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STRUCTURE AND FUNCTION IN CALIFORNIA GRASSLANDS

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Abstract. Functional and floristic properties of annual grasslands on serpentine and sandstone soils at an elevation of 180 m on Stanford University's Jasper Ridge were determined along an intuitive habitat gradient from northeast to southwest exposures. The most frequent species contributed the most to peak standing crop in only half the stands. *Stipa pulchra*, the only native species among the important species, was more important on serpentine than on sandstone sites. *Bromus mollis*, the other consistently important species, increased in importance with decreasing moisture supply on both soils. The sandstone grasslands sustained a greater biomass, were more productive, and were less diverse than serpentine grasslands. Within the grasslands as a whole, productivity was inversely related to diversity and positively related to dominance. Stability, however, was related to neither productivity, diversity, or dominance. Thus productivity may increase in such a system with no sacrifice in stability. Properties of sandstone grasslands were clearly related to the habitat gradient from cool, moist sites to warm, dry sites. There was no such relationship in serpentine grasslands. Dominance-diversity curves generally fit previously described models, except on southwestern serpentine exposures. The annual grassland vegetation is a mosaic of floristic composition and ecological properties, shifting in response to habitat patterns but without abrupt discontinuities.

INTRODUCTION

California's annual grasslands, occupying extensive areas in the Central Valley and along the Pacific Coast (Munz and Keck 1949, Biswell 1956, Kuchler 1964) (Fig. 1), form a vegetation type that is unique in North America: a distinct and extensive community type consisting largely of introduced species (Biswell 1956). Nearly 400 alien species have been recorded in these grasslands, and in most sites aliens constitute the major vegetative cover. Although most authors believe

that the prehistoric vegetation was perennial (Munz and Keck 1949, Wells 1964), historical evidence is meager and the earliest references are to annual prairies (Biswell 1956). Twenty-nine years of protection from grazing and fire produced grasslands in Monterey County which were still dominated by *Bromus rigidus*, *B. mollis*, *Avena fatua*, and *Erodium Botrys* (White 1966). Regardless of their initial cause, it seems likely that the current annual grasslands are more similar than the original prairies to the vegetation which would result from the elimination of disturbance.

This vegetation is essentially reconstructed de novo each growing season (Major and Pyott 1966). Because the soil is a reservoir of a considerable variety of potential occupants, the grassland composition is extremely responsive to fluctuations in habitat conditions. The variations in vegetation character from year to year and under different treatments were recognized early in the systematic investigation of California's grasslands (Talbot, Biswell, and Hormay 1939). Many ecologists have provided evidence of this vegetation's response to fire, grazing, and climatic oscillations (Hendrick 1948, Hervey 1949, Heady 1956, 1958).

The study reported here was designed to determine the effects of soil type and exposure upon composition, diversity, biomass, productivity, and stability of California's annual grasslands. Support was by NIH 5T1-GM-365-04, Division of Systematic Biology, Stanford University. Plant identifications were by J. Thomas. P. Raven, J. Thomas, R. Holm, L. Mason, and E. Leigh of



FIG. 1. Distribution of grasslands in California and location of Jasper Ridge (●) on San Francisco Peninsula.

the population biology group at Stanford University, together with A. Kruckeberg of the University of Washington, provided many helpful comments and discussions.

THE STUDY AREA

The Jasper Ridge Experimental Area, maintained by the Division of Systematic Biology at Stanford University, had been protected from grazing and burning for over 5 years previous to this study. Since annual communities may be expected to adjust comparatively rapidly to prevailing habitat state (White 1966), these grasslands are probably representative of California grasslands free of disturbance although they may not yet approach steady state. In fact, steady state for these communities may involve year-to-year changes with climatic oscillation.

Jasper Ridge is an inland Coast Range foothill on the San Francisco peninsula approximately 3 km long and 1 km wide with its long axis lying in a northwest-southeast direction. The protected area varies in elevation from 90 m along San Francisquito Creek to 200 m at the crest. Redwoods (*Sequoia sempervirens*) occur along the creek, oak-madrone forest (*Quercus agrifolia* and *Arbutus menziesii*) and chaparral (*Adenostoma fasciculatum*, *Ceanothus cuneatus*, and *Arctostaphylos crustacea*) occur on the shoulders of the ridge, and the crests are grasslands with an occasional individual of California blue oak (*Quercus douglasii*) interspersed. The parent material of the ridge is largely sedimentary rock, but it is traversed by a serpentine intrusion. Cooper's (1922) pioneering studies on the effects of serpentine-derived soil upon vegetation were done on Jasper Ridge.

The grasslands studied are located on sandstone (Fig. 2) and serpentine (Fig. 3) soils at an elevation of 180 m. The principal nutritional dif-



FIG. 2. General view of the sandstone grasslands looking north toward southeast (on the right) and southwest (on the left) exposures. Photograph taken on June 10, 1966.



FIG. 3. General view of the serpentine grasslands looking at the same exposures as in Fig. 2 on the same date. Note the large outcrops of undifferentiated serpentine and numerous large rocks.

ference in California sandstone and serpentine soils is the much lower calcium:magnesium ratio of the latter. McMillan (1956) found that this ratio averaged 2.95 for sandstone and 0.17 for serpentine, with the magnesium content being about six times greater in serpentine soils. The effects of this unique soil property upon vegetation are well known (Cooper 1922, Whittaker 1954a, 1954b, 1960, Walker 1954, Kruckeberg 1954, McMillan 1956).

