

## PRE-AGRICULTURAL GRASSLAND IN CENTRAL CALIFORNIA

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### ABSTRACT

An increasingly dogmatic paradigm maintains that central California's pre-agricultural grasslands were once entirely dominated by the bunchgrass *Nassella pulchra*. Evidence from early records and current relict vegetation, however, indicates they were spatially diverse. In moderate precipitation areas *Nassella pulchra* frequently dominated grasslands in foothills and occasionally also on sandy valley floors, but grassland on heavier soils in valleys and on many hillslopes was dominated by the rhizomatous graminoids *Leymus triticoides*, *Carex barbarae*, and *C. praegracilis*. Dominance shifted to spring-active annual forbs in low precipitation areas and probably to summer-active annual forbs (tarweeds) on infertile old terrace soils.

### INTRODUCTION

When I was seeking remnant examples of native perennial prairie in 1994 as models for grassland restoration in California's Central Valley, it soon became evident that there were at least an order of magnitude more remnants dominated by the rhizomatous native perennial grass *Leymus triticoides* (Buckley) Pilger than by native bunchgrasses like *Nassella pulchra* (A. Hitchc.) Barkworth. This observation was surprising since conventional botanical wisdom at that time assumed herbaceous valley vegetation was formerly dominated by bunchgrasses before nineteenth century land use changes caused their almost total replacement by exotic annual grasses (Heady 1977).

Examination of such apparent paradoxes has gradually led to a reevaluation of long-standing assumptions about the valley's original natural vegetation. In 1981, for example, two Madroño papers questioned the then generally accepted bunchgrass dominance paradigm (BDP). Bartolome and Gemmill (1981) first showed *N. pulchra* is not well-adapted for dominating pristine herbaceous vegetation. Then, three months later, Wester (1981) provided historical evidence that well before the post-1850 cattle introduction traditionally blamed for the demise of bunchgrasses, they were either rare or entirely absent in the San Joaquin Valley, a significant part of the area they were traditionally assumed to dominate.

The BDP remained one of California botany's most dominant paradigms through the 1990's, however, despite these and numerous other studies. Late in the decade Hamilton (1997) systematically demonstrated its creation was motivated by pre-existing theory rather than strong evidence, but it is too soon to determine if his work significantly impacted the surprisingly durable BDP. Meanwhile many California Floristic Province vegetation surveys uncritically claim its grasslands were once covered by bunchgrass prairies dominated by *N. pulchra* (Barbour and Christensen 1993; Schoenherr 1992; Sims

1988), while others treat the BDP with only mild scepticism and fail to suggest alternative hypotheses (Barbour et al. 1993). One excellent survey of the state's vegetation in that period (Holland and Keil 1989) acknowledged Wester's work and questioned BDP, but local publication limited its impact until a new edition (1995) was issued by a national publisher. California native grassland restoration efforts consequently still emphasize creating bunchgrass prairies even where their former presence is highly unlikely (Harker et al. 1993; Dremann 1995).

Evidence for BDP rests on Clements' (1920, 1934) observation of *N. pulchra* stands along railroads in the San Joaquin Valley near Fresno and his subsequent conclusion they were relicts of a formerly widespread bunchgrass prairie that once covered most California Floristic Province valleys and foothills. Hamilton (1997) amply demonstrated, however, that this conclusion was heavily influenced by and made to fit grassland theories Clements had previously developed outside California. As discussed above, Bartolome and Gemmill (1981) also demonstrated that *N. pulchra* is a semi-ruderal species adapted to disturbed fire-prone habitats like those seen by Clements along railroads because its abundant seeds can readily germinate on bare ground and thus permit rapid colonization of sites where disturbance has temporarily reduced competition from other species. Ironically Clements' BDP is alive and well even though his more famous climatic monoclimate theory from which it arose was discredited and subsequently discarded (Daubenmire 1968; Krebs 1972; Mueller-Dombois and Ellenberg 1974).

The fully developed BDP has several key assumptions:

1. "*Stipa* (= *N.*) *pulchra*, beyond all doubt, dominated the valley grassland" (Heady 1977).
2. Following Küchler (1964), the largest single area of former valley grassland in California included much of the Central Valley.
3. Replacement of native bunchgrasses by the ex-

otic annuals that presently dominate California grasslands started with overgrazing in the 1850's and accelerated during severe drought in the 1860's.

#### OBJECTIVES AND METHODS

To determine if BDP's assumptions are accurate I looked for evidence about the nature of central California's pre-agricultural grasslands in two places:

1. Historical accounts describing central California grassland during the period their domination by bunchgrasses was assumed by BDP.

