Factors Affecting Vegetation on a Serpentine Soil

I. Principal Components Analysis of Vegetation Data

Robert L. Koenigs, William A. Williams, and Milton B. Jones

II. Chemical Composition of Foliage and Soil

Robert L. Koenigs, William A. Williams, Milton B. Jones, and Arthur Wallace

I. Principal Component Analysis of Vegetation Data

Vegetation of 40 sample stands on serpentine soils was analyzed and used to indicate conditions that might limit the establishment of annual range species. Two groups of stands, "cypress" and "non-cypress," were defined by cluster analysis. Stands with *Cupressus sargentii* also contained *Arctostaphylos viscida* and occurred on mesic sites with lower Ca in the sub-surface soil. Stands without *C. sargentii* usually contained *Adenostoma fasciculatum* and *Quercus durata* and occurred on the drier sites with higher Ca.

Principal component analysis was carried out on the vegetation data in each group of stands, and simple and partial correlations were calculated between principal components and environmental variables. A moisture gradient within the cypress stands was associated mainly with the water-storage capacity of the soil. *Cupressus sargentii* was more abundant at lower water-storage capacities (and at lower elevations), while *Arctostaphylos viscida* was most abundant at the opposite end of the gradient. No correlations were found with soil chemical analyses.

The relations between principal components and environmental variables were less apparent within the non-cypress stands. *Adenostoma fasciculatum* and *Garrya congdoni* were most abundant where Ca contents in the soil were high while *Ceanothus jepsonii*, *Quercus durata*, *Bromus laevipes,* and *Sisyrinchium bellum* were most abundant at the opposite end of the gradient.

THE AUTHORS:

Robert L. Koenigs was Research Assistant and is now Environmental Consultant, 9232 Lomker Court, Santee, CA 92071. William A. Williams is Professor, Department of Agronomy and Range Science, Davis. Milton B. Jones is Agronomist, Department of Agronomy and Range Science, Hopland Field Station. Arthur Wallace is Professor, Laboratory of Nuclear Medicine and Radiation Biology, Los Angeles.

Robert L. Koenigs, William A. Williams, Milton B. Jones,
and Arthur Wallace

II. Chemical Composition of Foliage and Soil

INTRODUCTION

SERPENTINE SOILS have a unique combination of chemical characteristics that affect the vegetation found on them. Species growing on these soils are usually subjected to low concentrations of Ca, high concentrations of Mg, occasionally toxic levels of Ni, Cr, and Co, and deficiencies of Mo (Proctor and Woodell, 1975). N, P, K, and S deficiencies are known to be of importance on some serpentine soils (Jones, Williams, and Ruckman, 1977).

Several workers have demonstrated that different species, and even different races of a species, growing on the same soil will differ in their elemental composition (Collander, 1941; Lyon *et al.* 1971; Shewry and Peterson, 1975; Johnston and Proctor, 1977). These differences may reflect differences in mechanisms of adaptation to these soils (especially in the case of such inhospitable soils as serpentine soils), although they do not reveal what the mechanisms are or even what concentrations are optimum. Optimum concentrations of these elements need to be defined for each species.

Experimental work, where the growth medium is varied under controlled conditions, is necessary to accurately define these optima (Walker, Walker, and Ashworth, 1955; Marrs and Proctor, 1976). Nevertheless, the abundance and vigor of species in the field may prove to be related to soil and leaf concentrations of important elements. These relations might supply some information about optimum concentrations where experiment is impractical or where information is desired to help select species for further experimentation.

Four species dominate in the study area: *Cupressus sagentii, Quercus durata, Arctostaphylos viscida,* and *Adenostoma fasciculatum. Cupressus sargentii* and *Q. durata* are considered to be serpentine endemics (McMillan, 1956). *Arctostaphylos viscida* occurs both on and off serpentine in the Sierra Nevada, but is restricted to it in the Coast Range of California, U.S.A., where this study took place (J. Major, personal communication). Although *Adenostoma fasciculatum* is very widespread in chaparral in California, serpentine ecotypes may occur. *Arctostaphylos viscida* and *Q. durata* were the most widespread species in our study area. Sites containing *C. sargentii* had significantly lower concentrations of Ca in the soil than sites containing *Adenostoma fasciculatum* (Part I). *Arctostaphylos viscida* was more abundant where *C. sargentii* occurred, and *Q. durata* was more abundant where *Adenostoma fasciculatum* occurred.

