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DISTRIBUTION OF THE NATIVE GRASSES OF CALIFORNIA

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H I L G A R D I A

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DISTRIBUTION OF THE NATIVE GRASSES OF CALIFORNIA[1]

ALAN A. BEETLE[2]

THE GRASSES, supplemented by certain legumes, form the principal basis for range wealth. The natural forage value of the Gramineae as a whole makes an intensive study of their characteristics important, for the broader the knowledge concerning them the more readily may any problem be met. The following paper presents a picture of the current distributions of grasses in California, together with evidences of their floral origins by migration from other regions.

Vegetation has many characteristics which are not always apparent at first glance. For instance, certain elements of the vegetation are native in their location, some are native elsewhere and have only recently been introduced. Some are old species often representative of a primitive condition in their genus, still others appear to be recently evolved. Some of the migrants arrived in California from the north during glacial periods, some crossed the ocean, and others came from the south during interglacial periods. Some plants are distributionally restricted for a number of reasons, including: (1) specialization as to habitat or environmental repression, as the species of vernal pools; (2) recent origin (plants sometimes referred to as neoendemics or initiates), as the endemic varieties of *Distichlis spicata;* (3) ancient origin (paleoendemics or relics); and (4) genotypic specialization (genetic endemics). The limiting factors controlling distribution of grasses are then not always easily recognized, but some attempt has been made to appraise these historical and ecological factors which contribute to an understanding of the present botanical composition of the California rangeland.

Introduced grasses are frequently mentioned in order to complete the overall picture or because of contrast in distributional behavior. Principal attention is paid, however, to the native species, the limits of whose areas are stabilized by climatic and edaphic features interacting over a long period of time. Distributions of 184 California grasses are shown in the maps on pages 319–339. Not all the native species have been mapped but those omitted would not contribute anything new or disturbing. A few introduced species have been mapped where their area of adaptability seemed limited and already occupied.

[1] Received for publication June 20, 1946.

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The first comprehensive list of the grasses of California was made by Bolander (1864–65).[3] At that time he knew 112 species of grasses growing without cultivation, of which 31 were introductions. Soon thereafter Thurber (1880) listed 175 graminaceous species for the state. Now some 400 grasses are known, about one fourth of which are introductions. For convenience in handling the material presented in this study, California has been divided into areas on the basis of recurrent distributions. Neither these areas nor the habitats into which they may be subdivided are wholly contiguous in all their parts. Complex in the same way as biological units, distribution patterns are recognizable but not always disjunct. There are exceptions and overlappings.

THE NORTHERN FLORAL UNITS IN CALIFORNIA

The northern floral units in California occupy the mountain ranges of northern California southward in the Coast Ranges to Monterey Bay and southward in the Sierra Nevada to Tulare County; the mountain peaks of southern California, particularly the San Bernardino and San Jacinto mountains. This delimitation is arrived at after studying the distributions of the native grasses of northern California. Although not all grasses discussed under this heading occupy this whole area they all fall within its limits and are not found outside it. This area is by far the richest in California in numbers of Gramineae. The grasses are consistently of such typically north-temperate genera as *Melica, Festuca, Poa,* and *Glyceria.* They have all come to California from the north. One half or better are of the tribe Festuceae, about one fourth are of the Agrostideae, one eighth are of the Aveneae, and the remaining one eighth represent all other tribes.

The inclusion of northern California and the coastal pine forests with the Sierra Nevada as a homogeneous floral unit is substantiated by Cooke (1940, 1941) who, in two lists containing 487 species, varieties, subspecies, and forms, could find "no endemic plants"; most of the plants were "fairly common" though this uniform picture may have been disturbed partially by Swallen's subsequent description (1941) of *Glyceria cookei* (map 89). The endemic nature of *Panicum shastense* (map 93) is open to question and depends upon the interpretation of specific limits in *Panicum.*

The pine woods offer the only relief for the agrostologist from the host of introductions that have so altered the aspect of the California flora. Here, alone, native grasses are encountered to the near exclusion of all aliens. Their history is undoubtedly connected with that of the coniferous forests. If the fossil records of these conifers could be coördinated with the known ranges of the grass species and their nearest relatives, considerable light should be shed on the origin of many California grasses.

Northern Grasses That Reach Their Southern Limit in California (maps 1 to 27).—The general predominance of species of or from northern floras that are characteristic of northern California is emphasized when one picks up a flora of Nova Scotia (Dore and Roland, 1941–42) or of Alaska (Scribner and Merrill, 1910) and finds listed in either not only genera but species typical of the northern California floral unit—for example, *Agro-*

[3] See "Bibliography" for complete citations, referred to in the text by author and date of publication.

pyron trachycaulum, Alopecurus aequalis (map 60), *Cinna latifolia* (map 36), *Calamagrostis canadensis* (map 42), *Deschampsia caespitosa* (map 2), *Koeleria cristata* (map 58), *Trisetum spicatum* (map 35), *Poa palustris,* and *Festuca ovina* (map 55). Of these species, three—*Trisetum spicatum, Deschampsia caespitosa,* and *Koeleria cristata*—reappear in South America, as do *Phleum alpinum* (map 5), *Deschampsia danthonioides* (map 66), *D. elongata* (map 67), and a near relative of *Melica subulata* (map 9).

Of similar wide distribution northward are *Poa pratensis* (map 1), *Agrostis hiemalis* (map 3), *A. exarata* (map 17), *Glyceria pauciflora* (map 7), *G. borealis* (map 11), *G. striata* (map 22), *Festuca rubra* (map 8), *F. subulata* (map 15), *Beckmannia syzigachne* (map 13), *Puccinellia distans* (map 23), and *Deschampsia atropurpurea* (map 26). These grasses are never found in the Great Valley. They are, however, of wide distribution within the limits defined above—that is, they cover a considerable altitudinal range, often occurring in both the Coast Ranges and the Sierra Nevada. In the Coast Ranges they are not found south of Monterey Bay and in southern Sierra Nevada they are not found between Tulare County and the San Bernardino Mountains.

Of somewhat narrower distribution northward but of similar occurrence in California are *Glyceria elata* (map 4), *Trisetum cernuum* var. *canescens* (map 6), *Poa cusickii* (map 10), *Festuca idahoensis* (map 14), *Melica spectabilis* (map 19), *Festuca occidentalis* (map 21), *Puccinellia lemmoni* (map 25), and *Calamagrostis rubescens* (map 27).

Even more restricted but still within the same pattern are *Melica fugax* (map 12), *Festuca subuliflora* (map 20), and *Scribneria bolanderi* (map 24).

The continuous chain of the Sierran peaks is finally broken in Tulare County. A considerable element of the grass flora has, however, been able to bridge the barrier presented by the intervening low elevations and reappears on the San Jacinto, San Bernardino, and other peaks of southern California. The majority of these are found in the San Bernardinos; fewer are known from the other peaks. Species exemplifying this hiatus include, in part:

Agrostis exarata (map 17)
Phleum alpinum (map 5)
Agrostis idahoensis (map 39)
Deschampsia caespitosa (map 2)
Muhlenbergia filiformis (map 37)
Poa bolanderi (map 38)
Muhlenbergia richardsonis (map 40)
Festuca ovina (map 55)
Muhlenbergia andina (map 46)
Festuca viridula (map 48)
Glyceria elata (map 4)

Here they join a small group of grasses including *Muhlenbergia californica* (map 108), *Poa atropurpurea,* and *P. longiligula* (known also from Rock Creek Lake Basin, Inyo County), which are isolated in range but related to the Sierran species. They have not, on the other hand, been able to bridge the gap between these mountains and those of Mexico. True, *Agrostis exarata* is found in Mexico, but its migrational path was not south in the California Sierra Nevada but rather southward in the Rocky Mountain chain through New Mexico and western Texas.

Few annuals are really characteristic of this zone, and these usually occur only at the lower elevations; they are far outranked by the large number of perennials. Some of the introduced annuals listed under open range and

savanna, because of their wide tolerance and ready adaptability, are easily found here, but so are *Aira praecox* and *Festuca myuros,* which occur only within the area defined. The natives include *Festuca microstachys, Muhlenbergia filiformis,* and *Poa bolanderi. Muhlenbergia filiformis,* usually listed as a perennial, is treated here as an annual (or at least a very short-lived perennial) because it occurs on sandy stream banks and open washes associated with other very characteristic and typically tiny, annual species including *Eleocharis bella, Cyperus aristatus,* and many others.

The mountain meadows contain an impressive list of economically important introduced perennials:

Agropyron cristatum
Agropyron repens
Agrostis alba
Anthoxanthum odoratum
Arrhenatherum elatius
Bromus inermis
Dactylis glomerata
Festuca elatior
Phleum pratense
Poa bulbosa
Poa compressa
Poa pratensis

Except for sweet vernal grass (*Anthoxanthum odoratum*), a filler usually planted only for the fragrance it gives to hay, all the above introductions are of considerable economic importance. There can be no doubt that meadows in which they are well established are a greater economic resource to their owners than are mountain meadows, usually dominated by *Carex,* where the native vegetation is undisturbed. It must be remembered, however, in attempting to establish these grasses, to which areas of the state they are adaptable. It is not at all surprising that Sampson (1944) had no success in his attempts to reseed burned areas in the chaparral belt with six of the above listed species.

Agrostis alba and *Poa pratensis* have long been known in commercial seed mixtures. They were first brought into cultivation in the Old World and were among the first plants sown for hay in this country by settlers, the origin of the seed being the markets of the Old World. It has then usually been assumed that these grasses were introduced in all their occurrence in this country. Present-day study of ecotypes suggests that these species may have had a panboreal distribution and may have arrived in North America long before the white man. Subsequent crossing of the introduced with the native strains would have complicated the study of the origin of these grasses.

Grasses of High Elevations in the Sierra Nevada (maps 28 to 54).—Many grasses which are common at high elevations (about 7,000 to 9,000 feet) in the Sierra Nevada are not found elsewhere in California, except in the northern Inner Coast Range. In the Sierra Nevada they follow the mountains to Tulare County and then frequently reappear in the San Bernardino Mountains. They are not known in the Great Valley. A few that fit this California pattern are of a very widespread distribution northward—for example, *Trisetum spicatum* (map 35), *Cinna latifolia* (map 36), *Calamagrostis canadensis* (map 42), *Bromus ciliatus* (map 47), and *Danthonia intermedia* (map 51). Most of these grasses are more characteristic of a more restricted area—from British Columbia to Montana southward to California and New Mexico—for example, *Agrostis thurberiana* (map 28), *A. idahoensis* (map 39), *A. rossae* (map 43), *Bromus suksdorfii* (map 45), *Melica stricta* (map 29), *M. bulbosa* (map 44), *M. aristata* (map 30), *Poa pringlei* (map 31), *P. epilis*

(map 32), *P. bolanderi* (map 38), *Glyceria erecta* (map 33), *Danthonia unispicata* (map 34), *Muhlenbergia filiformis* (map 37), *M. andina* (map 46), *M. montana* (map 53), *Festuca viridula* (map 48), *Trisetum wolfii* (map 50), and *Stipa webberi*. Only a few are endemic to the Sierra Nevada—for example, *Trisetum cernuum* var. *projectum* (map 54), *Oryzopsis kingii*, and *Calamagrostis breweri* (map 41).

Alpine Grasses (maps 55 to 60).—There are only six truly alpine grasses in California, namely *Alopecurus aequalis* (map 60), *A. geniculatus* (map 59), *Glyceria californica* (map 57), *Koeleria cristata* (map 58), *Poa rupicola* (map 56), and *Festuca ovina* (map 55). The small number of alpines is remarkable and attests the youthfulness of the present alpine peaks. The species are specialized representatives, closely related to other members of their genera found on the lower slopes. None is endemic to the Sierra Nevada. Although isolated in the Sierran part of their range, specific differences have not been found in the Sierran material of *Koeleria cristata*, *Alopecurus geniculatus*, and *A. aequalis*.

Russell (1926) in his discussion of California climates states that "a narrow strip in the High Sierra . . . [is] mapped as Tundra Climate. . . . This treeless alpine area differs sufficiently from the Microthermal area to justify its being placed in another type and there is little doubt that it meets the Köppen requirement of having all monthly means below 50°F." The true alpine grasses of California are closely confined to this narrow strip, at least in their high Sierran phase.

Grasses of the Northern Coast Ranges and Low to Middle Elevations in the Sierra Nevada (maps 61 to 81).—Still following the pattern of the grasses of northern California—that is, in the Coast Ranges to Monterey Bay, in the Sierra Nevada to Tulare County, and reappearing on the peaks of some southern California ranges—are a group whose center of abundance is in the northern Coast Ranges but which occur also in the Sierra Nevada, usually at low elevations. These grasses are again of northern origin, and in most cases represent different species of the same genera already mentioned. They tend to have narrower distributions, mostly within the limits of British Columbia to Idaho and southward to California—for example, *Melica geyeri* (map 61), *M. harfordii* (map 62), *M. californica* (map 63), *Festuca elmeri* (map 64), *Poa rhizomata* (map 65), *Panicum occidentale* (map 69), *Panicum pacificum* (map 70), *Stipa lemmoni* (map 72), *Festuca californica* (map 74), *Poa howellii* (map 75), *Bromus orcuttianus* (map 79), *B. vulgaris* (map 81), and *B. laevipes* (map 80). Only two—*B. grandis* (map 73) and *Melica torreyana* (map 76)—are actually confined to California.

