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THE ECOLOGICAL STATUS OF STIPA PULCHRA (POACEAE) IN CALIFORNIA

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ABSTRACT

We present information clarifying the past and present role of the native perennial grass *Stipa pulchra* in the California grassland. *Stipa pulchra* occupies a diverse array of habitats in northern and central California, as shown from information collected on more than 1500 plots by the State Cooperative Soil-Vegetation Survey. *Stipa pulchra* did not increase in density over a 20-year period in ungrazed areas on the Hopland Field Station in northern California and was replaced by other perennial grasses and annuals on some plots. *Stipa pulchra* germinated more slowly than associated annual plants and *S. pulchra* seedlings apparently did not survive the period of rapid spring growth in annual grassland. In pot trials fewer *S. pulchra* germinated and plants grew poorly when grown with high densities of *Bromus mollis* and *Festuca megalaria*. High densities of *B. mollis* limited *S. pulchra* growth more dramatically than high densities of *F. megalaria*. We suggest that *S. pulchra* is the most common California native grass not because the species dominated the original California grassland, but because it is favored by disturbances common now. Disturbances that reduce associated annuals are important for colonization by *S. pulchra*.

Stipa pulchra Hitchc. has long been regarded as the most important perennial species of the California grassland. Because *S. pulchra* is the most common native grass now, it has often been assumed to have dominated the pristine grassland. Yet progress towards understanding the historical role of native species has been slow, primarily due to the lack of overlap between the destruction of California's grasslands and the arrival of scientific observers of vegetation. The introduction of domestic livestock and alien plant species of Mediterranean origin beginning in 1769 completely changed the grassland flora (Burcham, 1957). Early records do not document the change adequately, but today few grassland areas are dominated by native plants (Barry, 1972) and even locations with numerous native species contain large numbers of alien plants (Heady, 1977).

Because of the complete alteration of the vegetation, with introduction of essentially a new flora, ecologists must rely on circumstantial evidence and inference to a large degree when reconstructing the original grassland. Early explorers occasionally referred to the presence of bunchgrasses (Burcham, 1957), and the distribution of native

species of perennial grasses follows closely the extent of the present grassland (Beetle, 1947), although stands are widely scattered.

Clements (1920) called the *Stipa setigera* (synonym for *S. pulchra*) consociation a part of the *Agropyrum* (sic)-*Stipa* Association. Clements based his classification on stands of bunchgrasses along fenced railroad rights of way. Although *S. pulchra* is favored by frequent fires, such as would have occurred along railroad tracks (Biswell, 1956), Clements' designation of the climax California prairie as a perennial grassland has been accepted with little modification (Munz and Keck, 1949; Barry, 1972; Baker, 1976; Küchler, 1977; Heady, 1977) and surprisingly little additional evidence.

Observations of vegetational change in protected California grassland yield inconsistent results. Succession after elimination of livestock grazing often shows the return of perennial grasses, particularly near the coast (Heady, 1977). Yet many areas have not returned to perennials even after decades of protection (White, 1967). Disturbance such as fire and some seasonal grazing patterns favor *S. pulchra*.

Experimental work with *S. pulchra* has yielded limited results applicable to observed patterns of vegetation. Robinson (1968) concluded that clay soils and abundant soil nitrogen favored *S. pulchra* in the central coast. Yet most areas remained dominated by annual grasses. Hull and Muller (1977) investigated the causes of the replacement of *Avena* grassland by *S. pulchra* following a change from cattle to horses and an alteration of grazing patterns in the south coast. Hull and Muller strongly implicated an allelopathic component that altered the associated annual flora when *S. pulchra* became dominant. Saville (1977) found that stands of *S. pulchra* in northern California included an understory of *Festuca megalura*, whereas adjacent areas with similar soil were dominated by *Bromus* spp. Saville found striking differences in decomposition and productivity in adjacent perennial and annual grasslands.