2. Vegetation surveys of central California grassland areas dominated by native species. These started along the Cosumnes River in southern Sacramento County where my interest in the BDP problem began but ultimately included several other areas of interest. Each survey consisted of a sample stand (relevé) in essentially homogeneous vegetation and used Braun-Blanquet's cover-abundance scale (Mueller-Dombois and Ellenberg 1974) to estimate cover of all vascular plant species in the stand. In the scale 5 = >75% cover, 4 = 50–75%, 3 = 25–50%, 2 = 5–25%, 1 = numerous but <5%, and + = few. The scale also includes r for solitary individuals but all such records were assigned to +.

#### RESULTS

##### Historical records

Central California bunchgrass prairies dominated by *N. pulchra* were first clearly described by Fremont (1848) in 1845 and Bryant (1985) in 1846, well before they were purportedly replaced by exotic annual grasses in the Central Valley. The bunchgrass prairies described by Fremont and Bryant were located, respectively, in the Sierra Nevada foothills and the inner Coast Ranges, however, and both authors clearly distinguished these upland prairies from quite different more continuous grasslands they found on the nearby Central Valley floor.

While traveling through the Sierra Nevada foothills in 1845, for example, Fremont reported that "Emerging from the woods, we rode about sixteen miles over an open prairie, partly covered with bunch grass, the timber reappearing on the rolling hills of the River Stanislaus in the usual belt of evergreen oaks." (Fremont 1848). A year earlier, in contrast, while camped at the site of the present city of Sacramento he found that "Here the grass is smooth and green, and the groves very open; the large oaks throwing a broad shade among sunny spots. . . ." (McKelvey 1955). In my opinion Fremont's contrasting observations distinguish between *Leymus triticoides* prairie, which has a smooth aspect and numerous relict stands near Sacramento, and *Nasella*-dominated bunchgrass prairie, which has a rough aspect and many relict stands in the Sierra foothills.

Bryant similarly clearly distinguished central California prairies observed just four days and about 45 miles apart on an 1846 journey between what are now Sacramento and Alameda counties:

"September 14.—We crossed the Coscumne river [sic] about a mile from our camp, and travelled over a level plain covered with luxuriant grass and timbered with evergreen oak, until three o'clock, when we crossed the Micklelemes river [sic] . . . where . . . . The soil of the bottom appears to be very rich, and produces the finest qualities of grass.

"September 18.—. . . From this plain we entered a hilly country, covered to the summits of the elevations with wild oats and tufts or bunches of a species of grass, which remains green through the whole season." (Bryant 1985).

It is clear Bryant on September 18 is describing his first observation of a *Nasella* species on hills near the present city of Livermore, where bunchgrass prairie relicts are still frequent. If the "luxuriant grass" he had seen four days earlier along the Cosumnes and Mokelumne rivers was also a bunchgrass, he would have said so. More likely it was *Leymus triticoides*, which still dominates numerous prairie relicts along those rivers and is the only common native or non-native Central Valley grass associated with oaks which would be "luxuriant" in September before irrigation was widely introduced to the Central Valley in the 1860's and 1870's (Hundley 1992).

Contrary to popular impression, the grassland vegetation of central California valley floors was clearly described well before 1850. Early accounts by travelers leave little doubt domination of valley grasslands by bunchgrasses like *N. pulchra* was generally absent in the period BDP assumes it occurred. Jedediah Smith, for example, camped twelve miles south of the American-Sacramento river confluence on February, 1828, and wrote: "The whole face of the country is a most beautiful green, resembling a flourishing wheat field". (Burcham 1957). The hummocky tussocks of bunchgrass prairies never produce smooth grass canopies characteristic of wheat fields, but relict native prairies near the site of Smith's camp (see below) still resemble wheat fields because of their domination by *L. triticoides*, a rhizomatous native perennial grass whose name reflects its strong resemblance to wheat.

Two years earlier, in 1826, Captain Beechey reported that three members of his expedition (Collie, Marsh, and Evans) described how a valley floor near what is now the border between San Mateo and Santa Clara counties "opened out on a wide country of meadow land, with clusters of fine oak free from underwood. It strongly resembled a nobleman's park" (McKelvey 1955). The European

parks familiar to members of this British expedition are dominated by stoloniferous or rhizomatous grasses like *Agrostis tenuis* Sibth. and *Poa pratensis* L. (Hessayon 1990; Jenkins 1994) resembling *L. triticoides* much more than non-rhizomatous *N. pulchra*. The site of this observation is now covered by highly urbanized "Silicon Valley", but relict native prairies dominated by *L. triticoides* are still present nearby at a sea level ecotone with saltmarsh located just across San Francisco Bay at Coyote Hills Regional Park (personal observation). Relict bunchgrass prairies dominated by *N. pulchra* do occur in hills east and west of the bay but are absent from plains near sea level.

