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Edaphic Interactions in First-Year Growth of California Ponderosa Pine

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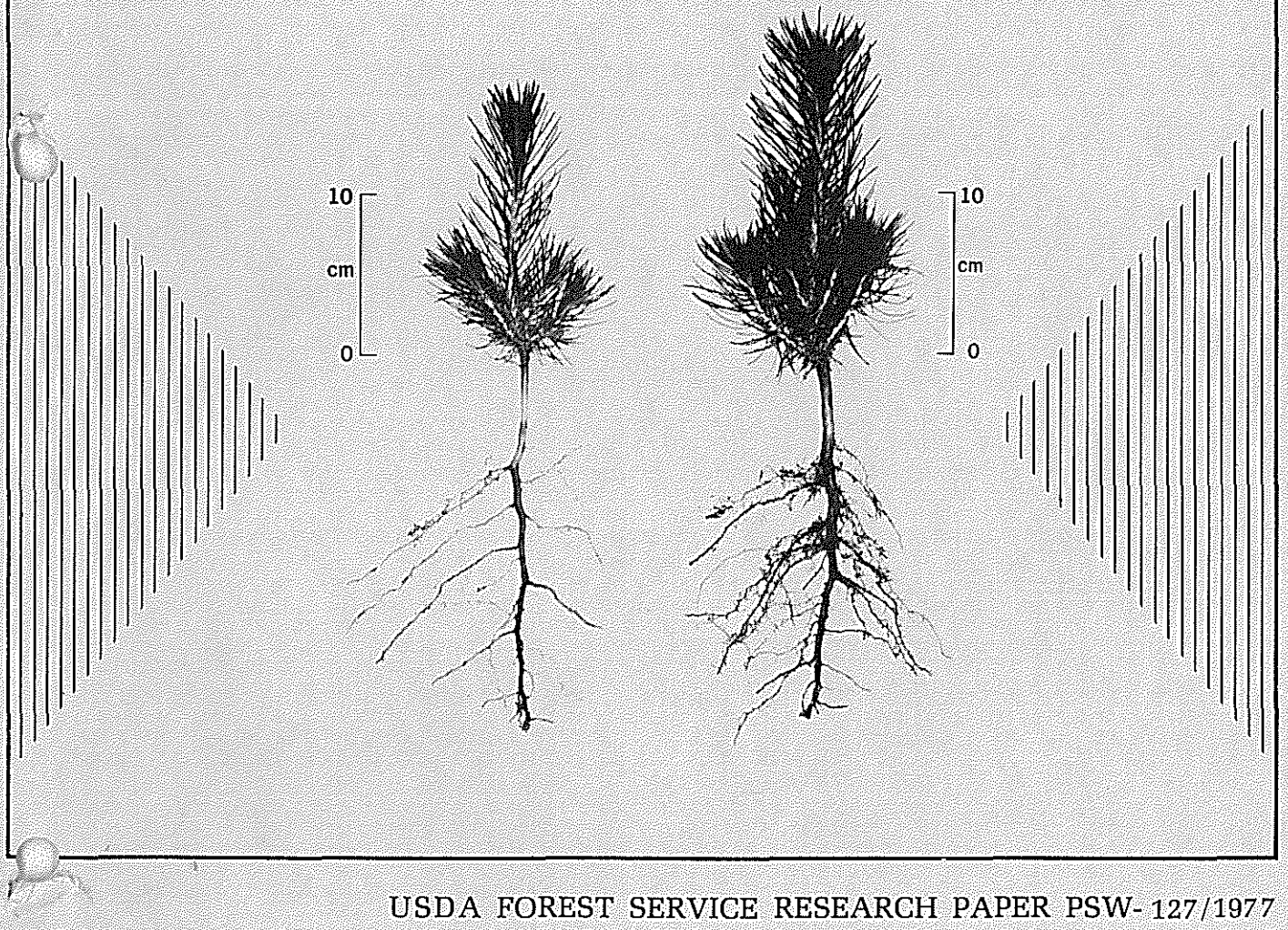

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The Author

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SUMMARY

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California's commercially important conifers may be specifically adapted to local forest soils. To investigate such adaptation, natural stands were selected on one ultramafic, infertile soil and on a nearby fertile soil in each of four widely separated areas that typify mixed conifer forests and climates in the northern Sierra Nevada. Seeds were collected from 11 or more randomly distributed ponderosa pines in each stand.

Mean seed weight and speed of germination were determined for each family. Grouped by geographic area, germinants of every family were planted in a greenhouse in fertile and ultramafic soils obtained from the A horizon in the seed-parent stands. Growth for each family was evaluated on both test soils when the seedlings were 4 to 7 months old.

Germination rates of individual families varied widely for every stand, but this variation was not associated with the equally wide variation in family seed weight. In speed of germination, differences were large between areas and insignificant between paired stands. Thus, climate may have influenced inherent germination rate, but local soil type has not.

For three areas, seedling growth indicated no genetic differentiation between stands on contrasting soils. Even though overall growth was much greater on fertile than on ultramafic soil, mean top weights of seedlings never differed by more than 1 to 4 percent on either soil, and no stand × soil interaction was found. For the fourth area, offspring from the ultramafic stand were consistently smaller on both soils than offspring from the stand on fertile soil, apparently because of the significantly lighter seeds from trees on the ultramafic soil. For reasons I discuss, these results do not rule out edaphic ecotypes.

Seedling root growth in every soil was generally greater for families with large seeds. Seedling top growth was also tied to family seed weight, but the degree of association depended on both the growth trait measured and test soil fertility. Seedling heights on fertile soil were not related to seed weight. Variation in seedling top weight on fertile soil was weakly associated with variation in seed weight, whereas the association ranged from weak to strong on infertile soil. Also, the top weight—seed weight relation was moderate to strong only when top and root growth were highly correlated. When they were not, the relation of top weight to seed weight was weak.

Highly significant differences in seedling growth were found among families from every stand. Up to three-fourths of the families from each stand showed roughly the same ranking on ultramafic as on fertile soil. The other one-fourth showed significant differential responses to soil type — identified by comparing relative top growth performances that could not be explained by family seed weight. Apparently, wide variation in seedling growth of wind-pollinated families and large family × soil interactions are characteristic of the typical populations of California ponderosa pine in the Sierra Nevada.

For artificial regeneration, the results clearly imply that seed collections made in local tree seed zones need not be separated by or restricted to particular soils. Presently, the offspring of diverse stands appear to have comparable growth potentials on a given soil. The superior growth of certain families on both fertile and infertile soils, and of certain others on a single soil, suggest family (parent tree) selection for fast seedling growth on either a specific soil or an array of nutritionally different soils.

