The Potential for Dominance by Stipa pulchra in a California Grassland

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ABSTRACT: In a California grassland where *Stipa pulchra,* a perennial bunchgrass, has regained dominance, *Avena fatua* is dramatically reduced in importance as compared to surrounding annual grasslands without *S. pulchra.* This study examined the potential of *S. pulchra* to reduce the importance of *A. fatua* in the perennial grassland compared to the annual grassland. Soil moisture was monitored frequently over two growing seasons and was not limiting to growth of *A. fatua* in the perennial grassland. Soil nutrients were examined by chemical analysis of field soils and by fertility experiments in greenhouse studies. Available nitrogen occurred at concentrations limiting to growth of *A. fatua* in both grasslands, but it occurred in lowest concentrations in the annual grassland where *Avena* abounded. Animal activity and light reduction did not support a hypothesis for reduction in abundance of *A. fatua.* The allelopathic potential of aqueous leachates of *S. pulchra* straw was experimentally tested on *A. fatua,* and demonstrated a slight toxicity as evidenced by the growth of *A. fatua.* Root exudates of *S. pulchra* reduced the shoot growth of *A. fatua.* This was especially pronounced when the two species were grown together. The importance of the allelopathic reactions to the pattern in the field is related to the phenology of the two species. A synergistic effect of allelopathic reaction and limitation of available nitrogen is suggested as one potential mechanism by which *A. fatua* is reduced in grasslands dominated by *S. pulchra.*

INTRODUCTION

The pristine grasslands of California are thought to have been dominated by perennial grasses (Beetle, 1947), and Clements (1934) suggested that *Stipa pulchra* (purple needlegrass) was the principal dominant in these grasslands. Clements' suggestion was based upon a single stand of *S. pulchra* adjacent to a railroad track near Fresno, Calif. Biswell (1956) disagreed with Clements' suggestion. These grasslands were virtually destroyed by domestic grazing animals in the 18th and 19th centuries, and when Burcham (1957) attempted to describe what was known of the original grasslands, he concluded that historical records were too incomplete to describe their composition or characteristics.

The grasslands are currently dominated by alien annual species which were introduced concurrently with the domestic grazing animals. The annual vegetation of the California grasslands has been referred to as the "California annual type" (Talbot *et al.,* 1939), and the vegetation type has been reviewed by Biswell (1956), Heady (1958) and Rossiter (1966). In the coastal valleys of California, and especially

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Southern California, *Avena fatua* (wild oats) dominates large areas of grasslands. In a few of these valleys, *Stipa pulchra* has regained dominance where grazing by domestic animals is curtailed (White, 1966, 1967). Where *S. pulchra* regains dominance, there is a marked change in the composition of the annual grass component of the grassland; *A. fatua* is reduced in importance (Robinson, 1969), and other annual grasses increase in importance. The purpose of this investigation is to determine if *S. pulchra* is capable of excluding *A. fatua* from grasslands.

STUDY AREA

A study area was selected in the Santa Ynez Valley of Santa Barbara Co., Calif., in which *Stipa pulchra* had regained dominance in a grassland previously composed of annual grass species. The study area was located on a ranch which was converted from cattle to horse grazing in the early 1960s. Because of the nature of the surrounding vegetation and topography, horses do not graze in this area as evidenced by the absence of both fecal material and hoofprints.

The study area consisted of two grassland stands ca. 100 m apart. The first was dominated by *Stipa pulchra* with contributions of several annual brome species, and will be referred to herein as the perennial grassland. The second was a grassland dominated by *Avena fatua,* and will be referred to as the annual grassland. The two grasslands were on a soil series described as Zaca clay (Carpenter *et al.,* 1927) which was derived from the Paso Robles formation (Dibblee, 1956). The soils are relatively heavy and dark with no distinct profile. The parent material is a loosely consolidated material derived principally from the detritus of the Monterey Shale formation (Dibblee, 1956). The perennial grassland is on a 10° NE-facing slope, and the annual grassland is on a 6° N-facing slope.

Climate.—The climate is strongly Mediterranean with cool, moist winters and hot, dry summers. The weekly precipitation totals (Fig. 1) for September 1971 to June 1973 were collected by the U.S. Weather Bureau at Cachuma Lake approximately 5 airline miles S of the study area. The data agreed with those collected on the site with a fencepost rain gauge. The 1972 growing season, or that period from the autumn of the previous year to the late spring of 1972, had below normal total precipitation (26.3 cm) most of which fell in one storm. The 1973 growing season, conversely, had above normal precipitation (74.2 cm) which was distributed throughout much of the growing season. Records have not been collected at Cachuma Lake sufficiently long for a reliable average annual precipitation, but it would be about 45 cm. The coolest air temperatures follow the early rains, and there is a gradual rise in temperature starting in February and March (Fig. 1).

METHODS AND RESULTS

ANALYSIS OF VEGETATION

The differences in composition between the two grasslands were determined by several methods. The relative abundance of species in

the two grasslands, the importance of *Stipa pulchra* to each grassland, and the differences in annual grass species were sampled separately.

The relative abundance of species in each grassland was computed on the basis of 40 circular samples of 125 cm² each. Nomenclature follows Munz and Keck (1959). Of the 27 forbs recorded, only two *(Amsinkia intermedia* and *Medicago hispida)* were more abundant in the annual grassland than in the perennial grassland. Several forbs were more abundant in the perennial grassland. Most notable among these were *Alchemilla occidentalis, Erodium cicutarium, E. moschatum, Tillaea erecta, Dodocatheon clevelandii* and *Fritillaria biflora.* The

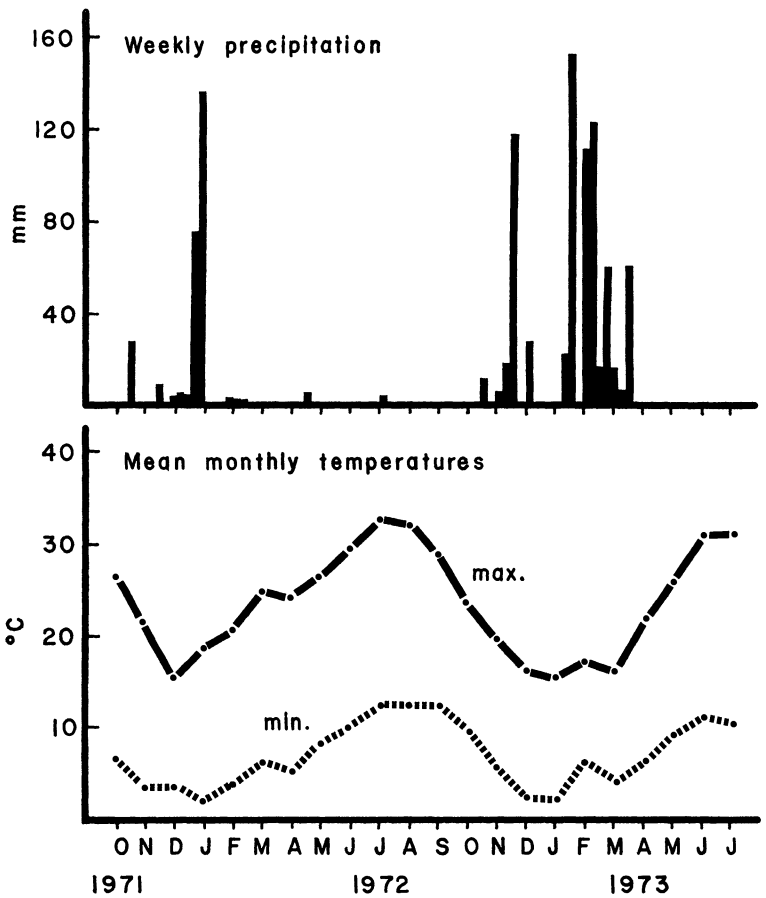

Fig. 1.—Precipitation and maximum and minimum temperatures recorded at Lake Cachuma encompassing the 1972 and 1973 growing seasons. Precipitation is presented as millimeters per week. Temperatures are presented as mean daily maxima (solid line) or minima (broken line) for each calendar month

conspicuous difference between the two grasslands was the contributions of the grass species.