A striking common feature of all these early accounts is the great similarity between what they reported and vegetation present in the same places today wherever landscapes have not been altered by agriculture or urbanization. That is not what the BDP predicts since it imagines California valleys were covered by *Nasella pulchra* before overgrazing in the 1850's and 1860's caused its replacement by exotic weedy species from Eurasia (Heady 1977). Traveler's reports from earlier periods make it clear, however, that two exotic Eurasian annuals, *Avena fatua* L. and *Erodium cicutarium* (L.) L'Hér., were common and dominant before 1850. Bryant's 1846 description, cited above, of wild oats and bunchgrass codominating a Coast Range hillside is a typical but not particularly early example of such reports (Bryant 1985). Oceanic pollen deposits of *E. cicutarium* in the Santa Barbara Basin demonstrate its abundance in the California Floristic Province by 1751–1765, well before California's first European settlement in 1769 and possibly the result of its introduction to the Baja Californian part of the province in the early 1750's by the Jesuit explorer Consag and subsequent explosive natural spread northward facilitated by openings created by pre-European burning. (Mensing and Byrne 1999). Its presence with *A. fatua* in adobe bricks of California's oldest European buildings (Burcham 1957) is consequently explained.

#### Vegetation surveys

Numerous small relict prairies are still extant in central California, where they are particularly frequent in Sacramento County near the places they were seen and described in the nineteenth century by Jedediah Smith, John C. Fremont, and Edwin Bryant. Most frequently these prairie remnants are dominated by *Leymus triticoides*, but two graminoid sedges, *Carex barbarae* Dewey and *C. prae-gracilis* W. Boott, are also often very important elements. Relict prairies near Sacramento occur both in the open and as groundcover in valley oak (*Quercus lobata* Nee) savannas, woodlands, and forests, which are all present at The Nature Conservancy's Cosumnes River Preserve in the southern part of the county. If "savanna" is interpreted

broadly enough to include open valley oak woodland, Griffin's (1977) statement "Relatively undisturbed savannas of *Quercus lobata* have not been available on prime alluvial soils for over a century ..." fortunately does not accurately describe the Cosumnes Preserve.

A variety of plant communities occur at the reserve in a sequence which changes with increasing distance from its streams. Riparian forest dominated by *Populus fremontii* S. Watson occurs in the immediate vicinity of the Cosumnes River and its associated sloughs but is replaced by closed-canopy valley oak forest a short distance away from them. As distance from the river and sloughs increases, space between valley oak crowns also progressively enlarges so a vegetation sequence from closed forest through open woodland to savanna is formed. This sequence appears to result from a correlation between distance from rivers and sloughs and increasingly unfavorable soil conditions that may include greater competition for groundwater (Walter 1979) rather than from historic land uses since it is most evident where signs of disturbance are scarcest. In the sequence at the preserve from closed forest to savanna, valley oak density per hectare declines from 540 to 2.7 and soil shifts from Cosumnes silt loam to Dierssen sandy clay loam. The former is an Aquic Xerofluent occurring on the Cosumnes River floodplain, and the latter, an Argic Durixeroll that is consequently much less permeable to both water and air, is on the rims of basins more distant from the river (Tugel 1991). The Cosumnes is one of California's few undammed rivers, and in most years large areas of the preserve are covered by winter flood waters, which often do not recede for several months.

At the preserve prairie vegetation is best developed as an understory in open valley oak forest. Cover estimates from twelve such stands are provided below (Table 1). All are on Cosumnes silt loam except 1 and 6, which respectively are on Dierssen sandy clay loam and Columbia sandy loam (Tugel 1991).

All the above stands were sampled between August and December, 1994, and are representative of open oak forest in the western and oldest part of the preserve. Some differences among them are evident, however. The lower valley oak cover of stand 3 indicates it is located at the open forest's outer edge ecotone with savanna, where soils become heavier and water stress greater. In contrast, significant *Vitis* and *Fraxinus* cover in stands 5–8 indicate their location is at open forest's inner edge ecotone with oak- and cottonwood- (*Populus*) dominated closed riparian forest, where soils are lighter and water stress reduced.

Similar open oak forest vegetation occurring on two recent additions to the preserve located east of its original oldest portion was sampled in May–June, 1995. The Orr Ranch addition, located immediately east of the original preserve, had been

TABLE 1. BRAUN-BLANQUET COVER-ABUNDANCE VALUES AND MEANS FOR SPECIES IN 12 OPEN OAK FOREST-RELICT PRAIRIE SAMPLE STANDS AT THE NATURE CONSERVANCY'S CONSUMNES RIVER PRESERVE. The cover class mean (with + assigned a value of 0.1) of each species is given at right.