This paper examines differences in the concentration of elements in the four species. To improve understanding of the adaptive strategies of these species, it also correlates their abundance and size with nutrient concentrations in leaf and soil.

METHODS

Forty sample stands were selected randomly from about 280 ha within the watersheds of Cedar and Pocock creeks (California, U.S.A.; latitude 38°47′N, longitude 122°22′W). Within each stand, three transects, each 15 m long and 7.5 m apart, were laid out parallel to each other and to the contour of the slope in spring and summer, 1975,

with the criterion that vegetation discontinuities be avoided. Soil samples were collected from both the A horizon (surface) and the B horizon (subsoil) by combining subsamples from two locations, along each of the three transects. The samples were then seived and air dried. K, Ca, and Mg were extracted from the soil samples with neutral 1.0 normal ammonium acetate and determined by atomic-absorption spectrophotometry.

The percentage cover of each of the four species (*Cupressus sargentii, Arctostaphylos viscida, Quercus durata,* and *Adenostoma fasciculatum*) was estimated by the line-intercept method along each transect. If a species occurred in the stand but was not intercepted by a transect, it was given a cover value of 0.1 percent. Quadrats (3 × 15 m) were centered over each trasect to determine the density of the species. Heights of all *Arctostaphylos viscida* and *C. sargentii* plants within each quadrat were measured.

Leaf samples were collected within each stand for each of the four species found in that stand. The samples were collected from new growth of plants scattered through-out each stand. Leaf samples were washed, dried, ground, and analyzed for K, Ca, Mg, Ni, and Cr using a 1.5-liter direct-reading emission spectrometer (Applied Research Laboratories [Wallace, Ramsey and Alexander, 1974]).

The 40 stands were divided objectively into two groups, cypress and non-cypress stands, by an agglomerative method of cluster analysis (Part I). Linear correlations of leaf-cation variables with soil-cation variables and of species abundance and size variables with both leaf and soil chemical composition were calculated separately for cypress and non-cypress stands. These correlations were also calculated for each species over its entire range. Presumably because of changes in species interactions as the plant community changed, results were not as good and not reported. Scattergrams were examined where nonlinear relations were suspected. Logarithmic functions were used to describe these relations but were not found to improve correlations significantly.

RESULTS

Soil analyses

Table 1 contains the mean concentrations of exchangeable cations in both the cypress and non-cypress stands. Concentrations of K and Ca and the Ca/Mg ratio were greater in the surface soil than in the subsoil, whereas Mg concentrations were greater in the subsoil. The only significant differences between cypress and non-cypress stands were in the Ca concentration and the Ca/Mg ratio in the subsoil, both being lower in the cypress stands. The concentration of exchangeable Mg was slightly greater in the cypress stands.

Concentrations of Ca in these soils were mostly in the middle of the range of values found in Table XI, compiled by Proctor and Woodell (1975). Exchangeable Mg, however, did reach extremely high concentrations in some of these soils (46 meq/100 g), resulting in some Ca/Mg ratios that were extremely low (0.01).

Leaf analyses

The concentrations of Ni (4.5 to 14.0 ppm; Table 2) and Cr (less than 1 ppm for all species) found in this study are quite low compared with Ni and Cr concentrations in serpentine plants compiled by Proctor and Woodell (1975) and Reeves, Brooks, and

TABLE 1. Concentration of exchangeable K, Ca, and Mg and Ca/Mg ratios in surface and subsoil horizons (± S.E.).**

	Cypress stands (n=17)	Non-cypress stands (n=17)
	meq/100 g	meq/100 g
Surface soil:		
K	1.00 ± 0.03	0.93 ± 0.07
Ca	6.76 ± 0.59	6.64 ± 0.43
Mg	28.7 ± 1.6	25.4 ± 1.1
Ca/Mg	0.27 ± 0.04	0.28 ± 0.03
Subsoil:		
K	0.65 ± 0.02	0.66 ± 0.05
Ca	2.51 ± 0.32 **	5.02 ± 0.45
Mg	34.4 ± 1.8	30.6 ± 1.4
Ca/Mg	0.08 ± 0.02 **	0.17 ± 0.02

**$p < .01$ for means of cypress and non-cypress stands compared with a t-test.

MacFarland (1981, Ni only). Those workers found concentrations of Ni in leaves ranging from undetectable to 10,000 ppm (dry weight basis), with only a few of their samples within the range we found. The same holds true for Cr, which was found in serpentine plants at concentrations up to 284 ppm. Cobalt and Mo were at concentrations below the minimum detectable limits of the analytical procedures used (1.5 ppm for Co and 0.2 ppm for Mo).

