Historical and Contemporary Lessons From Ponderosa Pine Genetic Studies at the Fort Valley Experimental Forest, Arizona

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Abstract—*Forest management will protect genetic integrity of tree species only if their genetic diversity is understood and considered in decision-making. Genetic knowledge is particularly important for species such as ponderosa pine (*Pinus ponderosa *Dougl. ex Laws.) that are distributed across wide geographic distances and types of climates. A ponderosa pine study initiated in 1910 at the Fort Valley Experimental Forest is among the earliest ponderosa pine genetic research efforts in the United States. This study contributed to the description of ponderosa pine's varietal differences, genetic diversity and adaptation patterns, and helped confirm the importance of using local seed sources. The role this and other pioneer studies had in improving forest management of ponderosa pine was, and still is critical. These early studies have long-term value because they improve our knowledge of responses to climate change and our understanding of genetic variability in physiology and pest resistance in older trees. More recently, studies of natural ponderosa pine stands at Fort Valley using molecular markers have shown the importance of stand structure and disturbance regimes to genetic composition and structural patterns. This knowledge is important to ensure ecological restoration efforts in ponderosa pine forests will also restore and protect genetic integrity into the future. Highlights of these historical and contemporary studies at Fort Valley are summarized and their applications to management of ponderosa pine forests are described.*

Historical Provenance Study

In a provenance experiment, seed is collected from many natural stands (*i.e.*, sources) and then grown in a common environment to study genetic diversity and adaptation patterns. Provenance research began in North America in the late 1800s

In: Olberding, Susan D., and Moore, Margaret M., tech coords. 2008. Fort Valley Experimental Forest—A Century of Research 1908-2008. Proceedings RMRS-P-53CD. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 408 p.

Table 1. Seed origins of ponderosa pine seed sources in a provenance study at the U.S. Forest Service Fort Valley Experimental Forest, Arizona (adapted from Silen unpublished data and Larson 1966).

National Forest	State	Latitude	Longitude	Elevation (ft)	Variety	# Planted
Coconino [a]	AZ	35° 05′	111° 35′	7400	*Scopulorum*	2784
Santa Fe	NM	36° 10′	106° 30′	8000	*Scopulorum*	84
Gila	NM	32° 30′	108° 20′	-- [b]	*Scopulorum*	87
San Isabel [a]	CO	38° 15′	107° 00′	8000	*Scopulorum*	791
Roosevelt	CO	44° 30′	116° 00′	5000	*Scopulorum*	200
Ashley	UT	37° 20′	107° 50′	--	*Scopulorum*	65
Manti-La Sal	UT	37° 50′	110° 00′	--	*Scopulorum*	84
Fishlake	UT	40° 30′	105° 15′	--	*Scopulorum*	14
Black Hills	SD	--	--	--	*Scopulorum*	273
Harney	SD	43° 45′	103° 30′	6000	*Scopulorum*	152
Bitterroot	MT	36° 00′	114° 20′	4600	*Ponderosa*	78
Boise	ID	43° 30′	114° 50′	5500	*Ponderosa*	26
Payette	ID	--	--	--	*Ponderosa*	65
Salmon	ID	45° 15′	114° 10′	4500	*Ponderosa*	43
Siskiyou	OR	42° 10′	123° 40′	2000	*Ponderosa*	22
Tahoe	CA	38° 50′	120° 15′	6500	*Ponderosa*	12
Klamath	CA	41° 30′	122° 40′	--	*Ponderosa*	0 [c]
Angeles	CA	34° 30′	118° 10′	6500	*Ponderosa*	0 [c]

[a] 607 of the seedlings from these San Isabel seed sources were propagated at the Monument Nursery in Colorado, and 372 seedlings of the Coconino seed source were propagated at the Fort Bayard Nursery in New Mexico. All other San Isabel and Coconino seedlings were propagated at the nursery in Fort Valley, AZ.

[b] -- Indicates unknown collection location data.

[c] All seedlings were killed in the Fort Valley nursery by freezing temperatures (-3 °F).

(Wright 1976). Three large pioneer studies of ponderosa pine were established in 1911-1927 by early United States Forest Service (USFS) scientists sent west in 1909. These three ponderosa pine racial variation trials (hereafter referred to as provenance tests) are among the earliest and now oldest existing provenance tests in North America. One of these tests was established by Gustaf A. Pearson at the Fort Valley Experimental Forest (35° 16'latitude, 111° 44' 30" longitude) in Arizona (Table1, Figures 1 and 2). This historical test included seed collected from 18 National Forests representing much of the range of ponderosa pine (Table 1). The other two tests were established in Idaho and Washington/Oregon and included Coconino sources collected from the Fort Valley Experimental Forest.