Sample stand:	1	2	3	4	5	6	7	8	9	10	11	12	$\bar{x}$
<i>Quercus lobata</i>	5	5	4	5	5	5	5	5	5	5	5	5	4.9
<i>Leymus triticoides</i>	4	3	1		5	5	5	2	2	4	2	1	2.8
<i>Carex barbarae</i>	3	4		1							5	5	1.5
<i>Carex praegracilis</i>	1		2	3				5	5	3	2	1	1.8
<i>Rosa californica</i>	1	1		1			1		1	+	1	1	0.6
<i>Lolium multiflorum</i>	2	3	5	4									1.3
<i>Lactuca serriola</i>	1	1	1	1							1		0.3
<i>Toxicodendron diversilobum</i>	+	+	2			1	2		1	+			0.5
<i>Rumex crispus</i>	2	1		1									0.3
<i>Cichorium intybus</i>	+	+	2	+				1	+	1	1	1	0.5
<i>Convolvulus arvensis</i>	+												0.0
<i>Lotus corniculatus</i>	1		1						+				0.2
<i>Phyla nodiflora</i>	1								1				0.2
<i>Lotus purshianus</i>	+												0.0
<i>Lepidium latifolium</i>	1												0.1
<i>Carduus pycnocephalus</i>		+											0.0
<i>Atriplex triangularis</i>		+											0.0
<i>Raphanus sativus</i>		+											0.0
<i>Rumex conglomeratus</i>		+					+	1	+	1	1		0.3
<i>Cirsium vulgare</i>		+			1					+	+		0.1
<i>Picris echioides</i>		+		1	1			+	1	1	+		0.4
<i>Cordylanthus pilosus</i>			2					+					0.2
<i>Gylcyrrhiza lepidota</i>			2										0.2
<i>Lathyrus jepsonii</i>			1										0.1
<i>Asclepias fascicularis</i>			1	+									0.1
<i>Foeniculum vulgare</i>			+										0.0
<i>Plantago lanceolata</i>			+	+									0.0
<i>Plantago major</i>								+					0.0
<i>Barbarea vulgaris</i>				1				+					0.1
<i>Cyperus eragrostis</i>				+				1	1				0.2
<i>Fraxinus latifolia</i>				1	2	2	2	1	2	1	2	2	1.3
<i>Epilobium brachycarpum</i>				+									0.0
<i>Vitis californica</i>					2	1	3	1					0.6
<i>Aster chilensis</i>								+					0.0
<i>Mentha pulegium</i>								+					0.0
<i>Euthamia occidentalis</i>					1		1					1	0.3
<i>Rubus ursinus</i>					2		2	+	1	+			0.4
<i>Acer negundo</i>												2	0.3
<i>Cornus glabrata</i>													0.2
<i>Rubus discolor</i>							1		1	1			0.3
<i>Xanthium strumarium</i>							2				+		0.0
<i>Salix exigua</i>						2						1	0.1
<i>Asparagus officinalis</i>		+			+			1	1	1			0.3
<i>Rumex pulcher</i>		1	+										0.1

acquired a short time before the survey, while the Valensin Ranch, located somewhat farther east near Highway 99, was acquired by the preserve after the survey. The superior floristic richness of the addition surveys (Table 2) reflects their spring-summer (rather than summer-fall) timing and the outstanding condition of open oak forest at Valensin Ranch. The Orr Ranch sample is on Dierssen sandy clay loam and the Valensin on Liveoak sandy clay loam (Tugel 1991).

Not all vegetation at the Cosumnes Preserve is open oak forest. Three stands representative, respectively, of open savanna (OS), oak-dominated closed riparian forest (OR), and cottonwood-dom-

inated closed riparian forest (CR) sampled in September, 1994, are provided below in Table 3. The open savanna sample stand is on Dierssen sandy clay loam, and the two riparian forest sample stands are on Columbia sandy loam (Tugel 1991).

The great difference between savanna and closed riparian forest vegetation is evident in Table 3 since valley oak is their sole species in common. The oak and cottonwood dominated types of closed riparian forest are much more similar, however, and have many species in common since both are subject to frequent extended flooding. Such flooding also prevents development of a graminoid understory, and its absence readily distinguishes them from open

TABLE 2. BRAUN-BLANQUET COVER-ABUNDANCE VALUES AND MEANS FOR SPECIES IN 2 OPEN OAK FOREST-RELICT PRAIRIE SAMPLE STANDS LOCATED, RESPECTIVELY, AT ORR AND VALENSIN RANCHES IN THE NATURE CONSERVANCY'S COSUMNES RIVER PRESERVE.

