

# Adaptive Genetic Variation in Sugar Pine

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**Abstract**—Sugar pines from range-wide provenances displayed a complex genetic structure in adaptive traits in four contrasting common gardens. Strong, rank-changing G-x-E interactions for 10- to 17-year survival and growth require restrictions in seed transfer across altitudes and coastal-interior transects. Geographic and altitudinal subdivisions on a regional scale correspond with major changes in climate, soil, and vegetation. Altitude of origin was the primary geographic variable influencing growth potential; coastal proximity also affected it. Genetic sources accounted for about 40 percent of the variability in growth. Central Sierra Nevada tests at contrasting low and high altitudes exhibited better growth for seed sources from altitudes similar to the test sites. However, distant sources from high elevation, southern and eastern origins had higher survival at the low (840 m) altitude site. Best survival (and growth) at the high (1860 m) altitude test was attained by sources from matching altitudes in the Sierra Nevada, peaking for 1850 m origins, and diminishing rapidly below 1530 m and above 2030 m. In Oregon tests, the local region had best growth, southern regions had least, and sources within region were interactive between the two contrasting coastal and interior tests. Seed transfer from southern Sierra Nevada northward is desirable to boost rust resistance (also growth and genetic diversity) in northern populations, where natural resistance is rare. Seed transfer up to 220 km northward along the Sierra Nevada west-slope may be advantageous and safe, if temperature regimes of seed source and planting site are matched, and if proven-superior sources are used.

**Key words:** sugar pine, tree genetics

## Introduction

Sugar pine (*Pinus lambertiana* Dougl.) is often described as the largest, noblest, and most beautiful of pines in the world. With long life and a remarkable capacity to sustain growth into old age, not reaching culmination of mean annual increment until 400 years, individual trees may reach enormous size, some over 76 m tall, 305 cm dbh (Larson and Woodbury 1916, Oliver 1996). Excellent wood qualities that include uniformity, stability, workability, and

finish ability, elevate the commercial value of sugar pine to most preferred species for paneling, cabinetry, and moulding (Willits and Fahey 1991).

Sugar pine ranges widely in latitude (over 14°) and in altitude (2750 m) from Baja California to northern Oregon (Critchfield and Little 1966). Sugar pine possesses wide ecological amplitude, having adapted to different temperature, humidity, and soil environments from coastal to inland montane forests. This late seral species is adapted to high elevations because of its short period of height growth, and to low elevations due to its tolerance of hot, dry sites. Distribution is nearly continuous through the Siskiyou and Klamath Mountains and along the western slopes of the Cascade and Sierra Nevada Ranges (Oliver 1996).

Rarely forming pure stands, sugar pine is typically a minor (less than 25 percent of canopy cover) but highly consistent (more than 70 percent constancy) component with high ecological value in mixed-conifer forests (Fites 1996). These majestic pines protect watersheds, provide large, edible seeds for wildlife forage and large snags for cavity nesting birds, enhance ecological diversity, and improve recreation. Best development has been observed in virgin stands on deep soils in the Stanislaus-Toulumne Experimental Forest, and Yosemite, Kings Canyon, and Sequoia National Parks.

Unfortunately, the high resource values and future of sugar pine are seriously threatened by its extreme susceptibility to an introduced disease, white pine blister rust (WPBR) caused by *Cronartium ribicola* Fisch. Natural regeneration is further impeded by poor seed dispersal, heavy seed predation, low tolerance of competition, and the lack of recurrent, non-stand-replacing fires (Oliver 1996). Needed are proper pest management, genetic conservation, and silviculture, using group selection harvest and artificial regeneration with resistant stock.

Genetic conservation programs in both California and Oregon aim to improve genetic resistance and to restore sugar pine in its native habitats (Samman and Kitzmiller 1996, Sniezko 1996). A major (dominant) gene (R) conveys resistance in natural populations. Natural resistance is rare (R frequency is less than 0.01) in northern populations, where the disease entered 75 years ago and spread southward in sporadic "wave years". Resistance is highest, but still very low, in southern Sierra populations (R<0.09). WPBR is absent below 35° N. "Slow rusting" and ontogenetic resistance mechanisms also exist (Kinloch and Davis 1996).

Management policy seeks to maintain the viability of sugar pine in mixed-conifer forests. Restoration will be needed most in the north, because of the greater impact of WPBR on local occurrence. Likewise, an adequate genetic base of durable resistant genotypes for restoration will be extremely difficult to find in northern populations. Moving resistant genotypes from southern populations to northern planting sites could help solve this problem.

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If sugar pine is closely adapted to regional or local environments, long-distance seed transfer could have adverse effects, e.g. maladaptation to “foreign” restoration sites or genetic “contamination” of local gene pools. If sugar pine is not closely adapted, then long-distance transfers would infuse vitally needed genetic diversity to maintain species viability and restore it towards pre-WPBR distribution.

Management policy in California aims to protect the natural genetic structure of sugar pine and all woody plant species (Kitzmilller 1976, 1990). The “default” policy restricts movement of seed (genes) to relatively short distances, defined by standard seed zones (fig. 1) and transfer guides (Buck and others 1970) that apply to all species (“one size fits all”).

Transfer is allowed within the local seed zone (152 m elevation band and ca 80 km), and, in certain cases, across climatically similar seed zones (305 m elevation band and ca 200 km). Developed 30 years ago, this general forest seed policy assumes highly structured sub-populations within species, which theoretically form as a result of high environmental heterogeneity, strong natural selection, and limited gene flow.

Natural selection promotes adaptation of populations to local environments. Climatic, edaphic, and biotic factors affect survival, health, and growth. These traits measure adaptability of seed sources to their transplant environment. Vigorous, healthy trees are expected when natural selection at test and seed origin environments sufficiently

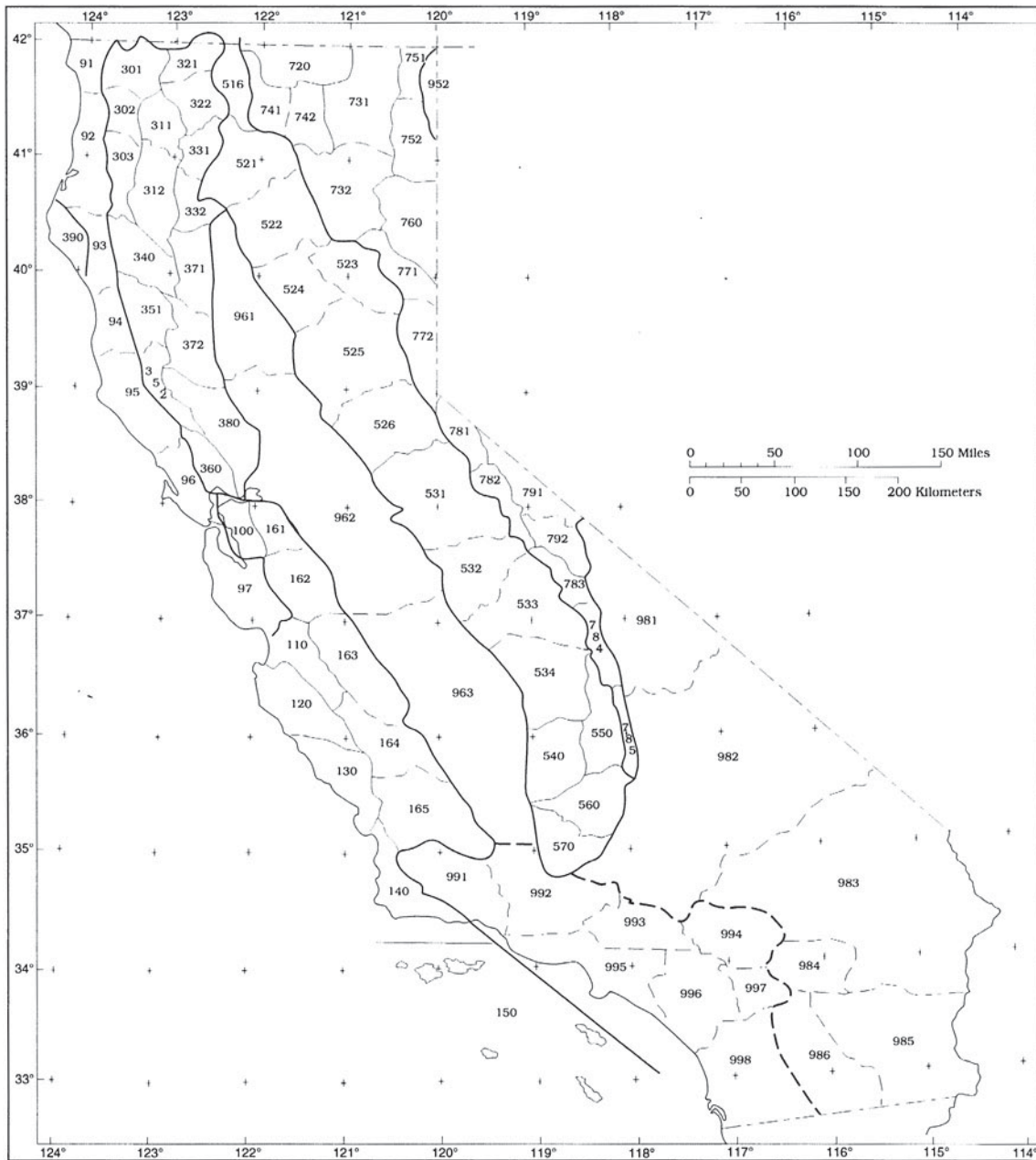


Figure 1—California tree seed zone map.

corresponds to favor similar genotypes. When test and seed origin environments differ widely, maladaptation is expected. Seed zones restrict seed transfer to similar origin and planting environments.

## Genetic Studies of Sugar Pine

Both conservation goals, maintaining species viability and protecting adaptive genetic structure, require knowledge of the nature and pattern of adaptive genetic variation. Together, allozyme and common garden studies provide this knowledge. Conkle (1996) reported strong allozyme differentiation into at least four groups (southern California-Baja, southern Sierra Nevada, northern Sierra Nevada, northern California-Oregon) with a north-south cline in gene frequency. Seed zones with steeper genetic gradients (more complex topography and climate) reflect higher genetic heterogeneity and transfer risk. Heterogeneity of allozyme multi-locus genotypes is a transfer risk parameter that estimates the proportion of genotypes that do not “match” the group (zone) and presumably are maladapted (Westfall 1991). Within Sierra Nevada seed zones, heterogeneity varied in a north-south clinal pattern (Kitzmilller, data filed 1995). The most heterogeneous was 24 percent within the southern-most seed zone 540 (fig. 1), and the least was 13 percent within the northern-most zone 524. Mendocino interior coast zones ranged between 8 to 13 percent, while California North Coast, Klamath, and Southern Cascade zones were 2 to 8 percent. Thus, heterogeneity and transfer risk within geographic seed zones was lower in northwestern California than in southern Sierra Nevada.”

In three separate nursery common gardens, sugar pine showed marked geographic variation in early growth and phenology. Altitudinal provenances (or the original geographic source of seed) from a central Sierra Nevada transect were highly differentiated (Harry and others 1983). Regional patterns were evident for 1185 families representing 27 California seed zones (Kitzmilller and Stover 1996). Campbell and Sugano (1987) found about 50 percent of the adaptive genetic variability in Oregon occurred among local populations. They developed larger and very different zones from the standard Oregon seed zones delineated in 1966 without the aid of genecological data.

Ideally, seed zones should be defined from long-term field trials. Such studies with associated species, ponderosa pine (*Pinus ponderosa* Dougl.) (Conkle 1973) and white fir (*Abies concolor* (Gordon & Glend.) Lind.) (Jenkinson data filed, 1985) have shown strong adaptation to altitudinal climatic gradients. In a 9-year California field study (Kitzmilller and Stover 1996), 37 sugar pine families at seven common garden sites expressed Genotype x Environment (G-x-E) interaction for height. Families originating in coastal influence belts, North Coast-Klamath Mountains (NC-KM), grew faster at three NC-KM sites than families from the northern Sierra Nevada (NSN). NSN families grew faster at the two coldest NSN sites, but no regional differences were expressed at the two NSN sites with long, warm growing seasons. Close inspection revealed that about 30 percent of the families were stable, with half ranking consistently high across all sites. Liberal transfer of seed was suggested for stable families if trends continued.

This paper presents recent results of the most comprehensive study of adaptation and G-x-E interaction in sugar pine established by the Institute of Forest Genetics, PSW Research Station, and the Siskiyou and Eldorado National Forests. This range-wide provenance trial was planted in 1984 in paired low and high elevation Sierra Nevada sites in northern California, and in 1988 in paired coastal and inland sites in southwest Oregon. Jenkinson (1996) reported early results (4- to 8-year). Seed source elevation was significant for 8-year growth of Sierra Nevada sources at the low elevation Sierra Nevada site. There, height was reduced by 10 percent and volume by 26 percent per 300 m rise in source elevation. At the high elevation Sierra Nevada site, where annual winter damage from wet, wind-driven snows became evident at 7-years, high sources were beginning to excel. Source elevation was less important for northern sources at both 4-year-old Oregon sites. Best early growth in all plantations was attained by sources from the middle to upper elevations of the most productive center of the species range.

My objectives are to further assess adaptation and G-x-E interactions in sugar pine for changes in early trends, and to determine the current results and their implications for seed transfer. This paper reports for the first time: (1) comparisons among all four tests for 10-year survival and growth, (2) paired comparisons for survival and growth after 13-years (Oregon) and 17-years (California), and (3) rust infection and health of rust-free trees.

## Materials and Methods

### Study Design and Establishment

Jenkinson (1996) detailed selection of seed sources, nursery and planting procedures, and early results. Seed sources represent 69 wild stands extending across environmental gradients associated with elevation, latitude, and distance from the Pacific Ocean (fig. 2, table 1). Provenance (seed source) samples were well distributed, except in California for the southern Cascades and interior north coast. Each was represented by offspring from 4 to 20 (predominantly 10) healthy, vigorous natural seed parents occurring 0.8 km to 3.2 km apart. The 69 sources were grouped by region (physiographic province) of origin.

Four contrasting common garden test locations were selected to represent and compare two main areas within the ecologically-variable species range: (1) compare range-wide provenance performance in coastal (Sundown) *versus* inland (Burnt Timber) forest environments within southwestern Oregon, and (2) compare range-wide provenance performance at low (Cannon) *vs* high elevation (Fitch-Rantz) forest environments within the Sierra Nevada.

Bayleton systemic fungicide was sprayed annually in autumn for 5-years to reduce blister rust infection. California tests were lightly irrigated the first two summers to ensure initial survival. Herbaceous vegetation was controlled intensively for 2-years using chemical and mechanical methods. Woody vegetation (including *Ribes*) was controlled every 3- to 5-years.