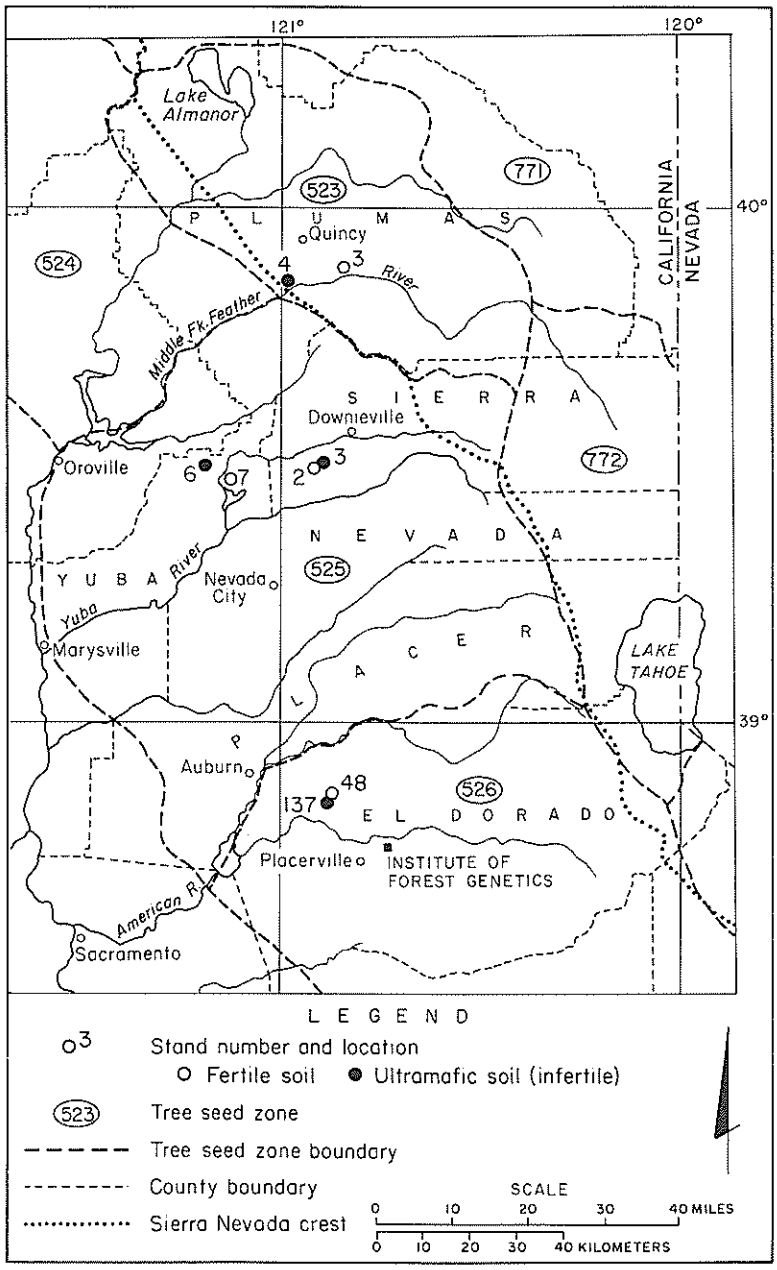


Figure 1 — To investigate local adaptation to soil fertility, natural stands of ponderosa pine were selected on an ultramafic soil and on a nearby fertile soil in four areas in the northern Sierra Nevada.

Extraordinary edaphic variation is a common feature of California's major forest types. Sharp contrasts in tree growth and species composition between stands on adjacent soils are evident in most geographic areas and tree seed collection zones. Edaphic adaptation is a distinct possibility, yet few published studies have considered whether any widespread forest tree is specially adapted to local soils.

In the Coast Ranges, Klamath Mountains, and Sierra Nevada, ultramafic rocks are widely distributed (Rice 1957) and have weathered to form highly infertile soils. In the northern Sierra Nevada, these ultramafic soils lie in roughly parallel and discontinuous belts, crossing rivers and divides at elevations from 500 to 6600 ft (Calif. Div. Mines and Geol. 1971). Many of these soils fail to support the typical mixed conifer forest. Jeffrey pine (*Pinus jeffreyi* Grev. and Balf) — absent from most mixed conifer associations below 5500 ft — and incense-cedar (*Libocedrus decurrens* Torr.) characterize most ultramafic soils down to 3000 ft, and Digger pine (*P. sabiniana* Dougl.) characterizes them below that elevation (Griffin 1965). Ponderosa pine (*P. ponderosa* Laws.), which thrives abundantly in the mixed conifer forest, forms only occasional stands on ultramafic soils. Sugar pine (*P. lambertiana* Dougl.) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) grow on them at middle and higher elevations, and white fir (*Abies concolor* [Gord. and Glend.] Lindl.) grows on such soils at high elevations only. California black oak (*Quercus kelloggii* Newb.) is excluded from all ultramafic soils except those in the Cornutt series.

Only Digger pine has been adequately sampled for investigation of soil adaptation (Griffin 1965). Seedling growth performances of offspring from 17 stands, 5 of which were restricted to infertile serpentinite soil, were compared on one nutritionally sterile serpentinite and on one fertile forest soil. Though differences among stands were great, no general adaptation of the serpentinite progenies to serpentinite soil was indicated.

Stands of ponderosa pine, like those of Digger pine, survive and grow on ultramafic soils in a wide variety of climates. On such soils, trees are chronically subject to nutrient deficiencies of calcium, nitrogen, phosphorus, and potassium. If these trees are specially adapted to function in such circumstances, growth of their offspring on the local soil might reflect this adaptation when compared to the growth of offspring from trees on fertile soil. In an earlier study, the ability of ponderosa pine seedlings to take up calcium and grow on soils low in available calcium was much greater in some single-tree progenies than it was in others (Jenkinson 1974).

This paper reports a study of selected stands of ponderosa pine for specific adaptation to local forest soils.

METHODS

To investigate edaphic adaptation, seedling growth performances of wind-pollinated families from trees in stands on an ultramafic soil and on a nearby fertile soil were evaluated and compared on both soils. Germination rate and mean seed weight were determined for every family. The parent stands were characterized and their climates were evaluated.

Stand Selection

Two natural stands of ponderosa pine, one on ultramafic and one on fertile soil, were selected in each of four geographic areas in the northern Sierra Nevada (*fig. 1; table 1*). Three areas — the Yuba, Sierra, and Plumas — represent the mixed phase of the mixed conifer forest — ponderosa

and sugar pines, incense-cedar, Douglas-fir, white fir, California black oak — that dominates the Cascade-Sierra Nevada mountain chain in California (Griffin and Critchfield 1972). The Yuba and Sierra areas are at low and middle elevations in the zone of maximum rainfall on the western slope. The Plumas area is the coldest and most northerly, and lies in a transition zone between the east and west slopes of the Sierra Nevada. The fourth area — El Dorado — is the most southerly and typifies the warm, dry, low-elevation west-side-pine phase dominated by ponderosa pine.

Except for soil, the site factors for each pair of stands are similar. Differences between soils are primarily due to parent material. The ultramafic soils, in addition to being markedly deficient in nutrients (Jenkinson 1974), are comparatively shallow and rocky.

