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PONDEROSA PINE PROGENIES: differential response to ultramafic and granitic soils

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CONTENTS

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SUMMARY

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Ponderosa pine *(Pinus ponderosa* Laws.*)* in Oregon and California typically grows on a wide variety of nutritionally contrasting soils ranging from highly fertile granitic to very infertile ultramafic types. Its presence on such diverse soils suggests edaphic adaptations in this widely distributed, commercially important forest tree.

Ultramafic soils are commonly deficient in calcium (Ca), nitrogen (N), phosphorus (P), potassium (K), and high in magnesium (Mg), but are also highly variable. Thus, ponderosa pines on these soils vary in growth and associated vegetation, yet contrast with those on adjacent, more fertile soils in their slower growth and different species associates.

This paper reports a study to explore inherent differences between trees in the capacities of their progenies to grow on granitic and ultramafic soils, and to determine whether differences are related to the nutritional conditions of soils supporting the seed parents.

Wind-pollinated progenies from selected ponderosa pines in northern California were grown on a granitic soil and on a range of soils derived from ultramafic rocks. Seed was collected from nine trees in six stands in the northern Sierra Nevada. Two trees were sampled on a granitic soil (Holland series); the other seven grew on soils (Henneke, Dubakella, Cornutt series are examples) that represent the full range of ultramafic parent materials. Survival, first-year growth, and nutrient uptake of selected progenies were compared in four greenhouse tests. The granitic test soil was chosen for its high fertility; the infertile ultramafic test soils were chosen for their range of parent rocks and chemical differences.

The progenies showed inherent differences in growth, nutrient uptake, and mycorrhizae formation, depending on the test soil. Growth differences between granitic and ultramafic progenies, and between ultramafic progenies, were mainly related to differences in Ca uptake. Progenies with the better growth consistently had higher Ca concentrations in the seedling roots, tops, or both. Large growth differences between progenies on some ultramafic soils, and smaller or no differences on other ultramafics and the granitic soil, were explained by progeny differences in the capacity to take up Ca and by differences in Ca availability among soils. Growth differences were greatest at moderate-to-low levels of Ca availability, and least at very low and high levels. Growth differences between progenies were not closely related to differences in mycorrhizae formation.

On the granitic and more common ultramafic soils, top growth was associated with shoot Ca concentration in the granitic progenies, and with Ca and N in ultramafic progenies. Root growth was related to root P (and possibly N) concentration in granitic progenies, but to N and K in the ultramafic progenies.

On a localized, extremely infertile ultramafic soil, all seedlings from granitic progenies died in less than 3 months, while about 20 percent of those from two ultramafic progenies were alive at 6 months.

When a severe water stress was imposed and rates of seedling mortality were noted, no difference in drought tolerance was found between progenies on either granitic or ultramafic soils.

The inherent variation in first-year growth and survival of these ponderosa pine progenies shows that some of the parent trees chosen for this study are better adapted than others to the nutritional conditions found in ultramafic soils. Although the possibility of hybridization or introgression with Jeffrey pine – which grows extensively on ultramafic soils – existed for several of the ultramafic progenies, the more likely explanation of the adaptive capacity observed is simply variability within ponderosa pine.

The inherent variation in growth and nutrient uptake of the progenies on ultramafic soils implies that similar variation may exist in adaptedness to other forest soils. Growth differences between the progenies were large enough to suggest selection for specific soil types by progeny-testing seed parents.

One of the most widely distributed trees in western North America, ponderosa pine *(Pinus ponderosa* Laws.*)* shows geographic and elevational variation that reflects climatic adaptations.[1] Its presence on a wide range of nutritionally contrasting soils – especially in Oregon and California - suggests there may also be edaphic adaptations in this forest tree.

Among the most infertile forest soils are those derived from ultramafic rocks. Such rocks consist mainly of ferromagnesian minerals, and soils formed on them are usually deficient in nitrogen, phosphorus, potassium, and calcium and high in magnesium (Krause 1958, Kruckeberg 1969, Walker 1954). Ponderosa pine occurs sparingly on these soils in a wide variety of climates in the Wenatchee Mountains of central Washington (Kruckeberg 1969), in the Strawberry Range of east-central Oregon, and in the North Coast Ranges, Klamath Mountains, and from below 2,000 to nearly 6,000 feet in the northern Sierra Nevada of California.

Ponderosa pine is known on soils formed on peridotites, serpentinites, slickentite – a highly-sheared serpentinite (Walker and Griggs 1953) – and other ultramafic rocks showing various degrees of alteration from peridotite to altered serpentinite. Because of such diversity in soil parent material, the stands vary greatly in tree growth, spacing, and associated species. Most of them are in sharp contrast with stands on adjacent fertile soils by their remarkably different vegetation, slower growth, and generally more open character.

Surprisingly few studies have dealt with edaphic adaptations in woody plants: Habeck (1958) compared the growth of white cedar *(Thuja occidentalis* L.*)* seedlings from upland (drained) and lowland (swampy) stands on both well-drained and poorly-drained soils; roots of upland seedlings were twice as long in well-drained, but only half as long in poorly-drained soil as roots of lowland seedlings. Griffin (1965) found no obvious differential response in first-year growth of seedlings from 17 Digger pine *(P. sabiniana* Dougl.*)* stands, including five on ultramafic soils, when the seedlings were grown on both an extremely infertile serpentinite (slickentite) and a fertile granitic soil. Kruckeberg (1967) outplanted lodgepole pine *(P. contorta* Dougl.*)* seedlings from three ultramafic and two non-ultramafic sources on an ultramafic soil, and found the ultramafic sources eventually showed much better top growth. Such apparently nutritional adaptations are common among the many investigated herbaceous species with ultramafic and non-ultramafic populations; plants from the former frequently show the better growth on ultramafic soil (Kruckeberg 1951, 1954, 1967).