METHODS

Beginning on January 1, 1966, and on the first of every month through July 1, 1966, three quadrats 1 m by $\frac{1}{2}$ m placed end to end perpendicular to the slope of the hill were harvested on northeast, northwest, southeast, and southwest slopes on sandstone and serpentine soil areas. Position of quadrats on slopes was random. Aboveground standing crop was dried at 105°C for 8 hr, and the yield of each quadrat was determined separately. During May, which represented the period of peak standing crop, two 5-m transects, one parallel and one perpendicular to the slope, were used to determine frequency and yield of individual species. Fifty random numbers were drawn from Snedecor (1956) to fix sampling points on each transect. At each of these points, frequency was determined by canopy interception and a 4-cm² area was harvested, sorted into species composition, and dried. Each species contribution to peak biomass was determined after drying. The sampling technique, though laborious, allowed a more direct comparison of floristic data (gathered along a transect) with biomass data (gathered by harvesting randomized blocks). Standing crop refers to total plant material present, including litter. Productivity is defined as change in standing crop with time.

TABLE 1. Relative importance of species on two soil types and four exposures in the Jasper Ridge grasslands—expressed as percentage of peak standing crop and as percentage frequency during the period of peak standing crop

Species	Sandstone				Serpentine			
	North-east	North-west	South-east	South-west	North-east	North-west	South-east	South-west
A. Standing crop								
<i>Avena fatua</i>	44.4		8.6					
<i>Medicago hispida</i>	0.7		3.7					
<i>Avena barbata</i>			1.7					
<i>Torilis nodosa</i>		1.8	0.9					
<i>Centaurea melitensis</i>			2.0					
<i>Festuca megalura</i>				0.2				
<i>Lolium multiflorum</i>	7.0	7.4		3.5				
<i>Erodium botrys</i>	4.4	0.8	5.9	8.3				
<i>Bromus rigidus</i>	35.4	67.8	42.6	22.6				
<i>Bromus mollis</i>	7.0	21.1	21.3	38.1	7.9	19.6	27.3	53.2
<i>Clarkia purpurea</i>	1.1	1.1	4.7	1.2	3.3	1.2	2.7	
<i>Hemizonia luzulaefolia</i>			1.2	8.3	11.8			5.9
<i>Eriastrum abramsii</i>				3.0				0.8
<i>Lotus subpinnatus</i>			0.2	3.7	4.0	6.5	3.6	14.4
<i>Stipa pulchra</i>				16.4	40.7	41.0	26.4	10.5
<i>Eschscholzia californica</i>					11.8	11.6	13.4	1.3
<i>Festuca grayii</i>					1.1	1.2	10.2	1.4
<i>Plantago erecta</i>					2.0	4.1	5.6	1.8
<i>Melica californica</i>					8.0	11.2		
<i>Linanthus androsaceus</i>					1.7	0.45		
<i>Brodiaea laxa</i>					0.35	3.0		
<i>Calochortus venustus</i>					3.3			1.0
<i>Agroseris heterophylla</i>					0.31			2.4
<i>Festuca dertonensis</i>					0.30		2.1	
<i>Achillea millefolium</i>					1.4			
<i>Polypogon monospermiensis</i>					0.20			
<i>Trifolium tridentatum</i>						0.10		
<i>Brodiaea pulchella</i>							4.0	
<i>Sitanion jubatum</i>							3.6	
<i>Lomatium utriculatum</i>								6.5
<i>Madia gracilis</i>							1.0	1.6
<i>Poa scabrella</i>								0.6
B. Frequency								
<i>Avena fatua</i>	31		4					
<i>Medicago hispida</i>	2		3					
<i>Avena barbata</i>			1					
<i>Torilis nodosa</i>		1	1					
<i>Centaurea melitensis</i>			3					
<i>Festuca megalura</i>				1				
<i>Lolium multiflorum</i>	11	8		1				
<i>Erodium botrys</i>	2	1	5	6				
<i>Bromus rigidus</i>	32	55	27	18				
<i>Bromus mollis</i>	20	34	43	63	24	30	40	53
<i>Clarkia purpurea</i>	2	1	4	2	4	3	4	
<i>Hemizonia luzulaefolia</i>			3	6	18			7
<i>Eriastrum abramsii</i>				2				1
<i>Lotus subpinnatus</i>			1	2	6	8	5	14
<i>Stipa pulchra</i>				4	14	20	14	3
<i>Eschscholzia californica</i>					4	12	3	1
<i>Festuca grayii</i>					3	4	21	4
<i>Plantago erecta</i>					10	10	4	4
<i>Melica californica</i>					2	8		
<i>Linanthus androsaceus</i>					5	2		
<i>Brodiaea laxa</i>					3	2		
<i>Calochortus venustus</i>					2			1
<i>Agroseris heterophylla</i>					1			4
<i>Festuca dertonensis</i>					1		5	
<i>Achillea millefolium</i>					1			
<i>Polypogon monospermiensis</i>					1			

TABLE 1.—Continued

Species	Sandstone				Serpentine			
	North-east	North-west	South-east	South-west	North-east	North-west	South-east	South-west
B. Frequency								
<i>Trifolium tridentatum</i>						1		
<i>Brodiaea pulchella</i>							2	
<i>Sitanion jubatum</i>							1	
<i>Madia gracilis</i>							1	6
<i>Lomatium utriculatum</i>								3
<i>Poa scabrella</i>								1

