

Contributions of dynamic environmental signals during life-cycle transitions to early life-history traits in lodgepole pine (*Pinus contorta* Dougl.)

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Abstract

Environmental signals are important triggers in the life-cycle transitions and play a crucial role in the life-history evolution. Yet, very little is known about the leading ecological factors contributing to the variations of life-history traits in perennial plants. This paper explores both the causes and consequences for the evolution of life-history traits (i.e., seed dormancy and size) in lodgepole pine (*Pinus contorta* Dougl.) across British Columbia (B.C.), Canada. We selected 83 lodgepole pine populations covering 22 ecosystem zones of B.C. and through their geographic coordinate, 197 climatic variables were generated accordingly for the reference (1961–1990) and future (2041–2070) periods. We found that dynamic climatic variables rather than constant geographic variables are the true environmental driving forces in seed dormancy and size variations and thus provide reliable predictors in response to global climate change. Evapotranspiration and precipitation in the plant-to-seed chronology are the most critical climate variables for seed dormancy and size variations, respectively. Hence, we predicted that levels of seed dormancy in lodgepole pine would increase across large tracts of B.C. in 2050s. Winter-chilling is able to increase the magnitude of life-history plasticity and lower the bet-hedge strategy in the seed-to-plant transition; however, winter-chilling is likely to be insufficient in the north of 49° N in 2050s, which may delay germination while unfavourable conditions during dry summers may result in adverse consequences in the survival of seedlings owing to extended germination span.

1 Introduction

In the context of global climate change, species have responded by tracking the environment for which they are best suited through local adaptation, range shift, range reduction, or a combination of these (Walther et al., 2002; Parmesan and Yohe, 2003; Cleland et al., 2007; Breshears et al., 2008). Knowledge about traits that vary with ecological niches should therefore help predict how these traits may evolve under cli-

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mate change. Life-history traits influence the fitness, as a last resort via their effects on fecundity as well as survival. Ecological and genetic trade-offs constrain the combinations of the life-history traits through evolution (Adler et al., 2014), which involves an adaptation to environments and is shaped by natural selection.

Climate change has already altered the timing of major life-history transitions, such as seed germination timing (from seed to plant). Timing is directional and completely asymmetric and the timing of seed germination is the earliest life-history trait that is expressed and sets the context for the traits that follow (Donohue et al., 2010). It is controlled by the level of seed dormancy, whereby dormant seeds await germination-cueing from the environment to release dormancy (Finch-Savage and Leubner-Metzger, 2006; Baskin and Baskin, 1998). Moreover, early developmental stages of plants are more sensitive to environment perturbations than adult stages and represent a major bottleneck to regeneration from seeds (Johnsen and Skrøppa, 1996; Hedhly et al., 2009). At the core of plant regeneration, temperature and water availability (or precipitation) are critical drivers for a plant's distribution (Woodward and Williams, 1987). Hence, climate-changed plant regeneration will be manipulated in both temperature- and moisture-controlled ecosystems (Walter and Breckle, 2002) and much of plant regeneration climate research has been directed at tundra and boreal forest, and treeline ecotones (reviewed in Walck et al., 2011).

As per fossil data, seed size remains small across all plants until the Cretaceous period (124 MYA). Seed size begins to increase after the limit of the Cretaceous-Tertiary period (65 MYA). One of the most popular explanations is that climate change gives rise to seed size variation, which took place during that period (Eriksson et al., 2000). Since the early 1950s, effects of environmental stimuli, such as, temperature and photoperiod on seed size and weight have been noted. *Chenopodium polyspermum* L. seeds from mother plants grown in long days have lower germination frequency and thicker seed coats when compared to seeds from short days (Pourrat and Jacques, 1975). Large seed size with more provisions stored for seedlings may be favorable in variable environments (Venable and Brown, 1988). Seed plants have a general trend

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of increasing embryo to seed ratio (E : S) in morphological seed dormancy and the shift in E : S is likely a heterochronic change, having vital implications to life history of seed plants (Forbis et al., 2002). A priori, the environment plays a crucial role in life-history traits in general and seed size in particular.

Adaptive phenotypic plasticity can underpin rapid phenological shifts in response to climate change and evolve when cues reliably predict fitness consequences of life-history decision (Simons, 2014). This was evident by the performance of seedlings produced by central European trees growing in central Norway as they expressed phenology similar to that of their adjacent ecotype and were exceedingly different from those produced at their original habitat (Skrøppa et al., 2010). Differences in adaptive traits between populations are inconsistent with the Mendelian genetic framework and probably modulated by epigenetic mechanisms (Yakovlev et al., 2012). Germination-cueing under favorable conditions is similar within species; however, these conditions do not persist throughout the seasons. Likewise, populations growing in different ecological niches may have different degree of exposure to unfavourable environments. As such, the prevention of germination of some seeds even under favourable conditions would be of significance. When environments fluctuate unpredictably, “bet-hedging” strategy (Slatkin, 1974) is expected to spread germination over time to reduce the risk of outright extinction. This results in the evolution of traits that maximizes the geometric-mean fitness by reducing fitness variance over generations (Gillespie, 1977). To date, much of the evidence for bet-hedging remains restricted to simple life-history plants (e.g. annuals) (Childs et al., 2010).