Perennial grass component.—The contribution of *Stipa pulchra* to the two grasslands was estimated by a line intercept method. A tape was extended for 10 m over the grassland, and along this transect the foliar cover of *S. pulchra* was recorded. This process was repeated along 10 separate transects in each grassland. The results which follow were obtained in February 1973. In the perennial grassland the foliar cover of *S. pulchra* was 33%, while its cover in the annual grassland was less than 3%. Thus, the designations of perennial and annual reflect an order of magnitude of difference in the cover of the perennial, *S. pulchra*. Foliar cover is a dynamic parameter in perennial grasslands during the period of a growing season. The foliar cover of *S. pulchra* is minimal in December and January and is maximal in April and May. The February results are presented to correspond to a period when the annual species are well-established and the perennial grasses are initiating new growth. These data give evidence for the ample space between the clones of *S. pulchra* for the growth of annuals.

Annual grass component.—The annual grass component of the two study sites was estimated with the use of a productivity sampling technique. For this method, a ring with an area of 125 cm^2 was the basic sampling unit. A sample consisted of all the aboveground biomass of the species falling within the ring. Sampling of disturbed areas such as gopher mounds and access trails was avoided. In the perennial grassland the sampling location was between the clones of *Stipa pulchra* in the space available for the growth of annual species. This technique is analogous to sampling the herbaceous species of a forest floor between the trees. The results contrast only the annual grass components of the two grasslands, and not the grasslands as a whole. For the purpose of experimentation and the avoidance of creating disturbance, the perennial grassland was divided into halves: one half was sampled in 1972, the second in 1973. Eighty samples were collected from each grassland in 1972 and 1973. This collection corresponds to 1 sq m from each grassland. Each sample was labeled, bagged and transported to the laboratory where it was stored at 4 C. Each sample was subsequently divided into species which were counted, dried and weighed.

There was a marked difference in the annual grass productivity between the two grasslands. The productivity in the perennial grassland was 65.1 and 286.3 g/m^2, and in the annual grassland was 272.1 and 453.8 g/m^2, respectively, for the 1972 and 1973 growing seasons. The relative annual grass productivity in the perennial grassland was 24 and 63% of that in the annual grassland for the two growing seasons. Productivity of both grasslands increased in 1973, a year of above average precipitation; however, the increase was greatest in the perennial grassland.

In the perennial grassland in 1972, the contribution of *Avena* spp. was 8.4 g/m^2 or 12.9% of the total annual grass productivity. The

species of *Avena* in the perennial grassland was almost entirely *A. barbata*. In the annual grassland, *Avena* spp. contributed 243 g/m² or 89.1% of the annual grass productivity. In this grassland *A. fatua* is nearly a pure stand. No effort was made to distinguish between *A. fatua* and *A. fatua* var. *glabrata* in the annual grassland. In 1973 the contribution of *Avena* spp. to the perennial grassland was 0.6 g/m² or 0.2%, whereas the contribution in the annual grassland was 422 g/m² or 92.9% of the total annual grass productivity. The differences between years in the contribution of *Avena* spp. to the annual grass productivity of the perennial grassland was a product of the arbitrary division of the perennial grassland into halves rather than a change in the success of *Avena* spp. in the grassland.

The contributions of other annual grass species varied between the grasslands and were primarily *Bromus* spp. In the annual grassland *B. rigidus* (ripgut brome) contributed 10.1 and 6.0%, and *B. mollis* (soft chess) contributed 0.8 and 1.0% of the annual grass productivity in 1972 and 1973, respectively. *Bromus rubens* (red brome) and *Festuca megalura* (foxtail fescue) were present in the annual grassland, but contributed less than 0.1% of the annual grass productivity in either sampling year. In the perennial grassland the *Bromus* spp. contributed nearly 100% of the annual grass productivity. For the perennial grassland in 1972 and 1973, respectively, *B. rigidus* contributed 11.4 and 59.0%, *B. mollis* contributed 57.3 and 9.8%, and *B. rubens* contributed 18.3 and 30.6% of the total annual grass productivity.

The two grasslands were distinct with respect to species composition. The annual grassland was predominately *Avena fatua* with minor contributions from *Bromus rigidus, B. mollis* and *Stipa pulchra*. The perennial grassland was predominately *S. pulchra* with important contributions from *B. rigidus, B. mollis* and *B. rubens*. The contribution of *A. fatua* in the perennial grassland was small and conspicuously reduced when compared to the annual grassland.

GRASS HABIT AND PHENOLOGY

The two principal grasses, *Stipa pulchra* and *Avena fatua*, differ in habit and phenology. *A. fatua* is an annual which is variable in the number of tillers produced. In low density an individual may be many-tillered, while in high density single culms predominate. *Stipa pulchra* is a clone-forming perennial. The clone basal area varies considerably in size depending on the age and the number of tillers. The distinction is tenuous between those clones which are formed of genetically identical individuals and those which are the convergent growth of several seedlings. Distances of 30 cm between clones are not uncommon.

Examinations of the root systems of *Avena fatua* and *Stipa pulchra* were made on several occasions by careful excavation and hydraulic removal of the soil. *Avena fatua* was primarily rooted in the upper 30 cm of the soil profile with an increasing concentration of roots above 20 cm. The roots of annual species formed a thick, tangled mat in the

first 5 cm of soil. *Stipa pulchra* was a much deeper-rooted species with roots extending to 1 m in depth with the greatest concentration of roots between 15 and 30 cm. The roots of the two species overlap in the vertical profile with the majority of the roots of *A. fatua* near the surface, and most of the *S. pulchra* roots lower in the soil profile.

The two grasses also differ phenologically. The annual *Avena fatua* germinates with the first rains in the late autumn or early winter. This is concurrent with a cooling trend (Fig. 1). As a result, growth is slow until late winter when air and soil temperatures increase and the annual grasses grow rapidly. Anthesis normally occurs in April, and seed set occurs the following month. The annual species passes the hot, dry summer months as seed, the parent plants having died by the end of June. *Stipa pulchra* is normally very slow in growth initiation during the cool months of early winter. Growth is usually initiated with the warming trend and, therefore, lags behind the annual species. Anthesis for *S. pulchra* is in May with seed set in late May or early June. The summer drought and high temperatures are tolerated as quiescent meristematic regions at or near the soil level, and these are supplied with water from the deep roots at a very slow rate.

ANALYSIS OF PHYSICAL FACTORS

Soil moisture.—Differences in the availability of soil moisture for *Stipa pulchra* and *Avena fatua* provide an obvious hypothesis for interaction between the two species. Precipitation is highly seasonal in Southern California, and the duration and frequency of rainfall are unpredictable. This unpredictability may result in periods of drought after the initiation of germination brought about by the first rains. The presence of the established root system of *S. pulchra* at the time of germination and early growth of *A. fatua* give credibility to this hypothesis.

Soil texture was analyzed by the hydrometer method (Bouyucos, 1936) of soils from the 0-5 and 10-15 cm depths in each grassland. The soils are categorized as clay-loams by the USDA soil classification system (Brady, 1974) in the 0-5 cm depth of both grassland soils and in the 10-15 depth of the annual grassland soil. The lower soil depth in the perennial grassland was a clay. The soils of the perennial grassland had a higher proportion of clay with less sand and silt than did the soils of the annual grassland.

The permanent wilting percentage (PWP) was determined on a 15-bar pressure plate (Soil Moisture, Inc.) for three sampling depths, 0-5, 10-15, and 25-30 cm. The PWP values in percent of dry weight for the annual grassland soil were 15.4, 14.4 and 17.1 and for the perennial grassland soil were 16.1, 15.7 and 20.3 for the three sampling depths. Each value represents the mean of 12 samples. The greater values in soil samples from the perennial grassland reflect the higher clay content of the soil.

During the growing seasons of 1972 and 1973, field soil moisture

was determined frequently. Triplicate samples were collected at three depths, 0-5, 10-15 and 25-30 cm, in both grasslands, and the soil moisture was determined gravemetrically. Field soil moisture is reported as a percent of oven dry weight. The permanent wilting percentage is subtracted from the field soil moisture to obtain available soil moisture.

At no time after the rain of 14 November 1973 was the available soil moisture in the perennial grassland lower than that in the annual grassland (Fig. 2). For the 0-5 cm depth in both grasslands, the available soil moisture was depleted to the PWP by approximately the same date. For the 10-15 cm and the 25-30 cm depths, the approximate date at which PWP was reached in the perennial grassland followed that for the annual grassland by 3 and 9 weeks, respectively.