Most of the seedlings used to establish the Fort Valley provenance test were grown by G.A. "Gus" Pearson in a nursery at Fort Valley. The nursery-grown seedlings were transplanted into the test site located west of the Experimental Forest Headquarters at 7,300 feet elevation. The seedlings were hand-planted at a 6-foot spacing, in rows oriented east-west. Each row represented one seed source and varied in length up to 660 feet. Survival was monitored annually until 1919, and then in 1928, 1951, 1964, and 1995. Heights were measured in 1928, and both height and diameter were measured in 1964 and 1995-1996. It is note-worthy that the 1995-1996 data were collected by Roy Silen, who was a retired project leader for genetics research, USFS Pacific Northwest Forest Research Station in Corvallis, Oregon. Roy Silen (who is now deceased) spent his personal time and resources during his retirement to measure this historical test because of his strong belief in the long-term value of such studies.

Figure 1 - Ponderosa pine racial variation study located in the Fort Valley Experimental Forest. Photograph by Mahalovich, June 1999.

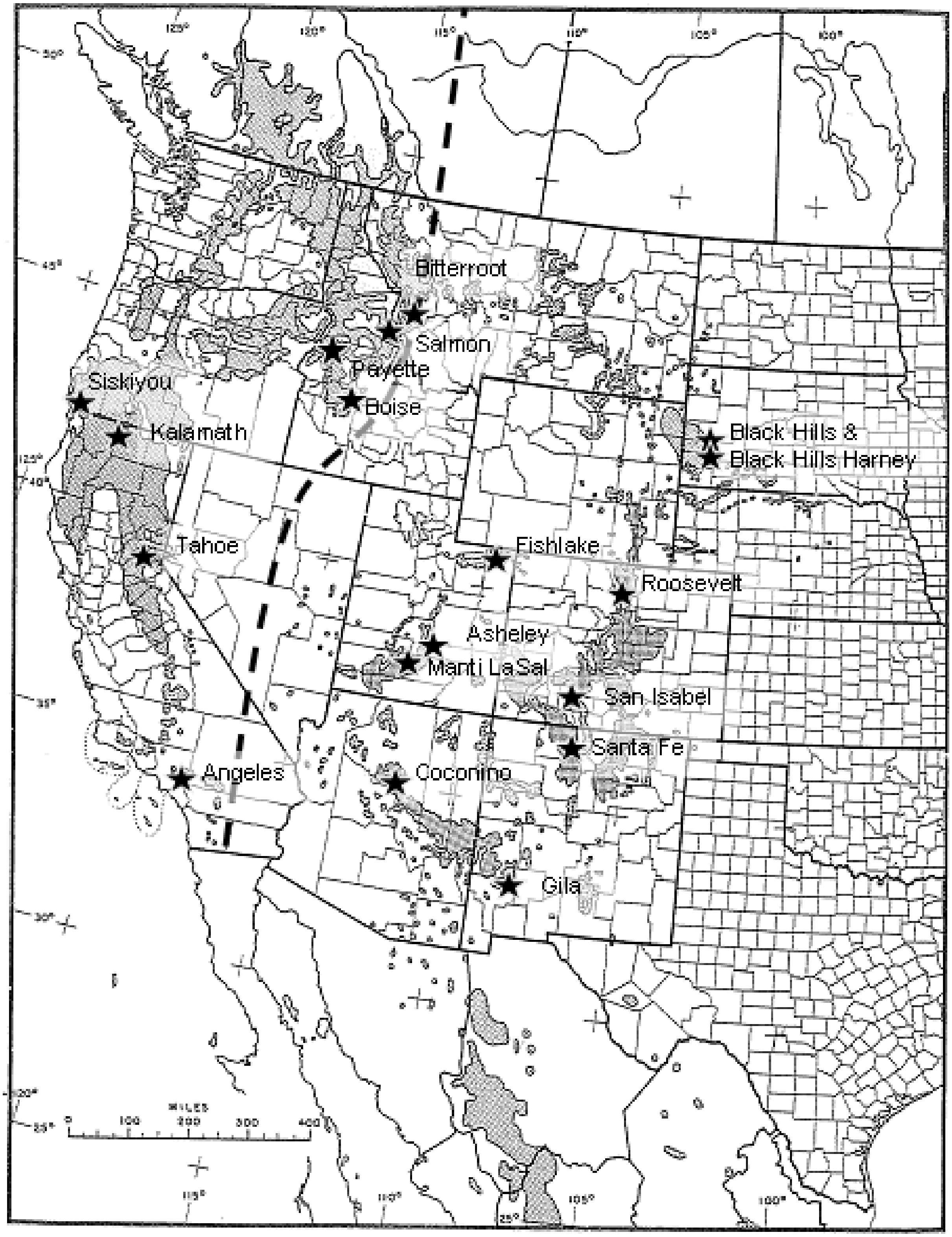

Figure 2 - Geographic range (adapted from Fowells 1965) and locations (★) of *Pinus ponderosa* sources included in the Fort Valley provenance study (adapted from Silen unpublished report and Larson 1966). Populations west of the dotted line are var. *ponderosa* and east of the dotted line are var. *scopulorum*.

Table 2. Performance of ponderosa pine seed sources in a provenance study at the U.S. Forest Service Fort Valley Experimental Station, Arizona (from Silen unpublished data and Larson 1966).

			Survival (%)			Mean Height (ft)			Volume per acre (ft^3)	
Seed Source	**Variety**	**Number Planted**	**5-yr**	**50-yr**	**80-yr**	**5-yr**	**50-yr**	**80-yr**	**50-yr**	**80-yr**
Coconino	*Scopulorum*	2784	29	21	19	1.2	26.6	32.0	507	1032
Santa Fe	*Scopulorum*	84	52	24	24	0.8	24.6	28.0	566	1748
Gila	*Scopulorum*	87	33	6	3	0.7	21.5	25.9	65	136
San Isabel	*Scopulorum*	791	34	17	16	1.1	22.9	26.1	304	560
Roosevelt	*Scopulorum*	200	26	7	6	0.7	19.8	20.4	94	97
Ashley	*Scopulorum*	65	35	12	8	0.5	21.0	20.4	94	97
