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The 1912 Douglas-Fir Heredity Study: Long-Term Effects of Climatic Transfer Distance on Growth and Survival

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Abstract

The 1912 Douglas-Fir Heredity Study is one of the first studies undertaken by the US Forest Service, and one of the first forest genetics studies in North America. The study considers provenance variation of 120 parent trees from 13 seed sources planted at five test sites in the Pacific Northwest. The unique, long-term nature of the study makes it valuable to revisit and consider its biological and historical significance. This analysis considers how far climatically Douglas-fir populations may be moved without incurring unacceptable declines in growth and survival. Results indicate that Douglas-fir seed sources may be moved at least 2° C cooler or warmer and still retain good long-term survival and productivity. However, projected future climate change beyond 2° C may lead to lower survival and productivity. One option to address these concerns is assisted migration; however, if seed sources are moved beyond 2–3° C to a cooler climate in anticipation of warming, or from a more continental to a maritime climate, we are likely to see increased mortality and associated losses in productivity in the near-term. Lessons from this study include: (1) pay attention to good experimental design; we were able to overcome limitations from the design by using new statistical approaches; (2) maladaptation may take time to develop; poorer survival was not evident until more than two decades after planting; and (3) long-term studies may have value for addressing new, unforeseen issues in the future.

Keywords: provenance test, adaptation, climate change, climatic transfer distance, forest history

The turn of the 20th century saw a great increase in the protection and management of forests in the United States. The Forest Reserve Act of 1891 allowed the President to establish forest reserves from public lands; the Organic Act of 1897 provided for the management of those reserves; and in 1905, the administration of all federal forestry activities was united under the newly formed US Forest Service within the Department of Agriculture. With the new emphasis on protection and management, there was increased interest in research and the application of "scientific forestry." The early 20th century also saw the establishment of the first forestry programs at universities in the United States. In 1898, for example, Cornell established a forestry program led by Bernard Fernow, an early forestry leader educated in Germany. One of his first students, a Russian immigrant named Rafael Zon, became head of the Forest Service's Office of Silvics, and a major proponent of forestry research. After touring Germany, Austria, and France in the winter of 1908, Zon wrote a memo to Gifford Pinchot, Chief of the Forest Service, proposing to establish forest experiment stations in the western United States similar to those he saw in Europe. The first experiment station was established in the spring of 1908 at Fort Valley on the

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Management and Policy Implications

- Douglas-fir seed sources may be expected to retain good growth and survival for changes in climate of 2° C warmer or colder, whether those changes occur by seed transfer or by climate change at a site. This is within current seed zone guidelines and within current observed levels of climate change. Thus, past reforestation practices have helped ensure productive forests.
- Climates are expected to warm more than 2° C over the next few decades, leading to lower survival and productivity of Douglas-fir stands. Assisted migration to move seed sources from warmer to colder climates has been suggested to ensure adaptation of future forest stands. Seed sources should not be moved, however, more than 2–3° C to a cooler climate in order to ensure good survival in the near-term.
- Movements from the more continental climates of the Cascade Range to the more maritime climates of the Coast Range should be avoided.
- There is value in long-term field studies. Changing objectives may lead to new insights.

Coconino National Forest in Arizona. Later, Zon argued for separating all research work from administration within the Forest Service, leading to the establishment of the Branch of Research in 1915.

Forestry research saw its beginnings in the Pacific Northwest with the arrival in 1908 of Thornton T. Munger, fresh from completing a masters degree in forestry from Yale University. Munger was assigned to the Section of Silvics at the Forest Service's new North Pacific District in Portland, Oregon, where he established some of the first forestry research plots in the western United States. These plots were important for demonstrating the high growth potential of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Prior to that, the species was seen primarily as a resource to be mined by the timber industry. Around the same time, fires burned through large areas of the Pacific Northwest. The Yacolt burn of 1902 was particularly damaging, burning 238,000 acres and killing 65 people near the Columbia Gorge. Because natural regeneration was largely ineffective, the Wind River Nursery, one of the first in the West, was established in 1909 to reforest the burned and cutover lands.

At the encouragement of Zon, Munger began studying the suitability of species and seed sources for reforestation. These studies likely stemmed from two important influences. First, exotic species were receiving a great deal of attention in Europe, particularly species from western North America, including Douglas-fir. Second, differences among seed sources were recognized in early European provenance tests, such as the first large-scale provenance study that was initiated in 1907 with Scots pine (Langlet 1971). Another important influence was the rediscovery of Mendel's Laws of Heredity in 1900 (Sandler and Sandler 1986). Surely, the activities in Europe and the new science of genetics must have contributed to the thinking and activities undertaken by Zon and Munger.

In 1912, Munger initiated two influential studies on the suitability of species and seed sources for the Pacific Northwest. The first study, known as the Wind River Arboretum Study, began with a few trials of eastern hardwood species and then grew to 152 conifer and hardwood species and varieties (Silen and Olson 1992). The Wind River Arboretum was important for demonstrating the superiority of native species in the Pacific Northwest, something that was not all that certain at the beginning. It appears, however, to be a one-way street—although Douglas-fir and other western species are important worldwide, most exotic species did not perform well in the Pacific Northwest (Silen and Olson 1992). The Wind River Arboretum has also been important to show the impact of tree development and climate over time. If foresters had put too much faith into early results, we might have seen many failed plantations of Siberian larch in the region.

The second study became known as the Douglas-Fir Heredity Study, one of the earliest forest genetics studies in North America. In the fall of 1912, Munger had a crew collect cones from 13 locations in the Coast and Cascade Ranges that differed in latitude, elevation, and soil type (Munger and Morris 1936). At some sites, parent trees were selected to reflect differences in stand age, stand density, and disease infection. The progeny from 120 maternal parent trees were grown at the Wind River Nursery, and then outplanted in 1915 and 1916 at six locations in western Oregon and Washington. The original objectives were to determine the best parents to use as seed trees after logging or for collecting seed for artificial regeneration. Munger was particularly interested in knowing whether the offspring of parents from different sites or classes of trees inherited different characteristics—hence the name of the study.