SPECIFIC PROPERTIES OF THE GRASSLANDS

The principal species in the grasslands of Jasper Ridge are generally grasses, although the composition varies considerably from site to site (Table 1). The only non-graminaceous species to occur with regularity among the dominant species is California poppy (*Eschscholzia californica*), which is important on all serpentine sites but the driest. It is, however, excluded from the sandstone grasslands. *Stipa pulchra* is an important dominant on all of the serpentine sites, but it penetrates the sandstone grasslands only at the dry end of the moisture gradient. If all the serpentine stands are summed, *S. pulchra* is the most important species on serpentine sites contributing an average of 30% of the total standing crop, although it shares dominance with *Bromus mollis* which contributes 27% of the total. The next most important species on the serpentine is *Eschscholzia californica* contributing 9% of the total standing crop. On the sandstone, the three most important species contribute much more to the total standing crop (77%) than the three most important serpentine species (66%). On the sandstone, *Bromus rigidus* contributes 42% of the total overall standing crop, followed by *B. mollis* (22%) and *Avena fatua* (13%).

Considering grasslands on both sandstone and serpentine soils, *B. mollis* was most important, contributing 24.4% of the total standing crop, followed by *B. rigidus* (21.2%), *S. pulchra* (16%), and *A. fatua* (6.7%). Together, these four grasses contributed 69% of the total peak biomass on the Jasper Ridge grasslands. Only one of these species, *S. pulchra*, is native to the California grasslands.

The biomass of populations is emphasized in this treatment because it seems a more realistic term for community evaluation than the commonly used floristic assessment, frequency. Although percentage standing crop and percentage frequency

are significantly correlated ($r = 0.794$; $.001 > P$), frequency emphasizes those species which are most conspicuous as a result of their numbers rather than those which contribute most to community structure. Even considering only the two top species per stand (according to biomass), the correlation between percentage frequency and percentage standing crop is high for both serpentine ($r = 0.849$; $.01 > P > .001$) and sandstone ($r = 0.677$; $.1 > P > .05$) sites. However, in spite of the high correlation between the two characters, serious errors may result from using one as an indicator of the other (Table 1). For instance, *B. mollis* is the most frequent species on every serpentine site, and yet on one of these sites it ranks fifth in terms of contribution to standing crop. And on southeast sandstone exposures, *B. mollis* is twice as frequent as *B. rigidus*, but contributes half as much to community biomass. Although the high correlation between the two characters demonstrates a high degree of correspondence, the areas where there is a lack of correspondence could lead to substantial distortions in community assessment. Although frequency data are much easier to collect, they are probably less reliable indicators of community structure and function than such parameters as biomass.

The distribution of *B. mollis* is directly related to the exposure gradient on both substrate types, although the magnitude of the response is more pronounced on serpentine (Fig. 4) than on sandstone (Fig. 5) soils. Waring and Major (1964) found that this grass was confined to the driest and most exposed sites in the vegetation of the Coast Ranges of northern California, and a similar response is evident in these central California coastal grasslands. On serpentine soils, the distribution of *B. mollis*, an introduced annual, and *S. pulchra*, a native perennial, are reciprocally related. *S. pulchra* is the most important species on the cool, moist northern slopes, but its impor-

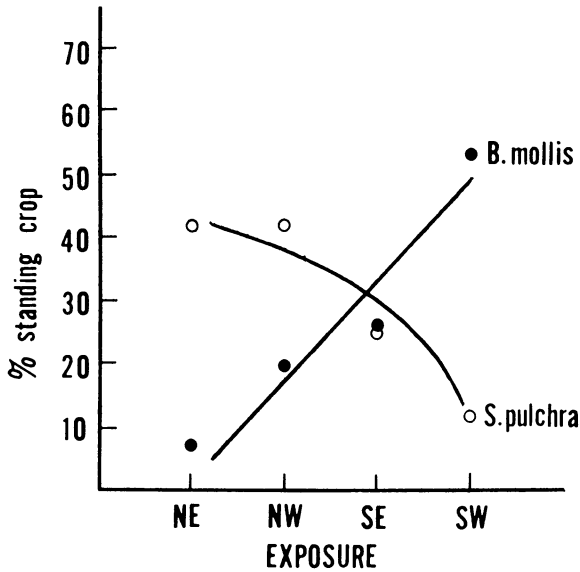


FIG. 4. Distribution of importance of *Bromus mollis* and *S. pulchra* in relation to the exposure gradient on serpentine soils.

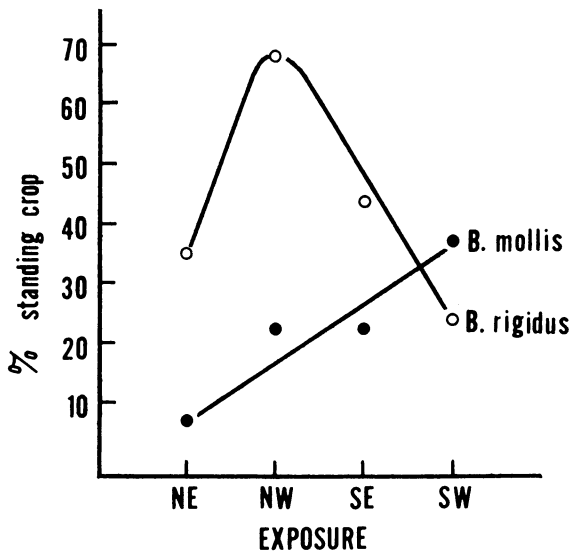


FIG. 5. Distribution of importance of *B. mollis* and *B. rigidus* in relation to the exposure gradient on sandstone soils.

