SERPENTINE VEGETATION IN CALIFORNIA

Serpentines intrude upon the California landscape mostly at moderate elevations and wholly west of the Sierra Nevada crest. Thus it is grassland, chaparral, oak woodland, and conifer forest that must meet the challenge of serpentine substrates. Moreover, since most serpentine outcrops are in a xeric, Mediterranean climate, the added stress of drought to chemical imbalance makes for even more severe environments. The net effect on plant life is the striking discontinuity between vegetation on the nonserpentine bedrock supporting normal vegetation and the plant cover on serpentine.

The serpentine barren is the most extreme manifestation of the effect of serpentine parent material. Some barrens have no plant cover whatsoever; more often the barren supports a sparse herbaceous or shrub/herbaceous cover with much intervening barren ground. The contact between normal and serpentine soils can be so abrupt that one imagines the vegetation on the serpentine side to have been severely burned or grazed. Yet this sharp contrast was not contrived by man, but by natural sorting of a select few plants tolerant to serpentine and exclusion of much of the adjacent flora. Contact zones are often sharp, and the species composition, density, and pattern of distribution in communities on either side of the contact are markedly distinct. Often the contrast in vegetation takes the form of a sudden shift in life-form spectrum and physiognomy. The most frequent shifts are from blue oak and digger pine to hard chaparral or a sparse grass–forb cover, or from chamise chaparral to a – scrub. Whittaker (1975) comments on this shift in life-form spectra as a worldwide phenomenon: in Quebec, the shift is from taiga to tundra; in Oregon, it is an abrupt transition from Douglas fir to open pine woodland; in California, it is from oak woodland to chaparral; in Cuba and New Caledonia, the shift can be dramatic, from tropical forest to savannah-scrub; and in New Zealand, it is from southern beech forest to tussock grassland.

Practically every major vegetation type at low to mid elevations from Santa Barbara County to the Oregon border is touched by the serpentine effect. Nearly always the serpentine–nonserpentine discontinuity occurs on residual soils, upslope from alluvial formations. The distribution of serpentine habitats can be overlain on a vegetation map of California (Kuchler, 1977) to reveal the many different vegetation types that can border serpentine. Besides the most common ones just mentioned, serpentine "islands" occur in redwood forest, yellow pine forest, coastal cypress–pine forest, Klamath and Coast Range montane forests, mixed evergreen forest, mixed hardwood forest, and California prairie and coastal sagebrush.

Discontinuity of vegetation type and floristic composition usually results when any of these vegetation zones is intruded by serpentine. The Kuchler map does not recognize these incursions of serpentine in the vegetation landscape, partly because of scale. Undoubtedly, though, particular patterns within the intricate mosaic of different vegetation formations in the north and south Coast Ranges do reflect the influence of the larger serpentine areas as

Kruckeberg, A.R. 1984 Serpentine Geology UC Press

they abut other formations. Chaparral–woodland contacts are likely to be serpentine–nonserpentine contacts; but since the variant floristic composition of chaparral is not differentiated, contacts due to serpentine are thus obscured in this map. The only formation on serpentine that Kuchler recognizes is the very restricted San Benito Forest (*Calocedrus decurrens* (Torr.) Florin) near New Idria.

Any more fine-grained view of cismontane California vegetation is bound to include communities of species peculiar to serpentine. Serpentine chaparral (Hanes, 1977, pp. 429-430) and serpentine grassland (Howell, 1970) are recognized as unique vegetation formations. Scattered through Barbour and Major (1977) are references to unusual range extensions, conifer distributions, plant groupings, and vegetation discontinuities on serpentines.