Grasses of the Northern Coast Ranges (maps 82 to 99).—This final group occupying northern California contains species mostly endemic to California and usually of very restricted range. They are, again, all found northward from Monterey Bay, and thus form a strong contrast to the Coast Ranges from Monterey Bay southward to San Diego County wherein there is not known a single endemic of narrow or restricted range.

Characteristic of the Outer Coast Range and extending into Oregon are *Deschampsia caespitosa* var. *holciformis* (map 90), *Hierochloe occidentalis* (map 91), *Phalaris californica* (map 92), and *Calamagrostis nutkaensis*

(map 98). Near the coast are the very rare *Hystrix californica* and *Agrostis californica* (map 99). More obviously specialized in habitat are *Poa napensis* (map 87) from a hot spring and *Calamagrostis crassiglumis* (map 95) from sphagnum bogs. Of the three species of *Pleuropogon*—*P. refractus* (map 84), *P. davyi* (map 85), and *P. californicus* (map 83)—two are endemic to California but fit the general scheme of northward relationship, for the only remaining known species in the genus are the very restricted *P. oregonus* and the circumboreal *P. sabinii.*

GREAT BASIN AND DESERT FLORAL UNITS IN CALIFORNIA

Desert Grasses (maps 100 to 126).—Species on nonalkaline soils in the desert include:

Native perennials
- *Aristida adscensionis* (map 118)
- *Aristida californica* (map 119)
- *Aristida divaricata* (map 120)
- *Aristida fendleriana* (map 121)
- *Aristida glabrata* (map 122)
- *Aristida glauca* (map 123)
- *Aristida parishii* (map 124)
- *Aristida purpurea* (map 125)
- *Aristida wrightii* (map 126)
- *Bouteloua aristidoides* (map 114)
- *Bouteloua barbata* (map 115)
- *Bouteloua curtipendula* (map 116)
- *Bouteloua gracilis* (map 100)
- *Bouteloua rothrockii* (map 117)
- *Hilaria rigida* (map 104)
- *Panicum urvilleanum* (map 103)
- *Poa bigelovii* (map 110)
- *Triodia pulchella* (map 113)

Native annuals
- *Cenchrus echinatus*
- *Cenchrus pauciflorus*

Introduced annual
- *Schismus barbatus*

Weeds of cultivated land
- *Eriochloa gracilis*
- *Eriochloa aristata*
- *Hordeum jubatum*
- *Leptochloa filiformis* (map 101)
- *Leptochloa uninervia* (map 102)

Introduced or subtropical economic grasses
- *Oryzopsis miliacea*
- *Panicum miliaceum*
- *Chloris gayana*
- *Chloris virgata*
- *Cynodon dactylon*

In connection with the flora of the extreme southern desert part of California, it is of interest to review the influence of the tremendously rich Mexican flora (Conzatti, 1943; Johnston, 1943) on that of California. The Mexican flora has roughly twice the number of native species that occur in California. This would indicate that so far as the grasses are concerned the relatively more stable geologic conditions that have existed in Mexico have been more favorable for the development and persistence of species than have the fluctuations in sea level, the glaciation, and the mountain unrest that have characterized California's past. Moreover, the sea and desert barriers that have existed through much of the past have been so effective in preventing a free interchange of species that, except for desert species and a few other exceptions the two floras are entirely distinct.

Although perhaps the best indicator species are tall, stiff *Hilaria rigida* (map 104) on the flats and low, fluffy *Triodia pulchella* (map 113) on the rocky slopes, in numbers *Aristida* (nine species) (maps 118 to 126) and *Bouteloua* (five species) (maps 100, 114 to 117) dominate the desert grass flora. This flora, in contrast to all the others found in California, has its strongest ties eastward and southward. *Bouteloua, Aristida,* and *Muhlenbergia* are well represented in the Mexican flora, each having one or two species in common with South American floras and in South America a second center of diversification. Clements (1934) postulates the "transformation of southeastern California from bunch-grass prairie to desert as a consequence of climatic changes" and describes *Hilaria rigida* as "derived directly from the adaptation of *Hilaria jamesii* (map 140) to a drying climate."

The close ties between the temperate floras of North and South America, already shown in the Sierran and Great Valley floras, are further demonstrated by the presence of these desert elements common to both hemispheres:

Aristida: compare the distributions of *A. ternipes* Cav. and *A. capillacea* Lam.
Bouteloua curtipendula (Griffiths, 1912)
Cenchrus echinatus (Hitchcock and Chase, 1920)
Cenchrus pauciflorus (Hitchcock and Chase, 1920)
Distichlis spicata (Hitchcock, 1927; Beetle, 1943*a*)
Muhlenbergia asperifolia (Hitchcock, 1927; Parodi, 1928; Beetle, 1943*c*)
Panicum urvilleanum (Hitchcock, 1935)
Sporobolus argutus (Hitchcock, 1927)
Stipa speciosa (Hitchcock, 1927)

In direct contrast to this North and South American relationship between the species of *Bouteloua, Muhlenbergia, Aristida,* and other genera is the situation in *Hierochloe.* The seven South American species of this genus (Parodi, 1941) show no immediate relationship to those of North America. They are concentrated in Magellanic floras (where *Muhlenbergia, Bouteloua,* and *Aristida* are entirely absent) and are linked to New Zealand by *Hierochloe redolens* ("Habita en el Ecuador, en el sur de Chile, y Argentina y en Nueva Zelandia"). Here is the strongest possible evidence in support of panantarctic dispersals.

Species of desert alkaline flats include:

Distichlis spicata var. *divaricata* (map 111)
Puccinellia parishii (map 112)
Sporobolus airoides
Sporobolus contractus (map 106)
Sporobolus cryptandrus

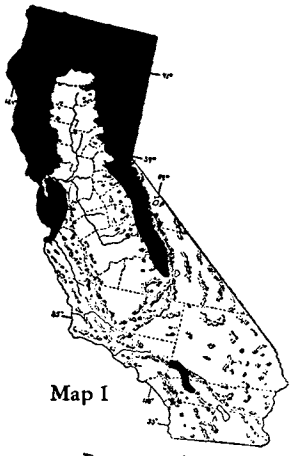
Great Basin Grasses.—The Great Basin has contributed a large number of grasses to the borders of California—that is, to the areas that lie eastward or southward of the Sierran crest, which has been almost without exception an effective barrier to their further dispersal. These Great Basin grasses include a number of alkali-tolerant species, *Poa ampla* (map 131), *Poa nevadensis* (map 132), *Puccinellia nuttalliana* (map 134), *Distichlis spicata* var. *stricta* (map 133), *Spartina gracilis* (map 137), and *Muhlenbergia asperifolia* (map 139). The other, alkali-intolerant species include a small but diverse Great Basin (and Colorado Desert) element:

Agropyron smithii (map 143)
Agropyron spicatum (map 144)
Blepharidachne kingii (map 127)
Elymus cinereus (map 136)
Festuca kingii (map 128)
Hilaria jamesii (map 140)
Oryzopsis hymenoides (map 138)
Poa fendleriana (map 129)
Poa leptocoma (map 130)
Stipa comata
Stipa speciosa (map 142)
Stipa williamsii (map 141)
Triodia mutica (map 135)

These Great Basin species occupy the area of transition between the mountains and the desert. The group meets the desert grasses in central San Bernardino County but in general does not overlap their distribution.

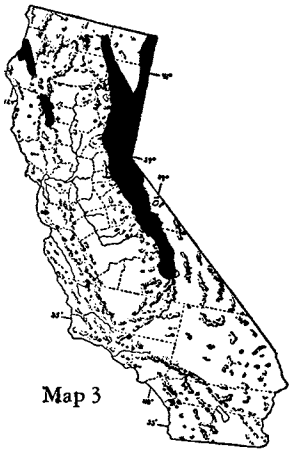
DISTRIBUTION MAPS FOR CALIFORNIA GRASSES

IN THE MAPS on the following pages, grasses with similar distributions are grouped together. Most of the grasses included are native species, but not all native species discussed in this paper are mapped. Those omitted would not affect the conclusions of the paper. The few introduced species mapped are ones that seem to have fully occupied the area to which they are adapted—that is, ones whose distribution has become relatively stable.