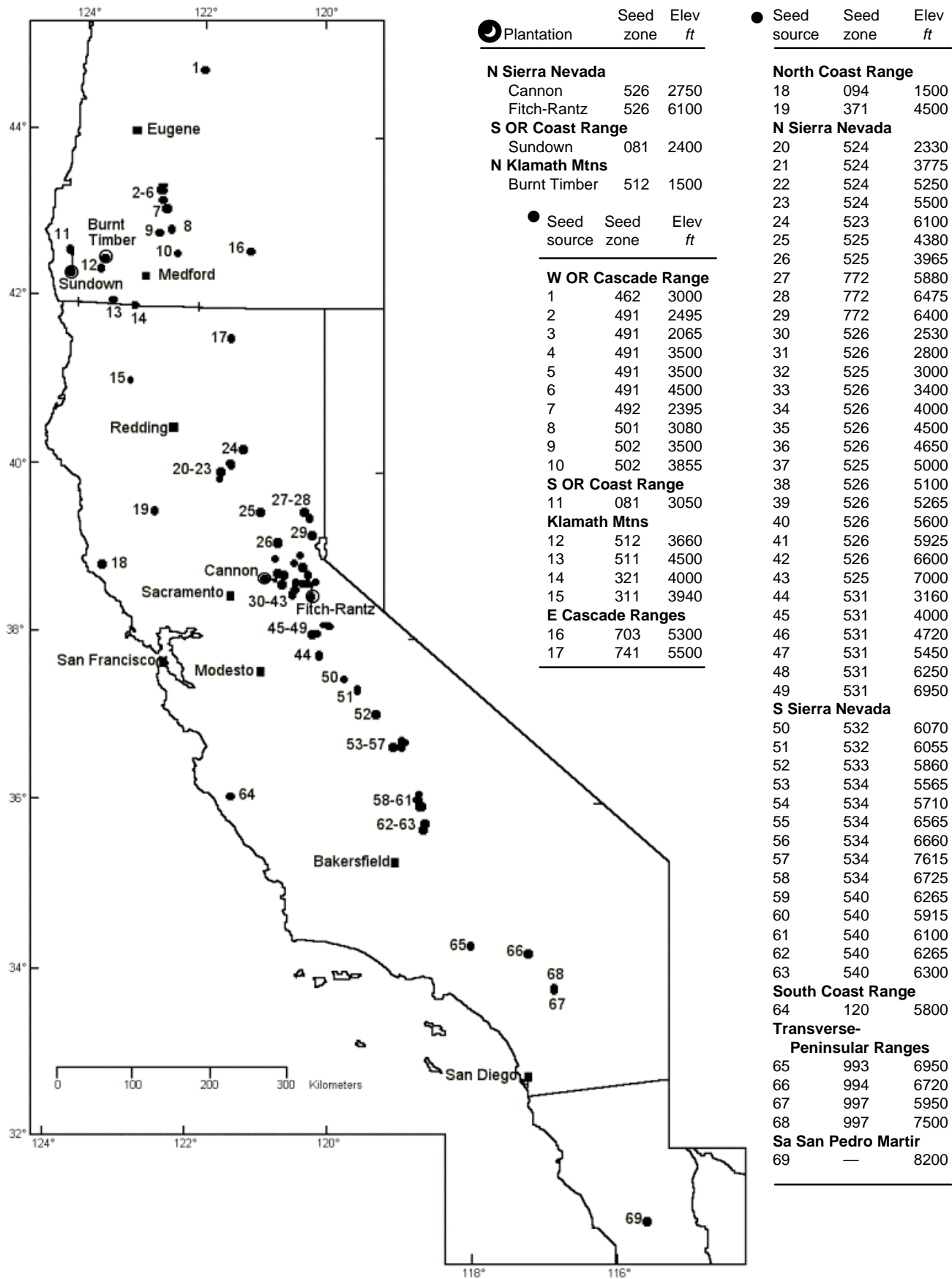


Figure 2—Sugar pine seed sources and locations of common garden tests.

**Table 1**—Seed sources of sugar pine evaluated in common gardens in northern California and southwest Oregon. Sources are listed by latitude and elevation.

Region <sup>a</sup>	Locale	County	Seed Zone <sup>b</sup>	Elevation		Lat °N	Lon °W	Tested In <sup>c</sup>	No. Fam	Map Code
				(ft)	(m)					
WOC	Breitenbush R	Marion	462	3000	915	44.80	122.03	C,F,_,_	4	1
WOC	Steelhead Ck	Douglas	491	2495	761	43.40	122.66	C,F,S,B	7	2
WOC	Grass Ck	Douglas	491	2065	595	43.35	122.70	C,F,S,B	10	3
WOC	Limpy Rock NE	Douglas	491	3500	1067	43.33	122.62	C,F,_,_	7	4
WOC	Limpy Rock SW	Douglas	491	3500	1067	43.33	122.62	C,F,S,B	10	5
WOC	OK Butte	Douglas	491	4500	1372	43.22	122.65	C,_,S,B	10	6
WOC	Camp Comfort	Douglas	492	2395	730	43.12	122.58	C,F,S,B	10	7
WOC	Woodruff Flat	Jackson	501	3080	939	42.87	122.49	C,F,S,B	10	8
WOC	Elk Ck	Jackson	502	3500	1067	42.85	122.68	C,_,S,B	10	9
WOC	Camp Ck	Jackson	502	3855	1175	42.60	122.38	C,F,S,B	10	10
SOC	Gold Beach	Curry	81	3050	930	42.60	124.15	C,_,S,B	10	11
KM	Pea Soup	Josephine	512	3660	1116	42.40	123.63	C,_,S,B	10	12
KM	Bolan	Josephine	511	4500	1372	42.05	123.43	C,F,_,_	10	13
KM	Dutch Ck	Siskiyou	321	4000	1220	41.98	123.07	C,F,S,B	10	14
KM	Salmon R	Siskiyou	311	3940	1201	41.08	123.10	C,F,S,B	10	15
EC	Black Hills	Klamath	703	5300	1616	42.64	121.20	C,F,_,_	10	16
EC	Glass Mtn	Siskiyou	741	5500	1677	41.60	121.50	C,F,_,_	20	17
NC	Fish Rock Rd	Mendocino	94	1500	457	38.87	123.46	C,F,S,B	10	18
NC	S Fk Elk Ck	Glenn	371	4500	1372	39.56	122.65	C,F,S,B	10	19
NSN	Forest Ranch	Butte	524	2330	710	39.93	121.65	C,F,S,B	10	20
NSN	Diamond I	Butte	524	3775	1151	40.02	121.63	C,F,S,B	10	21
NSN	Jonesville	Butte	524	5250	1601	40.12	121.48	C,_,S,B	10	22
NSN	Colby Mtn	Tehama	524	5500	1677	40.13	121.52	C,F,S,B	10	23
NSN	Stover Mtn	Plumas	523	6100	1860	40.28	121.30	C,F,S,B	10	24
NSN	Cal-Ida	Sierra	525	4380	1335	39.54	121.01	C,F,_,_	6	25
NSN	N Shirttail Cyn	Placer	525	3965	1209	39.18	120.75	C,F,_,_	6	26
NSN	Sierraville	Sierra	772	5880	1793	39.55	120.34	C,F,_,_	6	27
NSN	Little Truckee	Sierra	772	6475	1974	39.48	120.24	C,F,_,_	5	28
NSN	Upper Truckee	Placer	772	6400	1951	39.27	120.21	C,F,_,_	5	29
NSN	Pleasant Valley	Eldorado	526	2530	771	38.68	120.67	C,F,S,B	5	30
NSN	Crozier Loop	Eldorado	526	2800	854	38.82	120.72	C,F,S,B	10	31
NSN	Breedlove	Eldorado	525	3000	915	38.98	120.78	C,F,S,B	10	32
NSN	Big X Mtn	Eldorado	526	3400	1037	38.79	120.63	C,F,S,B	10	33
NSN	Big Mtn	Eldorado	526	4000	1220	38.57	120.52	C,F,S,B	10	34
NSN	Snow Mill Rd	Eldorado	526	4500	1372	38.71	120.46	C,F,S,B	10	35
NSN	Caldor Rd	Eldorado	526	4650	1418	38.62	120.47	C,F,S,B	10	36
NSN	Uncle Tom's	Eldorado	525	5000	1524	38.93	120.48	C,F,S,B	10	37
NSN	Tells Creek	Eldorado	526	5100	1555	38.89	120.37	C,F,S,B	10	38
NSN	Alder Ck	Eldorado	526	5265	1605	38.69	120.30	C,F,S,B	10	39
NSN	Pilliken	Eldorado	526	5600	1707	38.69	120.35	C,F,S,B	10	40
NSN	Sugarloaf	Eldorado	526	5925	1806	38.79	120.28	C,F,S,B	10	41
NSN	Mule Cyn	Eldorado	526	6600	2012	38.72	120.18	C,F,S,B	10	42
NSN	Bunker Hill	Placer	525	7000	2134	39.04	120.39	C,F,S,B	10	43
NSN	Groveland Stn	Tuolumne	531	3160	963	37.82	120.11	C,F,_,_	10	44
NSN	Sugar Pine	Tuolumne	531	4000	1220	38.08	120.20	C,F,S,B	10	45
NSN	Lyons Reservoir	Tuolumne	531	4720	1439	38.10	120.17	C,F,S,B	10	46
NSN	Summit Stn	Tuolumne	531	5450	1662	38.20	120.03	C,F,S,B	10	47
NSN	Pincrest	Tuolumne	531	6250	1905	38.19	119.98	C,F,S,B	10	48
NSN	Dodge Ridge	Tuolumne	531	6950	2119	38.18	119.97	C,F,S,B	10	49
SSN	Chowchilla Mtns	Mariposa	532	6070	1851	37.53	119.72	C,F,S,B	10	50
SSN	N Fk Willow Ck	Madera	532	6055	1846	37.41	119.53	C,F,S,B	7	51
SSN	Shaver Lake	Fresno	533	5860	1787	37.12	119.26	C,F,S,B	8	52
SSN	Landslide	Fresno	534	5565	1697	36.77	118.88	C,F,S,B	10	53
SSN	Happy Gap	Fresno	534	5710	1741	36.73	119.00	C,F,S,B	10	54
SSN	Lockwood Grove	Fresno	534	6565	2002	36.80	118.87	C,F,S,B	10	55
SSN	Hume Lake Rd	Tulare	534	6660	2030	36.73	118.88	C,F,S,B	10	56
SSN	Burton Mdws	Fresno	534	7615	2322	36.78	118.83	C,_,S,B	10	57
SSN	Hossack Mdw	Tulare	534	6725	2050	36.17	118.62	C,F,_,_	5	58
SSN	Black Mtn Grove	Tulare	540	6265	1910	36.11	118.65	C,F,_,_	9	59
SSN	Peyrone Camp	Tulare	540	5915	1803	36.03	118.62	C,F,_,_	6	60
SSN	Cunningham Grove	Tulare	540	6100	1860	36.02	118.58	C,F,_,_	10	61
SSN	Bull Run Basin	Tulare	540	6265	1910	35.81	118.54	C,F,_,_	6	62
SSN	Greenhorn Sum	Kern	540	6300	1921	35.74	118.56	C,F,_,_	9	63
SC	Junipero Serra	Monterey	120	5800	1768	36.15	121.42	C,F,S,B	10	64
T-P	San Gabriel	San Angeles	993	6950	2119	34.35	117.92	C,F,_,_	10	65
T-P	San Bernardino	San Bernardino	994	6720	2049	34.24	117.10	C,F,_,_	10	66
T-P	San Jacinto	Riverside	997	5950	1814	33.80	116.75	C,F,S,B	10	67
T-P	San Jacinto	Riverside	997	7500	2287	33.83	116.75	C,F,S,B	10	68
SSPM	Parque Nacional	Baja CA		8200	2500	31.00	115.57	C,F,_,_	10	69

<sup>a</sup>WOC: Western Oregon Cascades; SOC: South Oregon Coast; KM: Klamath Mt; NC: North Coast; NSN: Northern Sierra Nevada; SSN: Southern Sierra Nevada; SC: South Coast; T-P: Transverse- Peninsular.

<sup>b</sup>Buck et al 1970, Kitzmilller 1976, 1990.

<sup>c</sup>C=Cannon, F=Fitch-Rantz, S=Sundown, B=Burnt Timber.

## Measurements

Survival, height, and basal diameter at ground level (dg) through age 10 were taken in all four tests. In fall of 2000, at age 13, these same measurements were repeated at Sundown and Burnt Timber. At Cannon and Fitch-Rantz, survival, height, and diameter at breast height (db) were recorded in the fall of 2000 at age 17. Stem volume ( $\text{dm}^3$ ) of individual trees was calculated using the formula:  $v = 0.1 \pi d^2 h$ , where  $d = db$  or  $dg$  and  $h = \text{height}$ , in dm. At Sundown and Burnt Timber, 13-year volumes were based on dg. In contrast, 17-year volumes at Cannon and Fitch-Rantz were based on db. At California sites, tree injuries caused by blister rust, insects, weather, and stem defects (including forking) were recorded. A different crew measured Oregon tests; damage codes consisted mostly of blister rust (infected or not), which became readily apparent after 10-years. Other causes of injuries were difficult to evaluate on rust-infected trees. So, rust-free trees formed the base for assessing freedom from other injuries. For seed sources, rust infection and mortality were expressed as percent of surviving trees and of total planted trees, respectively.

## Design Differences between California and Oregon Tests

The study is really composed of two pairs of different experiments in terms of: year of establishment, provenance and family representation, number and size of block replications and of trees per source-plot, and measurement schedule (table 2). Cannon (CAN) and Fitch-Rantz (FIT) had 63 sources (provenances) in common. Sundown (SUN) and Burnt Timber (BUR) had 46 common sources. All four tests shared 42 sources and 10-year data in common for a combined analysis. An important difference in experimental design was family representation within source-plots. CAN/FIT source-plots consisted of 10 families each with one tree. SUN/BUR source-plots had 8 families with two contiguous trees each. The effect of families within source could be evaluated accurately only for SUN/BUR tests due to missing family-plots at CAN/FIT.

## Statistical Analysis

Statistical Analysis System (SAS) software (v. 8.1) was used exclusively. PROC SUMMARY computed simple means, within family plot variances, and correlations. Means were built sequentially starting at the family-plot level (that is, "mean of means" method). ANOVAs were based on family-plot (SUN/BUR pair) or source-plot means (CAN/FIT pair). INSIGHT computed simple and canonical correlations, simple and polynomial regressions, and contour-plot graphs to relate adaptability traits to two geographic variables using test-source means. PROC MIXED (method=REML, option=satterth) estimated variance components, least square means, and standard errors of means and of differences between two means using appropriate degrees of freedom for unbalanced subclasses. PROC GLM (option=test) generated accurate expected mean squares and synthesized the proper F-tests.