The stands on fertile soils are second growth that was naturally regenerated after repeated logging of the virgin forest. They might be described as even-aged, although each includes several distinct age classes. The stands on ultramafic soil are all-aged, and contain trees in five or more widely separated, poorly defined classes. All stands are on gentle-to-moderate slopes of ridges, divides, or other uplands.

Climate Evaluation

Climates were evaluated from data recorded at 16 upland stations (U.S. Dep. Commer. 1964a, 1964b, 1970). The El Dorado, Yuba, and Sierra areas are points on the temperature gradient associated with elevation on the west slope of the Sierra Nevada. The Plumas area, though comparable to the Sierra in elevation, lies east of the main crest (*fig. 1*) in a continental climate. Daily fluctuations of air temperature in the Plumas area vary

Table 1—*Seed sources of ponderosa pine selected on fertile (F) and ultramafic, infertile (I) soils in four areas in the northern Sierra Nevada*

Area (county), stand number, and locality	Soil series and parent material	Seed parents		
		Elevations	Ages	Arborescent associates[1]
		Feet (meters)	*Years*	
El Dorado:				
48 Garden Valley	Sites-like (F), marine	1920 to 1960 (585 to 597)	46 to 96	L, QuKe, QuCh
137 Johntown Creek	Henneke (I), serpentinite	1900 to 1950 (579 to 594)	85 to 217	S, LiDe
Yuba:				
7 Kennedy Ranch	Holland-like (F), granitic	2950 to 3000 (899 to 914)	43 to 58	L, AC, LiDe, QuKe, ArMz, S
6 Woodleaf	Dubakella (I), serpentinite	3050 to 3150 (930 to 960)	62 to 300	LiDe
Sierra:				
2 Gleason Spring	Lyonsville-like (F), volcanic	4640 to 4720 (1414 to 1439)	85 to 112	L, AC, PsMz, LiDe, QuKe
3 Brush Creek	a lithosol (I), slickentite	4560 to 4640 (1390 to 1414)	54 to 204	QuCh, PsMz, LiDe
Plumas:				
3 Spring Garden	Mariposa-like (F), marine	4840 to 4980 (1475 to 1518)	87 to 132	L, PsMz, LiDe, AC, QuKe
4 Rocky Point	Cornutt (I), peridotite	4900 to 5050 (1494 to 1539)	78 to 235	LiDe, L. PsMz, AC, QuKe, QuGaSe, J

[1] L: *Pinus lambertiana* Dougl.
S: *P. sabiniana* Dougl.
J: *P. jeffreyi* Grev. & Balf.
AC: *Abies concolor* (Gord. & Glend.) Lindl.
LiDe: *Libocedrus decurrens* Torr.
PsMz: *Pseudotsuga menziesii* (Mirb.) Franco
ArMz: *Arbutus menziesii* Pursh
QuKe: *Quercus kelloggii* Newb.
QuCh: *Q. chrysolepis* Liebm.
QuGaSe: *Q. garryana* var. *semota* Jeps.

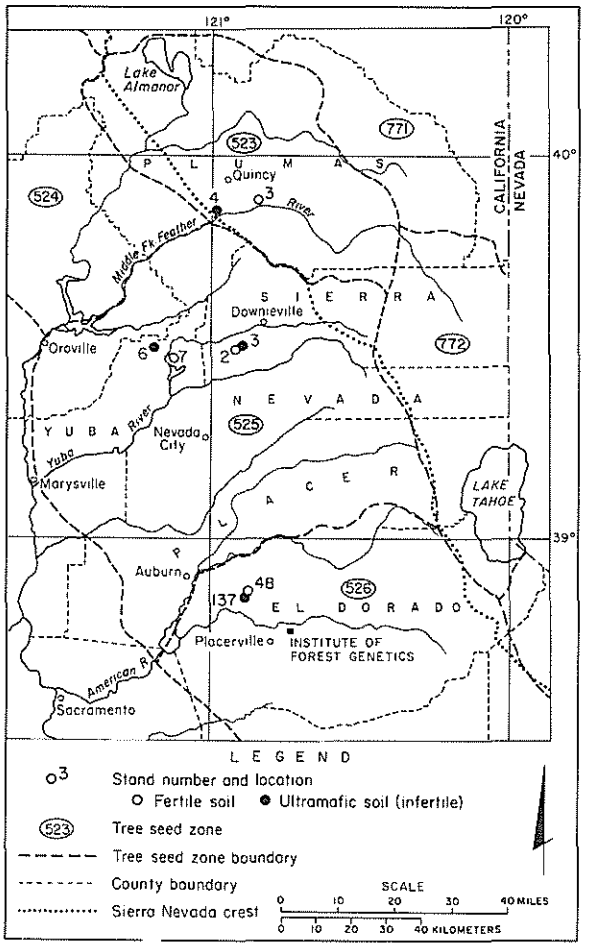


Figure 1 — To investigate local adaptation to soil fertiliy, natural stands of ponderosa pine were selected on an ultramafic soil and on a nearby fertile soil in four areas in the northern Sierra Nevada.

from 30 percent greater in winter to 80 percent greater in summer than fluctuations on the west slope (*fig. 2*).

The seasonal sum of air temperatures that support growth activity is greatest for the El Dorado area and least for the Plumas, where mean daily minimum temperatures are lowest and the winters are coldest. Growing seasons, estimated by summing days with a mean daily minimum above 0° C, are 12, 11, and 8 months in the El Dorado, Yuba, and Sierra areas, and roughly 5 months in the Plumas. The expected freeze-free periods, when minimum temperatures are consistently above −2° C, are 310, 265, 200, and 65 to 120 days (*fig. 2*).

Snowfall is 5 to 7 ft in the Plumas, 10 to 12 ft in the Sierra, and 4 to 6 ft in the Yuba area. The El Dorado area is below snowline.