Manti-La Sal	*Scopulorum*	84	45	21	20	0.6	28.7	30.8	825	1696
Black Hills	*Scopulorum*	273	41	18	16	1.2	27.6	27.2	667	963
Harney	*Scopulorum*	152	30	20	19	0.8	19.8	30.8	109	203
Fishlake	*Scopulorum*	14	0	0	0	0	0	0	0	0
Bitterroot	*Ponderosa*	78	0	0	0	0	0	0	0	0
Boise	*Ponderosa*	26	0	0	0	0	0	0	0	0
Payette	*Ponderosa*	65	0	0	0	0	0	0	0	0
Salmon	*Ponderosa*	43	0	0	0	0	0	0	0	0
Siskiyou	*Ponderosa*	22	0	0	0	0	0	0	0	0
Tahoe	*Ponderosa*	12	0	0	0	0	0	0	0	0

Although some results of the Fort Valley test are summarized by Pearson in a variety of reports (e.g., Pearson 1950), the first full analysis of the provenance test was not published until 1966 in a USFS Research Note written by M.M. Larson, a Forest Physiologist located at what was then the Rocky Mountain Forest and Range Experiment Station in Flagstaff, AZ. In this paper, Larson includes information from a 16-page unpublished progress report "Source of Seed—Western Yellow Pine" prepared by Gus Pearson in 1920 (on file at the Rocky Mountain Forest and Range Experiment Station, Flagstaff, AZ). Larson indicated that Pearson noticed varietal differences among seed sources both in the nursery and early on in the provenance test where *"despite the seemingly better health of the northern and western seed sources, these seedlings turned out to be sensitive to frost and drought."* It is likely these same climatic variables contributed to mortality over time. Larson (1966) reported that after 50 years, seed sources from only nine of the National Forests survived and mortality was greater than 75% for all sources (Table 2). These sources were still alive after 80 years but survival had decreased to an average of 15% (Table 2). Most of the variation in mortality occurred from 1913-1928 and mortality after that time was relatively evenly divided among the remaining sources. After 50 years, Larson (1966) reported that seed sources originating from National Forests in Arizona, Utah and Colorado (*e.g.*, locations most similar to the latitude and/or elevation to the test site) had the best survival, tallest heights and greatest diameters (Table 2), while trees originating from the northern and western sources did not survive. This variation can be attributed to varietal differences.

