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TERPENES OF PONDEROSA PINE AND FEEDING PREFERENCES BY POCKET GOPHERS

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Abstract—Yield and composition of essential oils were compared in foliage, stems, and roots of ponderosa pine seedlings, and preferences for the trees by pocket gophers were determined. Test seedlings represented nine widely separated provenances in the western United States. Seed source of the trees influenced gopher feeding preferences and resulted in varied tree damage. The damage ranged from 0 to 31%, suggesting that some sources might possess sufficient natural resistance to give trees practical protection from gophers in the field. There were no morphological differences among sources to explain differential tree damage. All sources contained essential oils in all tissues examined, but oil yield varied among and within tissue types. Oils were predominantly (76–97%) composed of monoterpene hydrocarbons. Oil composition varied by source, and different tissue types varied greatly in the yield and composition of their oils. Neither yield nor constituents of foliage oils were significantly correlated with gopher damage (or preference). In contrast, some components of stem and root oils were strongly related to preference. Results of correlation and discriminant analyses showed that some oil constituents could serve as indicators of resistance (or susceptibility) to gopher damage. Such important chemical variables, when verified, could be used in selections for ponderosa pine resistant to gophers.

Key Words—Terpenes, essential oils, gopher damage, gopher feeding preference, *Pinus ponderosa*, *Thomomys* spp.

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INTRODUCTION

Ponderosa pine (*Pinus ponderosa* Laws.) is the most important conifer in interior forests of the western United States. In some areas, however, attempts to regenerate the species have repeatedly failed because of pocket gophers (Geomyidae). Gophers damage and kill trees of ponderosa pine and other coniferous species, mostly by barking and root pruning (Moore, 1940; Dingle, 1956; Tevis, 1956; Hermann and Thomas, 1963; Crouch, 1969, 1971; Barnes et al., 1970).

Gophers may be controlled by poisoning (Crouch, 1933; Barnes et al., 1970), caging individual trees (Anthony et al., 1978), or application of herbicides which reduce the animals' food supply (Crouch, 1979). Potential control methods based on natural resistance of crop trees would be more environmentally or esthetically acceptable. Development of such methods requires determination of the gophers' preferences for the trees and the factors involved.

Natural resistance of herbivores occurs among and within plant species, and essential oils and their terpenoid components have been prominent among chemical factors postulated to influence the animals' feeding preferences (Radwan, 1974). For ponderosa pine, within-species variations in resistance have been observed with many animals other than gophers (Squillace and Silen, 1962; Read, 1971). Work with gophers, however, has been limited to one unpublished study. In laboratory tests, Cummins, (1975) found that gophers consumed significantly different amounts of ponderosa pine seedlings from various sources. The gophers also showed varied preferences for the different parts of seedlings as follows: stems > roots > needles > terminal buds.

The purpose of this study was to elaborate on the differential preferences of pocket gophers for ponderosa pine and to determine relationships between the pines' terpenes and observed preferences. We used progeny of nine widely separated provenances of ponderosa pine, tested preferences for the seedlings in gopher-proof enclosures, and determined yield and composition of essential oils isolated from different parts of the trees.

METHODS AND MATERIALS

Test Seedlings. Open-pollinated seeds were obtained from natural stands in nine national forests, covering most of the range of the species in the western United States. In January 1974, seeds, stratified at 3–5° C for 3 weeks, were sown at 3-mm depth in styroblock containers filled with 1:1:1 (by volume) mixture of peat moss, vermiculite, and Tumwater sandy loam soil. Containers were placed in a greenhouse where fluorescent light was available during a 12-hr photoperiod and temperatures were maintained at about 20° C. After germination was complete, seedlings were thinned to one per styroblock compartment. Seedlings were watered when necessary and supplied with a dilute solution of a complete fertilizer at biweekly intervals through May when they were placed outdoors. In September, seedlings were randomly selected from each source for use in the gopher preference tests at Moscow, Idaho, and chemical analysis in Olympia.

