VEGETATIONAL CHANGES IN THE CALIFORNIA ANNUAL TYPE

HAROLD F. HEADY
School of Forestry, University of California, Berkeley

INTRODUCTION

The objectives of the study were to describe fluctuations in the California annual type that occur within a growing season and from one year to the next. These are given for three sites. Other changes that are related to mulch manipulation, grazing, and fire are discussed.

Not only does this type of information have value in itself but it also has value in the interpretation of studies on the management of the vegetation for forage production. If sampling can be done at one time only, vegetational changes during the growing season necessitate that the sampling date be selected carefully. Otherwise, seasonal differences may be unknowingly confounded with those due to other causes.

That the annual-type vegetation differs greatly in any given place from one year to another is well known. Annual vegetation also changes with season and the pattern may differ from one site to another. The three types of changes are superimposed and must be determined before the effect of manipulation can be accurately evaluated.

The magnitude of these changes was measured in terms of number of plants per unit of area on plots located on the Hopland Field Station in Mendocino County. The results, therefore, are from a restricted area and are presented as such. They are not offered as norms to describe the "average California annual type." However, the principles found are in essential agreement with the work of others. Together they may be interpreted as giving the basic sequences and directions of change. It is assumed that these sequences are not fortuitous and that they would show a significant relation to those of other areas and years despite diversities between individual situations.

The term "California annual type" is used in this paper to denote that vegetation in California which is composed primarily of annuals. The type is a mixture of many species of grasses and broad-leaved herbs, and species that are native and introduced. Although many perennial species are present, individual perennial plants are scarce. The type is located below the 4,000 foot level in the Central Valley and intermittently in the Coast Ranges. It is the understory in the open areas of oak-woodland and to some extent in the chaparral types. Actually the type is a very broad one. It contains many sub-types which can be delineated by species composition or other characteristics, and related to the differences in soil and climate.

The term "vegetation" is used to signify a group of individual plants growing together. The size of area and complexity of the group is indicated only by the context in which the term appears. The term "vegetational change" is used to specify changes over time in the number of plants per unit of area or in relative species composition on a percentage basis.

Sincere appreciation is extended to members of the Faculty Seminar in Ecology at the University of California who offered many helpful suggestions during discussions of this paper.

METHODS

In early December of 1951, sixteen plots, each 10 feet on a side, were established in a 4 x 4 Latin square at three locations on the Hopland Field Station. This design was used so that location effects in two directions, rows and columns, could be measured and removed statistically from the treatment effects within each study site. Treatments were dates of sampling. The first set of four plots was sampled on an average date of December 7; the second set was sampled on February 6; the third on April 5; and the fourth on June 9. The sampling consisted of counting the number of annual plants by species or groups of species in ten quadrats of one square inch in each plot. The occasional perennial plant was omitted. Sampling was done on all plots at the same time every year.

The square inch quadrat was handled by cutting out a block of soil of that size with the aid of a measuring fork and stiff putty knife. The block was then carefully spread out or pulled apart and the live plants counted as they were discarded. In June all dry individuals were counted but undoubtedly some were missed because they had shattered. A total of 2,400 quadrats were taken in the five years.

The sampling during the fall and winter was on seedlings, when positive identification of all the species was impractical. *Bromus mollis*,[1] *Bromus rigidus*, and *Erodium botrys* were easily identified and recorded separately. The others were grouped either as "other grasses," "legumes," or "other

[1] Botanical nomenclature follows Hitchcock (1950) for grasses and Jepson (1923) for other plants.

broadleaved plants." Legumes were generally few in number and included *Lotus micranthus, Lupinus bicolor, Trifolium bifidum, T. ciliolatum, T. depauperatum, T. microcephalum, T. microdon,* and *T. variegatum.* The list of other grasses included *Aira caryophyllea, Avena barbata, Briza minor, Festuca dertonensis, Gastridium ventricosum, Hordeum hystrix,* and *Poa annua.* The principal other broadleaved plants were *Baeria chrysostoma, Cerastium arvense, Filago californica, Galium parisiense, Hypochoeris glabra, Lepidium nitidum, Linanthus ciliatus, Micropus californicus, Navarretia intertexta, Orthocarpus erianthus, Pentachaeta exilis, Plagiobothrys nothofulvus, Plantago erecta,* and *Spergula arvensis.* The total flora at the three locations numbered about 50 species with some variation from year to year and among the locations.

The Study Sites

Site I was in an area that had been ungrazed by domestic livestock for several years previous to and during the study. However, deer made frequent use of it in the winter months. One result of this protection from domestic animals was that large amounts of mulch were present throughout the five years of the study. Perennials were conspicuous and the common ones were *Elymus glaucus, Melica californica, Koeleria cristata, Achillea millefolium,* and *Eschscholtzia californica.* These were not observed either to increase or to decrease during the five years.

The soil of Site I consists of water-deposited material in a small fan below an extensive area of the Josephine soil series. The surface layer is a sandy loam containing many rock fragments. The reaction is slightly acid and the color is brown to reddish brown. Drainage throughout the soil is good. The exposure is southeast with a slope of about 10 percent. In the winter this area is shaded in the afternoons.

Site II was in a grazed pasture, about one-half mile from where sheep were fed. Grazing was estimated to be moderate. The soil is classed as Sutherlin fine sandy loam. It is 3 to 4 feet in depth with a brown, loamy, slighty acid surface layer which grades into a yellowish brown claypan that is neutral in reaction. Surface drainage is moderate but water moves slowly through the claypan. Occasionally after heavy rains small undulations in the soil surface contain free water for a few hours. No perennials were present. The slope is less than 10 percent toward the south.

Site III was in the same pasture with site II but near where sheep were fed every winter. It was grazed and trampled heavily before 1951. During the course of the study, grazing was still heavy but periods in the winter and spring without grazing allowed the plants to attain more growth than they had in previous years. The soil at this site also is classed as Sutherlin fine sandy loam, but it is only 2 to 3 feet thick, and lighter in color and less friable than at Site II. Surface drainage is rapid. Usually there was a moderate amount of mulch on the soil but it disappeared during each winter. Perennials were absent at the beginning of the study but periods without grazing allowed *Stipa pulchra* to increase during the five years. By 1956 it was numerous on the plots and in the vicinity. The slope is approximately 10 percent toward the southeast.

Normal Seasonal Development of Plants

Following germination and slight growth in the fall there was a period until about the middle of March or the first of April when growth was very slow. Little difference in height of plants could be seen between the December and February sampling dates. Fast growth of the plants was underway or about to begin at the time of the April sampling. All plants were dry by the June sampling time. However, in 1953 and 1956 a few sprigs of *Mendicago hispida* at Site II and a few grass stems at Site I were still green. In those two years a few plants were green under the oak trees in the vicinity of the plots. At Site I, *Bromus rigidus* was usually in the last stage of drying and appeared reddish in contrast to the light tan of the other species. *Aira caryophyllea* and *Briza minor* were the first grasses to mature and *Bromus mollis* was intermediate.

During every winter at Site I the plants were taller, more slender and grew in sparser stands than at the other sites. This was probably the result of large amounts of mulch, both matted on the soil and standing.

Site III was characterized by short plants at all seasons. In December and February few were over one inch in height and by June the vegetation was seldom over one foot in height. This was because the major species were short plants like *Aira, Briza, Gastridium, Trifolium, Erodium* and *Festuca* and there were few plants of *Bromus mollis* and *Bromus rigidus* (Figs. 1-3).

Bromus mollis and *Erodium botrys* gave Site II a characteristic appearance of a mixture of grass and broadleaved species (Fig. 4). In all years except 1954 the ground between these plants was essentially bare of the smaller grasses and broadleaved plants. In 1954 *Briza minor* and *Aira caryophyllea* were common, in 1953 and 1956 *Medicago hispida* was abundant but in 1954 there was none of it, and in 1952 *Gastridium ventri-*

FIG. 1. On February 2, 1955, at Site III the new plants were less than an inch tall and formed a green carpet beneath the dry standing plant material (See Figs. 2-3).