The analysis consisted of three parts: (1) 42 common sources for all four tests, (2) 63 common sources for the CAN/FIT pair, and (3) 46 common sources for the SUN/BUR pair. Analyses were made both across plantations and by individual test plantation. Models were developed using two sets of assumptions regarding fixed and random effects. One model assumed all factors random (REM) to estimate variance components for all factors studied (table 3a). Since test plantations and regions of seed origins were not actually selected at random, and since least square means are computed only for fixed effects, a more realistic mixed effects model (MEM) was also used. For this MEM, Plantations, Regions, and P-x-R interaction were assumed fixed, while Sources within Region and P-x-S(R) interaction were random (table 3b). Lastly, to compute least square means for S(R) and P-x-S(R) interaction, a third model was used where only Blocks and Error were assumed random. Least squares means were considered most useful for unbalanced data (e.g. missing source plots, unequal replication among tests, unequal sources within regions). G-x-E interactions were examined for cause attributable to scale effects or true rank changes according to Surles and others (1995).

The general run sequence was: (1) PROC MIXED for the REM to estimate variance components; (2) PROC GLM for

**Table 2**—General description contrasting the four common garden tests.<sup>a</sup>

Description	Cannon	Fitch-Rantz	Sundown	Burnt Timber
<b>State</b>	<b>California</b>	<b>California</b>	<b>Oregon</b>	<b>Oregon</b>
Year Planted	1984	1984	1988	1988
Blocks	6	6	5	5
Sources	68 (14OR53CA1M)	64 (10OR53CA1M)	46 (8OR38CA)	46 (8OR38CA)
Trees/Plot	10	10	16	16
Spacing	2.25 m	1.83 m	1.83 m	1.83 m
Elevation	838 m	1860 m	732 m	457 m
Latitude	38.73	38.68	42.55	42.52
Longitude	120.75	120.21	124.13	123.58
Aspect	south	east	south	south
Climate	warm, dry	cool, moist	cool, moist	warm, dry
Soil PM	volcanic basalt	granite	schist	metavolcanic
Forest Type	Lower M-C	Upper M-C	Coastal M-C	Inland M-C
Irrigate 2-Yrs	3 week interval	3 week interval	none	none
Measure Age	2,3,4,6,8,9,10,17	2,3,4,6,8,9,10,17	3,4,5,6,8,10,13	3,4,5,6,8,10,13

<sup>a</sup>(14OR53CA1M) indicates 14 Oregon, 53 California, and 1 Mexico seed sources in test.

**Table 3a**—ANOVA structure for the random model based on family plot means.<sup>a</sup>

Source of variation	DF	Expected mean square (EMS)
Plantations	p-1	$\sigma^2 + 4 \sigma_{PF}^2 + 32 \sigma_{PS}^2 + 100 \sigma_{PR}^2 + 148 \sigma_B^2 + 740 \sigma_P^2$
Blocks (P)	p(b-1)	$\sigma^2 + 313 \sigma_B^2$
Regions	r-1	$\sigma^2 + 4 \sigma_{PF}^2 + 8 \sigma_F^2 + 33 \sigma_{PS}^2 + 66 \sigma_S^2 + 147 \sigma_{PR}^2 + 293 \sigma_R^2$
PxR	(p-1)(r-1)	$\sigma^2 + 4 \sigma_{PF}^2 + 33 \sigma_{PS}^2 + 146 \sigma_{PR}^2$
Sources (R)	r(s-1)	$\sigma^2 + 4 \sigma_{PF}^2 + 9 \sigma_F^2 + 34 \sigma_{PS}^2 + 68 \sigma_S^2$
PxS(R)	(p-1)r(s-1)	$\sigma^2 + 4 \sigma_{PF}^2 + 34 \sigma_{PS}^2$
Families (SxR)	rs(f-1)	$\sigma^2 + 4 \sigma_{PF}^2 + 9 \sigma_F^2$
PxF(SxR)	(p-1)rs(f-1)	$\sigma^2 + 4 \sigma_{PF}^2$
Error	<sup>b</sup>	$\sigma^2$

<sup>a</sup> Includes family effect; coefficients are rounded to nearest whole number; p=number of plantations, b=number of blocks or replications within plantation, r=number of regions, s=number of sources within region, and f=number of families within source.

<sup>b</sup> Error degrees of freedom = p(b-1)(r-1) + p(b-1)r(s-1) + p(b-1)rs(f-1).

Synthesized Error Terms (computed by GLM):

Plantation: 0.47\*MS Blk(P) + 0.68\*MS PxR + 0.29\*MS PxS(R) + 0.01\*MS PxF(SxR) – 0.46\*MS Error;

Region: MS PxR + 0.97\*MS S(R) – 0.96\*MS PxS(R) + MS F(SxR) – 0.01\*MS PxF(SxR) – MS Error;

PxR: 0.96\*MS PxS(R) + 0.02\*MS PxF(SxR) + 0.02\*MS Error;

Sources (R): MS PxS(R) + 0.99\*MS F(SxR) – 0.99\*MS PxF(SxR) + MS Error;

PxS(R): 0.98\*MS PxF(SxR) + 0.02\*MS Error.

**Table 3b** – ANOVA structure for a mixed model based on source plot means.<sup>a</sup>

Source of variation	DF	Expected mean square (EMS)
Plantations	p-1	$\sigma^2 + 5 \sigma_{PS}^2 + \_ + 21 \sigma_B^2 + Q_P$
Blocks (P)	p(b-1)	$\sigma^2 + 46 \sigma_B^2$
Regions	r-1	$\sigma^2 + 5 \sigma_{PS}^2 + 10 \sigma_S^2 + \_ + Q_R$
PxR	(p-1)(r-1)	$\sigma^2 + 5 \sigma_{PS}^2 + Q_{PR}$
Sources (R)	r(s-1)	$\sigma^2 + 5 \sigma_{PS}^2 + 10 \sigma_S^2$
PxS(R)	(p-1)r(s-1)	$\sigma^2 + 5 \sigma_{PS}^2$
Error	p(b-1)(r-1) + p(b-1) r(s-1)	$\sigma^2$

<sup>a</sup> P, R, and P-x-R are assumed fixed effects; “\_” denotes their absence relative to random model; **bold** components would be absent from a mixed model with S(R) and PxS(R) also assumed fixed; coefficients are rounded to nearest whole number; p=number of plantations, b=number of blocks or replications within plantation, r=number of regions, s=number of sources within region, and f=number of families within source.

Synthesized Error Terms (computed by GLM):

Plantation: 0.47\*MS Blk(P) + 0.96\*MS PxS(R) – 0.42\*MS Error;

Region: 0.97\*MS S(R) + 0.03\*MS Error

the REM to make F-tests; (3) PROC GLM for a MEM to make F-tests for Plantations, Regions, and P-x-R, (4) PROC MIXED on the MEM to estimate and test differences between least square means of significant factors; (5) repeat 3 and 4 above for the Sources(R) level. The random *vs* fixed assumption affected the F-test outcome for the main effects: Plantations and Regions, because P-x-R was part of the error term in the REM but was not in the MEM. Similarly, the assumption for S(R) and P-x-S(R) affected the F-test outcome for P-x-R and for S(R) (table 3b).

Trees shorter than breast-height (BUR:132, FIT: 62) were discarded from growth analyses. All other trees were used, even rusted and injured trees. Results were similar whether rusted/injured trees were included or not. Rust on limbs had no effect on current height or diameter. Rust on stem reduced height by 4 to 5 percent, but had no effect on

diameter. Since this effect was rather small, and preservation of plot sample size was needed to prevent missing plots, all except severely stunted trees were analyzed. I also excluded trees that died after 10 years in my 10-year analysis across all tests.

## Results

### Survival, Rust Infection, and General Health

Survival was highest at SUN and BUR (73.3 and 72.5 percent, respectively) followed closely by FIT (69.3 percent). Survival was lowest at CAN (38.3 percent) due to progressive mortality from charcoal root rot (*Macrophomina*

phaseolina [Tassi] Goid). During the last nine years, mortality was 29 percent at CAN, 9 percent at FIT, 15 percent at SUN, and 8 percent at BUR. *Note:* Mortality the first 3-years was 23 (CAN), 16 (FIT), 2 (SUN), and 18 (BUR) percent.

Trees living with rust infection were very low at CAN (0.1 percent), much higher at FIT (19.3 percent) and BUR (20 percent), and highest at SUN (44 percent). No trees were recorded as dead from rust at CAN, SUN, or BUR, but 40 trees were rust-killed at FIT. The high post-establishment mortality at SUN was probably rust-related, though it was not so recorded. Of rust-free trees, 95 percent were healthy and without major stem defects at CAN, 65 percent at FIT, 98 percent at SUN, and 99 percent at BUR. Of surviving trees, 52 percent (in other words,  $0.65 \times (1-0.19)$ ) were healthy

at FIT and 95 percent were healthy at CAN. Only 36 percent of total trees planted at both California tests were healthy at 17-years (table 4).

The widest range in survival among sources (table 4) was at FIT (18 to 95 percent). At FIT, survival (and health) varied in a curvilinear pattern with elevation of origin ( $R^2=0.57$ ,  $n=64$ , ( $R^2=0.40$ ,  $n=64$ , respectively)), with highest survival (and health) occurring for sources that match the test site elevation (fig. 3). Survival and health of living trees was directly correlated at FIT ( $r=0.70$ ,  $n=63$ ); sources with higher survival were also healthier. Among tests, current survival is significantly correlated only for CAN x FIT ( $r=0.44$ ,  $n=63$ ). At CAN, survival based on regional means was highly correlated with elevation of origin ( $R^2=0.88$ ,  $n=10$ ); Trans-

**Table 4**—Survival, health, and rust infection by seed source and test plantation.<sup>a</sup>

Region	Locale	Seed Origin: <sup>b</sup>			Cannon		Fitch-Rantz				Sundown			Burnt Timber		
		MC	Sdz	Elev	Surv	Heal	Surv	Heal	LR	DR	Surv	Heal	LR	Surv	Heal	LR
				<i>m</i>	----- % -----											
WOC	Breitenbush R	1	462	915	24	92	48	20	13	2	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
WOC	Steelhead Ck	2	491	761	38	91	45	50	11		83	96	20	84	100	18
WOC	Grass Ck	3	491	595	30	89	58	48	17	2	74	98	29	79	96	13
WOC	Limpy Rock NE	4	491	1067	10	83	72	55	28		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
WOC	Limpy Roc SW	5	491	1067	20	100	50	33	20		78	100	37	75	100	20
WOC	OK Butte	6	491	1372	40	100	<i>np</i>	<i>np</i>	<i>np</i>		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
WOC	Camp Comfort	7	492	730	45	96	43	42	8		86	98	36	73	100	31
WOC	Woodruff Flat	8	501	939	48	90	43	65	23	2	56	100	38	75	100	17
WOC	Elk Ckn	9	502	1067	27	94	<i>np</i>	<i>np</i>	<i>np</i>		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
WOC	Camp Ck	10	502	1175	32	100	65	70	15	3	80	90	52	60	100	35
SOC	Gold Beach	11	81	930	22	100	<i>np</i>	<i>np</i>	<i>np</i>		74	97	36	59	100	23
KM	Pea Soup	12	512	1116	27	94	<i>np</i>	<i>np</i>	<i>np</i>		70	97	39	79	98	19
KM	Bolan	13	511	1372	45	89	50	40	7	4	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
KM	Dutch Ck	14	321	1220	12	86	43	40	23	2	68	100	59	81	100	18
KM	Salmon R	15	311	1201	53	91	88	65	13		65	100	63	56	100	22
EC	Black Hills	16	703	1616	43	100	92	69	18		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
EC	Glass Mtn	17	741	1677	43	100	55	72	24		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
NC	Fish Rock Rd	18	94	457	50	90	18	0	0		84	100	33	64	100	14
NC	S Fk Elk Ck	19	371	1372	12	86	55	48	12		74	100	66	61	100	8
NSN	Forest Ranch	20	524	710	38	96	27	46	19		86	98	28	78	100	16
NSN	Diamond I	21	524	1151	38	96	67	54	30		83	100	27	79	100	8
NSN	Jonesville	22	524	1601	43	96	<i>np</i>	<i>np</i>	<i>np</i>		75	100	65	63	100	44
NSN	Colby Mtn	23	524	1677	12	86	78	95	21	3	55	100	50	70	100	34
NSN	Stover Mtn	24	523	1860	32	100	85	86	14	3	75	100	43	79	100	17
NSN	Cal-Ida	25	525	1335	32	95	60	46	28	2	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
NSN	N Shirrtail Cyn	26	525	1209	23	93	73	64	25		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
NSN	Sierraville	27	772	1793	48	100	93	84	20		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
NSN	Little Truckee	28	772	1974	47	100	83	90	16		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
NSN	Upper Truckee	29	772	1951	50	100	83	76	16	3	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
NSN	Pleasant Valley	30	526	771	45	93	47	71	14		81	100	35	75	98	18
NSN	Crozier Loop	31	526	854	42	84	70	63	17		73	97	50	83	98	20
NSN	Breedlove	32	525	915	33	90	48	48	14		90	100	39	86	100	14
NSN	Big X Mtn	33	526	1037	20	100	53	52	22		88	100	43	64	100	25
NSN	Big Mtn	34	526	1220	25	100	77	77	15		75	100	32	90	100	28
NSN	Snow Mill Rd	35	526	1372	25	93	68	63	15		68	100	48	79	100	24
NSN	Caldor Rd	36	526	1418	35	90	62	78	38		78	91	45	58	100	15
NSN	Uncle Tom's	37	525	1524	37	91	77	62	15		73	100	52	79	100	22
NSN	Tells Creek	38	526	1555	30	100	92	65	22		78	100	53	80	100	23
NSN	Alder Ck	39	526	1605	42	100	92	80	16		83	100	48	85	100	19
NSN	Pilliken	40	526	1707	47	96	68	93	27		73	97	38	74	100	37

(con.)

Table 4 (Con.)

