

Vegetation Classification and Plant Community Stability: A Summary and Synthesis¹

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I have attempted not only to summarize each paper but also to refer to other information and papers so that the reader can evaluate its contribution. I take full responsibility for the interpretation of these papers in this summary. The first two papers deal with vegetation classification, the third paper contrasts California - Israel shrublands, two papers deal with chaparral succession, and the final paper presents a timely discussion on coastal sage scrub succession. Each author has made a significant contribution to the manner in which we classify and perceive the dynamics of Mediterranean-type vegetation.

A Mediterranean System

The classification of Mediterranean-type vegetations has been a challenge to biologists and geographers through the 20th Century. Barbero and Quezel herein build a strong case for phytosociological and bioclimatic analysis of Mediterranean-type plant associations. They claim that the traditional physiognomical and the more sophisticated ecophysiological and autecological studies used in the United States are not suitable methods for classifying Mediterranean-type ecosystems. They suggest that purely physiognomical methods portray only a small part of the total ecology of vegetation. Even strictly phytosociological methods have limited application in classifying ecosystems.

Barbero and Quezel (these proceedings) propose a correlation of ecological and dynamic approaches to be used in classifying ecosystems. They point out that problems arise when climatic criteria are the sole basis of classification. In America plant ecologists are aware of the severe limitations of the old Merriam life zones based upon thermal minima. Furthermore, Barbero and Quezel give evidence that climatic zones do not match vegetation zones based on physiognomy. They propose that the problem can be rectified by using bioclimatic criteria such as water balance by means of instruments or theoretically, using

coefficients. Summer drought is universally accepted as a bioclimatic component of Mediterranean-type vegetation.

Barbero and Quezel show that by not setting a limit on thermal minima, an entire scale of vegetation types emerges. Also, annual rainfall and humidity create bioclimatic zones that are useful in vegetation classification. Finally, altitudinal levels can be correlated with thermal criteria, species composition, and vegetation types.

It is stated that dynamic approaches to classifying ecosystems consider successional trends of vegetation and the development of stands of vegetation. Readers may find the use of the term "vegetation evolution" confusing since the authors are actually describing succession (vegetation change through time). The authors' traditional view of vegetation succession does not consider the different adaptive strategies of various species to perturbations nor the current debate on different types of succession (Drury and Nisbet 1973, Grime 1979). It is unclear how the authors determine successional stages and how such determinations are used in their classification scheme.

The authors identify the classical successional sequence of: annual grassland - perennial grassland - scrubs - pre-forest formation - climatic forest. If this classical sequence applies broadly to the entire Mediterranean rim it differs markedly from California chaparral succession. In California, chaparral replaces itself and does not give way to forest except in its upper elevational reaches. Disturbance initiates physiognomic changes (to herb and scrub phases) concomitant with shrub seedlings and crown sprouts. Over most of the chaparral lands of California, the climax vegetation is chaparral. The existence of herb and scrub phases, a few years after disturbance, are not obligate preparatory series to chaparral development.

Barbero and Quezel end their paper by suggesting various methods of classifying ecosystems for applied purposes. These are mapping, numerical analysis, and ecological zonation. Practitioners may find the reduction of vegetation parameters to numerical values of limited utility.

A California System

Paysen gives an extensive review of vegetation classification in California and describes a new system suited to various user needs. Justification for a new classification system is provided by showing that serious interdisciplinary communication problems exist due to divergent principles and uses of classification output. Earlier systems of vegetation classification

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cation are no longer suitable to resource managers and researchers due to changing perceptions of vegetation.

Historically, California's vegetation has been described in natural terms. Broad physiognomic types, such as grassland and timber, emerged when California's vegetation was viewed as a resource. Classification systems developed in relation to timber production and range values, neither of which included the shrublands with their watershed values. In the 1930's, fire management planning in southern California led to a major vegetation classification and mapping effort undertaken by Wieslander. The widely used Munz system of classifying vegetation into plant communities, first introduced in the late 1930's, leaves much to be desired since it is entirely subjective in nature. Several studies in the 1970's recognized habitat types and detailed vegetation composition, but fail to provide a universal system of classification.

The new vegetation classification system developed in California acknowledges the need resource managers have for an understanding of the nature of dynamics of vegetation in precise terms rather than phytosociological abstractions. It assumes that anyone in the field, practitioner and researcher alike, can classify a site-specific plant community by tabulating a few vegetation characteristics. This tabulation follows an aggregative hierarchy in logical sequence.