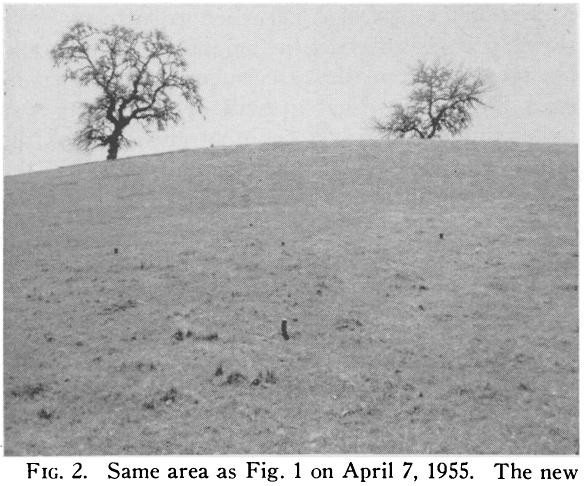


FIG. 2. Same area as Fig. 1 on April 7, 1955. The new plants were little taller but considerable mulch had been removed by grazing and decomposition.

cosum was present. It did not make a conspicuous appearance until June.

Several perennial grasses were present in the plots of Site I and these were always green, and in 1954 still flowering, during the first week of June (Fig. 5).

Number of Plants Per Unit of Area

The number of individual plants on a square inch of soil varied between zero and 91. Average numbers per square inch in sample sizes of 40 varied between 3.3 and 35.0 plants (Fig. 6). Converted to numbers per square foot, these are 475 to 5,040. The maximum calculated from the 91 is 13,104. In another study the number of plants on 4 separate square feet in mid-winter near Site III were 2,746, 3,014, 3,393, and 3,643.

From a study in Madera County, Biswell and Graham (1956) reported as many as 20,875 *Festuca megalura* seedlings per square foot in dense

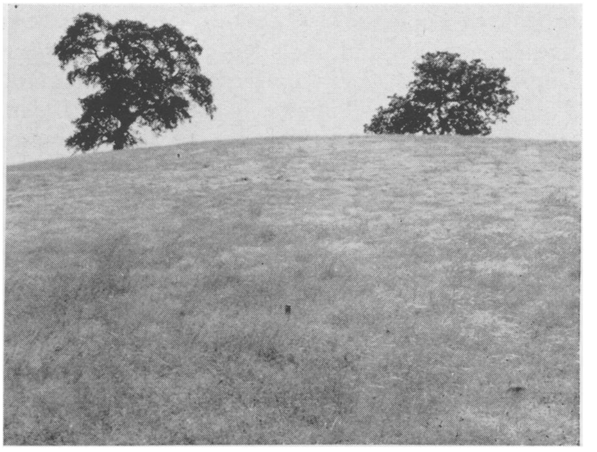


FIG. 3. Same area as Figs. 1-2 on June 6, 1955. All plants had matured at a height of about 6 inches. *Erodium botrys* was conspicuous even though it was overtopped by numerous grasses.

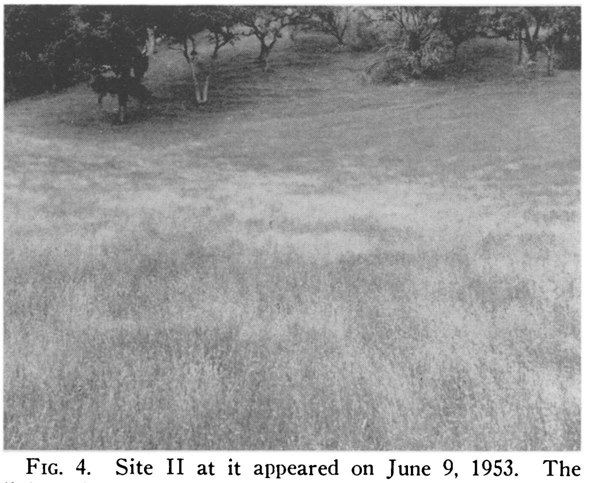


FIG. 4. Site II at it appeared on June 9, 1953. The light colored areas are mostly *Bromus mollis* and other grasses. The dark areas are *Erodium botrys* and *Medicago hispida*.

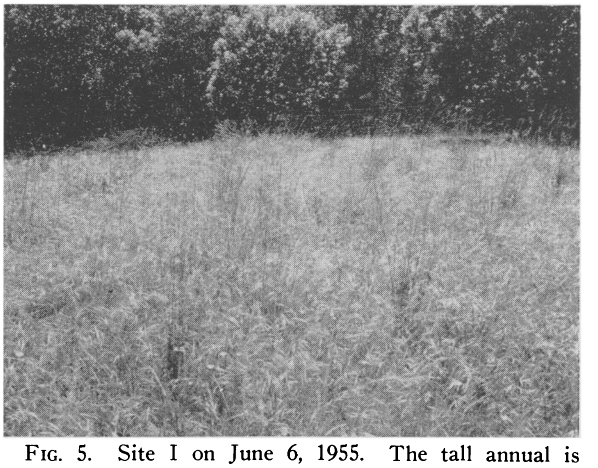
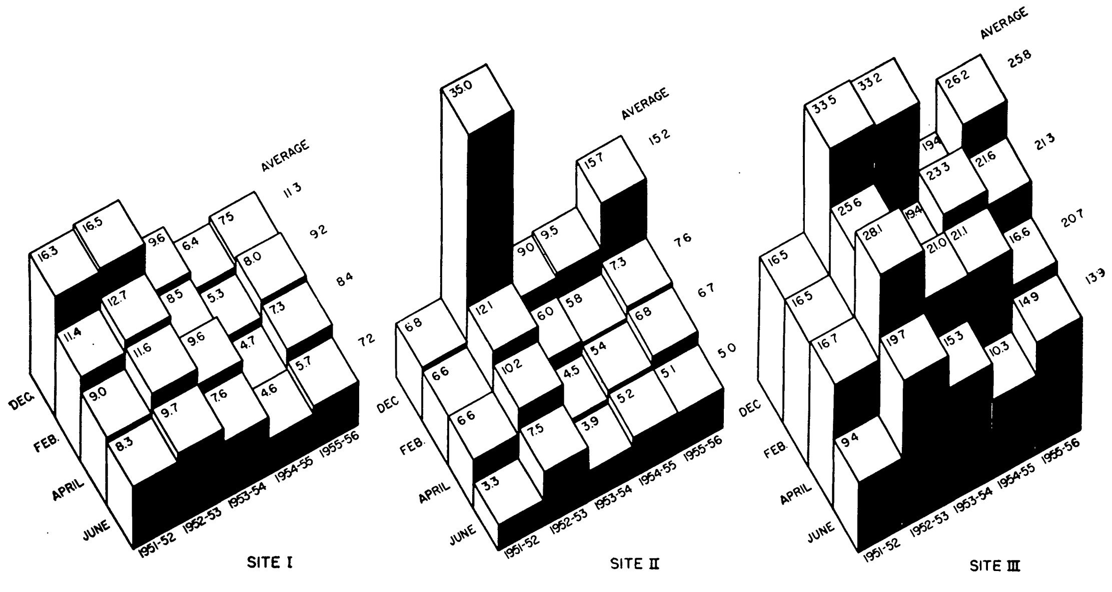


FIG. 5. Site I on June 6, 1955. The tall annual is *Bromus rigidus* and the large perennial bunch grass is *Elymus glaucus*. The annuals were dry and the seed beginning to fall but the perennial was still green.



AVERAGE NUMBER OF PLANTS PER SQUARE INCH

FIG. 6. Average numbers of plants per square inch for all species from a sample size of 40 for four seasons in each of five years.

stands; *Bromus mollis,* 17,433; and *Erodium botrys,* 1,048. In stands of average density dominated by the two grasses at maturity, they found between 1,805 and 7,830 plants of all species. Comparable numbers of mature plants in this study were 475 and 2,837. Reasons for the difference between areas in number of individuals per unit of area are not known.