Continuously changing environment is constantly selecting for new adapted genotypes resulting in greater genetic diversity (Jump et al., 2009). Adaptive evolution characterized by the genetic architecture allows population persistence in the long term (Lande and Shannon, 1996). However, sustained directional selection due to climate change could potentially eliminate a proportion of the genetic variation needed for continued adaptation. To date, it remains unclear whether adaptive evolution can keep pace with climate change (Etterson and Shaw, 2001).

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Life-history strategy for long-lived organisms is influenced primarily by survival (Adler et al., 2014). Evergreen coniferous forests in the Pacific Northwest are unique among the Northern Hemisphere temperate forests in their species composition and high productivity (Waring and Franklin, 1979). Our study species, lodgepole pine (*Pinus contorta* Dougl.), is an aggressive pioneer species distributed over wide geographic and ecologic ranges across British Columbia, Canada and is therefore expected to display wide spectrum of dormancy variation owing to adaptation to diversified local habitats (Plomion et al., 2007). Cone and seed production in lodgepole pine is not as cyclic as in many other conifers. Cone drop soon after seed maturation is commonly observed in coastal areas but lodgepole pine growing in the interior tend to be serotinous, indicating that mature cones do not drop or open to release seeds unless exposed to fluctuating high temperature during prolonged hot summer and low fall temperatures or due to fire or insect damage (Fowells, 1965; Owens et al., 1981, 1982). Most serotinous cones take several years to open and seeds are released in large quantities, consequently, any seed collection made from a single tree consists of a mixture of different seed-crop years. Before the cones eventually open, seeds are wrapped and sealed by scales and sticky resin without exposure to any germination cues (such as moisture, oxygen, etc.); thus we assumed that seed dormancy in lodgepole pine is least affected over its natural storage period.

Seed dormancy is an intrinsic attribute affecting regeneration dynamics and seed size is one of the vital determinants for the evolution of seed dormancy. The objectives of this study are to evaluate the contributions of local environmental effects during life-cycle transitions to seed dormancy and size variations of lodgepole pine populations across British Columbia, Canada and to predict how life-history traits evolve locally under ongoing climate change. Studies of seed dormancy and size allow investigating the relationship between these two life-history traits and their relationship with environments in life-cycle transitions. This study can also contribute to providing the missing empirical evidence of bet-hedging strategy in long life-history plants.

2 Methods

2.1 Plant materials, and current and future climate data

The 83 lodgepole pine seed lots used were representative of 83 different populations covering 22 ecosystem zones. The seed lots are distributed throughout the species' natural range across British Columbia (B.C.), Canada encompassing coastal area and interior regions with a spatial grid over latitudinal range from 49 to 60° N and longitudinal range from 115 to 132° W, which consist of tundra, boreal and temperate forests, and treeline ecotone ecosystems (Supplement Fig. S1). The studied populations were selected primarily based on two important climate variables; namely, mean annual temperature (MAT) and annual heat moisture index (AHM) (Fig. S2) (Wang et al., 2006) and geographic variables, including longitude, latitude, and elevation were also considered.

Climate data (197 climatic variables) of the 83 studied sites for the reference normal period 1961–1990 were generated using ClimateWNA version 4.85 (Wang et al., 2012). The same 197 climatic variables for the future period between 2041 and 2070 (or 2050s) were also projected using ClimateWNA. The future climate data were downscaled to point locations using a delta approach (Wang et al., 2012). We used three Representative Concentration Pathways (RCP) 2.6, 4.5 and 8.5 from the CGCM4 model output of the phase 5 of the Coupled Model Intercomparison Project (CMIP5), generated by the United States National Center for Atmospheric Research. The CCSM4 model output was included in the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5) (Stocker and Randall, 2013). In the prediction of seed dormancy indicators across B.C. for the reference period and 2050s, climate data were generated for each pixel at the spatial resolution of 800 × 800 m using ClimateWNA. The full list of climatic variables is given in Table S1 in the Supplement and the four most relevant variables for the present study were *Eref07* and *_summer* (July and summer hargreaves reference evaporation estimated based on temperature and solar radiation), *DD_0_summer* (summer degree-days below 0 °C), *PPT07* and 10

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(July and October precipitation (mm)), and T_{max07} (July maximum mean temperature (°C)).

2.2 Life-history traits' measurement

Germination parameters gauging timing of seed germination were estimated from cumulative germination curves fitting a mathematical function known as the four-parameter Hill function (El-Kassaby et al., 2008). Core germination parameters include dormancy index (DI, the difference of areas under germination curves (AUC) of control and treated seed), germination capacity (GC, the final germination fraction), time to germination (time at the onset of germination), and germination speed (GS, the time required to achieve 50 % germination of the total germinated seed) (graphically represented by Fig. S3, Liu and El-Kassaby, 2015). To simulate winter chilling in the seed soil bank and retain natural seed dormancy, seed germination was manipulated with or without 21-day moist-chilling treatment under 3 °C in lightproof chamber. Germination assay was performed as previously described (Y. Liu et al., 2013) and seed size was measured as the average of 1000-seed weight collected from each study site.