Varietal Differences

The 50-year Fort Valley results summarized by Larson (1966) were consistent but opposite in trend with results from the Idaho and WA-OR tests reported by Squillace and Silen (1962); in the northern tests, performance of the southern Rocky Mountain sources was the poorest. These 50-year trends corresponded with the range delineations of the two varieties (ponderosa and scopulorum, Figure 1). In addition, variation in seed source performance was roughly a continuum of decreasing height and survival with increasing distance from origin. This relationship was consistent with other early provenance test results and prompted Forest Service scientists such as Roeser (1962) to conclude that seed collections for a given area should be confined to local varieties. This is still sound advice today (Johnson et al. 2004). Results from tests such as at Fort Valley led to the development of seed transfer guidelines (e.g., Mahalovich and Rehfeldt 2005; 2003) to ensure that mistakes made in the movement of seed such as described for ponderosa pine in DeWald and Mahalovich (1997) do not happen again.

Climate-Genetic Relationships

We now know that the geographic patterns in genetic diversity that emerged from the historical provenance tests reflect adaptive responses associated with changes in temperature and precipitation (Rehfeldt 1993). However, at the time the first ponderosa pine provenance tests were established, variation among trees was believed to be partly inherited, but mechanisms controlling this variation were unknown. It was speculated that natural selection had some role, but evidence to support this idea was lacking (Morgenstern 1996). Results from the early provenance studies such as at Fort Valley contributed evidence that certain traits were partially inherited, and that geographic patterns had a genetic basis (Squillace and Silen 1962). These results added to the accumulating knowledge about inheritance, evolution and selective responses to varying intensities of natural and artificial selection (Wright 1976) which was used to initiate tree breeding. The early provenance tests enabled the best trees in the best seed sources to be identified as potential breeding stock. Results from provenance tests such as at Fort Valley contributed to the foundation of our knowledge and continue to inform ponderosa pine genetics and management (*e.g.*, Silen unpublished report, Mahalovich and Rehfeldt 2005; 2003, Baumgartner and Lotan 1987, Wang 1977, Larson 1966, Wells 1964a; 1964b, Roeser 1962, Squillace and Silen 1962, Pearson 1950, Munger 1947, Weidman 1939, Schreiner 1937).

Long-term tests such as at Fort Valley showed that early performance was not always a reliable predictor of later performance (Silen unpublished report). Non-local seed sources often tolerate average conditions of a site, but are usually poorly adapted to extremes of weather that occur less frequently but at regular intervals (Johnson *et al.* 2004, Silen unpublished report); they may perform well for several years, but then decline in health. At Fort Valley, nearly all the western and northern provenances (*i.e.*, var. *ponderosa*) died during the first decade, leaving only the *scopulorum* variety. However, it took another 70 years to sort the remaining provenances to a single best-yielding provenance (Coconino National Forest, Silen unpublished report). Some of the non-local provenances grew faster than the local

Table 3. Compatible ponderosa pine seed sources for planting at the Fort Valley Experimental Forest, Arizona, based on a seed transfer expert system (Mahalovich and Rehfeldt 2005).

Southwestern Ponderosa Pine Seed Transfer Expert System *Pinus ponderosa var. scopulorum*, Version 1.0				
Forest:				
Coconino NF				
Seed Source or Planting Site	**Seed Lot**	**Latitude**	**Longitude**	**Elevation**
Fort Valley Experimental Forest		35.27	111.74	7300
Results	June 06, 2008 • 07:52 PM			
Fort Valley Experimental Forest				
	Elevation Range			
Area	Lower	Upper		
COCONINO: MORMON LAKE	7100	7400		
COCONINO: PEAKS	6900	7700		
KAIBAB: CHALENDER-WILLIAMS	6900	7700		

source early on, but the local source slowly overtook and in the end, out-performed the others. Table 3 lists the seed sources and elevation bands based on a seed transfer expert system (Mahalovich and Rehfeldt 2005) that are considered local to the Fort Valley location. The long-term results from Fort Valley illustrate that shorter term studies may provide misleading information and highlights the value of historical long-term provenance tests.