Much variation in numbers of plants per unit of area occurred locally within but a few inches. The ratio of the standard deviation to the mean was usually between 30 and 40 percent. This indicated that a sample size of 40 should measure differences as small as approximately 10 percent of the means.

Changes in Total Numbers from December to June

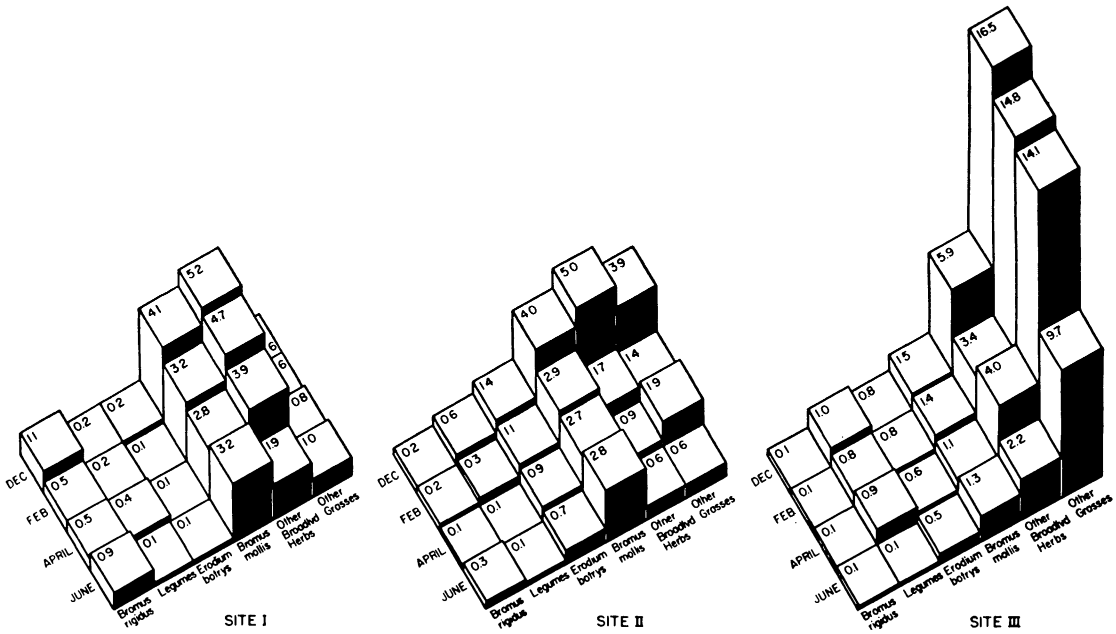
In nearly all cases, there was a reduction in numbers of plants from each sampling date to the next. Two exceptions occurred at Site I and four at Site III (Fig. 6). Thus, in a total of 45 separate comparisons, there were six that showed an increase in numbers from one date to the next. The numbers were equal in two other instances. An analysis of variance showed the reduction between December and June to be significant at the 0.05 level in all cases but 1953-1954 at Site I. The major part of the decrease occurred between December and February and at Site III between April and June. The changes were least between February and April.

Changes by Species from December to June

Diverse patterns of change were exhibited by the different species or groups. For two of the sites, much of the seasonal decrease was in the categories of broadleaved herbs and other grasses. Site I showed significant decrease only in the broadleaved herbs. The three species, *Bromus mollis, Bromus rigidus,* and *Erodium botrys,* and the legumes were fewer in number in June than in December, but the differences were not significant (Fig. 7).

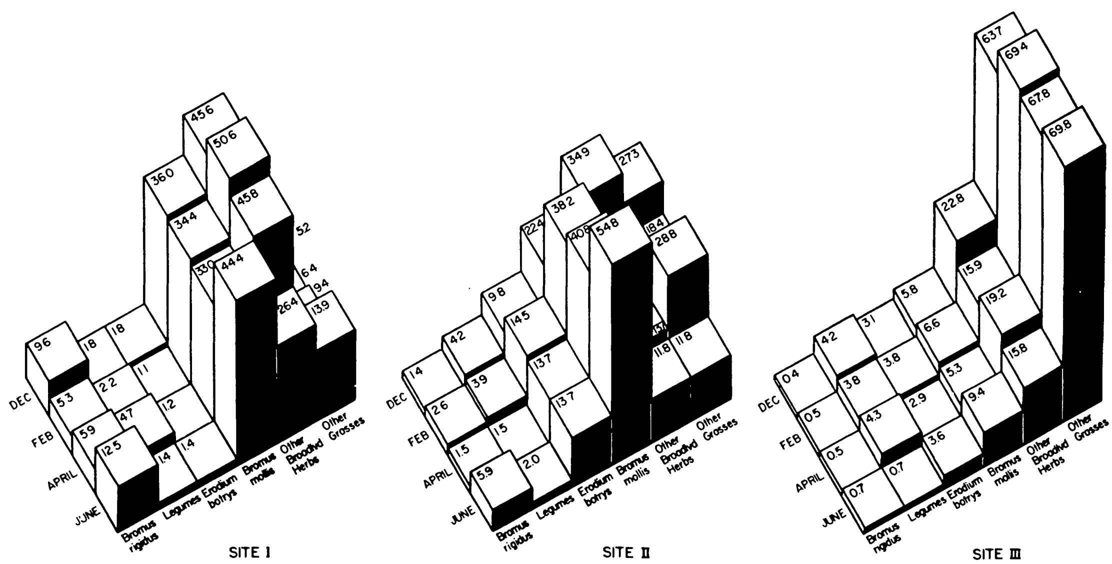
The relative responses by the different species and groups are shown by percentage botanical composition (Fig. 8). *Bromus mollis* and *Bromus rigidus* made up more of the vegetation in June than in December at all three sites. *Erodium botrys* was about the same proportion at all four times of sampling. The legumes generally comprised the least in June and the most in April, although not significantly so and not without exception. At Site I the other grasses increased in importance through the season and at Site II they were irregular. Where they comprised a high proportion of the vegetation (Site III), they held through the season with little change. Other broadleaved plants were irregular but in a decreasing trend.

The percentage botanical composition for *Bromus mollis* and *Erodium botrys* at Site II illustrates change on a year by year basis (Fig.



AVERAGE NUMBER OF PLANTS PER SQUARE INCH

FIG. 7. Average number of plants per square inch for three species and three groups of species at each of four seasons over a period of five years.

