



The Ecology of Serpentine Soils

R. H. Whittaker

Ecology, Volume 35, Issue 2 (Apr., 1954), 258-288.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28195404%2935%3A2%3C258%3ATEOSS%3E2.0.CO%3B2-T>

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Ecology is published by The Ecological Society of America. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Ecology

©1954 The Ecological Society of America

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2003 JSTOR

THE ECOLOGY OF SERPENTINE SOILS*

TABLE OF CONTENTS

I. INTRODUCTION	R. H. WHITTAKER 258
II. FACTORS AFFECTING PLANT GROWTH ON SERPENTINE SOILS.....	R. B. WALKER 259
III. PLANT SPECIES IN RELATION TO SERPENTINE SOILS.....	A. R. KRUCKEBERG 267
IV. THE VEGETATIONAL RESPONSE TO SERPENTINE SOILS.....	R. H. WHITTAKER 275

THE ECOLOGY OF SERPENTINE SOILS

I. INTRODUCTION

R. H. WHITTAKER

*Biology Section, Department of Radiological Sciences, General Electric Company,
Richland, Washington*

Areas of the soil-rock systems which may be grouped together as "serpentine" occur in many parts of the world and, wherever they occur, are known for their remarkable plant life. Many authors have described the flora and vegetation of serpentine areas in Europe: Sweden (Rune 1953),¹ Norway (Bjørlikke 1938), Finland (Kotilainen 1944, Rune 1953), Helgoland (Dahl 1912, 1915), Great Britain (Hunter & Vergnano 1952), Austria (Hayek 1923, Nevole 1926, Lämmermayr 1926, 1927, 1928a, 1928b, 1934, Kretschmer 1931), Czechoslovakia (Zlatník 1928a, 1928b, Suza 1928, Novák 1928), Switzerland (Beger 1922-3, Braun-Blanquet & Jenny 1926, Zollitsch 1927, Braun-Blanquet 1951), Yugoslavia (Pančić 1859, Novák 1928), Albania (Markgraf 1925, 1932), Greece (Boydell 1921, Turrill 1929), Italy (Messerli 1936, Negodi 1941, Bargoni 1943, Pichi-Sermolli 1948), Spain (Palacios 1936), and France (LeGendre 1919). Serpentine vegetation is reported also from the Ural Mountains (Novák 1926, Sočava 1927, Iljinski 1936), Southern Rhodesia (Blackshaw 1921), Japan (Yamanaka 1951-2, 1952, Kitamura 1950, 1952a, 1952b, Kitamura *et al.* 1950, 1952, 1953), Karakelang in Indonesia (Lam 1927), New Caledonia (Däniker 1939, Birrell & Wright 1945), New Zealand (Betts 1918, Cockayne 1921: 332), Cuba (Seifríz 1940, 1943, Carabia 1945, Beard 1953), Puerto Rico

(Holdridge 1945), Newfoundland (Fernald 1911), Quebec (Low 1884, Fernald 1907, Raymond 1950, Scoggan 1950, Rune 1953), British Columbia, and the United States. Apparently no information on vegetation is available from some areas of serpentine.

In the United States, scattered outcrops occur along the Appalachian chain from western Massachusetts through the largest Appalachian areas, those of Pennsylvania and Maryland (Harshberger 1903, 1904, Shreve 1910, Pennell 1910, 1913, 1930, Braun 1950: 248), south to Georgia (Radford 1948). The Pacific Coast states contain much more extensive areas of serpentine. The California formations (Mason 1946b, Kruckeberg 1951, and the following papers by Walker 1954, and Kruckeberg 1954) in the Sierra Nevada and the Central and North Coast Ranges total several thousand square miles. The major Oregon areas adjoin those of the California Coast Ranges and occupy much of the Siskiyou Mountain Range. The principal locations in Washington are about one hundred square miles in the Wenatchee Mountains in a belt lying just south of Mt. Stuart, about thirty square miles in the Twin Sisters Range southwest of Mt. Baker, and portions of the San Juan Islands.

These widely scattered serpentine areas have many features in common. In almost all cases they: (1) are sterile and unproductive either as farm lands or timber lands, (2) possess unusual floras, characterized by narrowly endemic species of great interest to the plant taxonomist and geneticist, and (3) support vegetation in striking physiognomic contrast with that on other soils. The problems of serpentine soils are thus both economically important and of special interest to biologists of several fields. The three features of

* A symposium originally presented at the meetings of the Northwest Scientific Association, Spokane, Washington, December 29, 1950, by R. H. Whittaker (presiding), Washington State College, R. B. Walker, University of Washington, and A. R. Kruckeberg, University of Washington.

¹ These citations are listed with those of the following paper by Whittaker (see p. 000). For additional European papers see Novák (1928), Pichi-Sermolli (1948), and Rune (1953).

serpentine areas above suggest three parts into which discussion of biological problems of serpentine may naturally be divided: the edaphic, concerning the soil itself and its relation to plant ecology; the autecological, dealing with the responses of plant species to serpentine and non-serpentine soils; and the synecological, considering

the peculiarities of serpentine vegetation. In the three papers following, students of these three aspects of the serpentine problem in the western United States will attempt to present a synthesis of what is known concerning the ecology of serpentine soils.

THE ECOLOGY OF SERPENTINE SOILS

II. FACTORS AFFECTING PLANT GROWTH ON SERPENTINE SOILS¹

RICHARD B. WALKER

Botany Department, University of Washington, Seattle, Washington

The distinctive vegetations of soils derived from serpentine and related rocks sharply set apart such areas from adjacent non-serpentine terrain in many regions of the world. The plant life of these serpentine areas varies greatly with location, topography, depth of soil, and other factors, but is usually sparse or stunted, and characterized by the presence of many species which seem to be restricted to the serpentine habitat. Many of the species present on adjacent non-serpentine soils fail to appear on the serpentine; others grow on the serpentine but are stunted, while only a few plants grow equally well on either type of soil.

These vegetational differences often serve to delineate the geologic discontinuities of an area even to the casual observer. An example of such differences is shown in Figure 1, a scene in Lake County, in the North Coast Ranges of California. On the left is a serpentine area (Soil W-30, Table II), on which the predominant woody species are Digger pine, *Pinus sabiniana* Dougl., chamise, *Adenostema fasciculatum* H. and A., leather oak, *Quercus durata* Jeps., musk-brush, *Ceanothus jepsonii* Greene, silk tassel bush, *Garrya condoni* Eastwood, and Christmas berry, *Photinia arbutifolia* Lindl., and on which a sparse herbaceous flora occurs, including *Chaenactis glabriuscula* D. C., *Clarkia concinna* (F. and M.) Greene, *Eriogonum nudum* Dougl., *Eriophyllum lanatum* (Pursh) Forbes, *Gilia capitata* Dougl., *Phacelia corymbosa* Jeps., *Plantago erecta* Morris, *Streptanthus glandulosus* Hook., and *S. Breweri* Gray. On the right, lies a non-serpentine hillside (Soil

W-53, Table II), on which is found an open stand of blue oak, *Quercus douglasii* H. and A., and a dense herbaceous cover which includes *Avena fatua* L., *Bromus* spp., *Brodiaea laxa* (Benth.) Wats., and numerous other species. The type of chaparral characteristic of serpentine areas covers thousands of acres in the California Coast Ranges, and can be distinguished at a glance from the oak-grass vegetation of hillsides of non-serpentine origin.

In other regions, comparable contrasts exist between serpentine and non-serpentine areas. In Oregon and Washington, slopes whose soils have been derived from serpentine or related rocks may be recognized readily by their barren, sparsely forested appearance, which contrasts with the presence of heavier forests on adjacent non-serpentine terrain. Robinson *et al.* (1935) describe the infertile and barren soils formed from serpentine rock in Maryland and Pennsylvania which support scrubby timber or poor farm crops, in contrast with the fertile soils of surrounding non-serpentine areas. The serpentine formations of Europe weather into sterile residual soils on which occur characteristic endemic species (Braun-Blanquet 1932, Novák 1928). Birrell and Wright (1945) described a serpentine soil in New Caledonia which bears a xerophyllous shrub vegetation from 3-5 feet high, a most unusual appearance in this region of high rainfall in which tropical forest is the ordinary plant cover. These examples serve to indicate that the uniqueness of serpentine floras is not a peculiarity of one region alone, but is world-wide in nature. A detailed discussion of the floristics of serpentine vegetation will be given by Whittaker (1954).

The striking differences often observed between the plant covers of serpentine and adjacent non-serpentine areas have naturally led to attempts to

¹ The material reported in this paper is largely taken from the author's dissertation for the Ph.D. degree in the Department of Botany, University of California, Berkeley. The encouragement and supervision of Professors A. R. Davis, H. L. Mason, and P. R. Stout, and the generous assistance of Dr. J. Vlamis are gratefully acknowledged.



FIG. 1. Barren, brush-covered serpentine hills (left) and blue-oak covered non-serpentine hillside (right) separated by a meadow of mixed rock origin. Lake County, California.

explain these phenomena in terms of the physical or chemical properties of the soil, or of the physiological characteristics of the plants. Frequently it has been supposed that plants restricted to, or endemic on, serpentine "require" some features of serpentine soil for proper growth, but the validity of this hypothesis can readily be attacked on the basis that a considerable number of these plants have been cultivated successfully in non-serpentine soils and even in culture solutions. Another common suggestion is that the endemic species grow well on the rather barren serpentine sites where competition is not severe, and are unable to survive on other soils where competition is more rigorous; but this is a suggestion that has been difficult to test experimentally. It is apparent that both the endemic and non-endemic species which grow successfully on these soils possess a "tolerance" for the serpentine habitat which is lacking in the greater number of plants which will not grow readily on this medium, and further that the non-endemic species possess some characteristic which is lacking in the endemic species. The problems of the possible restriction of endemic species to serpentine through competition and the differences which may exist between endemic and

non-endemic species will be discussed in the paper by Kruckeberg (1954) which follows. The balance of this paper will be devoted first to an outline of the general attributes of serpentine rocks and soils, followed by discussions of the various hypotheses which have been advanced to explain the tolerance or intolerance of plants for serpentine soil.

CHEMICAL PROPERTIES OF SERPENTINE ROCKS AND SOILS

Serpentine rock is essentially a magnesium iron silicate, formed by metamorphosis from peridotite. Although peridotite is often predominantly olivine, $(Mg, Fe)_2SiO_4$, varying amounts of pyroxenes and amphiboles are also present, so some Ca, Al, Na, and Ti are included. Also, in many instances chromite, $FeCr_2O_4$, and garnierite, $(Ni, Mg)SiO_3 \cdot nH_2O$, occur in appreciable proportions. These variations in the composition of the rock are reflected in the color, which may range from shiny green to bluish or almost black. Soils formed from the rock are usually reddish, brown, or gray in color at the surface, often changing to yellowish or greenish in the lower layers. Soils formed from un-serpentinized peridotite and peridotite-

serpentine mixtures have similar physical and chemical properties, so it will be convenient to refer to all these similar forms under the general term "serpentine soils" in this discussion. Since there is a wide range in the composition of the parent rocks, it is to be expected that the compositions of the resultant soils should vary considerably, especially in the secondary constituents such as calcium, potassium, and the heavy metals. Even small variation in these elements may have marked effects, however, on the ability of the soils to support plant growth.

While the total composition of the parent rocks is only one of the factors involved in the formation of soil, it is of considerable interest to examine analyses of some of these basic igneous rocks, and of soils of this origin (Table I). The contents of the major constituents, Si, Mg, and Fe, are in the same range in the rocks; aluminum is low in all cases; and values for all the other elements are under one per cent. Although the contents of calcium and the heavy metals are small, they will be seen to play important roles in some of the hypotheses which attempt to explain the intolerance of plants for serpentine soils. Magnesium content is reduced by weathering, and is seen to be much lower in the soils than in the rocks; it was noted by Robinson *et al.* (1935) that in most cases magnesium is lower in the surface soil than in the deeper soil layers. Loss of this element is striking in tropical soils such as the one from New Caledonia, in which the accumulation of iron is also particularly noticeable. Chromium is also especially high in the tropical soils, either because of its abundance in the parent rock or an accumulation similar to that of iron.

It is questionable whether the total analyses quoted above give reliable indications of the amounts of the various ions which are available for plant absorption. Important among the types of analyses which are intended to measure the levels of ions available to plants is the determination of the exchangeable cations by means of the ammonium acetate extraction method. The exchangeable cation values, as well as H-ion concentrations, for a number of serpentine and non-serpentine soils are given in Table II. The problems of the forms of chromium and nickel which exist in the soil and which may be absorbed by plants have been studied very little, but values for the exchangeable form of these ions are included in the table where available. Since the percentage of calcium present among the exchangeable cations is considered to be of particular importance in connection with soil fertility, this is also included in Table II. The table shows that magnesium much exceeds calcium except in the tropical soil

TABLE I. Total chemical analyses of certain rocks and soils

	Fresh serpentine rock, Cherry Hill, Maryland (Robinson <i>et al.</i> 1935) Per cent	Peridotite (90% olivine)†, Whatcom County, Washington (Pfeiffer 1945) Per cent	Serpentine soil material, Mt. Tamalpais, California (Robinson <i>et al.</i> 1935) Per cent	Serpentine surface soil, Dublin, Maryland No. 4722 (Robinson <i>et al.</i> 1935) Per cent	Serpentine soil, 5-15 in., New Caledonia (Birrell & Wright 1945) Per cent
SiO ₂	37.98	43.7	40.28	66.30	3.95
TiO ₂	0.10	**	0.12	0.83	—
Al ₂ O ₃	0.78	1.5	2.36	7.17	—
Al ₂ O ₃ +TiO ₂ ..	—	—	—	—	4.87
Fe ₂ O ₃	12.45	—	9.31	6.44	71.9
FeO.....	—	7.3	—	—	—
MnO.....	0.15	**	0.13	0.09	**
Cr ₂ O ₃	0.44	**	0.29	0.17	3.05
NiO.....	**	Trace	0.25	0.003	0.16
CaO.....	Trace	0.3	Trace	0.20	0.05
MgO.....	37.68	46.6	36.42	12.96	0.06
K ₂ O.....	0.06	**	Trace	0.66	—
Na ₂ O.....	0.01	**	0.02	0.53	—
P ₂ O ₅	0.03	**	0.02	0.03	—
SO ₃	0.52	**	0.08	0.13	—
Alkalis and undetermined..	—	—	—	—	0.84
Ignition loss...	10.35	+2.5	12.25	5.55	15.12

†From same area as soil W-207 (*cf.* Table II).

**Not determined.

— Included in another category.

from New Caledonia. The data also show that there is a considerable range of calcium levels among the serpentine soils, even though all are low in this element. It will be shown later how such differences may greatly influence the degree of infertility of a particular soil.

PHYSICAL CHARACTERISTICS OF SERPENTINE SOILS

Peridotite and serpentine formations are usually intrusions of great depth and often of ancient geologic origin; thus it might be anticipated that the soils would be deep, and such is the case in many of the Conowingo soils of Maryland, and in tropical soils which have been described (Robinson *et al.* 1935, Birrell and Wright 1945). On the other hand, many serpentine sites are in rolling or mountainous terrain, and the soils in such locations are usually shallow, presumably because the steepness of the slopes and the sparseness of the vegetation encourage continual erosion. In many cases, these soils are made up largely of relatively unweathered rock particles, and may be called lithosols; in many other instances, the shallow soils contain considerable clay and organic material and might better be called azonal soils of a relatively stable nature. Robinson *et al.* (1935) believe that some serpentine rocks are too low in alumina to form sufficient clay for the establishment of a normal soil covering, regardless of the topography. This hypothesis concerning insufficient clay formation may explain the existence of

TABLE II. *Exchangeable cations in soils*

Soil No.	Location and description	Parent material	pH	Exchangeable cations milliequivalents/100 gm soil						NH ₄ adsorp. capacity m. e./100 gm	% Ca
				Ca	Mg	K	Na	Ni	Cr		
(B & W)*.....	New Caledonia 0-5 in. layer	Serpentine	5.8	0.6	0.8	**	**	0.12	0.026	9.8	6.1
	5-15 in. layer		5.4	0.6	0.3	**	**	**	**	3.5	17
REB† 4722.....	Dublin, Maryland	Serpentine	5.85	0.16	4.09	0.06	0.13	0.012	0.006	**	**
W-30†.....	Lake Co., Calif.	Serpentine	6.80	2.12	12.1	0.11	0.05	0.026	0.001	14.2	14.9
W-37.....	Lake Co., Calif.	Serpentine	6.60	2.33	19.7	0.13	0.04	**	**	22.3	10.4
W-52.....	Marin Co., Calif.	Serpentine	6.35	3.20	11.2	0.37	0.13	0.003	**	17.0	18.8
W-53.....	Chelan Co., Wash.	Serpentine	6.62	2.03	5.95	0.20	**	**	**	8.66	23.4
W-207.....	Whatcom Co., Wash.	Peridotite	6.21	1.07	9.16	**	**	**	**	13.1	8.2
W-38.....	Solano Co., Calif.	Sandstone	7.20	11.1	3.2	0.23	0.09	**	**	13.1	84.7
W-53.....	Lake Co., Calif.	Sandstone	6.75	23.4	11.2	1.42	0.14	0.005	nil	30.6	76.4

*Data from Birrell and Wright (1945).

†Data from Robinson, Edgington, and Byers (1935).

‡The prefix *W* indicates data of the author.