Sample stand:	Valensin		
	Orr Ranch	Ranch	$\bar{x}$
<i>Quercus lobata</i>	5	5	5.0
<i>Leymus triticoides</i>	2	2	2.0
<i>Anthemis cotula</i>	2	+	1.1
<i>Cichorium intybus</i>	2		1.0
<i>Lolium multiflorum</i>	2	1	1.5
<i>Bidens frondosa</i>	1	+	0.6
<i>Stellaria media</i>	2	+	1.1
<i>Vicia sativa</i>	1		0.5
<i>Conium maculatum</i>	1	+	0.6
<i>Lythrum hyssopifolium</i>	1	1	1.0
<i>Carex praegracilis</i>	2	1	1.5
<i>Carex barbarae</i>	2	4	3.0
<i>Cyperus eragrostis</i>	+	1	0.6
<i>Lactuca serriola</i>	+	+	0.1
<i>Rumex conglomeratus</i>	1	1	1.0
<i>Raphanus sativus</i>	+	+	0.1
<i>Rumex crispus</i>	1	1	1.0
<i>Toxicodendron diversilobum</i>	1	+	0.6
<i>Sisymbrium officinale</i>	1	+	0.6
<i>Solanum americanum</i>	1	+	0.6
<i>Chenopodium ambrosioides</i>	1		0.5
<i>Sonchus oleraceus</i>	+		0.1
<i>Hordeum murinum</i>	+	+	0.1
<i>Bromus diandrus</i>	+	+	0.1
<i>Cirsium vulgare</i>	+		0.1
<i>Melilotus indica</i>	+		0.1
<i>Chlorogalum pomeridianum</i>	1	1	1.0
<i>Polygonum punctatum</i>		2	1.0
<i>Rumex pulcher</i>		1	0.5
<i>Rubus discolor</i>		+	0.1
<i>Xanthium strumarium</i>		1	0.5
<i>Ranunculus muricatus</i>		+	0.1
<i>Sonchus asper</i>		+	0.1
<i>Geranium dissectum</i>		+	0.1
<i>Rosa californica</i>		+	0.1
<i>Atriplex triangularis</i>		+	0.1
<i>Phyla nodiflora</i>		1	0.5
<i>Convolvulus arvensis</i>		+	0.1
<i>Stachys ajugoides</i>		+	0.1
<i>Brodiaea elegans</i>		+	0.1
<i>Ammi visnaga</i>		+	0.1
<i>Amaranthus albus</i>		+	0.1
<i>Anthriscus caucalis</i>		+	0.1
<i>Polypogon monspeliensis</i>		+	0.1
<i>Dipsacus fullonum</i>		+	0.1
<i>Maclura pomifera</i>		+	0.1
<i>Mimulus guttatus</i>		+	0.1
<i>Medicago arabica</i>		+	0.1
<i>Plantago major</i>		+	0.1
<i>Juncus xiphioides</i>		+	0.1

TABLE 3. BRAUN-BLANQUET COVER-ABUNDANCE VALUES FOR SPECIES IN REPRESENTATIVE OPEN SAVANNA (OS), OAK-DOMINATED CLOSED RIPARIAN FOREST (OR), AND COTTONWOOD-DOMINATED CLOSED RIPARIAN FOREST (CR) SAMPLE STANDS AT THE CONSERVANCY'S COSUMNES RIVER PRESERVE.

Sample stand:	OS	OR	CR
<i>Quercus lobata</i>	2	5	3
<i>Lolium multiflorum</i>	5		
<i>Distichlis spicata</i>	2		
<i>Lactuca serriola</i>	2		
<i>Rumex crispus</i>	1		
<i>Hirschfeldia incana</i>	2		
<i>Centaurea solstitialis</i>	1		
<i>Bromus hordeaceus</i>	2		
<i>Hordeum marinum</i>	2		
<i>Leymus triticoides</i>	2		
<i>Grindelia camporum</i>	1		
<i>Rumex pulcher</i>	+		
<i>Rubus ursinus</i>		5	1
<i>Vitis californica</i>		3	+
<i>Acer negundo</i>		2	
<i>Cyperus eragrostis</i>		2	2
<i>Rosa californica</i>		1	1
<i>Rubus discolor</i>		1	3
<i>Fraxinus latifolia</i>		1	3
<i>Cirsium vulgare</i>		1	
<i>Picris echioides</i>		1	1
<i>Rumex conglomeratus</i>		+	+
<i>Populus fremontii</i>			5
<i>Euthamia occidentalis</i>			2
<i>Plantago major</i>			1
<i>Oenanthе sarmentosa</i>			+
<i>Cephalanthus occidentalis</i>			2
<i>Polygonum punctatum</i>			1
<i>Artemisia douglasiana</i>			+
<i>Urtica dioica</i>			+

The lower cover of the native prairie grass *Leymus triticoides* in open savanna relative to open oak forest at the Cosumnes Preserve appears to contradict the early reports discussed above that suggest it once dominated many of California's open areas. Evidence of prairie remnants in open areas farther north in Sacramento County at the new Stone Lakes National Wildlife Refuge supports the reports, however, and suggests present scarcity of native prairie grass in the Cosumnes savannas results from former cultivation, which did not occur in the open forests. The preserve is now planting trees to restore extensive areas where they were removed to facilitate farming, but cultivation often occurred in the savannas without general removal of their widely scattered large valley oaks.