No significant rain falls in any area during July

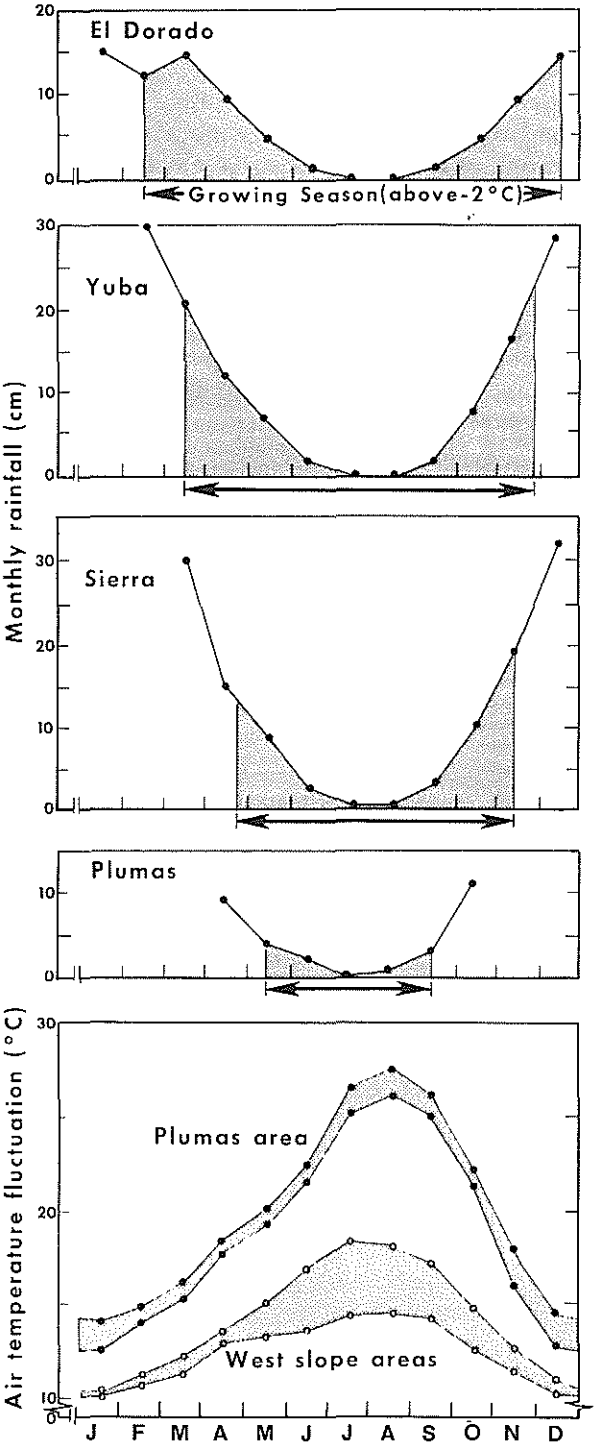


Figure 2 — Climate differs markedly for ponderosa pine west and east of the main Sierra crest: Above, significant spring rainfall overlaps the freeze-free period in the western El Dorado, Yuba, and Sierra areas, but not in the eastern Plumas area. Below, day-night air temperature differences in the Plumas area exceed those on the western slope. (The two curves which delimit each shaded zone are the smallest and largest mean daily fluctuations determined for local stations.)

and August, but the summer drought is most severe in the El Dorado area (*fig. 2*). The Plumas area resembles the dry El Dorado in late spring and the wet Yuba-Sierra zone in early fall. In spring (April-June), twice as much rain falls in both the Yuba and Sierra areas as in the Plumas. In fall (September-November), the El Dorado rainfall is usually just half that of the other areas.

In every area the higher plant water stresses probably develop on the ultramafic soil. Available water capacities are lower in these soils, and their sparse vegetation permits greater insolation and evaporative water loss.

Test Procedures

Seed collections were made in all areas in a good crop year. From 35 to 50 cones were picked from the upper crown of each of 12 randomly distributed trees in each stand, except in Sierra 2 (on fertile soil) where 11 trees were sampled. In the Yuba stands a larger collection, noted as Yuba II, was made three years later, when 18 trees — including 13 new ones — were sampled in each stand. Seeds were extracted from sun-dried cones, cleaned, and stored at 1° to 2° C.

Germination and seedling growth of the individual families were evaluated in a series of five tests at the U.S. Forest Service Institute of Forest Genetics, near Placerville (*fig. 1*).

The mean seed weight for each family was determined from the air-dry weight of 400 full seeds. These seeds were then stratified 60 days at 1° to 2° C in moist, Captan-treated sand, and germinated 14 days at 20° to 25° C on filter paper over wet sand in Petri dishes. During the first 5 days of germination, germinants of each family were stored at 5° C to slow their radicle growth and hold them in similar stages of development for initiating the seedling growth test.

The experimental design for the germination test was a randomized block with four replications — 100 seeds per dish and 4 dishes per family. Seeds were counted as germinated when the radicle emerged 2 mm. After 14 days, the remaining seeds were cut to verify soundness. To evaluate peak germination rates, the maximum mean daily germination was determined for each family (Czabator 1962).

By area, families from both stands were grown on both of the native soils in a greenhouse. The experimental design was a split-plot, randomized block with eight replications. Native soils were the major plots and individual families were the minor plots. Soil was dug from the A horizon in each stand, screened to 5 mm, blended, and transferred to polyethylene-lined containers measuring 9.5 cm square and 30 cm deep. Each container was planted with five germinants of a single family. Forty germinants per family — 8 five-seedling plots — were planted on each soil. The planting of most families was completed the same day, with germinants stored from 0 to 4 days. All plantings were first watered with a Captan suspension to control damping-off fungi, and thereafter with distilled water to avoid any addition of nutrients.

Seedlings were grown under a 16-hour photoperiod and harvested after 4 months (El Dorado), 5.5 months (Yuba, Sierra, Plumas), and 7 months (Yuba II). Individual seedling heights were measured from cotyledon scar to shoot apex, and tops were cut from roots at the cotyledon scar. The ovendry (65° C) weight of each top and the total ovendry root weight per container were recorded.

By area, the data for each seedling growth trait and for peak germination rate were subjected to analyses of variance. Data analyses included linear regressions of family growth traits and seed weight. Because the growth and seed weight relations were similar for offspring of stands evaluated on the same soil, coefficients of determination (r^2) were calculated on pooled data for each soil. Because some variation in growth was associated with seed weight, top weights for the individual families were adjusted to remove this effect and the adjusted data were analyzed. Significant differences among family means were identified by using Duncan's multiple range test and least significant difference procedures (Steel and Torrie 1960).

RESULTS

In the four areas sampled, mean seed weights of individual families from trees on ultramafic and fertile soils offered little evidence of stand adaptation to either local climate or local soil. Differences in mean seed weight between the El Dorado, Yuba, Sierra, and Plumas areas were not

significant (5 percent level). Trees on ultramafic soil in the Yuba area, apparently reflecting their nutrient-deficient and water-stressed condition, consistently produced smaller seeds than trees on fertile soil (*table 2*). In each of the other areas, however, the difference in seed weight between stands was not significant.

Mean seed weights of individual families varied widely, with roughly two-fold differences in most stands (*table 2*). In the higher-elevation Sierra and Plumas areas, but not El Dorado and Yuba, the variance of family seed weights was significantly less for families from trees on ultramafic soil than for those from trees on fertile soil.

Relation of Seedling Growth to Seed Weight and Soil Fertility

Among ponderosa pine families from every area, some variation in seedling growth was associated with variation in seed weight (*table 3*). The relation to seed weight varied with the growth trait measured and with fertility of the test soil. On fertile soils, the mean heights of individual families were not related to seed weight. On ultramafic soils from the El Dorado and Yuba areas, but not the Sierra and Plumas, several families with light seeds did produce shorter seedlings.

