

Predicting pollination phenology in lodgepole pine

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Common garden experiments and genetic work reveal extensive local adaptation in many forest tree species, especially boreal and temperate conifers (reviewed in @Alberto2013a). A locally adapted population only grows optimally in a subset of the range and may tolerate a more limited climatic range than the species as a whole. In northern hemisphere conifers, local adaptation often reflects strong trade-offs between avoidance of cold damage and competitive height growth (summarized in @Aitken2008a).

I will predict the timing of pollen shed and cone receptivity in lodgepole pine (*Pinus contorta* spp. *latifolia*) across its range

Study species Lodgepole pine is an ideal candidate with which to explore these questions. It is an economically and ecologically important tree species facing multiple threats from climate change [@Schneider2010; @Sambaraju2012; @Hamann2006]. Lodgepole pine has a very large geographical distribution (across 33° latitude and 31° longitude) encompassing a wide range of climates and soils (Figure 1) with widespread and significant local adaptation in many traits. For example, populations from both northern interior British Columbia and northern Idaho can survive in areas with mean annual temperatures between -4 and 6 °C, but the northern British Columbia population survives best where mean annual temperatures are ~ 1 °C and the Idaho population best at ~ 4 °C [@Rehfeldt1999a]. Local adaptation in lodgepole pine can be observed even at relatively small spatial scales when topographic variability is high: in a reciprocal transplant experiment, growth declines were observed when moving high elevation populations just 100m in elevation [@Rehfeldt1983]. Cone serotiny, an adaptive trait which allows for germination after fire events, is much more common in Rocky Mountain populations [@Morgenstern1996a] where fire is frequent. At smaller scales within the Rocky Mountain region, cone serotiny is predicted well by the type of disturbance that initiated the stand; serotinous cones are predominant in fire-initiated stands and open cones in other types [@Muir1985], with sharp boundaries between the two [@Lotan1976].

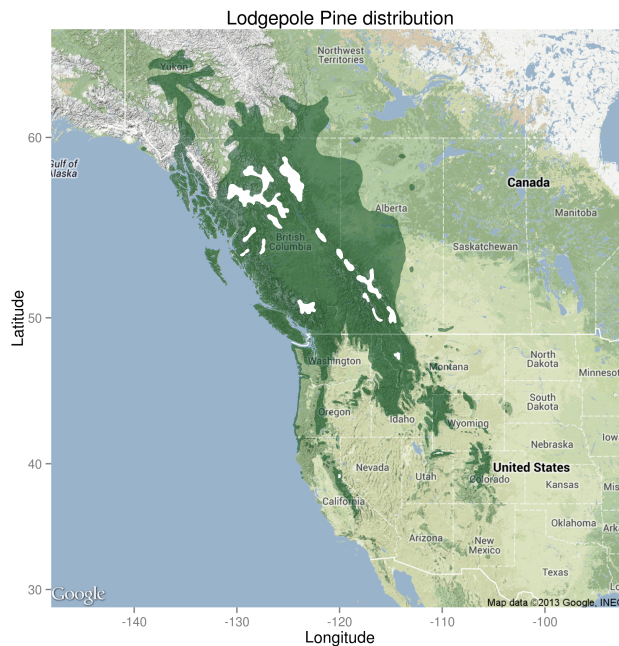


Figure 1: Rangemap of lodgepole pine. After @Little1971 .

Several other traits make *Pinus contorta* suitable for this project. Pollen movement is an important vector for identifying gene flow because outcrossing is common, pollen dispersal is extensive, and seed dispersal is relatively limited [Ennos1994]. Selfing is typically infrequent [Sorensen2001], though when lodgepole pine occurs at low frequencies within a stand, selfing can climb to 21% [Sorensen1993]. This project also builds on other landscape-scale work on adaptation in lodgepole pine: there is evidence for spatially varying levels of gene flow in the species as populations from areas with higher regional climate heterogeneity have higher genetic variance [Yeaman2006], and the relative roles of wind, phenology and divergent selection are unclear. Crucial to the scale of this project, decades of high quality reproductive and vegetative phenology data are available from seed orchards producing seed for reforestation for lodgepole pine from many locations throughout the range. Because of lodgepole's importance, the large scale genomics project AdapTree is producing detailed phenological and genetic descriptions of local adaptation in this species that will complement this project.