tance declines conspicuously toward the drier end of the habitat gradient. A somewhat different response than either of these is indicated in the pattern of *B. rigidus* distribution along the sandstone habitat gradient (Fig. 5). This species reaches its maximum importance at the intermediate exposures. On the wet end of the gradient, it is displaced by *Avena fatua*, which is important only on the wettest end of the spectrum, while on the dry sites it is displaced by *S. pulchra*, which penetrates the sandstone communities only

on the driest end of the gradient. The distribution of *S. pulchra* is particularly anomalous since it occurs on sandstone only on the driest sites but reaches its greatest development on serpentine soils on the moistest sites. It seems likely that the greater development of the introduced annuals on the sandstone soil effectively excludes *S. pulchra*, a native perennial, except where vigor of the introduced species is restricted by low moisture supply.

The distribution of biomass on the two substrates shows that *S. pulchra* penetrates the sandstone community only where this community's standing crop is reduced to near the serpentine level (Fig. 6). The substantial difference in

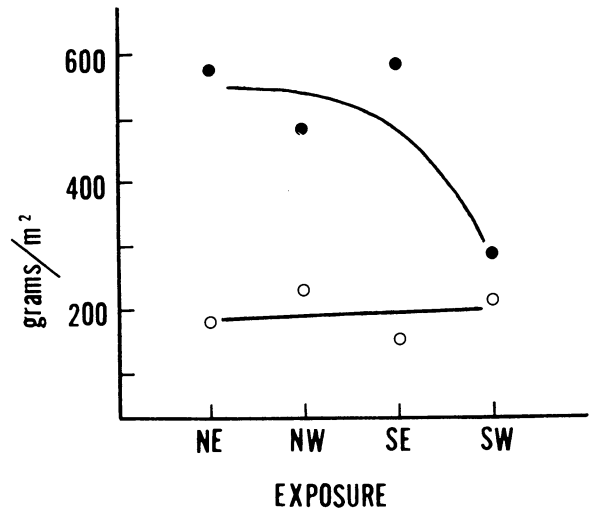


FIG. 6. Biomass of Jasper Ridge grasslands in relation to exposure and substrate. (Solid circles = sandstone; open circles = serpentine).

standing crop (here represented by peak biomass) between the two substrates is one of the most profound differences between grasslands on Jasper Ridge. Community biomass is twice as large on sandstone sites except at the driest exposure where it declines precipitously to near the serpentine level. Community biomass on serpentine, in contrast, is unaffected by exposure and maintains a similar level throughout the habitat gradient.

Productivity on sandstone was even more radically affected than biomass by the exposure gradient with a pronounced decrease in productivity from cool, moist sites to warm, dry sites (Fig. 7). While the biomass fell by about 54% along the habitat gradient, productivity declined by over 80%. By contrast, productivity on serpentine was unaffected by the moisture gradient, but this community was much less productive than the sandstone community except on the driest sites. It seems clear that the principal community limita-

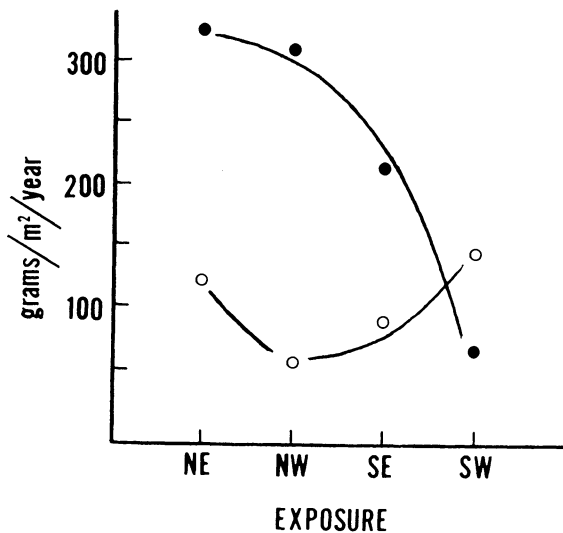


FIG. 7. Productivity of the Jasper Ridge grasslands in relation to exposure and substrate. (Solid circles = sandstone; open circles = serpentine).

tion on sandstone soils is the rapid drainage of these soils and the resulting low level of moisture on exposed slopes. The limitation to grassland development on serpentine seems to be something other than moisture, presumably the unfavorable nutritional properties of these soils (Cooper 1922, Whittaker 1954a, 1954b, McMillan 1956).

