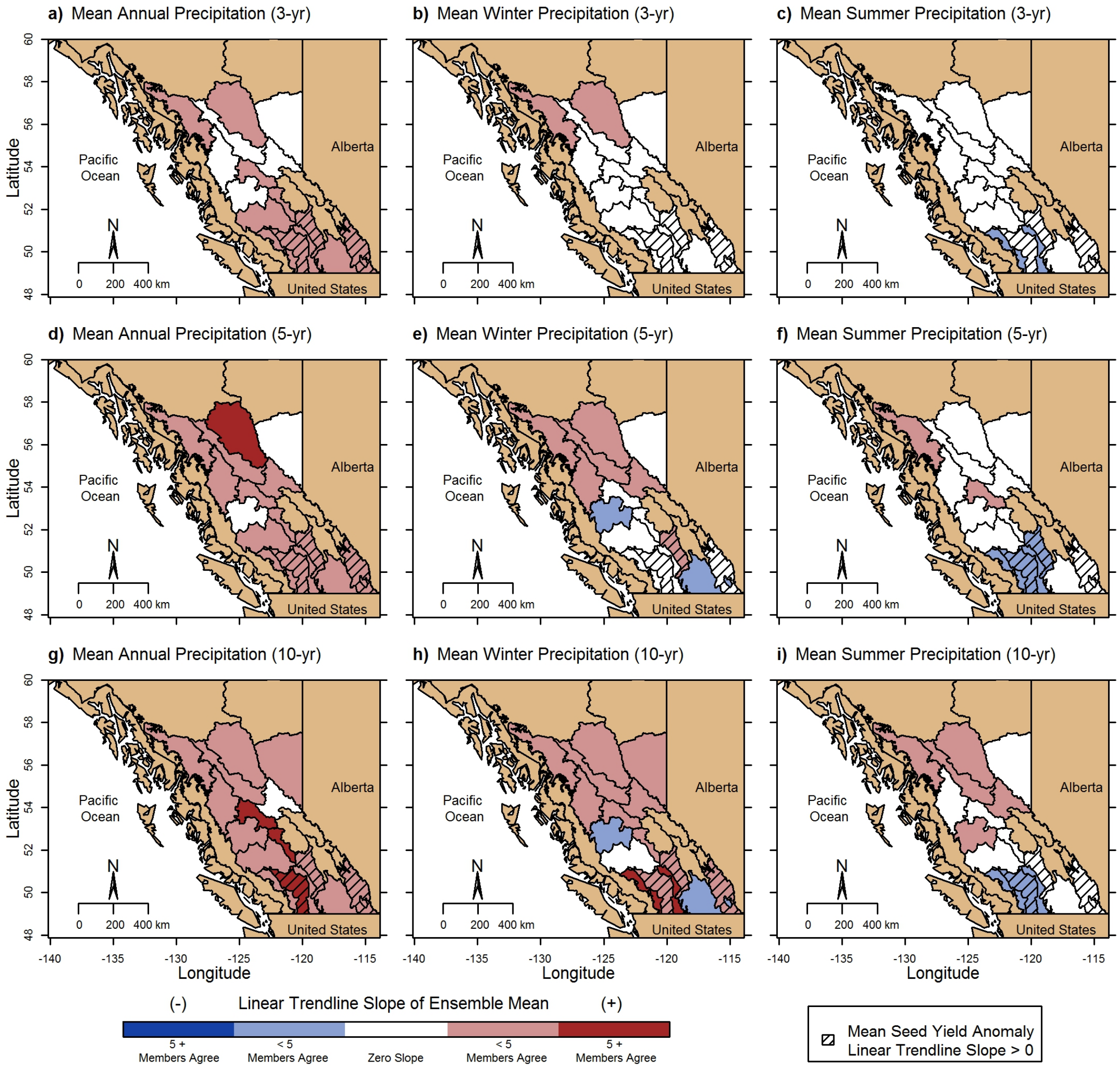

Figure 3.4: Signs of significant ($\alpha = 0.05$) linear trendline slopes (β) for ensemble mean climate variable anomalies of the corresponding seed planning zone (SPZ) under different climate schemes using 45 km x 45 km Canadian Regional Climate Model (CRCM) version 4.2.4 output with Global Circulation Model (GCM) boundary forcing: 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) are indicated by hatching. White SPZs indicate that the slope of the ensemble mean climate variable anomaly 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.