**Not determined.

only a thin soil mantle on many rather level areas. The textures of the soils vary from heavy clays to light loams, with a friable, gravelly loam being the most common type in western United States. From a series of detailed physical analyses, Robinson *et al.* (1935) concluded that serpentine soils possess no physical characteristic which would render them particularly unfavorable for plant growth, although in some cases the clay contents of the subsoils were high enough to impede drainage.

Undesirable physical characteristics, such as shallowness of the soil mantle, gravelly texture, low clay content, and steepness of topography which encourages erosion, have important effects on the vegetation of serpentine areas, since they result in reduced moisture and nutrient levels. On moister serpentine sites, such as north slopes, the plant cover is more abundant, and often includes additional species which are absent in drier situations. This presumably indicates, at least in western United States, that plants which are widespread on serpentine soils possess drought resistance as well as tolerance for serpentine soils. The various physical factors may have effects in connection with soils of diverse parent materials, however, so the peculiarities of serpentine soils do not appear to be explicable on the basis of physical characteristics.

HYPOTHESES ADVANCED TO EXPLAIN TOLERANCE AND INTOLERANCE FOR SERPENTINE SOILS

A number of hypotheses have been advanced which attempt to explain the peculiarities of serpentine soils on the basis of soil chemistry. The development of different viewpoints on the subject probably can be attributed to the fact that the soils studied came from different climatic regions and to the probability that two or more of the proposed factors may operate simultaneously in many of the

soils. A discussion of each of the major hypotheses follows in the succeeding paragraphs. Most of these hypotheses have stemmed from the studies by agriculturalists of the infertility of these soils for crop plant production. From the agricultural viewpoint, *serpentine infertility* is equivalent to *serpentine intolerance* by crop plants, so these two terms will be used interchangeably below.

(1) *Low levels of major nutrient elements*

Gordon and Lipman (1926) observed low levels of nitrate and phosphate ions in the soil extracts which they studied, showing that these ions limited the growth of barley. Later, Vlamis (1949) demonstrated that lettuce and barley responded markedly to nitrogen and phosphate additions to a serpentine soil. The nature of such response in both an agricultural species, the tomato, *Lycopersicon esculentum* Mill., and a non-endemic but serpentine-tolerant species, the wall-flower, *Erysimum capitatum* (Dougl.) Greene, is shown by the results of greenhouse pot culture experiments in Table III (Walker 1948a). The soil used was obviously very deficient in nitrogen and moderately deficient in phosphorus, although it is recognized that under natural conditions in which water or other factors may be limiting growth, such deficiencies would be less severe. It is also a common observation that many types of soils, regardless of origin, are deficient in these elements. In a recent experiment, a serpentine soil from Chelan County, Washington, showed a severe deficiency of sulfur when tested with tomato plants in pot cultures. No doubt deficiencies of major nutrient elements are common in serpentine soils, but there is little evidence that any such deficiency can serve as a general explanation of poor plant growth on these soils, because in agricultural practice, heavy applications of nitrogen,

TABLE III. *Effects of nitrogen, phosphorus, and potassium additions to a California serpentine soil (W-30) on the yields of tomato and wall-flower, Erysimum capitatum*

Fertilizer addition	Weight of shoot (dry gm)	Per cent of NPK yield
	<i>Tomato</i>	
None	0.61	12
NPK	5.06	100
	<i>Erysimum capitatum</i>	
None	0.24	7
NPK	3.42	100
PK	0.27	8
NK	1.82	53
NP	2.98	87

phosphorus, potassium, and sulfur have failed to correct their infertility.

(2) *Alkalinity*

Gordon and Lipman (1926) suggested that the alkaline reaction of serpentine soils contributes to their infertility. Whereas the Californian soils with which they worked are alkaline, this is not true for the majority of serpentine soils, and it is also known that many somewhat alkaline soils of diverse origins are quite fertile. It is apparent that alkalinity cannot serve, in any case, as a general explanation for serpentine infertility.

(3) *Low available molybdenum*

It has been found that a number of the Californian serpentine soils are deficient in available molybdenum (Walker 1948b, Johnson, Pearson, and Stout 1952). This can be demonstrated by growing agricultural species such as tomato and lettuce in pot cultures with heavy nitrogen and phosphate fertilization. As yet, no investigation has been made to determine whether or not this low molybdenum level is characteristic of serpentine soils in general, nor are any data available to indicate whether native plants may suffer from a deficiency of this element. Such deficiency in the field seems somewhat unlikely in view of the slow growth rates of the plants, so it appears reasonable to state at present that molybdenum deficiency may contribute to the infertility of some serpentine soils, but is probably not the dominant factor in any case.

(4) *Toxicity of chromium, nickel, or other heavy metals*

It has been proposed that the presence of toxic concentrations of heavy metals such as chromium and nickel may be responsible for the unfavorable nature of serpentine soils for plant growth (Robinson *et al.* 1935, Birrell and Wright 1945). Unquestionably, the chromium and nickel contents are generally higher in serpentine soils than in

those of other origins, and appreciable amounts of these metals may be absorbed by plants. The amounts absorbed may be as high as 86 parts per million Ni and 4.5 parts per million Cr in the dry leaf material of *Pancheria glabrosa* growing on a tropical soil with pH of 5.8 in the surface horizon (Birrell and Wright 1945). These values are considerably higher than the levels found in either field- or greenhouse-grown tissue from several neutral serpentine soils of western United States (Table IV). Little is known about the factors affecting the absorption of nickel and chromium from soils, but it is probable that the pH, the nature of the primary and secondary minerals, the concentrations of anions such as phosphate, and perhaps other soil characteristics have considerable influence on the uptake of the heavy metals. The importance of pH in nickel availability was stressed by Hunter and Vergnano (1952), who studied a glacial area in Scotland in which the parent material is largely serpentine rock. Oats growing on soils in this area accumulated 16 to 134 parts per million Ni in the expanded leaves,

TABLE IV. *Nickel and chromium analyses of leaf tissue collected on serpentine soils*

Species	Location	Reference*	Parts per million in dry leaf tissue	
			Ni	Cr
Blackjack oak	Dublin, Maryland	Robinson <i>et al.</i> (1935)	4	4
Red oak	Dublin, Maryland	Robinson <i>et al.</i> (1935)	5	3
<i>Pancheria glabrosa</i>	New Caledonia	Birrell and Wright (1945)	86.3	4.5
<i>Araucaria mulleri</i>	New Caledonia	Birrell and Wright (1945)	19.3	12.6
<i>Garrya congdoni</i>	Lake County, California		12	nil
<i>Quercus durata</i>	Lake County, California		8.2	0.30
<i>Arctostaphylos</i> sp.	Lake County, California		10	0.43
Marglobe tomato	Grown in pots on soil W-30 from Lake County, Calif.		29	1.5
<i>Pseudotsuga taxifolia</i> ...	Chelan County, Washington (Soil W-85)		3.7	0.32
Marglobe tomato	Grown in pots on soil W-85 from Chelan County, Washington		5.8	1.6

*Analyses not otherwise credited are those of the author.

the larger amounts being absorbed from the more acid soils and the smaller amounts from the less acid fields. Concentrations of 30-40 parts per million in the leaves of young plants caused moderate toxicity symptoms, and higher concentrations caused more severe chlorosis and necrosis, present in longitudinal stripes.

Toxicity symptoms were noted by the writer in tomato and sunflower (*Helianthus*) plants grown in culture solutions if the concentrations of chromium or nickel in the solutions were sufficiently high to reduce plant growth appreciably. However, tomato and sunflower were grown on several serpentine soils from western United States (in which the calcium was raised to a favorable level) with excellent growth and with absence of toxicity symptoms. This may be, of course, merely further evidence that plants absorb less nickel from these nearly neutral soils than from more acid ones. Another aspect of toxicity which needs investigation with respect to serpentine soils is the fact that additions of molybdenum may alleviate toxicities caused by excessive nickel, manganese, or other cations in culture solutions (Milliken 1948).

As yet, there is insufficient evidence at hand to evaluate the toxicity hypothesis critically. Large amounts of chromium and nickel may be absorbed from some acid serpentine soils, but much less is available to plants from neutral soils. While this toxicity factor is of much importance in specific areas, it seems unlikely that it is alone responsible for the world-wide peculiarity of the serpentine habitat.

(5) Status of calcium and magnesium in the soil

The predominance of magnesium over calcium in the ferro-magnesian rocks and soils was advanced by Loew and May (1901) as the reason for poor growth on serpentine soils. They determined the calcium and magnesium contents of many soils by acid extraction or by total analysis and related these values to the productivity of the soils, concluding that the Ca:Mg ratio in the soil should equal at least one for good plant growth. Recently Vlamis and Jenny (1948) have used low calcium saturation of the soil colloids as a modern replacement for the old ratio hypothesis, attributing little importance to the magnesium except that it makes calcium less available. The amounts of adsorbed calcium and magnesium in some serpentine and non-serpentine soils are listed in Table II. The quantity of calcium is low in every case, but there is considerable difference in the percentage saturation with this ion. Magnesium is the predominant cation in the neutral or moderately acid serpentine soils of the temperate zone, while it may

be almost entirely replaced by hydrogen in the highly weathered tropical ones.

Vlamis (1949) demonstrated the relationship between calcium saturation of the soil and the yield of barley and lettuce, obtaining yields which were very low at 10% saturation, increased sharply up to 20-25%, and leveled off at saturations above 25%. The author has performed a series of experiments involving both agricultural and native species which lend considerable support to the calcium saturation viewpoint (Walker 1948a). In the technique used, individual lots of the field serpentine soil were leached with chloride solutions varying in calcium and magnesium as desired. After leaching, excess salt was washed out with water; the soils were dried, fertilized with NPK, and used for greenhouse pot cultures. In this manner, soil lots were prepared in which calcium varied from 5% to 80% of the total exchangeable cations, with magnesium varying in a complementary manner from 94% to 19%, and potassium remaining in all cases at about 1%. The results of representative experiments in which tomato, *Lycopersicon esculentum* Mill., variety Marglobe, was compared with an endemic species of crucifer, the jewel flower, *Streptanthus glandulosus* var. *pulchellus* (Greene) Jeps., are given in Table V.

These data indicate that the growth of tomato is much restricted at the calcium level of the field soil, is reduced to nil as the saturation of 5.6% is reached, but increases strikingly at the calcium levels above that of the field soil. In contrast, the yields of the *Streptanthus* plants were little changed by the calcium level. This indicates that the endemic species is more tolerant of the low-

TABLE V. Yields and leaf composition of Marglobe tomato and *Streptanthus* grown on lots of serpentine soil (W-30) with varying Ca saturation

Per cent Ca saturation of soil	Average yield of shoot, dry grams	Per cent of yield on field soil	Leaf-tissue analyses, milliequivalents per 100 dry grams		
			Ca	Mg	K
<i>Marglobe tomato</i>					
5.6	0.03	1.1	**	**	**
8.3	0.09	3.2	27.7	442	28.5
12.5	2.16	82	30.8	246	59.9
13.5*	2.63	100	35.5	233	50.2
25	7.74	294	38.2	117	29.9
34	7.52	286	54.7	99.8	38.5
<i>Streptanthus glandulosus</i> var. <i>pulchellus</i>					
5.6	3.73	75	21.8	222	56.8
8.3	3.59	73	26.8	166	58.3
12.5	3.68	74	54.6	120	58.6
13.5*	4.95	100	52.1	121	42.7
25	4.42	89	85.7	84.2	51.2

*Unaltered field soil.

**Plants died before end of growth period.

calcium medium than tomato, which seems to offer a physiological explanation for serpentine tolerance. Similar experiments performed on other agricultural species (lettuce, *Lactuca sativa* L., var. Romaine, and sunflower, *Helianthus annuus* L., var. Russian Mammoth), and two other native species (serpentine-collected races of *Helianthus bolanderi* Gray, subsp. *exilis* (Gray) Heiser, and *Streptanthus glandulosus* Hook.) have given results of a similar nature. Native species which do not invade serpentine areas react to low calcium levels as do the agricultural species (Kruckeberg 1954).

Reasons for the differences in responses of various plants to soils of low calcium saturation are not apparent. One indication may lie in the results of calcium and magnesium analyses of the leaf tissue. In Table V it is seen that the *Streptanthus* absorbed somewhat more calcium than the tomato at comparable soil calcium levels, but the most noticeable difference is that the magnesium absorption of the tomato greatly exceeded that of *Streptanthus* at the very low calcium saturations. This excessive magnesium in the tissues could in some way hamper the normal utilization of the calcium which is present, perhaps simply by ion competition at membranes or sites of absorption, so that the ratio of calcium to magnesium is apparently more important than the absolute amount of calcium. In lettuce and tomato, a Ca:Mg ratio in the tissue of less than 0.20 is accompanied by reduced yield and at least incipient calcium deficiency, while ratios of less than 0.15 are associated with severe calcium deficiency symptoms and great reductions in yield.

The results reported above lend confirmation to the proposal of previous workers (Loew and May 1901, Vlamis and Jenny 1948) that the basic cause of serpentine infertility is the low calcium level, and the writer is of the opinion that in the larger picture of serpentine tolerance and intolerance this is likewise the principal factor. The role played by the other adsorbed cations in relation to calcium is not clear, however, and probably varies with different soils. The data given above indicate that ability to exclude magnesium may be a characteristic of the tolerant species, but in some tropical serpentine soils magnesium has been replaced to a large extent by hydrogen, and, in such cases, unbalance between calcium and magnesium can be of no importance. Vlamis and Jenny (1948) noted that large amounts of adsorbed potassium or strontium had effects similar to magnesium in inducing calcium deficiency. Although the relationships of adsorbed hydrogen to the other cations and to the general problems of soil infertility have received much attention (Hes-

lep 1951), there is a lack of agreement concerning effects of hydrogen. It is thus difficult to compare the usual high-magnesium serpentine soils with those in which most of the magnesium has been replaced with hydrogen. It is evident, however, that in the latter group, calcium saturation is extremely low and probably of considerable importance even if a factor such as heavy metal toxicity should predominate in controlling plant growth.

DISCUSSION

Low levels of adsorbed calcium have been shown to limit the growth of serpentine-intolerant species, as represented by a number of common crop plants, but serpentine endemic species are tolerant of calcium levels even lower than are usually found in natural serpentine soils. There is no doubt that only those plants which possess the ability to thrive on soils of low calcium status can long persist in serpentine areas, while plants lacking this ability will be excluded from them.

The effects of nickel and chromium depend upon their availability in the soil, the amounts absorbed by plants, and the sensitivity of individual species to these metals. The amounts absorbed from some soils by the native species appear to be sufficiently high that more sensitive species might be expected to be adversely affected, but this has not been confirmed by experimentation. On other soils, even though the total nickel and chromium contents are known to be high, absorption by sensitive crop plants is insufficient to induce toxicity. It is apparent that considerable experimentation involving serpentine soils from different regions will be necessary before aspects of toxicity can be evaluated fully.

It is concluded that the basic reason for the intolerance exhibited by most plants for serpentine soils is the low calcium level. In special cases, heavy-metal toxicity may be more influential than the calcium saturation, or at least serve as an additional major factor limiting plant growth. The possible effects of low available molybdenum and high magnesium concentrations have yet to be fully evaluated, but the influence of magnesium in accentuating calcium deficiencies must be of importance in most serpentine soils. Often factors not unique in serpentine sites, such as limited water retention and low levels of various major nutrients, contribute to making the serpentine environment unsuitable for many species. Plants which grow well on serpentine soils must therefore first be tolerant of low calcium levels and, in addition, be tolerant of one or more of the following: high concentrations of chromium and nickel, high magnesium, low levels of major nutrients, low

available molybdenum, and the drought and other undesirable aspects of shallow, stony soils.

SUMMARY

1. In an attempt to elucidate the factors involved in the tolerance of some plants for serpentine soils and the intolerance of others for this unusual growth medium, a description has been made of the physical and chemical properties of these soils, followed by an examination of the various hypotheses which have been advanced to explain the peculiarities of the soils with respect to plant growth. They differ from other soils in these principal characteristics: low contents of total and adsorbed calcium, high magnesium content, and high contents of chromium and nickel.

2. Serpentine areas usually support a stunted type of vegetation, unique in its species composition. Such an area located in California is described.

3. It is well-established that these soils are infertile for the growth of most plants, yet are tolerated by certain others. The following hypotheses, which have been advanced to explain tolerance and intolerance of serpentine soils, are examined: various physical factors, low levels of major nutrient elements (especially nitrogen and phosphorus), alkalinity, low available molybdenum, toxicity of nickel or chromium, and the status of calcium and magnesium in the soil. While all of these have effects under certain circumstances, experimental evidence favors the view that low calcium level is the basic cause of the peculiarity of serpentine soils, with the other factors of secondary importance.

4. It is concluded that plants which grow well on serpentine areas must first be tolerant of low calcium levels and, in addition, must be tolerant of one or more of the following in special situations: high concentrations of nickel and chromium, high magnesium, low levels of major nutrients, low available molybdenum, and unfavorable physical aspects of shallow soils.