The characteristics of serpentine chaparral are nicely summarized by Hanes (1977 pp. 429–430):

> Serpentine chaparral is an open, low type associated with serpentine soils from San Luis Obispo Co. northward through the Coast Ranges and foothills of the northern Sierra Nevada. The shrubs are characterized by apparent "xeromorphism" (peinomorphism, serpentinomorphism) and dwarfed stature resulting from reduced productivity and growth (Whittaker, 1954). The dominant shrubs are *Adenostoma fasciculatum* H. and A. and *Heteromeles arbutifolia* M. Roem., but noteworthy are several localized endemic shrub species, *Arctostaphylos viscida* and *Ceanothus jepsonii*.
>
> *Cupressus sargentii, Garrya congdonii*, and *Quercus durata* are unmistakable "indicator species" because of their typical restriction to, and numerical dominance on, serpentine soils (Kruckeberg, 1954). Serpentine chaparral may be associated with foothill woodland (*Pinus sabiniana Dougl.*) or montane coniferous forest (*P. jeffreyi* Grev. and Balf., *P. ponderosa* Dougl. ex P. and C. Lawson, *P. attenuata* Lemmon, *Pseudotsuga menziesii* (Mirbel) Franco) as an understory (Whittaker, 1954). The thousands of hectares of serpentine chaparral in the north Coast Ranges are easily distinguished from the oak–grasslands on hills of nonserpentine origin (Walker, 1954). Wells (1962) has described serpentine chaparral in San Luis Obispo Co., as has Vogl (1973) for the Santa Ana Mts., Orange Co.

(See figs. 15–19 for views of serpentine chaparral in the Coast Ranges.)

In his flora of Marin County, Howell (1970) recognizes two serpentine communities. The chaparral–Sargent cypress association on Mt. Tamalpais consists of several woody serpentine species, *Quercus durata, Ceanothus jepsonii, Arctostaphylos montana* Eastw., and the more arborescent *Cupressus sargentii*, along with many grasses and other herbs, some of which are obligate serpentine species. Serpentine grassland in Marin County is restricted to the Tiburon peninsula and includes some of the most restricted endemics of California: *Streptanthus niger, Castilleja neglecta* Zeile in Jeps., and *Calochortus tiburonensis*. Serpentine grassland is much more local than serpentine chaparral, and (without the Tiburon endemics) is to be expected elsewhere in coastal areas such as the Redwood, California Prairie, and Coastal Sagebrush associations. Annual fescues (*Festuca pacifica* Piper and *F. reflexa* Buckl), *Stipa pulchra* Hitchc., as well as naturalized Europeans like *Bromus rigidus* Roth., *B. mollis* L., and *Avena fatua* L., are the chief grass species of this formation.

McNaughton (1968) has made some revealing comparisons between serpentine and nonserpentine grasslands; his sample of the California grassland type was in the Jasper Ridge Reserve of Stanford University, in San Mateo County—the same site used by Cooper (1922) in his classic study of California chaparral. McNaughton found that the nonserpentine grassland at Jasper Ridge, which occurs on sandstone, had greater productivity and a higher annual yield of biomass, but that the serpentine grassland showed greater species diversity. The biological attributes of the sandstone grassland were correlated with the habitat gradient (cool, moist to warm, dry); no such relationship was found for the serpentine grassland.