Seed Origin: <sup>b</sup>		Cannon			Fitch-Rantz				Sundown			Burnt Timber				
Region	Locale	MC	Sdz	Elev	Surv	Heal	Surv	Heal	LR	DR	Surv	Heal	LR	Surv	Heal	LR
<i>m</i>																
NSN	Sugarloaf	41	526	1806	48	93	66	82	24	2	80	100	55	76	100	15
NSN	Mule Cyn	42	526	2012	50	97	85	81	29	3	60	86	54	68	97	30
NSN	Bunker Hill	43	525	2134	33	90	70	87	10	2	74	100	36	69	100	13
NSN	Groveland Stn	44	531	963	23	100	58	68	3		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
NSN	Sugar Pine	45	531	1220	37	100	68	70	27		81	97	45	71	100	21
NSN	Lyons Reservoir	46	531	1439	43	96	75	68	18		66	100	49	68	100	22
NSN	Summit Stn	47	531	1662	28	82	75	82	24	5	78	100	55	75	100	28
NSN	Pinecrest	48	531	1905	33	95	83	76	24	3	69	100	55	66	100	15
NSN	Dodge Ridge	49	531	2119	33	100	93	76	13		76	100	43	79	98	13
SSN	Chowchilla Mtn	50	532	1851	33	90	77	77	33	2	71	100	35	64	100	20
SSN	N Fk Willow Ck	51	532	1846	53	97	83	77	30		59	100	40	74	100	12
SSN	Shaver Lake	52	533	1787	65	97	87	80	23		88	100	44	86	100	10
SSN	Landslide	53	534	1697	43	100	95	61	23	3	63	95	56	68	100	33
SSN	Happy Gap	54	534	1741	42	100	77	76	28	2	65	95	58	80	100	27
SSN	Lockwood Grov	55	534	2002	42	100	83	69	28	2	64	100	61	74	100	20
SSN	Hume Lake Rd	56	534	2030	53	100	83	69	28	2	48	100	34	76	100	21
SSN	Burton Mdws	57	534	2322	<i>np</i>	<i>np</i>	73	63	14	2	56	94	64	56	100	18
SSN	Hossack Mdw	58	534	2050	32	95	75	59	36		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
SSN	Black Mtn Grov	59	540	1910	65	92	77	71	26		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
SSN	Peyrone Camp	60	540	1803	42	96	83	83	20	3	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
SSN	Cunningham G	61	540	1860	52	100	87	72	31		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
SSN	Bull Run Basin	62	540	1910	45	93	92	86	24		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
SSN	Greenhorn Su	63	540	1921	38	91	83	91	12	3	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
SC	Junipero Serra	64	120	1768	37	95	58	32	20		71	100	42	61	100	6
T-P	San Gabriels	65	993	2119	67	95	62	65	8	3	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
T-P	San Bernardino	66	994	2049	42	100	67	65	15	3	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
T-P	San Jacinto	67	997	1814	45	89	67	45	18		<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
T-P	San Jacinto	68	997	2287	63	100	68	45	2		85	100	29	64	100	8
SSPM	Parque Nacion	69		2500	63	95	52	59	6	3	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>

<sup>a</sup> *np* signifies not planted. Map Code 54 at Cannon had 4% LR.  
 Surv=Survival as % of trees planted. Heal= Healthy trees as percent of living rust-free trees.  
 LR= Trees living with rust infection as % of living trees. DR= Trees dead from rust as % of total trees planted  
<sup>b</sup> WOC: Western Oregon Cascades; SOC: South Oregon Coast; KM: Klamath Mts; NC: North Coast;  
 NSN: Northern Sierra Nevada; SSN: Southern Sierra Nevada; SC: South Coast; T-P: Transverse- Peninsular.

verse-Peninsular and Sierra San Pedro Martir sources had highest survival (fig. 4a). In contrast, based on regional means at FIT, survival varied in a curvilinear pattern with elevation of origin ( $R^2=0.68, n=9$ ); southern Sierra Nevada sources had highest survival (fig. 4b). Contour plots for survival pattern by latitude and elevation of origin likewise revealed distinctions between test sites.

Generally, sources with higher survival and health at SUN had lower survival and health at FIT ( $r=-0.40, r=-0.35, n=42$ ). At SUN, highest survival was associated with lower elevation of source origin ( $r=0.44, n=46$ ). At BUR, survival was not associated with source origin. Rust infection of sources was not consistent (not correlated) across test sites. Survival and rust infection of sources at FIT were weakly correlated ( $r=0.35, \text{quadratic } R^2=0.18, n=63$ ); sources with 11 percent or lower infection had less than average survival.

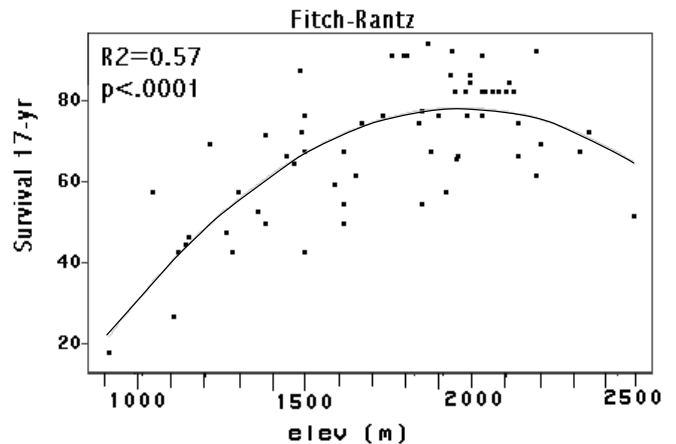


Figure 3—Association between 17-year survival and origin elevation for all provenances at Fitch-Rantz.

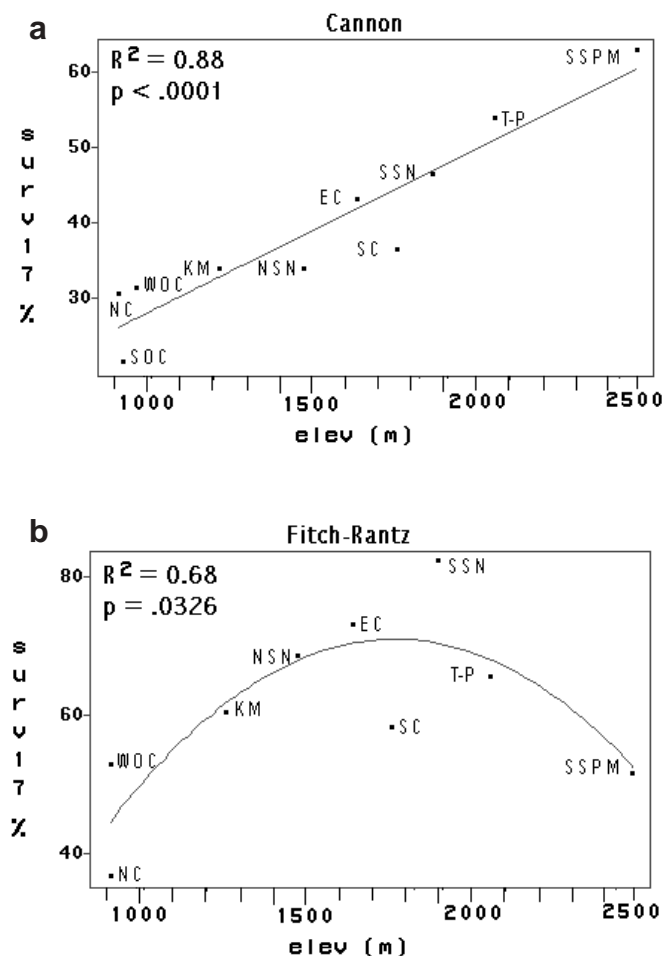


Figure 4—Association between 17-year survival and origin elevation for regions at: a. Cannon and b. Fitch-Rantz.

## All 4 Test Plantations: 42 Common Sources

**Genetic Structure in Adaptive Traits: ANOVA: 10-Year Growth**—All factors except Regions reflected significant differences for 10-year height across plantations (table 5). Plantations accounted for most of the variability in growth; trees at CAN and SUN grew much faster than trees at FIT and BUR (table 6). All pair-wise differences between test means were significant ( $p < 0.05$ ), except 10-year height at CAN and SUN were similar. The G-x-E interactions: P-x-R and P-x-S(R) were about twice the magnitude of their genetic main effects (Regions and Sources within Region) (table 5). Thus, height means for regions and sources within region changed ranking across test plantations. Together, genetic effects and their interactions accounted for about 11 percent of the total variability in height and volume (8 percent for diameter). Comparing across all four plantations, Regions and Sources(R) were about equal for height and diameter, but for volume, Sources(R) far exceeded Regions.

Analysis by plantation revealed that BUR, a xeric site, was a relatively poor site for expression of genetic differences in growth (table 5). At BUR, diameter and volume did

not vary significantly by genetic source, and differences were relatively weak for height. CAN was a good site for genetic expression, but only at the Sources(R) level. Genetic differences for all traits were expressed best at FIT, even with its short growing season; Regions were 2.5 to 4 times more variable than Sources(R). Together, genetic effects accounted for: 39, 65, and 30 percent in height, diameter, and volume, respectively. SUN also was excellent for total genetic expression for height (65 percent of total variability), and, at the Sources(R) level, for diameter and volume (35 percent).

The region effect was similar and small for growth at CAN and BUR, but it was very different at FIT and SUN, where Regions were about twice the magnitude of Sources(R) for height. Both sites expressing strong regional differences have low moisture stress and productive soils. But SUN has a strong maritime influence and long growing season without snow pack, while FIT has a short growing season with deep, persistent snow pack. Trees at SUN grew twice as much in height and three times as much in volume as trees at FIT (table 6). At SUN the region effect was due most notably to superiority of the western Oregon Cascade and North Coast sources, with Klamath Mts. and Sierra Nevada sources intermediate, and South Coast and Transverse-peninsular sources were distinctly inferior in growth (table 7). In contrast, at FIT, Sierra Nevada trees grew most, and North Coast and Transverse-Peninsular trees grew least. The Plantation-x-Region interaction was caused by region height differences between SUN and FIT, the two most climatically distinct tests.

**Seed Source Correlations Among All Test Sites (10, 13-, and 17-Year Data)**—Simple correlations between tests were consistently strongest for height, and consistently lowest when FIT was involved. Simple correlations between test-source means for growth traits among low altitude tests (CAN, SUN, BUR) were positive and mostly significant ( $r = 0.21$  to  $0.65$ ,  $n=42$ ,  $p < 0.05$  when  $r > 0.31$ ). But  $r$ -values are relatively low and show evidence for G-x-E interaction. Correlations between CAN and SUN source growth means were highest (0.48 to 0.65). CAN x BUR (0.34 to 0.48) followed by SUN x BUR (0.21 to 0.46) were lower still. Height at FIT was inversely related to height at SUN ( $r = 0.36$ ), but all other growth trait correlations between FIT and other sites were non-significant and generally negative. Survival was significantly correlated only for CAN x FIT ( $r = 0.44$ ,  $p < 0.01$ ).

Overall, source means were generally correlated between low altitude tests, but not impressively so. Ranking among sources at FIT were most different from ranking in other tests. These results imply relatively large genetic source x test environment interaction.

**Geographic Trends in Seed Source Means**—Simple correlations by test site between source mean growth traits and their geographic origin variables (elevation, latitude, longitude, and distance from test site to seed origin) were relatively high (table 8). Highest correlations were inverse associations between growth and source elevation, except at FIT, the high elevation test, where growth-source elevation correlations were always positive. Also, correlations at FIT were opposite in sign for source latitude and longitude from the other three tests. SUN exhibited the strongest correlations of all tests, with over 60 percent of the variation in height

**Table 5**—Variance component analyses combining all test plantations with 42 common seed sources for 10-yr height (h10), diameter (dg10), and volume (v10) across and by plantation.

Source of Variation	DF	h10			dg10			v10		
		VarC	%	PR > F	VarC	%	PR > F	VarC	%	PR > F
Plantations	3	7463	69	0.0001	680	69	0.0001	38	60	0.0001
Blocks(P)	18	444	4	0.0001	46	5	0.0001	3	5	0.0001
Regions	6	196	2	0.2325	32	3	0.0161	0	0	0.1891
Sources(R)	35	172	2	0.0061	17	2	0.0020	2	3	0.0028
P*R	18	376	3	0.0002	5	1	0.1995	0	1	0.2382
P*S(R)	105	395	4	0.0001	24	2	0.0001	5	7	0.0001
Error	680	1772	16		186	19		16	24	
	865	10818	100		990	100		64	100	
<b>Cannon</b>										
Regions	6	0	0	0.3607	3	1	0.2684	0	0	0.5206
Sources(R)	35	1012	20	0.0001	76	15	0.0021	16	24	0.0001
Blocks	5	756	15	0.0001	75	15	0.0001	8	12	0.0001
Error	157	3246	65		338	69		42	64	
	203	5014	100		492	100		66	100	
<b>Fitch-Rantz</b>										
Regions	6	507	28	0.0001	52	26	0.0001	1	23	0.0001
Sources(R)	35	200	11	0.0004	13	6	0.0205	0	6	0.0174
Blocks	5	124	7	0.0001	22	11	0.0001	1	13	0.0001
Error	196	969	54		112	57		3	57	
	242	1801	100		198	100		6	100	
<b>Burnt Timber</b>										
Regions	6	199	6	0.0569	15	5	0.0613	0	1	0.3639
Sources(R)	35	204	7	0.0344	6	2	0.2597	0	5	0.0963
Blocks	4	840	27	0.0001	72	26	0.0001	2	20	0.0001
Error	163	1877	60		190	67		6	74	
	208	3120	100		283	100		8	100	
<b>Sundown</b>										
Regions	6	1535	42	0.0008	17	7	0.0484	3	9	0.0677
Sources(R)	35	843	23	0.0001	82	35	0.0001	10	35	0.0001
Blocks	4	50	1	0.0298	14	6	0.0002	1	5	0.0006
Error	164	1197	33		121	52		14	51	
	209	3625	100		234			28	100	

**Table 6**—Least square means for test plantations by growth traits.<sup>a</sup>

Plantation	Trait - Least Square Mean			
	cm	mm	dm <sup>3</sup>	cm
<i>46 sources</i>	h13	db13	v13	hgr3
Sundown	466	130	72.8	146
Burnt Timber	284	76	17.8	95
Std Error	17.1	4.4	5.2	5.4
<i>63 sources</i>	h17	db17	v17	hgr7
Cannon	714	154	52.4	378
Fitch-Rantz	458	90	11.1	234
Std Error	14.4	3.1	2.4	9.8
<i>42 sources</i>	h10	dg10	v10	
Sundown	320	95.6	11.07	
Burnt Timber	188	49.8	2.19	
Cannon	325	108.9	14.31	
Fitch-Rantz	158	74.1	3.36	
Std Error	10	3.3	0.9	

<sup>a</sup> h=height, db=diameter breast height, db=diameter ground level, v=volume, hgr=recent 3- or 7-yr height growth increment; Based on three analyses: 10-yr-all plantations-42 common seed sources; 13-yr-SUN/BUR-46 common sources; 17-yr-CAN/FIT-63 common sources.

and 50 percent in volume associated with source elevation. Weakest correlations between growth and geographic variables other than elevation were for CAN.