This paper reports a study of wind-pollinated progenies from ponderosa pine trees growing on granitic and ultramafic soils in the northern Sierra Nevada of California. The study considered two questions: Are there inherent differences between trees in the capacities of their progenies to grow on ultramafic and granitic soils? If differences exist, are they related to the nutritional conditions of soils supporting the seed parents?

METHODS AND MATERIALS

The performances of the progenies were compared in four greenhouse tests:

Test A: Survival and growth of granite and slickentite progenies were compared on granitic and peridotite soils, both with and without water stress.

Test B: Survival of granite, serpentinite, and slickentite progenies were compared on granitic and slickentite soils, while growth and nutrient uptake of the same progenies were compared on granitic and serpentinite-peridotite soils.

Test C: Growth and nutrient uptake of granite and serpentinite progenies were compared on soil supporting the serpentinite parents and on granitic soil.

Test D: Growth and nutrient uptake of peridotite and serpentinite-peridotite progenies were compared on soil supporting the serpentinite-peridotite parent, and on granitic and peridotite soils.

Cones were collected from nine trees in six stands *(table 1);* the seeds were extracted in sunlight, cleaned, and stored at 1° C. The ultramafic test soils represented the full range in parent materials *(table 1).* To obtain additional chemical differences, soil was taken from both the A and B horizons *(table 2).* The granitic test soil was known to be fertile. Each soil

[1]See Callaham 1962; Callaham and Liddicoet 1961; Conkle 1973; Mirov, Duffield, and Liddicoet 1952; Squillace and Silen 1962; Weidman 1939; Wells 1964 a,b.

Table 1–*Origins of wind-pollinated ponderosa pine progenies and of ultramafic and granitic soils employed in the tests*

Item	Locality and California county	Elevation	Soil series
		Ft.; and m.	
Progeny:			
Granite[1]	Sand Mountain, El Dorado	4,300; 1,311	Holland
Slickentite a, b[2]	Brush Creek, Sierra	4,600; 1,402	(a lithosol)
Serpentinite	Ramshorn Creek, Sierra	2,800; 853	Henneke-like
Serpentinite a, b[2]	Johntown Creek, El Dorado	1,920; 585	Henneke
Peridotite	Rocky Point, Plumas	5,040; 1,536	Cornutt
Serpentinite-peridotite	Meadow Valley Creek, Plumas	3,750; 1,143	Weitchpec- or Dubakella-like
Soil:			
Granitic (quartz monzonite)	Ben Lomond Mountain, Santa Cruz	2,500; 762	Sheridan
Peridotite A, B[3]	Little Red Mountain, Mendocino	2,700; 823	Cornutt
Serpentinite A, B[3]	Johntown Creek, El Dorado	1,920; 585	Henneke
Serpentinite-peridotite A, B[3]	Meadow Valley Creek, Plumas	3,700; 1,128	Weitchpec- or Dubakella-like
Slickentite	Clear Creek, San Benito	3,200; 975	(a lithosol)

[1]Pooled collection from two trees.
[2]Two single-tree collections.
[3]Two horizons sampled.

was sifted with a 5-mm. screen, blended, and transferred to containers 28 cm. diameter by 30 cm. deep. To insure that germination vigor did not confound the growth comparisons, only seeds with similar germination speeds were planted. For test A, 10 or 12 germinants per progeny were sown in each container; for each of the other tests, seven or eight were sown. The tests were replicated two (A, D), three (B), or four (C) times.

Seeds were stratified 10 weeks at 5° C. and germinated at 23° C. During seedling establishment, the soils were surface-watered as needed and damping-off fungi were controlled with Captan fungicide. Thereafter soils were surface- and deep-watered weekly. Deionized water was used throughout to avoid the addition of essential elements. To eliminate greenhouse position effects, I randomized all containers and rotated them frequently.

Test A extended from early May to mid-December; B, C, and D extended from early May to late October in the following year. After growth ceased, the seedlings were lifted by washing out the roots and

Table 2–*Chemical analyses of ultramafic and granitic soils employed in greenhouse tests of ponderosa pine progenies*

Test soil	Profile sample depth	pH	Total		Replaceable			Cation exchange capacity	Ca++ saturation
			N	P	K^+	Ca^{++}	Mg^{++}		
	Cm.		*Percent*		*Meq./100g.*			*Meq./100g.*	*Pct.*
Granitic	0-60	4.8	0.138	0.130	0.80	1.56	0.72	3.45	45.2
Peridotite A	0-30	6.3	.056	.081	.11	1.28	.59	2.63	48.6
Peridotite B	60-90	6.6	.002	.024	.03	.12	.45	1.50	8.0
Serpentinite A	0-15	6.3	.073	.016	.08	3.64	12.7	17.3	21.0
Serpentinite B	20-45	6.4	.046	.011	.06	1.92	20.2	21.0	9.1
Serpentinite-peridotite A	0-20	6.2	.063	.044	.15	1.70	23.1	24.2	7.0
Serpentinite-peridotite B	40-60	6.4	.015	.025	.13	1.12	44.7	43.7	2.6
Slickentite	0-15	8.8	.001	.000	.02	.22	42.0	6.83	3.2

rinsed in de-ionized water. In test A, the lengths of the tap root and each lateral root longer than 0.5 cm. were measured for each seedling. To estimate mycorrhizae, I recorded the number of coralloid structures – short roots with multiple dichotomies covered with fungal mycelium (Slankis 1958). To evaluate total growth, the shoot and roots were separated 1 mm. below the cotyledon node and weighed after oven-drying 48 hours at 70° C.