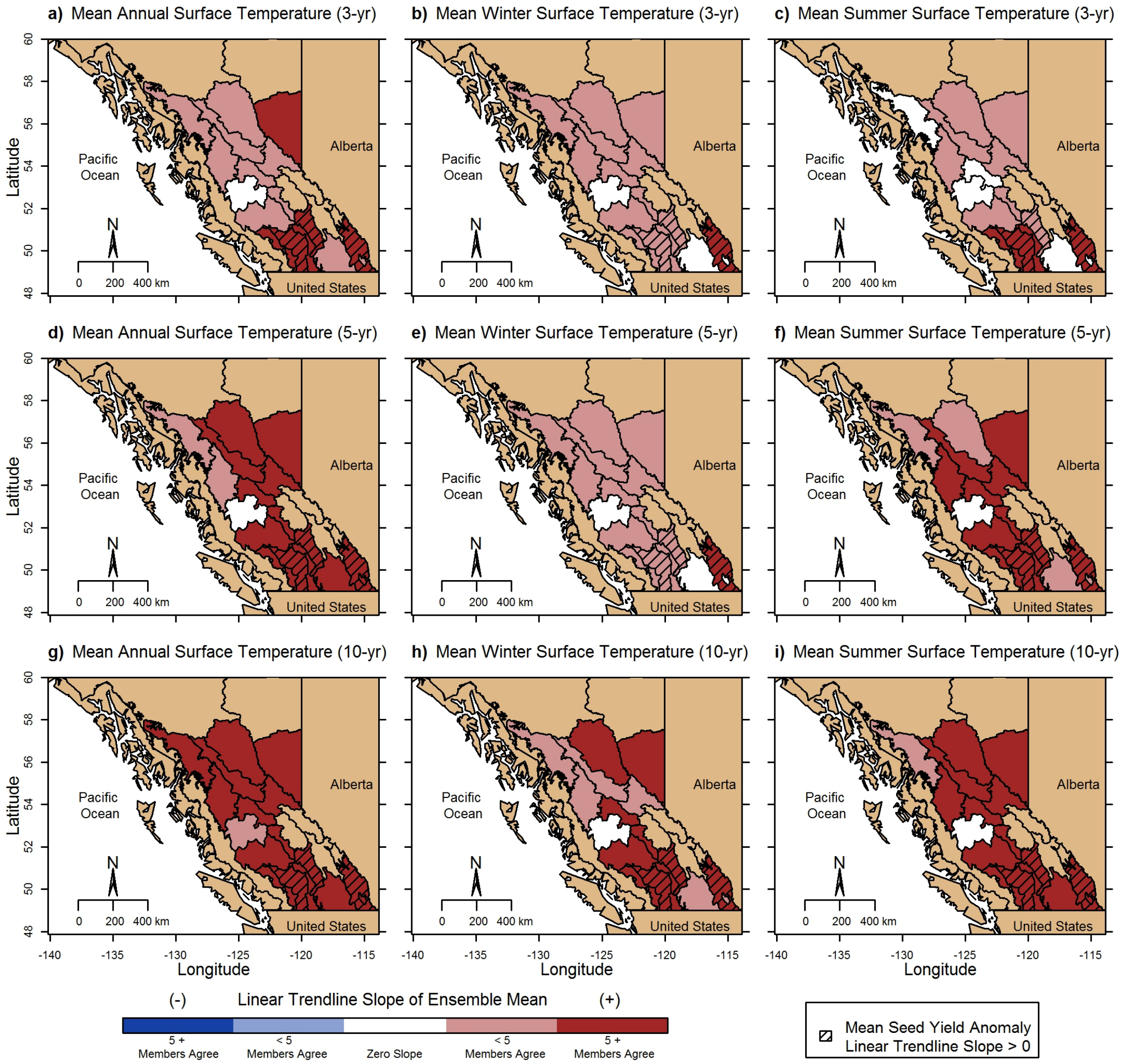

Figure 3.5: Signs of significant ($\alpha = 0.05$) linear trendline slopes (β) for ensemble mean climate variable anomalies of the corresponding seed planning zone (SPZ) under different climate schemes using 45 km x 45 km Canadian Regional Climate Model (CRCM) version 4.2.4 output with Global Circulation Model (GCM) boundary forcing: 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) are indicated by hatching. White SPZs indicate that the slope of the ensemble mean climate variable anomaly 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.

However, only three different SPZs show a trend in mean seed yield anomaly that is significantly different from zero: TOA, SA and EK (Figures 3.4 and 3.5; Table 3.3).

SPZs where CRCM45-NREA output showed reasonably strong correlations with the mean annual seed yield anomaly (Table 3.2) were the natural starting point for further analysis. 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 climate output. Several case studies were used to investigate the extent to which the conclusions of the reanalysis and GCM-driven CRCM output analyses could be consolidated with one another.

First, I focused on a single zone: Central Plateau (CP). Using CRCM45-NREA output, there was a strong positive correlation between the 5-year mean winter surface temperature anomaly and the mean annual seed yield anomaly, $r_{s(10)} = 0.748$, $p = 0.0074$ (Figure 3.6a). Using the GCM-driven CRCM output, the slope of the ensemble mean anomaly for the same climate scheme was found to be significantly different from zero, $\beta = 0.042$, $p = 0.0011$ (Figure 3.6b). However, the majority (5 or more) of ensemble members did not support this trend. The importance of satisfying this condition is clear when the fitted trendline of the ensemble mean is broken down into individual fitted trendlines of the ensemble members (Figure 3.6b). Although four members show a significant positive trend that agrees with the ensemble mean, the other four are not significantly different from zero, and some even allude to a negative trend. The variability between individual ensemble members of the CRCM is expected based on the