Arthur Sampson, California's first range plant ecologist, intensively investigated *S. pulchra* in the late 1920's and 1930's (Sampson and McCarty, 1930). His objectives centered around evaluation of native perennial grasses as forage for livestock. Unfortunately, the native bunchgrasses proved not only difficult to manage but less productive under grazing than the introduced annuals which had replaced them (Green and Bentley, 1957). Thus range improvement research shifted to non-native perennial species. Yet rangeland management has matured from a narrow, livestock centered discipline, into a broader science concerned less with a single product than a class of land. Restoration of native vegetation, including grasses, is now again a logical goal on many rangelands such as nature preserves and areas needing low-maintenance landscaping.

Heady (1977) summarizes the current attitude of vegetation ecologists towards this species: "*Stipa pulchra*, beyond all doubt, dominated

the valley grassland." *Stipa pulchra* is found on a wide variety of soil types, slopes and habitats (Barry, 1972), often with a different group of associated annuals than adjacent grassland without perennial grasses. Although grazing contributed to the decline of the native perennials, removal of grazing does not necessarily result in the return of perennial species, and never in the elimination of introduced annuals.

In this article we examine the present occurrence of *S. pulchra* in northern California and present information collected over a period of 20 years in a protected area. We next look at field patterns of establishment and mortality, and finally report results of studies investigating the interactions of seedlings of *S. pulchra* and introduced annuals. Our objective is to use these diverse data to help clarify the past and present role of *S. pulchra* in the California grassland.

METHODS AND RESULTS

Soil-vegetation survey plots. The State Cooperative Soil-Vegetation Survey has mapped soils and associated vegetation in California since 1947. Shortly after the establishment of the survey, personnel began inventorying understory vegetation. Acre plots were established in selected locations for intensive sampling. More than 1500 plots have now been located, primarily in the North Coast and the foothills of the Sacramento Valley. Of primary interest are data from a listing of all herbaceous species present on the plot and from a step-point sample taken if herbaceous cover exceeded 5 percent. In conjunction with the sampled soils and other environmental information, this set of plots forms a valuable resource for examining plant distribution.

Of the 1517 total type-acre plots available, 51 recorded the presence of *S. pulchra* (Fig. 1). These plots were examined to establish the types of habitat favoring *S. pulchra*. Because of the very large number of plots involved, the sample forms an extensive survey of the types of habitat occupied by *S. pulchra* in the North Coast and the Sacramento Valley. Rather than being restricted, *S. pulchra* occupies a wide diversity of habitats, particularly in the Sacramento Valley. On the 51 plots, *S. pulchra* varied in density from a trace to 8 percent cover and occurred on 33 different soil series at elevations from 30 to 890 m. It was found on plots with annual precipitation ranging from 56 to 127 cm with a single stand at 190 cm rainfall. Although more common on southerly slopes than on northerly slopes (73 versus 27 percent), all slope aspects were represented. *Stipa pulchra* most commonly occurred on plots with less than 5 percent woody cover. Plots with more than 50 percent canopy cover contained little *S. pulchra*, and no plants appeared on plots with more than 80 percent woody cover.

Permanent transects. Shortly following the establishment of the Hopland Field Station in Mendocino County 180 km north of San