Distance was expressed both as simple kilometer distance irrespective of direction ("Dist") and as north vs south direction-dependent (sources north of test latitude were given positive kilometer values, and sources south of test were given negative values). All test plantations except CAN expressed an association for better growth for sources closer in distance to the test site, "i.e." correlations between growth and "Dist" were negative (table 8). Close examination revealed one local source (Big X Mtn) with vastly superior growth at CAN, and some superior sources at FIT were transferred 250 km. For Oregon tests, nearly all sources originated southward, so both variables gave the same result. However, at FIT, better growth was associated with closer source distance, and southern sources tended to out-grow northern sources ("Dist1" negative r-values, table 8).

Canonical correlations (1<sup>st</sup> variates) between growth and geographic variables were higher for SUN (r=0.89), and FIT (r=0.86), and lower for CAN (r=0.80) and BUR (r=0.77). Height and elevation were weighted most. Sixty-three percent of the variance in the derived geographic origin variable was associated with the variance in the derived growth trait variable.

**Table 7**—Least square means and ranks by test, region and 10-yr height (h10), diameter (dg10), and volume (v10).

Region and Trait	Sundown		Burnt Timber		Cannon		Fitch-Rantz	
	Rank	LSM	Rank	LSM	Rank	LSM	Rank	LSM
<i>h10</i>								
W Oregon Cascade	1	375	1	224	3	338	4	153
Klamath Mts	3	348	2	197	1	369	3	158
North Coast	2	372	4	189	2	360	7	129
N Sierra Nevada	4	322	3	194	4	330	2	184
S Sierra Nevada	5	307	5	183	5	328	1	195
South Coast	6	258	6	170	6	277	5	151
Transverse-Peninsular	7	254	7	160	7	274	6	133
Plantation Mean		320		188		325		158
<i>dg10</i>								
W Oregon Cascade	1	106.4	1	58.4	5	109.4	5	73.0
Klamath Mts	4	100.1	4	49.9	3	116.0	4	73.5
North Coast	3	103.2	5	46.9	4	111.2	6	68.2
N Sierra Nevada	2	103.5	2	55.8	1	117.0	2	82.5
S Sierra Nevada	5	100.0	3	51.3	2	116.1	1	84.7
South Coast	6	79.1	6	46.3	6	100.7	3	76.5
Transverse-Peninsular	7	76.9	7	40.0	7	92.2	7	60.5
Plantation Mean		95.6		49.8		108.9		74.1
<i>v10</i>								
W Oregon Cascade	1	15.24	1	3.29	5	14.21	5	3.07
Klamath Mts	4	12.28	3	2.16	1	17.86	4	3.20
North Coast	2	14.61	5	1.91	3	16.66	6	2.19
N Sierra Nevada	3	12.47	2	3.01	2	16.67	2	4.69
S Sierra Nevada	5	11.33	4	2.16	4	15.88	1	5.27
South Coast	6	6.07	6	1.74	6	9.91	3	3.30
Transverse-Peninsular	7	5.47	7	1.10	7	8.96	7	1.80
Plantation Mean		11.07		2.19		14.31		3.36

**Seed Source Rank Changes Across Test Plantations**—Rank comparisons for the same 42 seed sources on the same four test sites for 10-year growth traits revealed clear genetic source interactions across tests (table 9). These interactions were not due to scale effects; rather they were determined to be true rank change interactions (Surles and others 1995). Major rank changes among tests for the same sources were evident between: Oregon sites, California sites, and states. Patterns of rank changes may reflect adaptive responses to different climates. Based on the subjective criterion of at least one quartile rank change (11+) in both height and volume, within the Oregon pair (coastal *vs* inland tests) 12 sources were interactive, five of which (Map Codes: 18, 23, 41, 45, 50) were highly so. Within the California pair (low *vs* high elevation tests), 18 sources were interactive, 12 of which (5, 7, 8, 14, 18, 24, 32, 33, 37, 39, 42, 51) were highly so. Some sources displayed specific preference for their “home” state (2, 3, 8, 50, 56). Among the four test sites, 18 sources (43 percent) were considered highly interactive. Some 13 sources were interactive only at FIT, being stable across all other tests; five low elevation sources were especially maladapted to FIT; eight mid to high elevation sources were especially well-adapted. Only 10 sources (24 percent) were relatively stable in rank across all tests (15, 19, 31, 34, 43, 46, 52, 55, 64, 68).

**Growth Trends Over Time**—Within-test simple correlations between 10-year total growth and subsequent 3- or 7-year growth increment were made to monitor potential trend changes among sources over time. Most recent 7-year

height increment at FIT was highly correlated with height at age 10 ( $r=0.94$ ,  $p<0.0001$ ), but much less so at CAN ( $r=0.62$ ,  $p<0.0001$ ). Corresponding values for recent 3-year increment and 10-year total were identical at both SUN and BUR ( $r=0.87$ ,  $p<0.0001$ ). Thus, the pattern of growth differences among sources at CAN changed to a greater degree during recent years compared to the other tests, which remain very stable.

## Cannon and Fitch-Rantz: 63 Common Seed Sources: 17-Year Data

**Genetic Structure in Adaptive Traits: ANOVA Variance Components and Means**—Analysis of 17-year data for CAN/FIT provided 21 additional sources to better represent regions and sources within regions. Forty-two of the 63 common sources were from the Sierra Nevada. Plantations accounted for the majority of variability in all traits (66 to 74 percent for growth, and 50 percent for form, Table 10). Trees at CAN grew 1.6 times more height and 4.7 times more volume as trees at FIT (table 6). Genetic sources accounted for 10 to 23 percent of total variability. Significant G-x-E interactions (P\*R, P\*S(R)) imply that growth trait differences among Regions and Sources(R) must be interpreted separately for each test plantation. G-x-E interactions (composed mainly of P\*R for height, and mainly P\*S(R) for volume) were 3 times the magnitude of genetic main effects (table 10).

**Table 8**—Simple correlations between seed source growth trait means and geographic origin variables at each test site.<sup>a</sup>

Test_Trait <sup>b</sup>	Elev	Lat	Lon	Dist	Dist1
Sun_h10	<b>-0.808</b>	<b>0.624</b>	<b>0.638</b>	<b>-0.637</b>	<b>-0.637</b>
Sun_dg10	<b>-0.565</b>	<i>0.330</i>	0.290	<i>-0.347</i>	<i>-0.347</i>
Sun_v10	<b>-0.698</b>	<b>0.424</b>	<b>0.423</b>	<b>-0.436</b>	<b>-0.436</b>
Sun_h13	<b>-0.792</b>	<b>0.638</b>	<b>0.653</b>	<b>-0.652</b>	<b>-0.652</b>
Sun_dg13	<b>-0.599</b>	<i>0.370</i>	<i>0.327</i>	<i>-0.378</i>	<i>-0.378</i>
Sun_v13	<b>-0.712</b>	<b>0.478</b>	<b>0.469</b>	<b>-0.484</b>	<b>-0.484</b>
Sun_hgr3	<b>-0.685</b>	<b>0.610</b>	<b>0.626</b>	<b>-0.624</b>	<b>-0.624</b>
Sun_dggr3	<b>-0.559</b>	0.396	<i>0.355</i>	<i>-0.379</i>	<i>-0.379</i>
Sun_vgr3	<b>-0.709</b>	<b>0.504</b>	<b>0.490</b>	<b>-0.507</b>	<b>-0.507</b>
Bur_h10	<b>-0.571</b>	<b>0.550</b>	<b>0.441</b>	<b>-0.517</b>	<b>-0.517</b>
Bur_dg10	<b>-0.413</b>	<i>0.362</i>	0.216	<i>-0.342</i>	<i>-0.342</i>
Bur_v10	<b>-0.398</b>	0.275	0.187	-0.264	-0.264
Bur_h13	<b>-0.580</b>	<b>0.590</b>	<b>0.495</b>	<b>-0.556</b>	<b>-0.556</b>
Bur_dg13	<i>-0.360</i>	<i>0.355</i>	0.207	<i>-0.339</i>	<i>-0.339</i>
Bur_v13	<b>-0.396</b>	<i>0.319</i>	0.224	-0.302	-0.302
Bur_hgr3	<b>-0.546</b>	<b>0.615</b>	<b>0.554</b>	<b>-0.582</b>	<b>-0.582</b>
Bur_dggr3	-0.155	0.256	0.138	-0.250	-0.250
Bur_vgr3	<i>-0.388</i>	<i>0.340</i>	0.242	<i>-0.320</i>	<i>-0.320</i>
Can_h10	<b>-0.633</b>	0.284	<i>0.367</i>	-0.045	<i>0.324</i>
Can_dg10	<i>-0.371</i>	0.017	0.050	<i>-0.378</i>	0.028
Can_v10	<b>-0.475</b>	0.064	0.134	-0.298	0.089
Can_h17	<b>-0.583</b>	0.302	<i>0.345</i>	-0.007	<i>0.333</i>
Can_db17	<i>-0.383</i>	0.052	0.094	<i>-0.315</i>	0.071
Can_v17	<b>-0.465</b>	0.101	0.161	-0.242	0.129
Can_hgr7	<i>-0.377</i>	0.256	0.233	0.048	0.268
Fit_h10	<b>0.551</b>	-0.292	<b>-0.460</b>	<b>-0.559</b>	<i>-0.360</i>
Fit_dg10	<i>0.389</i>	-0.276	<i>-0.351</i>	<b>-0.632</b>	<i>-0.314</i>
Fit_v10	<b>0.472</b>	<i>-0.323</i>	<b>-0.441</b>	<b>-0.603</b>	<i>-0.372</i>
Fit_h17	<b>0.556</b>	-0.268	<b>-0.463</b>	<b>-0.547</b>	<i>-0.339</i>
Fit_db17	<b>0.525</b>	-0.272	<b>-0.471</b>	<b>-0.609</b>	<i>-0.347</i>
Fit_v17	<b>0.475</b>	-0.279	<b>-0.426</b>	<b>-0.611</b>	<i>-0.331</i>
Fit_hgr7	<b>0.547</b>	-0.249	<b>-0.455</b>	<b>-0.529</b>	<i>-0.321</i>

<sup>a</sup> *Italics*:  $p < .05$ ,  $n=42$  **Bold**:  $p < .01$ ,  $n=42$ . Elev: elevation, Lat: latitude, Lon: longitude, Dist: seed origin distance from test site, Dist1: distance of northern (+) or southern (-) origins from test site.

<sup>b</sup> Sun,Bur,Can,Fit refers to test: Sundown, Burnt Timber, Cannon, Fitch-Rantz. h, db, dg, v, hgr, dggr, and vgr refers to trait: height, diameter breast height, diameter ground level, volume, recent 3- or 7-yr growth increment for height, diameter ground level, and volume respectively.

Analyses by test revealed large genetic source effects at both plantations, accounting for 38 to 40 percent for height and 32 to 40 percent for diameter and volume (table 10). Region of origin contributed most to growth variability at CAN/FIT, but Sources(R) was a highly significant contributor to growth in each test. Regions accounted for four times that of Sources(R) at FIT and 1.5 to two times Sources(R) at CAN. Regions were less interactive with plantations than Sources(R), perhaps because Regions were more highly buffered with broad genetic diversity. The P\*R interaction involved regions with high elevation persistent snow-packs, Eastern Cascade and Sierra Nevada Ranges grew more at FIT than coastal and milder regions which grew more at CAN (fig. 5). Seed source means were highly variable between tests (tables 10, 12).

#### **Growth and Geographic Origin Factors: Correlation and Regression**—Region height means at CAN decreased

with origin elevation ( $R^2=0.76$ ,  $p=0.001$ ,  $n=10$ ). At the source level, height of Sierra Nevada sources decreased linearly with increase in elevation ( $R^2=0.37$ ,  $p<0.0001$ ,  $n=42$ , fig. 6a). At FIT, growth of Sierra Nevada sources increased with source elevation in a curvilinear pattern peaking at 1860 m and then decreasing ( $R^2=0.44$ ,  $p<0.0001$ ,  $n=42$ , fig. 6b).

For 63 sources at both test sites, volume (v17) and previous 7-year height growth (hgr7) varied in curvilinear patterns with distance in miles north (+) or south (-) from test to seed origin (dist1), with  $R^2=0.22$ ,  $p=0.0006$  at CAN (fig. 7a) and  $R^2=0.38$ ,  $p<0.0001$  at FIT (fig. 7b) for v17. Corresponding values for hgr7 were only slightly lower. Best hgr7 growth occurred for sources nearest CAN. At FIT best growth occurred for sources near the site and up to 240 km south. Recent height growth (hgr7) was correlated with 10-year height more closely at FIT ( $r=0.93$ ) than at CAN ( $r=0.68$ ), just as it was in the 10-year 42-source analysis.