In June–July, 1995, two prairie remnants were located at Stone Lakes refuge in open grassland lacking valley oaks or other woody plants and subsequently sampled. The larger, which covered 930 m<sup>2</sup> and is on Dierssen sandy clay loam, is represented in Table 4 below by sample SL1, while the smaller, SL2, covered 56 m<sup>2</sup> and is on Clear Lake clay (Tugel 1991). Three contemporary samples

oak forest. Most species largely confined to the cottonwood-dominated phase of closed riparian forest, including *Populus fremontii* itself and *Cephalanthus occidentalis* L., are particularly adapted to very frequent flooding and associated coarse alluvial soils (Holstein 1984).

TABLE 4. BRAUN-BLANQUET COVER-ABUNDANCE VALUES FOR SPECIES AT FIVE SACRAMENTO COUNTY SAMPLE STANDS. Three (MC 1-3) are in oak forest along Morrison Creek and two (SL 1-2) are in relict prairies at Stone Lakes National Wildlife Refuge.

Sample stand:	MC1	MC2	MC3	SL1	SL2
<i>Quercus lobata</i>	5	5	5		
<i>Leymus triticoides</i>	1	4	5	5	5
<i>Rubus ursinus</i>	5		2		
<i>Sambucus mexicana</i>	1		1		
<i>Toxicodendron diversilobum</i>	2	1	2		
<i>Foeniculum vulgare</i>	+		1		
<i>Juglans hindsii</i>	+	+			
<i>Rubus discolor</i>	1		1		
<i>Cornus glabrata</i>	1				
<i>Rosa californica</i>	1				
<i>Vitis californica</i>	+		+		
<i>Prunus cerasifera</i>	+		1		
<i>Lactuca serriola</i>		2			
<i>Bromus diandrus</i>		2	+	2	
<i>Lolium multiflorum</i>		2	+		
<i>Stellaria media</i>		3	+		
<i>Sisymbrium officinale</i>		2			
<i>Sonchus oleraceus</i>		1	1		
<i>Rumex conglomeratus</i>		1	+		
<i>Raphanus sativus</i>		1	1	+	
<i>Convolvulus arvensis</i>		1	+	+	1
<i>Rumex crispus</i>		1	+		1
<i>Bidens frondosa</i>		1	+		
<i>Urtica urens</i>		+			
<i>Chenopodium berlandieri</i>		1	+		+
<i>Atriplex triangularis</i>		+	+		
<i>Chenopodium murale</i>		+			
<i>Xanthium strumarium</i>		+	1		2
<i>Asparagus officinalis</i>		+	1		
<i>Galium aparine</i>		+			
<i>Solanum americanum</i>			+		
<i>Lepidium latifolium</i>			+		
<i>Malva nicaeensis</i>			+		
<i>Cyperus eragrostis</i>			+		
<i>Avena fatua</i>				2	
<i>Vicia villosa</i>				2	
<i>Trifolium hirtum</i>				+	
<i>Hemizonia pungens</i>					1
<i>Rorippa palustris</i>					+
<i>Hirschfeldia incana</i>					1
<i>Helianthus annuus</i>					+
<i>Phyla nodiflora</i>					1
<i>Gnaphalium luteo-album</i>					+
<i>Anthemis cotula</i>					+
<i>Polygonum arenastrum</i>					1

from oak forest along Morrison Creek a short distance north of the refuge are provided for comparison. These resemble similar forest at the Cosumnes Preserve, and consist of one oak-dominated closed riparian forest sample, MC1, and two open oak forest samples, MC2 and MC3. All are on Egbert clay (Tugel 1991).

In July-August, 1995, five additional native prairie remnants varying in area from 230 to 470 m<sup>2</sup> and resembling the Stone Lakes remnants in having few woody plants were located and sampled on Coast Range hillslopes in northwestern Contra Costa County. They are represented below by samples

CC 1-5 in Table 5. CC 1 and 2 are on Sehorn clay, CC 3 and 4 are on Millsholm loam, and CC 5 is on Clear Lake clay (Welch 1977).

#### DISCUSSION

Several theoreticians important in the first half of the twentieth century like J.C. Willis, Sigmund Freud, and Frederic Clements later fell from favor when it became clear their theories did not describe reality. That happened for Clements in at least two areas. He was a leading American opponent of Darwinian evolution (Hagen 1992), the central para-

TABLE 5. BRAUN-BLANQUET COVER-ABUNDANCE VALUES AND MEANS FOR SPECIES AT 5 RELICT PRAIRIE SAMPLE STANDS ON COAST RANGE HILLSLOPES IN NORTHWESTERN CONTRA COSTA COUNTY.