Poa pratensis

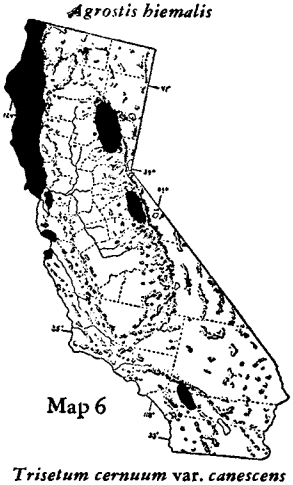
Deschampsia caespitosa



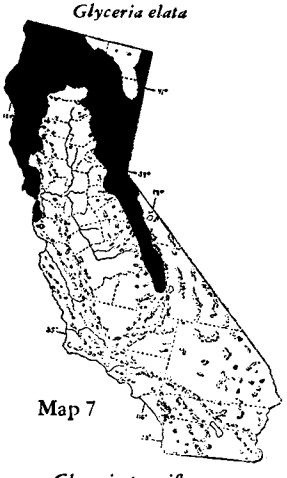
Agrostis hiemalis

Glyceria elata

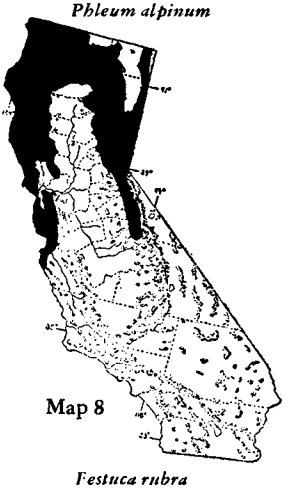
Phleum alpinum



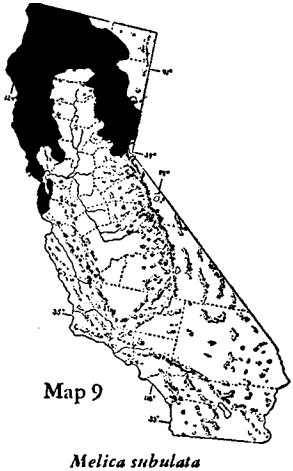
Trisetum cernuum var. *canescens*



Glyceria pauciflora



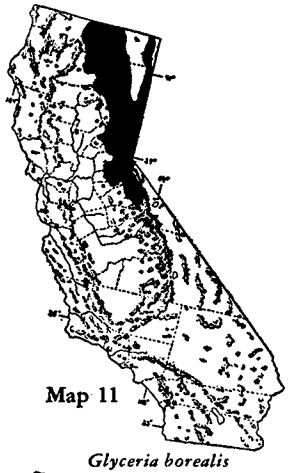
Festuca rubra



Melica subulata

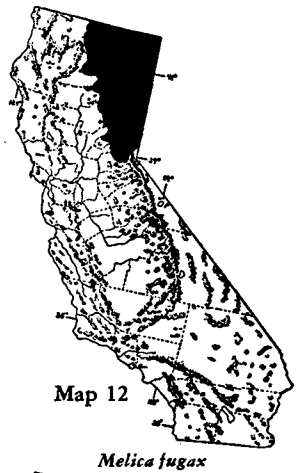
Map 10

Poa cusickii



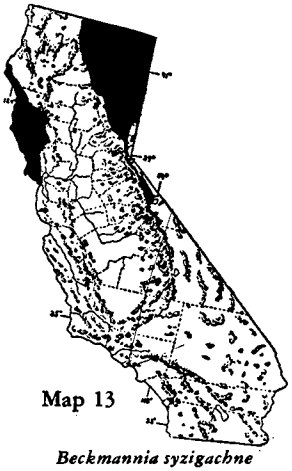
Map 11

Glyceria borealis



Map 12

Melica fugax



Map 13

Beckmannia syzigachne

Map 14

Festuca idahoensis

Map 15

Festuca subulata

Map 16

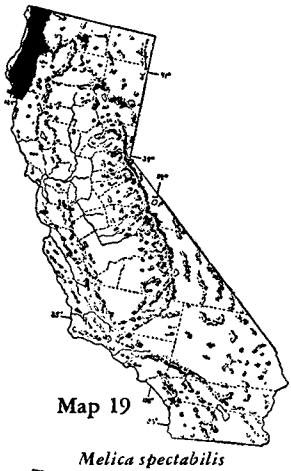
Deschampsia caespitosa var. *arctica*

Map 17

Agrostis exarata

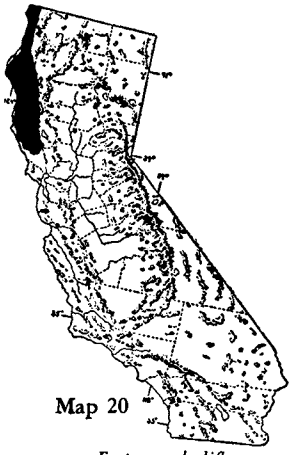
Map 18

Trisetum cernuum



Map 19

Melica spectabilis



Map 20

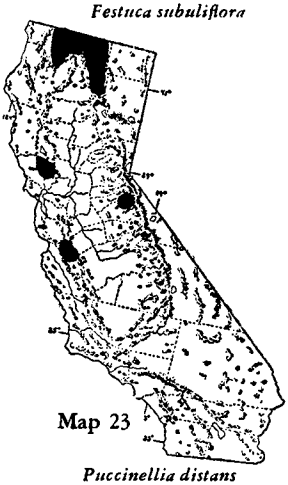
Festuca subuliflora

Map 21

Festuca occidentalis

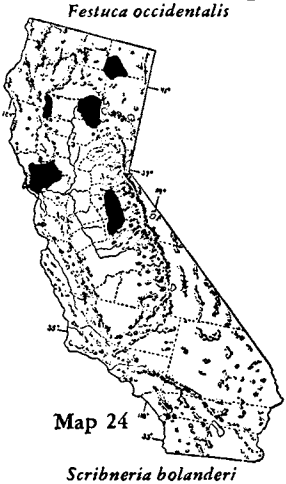
Map 22

Glyceria striata



Map 23

Puccinellia distans

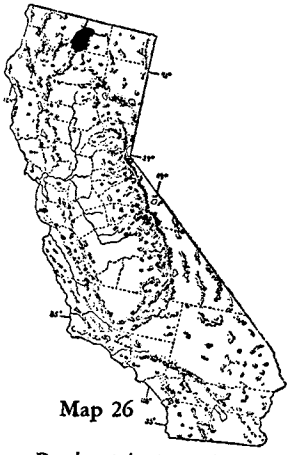


Map 24

Scribneria bolanderi

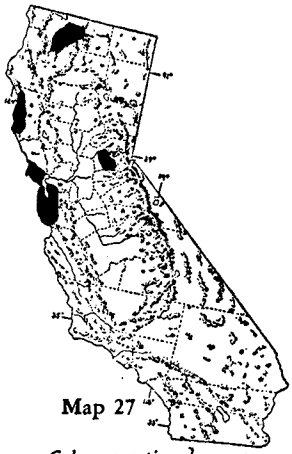
Map 25

Puccinellia lemmoni



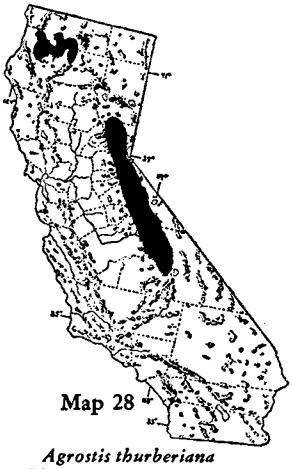
Map 26

Deschampsia atropurpurea



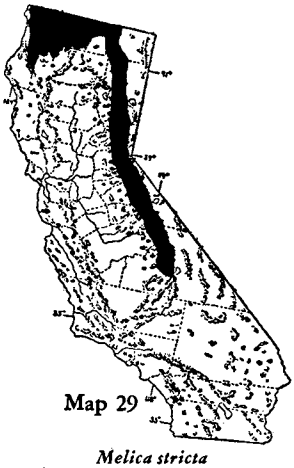
Map 27

Calamagrostis rubescens



Map 28

Agrostis thurberiana



Map 29

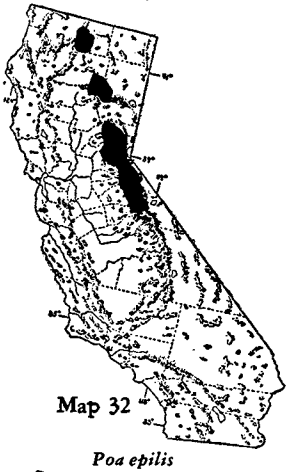
Melica stricta

Map 30

Melica aristata

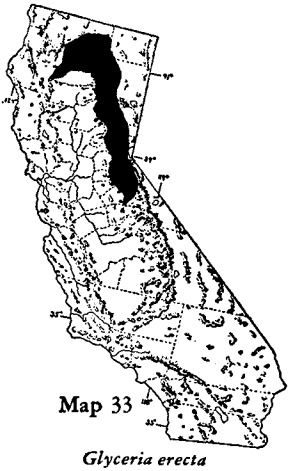
Map 31

Poa pringlei



Map 32

Poa epilis

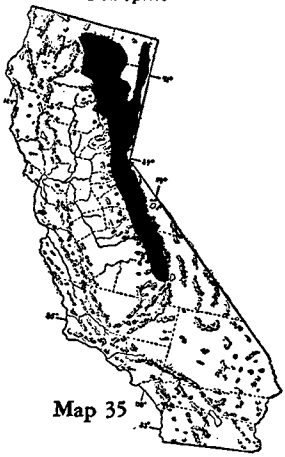


Map 33

Glyceria erecta

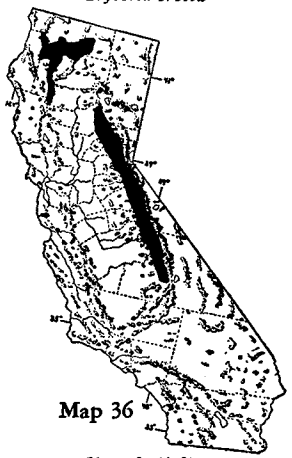
Map 34

Danthonia unispicata



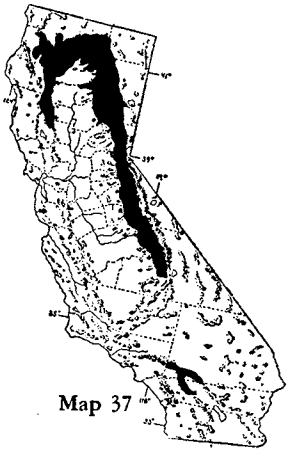
Map 35

Trisetum spicatum



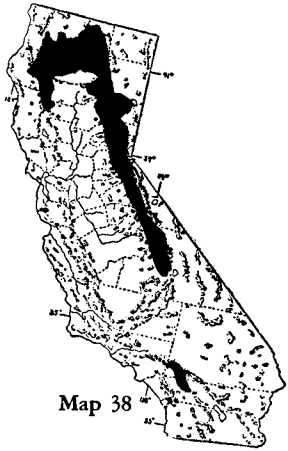
Map 36

Cinna latifolia



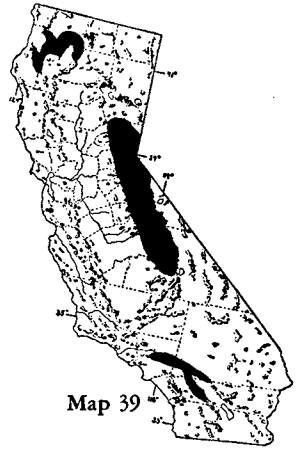
Map 37

Muhlenbergia filiformis



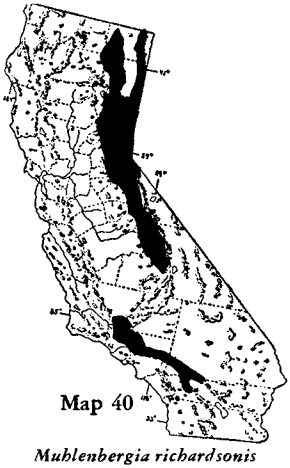
Map 38

Poa bolanderi



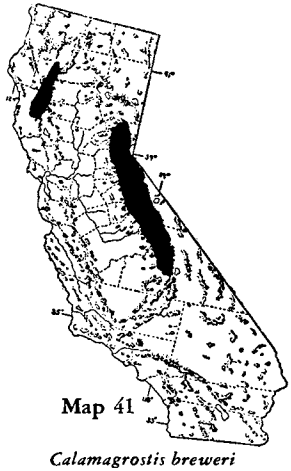
Map 39

Agrostis idahoensis



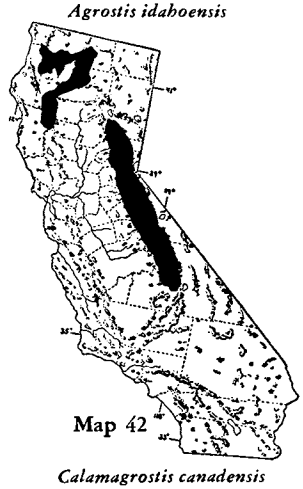
Map 40

Muhlenbergia richardsonis



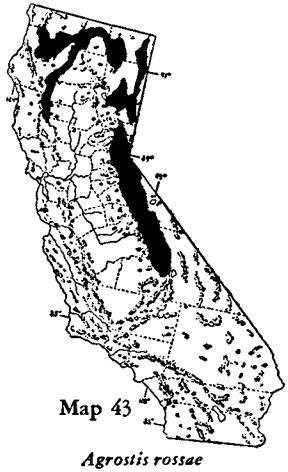
Map 41

Calamagrostis breweri



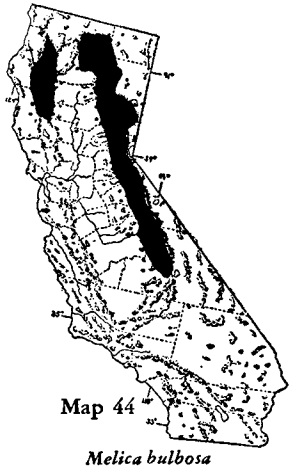
Map 42

Calamagrostis canadensis



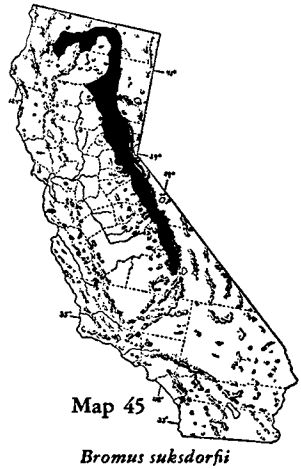
Map 43

Agrostis rossae



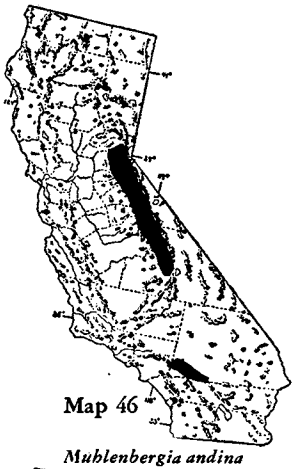
Map 44

Melica bulbosa



Map 45

Bromus suksdorfii

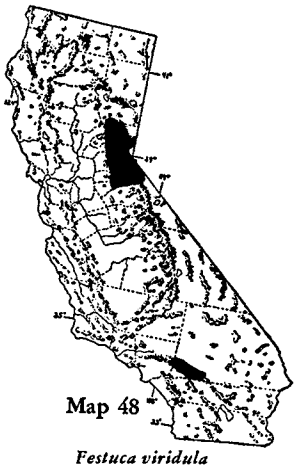


Map 46

Muhlenbergia andina

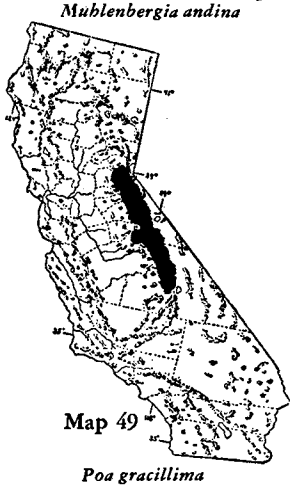
Map 47

Bromus ciliatus



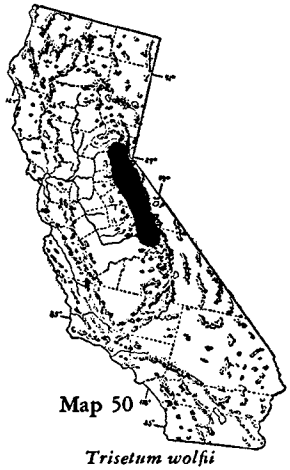
Map 48

Festuca viridula



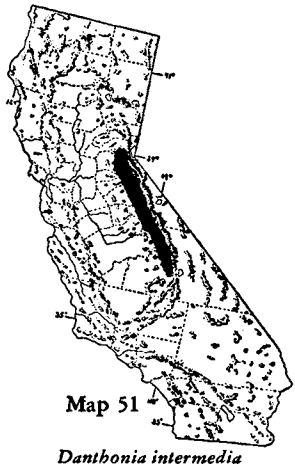
Map 49