Preference Test. In November 1974, test trees were planted in each of three 0.1-hectare gopher-proof enclosures located on the University of Idaho farm at Moscow. Each source was represented by 20 trees in each enclosure and trees were planted at approximately 1.5- × 1.5-m spacing in a completely random design. Seedlings were allowed to get established in the enclosures for 10 months. In September 1975, locally trapped gophers (*Thomomys* spp.) were placed in the enclosures, and the test was run until the end of April 1976. During that time, the enclosures contained some natural forage, and the animals had free access to the trees. Inspection for gopher feeding on the seedlings and seedling mortality was made periodically. Relative preference was ranked according to the percent of trees clipped or gnawed by gophers.

Processing Plant Material. Ten seedlings of each of the nine sources were used for chemical analysis. In January 1975, seedlings of each source were randomly divided into two samples of five seedlings each. Terminal buds were removed and discarded; and the seedlings were then divided into roots, stems, and foliage by severing each tree at the root collar and just below the live needles. Roots were washed free of soil and blotted with absorbent paper to remove surface moisture. The cut seedlings were pooled by part and sample; individual parts were thoroughly mixed, weighed, and subsampled for moisture determination and distillation of essential oils.

Chemical Analysis. Isolation and analysis of the oils have been described in detail before (Radwan and Crouch, 1978). Briefly, essential oils were obtained by steam distillation and collection in *n*-heptane. Oil solutions were analyzed by gas–liquid chromatography (GLC) using flame ionization detection and open tubular columns. Compounds were identified by their retention times, infrared spectra, and peak enrichment. Compounds were quantified by electronic integrator. Average oil yields per gram of tissue and percent composition of the oils were calculated based on two samples and two injections per sample.

Statistical Analysis. Gopher damage for each source was calculated by averaging the percent damage from the three gopher enclosures. Chemical composition for each source was determined by averaging the values of the two samples for each source and tissue type.

Individual relationships between each of the chemical variables measured in the different parts of the seedlings and percent gopher damage by source were evaluated by calculating the appropriate correlation coefficients (r) (Snedecor, 1961). Results were considered significant at $P < 0.10$.

Multivariate relationships between the chemical and damage variables were examined using stepwise discriminant analysis (Dixon, 1977). For this analysis, the populations were divided into two groups based on percent damage by gophers—low damage, 0–12%, and high damage, 16–31%. Stepwise discriminant analysis was also used to determine the chemicals which distinguished between the three different parts of seedlings. In this analysis, we assumed that the observations of each of the three tissue types were independent, when in fact they were related. This assumption, however, seemed reasonable in an analysis used for screening of variables. The F values for including variables in both discriminant functions was $P \leqslant 0.01$.

RESULTS AND DISCUSSION

Gopher Preference. The gophers fed on seedlings of all sources except those from Utah (#9) (Table 1). Like other animals (Squillace and Silen, 1962; Read, 1971), gophers discriminated among the pine sources tested, with damage ranging from 0 to 31%. In general, the gophers favored seedlings of sources from Arizona (#6), Washington (#7), Montana (#11), and Nebraska (#17) over seedlings of other sources. The least and most preferred trees were those from Utah (#9) and Arizona (#6), respectively. There were no obvious morphological differences among sources to explain the differential damage or the apparent variations in gopher preference observed.

Variations between sources of ponderosa pine, therefore, influenced the gophers' feeding preference and resulted in much varied tree damage. The 31%

TABLE 1. POCKET GOPHER DAMAGE TO DIFFERENT SOURCES OF PONDEROSA PINE SEEDLINGS IN AN ENCLOSURE FIELD TEST AT MOSCOW, IDAHO

Source identification number	National forest	Location	Gopher damage (%)
6	Coconino	central Arizona	31
7	Colville	northeastern Washington	16
9	Dixie	southcentral Utah	0
10	El Dorado	central California	10
11	Helena	western Montana	21
17	Niobrara	central Nebraska	17
18	Rogue River	southwestern Oregon	12
19	Roosevelt	northcentral Colorado	7
21	Umatilla	northeastern Oregon	12