Family root weight was always moderately to strongly associated with seed weight. Family top weight, however, was not consistently related to seed weight, but apparently was influenced by it through the relation to root growth. Thus, when top weight was strongly correlated with root weight, it was also moderately to strongly related to seed weight (r^2 = 0.41 to 0.72). When top weight was not strongly correlated with root weight, it was weakly related to seed weight (r^2 = 0.22 to 0.25). In four of the five tests, the weaker relation between top weight and seed weight was found on the fertile soil.

Germination

After 4 days, germination of seeds from trees in the Yuba and Plumas areas was from 13 to 27 times greater than that of seeds from the El Dorado and Sierra areas (*table 2*). Such differ-

Table 2 — *Seed weights and 4-day germination of ponderosa pine families from stands on fertile (F) and infertile (I) soils*

Area and stand	Seed weight		4-day germination	
	Family average[1]	Range of family means	Family average[1]	Range of family means
	Mg		*Percent*	
El Dorado:				
48 (F)	51	30 to 64	2.6	0 to 16
137 (I)	54	40 to 70	3.5	0 to 16
Yuba:				
7 (F)	60 a	40 to 88	79	62 to 95
6 (I)	44 b	32 to 63	83	39 to 99
Yuba II:				
7 (F)	53 a	41 to 66	76	34 to 98
6 (I)	42 b	27 to 53	78	37 to 97
Sierra:				
2 (F)	53	32 to 85	5.5	0 to 21
3 (I)	46	38 to 53	5.6	0 to 35
Plumas:				
3 (F)	52	35 to 65	78	48 to 95
4 (I)	47	43 to 58	67	33 to 98

[1]For an area, means followed by unlike letters differ significantly at the 5 percent level.

Table 3 — *Coefficients of determination (r^2) for seedling growth traits and seed weight of ponderosa pine families tested on fertile (F) and infertile (I) soils*[1]

Area and test soil	r^2 for ...				
	Seedling growth trait on seed weight			Height on top weight	Top weight on root weight
	Height	Top weight	Root weight		
El Dorado:					
Sites-like (F)	0.00	0.24*	0.50**	0.39**	0.54**
Henneke (I)	.55**	.64**	.36**	.70**	.71**
Yuba:					
Holland-like (F)	.00	.25**	.59**	.37**	.30**
Dubakella (I)	.24*	.70**	.90**	.44**	.80**
Yuba II:					
Holland-like (F)	.14*	.41**	.67**	.62**	.40**
Dubakella (I)	.42**	.72**	.81**	.60**	.72**
Sierra:					
Lyonsville-like (F)	.00	.58**	.74**	.17	.73**
a lithosol (I)	.13	.22*	.70**	.18*	.42**
Plumas:					
Mariposa-like (F)	.00	.22*	.70**	.47**	.22*
Cornutt (I)	.13	.41**	.70**	.72**	.71**

[1]Family means in regression were 23 for Sierra, 24 each for El Dorado, Yuba, and Plumas, and 36 for Yuba II. Asterisks designate values for r^2 significant at the 5 (*) and 1 (**) percent levels.

ences between areas were negligible at 14 days, when total germination was 91 to 99 percent.

Edaphic adaptation was not evident in speed of germination. Offspring from stands on fertile and infertile soils in the same area always had similar peak germination rates (*fig. 3*).

Without exception, the peak germination rate varied widely for individual families from the same stand (*fig. 3*). In one area, variation in peak rate was greater for families from trees on ultramafic soil than for those from trees on fertile soil: Family means ranged from 9 to 32 percent per day in Plumas stand 4, against 15 to 28 in Plumas stand 3. As with other areas, however, most of the families differed only in rate of germination, and with few exceptions had from 95 to 100 percent germination at 14 days.

Germination rates of families were independent of seed weight, except that a number of small-seed Yuba families germinated with exceptional speed ($r^2 = -0.18$).

Growth by Stand and Family

Overall, top growth of seedlings on fertile soil exceeded the growth on ultramafic soil by 50 percent or more, although even the fertile soils were somewhat deficient in nitrogen.

For the El Dorado, Sierra, and Plumas areas, analyses of the growth of offspring from both stands on both native soils indicated no genetic differentiation between the parent stands (*table 4*). There was no difference in any growth trait between stand offspring, and there was no differential response of stand offspring to soil fertility (stand × soil interaction). Average top weights of seedlings from the two stands — whether compared on ultramafic or on fertile soil — never differed by more than 1 to 4 percent (*fig. 4*). For the Yuba area, seedlings from the ultramafic stand were significantly smaller on both soil types, apparently because of the smaller seeds from parents on the ultramafic soil (*table 2*).

Although offspring from paired stands generally showed equal growth, large and highly significant differences in seedling growth were found among families from different trees in every stand (*table 4*, families/stand). On fertile soil, for example, El Dorado family 48-4 had inherently better growth than 3, 13, 11, and 5, and families 6 and 12 were superior to 5 and 2 (*fig. 4*). Such inherent family differences in seedling growth were just as evident on ultramafic soil, in comparisons of families with equivalent seed weights. Top growth for individual families ranged from below 80 to more than 120 percent of the stand mean, whether the seedlings were grown on ultramafic or on fertile soil.