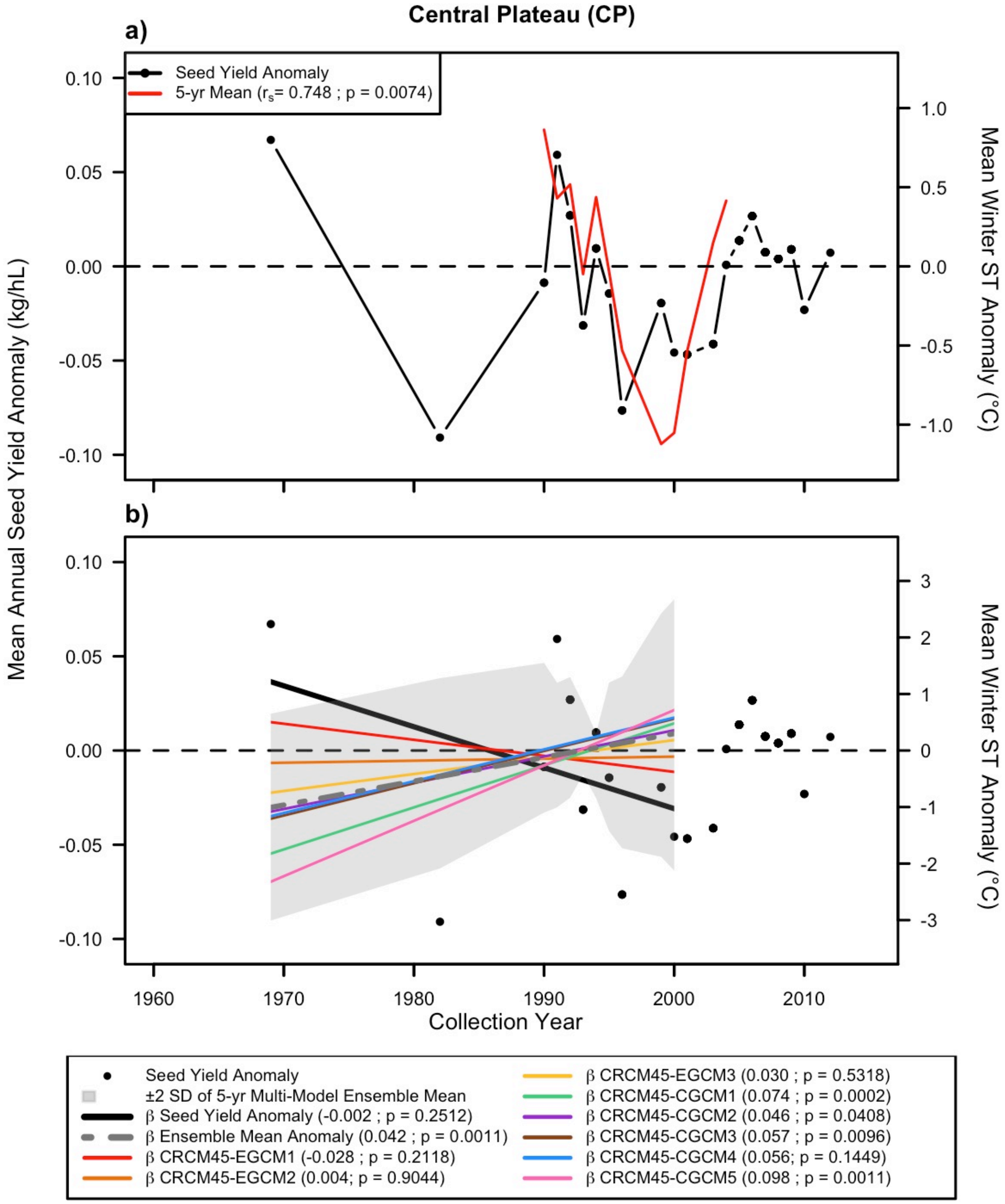

Figure 3.6: Temporal variation of mean annual *Pinus contorta* seed yield anomaly (kg/hL) for Central Plateau (CP) seed planning zone along with: a) 5-year mean winter surface temperature (ST) anomaly calculated using Canadian Regional Climate Model (CRCM) version 4.2.4 output from CRCM45-NREA, and b) Fitted linear trendlines of 5-year mean winter surface temperature (ST) anomaly for an ensemble of eight different 45 km x 45 km CRCM output runs with Global Circulation Model boundary forcing, as well as the ensemble mean. The fitted linear trendline for the mean annual seed yield anomaly is indicated in solid black.

use of different initial and boundary conditions for each simulation and the relatively short time period being analyzed. However, adhering to a strict criterion for majority allows for greater confidence in the overall trend of the ensemble mean. In the case of Central Plateau, violation of this requirement restricts any further comparison between the reanalysis and GCM-driven results.

Even in SPZs where CRCM45-NREA output was significantly correlated with the mean annual seed yield anomaly and the majority of ensemble members agreed with the significant trend found by the ensemble mean of GCM-driven climate output, the results were inconclusive for various reasons. In Hudson Hope (HH), for instance, CRCM45-NREA output of 5-year mean summer surface temperature anomalies were found to be negatively correlated with the mean annual seed yield anomaly, $r_{s(14)} = -0.624$, $p = 0.0116$, from 1984-2004 (Figure 3.7a). The ensemble mean of GCM-driven output of 5-year mean summer surface temperature anomalies showed a significantly positive increase, $\beta = 0.021$, $p < 0.0001$, from 1971-2000 (Figure 3.8a). Over the period of overlap with CRCM45-NREA, i.e. 1984-2000, the result is similar: $\beta = 0.021$, $p = 0.0003$. The trend in CRCM45-NREA 5-year mean summer surface temperature anomalies over this period is also significant and of the same sign: $\beta = 0.037$, $p = 0.0174$. However, since the slope of the mean annual seed yield anomaly was not significantly different from zero during both the 1971-2000 ($\beta = -0.001$, $p = 0.4843$) and 1984-2000 ($\beta = -0.003$, $p = 0.0583$) intervals, the results for this SPZ remain inconclusive.