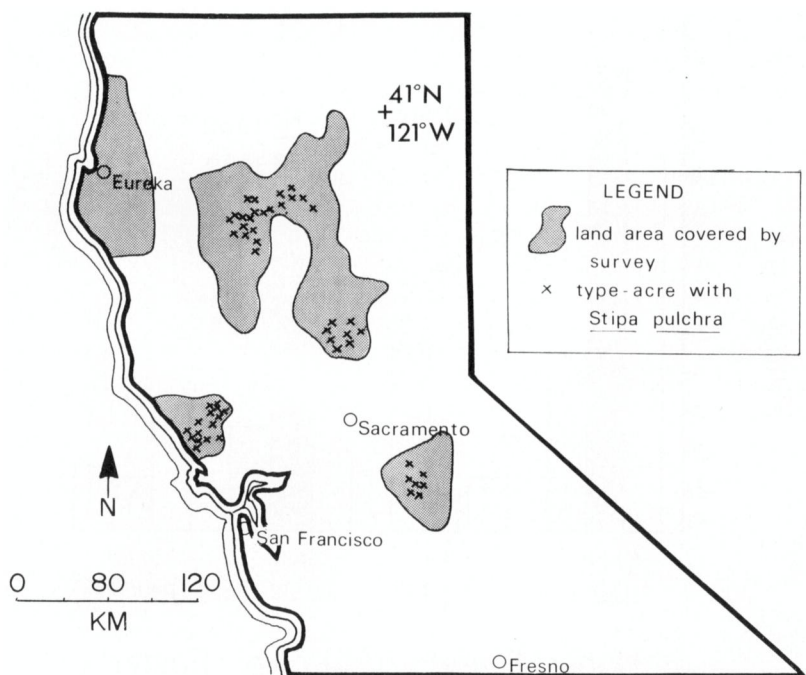


FIG. 1. Location of type-acre plots containing *Stipa pulchra*. Of 1517 acre-square plots established by the Soil-Vegetation Survey, 51 contained identified *S. pulchra* between trace and 8 percent cover.

Francisco, the University of California designated two "Biological Areas" to be excluded from grazing by domestic livestock. The areas were set aside in 1956 in pastures formerly heavily used by sheep. Biological areas on the Hopland Field Station are located in oak woodland/grass vegetation typical of the valleys of the North Coast Ranges. With a Mediterranean climate, the area has dry and warm summers, cool and wet winters. The Foster Biological Area is located at an elevation of about 300 m and receives an average of 95 cm annual precipitation. The Riley Biological Area averages 700 m in elevation, with 120 cm mean annual precipitation.

In 1958, two years after the establishment of the Biological Areas, 24 permanently marked, 30-m transects were established to monitor changes in perennial grass density. The transects formed four clusters composed of three transects each, replicated in each Biological Area. Within each Biological Area two clusters were located within woodland canopy cover, and two in open grassland. Transects were all on similar soils. Along the transect within a belt extending 0.76 m on either side, all perennial grasses were tallied by species. Sampling of

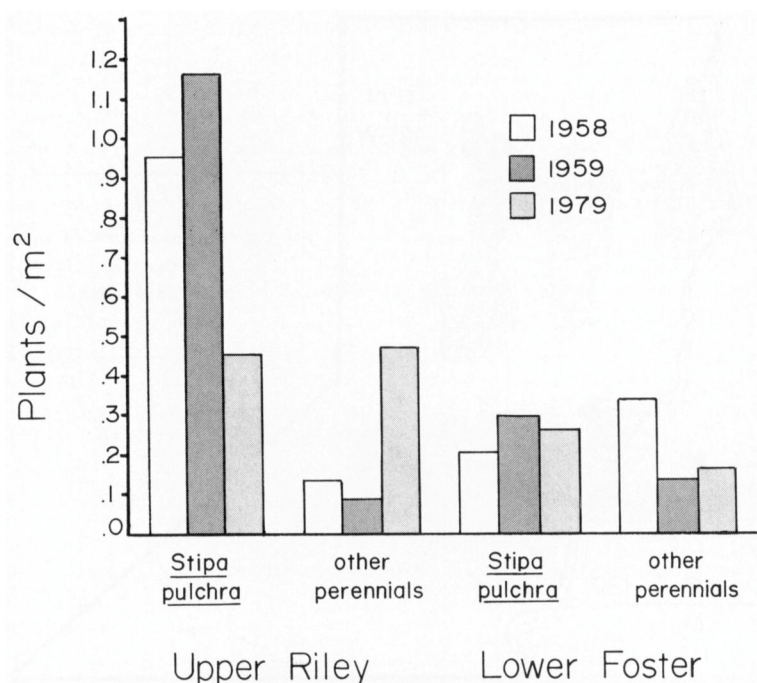


FIG. 2. Perennial grass species density on permanent transects on three sample dates. Transects were located at Hopland Field Station, Mendocino County in two "Biological Areas" ungrazed by livestock since 1956.

the transects was repeated in late summer of 1959 and 1979. An intensive search failed to relocate one transect cluster in the Foster area in 1979.

Numbers of perennial grasses varied widely between transects and even between clusters. This variability, coupled with systematic arrangement of the plots, precludes statistically supported conclusions concerning the differences between sample dates. However, because the plots are permanent, and thus represent repeated measures of the same spot, conclusions still have validity.