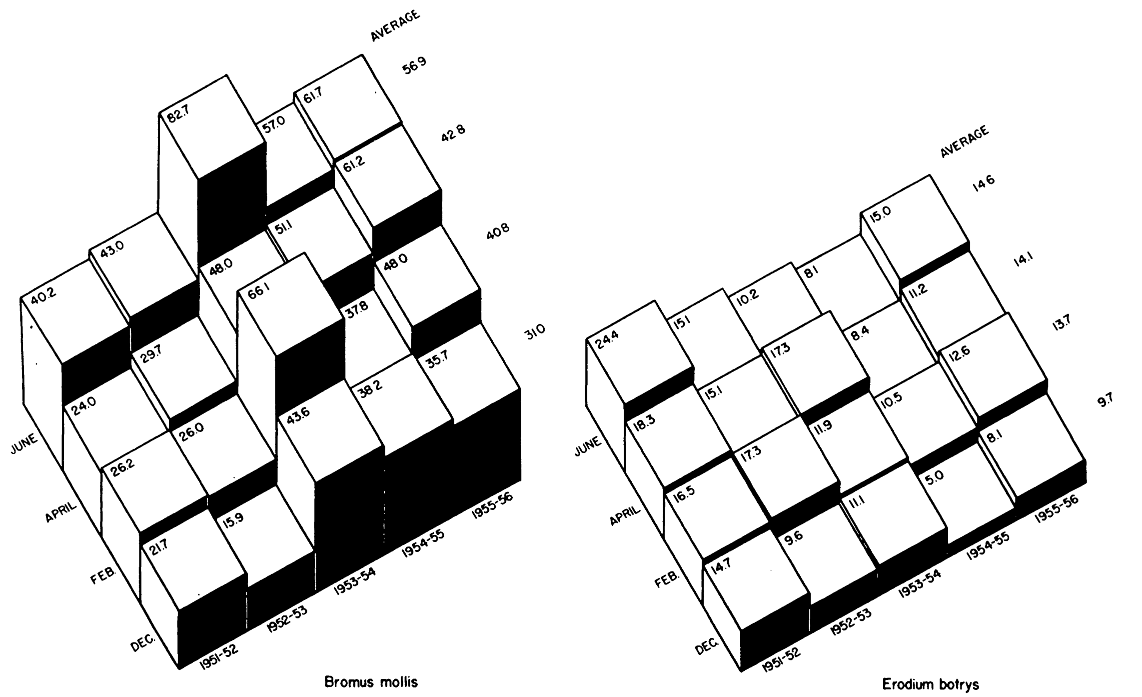


AVERAGE PERCENTAGE OF TOTAL NUMBERS

FIG. 8. Percentage botanical composition for the average numbers of plants per square inch shown in Figure 7.

9). (Note the reverse order of months in this Figure.) For *Bromus mollis* two of the April readings were lower than those from February and one February reading was lower than that in December. The differences in percentages between December and June are significant at the 0.01 level. Somewhat more irregularity existed with *Erodium botrys*. In three of the five years (1952, 1953, and 1956) this species made up more of the vegetation in June than in the previous December at the 0.05 level of significance.

From these data, it would seem that the species



PERCENTAGE OF TOTAL NUMBERS AT SITE II

FIG. 9. Percentage of the botanical composition contributed by *Bromus mollis* and *Erodium botrys* at Site II at four seasons for five years.

with individuals that are relatively small in stature and usually most numerous were the ones that exhibited the widest change in numbers. Even though all species showed mortality as the season progressed, the larger plants, or at least *Bromus mollis, Bromus rigidus,* and *Erodium botrys,* survived better than did the smaller ones. The decrease took place over and above a highly significant difference between years in their relative position.

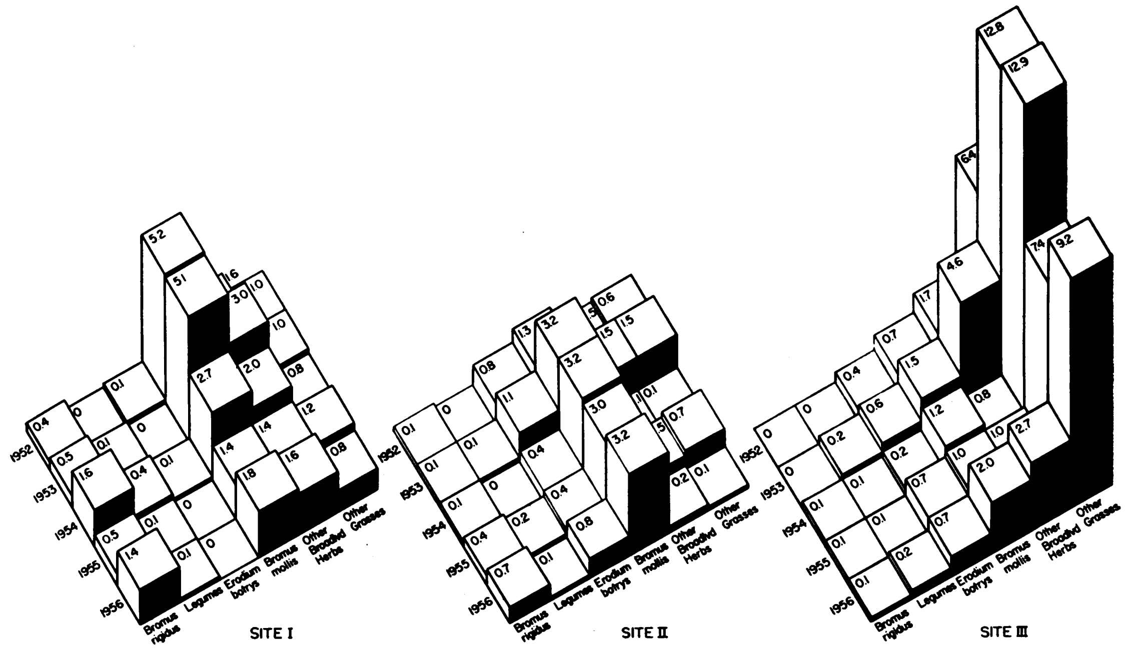
The pattern of change through each growing season was essentially the same whether density was high or low in December. From this fact it would seem that the relative proportion of plants by species for the entire growing season was established before December of each year. This may in part be due to differences in the amount of viable seed produced the previous year, depredations on the seed during the summer, and climatic conditions previous to and during the first days of the growing season. The relative importance of these factors and others can only be speculated upon at this point.

CHANGES FROM YEAR TO YEAR

The changes from one year to the next are perhaps the most striking of the differences mentioned so far. These have been shown in Figures 6 and 9 and are further illustrated by the numbers in June of each year (Fig. 10). The greatest numbers of plants per square inch at all four dates occurred in 1952-1953 (Fig. 6). This was without exception on the three study areas and was significant at the 0.05 level. The lowest numbers at Site I were in 1955 and in 1952 at the other sites. For the most part the same relative position was maintained through the seasons of each year.

The large numbers in 1953 were made up mostly of *Bromus mollis,* small grasses, and broadleaved plants. However, the general appearance on all three sites suggested predominance by either *Bromus mollis* or *Bromus rigidus* because they grew luxuriantly that year. The years 1952, 1954, and 1956 were also years of good grass growth but not so much so as 1953 (Figs. 11-12). In these years of moderate grass the vegetation showed much more of a mixture of species in the aspect than in 1953 and 1955.

The vegetation was short and dominated by *Erodium botrys* in 1955 except at Site I even though the plants were few in number that year. The two extreme years for growth and appearance of the vegetation were 1953 and 1955. The vegetation in the former was clearly dominated by



AVERAGE NUMBER OF PLANTS PER SQUARE INCH IN JUNE

FIG. 10. Average number of plants per square inch in June for three species and three groups of species in each of five years.

FIG. 11. The vegetation on Site III at maturity in 1952 (see Fig. 12).

FIG. 12. Same area as Fig. 11 but at plant maturity, 1954. The small grasses were about twice as numerous as in 1952. *Erodium botrys* was most numerous in 1952. In both years *Bromus mollis*, the few tall stems in the photos, was inconspicuous.

grasses and the latter was definitely a year favorable for *Erodium*.

Differences between Sites

Increasing numbers of plants per square inch were found on Sites I, II and III in that order. Changes in the vegetation betwen seasons and between years were more uniform on Site I than the others. The nature of these changes has been discussed. In this section the consistent differences between the sites over the five years will be discussed.

The sites were characterized in all five years by high proportions of certain species (Fig. 8). Site I had more *Bromus rigidus* than the other areas even though there was less than one per square inch on the average (Figs. 5 and 7). However, it was enough to give the area the general appearance of a stand of *Bromus rigidus* because the plants of this species were taller than the other grasses and broadleaved plants. *Erodium botrys* and the small grasses were inconspicuous.