Kruckeberg, A.R. 1984 Serpentine Geology UC Press

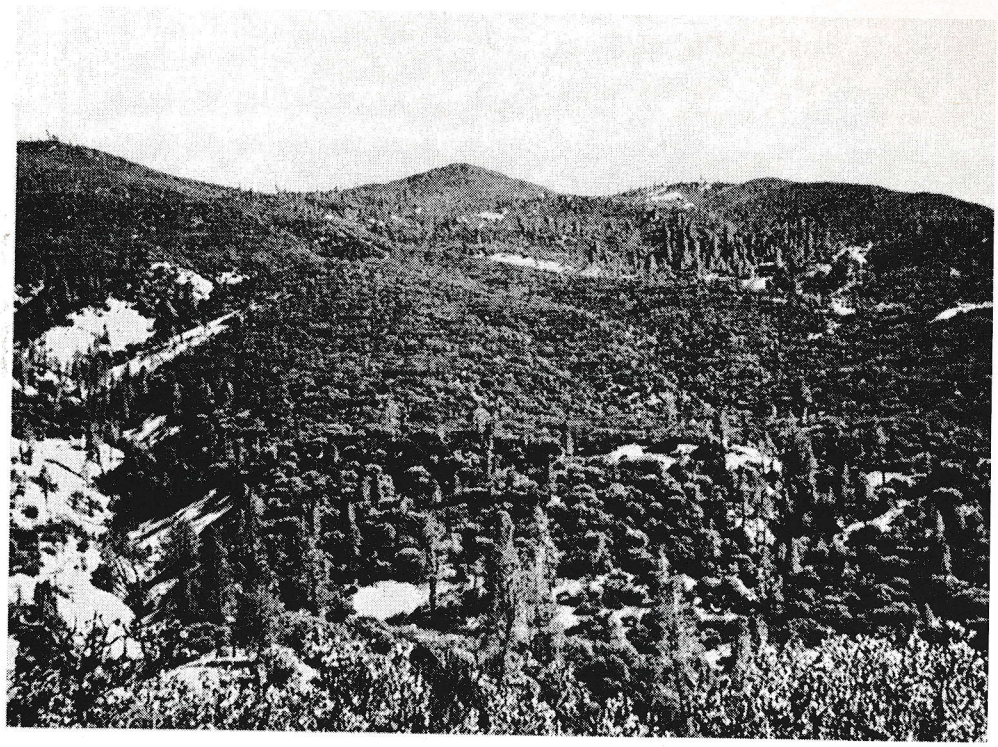


FIG. 15. Serpentine chaparral in the Clear Creek area, San Benito County. (Photo by J. Griffin.)

It is evident that California botanists have given more attention to the floristics of serpentine than to its effect on the synecology or autecology of the flora. I am aware of only a few other ecological studies of serpentine vegetation. Whittaker's (1960) study of the vegetation of the Siskiyou Mountains is a landmark paper, for here the concept of gradient analysis was successfully applied to vegetation on contrasting substrates. Though Whittaker's study sites were mainly in Josephine County, Oregon, the same vegetation types continue into northwestern California. Low-elevation serpentine vegetation occurs along the moisture gradient from open *Chamaecyparis lawsoniana* (A. Murr.) Parl.–*Pinus monticola* Dougl.–*Psuedotsuga* mesic forest, "through very distinctive forest–shrub stands with several conifers and a two-phase undergrowth of sclerophyll shrubs and grass to the [more xeric] *Pinus jeffreyi* woodlands."

In the same region as Whittaker's study, Zobel and Hawk (1980) have examined the autecology of *Chamaecyparis lawsoniana* (Port Orford cedar). This conifer is confined to wet ultramafics except at high altitudes and northern localities (in Oregon). It seems to be confined to sites of low moisture stress (minus 11 bars at predawn); certainly the high frequency of seeps and springy areas on ultramafics in the Siskiyou region of Oregon and California can account for Port Orford cedar's local fidelity to ultramafics. Though Zobel and Hawk do not comment on the chemical aspects of the substrates, it is not unlikely that Port Orford cedar has accommodated to the exceptional base status and nutrient levels of ultramafics while taking advantage of the mesic conditions. Zobel attributes the success of Port Orford cedar

Kruckeberg, A.R. 1984 Serpentine Geology UC Press



FIG. 16. Serpentine chaparral-cypress woodland at Carson Ridge, north slope of Mt. Tamalpais, Marin County.

on ultramafics to the wetness of the sites and the absence of competition from Douglas fir and other woody species.

South of the more mesic-mixed conifer vegetation on serpentine of the Klamath–Siskiyou country, vegetation in general—and particularly that on serpentine—shows the effect of increasing drought stress (both apparent and real—see below). Only a few ecological studies of this more xeric-appearing vegetation are on record. Wells (1962) found great diversity in vegetation pattern and floristic composition from his study of the vegetation on a variety of substrates (more than 15) in the San Luis Obispo region. Wells contended that serpentinite rock causes a change in the flora rather than a shift in vegetation type. Moreover, disturbance, especially fire, probably accounts for the physiognomic differences both within and between substrates. Wells cautions against the superficial inference that serpentine sites are xeric; despite xeric taxa like *Yucca, Quercus durata*, and other xeromorphic plants, the accommodations of *Umbellularia* and other more mesic and even riparian taxa suggest that serpentine sites in his study area may be more moist than is supposed. This idea is amplified by Hardham (1962) in her observations on the floristics of serpentine in the outer south Coast Ranges.