2.3 Data analysis and visualization

To investigate which climatic variables can most explain the observed patterns of seed dormancy and size variations, partial least squares (PLS) analyses was conducted using SAS[®] (vers. 9.3; SAS Institute Inc., Cary, NC) (Jose Crossa et al., 2013). The goal of PLS regression is to analyse multivariate response based on a large set of explanatory variables (i.e., climatic variables). This technique combines features from principle component analysis (PCA) and multiple regression (Abdi, 2007; Carrascal et al., 2009). In the PLS biplot, the angles between the environment vectors proximately correspond to the correlation coefficients among the environments. The cosine of the angle between two vectors approximates the correlation between them and the length of the vectors is proportional to the standard deviation within respective environments

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or genotypes (Yan, 2001; Yan and Tinker, 2006). Virtually, an ideal environment has the longest vector of all test environments (most discriminating and informative) and is closely located on the abscissa (most representative) (Liu and El-Kassaby, 2015). As a comparison, PCA for explanatory variables and canonical correlation analysis (CCA) dealing with both explanatory and response variables were also performed (Liu and El-Kassaby, 2015). To examine how seed dormancy and size varied in ecosystem zones, the two variables were analyzed collectively using multivariate analyses (MANOVA) with the aid of general linear model (GLM) procedure in SAS (Manly, 2005; Tabachnick and Fidell, 2012). To investigate how the most correlated climatic and geographic variables affect life-history traits, hierarchical models were established using PROC MIXED in SAS with errors split into population and ecosystem zones but having unequal variances at the population level (West et al., 2007; Raudenbush and Bryk, 2001). The most correlated climatic variables through the PLS analysis were used and the model was expressed as follows:

$$(\text{life-history trait})_{ij} = (\beta_0 + \varepsilon_j) + \beta_k \times P_{kij} + \beta_l \times T_{lij} + \varepsilon_{ij} \quad (1)$$

where i and j represent two levels, namely, i th population within j th ecosystem zone; P_{kij} and T_{lij} represent the k th precipitation- and l th temperature-based variable in i th population within j th ecosystem zone, respectively; ε_j and ε_{ij} represent errors from the ecosystem zone and population level, respectively. Intercept $(\beta_0 + \varepsilon_j)$ and coefficients $(\beta_k$ and β_l ($k, l = 1, 2, 3, \dots$)) were estimated using our experiment data. Analogously, fitting models using longitude, elevation, and latitude as independent variables were established. Using the foregoing climatic model for the reference period and 2050s via CCSM4 RCP 4.5, DI values were estimated for each pixel across BC at the resolution of 800×800 m and mapped across B.C for visualization.

To investigate the phenotypic plasticity of timing of seed germination, Pearson's product-moment correlation was calculated. The mean phenotypic plasticity of timing of seed germination is the magnitude of the average response of the population genotypes to specific environments and calculated as a population's mean AUC in the

chilling manipulation minus its corresponding value in the control (i.e., DI). To investigate the range of possible plastic response to dormancy and to determine its genetic contribution to the phenotypic variance, the following linear model was used:

$$DI_{ij} = \mu + G_i + E_j + GE_{ij} + \varepsilon \quad (2)$$

where DI_{ij} is dormancy index of i th genotype in j th environment, μ is the overall mean, G_i is the effect of the i th genotype, E_j is the effect of the j th environment, GE_{ij} is the interaction of i th genotype with j th environment, and ε is the random error. The range of phenotypic plasticity is interpreted as $G \times E$ variation ($V_{G \times E}$) and the extent of genetic control of a trait was calculated by broad-sense heritability ($H^2 = V_G / (V_G + V_{G \times E} + V_\varepsilon)$).

To evaluate bet-hedge strategy in seed germination, two potential traits were tested, i.e., germination capacity and time to germination. Specifically, germination capacity was the subject of Cohen's classic bet-hedging model (Cohen, 1966), in which dormancy is expected to evolve in proportion to the probability of encountering a "bad" year, which corresponds to no chilling manipulation in this study. Time to germination in a "bad" or "good" year (i.e., no chilling vs. chilling) represents within-season variation, which has been shown to be advantageous when germination success is unpredicted within season (Simons, 2009). The standard deviation (SD) for these two traits in a "good" and "bad" year was also calculated to measure the amount of variation across studied populations.

3 Results

3.1 Life-history traits strongly correlated with climatic variables in the plant-to-seed transition

Partial least squares (PLS) analyses for seed dormancy and weight indicated that the first and second components accounted for 15 and 13%, and 18 and 9% of the total variation, respectively (Fig. S4). The 15 most correlated climatic variables with respect

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to life-history trades were correlated with environmental factors related to temperature (Fig. 1). This indicates that temperature plays a major role in the development of life-history traits (Liu and El-Kassaby, 2015). By contrast, the PCA analysis showed several temperature-based variables, which were intrinsically correlated (Fig. S5). In addition, the PLS analyses classified the 83 population habitats into 21 and 20 major categories for seed dormancy and weight, respectively (blue arrows in Fig. S4).

The first canonical correlation analysis (CCA) was significant across all statistical tests (Table S2a). Seed dormancy and weight had moderate (0.66) and very strong (0.90) correlations with climate, moderate (0.59) and high (0.74) correlations with life-history traits (i.e., combination of seed dormancy and weight), and moderate (0.53–0.55) correlation with geographic, respectively, variables (Table 1a). This implies that the climatic variables were more important than the geographic variables in variations of life-history traits. Based on respective covariate matrices for “life-history traits”, “climatic ecology”, and “geographic ecology” canonical variates, 62.35 and 47.11 %, 62.85 and 45.06 %, 14.80 and 6.82 % of variance were explained by their corresponding canonical variates for the same group of variables and the other group of variables (Table 1b). Furthermore, multivariate analyses showed that ecosystem zones were significant for seed dormancy and weight, and had moderate correlation ($R^2 = 0.55$ – 0.56 , $P < 0.0001$) with life-history traits (Table 2).

