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Provenance Geographical and Climatic Characteristics Influence Budburst Phenology of Southwestern Ponderosa Pine Seedlings

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Abstract: Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm.) forests of the southwestern US are threatened by climate change and deforestation. Information about geographic patterns of provenance variation in budburst phenology is needed to make decisions about selecting seed sources for future planting. In this study, provenance variation in the budburst phenology of ponderosa pine seedlings was examined using common garden studies. Seedlings from 21 provenances, representing an elevational gradient in Arizona and New Mexico, were planted in July 2018 at a ponderosa pine-dominated field site in northern Arizona. Field budburst was monitored weekly on all seedlings in the spring of 2019. Field budburst was compared with budburst timing of the same provenances measured under greenhouse conditions. The hypotheses for this study were that (1) budburst varies among provenances, with earlier budburst in low-elevation provenances, and (2) differences in budburst timing among provenances are consistent for seedlings grown in greenhouse and field environments. Field results show that provenances vary in budburst date and that low- and middle-elevation provenances break bud sooner than high-elevation provenances. Field budburst date had a moderate, positive correlation with provenance mean annual precipitation ($r = 0.522$) and a moderate, negative trend with latitude ($r = -0.413$). Budburst date of provenances in the greenhouse had a moderate, positive trend with budburst date in the field ($r = 0.554$), suggesting application of greenhouse results to field plantings. Such information about provenance variation and environmental and geographic trends in budburst timing will be useful for developing species-specific seed transfer guidelines and effective assisted migration strategies in a changing climate.

Keywords: budburst; phenology; provenance variation; common garden; elevation; latitude; precipitation; *Pinus ponderosa*

1. Introduction

Tree species have considerable genetic variation among provenances and are generally adapted to local climate [1,2]. However, locally adapted provenances are likely to become locally maladapted [3,4] due to the inability to adapt or acclimate to rapid climatic change and associated disturbances. Forests of the southwestern US are already experiencing increases in warming, drought, and tree-killing disturbances [5]. An increase in temperature of over 1 °C occurred in the southwestern US between 2001–2010, and mean annual temperature is expected to increase between 3 and 5 °C by the end of this century [6].

Climate warming has already caused an earlier onset of spring in western North America forests [7,8] because tree budburst timing responds to many factors including temperature [9].

Earlier budburst due to warmer spring temperatures can have a positive impact on tree performance if early budburst promotes growth by lengthening the growing season, or a negative impact if early budburst results in spring frost damage that kills stems, buds, and leaves [9,10]. Spring frost damage has been predicted to increase in frequency with future climate warming due to early budburst [11]. Interactions among multiple factors, such as chilling requirements, temperature, photoperiod, and plant genotype, determine budburst timing [12]. Budburst can vary among tree populations due to local adaptation to the thermal environment [13]. In *Pinus*, genetic differentiation and clines in growth and phenology have been previously reported [14–16], including among populations of ponderosa pine (*Pinus ponderosa* Doug. Ex. Laws) from different elevations [17,18].

Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson var. *scopulorum* Engelm.) forests in the southwestern US are threatened by large-scale mortality due to drought, bark beetle attacks, and wildfires [19], with higher mortality at the low-elevation warm edge of the range [20]. Regeneration and establishment of ponderosa pine seedlings following drought and wildfires has been sparse [21,22]. In order to promote ponderosa pine regeneration in a warming climate, planting low-elevation trailing-edge provenances has been recommended when natural regeneration fails [18,23], as low-elevation provenances have been shown to have traits of drought adaptation [24,25]. However, movement of populations from low elevations to higher elevations could result in earlier budburst and a risk of spring frost damage [26]. Therefore, more information is needed about provenance variation in phenological processes in southwestern ponderosa pines under field conditions to make informed decisions about selecting seed sources for out-planting in a changing climate.

Results of studies performed in controlled greenhouse environments may or may not be scalable to field conditions [27]. Direct comparisons of results from greenhouse and field-based studies are required to determine the predictability of field performance from greenhouse studies. A study of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) found a similar pattern of variation in budburst timing among provenances in greenhouse and field environments [28]. This suggests that greenhouse results for budburst timing of provenances are relevant to field performance, but studies are needed for other species such as ponderosa pine.