Classification starts with a basic unit, the Association, and builds upward through the hierarchy in progressively broader descriptive terms. It is important to realize that the Association is considered independent of the ecology, phytosociology, or stage of development of the vegetation. The Association is named in terms of the relative crown cover of dominant overstory species and the dominant species in subordinate layers. Codominant species can be included in the Association name.

Associations are aggregated into Series based on dominant overstory species; into Subformations based upon leaf and stem morphology; into Formations based upon growth form. The Phase is a flexible qualifier category used to describe Associations of varying age, condition, or stage of development. Most of these vegetation parameters are readily determined by experienced field workers.

The greatest strength of this new classification system is that it is a system rather than a classification of vegetation. It is a universal framework into which any and all vegetation can be fit. If all future studies classify vegetation with this system, a large groundswell of information will be developed that will communicate vegetation information to all practitioners and researchers familiar with the

system. The vast array of Environmental Impact Reports (E.I.R.'s) prepared in the past decade would have contributed immeasurably to our knowledge of California vegetation had this system been in use. The same can be said of all mandated U.S. Forest Service resource inventories, as well as watershed management studies, fuel modification and type conversion studies, control and prescribed burn studies, and plant ecological and wildlife habitat studies.

Unfortunately Paysen's paper does not present results of trials and case studies. This void is particularly evident when one considers chaparral. Does the system chop chaparral into large, medium or small chunks? Several other questions may occur to the student of classifying methodology. Since both Subformations and Formations are based upon life form characteristics, what is the difference? Does growth form in Formations refer to plant height, crown diameter, or the physiognomy of the vegetation? Further, no indication is given of difficulties experienced with the system. One wonders what the training, experience, and commitment of the classifiers was or needs to be. Undoubtedly, uniform classification results will depend upon the background of those who use the system. Finally, the system needs and deserves a name. After all, if it is intended to communicate between disciplines, we all need to know what it is called.

The common language and the universal application of what I think should be called the California System of Vegetation Classification makes it the system that all people involved in vegetation work should adopt now and use consistently. Its widespread use throughout California could be the most significant, unifying vehicle in vegetation studies and vegetation management in the 1980's. One can only speculate as to its contribution to our understanding of the various vegetations we call chaparral.

California-Israel Shrublands

By contrasting and comparing the mediterranean-type vegetations of California and Israel, Shmida has given us insights into their unique features. Although they represent the same physiognomic types, the vegetative compositions of the two regions are distinctly different. This of course, is why the concept of convergent evolution has been so productive. It says, given groups of plants of different phylogenies and independent origin but exposed to similar environmental conditions through time, the plants will develop similar morphologies, physiologies, and physiognomies. Readers may question the validity of Shmida's extrapolations from Israel to the other Mediterranean rim countries.

Israeli maquis compared with California chaparral is taller, less dense, and less woody. Israeli maquis is also richer in species and genera, both in local stands and between regions. Chaparral is composed almost entirely of ever-green species where Israeli maquis contains many deciduous species. Few chaparral shrubs are spinescent stemmed but many have spinescent leaves. There is usually no herbaceous understory in the chaparral. Lignotubers and root-crown sprouting in chaparral are strong adaptations to fire, but there is no counterpart in Israel. California chaparral is more clearly fire adapted both in vegetative and sexual reproduction.

Montane chaparral invades the coniferous forest as an understory. In Israel there is no such invasion in the tree zone above; it is mainly deciduous.

Coastal sage scrub vegetation differs from Israeli phrygana in several respects. It is more restricted in distribution and may reflect a shorter exposure to overgrazing than in Israel. Students of coastal sage scrub ecosystems will note that dominant species (Encelia farinosa and Eriogonum fasciculatum) were not included but that Shmida included many desert species not commonly a part of sage scrublands. Rather than coastal sage scrub expanding into disturbed chaparral on a grand scale, we are seeing the demise of coastal sage scrub owing to urbanization. Sage scrub has more woody shrubs and fewer annuals than phrygana, yet in the springtime the intershrub spaces may support a diverse herb carpet. Several cacti and other succulents are components of coastal sage scrub.