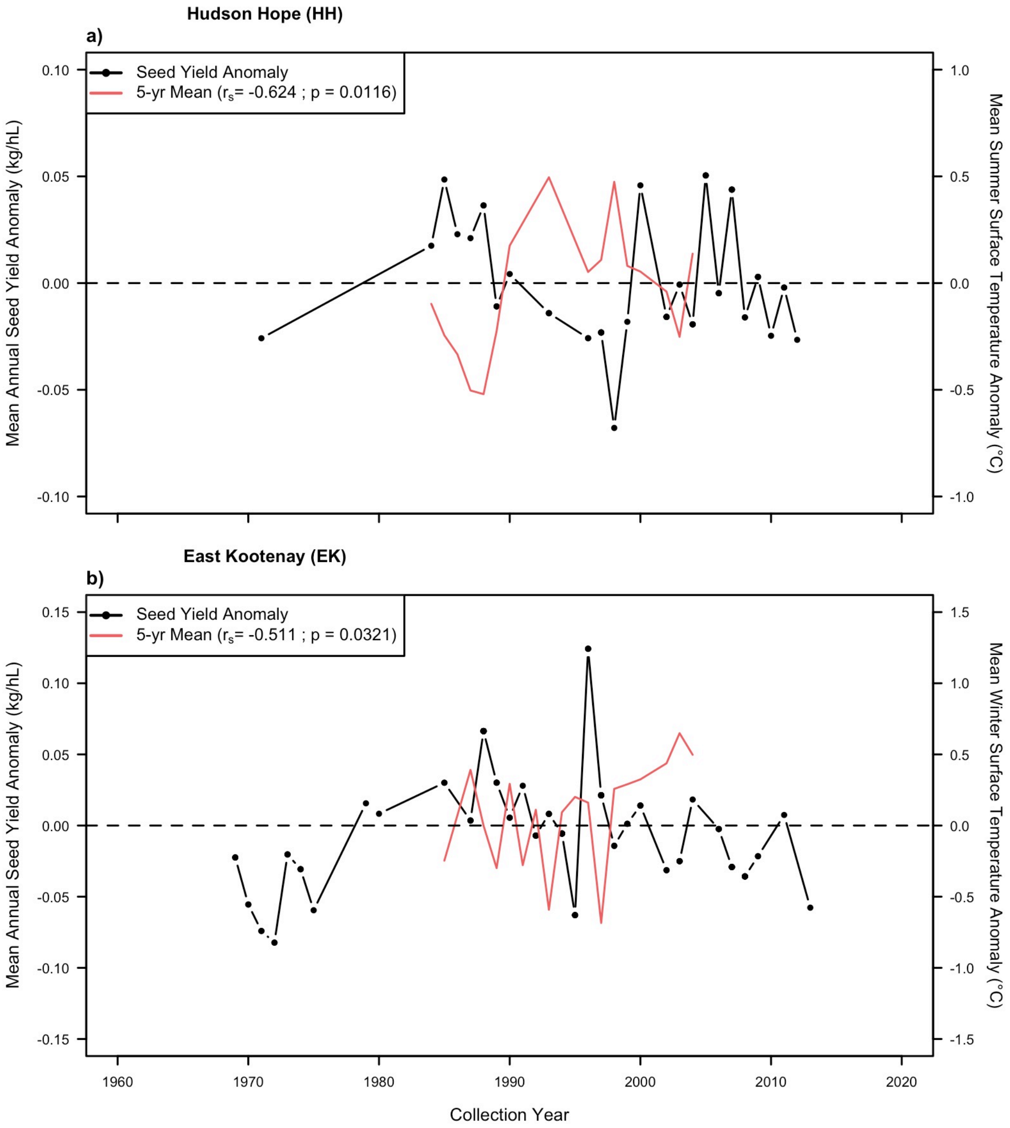

Figure 3.7: Temporal variation of mean annual *Pinus contorta* seed yield anomaly (kg/hL) along with: a) 5-year mean summer surface temperature (ST) anomaly in Hudson Hope (HH), and b) 5-year mean winter ST anomaly in East Kootenay (EK) calculated using Canadian Regional Climate Model version 4.2.4 output from CRCM45-NREA.

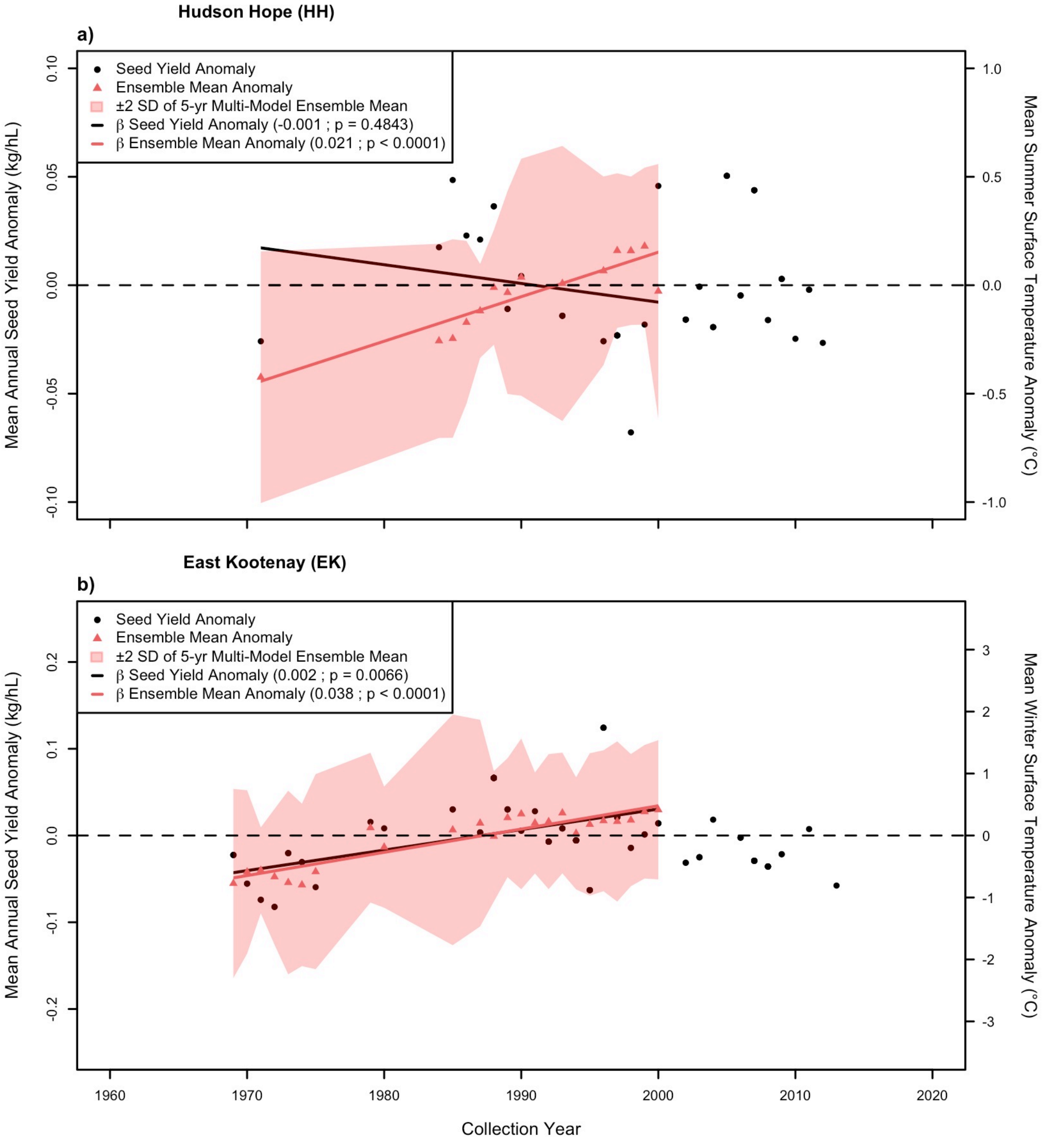

Figure 3.8: Temporal variation of mean annual *Pinus contorta* seed yield anomaly (kg/hL) along with: a) Fitted linear trendline of 5-year mean summer surface temperature (ST) anomaly in Hudson Hope (HH), and b) Fitted linear trendline of 5-year mean winter ST anomaly in East Kootenay (EK) calculated from the ensemble mean of eight 45 km x 45 km Canadian Regional Climate Model version 4.2.4 output runs with Global Circulation Model boundary forcing. The fitted linear trendline for the mean annual seed yield anomaly for each zone is indicated in solid black.