REFERENCES

- Birrell, K. S. and A. C. S. Wright.** 1945. A serpentine soil in New Caledonia. *New Zeal. Jour. Sci. Tech.* **27A**: 72-76.
- Braun-Blanquet, J.** 1932. *Plant sociology*. Transl. by G. D. Fuller and H. S. Conard. McGraw-Hill Book Co. New York.
- Gordon, A., and C. B. Lipman.** 1926. Why are serpentine and other magnesian soils infertile? *Soil Sci.* **22**: 291-302.
- Heslep, J. M.** 1951. A study of the infertility of two acid soils. *Soil Sci.* **72**: 67-80.
- Hunter, J. G., and O. Vergnano.** 1952. Nickel toxicity in plants. *Ann. Appl. Biol.* **39**: 279-284.
- Johnson, C. M., G. A. Pearson, and P. R. Stout.** 1952. Molybdenum nutrition of crop plants. II. Plant and soil factors concerned with molybdenum deficiencies in crop plants. *Plant and Soil* **4**: 178-196.
- Kruckeberg, A. R.** 1954. Plant species in relation to serpentine soil. *Ecology* **35**: 267-274.
- Loew, O., and D. W. May.** 1901. The relation of lime and magnesia to plant growth. I. Liming of soils from a physiological standpoint. II. Experimental study of the relation of lime and magnesia to plant growth. *U. S. Dept. Agr. Plant Ind. Bull.* **1**, 53 pp.
- Millikan, C. R.** 1948. Antagonism between molybdenum and certain heavy metals in plant nutrition. *Nature (London)* **161**: 528.
- Novák, F. A.** 1928. Quelques remarques relatives au problème de la végétation sur les terrains serpentiniques. *Preslia* **6**: 42-71.
- Pfeiffer, D. H.** 1945. Thermomineralogical changes of olivine from the Twin Sisters Mountains of Washington. Thesis 5113, University of Washington, Seattle.
- Robinson, W. O., Glen Edgington, and H. G. Byers.** 1935. Chemical studies of infertile soils derived from rocks high in magnesium and generally high in chromium and nickel. *U. S. Dept. Agr. Tech. Bull.* **471**.
- Vlaminis, J.** 1949. Growth of lettuce and barley as influenced by degree of calcium saturation of soil. *Soil Sci.* **67**: 453-466.
- Vlaminis, J., and H. Jenny.** 1948. Calcium deficiency in serpentine soils as revealed by adsorbent technique. *Science* **107**: 549.
- Walker, R. B.** 1948a. A study of serpentine soil infertility with special reference to edaphic endemism. Thesis, Ph.D., University of California, Berkeley.
- , 1948b. Molybdenum deficiency in serpentine barren soils. *Science* **108**: 473-475.
- Whittaker, R. H.** 1954. The vegetational response to serpentine soils. *Ecology* **35**: 275-288.

THE ECOLOGY OF SERPENTINE SOILS

III. PLANT SPECIES IN RELATION TO SERPENTINE SOILS

ARTHUR R. KRUCKEBERG

Department of Botany, University of Washington, Seattle, Washington

The North Bay counties (Napa, Lake, Marin, and Sonoma) of central California have afforded an ideal locale for study of the vegetational discontinuities associated with serpentine outcrops. Here, large areas of serpentine rocks are exposed; and one is impressed at once by the sharp contrasts among vegetation types. Walker (1954) has described in detail the distinct differences in vegetation that exist between the two soil phases of this mosaic of serpentine and non-serpentine formations. The gross differences in aspect between the two types of vegetation are particularized when a tabulation of species is made. The vegetation of non-serpentine areas consist mostly of species common to similar sites throughout central California whereas serpentine outcrops support a flora rich in endemic species. Such sclerophyllous shrubs as *Quercus durata* Jeps., *Ceanothus jepsoni* Greene, *Garrya congdoni* Eastwood, and even the small tree, *Cupressus sargentii* Jeps., are unmistakable "indicator" species because of their typical restriction to and numerical dominance on serpentine soils. Although not endemic to serpentine, *Adenostoma fasciculatum* H. & A. and *Photinia arbutifolia* Lindl. are likewise characteristic dominants in this vegetation pattern.

It is not these dominant woody species, however, which have made these serpentine areas celebrated as a source of rare and endemic plants. The transient spring flora of these dry serpentine hills still continues to be a source of "new or otherwise noteworthy" additions to the California flora. The list of diminutive annuals and herbaceous perennials that merit the serpentine endemic status is increased every year. From all accounts (Morrison 1938, 1941, Stebbins 1942, Mason 1946, Hoffman 1952), genera of the annual life-form are by far the richest source of variation throughout the serpentine mosaic of central California. One of the genera most characteristic of the serpentine areas is *Streptanthus*, which will serve as an example of some of the genetic problems of serpentine endemism.

The distributional responses of different plant species to serpentine soils raise three groups of problems: (1) Why are so many species excluded from serpentine soils?, (2) Why are other species, which occur with them off serpentine, able to

grow successfully on serpentine?, (3) Why is a third group of species restricted to serpentine soils? In this paper these three questions will be examined further, seeking genetic and ecologic, as well as edaphic, answers.

TOLERANCE TO SERPENTINE SOILS

From the careful work of Vlamis & Jenny (1948), Vlamis (1949), and Walker (1948, 1954), we may state a working hypothesis on serpentine tolerance: A major criterion for serpentine tolerance must be the capacity of serpentine plants to grow on soils of *low calcium* levels. It has been shown by these authors that crop plants, which grow poorly in serpentine soils, are unable to absorb sufficient calcium from them. In addition, Walker (1948) proposed that serpentine endemics appear to be characterized by their ability to obtain sufficient calcium, even at the low concentrations characteristic of serpentine soils. Some native species occur both on and off serpentine, however, and studies of these may further clarify the problem. We might expect to find, within species of this latter type, some populations adapted to serpentine and others not so adapted. The demonstration of such serpentine and non-serpentine races, if they do exist, would provide some basis for a genetic interpretation of serpentine endemism. These species which occur both on and off serpentine may be called *bodenwag* plants (Unger 1836) in contrast to *bodenstet* species which are restricted by a requirement for a specific chemical substance in the soil. The use of serpentine and non-serpentine populations of *bodenwag* species may be especially effective in the study of serpentine adaptation, since the populations being compared should be closely similar in every respect except that with which we are most concerned—adaptation to serpentine.

Seeds of a number of *bodenwag* species were collected from both serpentine and non-serpentine sites. These paired populations of the same species were then grown on serpentine soils adjusted to different levels of exchangeable calcium. Invariably, the serpentine populations were much more tolerant of low calcium levels (less than 25% exchangeable Ca) than the populations from other soils. Some of the most striking results were ob-

tained with two strains of the *Phacelia californica* Cham.—*P. imbricata* Jeps. complex. The non-serpentine strain was from Los Alamos Creek, Sonoma County, where it grows on soil derived from basalt; the serpentine strain came from the rather extensive serpentine outcrop on Tiburon Peninsula, Marin County. Seeds of these two strains were sown on triplicated 1600-gram aliquots of serpentine soil prepared in the following manner: The series represented by pot "A" in Figure 1 was treated with gypsum ($\text{Ca}_2\text{SO}_4 \cdot 2\text{H}_2\text{O}$) in the amount equivalent to 2 tons to the acre and pot "B" in amount equivalent to 4 tons to the acre, while "C" is unaltered serpentine soil and "D" the serpentine soil plus a nitrogen-phosphorus-potassium treatment ($\text{N}_3\text{P}_4\text{K}_2$). The photographs of Figure 1 show the rather clear-cut differences in growth response with these soil treatments. In line with Walker's hypothesis of tolerance to low calcium levels, it is seen that only the serpentine strain grew at the low calcium level of the field soil, whereas the non-serpentine strain required a significant calcium amendment before its growth became comparable to the serpentine form. The results of the NPK treatment shed additional light on the specificity of the effect of calcium on the growth of the two strains. Only the serpentine strain showed good growth on the fertilized serpentine soil. The non-serpentine strain grew no better on this soil than on the unaltered serpentine soil. Thus it is seen that an NPK amendment did

not ameliorate the poor growth of the non-serpentine strain on a soil of low calcium level.

The results of tissue analyses further substantiate the suggestion of Walker that serpentine species may absorb calcium in preference to other cations, notably magnesium. The most significant feature of the graph in Figure 2 is the difference between the two strains in amounts of calcium absorbed. Even though both strains showed increase in calcium absorption as calcium level in the soil was increased, there was a decided difference in the absolute amounts absorbed by each strain. At each of the three soil-calcium levels, the serpentine race had absorbed greater amounts of calcium and had absorbed less magnesium than had the non-serpentine race.

To complete the picture of the calcium effect, results of additional related experiments may be summarized:

(1) Several native *bodenveg* species were grown on a series of serpentine soils adjusted to levels of exchangeable calcium ranging from 3% to 80%. For the non-serpentine strains, the minimum calcium level for normal growth was 25% of the total exchange capacity of the soil. In sharp contrast, the serpentine strains showed vigorous growth at 13% and at least fair growth at 6%, the latter calcium level being well below that of unaltered serpentine soil.

(2) A fertile soil of the Yolo series was reconstituted so as to simulate a serpentine soil in low calcium and high magnesium levels. The growth of serpentine and non-serpentine strains of *Phacelia* on this "serpentine" Yolo soil was compared with that on an unaltered (control) Yolo soil. As might be expected, the low-calcium Yolo replica-



FIG. 1. Reaction of serpentine and non-serpentine strains of *Phacelia californica* to unaltered and reconstituted serpentine soil. Pot A: 2 tons/acre $\text{Ca}_2\text{SO}_4 \cdot \text{H}_2\text{O}$; pot B: 4 tons/acre $\text{Ca}_2\text{SO}_4 \cdot \text{H}_2\text{O}$; pot C: unaltered serpentine; pot D: serpentine plus $\text{N}_3\text{P}_4\text{K}_2$. Plants of serpentine and non-serpentine strains appear on right and left halves of pots, respectively.

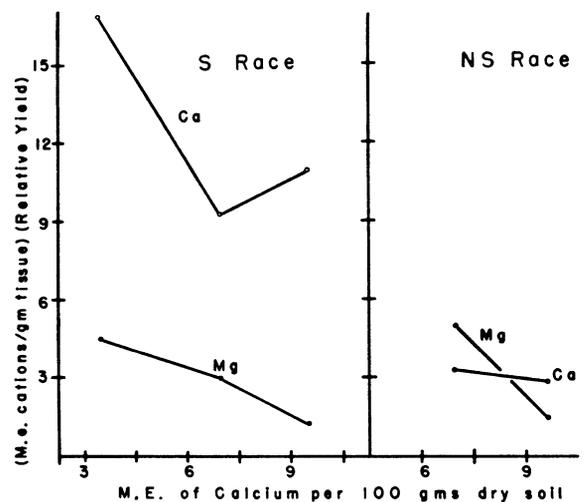


FIG. 2. Comparisons between serpentine (S) and non-serpentine (NS) strains of *Phacelia californica*. Total cation absorption (m.e. cations/gm tissue × relative yield) plotted against soil calcium level.

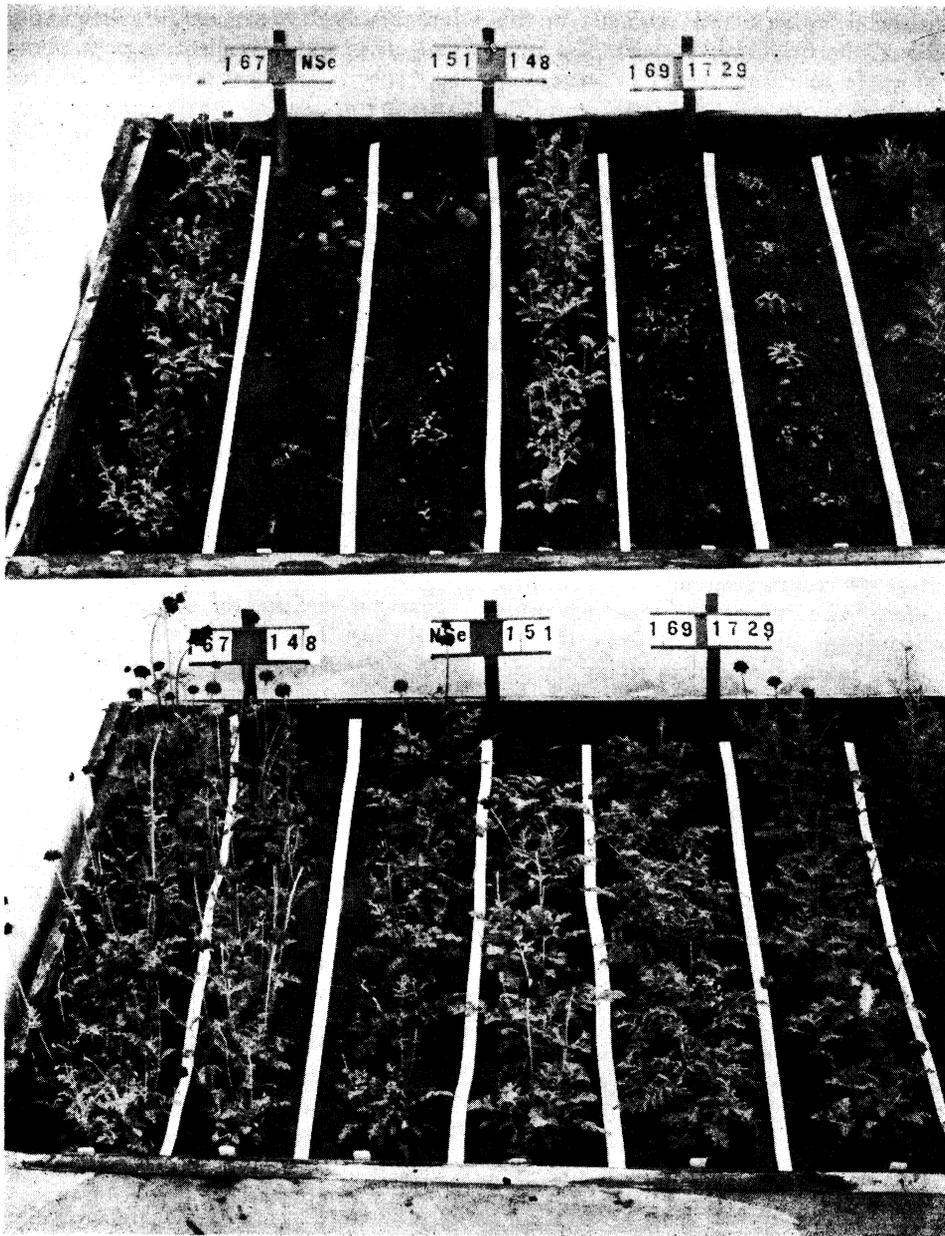


FIG. 3. Response of two serpentine and four non-serpentine strains of *Salvia columbariae* to serpentine soil (above) and non-serpentine soil (below). The serpentine strains are S-148 and S-167.

tions gave the same all-or-none picture that was so characteristic for the two *Phacelia* strains grown on unaltered serpentine soil. The non-serpentine strain was unable to grow in the "serpentine" Yolo soil, presumably because of the same adverse low calcium level as in the unaltered serpentine soil.

(3) Differences in response appeared among different *bodenvag* species. Of 21 species of several plant families tested, 12 showed definite differentiation into serpentine and non-serpentine races. Most of the annual and perennial herbs

other than grasses showed the differentiation into races, but none of the grass species studied did. Several examples of the rather definitive responses of races of *bodenvag* species to serpentine are cited elsewhere (Kruckeberg 1951). The clear-cut ecotypic response of biotypes to serpentine soil is typified in the example of the annual sage, *Salvia columbariae* Benth. (Fig. 3). In contrast, the herbaceous perennial, *Achillea borealis californica* (Poll.) Keck, gave a mixed response (Kruckeberg 1951). Some non-serpentine strains of *Achillea* were quite uniform in their intolerance

of serpentine, while others were variable in this respect. As yet, the uniform tolerance of a *non-serpentine* strain (a maritime form) to serpentine soil is unexplained.

(4) Results were obtained which point to differences in low-calcium tolerance even among serpentine endemics. Certain *Streptanthus* species (subsection *Hesperides*) grew quite well in a 3% calcium soil, while others (subsection *Pulchelli*) made a much poorer showing at this extremely low calcium level. These results seem to be correlated with field observations of the distribution on serpentine outcrops of these two groups of endemic *Streptanthi*. The former group (better adapted to the 3% level) is more frequently found on the barren patches of "raw" serpentine and on loose, fine talus. The other group (less tolerant of the 3% level) occurs predominantly where some development of the serpentine soil has taken place.

The experimental results seem in agreement with those of Walker. The importance of factors other than calcium-level for some plants cannot be excluded, but there is good reason to stress the degree of calcium saturation of the soil as of major significance in the serpentine problem. It appears probable that an important requirement for existence of serpentine endemics on serpentine soil is their capacity to obtain calcium at low levels. It may also be held that those species growing both on and off serpentine are able to do so because either their whole populations or, more frequently, their specially adapted serpentine populations possess that same adaptation to low calcium levels. The plants growing on serpentine may, in addition, be adapted to the low levels of other nutrients, to the openness and strong exposure to evaporation in the serpentine communities, and to other factors.

That such is the case is suggested by the phenomenon of "serpentinomorphism". Many serpentine populations show at least slight morphological distinction from non-serpentine populations of the same species, and some are distinctive enough to have been named as varieties. Often the serpentine populations are of reduced stature, with denser branches and smaller, thicker, more pubescent leaves than the non-serpentine population. These characteristics of serpentine plants are discussed by Pichi-Sermolli (1948) and Rune (1953). Pichi-Sermolli recognizes six tendencies: reduction in size of leaves and other organs, shrubbiness of growth, stunting or dwarfing, greater development of the root system, increased glaucousness, and reduced pubescence (there are contrary indications of increased pubescence in some species; consistency among different species need not always be expected). Most of these dif-

ferences, both in serpentine species compared with congeners and in serpentine populations of *boden-vag* species, are those to be expected of plants growing in dry and open situations. It thus seems likely that serpentine plants are physiologically adapted to the open characteristics of serpentine communities as well as to the special soil conditions, and that the physiological adaptations of serpentine plants may have some degree of morphological expression.