The results for the 1972 growing season were similar, but due to the reduced levels of precipitation there was considerable variation in the availability of soil moisture at the 0-5 cm depth. On six consecutive dates the higher level of available soil moisture alternated between the

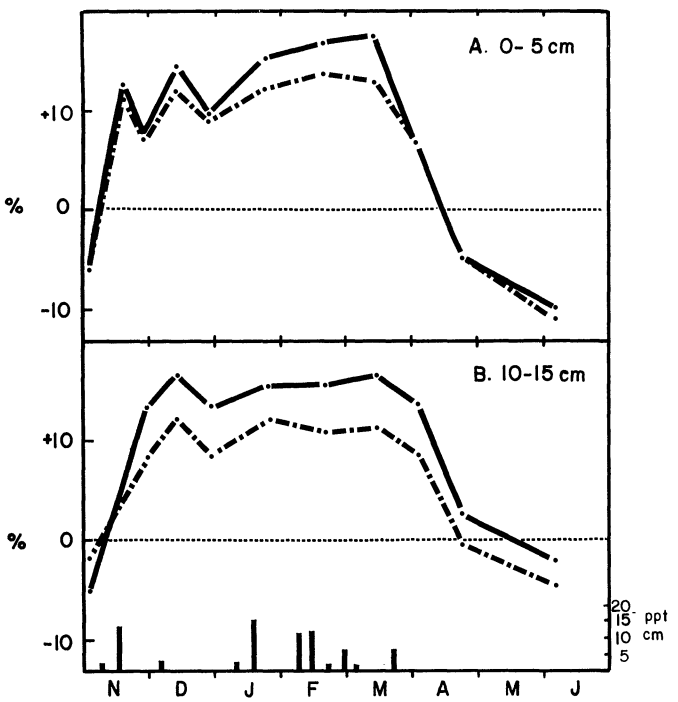

Fig. 2.—Available soil moisture as a percent of dry soil weight for the perennial (solid line) and annual (broken line) grassland soils at the 0-5 and 10-15 cm depth in 1973. The PWP is indicated by the horizontal broken line at 0%. The histograms represent weekly precipitation in cm

perennial and annual grassland. Levels of soil moisture at the 10-15 and 25-30 cm depths followed a pattern similar to that of the 1973 season, but the 25-30 cm depths reached PWP at approximately the same date in both grasslands.

Soil nutrients.—Soil mineral nutrients have been suggested by Robinson (1968) and White (1967) to be important in the perennial and annual grasslands. We proposed a working hypothesis that *Stipa pulchra* reduced the level of some mineral nutrient below the tolerance of *Avena fatua*. To test this hypothesis, field soils were analyzed for essential nutrients and fertility.

The soils of the annual and perennial grasslands were sampled for soil mineral nutrients four times during the year encompassing the 1973 growing season. The first sampling date was 2 August 1972. The second was 3 November 1972, following a rain of 1.2 cm on October 15 which initiated germination of the annual grasses. The third sampling date was 14 March 1973, which coincided with the maturation of the annual grasses. The final sampling date was 17 July 1973, a time at which all annual species had died. These sampling dates were chosen to assess changes in soil nutrients as a result of utilization.

Each grassland soil was sampled at six separate locations and at two depths on each sampling date. The August 1972 sample was an exception and consisted of only three locations. The specific location of each sample was selected to be representative, yet minimize disturbance to the grasslands. Sampling depths of 0-5 and 10-15 cm were chosen to investigate soil nutrient levels in the region of greatest concentration of annual grass roots. The soil was transported to the laboratory in sealed plastic bags and stored at 4 C until analysis was initiated. Prior to analysis, the soils were passed through a 2.0-mm mesh screen. Extractions of transient soil minerals, such as nitrate and ammonium, were performed within 48 hr after collection in the field. The results of the analyses for soil mineral nutrients for each sampling date were subjected to analysis of variance with the Newman-Kuels multiple range test at the 95% probability level (Woolf, 1968).

Soil nitrogen was typically found in greatest quantities as organic nitrogen, nitrate nitrogen and ammonium nitrogen. The level of organic nitrogen is an indication of the potential availability of nitrogen to plants. Nitrate nitrogen is considered to be the form most readily available to plants (Viets, 1965). Available nitrate was extracted from the soil and analyzed by the phenoldisulfonic acid method described by Bremner (1965). Levels of soil nitrate increased after the first rains and decreased as the plants approached maturity (Table 1). The levels of nitrate in the perennial grassland soil in November at the 0-5 cm depth were significantly greater ($P = 0.05$) than in the annual grassland soil. In August and March the mean soil nitrate levels were greater in the perennial grassland than in the annual grassland, but the differences were not significant. Similarly, there was no significant difference in the July soil nitrate levels of the annual grassland as com-

TABLE 1.—Soil chemical characteristics for the annual and perennial grassland soils at two depths and for three sampling dates. Nitrogen as nitrate, phosphorus as phosphate and sulfur as sulfate are presented as μg elemental nutrient/g dry soil weight. Potassium and divalent cations are presented as m. e./100g dry soil. Organic matter is presented as a percent of dry weight. Each value represents the mean of six samples

	November				March				July			
	Annual		Perennial		Annual		Perennial		Annual		Perennial	
	0-5	10-15	0-5	10-15	0-5	10-15	0-5	10-15	0-5	10-15	0-5	10-15 cm
NO_3-N	4.7[a]	2.8[a]	10.2[b]	0.8[a]	3.2[ab]	1.9[bc]	4.5[a]	0.6[c]	1.4[a]	1.5[a]	1.2[a]	1.3[a]
HPO_4-P	10.4[a]	8.7[a]	9.7[a]	7.9[a]	11.3[a]	8.1[b]	11.0[a]	8.8[b]	13.1[a]	9.3[b]	12.9[a]	7.0[b]
SO_4-S	0.5[a]	0.5[a]	0.9[b]	0.4[a]	0.1[a]	2.1[a]	1.2[a]	1.6[a]	0.6[a]	0.7[a]	0.7[a]	0.6[a]
K	1.0[a]	0.9[a]	0.7[ab]	0.5[b]	1.1[a]	0.8[a]	0.9[a]	0.7[b]	0.9[a]	0.8[a]	0.8[a]	0.5[b]
Divalent cations	17.4[a]	17.4[a]	18.1[a]	20.4[b]	17.5[a]	18.0[a]	22.3[b]	29.1[c]	16.8[a]	17.4[a]	23.1[b]	28.0[c]
Organic matter	4.6[a]	3.8[b]	3.0[c]	1.5[d]	4.0[d]	3.2[b]	4.8[a]	2.4[c]	5.1[a]	3.8[a]	5.1[a]	4.3[a]
pH	6.4[a]	6.6[b]	6.2[c]	6.7[b]	5.8[a]	5.9[a]	5.6[b]	5.8[a]	6.2[a]	6.3[b]	6.1[c]	6.3[b]

a, b, c, d—Shared letters within a characteristic and sampling date indicate no significant difference at P = 0.05

pared to the perennial grassland. The nitrate levels in the 10-15 cm depth (Table 1) were less than the 0-5 cm depths in both grassland soils, but the difference was significant only for the perennial grassland in November and for both grasslands in March. None of the samples showed a significant difference between the two grassland soils for the 10-15 cm depth. Levels of soil nitrate in the two grasslands were relatively low (Richardson, 1938); however, in all cases, the levels in the perennial grassland soil were the same or greater than in the annual grassland soil.

Organic nitrogen was extracted from soils by the Kjeldahl digestion method (Jackson, 1958). These digests were analyzed by the indolephenol blue method described by Tetlow and Wilson (1964). In a representative sample (July 1973) the soil organic nitrogen content at the 0-5 cm depth was 2.9 and 2.3 mg/g dry soil for the annual and perennial grassland, respectively. The values were not significantly different. The soil nitrogen content for the 10-15 cm depth was significantly lower than the 0-5 cm depth for both soils, and the nitrogen content of the annual grassland soil (1.7 mg/g) was significantly greater than the perennial grassland soil (1.2mg/g) at the 10-15 cm depth.

Soil ammonium was extracted by the method described by Bremner (1965), and analyses were performed by the method described by Tetlow and Wilson (1964). Ammonium levels in the November and March soil samples were below the sensitivity of the technique of analysis (3 μg-N/g soil). The July samples for ammonium in the annual grassland soil were 3.9 and 5.1 μg-N/g dry soil for the 0-5 and 10-15 cm depths, respectively. There was no significant difference for soil ammonium between the two grasslands or among depths.

Soil organic matter content was determined by loss on ignition at 700 C (Baer, 1964). Correction was made for the loss of water from the clay crystalline structure. Percent organic matter in the annual grassland soil was greater than in the perennial grassland soil at the 0-5 cm depth, but the only significant difference was in November (Table 1). Organic matter at the 10-15 cm depth was significantly greater in the annual grassland soil at the November and March sampling dates. There was a general increase in the organic matter content of the soils during the period of measurement.