The communities are also distinct floristically, and there are substantial differences between different exposures on the same substrate. A comparison of Jaccard's coefficients (Jaccard 1912) for the different substrates indicates that the grasslands are floristically distinct on the two substrates and that the floristic similarity changes regularly with exposure (Table 2). Floristic similarity

TABLE 2. Jaccard's coefficients for different substrates (sandstone \times serpentine comparison)

Exposure	Coefficient
Northeast.....	17.4
Northwest.....	23.5
Southeast.....	27.4
Southwest.....	34.8
Total flora.....	26.4

between grasslands on different substrates increased consistently along the moisture gradient with the similarity on the driest exposure being twice that on the wettest site. The pattern agrees well with the patterns of biomass and productivity along the exposure gradient with increasing community similarity, both floristically and functionally, with increasingly dry exposures. The

TABLE 3. Mean Jaccard's coefficients for different exposures (exposure \times 3 additional exposures for a given substrate)

Exposure	\bar{X} coefficient	
	Sandstone	Serpentine
Northeast.....	67.6	66.5
Northwest.....	66.2	62.8
Southeast.....	60.0	61.2
Southwest.....	58.8	57.1

within-soil type comparison presents quite a different pattern (Table 3). Within a given soil type, the community becomes floristically more distinct along the exposure gradient from cool, moist to warm, dry exposures on both soil types. There is consistently a greater floristic homogeneity within the sandstone community than on serpentine soils, although the difference is not conspicuous. The decreasing floristic affinities on both substrates along the habitat gradient, compared with the between-substrate comparison, indicate that as sites become increasingly drier, substrate becomes a less important determinant of floristic composition. With increasing dryness along the habitat gradient, the community becomes less similar to sites on the same substrate and more similar to sites on different substrates, although exposure is never the most important determinant of floristic properties.

The most conspicuous aspect of the species-diversity pattern within the grasslands is the floral poverty of northern exposures on sandstone (Fig.

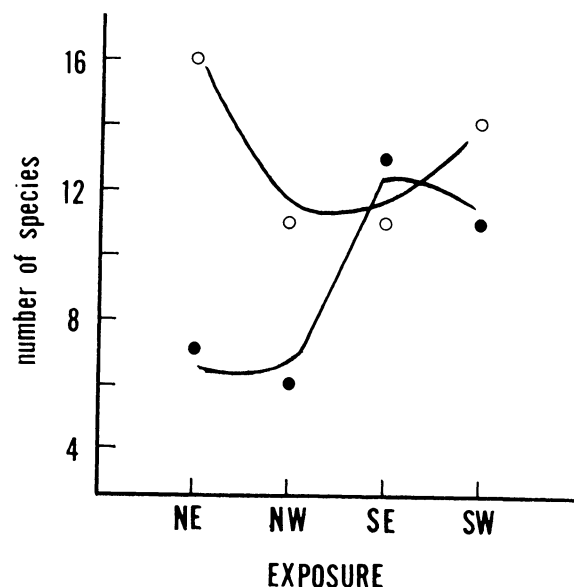


FIG. 8. Floristic diversity of the Jasper Ridge grasslands in relation to exposure and substrate. Solid circles = sandstone; open circles = serpentine).

8). Floristic richness of the serpentine community is independent of exposure, while the sandstone community is conspicuously affected by position along the habitat gradient. The serpentine community is more diverse than the sandstone community except on the southeast exposure. The greater diversity of the serpentine flora compared with the sandstone is probably at least partially a reflection of diverse microtopography on the serpentine. The serpentine is characterized by a considerable complement of undifferentiated material including numerous stone outcrops and large rocks (Fig. 3) compared with the uniform substrate in the sandstone area. The abundance of exposed rocks and boulders creates numerous microhabitats characterized by drainage off rock surfaces and differential soil depths. The pronounced difference in the sandstone grasslands along the exposure gradient, however, indicates that this difference between the substrates should not be overemphasized. An alternative explanation is that those highly productive species, such as *Avena fatua* and *Bromus rigidus*, which are extremely important on the moist end of the sandstone gradient may so monopolize the site resources under these conditions that subsidiary species are excluded. Their disappearance with drier conditions may allow less effective competitors to penetrate the community.

The concentration of biomass in a limited number of species, as an evaluation of dominance, is quite different between the two substrates and along the moisture gradient on both substrates (Fig. 9). The dominance pattern on sandstone

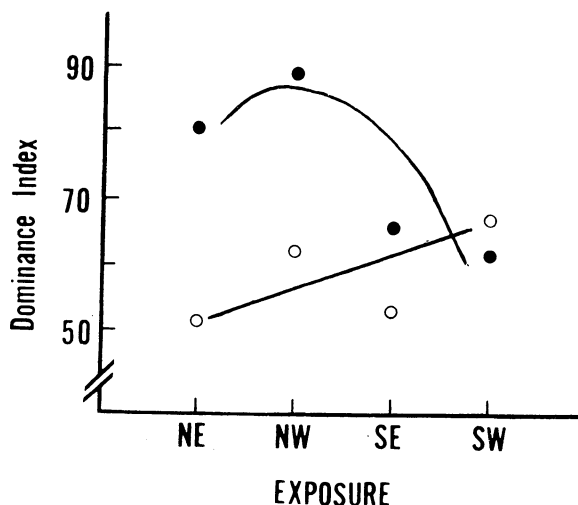


FIG. 9. Dominance index (percentage of peak standing crop contributed by the two most important species) of the Jasper Ridge grasslands in relation to exposure and substrate. (Solid circles = sandstone; open circles = serpentine).

