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Figure 1. Present and presumed historical distribution of grasslands in California; sites with remnants of the pristine prairie are named (from Barry 1981, with permission of the California Native Plant Society).

THE CALIFORNIA VALLEY GRASSLAND

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INTRODUCTION

Grasslands are distributed throughout California from Oregon to Baja California Norte and from the coast to the desert (Brown 1982) (Figure 1). This review will focus on the dominant formation in cismontane California, a community referred to as Valley Grassland (Munz 1959). Today, Valley Grassland is dominated by non-native annual grasses in genera such as Avena (wild oat), Bromus (brome grass) and Hordeum (barley), and is often referred to as the California annual grassland. On localized sites, native perennial bunchgrasses such as Stipa pulchra (purple needle grass) may dominate and such sites are interpreted to be remnants of the pristine valley grassland.

In northwestern California a floristically distinct formation of the Valley Grassland, known as Coastal Prairie (Munz 1959) or Northern Coastal Grassland (Holland and Keil 1989) is recognized. The dominant grasses include many native perennial bunchgrasses in genera such as Agrostis, Calamagrostis, Danthonia, Deschampsia, Festuca, Koeleria and Poa (Heady et al. 1977). Non-native annuals do not dominate, but on some sites non-native perennials like Anthoxanthum odoratum may colonize the native grassland (Foin and Hektner 1986).

Elevationally, California's grasslands extend from sea level to at least 1500 m. The upper boundary is vague because montane grassland formations are commonly referred to as meadows; a community which Munz (1959) does not recognize. Holland and Keil (1989) describe the montane meadow as an azonal community; that is, a community restricted not so much to a particular climatic zone but rather controlled by substrate characteristics. They consider poor soil-drainage an over-riding factor in the development of montane meadows and, in contrast to grasslands, meadows often remain green through the summer drought. Floristically, meadows are composed of graminoids; Cyperaceae, Juncaceae, and rhizomatous grasses such as Agropyron (wheat grass). Some bunchgrasses, such as Muhlenbergia rigens, are found in both montane meadows and moister grasslands. Forbs when present, are typically perennials. East of the interior ranges, grasslands are uncommon although native perennial bunchgrasses in genera such as Stipa, Hilaria and Aristida are common in steppe and desert scrub.

Today, Valley Grassland covers nearly 7 million ha or 17% of the state (Huenneke 1989), although other sources list less than half this amount (Jones and Stokes 1987). There is some evidence that extent of the grassland region has not changed since pre-European conditions, although the spatial distribution of grasslands has likely changed substantially (Huenneke 1989). That is, many current grasslands previously may have been dominated by other vegetation types and vice versa. Without question, many former grasslands have been converted to agricultural and urban use (Barry 1972).

The Valley Grassland community occurs in regions characterized by a broad range of climatic conditions. Average January temperatures may range from 5° to 15° C and July temperatures from 15° to 30° C (NOAA 1988). Annual precipitation ranges from approximately 12 cm to over 200 cm, although all sites are characterized by a summer drought of 4-8 months (Heady 1977). Grasslands are well developed on deep, fine-textured soils although they are not restricted to such conditions (Wells 1962, Adams 1964, Heady 1977).

TODAY'S CALIFORNIA ANNUAL GRASSLAND

Today, the California Valley Grassland is dominated by non-native species of European origin, both grasses and associated forbs (Table 1). Whereas the dominant grasses are all exotic species, the forbs may be either exotic or native (Tables 1 and 2). The origin of more than 70% of the non-native species is the Mediterranean region of Europe (Baker 1989). Presumably the very long history of civilization in that area has selected for aggressive ruderal taxa, which were pre-adapted to colonize California grasslands. Most species have propagules highly specialized for animal dispersal.

The composition of annual grasslands varies spatially and temporally, although the most common species are grasses such as Avena barbata, A. fatua, Bromus mollis, B. diandrus and Lolium multiflorum, and forbs such as species of Erodium (Heady 1956, Bartolome 1979). As is typical of many weeds, most have non-dormant seeds and usually there is relatively little seed carry-over from year to year (Evans and Young 1989, Young and Evans 1989). Different seed germination responses to annual variations in temperature and precipitation may account for much of the year to year variation in the species composition.

Disturbances such as fire and livestock grazing often alter species composition. In some cases, intense grazing or fires may replace non-native annuals with native annuals such as Eremocarpus setigerus, Trichostema lanceolatum, Madia spp., Lotus spp. and Trifolium spp. (Heady 1977, Parsons and Stohlgren 1989). Some of these are quite noxious and become more abundant due to avoidance by grazers. In some cases, allelopathic suppresion of competing vegetation may be involved. Trichostema lanceolatum, for example, produces a volatile oil which makes the plant quite redolent; lab assays indicates potential for allelopathic suppression of other plants but this is not borne out in field studies (Heisey and Delwiche 1985).

Invasion of the Pristine Valley Grassland

The story behind the invasion of the pristine California Valley Grassland illustrates how rapidly and thoroughly an exotic flora can dominate another landscape. It is thought that certain of today's naturalized alien species may have become established in California as early as the 16th century when the first Europeans explored our coastline (Heady 1977). Hendry (1931) reported Erodium cicutarium and a few other exotic annuals from adobe bricks used to build the earliest Spanish missions, suggesting these species were already established (at least in the vicinity of the missions) by the late 18th century. It is during this period that most exotic grassland species were probably introduced, and it seems quite likely that many of these taxa were well established in California by the beginning of the 19th century. There is some evidence that invasion of non-native species took place in waves, with Avena

Table 1. Non-native species dominating the modern annual grassland (nomenclature according to Munz 1959 except for Vulpia see Leonard and Gould 1974). See Table 2 for native taxa which often coexist with these taxa.