The higher-elevation plots in the Riley area contained greater densities of *S. pulchra* and other perennial species than the lower-elevation Foster plots (Fig. 2). Densities averaged 1.07 plants/m² on the upper transects and 0.37 plants/m² on the lower.

The differences between 1958 and 1959 are generally minor with the exception of a decrease in perennial species other than *S. pulchra* on the lower area. *Melica* spp. decreased from 0.17 to 0.09 plants/m² and *Danthonia californica* decreased from 0.07 to zero plants/m² on

the lower area. *Stipa pulchra* remained at nearly the same density. Between 1959 and 1979, density of *S. pulchra* changed little on the lower Foster area, even after more than 20 years without livestock.

On the upper Riley area *S. pulchra* declined in density between 1959 and 1979 (Fig. 2), while other perennial grasses, most notably *Elymus glaucus*, increased. Total perennial density changed little, with the exception of one cluster. On that cluster, in the absence of sheep grazing, the formerly abundant *S. pulchra* plants have been reduced from 2.18 to 0.05 plants/m², and have been replaced by the annuals *Carduus pycnocephalus* and *Taeniatherum asperum*.

Stipa pulchra was found both within the woodland zone and in the open grassland, although open areas contained more abundant *S. pulchra*. *Elymus glaucus* tended to occur more frequently under oak canopy, although it was also found in small numbers in open grassland. The perennial grass vegetation has changed little between 1959 and 1979, without a consistent increase of *S. pulchra*. In the Riley area other perennial grasses replaced *S. pulchra* between 1959 and 1979.

Germination, establishment, and mortality in the field. In conjunction with a study of the population dynamics of annual grassland reported elsewhere (Bartolome, 1979), field observations were made of the behavior of *S. pulchra* seedlings at the Hopland Field Station. At weekly intervals through the fall and biweekly throughout the 1974–1975 growing season, the composition of the grassland was determined. Sampling consisted of 125 6.45-cm² samples of soil taken on each sample date with attached plants on which all species were counted. Germinable seed in soil samples was also determined before the fall rains, during the first six weeks of the fall, and twice in spring. The plot had been ungrazed by livestock since 1958 and used for evaluation of the effects of removal of varying amounts of natural mulch. Initially dominated by introduced annuals, *S. pulchra* increased on the plot in the first few years following the initiation of treatment, then remained stable.

Although *S. pulchra* seedlings were relatively few, several conclusions may be drawn. First, *S. pulchra* may germinate more slowly than the associated annual species and did not reach a peak density until well into the fall growing season (Fig. 3). However, the absence of germinable seed after the second week of the season precludes a definitive conclusion. Introduced annuals reach near-maximum density within the first six weeks of the season (Bartolome, 1979). *Stipa pulchra* densities fall rapidly as a result of mortality during the initiation of rapid spring growth by the associated annuals. The drop in *S. pulchra* density in the spring contrasts to the annual species which suffer little mortality during the rapid growth period (Heady, 1958). No *S. pulchra* seedlings occurred in samples after April.