TABLE 2. YIELD AND GROSS COMPOSITION OF ESSENTIAL OILS OF PONDEROSA PINE

		Source identification number								
Item	Oil source[a]	6	7	9	10	11	17	18	19	21
Yield (area × 10^6)[b]										
Monoterpene	F	4.30	4.95	4.31	4.07	3.62	5.33	4.15	4.69	3.01
hydrocarbons	S	1.32	2.40	2.58	1.72	4.67	2.49	1.00	2.27	1.93
	R	4.15	3.24	2.37	2.32	4.70	3.90	1.77	1.73	2.99
Oxygenated	F	1.38	0.16	0.94	0.28	0.16	0.76	0.20	0.56	0.11
monoterpenes	S	0.21	0.16	0.19	0.19	0.30	0.50	0.13	0.54	0.20
	R	1.09	0.40	0.46	0.33	0.48	0.82	0.18	0.50	0.34
Total	F	5.68	5.11	5.25	4.35	3.78	6.09	4.35	5.25	3.12
	S	1.53	2.56	2.77	1.91	4.97	2.99	1.13	2.81	2.13
	R	5.24	3.64	2.83	2.65	5.18	4.72	1.95	2.23	3.33
Composition (%)										
Monoterpene	F	75.70	96.87	82.10	93.56	95.77	87.52	95.40	89.33	96.47
hydrocarbons	S	86.27	93.75	93.14	90.05	93.96	83.28	88.50	80.78	90.61
	R	79.20	89.01	83.75	87.55	90.73	82.63	90.77	77.58	89.79
Oxygenated	F	24.30	3.13	17.90	6.44	4.23	12.48	4.60	10.67	3.52
monoterpenes	S	13.72	6.25	6.86	9.95	6.04	16.72	11.50	19.22	9.39
	R	20.80	10.99	16.25	12.45	9.27	17.37	9.23	22.42	10.21

[a] F = foliage, S = stem, R = root.

[b] Area in arbitrary units determined by electronic integrator and calculated per gram dry tissue.

TABLE 3. MONOTERPENE HYDROCARBONS OF ESSENTIAL OILS OF PONDEROSA PINE

Component composition (%)[a]	Oil source[b]	Source identification number								
		6	7	9	10	11	17	18	19	21
α-Pinene	F	30.28	12.13	19.44	10.41	12.08	14.58	9.69	12.44	10.88
	S	37.01	6.48	18.34	5.49	5.48	7.11	5.64	6.72	5.12
	R	31.09	6.78	16.58	7.41	6.19	7.85	8.03	7.04	7.06
Camphene	F	1.48	1.40	0.94	0.80	0.59	1.19	0.57	1.00	0.46
	S	0.52	0.60	1.03	0.58	0.29	1.07	0.50	0.51	0.21
	R	0.87	0.65	1.03	1.03	0.37	1.16	0.89	0.45	0.44
Unknown 6	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	S	0.12	0.24	0.26	0.64	0.40	0.30	0.46	0.38	0.34
	R	0.72	1.37	0.75	2.64	1.67	1.07	1.76	1.13	1.24
β-Pinene + sabinene	F	20.25	38.05	27.84	33.95	39.69	33.65	42.26	34.10	36.09
	S	3.03	20.76	27.90	27.44	18.05	30.71	25.81	23.79	15.64
	R	7.30	22.81	21.81	33.61	25.97	30.38	30.57	25.22	25.29
3-Carene + myrcene	F	13.80	35.64	25.82	37.66	34.31	26.56	34.26	30.02	38.05
	S	38.25	54.66	38.31	42.33	53.61	34.27	46.74	37.91	50.92
	R	32.68	48.50	37.95	31.15	45.35	34.06	40.46	35.95	44.38
α-Terpinene	F	0.17	0.36	0.18	0.42	0.26	0.24	0.24	0.30	0.26
	S	0.22	0.39	0.30	0.26	0.45	0.33	0.27	0.24	0.33
	R	0.32	0.39	0.25	0.32	0.32	0.30	0.31	0.20	0.34