Species	(Life Form)*	Common Name
Poaceae		
Aira caryophyllea	(A)	hair grass
Avena barbata	(A)	slender wild oat
A. fatua	(A)	wild oat
Bromus omollis	(A)	soft chess
B. rigidus	(A)	ripgut grass
B. rubens	(A)	foxtail chess
B. tectorum	(A)	cheat grass, downy cheat
Hordeum leporinum	(A)	barley
Lolium multiflorum	(A)	Italian rye grass
Schismus barbatus	(A)	
Vulpia dertonensis	(A)	fescue
V. megalura	(A)	foxtail fescue
V. myuros	(A)	fescue
Apiaceae		
Torilis nodosa	(A)	hedge-parsley
Asteraceae		
Centaurea melitensis	(A)	star thistle, tocalote
C. solstitalis	(A)	star thistle, Barnaby's thistle
Hypochoeris glabra	(A)	cat's-ear
Sonchus spp.	(A)	sow-thistle
Brassicaceae		
Brassica spp.	(A)	mustard
Raphanus sativaus	(A)	radish
Caryophyllaceae		
Cerastium viscosum	(A)	
Silene gallica	(A)	
Stellaria arvensis	(A)	chickweed
Fabaceae		
Medicago hispida	(A)	bur-clover
Trifolium spp.	(A)	clover
Geraniaceae		
Erodium botrys	(A)	filaree
E. cicutarium	(A)	filaree
E. moschatum	(A)	filaree

* (A) = annual

spp. and Brasica nigra dominating in the early 19th century but later being reduced by an increased abundance of Bromus spp., Hordeum spp. and Erodium spp. (Burcham 1956).

Most authorities agree that the first half of the 19th century was the period of transition between native-dominated grasslands and non-native dominated grasslands (Burcham 1957, Dasmann 1966). This was a period of intensive cattle and sheep grazing and was marked by years of severe drought. The first of these in southern California occurred between 1828 and 1830, when no rain fell for 22 months. By 1840, species of Avena, Brasica and Erodium were already abundant in the Central Valley (Dasmann 1966, Wester 1981). In the following decades both cattle and sheep grazing intensified, partly to supply the demands of the increasing gold-rush generated population. Cattle numbers in California rose from approximately a quarter million in 1850 to 1.2 million (Burcham 1957, or 3 million according to Dasmann 1966) by 1860. Between 1862 and 1864 the state was again struck with two severe drought years. Livestock reportedly consumed all available forage and then died en masse, leaving only about half a million cattle by 1870.

This report by one early traveler, William Brewer, while crossing the coast range in 1863, provides some insight into the extent of destruction (Dasmann 1966): "Our road lay over the mountains. They are perfectly dry and barren, no grass---here and there a poor gaunt cow is seen, but what she gets to eat is very mysterious...The ride was over the plain, which is utterly bare of herbage. No green thing greets the eye, and clouds of dust fill the air. Here and there are carcasses of cattle, but we see few living ones."

It is hypothesized that the populations of the native perennial grasses were severely reduced by these conditions, whereas the impact on the non-native annual grasses and forbs was minimal. Several factors were involved but one critical factor is the perennial nature of the native bunchgrasses. Such plants are in a precarious position for survival during extended drought, even without grazing. One effect of grazing was to reduce root growth and thus make the plants more susceptable to drought (Parker 1929). Irresponsible overgrazing during droughts was the coup de grace and persistence was possible only as seed. Annuals, by their nature, however, are commonly far more prolific seed producers, some of which may persist for more than a year. Once established, annuals represent formidable competitors, making recovery of the native species even more difficult.

Evidence of the mechanisms for replacement of perennials by annuals is documented in several California studies. In one investigation, a grassland dominated by the native bunchgrasses Stipa pulchra and Aristida hamulosa, had no viable seeds in the soil, rather the seed bank was dominated by associated non-native annuals (Major and Pyott 1966). Other studies indicated that Stipa pulchra seedlings established very poorly in the presence of annual grass seedlings (Robinson 1971, Bartolome and Gemmill 1981). This may be tied to the rapid soil moisture depletion by annual grasses (Hull and Muller 1977) which could occur prior to the late spring peak in S. pulchra growth (Sampson and McCarty 1930). To further exacerbate the recovery of native perennials, species such as S. pulchra and Poa scabrella have slower growth rates, less root biomass, and shallower rooting depths than non-native annual grasses (Jackson and Roy 1985). Examples of