In the hierarchical model for seed dormancy using climatic variables, the climatic variables *Eref07*, *Eref_summer*, and *DD_0_summer* were significant (Table 3a). This indicates that summer moisture and temperature, the period corresponding to the plant-to-seed transition, played an important role in the development of seed dormancy. The intercept including error from ecosystem zones was not significant (Table 3a). For seed weight, variables *PPT07* and *PPT10*, *Tmax07*, and intercept were significant (Table 3b), indicating that July temperature and precipitation and October precipitation were important to seed weight. Compared to seed dormancy, ecosystem zones, ecological boundaries in geography, had a greater impact on seed weight variation. In the geographic variable-based hierarchical model for seed dormancy, only longitude and inter-

cept were significant (Table S4a and Fig. S6a). For seed weight, longitude, elevation and intercept were significant (Table S4b and Fig. S6b), indicating that longitude was an important geographic factor in life-history traits and geographic factors had greater influence on the variation of seed weight than seed dormancy. Considering all these results collectively, life-history traits were significantly influenced by precipitation as well as temperature in the plant-to-seed chronology, and roughly distributed in a longitude pattern.

3.2 Prediction of life-history traits in response to climate change

Using current climate data, seed dormancy predicted had a moderate linear relationship ($R^2 = 0.47$, $P < 0.0001$) with that observed (Fig. 2), which was used for the correction of the climate scenario predicted in 2050s. Seed dormancy predictions using three greenhouse gas emission scenarios (RCP2.6, 4.5, and 8.5) showed that DI in 2050s would increase (Fig. 2). In general, the spatial pattern of DI across the entire province showed that the seed dormancy in the south of B.C. would pronouncedly increase and the territory previously not suitable for pines to establish (grey area in 1970s) is expected to shrink in 2050s, which are presumably responses to climate change (Fig. 3). In addition, seed weight “predicted” had a low moderate linear relationship ($R^2 = 0.34$, $P < 0.0001$) with observed values (Fig. S7).

3.3 Correlated response in plasticity to timing of seed germination after “winter-chilling”

Among the 83 lodgepole pine populations, variance of seed dormancy was significantly explained by genotype and environment (Table 2b). Estimate of broad-sense heritability (H^2) was 0.54 corresponding with the observed variance component for genotypes (Table 2b), indicating that genetic components have moderate influence on seed dormancy variation. In response to significant $G \times E$ interaction (Table 2b), a plot of the reaction norms of AUC showed a range shift, nonparallelism, and crossing between

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moist-chilling and control (Fig. 4), where $G \times E$ accounted for 39% of the variance and was attributed to crossing of reaction norms (Table 2b), indicating that environments changed the adaptive values of the life-history trait.

A moderate correlation ($R^2 = 0.53$, $P < 0.0001$) between AUC and phenotypic plasticity under chilling treatment (Fig. 4) indicates that populations that germinated after chilling treatment were more plastic. However, no treatment prior to germination, such as a correlation ($R^2 = 0.04$, $P = 0.3479$) was weak and not statistically significant (Fig. 4). Therefore, germination after the chilling treatment was able to increase the magnitude of phenotypic plasticity, which was a response to subsequent predictable environments.

3.4 Expression of bet-hedge under manipulated environmental uncertainty

Relative to “bad-year” simulation, “good-year” resulted in higher and uniform germination capacity and shorter time to germination across the 83 populations (Fig. 5). The standard deviation (SD) of germination capacity and time to germination were evenly distributed on the two sides of respective average line for both good- and bad-year across populations (Fig. 5) and “good-year” had lower average STD germination capacity and STD time to germination (Fig. 5). This indicates that, though bet-hedge is a risk strategy for unpredictable environments, “good-year” can lower the risk by means of allowing higher germination capacity and shorter time to germination across populations.

4 Discussion

Climate change is accelerating plant life-cycle transitions coordinated with the seasons. In life-cycle transitions, the environment plays a critical role in the development of life-history traits and in response to environmental stimuli, intrinsic mechanisms of genetics, epigenetics, phenotypic plasticity, bet-hedge strategy, and adaptive evolution take effect (Fig. 6). In this study, we found that seed dormancy and size were most

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correlated with evapotranspiration, and precipitation and maximum mean temperature during the plant-to-seed transition, respectively, using 83 lodgepole pine populations across British Columbia (B.C.), Canada. We predicted that the range of seed dormancy variation would increase across B.C. in 2050s. Moreover, winter-chilling can increase the magnitude of life-history plasticity (predictable factor) and lower the bet-hedge strategy (unpredictable factor). However, future climate may bring about insufficient winter-chilling required to decay seed dormancy, thus resulting in adverse consequences for the timing of phenology and the growth and establishment in lodgepole pine. This study allowed us to gain insights in the role of dynamic environments in shaping life-history characteristics.

4.1 Environmental conditions in the plant-to-seed transition

In the plant-to-seed chronology, the sexual reproductive of plants is vulnerable to climate change as influenced by the maternal environment (Hedhly et al., 2009; Donohue, 2009; Schmitt et al., 1992a), and temperature is involved in both genetically-based and environmentally-induced parental effects (Lacey, 1996). Global warming has resulted in an upward shift in species optimum elevation and latitude (Chen et al., 2011; Lenoir et al., 2008; Parmesan and Yohe, 2003), an observation similar to that reported by Parmesan (2006) as he pointed out that the best places to seek potential changes in species ranges is at their altitudinal and latitudinal treelines (Parmesan, 2006). This suggested that climatic variables are the real causes of species' responses to environmental signals. Compared with last three decades, the Pacific Northwest is expected to warm about 0.8–2.9 °C by mid-century (Leung et al., 2004; Duffy et al., 2006; Mote et al., 2008), and 1.5–5.4 °C by the end of the century (Mote et al., 2008). Warming in this region will be probably greater in summer (3.9 °C on average) than in winter (2.7 °C) (Mote et al., 2008).