Dynamics of Chaparral Change

Succession has been a fruitful concept in understanding the dynamics of California chaparral since the turn of the century (Plummer 1911, Clements 1916, Cooper 1922). Yet more recent studies have shown that classical "replacement" succession does not apply to California chaparral (Hanes 1971, 1977). Dr. Vogl contrasts chaparral with classical succession, showing that the absence of seral stages with their site modification properties makes chaparral distinctive. There are several additional features that need to be emphasized, however.

Dr. Vogl is correct in his description of primary chaparral succession as direct, that is, invasion of a site by climax species. It is important to note that primary chaparral succession does not involve the complete spectrum of chaparral plant species. Rather, only a few half-woody and woody species colonize virgin sites. These include California buckwheat (Eriogonum fasciculatum), chaparral yucca (Yucca whipplei) pricklypear cactus (Opuntia spp., yerba santa (Eriodictyon spp.)), and

chamise (Adenostoma fasciculatum). Increased species diversity on colonized sites seems to be a protracted process, and if the substrate is unstable, species diversity remains low indefinitely.

Primary chaparral succession occurs on broken rock surfaces in mountains and on alluvial fans and washes in valleys. Alluvial scrub, the vegetation that develops on floodplains (Cooper 1922, Smith 1980), reveals many vegetation dynamics that result from periodic flooding; (1) New substrates are formed by stream deposits during intense winter storms. (2) Colonization is accomplished by seeds of ruderals, subshrubs of coastal sage scrub, and woody chaparral species. (3) Mature stands are composed of a rich flora of springtime herbs and extensive stands of subshrubs punctuated with large ever-green chaparral shrubs. In this vegetation type there does not seem to be a decline in productivity or species diversity, or an increase in senility with age. For these and other reasons it is a suitable vegetation type upon which to test conceptual models of succession.

Chaparral contrasts with many ecosystems in that there is little if any increase in species diversity as the stand matures (Horton and Kraebel 1953, Patric and Hanes 1964). In fact, if one considers the ruderals (annuals) as part of the chaparral, there is a dramatic reduction in species diversity within the first five years after fire. Even by excluding the ruderals of the herb phase, the number of individuals and the demise of some woody species results in stands of low species diversity. This is particularly true on the more xeric sites that support chamise chaparral (Hanes 1971). This "unstocking" of chaparral stands as they mature is a unique feature that correlates with a decline in live tissues of those plants that remain (Hanes 1971).

In Dr. Vogl's conceptual model of chaparral succession, the process is considered cyclic rather than linear retrogressive. The cycle or pulse is initiated by a perturbation, mainly fire. Like an off-centric at the top of a wheel, fire results in high initial productivity and species diversity that gradually decrease through time until the next perturbation accelerates them again. Dr. Vogl raises an interesting point when he states, "The concern in chaparral is not so much if chaparral will recover after fire and how long it will take, but rather how rapidly the system will decline without fire". We know that chamise chaparral stands 60-90 years old have very low productivity and species diversity, and are often decadent (Hanes 1971). In more mesic chaparral, such as scrub oak chaparral, the rate of vegetation decline is much more protracted, perhaps two to three times as long.

Dr. Vogl's claim that decreased erosion leads to chaparral replacement by grassland and

savanna or forest should lead readers to some questions and debate. There are numerous steep sites occupied by oak and pine forests. Steep rocky slopes are not the exclusive domain of chaparral. Surely there are many other factors than steep slope gradients and high erosion rates that account for the presence of California chaparral on the millions of acres (hectares) upon which it grows.

Chamise Chaparral Succession

Rundel's study of chaparral succession is significant in several ways: (1) It deals with the chamise chaparral in Sequoia National Park in central California mountains, (2) the pattern of succession is the same as that found in Southern California and Coastal Northern California studies, (3) it reveals important soil-plant interactions, and (4) it provides useful information to land managers in relation to fire intensity and season.

Rundel proposes that first pulse or herb phase of post-fire chaparral succession serves as a reservoir for nitrogen on burned sites. Without this tie-up by herbs, soil nitrogen would be vulnerable to erosion from the site. The woody species, present in the early stages of plant succession, also tie up nutrients but to a lesser extent than the herbs. Heavy livestock grazing during the herb phase reduces the protective cover and exposes nutrients to leaching and run-off.