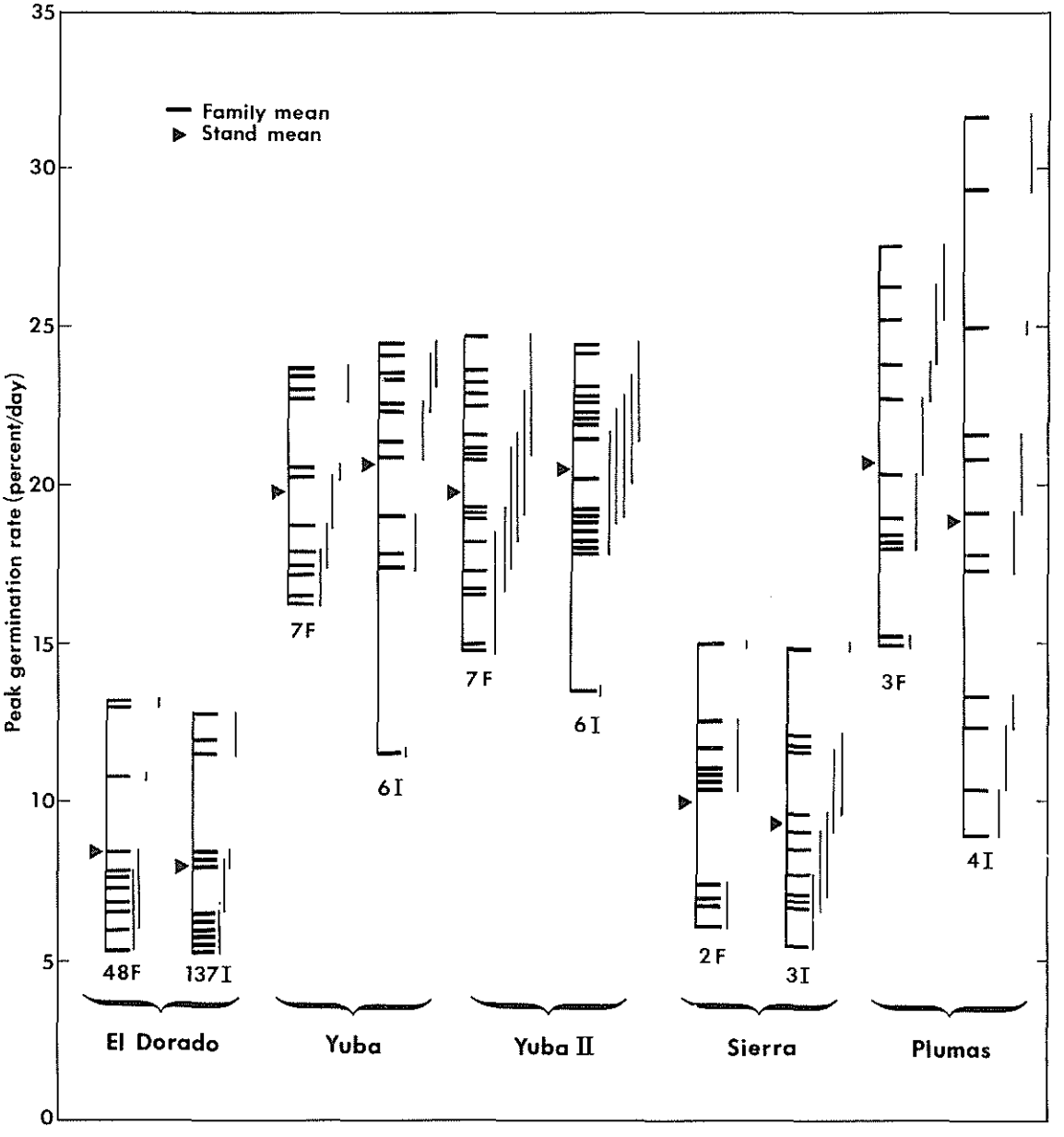


Figure 3 — Speed of germination for ponderosa pine differed between areas and among families from the same stand, but not between paired stands. Seeds tested were from trees in stands on fertile (F) and infertile (I) soils, and represent two crop years in the Yuba area. Family means not common to a bar differ significantly at the 5 percent level.

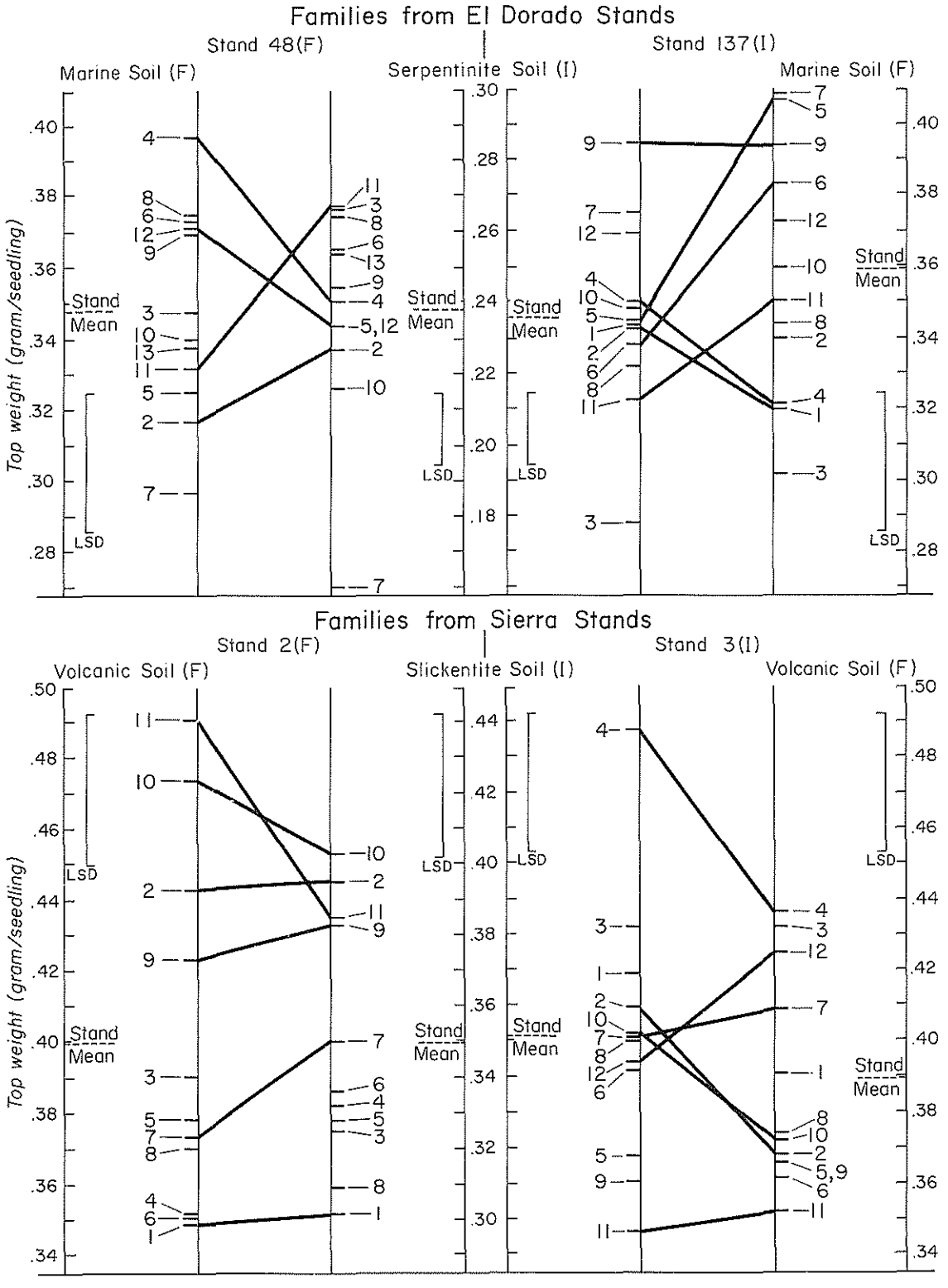
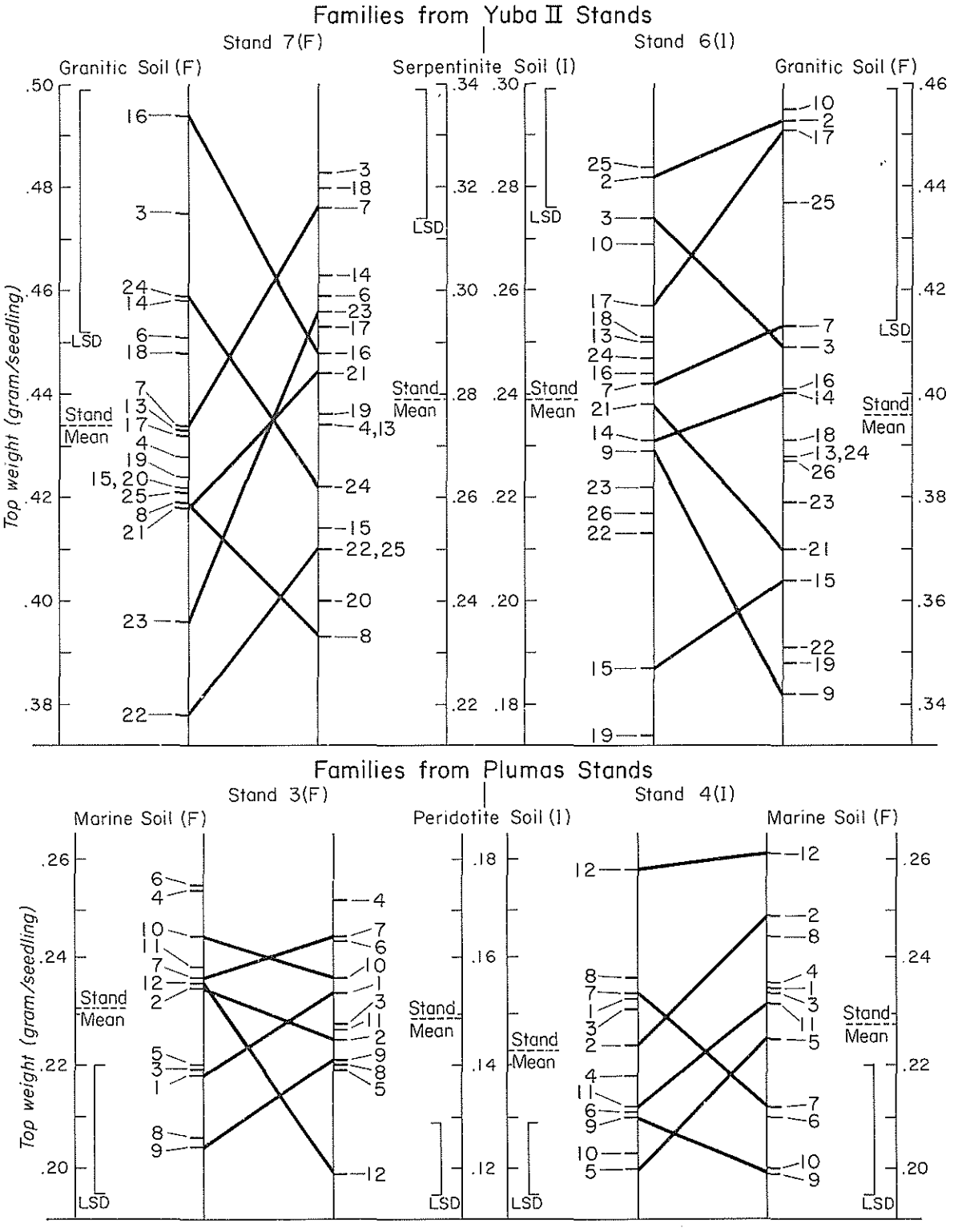