In the hierarchical model for seed dormancy, the climatic variable, summer degree-days below 0 °C (*DD_0_summer*) was not equal to zero only for 16 out of the total 83 study populations and was projected to be zero for 80 populations in 2050s. We

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performed approximation by removing *DD_0_summer* from the model and the result of seed dormancy projection could be interpreted as: given the current-future difference in July hargreaves reference evaporation (*Eref*) is more than one third higher than that in summer *Eref* (June to August period), seed dormancy will increase in 2050s, and if such a difference is less than one third higher, seed dormancy will diminish. These results also suggest that the allocation of summer *Eref* in July (i.e., seed development period) was critical in the development of seed dormancy.

The ecosystem zones were significant in analyses of life-history traits using MANOVA (Table 2a) but not significant for seed dormancy and weight models (Table S2). This indicates that dynamic climatic variables are true driving effects on modulating life-history traits. On the other hand, gene flow as a single pollen grain carries half the number of alleles and may yield effective distance spanning from a few centimetres to thousands of kilometres (Nathan et al., 2008). The “abundant center” model dealing with the population position across species’ ranges and its evolutionary potential also has implications (Volis et al., 2014; Etterson and Shaw, 2001; Parmesan, 2006), that is, compared with core populations, locally adapted peripheral populations had lower adaptive potential and were outperformed in the novel environment. Ecosystem zones like other geographic variables are not individual units to classify life-history traits.

A number of ecologically and evolutionary relevant genes have been identified in *Arabidopsis* and some annuals, such as *FLC* (Flowering Locus C), *SCR/SP11* (S-locus Cysteine-Rich protein/S-locus Protein 11) (Shimizu et al., 2011; Amasino, 2010), thus providing genetic diversity in adaptive evolution. Moreover, both seed dormancy (genes in ABA and GA signalling circuit) and flowering (such as *FLC*) were modulated by epigenetic mechanisms (Müller et al., 2012; Chinnusamy et al., 2008; Bossdorf et al., 2008), indicating that epigenetic changes play a significant role in evolution and ecology and the environment signals working on genes by epigenetic modification were crucial for life-history traits. In recent years, much progress has been made in uncovering genes acting on different seed compartments i.e., embryo, endosperm, and seed coat, which modulate seed development (Le et al., 2010). Processes that regulate

seed size and development are coordinated across several morphologically distinct sub-regions (Belmonte et al., 2013) and the complex cross-talk and integration of signals from different components of the seed together determine its final size (Garcia et al., 2005).

4.2 Temperature signals in winter-chilling

Winter dormancy is an important adaptive strategy, as it prevents plants from flushing during short warm periods in the winter. Winter chilling is an important environmental signal for plant life histories, which accelerates flowering through vernalization in winter annuals and alleviates both bud and seed dormancy, allowing the onset of growth in springs (Penfield, 2008; Penfield and Springthorpe, 2012). Seeds take advantage of environmental temperature as a key signal to coordinate timing of seed germination, allowing plants to synchronize their life histories with the seasons. Low temperature can promote dormancy at the inception of seed maturation, but promotes dormancy alleviation in mature seeds after imbibition. It is therefore assumed that chilling plays a dual role in regulating dormancy (Batlla and Benech-Arnold, 2010).

With substantial climate warming ($> 3^{\circ}\text{C}$), chilling may be insufficient in many woody perennials, such as, poplar, western hemlock, and Sitka spruce, resulting in delayed bud burst and poor growth (Cannell and Smith, 1986; Murray et al., 1989; Morin et al., 2009). We predicted that winter-chilling days (*DD_0_winter*) would on average decrease by 24% across the 83 study habitats in 2050s relative to present (Fig. S8), which may lead to insufficient dormancy alleviation through winter-chilling. However, spring and annual heat sums (*DD5_spring* and *DD5*) would increase by 95 and 49%, respectively, in 2050s (Fig. S8), resulting in earlier springs and advanced vegetative green-ups and an increase in growing season length (Robeson, 2004; Schwartz et al., 2006). In 2050s, inadequate winter-chilling may delay germination and an extended germination span leads to adverse conditions during dry summers. As such, future climate will change the timing of conifer phenology and may give rise to adverse consequences.

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In terms of molecular mechanisms in alleviation of seed dormancy via winter-chilling, several studies demonstrated that moist-chilling involves changes in levels of ABA, GAs, and auxin, and transcripts in respective signaling cascades, GA3 oxidase 1, for example (Yamauchi et al., 2004; Ali-Rachedi et al., 2004; X. D. Liu et al., 2013).

4.3 Germination cues in the seed-to-plant transition

Changes in climate can alter patterns of phenology and thus multiple life-history traits. In response to climate change, phenotypic plasticity associated with life-history traits (Pigliucci, 2001; Chevin et al., 2010; Franks et al., 2014; Liu and El-Kassaby, 2015) and genetically based trait responses (Bradshaw and Holzapfel, 2001, 2008; Thompson et al., 2013) were well documented. In the long run, only the species that can respond by phenotypic plasticity and/or genetically based local adaptation can persist (Jump and Penuelas, 2005). However, the revolutionary response to climate change may be attenuated due to constraints causing a time lag between the environmental change and an observed evolutionary response (Etterson and Shaw, 2001; Davis et al., 2005). In tree populations, the extent of the constraints will hinge on phenotypic variation, strength of selection, fecundity, interspecific competition, and biotic interaction (Aitken et al., 2008).