Sample stand:	CC1	CC2	CC3	CC4	CC5	$\bar{x}$
<i>Leymus triticoides</i>	3	4	5	5	5	4.4
<i>Silybum marianum</i>	1				+	0.2
<i>Carduus pycnocephalus</i>	1	1	2	2	2	1.6
<i>Sonchus oleraceus</i>	1					0.2
<i>Lactuca serriola</i>	1	1	1	1	1	1.0
<i>Avena fatua</i>	2	1			1	0.8
<i>Brassica nigra</i>	4					0.8
<i>Toxicodendron diversilobum</i>		2				0.4
<i>Aira caryophylla</i>	3		2	2		1.4
<i>Vulpia myuros</i>	2	2	2	2		1.2
<i>Conium maculatum</i>			1			0.2
<i>Epilobium brachycarpum</i>			1	1		0.4
<i>Picris echioides</i>			1		1	0.4
<i>Brassica rapa</i>			1		1	0.4
<i>Chlorogalum pomeridianum</i>			1			0.2
<i>Hirschfeldia incana</i>			1			0.2
<i>Clarkia unguiculata</i>			2	1		0.6
<i>Madia gracilis</i>			2			0.4
<i>Phleum pratense</i>			2			0.4
<i>Sonchus asper</i>			1			0.2
<i>Bromus madritensis</i>			1			0.2
<i>Scrophularia californica</i>				+		0.0
<i>Amsinckia menziesii</i>				1		0.2
<i>Gnaphalium californicum</i>				1		0.2
<i>Geranium dissectum</i>					1	0.2
<i>Bromus diandrus</i>					1	0.2

digm of biology, and developed monoclimate theory, which assumed vegetation in each climate zone converges toward a common type (Hamilton 1997). Monoclimate was long influential but has gradually failed as evidence accumulated that climate is one of the least stable environmental factors. In California, for example, the climate 150 years ago in the Little Ice Age was significantly colder and wetter than at present during the lifetimes of many individual trees in old growth forests (Bradley 1999; Fagan 2000).

Theories inaccurately describing reality are clearly social constructions even when arising within science, but recently some elements in the humanities have claimed all science and even reality itself is a social construct (Gross and Levitt 1994; Sokal and Bricmont 1998). Such claims may just be new weapons in an old war for academic influence, but science still needs to police itself and eliminate any lingering social constructs it still contains. The BDP appears to be a good example, but Clements should not entirely be blamed for that. He eventually recognized *Leymus triticoides* formerly dominated much of the Central Valley (Clements and Shelford 1939), but by that time his academic influence had waned (Hagen 1992) and the world was more preoccupied by war than science. It was later figures like Heady (1977) who provided the dogmatic character of today's BDP. Before then opinion regarding California grassland ecology was more eclectic. The conclusions of Biswell (1956) and

Burcham (1957), for example, are generally compatible with my field observations; those of Heady are not.

So what were California's pre-agricultural grasslands really like? The vegetation samples reported above and numerous other field observations suggest sufficient relict evidence remains to reasonably reconstruct their basic nature. *Leymus triticoides* dominated most central California grasslands on sites with clay or loam soil, flat to moderately sloping topography, precipitation above 250 mm per year, and moderate to high fertility. Relict stands of *L. triticoides* are frequent on such sites, but more often they are dominated by *Lolium multiflorum* Lam., *Bromus diandrus* Roth, or *Avena fatua*. Similarly frequent relict stands of *Nassella pulchra* suggest pre-agricultural dominance shifted to it on sites with steeper slopes, coarser soils, and lower fertility; which today are most frequently dominated by *Bromus hordeaceus* L., *Avena barbata* Link, *Cynosurus echinatus* L., and *Taeniatherum caput-medusae* (L.) Nevski. Wester (1981) previously argued that arid valleys like the southern San Joaquin with precipitation <250 mm per year were pre-agriculturally dominated by annual rather than perennial species. Such annuals were largely spring-active forbs.