A field common garden study was used to investigate variation in budburst phenology among 21 southwestern ponderosa pine provenances obtained from different elevations across Arizona and New Mexico. The hypotheses for this study were that (1) budburst varies among provenances, with earlier budburst in low-elevation provenances, and (2) differences in budburst timing among provenances are consistent for seedlings grown in greenhouse and field environments. The objective was to determine if the pattern of earlier budburst by low-elevation provenances found in an earlier greenhouse study was maintained, muted, or amplified under field conditions.

2. Materials and Methods

2.1. Provenance Information

Ponderosa pine seeds from 21 provenances were used in this study representing a wide elevational range from Arizona and New Mexico (Figure 1). Seeds were obtained for 19 of the 21 provenances from collections at the Northern Arizona University (NAU) Greenhouse Facility located in Flagstaff, Arizona, and New Mexico State University's John T. Harrington Forestry Research Center located in Mora, New Mexico. Seeds were collected for the remaining two provenances in the year 2017. Each provenance consisted of seeds from 3–6 mother trees or a pooled collection without mother tree level information. The selected provenances varied in elevation, mean annual temperature (MAT), and mean annual precipitation (MAP) (Table 1). Climatic information for each provenance was obtained from PRISM (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 19 September 2020). Provenance origins ranged in MAT from 5.7 °C to 14.2 °C, in MAP from 364 mm to 767 mm, and in elevation from ~1600 m to ~2800 m. Provenance elevation had a moderate, positive correlation with MAP (r = 0.500, p = 0.020) and a strong, negative correlation with MAT (r = −0.902,

$p < 0.0001$); MAT had a moderate, negative correlation with MAP ($r = -0.434$, $p = 0.048$). Latitude had a moderate, negative trend with MAT ($r = -0.406$, $p = 0.067$) and longitude had a moderate, positive trend with elevation ($r = 0.370$, $p = 0.098$) (Table 2).

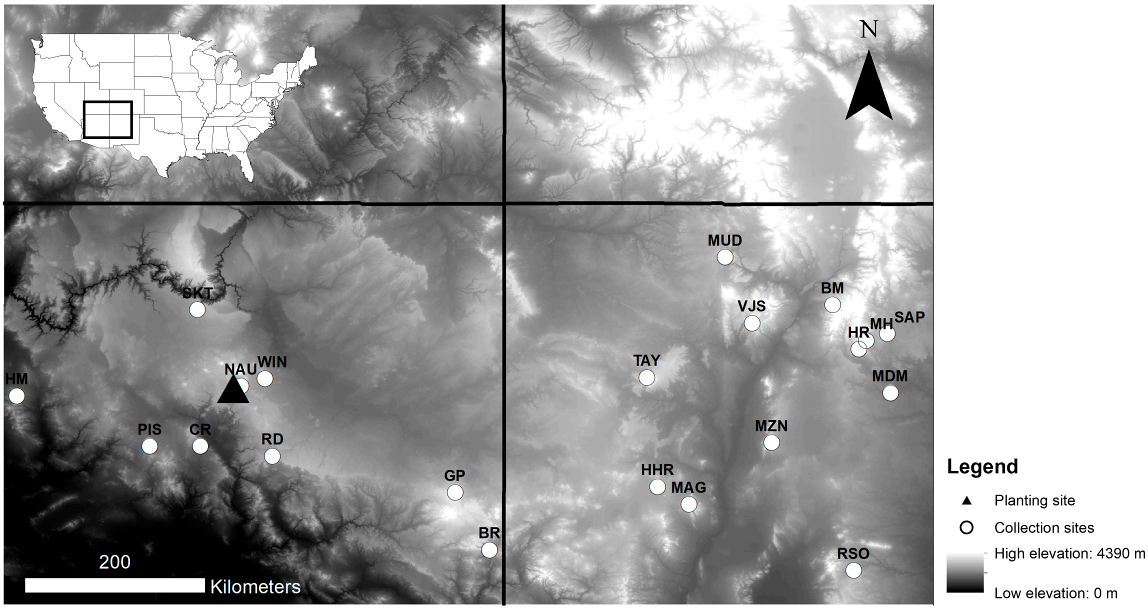

Figure 1. Location map of the 21 provenance collection sites (white circles) of *Pinus ponderosa* and the location of the field common garden (black triangle).