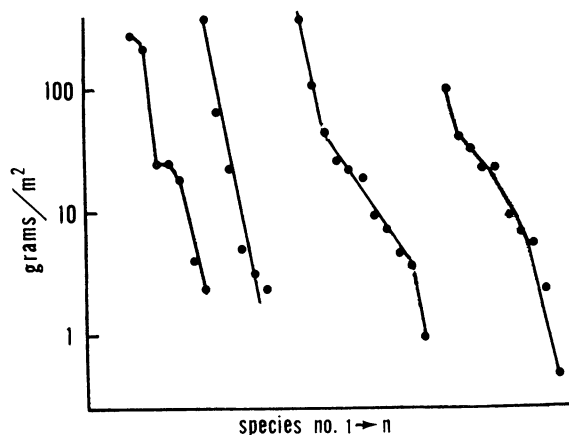


FIG. 10. Dominance-diversity curves for stands on different exposures on the sandstone soil. Curves arranged in the order of previous figures: NE, NW, SE, and SW exposures.

is essentially the inverse of the diversity curve with the conspicuous differences being between north and south slopes. There is more pronounced dominance on sandstone than on serpentine substrates, and dominance on the sandstone is more pronounced on northern exposures and declines abruptly with decreasing moisture. On the serpentine soil, however, there is a slight tendency for dominance to increase from cool, moist to warm, dry sites.

Dominance-diversity curves (Preston 1948, Whittaker 1965) for the sandstone sites generally fit the steep geometric series of floristically poor sites, although there is some deviation (Fig. 10). Diversity increases along the moisture gradient, as indicated previously, with an accompanying decrease in dominance. There is pronounced single species dominance on all sites except the northeast exposure where dominance is shared. In addition, the proportion of the total community resources represented by the top species-niche decreases from moist to dry sites. The greater diversity of the serpentine community is evident in the dominance-diversity curves (Fig. 11). All sites except the southwest fit the logarithmic series of Preston (1948) characteristic of most well-developed plant communities (Whittaker 1965). The southwest slope, however, fits none of the conventional models of community structure and represents a community with essentially three niche groups: a top niche occupied by a single dominant and two subsidiary niches partitioned among relatively coequal species. These biomass-based dominance-diversity curves indicate that the structure of these grasslands changes conspicuously along the habitat gradient and between the two soil types. Both lumping the total data for a

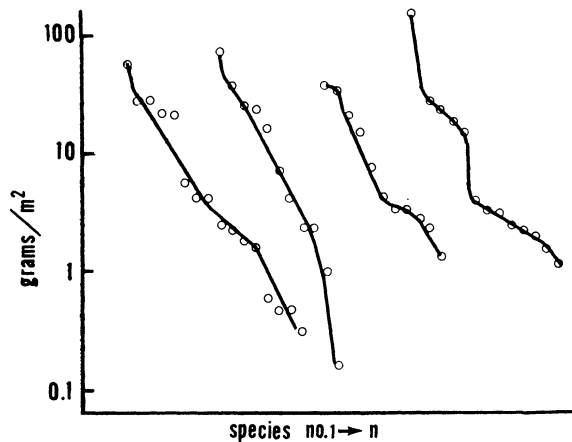


FIG. 11. Dominance-diversity curves for grasslands on different exposures on the serpentine soil. Curves arranged as in Fig. 10.

given substrate and combining all sites give the familiar lognormal distribution when plotted according to Preston's octave plot (Preston 1948). This distribution, however, is what one would expect for a universe, and such a loss of information based on arbitrary or intuitive stand grouping seems neither desirable nor justified. It is clear, based on the dominance-diversity curves and on functional and floristic properties, that the grasslands vary conspicuously on different substrates and on different exposures and that arbitrarily grouping them would sacrifice considerable information about the total grassland dynamics.

These California grasslands represent a floristic and functional continuum of intergrading biomass, productivity, diversity, and species composition. On a floristic basis, there is good reason to separate the grasslands by soil type according to their conspicuously low Jaccard coefficients. However, the biomass of the southwestern sandstone site is much nearer to serpentine communities than to its adjacent sandstone sites. In terms of diversity, the south-facing sandstone exposures are much more similar to serpentine grasslands than to north-facing sandstone slopes. There can be little doubt that substrate has a profound effect upon community properties. But the grassland is a responsive community, and substrate-induced differences in community properties are modified along exposure gradients.

GENERAL PROPERTIES OF THE GRASSLANDS

Turning to the general properties of the Jasper Ridge grasslands, what is the relevance of models of community structure to an interpretation of the ecology of these grasslands? One of the most widely discussed models of community structure is the one Margalef (1958, 1963, 1965) proposed

based on his studies of marine plankton ecosystems. In this community model, diversity is inversely related to dominance and productivity and directly related to stability. A similar conclusion was derived in Leigh's examination of quasi-Hamiltonian systems of equations, although he restricted his development to predator-prey interactions (Leigh 1965). According to this model, which is in general accord with Margalef's, stability of a species increases with an increase in that species' predators. A proliferation of alternative avenues of energy flow is the generally advanced explanation for this increased stability (Solomon 1953, Burnett 1960). Watt (1965), however, concludes from his studies of biological control of insects that, at carnivore or herbivore trophic levels, stability decreases with the number of predators. Patten's (1963) studies of planktonic communities in the York River, Virginia, indicated that high productive capacity in this community was associated with high diversity.