While lodgepole pine has four subspecies (*P. contorta* spp. *contorta*, *P. contorta* spp. *murrayana*, *P. contorta* spp. *bolanderi*, and *P. contorta* spp. *latifolia*), I will be focusing solely on *latifolia*. The smaller distributions and lower economic values of the *contorta*, *murrayana*, and *bolanderi* subspecies unfortunately limit data availability. Hereafter, lodgepole pine refers to *P. contorta* spp. *contorta* only unless otherwise noted. This includes references to the range of the species; only spp. *contorta* is under consideration.

My research will proceed in three stages, which I've divided into chapters. In the first stage, I will model pollination phenology.

Research Chapter 1: Model pollination phenology

As the climate changes, spring phenological events like budburst and flowering will advance, especially for plants active in rapid seasonal transitions and short growing seasons [Pau2011], like many high elevation and latitude conifers. This effect is already obvious in many species [Parmesan2006; Franks2014]. Changes in pollination phenology can affect fecundity, gene flow, and even range size in a species and have effects on dependent species [Inouye2008; Chuine2001a]. Lodgepole pine, an ecologically and economically important species in western North America, is of particular interest because of extensive local adaptation; current and future gene flow could have significant adaptive consequences.

In conifers, pollen is shed from male strobili and must arrive at receptive female strobili for successful pollination. Shifts in the timing of pollen shed and cone receptivity (pollination phenology) in lodgepole pine and other conifers could lead to gene flow changes that hinder or promote adaptation under climate change, decrease fitness, and even affect reforestation via seed orchard productivity declines. In order to investigate the effects of gene flow on adaptation in lodgepole pine under climate change, we must first be able to predict pollination phenology.

Predicting pollination phenology will also have practical benefits. Seed orchard managers in British Columbia are particularly concerned about protandry, when all pollen in an area is shed before cones become receptive (*personal communication, Chris Walsh, Former Seed Orchard Manager, Kalamalka Seed Orchards, February 13, 2013*). Protandry occurs in particularly hot and dry years [Owens2005]. If this pattern holds, protandry could become more common in natural populations, leaving some populations pollen limited and likely hampering local adaptation.

I will use pollination phenology and temperature data to fit a mechanistic model predicting pollen shed and cone receptivity across the entire range of *Pinus contorta* var. *latifolia* and consider how the date and length of pollination phenology periods vary normally and under several climate change scenarios. Specifically, I will answer 1) What is the relationship between temperature and pollen shed and temperature and cone receptivity timing and length? 2) How strong is the genetic versus environmental effect on pollination phenology? 3) How many days will pollination phenology shift under the next 30, 60, and 90 years of climate change 4) Will protandry become more common?

Phenology Modeling

Scientists have modeled plant phenology for centuries with an overwhelming variety of model structures. Predictive phenology models are usually mechanistic, but the parameters are rarely directly measured since many stages of development are unseen. Instead, models rely on dates of a few visible stages of development, such as budburst or flowering. Modeling frameworks have different assumptions about how sensitive development is to chilling and warming (or “forcing”) and how sensitivity changes throughout the winter and spring. These assumptions are very difficult to test because of the difficulty of observing internal development. While numerous assumptions spawned even more numerous models, Isabelle Chuine noticed that all of the major budburst models could be represented by different parameterizations of the Gompertz function, a special case of the generalized logistic function [Chuine2000].