Table 1. Provenance name, code, latitude, longitude, elevation, mean annual temperature (MAT), and mean annual precipitation (MAP) ordered by increasing elevation. Climate data (30 year normal, 1981–2010) are from PRISM (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 19 September 2020). Values are means over mother trees at each provenance.

Provenance (code)	Latitude/Longitude	Elevation (m)	MAT (°C)	MAP (mm)
Cherry Road (CR) [1]	34.586/−112.057	1592	14.2	408
Blue River (BR)	33.555/−109.193	1674	11.8	581
Mesa Del Medio (MDM)	35.116/−105.217	1714	12.3	397
Prescott—Iron Springs Road (PIS) [1]	34.585/−112.559	1846	11	546
Townsend Winona (WIN)	35.254/−111.415	1934	10.2	398
Hualapai Mountains (HM) [1]	35.084/−113.875	1969	11.5	403
Ruidoso Service Office (RSO) [1]	33.350/−105.583	1976	11.1	506
Sapello Rt. 3 (SAP)	35.700/−105.250	2050	9.8	456
South Kaibab Tusayan Dist. (SKT)	35.939/−112.084	2067	8.9	410
Northern Arizona University (NAU)	35.182/−111.655	2104	8.4	540
Rim District (RD) [1]	34.487/−111.343	2244	9.4	767
HH Ranch (HHR) [1]	34.183/−107.525	2270	9.2	364
Mineral Hill (MH) [1]	35.633/−105.461	2277	8.5	528
Mud Springs (MUD)	36.463/−106.859	2277	6.9	443
Manzano Mountains (MZN)	34.623/−106.400	2366	8.6	638
Vallecitos-Jemez Springs (VJS)	35.809/−106.589	2436	6.8	571
Hartman Ridge (HR)	35.550/−105.533	2500	8.8	526
Borrego Mesa (BM) [1]	35.990/−105.794	2560	6.3	470
Magdalena Mountains (MAG)	34.006/−107.215	2565	8.9	512
Green's Peak (GP) [1]	34.126/−109.535	2760	5.7	671
Mount Taylor (TAY) [1]	35.266/−107.633	2814	6.1	722

[1] Provenances used in earlier greenhouse study [25].

Table 2. Correlation coefficients between provenance environmental characteristics and budburst date (n = 21). Values in parentheses are p values. Boldface type indicates significance ($p < 0.05$).

	Budburst Date	Elevation	MAT	MAP	Latitude
Budburst date					
Elevation	**0.528 (0.013)**				
MAT	−0.353 (0.116)	**−0.902 (<0001)**			
MAP	**0.522 (0.015)**	**0.500 (0.020)**	**−0.434 (0.048)**		
Latitude	−0.413 (0.062)	0.203 (0.375)	−0.406 (0.067)	−0.243 (0.287)	
Longitude	0.058 (0.802)	0.370 (0.098)	−0.324 (0.151)	0.029 (0.898)	0.139 (0.546)

2.2. Field Planting

Seedlings used for field planting were grown at the John T. Harrington Forestry Research Center of New Mexico State University in Mora, NM. Seedlings began as seeds that were sown in March 2018 into 164 mL containers and placed in racks with 98 container capacities (Ray Leach Cone-tainers-SC10 Super, RL98 Tray, Stuewe & Sons, Inc., Tangent, OR, USA). Media was a 2:1:1 mixture of sphagnum peat, perlite, and vermiculite (v:v:v). Seedling emergence rates were uniform across sources with the majority of germination occurring within 14 days after sowing. For the initial three weeks, seeds and germinates were misted 5 times daily, followed by overhead irrigation after total soil moisture dropped to approximately 75% of container capacity based on gravimetric weights. Supplemental lighting (metal halide lamps; range of 75–125 1.55 µmmol m^{-2} s^{-1}) was provided when necessary to maintain an 18 h photoperiod. Daytime and nighttime temperatures were maintained at 21–26 °C and 18–22 °C, respectively. A starter fertilizer (Peters Professional 25–30 ppm 10-30-20 N-P-K) was applied once per week after planting for a total of 5 weeks, followed by a grower fertilizer (Peters Professional 75–150 ppm 21-5-20 N-P-K) applied once per week, and finally a finisher fertilizer (Plant Marvel Nutriculture 4-25-35 N-P-K) applied once per week.