Differences in plasticity exist among populations, but plasticity presumed to be adaptive may often be neutral or maladaptive (Caruso et al., 2006). Only when there exists a balance between adaptive and non-adaptive (bet-hedging) plasticity, can we expect an optimal balance to exist, and possibly varies among populations. Moreover, germination characters are expected to exhibit phenotypic plasticity to environmental variables experienced not only by seed following dispersal but also by seed parents prior to dispersal (Schmitt et al., 1992b).

It is noteworthy that seed dormancy and germination is a quantitative trait that interacts with environment factors (Bentsink et al., 2007). Some QTLs associated with germination phenology in *Arabidopsis* can attain allele frequencies approaching fixation within a single generation even though they started with frequencies below

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50 % (Huang et al., 2010), indicating strong directional selection. Seed dormancy in *Arabidopsis* was associated with a cohort of genes controlled by seasonally distinct hormone-signalling pathways in the seed soil bank, such as *DOG1* (Delay Of Germination 1), *MFT* (Mother of Flowering Timing), *DELLAs* (repressors of germination potential and GA signalling), and *PIFs* (Phytochrome Interacting Factors) (Footitt et al., 2014; Footitt et al., 2011). In addition, photoperiod can affect seed dormancy and germination and phytochromes were the most investigated photoreceptors. Phytochromes are temperature- and light-dependent in association with GA pathway via the bHLH transcription factor *SPATULA* (SPT) (Heschel et al., 2007). SPT is a light-stable repressor of seed germination and mediates the germination response to temperature through temperature-sensitive changes in its transcription (Penfield et al., 2005).

Taken together, we reinforced the importance of climatic signals with an emphasis on the process of seed set to the formation of early life-history traits (i.e., seed dormancy and weight). Variations of life-history traits may be acquired through signal transduction cascades and/or gene/protein imprinting triggered by specific environmental variables, such as, evapotranspiration and precipitation. The period of winter chilling exerts a pronounced influence on the range of life-history plasticity and the variation of bet-hedge strategy when the life-history trait expressed (i.e., seed emergence). In response to previous memory during seed development and different genetic architectures that every individual harbours, germination behaviour (e.g., timing of seed germination) varies even given same optimal germination cues.

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coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

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Table 1. Canonical correlation analysis between individual variables and their own and opposite set of variables.

(a) Variables	Life-history traits	Climatic Ecology ¹	Geographic Ecology ²	
Life-history traits	Seed weight	0.7429	0.9021	0.5481
	DI	0.5909	0.6582	0.5327
(b) Canonical variate	% explained variance by			
	Their own	The opposite		
Life-history traits	62.35 %	47.11 %		
Climatic Ecology	62.85 %	45.06 %		
Geographic Ecology	14.80 %	6.82 %		

¹ Based on the PLS analysis, 27 most correlated climatic variables for seed dormancy (DI) and weight were used as Climatic Ecology (three climatic variables were strongly correlated with both seed dormancy and weight). ² Geographic Ecology consists of latitude, longitude, and elevation.

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Table 2. Multi- and uni-variate analyses for life-history traits. (a) MANOVA table reporting the correlation of seed dormancy (DI) and weight with ecosystems; (b) ANOVA table reporting significant effect of the genotype on phenotypic variance and associating broad-sense heritability (H^2).

(a) SOV	Parameters						
	DF	DI			Seed weight		
		Mean squares	F value	R^2	Mean squares	F value ¹	R^2
Ecosystem zones	21	130.3132	3.50 [*]	0.55	0.3011	3.63 ^{**}	0.56
corrected error	61	37.1821			0.0829		
(b) SOV	DF	EMS	Mean squares	F value ²	Variance components	H^2	
Genotype (G)	82	$\sigma_\varepsilon^2 + 8\sigma_G^2$	346.8691	67.01 ^{**}	54.02%	0.54	
Environment (E)	1	$\sigma_\varepsilon^2 + 4\sigma_{G \times E}^2 + 332\varphi_E$	89393.0625	17268.20 ^{**}	— ³		
$G \times E$	82	$\sigma_\varepsilon^2 + 4\sigma_{G \times E}^2$	129.8935	25.09 ^{**}	39.43%		
Error (ε)	498	σ_ε^2	5.1767		6.55%		

SOV, source of variation; DF, degrees of freedom; EMS, expected mean squares. ¹ $P < 0.025$ (= 0.05/2 dependent variables). ² $P < 0.05$. ³ No variance components or percent of total variation were estimated for the fixed effect (E).

Table 3. Parameter estimates and statistical tests for the climatic variables-based hierarchical models regarding seed dormancy and weight.