Dominance and diversity are inversely related in the Jasper Ridge grasslands (Fig. 12). The

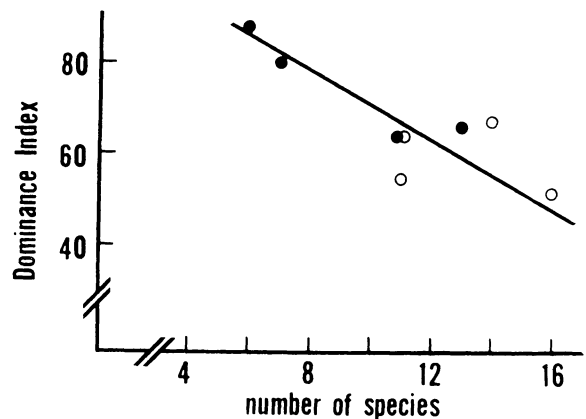


FIG. 12. Relationship between dominance and diversity of grasslands on sandstone (solid circles) and serpentine (open circles) soils on Jasper Ridge.

inverse correlation between these two properties ($r = -0.842$) is highly significant ($.01 > P > .001$). The serpentine grasslands are more diverse, on the whole, than the sandstone grasslands, and this diversity is accompanied by decreased dominance. Even within a substrate type there is a pronounced decrease in dominance with increasing diversity. The tendency for community biomass to be concentrated in the top species on the dominance-diversity curve decreases as the community becomes more diverse.

There was a significant ($.01 > P > .001$) positive correlation ($r = 0.852$) between dominance and productivity in the grasslands (Fig. 13). Conversely, there was a highly significant ($.01 >$

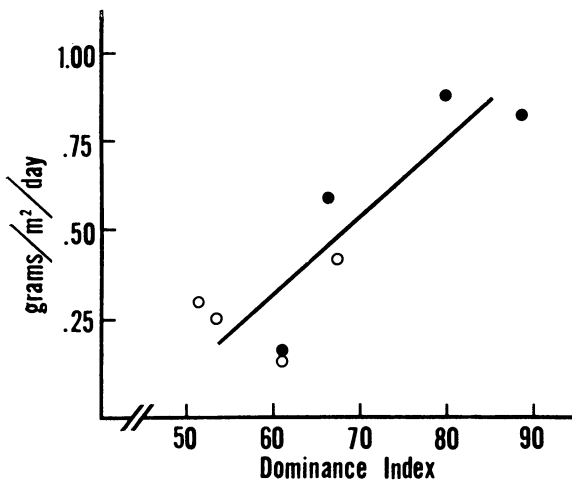


FIG. 13. Relationship between dominance and productivity of grasslands on sandstone (solid circles) and serpentine (open circles) soils on Jasper Ridge.

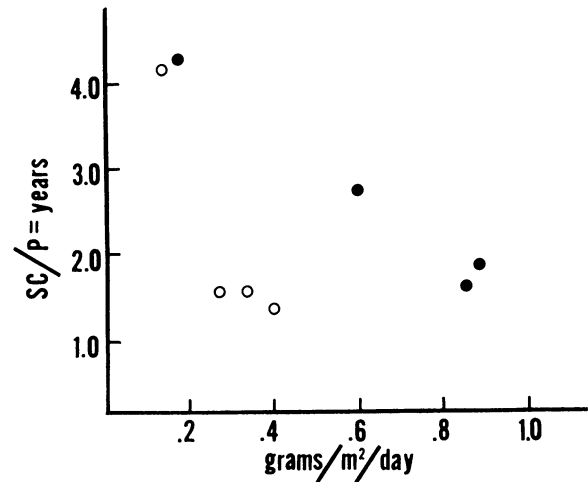


FIG. 14. Relationship between community stability (as indicated by turnover time) and productivity of the grasslands on sandstone (solid circles) and serpentine (open circles) soils on Jasper Ridge.

$P > .001$) inverse correlation ($r = -0.901$) between number of species in the stand and stand productivity. The efficiency of the grasslands as a photosynthetic energy accumulator decreases with increasing diversity. The most efficient stands are species-poor stands in which biomass is accumulated principally in the top species on the dominance-diversity curve. As more and more species penetrate the community, the productive efficiency of the community decreases. This indicates that community diversification, rather than increasing efficiency through more complete utilization of site resources, actually decreases efficiency, perhaps through niche overlap.

The third, and perhaps most important, tenet of Margalef's model is that diversity is directly related to stability. According to the model, diversity in the community generates stability but is accompanied by a decrease in system productivity. Community stability in the grasslands was assessed as turnover time, the ratio between biomass and productivity. The turnover times all exceeded 1 year, which is the presumed turnover time in grasslands of this type. However, there is a considerable accumulation of litter from year to year and in spite of the comparatively low complement of perennials in these grasslands, the accumulated standing crop is one to four times the annual productivity. It may be argued that in such a system the turnover time is not an accurate assessment of community stability. However, in the absence of grazing and repeated burning, this accumulated standing crop represents a reservoir of energy and stored minerals of the same type as that which contributes most of the standing crop in woody communities (Heady

1956). According to the model, then, productivity and turnover time should be inversely related. Although the relationship (Fig. 14) holds on the sandstone soil ($r = -0.970$; $.05 > P$), it does not hold for either the serpentine sites ($r = -0.870$; $P > .1$) or the grasslands as a whole ($r = -0.531$; $P > .1$). Neither do the regressions of dominance ($r = 0.216$; $P >> .1$) or diversity ($r = -0.003$; $P >> .1$) on turnover time fit the predictions of the model. In these grasslands, stability is independent of productivity, diversity, and dominance.