Mean K concentrations were similar for all species averaging 16 meq/100 g. Accumulation ratios, the ratios of exchangeable K in the leaf to exchangeable K in the soil, also were similar among species, since all species accumulated K similarly from soil.

Calcium concentrations, Ca/Mg ratios, and the abilities of species to accumulate Ca were all much more variable than were K concentrations. All four species fell into the same order with respect to average values for these three variables: thus, in ascending order, *Adenostoma fasciculatum, Quercus durata, Arctostaphylos viscida,* and *Cupressus sargentii.* Variation among the species was greatest for the Ca accumulation ratios, ranging from 3.3 to 21.1. Our Ca concentrations fell in the middle of the range reported by Proctor and Woodell (1975). Only two species in their table, however, have Ca/Mg ratios greater than the mean ratios we found for *C. sargentii* and *Arctostaphylos viscida.*

Magnesium concentrations and accumulation ratios were lowest in *Arctostaphylos viscida* (20.6 meq/100 g, 0.66) and highest in *Adenostoma fasciculatum* (33.7 meq/ 100 g, 1.15). Most species reported on by Proctor and Woodell (1975) had Mg concentrations greater than those in *Adenostoma fasciculatum,* and all species had higher ratios.

Arctostaphylos viscida and *Quercus durata* were the only species that occurred in enough of both the cypress and non-cypress stands for comparisons to be made between the two groups. Table 3 shows the comparisons that produced significant differences. Exchangeable Ca in the soil was greater in the non-cypress stands, and both Ca concentration and Ca/Mg ratio in the leaves of *Arctostaphylos viscida* reflect this. *Quercus durata,* however, had a greater Ca/Mg ratio in leaves collected from the cypress stands. Differences in the accumulation of both Ca and Mg contributed to this difference.

Table 2. Concentrations of selected elements and Ca/Mg ratios in leaf tissue and accumulation ratios using subsoil concentrations ($\pm$ S.E.).

Element	Cupressus sargentii	Arctostaphylos viscida	Quercus durata	Adenostoma fasciculatum
In leaf				
Ni ppm	10.2 $\pm$ 0.4	4.5 $\pm$ 0.4	11.7 $\pm$ 0.5	14.0 $\pm$ 0.8
Cr ppm	0.38 $\pm$ 0.04	0.60 $\pm$ 0.06	0.89 $\pm$ 0.09	0.76 $\pm$ 0.20
K meq/100 g	16.9 $\pm$ 0.8	15.3 $\pm$ 0.5	16.9 $\pm$ 0.5	15.9 $\pm$ 0.5
Mg meq/100 g	28.8 $\pm$ 1.6	20.6 $\pm$ 0.8	23.9 $\pm$ 0.8	33.7 $\pm$ 0.8
Ca meq/100 g	39.4 $\pm$ 1.5	26.9 $\pm$ 2.0	16.0 $\pm$ 0.5	15.6 $\pm$ 1.0
Ca/Mg[1]	1.44 $\pm$ 0.11	1.29 $\pm$ 0.08	0.69 $\pm$ 0.04	0.44 $\pm$ 0.03
Accumulation ratio				
Leaf K/Soil K[1]	27.2 $\pm$ 1.6	25.2 $\pm$ 1.1	26.6 $\pm$ 1.1	27.2 $\pm$ 2.0
Leaf Mg/Soil Mg[1]	0.90 $\pm$ 0.04	0.66 $\pm$ 0.03	0.82 $\pm$ 0.04	1.15 $\pm$ 0.06
Leaf Ca/Soil Ca[1]	21.1 $\pm$ 3.7	10.0 $\pm$ 1.2	5.2 $\pm$ 0.7	3.3 $\pm$ 0.2

[1] Units are $\frac{meq/100\ g}{meq/100\ g}$

Table 3. Values of Ca and Ca/Mg ratio in leaf tissue for two shrub species and Ca and Mg accumulation ratios using subsoil concentrations ($\pm$ S.E.).