In East Kootenay (EK), CRCM45-NREA output of 5-year mean winter surface temperature anomalies were found to be negatively correlated with the mean annual seed yield anomaly, $r_{s(16)} = -0.511$, $p = 0.0321$, from 1985-2004 (Figure 3.7b). The ensemble mean of GCM-driven output of 5-year mean winter surface temperature anomalies showed a significantly positive increase, $\beta = 0.038$, $p < 0.0001$, from 1969-2000 (Figure 3.8b). Both the GCM and reanalysis-driven CRCM output captured significant relationships in this SPZ under this climate scheme (Table 3.2 and 3.3). In addition, the slope of the mean annual seed yield anomaly was significantly different from zero in EK from 1969-2000, $\beta = 0.002$, $p = 0.0066$ (Figure 3.8b). This single climate scheme and SPZ were the only case where a sound comparison between all elements of the study was possible, because all of the necessary criteria were met: a significant temporal correlation between the mean annual seed yield anomaly and the anomaly of CRCM45-NREA output, a significant overall trend in the ensemble mean anomaly of GCM-driven CRCM output supported by five or more ensemble members, and a significant overall trend in the mean annual seed yield anomaly. However, when the overall trends of these components were investigated by fitting linear trendlines for the overlapping period from 1985-2000, the slopes of the ensemble mean GCM-driven climate anomaly ($\beta = 0.014$, $p = 0.0552$), reanalysis-driven climate anomaly ($\beta = 0.013$, $p = 0.5219$) and seed yield anomaly ($\beta = -0.001$, $p = 0.5865$) were not significantly different from zero.

It is not surprising that the conclusions of the GCM-driven and reanalysis-driven analyses cannot be consolidated beyond the level of local correlations, since the geographic pattern of their results are fundamentally different. For example, the GCM-based analyses exhibit a relatively consistent positive trend in nearly all schemes of the surface temperature anomaly, particularly in southern SPZs where the mean annual seed yield anomaly also showed a positive trend (Figures 3.5 and 3.9). In contrast, analyses using CRCM45-NREA output did not capture significant correlations in these same SPZ under the majority of the surface temperature schemes (Figure 3.3). Analyses using 10-year surface temperature anomalies of GCM-driven CRCM output indicate that in all three zones where a significant positive trend in the mean annual seed yield anomaly was detected—EK, TOA and SA—the ensemble mean and majority of ensemble members also show a significant positive trend (Figure 3.9). When this same analysis is isolated from 1988-2000—the period overlapping with CRCM45-NREA output—a significant positive trend in the ensemble mean remains (Table 3.4). The CRCM45-NREA output also shows a significant positive trend over the same interval for the same climate schemes in each of the three zones, with the exception of the mean winter surface temperature anomalies, which had slopes that were not significantly different from zero (Table 3.4). The lack of trend in the reanalysis-based mean winter surface temperature anomalies is not a concern because the ensemble mean anomaly, while significant, becomes unsupported by the majority of ensemble members for this particular climate scheme from 1988-2000 (Table 3.4). As a result, there are considerable differences between the results of individual ensemble members of the GCM-driven CRCM, with some showing a non-significant slope during this interval. In addition, the slopes of all nine CRCM45-NREA anomalies shown in Table 3.4 always fall well within the range of slopes expressed by the ensemble members of the GCM-driven CRCM. Thus, there is no reason to suspect that the single realization of CRCM45-NREA output is unreasonably different from the output generated by the eight GCM-driven ensemble runs of CRCM.