GENETIC ASPECTS OF SERPENTINE ADAPTATION

The foregoing results, together with field observations, may provide some basis for considering genetic and evolutionary aspects of the serpentine problem. One of the characteristic genera of serpentine plants in California, *Streptanthus*, is especially instructive in this respect (Kruckeberg 1951). All of the dozen or more species of the section *Euclisia* of this genus are serpentine plants, occurring here and there in northern California, the total range of a species being in some cases only a few square miles of serpentine. Some of these species are quite strictly confined to serpentine, others occur predominantly on serpentine but also maintain substantial populations on other soil materials. Still other species of *Streptanthus* have not been observed on serpentine, or occur predominantly on other rocks but maintain populations on serpentine.

It was, in part, some of these annual species endemic to serpentine outcrops that led Stebbins (1942) to seek a genetic explanation of endemism. Stebbins proposed that there are two types of endemics. The "depleted" species is an old (but not necessarily senescent) species which has acquired endemic status through the loss of most of its biotypes which formerly allowed the species to exploit a greater variety of habitats. Thus, by "biotype depletion," the species has been pared down to but one or a few biotypes specifically adapted to serpentine or some other local or specialized habitat. The other type of endemic, the "insular" species (which may occur as well on a continent as on an island) could have originated from a few isolated individuals pre-adapted to a specific habitat situation. Such a species, *ab initio*, is an endemic. The "depleted" and "insular" species are suggestive of the more familiar concepts of paleo- and neoendemic species, but may have little to do with age of the species.

Both types of species origin may be postulated for the serpentine endemics in *Streptanthus*. It is probable, moreover, that we can observe depletion in progress in some species. *Streptanthus glandulosus* Hook. is the most wide-spread serpentine species of the genus in California. It occurs

mainly on serpentines from San Luis Obispo County north to Del Norte County, but occasional non-serpentine localities for the species are also encountered. *Streptanthus glandulosus* was submitted to the same experimental procedures as other *bodenwag* species, with seed of both serpentine and non-serpentine strains grown reciprocally on non-serpentine and serpentine soils (Kruckeberg 1951). The non-serpentine forms proved to be much less tolerant of serpentine soil than their serpentine relatives; at least two biotypes of different physiological tolerance are present in the species. *Streptanthus glandulosus* may consequently be interpreted as a species originally possessing several edaphic biotypes, of which the non-serpentine biotypes are almost eliminated from the population, leaving the species very nearly a depleted serpentine endemic. This interpretation seems generally more plausible than that a serpentine species is extending its range off serpentine. While *S. glandulosus* appears to be only a few steps from complete serpentine endemism, such congeners as *S. breviflorus* Gray, *S. barbiger* Morrison (*in ed.* 1941), and *S. batrachopus* Morrison are obligate serpentine endemics.

On this basis, a reasonable, if necessarily somewhat speculative, interpretation of the development of serpentine endemism in a genus may be suggested. A species characteristic of normal soils extends its range into an area where serpentines alternate with other soil types. Among the populations of the species are some individuals at least partially adapted to low calcium levels and other conditions on serpentine; seeds of these individuals may fall on serpentine soils or the transitional soils along the margin of a serpentine area, develop to maturity, and reproduce. Among the progeny, those individuals survive that are best adapted to the environment on serpentine. In time, through this selection, various genes favorable for survival on the serpentine sites accumulate, while other genes of this originally non-serpentine population are eliminated by the selective action of the serpentine environment. The serpentine population thus develops its own genetic pattern of adaptation to serpentine environments; it becomes a biotype distinct from that on nearby non-serpentine soils within the confines of a *bodenwag* species. If, now, the non-serpentine biotypes gradually lose ground in competition with other plants until they ultimately become extinct, the species has become a depleted serpentine endemic. It has, step by step, gone through a hypothetical sequence from serpentine exclusion to serpentine endemism which appears to exist contemporaneously among the different species of a genus (*e.g.*, *Streptanthus*).

Once established on serpentine, the species may

branch out further. Occasional seeds from one outcrop or area of serpentine may reach other outcrops or areas, to which they are fairly well pre-adapted. The soils of various serpentine outcrops may be significantly different, however, and the plants growing on them may encounter somewhat different microclimates and different associates. In adaptation to these environmental differences and by genetic drift, the separated populations of the species may gradually diverge into different biotypes and eventually different "insular" species. An additional possibility is that a *bodenwag* species coming in contact with a number of serpentine outcrops may, on each, differentiate into a local biotype; and these may, with further divergence and extinction of or separation from the parent species, become local serpentine endemics. In either of these ways there may arise those clusters of closely related serpentine species, each on its own outcrop or area, which we observe in genera such as *Streptanthus*.

Interpretation of the autecology and evolution of serpentine plants requires recognition of edaphic biotypes within the species. These adaptively differentiated populations within the species, or *ecotypes*, are very well known in modern biosystematics through many studies, beginning with the pioneer work of Turreson (1922). The outstanding work of the team of Clausen, Keck, and Hiesey (1940, 1948) has shown, for example, the existence of chains of more or less discrete, climatically adapted types in various perennial species ranging from sea-level to above timberline in California. Such physiologically adapted habitat-types probably exist either as discrete populations or as complex gradients of variation in most widespread species occupying diverse habitats. Almost all the reported ecotypes have been delimited on the basis of climatic, or climatic and geographic, criteria.

The demonstration of edaphic ecotypes implies the existence of a level of ecotypic variation within the species in addition to the climatic and geographic level. The relation of the edaphic-local and climatic-geographic ecotypes may be illustrated by some of the work of Clausen, Keck, and Hiesey. In their report of transplant work on clones of the herbaceous perennial *Achillea borealis californica* (Poll.) Keck (Clausen, *et al.* 1948), the existence of climatic races in the species along an altitudinal transect was established. One of these ecotypes, that of the inner Coast Ranges and Sierra Nevada foothills, was studied by the present author (Kruckeberg 1951) in relation to serpentine and non-serpentine soils; the existence of at least two edaphic ecotypes was shown. There are thus edaphic subdivisions within climatic ones

in this species, *i.e.*, ecotypes within ecotypes. Moreover, since the geographic area occupied by the foothill climatic ecotype is very diverse lithologically and therefore is a mosaic of different soil types, additional edaphic ecotypes may very well be expected. The superposition of ecotype on ecotype at least suggests that there exists a much more complex genotypical response to the habitat than is implied in consideration of single environmental factors. Viewed from a holistic standpoint, ecotypic differentiation must be in relation to the whole pattern of selective forces in the environment. Analysis of either a climatic or edaphic ecotype by itself thus takes a segment of the species population out of context from the whole of its pattern of response to edaphic, climatic-geographic, and biotic environmental factors in relation to which its various sub-populations are maintained. To be sure, the holistic viewpoint is untenable as an experimental approach, for these various factors must be analyzed one by one. A holistic interpretation of the causes of vegetational patterning can become an experimentally substantiated concept only when analyses of each factor has been achieved and the results integrated into a unified picture.

EXCLUSION OF SERPENTINE ENDEMIC FROM NON-SERPENTINE SOILS

If the preceding discussion offers some interpretation of serpentine adaptation, there remains the problem of serpentine restriction—why some species do not grow on soils other than serpentine. One possible answer would be that the serpentine endemics “need” some condition of serpentine soils. While it is hard to conceive of a plant “needing” a very short supply of calcium, serpentine plants might still conceivably be so adapted that they require high levels of magnesium, iron, nickel, chromium, or some other substance in abundant supply in at least some serpentine soils. It is easily shown by experiment that such is not the case. Plants of many serpentine species and serpentine populations of *bodenzag* types have been grown by the author and others on serpentine and non-serpentine soils. The growth of these serpentine plants is usually better on the non-serpentine than on the serpentine soils, and apparently no case has been reported in which growth of a serpentine species is inhibited by the conditions of a non-serpentine soil. While these results would have surprised some previous investigators (Novák 1928, Lämmermayr 1927, Morrison 1941), who were convinced that serpentine species were restricted to serpentine because of some essential substance furnished by that soil, it seems clear that we must seek elsewhere for the explanation of serpentine restriction.

Field observation may offer some suggestions. Even to the unpracticed eye, the demarcations between serpentine and non-serpentine vegetation, where swaths of chaparral cut through the oak woodlands, are remarkably abrupt. Such conspicuous discontinuity could conceivably be produced directly by edaphic discontinuity if the serpentine species did require some special substance in serpentine soil, but it is also suggestive of a dynamic discontinuity between kinds of individuals from different populations or species. The serpentine vegetation itself may appear from a distance to be an almost impenetrable scrub, except for the scattered bare spots. Yet, on foot in the head-high brush, one notices that each sclerophyllous bush is separated from its neighbor by a rather uniform distance. Under the shrubs and in the intervening spaces there are only scattered herbaceous plants; most of the ground surface is bare serpentine soil, lightly covered in places by dead sclerophyll leaves. The bare areas of serpentine rock appear to be truly pioneer habitats, only beginning to be occupied by plants, while the chaparral is also an “open” community with much apparently unoccupied space for plant growth. This open appearance above the soil surface does not necessarily mean that more serpentine plants can grow there than at present; the chaparral appears in fact to be in a stable and self-maintaining condition with its present population. In contrast to this open community on serpentine, however, adjacent plant communities on other soils appear “closed,” having either a forest canopy, though not a dense one (in the black oak-madrone forest), or an open tree stratum with a closed herb stratum dominated by grasses (in the blue oak woodland).

A working hypothesis on the restriction of serpentine plants to serpentine thus suggests itself. The serpentine endemics are able to maintain themselves in open serpentine communities where competition is not severe, but not in the more rigorous competition of non-serpentine communities.

The first step toward an evaluation of this hypothesis would be to determine whether non-serpentine plants affect the growth of serpentine endemics when the two are grown together on a fertile non-serpentine soil. The next step—if competition, *per se*, is demonstrated in the initial step—would be to dissect the competition factor into its components. That is to say, to analyse experimentally this apparent biotic effect. Is the effect produced by competition for some factor limiting in the environment, or, as suggested by H. L. Mason (oral comm.), does some specific element of the environment (biotic, edaphic, etc.) inhibit the growth of the serpentine endemic spe-

cies? The first step should be a fairly simple one; the next step—the analysis of competition—is the difficult one. As yet, results from the first procedure only can be presented.

A rather simple procedure was followed in the first experiments. Identical mixtures of weed seed—mustard (*Brassica*), filaree (*Erodium*), perennial rye-grass (*Lolium*), bur clover (*Medicago*), wild oats (*Avena*)—and endemic *Streptanthus* seed were sown on each of two unaltered soils, a fertile Yolo fine sandy loam and un-screened serpentine soil (Henecke gravelly clay loam). These cultures were periodically irrigated, and within a week or so significant differences in the two could be detected. At maturity, the two bins had a remarkably different aspect. The Yolo bin was covered with a lush growth of mustard, bur clover, and wild oats—but not a single endemic. From a distance the serpentine bin appeared rather barren, but closer inspection showed that it was covered with a good scattering of *Streptanthus* and rather stunted growth of grasses (mostly rye-grass and wild oats). Conspicuous on the serpentine was the absence of even a single seedling of mustard, while other dicot weeds soon died. Knowing from previous greenhouse cultures that *Streptanthus* do well on Yolo soil by themselves, it seemed apparent that the weedy annuals in some way affected the growth of the endemics. That this is a reasonable explanation is further suggested by the fact that during the early seedling stages on the Yolo soil, several seedling *Streptanthus* were observed. These disappeared as the weed crop matured.

Encouraged by these results, similar competition bins (Figure 4) were set up the following year, but on a larger scale. By this time it had been established that calcium amendments to serpentine made it possible for non-serpentine plants to do well on that otherwise infertile medium. Hence, a calcium-reconstituted serpentine soil was the medium for one competition plot, in addition to the unaltered serpentine and Yolo soil bins. These three bins were sown with a mixture of weed and *Streptanthus* seed. On the unaltered soils, results identical with those of earlier experiment were observed. In addition, the expected results on the calcium-altered serpentine bin were realized. Here, mustard, clover, and filaree sprouted freely, while *Streptanthus* plants were conspicuously absent.

In these experiments with competing plants, a serpentine plant occupies a serpentine environment while its potential competitors are excluded by edaphic factors. On the non-serpentine soil, in contrast, the serpentine plant is excluded by the presence of other plants, though very well able to



FIG. 4. Appearance of competition during seedling stage in bins. All three soil bins were sown with identical mixtures of endemic and weed seed. Bin A contains unaltered serpentine soil; Bin B, non-serpentine soil; Bin C, calcium-reconstituted serpentine soil. Note absence of *Brassica* seedlings on serpentine (Bin A), but their presence when calcium has been added to serpentine (Bin C).

grow on non-serpentine soil in their absence. It would be premature to consider that these experiments fully substantiate the hypothesis offered. The "competition" should be further analyzed to determine what actual factors exclude the serpentine plants from an environment occupied by non-serpentine plants, and alternative possibilities should be further considered. An interpretation of the reciprocal exclusion of many serpentine and non-serpentine plants from non-serpentine and serpentine soils may, however, be at least tentatively offered. Some *bodenrag* species are able to range from non-serpentine onto serpentine soils because their serpentine populations, at least, are adapted

to low soil calcium levels (and other factors); these species usually contain distinct serpentine ecotypes. Other species lacking these adaptations are excluded and their populations abruptly limited at the margin of the serpentine area. Still other species adapted to serpentine soils and the open serpentine communities are unable to maintain themselves against the rigorous competition of non-serpentine plant communities; their distributions are consequently terminated along the same serpentine border, though by dynamic or biotic, rather than simply edaphic factors. Perhaps on this basis the contrasts and discontinuities so impressive in the foothill mosaic of woodland and chaparral may be understood.

SUMMARY

1. In California, the chaparral vegetation on serpentine includes some genera of annual herbs that show a striking development of serpentine endemism and provide material for its study.

2. Experimental results are reported which support those of Walker (1954) in showing that tolerance of low calcium levels is a principal adaptation required for growth of plants on serpentine soils. *Bodenwag* species occurring both on and off serpentine are able to do so because their serpentine populations are adapted to low calcium levels. It is shown that in most cases the population on serpentine is ecotypically distinct from that on non-serpentine soils.

3. All degrees of serpentine tolerance appear in the genus *Streptanthus*. Adaptation to serpentine followed by "biotype depletion" (Stebbins 1942), and the development of some isolated populations into "insular" endemics provide reasonable evolutionary explanations for serpentine endemism.

4. Experiments are reported showing that serpentine plants may be restricted to serpentine by intolerance of the more rigorous competition in non-serpentine plant communities. Thus, edaphic factors on the one hand, biotic or dynamic factors on the other, may produce the sharp discontinuities between serpentine and non-serpentine vegetation.

REFERENCES

- Clausen, J., D. D. Keck, and W. M. Hiesey. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Inst. Wash. Publ. 520: 1-452.
- . 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea*. Carnegie Inst. Wash. Publ. 581: 1-129.
- Kruckeberg, A. R. 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. Amer. Jour. Bot. 38: 208-419.
- Lämmermayr, L. 1927. Materialien zur Systematik und Ökologie der Serpentinflora. II. Das Problem der "Serpentinpflanzen."—Eine kritische ökologische Studie. Sitzber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. I, 136: 25-69.
- Hoffman, F. W. 1952. Studies in *Streptanthus*. A new *Streptanthus* complex in California. Madroño 11: 221-233.
- Mason, H. L. 1946. The edaphic factor in narrow endemism. II. The geographic occurrence of plants of highly restricted patterns of distribution. Madroño 8: 241-257.
- Morrisson, J. L. 1938. Studies in the genus *Streptanthus* Nutt. I. Two new species in the section *Euclisia* Nutt. Madroño 4: 204-208.
- . 1941. A monograph of the section *Euclisia* Nutt., of the genus *Streptanthus* Nutt. Ph.D. Thesis, Univ. of California, Berkeley.
- Novák, F. A. 1928. Quelques remarques relatives au problème de la végétation sur les terrains serpentiniques. Preslia 6: 42-71.
- Pichi-Sermolli, R. 1948. Flora e vegetazione delle serpentine e delle altre ofioliti del 'alta valle del Tevere Toscana'. (English summary.) Webbia 6: 1-380.
- Rune, O. 1953. Plant life on serpentines and related rocks in the North of Sweden. Acta Phytogeog. Suecica 31: 1-139.
- Stebbins, G. L., Jr. 1942. The genetic approach to problems of rare and endemic species. Madroño 6: 241-272.
- Turesson, G. 1922. The genotypical response of the plant species to habitat. Hereditas 3: 211-350.
- Unger, F. 1836. Über den Einfluss des Bodens auf die Verteilung der Gewächse, nachgewiesen in der Vegetation des nordöstlichen Tirols. Wien. (Cited by Zlatnik, A. 1928. Études écologiques et sociologiques sur le *Sesleria coerulea* et le *Seslerion calcariae* en Tchécoslovaquie. Trav. Soc. Roy. Sci. Bohême, Cl. Sci., N. S. 8 (1): 1-116.)
- Vlams, J. 1949. Growth of lettuce and barley as influenced by degree of calcium saturation of soil. Soil Sci. 67: 453-466.
- Vlams, J. and H. Jenny. 1948. Calcium deficiency in serpentine soils as revealed by adsorbent technique. Science 107: 549.
- Walker, R. B. 1948. A study of serpentine soil infertility with special reference to edaphic endemism. Ph.D. Thesis. Univ. of California, Berkeley.
- . 1954. Factors affecting plant growth on serpentine soils. Ecology 35: 259-266.