To evaluate nutrient uptake, the shoots and roots were separately combined by progeny and container, milled to pass a 40-mesh screen, and analyzed for nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) in duplicate 100-mg. samples. Nitrogen was determined by a micro-Kjeldahl method (Jackson 1958). P, K, Ca, and Mg were determined on samples wet-ashed in nitric-perchloric acid (Johnson and Ulrich 1959): P was determined by a molybdenum blue colorimetric method, K by flame emission, and Ca and Mg by atomic absorption. Growth and element concentration data were analyzed by variance and multiple regression analyses, and means were compared by t-tests (Steel and Torrie 1960).

To evaluate the test soils, replaceable K^{+}, Ca^{++}, and Mg^{++}, total N and P, cation exchange capacity, and pH were determined on duplicate samples passed through a 2-mm. screen *(table 2)*. Nitrogen was determined by a micro-Kjeldahl method, and P by nitric-perchloric acid digestion and a modified molybdenum blue method (Jackson 1958). The cations were extracted with neutral 1N ammonium acetate and determined as noted above. The cation exchange capacity was estimated by Ca^{++} saturation of the exchange complex (Rich 1961, 1962) and pH was determined on a saturation paste.

Table 3–*Growth of 35-day-old granite (G) and slickentite progenies (Sk) on granitic and peridotite soils (test A)*[1]

Soil and progeny	Shoot weight	Root weight	Lateral root length
	Gram		Cm.
Granitic:			
G	0.034	0.050	61
Sk a	.039	.048	53
Peridotite A:			
G	.028 b	.048 b	61 b
Sk a, b	.035a	.063a	91a
Peridotite B:			
G	.021 b	.042 b	64 b
Sk a, b	.028 a	.050 a	91 a

[1]Means followed by unlike letters differ significantly at the 5 percent level.

RESULTS

Survival, Growth, Nutrient Uptake

Test A: At 35 days after sowing, the slickentite progenies showed better growth than granite progenies on the peridotite soils, but not on granitic soil *(table 3)*. On peridotite, the slickentite progenies had 25 to 33 percent greater shoot weight, 19 to 31 percent greater root weight, and 42 to 50 percent longer roots. All tap roots were down 28 to 30 cm., and no mycorrhizae were evident at this stage.

Many ultramafic soil sites are thinly vegetated, and unusually hot and dry during the summer. In such circumstances, seedling establishment probably requires adaptation to extended periods of high water stress as well as to nutritional deficiency. To check this possibility, I discontinued watering half of the seedlings when they were 2 months old.

No difference in drought tolerance between progenies was found. After 8 weeks of water stress, all seedlings on granitic soil (a loamy sand) were dead *(table 4),* and rates of mortality were similar. After 15 weeks of stress – when watering was resumed – all seedlings on the peridotite soils (sandy clay loam, clay loam) still appeared healthy, though subsequent losses on peridotite-B soil were probably related to the stress period.

At 7 months, slickentite progenies continued to show better growth than the granite progenies on both peridotite soils *(table 4)*. Growth differences were large on peridotite-A, relatively small on the very infertile peridotite-B, and – except for shoot weight – not significant on the fertile granitic soil. On peridotite-A soil with no water stress, slickentite progenies averaged 60 percent more shoot weight, 55 percent more root weight, 53 percent more root elongation, and 81 percent more mycorrhizae. Severe water stress reduced the differences, but the slickentite progenies still showed 29 percent more shoot

Table 4–*Survival and growth of granite (G) and slickentite progenies (Sk) on granitic and peridotite soils under two watering regimes (test A)*[1]

Soil and progeny	Survival	Shoot weight	Root weight	Lateral root length	Coralloid structures
	Pct.	Grams		Cm.	
Water adequate					
Granitic:					
G	100	0.74 b	0.93	545	0.4
Sk a, b	100	.92 a	1.07	546	1.2
Peridotite A:					
G	100	.30 b	.38 b	204 b	16 b
Ska,b	100	.48 a	.59 a	312 a	29 a
Peridotite B:					
G	100	.19 b	.33 b	256 b	14
Sk a. b	100	.22 a	.40 a	303 a	16
Water limiting					
Granitic:					
G	0	–	–	–	–
Ska,b	0	_	_	–	_
PeridotiteA:					
G	100	.14 b	.20 b	152 b	1.5
Ska,b	100	.18 a	.28 a	201 a	3.0
PeridotiteB:					
G	80	.092	.17 b	183	.7
Ska,b	85	.11	.21 a	207	2.4

[1]Means followed by unlike letters differ significantly at the 5 percent level.

weight, 40 percent more root weight, and 32 percent more root elongation. On peridotite-B soil the watering regime exerted little, if any, influence on progeny differences. With or without water stress, slickentite progenies had higher shoot and root weights and greater root elongation than the granite progenies.

While root elongation was the same for progenies on granitic soil, it was consistently greater for the slickentite progenies on peridotite soil, suggesting an adaptation for improving nutrient uptake from nutrient-deficient soil. Regression coefficients for root length on weight in peridotite soil were 0.94 with 35-day-old seedlings and 0.78 with 7-month-old seedlings. Since root elongation could be estimated by root weight, length measurements were discontinued.

Test B: During this test, water was never limiting, and no seedlings died on either the granitic or serpentinite-peridotite soils. On slickentite soil, however, all of the granite seedlings died within 3 months and roughly 20 percent of the ultramafic seedlings survived 6 months *(fig. 1).* Eight days after planting, all seedlings were in the expanded-cotyledon stage and appeared healthy, but their subsequent epicotyl growth was severely stunted. Ten weeks later, when the last granite seedling was dead, 37 percent of the slickentite and 27 percent of the serpentinite seedlings were still living.

On the granitic and serpentinite-peridotite (SP) soils, both ultramafic progenies showed better root growth than the granite progenies, averaging 16 percent more growth in granitic and SP-B, and 21 percent more in SP-A soil *(table 5).* The slickentite progeny consistently had the highest shoot Ca concentrations, arid on SP-A soil both ultramafic progenies had higher root Ca concentrations.