The Fort Valley study has had approximately 100 years to respond to climate change and provide a testing ground for suggested management recommendations to address climate change. Local seed sources of the native variety *scopulorum* have persisted over time at Fort Valley. The Coconino National Forest seed source at 7,400 feet has one of the highest percent survival followed by the Santa Fe National Forest source at 8,000 feet; however the non-local Santa Fe source is more productive as measured by height at age 80 (Table 2). The performance of seed sources at ages 50 and 80 in the historical tests are beginning to demonstrate a restoration principle used in mining reclamation (Mahalovich personal communication, USDA Forest Service *in press*), where seed sources adapted to extreme environments (higher latitudes and higher elevations) are utilized to revegetate these sites. Possible mitigation in the form of revising seed and plant movement guidelines emphasizing a warming trend (IPCC 2007), recommend species and seed sources from more southerly latitudes and lower elevations (Arbor Day Foundation 2006). Long-term data from the Fort Valley and Idaho studies do not support the selection of southerly latitude or lower elevation seed sources after 10 decades, rather local or local and higher in elevation sources have survived and been more productive. Although mortality has been high, which is to be expected in these types of studies, the Fort Valley test exists today and represents a long-term study with historical and contemporary value.

Contemporary Genetic Studies

Results of the pioneer provenance tests demonstrated that genetic diversity is the raw material on which evolution operates. One goal of ecological restoration is to restore evolutionary processes. Genetic knowledge gained from provenance tests has direct bearing on the success of ecological restoration (Falk and Holsinger 1991, Young and Clarke 2000) because knowing how genes are distributed and what controls the patterns of genetic diversity enables practitioners to restore genetic diversity patterns to meet specific management objectives.

Contemporary genetic research using molecular techniques demonstrated that the genetic diversity of ponderosa pine trees established at Fort Valley prior to Euro-American settlement differed from trees established since then (Kolanoski 2002). It was also revealed that the clumpy spatial structure of historical southwestern ponderosa pine stands (White 1985) also corresponded to a clumpy genetic pattern. Regeneration within clumps was likely protected from frequent fire. Over time this created small "genetic neighborhoods" where trees within a clump were more closely related to each other than to trees between clumps. Inbreeding was avoided by high pollen movement in the open areas maintained by frequent fire between clumps of trees. As tree densities increased and the open spaces between clumps filled in, pollen movement was restricted and the regeneration that became established between clumps differed genetically from the older trees. Thinning to healthier densities will restore pollen flow, but full restoration of genetic diversity patterns also requires restoration of a clumpy versus evenly spaced forest structure (DeWald 2003, Kolanoski 2002).

In addition to changes in pollen movement, contemporary or "rapid" evolution also likely contributed to the genetic differences between the generations (Stockwell *et al.* 2003). The older trees established themselves in environmental conditions unlike those their contemporary progeny faced. Older pines generally experienced relatively little within-species competition during stand development because of frequent low-intensity fires. In contrast, the modern dense, shaded conditions created a different environment during the establishment of the younger trees that were likely selected for different genetic material. The different genetic material in the younger trees may have future adaptive value and a conservative approach would be to maintain this genetic diversity (Buchert *et al.* 1997, El-Kassaby and Ritland 1996) along with that preserved in the old trees. Although thinning will help pollen move among the clumps of trees, it can also alter genetic diversity through losses of genetic material from the population of trees being thinned. Therefore, a sufficient number of the younger generation trees should be maintained along with the older trees in thinned stands. This can be accomplished by varying thinning densities across the landscape (DeWald 2003, Kolanoski 2002).

Genetic diversity allows populations to respond to, and evolve with the dynamic nature of the environment. Therefore, a primary objective of forest management should be to conserve and maintain genetic diversity of organisms and populations within forest ecosystems (DeWald and Mahalovich 1997). Absence of genetic information for adaptive traits leads to poor management decisions. Likewise, prematurely changing management recommendations involving seed transfer in the context of climate change models emphasizing warming, may also lead to poor management decisions if we ignore hard data from long-term racial variation and provenance tests. In this regard, the historical ponderosa pine provenance study initiated at Fort Valley is still providing important information today, and along with contemporary genetic research helps provide the genetic knowledge critical to successful management of the ponderosa pine ecosystem.

References

Arbor Day Foundation. 2006. Hardiness zone map (2006 arborday.org Hardiness Zone Map). http://www.arborday.org/media/Zones.cfm.

Baumgartner, D.M.; Lotan, J.E. tech eds. 1987. Ponderosa pine: The species and its management. Proceedings of a symposium. 1987; September. 29-October1; Washington State University, Pullman WA.

Buchert, G.P.; Rajora, O.P.; Hood, J.V.; Dancik, B.P. 1997. Effects of harvesting on genetic diversity in old-growth eastern white pine in Ontario, Canada. Conservation Biology. 11: 747-758.

DeWald, L.E.; Mahalovich, M.F. 1997. The role of forest genetics in managing ecosystems. Journal of Forestry. 95: 12-16.