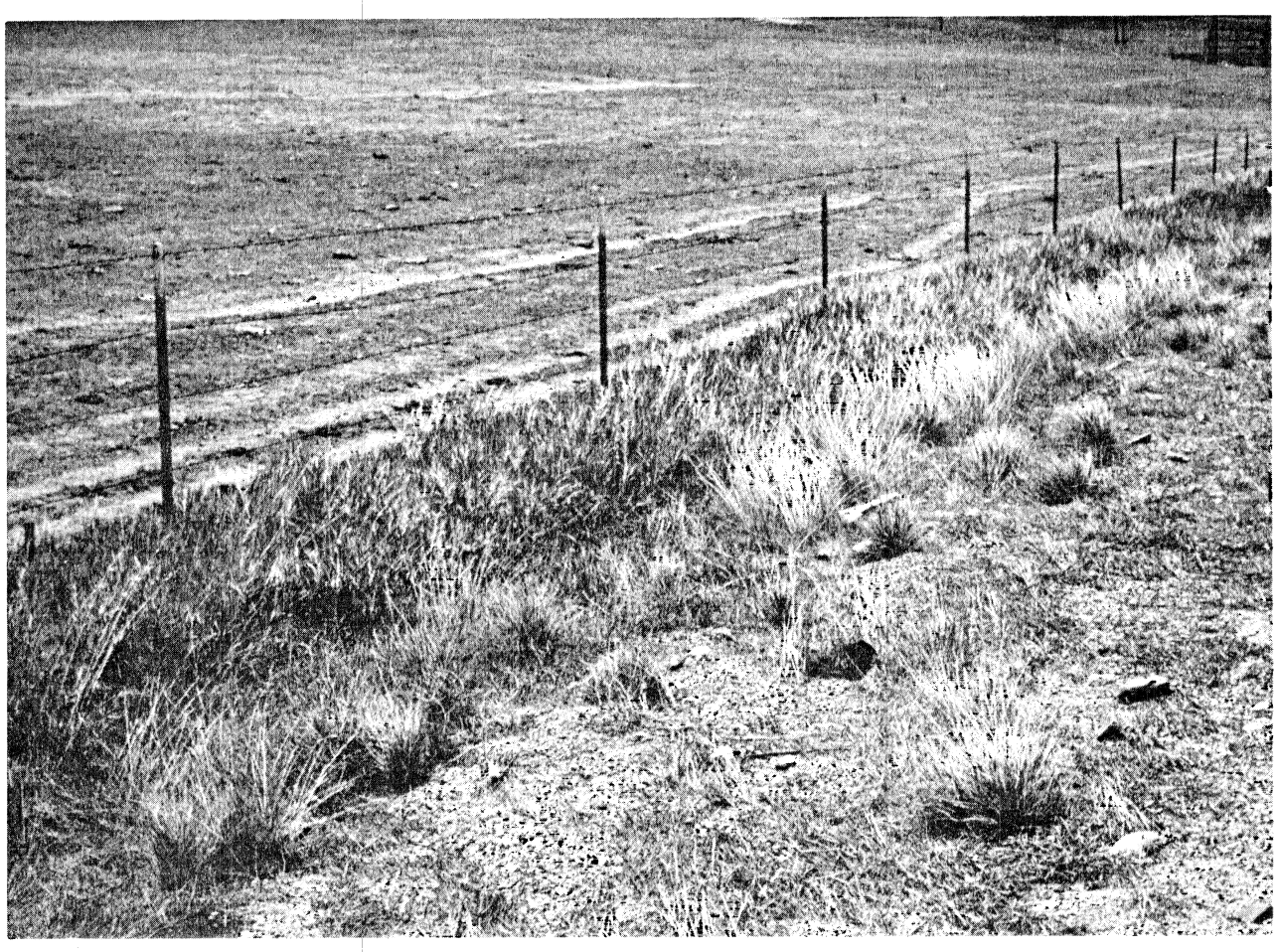

Figure 2. Overgrazed annual grassland within fenced enclosure and "relict" perennial bunchgrasses (Stipa pulchra and Aristida wrightii) outside of the fence; Warner Valley, San Diego Co.

grazing-induced displacement of native bunchgrasses can still be observed today (Figure 2).

It is curious that these exotic grasses, which have formed extensive annual grasslands in California, do not dominate the landscape in their region of origin, the Mediterranean Basin (Jackson 1985). Stable grasslands are uncommon in the moister portions of that region, although they may dominate in drier parts of the eastern Mediterranean (Blumler 1984). Perhaps what is most unique about California annual grasslands is the comparative stability of these ecosystems. Few ecosystems in the world are dominated by non-native annuals with relatively little threat of being displaced by perennials.

Apparently the dominance by exotic annual species in California is partly explained by the fact that, relative to much of the Mediterranean Basin, the climate here is more arid. Commonly, the proportion of annuals in a flora increases as aridity increases, and this is true in California (Richerson and Lum 1980). Further, in light of the increasing aridity

in California during the last 10,000 years (Johnson 1977, Heusser 1978), perhaps the invasion of native perennial grasslands by annual species is the culmination of a process which began thousands of years ago. For example, southern California plant communities during the late Pleistocene Epoch (20,000-40,000 years before present) were comparable to those currently found 300 km to the north (Warter 1976). Obviously, the pristine California prairie or grassland existed under a somewhat moister climate, than that of the modern grasslands.

PRISTINE CALIFORNIA VALLEY GRASSLAND

Distribution and composition of California grasslands, prior to the invasion by European annual grasses, is still a matter of some debate. Clements (1934) suggested that the pristine prairie in California had previously been dominated by Stipa pulchra (purple needle grass) (Figure 3). This conclusion was largely based on the observation of nearly pure stands of this native bunchgrass along railway rights-of-way. Clements believed these stands were "relicts" of what dominated the region in previous eras. Heady (1977) stated that: "The pristine California prairie appears to have been little different in distribution from the present-day grasslands, except the areas taken for cultivation... Stipa pulchra, beyond all doubt, dominated the valley grassland." These points, however, are not universally accepted.