(a) Seed dormancy model					
Effect	Estimate	Standard Error	DF	Statistic	<i>P</i>
Intercept ¹ (β_0)	2.4819	7.9418	21	$t = 0.31$	0.7577
<i>Eref07</i> (β_1)	2.7076	0.8932	58	$F = 9.19$	0.0036
<i>Eref_summer</i> (β_2)	-0.9284	0.3354	58	$F = 7.66$	0.0076
<i>DD_0_summer</i> (β_3)	6.5170	1.8480	58	$F = 9.06$	0.0039
(b) Seed weight model					
Effect	Estimate	Standard Error	DF	Statistic	<i>P</i>
Intercept ¹ (β_0)	1.3290	0.3799	21	$t = 3.50$	0.0021
<i>PPT07</i> (β_1)	0.0046	0.0019	58	$F = 5.66$	0.0207
<i>PPT10</i> (β_2)	-0.0014	0.0007	58	$F = 4.68$	0.0346
<i>Tmax07</i> (β_3)	0.0721	0.0150	58	$F = 23.11$	< 0.0001

¹ residual from the ecosystem zone (ε_j) is integrated into “intercept” (Table S3).

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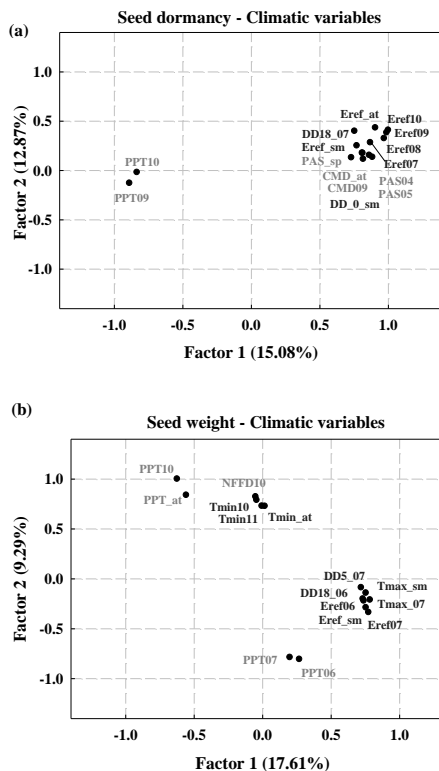


Figure 1. The 15 most correlated climatic variables with seed dormancy (a) and size (b) after partial least squares (PLS) regression. Note: (1) three variables (*Eref07* and *_summer*, and *PPT10*) were highly correlated with both seed dormancy and size; (2) fonts in black and grey represent the temperature- and precipitation-based climatic variables, respectively; (3) see Table S1 for full names of abbreviated variables.

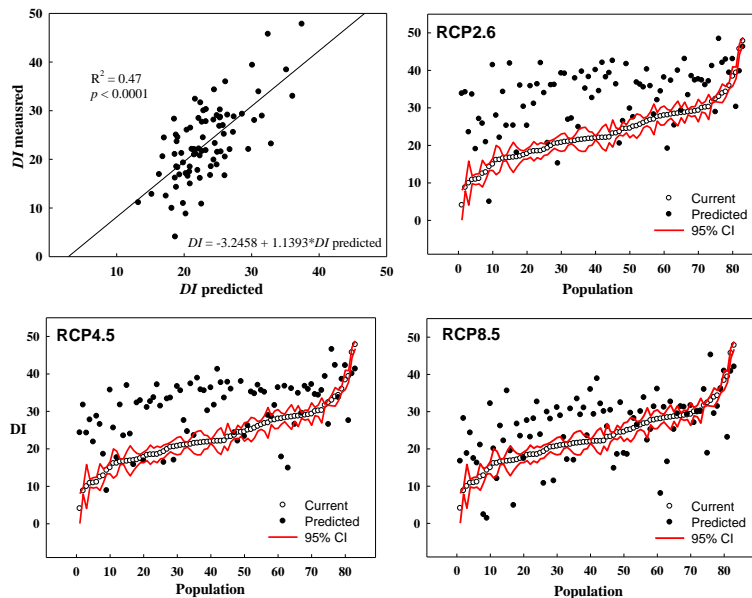


Figure 2. Seed dormancy (DI) prediction in 2050s. **(a)** Linear relationship between predicted DI and DI used for the correction of predicted seed dormancy; **(b)** Corrected seed dormancy prediction using Representative Concentration Pathways (RCP) 2.6, 4.5 and 8.5, respectively. Note: (1) model for seed dormancy prediction, $DI = (2.4819 + \text{ecosystem zone}) + 2.7079 \times Eref07 - 0.9284 \times Eref_summer + 6.6170 \times DD_0_summer$ (refer to Table S2 for intercept adjustment in each ecosystem zone); (2) the population was ranked as per its current DI in ascending order and 95% confidence interval (CI) was plotted.

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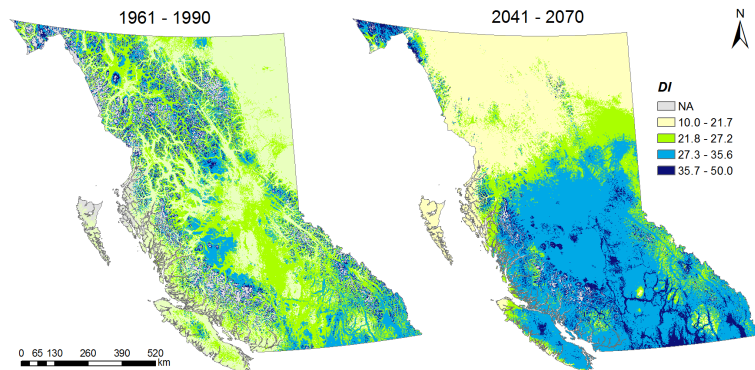


Figure 3. Map of predicted seed dormancy using climatic model for the reference period and 2050s in lodgepole pine across British Columbia. Note: DIs are classified into five categories and represented by different colours on the map. The higher the value, the more dormant the seeds.