	Arctostaphylos viscida		Quercus durata	
	Cypress stands	Non-cypress stands	Cypress stands	Non-cypress stands
Ca meq/100 g	22.5 $\pm$ 2.0**	33.9 $\pm$ 4.0	18.0 $\pm$ 1.5	15.5 $\pm$ 1.0
Ca/Mg[1]	1.11 $\pm$ 0.10**	1.61 $\pm$ 0.19	0.81 $\pm$ 0.05*	0.66 $\pm$ 0.05
Leaf Mg/ Soil Mg[1]	0.66 $\pm$ 0.04	0.66 $\pm$ 0.05	0.66 $\pm$ 0.05 **	0.82 $\pm$ 0.04
Leaf Ca/ Soil Ca[1]	11.88 $\pm$ 2.00	8.58 $\pm$ 1.53	8.73 $\pm$ 1.84 **	3.59 $\pm$ 0.42

* and ** indicate $P < .05$ and $P < .01$ for means of cypress and non-cypress stands with a t-test.

[1] Units are $\frac{meq/100\ g}{meq/100\ g}$

Correlations

Exchangeable K and Mg in the soil were not correlated significantly with many leaf-cation variables (Table 4). Exchangeable K was correlated positively with the concentration of K in the leaves of *Quercus durata* only in the non-cypress stands, and exchangeable Mg was correlated negatively with the Ca/Mg ratio only in the leaves of *Cupressus sargentii.*
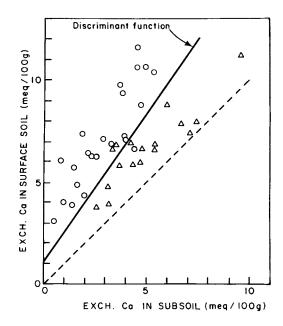
Table 4. Significant correlations (P<.05) of leaf-cation variables with subsoil-cation variables and K x Mg interaction in surface and subsoil.

Leaf-cation variables (n)	Subsoil-cation variables				Soil KxMg interaction	
	K	Ca	Mg	Ca/Mg	Surface	Subsoil
Cypress stands						
Cupressus sargentii (15)	Ca		.60		.56		-.54
	Mg				-.58		
	Ca/Mg		.66**	-.64**	.76**		-.52
Arctostaphylos viscida (17)	Ca					-.56	
	Ca/Mg		.53			-.50	
Quercus durata (11)	Ca/Mg					-.62	
Non-cypress stands						
Arctostaphylos viscida (9)	Mg					-.68	
Quercus durata (17)	K	.62**					.57
	Ca		-.68**		-.65**		
	Ca/Mg		-.58				
Adenostoma fasciculatum (15)	Ca		.71**		.60		
	Ca/Mg		.64**		.55		

**P < .01.

Several more significant correlations can be found between leaf-cation variables and the soil K × Mg "interaction term," a variable arrived at by multiplying K concentration by Mg concentration. This term should reflect the joint influence of these two variables. The K × Mg term is the only variable included in Table 4 from the surface soil for two reasons. Correlations were higher with this variable than with its subsoil counterpart, unlike the rest of the correlations of surface-soil variables with leaf cations. Secondly, K and Mg alone were not correlated significantly with the leaf-cation variables. All significant correlations of Ca concentrations or Ca/Mg ratios in leaves with the K × Mg interaction terms were negative, and all occurred within the cypress stands.

Exchangeable Ca and Ca/Mg ratio in the subsoil were correlated significantly only with Ca and Ca/Mg ratio in the leaves, with one exception: the correlation between the Ca/Mg ratio in the soil and Mg in leaves was negative in *Cupressus sargentii.* The other correlations are positive for all species except *Quercus durata.*

Correlations between leaf cations and soil cations tend to be better when the subsoil is included. The reason could be that the composition of the surface soil is dependent on species composition. Figure 1 plots all 40 sites according to their surface and subsoil Ca concentrations. In all cases there was more Ca in the surface than in the subsoil, and, according to Table 2, concentrations of Ca were also higher in leaves than in the subsoil. Discriminant analysis was performed on these data to determine whether the apparent separation of cypress stands from non-cypress stands was significant (Dixon, 1973). The discriminant function was found to be highly efficient at separating the two groups of sites (Wilks' lambda = 0.34 and canonical correlation = 0.81). The species that are dominant in the cypress stands had higher Ca accumulation ratios than those in the non-cypress stands (Table 2), and cypress stands had more Ca in the surface soil at any given level of subsoil CA (see figure).

The location of sites with respect to surface and subsoil exchangeable Ca. All sites have a higher concentration of exchangeable Ca in the surface than in the subsoil (---). The discriminant function (———) significantly separates cypress (o) from non-cypress stands (△). Wilks' lambda = 0.34 and canonical correlation = 0.81.