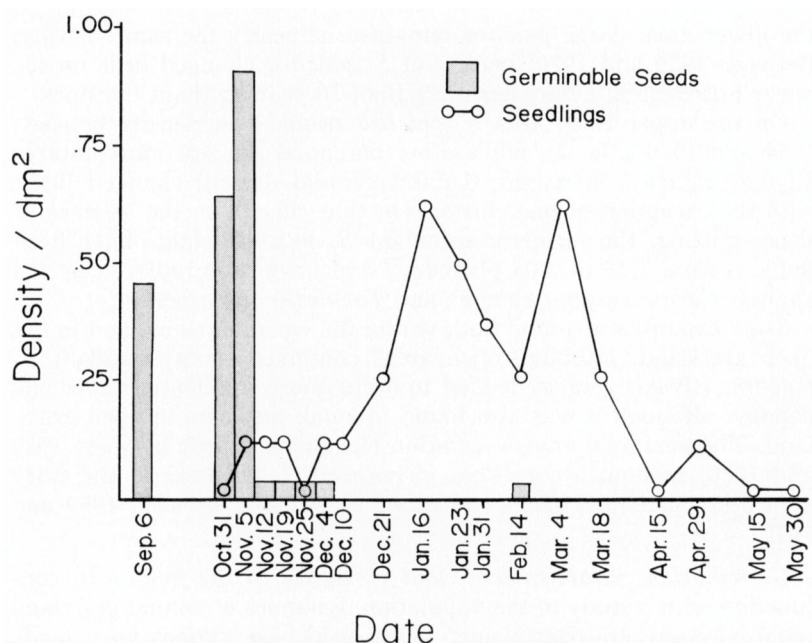


FIG. 3. Number of *Stipa pulchra* seedlings and germinable seeds in a sample of 125 6.45 cm² plots at the Hopland Field Station, Mendocino County during the 1974–1975 growing season.

Species interactions. Because annual plant density was high on the study plot, as it generally is wherever *Stipa* is observed, further investigation of the interaction of *S. pulchra* with annual species was initiated. Regardless of the historical role of *S. pulchra* in the pristine native grassland, today a major factor in its persistence is the nature of interactions with the introduced annual grasses. The key period for observing such interactions would be during germination and seedling establishment. Poor early germination or growth would precipitate later spring mortality. We examined *S. pulchra* in two pot experiments, one growing *S. pulchra* alone and the second in combination with annual grasses.

In both experiments, *S. pulchra* seeds were sown in plastic pots 14.6 cm in diameter. Pots were divided into blocks consisting of seeds gathered from three different locations (two coastal and one inland valley site). Cultures were grown at Oxford Tract at the University of California, Berkeley. The first experiment was conducted indoors in a greenhouse from 30 January to 30 March 1978. The interspecific experiment matured outdoors on benches from 30 May to 30 July 1978. In both experiments, observations were taken most frequently