Site III contained a high percentage of small grasses such as *Festuca dertonensis, Aira caryo-*

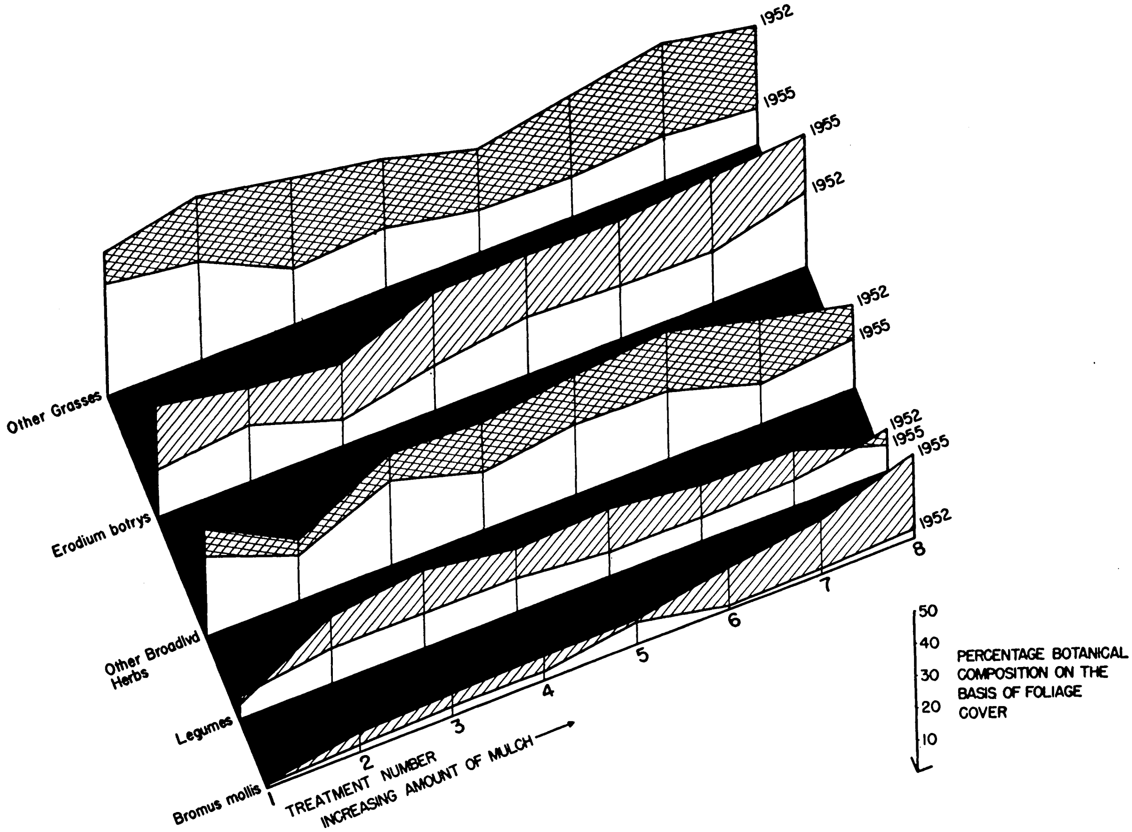


FIG. 13. Percentage botanical composition at plant maturity for two species and three groups of species on a basis of foliage cover. The treatments were amounts of mulch in September of the year preceding and varied from none to approximately 3200 pounds per acre.

phyllea, Briza minor, and *Gastridium ventricosum.* In December and February when the grasses were short, *Erodium botrys* was also conspicuous (Figs. 1-3 and 11-12). Legumes were most numerous at Site III and at times in mid-spring they made a conspicuous show of color.

Site II had the appearance of predominance by *Bromus mollis* even though it was not as numerous as on Site I. This is because *Bromus rigidus* was scarce at Site II. *Erodium botrys* and *Medicago hispida* were also a conspicuous part of the vegetation (Fig. 4). On this site, those species in the categories of other broadleaved plants and other grasses were never very conspicuous even though they were numerous in December. *Daucus pusillus* was another major species here.

Changes Due to Treatment

Vegetational changes in the California annual type have been related to several kinds of treatments (Biswell 1956). Talbot, Biswell, and Hormay (1939) and Bentley and Talbot (1951) described vegetational changes on the San Joaquin Range that were associated with rodent activities and the intensity of grazing by cattle. Jones and Love (1945) described a grazing system whereby early heavy grazing and late deferment were observed to result in a higher proportion of taller grasses and a lower proportion of the early maturing small weeds and grasses. Fertilization has been reported to result in higher proportions of legumes if with phosphorous and more grass if with nitrogen in the presence of sufficient phosphorus (Martin and Berry 1956, Williams, Love, and Conrad 1956). Sulphur fertilization has increased the amount of legumes for a year or so (Conrad 1951, Arkly, Helphinstine, and Williams 1955) and then an increase of grass (Bentley and Green 1954). Burning has also been found to be a treatment effecting changes in species composition. Hervey (1949) reported an increase in weedy vegetation following a grass fire on annual range but if weeds were already dominant litle change was observed. These shifts in composition were probably the result of variations in the amount and position of mulch. The influence of mulch on annual vegetation has been described for the San Joaquin Experimental

Range (Talbot and Biswell 1942) and for the Hopland Field Station (Heady 1956). Some of the data in the latter publication will illustrate the important points (Fig. 13).

In reading the chart, the height of the vertical lines gives the relative importance of each species. The shaded portion shows the difference in percentage composition between the two years. The convergence, crossing, and divergence of the two lines for each year and their position above the base line show the effect of mulch on percentage composition.

Bromus mollis increased in percentage composition with an increase in the amount of mulch. The legumes were low with both extreme amounts of mulch. *Erodium botrys* was not materially affected by the amounts of mulch. *Orthocarpus erianthus, Hypochoeris glabra,* and *Baeria chrysostoma* were conspicuous on the plots with no mulch. In both years shown in the diagram the small grasss were present in large numbers on all plots. They were less abundant with large amounts of mulch.

Figure 13 also shows that the vegetation was different in botanical composition between the two years, regardless of treatment. The small grasses and weeds were sparse in 1955. 1952 was a poor year for legumes and *Erodium botrys. Bromus mollis* was not materially different in the two years. The effects of the mulch treatments can be evaluated only in relation to the yearly differences for all species.

Relation of Weather to Seed Germination

The data presented indicate that many seeds had germinated by December in all years and locations. However, ungerminated seed was seen at that time and some of the seedlings had not developed true leaves. In December of 1954 there were two age classes of the large species such as *Erodium botrys, Bromus rigidus,* and *Bromus mollis.* One crop had survived germination in late August and the other had started in November. In December of 1955 seedlings of the *Trifolium* species were found from the cotyledon to the three-leaved stage and much *Bromus mollis* had recently germinated. An occasional new plant of some of the broadleaved species was observed in February of 1952, 1954 and 1955. Otherwise no germination was observed through the late winter and spring months. Ungerminated seed of *Medicago hispida* was present at all times at Site II (Fig. 14). Not all germination occurred at the same time each year nor was it normally spread over as long a period as in 1954. There seems to be little germination after the first of each year or even after December 1. Well distributed late rains fell in May and June of 1953.

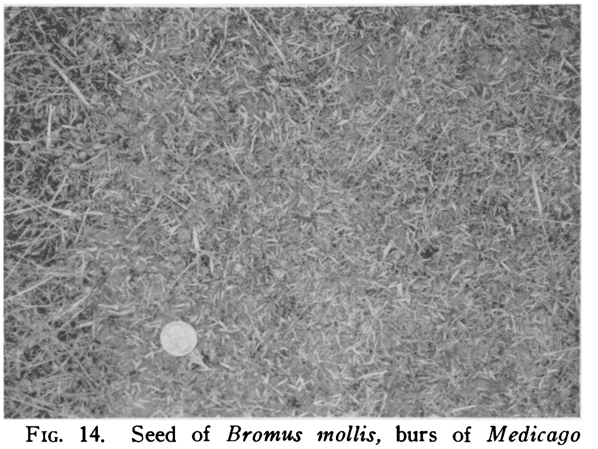


Fig. 14. Seed of *Bromus mollis,* burs of *Medicago hispida,* and heads of *Gastridium ventricosum* on the soil surface at Site II, July 15, 1953.

Plants of *Bromus mollis* continued to develop new culms throughout the spring and seed from the earliest ones had shattered by June. A few of these germinated immediately but none were observed to develop to flowering.