Poa gracillima



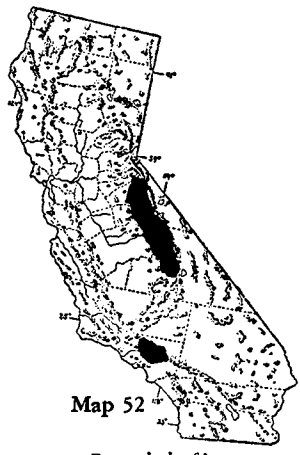
Map 50

Trisetum wolfii



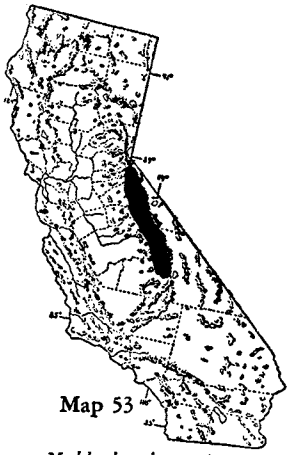
Map 51

Danthonia intermedia



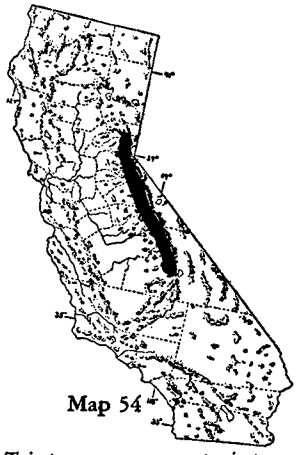
Map 52

Poa suksdorfii



Map 53

Muhlenbergia montana



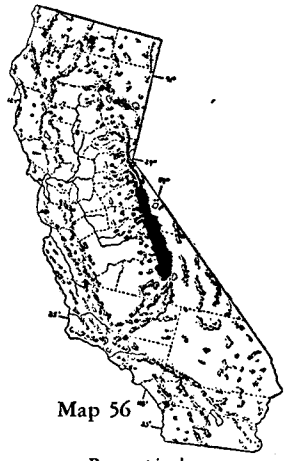
Map 54

Trisetum cernuum var. *projectum*

ALPINE GRASSES

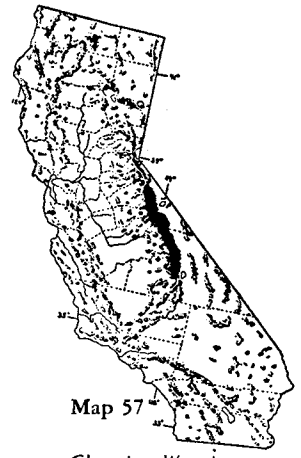
Map 55

Festuca ovina



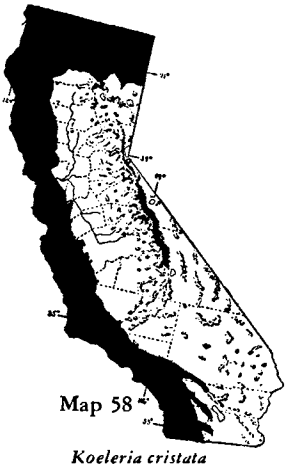
Map 56

Poa rupicola



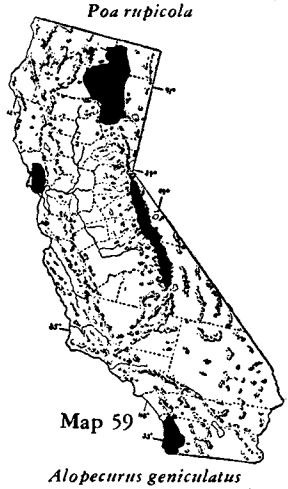
Map 57

Glyceria californica



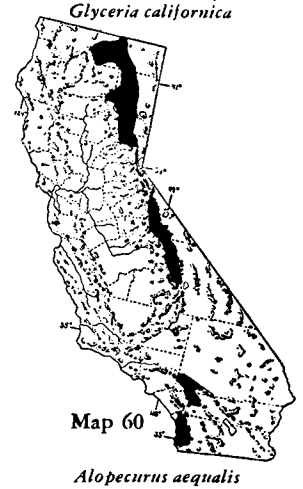
Map 58

Koeleria cristata



Map 59

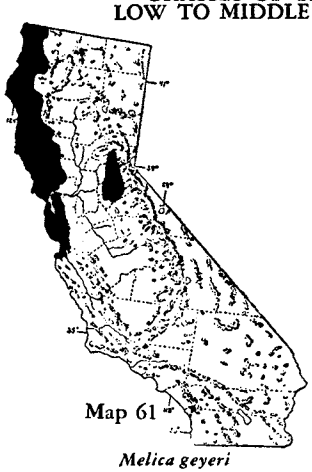
Alopecurus geniculatus



Map 60

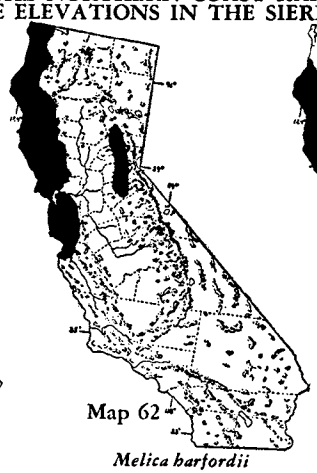
Alopecurus aequalis

GRASSES OF THE NORTHERN COAST RANGES AND LOW TO MIDDLE ELEVATIONS IN THE SIERRA NEVADA



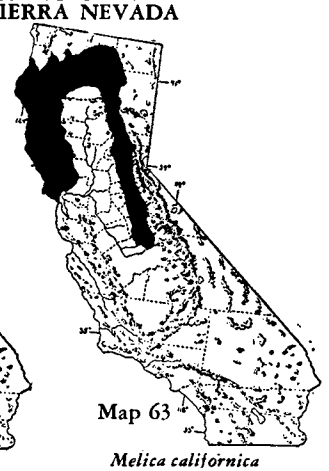
Map 61

Melica geyeri



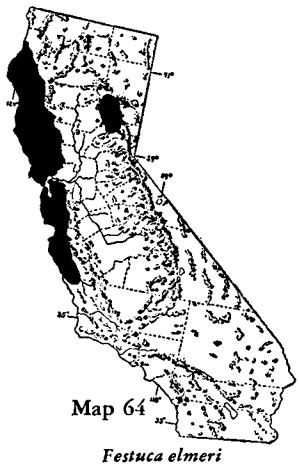
Map 62

Melica harfordii



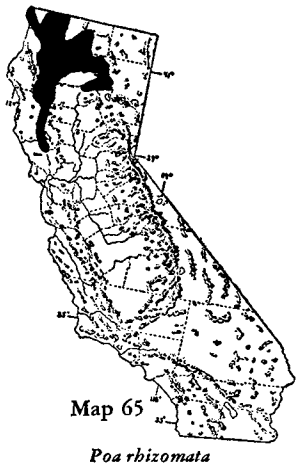
Map 63

Melica californica



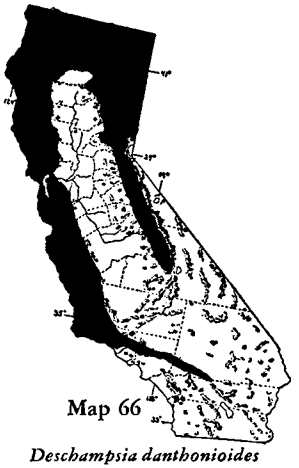
Map 64

Festuca elmeri



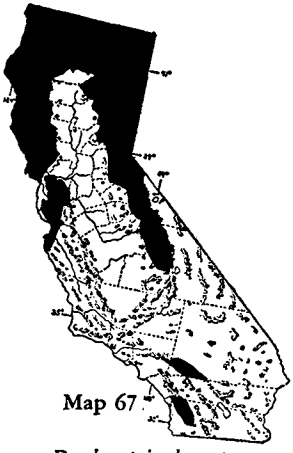
Map 65

Poa rhizomata



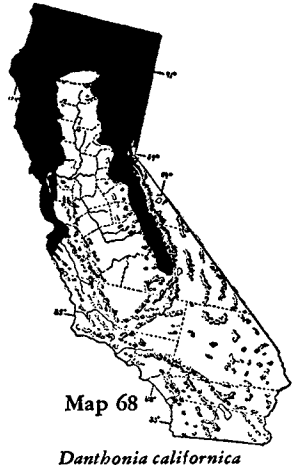
Map 66

Deschampsia danthonioides



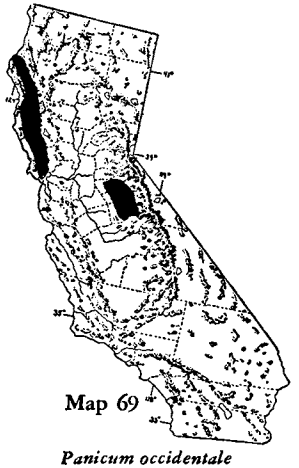
Map 67

Deschampsia elongata



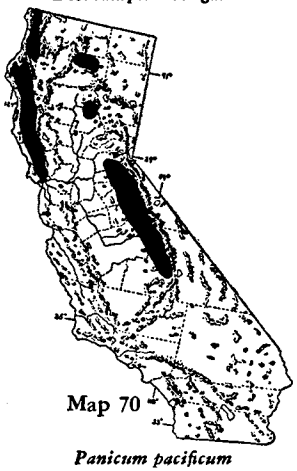
Map 68

Danthonia californica



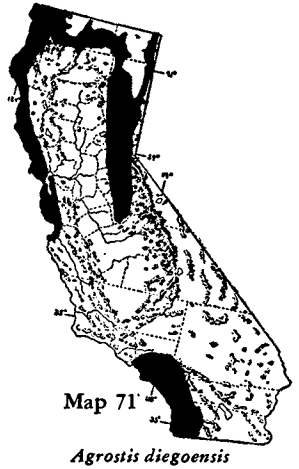
Map 69

Panicum occidentale



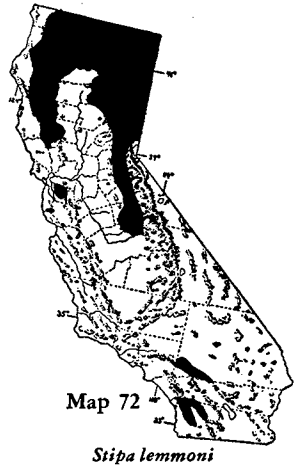
Map 70

Panicum pacificum



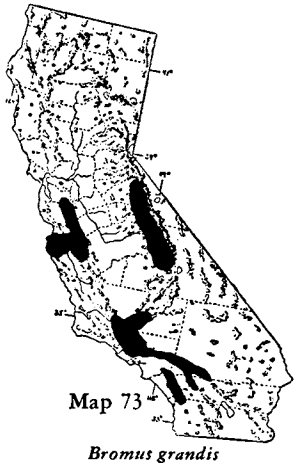
Map 71

Agrostis diegoensis



Map 72

Stipa lemmoni

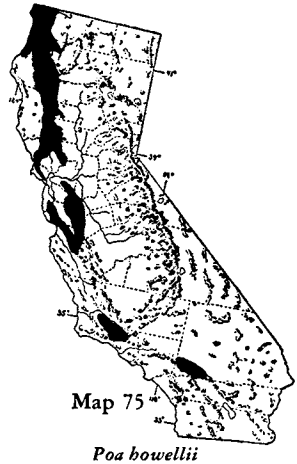


Map 73

Bromus grandis

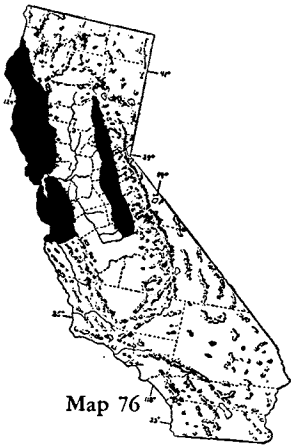
Map 74

Festuca californica



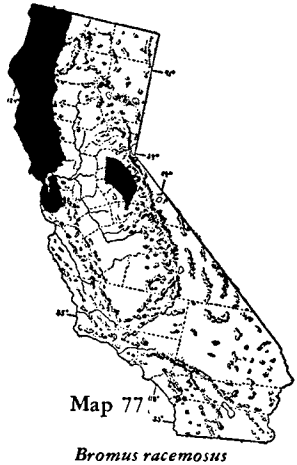
Map 75

Poa howellii



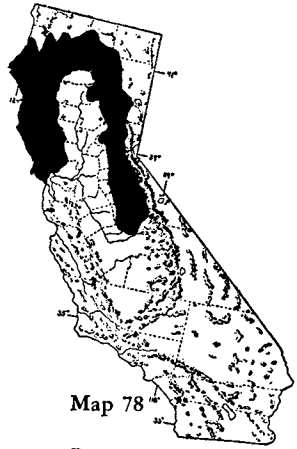
Map 76

Melica torreyana



Map 77

Bromus racemosus

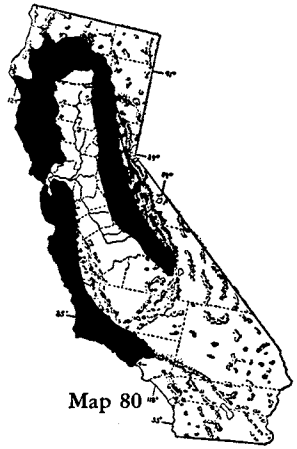


Map 78

Bromus commutatus

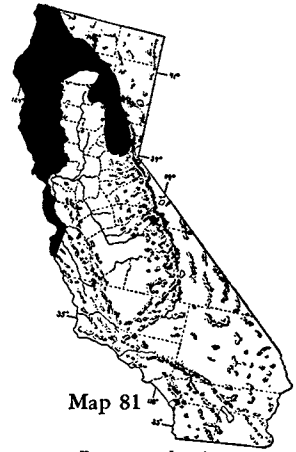
Map 79

Bromus orcuttianus



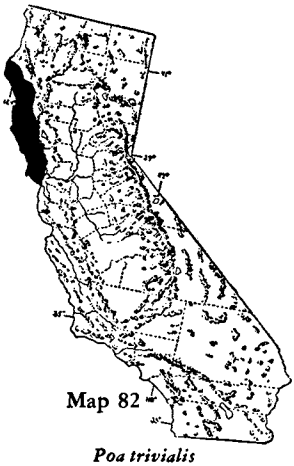
Map 80

Bromus laevipes



Map 81

Bromus vulgaris

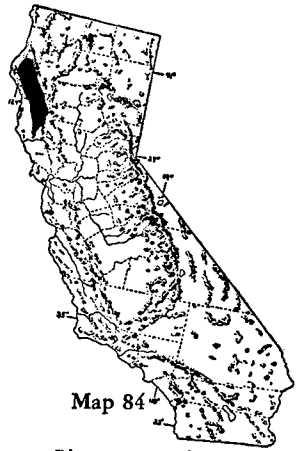


Map 82

Poa trivialis

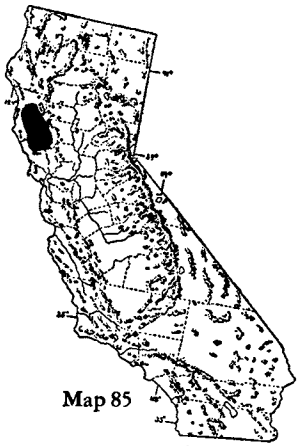
Map 83

Pleuropogon californicus



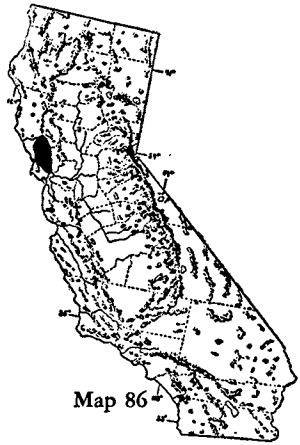
Map 84

Pleuropogon refractus



Map 85

Pleuropogon davyi

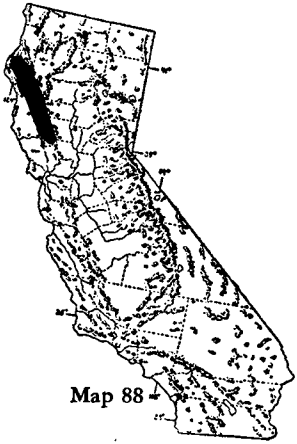


Map 86

Glyceria leptostachya

Map 87

Poa napensis



Map 88

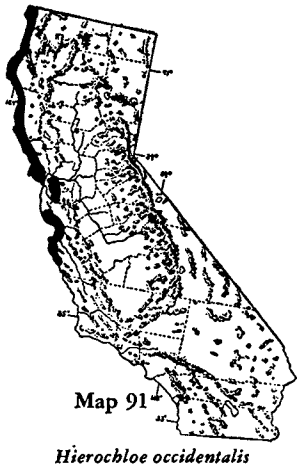
Glyceria occidentalis

Map 89

Glyceria cookei

Map 90

Deschampsia caespitosa var. *holciformis*