Early results by Munger and Morris (1936) found no important differences among the progeny of parents differing in age, stand density, fungal infection, or soil type. However, high-elevation sources grew best at the high-elevation test site, and the coastal seed source grew best at the milder coastal site. Despite this evidence for local adaptation, two sources from the central Washington Cascades, near Granite Falls and Darrington, grew well across all test sites. In contrast to growth, they did not find large differences in mortality among the seed sources at any of the test sites. These results, combined with anecdotal evidence of poor growth of off-site plantations compared to adjacent naturally regenerated stands, spurred the development of the first seed collection guidelines and seed zones for the Douglas-fir region (Isaac 1949). In 1939, the USDA established a "Forest Seed Policy" that required the use of seed of known origin, and recommended that seed be planted within 100 miles and 1,000 feet in elevation from its origin. In 1942, Munger divided the region into nine "provenances" that he considered to be climatically homogenous. Beginning in the 1950s, Roy Silen of the US Forest Service Pacific Northwest Research Station was instrumental in continuing to measure the study over the next half century. He reported on 50-year results in a Station annual report in 1963, and at two conferences in 1964 (Silen 1963, Silen 1965, Silen 1966). His findings strongly influenced ideas of fine-scaled local adaptation in the region. By 1962, a system to certify forest tree seed was established for Oregon and Washington, and in 1966, seed-zone maps were developed that continue to be widely used. In addition to seed zones, family differences observed in the Douglas-Fir Heredity Study were influential in promoting tree improvement programs in the 1960s.

Despite the influence of the Douglas-Fir Heredity Study, little has been published since the reports in 1936 and the 1960s. The unique, long-term nature of the study makes it particularly valuable to revisit and consider its biological and historical significance. Although the study has limitations associated with the experimental design, new statistical techniques allow us to better evaluate the results. Furthermore, the increasing concern over climate change brings renewed interest in understanding adaptive responses of populations to climate, and the climatic distance that populations may be moved in anticipation of continued warming. With this in mind, the objectives of this analysis were to explore (1) the climatic distance that Douglas-fir populations can be moved while maintaining acceptable growth and survival, and (2) how tree growth and survival change over time and in response to specific climatic events. A secondary goal is to provide the historical context for this unique, long-term study.

Materials and Methods

Provenances

In the fall of 1912, cones were collected from 120 open-pollinated Douglas-fir trees from 13 seed sources (also referred to as provenances) in western Oregon and Washington (Table 1A; Figure 1). The number of parent trees per source location varied between three and 21. Three provenances (Santiam, Palmer, and Race Track) were chosen to represent higher elevation locations, and one provenance (Lakewood) came from an area of glacial outwash soils with poor site quality. Different parents were selected within provenances to contrast different age classes and open-grown versus dense competition from neighboring trees. In addition, trees were selected within the Wind River and Gates provenances to explore differences between parents infected versus uninfected with the red ring rot pathogen (*Phellinus pini*). Munger and Morris (1936) found little difference in heights and survival between parents chosen from different age classes, stand densities, and infection status within sites, and little difference between the Lakewood provenance from poor soils and the other sites. These results are consistent with our findings; thus, our analysis focused on differences among provenances as related to the climates of the source locations.

Test plantations

Seeds from the 120 parent trees were sown at the Wind River Nursery in the springs of 1913 and 1914, grown for two growing seasons, and then outplanted at six test sites in the springs of 1915 and 1916 (Table 1B). The test sites were chosen to represent typical planting sites in the study area (Figure 1). A fire in 1917 destroyed the middle elevation site in the northern Oregon Cascades; thus, this site was abandoned (and not included in Table 1B). The 1917 fire also destroyed part of the Upper Mt Hood site. Shortly after planting, the 1915 portion of the Stillaguamish site and the 1916 portion of the Hebo site were damaged by mountain beaver and were not measured again until 1963 (Silen 1963). Additional early mortality was mostly caused by falling snags. Trees that died before 1917 and trees that had been killed by fire were excluded from the data analyses, as were the 1915 portion of the Stillaguamish plantation and the 1916 portion of the Hebo plantation.

Table 1. Location and climate information* for provenances and test sites used in the Douglas-Fir Heredity Study (sorted by decreasing mean annual temperature).

Name	Latitude (°)	Longitude (°)	Elevation (m)	MAT (° C)	MCMT (° C)	MWMT (° C)	TD (° C)	MAP (mm)	MSP (mm)
A. Provenances									
Portland	45.489	–122.730	90	11.0	3.5	18.8	15.2	1,150	200
Lakeview	47.176	–122.592	30	10.7	3.8	17.9	14.1	1,063	198
Benton	44.642	–123.580	215	10.5	3.8	17.7	13.8	1,716	236
Carson	45.718	–121.825	120	10.4	1.7	18.8	17.1	1,721	244
Gates	44.750	–122.417	290	9.9	2.8	17.6	14.7	1,748	312
Granite Falls	48.104	–121.917	120	9.6	2.3	17.1	14.8	1,939	413
Hazel	48.263	–121.844	275	8.9	1.6	16.7	15.0	2,340	476
Darrington	48.254	–121.592	150	8.9	0.8	17.1	16.3	2,418	403
Wind River	45.823	–121.958	410	8.9	0.2	17.9	17.7	2,444	297
Fortson	48.267	–121.725	150	8.5	0.9	16.4	15.5	2,689	507
Race Track	45.897	–121.850	790	7.2	–0.7	15.9	16.6	2,628	332
Santiam	44.661	–121.907	975	7.1	–0.6	16.0	16.6	2,041	298
Palmer	45.559	–122.001	915	6.8	–0.7	15.0	15.7	3,372	548
B. Test sites									
Wind River	45.792	–121.927	353	9.0	0.3	17.9	17.7	2,626	316
Hebo	45.148	–123.756	638	8.3	2.5	14.7	12.2	2,675	393
Stillaguamish	48.075	–121.606	579	7.7	–0.5	15.8	16.4	3,250	653
Lower Mt Hood	45.268	–121.821	853	6.9	–0.8	15.4	16.2	2,014	349
Upper Mt Hood	45.263	–121.774	1,372	5.4	–2.0	14.2	16.1	1,912	330

Note: MAT, mean annual temperature; MCMT, mean coldest month temperature; MWMT, mean warmest month temperature; TD, continentality as determined by the difference between MWMT and MCMT; MAP, mean annual precipitation; MSP, mean summer precipitation.
*Climatic information derived from ClimateNA (Wang et al. 2016).