THE ECOLOGY OF SERPENTINE SOILS

IV. THE VEGETATIONAL RESPONSE TO SERPENTINE SOILS¹

R. H. WHITTAKER

*Biology Section, Department of Radiological Sciences, General Electric Company,
Richland, Washington*

The distinctiveness of serpentine vegetation has been indicated in the preceding papers. Although the types of serpentine vegetation in different parts of the world are diverse, some common characteristics or tendencies may suggest themselves when serpentine vegetation is in each case compared with adjacent vegetation on other soils. As a basis for considering these tendencies, a particular area of serpentine vegetation, that of the Siskiyou Mountains of southwestern Oregon, will be treated in detail. The present paper will discuss Siskiyou serpentine vegetation first in terms of populations and vegetation structure, or physiognomy, and second in terms of flora or species composition, and will then seek to interpret the vegetational response to serpentine soils.

Just north of the California-Oregon boundary, west from O'Brien, Oregon, is one of the extensive areas of serpentine vegetation in the Siskiyou Mountains, occupying an almost continuous area of more than 150 square miles of peridotite and serpentine (Wells *et al.* 1949). Across the Illinois Valley from it, in and near the Oregon Caves National Monument, "typical" vegetation for the area occurs on quartz diorite and other rocks. A comparison of vegetation in these two areas formed the basis of the study. So different are their vegetations that one might imagine one had traveled to another part of the continent in crossing the few miles from the diorite area to the serpentine, if it were not difficult to think of another area much resembling the Siskiyou serpentines. The mountains of diorite and other rocks east of the Illinois Valley are covered by dense evergreen forests and are valuable timber lands for the Douglas fir and Port Orford cedar these forests contain. Pines and other conifers in open, stunted

¹ A contribution from the Department of Zoology, Washington State College, completed before joining General Electric Co. This study was supported in part by the funds for biological and medical research of the State of Washington Initiative Measure No. 171. The author is much indebted to M. Ownbey and A. Cronquist for determining the specimens of the difficult flora of the Siskiyou; the voucher specimens have been deposited in the herbarium of Washington State College. All three authors are indebted to H. L. Mason and W. D. Billings for critical readings of the manuscripts before they were submitted for publication.

stands, which the loggers are generally content to leave alone, occupy the serpentine area. Both too steep and too infertile for farming, the serpentine mountains are almost without present economic value except for limited grazing and mining.

The approach of gradient analysis (Whittaker 1951, 1952, *cf.* Curtis and McIntosh 1951, Brown and Curtis 1952) was used for the study. Vegetation site-samples were taken at random, so far as possible, over the mountain surface. Each sample included a stand-count of trees for 0.1 or 0.2 hectare, undergrowth counts for 25 square-meter plots, and data on soil material, topographic position, and location. Fifty of these samples for undisturbed stands in each area at elevations between 2,000 and 3,000 feet were used in the tabulations. The samples were first arranged into transects by topographic position, and the plant species were grouped into four classes, from mesic to xeric, on the basis of the positions of their populations along the moisture gradient. Weighted averages of stand composition based on these classes give a more sensitive expression of the moisture relations of stands (*cf.* Curtis and McIntosh 1951, Brown and Curtis 1952). Using these weighted averages, the samples were arranged in series from most mesic to most xeric and grouped into ten sets of five samples each along the moisture gradient. The resulting tables² showing the change in plant populations from most mesic ravines to most xeric southwest slopes on diorite and on serpentine are the basis of the following comparison and interpretation of these vegetations.

DESCRIPTION OF DIORITE AND SERPENTINE VEGETATION

In the diorite area, well-developed, closed mountain forests prevail. In ravines Douglas fir, *Pseudotsuga taxifolia* (Lamb.) Britt., and Port Orford cedar, *Chamaecyparis lawsoniana* Parl., dominate the stands, with a low-tree stratum in which deciduous species are more important than

² A monograph on the vegetation of peridotite, olivine gabbro, and quartz diorite is in preparation. Since it is expected that data for the three transects will be presented together at that time, the extended tables for two of the soil materials are not given with this shorter account.

sclerophylls. *Gaultheria shallon* Pursh and *Berberis nervosa* Pursh are important shrubs, occurring along with a variety of mesic herbs of wide distribution. As one proceeds from these ravines to northerly and easterly slopes, Port Orford cedar and the other species mentioned, except Douglas fir, gradually decrease in numbers until no longer present. In the absence of cedar, Douglas fir is the canopy dominant (with some *Pinus lambertiana* Dougl.) above a dense lower tree-stratum of sclerophyllous trees, mainly tanoak, *Lithocarpus densiflorus* (H. & A.) Rehd. As one follows the moisture gradient from intermediate slopes to xeric southerly ones, the Douglas fir canopy becomes more and more open until, on the driest slopes, these large trees are only scattered above a canopy of sclerophylls including canyon liveoak, *Quercus chrysolepis* Liebm., chinquapin, *Castanopsis chrysophylla* Dougl.) A. DC., and madrone, *Arbutus menziesii* Pursh, as well as tanoak (Fig. 1). Undergrowth coverage in the diorite stands is low, except in mesic sites. In general character, the diorite vegetation is a pattern of closed forests dominated by Douglas fir and the sclerophylls, with progressive change from Douglas fir, Port Orford cedar, and deciduous species in more mesic sites toward stands of sclerophylls with Douglas fir in more xeric ones.

Port Orford cedar and Douglas fir appear also as dominants at the mesic extreme of the pattern on serpentine, but form open stands of smaller trees along with western white pine, *Pinus monticola* Dougl., and other species (Fig. 2). *Rhododendron occidentale* (T. & G.) Gray is the most important shrub. The herb stratum shows an unusual mixture of rare serpentine species (*Trillium rivale* Wats., *Lilium howellii* Johnst., *Cypripedium californicum* Gray) with more familiar species from bogs and marshes (*Darlingtonia californica* Torr., *Rudbeckia californica* Gray, *Helenium bigelovii* Gray, *Tofieldia glutinosa* spp. *occidentalis* (Wats.) C. L. Hitchc.). In intermediate sites, mixed stands of Douglas fir, white pine, sugar pine, *P. lambertiana* Dougl., Jeffrey pine, *P. jeffreyi* Grev. and Balf., and incense cedar, *Libocedrus decurrens* Torr., occur (Fig. 3), with a rather dense stratum of shrubs (*Quercus chrysolepis* var. *vaccinifolia* (Kell.) Engelm., *Lithocarpus densiflorus* var. *montanus* (Mayr.) Rehd., *Vaccinium parvifolium* Smith, *Arctostaphylos nevadensis* Gray, an unnamed shrubby variant of *Umbellularia californica* Nutt., *Rhamnus californica* var. *occidentalis* How., *Garrya buxifolia* Gray, *Rosa gymnocarpa* Nutt., *Berberis pumila* Greene, and *Amelanchier gracilis* Heller). This shrub layer is dominated by sclerophyllous species, many of them shrubby varieties of the sclerophyllous trees of

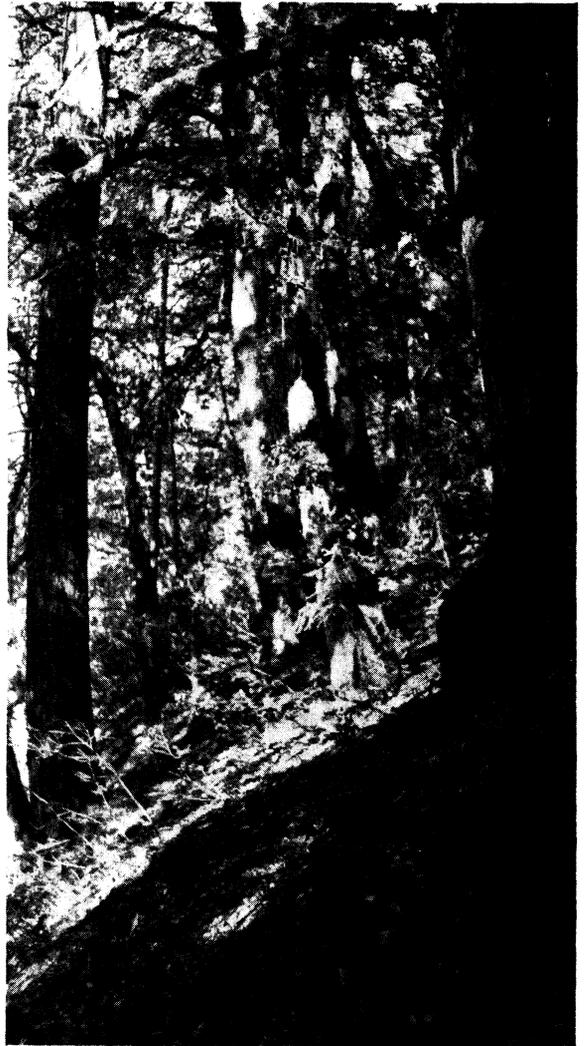


FIG. 1. A xeric stand on quartz diorite, open south slope above Grayback Creek, Siskiyou Mountains, southwestern Oregon, at 2300 ft. elev. *Pseudotsuga taxifolia* with *Lithocarpus densiflorus*, *Quercus chrysolepis*, and *Arbutus menziesii*; *Pinus lambertiana*, *Rosa gymnocarpa*, *Boschniakia hookeri* Walp., and *Apocynum pumilum* (Gray) Greene present. October 10, 1951.

diorite or shrubby congeners of these trees. The tree layer, however, is almost entirely coniferous. The broadleaved trees so important on diorite are conspicuous by their absence from serpentine, except for occasional madrones. It is as if, with the opening and reduction in size of the forest on serpentine, the broadleaf tree stratum had been dwarfed to a shrub layer.

In more mesic sites, shrub coverage may be 80 per cent or more, with scattered open patches of grass; but in more xeric sites, the shrubs themselves occur only in scattered patches. The undergrowth of intermediate sites on serpentine has a distinct two-phase structure which is often con-



FIG. 2. A mesic stand on serpentine in a ravine near the Wimer Road, Siskiyou Mountains, southwestern Oregon, at 2100 ft. elev. *Chamaecyparis lawsoniana*, *Pinus lambertiana*, and *P. monticola*, *Rhododendron occidentale*, *Darlingtonia californica*, *Helenium bigelovii*, *Lilium occidentale* Purdy, *Carex* spp. July 21, 1951.



FIG. 3. An intermediate stand on serpentine on an open east slope of Josephine Mtn., Siskiyou Mountains, southwestern Oregon, at 3800 ft. elev. *Pinus monticola* with *Libocedrus decurrens* and *Pinus jeffreyi*; shrub coverage 50 per cent with *Quercus chrysolepis* var. *vacciniifolia* predominant, *Rhamnus californica* var. *occidentalis*, and *Garrya buxifolia*. July 20, 1950.

spicuous in sampling quadrats along a tape; the sampler finds himself working in shrubs for a few meters, then in grass, then back in shrubs. As if to make this two-phase structure the more apparent, there is a reversal of phase along the gradient. The shrubs form the continuous phase in the more mesic sites but decrease along the moisture gradient while the grass increases, until the shrubs are the discontinuous phase in the grass of more xeric sites. The tree and herb populations respond to the difference of environment of the two phases. While the same tree species grow in both, there is a difference of relative abundance in the two phases probably determined by effects of the different undergrowth environments on seedling survival. The more mesic tree species, Douglas fir,

white pine, and sugar pine, tend to be concentrated in the shrub phase and the more xeric Jeffrey pine in the grass phase, while incense cedar shows no clear preference.

The shrub stratum just described is absent from most xeric sites, and here the whole vegetation resembles the grassy phase of subxeric sites. Jeffrey pine is the dominant tree, often with no other species but incense cedar present, and forms a very open stand above a grassy floor (Fig. 4). The community is thus a woodland or "temperate savanna," which perhaps may best be described as pine steppe and compared with similar communities formed by *Pinus sylvestris* and other species in Europe. Scattered *Arctostaphylos viscida* Parry may appear as a high shrub stratum, with *Con-*

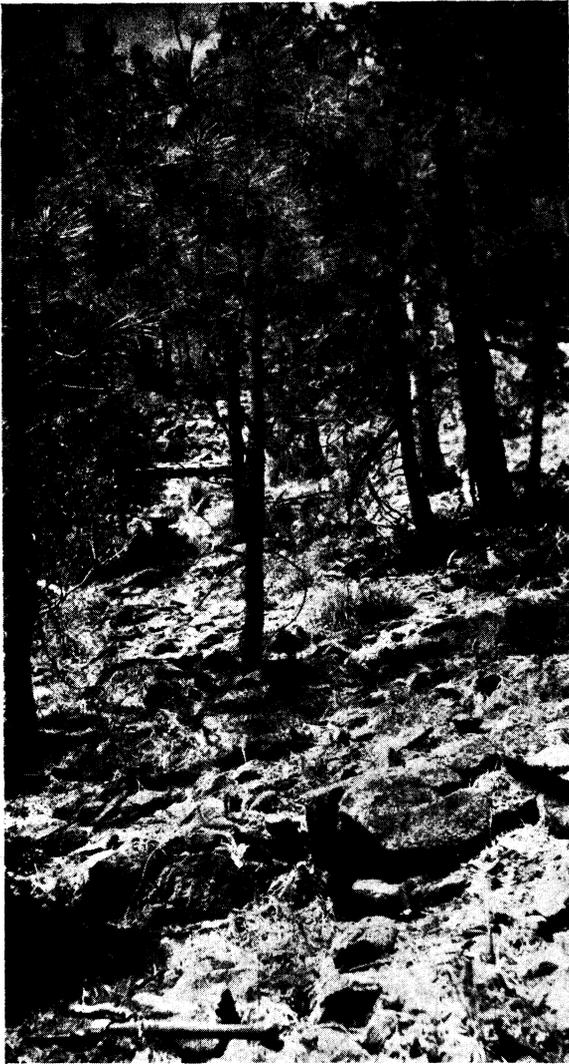


FIG. 4. A xeric stand on serpentine on an open southeast slope above Rough-and-Ready Creek, Siskiyou Mountains, southwestern Oregon, at 1900 ft. elev. *Pinus jeffreyi* with *Libocedrus decurrens* and *Pseudotsuga taxifolia*; sparse shrub coverage of *Arctostaphylos viscida* with *Quercus chrysolepis* var. *vaccinifolia* and *Umbellularia californica*; *Xerophyllum tenax* (Pursh) Nutt. and grass spp. The soil is rockier and less developed than in most similar stands. July 17, 1950.

volvulus polymorphus Greene and *Rhamnus californica* var. *occidentalis* the only other shrub-layer species present. The grasses are widespread *bodevzag* species; *Stipa lemmoni* (Vas.) Scribn. and *Sitanion jubatum* J. G. Sm., are usually most important. Among the herbs other than grasses are some of the many Siskiyou and Klamath endemics of the serpentine area. A few of these endemics which occur with square-meter frequencies of 5 per cent or more for the whole transect (*Vancouveria chrysantha* Greene, *Lomatium howellii* (Wats.) Jeps., *Galium ambiguum* Wight,

Iris bracteata Wats., *Hieracium cynoglossoides* var. *nudicaule* Gray, *Sanicula peckiana* Macbr., *Horkelia sericata* Wats., and the prostrate *Ceanothus pumilus* Greene) may be mentioned as most important.

The pattern of low-elevation serpentine vegetation is thus one in which pine species share dominance with other conifers in the open stands of small trees, a pattern which changes continuously along the moisture gradient from Port Orford cedar-white pine-Douglas fir stands in ravines, through mixed pines and Douglas fir with two-phase undergrowth in intermediate sites, to the Jeffrey pine steppe on xeric slopes. The contrast with the diorite vegetation pattern may be illustrated by a transect diagram (Fig. 5) as well as by photographs. The Douglas fir-sclerophyll forest on diorite (the Mixed Evergreen Forest of Munz and Keck 1949) is a widespread vegetation type of the Klamath Mountain region and northern Coast Ranges. The Jeffrey pine steppe of xeric serpentine sites is, in superficial appearance, part of a vegetation type of even wider range, the yellow pine steppes dominated by *Pinus ponderosa* and relatives. The remaining serpentine vegetation types, however, are as distinctive and anomalous in vegetation structure as in floristics.

Exclusion of growth-forms important on one soil from the vegetation on the other is responsible for much of the contrast of diorite and serpentine vegetation. The broad-leaf trees are absent or represented only by shrubs on serpentine; the pines (except sugar pine), grasses, and characteristic sclerophyllous shrubs of serpentine are absent or of minor importance on diorite. Some further basis of the contrast may be seen in the effects of serpentine on the population of Douglas fir. The average population density of this tree on serpentine is less than half that on diorite, comparing the whole transects (average number of stems 1 inch and above d.b.h. per hectare, 177 on diorite vs. 78 on serpentine). The trees on serpentine are, furthermore, noticeably smaller. Increment borings indicate a growth rate on serpentine about two-thirds that on diorite (average diameters at 100th ring, breast height, of 11.4 inches for 20 diorite stems, 7.4 inches for 5 serpentine stems). With the sclerophyllous trees nearly excluded and Douglas fir kept to a low population of small trees, the serpentine stands are necessarily open ones.