Modeling pollination phenology in conifers is not new, but it is uncommon. Simple heat accumulation thresholds (*Pinus taeda*) [Boyer1978] or elevation (*Pinus flexilis*) [Schuster1989] were used previously to explain or predict pollen shed in limited spacial and temporal contexts. Owens2006 reports that lodgepole pine pollen shed and cone receptivity occur when degree days reach about 500 at a threshold of 5 °C, but this is the only report of pollination phenology modeling for lodgepole pine and no details are provided. (Degree days are used to measure heating or cooling from a base temperature over time.) Models of lodgepole pine vegetative phenology, on the other hand, are better represented in the literature (e.g. Chuine2001), and pollen shed and cone receptivity are not expected to have additional or more complex triggers or model forms than budburst [Chuine2013a].

Previous models for lodgepole pine have fitted spring growth phenology models without considering chilling [Chuine2001] and, in general, budburst models for boreal tree species have not required chilling to give accurate predictions [Linkosalo2000]. For lodgepole pine growing in natural environments, chilling is always met and should continue to be met under the next century of climate change; in the AdapTree project, lodgepole pine seedlings grown for three to four weeks at 4 °C met their chilling requirements. Thus, I expect to be able to disregard the state of chilling and fit only Equations ?? and ??. Once the model is parameterized I will be able to calculate the timing of pollen shed and cone receptivity across the lodgepole pine species range using location specific climate data from seed orchards and ClimateWNA [Wang2012]. I will validate the model by comparing predictions to phenological measurements from the National Phenology Network.

Data

PMP requires dates of phenological events and temperature data. I will use pollination phenology data from British Columbian seed orchards and climate data from ClimateWNA and seed orchards.

Phenology Data

Trees selected from across the British Columbia portion of the lodgepole pine range are grown in both large scale provenance trials and seed orchards, which are similar to common gardens, as part of tree breeding programs. There are two types of orchards: first generation and second generation. Each orchard contains trees that are the descendants of seeds and scions collected from mother trees in one particular provenance. First generation orchards have not undergone selective breeding but may be subject to selection through the process of choosing mother trees (called “plus” trees by tree breeders), testing and selection of mother tree offspring, or culling of unfavorable trees in the orchard. First generation orchard trees are clones of mother trees and their offspring grafted onto rootstock. There are three types of first generation orchards subject to different levels of selection: 1.0, 1.5, and 1.75 generation orchards. All orchards are subject to selection based on mother tree selection. In 1.5 generation orchards, superior offspring of mother trees are selected for the orchard or poor trees are culled from the orchard. This selection may be strong; more than 50% of offspring can be rejected in this process due to poor growth form [Ukrainetz2011]. In 1.75 generation orchards, data from 10 year tests of mother tree offspring are used to select 40 of the best genotypes for a given provenance.

Offspring from controlled crosses between trees in first generation orchards are tested in field trials and the best trees are then cloned and grafted onto root stock in advanced generation orchards.

I contacted Seed Orchard Managers and other forestry professionals across British Columbia in 2012 and received pollination phenology data from C. Walsh, previously at Kalamalka Seed Orchards (now retired), R. Wagner at the Prince George Tree Improvement Station, and J.E. Webber previously at the Glyn Road Research Station (now retired).

So far, I have obtained records for 17 of the 26 lodgepole pine seed orchards in British Columbia. Orchards include the offspring of trees from 6 of the 7 BC seed planning zones (SPZs) (Figure 2) grown at at 7 sites across BC. SPZs are biogeoclimatic and political units used for seed planting purposes by British Columbia. SPZs are divided into elevation bands called Seed Planning Units (SPUs), which form this project's provenances. At least 13 of the seed orchards are first generation orchards and should faithfully represent their provenances. These first generation orchards represent 6 provenances at 5 sites. Second generation orchards have been selectively crossed and this may skew the mean or variance of phenology for a provenance if pollination phenology varies by provenance.

Most provenances are represented at 2 to 3 sites and have at least three years of data at a given site spanning 1997-2012 (Figure 3). The Prince George Tree Improvement Station (PGTIS) provides a continuous 15-year record of its three orchards' phenology.