DeWald, L.E. 2003. Conserving genetic diversity during restoration thinning. Pages 226-227 In P. Friederici, ed. Ecological restoration of southwestern ponderosa pine forests. Island Press, Washington, D.C.

El-Kassaby, Y.A.; Ritland, K. 1996. Impact of selection and breeding on the genetic diversity in Douglas-fir. Biodiversity and Conservation. 5: 795-813.

Falk, D.A.; Holsinger, K.E. eds. 1991. Genetics and conservation of rare plants. New York: Oxford University Press.

Fowells, H.A. compiler. 1965. Silvics of forest trees of the United States. USDA Forest Service Agriculture Handbook N. 271. Washington, D.C.

IPCC 2007. The Fourth Assessment Report (AR4). Working Group III Report "Mitigation of Climate Change". http://www.ipcc.ch/ipccreports/index.htm

Johnson, C.R.; Sorensen, F.C.; St. Clair, J.B.; Cronn, R.C. 2004. Pacific Northwest forest seed zones: A template for native plants? Native Plants. 5: 131-140

Kolanoski, K.M. 2002. Genetic variation of ponderosa pine in northern Arizona: Implications for restoration. MS Thesis, Northern Arizona University, Flagstaff, AZ.

Larson, M.M. 1966. Racial variation in ponderosa pine at Fort Valley, Arizona. USDA Forest Service Research Note RM-73. 7 p.

Mahalovich, M.F.; Rehfeldt, G.E. 2005. Southwestern Ponderosa Pine Seed Transfer Expert System *Pinus ponderosa* var. *scopulorum*, Version 1.0.

Mahalovich, M.F.; Rehfeldt, G.E. 2003. Ponderosa Pine Seed Transfer Expert System *Pinus ponderosa* var. *ponderosa*, Version 2.1d.

Morgenstern, E.K. 1996. Geographic variation in forest trees: Genetic basis and application of knowledge in silviculture. UBC Press Vancouver. 209 p.

Munger, T.T. 1947. Growth of ten regional races of ponderosa pine in six plantations. Res. Notes 39. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experimental Station. 4 p.

Pearson, G.A. 1950. Management of ponderosa pine in the Southwest. USDA Monograph 6, 218 p.

Rehfedlt, G.E. 1993. Genetic variation in the Ponderosae of the Southwest. American Journal of Botany. 80(3): 330-343.

Roeser, J., Jr. 1962. The importance of seed source and the possibilities of forest tree breeding. Journal of Forestry. 24: 38-51.

Schreiner, E.J. 1937. Improvement of forest trees. USDA Yearbook 1937: 1242-1279.

Soller, E.A. 2003. Using native seed for revegetation: Science and policy. Flagstaff, AZ: Northern Arizona University. MS Thesis.

Squillace, A.E.; Silen, R.R. 1962. Racial variation in ponderosa pine. Forest Science Monograph. 2: 1-27.

Steinhoff, R.J. 1970. Northern Idaho ponderosa pine racial variation study: 50-year results. Res. Note INT-118. Ogden, UT: U.S. Department of Agriculture, Intermountain Forest and Range Experiment Station. 4 p.

Stockwell, C.A.; Hendry, A.P.; Kinnison, M.T. 2003. Contemporary evolution meets conservation biology. Trends in Ecology and Evolution. 18: 94-101.

USDA Forest Service. *In press*. FSH 2409.26f. Seed Handbook. USDA Forest Service, Southwestern Region, Albuquerque, NM. 233 p.

Wang, Chi-Wu. 1977. Genetics of ponderosa pine. USDA FS Res Pap WO-34. 24 pages.

Weidman, R.H. 1939. Evidences of racial influence in a 25-year test of ponderosa pine. Journal of Agriculture Research. 59: 855-887.

Wells, O.O. 1964a. Geographic variation in ponderosa pine. I. The ecotypes and their distribution. Silvae Genetica. 13: 89-103.

Wells, O.O. 1964b. Geographic variation in ponderosa pine. II. Correlations between progeny performance and characteristics of the native habitat. Silvae Genetica. 13: 125-132.

White, A.S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. Ecology. 66: 589-594.

Wright, J.W. 1976. Introduction to Forest Genetics. Academic Press, New York. 463 p.

Young, A.G.; Clarke A.G. eds. 2000. Genetics, demography, and viability of fragmented populations. Cambridge, UK: Cambridge University Press.