Distribution of the Pristine Valley Grassland

Cooper (1922) believed that many "modern" annual grasslands were formerly dominated by chaparral and not formerly part of the pristine prairie. Repeated burning, often intentionally for the purpose of "type-conversion", was sufficient to eliminate the woody vegetation and replace it with weedy annuals. Cooper (1922) gave numerous examples of former brush-covered sites in northern California, which had been converted to grassland. Bauer (1930) and Wells (1962) also supported the idea that many modern grasslands in coastal California occur on sites formerly occupied by shrub vegetation. Naveh (1967) has suggested that annual grasslands in Israel had a similar origin from degraded shrublands.

Such "type conversion" from woody to herbaceous vegetation, through repeated burning, has been well documented (e.g., Arnold et al. 1951, Zedler et al. 1983). Russell (1983) has found evidence from pollen cores that, following European colonization of Point Reyes, shrubs decreased and grasses increased. However, such a process of land clearing by burning may have begun prior to the arrival of Europeans (Burcham 1960). Timbrook et al. (1982) contended that the Chumash of coastal southern California did frequent burning as a means of encouraging native annual species and collecting the seed for food. Such sites would have been highly susceptible to invasion by the aggressive weedy colonizers.

Historical studies of changes in annual grassland distribution provide further evidence that annual grasses have displaced shrubs on many sites. In the absence of disturbance by fire and grazing, many areas are often recolonized by coastal sage scrub or other woody plants (Woolfolk and Reppert 1963, McBride and Heady 1968, Oberbauer 1978, Hobbs 1983, Freudenberger et al. 1984, Hobbs and Mooney 1986). The rate of invasion, though, may be relatively slow on some sites (White 1966, Davis and Mooney

Figure 3. Stipa pulchra, purple needle grass, by Melanie Keeley.

1985). An example of historical changes in the grassland-shrubland interface is shown in Figure 4.

In contrast to Cooper's contention, Dodge (1975) suggested that, prior to the European invasion, fires were so frequent that vast stretches of coastal California capable of supporting chaparral were covered by grassland. He contended that since the arrival of Europeans, shrublands have invaded and colonized former grasslands. This theory is largely based on the diary of Fray Juan Crispi, a member of the Portola Expedition which, in 1769,traveled from San Diego to San Francisco (Bolton 1927). Crispi made mention of grasslands numerous times throughout the diary and Dodge (1975) pointed out that today, chaparral, not grassland, dominates the route traversed by the Portola party. These conclusions, however, deserve careful scrutiny. Contemporary highways commonly follow historical routes and thus the grass-covered route traveled by Portola has been replaced today, not by chaparral, but by concrete and asphalt. Additionaly, as Oberbauer (1978) pointed out, the diary of Fray Juan Crispi is not an unbiased account of the vegetation, as this padre's function was to convince the church to set up missions in the New World. Additionally, many of the grasslands he referred to were undoubtedly lowland marshy sites. This is suggested by countless references to "green pasture" in the months of July and August. In southern California, upland sites dominated by herbaceous plants do not remain green through the summer drought.

In summary, annual grasslands exist today on sites which, prior to invasion by Mediterranean annuals, were brushlands in some instances and native perennial grasslands in other cases. Throughout the coastal and transverse ranges of southern California, annual grasslands occur on steep, rocky slopes which probably were never dominated by native bunchgrasses (Figure 5). Throughout the state, on more level terrain of heavy clay substrates, annual grasslands likely occupy sites previously held by native grasses. These conclusions are supported by some experimental work. For studies by Robinson (1971) suggest that native bunchgrasses never formed grasslands on nutrient poor rocky soils. On the otherhand, there is evidence to support the claim made by Shreve (1927) that grasslands were an edaphic climax on deeper soils (Wells 1962, Robinson 1971).

Floristic Composition of the Pristine Valley Grassland

In terms of species composition not everyone agrees that all native grasslands were dominated by perennial bunchgrasses. Hoover (1936), Twisselmann (1967) and Wester (1981) contended that the aridity of the San Joaquin Valley favored an annual flora. This notion is supported by early descriptions made by Muir (1883) and later by Rountree (1936). These authors made reference to annual taxa in more than 30 genera, largely the same ones thought to be components of the pristine grassland (see below). Perennials were either geophytes or suffrutescents and, since grasses formed a minor part of this formation, Hoover (1970) suggested that such a formation, still evident today, be called the Interior Herbaceous community.

It is very likely true that many grasslands were dominated by native bunchgrass species, particularly Stipa pulchra (Figure 3). This idea is based on early historical accounts (Clements 1934), presence of micro-fossils (Bartolome et al. 1986) and the widespread distribution of what are considered relict stands of this