THE FLORISTICS OF SERPENTINE AND DIORITE

The species listed for the two transects may provide a basis for floristic comparison also. When species which occur only once or twice in the fifty samples of a transect are excluded, about a hun-

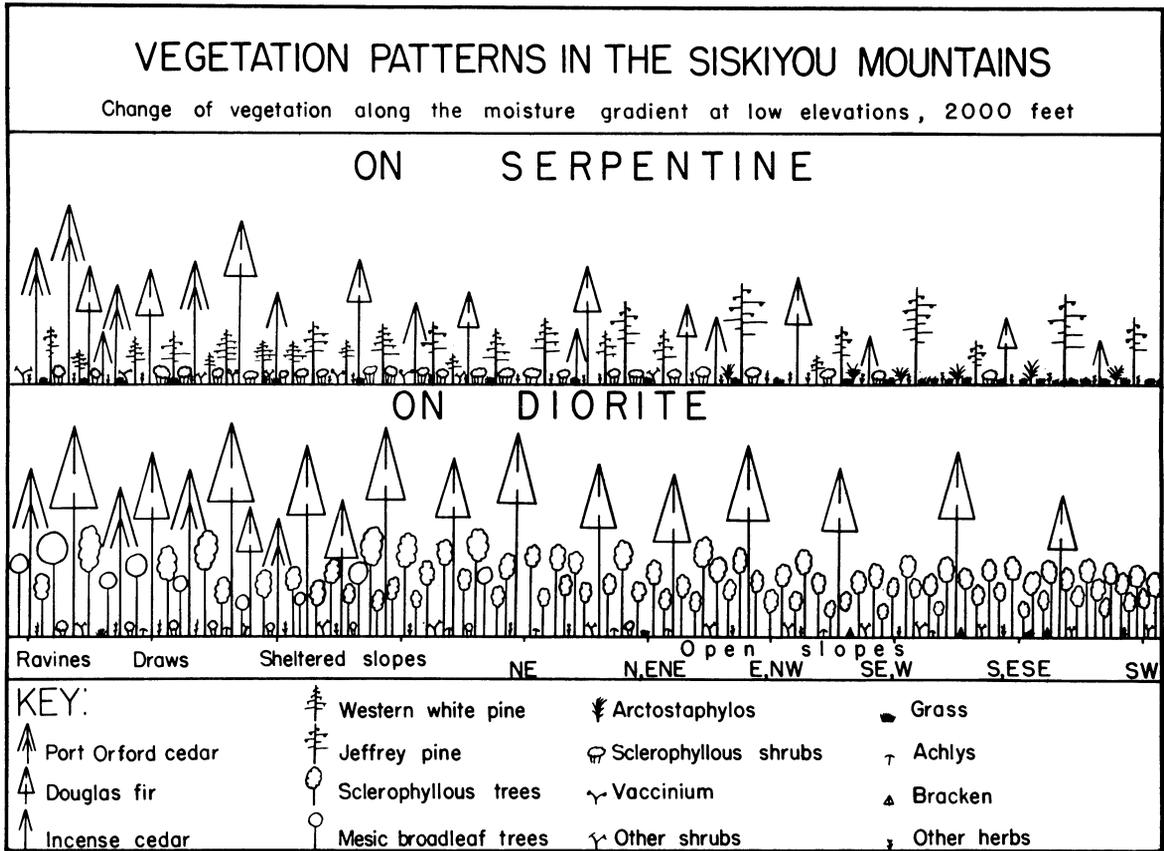


FIGURE 5. Transect diagrams of vegetation pattern sites on serpentine and on quartz diorite, from most mesic sites on left to most xeric sites on right, Siskiyou Mountains, southwestern Oregon.

s on serpentine and on quartz diorite, from most mesic sites on left to most xeric sites on right, Siskiyou Mountains, southwestern Oregon.

dred species remain for each—101 on diorite, 113 on serpentine. These numbers may indicate well enough that the vegetation on Siskiyou serpentines is by no means floristically impoverished. The breakdown of the two floras in terms of major growth-forms (Table I) shows a more evident contrast. Half as many tree species maintain themselves on serpentine as on diorite; all but one

of these are conifers and four of them are pines. The number of shrub species is reduced slightly on serpentine; but the greatest change in composition of this stratum is the dominance on serpentine of the evergreen-sclerophyllous shrubs, which are a minority on diorite. The herb stratum on serpentine is distinctly richer floristically than on diorite, and includes about twice as many grasses and sedges.

TABLE I. Floristic measurements of range and area for serpentine and diorite floras in the Siskiyou Mountains. Based on 113 serpentine and 101 diorite species occurring in the low-elevation composite transects. Diorite left; serpentine right (bold face)

	Grasses & sedges	Other herbs	Shrubs	Trees	Total
Number of species	8 17	58 71	19 17	16 8	101 113
Number of endemics	0 0	2 25	0 5	0 0	2 30
Extent: North	4.4 3.3	3.7 1.9	3.6 1.6	3.2 2.6	2.6 2.1
East	4.2 3.9	3.1 1.9	2.5 1.7	2.2 2.4	2.8 2.2
South	2.9 3.0	2.8 1.7	2.6 2.2	3.1 3.6	2.8 2.1
Direction of greatest extent: North	3 4	27 19	13 3	7 2	50 28
East	3 8	12 8	0 0	0 0	15 16
South	0 4	7 19	4 9	6 4	17 36
Indeterminate	2 1	12 25	2 5	3 2	19 33

The extent of the floristic contrast may be further shown by some such measure as Jaccard's (1912, 1932) coefficient of community. Of the lists of 101 and 113 species, 22 are shared of a total of 192 species occurring in either or both. A coefficient of $100 \times 22/191 = 11.5\%$ results, a value which is surely phenomenally low for two areas of vegetation a few miles from each other under the same general climate. Comparing various districts of Switzerland, Jaccard (1932: 171) obtained values ranging from 50% to 56%, comparing floras of gneiss and limestone soils in one district produced a value of 48%. Use of species lists as large as Jaccard's (300 or more), taken for all elevations and soils on opposite sides of the Illinois Valley would raise the coefficient but ob-

scure the real contrast of diorite and serpentine floras at comparable elevations. Since, as shown by Kruckeberg (1954), the populations of most *bodenwag* species are distinct, the actual percentage of ecotypic populations which are shared by the two vegetations within the limits of the study areas is well below 11.5%.

A breakdown by floristic areas further illustrates the contrast (Table II). The extent of narrow endemism for which serpentine vegetation is perhaps more celebrated than any other feature is at once apparent. Seventeen of the serpentine species are restricted to the narrower area of the Siskiyou Mountains along the California-Oregon border; thirteen others are restricted to the broader Klamath Mountain region of northern California and southern Oregon. These are a small fraction of the narrow endemics of serpentines and other soils in the Siskiyou. In the diorite transect, a single Siskiyou endemic appears (*Tauschia kelloggii* (Gray) Macbr.) Half of the diorite flora (50%) is made up of widespread western and nearctic species. These are reduced to 30% in the serpentine vegetation, in which the endemics together with the less widespread Sierran and Coastal groupings made up the majority.

TABLE II. Representation of floristic areas in serpentine and diorite floras, Siskiyou Mountains. Percentages in various floristic groupings of 113 serpentine species and 101 diorite species occurring in the low-elevation composite transects

Floristic grouping	Serpentine	Diorite
Siskiyou endemic.....	15	1
Klamath endemic.....	12	1
Cascadian.....	2	1
Sierran.....	11	4
Sierra-Cascadian.....	3	8
Sierra-Coastal.....	10	6
Coastal.....	17	29
Western.....	21	34
Nearctic.....	9	16

A further means of expressing some floristic features quantitatively has been developed for this comparison. The range of each species was expressed in terms of the distance of its extent north, east, and south of the Siskiyou, by a scale in which 0 indicated restriction to the Siskiyou in a given direction, 1 restriction to the Klamath Mountain region, and each further unit a 200-mile interval to the limits of the continent. The contrast in average extent of range is at once apparent (Table I). In the grouping of herbs other than grasses, the diorite flora has almost twice the average extent in a given direction, hence almost four times the average area of distribution. A similar contrast appears among the shrubs but is

less apparent in the other two growth-forms. The designations "Californian" and "Northwestern" were not considered very meaningful for the breakdown of Table II, but the contrast in direction of greatest extent is revealing. Numbers of species with their greatest extent of range to the north or to the south may be compared in Table I. About twice as many species have their greatest range to the north on diorite as on serpentine, and about twice as many species have their greatest range to the south on serpentine as on diorite. In this sense, the serpentine flora may be described as Californian and the diorite flora as Northwestern in affinities, although both occur in the floristic center lying between these two regions.

SUCCESSIONAL STATUS OF SERPENTINE VEGETATION

It has been one of the assumptions of the climatic climax theory (Clements 1928, 1936, Phillips 1934-5, Cain 1939) that the distinctive vegetation of special soils is seral or successional and, given time for development of soil maturity, will converge to essential identity with the climatic climax vegetation on more typical soils (Clements 1928: 284-5, Cain 1939: 150, Daubenmire 1947: 55). This assumption implies that much or all of the physiognomic and floristic peculiarity of serpentine vegetation should disappear when it reached the climax. It further suggests that the normal process of ecological succession should develop mature soils on serpentine as productive as soils developed from other rocks. Criticisms of the climatic climax theory have been considered elsewhere by the author (Whittaker 1951, 1953). Without reviewing these here, the following evidences on whether the Siskiyou serpentine vegetation is seral or climax may be adduced:

1. Seedling data from undergrowth quadrat counts show that the dominant trees on serpentine are reproducing (except knobcone pine, *P. attenuata* Lemm.). There is no evidence that the sclerophyllous trees of diorite are effectively entering the serpentine stands, as trees. The size-distributions of trees on serpentine show the J-curve form (Meyer and Stevenson 1943) of self-maintaining stands (except knobcone pine and Jeffrey pine steppe). The serpentine vegetation shows the characteristics of self-maintenance to be expected of vegetation stabilized in relation to its site.

2. The soils on both diorite and serpentine are shallow and rocky soils of mountain slopes, and there is no evidence that those on serpentine are less mature than those on diorite. Valley and outwash serpentine soils along the western edge of the Illinois Valley support serpentine vegetation.

3. Islands or exclaves of each rock in the area of the other show the persistence of differences in vegetation. Islands of other soils in the serpentine area support sclerophyllous trees or Douglas fir-sclerophyll stands. Islands of serpentine in the diorite area bear open stands dominated most frequently by knobcone pine and Jeffrey pine, which are serpentine species in the areas studied, and have serpentine undergrowth flora, the extent of development of which seems roughly proportional to extent of the outcrop and proximity to major serpentine areas.

4. The stand-to-stand regularity or predictability of patterning (Whittaker 1953) indicates that serpentine vegetation is stabilized, so that similar climax populations have been established in similar sites.

5. Successions in the two areas are different. Plants of bare serpentine rock and exposed serpentine soil are, as indicated by Kruckeberg (1954), serpentine plants together with some *bodenvag* grasses; such sites in the diorite area bear more familiar plants of newly exposed or disturbed situations. Recent, more severe burns are indicated on diorite by dense young stands of sclerophyllous trees, but on serpentine by stands of knobcone pine.

These lines of evidence point uniformly toward the same conclusion: Siskiyou serpentine vegetation is not a seral stage to the vegetation of other soils but is a distinctive climax of its own distinctive successions. Conclusions on climax status must allow for the extent of past fires in the Siskiyou; both the diorite and serpentine vegetations have been burned. In the dry-summer climate of this area, light summer fires are part of the environmental complexes in relation to which the present vegetations of both areas have developed. Only some stands, affected by more severe fires, are clearly successional. Allowing for the effects of fire, the author would interpret the serpentine vegetation of the Siskiyou as a complex and fully developed climax pattern in its own right, part of the still more intricate pattern of vegetation on serpentine, diorite, gabbro, and other rock types represented in the Siskiyou Mountains. Whatever the interpretation according to the three climax hypotheses (Whittaker 1953)—as a stabilized edaphic sub-climax, as one of a number of edaphic climaxes of the area, or as a climax pattern itself—, there is no reason to believe that the Siskiyou serpentine soils and vegetation are becoming more like those of surrounding, economically more valuable areas.

INTERPRETATION AND CONCLUSION

Impressive as some of the contrasts of serpen-

tine and non-serpentine areas are individually, it seems appropriate to try to draw together these details of the three papers in concluding the symposium.

It was shown by Walker and Kruckeberg that a deficiency of calcium underlies the effects of serpentine soils. With due allowance for other peculiarities of serpentine soils, and for the individuality of both serpentine soils and plant species, we may consider the nutrient deficiency, especially of this element, as the most crucial and general characteristic of serpentine soils affecting plants.

Plant species encountering serpentine soils within their ranges show various distributional responses, ranging from complete exclusion from serpentine to complete restriction to serpentine. Species restricted to serpentine are characterized by tolerance of the low calcium levels in these soils. Some *bodenvag* species naturally tolerant of low calcium levels may be able to grow on serpentine without ecotypic differentiation; but most plant species, as Kruckeberg has shown, are able to occupy serpentine habitats only as distinct edaphic ecotypes. The physiological adaptation of these serpentine plants to low calcium levels and other peculiarities of serpentine habitats is often expressed morphologically, in serpentinomorphism.

When species occur both on and off serpentine soils, the non-serpentine populations may in time lose out in competition with other plants, leaving the serpentine populations isolated on their soil. Many serpentine species have probably become, or are becoming, serpentine endemics by this process of "biotype depletion." Other endemics have arisen as "insular" species by the differentiation of a local, serpentine-adapted population from the population of a parental species. Kruckeberg's experiments indicate that in either case, these endemics are probably restricted to serpentine by their intolerance of the more rigorous competition on other, more typical soils. As may often be the case with the populations of special or extreme habitats, these are able to survive in environments of especially exacting physical conditions to which they are adapted, but are unable to compete elsewhere with other species which are excluded by those conditions.

While each species responds to serpentine soil according to its own potentialities, some relative differences of response among plant growth-forms appear. The experimental data of Kruckeberg and the field data of the author indicate that grasses are more easily able to occupy serpentine environments than are many other herbs and suggest that some grass species may do so without ecotypic differentiation. The field data for coniferous trees suggest they may occupy serpentine

habitats with the same facility; all the diorite conifers except *Taxus brevifolia* Nutt. (as a shade-plant necessarily excluded from serpentines in this area) occur also on serpentine. Deciduous trees are virtually excluded from Siskiyou serpentines; and, although stands of oaks and other deciduous trees occur on serpentine in some areas, deciduous forests on serpentine are on the whole much less extensive than coniferous stands. The evergreen-sclerophyllous shrubs appear more successful than deciduous shrubs on serpentine in the Siskiyou and in most, but not all, other areas. Although these can be only tendencies, it may be suggested that the needle-leaved or coniferous trees (and especially pines), evergreen-sclerophyllous shrubs, and grasses (and sedges) succeed more generally on serpentines than broad-leaf trees, broad-leaved deciduous shrubs, and many broad-leaved herbs. Most serpentine vegetations throughout the world appear to be dominated by some one or by some combination of these three adaptable growth-forms—coniferous trees, sclerophyllous shrubs, and grass-like plants.

The physiognomy of serpentine vegetation may further be understood on the basis of stunting or impoverishment of growth, referred to by all three authors. The reduction of both population level and growth rate in Douglas fir on serpentine has been mentioned; from this and the exclusion or reduction to shrubby equivalents of the broad-leaved trees, the stunted, open appearance of Siskiyou serpentine vegetation results. The openness of the tree stratum permits species intolerant of the shade of a closed canopy to reproduce; thus several pine species are able to maintain populations on serpentine. The sparse canopy coverage permits much light to reach lower strata, and may also imply a reduced demand on the available soil water by the trees. A development of undergrowth far beyond that on diorite is thus possible. Floristically, the undergrowth on serpentine in the Siskiyou is richer in species than that on diorite; in relation to physiognomy, the serpentine undergrowth is of greater coverage and more massive.

Similar physiognomic effects appear in other serpentine vegetations which have been described, almost all of them from forest climates. Sparse alpine meadow or tundra-like communities (eastern Canada and Scandinavia, Fernald 1907, 1911, Rune 1953) and open coniferous stands (north Urals, Sočava 1927) occur in northern forest or taiga regions. In temperate lower latitudes, serpentine vegetations include pine steppe (Europe, Beger 1922-3, Suza 1928, Zlatnik 1928a, Kretschmer 1931, Markgraf 1932, Bargoni 1943; Japan, Kitamura and Momotani 1952, Kitamura and Murata 1952, Yamanaka 1952; eastern

United States, Radford 1948; and Oregon, present paper) and other open coniferous stands (Washington and Oregon; south Urals, Iljinski 1936; Spain, Palacios 1936; Japan, Yamanaka 1952), deciduous forest (Yugoslavia, Pančić 1859; Albania, Markgraf 1932; eastern United States, Harshberger 1903, 1904, Pennell 1910, Radford 1948) and deciduous shrubs (Japan, Yamanaka 1952), chaparral (California), live-oak (Spain, Palacios 1936), and *lande* (France, LeGendre 1919), and edaphic steppe (Italy, Messeri 1936, Pichi-Sermolli 1948; Czechoslovakia, Suza 1928; eastern United States, Pennell 1910, Braun 1950: 248). In tropical climates, serpentines support savanna (Karakelang, Lam 1927; Cuba, Carabia 1945, Beard 1953), and scrub (New Caledonia, Däniker 1939, Birrell and Wright 1945; Cuba, Seifriz 1940). In south temperate New Zealand, luxuriant *Nothofagus* forests are replaced on serpentine by tussock grassland and shrub communities (Betts 1918, Cockayne 1921). The physiognomic types on serpentine are varied; but in each of these the tree stratum is reduced and the lower strata increased, compared with vegetation on other adjacent soils: the concentration of plant life in the community moves down one or two stories.