Test C: On granitic soil, the granite progenies averaged slightly more growth than the serpentinite-b progeny, while the serpentinite-a progeny showed about 15 percent more shoot and root growth and 50 percent higher shoot Ca concentrations than the granite progenies (*table* 6). The granite progenies had higher P and K concentrations in the shoots, and higher P in the roots.

Both serpentinite progenies clearly showed a greater capacity to grow on the serpentinite soils than did the granite progenies. On A-horizon soil, the serpentinite progenies had 27 and 37 percent more shoot growth, 36 and 58 percent more root growth, and

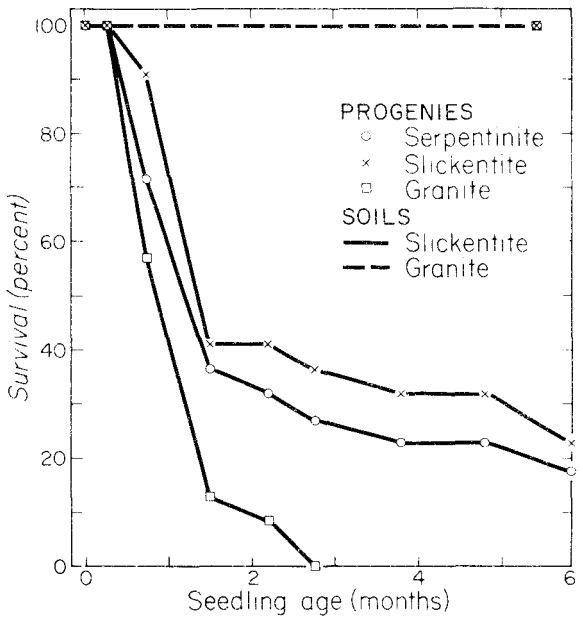

Figure 1–Survival of ponderosa pine on granitic and slickentite soils (test B).

Table 5–*Growth and element uptake Of granite (G), serpentinite (S), and slickentite progenies (Sk) on granitic and serpentinite-peridotite soils (test B).1*

Soil and progeny	Shoot						Root						Coral-loid struc-tures
	Weight	N	P	K	Ca	Mg	Weight	N	P	K	Ca	Mg	
	Gram	*Mmole/g.*	*µmole/g.*	——	*Meq./g.*	——	*Gram*	*Mmole/g.*	*µmole/g.*	——	*Meq./g.*	——	
Granitic:													
G	0.36	1.34	50	0.35	0.18 b	0.11	0.50 b	0.63	32	0.22	0.18	0.18	3.7
S	.41	1.48	45	.29	.18 0	.13	.57 a	.67	27	.22	.20	.20	7.3
Sk b	.41	1.50	47	.32	.25 a	.16	.59 a	.67	29	.23	.19	.21	7.0
Serpentinite-peridotite A:													
G	.22	1.50	42	.20	.061 ab	.42	.33 b	.57	24	.13	.09 b	.39	28
S	.24	1.50	39	.20	.052 b	.42	.38 a	.58	22	.12	.16 a	.36	28
Sk b	.25	1.57	37	.18	.066 a	.44	.42 a	.57	19	.11	.17 a	.39	27
Serpentinite-peridotite B:													
G	.16	.98	36	.15	.046 0	.35	.28 b	.47	19	.099	.13	.30	19
S	.16	.93	35	.14	.052 ab	.37	.32 a	.44	20	.084	.13	.31	26
Sk b	.18	.98	36	.17	.061 a	.38	.33 a	.44	19	.086	.14	.30	27

[1] Means followed by unlike letters differ significantly at the 5 percent level.

Table 6–*Growth and element uptake of granite (G) and serpentinite progenies (S) on granitic and serpentinite soils (test C)*[1]

Soil and progeny	Shoot						Root						Coral-loid struc-tures
	Weight	N	P	K	Ca	Mg	Weight	N	P	K	Ca	Mg	
	Gram	*Mmole/g.*	*µmole/g.*	——	*Meq./g.*	——	*Gram*	*Mmole/g.*	*µmole/g.*	——	*Meq./g.*	——	
Granitic:													
G	0.44 ab	1.49 ab	46 a	0.32 a	0.20 b	0.14	0.59 ab	0.76	35 a	0.31	0.23	0.14	1.2
S a	.51 a	1.61 a	39 b	.27 b	.30 a	.17	.68 a	.82	27 b	.32	.24	.14	2.3
S b	.42 b	1.42 b	38 b	.26 b	.22 b	.16	.55 b	.78	28 b	.26	.23	.15	9.2
Serpentinite A:													
G	.32 b	1.55	37	.18	.072 b	.35	.36 b	.64	22	.15	.25	1.02 b	26 b
S a	.43 a	1.58	38	.18	.093 a	.41	.57 a	.63	22	.15	.22	.98 b	28 b
S b	.40 a	1.47	35	.17	.088 a	.39	.49 a	.65	19	.14	.23	1.46 a	43 a
Serpentinite B:													
G	.26 b	1.38	32	.18	.064	.34	.33 b	.59	22	.12	.27	1.30 b	37 b
S a	.37 a	1.31	30	.15	.066	.39	.50 a	.56	20	.12	.27	1.31	62 a
S b	.75 a	1.36	35	.16	.060	.37	.48 a	.55	20	.12	.30	2.54 a	63 a

[1]Means followed by unlike letters differ significantly at the 5 percent level.

about 25 percent higher shoot Ca concentrations. The serpentinite-b progeny also had about 46 percent high root Mg concentrations and roughly 60 percent more mycorrhizae than the serpentinite-a and granite progenies. On B-horizon soil the serpentinite progenies had 36 and 45 percent more shoot growth, 43 and 51 percent more root growth, and about 70 percent more mycorrhizae. The serpentinite-b progeny again had much higher root Mg concentrations than the others (95 percent more than the granite progenies), and evidently was an inherent magnesium accumulator.