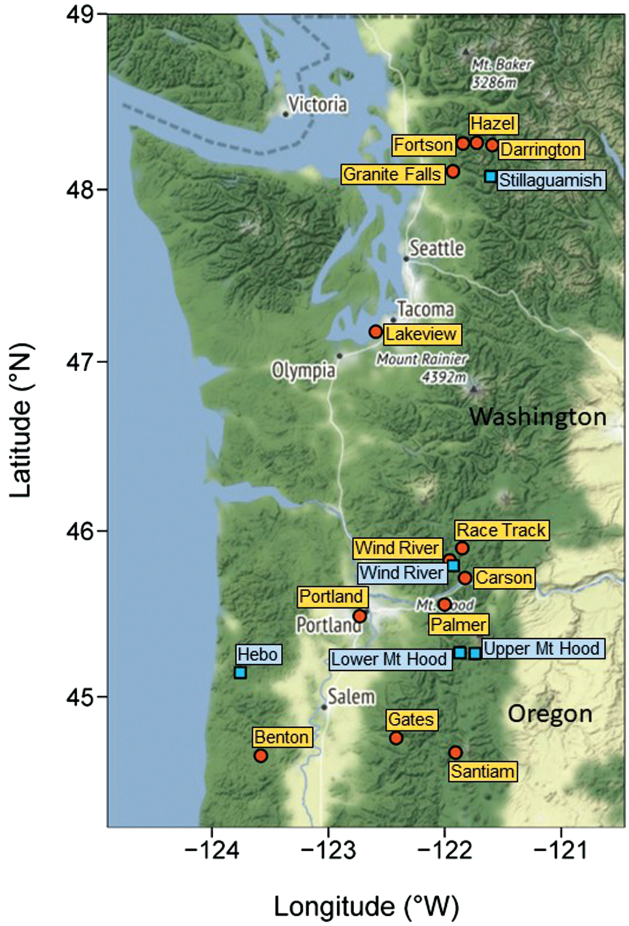

Figure 1. Map of provenances (orange circles) and test sites (blue squares) in the Douglas-Fir Heredity Study.

The field design at each test site was family row plots with 20 trees per row in 1915, and 10 trees per row in 1916. Because families and provenances were replicated across years, but not within years, we treated the 1915 and 1916 plantings as blocks during data analysis. Trees were planted at a 2.1 m × 2.1 m spacing, and filler trees were used when necessary to fill out a row. In the 1915 plantings, an additional 11 families from five of the 13 provenances were planted in 100-tree row plots across the length of the plantation (included in the analysis) with the idea of accounting for microsite variation at each site. Although ultimately not fruitful, this was an idea that was quite forward-thinking for its time. Within each planting year, families were grouped by provenance; that is, family row plots from the same provenance were planted adjacent to one another. Border rows were not planted around each plantation, although adjacent trees were of similar size and likely resulted from regeneration at about the same time. The study was not thinned at any test sites.

Although survival and heights were measured in early years, complete records were only available beginning in 1923. Survival was measured after planting and approximately every 10 years between 1923 and 1993, and in 2013. Trees that died before 1917 were excluded from the analysis with the assumption that much early mortality may be due to poor planting. Diameter was measured at breast height on all trees approximately every 10 years from 1931 to 1993, and in 2013. Height was measured on all trees in 1923, 1931, 1963, 1993, and 2013. We also calculated individual tree volume (using methods of Poudel and Hailemariam 2016) and volume per hectare for those years in which both height and diameter measurements were available.

Data Analysis

We hypothesized that provenance performance was related to the climatic difference between the test site and the seed-collection location (i.e., where the parent trees were exposed to climatic selection pressures). The variation among provenances for each trait in each year of evaluation was analyzed with the SAS GLIMMIX procedure (SAS Institute 2014), using restricted maximum likelihood and a fully random model. The replicated plantings of families from each provenance in 1915 and 1916 provided a measure of the nongenetic variation within test sites. The statistical model used for the across-site analyses was as described below. A similar reduced model was used for analyses of individual sites.

$$\begin{aligned} Z_{sypfn} = \; & \mu + S_s + Y_y + SY_{s\cdot y} + P_p + SP_{s\cdot p} + YP_{y\cdot p} \\ & + SYP_{s\cdot y\cdot p} + F_{f(p)} + SF_{s\cdot f(p)} + YF_{y\cdot f(p)} \\ & + SYF_{s\cdot y\cdot f(p)} + \varepsilon_{n(sypf)} \end{aligned}$$

where Z_{sypfn} is the observation for the nth tree in the fth family in the pth provenance in the yth planting year at the sth test site; S_s is the effect of the sth test site; Y_y is the effect of the yth planting year; $SY_{s\cdot y}$ is the interaction of the sth test site and yth planting year; P_p is the effect of the pth provenance; $SP_{s\cdot p}$ is the interaction of the sth test site and pth provenance; $YP_{y\cdot p}$ is the interaction of the yth planting year and pth provenance; $SYP_{s\cdot y\cdot p}$ is the interaction of the sth test site, yth planting year, and pth provenance; $F_{f(p)}$ is the effect of the fth family in the pth provenance; $SF_{s\cdot f(p)}$ is the interaction of the sth test site and fth family in the pth provenance; $YF_{y\cdot f(p)}$ is the interaction of the yth planting year and fth family in the pth provenance; $SYF_{s\cdot y\cdot f(p)}$ is the interaction of the sth test site, yth planting year, and fth family in the *p*th provenance; and $\varepsilon_{n(sypf)}$ is the random, independent error, ~$N(0, \sigma^2)$. The overall mean (μ) is a fixed effect, and all other effects in the model are random.