Limonene	F	4.41	2.51	2.57	3.27	2.13	3.65	1.89	4.49	2.84
	S	3.07	2.67	2.51	5.52	5.55	3.34	2.61	4.97	5.89
	R	2.32	2.40	1.96	6.02	4.70	2.74	3.23	3.28	4.27
β-Phellandrene	F	3.04	1.72	1.78	1.62	1.74	3.33	1.65	2.39	1.55
	S	0.81	1.27	1.33	1.26	1.63	1.88	1.04	1.84	1.49
	R	0.83	1.17	1.01	1.38	1.32	1.52	1.21	1.19	1.28
Ethyl caproate	F	0.18	0.02	0.10	0.00	0.00	0.40	0.00	0.54	0.00
	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	R	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
γ-Terpinene	F	0.36	0.71	0.46	0.68	0.67	0.49	0.62	0.52	0.67
	S	0.36	0.71	0.38	0.57	0.66	0.51	0.51	0.50	0.76
	R	0.41	0.50	0.31	0.39	0.41	0.39	0.41	0.30	0.51
p-Cymene	F	0.14	0.21	0.10	0.26	0.12	0.14	0.12	0.14	0.12
	S	0.21	0.24	0.29	0.11	0.26	0.29	0.14	0.16	0.15
	R	0.40	0.33	0.29	0.28	0.28	0.28	0.33	0.22	0.25
Terpinolene	F	1.57	4.12	2.78	4.57	4.23	3.37	4.06	3.34	5.56
	S	2.94	5.85	2.54	5.82	7.58	3.41	5.02	3.74	9.91
	R	2.32	4.32	2.32	3.41	4.19	2.64	3.48	2.11	4.69

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[a] Percent of total terpenes.

[b] F = foliage, S = stem, R = root.

TABLE 4. OXYGENATED MONOTERPENES OF ESSENTIAL OILS OF PONDEROSA PINE

Component composition (%)[a]	Oil source[b]	Source identification number								
		6	7	9	10	11	17	18	19	21
Unknown 20	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	R	0.66	0.74	0.44	0.73	0.42	0.44	0.70	0.40	0.46
Fenchyl alcohol	F	8.36	0.25	2.45	0.97	0.40	2.32	0.66	1.43	0.28
	S	9.46	2.02	4.82	4.76	1.25	11.38	3.10	11.50	2.20
	R	13.99	3.08	10.99	4.10	2.56	11.62	1.98	15.62	2.73
Terpinen-4-ol	F	0.46	0.58	0.51	0.76	0.67	0.70	0.63	0.79	0.77
	S	0.31	0.44	0.16	0.73	0.66	0.59	0.76	0.75	1.22
	R	0.58	0.47	0.41	0.45	0.43	0.44	0.49	0.37	0.44
Unknown 31	F	9.36	0.13	7.44	0.37	0.19	0.00	0.49	0.00	0.00
	S	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	R	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unknown 33	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	S	0.51	0.26	0.39	0.33	0.22	0.43	0.64	0.65	0.25
	R	0.52	0.79	0.41	0.90	0.60	0.43	0.65	0.64	0.68
Citronellyl acetate	F	1.04	0.53	1.02	0.69	0.60	0.65	0.56	1.42	0.48
	S	0.27	0.20	0.00	0.40	0.08	0.49	0.00	0.89	0.18
	R	0.38	0.20	0.27	0.14	0.11	0.28	0.02	0.37	0.05