Map 91

Hierochloe occidentalis

Map 92

Phalaris californica

Map 93

Panicum shastense

Map 94

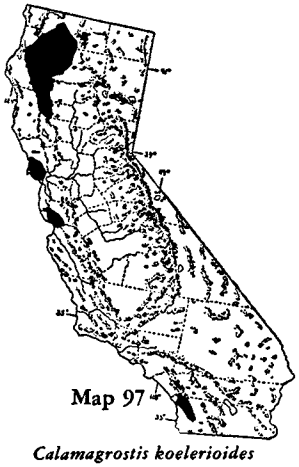
Panicum scribnerianum

Map 95

Calamagrostis crassiglumis

Map 96

Calamagrostis foliosa



Map 97

Calamagrostis koelerioides

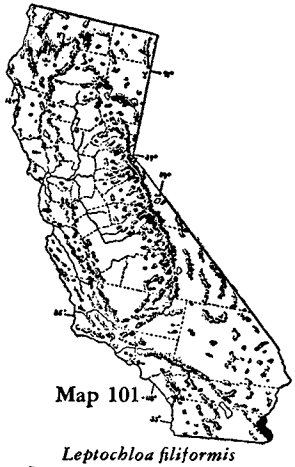
Map 98

Calamagrostis nutkaensis

Map 99

Agrostis californica

Bouteloua gracilis



Leptochloa filiformis

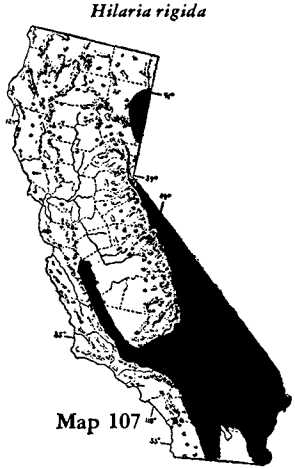
Leptochloa uninervia

Panicum urvilleanum

Hilaria rigida

Muhlenbergia porteri

Sporobolus contractus

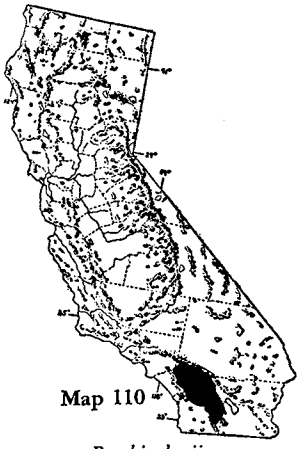


Stipa speciosa

Muhlenbergia californica

Map 109

Melica frutescens

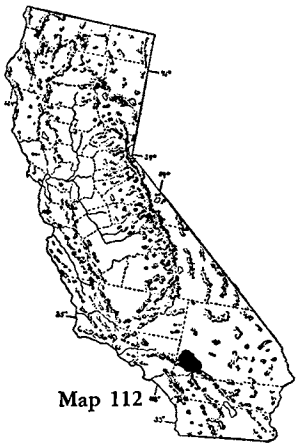


Map 110

Poa bigelovii

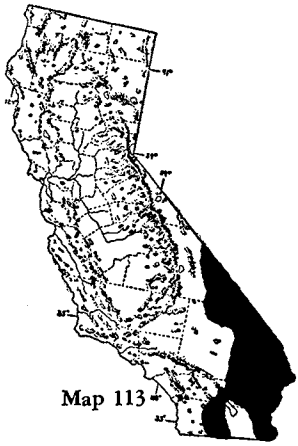
Map 111

Distichlis spicata var. *divaricata*



Map 112

Puccinellia parishii



Map 113

Triodia pulchella

Map 114

Bouteloua aristidoides

Map 115

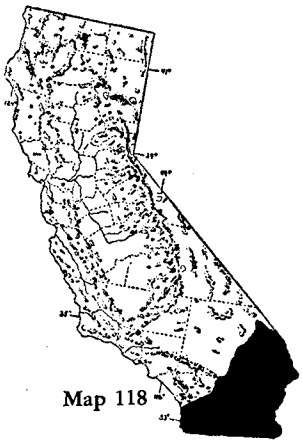
Bouteloua barbata

Map 116

Bouteloua curtipendula

Map 117

Bouteloua rothrockii

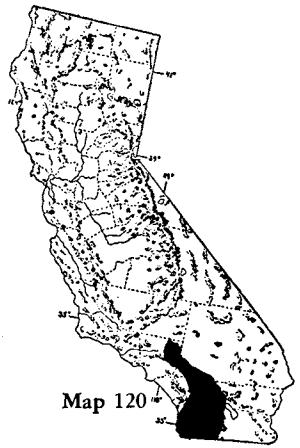


Map 118

Aristida adscensionis

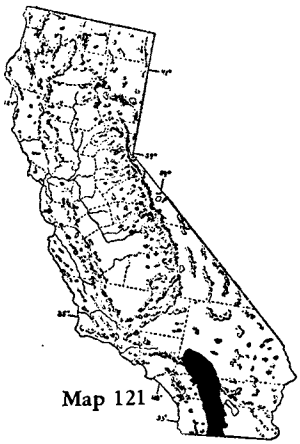
Map 119

Aristida californica



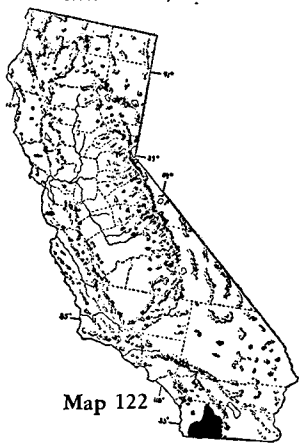
Map 120

Aristida divaricata



Map 121

Aristida fendleriana



Map 122

Aristida glabrata

Map 123

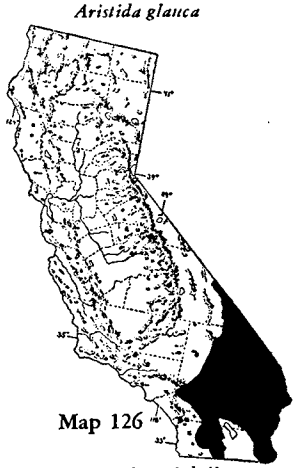
Aristida glauca

Map 124

Aristida parishii

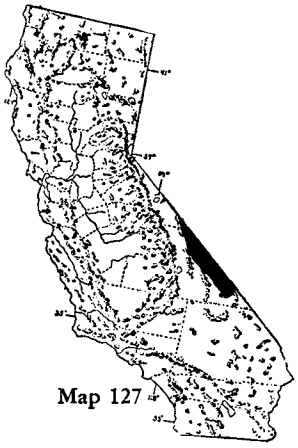
Map 125

Aristida purpurea

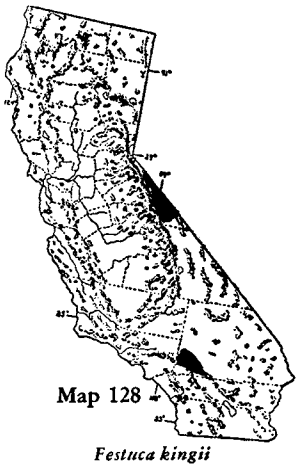


Map 126

Aristida wrightii



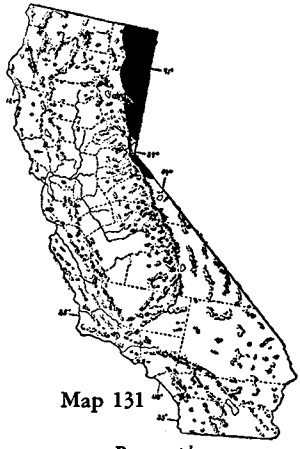
Blepharidachne kingii



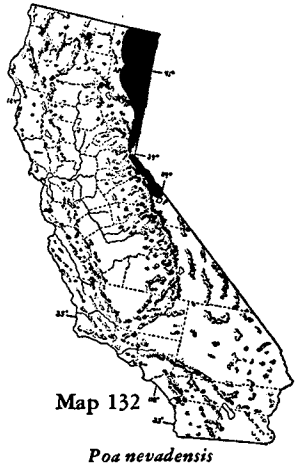
Festuca kingii

Poa fendleriana

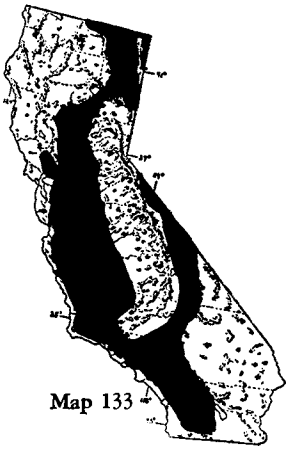
Poa leptocoma



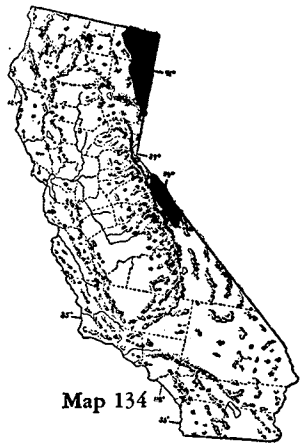
Poa ampla



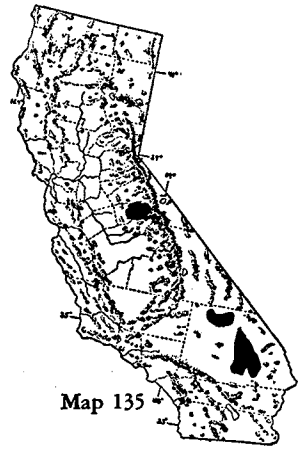
Poa nevadensis



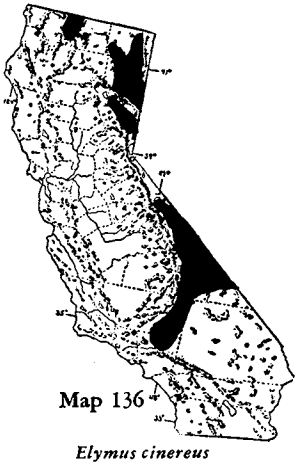
Distichlis spicata var. *stricta*



Puccinellia nuttalliana

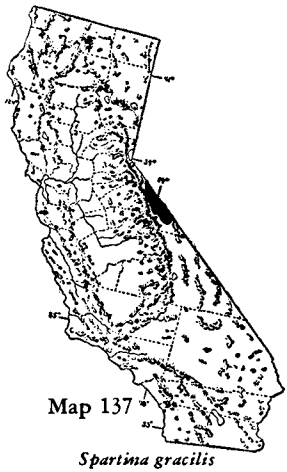


Triodia mutica



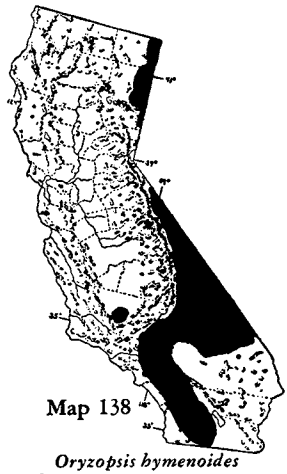
Map 136

Elymus cinereus



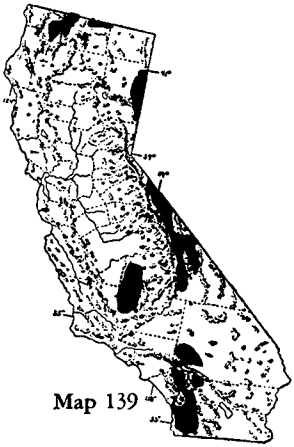
Map 137

Spartina gracilis



Map 138

Oryzopsis hymenoides



Map 139

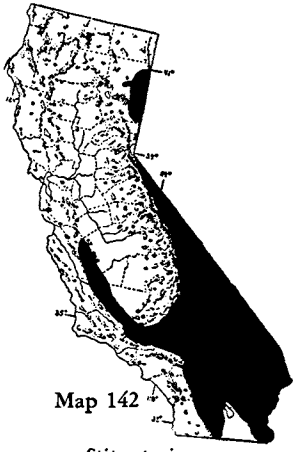
Muhlenbergia asperifolia

Map 140

Hilaria jamesii

Map 141

Stipa williamsii

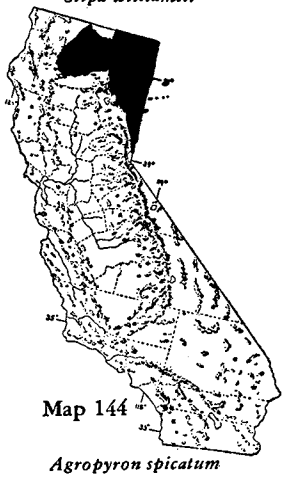


Map 142

Stipa speciosa

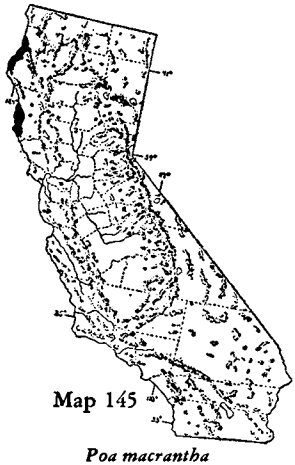
Map 143

Agropyron smithii



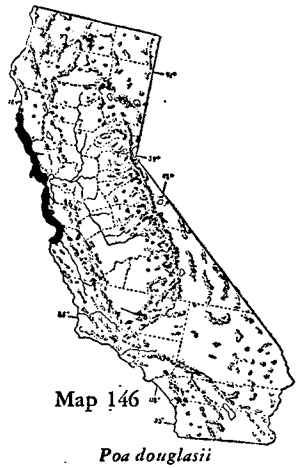
Map 144

Agropyron spicatum



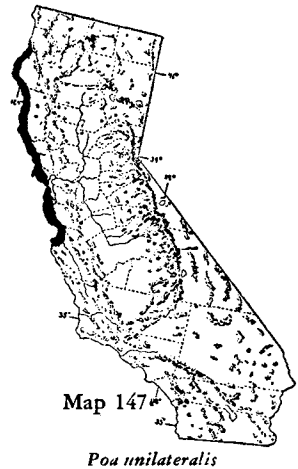
Map 145

Poa macrantha



Map 146

Poa douglasii

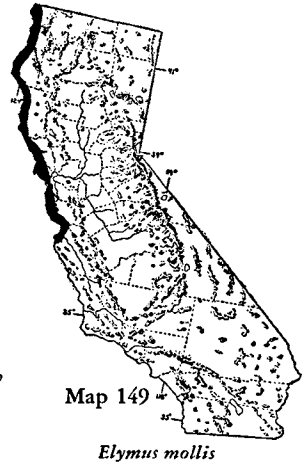