Three interesting questions remain:

1. Is *L. triticoides* always *L. triticoides*?

Stebbins and Walters (1949) concluded from

their chromosome and hybridization studies of *L. triticoides* and *L. condensatus* (C. Presl) A. Löve that much of the grass traditionally called *L. triticoides* in central California is actually a largely sterile hybrid between that species and *L. condensatus*. They strongly implied the hybrid, which they called *Elymus triticoides* Buckl. ssp. *multiflorus* Gould and distinguished from typical *L. triticoides* by its possession of 3 to 7 rather than 2 spikelets per central spike node, is much more common than either of its parents and includes all hillslope populations like those from northwestern Contra Costa County sampled above. I don't doubt their conclusions since the senior author's contributions to California plant evolution remain unequalled and partial sterility arising from natural hybridization accounts for the rarity of viable seed in the central California grass currently most often called *L. triticoides*. Nevertheless, the current name for *E. triticoides* ssp. *multiflorus* is *L. ×multiflorus* (Gould) Barkworth, a grass far too large (Barkworth 1993) to match Stebbins and Walters' abundant hybrid or any of the *Leymus* populations sampled above. Recent central California local floras (Best et al. 1996; Ertter 1997; Matthews 1997; Oswald and Ahart 1994) also fail to follow Stebbins and Walters' taxonomy since all treat *L. triticoides* as common and *L. ×multiflorus* as rare to completely absent. Hybrid or not, the common central California *Leymus*, because of its small size and strongly rhizomatous habit, is physiognomically close to typical *L. triticoides* and distant from *L. condensatus*, which is only weakly rhizomatous and one of California's largest native upland grasses. All stands sampled above matched *L. triticoides* in size and were strongly rhizomatous; so much so that stands and single clones were probably often equivalent. Consequently the name *L. triticoides* is applied here to all samples even though, following Stebbins and Walters (1949), it is likely their fertility is depressed through introgression from the *L. condensatus* genome.

2. If the BDP is wrong, why is *Nassella pulchra* at Jepson Prairie?

*Nassella pulchra* is common on the Central Valley floor in at least one place, the Jepson Prairie Preserve located in Solano County at the northern edge of the Montezuma Hills. Since the preserve has generally flat topography, the above discussion might lead to the expectation it is dominated by *Leymus triticoides*, which is actually rare to absent there. How is that accounted for? One explanation, of course, is that the BDP is true despite arguments against it provided here. Wester (1981) provided another when he concluded "Areas of bunchgrass [at Jepson Prairie] occupy relatively moist sites influenced by the cool, humid, maritime air able to penetrate to this part of the Central Valley through the San Francisco Bay gap. These conditions are not typical over the remainder of the Valley." His

conclusion has merit since the distribution of *Nassella pulchra* in California closely matches oak woodland (Beetle 1947; Dremann 1987), and several species associated with that vegetation type occur on the Central Valley only where the flow of maritime air is strongest. Examples are the occurrence of the trees *Quercus agrifolia* Nee and *Aesculus californica* (Spach) Nutt. (Griffin and Critchfield 1972; personal observation) and the mammals *Sylvilagus bachmani riparius* (riparian brush rabbit) and *Neotoma fuscipes riparia* (riparian woodrat) (Zeiner et al. 1990) in a localized area of the Central Valley floor that includes San Joaquin and southern Sacramento counties. What Wester's hypothesis does not explain is why *L. triticoides* rather than *N. pulchra* is dominant in northwestern Contra Costa County, where flow of maritime air is even stronger than at Jepson Prairie.

As discussed above, *L. triticoides* is favored by heavy clay and loam soils and *N. pulchra* by lighter ones since bunchgrasses are better adapted for drought stress than rhizomatous grasses (Grime 1979). The clay favored by *L. triticoides* holds more water than the light, frequently sandy soils hosting *N. pulchra* (Kramer 1969), and the latter's usual occurrence on slopes also accelerates runoff and consequent drought stress. In northwestern Contra Costa County, for example, *L. triticoides* occurs on a series of relatively heavy soils: Clear Lake, Diablo, and Sehorn clays; Conejo, Lodo, and Los Osos clay loams; and Los Gatos, Millsholm, and Tierra loams (Welch 1977). At Jepson Prairie, in contrast, *N. pulchra* occurs on a light soil, San Ysidro sandy loam (Bates 1977); an environmental factor accounting for the vegetational difference between the two relict prairie areas better than maritime air flow. Light soils may also account for Clements' momentous observation of *N. pulchra* near Fresno since a large area of sandy soil derived from Kings Canyon's glacial outwash occurs near there (Storie and Weir 1951). Even on generally flat valley floors aeolian movement of sand creates hummocky microtopography (Selby 1985) containing small versions of the slopes favored by *N. pulchra*. Grassland on sandy soil is among California's least known vegetation types since its ease of cultivation made it particularly attractive to early valley farmers. Consequently a high percentage of California's extinct plant species (e.g., *Eriogonum truncatum* Torrey and A. Gray and *Monardella leucocephala* A. Gray) were associated with sandy grassland (Skinner and Pavlik 1994). *N. pulchra* at Jepson Prairie now faces a different threat, overprotection. It has steadily declined there since preserve establishment eliminated even the light grazing required to maintain grass diversity by causing release from exotic annual competition (Howe 1999). Ironically grazing elimination at Jepson Prairie was motivated by BDP myths.

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