Test D: The two ultramafic progenies used in this test displayed equal shoot growth on granitic soil *(table 7)*. However, the serpentinite-peridotite (SP) progeny had 32 percent more root growth, and about 30 percent higher shoot Ca and K concentrations than the peridotite progeny. On the peridotite soils, growth differences were not significant, although the SP progeny had slightly better growth and 30 percent higher shoot Ca concentrations on peridotite-A soil.

On SP-A soil, the SP progeny showed 45 percent more shoot growth, 49 percent more root growth, and 43 percent higher shoot Ca concentrations, while the peridotite progency had higher root P and Mg concentrations. On SP-B, the SP progeny showed 22 percent more root growth and 85 percent higher shoot Ca concentrations, while the peridotite progeny had higher root P concentrations and 62 percent more mycorrhizae.

Nutrients Limiting Growth

Interpretation of the relationship between plant growth and element concentrations in plant tissues normally depends on a knowledge of the critical concentration curves developed for the species. A typical curve has a near-vertical arm (element deficient) and a near-horizontal arm (element adequate). The smooth transition between the arms includes the critical concentration, a value associated with growth 5 to 10 percent below maximum (Ulrich 1961).

In the present study, scatter diagrams relating growth to element concentration showed relationships comparable to those in critical concentration curves *(fig. 2)*. Ca showed a typical curve for the shoots, and K for the shoots and roots. N and P showed only the vertical arm of the curve for the roots. Established forms of such curves were used to describe the relationships between seedling growth and element concentrations, and to identify those elements which probably limited growth of the granite and ultramafic progenies.

Table 7–*Growth and element uptake of peridotite (P) and serpentinite-peridotite progenies (SP) on granitic, peridotite, and serpentinite-peridotite soils (test D)*[1]

Soil and progeny	Shoot						Root						Coralloid structures
	Weight	N	P	K	Ca	Mg	Weight	N	P	K	Ca	Mg	
	Gram	*Mmole/g.*	*µmole/g.*	—— *Meq./g.* ——			*Gram*	*Mmole/g.*	*µmole/g.*	—— *Meq./g.* ——			
Granitic:													
P	0.37	1.78	44	0.27 b	0.23 b	0.15	0.53 b	0.82	34	0.28	0.24	0.21	8.7
SP	.38	1.94	50	.36 a	.30 a	.16	.70 a	.81	28	.30	.21	.19	1.6
Peridotite A:													
P	.20	1.85	40	.19	.10 b	.12	.41	.71	29	.14	.16	.12	23
SP	.23	1.98	50	.19	.13 a	.11	.47	.74	26	.12	.16	.10	15
Peridotite B:													
P	.14	1.38	39	.13	.071	.18	.40	.53	20	.076	.10	.10	15
SP	.15	1.53	48	.15	.077	.19	.45	.55	20	.071	.11	.10	15
Serpentinite-peridotite A:													
P	.20 b	1.56	51	.20	.051 b	.38	.35 b	.59	30 a	.15	.25	.38 a	59
SP	.29 a	1.60	44	.21	.073 a	.41	.52 a	.61	22 b	.14	.19	.30 b	54
Serpentinite-peridotite B:													
P	.16	1.09	32	.14	.034 b	.32	.31 b	.48	23 a	.11	.17	.23	39 a
SP	.17	1.17	36	.16	.063 a	.38	.38 a	.46	17 b	.10	.14	.22	24 b

[1]Means followed by unlike letters differ significantly at the 5 percent level.