Soil *p*H was measured by the glass electrode method on an Instrumentation Laboratory electrometer, Model 265, using a 1:1 mixture of soil and distilled water. Soil *p*H increased with soil depth (Table 1), and the difference was significant for all samples except for the annual grassland soil collected in March. The annual grassland soils had a *p*H significantly higher than in the perennial grassland soil at the 0-5 cm depth for all sampling dates. The greatest difference was 0.22. There were no significant differences in *p*H between the grassland soils at the 10-15 cm depth.

Phosphorus, as available phosphate in an aqueous extract, was determined by the molybdenum blue colorimetric method of Dickman

and Bray (1940). Phosphate concentrations decreased significantly with depth for both grassland soils in the March and July samples (Table 1). There was no significant difference between the two grassland soils for any sampling date or depth.

Available potassium was extracted with ammonium acetate and analyzed on an Instrumentation Laboratory Model 143 flame photometer. Potassium decreased with depth, but this difference was significant only in the perennial grassland soil in the March and July collection (Table 1). The perennial grassland soil consistently had lower levels of available potassium than the annual grassland soil for all depths. There was, however, no significant difference between the grassland soils in the levels of available potassium at the 0-5 cm depth. Potassium levels at the 10-15 cm depth were significantly lower in the perennial grassland soil than in the annual grassland soil for all sampling dates.

Calcium and magnesium were determined in the same ammonium extract as was potassium by using the total hardness complexiметric method for the divalent cations (American Public Health Association, 1965). The divalent cations were significantly greater in the perennial grassland soils than in the annual grassland soils at both sampling depths (Table 1).

Sulfate levels were determined by the barium chloride turbidimetric method (Bardsley and Lancaster, 1965). For only one sampling date, November 1972, was there a significant difference between the grassland soils, when the 0-5 cm sample of the perennial grassland soil had more sulfate sulfur than all other samples (Table 1).

Comparison of levels of soil mineral nutrients alone has little meaning without some knowledge of the requirements of the plants. To evaluate the effect of mineral nutrients on growth of *Avena fatua,* a greenhouse experiment was established using field soil. Soils were collected from the 0-5 cm depth on 27 October 1973 for the first experiment and on 29 January 1974 for the second experiment. The soils were air-dried and passed through a 6.4-mm (0.25 inch) mesh screen. Because of the high clay content and contractibility of the field soils, the soil for each pot was mixed with crystal silica sand at a ratio of 4:1 (500 g soil : 125 g sand). To each pot, with either perennial or annual grassland soil, was added 250 ml of treatment solution after Machlis and Torrey (1956). In the first experiment the treatment solutions consisted of deionized water (None), full nutrient solution (Full), nutrient solution without nitrogen (−N), nutrient solution without phosphorus (−P), and nutrient solution without potassium (−K). The second experiment included an additional nutrient solution without sulfur (−S). For each treatment there were five pots, and each pot was planted with six *A. fatua* seeds which were thinned to the four largest individuals after 1 week. Twice during the experiment, 100 ml of the treatment solution was added to each pot. The treatments were arranged in five randomized blocks in the greenhouse. After 36 days for the first experiment and 38 days for the second, the shoot of

each plant was harvested, dried at 70 C for 48 hr, and weighed on an analytical balance. The results were subjected to analysis of variance and the Newman-Kuels multiple range test (Wolfe, 1968) using the 99% confidence level.

In all treatments and for both experiments, the mean dry weight of *Avena fatua* grown in the perennial grassland soil was significantly greater than that grown in the annual grassland soil (Fig. 3). There was no significant reduction in the growth of *A. fatua* in either soil when nutrients were supplied without potassium or without phosphorus as compared to when the soils were supplied with the full nutrient solution. This suggests that these two nutrients are present in adequate supply in both soils. There was a significant reduction in growth of *A. fatua* in the soils with no nutrients added compared to the addition of the full nutrient solution. There was the same reduction in growth in the treatments where nutrient solution without nitrogen was added to the soil. Finally, growth in which sulfur was deleted from the nutrient solution was intermediate, and statistically different from the growth in soils with the full nutrient addition treatment and from growth in soils with the no addition treatment.

Light.—In grasslands, the diminution of light is manifested in a vertical gradient from full sunlight above the culms to reduced values at soil level. The degree to which light is diminished is dependent upon several biotic and abiotic factors. The angle of incidence, as influenced

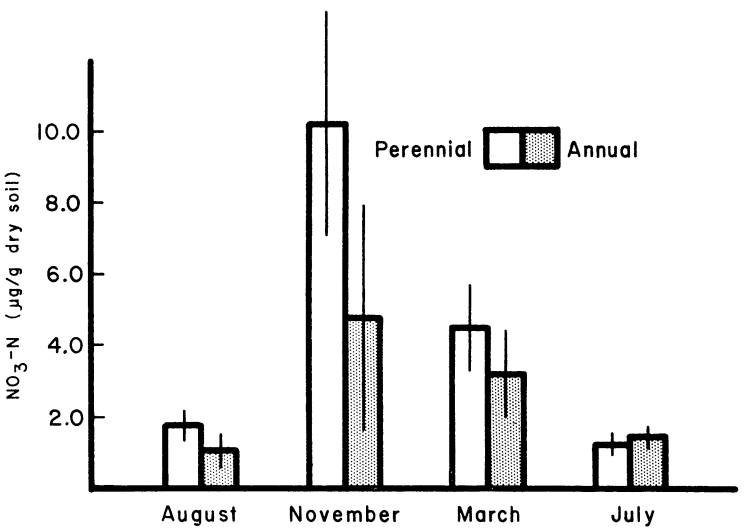

Fig. 3.—Field soil fertility analysis as mean dry weight (mg) of shoots of *A. fatua* when grown in soil from the perennial grassland (open) and from the annual grassland (shaded) under four nutrient treatments. Vertical bars within the histograms represent the confidence limits of the sampling means at P = 0.01

by latitude and topography, will directly affect light penetration in a grassland. The phenological state of the vegetation and its density will affect light. Finally, differences between species will affect the penetration of light.

The slopes of the two grasslands are similar in direction and inclination; furthermore, a similar pattern to that described is observed in grasslands with no slope.

With the first heavy rains, the straw of *Stipa pulchra* is lodged to the ground forming a mat 1-2 cm thick between the clones. The associated species, *Bromus mollis* and *B. rubens,* are also easily lodged. As a result of this lodging action by rains, the areas between clones of *S. pulchra* are well lighted to the surface of the detrital material. In the annual grassland, *Avena fatua* is not as readily lodged, and some of the previous year's culms may remain erect after the initiation of growth in the winter. Those culms which are lodged often form a deep mat up to 5 cm in depth.

Field observations indicated that light penetration above the litter layer is dependent on the height of the annual grass species. To illustrate, a vertical profile of light was measured in both types of grassland on a clear day, 15 January 1974. Light was measured with an ISCO Model SR solar radiometer with remote sensor which was leveled before each measurement. The wavelengths of 450 and 675 nm were selected to approximate those used in photosynthesis. Light measured at 6, 10, 15, 20, 25 and 30 cm above the soil surface is expressed as a percent of full sunlight as measured above all grass species at 30 cm. Use of the percent value was necessitated by the time required for the measurements. The data (Table 2) are the means of three measurements at each height. The mean height of *Avena fatua* in the annual grassland was approximately 16 cm, and the mean height of the annual grass species of the perennial grassland was approximately 8 cm. The data indicate that more light penetrated to the 6- and 10-cm heights in the perennial grassland than in the annual grassland.

Animal activity.—The influence of animals in annual grasslands has been described by several authors (Marshall and Jain, 1970; Batzli and

TABLE 2.—Light intensity of selected wavelengths (450 and 675 nm) along a vertical profile above the ground in the annual and perennial grasslands. Values are means of three samples and are expressed as a percent of light intensity recorded at 30 cm

	Percent of intensity at 30 cm			
	Annual		Perennial	
	Wavelength (nm)		Wavelength (nm)	
Height (cm)	450	675	450	675
6	11.8	10.6	54.2	54.1
10	21.7	21.5	88.1	86.2
15	35.9	51.3	89.7	86.0
20	95.8	100.0	90.6	83.6
25	95.0	97.1	94.4	99.5
30	100.0	100.0	100.0	100.0

Pitelka, 1970). These studies demonstrated that rodents have an effect on the composition of grasslands, but this effect is insufficient to eliminate completely a grass species from the grassland.