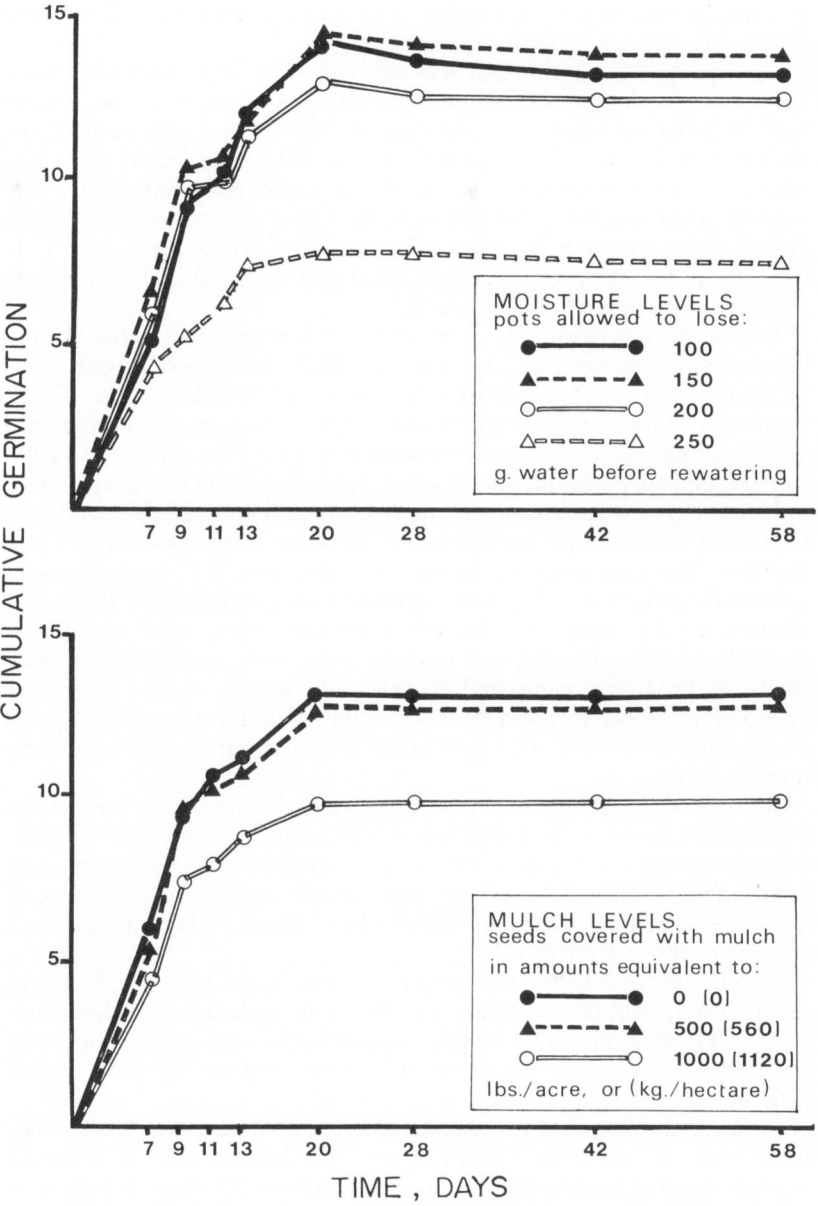


FIG. 4. Cumulative average number of *Stipa pulchra* seeds germinating out of 25 under four moisture regimes and three mulch levels in pots.

toward the beginning, during the initial rapid growth period, and less frequently later as growth rates leveled off.

In order to follow plant growth through time, nondestructive measures of growth (number of germinated seeds, length of the longest leaf, number of leaves and number of tillers) were recorded in the above experiments. A separate height-weight experiment was conducted to determine the relationship of these parameters to early-growth plant biomass. Length of longest leaf and number of leaves correlated best with biomass ($r^2 = 0.84044$, $p < 0.001$ and $r^2 = 0.83716$, $p < 0.001$, respectively) confirming the validity of using these measures to describe plant growth.

For the first experiment, *S. pulchra* seeds were sown alone at densities of 25 seeds per pot, and were subjected to three different levels of mulch cover and four different treatments of moisture stress. Mulch treatments consisted of leached and dried annual grass straw placed on top of the pots in weights corresponding to 0, 560, and 1120 kg/ha. For the moisture treatments, an alteration of wet and dry periods was induced, because it corresponds more closely to actual field conditions than does maintaining moisture at a constant level. With a soil tensiometer, the approximate relationship of pot weight to four soil water potentials (-3, -6, -12, and -15 bars) was established. Pots were allowed to dry down to established weights, then were rewatered. Instrumentation, and the fact that measurements were taken in relatively shallow pots compared to field soil depths, render only very approximate estimates of actual potential; thus the treatments should be thought of in terms of a gradation from constantly moist to infrequently moist.

Results of the above experiment showed that the final number of germinated seeds per pot differed significantly between seed sources, suggesting that there may be considerable genetic variability in natural populations. Of the 25 seeds per pot, an average of 12.75, 12.0, and 6.85 seeds germinated from Mendocino, Marin, and San Joaquin County sources, respectively.

Germination patterns were much more strongly impeded by treatments throughout the experiment than was growth of established seedlings. Germination was highly significantly suppressed both by the highest levels of moisture stress and the highest levels of mulch (Fig. 4).

In the second experiment, constant densities of perennial grass seeds were sown in pots in combination with varying densities and species of annual grasses. Encircling five *S. pulchra* seeds in plastic pots 14.6 cm in diameter were annual seeds at densities of 1, 3, 9, 18, and 54 seeds per *Stipa* seed. These numbers of annuals correspond to field densities of 300, 900, 2700, 5100, and 16,000 seeds/m², typical of low to moderate densities observed in the field (Bartolome, 1979).

To reduce genetic variation in the annual grasses, we used commercial strains of *Bromus mollis* and *Festuca megalura*. *Festuca megalura*, often mistakenly referred to as a native species (Lonard and Gould, 1974), commonly occurs in *S. pulchra* stands. *Bromus mollis* is the most widely distributed annual grass species in California (Janes, 1969).