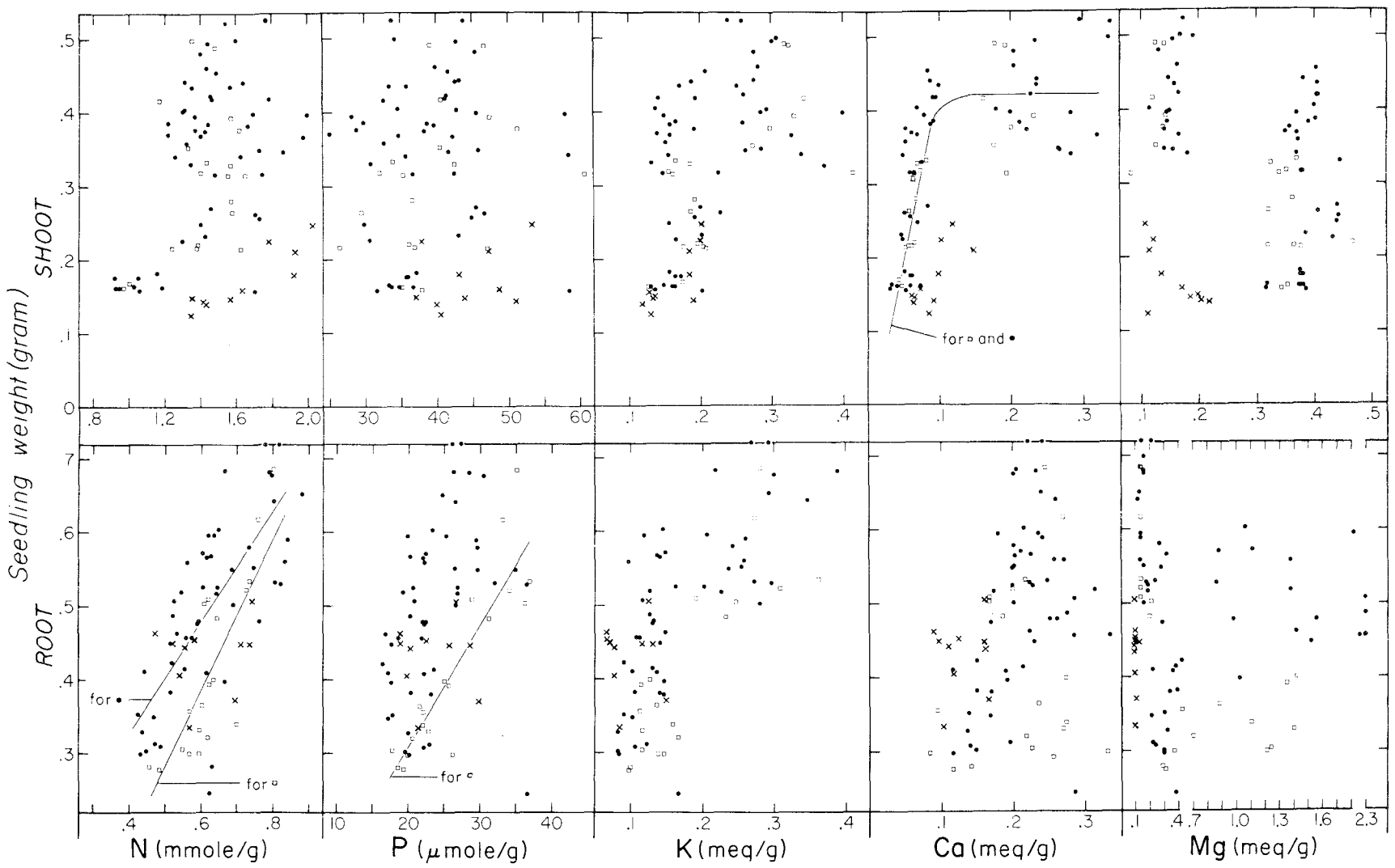

Figure 2–Growth and nutrient concentrations of ponderosa pine. ❑ shows granite and • ultramafic progenies tested on granitic, serpentinite, and serpentinite-peridotite soils. X shows progenies grown on peridotite soils.

Curves were fitted to the shoot and root weights and corresponding N, P, K, Ca, and Mg concentrations by using stepwise multiple regression analysis. For seedlings on granitic, serpentinite, and serpentinite-peridotite soils, there were 50 observation sets for six ultramafic and 19 for two granite progenies. Each set included the mean shoot or root weight and the corresponding element concentrations for a given progeny and container. On peridotite soils 10 sets of data for two ultramafic progenies were analyzed separately because their patterns generally differed from those obtained on other soils *(fig. 2)*. Log transformations – $\log_e Y = a + b(\log_e X)$ and $\log_e Y = a + b(\log_e X) + c(\log_e X)^2$ – showed the best fit of the data, i.e., consistently higher coefficients of multiple determination (R^2), and were used throughout.

Simple regressions showed growth to be either positively or not correlated with N, P, K, and Ca concentrations. With Mg they showed growth to be mainly negatively correlated, although many of the larger ultramafic shoots and roots had very high Mg concentrations *(fig. 2)*. Because its inclusion did not alter the outcome, Mg was dropped from the multiple regressions.

For the granite and ultramafic progenies tested on granitic, serpentinite, and serpentinite-peridotite soils, multiple regression showed that shoot growth was significantly positively correlated with N and Ca, but not P and K *(table 8)*. Comparison of standard partial regression coefficients showed that Ca was only 1.4 times more important than N for explaining variation in shoot growth of ultramafic progenies, but 3.7 times more important for granite progenies. Moreover, inclusion of the quadratic for Ca (to obtain a better fit for shoot weight and Ca concentration data) dropped N from significance in the granite progenies, and the R^2 with N, P, K, and Ca in the regression was no greater than that with Ca alone *(table 8)*. Calcium seemingly was more limiting for shoot growth of granite than ultramafic progenies. Since the calcium deficiency was less severe in ultramafic progenies, the element in next shortest supply, N, was also limiting their shoot growth.

Using this same approach, I found different relationships for the roots. For the granite progenies, root growth was significantly positively correlated with P alone when N, P, K, and Ca were included in the regression. When just N and P were included, R^2 was slightly higher and root growth was correlated with both N and P. Comparison of the standard partial regression coefficients indicated P was twice as important as N for explaining the variation in growth. For the ultramafic progenies, root growth was significantly positively correlated with N and K, but not P. Comparison of the standard partial regression coefficients suggested N and K were equally important for explaining the variation in growth.

For ultramafic progenies on peridotite soils, the only significant standard partial regression coefficient was obtained for shoot N concentration. Since these N concentrations were not especially low, no element could really be singled out as limiting. It may be significant, however, that in all tests the lowest shoot and root K and Mg concentrations were found in seedlings on peridotite soils *(fig. 2)*.

Table 8–*Coefficients of multiple determination (R^2) for growth and nutrient concentrations in ponderosa pine progenies tested on granitic, serpentinite, and serpentinite-peridotite soil*[1]

Progeny and dependent variable (wt., g.)	Independent variables (conc.)	R^2
Granite:		
Shoot	N*, P, K, Ca**	0.78
	N, P, K, Ca, Ca^2	.81
	Ca, Ca^2	.82
Root	N, P**, K, Ca	.84
	N*, P**	.86
Ultramafic:		
Shoot	N**, P, K, Ca**	.63
	N**, P, K, Ca, Ca^2	.69
	Ca, Ca^2	.55
Root	N*, P, K*, Ca	.62

[1]All values of R^2 were significant at the 1 percent level. Asterisks designate significant positive correlations at the 5 (*) and 1 (**) percent levels.