If the numbers of plants in December are taken to indicate favorable or unfavorable conditions for germination and establishment up to that time, it should be possible to correlate plant numbers with climatic conditions. November mean minimum temperatures were about 5 degrees less in 1955 than in the other years and about 5 degrees higher in 1953 (Table I). The total number of plants per square inch was neither lowest nor highest in those years (Fig. 6). Mean maximum temperatures were not greatly different for the Novembers of the 5 years.

On the other hand the greatest number of plants on all sites in December occurred in 1952. That is the year of least rainfall previous to that date and also a year when sufficient moisture to start the plants was late in arriving (Fig. 15). Temperatures were about average during the last two weeks of November of 1952.

The time between sufficient rain for germination and the December sampling in 1953 was the shortest period in five years. Temperatures were warm. *Bromus rigidus* had reached a height of six inches and was stooling, and there were large numbers of all grasses. Many seeds of *Medicago hispida* had germinated but a high proportion of the seedlings were dead because the soil surface was dry before they could become established.

Relation of Weather to Seedling Survival

The total rainfall at headquarters of the Hopland Field Station ranged between 24.8 and 50.9

TABLE I. Temperatures on the Hopland Field Station

	Mean Minimum Temperature				Number of Days with Temp. 31°F and below				Minimum Temperature			
	1952-53	1953-54	1954-55	1955-56	1952-53	1953-54	1954-55	1955-56	1952-53	1953-54	1954-55	1955-56
July.....		48.7	49.2	44.4		0	0	0		41	42	37
Aug......		47.6	46.8	43.5		0	0	0		42	41	37
Sept......		48.0	42.2	40.9		0	0	0		35	35	32
Oct......		39.5	36.9	36.1		0	8	2		32	27	27
Nov......	36.7	42.0	35.8	30.9	5	2	5	19	27	30	24	24
Dec......	39.8	35.5	29.0	32.0	0	11	23	15	32	25	17	19
Jan......	41.0	33.6	25.5	31.5	2	14	28	14	29	25	19	18
Feb......	35.1	34.4	27.1	24.0	10	8	22	27	29	29	20	16
Mar......	36.3	35.7	28.9	27.2	6	8	21	25	24	27	21	18
Apr......	40.3	41.7	31.8	32.3	3	1	15	9	29	30	24	25
May.....	41.1	42.1	39.5	36.7	0	1	0	6	35	30	33	31
June.....	45.1	46.1	42.8	41.9	0	0	0	0	40	36	33	33
	Total..................				26	45	122	117				
	Date of first frost.........					Nov. 18	Oct. 24	Oct. 6				
	Date of last frost.........				Apr. 9	May 1	Apr. 20	May 14				
	Mean Maximum Temperature				Maximum Temperature							
July.....		93.9	92.3	86.8		103	104	100				
Aug......		84.5	83.4	94.2		100	100	102				
Sept......		88.4	83.5	89.6		107	100	111				
Oct......		76.1	75.3	77.8		94	92	91				
Nov......	63.8	61.3	63.1	61.2	75	81	75	83				
Dec......	52.7	56.7	52.0	53.8	61	67	58	63				
Jan......	56.8	52.3	51.2	50.8	65	61	62	55				
Feb......	62.3	64.2	58.5	55.4	73	80	68	68				
Mar......	61.8	58.8	64.0	63.7	79	76	83	76				
Apr......	68.4	71.0	60.6	66.6	89	92	75	83				
May.....	69.9	77.9	75.3	74.2	86	92	94	91				
June.....	78.4	79.8	81.3	83.4	96	105	99	106				

inches for the five growing seasons beginning July 1, 1951 (Fig. 15). The first shower was recorded on July 19 and the last on June 29. However, the effective growing season is much shorter than that. Germination ordinarily begins with the first rain of one-half to one inch and growth ends with dry soil in May or June. The range in date for the first rain of one-half inch or more was eleven weeks, from August 25 to November 13. There was a long dry period after the August 25 rain, until October 7 when 0.5 inch fell and the next was November 8-17 when 5.8 inches occurred. During the five years the range in date of the beginning of continuous wet soil was October 1 to November 13 (Table II). This is the range in time when the hills became green.

In 4 of the 5 years the last effective rain for growth of plants was between April 17 and May 8. These rains varied between 0.8 and 3.9 inches. In 1953 growth was exceptionally good because the soil was wet until June. That year the grasses and certain other species matured before the soil was dry and there were many species of summer growing annuals that were conspicuous. Many species were found in 1953 that were not seen in 1952.

The luxuriousness of the vegetation seemed to be related to the pattern of rainfall, length of dry periods and temperatures after a mid-winter date of approximately January 20. The rainfall ranged between 1.6 and 5.6 inches after a date of March 5. This is approximately the date when temperatures were high enough to permit accelerated growth. Winter dry periods of over 20 days occurred in 3 of the 5 years. There were 48 days in 1953, 38 days and a second period of 47 days in 1955 and 22 days in 1956. Four of the years had a wet period between February 20 and March 20 but it did not occur in the other year until April 16 to 30. In that year it was the last rain of the season.

Three years were very different in these patterns. One, 1953, was the warmest winter and had scattered spring rains of sufficient amount to allow the vegetation to develop even though there were 48 days of dry weather between January 21 and March 19. Numbers of plants were highest throughout that year. In 1955 there were 86 days between January 21 and April 16 with only 2.9 inches of rain and the winter was relatively cold. This was followed by 3.9 inches in late April which was sufficient to permit fair forage production of some species but *Festuca dertonensis*, for example, was mature and did not respond.