Map 147

Poa unilateralis

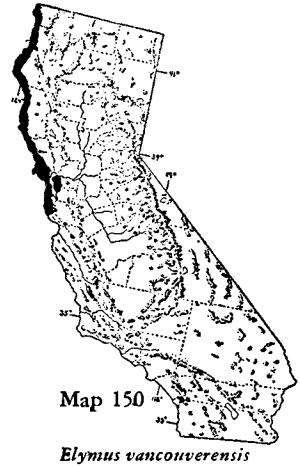
Map 148

Puccinellia grandis



Map 149

Elymus mollis

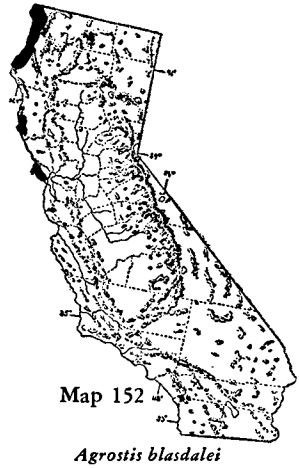


Map 150

Elymus vancouverensis

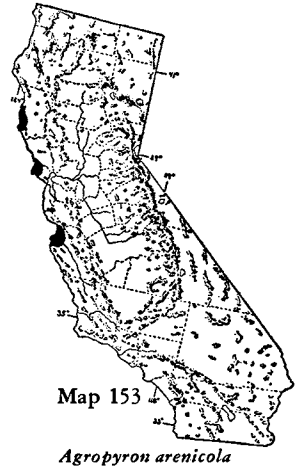
Map 151

Elymus virescens



Map 152

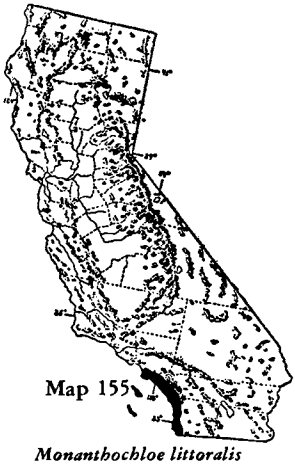
Agrostis blasdalei



Map 153

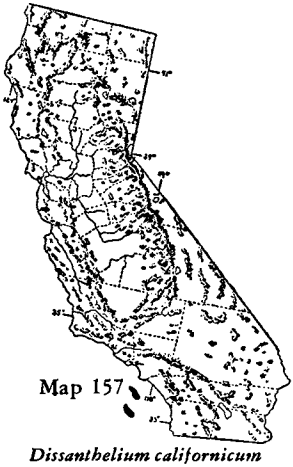
Agropyron arenicola

Phragmites communis



Monanthochloe littoralis

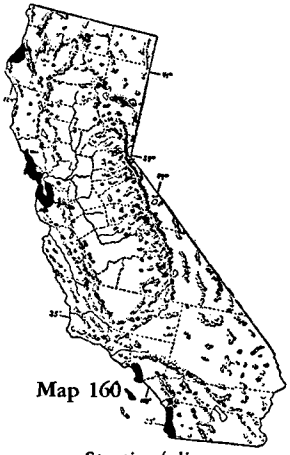
Distichlis spicata var. *stolonifera*



Dissanthelium californicum

Lepturus cylindricus

Pholiurus incurvus



Spartina foliosa

Ammophila arenaria

Muhlenbergia microsperma

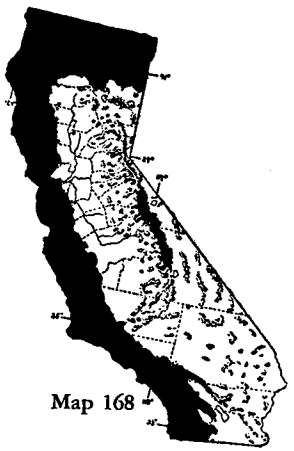
Muhlenbergia rigens

Stipa cernua

Stipa pulchra

Stipa lepida

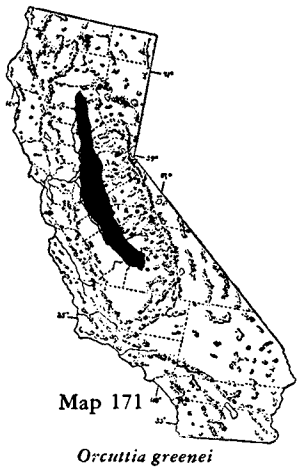
Melica imperfecta



Koeleria cristata

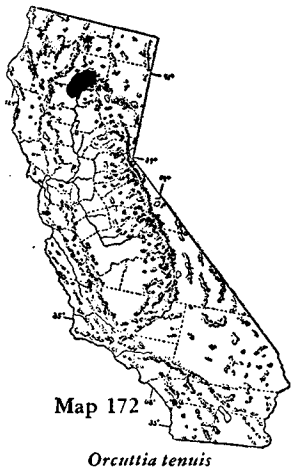
Stipa coronata

Elymus condensatus



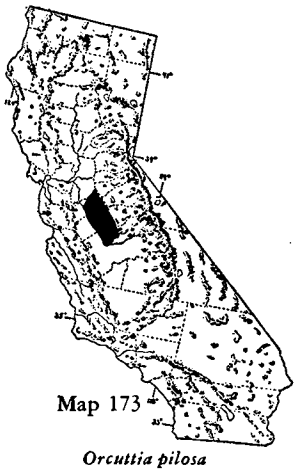
Map 171

Orcuttia greenei



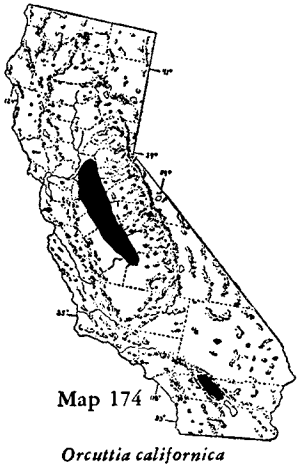
Map 172

Orcuttia tenuis



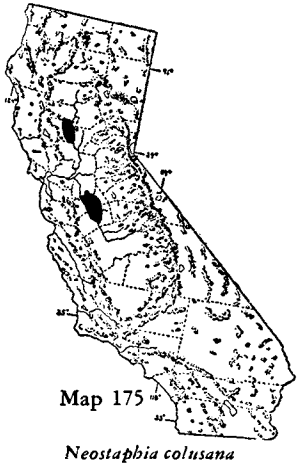
Map 173

Orcuttia pilosa



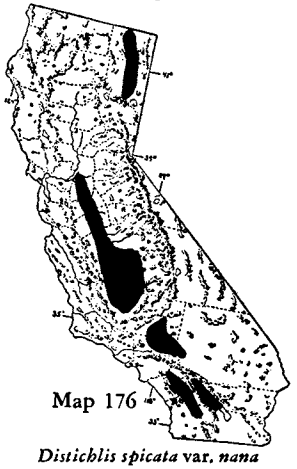
Map 174

Orcuttia californica



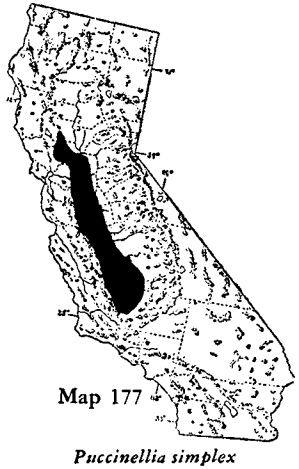
Map 175

Neostapbia colusana



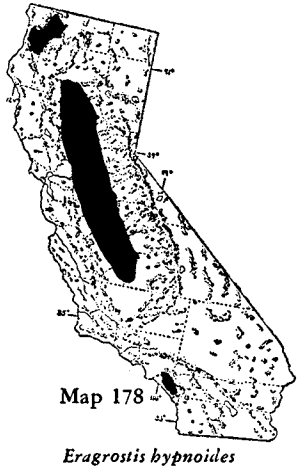
Map 176

Distichlis spicata var. *nana*



Map 177

Puccinellia simplex



Map 178

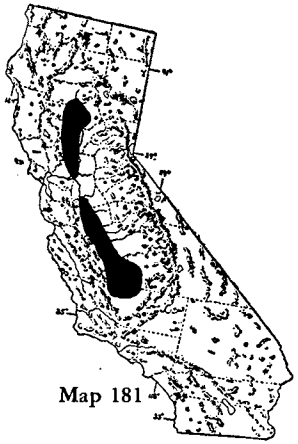
Eragrostis hypnoides

Map 179

Eragrostis orcuttiana

Map 180

Deschampsia danthonioides var. *gracilis*

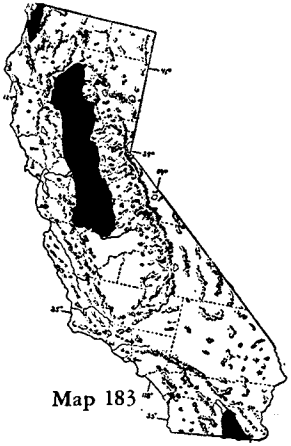


Map 181

Leptochloa fascicularis

Map 182

Aristida hamulosa



Map 183

Aristida oligantha

Map 184

Alopecurus saccatus

THE CENTRAL VALLEY AND COASTAL FLORAL UNITS IN CALIFORNIA

ANALYSIS BY DISTRIBUTION

Coastal Grasses (maps 145 to 161).—Many of the coastal grasses are typical of the northern grasses discussed earlier—that is, they occur only north of Monterey Bay and belong to genera whose distributions are north temperate. They tend to be concentrated at such points along the coast as Humboldt Bay, Point Arena, Point Reyes, and the Monterey Peninsula. This is partly, but not wholly, due to restrictions of habitat. The disrupted ranges of the very rare *Agrostis blasdalei* (map 152) and *Agropyron arenicola* (map 153) illustrate this. Other representatives of northern genera that are restricted to coastal habitats include two closely related *Poa* species—*P. macrantha* (map 145) and *P. douglasii* (map 146)—the giant ryes, *Elymus mollis* (map 149) and *E. vancouverensis* (map 150), and the rare and little-known *Puccinellia grandis* (map 148).