Estragole	F	0.00	0.19	0.00	0.07	0.14	0.02	0.11	0.11	0.10
	S	0.00	0.98	0.00	0.00	0.31	0.00	0.81	0.00	0.59
	R	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
α-Terpineol	F	0.99	0.96	1.63	2.12	1.63	1.57	1.94	1.69	1.29
	S	0.31	0.38	0.41	1.82	0.58	1.10	1.44	1.22	1.13
	R	1.06	1.63	1.23	3.02	1.10	1.86	2.49	1.83	1.17
Borneol	F	0.23	0.16	0.00	0.00	0.28	1.50	0.23	1.22	0.16
	S	0.33	0.44	0.00	0.00	1.03	1.67	1.23	1.59	1.10
	R	0.36	0.33	0.06	0.00	0.21	0.71	0.22	0.86	0.22
Unknown 41	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	S	0.32	0.32	0.80	0.00	0.37	0.61	1.27	0.74	0.12
	R	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unknown 43	F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	S	2.00	1.14	0.28	1.98	1.48	0.09	2.07	1.46	2.39
	R	0.86	2.31	0.48	1.84	3.03	0.38	1.92	1.04	3.40
Other unknowns	F	3.89	0.39	4.99	1.42	0.30	5.72	0.04	4.10	0.46
	S	0.00	0.00	0.00	0.00	0.12	0.46	0.00	0.49	0.12
	R	2.38	1.30	1.48	1.23	0.84	1.51	0.90	1.86	1.17

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[a] Percent of total terpenes.

[b] F = foliage, S = stem, R = root.

maximum difference in damage suggests that some ponderosa pine sources might possess sufficient resistance to give the trees appreciable protection from gophers in the field.

Yield and Composition of Essential Oils. Total yield of essential oils as well as yields of the monoterpene hydrocarbons and oxygenated monoterpenes are shown in Table 2. Total yield per gram dry tissue was lowest in the stems and highest in the foliage. Also, total yield of each tissue type varied by source.

As expected, the oils of the different seedling parts were predominantly (76–97%) composed of monoterpene hydrocarbons. This agrees with results obtained by others with ponderosa pine needle oil (Zavarin et al., 1971). Results also indicate that, on the basis of the monoterpenoid hydrocarbons and oxygenated compounds, ponderosa pine oil is similar to that of other conifers, such as Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Radwan and Crouch, 1978) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (von Rudloff, 1975).

The oils of the different parts of seedlings contained some 30 compounds each, but many were present in small or trace amounts (Table 3 and 4). Most abundant compounds present in the oils were the monoterpene "hydrocarbons" α-pinene, β-pinene + sabinene, 3-carene + myrcene, limonene, and terpinolene, and the oxygenated monoterpenes fenchyl alcohol and α-terpineol.

Composition of the oils differed by source. The sources, however, tended to fall roughly into four geographical groups as follows: northern, sources 7, 11, and 21; west-central, sources 10 and 18; eastern, sources 17 and 19; and southern, sources 6 and 9. Within each of the four groups, oils of one or more seedling parts had similar levels of some terepenes. For example, the northern sources were high in 3-carene + myrcene and γ-terpinene and low in fenchyl alcohol. In contrast, the southern sources were high in α-pinene and fenchyl alcohol and low in γ-terpinene, terpinolene, and α-terpineol.

Oil Composition of Different Tissues. Averaged over the nine sources, different tree parts varied greatly in the yield and chemical composition of their oils. Nineteen chemical variables had F values which were significant at $P \leqslant 0.05$ or $P \leqslant 0.01$ (Table 5). Differences in oils, however, were mostly quantitative, with qualitative differences noted in only seven components. These compounds, which were not always detected in oils of all tissue types, include unknowns 6, 20, 33, 41, and 43, ethyl caproate, and estragole.

The six most important variables which distinguished between the three tissue types were p-cymene, citronellyl acetate, and unknowns 6, 20, 33, and 41. The first variable in the discriminant function was unknown 20. This component, however, did not distinguish between stems and foliage because it was not detected in either tissue. The discriminant function with unknowns 20 and 33 correctly distinguished between the three tissues.