For growth measurements, we first performed analyses for each trait–year variable at each site to identify outliers. Observations with studentized residuals that were greater than three were excluded from further analyses. The intercept from the linear model for each site was used as an estimate of the site mean. For the combined analysis of growth traits across sites, data were divided by the square root of the error variance at each site to remove scale effects and standardize the variance (White 1996). A generalized linear model with a logit link function was used to analyze survival traits. Likelihood ratio chi-square tests were used to determine which trait–year combinations had significant variance components for sites, provenances, and site × provenance interactions. To investigate relations between provenance performance and provenance climatic origin, we used Best Linear Unbiased Prediction (BLUP) estimates for site × provenance interactions for trait–year variables that were significant in the across-site analysis using a p-value of <0.10. Climates of test sites and source locations were determined using 30-year normal data (1961–90) from ClimateNA (Wang et al. 2016). Pearson correlation coefficients between site × provenance BLUPs and source climates were estimated at each site. To further characterize the effects of climate variables on adaptation across a range of environments, we obtained linear and quadratic equations for the regression of site × provenance BLUPs on climatic transfer distances. These analyses accounted for differences in site productivity in two ways. First, because we standardized the observations by plantation, subsequent analyses were based on standardized BLUPs that accounted for differences in site productivity. Second, although the random effects model included the main effects of site and provenance, the pooled transfer function used only the site × provenance BLUPs—essentially, deviations from the main effects. Site main effects may result from differences in climate, soils, topography, competing vegetation, and management, whereas provenance main effects may result from differences in climatic origin, demographic history, and sampling error. By omitting the main effects from the pooled transfer function, we reduced the impact of these confounding factors, resulting in a transfer function that is broadly applicable to the provenances and sites we studied. For ease of interpretation, site × provenance BLUPs for survival were centered on the mean percent survival across sites. This was obtained using the inverse link function for the intercept from the combined logistic regression analysis. Climatic transfer distances were estimated for each climate variable as the test site climate minus the source climate.

Results

Test sites differed in growth and survival (Tables 2 and 3). In particular, trees at the three warmer sites of Wind River, Hebo and Stillaguamish were taller and had a greater diameter than those at the two cooler sites of Lower Mt Hood and Upper Mt Hood (Table 2). Survival by ages 18 and 19 was high at all sites (78–92 percent). Survival declined substantially over time, ranging from 31 percent at Lower Mt Hood to 15 percent at Stillaguamish by 2013. Some decades showed higher rates of mortality, including the 1930s at Upper Mt Hood, the 1940s at Stillaguamish, the 1950s at Hebo, and the 1960s at Wind River (Figure 2).

Provenance × site interactions provide evidence for local adaptation to climate. A provenance × site interaction was found for survival for measurements taken in 1941 and later ($p < 0.10$) and was particularly strong by 2013 ($p = 0.008$) (Table 3). A provenance × site interaction for survival, however, was not found in 1931. The differential survival of provenances at different sites appeared to be driven by factors arising

Table 2. Test site means for growth and survival traits in 1931 and 2013.

	1931			2013			
Test site	Height (m)	Diameter (cm)	Survival (percent)	Height (m)	Diameter (cm)	Volume/hectare (m^3 ha^{-1})	Survival (percent)
Wind River	4.5	6.0	78	39.9	42.8	783	20
Hebo	6.3	8.4	88	33.5	47.6	523	16
Stillaguamish	5.2	6.1	84	36.0	44.0	726	15
Lower Mt Hood	1.9	2.2	92	26.0	29.3	483	31
Upper Mt Hood	1.6	1.4	86	19.0	30.4	354	23

Table 3. Tests of significance (*p*-values) for site, provenance, and site × provenance variance components from BLUP analysis (prob > chi-square for likelihood ratio tests).

	Year								
Trait and source of variation	1923	1931	1941	1953	1963	1973	1983	1993	2013
Height									
Site	0.415	0.581			0.000			0.000	0.002
Provenance	0.094	0.105			0.312			0.254	0.157
Site × provenance	1.000	1.000			1.000			1.000	1.000
Diameter									
Site		0.006	0.040	0.063	0.011	0.005	0.008	0.002	0.002
Provenance		0.844	0.369	0.519	0.986	1.000	1.000	1.000	0.755
Site × provenance		0.014	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Volume									
Site		0.031			0.016			0.065	0.504
Provenance		0.693			1.000			1.000	0.330
Site × provenance		0.146			1.000			1.000	1.000
Volume/hectare									
Site		0.051			0.031			0.195	0.280
Provenance		0.811			1.000			1.000	1.000
Site × provenance		0.590			0.423			0.480	0.092
Survival									
Site	0.241	0.031	0.004	0.002	0.004	0.008	0.008	0.043	0.020
Provenance	1.000	1.000	0.371	0.598	0.348	1.000	1.000	1.000	1.000
Site × provenance	1.000	0.937	0.010	0.091	0.037	0.070	0.096	0.080	0.008

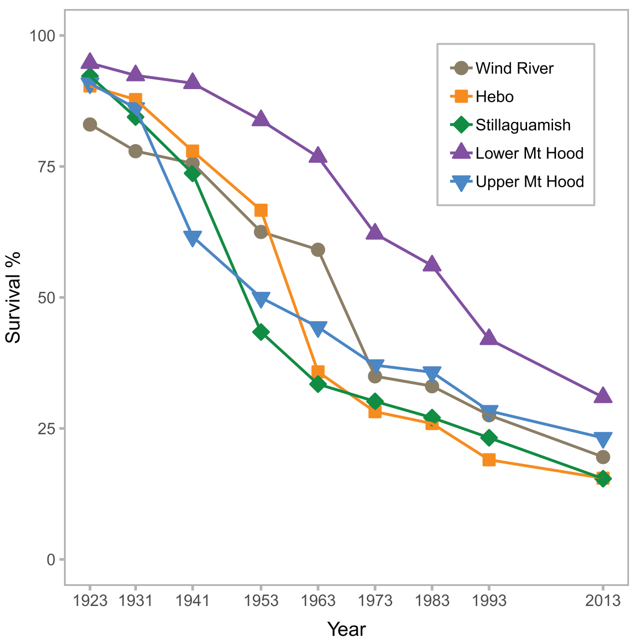

Figure 2. Survival over time at the five test sites of the Douglas-Fir Heredity Study.

between measurements in 1931 and 1941. Evidence for differences in growth among provenances planted at different sites was weak, except for diameter in 1931 ($p = 0.014$). Results from the 1931 measurement are consistent with the earlier findings of Munger and Morris (1936). Adaptation is evident for survival, but not for growth, at least not for those trees that survived beyond 1931.