Four species of rodents have been identified which may have an important effect on the two grasslands. *Microtus californicus* (California meadow vole) is a run-building species which forages on seeds and foliage. *Reithrodontomys megalotis* (harvest mouse) does not build runs but utilizes existing runs; and it, too, consumes seeds and foliage. The valley pocket gopher *(Thomomys bottae)* is a tunnel-building species which consumes foliage and roots. The bush rabbit *(Sylvilagus bachmani)* is an infrequent visitor to the grasslands and consumes grass foliage.

Several experiments were designed to ascertain the potential impact of rodents in the grasslands. The first experiment was a paired exclosure design to examine the total influence of seed foraging and grazing by rodents. The exclosure was constructed 1.2 m on a side from 6.4 mm (0.25 in) mesh hardware cloth. The exclosure margins were excavated so that the hardware cloth was buried to a depth of 25 cm in the soil and the remaining 50 cm were aboveground. To the top of the hardware cloth, a 20-cm width of aluminum flashing was attached. This design prevented the harvest mouse and meadow vole from tunneling beneath the exclosures, and the flashing prevented the harvest mouse from climbing the hardware cloth. The buried hardware cloth was ineffective in discouraging pocket gophers; however, their holes were filled to prevent other rodents from using their tunnels. Snap traps were used for the 1st year, but the exclosure proved to be effective and the traps were discontinued. The control for the exclosure is termed a false exclosure. It was constructed from the same materials as the exclosure but did not extend to the ground, and no excavation was made. This enabled rodents to pass into the false exclosure unobstructed. The exclosure and false exclosure constitute a pair, and two pairs were constructed for each grassland before the initiation of the 1972 growing season.

The effect of the exclosure was estimated after two growing seasons by the productivity sampling techniques previously described. Eight samples per exclosure were collected. In the exclosures of the perennial grassland, *Avena* spp. increased in frequency and in percent of the total sample weight as compared to the false exclosures (Table 3). There was a similar increase in *Bromus rigidus*. There was little or no change in the frequency or in the percent of total sample weight between the exclosures and false exclosures in the annual grassland.

To evaluate the potential effect of grazing on seedlings of *Avena fatua,* seeds were planted and marked with toothpicks in both grasslands. Ten plots with 20 seeds each were established after the first rain in the perennial and annual grasslands. These were carefully monitored at frequent intervals to establish possible causes of mortality (Table 4). The difference between the annual and perennial grasslands was pri-

marily the result of germination. The criterion for germination was initially the presence of a coleoptile, but after several weeks ungerminated seeds were removed and examined for radicle emergence. In the perennial grassland 45.0% of the seeds failed to show evidence of germination, while in the annual grassland 17.5% of the seeds failed to germinate. The difference was significant at the 95% confidence level. Most instances of grazing did not result in mortality. If all forms of mortality (excluding germination failure) are summed, there is no significant difference between the perennial grassland (14.5%) and the annual grassland (17.5%). Grazing was slightly greater in the annual grassland than in the perennial grassland.

Estimates of seed harvesting were done two ways. One was the establishment of seed caches in which 20 seeds each of *Bromus rigidus* and *Avena fatua* were placed on the top of soil held in a 15-cm glass petri dish. The dish was set into the ground so that the rim of the dish, and, therefore, the seeds, was flush with the surrounding soil. The litter was replaced. Twelve caches in each grassland were established in June for the summers of 1972 and 1973 and were collected before the first

TABLE 3.—Percent of total shoot weight and frequency for exclosures and for false exclosures from the two grasslands for each of the principal annual grass species

Location, species	False exclosure		Exclosure	
	% Total weight	Frequency	% Total weight	Frequency
Perennial grassland				
Avena spp.	0.4	6.3	10.3	50.0
Bromus rigidus	0.9	6.3	34.0	50.0
B. mollis	75.9	100.0	32.0	93.8
B. rubens	22.1	93.8	23.1	93.8
Annual grassland				
Avena spp.	94.2	100.0	95.4	100.0
B. rigidus	4.4	81.3	3.2	93.8
B. mollis	1.0	75.0	1.4	87.5
B. rubens	0.3	18.8	0.0	6.3

TABLE 4.—Incidence of grazing and fate of seeds of *A. fatua* as a percent of total seeds planted in the annual or perennial grasslands. Percent based upon 200 seeds planted per grassland

	Fate of seeds planted (%)					
	Germination	Survival	Seeds missing or destroyed	Unaccounted for[1]	Died	Seedlings grazed (%)
Annual	82.5	65.0	6.0	4.5	7.0	6.0
Perennial	55.0*	39.5*	6.0	2.0	7.5	2.5

* Significant difference between grasslands (within column) at P = 0.05

[1] Designates seeds for which identifying marker was destroyed.

rains in the autumn. All seeds which exhibited damage or were missing are listed (Table 5). The data indicate that foraging in the annual grassland was greater than in the perennial grassland.

The second method was the use of 5 × 10-cm glass plates to which seeds of *Avena fatua* and *Bromus rigidus* were affixed with a plastic tape. One hundred of these plates were placed in a 10-m sq grid in each grassland. The plates were placed in the grassland in the early morning and picked up 48 hr later. The dates of the experiments coincided with the dark phases of the moon from June to October 1972. These dates were chosen to standardize experimentation with respect to rodent activity and predator detection under different moonlight conditions. The perennial grassland had fewer total harvested seeds than the annual grassland (Table 6). *Avena fatua* was the preferred seed in the annual grassland.

ALLELOPATHY

Allelopathy, the term originally coined by Molisch (1937), has been suggested as an important factor in the dominance of vegetation (Muller, 1969). Allelopathy is defined as the process by which a plant releases into the environment a chemical compound which inhibits the growth of another plant in the same or a neighboring habitat (Muller, 1969). Many studies on the allelopathic potentials of plants have been published (Rice, 1974); however, comparatively little work has been published on allelopathy in grasslands.

TABLE 5.—Percent of seeds grazed or damaged for two species in seed cache experiments in the annual and perennial grasslands in 2 years. Values represent the means of 12 samples for each grassland

Year	*Avena fatua*		*Bromus rigidus*	
	Annual	Perennial	Annual	Perennial
1972	35.9	4.6**	9.2	3.1*
1973	17.9	8.3	29.6	4.6**

* Significant difference between grasslands within year and seed species at P = 0.05

** Significant difference between grasslands within year and seed species at P = 0.01

TABLE 6.—Forty-eight-hr seed plate experiments. Data represent the number of plates with missing or damaged seeds of *A. fatua* or *B. rigidus* for five samples in the annual and perennial grasslands

Month	*Avena fatua*		*Bromus rigidus*	
	Annual	Perennial	Annual	Perennial
June	1	3	2	5
July	6	0	0	0
August	4	1	0	0
September	11	0	0	0
October	5	0	0	0
	—	–	–	–
Total	27	4	2	5

The allelopathic capabilities of *Avena fatua* are described by Tinnin and Muller (1972). They demonstrated that *A. fatua* has a sufficient allelopathic potential to exclude several herb species from a grassland. The pattern which is described (Tinnin and Muller, 1971) is established after the first rains in the autumn. The toxins are released in the form of water-soluble phenolic acids which are leached from the straw by rain.

We proposed a working hypothesis that *Stipa pulchra* produces phytotoxins which affect *Avena fatua*. Our investigation examined three potential sources of phytotoxins: toxins from the straw, toxic decomposition products and toxic root exudates.

Straw phytotoxins.—The allelopathic potential of *Stipa pulchra* was examined using bioassay experiments in the laboratory and growth experiments in the greenhouse. Bioassay experiments are standardized techniques in which seeds are exposed to different treatments and the growth of radicles is compared. The technique most often used in this study was the standard sand bioassay. In this technique 50 g of river bottom sand, trapped between 1.00 and 0.25-mm mesh screens, are added to a 100 × 15-mm petri dish. Seeds of the test species are permitted to imbibe in the treatment solution for 2 hr prior to placement in the sand. Twenty seeds are added to a dish in a peripheral and circular pattern so that the radicles will grow toward the center of the dish. A normal sand bioassay design consists of four plates or 80 seeds per treatment. The sand is then moistened with 10 ml of the treatment solution, and the dish is sealed with parafilm and the petri dish cover. The treatments are placed in a dark growth chamber at 26 C for 48 hr after which time the elongation of each radicle is measured to the closest millimeter. Control treatment solutions are normally of glass-distilled water. Results of treatments were analyzed by the t-test or analysis of variance where appropriate.