In July 2018, the greenhouse grown seedlings were planted in a field common garden study at the Arboretum Forest site of the Southwest Experimental Garden Array (SEGA; https://sega.nau.edu; Figure 1) located 10 km from Flagstaff, Arizona (latitude 35.16, longitude −111.73, and elevation 2200 m). The mean annual temperature at the study site was 7.6 °C, and the mean annual precipitation was 555 mm (1981–2010). During the year of assessment (2019) the mean annual temperature was 6.9 °C, and the annual precipitation was 636 mm. Seedlings were planted in a randomized complete block design at a spacing of 1.2 m between seedlings. Forty-eight seedlings from 21 provenances each were planted across 4 blocks (1008 total seedlings). Each provenance was planted as a 12-tree linear plot, randomly positioned within each block.

2.3. Budburst Phenology

Budburst timing was visually assessed on all live seedlings (658 total; 350 omitted from analysis due to rabbit herbivory; Table 3) in each block of the field planting once per week between May and June, 2019. The protocol used to define budburst was the same as was used in an earlier greenhouse study, where budburst was defined as the Julian date when new needles emerged from the terminal bud [25]. Results from this earlier study [25] were used to compare provenance differences in budburst between our field planting and the greenhouse planting. In the earlier greenhouse study, seedlings were grown from seed at the Northern Arizona University Greenhouse Facility starting in February 2018. Seedlings were watered thrice per week, fertilized twice per week, and exposed to temperatures between 21 and 26 °C, except during the winter dormancy period (mid-November through mid-January), when the seedlings were watered once per week, not fertilized, and exposed to temperatures between 5 and 10 °C. Ten of the 21 provenances used for the field study were included in the greenhouse study (Table 1). For these ten provenances in the greenhouse, budburst was visually accessed on 80 seedlings per provenance (800 total), twice per week, between January and February, 2019.

Table 3. Mean budburst for each provenance, with standard errors in parentheses (ordered by increasing elevation). Means followed by the same letter do not differ significantly ($p \leq 0.05$; Tukey's honestly significant difference (HSD) tests; provenance main effect $p = 0.0009$).

Provenance	Number of Seedlings	Budburst Date (Julian Days)
CR	24	162.7 ab (1.05)
BR	29	165.4 ab (1.05)
MDM	31	163.2 ab (1.37)
PIS	36	165.2 ab (0.84)
WIN	33	163.2 ab (1.60)
HM	41	166.1 ab (0.74)
RSO	28	165.1 ab (0.69)
SAP	30	165.5 ab (0.84)
SKT	39	161.4 b (1.34)
NAU	30	165.9 ab (0.39)
RD	27	166.6 a (0.84)
HHR	39	166.1 ab (1.30)
MH	36	165.8 ab (0.83)
MUD	30	164.2 ab (1.20)
MZN	26	165.0 ab (0.49)
VJS	36	163.2 ab (0.52)
HR	26	163.1 ab (1.47)
BM	30	165.1 ab (0.50)
MAG	18	169.4 a (2.13)
GP	37	168.1 a (1.06)
TAY	32	168.9 a (0.93)