It is familiar that increasingly favorable environments (moisture and temperature especially) permit increased closing, elevation, and differentiation into strata of the community (Dansereau 1951: 219). In serpentine vegetation we see the generalization in reverse: with less favorable environment (nutrients) there is opening, lowering, and reduction of the community toward the lower strata. Differences in relative productivity of natural communities and relative amount of plant life or biomass maintained in them must underlie these phenomena. Increasingly favorable conditions of temperature, moisture, and nutrients permit increasing community productivity and with this increasing development of community structure from the lower strata upward.

There is thus a very rough parallelism in the effects of decreased moisture, temperature, and nutrients on vegetation structure, to which may be related another peculiarity of serpentine vegetation. Serpentine vegetation is xeromorphic. In the morphology of some of its species and in the morphology of the vegetation itself it shows some of the marks of adaptation to dryness. In the various occurrences of serpentine vegetation cited, the serpentine vegetation is in each case a step more xeric in appearance than vegetation on other soils. Physical characteristics of serpentine soil described above by Walker (1954) may contribute to the dryness of serpentine habitats; but in some cases; as in the Siskiyou, physical characteristics

of serpentine and non-serpentine soils are similar. Since the serpentine vegetation occurs side by side with other vegetation, receiving the same rainfall, its physiognomic response may best be interpreted as a pseudo-xeromorphism. The effects of decreased moisture are simulated by the effects of decreased nutrients, because basic productivity is reduced in both cases and because some of the same plant growth-forms are adapted to both dryness and infertility.

Characteristics of vegetation which parallel these in part, although in response to different edaphic factors, appear on some other special soil parent-materials: gypsum (Dziubałowski 1923, 1926, Weiss 1924, Mrugowsky 1931, Sokolowa 1935, Leontjev 1935, Emerson 1935, Campbell and Campbell 1938, Meusel 1939, 1941, Johnston 1941, Waterfall 1946, Braun-Blanquet 1951, Gilliland 1952) and magnesite (Lämmermayr 1928a, 1928b, 1933, 1934, 1935, Björkman 1937), some dolomites and limestones, as in the cedar glades of eastern North America (Harper 1926, Freeman 1933, Erickson *et al.* 1942, Quarterman 1950a, 1950b) and European edaphic steppe and pine steppe from Balkan *Karst* north to Baltic *Alvar* vegetation (Turrill 1929, Allorge 1921-2, Kaiser 1926, Dziubałowski 1926, Zlatník 1928a, Kozłowska 1928, Gams 1930, 1938, Klika 1932, 1933; Du Rietz 1923, Sterner 1925, Vilberg 1929, Jalas 1950, Albertson 1950), Appalachian shale barrens (Steele 1911, Wherry 1930, Core 1940, Allard 1946, Platt 1951), zinc and copper soils (Schwicklerath 1931, Robyns 1932, Braun-Blanquet 1951, Rune 1953), Australian soils low in phosphate (Beadle 1953), porphyry hills in Germany (Meusel 1940), and altered andesite in Nevada (Billings 1950). One notable reversal of the tendency for serpentine vegetation to be of reduced stature compared with the vegetation of other soils appears where two of these edaphic vegetation types meet on the Greek island of Euboea—*Karst* steppe on limestone and pine forest on serpentine (Boydell 1921, Turrill 1929). To varying degrees these other vegetations of special soils also resemble serpentine vegetation in floristic peculiarity and occurrence of endemic species. Rune (1953) has recently suggested that relict and paleoendemic species tend to be more characteristic of soils of high calcium or magnesium content (serpentine, magnesite, limestone and dolomite, gypsum), neoendemic populations of soils characterized by heavy metals—nickel (serpentine), zinc (calamine), copper, and perhaps others. As serpentine soil combines chemical properties of both groups of soils, so serpentine floras include both paleoendemics and neoendemics (Rune 1953: 108).

Rune's description of serpentine communities

across the North Atlantic from one another also illustrates a major contrast in the floristics of serpentines in far-northern and southern regions. The serpentine communities of Scandinavia and eastern Canada are relatively poor in numbers of species and extent of narrow endemism, compared with southern serpentine areas. In the western United States, the serpentine vegetation of Washington is not floristically rich and includes few, if any, narrowly endemic species. The major serpentine areas from the Siskiyou Mountains south into California are floristically rich and are remarkable for the extent of narrow endemism among their species, as are tropical serpentines still farther south. It is possible that contrast between serpentine and non-serpentine soils is less marked in humid far-northern climates. Serpentine rocks are of varied chemical properties and are subject to processes of soil-formation which differ in different climates. The relative importance of endemics vs. *bodenwag* species among serpentine floras may presumably be partly correlated with the extent of contrast between serpentines and adjacent soils (and hence the degree to which serpentine areas represent environmental extremes, Detling 1948).

It is also true that the northern serpentine areas have been exposed to glaciation, and there has consequently been much less time for the processes described by Kruckeberg to produce endemic serpentine species and distinctive serpentine ecotypes. The surrounding, non-serpentine floras of the northern regions are less rich, and hence offer a smaller stock of species from which these processes can, in time, produce distinctive serpentine floras. The northern serpentine areas are also relatively small (though some are larger than some southern areas with rich serpentine floras), and the extent of development of serpentine floras is partly related to extent of serpentine areas. The information on serpentine floras permits no real evaluation of the significance of extent of serpentine area, time the serpentine surface has been exposed, and richness of surrounding flora. The information is not inconsistent, however, with the possibility that both richness in species and extent of endemism in serpentine floras are partially correlated with each of these. Age, area, and richness in species are not causal factors affecting plant populations (Mason 1946a), but may have indirect relations with the number of species which occupy a serpentine area as ecotypes and endemics. It is of interest to compare these considerations on the floras of serpentines, as edaphic islands, with those on the floras of oceanic islands (Szymkiewicz 1938, Cain 1944: 215-21, Mason 1946a).

The physiognomic distinctiveness of serpentine

vegetation may suggest some further interpretation of its floristic peculiarities. The openness of serpentine vegetation implies penetration of more light to the lower strata, greater exposure to air movement and evaporation, exposure to higher afternoon temperatures, and retention of heat by the exposed rocks and soil. Any autecological interpretation of the Siskiyou serpentine flora described here must allow for this contrast in light, evaporative, and temperature conditions. Microclimates around the foliage of herbs and shrubs on serpentine are at times drier, and tend to induce greater loss of water by transpiration, than microclimates within the forests on diorite. Possession of morphological characteristics of growth in dry and exposed conditions by species of drier serpentine sites may thus be no accidental imitation of xeromorphism. To the warmer and drier conditions in communities of serpentine and other special soils may be related also the xerothermic character of some of their relict species and the interpretation of some of these communities as xerothermic in character by European authors (Suza 1921, 1935, Gams 1930, Sillringer 1931, Klika 1933, Meusel 1939, 1940, 1941).

The necessity of considering environmental factors as parts of a complex has been indicated by Kruckeberg and recently stated by Billings (1952). If we consider environment and natural community together as forming the ecosystem, then serpentine vegetation offers an *ecosystemic* environment differing widely in edaphic, microclimatic, and biotic characteristics from that on diorite. On this basis, we may understand why so few species have succeeded in bridging, even with ecotypic differentiation, the diverse and fundamental differences between diorite and serpentine habitats within the limits of the study areas. We may also understand, however, why a number of species which have failed to occupy both soils within these limits have been able to do so elsewhere under different conditions. Thus a number of the Siskiyou "serpentine species" of this study occur on non-serpentine soils in drier or more exposed habitats at higher elevations, farther east in the Siskiyou, or farther south into California. On the other hand, a number of "diorite species" excluded from serpentine at lower elevations enter denser forest stands on serpentine at higher elevations. The fundamental contrast in total-environment thus may provide a better explanation than edaphic difference alone for the low coefficient of community obtained and for the contrast in per cent of endemism and extent of average range in the two floras. The contrast in total-environment may also account for the difference in floristic affinities between the serpentine flora and the shade

plants of the diorite forests. Even apart from species shared with serpentine chaparral in California, we might expect more of the species of open serpentine vegetation to extend southward into the drier woodland, chaparral, and grassland vegetation of California, more of the species of closed forests on diorite to extend into mesophytic forests of the Northwest.

The natural communities on serpentine and diorite differ in almost every feature we can describe or measure. Underlying their various contrasts is a fundamental difference in nutrient conditions and one which is not counteracted by succession even as hundreds of feet of serpentine rock are weathered down through thousands of years. It is unreasonable to expect the mature ecosystems or climaxes on the two soils, developing in relation to differing nutrient levels and representing different nutrient economies, to converge. If we regret that serpentine soils will not in time become fertile, our regret may well be tempered by the consideration that their very lack of value will help to save from exploitation these areas of extraordinary interest.

SUMMARY

1. Vegetations of low elevations on serpentine and on quartz diorite were compared with techniques of gradient analyses in the Siskiyou Mountains of southwestern Oregon.

2. The vegetation pattern on diorite is characterized by closed Douglas fir-sclerophyll forests, whereas open, stunted stands of pines and other conifers appear on serpentine. Undergrowth in intermediate sites on serpentine shows an unusual development of a two-phase structure of grass and shrub patches, and in all sites on serpentine numerous endemic herb species occur.

3. Relatively few plant species occur on both diorite and serpentine, and the two floras are shown to be in marked contrast in representation of floristic regions. A means of expressing average range and direction of greater extent for a flora was devised. This shows the serpentine flora to be much more restricted in average extent and to have its greatest extent toward the south, in contrast to the diorite flora.

4. Evidence indicates that Siskiyou serpentine vegetation is climax, although affected by fires.

5. Serpentine vegetations appear in general to be characterized by apparent xeromorphism resulting from basic reduction of productivity, reduction of structure toward the lower strata, and dominance of conifers and especially pines, sclerophyllous shrubs, and grasses. As parts of ecosystems differing fundamentally in nutrient economy, vegetation patterns on serpentine and diorite

differ in almost every respect which can be described or measured.

REFERENCES

- Albertson, N.** 1950. Das grosse südliche Alvar der Insel Öland. Eine pflanzensoziologische Übersicht. *Svensk. Bot. Tidskr.* **44**: 269-331.
- Allard, H. A.** 1946. Shale barren associations on Massanutten Mountain, Virginia. *Castanea* **11**: 71-124.
- Allorge, P.** 1921-2. Les associations végétales du Vexin français. *Rev. Gén. de Bot.* **33**: 481-544, etc., **34**: 71-79, etc. (16 sections).
- Bargoni, Ida.** 1943. Osservazioni fenologiche sulle serpentine dell'Impruneta (Firenze). *Nuovo Giorn. Bot. Ital.* **50**: 232-251.
- Beadle, N. C. W.** 1953. The edaphic factor in plant ecology with a special note on soil phosphates. *Ecology* **34**: 426-428.
- Beard, J. S.** 1953. The savanna vegetation of northern tropical America. *Ecological Monog.* **23**: 149-215.
- Beger, H. K. E.** 1922-3. Assoziationsstudien in der Waldstufe des Schanfiggs. *Jahresber. Naturf. Gesell. Graubündens, N. F.* **61** (Beilage) : 1-96, **62** (Beilage) : 97-147.
- Betts, M. Winifred.** 1918-20. Notes on the autecology of certain plants of the Peridotite Belt, Nelson: I. Structure of some of the plants. *Trans. New Zealand Inst.* **50**: 230-242 (reviewed *Jour. Ecology* **8**: 155, 1921), **51**: 136-156, **52**: 276-314.
- Billings, W. D.** 1950. Vegetation and plant growth as affected by chemically altered rocks in the western Great Basin. *Ecology* **31**: 62-74.
- . 1952. The environmental complex in relation to plant growth and distribution. *Quart. Rev. Biol.* **27**: 251-265.
- Birrell, K. S., & A. C. S. Wright.** 1945. A serpentine soil in New Caledonia. *New Zealand Jour. Sci. & Technol.* **27A**: 72-76.
- Björkman, G.** 1937. Floran i trakten av Äpartjåkks magnesit-fält. *Svenska Vetensk. Akad. Skr.* **33**: 1-36.
- Bjørlykke, B.** 1938. Vegetasjonen på olivinsten på Sunnmøre. *Nyt Mag. f. Naturvid.* **79**: 51-126.
- Blackshaw, G. N.** 1921. Magnesia impregnated soils. *So. African Jour. Sci.* **17**: 171-178.
- Boydell, H. C.** 1921. The magnesite deposits of Euboea, Greece. *Econ. Geol.* **16**: 507-523.
- Braun, E. Lucy.** 1950. Deciduous forests of eastern North America. *Blakiston and Co., Philadelphia.* 596 p.
- Braun-Blanquet, J.** 1951. *Pflanzensoziologie: Grundzüge der Vegetationskunde.* Springer, Wien. 2 Aufl. 631 p.
- Braun-Blanquet, J., & H. Jenny.** 1926. Vegetations-Entwicklung und Bodenbildung in der alpinen Stufe der Zentralalpen (Klimaxgebiet des *Caricion curvulae*). Mit besonderer Berücksichtigung der Verhältnisse im schweizerischen Nationalparkgebiet. *Neue Denkschr. Schweiz. Naturf. Gesell.* **63**: 181-349.
- Brown, R. T., & J. T. Curtis.** 1952. The upland conifer-hardwood forests of northern Wisconsin. *Ecological Monog.* **22**: 217-234.
- Cain, S. A.** 1939. The climax and its complexities. *Amer. Midland Nat.* **21**: 146-181.
- . 1944. *Foundations of plant geography.* Harper and Bros., New York. 556 p.
- Campbell, R. S., & Imogene F. Campbell.** 1938. Vegetation on gypsum soils of the Jornada Plain, New Mexico. *Ecology* **19**: 572-577.
- Carabia, J. P.** 1945. The vegetation of Sierra de Nipe, Cuba. *Ecological Monog.* **15**: 321-341.
- Clements, F. E.** 1928. *Plant succession and indicators: A definitive edition of plant succession and plant indicators.* Wilson, New Nork. 453 p.
- . 1936. Nature and structure of the climax. *Jour. Ecology* **24**: 252-284.
- Cockayne, L.** 1921. The vegetation of New Zealand. Vol. **14** in *Die Vegetation der Erde.* Engelmann, Leipzig. 364 p.
- Core, E. L.** 1940. The shale barren flora of West Virginia. *Proc. West Virginia Acad. Sci.* **14**: 27-36.
- Curtis, J. T., & R. P. McIntosh.** 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* **32**: 476-496.
- Dahl, O.** 1912. Botaniske undersøkelser i Helgeland. I. *K. Norske Vidensk. Selsk., Kristiana, Skr., I. Mat-nat. Kl.* **1911** (6) : 1-221.
- . 1915. Botaniske undersøkelser i Helgeland. II. *K. Norske Vidensk. Selsk., Kristiana, Skr., I. Mat-nat. Kl.* **1914**(4) : 1-178.
- Däniker, A. U.** 1939. Neu-Caledonien. *Vegetationsbilder* **25**(6) : 1-9, Taf. 31-36.
- Dansereau, P.** 1951. Description and recording of vegetation upon a structural basis. *Ecology* **32**: 172-229.
- Daubenmire, R. F.** 1947. *Plants and environment: A textbook of plant autecology.* Wiley, New York. 424 p.
- Detling, L. E.** 1948. Environmental extremes and endemism. *Madroño* **9**: 137-149.
- Du Rietz, G. E.** 1923. Studien über die *Helianthemum oelandicum*-Assoziationen auf Öland. *Svensk. Bot. Tidskr.* **17**: 69-82.
- Dziubałowski, S.** 1923. La distribution et l'écologie des associations steppiques sur le plateau de la Petite Pologne. *Acta Soc. Bot. Poloniae* **1**: 185-200.
- . 1926. Les associations steppiques sur le plateau de la Petite Pologne et leurs successions. *Acta Soc. Bot. Poloniae* **3**: 164-195.
- Emerson, F. W.** 1935. An ecological reconnaissance in the White Sands, New Mexico. *Ecology* **16**: 226-233.
- Erickson, R. O., L. G. Brenner, & J. Wraight.** 1942. Dolomitic glades of east-central Missouri. *Ann. Missouri Bot. Gard.* **29**: 89-101.
- Fernald, M. L.** 1907. The soil preferences of certain alpine and subalpine plants. *Rhodora* **9**: 149-193.
- . 1911. A botanical expedition to Newfoundland and southern Labrador. *Rhodora* **13**: 109-162.
- Freeman, C. P.** 1933. Ecology of the cedar glade vegetation near Nashville, Tennessee. *Jour. Tennessee Acad. Sci.* **8**: 141-228.
- Gams, H.** 1930. Über Reliktföhrenwälder und das Dolomitphänomen. *Veröff. Geobot. Inst. Rübel Zürich* **6**: 32-80.
- . 1938. Über einige flechtenreiche Trockenrasen Mitteldeutschlands. *Hercynia* **1**: 277-284.
- Gilliland, H. B.** 1952. The vegetation of eastern British Somaliland. *Jour. Ecology* **40**: 91-124.