The phytotoxic effect of the aqueous leachate of *Stipa pulchra* straw was determined by the standard sand bioassay. The aqueous leachate was prepared by adding 5 g of cut straw to 100 ml glass-distilled water and shaking for 30 min on a mechanical shaker. This extract was vacuum-filtered through Whatman #42 paper. The extract was then concentrated under vacuum at 37 C until it was one-fourth the original volume. Portions of this concentrated extract were then diluted 1:1 and 1:3 with glass-distilled water. This provided extracts of one, two and four times the original concentration (1X, 2X, 4X). Each of these solutions and a control of glass-distilled water constituted the various treatment solutions for the sand bioassay. Seeds of *Avena fatua* were used as the test species. Growth of *A. fatua* radicles in the 1X, 2X and 4X extract treatments was 89.3, 84.5 and 69.9% of control, respectively. There was no observed inhibition of germination. Growth in the 1X and 2X extract treatments was significantly ($P = 0.01$) reduced as compared to the control, but the two treatments were not significantly different from each other. The results of the 4X extract treat-

ments were significantly reduced when compared to all other treatments.

An experiment was designed to determine if the leachate from *Stipa pulchra* straw is concentrated in soil. A soil column was constructed of plastic tubing, 3.1 cm in inside diam, and cut into 2.5-cm segments. Successive segments were held together by collars so that the column would not leak, but could be divided into separate segments. The soil was held in the column with the use of cotton gauze covering the open end of the lowest segment. Two columns were filled with clay soil collected near the grasslands. To one column was added an excess of the 2X concentration of leachate prepared as above. To the second column was added an excess of glass-distilled water. The excess was collected after it percolated through the soil column, and was approximately one-half of the total amount added to the column. In the first experiment, the radicle elongation of seeds imbibed in the solutions passed through the soil columns was compared in sand bioassay to the elongation of radicles of seeds in the same solutions not passed through the soil columns. There was no significant reduction in the toxicity of the leachate when comparing the 2X straw leachate to the 2X leachate after passing through a soil column.

In the second experiment, the soil column was divided into halves after the 2X leachate or water treatments passed through. To the 0-5 and 5-10 cm segments was added 90 ml of glass-distilled water and this was placed on a mechanical shaker for 30 min, decanted and centrifuged at 3200 rpm for 30 min. This solution was then vacuum-filtered through Whatman #42 filter paper. If we assume no adsorption in the soil column, this method corresponded to a dilution of the 2X leachate at ratio of 1:1. The four solutions were then compared in a standard sand bioassay against a control of glass-distilled water. The results indicate a reduction in test over the control for that segment of the soil column, but the differences were not significant at $P = 0.05$.

The effect of *Stipa pulchra* straw on the growth of *Avena fatua* in the greenhouse was tested to determine if the phytotoxic potential of the straw is continued after seed germination and radicle elongation. Straw of *S. pulchra* was cut into segments 2-3 cm long, and 5 g of this material placed on top of pots filled with sand. The controls consisted of the addition of spongerock to the same depth as that of the straw. In each pot six *A. fatua* seeds were planted. The pots were sprayed from above with a 0.25-strength Hoagland's solution as needed. After 1 week each pot was thinned to the four largest individuals. The experiment lasted 36 days after which time the shoots were cut at soil level, dried at 70 C for 48 hr and weighed. The experiment was duplicated, and the percent reduction in both experiments is approximately the same (91.0 and 91.1%). Only in the second experiment, however, was the reduction significant ($P = 0.05$).

Decomposition products.—Patrick and Koch (1958) presented evidence that if the organic material tested was allowed to decompose in

the presence of soil, a phytotoxic chemical is released. To test this possibility for *Stipa pulchra* straw, soils were collected from a perennial grassland. One cm of sand was added to six plastic trays with holes to provide drainage. Each tray measured 27.5 × 19.0 × 6.5 cm. To these trays 2.0 cm of soil passed through a 2.0-mm mesh screen was added. These trays were then divided into three treatments of two trays each. The first treatment was the addition of 25 g cut straw to the top of the soil. The second treatment consisted of mixing 25 g of straw in the soil. The third treatment consisted of a control to which no straw was added. These trays were watered with a mist sprayer at frequent intervals and were stored in the dark at room temperature. One tray in each treatment was analyzed for toxicity after 15 days and the second after 47 days. For analysis, the soil was removed from the trays and dried until it could be passed through a 2-mm screen to remove the decaying straw. To four petri dishes for each treatment were added 50 g of the moist soil and 5 ml of glass-distilled water. The toxicity of each soil treatment was then analyzed in soil in a manner similar to a sand bioassay (Gliessman and Muller, 1972). There was no significant reduction ($P = 0.05$) in radicle elongation or germination for seeds subjected to any straw treatment or period of incubation.

Phytotoxic root exudates.—A third possible mode of phytotoxic influence on *Avena fatua* is through exudations from the living roots of *Stipa pulchra.* Naqvi (1969) found that toxic phenolic acids are exuded by living roots of *Lolium multiflorum,* and Martin (1957) found that *Avena sativa* exuded a toxin (scopoletin) from root tips. For *S. pulchra* this possibility was examined through several types of experiments. In the first experiment, the roots of *S. pulchra,* actively growing in five pots of sand in the greenhouse, were leached over a 3-hr period with 0.25-strength Hoagland's solution. The control treatment consisted of the 0.25-strength Hoagland's solution which was not leached through pots. The treatment solutions were then filtered through Whatman #42 filter paper and concentrated four times under vacuum at 28 C. The *p*H of each solution was adjusted to 6.9 with the addition of small amounts of NaOH or HCl. The treatment solutions were tested against *A. fatua* in a standard sand bioassay. There was no inhibition in germination. The elongation of *A. fatua* radicles treated with the concentrated leachate solution was 102% of the control and was not significantly different from control.

The effect of possible root exudates on the growth of *Avena fatua* was tested in a greenhouse experiment. An excess of solution was added three times weekly to 10 pots of *Stipa pulchra* growing in sand, and the leachate was collected beneath the pots. The first leaching in each week utilized 0.5-strength Hoagland's solution, and subsequent leachings were with deionized water only. The leachate was added to each of 10 pots. The control consisted of the same additions which had not been leached through pots. Levels of mineral nitrogen and phosphorus were monitored in the leachates, and additions of $Ca(NO_3)_2$ and

KH_2PO_4 were made to equalize nutrient concentrations between the test and control solutions. In each pot six seeds of *A. fatua* were planted, and these were thinned to the four largest individuals after 1 week. After 40 days the *A. fatua* were cut at soil level, dried at 70 C for 48 hr and weighed. The mean dry weight of the leachate treatment was 79% of the control, a significant reduction at $P = 0.05$. A repetition of this experiment provided similar results.

A third experiment was designed to evaluate the phytotoxic potential of *Stipa pulchra* on *Avena fatua* when both species were growing in the same pot. For this experiment, 32 6-inch (15.2-cm) pots were divided into two groups. For the first group, nursery stock soil (a sandy loam) was added to each pot in a plastic bag which was carefully extended to be flush with the interior of the pot. For the second group, an equal weight of the same soil was halved and each half placed in a plastic bag. The two bags of soil were placed in each pot so that the volumes were identical in shape; therefore, the soil volumes of the two groups were exactly the same, but the second group had that volume divided into two identical portions by the plastic bags. The plastic bags were punctured at the bottom to allow drainage. To one half of each of these groups was added an aluminum partition which extended from the soil surface to 45 cm above soil level. The partition was on the same diameter as the separation of soil volumes. Figure 4A presents a diagrammatic view of the soil volume separation, and Fig. 4B shows