Results from pot trials support field observations reported above. *Stipa pulchra* seeds germinated more slowly and attained a lower density after 40 days with high densities of both *Festuca megalura* and *Bromus mollis* (Fig. 5) compared to control. Seedlings grew more slowly as represented by fewer leaves at high density (Fig. 5). Of particular interest, however, is the different effect of the two annual species. *Bromus mollis* appeared to have a much more detrimental effect on perennial seedlings than *Festuca megalura*. This effect shows up particularly well when comparisons are made between the two species averaging overall values for density versus both number of seeds germinating and leaf number per seedling. *Bromus mollis* showed a significant negative correlation with density and number ($r = -0.7554$, $p < 0.01$) and size ($r = -0.5979$, $p < 0.01$) of perennial seedlings at 40 days, whereas the relationship for *Festuca*, although present, is not significant at the 5 percent level. Values for length of the longest leaf and number of tillers show the same results as for number of leaves, and thus are not presented graphically.

CONCLUSIONS

Evidence presented helps clarify the ecological role of *Stipa pulchra* in California grasslands. Although *S. pulchra* has often been described as the dominant and even the equivalent of undisturbed California prairie, the results and observations above suggest a lesser role.

Permanent transects at the Hopland Field Station failed to show an increase of *S. pulchra* over twenty years of protection from grazing by livestock. Indeed, *S. pulchra* decreased with protection on the Riley area, was replaced by other perennial grasses in one cluster, and by annuals in another. This lack of directional change is supported by similar *Stipa* stands examined at the Hastings Reservation by White (1967). The Soil-Vegetation Survey shows that *S. pulchra* occurs on a wide variety of sites, with broad distribution in the northern part of the state, and probably similar distribution throughout its range. *S. pulchra* is far from a rare or endangered species.

Experimental results also support the idea that *S. pulchra* is opportunistic, with few of the characteristics of typical climax species. *S. pulchra* germinates readily under all but severe moisture stress. It appears to establish most readily on bare ground, rather than under a cover of mulch. One might anticipate a climax species to prefer a