Table 5 contains all of the significant (P < .05) correlations of species abundance and size variables with subsoil and leaf-cation variables. Heights of both *Cupressus sargentii* and *Arctostaphylos viscida* were correlated negatively with exchangeable K in the soil and correlated positively with the concentration of K in their leaves (the latter only in the cypress stands). The only other correlation with K was between the density of *A. viscida* in cypress stands and leaf K.

Species variables were correlated with only a few soil cation variables other than K. Soil Ca was correlated positively with the cover of both *Cupressus sargentii* and *Adenostoma fasciculatum*. Soil Mg was correlated negatively with the cover of *C. sargentii*, and the Ca/Mg ratio was correlated negatively with the density of *C. sargentii*.

Species variables were correlated more often with leaf-cations than with soil cations. Leaf Ca was correlated negatively with the density of *Arctostaphylos viscida* in the cypress stands and correlated positively with the cover of *Adenostoma fasciculatum*. The cover of *Quercus durata* was correlated negatively with leaf Mg in both cypress and non-cypress stands, and the height of *Cupressus sargentii* was correlated positively with leaf Mg. The Ca/Mg ratio in the leaves was the variable correlated most often with species variables. The density of *C. sargentii* correlated positively with the leaf Ca/Mg ratio in the cypress stands, whereas the density of *Arctostaphylos viscida* was correlated negatively with it. In the non-cypress stands, the cover of *Arctostaphylos viscida* was correlated negatively with the leaf Ca/Mg ratio, and the percentages of cover for both *Q. durata* and *Adenostoma fasciculatum* were correlated positively with it.

Table 5. Significant correlations (P<0.05) of species abundance and size variables with subsoil-concentrations and leaf tissue concentrations of K, Ca, and Mg, and Ca/Mg ratios, within the cypress and non-cypress groups of sites.**

Species variables	Subsoil concentration					Leaf concentration				
	n	K	Ca	Mg	Ca/Mg	n	K	Ca	Mg	Ca/Mg
Cypress stands										
Cupressus sargentii										
Cover %	15		.54	-.51		15				
Height	15	-.59				15	.70**		.52	
Density	15				.51	15				.58
Arctostaphylos viscida										
Height	17	-.50				17	.51			
Density	17					17	-.57	-.53		-.48
Quercus durata										
Cover %	17					11			-.71	
Non-cypress stands										
Arctostaphylos viscida										
Cover %	17					9				-.68
Height	17	-.60				6				
Quercus durata										
Cover %	17					17			-.54	.49
Adenostema fasciculatum										
Cover %	17		.49			15		.75**		.60

**P <.01.

DISCUSSION

Some of the soils were extreme examples of serpentine soils with respect to Mg concentrations and Ca/Mg ratios (Table 1); yet, even the mean concentration of Mg in the leaves of *Adenostema fasciculatum* (Table 2) was less than most Mg concentrations compiled by Proctor and Woodell (1975). Only two species in Table XII from their review article have higher Ca/Mg ratios than those found in the leaves of *Cupressus sargentii* and *Arctostaphylos viscida,* and not one species had a Mg accumulation ratio less than our highest mean accumulation ratio. It apears that the species in this study are well-adapted to high concentrations of exchangeable Mg in the soil by an ability to exclude Mg from their leaves, as has been shown for other species (Walker, 1954; Madhok and Walker, 1969; Marrs and Proctor, 1976). *Quercus durata,* however, appears to have exceeded its optimum Mg concentration in some instances, since its cover was correlated negatively with leaf Mg in both the cypress and non-cypress stands. The cover of *C. sargentii* was correlated negatively with soil Mg but not with leaf Mg. It would be interesting to see if any of these species accumulated Mg in some other tissue.

Cupressus sargentii appears to be the species best adapted to the low Ca concentrations found in our serpentine soils, while *Adenostoma fasciculatum* appears to be the least adapted. Soils supporting *C. sargentii* had a lower Ca concentration than soils supporting *A. fasciculatum;* yet *C. sargentii* had the highest concentrations of Ca in leaves and *A. fasciculatum* had the lowest concentrations. The mean Ca accumulation ratios for *A. fasciculatum* and *C. sargentii* were respectively 3.3 and 21.1. Despite these vast differences, the percentage of cover for both species was correlated positively (P < .05) with soil Ca (Table 5), indicating that both may be growing at sub-optimal concentrations of Ca. Thus, although *C. sargentii* may have a Ca requirement just as high or higher than the other species, it is able to grow on soils with extremely low concentrations of exchangeable Ca due to an ability to accumulate Ca selectively (Walker, Walker, and Ashworth, 1955). *Arctostaphylos viscida* had the second-highest Ca accumulation ratio, yet it appears to be adapted to low Ca concentrations by a low Ca requirement. This seems to be the case with many species, in the absence of toxic elements (Wyn Jones and Lunt, 1967; Main, 1974). The cover and density of *A. viscida* were correlated negatively with leaf Ca and/or Ca/Mg ratio, perhaps indicating Ca toxicity. *A. fasciculatum* had neither a low Ca-requirement nor an ability to take up sufficient Ca from the extremely Ca-deficient sites. Soil calcium concentrations should be highest where *A. fasciculatum* is most abundant. Introduced species, being unadapted to the low Ca concentrations found in serpentine soils, would be most likely to succeed on these sites.