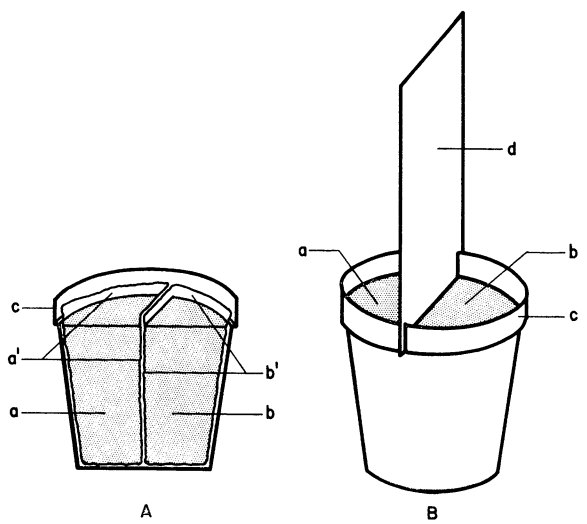

Fig. 4.—Diagrammatic representation of pots with root or shoot separation. Fig. 4A is a cutaway diagram of the pot (c) with the root separation treatment. The two soil volumes, a and b, are held in plastic bags, a′ and b′. Fig. 4B is a diagram of the pot (c) with the shoot separation treatment. The two aerial portions of the pot, a and b, are separated by the partition, d

the shoot partition. The resultant treatment pots were as follows: I, Separation of roots and shoots (Full); II, separation of shoots only (Shoot); III, separation of roots only (Root); and IV, no separation (None). For each of these four treatment types there were a test and control. The test consisted of a pot with *S. pulchra* growing in one half of the pot and *A. fatua* in the other half. The corresponding control consisted of *A. fatua* in one half of the pot and the absence of *S. pulchra* in the other half of the pot. Each of the *S. pulchra* clones consisted of 7-8 active growth points, and each was started about 3 months prior to the initiation of the experiment. For the effect of *S. pulchra* on the growth of *A. fatua,* six seeds of the latter were planted per pot, and these were thinned to four after 1 week. Full-strength Hoagland's solution was added to each pot at the initiation of the experiment and after 17 days. Otherwise, the pots were watered with deionized water as needed. The pots were randomly arranged on a slowly rotating turntable so that the diameter of the separation was parallel to the radius of the turntable. After 41 days the shoots of *A. fatua* were cut at soil level, dried at 70 C for 48 hr and weighed.

The mean dry weight of *Avena fatua* shoots, grown in test with its roots intermingled with those of *Stipa pulchra* and no shoot separation (None), was significantly reduced ($P = 0.01$) when compared with its corresponding control (Fig. 5). A similar reduction resulted when the

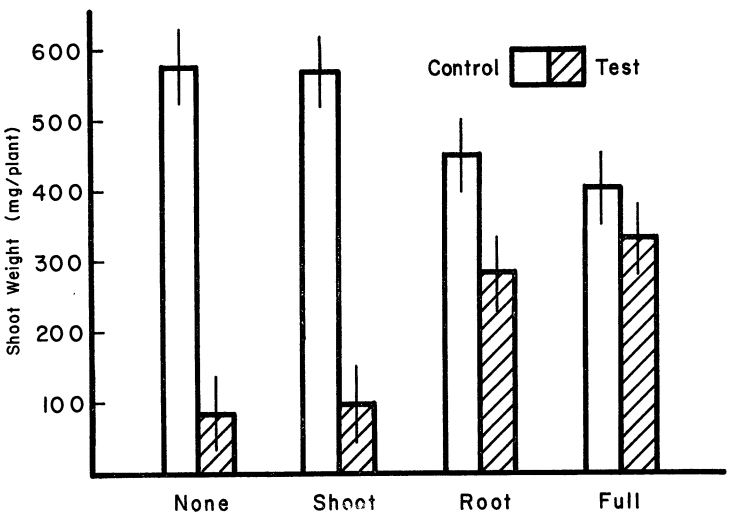

Fig. 5.—Mean dry weight (mg) of *A. fatua* shoots when grown in pots with various forms of separation from the roots and shoots of *S. pulchra:* full separation (Full), root separation (Root), shoot separation (Shoot) and no separation (None). The open histograms are the control treatments, and the hatched histograms are the test treatments. The vertical bars within the histograms represent the confidence limits of the sampling means at $P = 0.01$

roots of the two species were intermingled but the shoots were separated (Shoot). The mean dry shoot weight of *A. fatua* for the treatments with the intermingling of roots (None and Shoot) was 17.2 and 14.7% of the corresponding controls. There was a significant reduction of the mean dry weight when comparing the control treatments of the full soil volume (None and Shoot) to the control treatments of half soil volume (Root and Full). There was no significant effect of the partition on the growth of control treatment in either soil volume. There was a significant reduction of growth of test treatment as compared to control when the roots were separated, but the shoots were intermingled (Root).

DISCUSSION

The analysis of the vegetation demonstrated a considerable difference between the two grasslands with respect to the composition of the annual grass components. *Avena fatua* was abundant in the annual grassland, but conspicuously less abundant in the perennial grassland. The three brome species, *Bromus rigidus, B. mollis* and *B. rubens,* replaced *A. fatua* between the clones of *Stipa pulchra* in the perennial grassland. McNaughton (1968), Robinson (1968) and White (1966, 1967) suggest that *B. mollis* is more abundant when found with *S. pulchra,* and from their data *A. fatua* appears to be reduced in importance. Their data agree with the results of the vegetation analysis in this study. In other areas of Santa Barbara County, *Festuca megalura* may replace *B. mollis* in importance in areas dominated by *S. pulchra,* but the reduction of *A. fatua* is still evident. All of these studies have been in the coastal valleys of California. Further study would be required to determine if this pattern is maintained in interior valleys of California where *S. pulchra* may have reestablished.

Soil moisture.—Levels of available soil moisture were similar or greater in the perennial grassland than in the annual grassland. This agrees with Robinson (1968) and White (1967). The data suggest that the annual species, and not the perennial species, are responsible for the rapid depletion of available water. With a decrease in the total cover of the annual species per unit area of the perennial grassland, there is a decreased utilization of soil moisture which results in moisture available later in the growing season. In addition, the delayed initiation of foliar growth and the deeper rooting depth of *Stipa pulchra* decrease the capability of the perennial to reduce the levels of available soil moisture at the surface where the annual grasses are rooted. A hypothesis for the reduction of *Avena fatua* in the perennial grassland as a result of moisture depletion by *S. pulchra* is untenable.

Soil mineral nutrients.—The suggestion that soil mineral nutrients are limiting to growth in California grassland soils is not new (Love, 1952). Rossiter (1966) reviewed the literature on deficiencies of potassium, nitrogen, phosphorus and sulfur in the annual-type pasture. Jenny *et al.* (1950) found that in California 56% of the older alluvial

soils and 71% of the claypan soils tested were deficient in available nitrogen and phosphorus. A fertilization experiment in the same grasslands examined in this study indicated that there was a soil nutrient deficiency (Hull and Muller, 1976). In that study the addition of a complete fertilizer to the soils of both grasslands elicited an increase in the mean dry weight of the annual grass species present. The results indicated that although *Avena fatua* increased in mean dry weight, this increase was not as great as that of *Bromus rigidus, B. mollis* and *B. rubens*. The authors suggested that each of the species responded differentially to the addition of fertilizer.

In a soil such as that under study, which is described as calcareous (Carpenter *et al.,* 1927), the availability of divalent cations, most notably calcium and magnesium, is generally high. This is reflected by the relatively high level of exchangeable divalent cations (Table 1). The soil *p*H (Table 1) was in a range which is favorable for the availability of essential soil nutrients. The levels of soil organic matter (Table 1) and organic nitrogen are characteristic of grassland soils (Brady, 1974).

The greenhouse experiment in which essential soil nutrients were selectively withheld from nutrient solutions added to field soil indicated that nitrogen and sulfur, but not potassium and phosphorus, limited growth of *Avena fatua*. Comparisons of the growth responses of *A. fatua* with respect to available nitrogen and sulfur in the greenhouse (Fig. 3) and comparisons of the levels of these two nutrients in the field soil (Table 1) indicate that these elements are not more limiting in the perennial grassland soil than in the annual grassland soil. When levels of mineral nutrients are demonstrated to be limiting to growth in a soil, competition for that supply of nutrients is axiomatic. Interspecific or intraspecific competition for a limited resource cannot be separated by field measurements of the levels of that resource. However, if a species is to reduce the level of a resource below the tolerance of another species, some competitive advantage must be held by the first species. Harris (1967) documents such a competitive advantage of *Bromus tectorum* over *Agropyron spicatum* for available soil moisture. *Stipa pulchra*, with its deeper root system and temperature-delayed initiation of growth, demonstrates no such competitive advantage over *A. fatua*. In addition, there is no evidence that the levels of the limiting nutrients are decreased below those levels that *A. fatua* tolerates in the annual grassland. These data do not support a hypothesis of exclusion of *A. fatua* by *S. pulchra* through competition for mineral nutrients.