Figure 4—Seedling growth of ponderosa pine on fertile (F) and infertile (I) soils indicated little or no genetic differentiation between parent stands in any area, but varied widely among families of every stand and



demonstrated large family X soil interactions. On each soil, family means separated by the least significant difference (LSD) differ significantly at the 5 percent level. Diagonal lines identify groups of families that show inherent differential response to soil type.

Table 4 — *Significance of variation associated with stands, families, and soil interaction in seedling growth of ponderosa pine tested on fertile and infertile soils*[1]

Area and source of variation	Seedling growth trait			
	Height	Top weight	Top weight adjusted[2]	Root weight
El Dorado:				
Stands	ns	ns	ns	ns
Stand × soil	ns	ns	ns	ns
Families/stand	***	***	***	***
Families/stand × soil	***	*	**	ns
Yuba:				
Stands	ns	***	***	***
Stand × soil	ns	***	***	***
Families/stand	***	***	***	***
Families/stand × soil	ns	***	ns	***
Yuba II:				
Stands	***	***	***	***
Stand × soil	ns	ns	ns	ns
Families/stand	***	***	***	***
Families/stand × soil	ns	**	**	ns
Sierra:				
Stands	ns	ns	ns	ns
Stand × soil	ns	ns	ns	ns
Families/stand	***	***	***	***
Families/stand × soil	ns	ns	ns	ns
Plumas:				
Stands	ns	ns	ns	ns
Stand × soil	ns	ns	ns	ns
Families/stand	***	***	***	***
Families/stand × soil	***	*	**	ns

[1]Variation was significant at the 10 (*), 5 (**), and 1 (***) percent levels, or was not significant (ns).

[2]Effect of family seed weight was removed before analysis.

Many families displayed the same rankings on both soils (*fig. 4*). Thus, seedling growth was consistently good for some families — e.g., El Dorado 48-6 and 8, 137-7 and 9; Yuba II 7-3 and 14, 6-2 and 25; Sierra 2-2 and 10, 3-3 and 4; Plumas 3-4 and 6, 4-8 and 12 — and consistently poor for others — e.g., El Dorado 48-7 and 137-3; Yuba II 7-8 and 22, 6-15 and 19; Sierra 2-1 and 8, 3-9 and 11; Plumas 3-8 and 9, 4-9 and 10.

Strong family × soil interactions were indicated for seedling height, top weight, or both for families from the El Dorado, Yuba, and Plumas areas (*table 4*). In fact, at least one-fourth of the families from every stand — including the Sierra stands — showed significant changes in their relative growth performances on ultramafic and fertile soils (*fig. 4*). In El Dorado stand 137, for example, families 4, 5, 1, and 6 showed average top growth on serpentinite soil, but 5 and 6 were superior to 4 and 1 on marine soil. In Yuba II stand 7, family 16 outperformed 7, 20, and 21 on granitic soil, and 24 topped 23 and 22; but on serpentinite soil, 7 outperformed 16 and 21, which in turn surpassed 20, and 23 topped 24 and 22. These and other differential responses to soil were identified through relative growth performances that could not be explained by family differences in seed weight.

DISCUSSION

In the northern Sierra Nevada, wind-pollinated families of ponderosa pine vary widely in first-year seedling growth. The differences among progenies of randomly selected trees in natural stands are invariably great, regardless of the local soil and climate.

Family Variation and Artificial Regeneration

The patterns of variation have several implications for tree seed collection and reforestation programs. For every seed parent stand selected, we can expect that three-fourths of the families will show roughly the same relative rankings for seedling growth on fertile as on infertile soil. One-sixth of the families will produce superior seedlings on both soil types, and the others will produce mostly average or inferior seedlings.