DISCUSSION AND CONCLUSIONS

Ponderosa pine trees clearly differ in the inherent capacities of their wind-pollinated progenies to grow on ultramafic soils. Their progenies also differ in amount of mycorrhizae formation, but this variation does not explain the growth differences between progenies: In test A, slickentite and granite progenies differed significantly in mycorrhizae formation on only one peridotite soil, and then only when water

was not limiting. But on both peridotite soils the progenies differed in growth whether or not water was limiting. All of the test B progenies had similar amounts of mycorrhizae on ultramafic soils, but the ultramafic progenies showed better root growth than the granite progenies on both serpentinite-peridotite soils. In test C, serpentinite and granite progenies different in mycorrhizae formation on only one serpentinite soil, even though the serpentinite progenies showed much greater growth on both serpentinite soils. And in test D, the serpentinite-peridotite progeny had greater root growth on both serpentinite-peridotite soils, but much less mycorrhizae formation on one of them than the peridotite progeny. On the fertile granitic soil, where mycorrhizae formation was always minimal, several progenies differed significantly in growth but not in mycorrhizae formation. Apparently, growth differences between progenies are not closely related to differences in mycorrhizae formation.

Growth differences between ultramafic and granitic progenies (tests B, C) and between ultramafic progenies (test D) were consistently associated only with differences in tissue Ca concentration: progenies with better growth had higher Ca concentrations in the roots, shoots, or both. The large differences between progenies in the capacity to grow on some ultramafic soils, and smaller or no differences on other ultramafic and granitic soils, can be explained by differences in capacity to take up Ca – especially from soil low in available calcium – and by differences in calcium availability among soils.

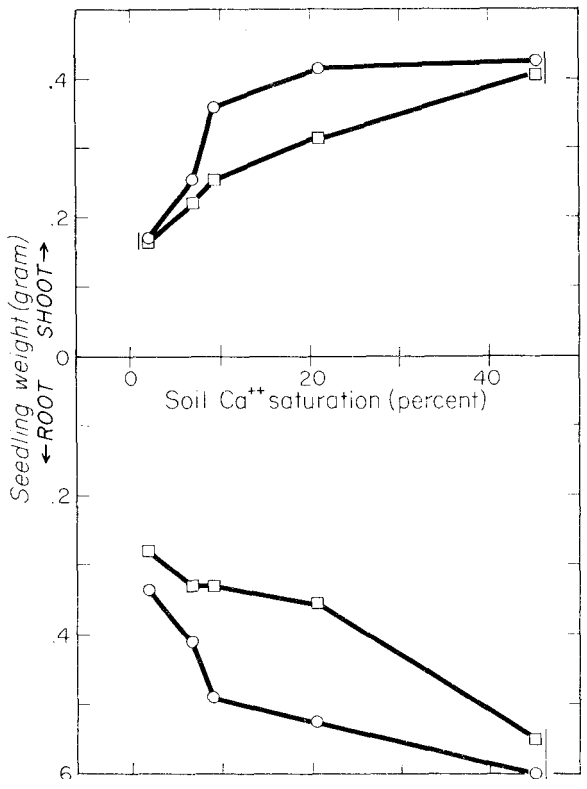

Figure 3–Influence of soil calcium availability on the growth of ponderosa pine. ❑ shows granite and ❍ ultramafic progenies. Means not common to a vertical bar differ significantly at the 5 percent level.

Seedling growth on granitic and the more common ultramafic soils (serpentinite and serpentinite-peridotite) was closely related to soil Ca^{++} saturation, an index to soil calcium availability *(fig. 3)*. All progenies showed about equally good growth when calcium availability was high, and poor growth when it was very low.

The consistently better growth of ultramafic progenies in the 5 to 25 percent Ca^{++}-saturation range suggests they were the more efficient calcium absorbers. And comparison of seedling Ca contents shows that ultramafic progenies did take up more Ca than did the granite progenies *(fig. 4)*. With increases in Ca^{++} saturation above 7 percent, shoot Ca content – roughly proportional to Ca^{++} saturation from 2.5 to 45 percent - increased at greater rates in ultramafic progenies. Root Ca content of ultramafic progenies increased sharply with increase in Ca^{++} saturation from 2.5 to 9 percent and was essentially unchanged thereafter; in granite progenies root Ca content increased sharply with increase in Ca^{++} saturation from. 7 to 9 percent, and continued to increase to the 45 percent level. With calcium availability between 2.5 and 25 percent, ultramafic progenies always showed more root growth (tests A-C) and higher root Ca contents than did the granite progenies.

On soil with very low Ca^{++} saturation *(fig. 3),* differences in both growth and calcium uptake between granite and ultramafic progenies were greatly diminished. The cause may have been the near-zero calcium availability for all progenies, a relatively greater deficiency of some other essential element, and/or incipient magnesium toxicity. Lack of appreciable growth differences on soil with 45 percent Ca^{++} saturation simply reflects a level of calcium availability sufficient for maximum growth of both granite and ultramafic progenies, and several of the latter undoubtedly absorbed Ca in luxury amounts.

Relationships between seedling shoot growth and Ca concentration are direct evidence that the granite and ultramafic progenies responded differentially to calcium availability. Variation in shoot Ca concentration explained 82 percent of the variation in shoot growth of granite progenies, but only 55 percent in