Significant relations ($p < 0.05$) with climate variables were consistently found at Upper Mt Hood and Hebo for survival from 1941 to 2013. Regressions of survival on transfer distances across sites indicate that the patterns of survival in 1941 and 2013 can be described by a quadratic function primarily driven by responses at Upper Mt Hood and Hebo (Figure 3, Table 4). When provenances from locations with warmer winters were transferred to the cooler Upper Mt Hood site, they had lower survival than provenances transferred from cooler locations, in both 1941 and 2013 (Figure 3A, 3C). When provenances from locations with colder, more continental climates were transferred to the warmer, more maritime climate at Hebo, they had lower survival than provenances transferred from maritime climates, in both 1941 and 2013 (Figure 3B, 3D). In general, survival declined when provenances were moved more than 2° C mean coldest month temperature (MCMT) to a colder or warmer winter temperature, or when provenances were moved than more

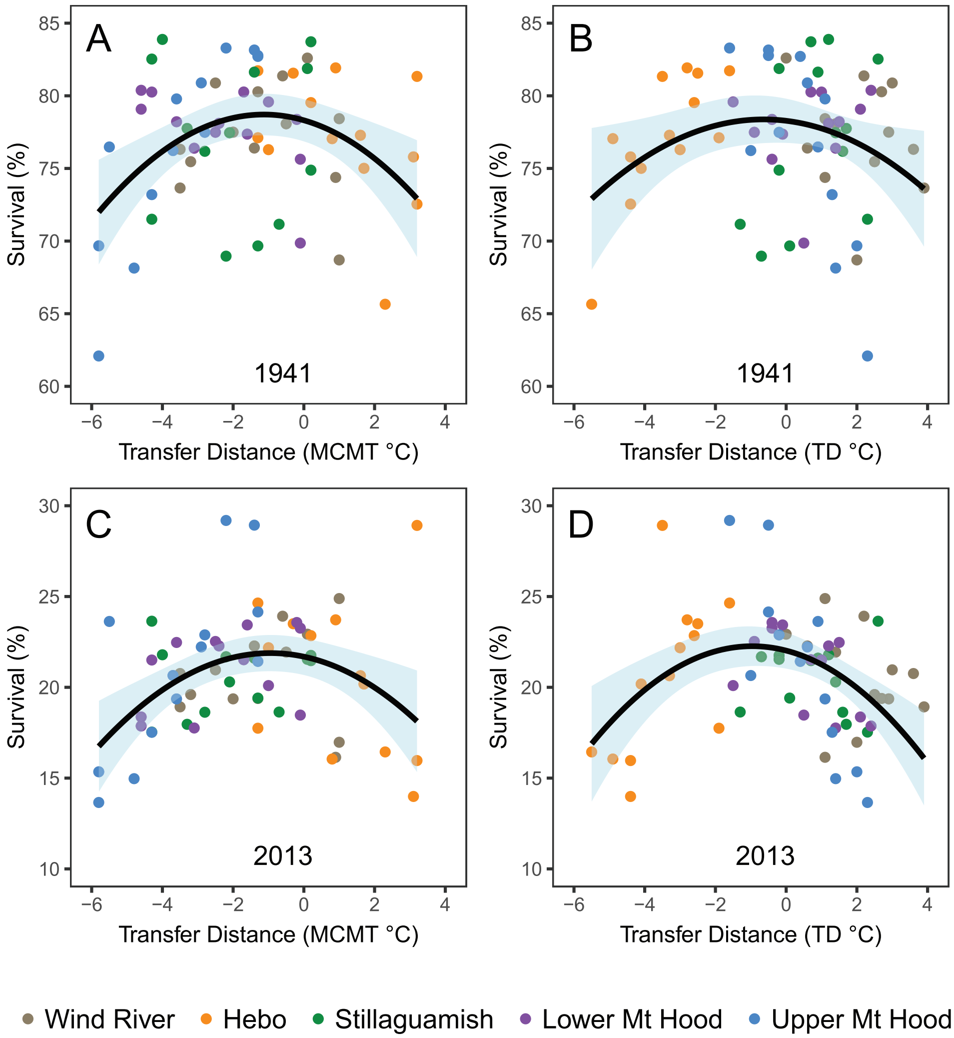

Figure 3. Transfer functions for survival in 1941 and 2013 as a function of climatic transfer distance (site minus provenance) for mean cold month temperature (MCMT) and continentality (TD).

2° C in continentality (TD) from a more continental climate (larger TD) to a more maritime climate (smaller TD) (Figure 3). Although adjusted R^2 values were low for the quadratic models across all sites (0.07–0.20), R^2 values for the within-site regressions for the best models at Upper Mt Hood and Hebo, which may include more than one climate variable, were quite high (0.52–0.79). The importance of the Upper Mt Hood and Hebo test sites for understanding adaptation and the effects of seed transfer are reflected in the correlations between seed source climates and growth or survival at each test site (Table 5). Consistent and significant correlations ($p < 0.05$) between provenance values and the climate of seed sources were found only at the Upper Mt Hood and Hebo test sites. The strongest correlations were found for MCMT and TD, although May–September precipitation was also important for survival at Hebo.

Discussion and Conclusions

Understanding the consequences of a changing climate, whether from moving populations or from climate change over time, requires testing climatically diverse provenances across a wide range of climates. Fortunately, the Douglas-Fir Heredity Study included two climatically distinct test sites—Upper Mt Hood and Hebo. The patterns of provenance survival were distinctly different between Upper Mt Hood, the colder high-elevation site, and Hebo, the coastal site with warmer winters and cooler summers.