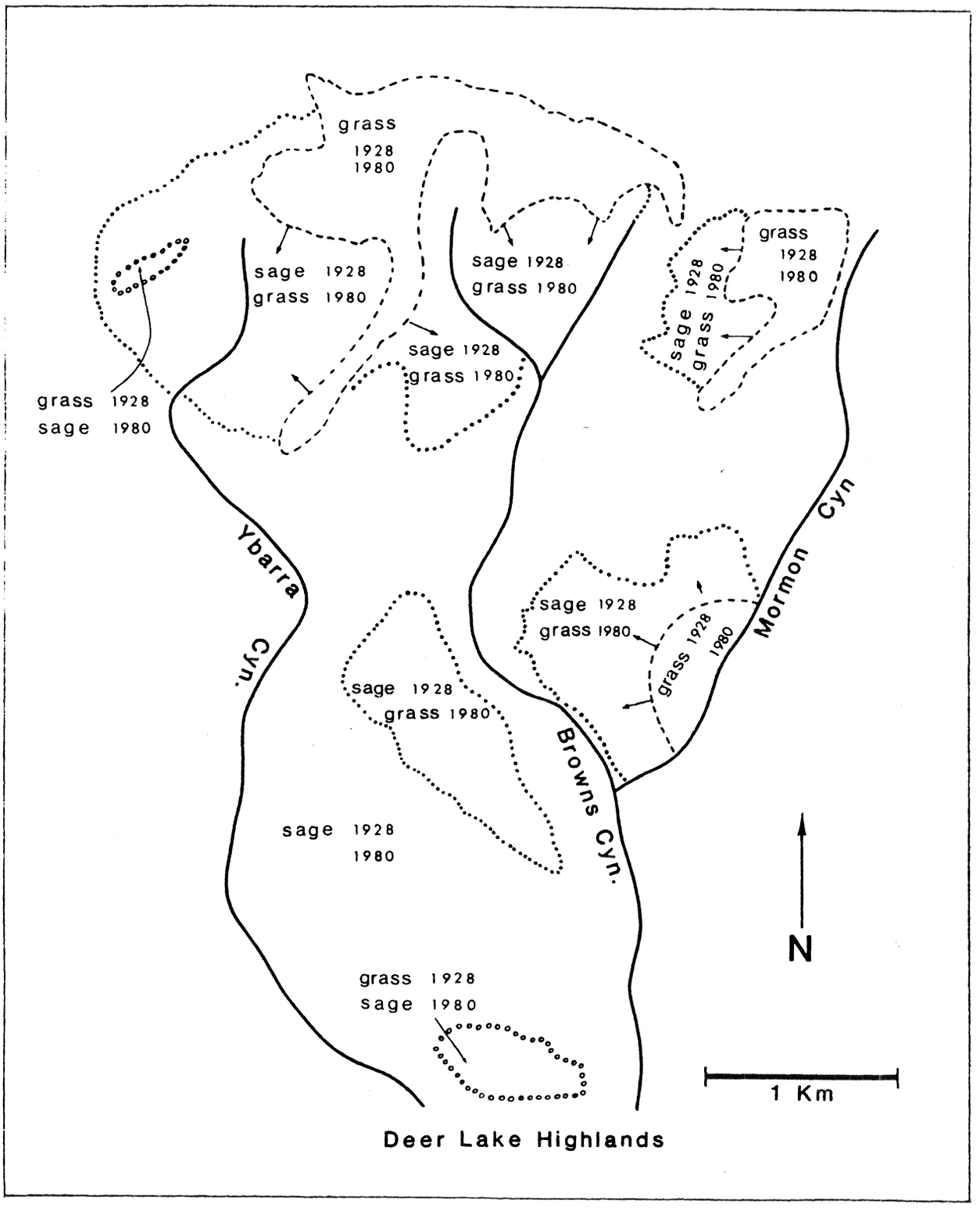

Figure 4. Historical and present day vegetation patterns (as of 1980) on a portion of Oat Mountain, Los Angeles Co. (from Freudenberger et al. 1987, with permission of the Southern California Academy of Sciences).