**Table 9**—Ranking among 42 common sources within test for 10-yr height (h10), diameter (dg10), and volume (v10).

Regn	Seed Origin: Locale	Sdz	Elev m	Map Code	SUN h10	BUR h10	CAN h10	FIT h10	SUN dg10	BUR dg10	CAN dg10	FIT dg10	SUN v10	BUR v10	CAN v10	FIT v10
WOC	Steelhead Ck	491	761	2	5	8	29	38	18	19	36	40	11	19	30	38
WOC	Grass Ck	491	595	3	7	4	14	26	8	8	26	32	7	5	25	32
WOC	Limpy Rock SW	491	1067	5	17	2	13	40	34	2	33	36	32	2	29	39
WOC	Camp Comfort	492	730	7	1	14	8	36	3	22	23	33	2	24	18	35
WOC	Woodruff Flat	501	939	8	3	6	19	34	2	12	17	35	3	12	17	37
WOC	Camp Ck	502	1175	10	16	7	17	31	31	18	21	26	27	15	23	30
KM	Dutch Ck	321	1220	14	11	23	5	39	29	34	11	39	25	35	7	40
KM	Salmon R	311	1201	15	15	19	15	23	23	23	25	24	22	18	19	21
NC	Fish Rock Rd	94	457	18	2	32	4	42	9	41	15	41	4	39	9	42
NC	S Fk Elk Ck	371	1372	19	19	15	26	28	30	28	34	37	28	22	24	34
NSN	Forest Ranch	524	710	20	13	20	9	33	14	16	16	23	14	17	14	31
NSN	Diamond I	524	1151	21	12	3	3	25	12	3	3	16	10	3	3	18
NSN	Colby Mtn	524	1677	23	33	17	35	16	37	13	39	31	36	13	40	29
NSN	Stover Mtn	523	1860	24	14	24	31	3	20	25	40	11	20	27	39	5
NSN	Pleasant Valley	526	771	30	24	10	27	37	19	7	30	38	16	7	28	36
NSN	Crozier Loop	526	854	31	6	11	6	17	6	5	1	21	6	11	2	16
NSN	Breedlove	525	915	32	10	1	1	32	17	1	2	30	12	1	1	28
NSN	Big X Mtn	526	1037	33	8	21	2	30	4	14	5	25	5	16	4	22
NSN	Big Mtno	526	1220	34	9	16	10	12	5	9	4	4	8	8	5	9
NSN	Snow Mill Rd	526	1372	35	22	12	22	22	15	11	7	6	21	6	11	12
NSN	Caldor Rd	526	1418	36	23	28	16	29	16	27	12	19	18	29	12	26
NSN	Uncle Tom's	525	1524	37	31	30	37	14	24	33	22	9	26	36	32	10
NSN	Tells Creek	526	1555	38	38	22	20	7	39	10	13	8	39	14	15	7
NSN	Alder Ck	526	1605	39	29	42	32	4	26	40	20	3	29	41	22	3
NSN	Pilliken	526	1707	40	28	27	23	11	22	24	18	14	24	25	20	13
NSN	Sugarloaf	526	1806	41	26	9	38	15	25	4	37	15	23	4	35	19
NSN	Mule Cyn	526	2012	42	37	39	39	1	35	31	32	2	35	26	38	4
NSN	Bunker Hill	525	2134	43	34	31	36	27	33	35	28	27	34	32	36	23
NSN	Sugar Pine	531	1220	45	4	33	12	24	1	32	8	28	1	34	10	25
NSN	Lyons Reservoir	531	1439	46	25	18	25	13	13	17	27	17	17	9	26	15
NSN	Summit Stn	531	1662	47	30	35	24	5	27	29	14	5	30	31	16	2
NSN	Pinecrest	531	1905	48	39	41	42	18	36	30	41	22	38	30	37	24
NSN	Dodge Ridge	531	2119	49	32	26	34	19	28	20	31	18	31	21	34	17
SSN	Chowchilla Mtn	532	1851	50	21	37	11	2	10	39	9	10	13	40	8	8
SSN	N Fk Willow Ck	532	1846	51	18	29	30	6	7	26	24	1	9	28	27	1
SSN	Shaver Lake	533	1787	52	20	5	7	10	11	6	6	12	15	10	6	11
SSN	Landslide	534	1697	53	40	25	28	20	40	21	29	20	40	20	33	20
SSN	Happy Gap	534	1741	54	27	13	21	8	21	15	19	7	19	23	21	6
SSN	Lockwood Grov	534	2002	55	35	38	33	21	38	38	35	34	37	38	31	27
SSN	Hume Lake Rd	534	2030	56	36	36	18	9	32	36	10	13	33	37	13	14
SC	Junipero Serra	120	1768	64	41	34	40	35	41	37	38	29	41	33	41	33
T-P	San Jacintos	997	2287	68	42	40	41	41	42	42	42	42	42	42	42	41

## SUN and BUR: 46 Common Seed Sources: 13-Year Data

**Genetic Structure in Adaptive Traits: Variance Components and Means**—The family-plot structure at Oregon test plantations allowed estimation of variance components that included among-families and within-family plots (table 11). Plantations accounted for 42 to 51 percent of the total variability in growth traits. Trees at SUN grew 1.64 times taller and 4 times more volume than BUR at 13-years (table 6). Regions, Families, and Plantations-x-Sources(R) were highly significant for 13-year height. Applying a fixed assumption for P-x-R interaction (MEM) resulted in significance for Regions main effect for all traits (not shown). About

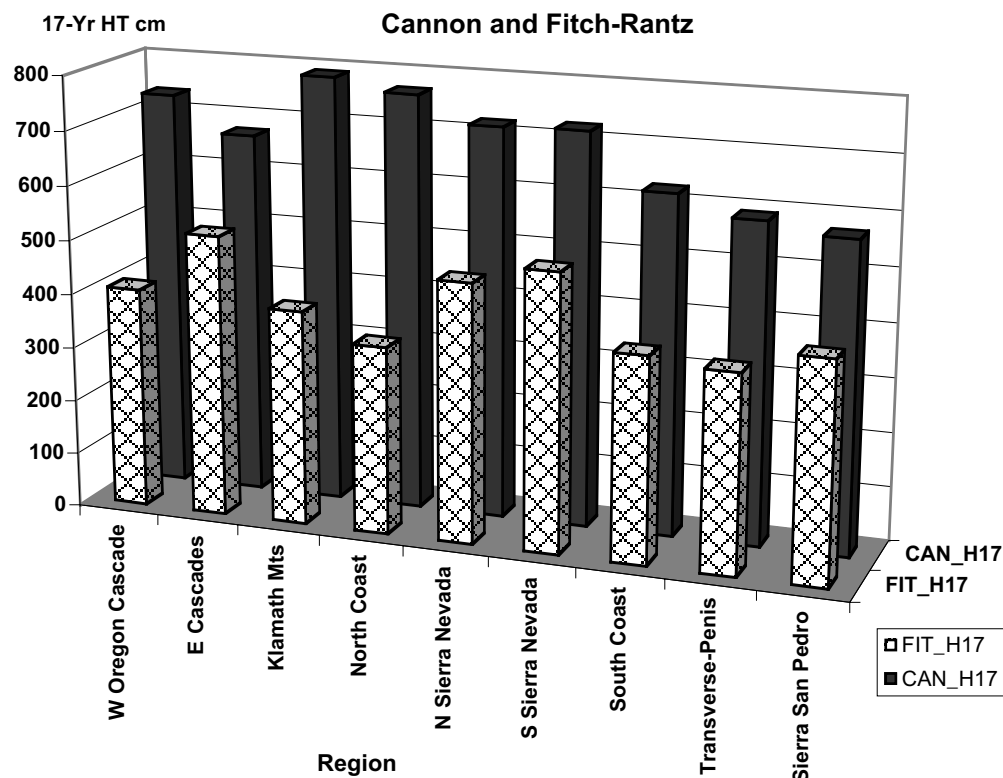
10 percent of all variability in 13-year height was attributable to genetic main effects and their interactions with plantations (table 11). The within-family plot variance is composed of confounded genetic and environmental factors. Within-family plot variance was similar but slightly smaller than the among-family plot (experimental error).

Genetic sources at SUN accounted for 25 percent of the total variability in 13-year height including the within-plot component (or 38 percent excluding it). Corresponding values at BUR were only 11 percent (or 16 percent) and about the same magnitude as Blocks. Although Regions and Sources(R) were significant for 13-year height, Regions was larger at SUN, while Sources(R) was larger at BUR. Effect of Regions was not significant for 13-year diameter and

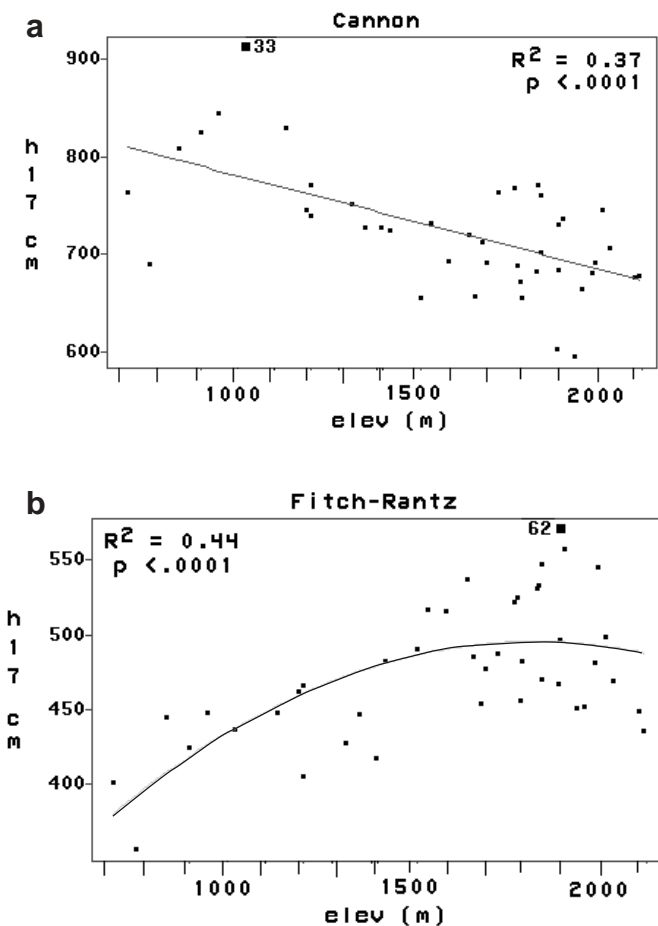
**Table 10**—Variance component percent of total variability and F-tests for growth traits of 63 common seed sources at Cannon and Fitch-Rantz.<sup>a</sup>

Source of Variation	DF	h17		dbh17		v17		h17/dbh17		hgr7	
		%	Pr > F	%	Pr > F	%	Pr > F	%	Pr > F	%	Pr > F
Across Tests:											
Plantations	1	73	0.0001	74	0.0001	68	0.0001	48	0.0002	67	0.0001
Blocks(P)	10	2	0.0001	2	0.0001	2	0.0001	2	0.0001	3	0.0001
Regions	8	2	0.1630	3	0.0399	3	0.1088	2	0.2808	3	0.2038
Sources(R)	54	0	0.8324	0	0.5797	0	0.5967	2	0.0897	0	0.9388
P*R	8	5	0.0016	3	0.0051	3	0.0532	15	0.0001	6	0.0005
P*S(R)	54	3	0.0001	3	0.0001	6	0.0001	4	0.0024	3	0.0001
Error	537	14		15		20		28		18	
By Test: Cannon											
Regions	8	25	0.0003	21	0.0001	15	0.0031	12	0.0001	18	0.0009
Sources(R)	54	15	0.0001	11	0.0012	17	0.0001	0	0.5933	8	0.0040
Blocks	5	7	0.0001	3	0.0043	4	0.0020	7	0.0001	5	0.0001
Error	243	52		64		64		80		69	
By Test: Fitch-Rantz											
Regions	8	31	0.0001	33	0.0001	29	0.0001	35	0.0001	32	0.0001
Sources(R)	54	7	0.0007	7	0.0002	9	0.0001	12	0.0001	11	0.0001
Blocks	5	11	0.0001	11	0.0001	12	0.0001	3	0.0012	12	0.0001
Error	243	51		48		50		50		45	

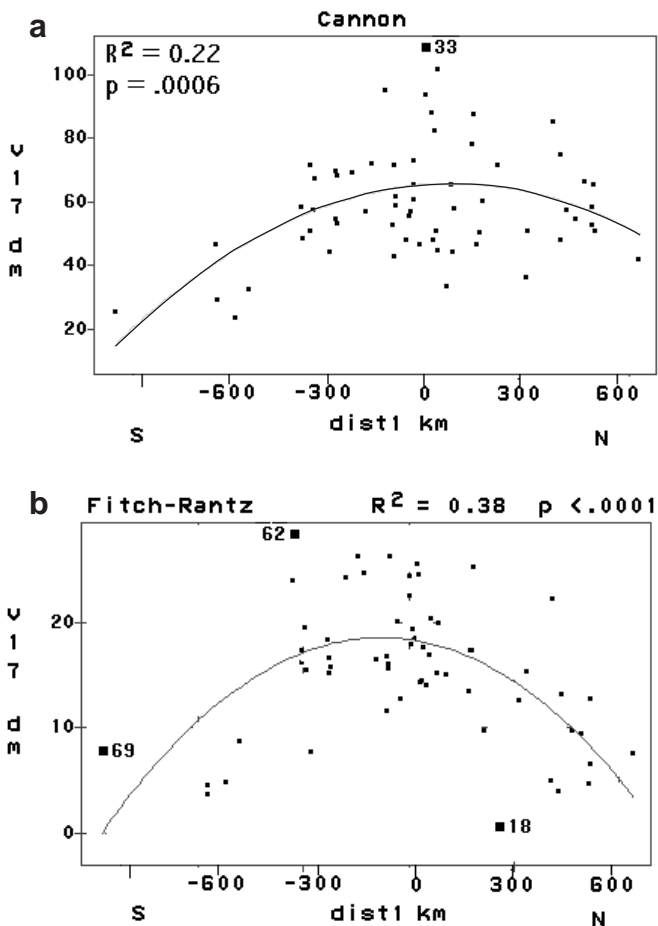
<sup>a</sup> h, dbh, v, hgr: height, diameter breast height, volume, and recent periodic height increment. Random Effects Model was assumed to estimate variance components and F-tests.



**Figure 5**—Mean 17-year height for regions at Cannon and Fitch-Rantz.



**Figure 6**—Association between 17-year height and origin elevation for Sierra Nevada provenances at: a. Cannon and b. Fitch-Rantz.



**Figure 7**—Association between 17-year volume and provenance distance north(+) or south(-) of test locations for: a. Cannon and b. Fitch-Rantz.

volume in either test. Effect of families was relatively small for all traits but was significant at SUN (table 11).

Ranking of regions for h13 was: WOC > NC > KM > SOC > NSN > SSN > SC > T-P. Significant ( $p < .05$ ) differences between Region means across tests for h13 were: WOC > NSN, SSN, SC, T-P; SOC > T-P; KM > SSN, SC, T-P; NC > SSN, SC, T-P; NSN > T-P; where: WOC = Western Oregon Cascade, SOC = South Oregon Coast, KM = Klamath Mountains, NC = North Coast, NSN = Northern Sierra Nevada, SSN = Southern Sierra Nevada, SC = South Coast, and T-P = Transverse-Peninsular. Seed sources within region varied greatly between test sites (table 12).

**Stability in Performance Across Plantations: Correlations and Regressions**—Simple correlations between test plantation-seed source means, a measure of G-x-E interaction, were significant only for height ( $r=0.53$  for h10,  $r=0.51$  for h13,  $r=0.37$  for hgr3,  $n=46$ ). This indicates substantial differences in performance ranking of sources between SUN and BUR that are increasing with age.

**Growth and Geographic Origin Factors: Correlation and Regression**—Growth was inversely correlated with elevation of origin for region means (fig. 8a, 8b) and for source means (fig. 8c, 8d). Among traits, height was most

highly correlated with seed origin. Among seed origin variables, elevation was most highly correlated with growth. SUN provided the strongest pattern of growth with seed origin for source means: 64 percent of the variation in 13-year height was associated with elevation. The corresponding value at BUR was 40 percent. Based on regional means, 85-86 percent of the variation in height was associated with region mean elevation at both sites. The dominant pattern was that growth decreased linearly with increasing elevation and with decreasing latitude and longitude of seed origin. Using canonical correlation, the derived seed origin variable accounted for 79 percent of the variation in the derived growth variable for SUN, and 61 percent for BUR. Further, the derived growth variable for SUN accounted for 62 percent of the variation in the derived growth variable for BUR. So, the implied adaptive pattern of growth response was somewhat different at these Oregon sites.