We have been assuming that the difference between cypress and non-cypress stands in the composition of vegetation reflects, in part, the difference in Ca concentrations in the soil. Others have shown that chemical differences in soil can produce vegetational differences (Billings, 1950; Waring and Major, 1964; McColl and Humphreys, 1967; Webb, 1969). All the same, it may be that the soils supporting cypress stands are lower in Ca because the species growing on these soils are better Ca accumulators, depleting the subsoil of Ca and depositing it in the litter. If that were true, we would expect subsoil Ca content to decline with increasing age. Soil samples taken both under vegetation and from bare soil need to be compared to settle the question.

Soil Mg concentrations were high in many of the samples taken in this study, yet they were correlated with only one species variable. Magnesium in combination with K, however, was correlated negatively with Ca concentration and/or Ca/Mg ratio in the leaves of all species in the cypress stands (Table 4). Vlamis (1949) found that adding K or Mg to a serpentine soil could cause a competitive inhibition of Ca uptake by plants growing there. It is interesting that in our study this relationship occurs only within the cypress stands, where soil Ca concentrations are lower. Madhok (1965; cited by Proctor and Woodell, 1975) suggested that at lower Ca concentrations in the medium, a Ca carrier more subject to interference is active in Ca uptake.

The finding most difficult to explain is the negative correlation between leaf Ca in *Quercus durata* and soil Ca within non-cypress stands. A competitive interaction with another species may account for the peculiarity. In fact, the cover of *Q. durata* is correlated negatively with the cover of *Adenostoma fasciculatum* (r = − 0.78; P < .01), an indication that a competitive relationship could exist.

The methods used in this study indicate a variety of possible adaptations to the extreme conditions found on serpentine soils. This information could provide a means for using some of the species as indicators of the chemical environment of these serpentine soils. First, however, further studies are needed under controlled conditions to test the hypotheses put forward in this paper.