- Harper, R. M.** 1926. The cedar glades of middle Tennessee. *Ecology* 7: 48-54.
- Harshberger, J. W.** 1903. The flora of the serpentine barrens of southeast Pennsylvania. *Science, N. S.*, 18: 339-343.
- . 1904. A phyto-geographic sketch of extreme southeastern Pennsylvania. *Bull. Torrey Bot. Club* 31: 125-159.
- Hayek, A.** 1923. Pflanzengeographie von Steiermark. *Mitt. Naturw. Ver. f. Steiermark* 59(Beih.): 1-208.
- Holdridge, L. R.** 1945. A brief sketch of the Puerto Rican flora. Pp. 81-83 in *Plants and plant science in Latin America*, ed. F. Verdoorn. *Chronica Botanica*, Waltham, Mass.
- Hunter, J. G., & O. Vergnano.** 1952. Nickel toxicity in plants. *Ann. Appl. Biol.* 39: 279-284.
- Iljinski, A. P.** 1936. Zur Phytocoenologie der Lärchenwälder des Ilmengebirges (Süd-Ural). *Ber. Schweiz. Bot. Gesell.* 46: 85-93.
- Jaccard, P.** 1912. The distribution of the flora in the alpine zone. *New Phytol.* 11: 35-50.
- . 1932. Die statistisch-floristische Methode als Grundlage der Pflanzensoziologie. *Handb. Biol. Arbeitsm.* ed. E. Abderhalden XI, 5(1): 165-202.
- Jalas, J.** 1950. Zur Kausalanalyse der Verbreitung einiger nordischen Os- und Sandpflanzen. (Finnish summary.) *Ann. Bot. Soc. Zool. Bot. Fenn. Vanamo* 24(1): 1-362.
- Johnston, I. M.** 1941. Gypsophily among Mexican desert plants. *Jour. Arnold Arboretum* 22: 145-170.
- Kaiser, E.** 1926. Die Pflanzenwelt des Hennebergisch-Fränkischen Muschelkalkgebietes. Eine pflanzensoziologische Monographie. *Repert. Spec. Novarum Regni Veg. Beih.* 44: 1-280.
- Kitamura, S.** 1950. Adaptation and isolation on the serpentine areas. (Japanese.) *Acta Phytotax. Geobot.* 12: 178-185.
- . 1952a. Serpentine flora of Mt. Shibutsu, Prov. Kodzuke, Japan. (Japanese.) *Acta Phytotax. Geobot.* 14: 174-176.
- . 1952b. Serpentine flora of Mt. Hayachine, Prov. Rikuchu, Japan. (Japanese.) *Acta Phytotax. Geobot.* 14: 177-180.
- Kitamura, S., M. Hiroe, & G. Nakai.** 1950. Serpentine flora near Sekinomiya, Prov. Tazima. (Japanese.) *Acta Phytotax. Geobot.* 12: 185-186.
- Kitamura, S., & Y. Momotani.** 1952. Serpentine flora of Island Sugashima, Prov. Shima, Japan. (Japanese with English summary.) *Acta Phytotax. Geobot.* 14: 118-119.
- Kitamura, S., & G. Murata.** 1952. Serpentine flora of Prov. Awa, Shikoku, Japan. (Japanese with English summary.) *Acta Phytotax. Geobot.* 14: 120-122.
- Kitamura, S., G. Murata, & K. Torii.** 1953. Serpentine flora of Mikawa Province. (Japanese.) *Acta Phytotax. Geobot.* 15: 1-4.
- Klika, J.** 1932. Der *Seslerion coerulacae*—Verband in den Westkarpathen. (Eine vergleichende soziologische Studie.) *Bot. Centbl. Beih.*, Abt. 2, 49: 133-175.
- . 1933. Studien über die xerotherme Vegetation Mitteleuropas. II. Xerotherme Gesellschaften in Böhmen. *Bot. Centbl. Beih.*, Abt. 2, 50: 707-773.
- Kotilainen, M. J.** 1944. Kasvit erikoislaatuisten substraatin indikaattoreina. *Årsbok Soc. Sci. Fenn.* 22B(6): 1-18.
- Kozłowska, A.** 1928. Études phyto-sociologiques sur la végétation des roches du plateau de la Petite-Pologne. *Bull. Internat., Acad. Polonaise Sci. & Let., Cl. Sci. Math. & Nat., Sér B, Sci. Nat.* 1927(Suppl. 2): 1-56.
- Kretschmer, Lotte.** 1931. Die Pflanzengesellschaften auf Serpentin in Gurhofgraben bei Melk. *Verhandl. Zool.-Bot. Gesell. Wien* 80: 163-208.
- Kruckeberg, A. R.** 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. *Amer. Jour. Bot.* 38: 408-419.
- . 1954. The ecology of serpentine soils. III. Plant species in relation to serpentine soils. *Ecology* 35: 267-274.
- Lam, H. J.** 1927. Een plantengeografisch Dorado. *Handel. 4de Ned.-Indisch Natuurwetensch. Congr., Weltevreden (Java)* 1926: 386-397.
- Lämmermayr, L.** 1926. Materialien zur Systematik und Ökologie der Serpentinflora. I. Neue Beiträge zur Kenntnis der Flora steirischer Serpentine. *Sitzber. Akad. Wiss. Wien, Math.-nat. Kl., Abt. I*, 135: 369-407.
- . 1927. Materialien zur Systematik und Ökologie der Serpentinflora. II. Das Problem der "Serpentinpflanzen"—Eine kritische ökologische Studie. *Sitzber. Akad. Wiss. Wien, Math.-nat. Kl., Abt. I*, 136: 25-69.
- . 1928a. Weitere Beiträge zur Flora der Magnesit- und Serpentinböden. *Sitzber. Akad. Wiss. Wien, Math.-nat. Kl., Abt. I*, 137: 55-99.
- . 1928b. Vierter Beitrag zur Ökologie der Flora auf Serpentin- und Magnesitböden. *Sitzber. Akad. Wiss. Wien, Math.-nat. Kl., Abt. I*, 137: 825-859.
- . 1933. Floristische Ergebnisse einer Begehung der Magnesitlagerstätten bei Dienten (Salzburg). *Sitzber. Akad. Wiss. Wien, Math.-nat. Kl., Abt. I*, 142: 233-242.
- . 1934. Übereinstimmung und Unterschiede in der Pflanzendecke über Serpentin und Magnesit. *Mitt. Naturw. Ver. f. Steiermark* 71: 41-62.
- . 1935. Notizen zur Flora über Gips, Dolomit, Phyllit, und Magnesit in Steiermark. *Mitt. Naturw. Ver. f. Steiermark* 72: 27-38.
- LeGendre, C.** 1919. Flore des terrains de serpentine de la Haute-Vienne. *Bull. de Géog. Bot. [Le Mans]* Tome 29/Ann. 27: 19-34.
- Leontjev, A. M.** 1935 (1937). Die Vegetation des Weissmeer-Kuloi Gebeits. (Russian with German summary.) *Geobotanica, Acta Inst. Bot. Acad. Sci. URSS, Ser. 3, 2*: 81-222.
- Low, A. P.** 1884. Report on explorations and surveys in the interior of the Gaspé Peninsula. *Rept. Geol. Surv. Canada* 1882-4, Pt. F: 1-21.
- Markgraf, F.** 1925. Botanische Reiseindrücke aus Albanien. *Repert. Spec. Novarum Regni Veg. Beih.* 36: 60-82.
- . 1932. Pflanzengeographie von Albanien, ihre Bedeutung für Vegetation und Flora der Mittelmeerlande. *Bibliotheca Bot.* 105: 1-132.
- Mason, H. L.** 1946a. The edaphic factor in narrow endemism. I. The nature of environmental influences. *Madroño* 8: 209-226.

- . 1946b. The edaphic factor in narrow endemism. II. The geographic occurrence of plants of highly restricted patterns of distribution. *Madroño* 8: 241-257.
- Messeri, A.** 1936. Ricerche sulla vegetazione dei dintorni di Firenze. 4. La vegetazione delle roccie ofiolitiche di Monte Ferrato (presso Prato). *Nuovo Giorn. Bot. Ital.* 43: 277-372.
- Meusel, H.** 1939. Die Vegetationsverhältnisse der Gipsberge im Kyffhäuser und im südlichen Harzvorland. Ein Beitrag zur Steppenheidefrage. *Hercynia* 2: 1-372.
- . 1940. Die Grasheiden Mitteleuropas. Versuch einer vergleichend-pflanzengeographischen Gliederung. *Bot. Archiv* 41: 357-418, 419-519.
- . 1941. Die Steppenheiden des Kyffhäusers, gesehen im Rahmen der eurosibirischen Hügelsteppenvegetation. *Ber. Deutsch. Bot. Gesell.* 59: 272-276.
- Meyer, H. A., & D. D. Stevenson.** 1943. The structure and growth of virgin beech-birch-maple-hemlock forests in northern Pennsylvania. *Jour. Agr. Res.* 67: 465-484.
- Mrugowsky, J.** 1931. Die Formation der Gipspflanzen. Beiträge zu ihrer Soziologie und Oekologie. *Bot. Archiv* 32: 245-341.
- Munz, P. A., & D. D. Keck.** 1949. California plant communities. *El Aliso* 2: 87-105.
- Negodi, G.** 1941. Studi sulla vegetazione dell'Appennino Emiliano e della pianura adiacente. II. La flora e la vegetazione dei serpentini di Varana. *Annali di Bot.* 22: 117-142.
- Nevole, J.** 1926. Flora der Serpentinberge in Steiermark (Oesterreich). *Práce Moravské Přírod. Společ.* 3(4): 59-82.
- Novák, F. A.** 1926. Vegetace na hadcových půdách v západním Srbsku. *Věda Přírodní* 7: 269-274, 289-294.
- . 1928. Quelques remarques relatives au problème de la végétation sur les terrains serpentiniques. *Preslia* 6: 42-71.
- Palacios, M. Laza.** 1936. Algunas observaciones geobotánicas en la Serranía de Ronda. *Bol. Soc. Españ. Hist. Nat.* 36: 39-46.
- Pančić, J.** 1859. Die Flora der Serpentinberge in Mittel-Serbien. *Verhandl. Zool.-Bot. Gesell. Wien* 9: 139-150.
- Pennell, F. W.** 1910. Flora of the Conowingo Barrens of southeastern Pennsylvania. *Proc. Acad. Nat. Sci. Philadelphia* 62: 541-584.
- . 1913. Further notes on the flora of the Conowingo or Serpentine Barrens of southeastern Pennsylvania. *Proc. Acad. Nat. Sci. Philadelphia* 64: 520-539.
- . 1930. On some critical species of the Serpentine Barrens. *Bartonia* 12: 1-23.
- Phillips, J. F. V.** 1934-5. Succession, development, the climax, and the complex organism: An analysis of concepts. Parts I-III. *Jour. Ecology* 22: 554-571; 23: 210-246, 488-508.
- Pichi-Sermolli, R.** 1948. Flora e vegetazione delle serpentine e delle altre ofioliti dell'Alta Valle del Tevere (Toscana). (English summary.) *Webbia* 6: 1-380.
- Platt, R. B.** 1951. An ecological study of the mid-Appalachian shale barrens and of the plants endemic to them. *Ecological Monog.* 21: 269-300.
- Quarterman, Elsie.** 1950a. Ecology of cedar glades. I. Distribution of glade flora in Tennessee. *Bull. Torrey Bot. Club* 77: 1-9.
- . 1950b. Major plant communities of Tennessee cedar glades. *Ecology* 31: 234-254.
- Radford, A. E.** 1948. The vascular flora of the olivine deposits of North Carolina and Georgia. *Jour. Elisha Mitchell Sci. Soc.* 64: 45-106.
- Raymond, M.** 1950. Esquisse phytogéographique du Québec. *Mém. Jard. Bot. Montréal* 5: 1-147.
- Robyns, W.** 1932. Over plantengroei en flora der kopervelden van Opper-Katanga. (French summary.) *Natuurw. Tijdschr.* 14: 101-106.
- Rune, O.** 1953. Plant life on serpentines and related rocks in the North of Sweden. *Acta Phytogeog. Suecica* 31: 1-139.
- Schwickerath, M.** 1931. Das *Violetum calamariae* der Zinkböden in der Umgebung Aachens. Eine pflanzensoziologische Studie. *Beitr. z. Naturdenkmalpf.* 14: 463-503.
- Scoggan, H. J.** 1950. The flora of Bic and the Gaspé Peninsula, Quebec. *Nation. Mus. Canada., Ottawa, Bull.* 115: 1-399.
- Seifriz, W.** 1940. Die Pflanzengeographie von Cuba. *Bot. Jahrb.* 70: 441-462.
- . 1943. The plant life of Cuba. *Ecological Monog.* 13: 375-426.
- Shreve, F.** 1910. The ecological plant geography of Maryland, Midland Zone; Lower Midland District. Pp. 199-219 in *The plant life of Maryland*, by F. Shreve, M. A. Chrysler, F. H. Blodgett, & F. W. Besley. Johns Hopkins Univ. Press, Baltimore.
- Sillringer, P.** 1931. Reliktini ostrovi teplomilné vegetace v nízkých Tatrách. *Preslia* 10: 156-166. *Biol. Abstr.* 8: 5332, 1934.
- Sočava, V.** 1927. Botanische Beschreibung der Wälder des Polar-Urals vom Flusse Nelka bis zum Flusse Hulga. (Russian with German summary.) *Trav. Mus. Bot. Acad. Sci. URSS* 21: 1-78.
- Sokolowa, L. A.** 1935 (1937). Die geobotanischen Bezirke der Onega-Dwina Wasserscheide und der Onega Halbinsel. (Russian with German summary.) *Geobotanica, Acta Inst. Bot. Acad. Sci. URSS, Ser.* 3, 2: 9-80.
- Steele, E. S.** 1911. New or noteworthy plants from the eastern United States. *U. S. Nat. Mus., Contrib. U. S. Nat. Herb.* 13: 359-374.
- Sternier, R.** 1925. Einige Notizen über die Vegetation der Insel Öland. *Svensk Bot. Tidskr.* 19: 303-322.
- Suza, J.** 1921. Xerothermni květena podkladů serpentínových na dolním toku Jihlavky. *Časopis Moravsk. Mus. Zem.* 20: 1-32 (*vide* Novák 1928).
- . 1928. Guide géobotanique pour le terrain serpentineux près de Mohelno dans la Moravie du sud-ouest (Tchécoslovaquie). *Acad. Tchèque Sci., Bull. Internat., Rés. Trav. Prés. Cl. Sci. Math. Nat. & Méd.* 29: 313-346. (French summary from the Czech, *Rozpravy České Akad. Věd a Umění Tr.* 2, 37(číslo 31): 1-116, 1928.)
- . 1935. Das xerotherme Florengebiet Südwestmährens (Č S R.). *Bot. Centbl. Beih., Abt. B.* 53: 440-484.
- Szymkiewicz, D.** 1938. Quatrième contribution statistique à la géographie floristique. *Acta Soc. Bot. Poloniae* 15: 15-22.

- Turrill, W. B.** 1929. The plant-life of the Balkan Peninsula. A phytogeographical study. Clarendon, Oxford. 490 p.
- Vilberg, G.** 1929 (1930). Erneuerung der Loodvegetation durch Keimlinge in Ost-Harrien (Estland). Acta et Comment. Univ. Tartu, A, 18(1): 1-117.
- Walker, R. B.** 1954. The ecology of serpentine soils. II. Factors affecting plant growth on serpentine soils. Ecology 35: 259-266.
- Waterfall, U. T.** 1946. Observations on the desert gypsum flora of southwestern Texas and adjacent New Mexico. Amer. Midland Nat. 36: 456-466.
- Weiss, R. F.** 1924. Die Gipsflora des Südharnes. Eine Vegetationsskizze. Bot. Centbl. Beih., Abt. B, 40: 223-252.
- Wells, F. G., P. E. Hotz, & F. W. Cater, Jr.** 1949. Preliminary description of the geology of the Kerby Quadrangle, Oregon. Oregon Dept. Geol. & Mineral Indust., Bull. 40: 1-23.
- Wherry, E. T.** 1930. Plants of the Appalachian shale-barrens. Jour Wash. Acad. Sci. 20: 43-52.
- Whittaker, R. H.** 1951. A criticism of the plant association and climatic climax concepts. Northwest Sci. 25: 17-31.
- . 1952. A study of summer foliage insect communities in the Great Smoky Mountains. Ecological Monog. 22: 1-44.
- . 1953. A consideration of climax theory: The climax as a population and pattern. Ecological Monog. 23: 41-78.
- Yamanaka, T.** 1951-2. Sociological studies on the serpentine vegetation. (Japanese with English summary.) Bull. Fac. Educ. Kôchi Univ. 1: 95, 2: 59 (*vide* Yamanaka 1952).
- . 1952. Studies in the vegetation and the flora on serpentine. Research Repts. Kôchi Univ. 1(9): 1-8.
- Zlatník, A.** 1928a. Études écologiques et sociologiques sur le *Sesleria coerulea* et le *Seslerion calcariæ* en Tchécoslovaquie. Trav. Soc. Roy. Sci. Bohême, Cl. Sci., N. S. 8(1): 1-116.
- . 1928b. Les associations végétales et les sols du terrain serpentineux près de Mohelno. Acad. Tchèque Sci., Bull. Internat., Rés. Trav. Prés. Cl. Sci. Math. Nat. & Méd. 29: 333-337 (Ch. IV *in* Suza 1928).
- Zollitsch, L.** 1927. Zur Frage der Bodenstetigkeit alpinen Pflanzen unter besonderer Berücksichtigung des Aziditäts- und Konkurrenzfaktors. Flora, N. F. 22: 93-158.