Provenances and sites included in my data exclude the coldest and wettest parts of the range. Figure 4 shows the 1961-1990 climate normal mean annual temperature (MAT) and mean annual precipitation (MAP) for data from all lodgepole pine provenances in BC, provenances included in my data set, and sites where provenances were grown. Orchard sites are generally much warmer and drier than many locations where lodgepole pine grow. I may have difficulty extrapolating into the coolest and wettest parts of the lodgepole pine range, depending on actual yearly conditions at sites for which I have data. However, this may be advantageous when it comes to predicting phenology under climate change.

Climate data

To quantify accuracy of the model, I will calculate the difference in variance within and between populations. Only phenological differences larger than the within population variance will be considered. The maps and parameters of these models can be compared to answer the following questions

Questions and expected results

- 1) How strong are the genetic vs. environmental effects on pollination phenology?

To answer this question I will compare the parameters of models fit by provenance. If different provenances have significantly different model parameters - that is, have different heat sum requirements for pollen shed and cone receptivity by provenance, then the rest of my project will be limited to the provenances I have data from. If not, I can use the same models across the entire range when predicting phenological events.

The budburst and spring pollination phenology of temperate tree species is determined by temperature, and there may be some regional variation in the temperatures required for pollen shed and cone receptivity; in lodgepole pine, the threshold for shoot elongation was 5.1 °C for coastal and interior provenances, but 6.5 °C for northern provenances [Chuine2001].

However, seedling spring vegetative phenology data from four growth chamber temperature and moisture treatments in the AdapTree project suggests that budburst shows substantial clinal variation (> 10% of phenotypic variance explained) only in the coldest treatment tested (MAT of 1 °C), and much colder than the seed orchard locations (Figure 4, Figure 5, Liepe2014 (submitted)). Analysis of phenotypic data from an outdoor common garden in Vancouver (*personal communication, Ian MacLachlan, AdapTree Graduate Student, January, 1 2015*) also shows that very little variation exists among provenances for spring phenology, regardless of whether seedlings originate from wild-stand or selectively bred seed orchard seedlots.