LITERATURE CITED

BILLINGS, W. D.
  1950.   Vegetation and plant growth as affected by chemically altered rocks in the western Great Basin. Ecol. 31:62-74.
COLLANGER, R.
  1941.   Selective absorption of cations by higher plants. Plant Physiol. 16:691-720.
DIXON, W. J.
  1973.   BMD Biomedical Computer Programs. Los Angeles: Univ. Calif. Press. 773 pp.
JOHNSTON, W. R., and J. PROCTOR
  1977.   Metal concentrations in plants and soils from two British serpentine sites. Plant and Soil 46:275-78.
JONES, M. B., W. A. WILLIAMS, and J. E. RUCKMAN
  1977.   Fertilization of *Trifolium subterraneum* L. growing on serpentine soils. Soil Sci. Soc. Amer. J. 41:87-89.
LYON, G. L., P. J. PETERSON, R. R. BROOKS, and G. W. BUTLER
  1971.   Calcium, magnesium, and trace elements in a New Zealand serpentine flora. J. Ecol. 59:421-29.
MADHOK, O. P.
  1965.   Magnesium nutrition of *Helianthus annus* L. and *H. bolanderi* Gray subspecies *exilis* Heiger. Ph.D. Thesis, Univ. of Washington, Seattle.
MADHOK, O. P., and R. B. WALKER
  1969.   Magnesium nutrition of two species of sunflower. Plant Physiol. 44:1016-22.
MAIN, J. L.
  1974.   Differential responses to Mg and Ca by native populations of *Agropyron* species. Am. J. Botany 61:931-37.
MARRS, R. H., and J. PROCTOR
  1976.   The response of serpentine and non-serpentine *Agrostis stolonifera* to magnesium and calcium. J. Ecol. 64:953-64.
McCOLL, J. G., and F. R. HUMPHREYS
  1967.   Relationships between some nutritional factors and the distributions of *Eucalyptus gummifera* and *E. maculata*. Ecol. 48:766-71.
McMILLAN, C.
  1956.   The edaphic restriction of *Cupressus* and *Pinus* in the coast ranges of central California. Ecol. Monographs 26:177-212.
PROCTOR, J., and S. R. J. WOODELL
  1975.   The ecology of serpentine soils. Adv. Ecol. Res. 9:255-366.
REEVES, R. D., R. B. BROOKS, and R. M. MACFARLANE
  1981.   Nickel uptake by Californian *Streptanthus* and *Caulanthus* with particular reference to the hyper-accumulator *S. polygaloides* Gray *(Brassicaceae)*. Amer. J. Bot. 68:708-12.
SHEWRY, P. R., and P. J. PETERSON
  1975.   Calcium and magnesium in plants and soil from a serpentine area on Unst, Shetland, Scotland. J. Appl. Ecol. 12:381-92.
VLAMIS, J.
  1949.   Growth of lettuce and barley as influenced by degree of calcium saturation of soil. Soil Sci. 67:453-66.
WALKER, R. B.
  1954.   The ecology of serpentine soils. II. Factors affecting plant growth on serpentine soils. Ecol. 35:259-66.
WALKER, R. B., WALKER, H. M., and P. R. ASHWORTH
  1955.   Calcium-magnesium nutrition with special reference to serpentine soils. Plant Physiol. 30:214-21.
WALLACE, A., E. M. ROMNEY, and G. V. ALEXANDER
  1974.   Variation in the simultaneous analysis by emission spectrography of 24 elements in plant material. Commun. Soil Sci. Plant Anal. 5:45-50.
WARING, R. H., and J. MAJOR
  1964.   Some vegetation of the California coastal redwood region in relation to gradients of moisture, nutrients, light, and temperature. Ecol. Monographs 34:167-212.
WEBB, L. J.
  1969.   Edaphic differentiation of some forest types in eastern Australia. II. Soil chemical factors. J. Ecol. 57:817-30.
WYN JONES, R. G., and O. R. LUNT
  1967.   The function of calcium in plants. Bot. Rev. 33:407-26.

APPENDIX

Table 1. Species composition at each site. Species followed by an asterisk have the percentage cover recorded. The remaining species have values recorded corresponding to the number of m plots in which they were found at each site. Zeros indicate that a species was present within a stand but not found within the sampling areas.

Species	Site #							Cypress												Intermediate Stands				
	25	28	29	24	26	37	33	7	8	32	27	13	19	12	10	11	36	39	38	1	30	5	20
Umbellularia californica *	.	.	.	.	.	.	.	.	.	.	.	0	.	.	.	.	.	.	.	.	.	.	.
Cupressus macnabiana *	.	.	.	.	.	.	.	.	.	.	.	0	.	.	.	.	.	.	.	.	.	.	.
C. sargentii *	17	14	14	15	19	28	26	59	.	.	44	43	36	36	26	33	23	.	.	.	45	45	66
Arctostaphylos viscida *	38	45	44	52	39	46	28	38	47	36	12	28	18	12	49	42	33	51	53	76	34	33	0
Ceanothus jepsonii *	.	.	0	0	.	.	.	.	0	0	2	1	1	0	0	0	.	.	.	.	9	9	0
Quercus durata *	.	.	.	0	0	2	4	3	9	.	2	8	5	8	2	2	1	11	5	0	8	29	10
Galium andrewsii	.	.	.	.	.	.	0	0	.	.	.	2	2	.	1	3	2	4	1	0	3	3	5
Zigadenus fremonti	.	.	.	.	.	.	.	1	.	.	0	2	2	2	2	1	10	3	3	2	0	.	.
Adenostoma fasciculatum *	.	.	.	.	.	.	.	.	.	.	.	0	2	0	.	1	.	3	3	2	0	8	0
Heteromeles arbutifolia *	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0	2	0	8	0
Garrya congdoni *	.	.	.	.	.	.	.	.	.	0	.	.	.	.	.	.	.	0	4	0	0	10	.9
Monardella viridis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0	.	3	3	.5
Galium nuttallii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	1	5	1
Iris macrosiphon	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1
Pinus sabiniana *	.	.	.	.	.	.	.	.	.	.	.	.	0	.	.	.	.	.	.	.	.	.	.
Melica torreyana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	7
Sitanion hystrix	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	.	.	9
Bromus laevipes	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Eriophyllum lanatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Lomatium marginatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca reflexa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
Chloragalum pomeridianum	.	.	.	.	.	.	.	.	.	.	.	0	.	.	.	.	.	.	.	.	.	.	.
Stipa lepida	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linum (?)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sisyrinchium bellum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eriodictyon californicum *	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	.	.
Polygala californica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhus diversiloba	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Castilleja foliolosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ceanothus cuneatus *	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhamnus crocea spp. ilicifolia *	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0	0
Symphoricarpus mollis *	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Featuca californica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cercocarpus betuloides *	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sanicula tuberosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calochortus amabilis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Galium bolanderi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Brodeae laxa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 1 (continued).