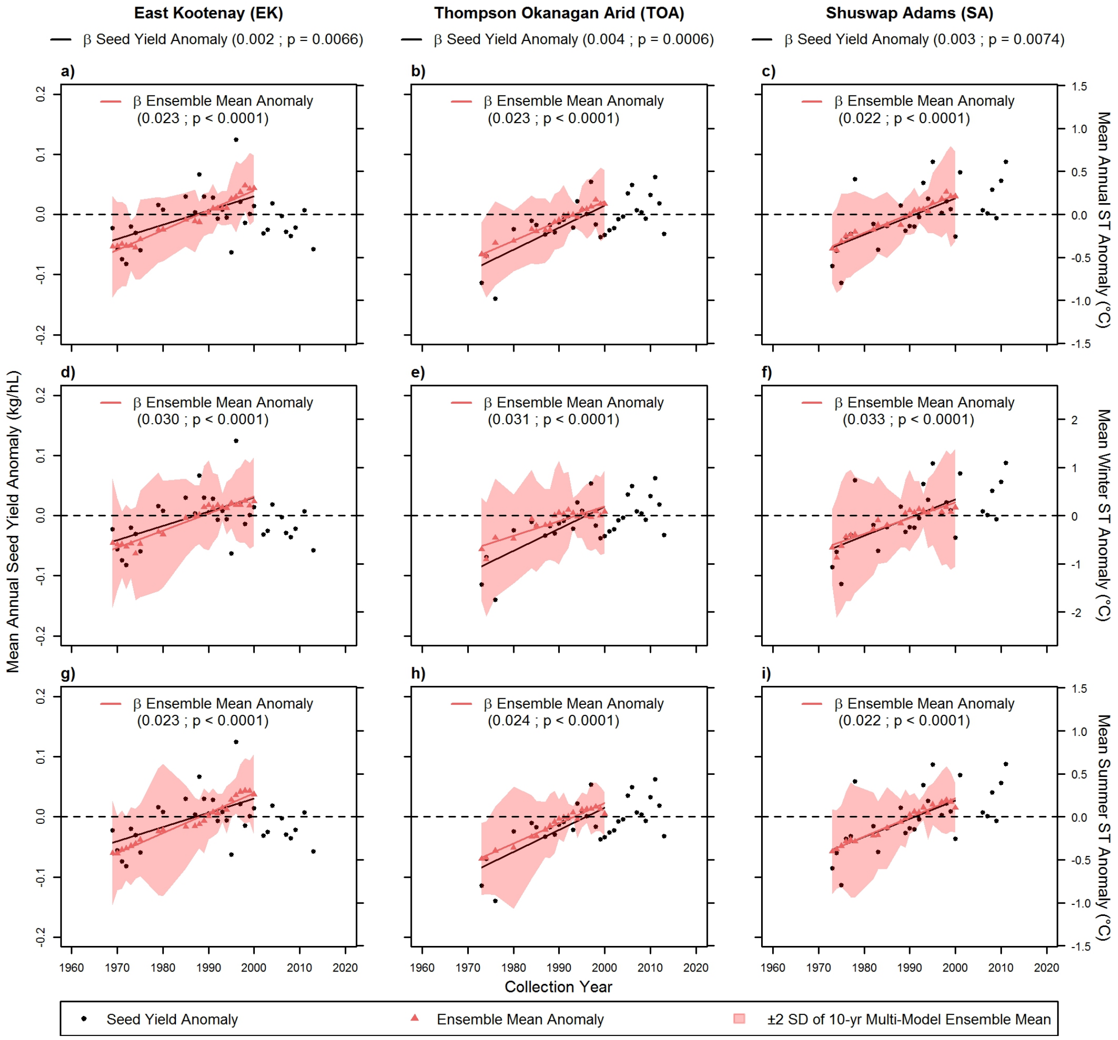

Figure 3.9: Temporal variation of mean annual *Pinus contorta* seed yield anomaly (kg/hL) for seed planning zones East Kootenay (a, d, and g), Thompson Okanagan Arid (b, e, and h) and Shuswap Adams (c, f and i). The fitted linear trendline for the mean annual (a-c), winter (d-f) and summer (g-i) surface temperature (ST) anomalies are calculated for each zone using the ensemble mean of eight 45 km x 45 km Canadian Regional Climate Model version 4.2.4 output runs with Global Circulation Model boundary forcing. The fitted linear trendline for the mean annual seed yield anomaly for each zone is indicated in solid black.

Table 3.4: Slopes (β) of fitted linear trendlines of 10-year surface temperature (ST) anomalies for the seed planning zones (SPZs) featured in Figure 3.9: East Kootenay (EK), Shuswap Adams (SA) and Thompson Okanagan Arid (TOA). Trendlines were calculated for the interval of 1988-2000 for: the ensemble mean anomaly determined from GCM-driven CRCM output, and the reanalysis anomaly determined from CRCM45-NREA output. Many of the slopes were significantly different from zero (α = 0.05). All slopes determined from CRCM45-NREA output fell within the range of slopes calculated for individual ensemble members of the GCM-driven CRCM output.

SPZ	ST Anomaly	β Ensemble Mean	p-value	Num. of Ens. Members in Agreement	Min Ens. Member Slope	Max Ens. Member Slope	β Reanalysis output	p-value
EK	Annual	0.034	< 0.0001	6	-0.013	0.077	0.021	0.0188
	Winter	0.014	0.0042	4	-0.085	0.135	0.013	0.4894
	Summer	0.034	< 0.0001	6	0.001	0.070	0.021	0.0375
SA	Annual	0.027	< 0.0001	6	-0.037	0.077	0.036	0.0026
	Winter	0.013	0.0374	2	-0.109	0.142	0.038	0.0775
	Summer	0.017	0.0003	5	-0.024	0.061	0.031	0.0028
TOA	Annual	0.024	< 0.0001	5	-0.031	0.077	0.036	0.0013
	Winter	0.011	0.0412	3	-0.116	0.124	0.028	0.1204
	Summer	0.015	0.0004	5	-0.020	0.055	0.028	0.0005

A more concerning issue is that the slope of the mean annual seed yield anomaly is not significantly different from zero in EK ($\beta = -0.002$, $p = 0.5601$), TOA ($\beta = 0.0004$, $p = 0.8491$) or SA ($\beta = 0.001$, $p = 0.7505$) when the interval is isolated from 1988-2000. This eliminates any possibility for a confident comparison between seed yield and climate, despite promising consistencies between the trends of the reanalysis and GCM-driven CRCM output. Even when the trailing-mean is relaxed to 5 years or 3 years in an effort to lengthen the common interval, results based on trends in the seed yield, CRCM45-NREA output and GCM-driven CRCM output remain inconclusive.

Discussion

SPZs where the CRCM45-NREA output found reasonably strong correlations with the mean annual seed yield anomaly (Table 3.2) were the natural starting point for further analysis. Meteorological reanalysis represents our best estimate of the observed climate on large scales. CRCM dynamically downscales 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 climate output. This ensemble of GCM-driven runs was used to smooth climate variability in an effort to find a climate change signal. Natural variability in surface temperature and precipitation is typically quite high over the relatively short time periods analyzed in this study. Furthermore, this variability increases over smaller regions, which may explain why it was so difficult to detect non-zero trends in the climate output for specific SPZs. Averaging individual ensemble members of the GCM-driven CRCM made the signal much clearer, but this is not an option with the single realization of the reanalysis-driven CRCM. Since the two different CRCM analyses could only be compared over the relatively short interval where they overlapped, my conclusions were limited by a lack of temporal coverage, particularly for the reanalysis-driven realization. The seed data were also highly localized, typically of short duration, and an amalgamation of many solitary seedlot collections, which confounded the results even further. While investigations using the reanalysis and GCM-driven CRCM output independently produce interesting results, their joint implications are unclear, for the reasons mentioned above.