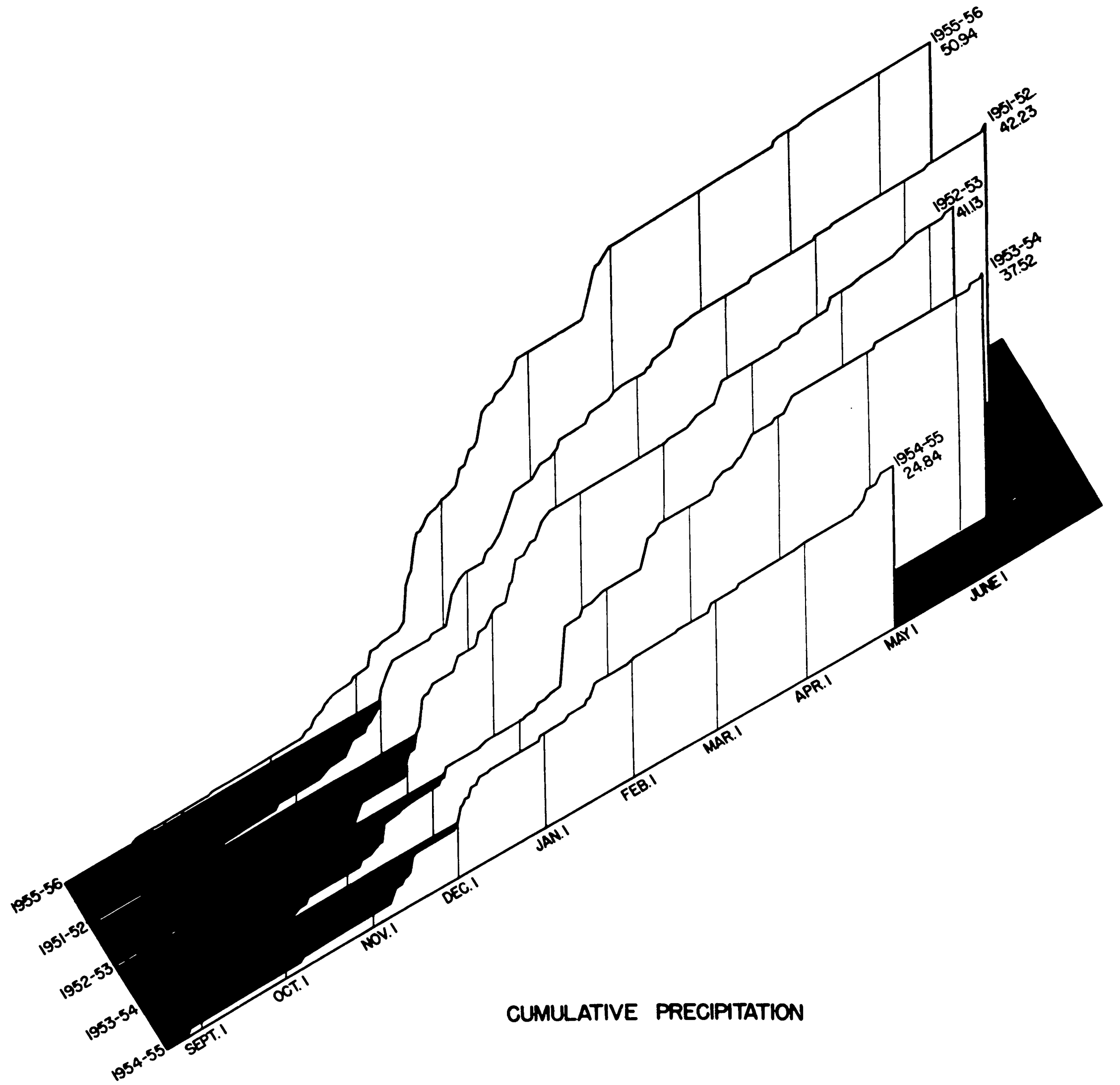


FIG. 15. Cumulative precipitation on the Hopland Field Station during each of five growing seasons. Horizontal portions of the graph indicate periods without precipitation.

The number of plants per square inch was low during that year. In 1956 the total precipitation for the season was high but there was only 1.62 inches after March 5. That spring was a cold one. The grasses did not do well, but *Erodium botrys,* on the other hand, made excellent growth.

In the fall of 1954, *Medicago hispida, Erodium botrys,* and *Bromus mollis* germinated after August rains. Many plants of the latter two species lived through the ensuing drought but those of *Medicago* did not.

In two of the years, 1952 and 1954, there was over one inch of rain in June. In neither of these years were the summer growing plants obviously more abundant than in years of no late rain.

On numerous occasions during the December and February samplings, frost heaving of the soil was observed where mulch or moss was scarce. Some plants were actually lifted from the soil. The most severe damage occurred at Site II where frost heaving resulted in small areas of bare soil. Plants of all species except *Bromus mollis* and *Erodium botrys* were susceptible. Frost heaving may explain the pattern of botanical composition at Site II.

Heaving of plants from the soil by frost was not observed in Site I and only in slight amounts in February of 1952 and 1954 at Site III. There was always a protective layer of mulch or moss on these areas during the winter and they were less subject to cold air drainage than Site II.

Frost or freezing did occur at all the sites as

TABLE II. Patterns of precipitation on the Hopland Field Station

	1st rain of ½″ or more		Second rain if 1st less than 1 inch		Last effective rain for growth		Winter dry periods over 20 days		Rain after T. begins to rise		Rain after veg. dries	
Season	Date	Amt.	Date	Amt.	Date	Amt.	Date	Amt.	Date	Amt.	Date	Amt.
1951-52	Oct. 1	0.50	Oct. 24	1.00	Apr. 30 May 8	0.85	None		Mar. 19	2.80	June 6-29	1.53
1952-53	Nov. 12-16	2.74			June 6-10	0.85	Jan. 21-Mar. 9 48 days	0.43	Mar. 29	5.64	None	
1953-54	Oct. 14-19	1.46			May 3	0.75	None		Apr. 5	2.12	June 5-9	1.07
1954-55	Aug. 25-29	1.07	Oct. 7-8	0.50	Apr. 17-30	3.86	Jan. 21-Feb. 26 38 days	0.69	Jan. 20	6.96	None	
			Nov. 8-17	5.84			Mar. 1-Apr. 16 47 days	0.60	Apr. 30	None		
1955-56	Nov. 13-24	4.22			Apr. 25-27	0.92	Jan. 28-Feb. 18 22 days	0.02	Mar. 5	1.62	June 19	0.09

evidenced by damaged leaves of the grasses. Frost injury of range annuals has been examined by Laude and Berry (1957). Although frost heaving has been observed to result in seedling mortality, it cannot be considered the sole cause in the death of plants because the decrease in number occurred where frosts were light as well as where they were heavy.

Relation of Grazing to Changes in Seedling Numbers

Both sites II and III were in a pasture grazed by sheep (Fig. 16). Site III was closely grazed and heavily trampled because it was located close to a feeding place. Grazing was estimated to be close in December of 1951; February of 1952, 1953, and 1956; and April of 1954 and 1955.

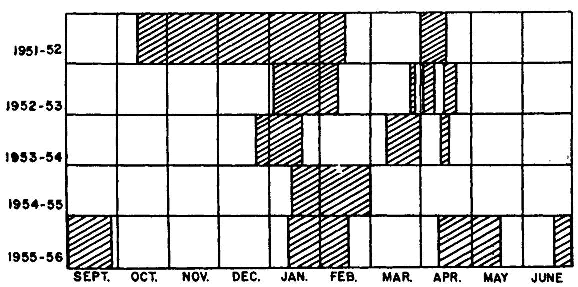


FIG. 16. Periods of grazing, 1951-1956, when Sites II and III were used by sheep.

Site II was located about one half mile from where the animals were fed. This site was grazed frequently and was recorded as closely grazed in December of 1951, and February of 1952 and 1956. In June of 1956 use was selective on patches of *Bromus mollis* and *Medicago hispida*. Usually the grazing was moderate at Site II. The intensity of grazing was indicated by the number of sheep pellet groups on an area of 40 by 40 feet (Table III).

TABLE III. Number of sheep pellet groups on an area 40 by 40 feet

	February		April	
	Site II	Site III	Site II	Site III
1953	37	65	13	92
1954			92	152
1955	19	44		
1956	21	75		

One might expect that grazing would be on the tallest plants first and that this would result in fewer tall plants and more of the short ones. Since *Bromus mollis* and *Bromus rigidus* were the tallest plants immediately after germination as well as at maturity, it would be logical to assume that they would be grazed most intensively throughout the growing season. Removal of the uppermost node stops growth of that culm but does not kill the plant. Additional growth is gained by the proliferation of new culms (Laude 1957). Both tall species showed an increase in proportion of total numbers as the season progressed and all species decreased in numbers with or without grazing. Therefore, changes in the numbers of plants per unit of area could not be related to differential grazing.

Deer on the Hopland Field Station graze the green herbaceous plants during the winter months. They no doubt used all three sites but only on Site I was their use evident in grazed plants and trails across the plots. This is a small area of grassland adjacent to a large timbered area and therefore deer were attracted to it. Only once was deer use recorded for April. Generally their diet switches to other forages in early spring. By plant maturity all evidence of grazing on herbaceous plants was eliminated.

Rodents, mainly mice, were common at Site I and their activities were always conspicuous. There were no signs of mouse activity at the other two sites. A colony of ground squirrels made numerous trails through the vegetation at Site II. The influence of these animals upon the changes in composition was estimated to be slight.

Relation of Mulch to Changes in Seedling Numbers

The change in general appearance at Site I through the growing season was from large amounts of standing dry plant materials in December to patchy dry and green plants in midwinter and finally to an even stand of tall grass at plant maturity. Usually there was a heavy matted mulch on the soil surface for most of the winter. The mat tended to disappear in late spring but in 1956 little was present after February.

At Site II, mulch was always less in amount and more patchy in appearance than that on Site I. The trampling and grazing of both sheep and deer removed the mulch or matted it on the soil where decomposition proceeded at a fast rate.

Site III was still more heavily grazed and trampled than Site II and consequently, less mulch was present there. The mulch was ordinarily patchy in December and varied from none in 1951 to a nearly complete cover in 1954. Essentially all was gone by June of every year.