Animal activity.—In combining the results of the various experiments to estimate the impact of animals on *Avena fatua* in the perennial grassland, a contradiction is apparent between the results of the exclosure experiment and those of the seed and seedling grazing experiments. Observations indicated that disturbance resulting from excavation in the installation of the exclosures altered the soil environment

and may have brought dormant *A. fatua* seeds to the surface. Thurston (1962) has documented that seeds of *A. fatua* can survive burial for several years, and Major and Pyott (1966) have identified 7-year-old viable seed of *A. fatua* from field collections. The results of the other experiments fail to corroborate the results of the exclosure experiment. This suggests that disturbance, rather than lack of rodents, may have caused the increased density of *A. fatua* in the exclosures. Marshall and Jain (1970) presented evidence for low levels of animal harvesting of seeds of *A. fatua* and *A. barbata*. Batzli and Pitelka (1970) conversely presented data indicating that *Microtus californicus* harvested large numbers of seeds of *A. fatua* and *Bromus rigidus,* and they suggested that a large change in the standing crop of grasses occurred when the *Microtus* population was high.

The seedling grazing experiment (Table 4), the seed cache experiment (Table 5) and the seed plate experiment (Table 6) demonstrated that levels of animal activity were not greater in the perennial grassland than in the annual grassland. No distinction can be made between rodents and any other animal that might be consuming seeds or plants on the basis of these data. The data, however, do not support a hypothesis that the maintenance of the observed vegetational pattern is caused by animal activity. The duration of this study must be considered in the interpretation of these results. There are no data with which to estimate the impact of animals in the original establishment of the pattern of exclusion of *Avena fatua* from the perennial grassland.

Light.—To support a hypothesis of competition by *Stipa pulchra* with *Avena fatua* for photosynthetically active light, the data should reflect a diminution of that resource below the tolerance of *A. fatua*. Robinson (1968) presented evidence that *A. fatua* and *S. pulchra* had similar photosynthetic rates at two light intensities and three temperatures. This suggests that both species have similar tolerances to light reduction. Light, as measured in the spaces between the clones of *Stipa pulchra,* showed no diminution below that tolerated in the annual grassland (Table 2). Light was diminished by the presence of the annual species as the soil was approached. In the perennial grassland the annual species were lower in stature than in the annual grassland; therefore, a higher proportion of sunlight penetrated into the spaces available for growth of annual species. These data do not support the hypothesis of competition for light by *S. pulchra*.

Allelopathy.—Aqueous leachates of straw of *Stipa pulchra* produced significant reductions in growth of *Avena fatua* as compared to control in both bioassay and greenhouse experiments. These reductions were relatively small as compared to control, and no inhibition of germination was observed. Similar experiments by other workers on different phytotoxic sources and test species have indicated substantially greater inhibitions in growth (Tinnin and Muller, 1972; Chou and Muller, 1972; Gliessman and Muller, 1972). The quantities of straw used in these experiments are difficult to compare with those in the field be-

cause, under field conditions, the lodging of straw creates an uneven pattern of distribution.

Growth of plants in bioassay media or in the greenhouse is much accelerated over that under field conditions. In the field, obvious signs of germination occur a week to 10 days after the first autumn rains. In the laboratory, however, the same signs of germination are observed within 48 hr. The differences are primarily related to temperature. Laboratory temperatures are optimal for growth, whereas field temperatures are low. The relationship between a low level of phytotoxic effect and low temperatures is not fully understood. A small reduction in respiration and growth resulting from low temperatures could be intensified by phytotoxins, and this, potentially, could reduce the success of a species under field conditions.

The possibility that the phytotoxins from *Stipa pulchra* are concentrated in the soil was not substantiated by the soil column experiment. In this case the concentrating effect due to differential adsorption in heavy soil suggested by del Moral and Muller (1970) was not supported by laboratory results. However, this does not negate the possibility that undisturbed soil might, to a greater extent, concentrate plant toxins under field conditions. In the field the bulk density of the soil is greater, resulting in slower percolation rates, and the application of leachate is slower and much longer in duration. This combination could result in a somewhat higher adsorption of toxic materials.

The thesis that microbial decomposition of straw of *Stipa pulchra* adds phytotoxins to field soil was not substantiated by laboratory experiments. Field observations indicated that the accumulation of litter in the annual grassland was greater than in the perennial grassland. The difference may be related to an intrinsic difference between the types of litter, or it may be the result of increased microbial activity in the perennial grassland. The importance of microbial activity as it relates to straw type and effects on establishment of annual grass species needs further study.

The importance of root exudates produced by *Stipa pulchra* is evidenced in greenhouse experiments. These were not corroborated by bioassay experiments in which there was neither reduction of radicle elongation nor inhibition of germination. Evaluation of the greenhouse results must include consideration of the habit and phenology of the two species. In experiments where the roots of *Avena fatua* and *S. pulchra* are confined to the same volume held by a 6-inch pot, there may be an intermingling of roots in excess of that in the field. This is especially important in view of the shallow nature of the roots of *A. fatua* and the deeper roots of *S. pulchra*. Probably a more important consideration is that the *S. pulchra* plants were grown in the pots under greenhouse conditions for 3 months prior to the initiation of the experiment. In the field, active shoot growth of *S. pulchra* follows the initiation of growth of *A. fatua* by about 2 months. Interpretation of the results of the root exudate experiments necessitates an understand-

ing of the physiological condition of the roots of *S. pulchra* following the first rains and before shoot growth. It is not known if roots of *S. pulchra* are capable of releasing a phytotoxic exudate before active growth of the shoots. The phytotoxins may be retained in the soil over the dry summer months and their toxicity expressed in the autumn. This has been shown to be a mechanism of interaction in the case of volatilized terpenes from *Salvia leucophylla* shrubs on the same soil type (Muller, 1966). The potential for soils to retain water-soluble phytotoxins is not known.

In general, the phytotoxic potential of *Stipa pulchra* is limited and somewhat dependent upon unknown parameters in the soil. The importance of slight reduction in growth of a species susceptible to the phytotoxins cannot be dismissed. Any factor which reduces the ability of a species to grow may predispose it to some pathogen or other vicissitude of the environment in which it is found.

CONCLUSIONS

Examination of the data provides two potential factors, phytotoxins and nitrogen availability, which have the potential for limiting growth. Available nitrogen, although present in quantities limiting to growth of *Avena fatua* in the perennial grassland, is not more reduced in the perennial grassland soil than in the annual grassland soil. Logically, available nitrogen could not be the sole factor limiting the growth of *A. fatua* in the perennial grassland. This statement, however, assumes that *A. fatua* has the same potential to occupy a soil volume. One probable effect of a soil-borne phytotoxin is to reduce the rooting volume of *A. fatua.* This reduced volume would necessarily reduce the total amount of nitrogen available to the plant. In this manner, the effect of phytotoxins produced by *Stipa pulchra* may act synergistically with a limited supply of nitrogen to reduce the growth of *A. fatua.*

This study has examined exclusively the potential of *Stipa pulchra* to exclude *Avena fatua* from the perennial grassland. The combined impact of the associated species has not been considered. Because of the association of *S. pulchra* with the several brome species, the examination of the physical environment has included the reaction of these annual grasses upon the environment of the perennial grassland. Therefore, discussions of the availability of nutrients, light and moisture, and the activity of animals have tacitly included the effect of the brome species. A consideration of the grassland as a whole must include the reactions of these species. The allelopathic potential of each of the brome species toward *A. fatua* has not yet been determined.

Although this study investigated an existing pattern in which *Avena fatua* was excluded, it is reasonable to suggest that the mechanism of maintenance is related to the mechanism of establishment of the pattern. That is, the mechanism by which reinvasion of *A. fatua* is prevented is similar to the mechanism by which *A. fatua* was originally excluded from the grassland. Observation has indicated that the inva-

sion of *Stipa pulchra* occurred in annual grasslands dominated by both *A. fatua* and *Bromus rigidus*. This is supported by White's (1966) statement that *S. pulchra* increased in old fields having different annual vegetation. White (1966) also implied that the establishment of a grassland dominated by *S. pulchra* takes 15-20 years. Concomitant with the attainment of dominance of *S. pulchra* is a diminution of importance of *A. fatua* and an increase in importance of the brome species. This change in the composition of the annual grass species is related to the effect of *S. pulchra* on *A. fatua*. *Avena fatua* has been shown to be allelopathic toward *B. rigidus* (Tinnin and Muller, 1972), and the reduction of the former may result in an increase in the brome species. The mechanism by which *A. fatua* prevents the invasion of *S. pulchra* in large areas where grazing has been reduced requires further study.

In summary, the exclusion of *Avena fatua* from a perennial grassland dominated by *Stipa pulchra* is probably the result of a complex synergistic relationship between low levels of available nitrogen and a phytotoxin produced by *S. pulchra*. The presence of other annual grasses in the perennial grassland contributes to the complexity of the mechanism.

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