Although it has long been postulated that climate influences the annual seed production of trees, the complexities of biological and climate systems makes exploring these relationships difficult. 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 *Dacrydium cupressinum* Lamb. (rimu) in New Zealand, but climate data was limited to observations made over 50 km away. In addition, no significant correlations were found between total seedfall and rainfall, which was attributed to consistently heavy precipitation in the region (Norton and Kelly 1988), but may have simply been a limitation of non-local climate observations. 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 strongly match the patterns of variability of either annual rainfall or mean temperature. Lodgepole pine does not experience mast years (Elliott 1974). Although the present study found significant correlations between the mean annual seed yield anomaly of lodgepole pine and climate variables from a reanalysis-driven run of CRCM (Table 3.2), as well as significant overall trends using an ensemble of GCM-driven CRCM output (Table 3.3), the combined implications of these analyses remain unclear.

Preferential harvesting by seed predators such as red squirrels and red crossbills has also been found to influence several lodgepole pine cone and seed traits. These interactions are hypothesized to have an even greater impact on lodgepole pine seed than abiotic factors (Benkman 1999). Benkman (1999) found that in areas where red squirrels are prevalent, cones tend to be wider and harder and contain fewer seeds. Since squirrels must remove the cones from the trees, they preferentially harvest cones that are narrow and have more seeds in order to maximize their feeding rate and energy return per unit effort (Smith 1970). In areas where crossbills are the predominant seed predators, lodgepole pine trees tend to have more seeds per cone, but also larger and thicker scales (Benkman et al. 2001). These traits may be a defense response to crossbill feeding, which does not require cone removal prior to seed extraction and favors the harvest of thin scales (Benkman 1987; Benkman 1989). The present study did not include any information about seed predation, or the subsequent co-evolutionary responses to predation. Thus, the extent to which selective pressures from predation may be contributing to the variability observed in lodgepole pine seed yield throughout BC is indeterminable.

It is important to emphasize that the current study only 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). In fact, extensive environmental tolerance has made *Pinus contorta* a prime exotic species for introduction in many native forests around the world. In Sweden, for example, lodgepole pine has been planted alongside native Scots pine (*Pinus sylvestris* L.) over the last 30 years for reforestation and wood production purposes (Elfving et al. 2001). Since the present study examined the seed production of *P. contorta* over a wide geographic range, the conclusions are undoubtedly influenced to some extent by the broad environmental adaptability and tolerance of the species.

Lodgepole pine populations throughout BC have been found to be significantly different from one another in terms of their genetic variability, growth and survival (Xie and Ying 1995; Rehfeldt et al. 1999). However, Wheeler and Guries (1982b) found that the genetic variability between populations was less than that contained within the populations. Berland (2013) hypothesized that this genetic variation within populations may be responsible for the relative stability of reproductive traits—namely, the average number of seeds per cone—across climate regimes in BC. Interestingly, my work found that seed yield was relatively consistent between 18 different seed planning zones in BC

(Figure 2.3), despite these regions having very different climates (Figure 3.1). 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 (Figures 3.4 and 3.5; Table 3.3). Despite natural year-to-year variability, the remaining SPZs seem to be maintaining a relatively constant overall reproductive output over the past few decades. For lodgepole pine, high genetic variation is maintained through long distance dispersal (Critchfield 1980), high outcrossing rates (Liewlaksaneeyanawin 2006), and an intolerance of natural self-fertilization (Yeh and Layton 1979). In addition, phenotypic plasticity may reduce selective environmental pressures on the reproductive capacity of lodgepole pine, thereby allowing the species to occupy a diverse range of environments (Rehfeldt et al. 1999). Thus, the exceptional adaptability of lodgepole pine could potentially mask any underlying relationship between climate and reproduction. Furthermore, lodgepole pine seems to be undergoing range expansion at its northern distribution limits with no evidence of strong climatic restrictions of 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 environmental scope than was previously recognized.

Since the results of this study were not robust enough to be supported by different historical outputs of CRCM, future projections were not attempted. It is not appropriate to extrapolate to future periods until historical relationships can be reliably predicted and replicated. However, subsequent research should strive to project future relationships between climate and the reproductive characteristics of lodgepole pine, as the results will have important implications for reforestation and breeding programs. Since natural populations are adapted to a wide range of environments (Wu and Ying 2001), the success of such programs will require that adaptive traits be specifically matched to the local environmental conditions, with an inherent malleability to future climate.

Study Limitations

Differences in natural stand *P. contorta* seed production in BC was examined using perhaps one of the most spatially and temporally extensive data sets ever collected for a single species, but there were still significant limitations of the seed collection data. While extensive, the seedlot data was not necessarily the most ideal for finding relationships with CRCM output, primarily because climate output is a time series with annual variability. In contrast, the seedlots used in this study were only collected on a single occasion and were never revisited; meaning that only a pseudo time series for seed yield could be created for each zone by combining seedlots. As a result, each year of collection was not represented in each zone, and violation of the requirement for affiliated climate output and seed yield data further limited the correlation and trend calculations.

Temporal limitations of the climate output, particularly the reanalysis-driven CRCM realization, further hindered the conclusions of this study. The reanalysis and GCM-driven output typically overlapped over a period of less than 20 years, restricting the interval over which they could be compared. In addition, the seed collections were highly localized and of short duration. As a result, it was exceptionally difficult to relate these biological observations to climate data or models having similar properties because the overall trends observed in climate variables such as surface temperature and precipitation over a 20-year period are comparable to natural variability in the climate system.

In addition, northern zones were under-represented in this analysis due to a lack of seedlot collections in these regions. Since climate change is expected to be more pronounced at higher latitudes (IPCC 2007), their exclusion may have non-trivial consequences for the overarching conclusions of this study.

In general, stronger significant correlations with the mean annual seed yield anomaly were found using CRCM45-NREA output when the number of trailing-mean years was increased, likely because a larger window restricted the number of points—corresponding to the seed yield data and associated CRCM output—that were included in the rank correlation (Table 3.2).

Another issue arose due to the fact that climate variables could be back-averaged 3, 5 or 10 years to account for serotiny, but there was not consistent enough seedlot data in each zone to calculate this same trailing-mean for seed yield. In addition, the serotinous nature of lodgepole pine made the age-range of cones for each seedlot collection highly ambiguous and made comparison to an appropriate climate window challenging, especially since a single length of the trailing-mean was not consistently better than the others.