The seed source climate variable most closely associated with survival at the Mt Hood site was MCMT. Provenances transferred to sites that were more than 2° C colder suffered greater mortality. For example, if provenances are moved from locations that are 6° C colder MCMT, we predict that 100-year survival will

Table 4. Regression equations for survival (Y_{ij}) of the *i*th provenance at the *j*th site as a function of transfer distance (X) for mean cold month temperature (MCMT) and continentality (TD) using the quadratic model $Y_{ij} = \beta_0 + \beta_1 X + \beta_2 X^2$.

	β_0	β_1	β_2	$P > \lvert t \rvert$ for β_2	Multiple R^2
MCMT					
1941	78.31	–.70	–.31	0.0017	.15
2013	21.69	–.41	–.22	0.0014	.17
TD					
1941	78.28	–.30	–.23	0.0296	.07
2013	22.02	–.50	–.26	0.0003	.20

Table 5. Pearson correlation coefficients between provenance values and the climate of source locations for the Upper Mt Hood and Hebo test sites.

Trait	Year	MAT	MCMT	MWMT	TD	MAP	MSP
Upper Mt Hood							
Diameter	1931	–.82	–.80	–.70	.49	.64	.51
Survival	1931	–.45	–.28	–.62	–.18	.58	.64
Survival	1941	–.77	–.88	–.53	.77	.67	.47
Survival	1953	–.68	–.78	–.46	.68	.50	.38
Survival	1963	–.70	–.77	–.49	.64	.51	.39
Survival	1973	–.67	–.77	–.42	.70	.48	.31
Survival	1983	–.68	–.78	–.43	.72	.49	.30
Survival	1993	–.67	–.80	–.37	.79	.48	.22
Survival	2013	–.57	–.75	–.24	.85	.41	.14
Volume/hectare	2013	–.56	–.73	–.23	.83	.37	.05
Hebo							
Diameter	1931	.33	.39	.14	–.43	–.07	–.06
Survival	1931	.37	.36	.27	–.26	–.27	–.12
Survival	1941	.16	.40	–.16	–.75	–.07	.28
Survival	1953	.15	.40	–.18	–.76	–.03	.35
Survival	1963	.13	.31	–.18	–.63	.18	.57
Survival	1973	.15	.35	–.16	–.67	.14	.50
Survival	1983	.16	.36	–.16	–.69	.15	.49
Survival	1993	.23	.43	–.09	–.71	.09	.40
Survival	2013	.12	.30	–.17	–.62	.21	.47
Volume/hectare	2013	.08	.26	–.15	–.54	.17	.36

Note: $\lvert r \rvert > .55$ is statistically significant at $p = 0.05$ ($N = 13$)|. MAP, mean annual precipitation; MAT, mean annual temperature; MCMT, mean coldest month temperature; MSP, mean summer precipitation; MWMT, mean warmest month temperature; TD, continentality as determined by the difference between MWMT and MCMT.

be 16 percent compared to 22 percent for provenances from a local or similar climate. Thus, given an initial planting density of 2,200 trees/hectare, low elevation sources, such as Benton, moved to a high-elevation site, such as Upper Mt Hood, are expected to have 351 trees/hectare compared to 483 trees/hectare for the local source (i.e., 27 percent fewer trees). Although cold damage was not measured during the life of the stand, the differential survival of provenances was probably a consequence of maladaptation to cold. Common garden studies have found a strong relation between seed source climate and cold damage (Benowicz et al. 2001, Bower and Aitken 2006, St.Clair 2006, Bansal et al. 2015). Genetic clines associated with cold temperatures have been found in several other Douglas-fir studies (e.g., St.Clair et al. 2005, Leites et al. 2012, Rehfeldt et al. 2014). Leites et al. (2012), however, found evidence that local seed sources were not best;

seedlings from warmer environments had better height growth than local sources when grown in cold environments. The differences with our study, however, may be attributed to evidence for adaptation as measured by survival over decades as compared to seedling growth.

The climate variable that was most closely associated with survival at the Hebo plantation was continentality (TD). Provenances transferred between locations differing by more than 2° C in continentality are expected to suffer higher mortality than provenances transferred from a local or similar climate (Figure 3). This difference is equivalent to moving provenances from the east end of the Columbia Gorge to the Hebo site in the Coast Range. For example, we predict that moving provenances 5.5° C in continentality to a more maritime climate, such as from Wind River to Hebo, would lead to 17 percent survival compared to 22 percent for the local sources after 100 years. This is equivalent to 373 trees/hectare compared to 483 trees/hectare (i.e., 23 percent fewer trees).

A clue as to the cause of differential mortality at Hebo is found in a Forest Service report from 1942 (Munger and Morris 1942). In the report, it was noted that *Rhabdocline* needle disease was found on a large proportion of the trees at the Hebo plantation in 1938. The authors concluded that trees from some seed sources were more susceptible to the disease, although they did not indicate which seed sources. The presence of *Rhabdocline* needle disease in 1938 is consistent with our results that the provenance × site interaction for survival becomes large between 1931 and 1941. A more recent study found that moving Douglas-fir seed sources more than 3° C in continentality, from a continental to a maritime climate, increased the probability of *Rhabdocline* infection by more than 25 percent (Wilhelmi et al. 2017). Thus, the effects of *Rhabdocline* may explain the associations between survival and TD. Wilhelmi et al. (2017) also found that *Rhabdocline* disease increased when seed sources were moved to locations with more summer precipitation and warmer winter temperatures, which is consistent with our findings (Figure 3). In general, *Rhabdocline* disease has not been a problem in Douglas-fir plantations, probably because the use of seed zones has limited long-distance seed transfers. Wilhelmi et al. (2017) concluded that *Rhabdocline* disease was primarily associated with long-distance transfers from the continental California Sierra and Klamath Mountains to the maritime areas of western Oregon and Washington. Our long-term results suggest that transfers from the Cascades to the Coast Range, that is, transfers as short as 160 km, may also be a concern.