2.4. Data Analysis

Analysis of variance (ANOVA) was used to test for differences in budburst date among the 21 provenances in the field study. We used a mixed-effects model with provenance as a fixed effect and block as a random effect. In order to examine the influence of provenance elevation on budburst phenology, provenances were assigned to elevational groups, which were included in the ANOVA. Elevational groups were defined as follows [25]: low elevation < 2000 m; middle elevation = 2000 to 2500 m; high elevation > 2500 m. The analysis was conducted on block-level means because individual seedlings were regarded as observational units and row plots of provenances within blocks were regarded as experimental units. Tukey's honestly significant difference (HSD) test was used to detect significant differences between means ($\alpha = 0.05$) among provenances and elevation groups. The relationship between field-measured and greenhouse-measured budburst date was investigated on a subset of field provenances (10 total; Table 1) that was also used in an earlier greenhouse common garden study. The relationships between field and greenhouse budburst dates (n = 10) and between field budburst date and environmental characteristics of provenance locations (n = 21) were evaluated on provenance means with correlation and regression analyses. Strength of relationship was interpreted as weak when the absolute value of the correlation coefficient (r) was between 0 and 0.3, moderate between 0.3 and 0.7, and strong between 0.7 and 1.0 [29]. JMP Pro version 14 (SAS Institute Inc., Cary, NC, USA) was used to perform all analyses.

3. Results

Budburst date in the field planting differed significantly among provenances ($p = 0.0009$; Table 3), ranging from 161.4 Julian days for South Kaibab Tusayan Dist. (SKT) to 169.4 Julian days for Magdalena Mountains (MAG).

Budburst date in the field planting also differed significantly among elevation groups ($p = 0.0026$; Table 4). Low- and middle-elevation provenances had similar budburst dates of about 164 Julian days.

However, high-elevation provenances broke bud about 3 days later (mean budburst = ~167 Julian days) than low- and middle-elevation provenances.

Table 4. Mean budburst for each elevation group, with standard errors in parentheses. Means followed by the same letter do not differ significantly ($p \leq 0.05$; Tukey's honestly significant difference (HSD) tests; provenance main effect $p = 0.0026$).

Elevation Group	Budburst Date (Julian Days)
Low elevation	164.6 b (0.39)
Middle elevation	164.6 b (0.22)
High elevation	167.7 a (0.52)

Correlation analysis revealed some interesting relationships between mean provenance budburst date in the field planting and environmental and geographical characteristics (Table 2). Specifically, budburst date had a moderately positive correlation with elevation (r = 0.528, $p = 0.013$) and MAP (r = 0.522, $p = 0.015$) and a moderately negative trend with latitude (r = −0.413, $p = 0.062$) (Figure 2).

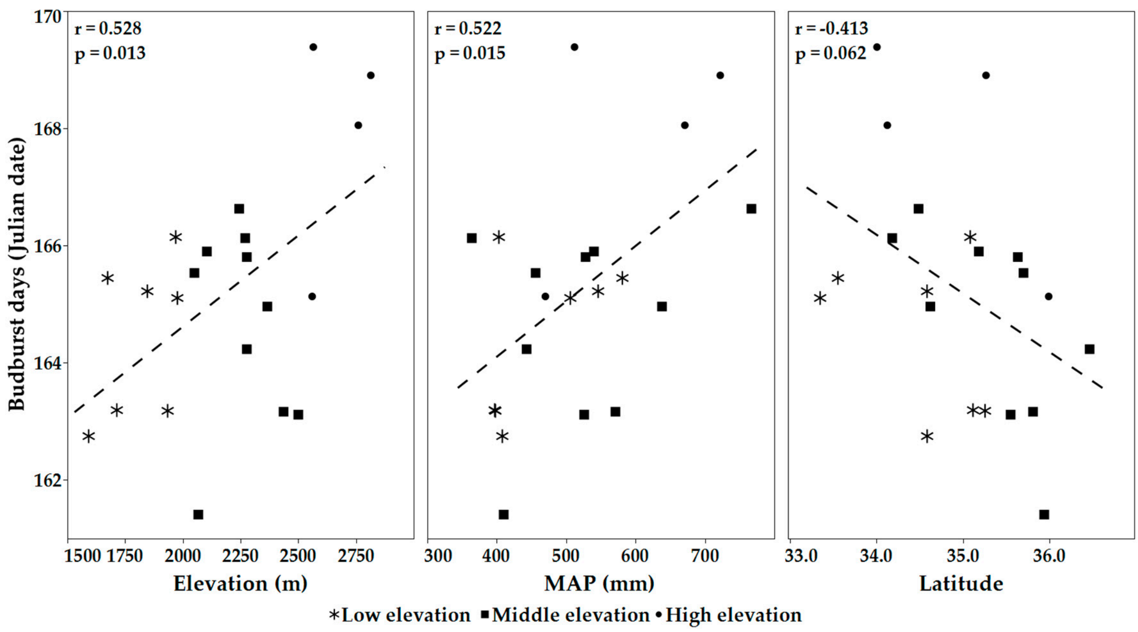

Figure 2. Relationships between provenance mean budburst date and elevation, mean annual precipitation (MAP), and latitude ($n = 21$). Elevation group is shown by different symbols.