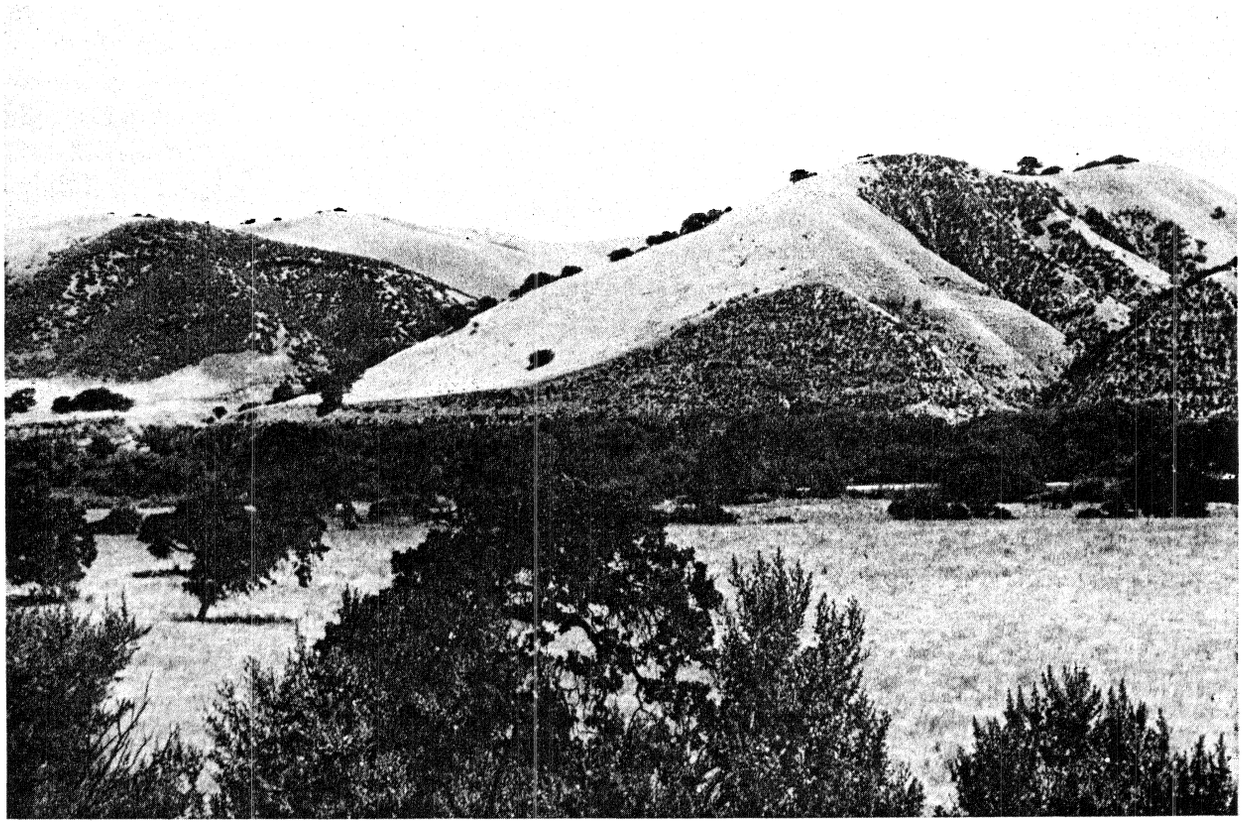

Figure 5. Example of present day grassland distribution in central Coast Range, San Luis Obispo Co. Annual grasslands on deep soils in the valley bottoms probably have replaced perennial bunchgrass vegetation. Grasslands on the slopes are interpreted as former coastal sage scrub sites which have been converted to annual grasslands by repeated disturbance.

species (Figure 1). These stands occur on a diversity of soil types throughout the state (Bartolome 1989).

Such 'relict' stands of Stipa pulchra always contain a sizable component of non-native annual grasses; particularly, species of Avena and Bromus. Studies have shown that simply excluding grazing from a site does not result in a rapid return to dominance by S. pulchra.

In the Central Valley, annual grasslands protected from livestock grazing for more than 40 years still lack a native perennial bunchgrass flora (Heady 1977). On Hastings Reservation in Carmel Valley, White (1967) noted that sites protected from grazing for 27 years had, on average, only 11% coverage by S. pulchra, comparable to that on grazed sites. Bartolome and Gemmill (1981) report similar findings for sites free of grazing for 20 years at Hopland Field Station in northern California. Other studies have also shown complete protection from grazing does not markedly increase dominance by S. pulchra. In

some cases total exclusion of grazing may favor some non-natives over S. pulchra (Goode 1981).

A study by Bartolome and Gemmill (1981) provides one explanations for the failure of native species to increase upon the cessation of grazing. They reported that S. pulchra establishes seedlings most readily on bare ground but poorly under a cover of litter, a sitation typical of an undisturbed grassland. They suggested that one should expect a "climax" species to recruit seedlings without disturbance and therefore this species probably was not the dominant grassland species of the pristine prairie. Their assumption as to the conditions under which a climax grassland species should reproduce, needs to be evaluated carefully.

Although very few studies anywhere in the world have focused on reproduction of perennial grassland species, the little data that are available suggests that reproduction is likely to be tied to fires. Most perennial grasslands are relatively closed to seedling recruitment, and perennial species not only resprout after fire, but are vigorous flower producers the first season after burning (Keeley 1981, Glenn-Lewin et al. 1990). These tendencies also hold true for Califonian bunchgrasses such as Stipa pulchra (Ahmed 1983), Stipa lepida (Keeley and Keeley 1984), and Sitanion hystrix (Young and Miller 1985); although the optimal timing of seedling recruitment in S. pulchra is in the second postfire year (Ahmed 1983). Indians perhaps played a critical role in maintaining these grasslands by frequent burning for the purpose of collecting grass seeds (Bean and Lawton 1973). If fires are important to regeneration, intensive grazing would have an additional negative effect on these species by keeping fuel loads below the level sufficient for fires. Other forms of disturbance may also provide safesites for seedling establishment. For example, Hobbs and Mooney (1985) suggested that gopher mounds, may be important sites of establishment by native species such as S. pulchra. Additionally, personal observations reveal that S. pulchra readily establish on road cuts.

Consistent with the suggestion by Bartolome and Gemmill (1981), are the observations by McNaughton (1968). He reported that Stipa pulchra accounted for up to 41% of the standing crop production on serpentine soils but was largely excluded on sandstone derived soils which were dominated by Avena fatua and Bromus rigidus. Serpentine substrates are low in calcium and high in magnesium, and these conditions result in low productivity compared to grasslands on other substrates. In McNaughton's study, species diversity was much greater on the more open S. pulchra dominated site and was largely due to native annuals. Others have also noted an increase in the balance between Stipa pulchra and non-native annuals as site productivity goes down (Blumler 1984, Huenneke et al. 1990).

There is some reason to believe that grasslands seldom had more that two-thirds coverage by S. pulchra (Biswell 1956, Burcham 1957, Oberbauer 1978, Goode 1981). Today, S.pulchra stands are never completely dominated by this species and often 60% is the greatest coverage one encounters. Thus, it seems likely that the pristine prairie was a mixture of perennial bunchgrasses and forbs. Based on the present occurrences and historical records, associated native species that comprised the pristine grassland are listed in Table 2. A typical stand may have had 50-75% coverage by S. pulchra and other bunchgrasses. The interstitial spaces between grasses were likely occupied by annual forbs and geophytes of the Liliaceae and Amaryllidaceae. Annual grasses were

Table 2. Native species thought to be important components of the pristine grassland of California (nomenclature according to Munz 1959). Based on literature cited in text.