In our understanding of chaparral dynamics the picture continues to emerge that the shrubs composing the mid-successional stand are of two types; short-lived and long-lived. Within the short-lived group some Rundel found were half shrubs such as Malacothamnus, Lotus, Eriodictyon, and Dendromecon, whereas the others are woody shrubs having developed from seed, but die out of the stand when it is middle-aged. Many species of Ceanothus are of this type. These drop-outs can be explained on the basis of competition, and yet differences in life span and tolerance to stress must be considered (Grime 1979).

Senility of old chamise chaparral has been recognized for some time (Hanes 1971). However, its cause has only been speculative until recently (Rundel and Parsons 1980). Limited nutrient availability, especially nitrogen, may contribute to the decline of chamise chaparral. More work is needed to show whether the fire-induced pulse results in a high input of nitrogen by the young vegetation. If the initial input must serve the chaparral throughout its development and maturation, then a deficiency could help explain the low productivity of old stands.

Not all resprouting shrubs survive fire (Hanes and Jones 1967). Even though Rundel's data show unusually high percentages of rootcrown kill, his findings serve as a caution at this time of increasing interest in control burning. Old stands of chaparral with high fuel loads can generate heat sufficient to kill many rootcrowns. Rootcrown mortality from fire is also correlated with the season of the year as it relates to starch reserves in the roots. Low starch reserves in late spring and early summer reduce resprouting potentials. But low moisture content in the soil reduces the impact of fire on seed reserves (Dunn & Poth 1979). Resource managers must fit control burn schedules to their post-fire vegetation needs.

Coastal Sage Scrub Succession

Westman's paper on coastal sage scrub succession is timely. For too long botanists and land managers alike have treated coastal sage scrub and chaparral as one vegetation type. Several characteristics argue against this practice. Among them are leaf type (mesophyllous, drought deciduous), half-woody (subligneous) stems, and greater drought tolerance. When compared to the hard (sclerophyllous), evergreen leaves of chaparral shrubs, and their woody stems and greater stature, it is unfortunate that these distinctly different Mediterranean-type vegetations have been considered as one. The use of soft chaparral when speaking of coastal sage scrub is an unfortunate misnomer that should be abandoned.

Westman provides ample evidence for treating coastal sage scrub as distinct from chaparral in structure, composition, physiognomy, phenology, physiology, habitat, and distribution. Two major formations are recognized: northern coastal scrub and southern coastal sage scrub. The southern formation is further subdivided into Venturan, Riversidian, and Diegan.

As with chaparral, the leaf is the single most diagnostic feature of coastal sage scrub vegetation. It is small to medium size, mesophyllous, drought-intolerant, has higher transpiration rates than chaparral sclerophylls, and is susceptible to SO₂ damage.

Three leaf duration features are described: (1) short (1-2 months), (2) small leaves on lateral stems during summer drought, (3) recovery after prolonged wilt. Westman proposes that photoperiod may be the trigger mechanism for seasonal leaf dimorphism rather than drought. Yet his findings indicate a higher incidence of leaf dimorphism on recent burns where environmental conditions are more stressful.

Coastal sage scrub is known for its aromatic properties and subligneous stems. The leaf oil content of dominant species is high, resulting in high flammability. Both coastal scrub and chaparral vegetations are fire types. Yet due

to the lower fuel loading from both live and dead stems, scrub communities support low fire intensities. Such low fire heat allows for abundant seed survival and the sprouting of burned rootcrowns, even though they lack root-crown burls (lignotubers).

The subligneous stems and the mesophytic leaves of coastal scrub species have other implications as described by Dr. Westman. Decomposition rates are high, resulting in rapid nutrient turnover. The life expectancy of most sage scrub species is generally short (10-30 years), and so the death and decomposition of entire plants accelerates nutrient turnover.

A unique feature of coastal scrub species is their ability to colonize disturbed sites as well as replace dead companions in intact stands. This feature allows scrub species to invade burned chaparral sites at low elevations, form enclaves within chaparral stands, and to maintain a climax community of coastal sage scrub with a mosaic of shrub ages.

Dr. Westman has laid a strong foundation in our understanding of the coastal sage scrub vegetation of California. It should be clear that this vegetation is a unique Mediterranean-type, distinct from chaparral, and that its compositional features as well as its vegetation dynamics demand attention from scientists and practitioners.

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