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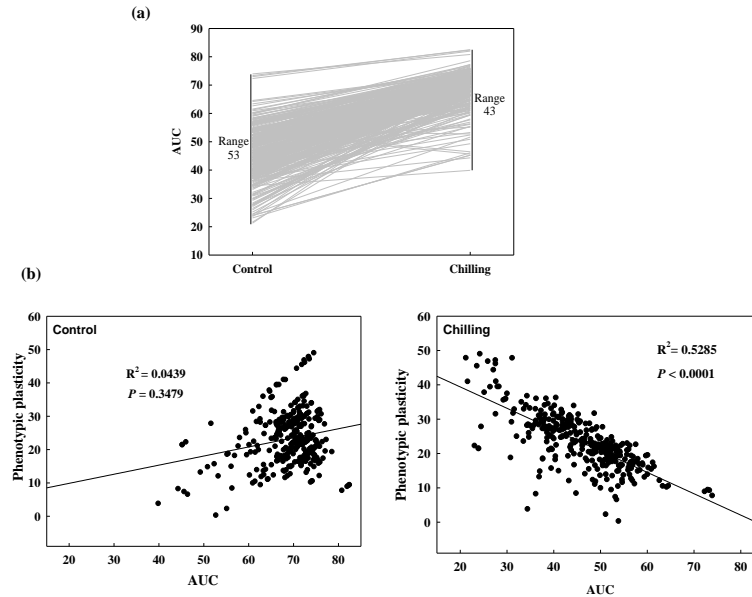


Figure 4. Studies of phenotypic plasticity. **(a)** Reaction norms for AUC with or without moist-chilling treatment across the 83 populations; **(b)** Relationship between phenotypic plasticity and AUC with or without moist-chilling treatment. Best fit lines based on linear models are provided.

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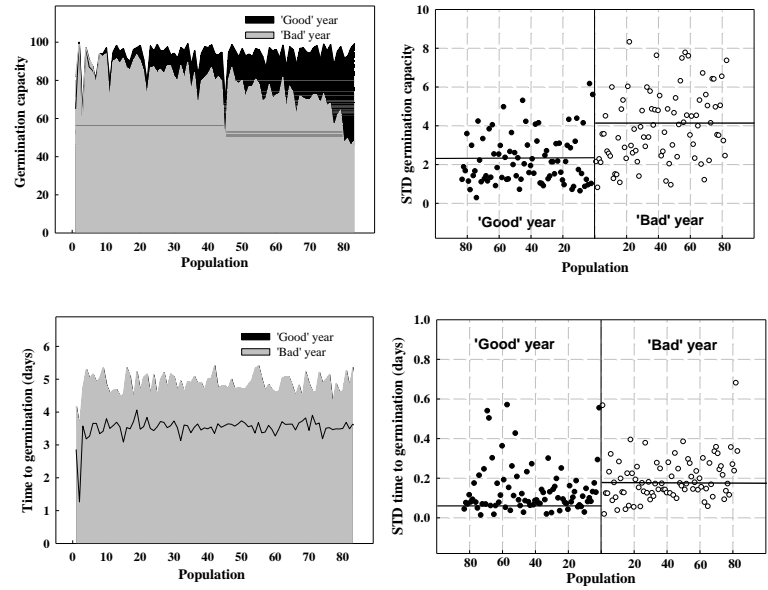


Figure 5. Studies of bet-hedge strategy. Bet-hedge dormancy involving germination capacity and time to germination (left) and their SD (right) in response to “good-year” and “bad-year” treatments. Note: the population was ranked as per its current DI in ascending order.

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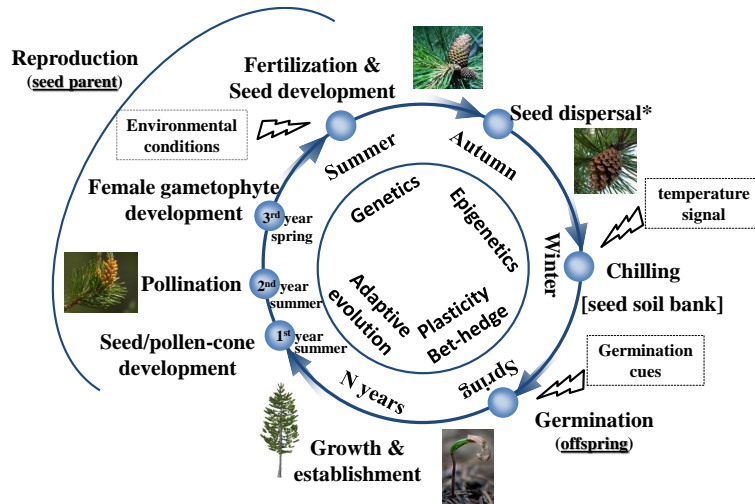


Figure 6. Important environment stages and intrinsic mechanisms in the life cycle of lodgepole pine for life-history traits. Note: (1)*, seed dispersal may not occur in the following season and textitmay take years until the cone drops and seeds release in nature; (2) the reproduction cycle of (lodgepole) pine undergoes three years, that is, seed/pollen cone initiation (August, September, October)→ dormant (November, December, January, February, March) → pollen development (April, May) → pollination (June) → female gametophyte development (July, August)→ dormant (September, October, November, December, January, February, March, April)→ female gametophyte development (May, June).

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