Species	Site #	6	22	2	9	3	31	23	15	40	17	34	21	16	35	14	4	18
									—Non-Cypress Stands—									
Umbellularia californica	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cupressus macnabiana	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
C. sargentii	*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Arctostaphylos viscida	*	14	13	7	3	16	0	.	0	14	0	2	.	.	.	.	0	.
Ceanothus jepsonii	*	11	10	2	18	1	9	2	2	2	0	2	2	.	0	0	0	0
Quercus durata	*	13	24	16	34	26	56	3	13	2	13	70	29	3	6	8	4	51
Galium andrewsii		3	5	1	.	4	2	17	1	9	6	2	.	5	3	0	3	1
Zigadenus fremonti		1	0	.	.	.	.	6	.	6	.	0	.	.	.	.	.	4
Adenostoma fasciculatum	*	5	35	16	2	22	1	27	34	32	47	3	28	58	58	51	59	.
Heteromeles arbutifolia	*	0	6	3	9	9	4	4	6	2	2	3	6	2	2	5	13	18
Garrya congdoni	*	0	0	.	0	0	2	1	3	0	5	0	1	0	0	2	8	0
Monardella viridis		1	0	1	7	10	5	6	1	7	6	11	9	2	4	3	6	8
Galium nuttallii		1	6	5	6	7	4	4	2	5	5	4	6	.	1	3	.	3
Iris macrosiphon		1	1	1	3	1	.	2	0	.	.	.	.	2	.	.	.	.
Pinus sabiniana	*	.	20	7	0	10	0	0	0	0	0	0	.	.	2	.	.	.
Melica torreyana		8	9	8	5	3	8	4	1	4	1	4	6	8	8	2	0	.
Sitanion hystrix		6	9	8	.	2	7	11	1	8	0	2	1	1	0	.	.	2
Bromus laevipes		0	5	4	2	9	3	5	3	5	1	8	9	7	.	.	.	2
Eriophyllum lanatum		0	3	2	.	4	2	6	2	3	2	5	7	1	.	4	.	8
Lomatium marginatum		1	0	.	8	8	2	3	1	7	11	9	3	12	.	12	11	.
Festuca reflexa		.	.	7	.	6	6	1	2	.	1	0	3	.	.	.	.	.
Chloragalum pomeridianum		.	.	1	1	5	10	7	.	3	0	2	7	7	2	.	.	.
Stipa lepida		.	4	.	.	5	1	.	2	11	8	.	1	2	8	.	4	.
Linum (?)		.	.	.	.	4	1	2	2	1	10	2	6	6	3	.	.	.
Sisyrinchium bellum		.	0	.	.	3	3	7	2	2	3	1	5	0	.	3	.	.
Eriodictyon californicum	*	2	.	.	.	0	0	.	5	1	.	0	.	1	.	.	2	.
Polygala californica		.	.	.	4	.	0	.	.	.	.	.	.	.	.	4	.	0
Rhus diversiloba		.	.	.	0	0	0	.	.	.	.	.	.	0	.	.	.	0
Castilleja foliolosa		.	.	.	1	1	.	.	.	.	.	.	.	.	1	1	1	2
Ceanothus cuneatus	*	.	.	.	.	.	.	.	.	.	.	.	0	0	0	0	0	0
Rhamnus crocea spp. ilicifolia	*	.	.	.	.	.	.	.	.	3	.	1	.	.	.	.	0	0
Symphoricarpus mollis	*	.	.	.	.	.	.	0	.	0	.	.	4	.	.	.	0	4
Featuca californica		.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	9
Cercocarpus betuloides	*	.	1	.	.	.	.	.	.	.	.	1	6	1	.	.	.	.
Sanicula tuberosa		.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Calochortus amabilis		.	.	.	3	.	.	.	.	3	0	0	.	.	.	3	.	0
Galium bolanderi		.	.	.	.	.	.	.	.	0	2	4	2	.	.	.	.	.
Brodeae laxa		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

ACKNOWLEDGMENTS