Grasses which occur south of Monterey Bay (often as well as northward) are more typically of south-temperate genera and are often introduced; for example, *Lepturus cylindricus* (map 158), *Pholiurus incurvus* (map 159) and *Ammophila arenaria* (map 161).

Grasses of the Southern Coast Ranges and Great Valley (maps 162 to 170).—The native grass flora of the Coast Ranges from Monterey County south is very meager. The most typical are a trio of *Stipa* species, *S. cernua* (map 164), *S. pulchra* (map 165), *S. lepida* (map 166), and two *Muhlenbergia* species, *M. microsperma* (map 162), and *M. rigens* (map 163). These grasses may extend northward from Monterey Bay although, with the exception of *Koeleria cristata* (map 168), they do not reach the Oregon border. The abrupt termination in northward distribution at Monterey Bay of *Muhlenbergia microsperma, M. rigens, Stipa coronata* (map 169), and *Elymus condensatus* (map 170) emphasizes the importance of the area as the most critical in the Coast Ranges; see discussion of the southern termination of northern grasses.

Stipa cernua and *S. pulchra* occupy both the central valley and the southern Coast Ranges without a break in their distribution. This distribution, but with hiatus involving the western half of the valley and the Inner Coast Range, is found with *Andropogon virginicus* var. *hirsutior*,[4] *Muhlenbergia microsperma, M. rigens, Aristida hamulosa* (map 182), *Deschampsia danthonioides* var. *gracilis* (map 180), and *Sporobolus microspermus.*

Great Valley Grasses (maps 171 to 184).—The four species of *Orcuttia, O. greenei* (map 171), *O. tenuis* (map 172), *O. pilosa* (map 173), and *O. californica* (map 174), as well as *Neostaphia colusana* (map 175) lend a strong degree of endemism to the grass flora of the Great Valley. These grasses are all rare and specialized in habitat (see discussion under "Vernal Pools," p. 347–8). The grasses of the Great Valley are not found in the surrounding hills although they may occupy various of the low valleys which are adjacent

[4] The California phase of *Andropogon virginicus* L. should be treated as *Andropogon virginicus* var. *hirsutior* (Hack.) Hitchc., f. *tenuispatheus* (Nash) comb. nov. (*A. glomeratus tenuispatheus* Nash, *in* Small, Fl. S.E. U.S. **61**. 1903; *A. tenuispatheus* Nash, *in* Gramineae. N. Amer. Fl. **17**: 113. 1912.)

to the Great Valley—for example, *Alopecurus saccatus* (map 184), *Eragrostis hypnoides* (map 178), and *E. orcuttiana* (map 179). All the species are annual except *Aristida hamulosa* (map 182) and *Distichlis spicata* var. *nana* (map 176).

ANALYSIS BY HABITAT

Central California, as defined here, includes the Great Valley (San Joaquin and Sacramento valleys) and the surrounding upper Sonoran zone (to an elevation of about 3,000 to 4,000 feet) which is characteristically either open grassland, parklike savanna (the scattered trees usually oaks or digger pine), or chaparral. These habitats tend to be zonal in distribution (Piemeisel and Lawson, 1937), the alkali flats of the poorly drained bottomlands being bordered by grassland, and then chaparral or savanna on the slopes.

Open grass slopes dominate this area, and their typical golden color during most of the year is produced by dry grass straw. The first fall rains germinate the seeds of the annuals and renew the vegetative growth of the perennials. Duration of the growth depends upon the season; the hills stay green for the colder, wetter months, and in early spring begin to turn as the annuals rapidly mature and dry. The last seeds of the annuals are usually shed by the middle of April. Most of the perennials mature nearly as rapidly as the annuals, with the last of them maturing by June. Prolongation of the period of grazing on green feed at this period is one of the important range problems.

The only major break in the coastal hills occurs at San Francisco Bay where the great rivers, having converged, finally enter the ocean. This break considerably affects the climate of the region far into the valley but not sufficiently to form a barrier to plant dispersal. The annual rainfall in this central portion of the Great Valley reaches an average of 15 inches, but tapers off to the north and to the south. The Coast Ranges are lowest at San Francisco Bay (and Suisun Bay), and become higher and steeper northward and southward.

Coastal California is an area of highly specialized habitats. In some places chaparral, open grassland, or oak savanna approach the ocean, but more often there is an intervening strip, usually very narrow, of either coniferous woods (redwood, Monterey cypress, or Douglas-fir), or sand dunes or salt marsh. All owe their existence to, and are modified by, the proximity of the ocean, though in different ways—the salt in the marshes, the wind against the bluffs, the fog in the redwood belt.

All the habitats mentioned may occur also on the islands off the coast of California, to which the rare *Dissanthelium californicum* (map 158) is the only grass species known to be endemic. See Eastwood (1941) for a list of the species that have been collected on the islands.

Grasses of the Grassland and Savanna.—Parts of this portion of California appear to have been originally as nearly a climax type of grassland as the more extensive prairies of the interior of North America. The California grasslands were then dominated by bunch grasses liberally supplemented by erect perennials and a few stoloniferous perennials and interspersed with annuals. These areas differ in two respects from similar areas elsewhere in the world: (1) the identity of the perennial species; (2) the number and importance of the annuals. In character the California grassland is related

to similar areas in eastern Oregon, eastern Washington and adjacent Idaho, and in western Montana. Together they comprise the Pacific bunch-grass area, as distinguished from the tall-grass and short-grass prairies of the Great Plains (McArdle, *et al.,* 1936). A far greater proportion of the species in the Pacific bunch-grass area, and even in the California area, trace their origins northward than is true in the tall-grass prairie (Weaver and Fitzpatrick, 1932) or the short-grass prairie, where a large southern element is usually dominant. Only *Koeleria cristata* occupies an important place in both the tall-grass and the Pacific bunch-grass floras.

The original appearance of the California grasslands is not a matter of historical record. Spanish settlers tilled the soil and grazed the hills for many years without caring to write about their surroundings in anything but the most general terms. As evidenced by adobe-brick studies (Hendry, 1931) such introductions as *Poa annua, Hordeum murinum,* and *Lolium multiflorum* made headway almost immediately. It is popularly supposed that the native bunch-grass perennials were far more abundant at the time and that they have since tended to disappear under the stress of cultivation, heavy grazing, and the competition of introductions. Since this area coincides with that principally occupied by California's enormous agricultural industry, such displacement is to be expected. Certainly in this portion of California no undisturbed remnants of the original flora remain (disturbance includes the effect of plant on plant as well as man on a plant community), and because of this its appearance is a matter for speculation only. Clements (1934) describes from observations made in 1918 the obliteration of "many hundred miles of a nearly continuous consociation of *Stipa pulchra,*" and the establishment of "the wild oats as the one great dominant throughout." There is no evidence, however, that any grass ever recorded for California has become extinct.

The number of strong contrasts between the California grassland and that of the Great Plains eliminates the possibility of any great similarity between the two. The California range is predominantly annual and therefore strongly fluctuating, whereas the Great Plains area is predominantly perennial and therefore potentially stable. The California range developed under a natural system of year-round grazing by deer, whereas the Great Plains area developed under a natural system of rotation grazing by buffalo. In California today introductions are predominant, and the state of the virgin range can no longer be considered a clue to its potential carrying capacity. In the Great Plains area natives are predominant today, and the state of the virgin range is an index to the carrying capacity. In California controlled grazing began around 1773, but on the Great Plains controlled grazing started about 1880. The two areas differ in the identity of both the native species and the introduced, often weedy species. They differ also in the degree of variability of the factors which influence the determination of grazing capacity. The difficulties in determining the carrying capacity of a given area are multiplied proportionately to: (1) the diversity of the vegetation; (2) the variability of the rainfall; (3) the variability of the climate; (4) the variability of slope; (5) the variability of the altitude; and (6) the diversity of soil types. Even within the counties of California all of the factors are present in a degree of variability not met in whole states in the Great Plains region.

The native bunch grasses (that is, nonstoloniferous types), whose conspicuous scattered clumps give the California part of the Pacific grassland its characteristic aspect, include:

Agrostis ampla
Andropogon virginicus var. *hirsutior*
Aristida hamulosa
Bromus carinatus
Bromus laevipes
Danthonia californica
Elymus condensatus
Elymus glaucus
Koeleria cristata
Melica californica
Melica imperfecta
Muhlenbergia rigens
Panicum pacificum and allies
Sitanion hystrix
Sitanion jubatum
Stipa cernua
Stipa lepida
Stipa pulchra

Successfully introduced stoloniferous perennials in this area are few because of moisture limitations (compare *Agrostis stolonifera, Phalaris arundinacea,* and *P. tuberosa* var. *stenoptera*). Of the grasses in this area, only *Elymus triticoides* is strongly rhizomatous.

Introduced perennials
Agrostis retrofracta
Agrostis tenuis
Danthonia pilosa
Lolium perenne

Native annuals
Agrostis exigua
Aristida oligantha
Bromus trinii
Eragrostis hypnoides
Eragrostis orcuttiana
Festuca megalura
Festuca microstachys
Festuca octoflora
Phalaris angusta
Scribneria bolanderi

Introduced annuals
Avena barbata
Avena fatua
Avena sativa
Briza maxima
Briza minor
Bromus mollis
Bromus commutatus
Bromus racemosus
Bromus rigidus
Bromus rubens
Elymus caput-medusae
Festuca dertonensis
Hordeum gussoneanum
Hordeum murinum
Lagurus ovatus
Lolium multiflorum
Lolium temulentum
Phalaris canariensis
Phalaris caroliniana
Phalaris minor
Phalaris paradoxa

The following introduced grasses are found in California only as weeds on disturbed or cultivated ground and usually at low elevations:

Aegilops triuncialis
Avena sterilis
Digitaria filiformis
Digitaria sanguinalis
Echinochloa colonum
Eleusine indica
Eragrostis cilianensis
Eragrostis poaeoides
Setaria lutescens
Setaria viridis

Southward from San Francisco Bay occur spontaneously a number of introductions of subtropical origin. Sometimes they occur on the open range, in rock crevices, in chaparral, or in oak woods, seemingly without regard to the habitats defined by the native vegetation. Unlike the introductions from the Mediterranean region, which are usually very abundant, make poor forage,

and have harsh awns which cause mechanical injury to stock (for example, *Bromus* spp. and *Hordeum* spp.), these species are generally palatable and not mechanically injurious, but are much less aggressive.

Perennials	Annuals
Andropogon saccharoides	*Lamarckia aurea*
Imperata hookeri	*Schismus arabicus*
Pennisetum villosum	*Sorghum vulgare*
Sorghum halepense[5]	
Tricholaena rosea	

Phalaris platensis Henrard, an Argentine species, is reported to be very similar in characteristics to *P. lemmoni* (Henrard, 1938). The fact that *P. angusta* is considered native to both Chile and California, indicates that the genus is a real link between the floras of the two regions. Among the native California grasses of similar habitat additional links may be found in *Poa secunda* Presl, and *Bromus trinii* Desv. (Beetle, 1943*b*). This connection between a flora of California and one of temperate South America must be considered to have a history independent of the connections found in both the deserts and the mountains of the same regions (see p. 311 and 316). Campbell (1944) states that "species common to Chile and central southern California . . . may be explained as due to migration along the great mountain system of the Pacific Coast." It seems unlikely that the variously adapted species of grassland, desert, and mountain, all took the same route; thus desert species may have traveled a dry continental shelf similar to Lower California.

The genus *Panicum* (in number of described species one of the largest of all genera) as a whole and especially the subgenus Dichanthelium whose center of distribution is the coastal plain of the southeastern United States (Hitchcock and Chase, 1910), has found the mountains, deserts, and ocean surrounding California difficult barriers to traverse. Three perennial species (*P. scribnerianum, P. pacificum,* and *P. occidentale*), none of them common, are found at scattered localities, usually in at least semishade. A fourth, *P. thermale,* is known from the vicinity of the hot springs of Sonoma County. Thus the southeastern United States, recognized as a center of origin and dispersal for many nonboreal plants and animals of the greater part of the eastern United States (Adams, 1902), has made only a minor, occasional, accidental contribution to the flora of California; this holds true for the flora of California in general as well as for the grasses. It is apparent that the ocean to the west, the desert to the south, and the mountains to the east have long been barriers to the immigration of species to California from other floras. Only the north-to-south immigration route along the Coast Ranges and the Sierra Nevada into Oregon and Washington has been responsible for any appreciable contribution to the California grass flora from the Tehachapi Mountains northward.