Conclusion

This study investigated the relationship between climate variation and the seed production of *P. contorta* in BC using output from the Canadian Regional Climate Model. Analyses conducted using reanalysis and GCM-driven CRCM output independently found significant relationships with the mean annual seed yield anomaly in particular seed planning zones. Ultimately, the conclusions of correlation analyses performed using CRCM45-NREA output could not be consolidated with those of trend analyses conducted using CRCM output driven by GCMs, leaving the relationship between climate and seed yield indecipherable. Temporal limitations of the seed collections and climate output, along with indefinite age-ranges for each cone collection, hindered the present study and may have contributed to the inconclusive results. Seed production was found to be relatively stable across the climate gradients represented by the seed planning zones, supporting earlier work by Berland (2013), which found that the average number of seeds per cone was relatively consistent over a wide range of climate regimes. Although the cause of this stability is unknown, the exceptional 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.

CHAPTER 4: CONCLUSION

Conclusion

The first half of this thesis investigated differences in *P. contorta* seed production between 18 natural stand SPZs from the interior of BC. Archived records of seedlots were utilized in order to compare mean seed production. Lodgepole pine in NST was found to have a significantly higher mean seed yield (kg seed/hL cone) compared to all other zones, with the exception of HH. In addition, the variance in seed yield for NST was found to be an order of magnitude higher than that of other SPZs, indicating that seed production is exceptionally variable in this region. Although this study was unable to attribute these differences to any genetic or environmental factors, transitional ecosystems such as NST present a unique opportunity to investigate how environmental variability and selection pressure may lead to adaptive evolution. Understanding how reproduction varies geographically in natural stands over a historical period is an essential baseline for future projections. These findings suggest that climate adaptation and mitigation strategies for some areas of the province may need to be more heterogeneous and malleable than for other regions.

The second portion of this thesis evaluated the relationship between climate variation and the seed production of *P. contorta* in BC using output from CRCM; climate output from GCMs and meteorological reanalysis was dynamically downscaled using this regional climate model. The dynamical downscaling technique, which retains information describing physically consistent processes in the climate system, was utilized in the hope of providing more realistic outcomes for the highly complex terrain of the province. Previous studies examining population-scale responses of lodgepole pine to climate have been conducted using statistically downscaled climate output, but this was the first study to expand on that breadth of knowledge using dynamically-downscaled climate output.

Statistically significant correlations between the mean annual seed yield anomaly and the anomaly of both total precipitation and 2-metre surface air temperature were found under a variety of climate schemes in a number of seed planning zones using the reanalysis-driven CRCM output. For many climate schemes, the probability that an equivalent or greater number of significant local correlations would have been observed by chance was no higher than 0.05, resulting in the declaration of global field significance at that level. Analysis of overall climate trends using the GCM-driven CRCM output revealed that increasing surface temperature trends were associated with increasing trends in the mean annual seed yield anomaly in EK, TOA and SA. While investigations using the reanalysis and GCM-driven CRCM output independently captured significant relationships between seed yield and climate variables, their joint implications were unclear. The lack of robustness of the results to shifts in the CRCM boundary forcing during the historical period did not justify consideration of future projections. These inconclusive results may be attributed to ambiguous age ranges of each cone collection and temporal restrictions of the seed collection data and reanalysis-driven climate output.

However, findings from the first half of the thesis provide an interesting supplemental result: with the exception of NST, seed production was found to be relatively stable across SPZs, which represent a wide range of climate regimes. Indeed, only three of the 18 seed planning zones showed a significantly non-zero trend in their mean annual seed yield anomaly based on cone collections made over the past 50 years—

namely, EK, SA and TOA. It is possible that the extraordinary adaptability of lodgepole pine and the high genetic variation in natural populations may invest this species with a reduced sensitivity to decadal-scale climate change.

Further Research

A number of shortcomings can be addressed in future research in order to gain a better understanding of the broad-scale impacts of climate on lodgepole pine seed production. Increasing the spatial coverage of cone collections within each BC SPZ—especially those in more northern regions—would allow for a more realistic representation of the natural variation in lodgepole pine populations throughout the province. Additional sampling at the geographic limits of the lodgepole pine range, as well as in extreme environments, would be important to describe the full extent of natural variation for the species over a broader scope of climatic regimes.

Future research investigating the effects of climate must also address the temporal limitations of cone collections. The seedlots used in this study were only collected on a single occasion and could only be combined to give a pseudo time series of seed yield for each zone. Since climate output varies temporally and is specific to a given locality, it is essential that cone collections be made at a similar frequency in order for more complete correlations between climate and seed production to be calculated.

Difficulties isolating long-term biological and climatological trends during the relatively short overlapping time intervals of the climate output analyses may be avoided by using reanalysis-driven CRCM output or observations from nearby meteorological stations that extend into the more recent past.

Issues introduced by the serotinous nature of lodgepole pine would need to be resolved by knowing the precise age of cones included in the collections. Climate output could be assigned more appropriately to each collection based on the specific time period in which the cones developed. Isolating the exact age of the cones would eliminate any need to calculate multiple trailing-means for climate variables and would minimize ambiguity in this respect.

The relative stability of lodgepole pine reproductive characteristics across climate regimes may be due to high genetic variation. To investigate this hypothesis, the degree of genetic variability in populations of *P. contorta* should be estimated. Comparing the extent of this variability to various reproductive traits of the same populations may indicate that increased heterozygosity stabilizes the reproductive capacity of the species over a broad range of environmental conditions.

It is unlikely that surface temperature and total precipitation are the only climate variables potentially influencing the seed production of lodgepole pine. Thus, subsequent studies should utilize other variables of dynamically-downscaled climate output as they become available for BC, and compare their results to those obtained using climate output downscaled by statistical methods. These variables should be biologically-relevant and represent a meaningful climatic indicator for lodgepole pine reproduction. For instance, the difference in mean temperature of the warmest and coldest month of the year, or ‘continentality’, the number of frost-free days, and the number of growing degree days above 5 °C would be suitable choices for further analyses. Ideally, if the relationship between climate and seed yield of natural stand lodgepole pine can be consistently quantified based on historical trends, it can then be carefully extended to future projections of climate.

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