One-fourth of the families from every selected stand will show marked differential responses to soil nutrient status. Family × soil interactions apparently characterize California ponderosa pine, and may prove to be typical of other widespread forest trees. Investigations of both conifers and hardwoods have found interactions between families, clones, or provenances, and soils of differing nutritional status (Brown 1970, Cunningham 1971, Curlin 1967, Giertych 1970, Goddard and others 1976, Jahromi and others 1976, Jenkinson 1974, Ohba and others 1965, Pritchett and Goddard 1967, Roberds and others 1976, Zobel and Roberds 1970).

Because similar distributions of family growth potentials may be expected from stands growing on completely different soils, the tree seed collection zones for reforestation (Buck and others 1970) need not be subdivided by soil type. The base level program for ensuring native genetic variability in planting stock (Kitzmiller 1976) — pooled seed collections from one or more trees in each of 20 widely distributed stands in a particular zone — should normally retain the distribution of seedling growth response, or adaptability, found within each zone sampled in my study (*fig. 1*).

The magnitudes of the genetic differences in family performance strongly suggest that parent trees can be selected for fast seedling growth on either a wide range of nutritionally different soils or a specific soil. Selected ponderosa pines might be profitably screened for both broad and specific edaphic adaptation by growing their offspring on typically diverse soil series within the native climatic environment, or the appropriate tree seed zone.

Optimizing the seedling culture regime greatly diminishes the effects of family seed weight on first-year growth, an outcome desired in any progeny test. Top growth of seedlings from individual families in the present study was related very weakly or not at all to seed weight when soil nutrients were in adequate supply, but there were appreciable effects on infertile soil. In forest tree nurseries and greenhouses where water and nutrients are properly supplied and the growing season is six months or longer, the influence of family seed weight on seedling top growth is always negligible (Brown and Goddard 1959, Hanover and Barnes 1963, Hanover and Reicosky 1972, Jenkinson 1975, Morgenstern 1969, Stonecypher and others 1966). In less favorable environments with short growing seasons or summer drought, seed effects may persist (Morgenstern 1969), even up to five years for ponderosa and Jeffrey pine grown and outplanted in the Plumas area (Fowells 1953).

Climatic Effects on Germination

The rapid germination of seeds from most trees in the Plumas stands (fig. 3) may reflect the presence of selective climatic forces. In this climatic and vegetational transition zone between the east and west slopes, the onset of the freeze-free period practically coincides with that of the summer drought (*fig. 2*). The brief time available for germination and radicle elongation should therefore favor rapid germinators and discriminate against slow ones. Here, as for ponderosa pine in the Southwest, late and slow germinators produce seedlings that almost certainly are more subject to high water stress and drought kill (Larson 1961, 1963), and to frost heaving (Heidmann 1976).

Although families from the stand on fertile soil were all fast germinators, 4 of 12 from the ultramafic stand 9 miles west were comparatively slow. Persistence of slower germinators in a stand so near the main Sierra crest suggests the influence of west-slope climate. A topographic conduit for such influence exists, as the ultramafic population rims the canyon of the Feather River Middle Fork, which cuts completely through the Sierra Nevada (*fig. 1*).

As native climate may explain the rapid germination of most Plumas families, it may also explain the comparatively slow germination of seeds from all four stands in the El Dorado and Sierra areas *(fig. 3)*. Germination and growth conditions are favorable for a much longer time on the west slope than in the Plumas area, because the overlaps of spring rain and freeze-free period are much greater *(fig. 2)*. In these milder environments, occasional hard freezes ranging from -3° to -12° C are likely in spring (U.S. Dep. Commer. 1964, 1970), and early or fast germinators may be subject to frost heave and freezing. A single exposure to night temperature below -6° C is lethal for 1-week-old seedlings of ponderosa pine from the east slope of the Cascade Range in southern Oregon (Cochran and Berntsen 1973), and presumably this cold exposure also kills west-slope seedlings.

More difficult to explain are the germination rates of seeds from the Yuba stands, which are just as rapid as those of the Plumas. Both Yuba stands are on uplands adjacent to the canyon carved by the North Yuba River *(fig. 1)*, and may be disposed to cold air flows. The river breaches the Sierra crest (7000 to 8500 ft) at elevations of 3900 to 4900 ft, draining the high country fronting the Sierra Valley, and snow in the Yuba stands often melts late in spring. Thus, continental-climate influence may reach the Yuba area, and drought may quickly follow onset of the freeze-free period. Although near the same canyon, the Sierra stands probably escape this influence, as they are 1800 ft above the river and on south slopes in another drainage.

Are There Edaphic Ecotypes?

The growth of ponderosa pine seedlings on ultramafic and fertile soils collected in the seed parent stands revealed no clear stand adaptation to soil fertility. In the Yuba test, seedlings from trees in the serpentinite stand were consistently smaller on both native soils than seedlings from the nearby stand on fertile soil. This result was also found in Digger pine, when offspring from trees on serpentinite soil grew poorest on that soil while offspring native to the closest nonserpentinite stand grew best (Griffin 1965). On both of these serpentinite collection sites, the understory varied from sparse to none. In such hostile circumstances, the lower nutrient and water demand of slow-growing seedlings may occasionally favor their survival.

In the El Dorado, Sierra, and Plumas tests, growth of offspring from ponderosa stands on ultramafic and fertile soils was the same on ultramafic soil, and also on fertile soil. There are two possible explanations for these results:

- Edaphic ecotypes do not exist in ponderosa pine because soil nutrient status is not an important selective factor, or because gene migration prevents ecotype formation.
- Edaphic ecotypes do exist, but they were not demonstrated because off-site pollen — in wind-pollinated offspring — masks adaptation of the seed parents, or because adaptation is not expressed in early seedling growth.

Studies in Scots pine (*P. sylvestris* L.) and Norway spruce (*Picea abies* [L.] Karst.) show that extensive gene flow through pollen dispersion is characteristic of widely distributed conifers (Koski 1970). Nonlocal pollen of those species in Finland accounts for more than 60 percent of the pollination in near-pure stands, a condition that may also hold for ponderosa pine. Soil type boundaries do not restrict pollen flight, and the distance from the center of any sampled ultramafic stand to stands on more fertile soil varies from less than 0.3 to 1 mile.

Adaptation to infertile and arid soils may be reflected not in first-year growth of seedlings, but in the relative ability of the seedlings to continue growth in subsequent growing seasons. Adaptation to ultramafic soils in particular requires an ability to function indefinitely while subjected to chronic nutrient deficiencies and long periods of high water stress. Differential survival and growth under severe edaphic stress may then become evident in later years. This interpretation explains the eventual better growth of seedlings from ultramafic compared to nonultramafic sources of lodgepole pine (*P. contorta* Dougl.) outplanted on ultramafic soil (Kruckeberg 1967). Growth on the planting site was the same for all sources for two growing seasons, but in the third season the seedlings from ultramafic sources continued fair growth while others did not. To look for a similar delay of adaptive expression in ponderosa pine, I have outplanted seedlings of all families from my El Dorado stands on the serpentinite and marine soils supporting the seed parents and will evaluate their growth when the plantations are older.

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