## Discussion

Sugar pine displayed a complex genetic structure in adaptive traits. Strong G-x-E interactions were expressed for

**Table 11**—Variance components, percent of total variability, and F-tests for 13-yr height diameter, and volume for 46 common seed sources at Sundown and Burnt Timber across and by plantation.

Source of Variation	DF	h13			dg13			v13		
		VarC	%	PR > F	VarC	%	PR > F	VarC	%	PR > F
Plantations	1	15964	49	0.0001	1464	51	0.0001	262	42	0.0001
Blocks(P)	8	975	3	0.0001	59	2	0.0001	9	1	0.0001
Regions	7	1548	5	0.0050	47	2	0.0590	11	2	0.1489
Sources(R)	38	337	1	0.1244	15	1	0.3925	2	0	0.3397
Family(R S)	321	151	0	0.0001	11	0	0.0004	3	1	0.0158
P*R	7	0	0	0.5367	0	0	0.9389	0	0	0.3053
P*S(R)	38	1092	3	0.0001	84	3	0.0001	33	5	0.0001
P*F(R S)	320	0	0	0.9996	0	0	0.9982	0	0	0.9031
Block * (R,S,F)	2495	6983	21		653	23		161	26	
Within Fam Plot	2094	5472	17		556	19		140	22	
		32522	100		2889	100		622	100	
<i>Burnt Timber</i>										
Regions	7	570	4	0.0180	21	2	0.1053	1	1	0.4006
Sources(R)	38	1031	7	0.0001	70	6	0.0001	10	7	0.0001
Families(R S)	320	0	0	1.0000	0	0	0.9999	0	0	1.0000
Blocks	4	1722	12	0.0001	107	9	0.0001	11	9	0.0001
Blocks*R,S,F	1219	6738	46		602	49		67	51	
Within Fam Plot	1062	4450	31		435	35		42	32	
		14510	100		1236	100		130	100	
<i>Sundown</i>										
Regions	7	2460	13	0.0013	15	1	0.1054	19	3	0.0602
Sources(R)	38	1852	10	0.0001	148	9	0.0001	62	10	0.0001
Families(R S)	320	359	2	0.0078	26	2	0.0224	11	2	0.0194
Blocks	4	235	1	0.0001	11	1	0.0002	6	1	0.0001
Blocks*R,S,F	1276	7166	39		699	44		249	42	
Within Fam Plot	1032	6528	35		682	43		240	41	
		18600	100		1581	100		587	100	

**Table 12**—Least square means for growth traits by test plantation and seed source.<sup>a</sup>

Seed Origin: Locale	Seed Origin:			Cannon			Fitch-Rantz			Sundown			Burnt Timber			
	MC	Sdz	Elev	h17	db17	v17	h17	db17	v17	h13	dg13	v13	h13	dg13	v13	
Breitenbush R	1	462	915	<i>m</i>	<i>cm</i>	<i>mm</i>	<i>dm<sup>3</sup></i>	<i>cm</i>	<i>mm</i>	<i>dm<sup>3</sup></i>	<i>cm</i>	<i>mm</i>	<i>dm<sup>3</sup></i>	<i>cm</i>	<i>mm</i>	<i>dm<sup>3</sup></i>
Steelhead Ck	2	491	761	716	144	51.6	398	69	7.8	532	144	95.3	321	82	21.7	
Grass Ck	3	491	595	740	163	66.0	444	85	13.1	548	149	106.3	359	94	32.2	
Limpy Rock NE	4	491	1067	799	154	61.4	374	65	4.9	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	
Limpy Rock SW	5	491	1067	736	142	53.0	388	70	6.6	485	125	69.2	386	99	38.4	
OK Butte	6	491	1372	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	
Camp Comfort	7	492	730	822	157	68.2	420	81	9.7	609	157	127.8	316	80	19.6	
Woodruff Flat	8	501	939	705	152	55.6	423	77	8.4	543	153	120.4	330	91	26.7	
Elk Ckn	9	502	1067	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	
Camp Ck	10	502	1175	733	152	56.5	450	85	13.4	485	129	71.3	320	82	20.7	
Gold Beach	11	81	930	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	487	129	69.9	299	75	16.5	
Pea Soup	12	512	1116	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	495	131	73.7	318	81	23.2	
Bolan	13	511	1372	793	171	75.3	374	66	4.3	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	
Dutch Ck	14	321	1220	859	174	85.8	349	61	5.4	499	132	77.2	294	73	14.3	
Salmon R	15	311	1201	714	141	51.4	464	87	15.6	516	144	92.6	304	80	20.5	
Black Hills	16	703	1616	726	141	50.0	587	106	22.5	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	
Glass Mtn	17	741	1677	616	123	37.2	452	86	12.8	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	
Fish Rock Rd	18	94	457	828	161	72.4	263	33	0.0	587	148	116.5	278	71	14.6	
S Fk Elk Ck	19	371	1372	707	158	63.8	429	83	9.9	486	133	76.0	306	77	19.9	
Forest Ranch	20	524	710	762	170	78.0	469	103	13.9	504	143	90.0	284	83	19.7	
Diamond I	21	524	1151	834	182	89.7	457	89	17.6	504	143	93.5	345	96	31.5	

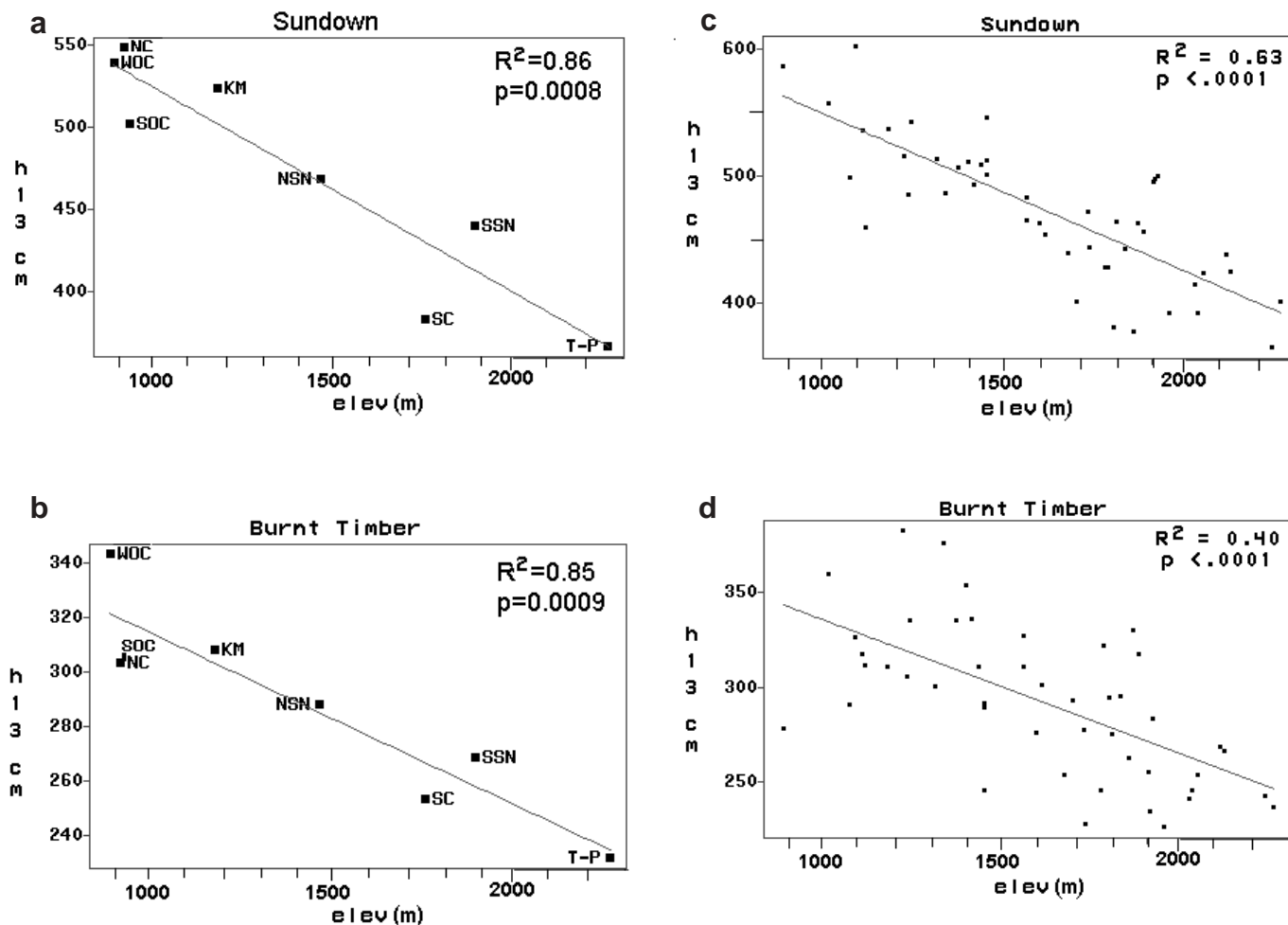
(con.)

Table 12 (Con.)

Seed Origin:				Cannon			Fitch-Rantz			Sundown			Burnt Timber		
Locale	MC	Sdz	Elev	h17	db17	v17	h17	db17	v17	h13	dg13	v13	h13	dg13	v13
			<i>m</i>	<i>cm</i>	<i>mm</i>	<i>dm<sup>3</sup></i>	<i>cm</i>	<i>mm</i>	<i>dm<sup>3</sup></i>	<i>cm</i>	<i>mm</i>	<i>dm<sup>3</sup></i>	<i>cm</i>	<i>mm</i>	<i>dm<sup>3</sup></i>
Jonesville	22	524	1601	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	475	132	70.9	269	72	15.9
Colby Mtn	23	524	1677	642	142	44.2	487	96	17.6	412	119	51.8	300	89	24.5
Stover Mtn	24	523	1860	706	151	52.6	548	109	25.6	492	140	82.8	287	80	19.4
Cal-Ida	25	525	1335	756	164	67.4	434	92	15.3	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
N Shirrtail Cyn	26	525	1209	746	188	102.5	486	106	20.6	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
Sierraville	27	772	1793	686	158	59.0	526	102	20.3	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
Little Truckee	28	772	1974	664	144	45.3	462	91	15.5	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
Upper Truckee	29	772	1951	595	129	34.1	460	99	17.2	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
Pleasant Valley	30	526	771	690	140	47.3	424	78	9.6	454	136	78.1	306	89	27.2
Crozier Loop	31	526	854	812	185	95.7	455	92	17.9	538	157	111.4	307	91	25.6
Breedlove	32	525	915	815	179	87.3	457	93	14.3	516	145	98.1	383	105	56.1
Big X Mtn	33	526	1037	908	189	107.0	448	90	14.5	517	152	101.9	287	88	22.3
Big Mtn	34	526	1220	743	170	74.7	476	102	20.4	515	155	104.3	288	86	24.9
Snow Mill Rd	35	526	1372	712	165	66.2	461	98	18.8	465	147	85.2	301	88	27.2
Caldor Rd	36	526	1418	735	153	61.5	452	92	13.0	458	142	83.5	272	81	17.9
Uncle Tom's	37	525	1524	640	148	47.1	502	113	24.8	437	139	75.5	246	72	12.8
Tells Creek	38	526	1555	723	176	81.4	518	109	25.8	406	121	52.3	296	95	26.7
Alder Ck	39	526	1605	685	150	56.2	512	105	22.9	443	136	70.3	228	69	10.7
Pilliken	40	526	1707	682	151	56.3	485	102	18.3	455	138	79.9	270	85	18.7
Sugarloaf	41	526	1806	655	146	51.6	483	106	19.6	464	136	77.8	316	97	30.7
Mule Cyn	42	526	2012	701	146	49.6	547	109	24.7	399	123	53.2	242	75	17.4
Bunker Hill	43	525	2134	678	143	45.4	456	92	14.8	422	127	60.0	258	75	17.0
Groveland Stn	44	531	963	829	187	95.6	448	91	16.8	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
Sugar Pine	45	531	1220	763	166	71.9	410	84	11.8	544	166	127.2	249	72	13.6
Lyons Reservoir	46	531	1439	726	159	59.7	483	95	17.0	449	141	81.4	311	86	29.1
Summit Stn	47	531	1662	705	162	62.6	542	112	26.6	427	136	70.0	249	75	14.8
Pinecrest	48	531	1905	601	138	42.5	467	94	15.9	385	119	47.3	239	80	17.9
Dodge Ridge	49	531	2119	686	151	54.5	461	97	16.3	439	134	68.9	271	82	19.8
Chowchilla Mtn	50	532	1851	769	168	72.8	544	113	25.0	503	150	98.3	238	72	12.5
N Fk Willow Ck	51	532	1846	683	155	57.6	546	115	26.6	500	152	99.3	249	78	15.4
Shaver Lake	52	533	1787	769	167	70.1	536	112	24.6	473	142	81.5	324	92	27.7
Landslide	53	534	1697	713	150	55.5	465	94	15.5	381	112	44.6	292	82	22.0
Happy Gap	54	534	1741	772	165	69.8	492	93	16.9	451	140	78.8	299	84	18.3
Lockwood Grove	55	534	2002	690	152	54.8	485	90	16.0	393	118	49.0	237	66	11.3
Hume Lake Rd	56	534	2030	746	165	70.5	499	98	18.7	399	125	57.7	251	77	15.8
Burton Mdws	57	534	2322	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	392	120	54.7	234	66	11.4
Hossack Mdw	58	534	2050	693	159	64.8	477	94	15.7	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
Black Mtn Grove	59	540	1910	731	152	58.1	500	105	19.7	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
Peyrone Camp	60	540	1803	673	147	51.6	463	91	16.5	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
Cunningham Gr	61	540	1860	761	165	72.2	488	95	17.6	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
Bull Run Basin	62	540	1910	674	141	47.6	578	118	28.8	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
Greenhorn Sum	63	540	1921	737	157	59.3	559	109	24.3	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
Junipero Serra	64	120	1768	626	142	44.9	378	70	8.0	379	109	42.5	261	73	15.3
San Gabriels	65	993	2119	604	128	33.4	423	81	8.9	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
San Bernardino	66	994	2049	517	108	24.2	353	63	5.0	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
San Jacintos	67	997	1814	662	143	47.4	343	59	4.8	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>
San Jacintos	68	997	2287	578	121	29.9	340	58	3.9	367	110	38.8	230	61	9.3
Parque Nacional	69		2500	571	114	26.5	404	72	8.1	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>	<i>np</i>

<sup>a</sup>MC=mapcode. Sdz=Seed Zone. h17,h13=total height at 17-,13- yrs; v17,v13=total volume at 17-,13-yrs; db17=diameter breast height at 17-yrs; dg=diameter at ground at 13-yrs.