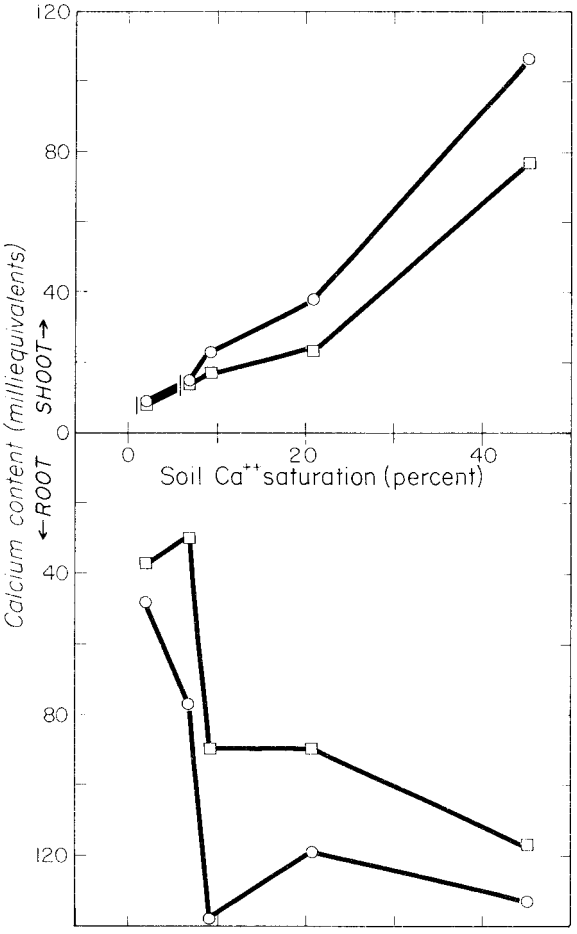

Figure 4—Influence of soil calcium availability on the calcium uptake of ponderosa pine. ❑ shows granite and ultramafic progenies. Means not common to a vertical bar differ significantly at the 5 percent level.

ultramafic progenies. Ultramafic progenies absorbed more Ca, and translocated more Ca to seedling tops. Because Ca generally was more limiting for shoot growth of the granite progenies, their growth was the more closely related to shoot Ca concentration.

Differences between the granite and ultramafic progenies with respect to their N relationships were probably related to the differential uptake of Ca. Some ultramafic progenies appear to have absorbed and translocated sufficient Ca to cause N — apparently the element in next shortest supply — to become limiting for shoot growth. Nitrogen probably did not effectively limit shoot growth of the granite progenies because Ca, the element in shortest supply, was always translocated in too-small amounts.

At least in part, differences between element concentrations in the shoots and roots reflected differences between tissues in their relative requirements for nutrients, and in relative mobilities of elements in the seedlings. Thus nitrogen, which is highly mobile in plants, was generally in much higher concentration in the shoots. In contrast, Ca, the least mobile element, was in roughly three times greater concentration in the roots, where it apparently even accumulated to excess. The low mobility of Ca helps to explain why Ca was deficient in shoots but not in roots. Conversely, the high mobilities of N, P, and K may partly account for their seeming deficiencies in roots.

The most extreme nutritional condition was found on slickentite, a more localized soil than serpentinite and serpentinite-peridotite. No granite and only 20 percent of the ultramafic progenies even survived on this soil. The survival of some ultramafic seedlings was probably related to their better root growth and greater capacity to take up Ca, and perhaps other elements, at extremely low soil calcium availability. The slickentite soil was nutritionally sterile. Its very low Ca^{++} saturation, alkaline pH, and Mg/Ca ratio (190) all indicate a severe calcium deficiency. Another striking feature of the slickentite soil was its seemingly absolute phosphorus deficiency, but it was not determined whether ultramafic seedlings survived because the seeds contained more P than those from granite parents. Finally, the very high amount of replaceable Mg^{++}, six times the capacity of the exchange complex, indicates magnesium toxicity (Proctor 1970) as the lethal agent. In this root environment, progenies with an inherently great capacity to take up Ca would be expected to show tolerance because Ca exerts a protective action against toxic effects of other cations (Bonds and O'Kelley 1969; LaHaye and Epstein 1969; Wyn Jones and Lunt 1967).

Soil calcium availability was evidently of primary importance for determining amounts of pine seedling growth on the more common ultramafic soils (serpentinite, serpentinite-peridotite) and possibly slickentite. Numerous investigations have already implicated low calcium availability as the general "serpentine factor" affecting growth of herbaceous plants (Krause 1958; Kruckeberg 1954; Martin, Vlamis, arid Stice 1953; Walker 1954; Walker, Walker, and Ashworth 1955; Vlamis 1949; Vlamis and Jenny 1948).

Peridotite soils differed from all of the other soils in seedling growth and nutrient uptake *(fig. 2).* Growth was much less throughout a wide range of Ca^{++} saturation than it was at similar saturations on

other soils *(table 2).* There are several possible explanations for this response. The very low amounts of Ca in the peridotite soils may restrict plant growth even though Ca^{++} saturation of the exchange complex is high (Jenny and Cowan 1933; Key, Kurtz, and Tucker 1962). Errors in determining cation exchange capacity, caused by clay fractions high in amorphous or poorly-crystalline sesquioxides (Rich 1962), could produce erroneously high Ca^{++} saturation percents. Also, as noted earlier, essential elements other than Ca – K and even Mg – may limit seedling growth on peridotite soils.

The first-year survival and growth differences of the ponderosa pine progenies show that some of the parent trees chosen for this study are much better adapted than others to the nutritional conditions found in ultramafic soils. Two explanations of this adaptive capacity are possible. The first is simply variability within this species. The second is Jeffrey pine *(P. jeffreyi* Grey. & Balf.*)*, which grows extensively on ultramafic soils and is known to hybridize with ponderosa pine (Haller 1962; Righter and Duffield 1951). Several of the ponderosa pine seed parents were growing within a few hundred feet of Jeffrey pine, so the possibility of hybridization or introgression exists. However, these species differ in flowering time (Duffield 1953), cross with difficulty (Critchfield 1966) and only occasionally hybridize in nature (Haller 1962). Since both the seed parents and the seedlings were typically ponderosa pine in morphology, the more likely explanation of adaptive capacity is variability within the species.

The inherent variation in growth and nutrient uptake of these progenies on ultramafic soil implies that similar variation may exist in adaptation to other forest soils. Growth differences were large enough to suggest that selection for specific soil types by progeny-testing seed parents may have merit. Field studies in progress should determine whether edaphic ecotypes exist in ponderosa pine.

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