Early results from the Douglas-Fir Heredity Study, and anecdotal evidence of maladapted plantations, prompted the development of seed transfer guidelines and seed zones in the Pacific Northwest. In particular, the seed zones developed for Oregon and Washington in 1966 have been widely accepted and used (Randall 1996). The Oregon/Washington seed zones are delineated as 152-m elevation bands intersected with a geographic delineation. The elevation bands are a critical component of seed zones because of the strong relation between elevation and cold temperatures. Using GIS, we characterized the climatic width of the Oregon/Washington seed zones to compare with the transfer functions from the Douglas-Fir Heredity Study. The average climatic width for winter temperatures (MCMT) of the 673 seed zones/elevation bands in western Oregon and Washington (defined as west of the Cascade crest) is 2.0° C. However, there is considerable variation among seed zones, with 5 percent of them exceeding a climatic width of 4.1° C. Thus, based on experience from seed zones, managers may feel confident that they can move seed sources up to 2° C MCMT, and perhaps as much as 4° C. This is consistent with our findings. When considering movements from a continental to a maritime climate, the average climatic width of TD within seed zones in western Oregon and Washington is 2.0° C, which, again, is close to the acceptable transfer distance that we observed at the Hebo site. Managers have been using these seed zones for more than a half century, and the consensus is that they have been effective in ensuring adapted, healthy, and productive plantations. However, as climates start to warm beyond 2° C, the adage that "local is best" may no longer be true, and resource managers are beginning to reconsider the use of local seed zones.

One conclusion by early researchers of both the Douglas-Fir Heredity Study and the Wind River Arboretum is that evidence for maladaptation may take time. Our results support that conclusion because maladaptation, as measured by differences in survival, was not evident until two decades after planting. Local adaptation, as indicated by differential survival of provenances, first became apparent in 1941 at ages 28 and 29 (Table 3). Between 1931 and 1941, survival dropped from 86 percent to 62 percent at the Upper Mt Hood plantation (Figure 2). Cold events in the winters of 1930 and 1937 may have contributed to this mortality and the differences among provenances. For example, MCMT values in those years were −9.4° C and −8.8° C, respectively, compared to an average for the 1930s of –2.2° C (data derived from ClimateNA). In western Oregon and Washington, a particularly well-documented cold event occurred in November 1955, when there was a week-long cold wave after an unusually mild October (Duffield 1956). Mortality over the next few years was high across much of the region, mostly from cambial damage (Childs 1961). The Hebo plantation seemed to be particularly affected (Figure 2)—mortality increased between 1953 and 1963, and frost cracks were observed in the dead trees (Roy Silen, pers. obs.). The Hebo site may have been particularly affected by the cold wave because the mild environment at the site would have resulted in lesser cold acclimation (see Bansal et al. 2015). However, the 1955 cold event appears to have affected all provenances equally since the provenance × site interaction, and the relative rankings for survival were unchanged. Instead, differences among provenances in maladaptation at the Hebo site may have arisen earlier as trees gradually died because of *Rhabdocline* needle disease.

Although maladaptation may not become apparent for decades in provenance tests, short-term genecology studies may shed light on patterns of variation in adaptive traits such as phenology, cold hardiness, drought resistance, and growth potential (e.g., St.Clair et al. 2005, Rehfeldt et al. 2014, and studies cited therein). Such short-term studies may be valuable for delineating seed zones and breeding zones, but long-term field studies are needed to inform managers about the long-term consequences of different transfer limits and evidence for local adaptation.

The Douglas-Fir Heredity Study is one of the longest-running forestry studies in the North America and perhaps the world. What have we learned over the past 100 years? First, experimental design and statistics have evolved over the last century. Since the establishment of the study, field tests routinely use randomization and replication with blocking. More recently, new analytical approaches—mixed models and BLUPs—allow better estimates of different sources of variation of interest to the researcher. These new approaches allow us to revisit older studies to better evaluate variation because of provenances, test sites, and their interactions. This study also highlights the value of sampling across a large climatic range for both plantations and provenances. We would have learned very little from this study without the inclusion of the warmest and coldest test sites. Provenance tests should emphasize a wide sampling of test sites and provenances across climatic gradients of adaptive significance (e.g., cold temperatures, aridity, and continentality). A well-designed study with respect to climate is more efficient and allows a better determination of response and transfer functions (Wang et al. 2010).

Second, the use of conservative seed zones, breeding zones, and seed transfer guidelines has probably increased plantation survival and productivity compared to plantations established during the first half of the 20th century. These seed zones and breeding zones probably kept operational seed transfers within the transfer limits we identified. However, clinal variation and large provenance variation around the transfer function, combined with large genetic variation within populations, may indicate some lost opportunities to select and deploy genetic material over a larger area with accompanying economies of scale.

Third, although the early researchers established the Douglas-Fir Heredity Study with different objectives in mind, the study has proven useful for evaluating new objectives associated with reforestation and climate change. Initial results did not shed much light on questions of which trees should be left as leave trees or from which trees to collect for reforestation. The study did, however, point to concerns about moving seed sources between very different elevations, contributing to the development of seed zones and seed movement guidelines. The study also proved valuable for promoting early tree improvement programs by demonstrating differences among parent trees within provenances (Roy Silen, pers. commun.). This current analysis of the results of the study points to implications for the adaptation of native stands to climate change, and possible management options for responding to concerns. Results indicate that Douglas-fir populations are adapted to the local climates that they have experienced over the past century. This suggests that climate change may not be a big problem if the amount of climate change is within 2° C, and extreme climatic events do not occur with frequency. To date, climate change has not exceeded 2° C for most of North America; however, the climate is expected to be strikingly warmer by midcentury. This study considered climatic transfers to warmer climates only up to about 3° C (MCMT) accompanied by a transfer from a continental to a more maritime climate, resulting in decreased survival and productivity. New studies may be required to explore greater climatic transfer distances with and without a concomitant change in continentality. If climate change exceeds a 2–3° C increase, moving populations from warmer to cooler locations to be adapted to future climates would hold promise for responding to concerns of maladaptation. However, managers should not move populations beyond 2–3° C to cooler climates to avoid risk of cold damage in the near-term. Finally, considerable variation may be found among and within populations. This means that there is some potential for natural selection (e.g., Warwell and Shaw 2019) (as well as human selection within tree-improvement programs), but that depends on generation turnover and the establishment of new stands. One management option to take advantage of genetic variation is to use mixtures of provenances to allow for natural selection and human selection by thinning.