Standard errors of means: Sundown and Burnt Timber: h13=28.3 cm, dg13=8.0 mm, v13=9.5 dm<sup>3</sup>; Cannon and Fitch-Rantz: h17=37.9 cm, db17=8.3 mm, v17=34.9 dm<sup>3</sup>.



**Figure 8**—Association between 13-year height and origin elevation for: a. regions at Sundown, b. regions at Burnt Timber, c. provenances at Sundown, and d. provenances at Burnt Timber.

survival and growth among four contrasting test environments. These were true rank-change interactions that require restrictions in seed transfer within the species range. Only 24 percent of the sources were stable in performance across four tests, and 43 percent were highly unstable. Regions of seed origin were defined to represent broad climatic zones that might prove useful for guiding seed transfer. Region means were also interactive with test environments. Although Regions ranked similarly at the three low elevation tests, ranking changed at the FIT environment. Therefore, both regions and sources within regions with high performance on one or more test sites often had low performance on another.

Common garden test environments greatly affected performance of sugar pine. These four test environments represent a temperature and moisture gradient from the very mild, maritime climate (SUN), to moderate-stress summer, mild winter climate (BUR and CAN), to cool, short, dry summers and long, cold winters with heavy snow-packs (FIT).

## Source-Test Response Patterns

SUN represents mild, humid, and productive northern maritime environments for sugar pine having low diurnal temperature fluctuation. Although high rust infection will greatly reduce survival at SUN, previous and current results show a strong regional geographic genetic variation pattern that is increasing with time. Best growth occurred for sources originating below 1220 m and most commonly from the local region. Growth at SUN was highest with mesic, mild-site western Oregon Cascade (WOC) and north coastal sources (NC). Height based on region means at SUN (as well as at BUR and CAN) followed an inverse linear elevation cline.

BUR represents warm, dry, very low elevation, south-facing environments in the interior Klamath Mountains with moderately high moisture stress for sugar pine, even though survival was high. Trees at BUR expressed weaker geographic patterns than those at SUN. Like SUN, and CAN, best growth occurred for sources originating below

1220 m. But in contrast to SUN, the more inland BUR site favored sources from moderate moisture stress sites farther inland in the western Oregon Cascades (WOC), Klamath Mountains (KM), and some Northern Sierra (NSN) sources.

CAN represents the lowest elevations for sugar pine in the Sierra Nevada, where growing seasons are long, winters are wet and mild, and summers are hot and dry. Survival at CAN was higher for southern California sources (below 38° N and above 1830 m elevation), but growth was better for sources originating above 38° N between 850 m and 1160 m elevation in the northern Sierra Nevada (up to 330 m higher than CAN). Survival based on region means at CAN closely follow a positive elevation cline. High survival of southern California sources suggests they may have higher resistance to charcoal root rot and/or higher drought resistance. Northern low elevation sources may have higher shoot growth potential due to natural selection in mesic, stable temperature climates with long growing seasons, rich, deep soils, and high competition for rapid height growth. Sites with long growing seasons and mild winters favor sources from low to middle elevation that are genetically flexible to extend their growth periods.

FIT is unique in this study in representing typical upper mixed-conifer forest sites with short, cool growing seasons and long, cold winters with persistent snow-packs. Adaptive genetic variation in survival and growth was most pronounced at FIT, and displayed opposite geographic patterns from those at the other test locations. Short-growing seasons and harsh cold winters with persistent snow packs favor trees that cease growth and enter dormancy early enough to escape freeze damage and those that heal stem injuries from snow bend and tearing of primary branches. Winter damage occurred annually, but reduced growth of low elevation sources was detected only after 7 years at FIT (Jenkinson 1996). This environment presented strong selection pressure against sources from distant origins at low or high elevations relative to the test site. Best survival, health, and growth developed for certain sources originating from 1550 m to 2020 m in the Sierra Nevada, with a higher likelihood of success for sources originating within 150 m elevation of the site. At FIT, southern Sierra Nevada sources (and 3 northern, eastside sources: Black Hills, Stover Mt, and Sierraville) tended to exhibit greater diameter and volume than others.

## Seed Transfer Considerations: Matching Seed Source and Planting Site

Clearly, different seed sources should be used in mild, coastal Oregon sites like SUN than in upper mixed-conifer sites like FIT in the Sierra Nevada. Also, different seed sources should be used at low elevation sites like CAN than at middle to upper altitudes in the Sierra Nevada. Moisture-stressed sites (like CAN and BUR) at very low elevations in the Klamath and Sierra Nevada Mountains may require more site-specific matching of seed source to local site conditions, because regional effects were not as strongly expressed as they were for the two mesic sites. Such site-specific matching would be safest within local region, but some transfers across regions with known superior provenances

may be successful (for example, Diamond and Breedlove to BUR, and Dutch Ck to CAN).

Extrapolation to predict safe seed transfers to other planting sites not represented in this study appears risky due to the high G-x-E interactions. Each test site displayed some selective advantage for the local climatic region and/or certain local sources. Local sources appear “safest though not necessarily best”. Even so, certain long distant transfers within a broad altitudinal band were among the best performers. The growth-elevation response pattern showed that the best source elevation was higher south of the site and was lower north of the site across a wide geographic distance. This suggests that elevation may be a “surrogate” for mean annual temperature (MAT).

MAT changes across gradients in elevation, latitude, and distance from the ocean. From long-term temperature and precipitation data recorded at 41 climate stations, MAT lapse rate was determined to be ca 1.62° C per 300 m rise in elevation and ca 0.55° C per 1° rise in latitude (ca 110 km) along the Sierra Nevada western slope (Ledig, data filed 1995). A general guide is to use provenances from ca 1 m higher in elevation than the plantation site per 1 km transfer northward. Applying this guide to the nearly 600 km span along the west-side Sierra Nevada predicts that a northernmost site should have a similar MAT as a southernmost site at 600 m higher elevation.

In general, seed transfer should be most restricted at higher altitudes. When geographic distances for transfer are shorter, the elevation range can be somewhat broader. As the distance of transfer increases, the range in acceptable elevation decreases. For high altitudes like FIT, in central Sierra Nevada, seed from northern or southern Sierra Nevada origins could be used provided source mean annual temperature (MAT), and perhaps even diurnal temperature variation (DT) during elongation, are matched closely with the temperature regime at the planting site. Transfer risk might be substantially reduced if provenance and restoration site temperatures are harmonized, and if stable, proven-superior provenances are used.

Sugar pine at mid to upper elevations has a comparatively short period of shoot elongation (51 days), only about 60 percent as long as and beginning later than ponderosa pine (81 days) and incense-cedar (*Calocedrus decurrens* Torr.) (91 days), but is similar to white fir (46 days) (Fowells 1941). Thus, sugar pine shoot growth is very rapid during a time (late May to mid July) when the temperature range is rather narrow and soil moisture is high. This suggests that sugar pine may be closely adapted to a specific and fairly narrow range of temperature for optimum growth at upper elevations. This delayed and brief growth period is still early enough to avoid drought and to allow “hardening” prior to onset of harsh weather. The temperature regime during elongation may be important to adaptation of sugar pine. Growth of ponderosa pine was inversely related to the diurnal range of temperature (DT) during elongation at the planting site (Church and others, data filed 2000). Sites with wide diurnal temperature fluctuation may selectively favor sources that grow slower (have lower energy efficiency) in a given narrow temperature range, but grow faster (have higher energy efficiency) over broader temperature ranges.

## Transfer Northward to Enhance Rust Resistance

Seed transfer from south to north is the most desirable direction of movement to boost rust resistance in northern populations, where natural resistance is extremely low. Furthermore, many southern populations had higher survival potential in the low elevation plantation and high growth potential at the upper elevation site, in addition to having highest rust resistance. These results suggest significant potential advantages of seed transfer northward.

For northern (or central) Sierra Nevada sites, seed transfer northward about 220 km from central (or southern) Sierra Nevada zones may be done with success by adjusting elevation to match temperature. And, to avoid significant growth losses relative to local sources, proven (tested) high-growth provenances should be transferred. Before transfer, rust resistant families should be tested for stable high performance in contrasting environments. Similarly, transfer of northern Sierra Nevada provenances to California Klamath Mountain sites might be done successfully. Other transfers such as: Sierra Nevada or Klamath Mountains to the Cascade Range, southern California to Sierra Nevada, or elsewhere are not recommended.

## References

- Buck, J. M., Adams, R. S., Cone, J., Conkle, M. T., Libby, W. J., Eden, C. J., and Knight, M. J. 1970. California Tree Seed Zones. Forest Service, California Region and Forestry, Misc. Pub. 5 pp.
- Campbell, R. K., and A. I. Sugano. 1987. Seed zones and breeding zones for sugar pine in southwestern Oregon. Res. Pap. PNW-RP-383. Portland, OR. USDA Forest Service, Pacific Northwest Res. Sta. 18 p.
- Church, J. N., Kitzmilller, J. H., Boom, B. A., Lunak, G. A., Greenwood, K. L., and R. S. Criddle. 2002. 15-year height of *Pinus ponderosa* is correlated with mean diurnal temperature variation during bud elongation. Data filed at UC Davis Dept Environ Hort., Davis, CA.
- Conkle, M.T. 1973. Growth data for 29 years from the California elevational transect study of ponderosa pine. Forest Science 19:31-39.
- Critchfield, W. B. and E. L. Little, Jr. 1966. Geographic distribution of the pines of the world. USDA Forest Service Misc. Publ. 991.
- Fites, J. A. 1996. Ecology of sugar pine in late successional mixed-conifer forests in the northern Sierra Nevada and southern Cascades (Abstract). In: Kinloch, Bohun B., Jr., Mellisa Marosy, and May E. Huddleson (eds.). 1996. Sugar Pine: Status, Values, and Roles in Ecosystems. Proceedings of a Symposium presented by the California Sugar Pine Management Committee. University of California, Division of Agriculture and Natural Resources, Davis, California. Publication 3362. p. 38.
- Fowells, H. A. 1941. The period of seasonal growth of ponderosa pine and associated species. Journal of Forestry 39(7):601-608.
- Harry, D. E., J. L. Jenkinson, and B. B. Kinloch. 1983. Early growth of sugar pine from an elevational transect. Forest Science 29:660-669.
- Jenkinson, J. L. 1996. Genotype-environment interaction in common garden tests of sugar pine. In: Kinloch, Bohun B., Jr., Mellisa Marosy, and May E. Huddleson (eds.). 1996. Sugar Pine: Status, Values, and Roles in Ecosystems. Proceedings of a Symposium presented by the California Sugar Pine Management Committee. University of California, Division of Agriculture and Natural Resources, Davis, California. Publication 3362. pp. 54-74.
- Kinloch, B. B., and D. Davis. 1996. Mechanisms and inheritance of resistance to blister rust in sugar pine. In: Kinloch, Bohun B., Jr., Mellisa Marosy, and May E. Huddleson (eds.). 1996. Sugar Pine: Status, Values, and Roles in Ecosystems. Proceedings of a Symposium presented by the California Sugar Pine Management Committee. University of California, Division of Agriculture and Natural Resources, Davis, California. Publication 3362. pp. 125-132.
- Kinloch, B. B., Davis, D., and G. E. Dupper. 1996. Variation in virulence in *Cronartium ribicola*: what is the threat? In: Kinloch, Bohun B., Jr., Mellisa Marosy, and May E. Huddleson (eds.). 1996. Sugar Pine: Status, Values, and Roles in Ecosystems. Proceedings of a Symposium presented by the California Sugar Pine Management Committee. University of California, Division of Agriculture and Natural Resources, Davis, California. Publication 3362. pp. 133-136.
- Kitzmilller, J. H., and P. Stover. 1996. Genetic variation in the growth of sugar pine progenies in California plantations. In: Kinloch, Bohun B., Jr., Mellisa Marosy, and May E. Huddleson (eds.). 1996. Sugar Pine: Status, Values, and Roles in Ecosystems. Proceedings of a Symposium presented by the California Sugar Pine Management Committee. University of California, Division of Agriculture and Natural Resources, Davis, California. Publication 3362. pp. 83-98.
- Kitzmilller, J. H. 1976. Tree improvement master plan for the California region. USDA Forest Service, Pacific Southwest Region. San Francisco. California. 96p.
- Kitzmilller, J. H. 1990. Managing genetic diversity in a tree improvement program. For. Ecol. Manage. 35:131-249.
- Larson, L.T., and T.D. Woodbury. 1916. Sugar Pine. USDA Forest Service Bull. 426. Washington, DC.
- Ledig, T. 1995. Data filed at Institute of Forest Genetics, Placerville, CA.
- Oliver, W. W. 1996. Silvics of sugar pine: clues to distribution and management. In: Kinloch, Bohun B., Jr., Mellisa Marosy, and May E. Huddleson (eds.). 1996. Sugar Pine: Status, Values, and Roles in Ecosystems. Proceedings of a Symposium presented by the California Sugar Pine Management Committee. University of California, Division of Agriculture and Natural Resources, Davis, California. Publication 3362. pp. 28-33.
- Samman, S. and J. H. Kitzmilller. 1996. The sugar pine program for development of resistance to blister rust in the Pacific Southwest Region. In: Kinloch, Bohun B., Jr., Mellisa Marosy, and May E. Huddleson (eds.). 1996. Sugar Pine: Status, Values, and Roles in Ecosystems. Proceedings of a Symposium presented by the California Sugar Pine Management Committee. University of California, Division of Agriculture and Natural Resources, Davis, California. Publication 3362. pp. 162-170.
- Sniezko, R. A. 1996. Developing resistance to white pine blister rust in sugar pine in Oregon. In: Kinloch, Bohun B., Jr., Mellisa Marosy, and May E. Huddleson (eds.). 1996. Sugar Pine: Status, Values, and Roles in Ecosystems. Proceedings of a Symposium presented by the California Sugar Pine Management Committee. University of California, Division of Agriculture and Natural Resources, Davis, California. Publication 3362. pp. 171-178.
- Surles, S. E., T. L. White, and G. R. Hodge. 1995. Genetic parameter estimates for seedling dry weight traits and their relationships with parental breeding values in slash pine. Forest Science 41(3):546-563.
- Westfall, R. D. 1991. Developing seed transfer zones. In: Fins, L. and Friedman, S. T. (Eds) Handbook of Quantitative Forest Genetics. pp. 313-395.
- Willits, S, and T. D. Fahey. 1991. Sugar pine utilization: a 30-year transition. Res. Pap. PNW-RP-438. Portland, OR. USDA Forest Service, Pacific Northwest Res. Sta. 21 p.