A moderate, positive trend (r = 0.554, $p = 0.096$; Figure 3) was found between budburst dates measured in the field planting and those measured in the greenhouse planting for the same 10 provenances (Table 1). Budburst occurred much earlier in the greenhouse (Julian days 41 to 45), which was warmed up in mid-January to promote early growth, compared with the field, where budburst occurred in late June (Julian days 163 to 169). In addition, for the same 10 provenances, the budburst range of about 4 days in the greenhouse was less than the range of about 6 days in the field.

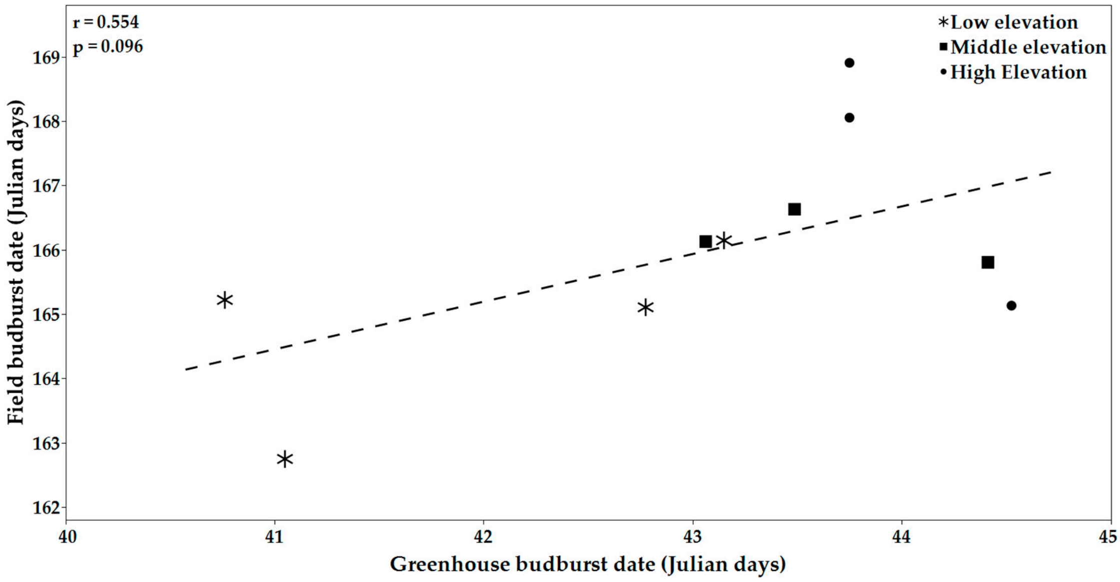

Figure 3. Relationships between mean budburst date measured under greenhouse and field conditions for the same provenances (n = 10).

4. Discussion

This study investigated variation in budburst phenology among 21 provenances of southwestern ponderosa pine using observations of a field common garden study in the first spring after planting, and of a greenhouse study of 10 of the same provenances. The goal of this study was to test the hypotheses that (1) timing of budburst would vary among provenances in a field planting, and low-elevation provenances would break bud sooner because budburst timing is often genetically controlled and associated with spring frost hardiness [30,31]; and (2) provenance variation in budburst timing measured under field conditions would be related to budburst timing of the same provenances measured under greenhouse conditions. In addition, correlations between field budburst date and provenance environment and geographic characteristics were examined. While the results strongly suggest genetic differences in budburst phenology among southwestern provenances of ponderosa pine, other explanations such as epigenetic and maternal influences were not investigated.