Species	(Life Form)*	Common Name
Poaceae		
Aristida spp.	(P)	triple-awned grass
Danthonia californica	(P)	California oat grass
Elymus glaucus	(P)	blue rye grass
E. triticoides	(P)	creeping rye grass
Festuca idahoensis	(P)	fescue
Koeleria cristata	(P)	June grass
Melica californica	(P)	California melic
M. imperfecta	(P)	small-flowered melic
Muhlenbergia rigens	(P)	deer grass
Poa scabrella	(P)	pine blue grass
Sitanion hystrix	(P)	squirreltail
Sitanion jubatum	(P)	squirreltail
Stipa cernua	(P)	noding needle grass
S. lepida	(P)	foothill needle grass
S. pulchra	(P)	purple needle grass
Amaryllidaceae		
Allium spp.	(P)	wild onion
Bloomeria spp.	(P)	golden-stars
Brodiaea spp.	(P)	brodiaea
Muilla spp.	(P)	
Liliaceae		
Calochortus spp.	(P)	mariposa lily
Fritillaria spp.	(P)	chocolate lily
Apiaceae		
Lomatium spp.	(P)	
Sanicula spp.	(P)	snakeroot
Asteraceae		
Baeria chrysostoma	(A)	goldfields
Calycadenia spp.	(A)	rosinweed
Chaenactis spp.	(A)	
Hemizonia spp.	(A)	tarweed
Holocarpha spp.	(A)	tarweed
Lasthenia spp.	(A)	
Layia spp.	(A)	tidy-tips
Madia spp.	(A)	tarweed
Malacothrix spp.	(A)	
Microseris spp.	(A)	
Stylocline spp.	(A)	
Boraginaceae		

Table 2 (continued)

Amsinkia spp.	(A)	fiddle-neck
Crythantha spp.	(A)	
Plagiobothrys spp.	(A)	
Brassicaceae		
Streptanthus spp.	(A)	
Euphorbiaceae		
Eremocarpus setigerus	(A)	turkey-mullein, doveweed
Fabaceae		
Astragalus spp.	(A)	locoweed
Lotus spp.	(A)	bird's-foot-trefoil
Lupinus spp.	(A)	lupine
Trifolium spp.	(A)	clover
Lamiaceae		
Salvia columbariae	(A)	chia
Trichostema lanceolatum	(A)	vinegar weed
Malvaceae		
Sidalcea malvaeflora	(P)	checker
Onagraceae		
Clarkia spp.	(A)	farewell-to-spring
Camissonia spp.	(A)	smilie-flower
Papaveraceae		
Eschscholzia spp.	(A,P)	California poppy
Platystemon californicus	(A)	cream-cups
Plantaginaceae		
Plantago spp.	(A)	plantain
Polemoniaceae		
Gilia spp.	(A)	gilia
Linanthus spp.	(A)	
Polygonaceae		
Chorizanthe spp.	(A)	
Eriogonum spp.	(A,P)	wild buckwheat
Portulacaeae		
Calandrinia spp.	(A)	
Capmontia spp.	*(A)	miner's lettuce
Ranunculaceae		
Delphenium spp.	(P)	larkspur
Ranunculus spp.	(P)	butter-cups
Scrophulariaceae		
Collinsia spp.	(A)	Chinese-houses
Orthocarpus spp.	(A)	owl's-clover

* (A) = annual, (P) = perennial.

probably never very important in the pristine grassland (Crampton 1974).

Differences in community composition of the pristine grassland have been noted by Beetle (1947) and Crampton (1974). On the drier soils of valleys and slopes, Stipa pulchra would have coexisted with other perennial bunchgrasses such as S. cernua, Poa scabrella, Elymus glaucus, Melica californica, M. imperfecta, Bromus carinatus, Koeleria cristata and Danthonia californica. On rich alluvial soils, Central Valley grasslands were dominated by both bunchgrasses and rhizomatous perennials;including species such as Elymus triticoides, Agropyron trachycaulum, A. subsecundum, Hordeum brachyantherum, Muhlenbergia rigens, Calamagrostis rubescens and Sphenopholis obtusata.

Substrate characteristics may also influence composition of the grassland community. On alkaline flats the above taxa are replaced by the rhizomatous perennial Distichlis spicata and the bunchgrass Sporobolus airoides, plus several annuals specialized to alkaline sites. On gravelly ridges and serpentine soils, Sitanion jubatum is common. Depressions, underlain by an impervious hardpan soil, support a completely different flora. These vernal pool communities are dominated by native annual grasses and forbs adapted to a temporary aquatic environment (Holland and Jain 1977). These azonal communities support a rich endemic flora and non-natives have not successfully invaded most vernal pool communities. This is due to the fact that most non-native grassland species germinate in cool weather, when the pools are filled. Higher temperatures later in the season, when the standing water has evaporated, may preclude grassland establishment. In years of very low rainfall, when the pools fail to fill with water, grassland species may dominate to the center of the pool basin (Keeley personal observations).

In the coastal foothills, certain grasses, such as Stipa lepida, S. coronata, Elymus condensatus and Agrostis diegoensis, become important. All of these, however, also occur in close association with coastal sage scrub and chaparral vegetation and may never have been components of true grasslands (Keeley and Keeley 1984, Goode 1981, Keeley personal observations). Towards the interior of the state, species of Aristida, Bouteloua, Stipa comata, S. speciosa, Oryzopsis hymenoides and Hilaria rigida dominate.