Lodgepole Pine Seed Planning Units

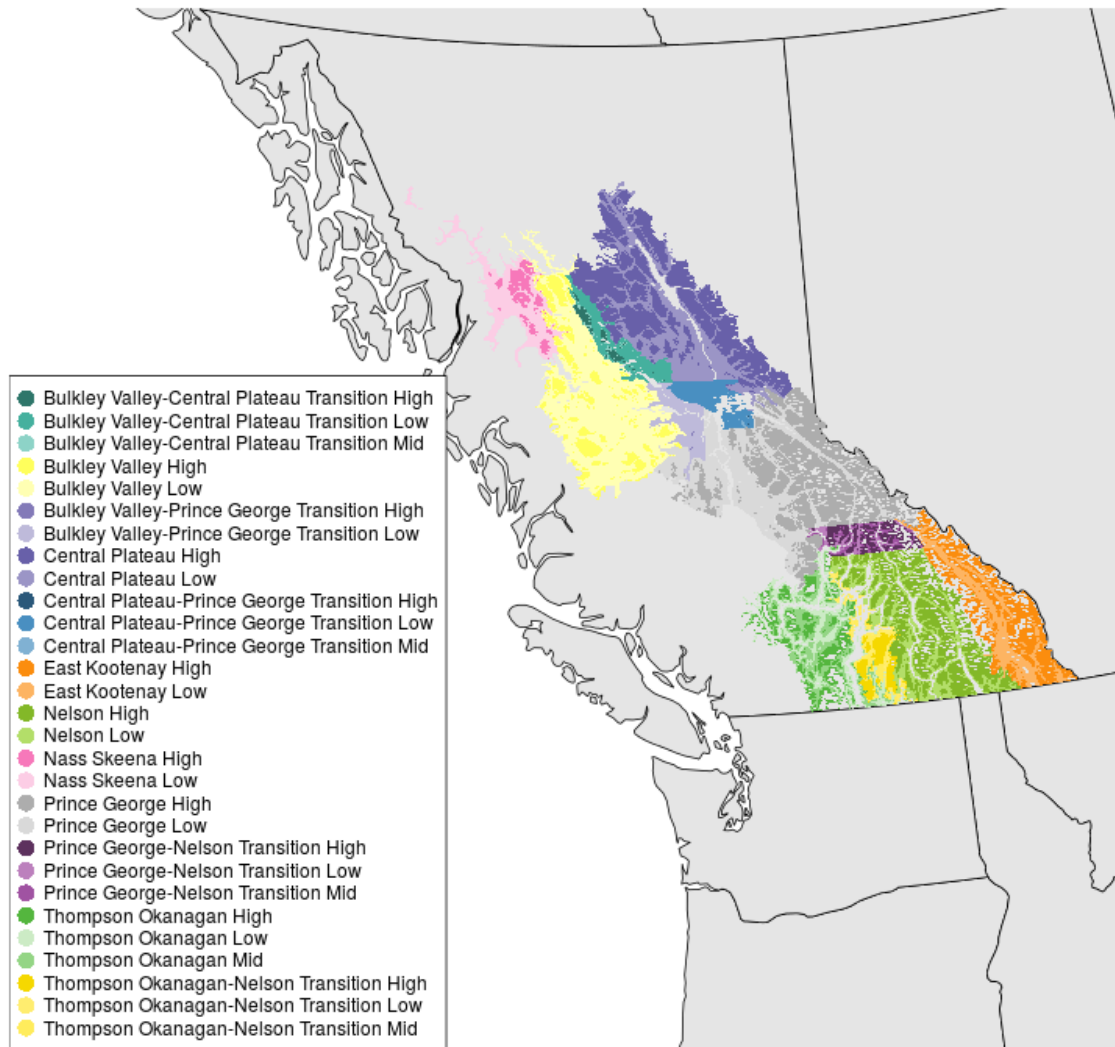


Figure 2: Map of Seed Planning Units (SPUs). Seed planning units are biogeoclimatic and political units used for seed planting purposes by British Columbia. Seed planning units form this project's provenances. High, Low, and Mid refer to elevational bands. Data is also available for East Kootenay Low, but will likely not be included in any analysis as it includes only one year at one site.

	Kalamalka	KettleRiver	PGTIS	PRT	Sorrento	TOLKO	Vernon	Total
Bulkley Valley Low	5	0	17	0	2	0	3	27
Central Plateau Low	0	0	15	0	0	0	4	19
Nelson Low	5	0	0	3	0	0	0	8
Prince George Low	0	2	18	0	0	0	4	24
Thompson Okanagan High	0	0	0	0	0	3	0	3
Thompson Okanagan Low	0	0	0	6	0	0	0	6
Total	10	2	50	9	2	3	11	87

Figure 3: Contingency table of Seed Planning Units (rows) and Seed Orchard Sites (columns). Seed Planning Zones, used as provenances in this project, are usually represented at multiple years and multiple sites. There is particularly good representation at PGTIS.