An early publication from 1917 describing the establishment of the Douglas-Fir Heredity Study promoted the value of such long-term studies (Kraebel 1917). The author states: "The imagination refuses to venture concerning the methods of study at so distant a time. The largeness of the idea is at once gratifying and disturbing, for one feels both the importance of the work and the responsibility of doing rightly the early steps in that work, lest the initial errors and omissions grow in magnitude with the advancing years." We can imagine that the early researchers never envisioned the results from this study informing management of forests in response to climate change. This article is a testament to their long-term vision.

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Literature Cited

Bansal, A., J.B. St.Clair, C.A. Harrington, and P.J. Gould. 2015. Impact of climate change on cold hardiness of Douglas-fir (*Pseudotsuga menziesii*): Environmental and genetic considerations. *Glob. Change Biol.* 21:3814–3826.

Benowicz, A., S.J. L'Hirondelle, and Y.A. El-Kassaby. 2001. Patterns of genetic variation in mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) with respect to height growth and frost hardiness. *For. Ecol. Manag.* 154:23–33.

Bower, A.D. and S.N. Aitken. 2006. Geographic and seasonal variation in cold hardiness of whitebark pine. *Can. J. For. Res.* 36:1842–1850.

Childs, T.W. 1961. Delayed killing of young-growth Douglas-fir by sudden cold. *J. For.* 59(6):452–453.

Duffield, J.W. 1956. *Damage to western Washington forests from November 1955 cold wave. Research Notes*. USDA Forest Service Pacific Northwest Forest and Range Experiment Station Research Note 129, Portland, OR. 8 p.

Isaac, L.A. 1949. *Better Douglas Fir forests from better seed*. University of Washington Press, Seattle, WA. 65 p.

Kraebel, C.J. 1917. Choosing the best tree seeds. *J. Hered.* 8:483–492.

Langlet, O. 1971. Two hundred years genecology. *Taxon* 20(5/6):653–723.

Leites, L.P., A.P. Robinson, G.E. Rehfeldt, J.D. Marshall, and N.L. Crookston. 2012. Height-growth response to climatic changes differs among populations of Douglas-fir: A novel analysis of historic data. *Ecol. Appl.* 22(1):154–165.

Munger, T.T., and W.G. Morris. 1936. *Growth of Douglas-fir trees of known seed source*. USDA Technical Bulletin No. 537, Washington, DC. 40 p.

Munger, T.T., and W.G. Morris. 1942. *Further data on the growth of Douglas-fir trees of known seed source*. RS-NW Genetics Racial Variation Douglas-Fir, USDA Forest Service Pacific Northwest Forest and Range Experiment Station, Portland, OR. 12 p.

Poudel, K.P. and T. Hailemariam. 2016. Calibration of volume and component biomass equations for Douglas-fir and lodgepole pine in Western Oregon forests. *Forest. Chron.* 92(2):172–182.

Randall, W.K. 1996. *Forest tree seed zones for western Oregon*. Oregon Department of Forestry, Salem, OR.

Rehfeldt, G.E., L.P. Leites, J.B. St.Clair, B.C. Jaquish, C. Sáenz -Romero, J. López -Upton, and D.G. Joyce. 2014. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Clines in growth potential. *For. Ecol. Manag.* 324:138–146.

Sandler, I., and L. Sandler. 1986. On the origin of Mendelian genetics. *Am. Zool.* 26:753–768.

SAS Institute Inc. 2014. *SAS/STAT® 13.2 User's guide*. SAS Institute Inc., Cary, NC.

Silen, R.R. 1963. *The 1912 Douglas-fir heredity study*. USDA Forest Service Pacific Northwest Forest and Range Experiment Station Annual Report, Portland, OR.

Silen, R.R. 1965. Regeneration aspects of the 50-year-old Douglas-fir heredity study. Proceedings 1964 Annual Meeting of the Western Reforestation Coordinating Committee, Spokane, WA.

Silen, R.R. 1966. A 50-year racial study of Douglas-fir in western Oregon and Washington. Proceedings of the 1965 Annual Meeting of the Western Forest Genetics Association, Olympia, WA.

Silen, R.R., and D.L. Olson. 1992. *A pioneering exotic tree search for the Douglas-fir region*. USDA Forest Service Pacific Northwest Research Station Gen. Tech. Rep. PNW-GTR-298, 44p.

St.Clair, J.B. 2006. Genetic variation in fall cold hardiness in coastal Douglas-fir in western Oregon and Washington. *Can. J. Bot.* 84:1110–1121.

St.Clair, J.B., N.L. Mandel, and K. Vance-Borland. 2005. Genecology of Douglas fir in western Oregon and Washington. *Ann. Bot.* 96:1199–1214.

Wang. T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One* 11(6):e0156720.

Wang, T., G.A. O'Neill, and S.N. Aitken. 2010. Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecol. Appl.* 20:153–163.

Warwell, M.V., and R.G. Shaw. 2019. Phenotypic selection on ponderosa pine seed and seedling traits in the field under three experimentally manipulated drought treatments. *Evol. Appl.* 12:159–174.

White, T.L. 1996. Genetic parameter estimates and breeding value predictions: Issues and implications in tree improvement programs. P. 110–117 in *Tree improvement for sustainable tropical forestry*, Dieters, M.J., A.C. Matheson, D.G. Nikles, C.E. Harwood, and S.M. Walker (eds.). QFRI IUFRO Conference, Caloundra, Queensland, Australia.

Wilhelmi, N.P., D.C. Shaw, C.A. Harrington, J.B. St.Clair, and L.M. Ganio. 2017. Climate of seed source affects susceptibility of coastal Douglas-fir to foliage diseases. *Ecosphere* 8(12):e02011.