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 bodewag plants (Unger 1836) in contrast to bodenstel species which are restricted by a requirement for a specific chemical substance in the soil. The use of serpentine and non-serpentine populations of bodewag 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 bodewag 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 (CaSO₄.2H₂O) 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 (N₃P₄K₂). 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 *bodenwag* 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 Ca₃SO₄·H₂O; Pot B: 4 tons/acre Ca₃SO₄·H₂O; Pot C: unaltered serpentine; Pot D: serpentine plus N₃P₄K₂. Plants of serpentine and non-serpentine strains appear on right and left halves of pots, respectively.](image1)

![Fig. 2. Comparisons between serpentine (S) and non-serpentine (NS) strains of *Phacelia californica*. Total cation absorption (me. cations/gm tissue × relative yield) plotted against soil calcium level.](image2)
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 bodewag 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 bodewag 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 differ-
ces 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 cor-
related with field observations of the distribution
on serpentine outcrops of these two groups of
demic 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 ex-
cluded, but there is good reason to stress the de-
gree of calcium saturation of the soil as of major
significance in the serpentine problem. It appears
probable that an important requirement for exist-
ence 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 pos-
sess that same adaptation to low calcium levels.
The plants growing on serpentine may, in addi-
tion, be adapted to the low levels of other nutri-
ents, to the openness and strong exposure to evap-
oration in the serpentine communities, and to
other factors.

That such is the case is suggested by the phe-
nomenon of "serpentinomorphism" Many ser-
penite populations show at least slight morpho-
logical 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 popula-
tion. These characteristics of serpentine plants are
discussed by Pichi-Sermolli (1948) and Rune
(1953). Pichi-Sermolli recognizes six tenden-
cies: reduction in size of leaves and other organs,
shrubiness of growth, stunting or dwarving,
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 condi-
tions, and that the physiological adaptations of
serpentine plants may have some degree of mor-
phological expression.

Genetic Aspects of Serpentine Adaptation

The foregoing results, together with field obser-
vations, may provide some basis for considering
genetic and evolutionary aspects of the serpentine
problem. One of the characteristic genera of ser-
penite plants in California, Streptanthus, is espe-
cially 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 ma-
terials. Still other species of Streptanthus have
not been observed on serpentine, or occur pre-
dominantly on other rocks but maintain popula-
tions 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 en-
demics. The "depleted" species is an old (but
not necessarily senescent) species which has ac-
quired 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 spe-
cialized 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" spe-
cies 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 deple-
tion in progress in some species. Streptanthus
 glandulosus Hook. is the most wide-spread serpen-
tine 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 (Kruckenberg 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. brevicaulis* Gray, *S. barbigera* Morrison (*in ed. 1941*), and *S. hartwegii* 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 biocenametrics through many studies, beginning with the pioneer work of Tutreeson (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 (Kruckenberg 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 Endemics 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 bodewag 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, Lämmernayr 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 serpentine 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 unscreened 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 Streptanthi 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 Streptanthi 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 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 *bodenwag* 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. *Bodewag* 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**