The first hypothesis was supported by significant differences in budburst date among provenances and elevation groups, along with a moderate positive correlation between budburst date and provenance elevation. The maximum difference in field budburst date among provenances was eight days. To understand the ecological significance of this difference, additional field common garden studies at elevations higher than those of the current study are needed to see if this difference is amplified or maintained. Amplification of this difference could predispose seedlings to spring frost damage. On the contrary, if this difference is not amplified, it suggests an opportunity for management in the form of flexibility for seed transfer guidelines pertaining to drought and/or heat resistance. The current study also used observations of seedlings during only the first spring after planting in a year when spring frost damage did not occur. A more complete understanding of the ecological importance of this amount of variation in budburst will require observations over more years [32], especially years with pronounced late-spring frosts.

The pattern of low-elevation provenances breaking bud earlier than high-elevation provenances is likely a result of local adaptation to warm spring temperatures at lower elevations and has been shown to be a highly species-specific response [32]. Similar elevational influence on budburst has been reported in an earlier study showing provenance variation and a negative correlation between elevation and growth potential and duration of shoot elongation in ponderosa pines from Colorado [13]. In addition, the finding in the field study of earlier budburst of low-elevation provenances is consistent with an earlier greenhouse study of some of the same provenances [25]. However, results in this study are different from a recent field common garden study in California showing no significant difference in budburst phenology among four provenances of ponderosa pine from different elevations [14], suggesting that findings from one region of ponderosa pine are not always applicable to other regions. Elevation of provenances in that study ranged from ~145 m to ~1920 m as compared to ~1600 m to 2800 m in this study.

In addition to an elevational trend, a moderate, positive correlation between provenance MAP and budburst timing was found in the current study, showing that provenances from drier areas broke bud sooner than provenances from wetter areas. This result is similar to a study of Douglas fir that reported earlier budburst of provenances from areas with low summer rainfall [33]. However, the result is different from a study involving 35 provenances of cork oak (*Quercus suber* L.) where no correlation was found between budburst and provenance precipitation and elevation [34]. Such information may have implications for assisted migration of seed sources from drier areas to high-elevation, colder sites that are expected to become drier in the future with climate warming.

An interesting latitudinal trend of earlier budburst by northern provenances was also found in the current study. The results of this latitudinal pattern are different from a study involving beech (*Fagus sylvatica* L.) provenances in northern Poland showing later flushing by northern provenances [35]. The latitudinal pattern could be the result of earlier fulfillment of the chilling hour requirement by northern provenances, as days to budburst have been shown to decrease as chilling hour accumulation increases in ponderosa pine [36].

The lack of significant correlation between budburst date and MAT ($p = 0.116$) was surprising considering the strong, negative correlation between elevation and MAT ($p < 0.0001$) and a moderate, positive correlation between budburst date and elevation ($p = 0.013$). This result may be due to the lack of direct temperature and precipitation data measured on site for the provenances. The provenance environmental data were obtained using PRISM from an interpolation equation that predicts temperature and precipitation largely from elevation in a particular region [37]. This approach likely does not capture all ecologically relevant microsite climatic variation.

A moderate, positive trend was documented between budburst timing in field and greenhouse environments for the same ten provenances. This relationship is consistent with our second hypothesis and may have applications for investigating provenance variation in phenology in greenhouse experiments. However, the correlation for the relationship had a p value of 0.096 and a sample size of only 10 provenances and therefore must be interpreted with caution. To our knowledge, this is the first report for ponderosa pine provenances of a direct comparison of budburst phenology between field and greenhouse studies. Similar results were reported in a study of Douglas fir provenances, which suggests that greenhouse studies have potential for investigating provenance differences in budburst and predicting patterns in field plantings [24].

5. Conclusions

In conclusion, budburst timing varies among provenances of southwestern ponderosa pine. These variations are mainly related to provenance elevation, precipitation, and latitude; low-elevation, drier, and high-latitude provenances break bud sooner than higher elevation, wetter, and lower latitude provenances. In addition, geographic patterns in budburst timing from greenhouse experiments may be applicable to field plantings. More information about budburst timing and risk of spring frost damage is needed for developing species-specific seed transfer guidelines and effective assisted-migration strategies in a changing climate.

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