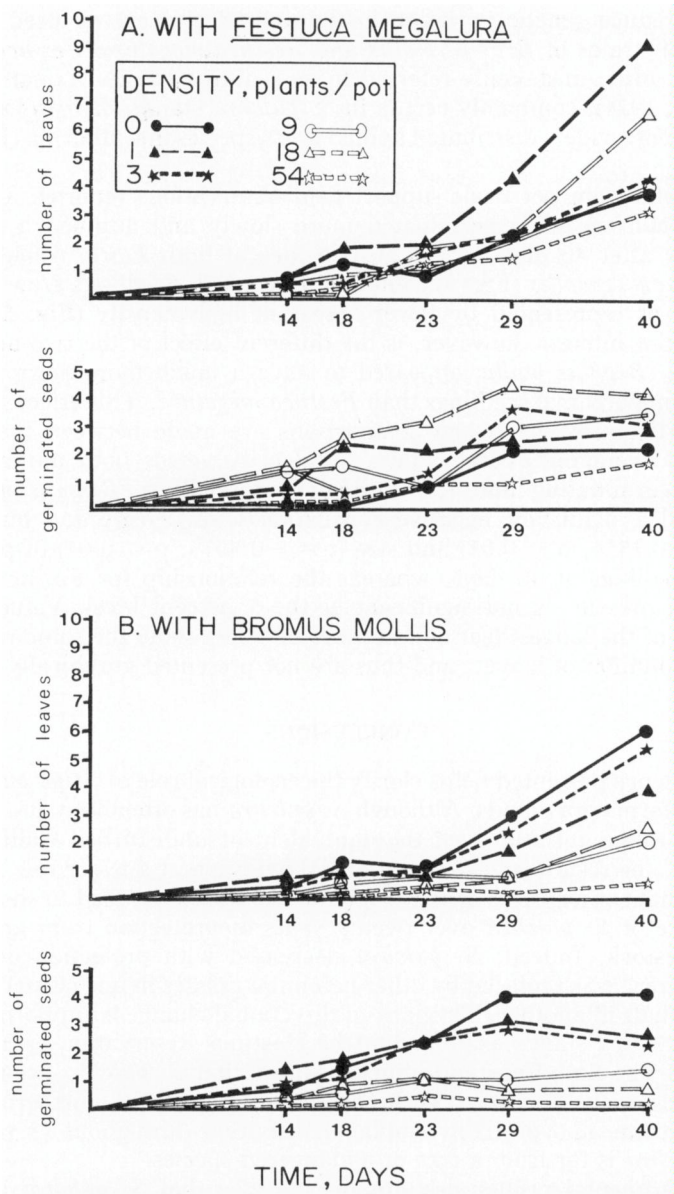


FIG. 5. Cumulative number of leaves per plant and number of germinated seeds of *Stipa pulchra* germinated in pots with six densities of A. *Festuca megalura* and B. *Bromus mollis*.

higher litter cover or at least be adapted to such conditions. It cannot compete successfully against a rapidly-growing, robust annual such as *Bromus mollis*, yet *S. pulchra* possesses some similar germination features (rapid germination, germination on bare sites) to those of the annuals with which it now grows. Where the annual cover is dense, *S. pulchra* seedlings often do not survive. Where the annual cover is reduced either by fire, grazing, or disturbance, *S. pulchra* seedlings thrive. Once established, a *S. pulchra* plant can persist under moderately heavy grazing.

Its vigorous seeding habit and substantial quantities of viable seed place *S. pulchra* in a position to occupy suitable sites rapidly following disturbance of the annual cover. *Stipa pulchra* may have occupied a similar status in the pristine grassland, occupying areas of disturbance such as land slips and burned areas. Thus when the first ecologists observed relicts of the grassland they saw *S. pulchra*, not as the remnant climax species, but the native perennial species best able to thrive under disturbance. Far from being the dominant of the California prairie, it was a survivor because it is adapted to disturbance and does well when not grazed heavily in the spring. The dominants of the original prairie remain undetermined.

The major questions remain: What was the nature of the pristine grassland, and did the new annuals from the Mediterranean replace native annuals or native perennials? What were the dominants of the pristine vegetation? These questions may be answerable through an expanded application, i.e., more native species, of the methods used in this study. Clearly, the evidence to date points to a role for *S. pulchra* not necessarily as the dominant pristine grass of California, but a native species adapted to disturbance. *Stipa pulchra* is clearly not in danger of elimination, having survived under 200 years of heavy grazing and frequent burning.

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NOTEWORTHY COLLECTIONS

LUPINUS CITRINUS Kell. (FABACEAE).—USA, CA, Madera Co., Indian Lakes Estates, Rd. 417, 3.1 km e. of jct. with Hwy 41 (T8S R21E S28 ne.¼), 685 m; 8 May 1974, *Wells s.n.* (CAS); 11 May 1980, *Hamon 8042A* and *8042B* (UC); 8 Jun 1980, *Bartel 1019* (UC). Open decomposing granite outcrops in digger pine/oak woodland. Associated with *Calyptidium pulchellum*, *Cryptantha flaccida*, *Mimulus bicolor*, *M. dudleyi*, *Parvisedum congdonii*, and *Pectocarya penicillata*.

Previous knowledge. Reported from Fresno and Mariposa Cos. (Munz, A Calif. fl. 1959) and also as Fresno Co. endemic (Jepson, Fl. Calif. 2:277. 1936; Abrams, Ill. fl. Pacific states 2:494. 1944). Mariposa Co. reports erroneous and probably based on either incorrect county notation on label [28 May 1903, *Congdon s.n.* (UC)] or label data transposed during remounting [11 May 1902, *Congdon s.n.* (MIN)].

Significance. First record for Madera Co., a range extension wnw. of 29 km. Considered rare and endangered by CNPS (Smith et al., CNPS Spec. Publ. 1, ed. 2. 1980). Under review as endangered species by the U.S. Fish & Wildlife Service (Fed. Reg. 45:82520. 1980).

STREPTANTHUS FARNSWORTHIANUS J. T. Howell. (BRASSICACEAE).—USA, CA: Madera Co., Mammoth Pool Rd., 3.5 km e. of jct. with Italian Bar Rd. (T9S R23E