DISCUSSION AND CONCLUSIONS

The principal defect of these studies of the California grasslands is the lack of information on underground portions of the community which may contribute significantly to community biomass and productivity (Bray 1963). Attempts to sample the underground portions of the community during the first sampling period proved unsatisfactory. Because of the nature of the serpentine soil, with large amounts of undifferentiated material, it was impossible to obtain a reasonable sample of underground biomass. This information, essential to a complete understanding of community ecology, will require a large investigative team or more sophisticated sampling methods than were available for this study.

The information currently available does, however, provide considerable insight into the structure and function of the California grasslands. The serpentine grasslands are more diverse than those on sandstone, and the latter are particularly poor in species. For instance, treating the ser-

pentine and sandstone grasslands as a unit and calculating diversity as the slope of the regression

$$\log Y = a + bX$$

where Y is the number of individuals and X is the number of species (Monk and McGinnis 1966) gives $b = 0.333$ for the sandstone and $b = 0.060$ for the serpentine. The serpentine grasslands are moderately diverse, falling between wet and dry southern mixed hardwood forests, while the sandstone community is less diverse than any community reported by Monk and McGinnis.

The species composition of the Jasper Ridge grasslands is similar to that reported previously for annual grasslands in various regions of California (Talbot, Biswell, and Hormay 1939, Biswell 1956, Heady 1956, 1958, Major and Pyott 1966, White 1966, Naveh 1967). The Jasper Ridge studies indicate that the importance of certain species, notably *Bromus mollis*, may be over-emphasized in the reliance upon floristic data. The mean frequency of this species in the grasslands was 38.4%, while its mean contribution to peak standing crop was 24.4%. Frequency overestimates the importance of this species by over 57% in these grasslands. This evaluation is one of degree, however. Whether ranked by frequency or standing crop, *B. mollis* is still the most important species in the grasslands as a whole although its importance changes conspicuously with the moisture gradient. The next most important species in terms of mean standing crop were *B. rigidus* (21.1%), *S. pulchra* (15.9%), and *A. fatua* (6.7%). The importance of *B. rigidus* is particularly striking since it was restricted to the sandstone. Even more surprising was the contribution of *A. fatua* which occurred only on the east slopes of the sandstone. The most important species on serpentine and their contribution to biomass were *S. pulchra* (29.7%), *B. mollis* (27.0%), *Eschscholzia californica* (9.3%), and *Lotus subpinnatus* (7.1%). The most important sandstone species were *B. rigidus* (42.1%), *B. mollis* (21.8%), and *A. fatua* (13.4%). No other sandstone species contributed more than 5% of the total peak biomass. The upper species on the dominance-diversity curve were comparatively more important on the sandstone, while the converse was true for the lower species on the curve.

The concept of the individualistic plant association (Gleason 1939) and the idea of the vegetation continuum (Curtis and McIntosh 1951) are both supported primarily by floristic data, and few data from functional studies have been applied to the problem of the nature of plant communities. In these studies of California grasslands

there seems to be even less reason to draw sharp lines based on the data on community biomass or productivity than on the basis of floristics. Although the sandstone and serpentine grasslands are relatively distinct floristically, there is a tendency toward convergence as the site becomes increasingly dry and there is complete overlap of biomass and productivity. Certain species (*B. mollis*, for instance) respond identically to the habitat gradient on the two soil types. Others (*S. pulchra*) are radically different in their response to the habitat gradient on the two soil types. As in their biomass, productivity, and species composition, so there is a tendency toward convergence in dominance-diversity relationships. The dominance-diversity curves could be arranged as a series from cool, moist sites on sandstone to warm, dry sites on serpentine with a complete intergradation of form in the curves. The Jasper Ridge grasslands are a system of inter-acting populations and "the balance among populations shifts with change in environment so that (the) vegetation is a pattern of populations corresponding to the pattern of environmental gradients" (Whittaker 1953).

There is, however, considerable order in these grasslands and this order is manifested in the relationships among productivity, standing crop, dominance, and diversity. Previous comparisons of terrestrial plant communities have emphasized the floristic composition of the communities, but equally important are the functional properties of the vegetation. Reliance upon floristic techniques reduces one to saying that communities are different if they share no species in common. However, the regular relationships among functional properties of these grasslands, which fit the model Margalef (1958) has proposed for planktonic communities, suggest that communities with different species composition, even different growth forms and totally different habitat spectra, have much in common. Although the widespread acceptance of Margalef's model among ecologists is emphasized by the casual manner in which it is often incorporated into discussions (Woodwell 1967), there is a paucity of data on terrestrial plant communities which can be clearly related to this model. The data on the California grasslands suggest that the model has general application. In the grasslands, dominance and diversity are inversely related and increased productivity is generated by increased dominance. The populations represent a responsive mechanism adjusting the community to habitat conditions along the exposure-substrate gradient. The interplay among species populations results in modifications of community productivity, biomass, dominance, and

diversity, in response to the habitat gradient. In one important respect, however, the grasslands do not fit Margalef's model. According to the model, diversity is a mechanism which generates community stability, and a price in stability is paid for increasing productivity. The model is logically satisfying because it indicates that something cannot be gotten for nothing: increasing productivity generates a stability cost; increasing stability generates a productivity cost. The grasslands, however, show no relationship between stability and productivity, dominance, or diversity. Although the data are not exhaustive, it suggests the possibility that productivity may be optimized without jeopardizing community stability. However, the Margalef model emphasizes successional states and the grasslands are a spatial rather than a temporal field. When they become available, data on successional sequences similar to those recorded here for the California grasslands will be particularly important in testing the applicability of the model to terrestrial systems.

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