TABLE 5. CHEMICAL VARIABLES SHOWING SIGNIFICANT DIFFERENCES BETWEEN DIFFERENT PARTS OF PONDEROSA PINE SEEDLINGS

	Mean value[b]				
Item[a]	Foliage	Stem	Root	*F* value	Statistical significance[c]
Unknown 6	0.00	0.35	1.37	36.6	**
β-Pinene + sabinene	33.99	21.46	24.77	6.6	**
3-Carene + myrcene	30.68	44.11	38.94	8.0	**
β-Phellandrene	2.09	1.39	1.21	9.4	**
Ethyl caproate	0.14	0.00	0.00	4.2	*
γ-Terpinene	0.58	0.55	0.40	6.0	**
p-Cymene	0.15	0.21	0.30	14.6	**
Terpinolene	3.73	5.20	3.28	3.4	*
Unknown 20	0.00	0.00	0.55	126.8	**
Fenchyl alcohol	1.90	5.61	7.41	3.9	*
Unknown 33	0.00	0.41	0.62	52.4	**
Citronellyl acetate	0.78	0.28	0.20	13.3	**
Estragole	0.08	0.30	0.00	4.0	*
α-Terpineol	1.54	0.93	1.71	5.0	*
Unknown 41	0.00	0.51	0.00	15.0	**
Unknown 43	0.00	1.43	1.70	12.3	**
Other unknowns	2.37	0.13	1.41	6.2	**
MTH yield	4.27	2.26	3.02	10.2	**
Total terpene yield	4.78	2.53	3.53	9.2	**

[a] MTH = monoterpene hydrocarbons.
[b] Means of all nine sources. Yield = area ($\times 10^6$) in arbitrary units determined by electronic integrator and calculated per gram dry tissue. All other values are percents.
[c] *, $P \leq 0.05$; **, $P \leq 0.01$.

Some of the discriminating properties which separated the tissues indicated that important characteristics of the oils were: high concentrations of *p*-cymene, and unknowns 6, 20, and 33 in the roots; medium levels of *p*-cymene, citronellyl acetate, and unknowns 6 and 33 in the stem; and absence of unknowns 6, 20, 33, and 41 from the foliage.

Relationships of Oil Yield and Composition to Gopher Preference. Correlation analysis between yield and chemical components of the oils and gopher preference, as measured by observed gopher damage to seedlings, resulted in six significant correlation coefficients. Neither yield nor constituents of foliage oils were significantly correlated with feeding preference. In contrast, the β-pinene + sabinene component of stem oils was negatively related to preference ($r = -0.74$, $P \leq 0.05$). The other five significant correlations involved root oils. All were positive and included *p*-cymene ($r = 0.65$, $P \leq 0.10$), terpinen-4-ol ($r = 0.76$, $P \leq 0.05$), yield of monoterpene hydrocarbons ($r = 0.77$, $P \leq 0.05$), yield of oxygenated monoterpenes ($r = 0.66$, $P \leq 0.10$), and total terpene yield ($r = 0.80$, $P \leq 0.01$).

Discriminant analysis of the high- and low-gopher-damage seedlings showed that total terpene yield of root oils was the variable most closely associated with preference; the average yield was almost twice as high in the high-damage sources as that of the low-damage trees. The discriminant function with total terpene yield of root oils and monoterpene hydrocarbon yield in foliage oils correctly classified all sources in their correct damage group. Association of the monoterpene hydrocarbon and total terpene yields with feeding preference is in agreement with results of the correlation analyses.

Results of the correlation and discriminant analyses suggest important possible practical applications. For example, the β-pinene + sabinene component of stem oil, which was negatively correlated with preference may be useful as a measure of pine resistance to damage by gophers. On the other hand, high levels of p-cymene, terpinen-4-ol, monoterpene hydrocarbon yield, oxygenated monoterpene yield, and total terpene yield in root oils might serve as indicators of potential high susceptibility to damage.

In general, the components which best distinguished between the different tree parts (Table 5) were not the same as those associated with gopher damage in the previous analysis. Some of these components, however, could be influential in determining feeding preference. Of particular importance is the component β-pinene + sabinene. This component, which was negatively correlated with gopher damage, was also found in highest levels in the foliage, the least preferred seedling tissue (Cummins, 1975).

CONCLUSIONS

This study helped generate hypotheses concerning the relationships between yield and composition of oil and damage by gophers in ponderosa pine seedlings. Additional research in now needed to confirm these relationships. Chemical variables associated with resistance (or low preference), when verified, could be used for indirect selection of planting or breeding stock suitable for areas where pocket gophers are a serious obstacle to reforestation of ponderosa pine. Alternatively, some of the same components could be tested for biological activity and possible development as repellents.

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