The vegetation on the only known locality of serpentine in southern California—in the Santa Ana Mountains—was studied by Vogl (1973). The hydrothermally altered serpentinite

Kruckeberg, A.R. 1984 Serpentine Geology UC Press



FIG. 17. Serpentine chaparral on the Paskenta-Covelo road, western Tehama County. *Quercus durata* and *Ceanothus jepsonii* are codominant shrubs.

supports a locally restricted stand of knobcone pine (*Pinus attenuata*). Other notable taxa restricted to this local ultramafic outcrop are *Ceanothus papillosus* T. and G. var. *roweanus* McMinn and *Ribes malvaceum* Sm. var. *viridifolium* Abrams. The pine appears to be restricted to serpentinite here, due to the lack of competition with the chaparral species common on adjacent nonserpentine habitats as well as its adaptation to low nutrient levels. Vogl further supports the increasing realization that ultramafic soils can have a higher water-holding capacity than nearby nonserpentine soils: "The water-retaining capacity of the serpentinite is nearly double that of the chaparral soils. This soil characteristic, the frequent fogs, the location of the pines in fog gaps, . . . contribute to the persistence of the pines. . . ." The knobcone pine habitat is held in a successional state by fire, to which the closed-cone attribute is uniquely adapted.

Californian species of *Cupressus* and of the closed-cone pine group are characteristically restricted to serpentinite and other edaphically atypical soils. McMillan (1956) did extensive field and greenhouse studies of these coniferous species as well as of a number of associated herbaceous taxa. Since low calcium and reduced nitrogen and phosphorus levels were com-

Kruckeberg, A.R. 1984 Serpentine Geology UC Press



FIG. 18. Serpentine chaparral landscape on the Paskenta-Covelo road, western Tehama County.

mon to both the serpentine and acid soils, McMillan expected that reciprocal progeny testing would show a "common denominator" effect: that is, a given strain of conifer species would be tolerant to acid *and* serpentine soils. Instead, edaphic tolerance appeared to express itself in a highly individualistic manner. However, tolerance to both acid and serpentine soils seems to occur in *Rhododendron occidentale* (T. and G.) Gray. It has been proposed that this azalea can thrive where the percentage of exchangeable calcium is low—as it is on both serpentine and the acid soils in California where the plant "normally" occurs (Leiser, 1957).

Principal components analysis of data from serpentine vegetation in eastern Napa County (Koenigs et al., 1982) achieved a grouping of "cypress" and "non-cypress" stands. "Stands with *Cupressus sargentii* also contained *Arctostaphylos viscida* and occurred on mesic sites with lower Ca in the sub-surface soil. Stands without *C. sargentii* usually contained *Adenostoma fasciculatum* and *Quercus durata* and occurred on the drier sites with higher Ca."

Kruckeberg, A.R. 1984 Serpentine Geology UC Press



FIG. 19. Serpentine chaparral with scattered digger pine (*Pinus sabiniana*) in a mixed conifer forest setting, north fork of Beegum Creek area, Trinity County.

The abrupt discontinuity between serpentinite and other substrates often evokes a sharp break in plant communities—both in life-form and in species composition. The only ecological analysis of such a contact discontinuity for Californian vegetation is in the paper by J.T. Gray (1979), in which the vegetation along elevational gradients in the north Coast Ranges and the Sierra was studied. In his work on the Coast Range sequence at Snow Mountain (Lake County), Gray noted an abrupt change from chaparral woodland on lower-elevation serpentinites to montane coniferous forest on higher-elevation nonserpentine parent materials. The attributes of a clear-cut break in vegetation type are mainly floristic, but the shift in taxa also includes a shift in life-form. Along the Snow Mountain transect, Gray found the common woody plants of serpentinite (*Pinus sabiniana, Ceanothus cuneatus* (Hook.) Nutt., *Quercus durata* and *Adenostoma fasciculatum*) giving way to *Pinus ponderosa, Quercus chrysolepis* Liebm., *Arctostaphylos canescens* Eastw., *Pinus lambertiana* Dougl., and *Abies concolor* (Gord. and Glend.) Lindl. on other substrates. The sharp break in vegetation type at 1250 m coincides with the change from ultramafic to normal soils.