Biogeography

Native grassland taxa such as Stipa, Elymus, Festuca and Poa are considered to have affinties with cool-temperate regions and are most similar to the flora making up the Palouse Prairie of eastern Oregon and Washington (Sims 1988). Both of these regions are affected by the mediterranean climate of winter rains and summer droughts, which has selected for growth restricted to the cool season. This behavior is so strongly ingrained in the genome of these taxa that artificial watering during the summer cannot prevent dormancy in Stipa pulchra and some others (Laude 1953).

Summer drought may account for the successful invasion by non-native annual grasses in both central California and eastern Oregon. Grasslands which dominate the Great Plains have summer rainfall and annuals have not successfully colonized these prairies (Sims 1988). However, other factors may be involved; the sod-forming (rhizomatous) nature of grasses in the Great Plains may resist invasion better than the bunchgrass life form which dominate grassland of the

Pacific states. Some have suggested that the Great Plains were adapted to more intensive grazing by bison and that the California grasslands had evolved under a regime of weak grazing by deer and antelope (Clark 1956, but c.f. Berry 1972). However, examination of the highly diverse Pleistocene fauna exhibited at the L.A. County Paige Museum, which houses fossils removed from the southern California La Brea Tar Pits, should be sufficient to convince one that this conclusion deserves further scrutiny (see also Wagner 1989).

PRESERVATION OF THE REMAINING PRISTINE VALLEY GRASSLAND

Nearly a fifth of the State was once covered by perennial grasslands, yet today only 0.1% of those remain (Barry 1972). Of the existing grasslands in California, less than 1% are protected within federal, state or private preserves (Jones and Stokes 1987). The California Natural Diversity Data Base has identified Purple Needle Grass Grassland as a community which needs priority monitoring and restoration efforts. Communities with 10% or greater overall cover of S. pulchra constitute significant communities that require special protection as remnants of the once widespread pristine California prairie. In all cases, native perennial grasses coexist with non-native weedy annuals. Some consider these exotic grasses to be a permanent part of our landscape and perhaps best viewed as "residents" (Kay et al. 1981) or "new natives" (Heady 1977). Attempts to eliminate these non-natives have been unsuccessful. However, some restoration treatments appear to have potential for increasing the balance of natives to non-natives.

Evidence suggests that perennial bunchgrasses are well adapted to frequent burning (Clements 1934, Wells 1962). Some authors have reported that burning will favor native bunchgrasses over non-native annuals (McClaran 1981, Ahmed 1983). However, other studies have reported no increase in Stipa pulchra following burning (Garcia and Lathrop 1984) or a decrease in density of Muhlenbergia rigens under some burning regimes (Lathrop and Martin 1982). Clearly much more research is needed in this area. In light of the differences in phenology and life history between perennial bunchgrasses and annuals, it would be instructive to know how burning in different seasons affects the ratio of natives to non-natives. Since the annual grasses reach reproductive maturity as much as a month earlier than the perennial bunchgrasses (Jackson and Roy 1986), precise timing may alter the balance of reproductive success between these two components.

There is evidence that seeding of Stipa pulchra may be an effective means of increasing the importance of this species on disturbed sites (Rogers 1981, Garcia and Lathrop 1984). Others (e.g., Kay et al. 1981), however, have reported that seeding with S. pulchra does not result in a density sufficient to make this a useful plant for restoration projects. However, since bunchgrasses did not occur in monocultures in the pristine prairie, perhaps, a mixture of native perennials and annuals would be successful.

The observation by McNaughton (cited above), of an inverse relationship between site productivity and dominace by Stipa pulchra, suggests that fertilizing may not enhance restoration of bunchgrasses. This observation also would be supported by experiments of Garcia and Lathrop (1984) which showed that fertilization enhanced the production

of annual grasses far more than the production of S. pulchra. Huenneke et al. (1990) found that fertilizing with nitrogen and phosphorous significantly increased the growth of non-native annual grasses on sites with S. pulchra.

SOUTHERN CALIFORNIA SITES WITH PRISTINE VALLEY GRASSLAND

Figure 1 illustrates extant native grasslands in the state. The following areas in southern California have sizable populations of Stipa pulchra and/or other native bunchgrasses and are interpreted to be fragments of the pristine prairie (Oberbauer 1978, Goode 1981, Barry 1981, Howard 1981, Keeley personal observations). Some of these sites have excellent assemblages of native annual forbs which often generate spectacular spring colors. All sites have substantial non-native cover.

1. Cuyamaca Rancho (eastern San Diego Co.)
2. Santa Ysabel Valley (eastern San Diego Co.)
3. Warner Valley (eastern San Diego Co.)
4. Palomar Mountain State Park (eastern San Diego Co.)
5. San Onofre State Beach and other parts of surrounding Camp Pendleton (western San Diego Co.)
6. Santa Rosa Plateau, Nature Conservancy Preserve and surrounding areas still undeveloped (western Riverside Co.)
7. La Jolla Valley and other sites in Malibu Creek, Pt. Mugu and Leo Carrillo State Parks (western Ventura Co.)
8. Antelope Valley Poppy Preserve (northern Los Angeles Co.)
9. Hungry Valley State Recreation Area (northern Los Angeles Co.)

CONCLUSIONS

California grasslands are dominated on most sites by non-native annual species. These taxa invaded and became established on brush covered sites following repeated burning and on native perennial bunchgrass sites following drought and overgrazing. Pockets of the pristine perennial bunchgrass prairie are extant on disjunct sites throughout the state, and are in need of protection. Much more research will be needed before restoration techniques capable of returning non-native grasslands to their former type will be readily available.

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