The changes associated with amounts of mulch illustrate progressive changes in the annual type. Grazing and fire destroy the mulch; as a result certain species increase. With large amounts of mulch other species are abundant. With no grazing or fire to remove the mulch, *Bromus mollis* and *Bromus rigidus* become the major species in the annual grass type in this location. Others do not replace them and therefore they may be considered the highest species successionally among the annuals.

The amount of mulch greatly influences the speed of early fall growth. Three weeks after the first fall rains *Bromus mollis* was found to be about 2 inches taller on the areas with the most mulch than where there was none. Thus, conditions favor this species at the time of earliest growth because the other species do not respond as quickly. The result is that herbage in grams per square foot was found to be about two and one-half times greater with all the mulch than where there was none.

Discussion

All the changes given in this paper are included under the title of "vegetational changes." Five levels of change have been discussed by Major (1951) as seasonal, annual, successional, historical, and genetical. The data from the square-inch plots illustrate the first two types; the data from the study involving manipulation of mulch illustrate the third or successional change.

Seasonal and annual changes are of the nature of fluctuations in that no evidence of a constant direction toward the dominance or disappearance of one or more species was found. The fluctuation suggests a response by each species population to the incoming heat, moisture, and light as modified by the vegetation itself. The magnitude of these incoming factors varies from season to season and year to year, as does the vegetation. The implied relationships are mentioned because they are usually given as the cause of changes in the California annual type. However, no correlations that suggest cause and effect, except the most general, could be found among the vegetational changes on the three sites. This may be because the only weather data available was of the usual type collected by a standard station about one mile distant. Data on the microclimate might well have shown clearcut relationships between vegetational changes and the micro-environment.

The data from the study on the vegetational changes that were associated with manipulating mulch are presented to illustrate directional changes. These are plant succession. Actually, the data document only one way by which man can influence vegetation of the type studied.

Ecologists have usually studied succession by comparing the vegetation in different areas to arrive at successional stages or sequences by deductive reasoning. But succession is a natural change over time on *one* area. The changes are directional; eventually they may lead to a stabilized vegetation, and they exhibit the oscillations mentioned above. Exclusively inferential conclusions are to be avoided whenever possible because they may be in error as generalities and because they do not allow prediction with accuracy of the details in the successional pattern. Quantitative data are needed on the vegetation of one area over time and should be taken in such a way that the non-directional fluctuations are also measured and separated from successional changes. The separation may or may not be important. In the California annual type, yearly fluctuations are as contrasting as successional stages in many other vegetational types.

Ordinarily it takes years of continued sampling to gather data on succession, consequently deductive methods are often used. One approach to shorten the time scale is to vary a factor experimentally in such a way that the resulting treatments approximate those that occur over a longer time scale. This was attempted by manipulating the natural mulch. The associated vegetational differences that developed with all mulch removed, none removed, and some intermediate treatments might well indicate the succession of plants in response to natural accumulation of organic material.

The hypothesis was that varying amounts of mulch would favor different kinds of plants, which was found to be true. The deduction was made that the changes in botanical composition represent a successional series. Stable vegetation of the California annual type was assumed to require mulch accumulation to a point where annual increment and decomposition reach stability. This point is as yet untested. Stability is interpreted to include seasonal and annual oscillations.

In the mulch study, the seasonal variations in vegetation were by-passed in the sampling procedure by reading the plots at plant maturity each year. The yearly changes are shown. Above these are the successional changes, which have already been discussed. In the following outline a division of the successional changes is proposed.

I. Primary succession. This type begins on new areas at the same time *zero* as the beginning of soil formation.

II. Secondary succession. Here is included those directional changes toward stability which occur after destruction, partial or complete, of existing vegetation. The destruction may be the result of natural catastrophes or man caused. Time limits on the speed of destruction are not implied. Secondary succession can be divided into two categories:

1. Those beginning from a natural catastrophe.
2. Those beginning from a man controlled cause and so named according to the cause; such as fire; grazing, logging, fertilization, and selective kill of certain species by chemicals. In this context nature plays an important role. A different cultivated crop on a certain field each year would not qualify, but the directional change following abandonment of the field from cultivation would qualify.

Ordinarily, secondary succession should be distinguished from primary succession on the basis of correlation with time zero in process of soil formation. In secondary succession, seldom are both soil and vegetation destroyed to the same extent. The balance is unstable and successional changes occur rapidly until they are in more or less stability with the soil. This implies that soil is ordinarily not set back as far as the vegetation.

Summary

1. Changes in the California annual type were studied on three sites during five successive growing seasons, 1951 to 1956. The sites were located on the Hopland Field Station in Mendocino County. The field data were collected by counting the number of plants by species on quadrats of one square inch in size.

2. The three sites were characterized by distinctly different combinations of annual plants throughout the study.

3. The seasonal growth pattern proceeds from germination, usually in November, through a short period of moderate growth, then a longer winter period when growth is slow, and finally ends with about a month of fast growth in April and May.

4. Average number of plants per square inch varied between 3.3 and 35.0 with different situations.

5. All species decreased in numbers per unit of area from December to June.

6. *Bromus mollis, Bromus rigidus,* and *Erodium botrys* decreased less in numbers per unit of area than the others and, thus, increased in percentage botanical composition.

7. The numbers of plants per unit of area varied greatly between years as also did the various species. For example, 1953 was a year when the grasses clearly dominated the vegetation. *Erodium botrys* constituted a larger portion of the vegetation in 1955 than in other years.

8. The patterns of seasonal and yearly change were recorded on the three sites, with different combinations of the botanical composition of the annual species.

9. Changes in the annual-type vegetation due to such items as grazing, seeding, fertilization, and fire are reviewed and the influence of mulch on percentage botanical composition is illustrated.

10. Data and observations indicate that most of the germination occurs in a short period after the first fall rains of 0.5 to 1 inch. Cause for the differences in total numbers of plants between years was not found.

11. The changes were examined in relation to the patterns of rainfall and temperatures and to grazing.

12. The results are discussed as illustrations of seasonal, annual and successional changes in vegetation.

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GROWTH OF NATIVE AND EXOTIC PLANTS UNDER CONTROLLED TEMPERATURES AND IN THE SAN GABRIEL MOUNTAINS CALIFORNIA[1]

HENRY HELLMERS AND WILLIAM C. ASHBY[2]

INTRODUCTION

Plant selection is one phase in the development of methods for soil stabilization in the San Gabriel Mountains of California (Sinclair 1954, Horton 1949). The climate—hot, dry, rainless summers and cool, wet winters—excludes many species of plants from the flora of these mountains. The studies reported here served as a rapid preliminary screening process to select exotic species for erosion-control plantings. Of 24 exotics tested, only one appeared outstanding for erosion control. Three leguminous species were well adapted and were considered desirable for their soil-improving possibilities. The study provided an insight into the autecology of the test species.

The main vegetation type in these mountains at elevations from 1,000 to 6,000 feet is known as chaparral, and is primarily composed of evergreen sclerophyllous shrubs. Jepson (1925) describes the species of the chaparral, which he considers a fire type formation in his discussion of the vegetation of California. An important reference chiefly concerned with the chaparral in northern California is Sampson (1944). Horton and Kraebel (1955) give detailed information on the local southern California species, and on the environment with particular reference to the major factor of fire and its consequences. Many of the species have deep and spreading root systems (Hellmers, Horton, Juhren, and O'Keefe 1955).

Various attributes of the climate in southern California, including several classifications in terms of climatic regions, are presented by Visher (1954). In the Köppen classification this area is represented as a *Cs*, Mediterranean, region. Figure 1 presents data for a station at 2,800 feet within the chaparral formation. The dry season often exceeds 6 months' duration, and has maximum air temperatures of 30° to 40°C. During

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[2] William C. Ashby's present address: Botany Department, University of Chicago, Chicago, Illinois.