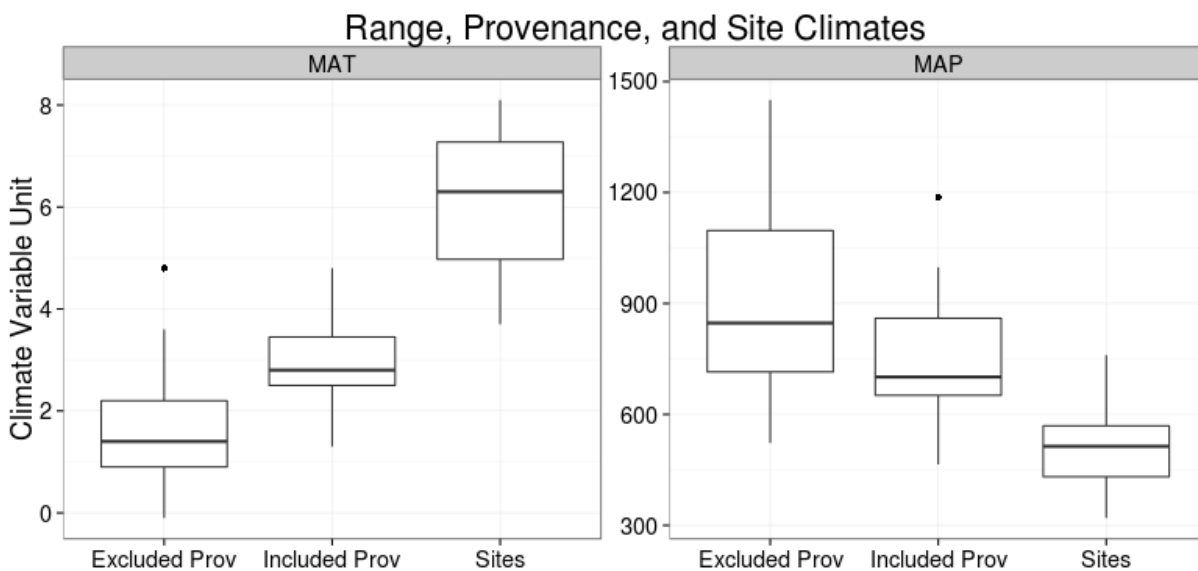


Figure 4: Provenance (SPU) climates of data included in this proposal, provenances not included in this proposal, and sites where provenances were grown. MAT is mean annual temperature and MAP is mean annual precipitation.

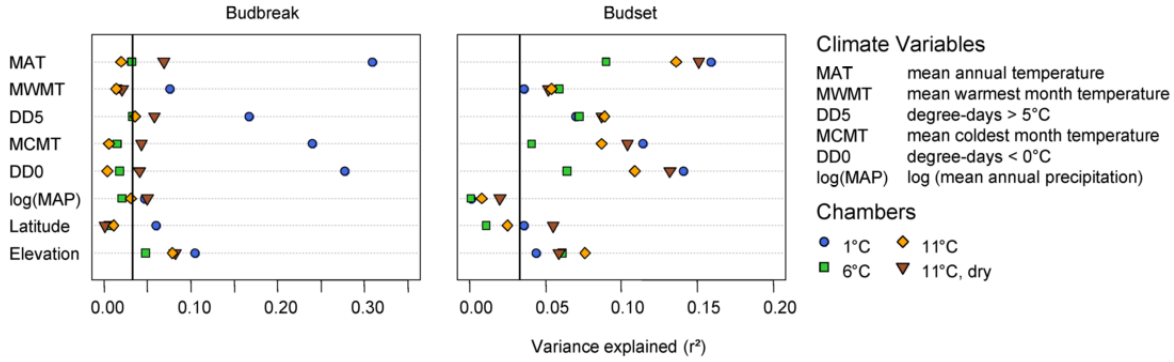


Figure 5: Variance in budbreak and budset for lodgepole pine explained by provenance climate. Seedlings from 281 locations across lodgepole’s BC range were grown in growth chambers under four treatments: approximated seasonal and daily variation in temperature for geographic locations with a MAT of 1, 6, and 11 °C, with the warmest treatment having a dry and wet version. Pearson’s correlation coefficient between phenotypic traits in lodgepole pine and provenance climates are presented. The vertical line represents the critical r^2 value after an adjustment for multiple inferences. From @Liepe2014 (submitted).

- 2) How does faster spring warm-up like we expect under climate change affect within population mating success and frequency of outcrossing?

I expect that faster spring warm-up will condense as well as advance growth initiation dates and also shorten pollination phenological periods by speeding development prior to and during the phenological period. This should further synchronize populations in similar climates and act as a barrier to breeding with populations in more different climates. On the other hand, it could favor outcrossing over selfing by causing protandry - pollen shed in advance of cone receptivity. Based on anecdotal reports from seed orchards managers, I expect protandry (and thus outcrossing) to increase under climate change.

I will examine the variability of the start date across the range (t_1) to see if it shrinks in warmer years and as the climate changes. I will also calculate overlap between within population cone receptivity and pollen shed under current conditions and with climate warming and see if the heat sum requirements for cone receptivity and pollen shed are different.