[5] At first glance, the California ranchers who have had trouble with Johnson grass may well be startled to find it listed as "less aggressive." Reference here is made, however, to the occurrence of these grasses on the dry, open range, a very different habitat from cultivated fields or irrigated pastures. In this connection it is interesting to note the apparently greater drought resistance of the bunch-grass type of perennial over stoloniferous or rhizomatous types. This accounts for the general rarity of introduced perennials on the range, as well as the general prevalence of introduced perennials in lawns and irrigated pastures.

Grasses of the Alkaline Flats.—Species of alkaline flats include:

Native perennials
- *Distichlis spicata* var. *nana*
- *Distichlis spicata* var. *stricta*
- *Puccinellia distans*
- *Puccinellia lemmoni*
- *Sporobolus airoides*

Native annuals
- *Hordeum pusillum*
- *Leptochloa fascicularis*
- *Puccinellia simplex*

The presence of any of the above is an indication of alkaline soil though *Distichlis spicata* var. *stricta* and *Puccinellia simplex* have the strongest tolerance. Alkaline soils are characterized by poor drainage, high evaporation, and an accumulation of soluble salts. These are not necessarily salts of alkaline reaction but include chlorides, sulfates, and carbonates and bicarbonates of sodium, potassium, calcium, and magnesium. Northward in the Great Valley the alkaline soils are all on the west side, but southward they are more common and occur on both sides of the valley.

With the exception of *Leptochloa fascicularis,* the species listed above represent typically north-temperate genera. Judging both from their centers of variation and the location of related species, the species of wide range listed above are probably immigrants to California. These include *Puccinellia distans, Hordeum pusillum,* and *Leptochloa fascicularis* (and probably also *Agropyron smithii,* which is of limited occurrence in northeastern California). This does not imply that they are not native in their occurrence, but simply that the impetus which resulted in their formation was elsewhere and that they subsequently found California a favorable environment. The remaining elements, on the other hand—varieties of *Distichlis spicata* and the species of *Puccinellia* which are narrow in range—may have been developed *in situ.* This appears to be particularly true of *Distichlis.* Here the origin of *Distichlis* from *Uniola,* or at least some ancestor with perfect florets, seems evident; dioeciousness is too rare in the Festuceae to be considered primitive where corroborative evidence is wholly lacking. Within *Distichlis* the species of larger plant body (for example, *D. texana*) are more characteristic of the Festuceae and are less specialized as to habitat; they might be regarded as precursors of the halophytic *D. spicata,* which has achieved a particularly wide range because of its adaptation to alkaline habitats.

Grasses of Aquatic Habitats.—The true aquatics include:

Native grasses
- *Alopecurus carolinianus*
- *Alopecurus howellii*
- *Alopecurus geniculatus*
- *Alopecurus saccatus*
- *Glyceria leptostachya*
- *Glyceria occidentalis*
- *Glyceria pauciflora*
- *Leersia oryzoides*
- *Paspalum distichum*
- *Phragmites communis*

Introduced perennials
- *Alopecurus pratensis*
- *Arundo donax*
- *Paspalum dilatatum*
- *Paspalum urvillei*
- *Setaria geniculata*

Introduced annuals
- *Agrostis semiverticillata*
- *Echinochloa crusgalli*
- *Polypogon interruptus*
- *Polypogon maritimus*
- *Polypogon monspeliensis*

All of the native perennial aquatics listed are of wide distribution, at least on the North American continent, except *Alopecurus howellii, A. saccatus,*

and *Glyceria leptostachya,* which are confined to the northwestern corner of the United States from southern Washington to northern California. Both *Alopecurus* and *Glyceria* are north-temperate genera, and their California distributions fit the picture of predominantly northern origins proposed for species of other habitats.

Grasses of the Vernal Pools.—In vernal pools are found:

Introduced annuals
- *Crypsis aculeata*
- *Heleochloa schoenoides*

Native annuals
- *Agrostis microphylla* and its varieties
- *Deschampsia danthonioides* var. *gracilis*
- *Neostaphia colusana*
- *Orcuttia californica*
- *Orcuttia greenei*
- *Orcuttia pilosa*
- *Orcuttia tenuis*
- *Phalaris lemmoni*
- *Pleuropogon californicus*

The vernal pool represents an unusual habitat requiring considerable adaptation on the part of the plants inhabiting it. Water collects in pockets during the rainy season and, because of the high water table and poor drainage, remains as a small lake until late in the spring. When the water finally disappears as a result of evaporation, the annuals germinate (usually at a time when the surrounding vegetation has fully matured). Although their seeds have germinated in an aquatic habitat, these annuals must grow and mature in the hottest summer temperatures on dry, cracked soils. An odorous viscid pubescence reduces their transpiration rate. All are intolerant of salinity. None are perennial.

Both *Deschampsia danthonioides* var. *gracilis* and *Crypsis aculeata* are common; *Phalaris lemmoni* is frequent. The rest of the plants are rare, their habitat being limited and frequently disturbed by cultivation.

Orcuttia, Neostaphia, and *Pleuropogon,* all related according to Hoover (1941), are the rarest and most unusual genera of California grasses. Obscure as to relationship and highly specialized in habitat, the origin of the species of these three genera represents a difficult and as yet unsolved problem. The relationship between *Orcuttia* and *Neostaphia,* viscid annuals of unpleasant odor, is easier to see than any relationship between these two and *Pleuropogon. Pleuropogon,* a genus of five species and one variety (Benson, 1941), in its northern origin through *P. sabinii,* its generally perennial habit, and its aquatic habitat, not to mention the general morphological characters of inflorescence and spikelets, suggests a close relationship to *Glyceria.* The endemic species of *Pleuropogon, Orcuttia,* and *Neostaphia* agree with the Great Valley endemics of other families in belonging to distinctly California genera.[6] Hoover considers them to be endemics of recent (that is, derived) origin. They would then be called neoendemics, or initiates. This appears to be borne out by the fact that the valley floor was submerged in recent geological time. On the other hand, the isolated position of these genera (that is, the absence in the flora of close relatives, or links to other more common

[6] Hoover, R. F. Endemism in the flora of the Great Valley of California. A thesis submitted in partial fulfillment of requirements for the degree of Doctor of Philosophy, University of California. 175 p. 1937.

genera) suggests a long history. It may well be that these plants are restricted in range, not because they are very young nor because they are very old, but because in evolution they have become too selective as to habitat.

Chaparral Grasses.[7]—The most characteristic grass species of the chaparral belt include:

Southern	More northern
Melica frutescens	*Calamagrostis densa*
Muhlenbergia microsperma	*Agrostis diegoensis*
Stipa parishii	*Melica imperfecta*
Stipa coronata	*Melica torreyana*
Stipa lepida	

Only in the southern part of the state have grass species very successfully responded to the influence of the chaparral and become so restricted as seldom to be found outside the belt. *Stipa coronata* and *S. lepida* are common and conspicuous elements; the others are somewhat rare. Apparently these species originated in, or near, their present localities, for they have no near relatives in distant floras. According to Clements (1934) the grassland is accomplishing a "gradual encroachment" on the chaparral, but the two vegetational zones have existed "since the last great pulsation of the Pleistocene," as evidenced "by the universal absence of chaparral relicts."

Northward the pure chaparral has no characteristic grass species. Here are found *Calamagrostis densa* (obviously a narrower adaptation of *C. koelerioides*) and occasionally *Melica torreyana* and *Agrostis diegoensis*. Where there are especially dense stands of hard chaparral (for example, pure stands of *Adenostema* or *Arctostaphylos*) not only the grasses but nearly all other herbaceous species are generally forced out by the competition. Where the chaparral tends to be "soft," composed of mixtures of *Arctostaphylos, Quercus, Rhamnus, Ceanothus,* and similar plants, perennial species are frequent, but are species characteristic of oak woods or open ranges, such as *Stipa pulchra, S. californica, Melica californica, Sitanion hystrix, Poa secunda, Bromus carinatus, Elymus glaucus,* and *Koeleria cristata.* Introduced weedy annuals spring up whenever sufficient moisture is available (*Bromus rubens, B. mollis, Avena barbata, Gastridium ventricosum,* and *Aira caryophyllea*) but introduced perennials are absent. Not one of the twenty-one species listed by Sampson (1944) as "common to chaparral areas" is confined in its distribution to that area, but are the characteristic species of the oak woods and open grasslands.

Cooke (1940) in discussing *Stipa californica* in the Mount Shasta area, says:

> [It is] generally confined to the chaparral but also present throughout the transition zone and scattered through the Canadian zone. If the chaparral should be discussed as a grass association it could be called an *Elymus glaucus–Stipa californica–Bromus carinatus* association.

Grasses of Coastal Bluffs and Sand Dunes.—Along the strand the characteristic species include:

Native	Native (*continued*)
Agropyron arenicola	*Agrostis pallens*
Agrostis blasdalei	*Calamagrostis foliosa*
Agrostis californica	*Elymus mollis*

[7] For a discussion of the ecology of and distribution of the chaparral belt, see Sampson (1944) and Jepson (1925).

Native (*continued*)
Elymus vancouverensis
Elymus virescens
Poa confinis
Poa douglasii
Poa macrantha
Poa unilateralis

Introduced annuals
Holcus lanatus
Holcus mollis

Introduced perennials
Agropyron junceum
Ammophila arenaria

Like the endemics of the neighboring bog flora and unlike the endemics of the vernal pools of the Great Valley, these species are probably relics. They reached California a long time ago and have since adapted themselves to only the most specialized habitats. It is perhaps more than a coincidence that *Agrostis blasdalei* and *A. pallens,* occupying isolated coastal situations, should be the only California representatives of their section of *Agrostis.* Other members of the section are found southward in the mountains of Mexico (*A. tolucensis* H.B.K.) and the mountains of Peru (*A. bromoides* Gr.). The species related to *Poa unilateralis* are also mountain inhabiting, but are found well represented in the California Sierra Nevada. Only *Elymus virescens,* most widespread of the three listed and the commonest (California north to Alaska), appears to be of recent origin, its nearest relative being the abundant *E. glaucus* of the Great Valley and the foothills.

Cooper (1936), in a comprehensive survey of the distribution and origin of the strand and dune flora of the Pacific Coast, concludes that *Poa confinis, P. douglasii, P. macrantha,* and the two dune species of *Elymus* (lumped by Cooper as *E. arenarius*) are, together with other associated species, of "subarctic or north temperate origin." The three *Poa* species—apparently closely related, for all fall into the section Pratenses—are related to *P. eminens* Presl of coastal northeastern Asia and arctic America and *P. labradorica* Steud., of the coast of Labrador. *Elymus* was first considered circumboreal in distribution, the North American material often being separated as var. *villosus* (St. John, 1915), but the latest taxonomic thought not only separates the New World material (as *E. mollis*) from the Old World, *E. arenarius,* but further distinguishes on the Pacific Coast *E. vancouverensis* Vasey. Although the origins of *Agrostis pallens* and *Agropyron arenicola* are more obscure, they belong to genera of principally north-temperate development, and they offer no evidence against the general picture of a migration southward of the grass species inhabiting the California sand dunes. Further evidence for the northern origin of the grasses in the dune flora is seen in the near absence of grasses on the strand formation of the southern California coast (McKenny, 1901).

There are only two introduced perennials on the dunes, *Ammophila arenaria* and *Agropyron junceum,* both from seashore sands and dunes of Europe, the former well established over a broader range than any of the native species, the second established only locally.

Salt-Marsh Grasses.—The ten species found in salt marshes are:

Native (all perennials)
Distichlis spicata var. *stolonifera*
Hordeum nodosum var. *boreale*
Monanthochloe littoralis
Puccinellia nutkaensis
Spartina foliosa

Introduced
Agrostis palustris
Lepturus cylindricus
Lolium strictum
Lolium subulatum
Pholiurus incurvus

Only the five introduced species, all from the salt marshes of Europe, have a similar background for their appearance in the California flora. It is striking that all but *Agrostis palustris* should be annuals, whereas no native annual grasses appear in the salt marshes. The general poverty of the salt-marsh floras probably attests to their recent formation, which is further evidenced by comparatively recent radical changes in the elevation of the California land mass.

Distichlis spicata is of wide occurrence throughout the Americas (Beetle, 1943*a*). Variety *stolonifera* intergrades with the inland variety *stricta,* and these may be presumed to be closely related. Variety *stolonifera* has neither become completely adapted to the salt-marsh habitat nor lost its connection with the inland flora. This situation is similar to that found in the introduced *Agrostis palustris,* whose affinities with the common pasture grass, *A. alba* (red top), are marked.

The dioeciousness of *Monanthochloe littoralis* is not an indication of relationship with *Distichlis,* in spite of the rare occurrence of the condition in the Festuceae. *Monanthochloe* is a small genus (probably only two species) ranging across the North American subtropics, from whence it came to California.

In contrast is the probable origin of *Puccinellia grandis,* which ranges north to Alaska; there its range coincides with that of at least twelve other related species (Swallen, 1944).

Finally, *Spartina foliosa* is similar to and probably related to *S. alterniflora* of the Atlantic Coast of North America; its method of reaching the California coast is in doubt.

Grasses of Bogs.—*Agrostis longiligula* and *Calamagrostis bolanderi* are the only two grasses within this habitat which need special mention. The true coastal bogs, strongly peaty and containing peat moss, have a flora independent of that of the recent bogs of both the Sierra Nevada and the Coast Ranges, whose species are essentially the same as those of the pine woods which surround them. It is likely that intensive search would reveal more bogs in the coastal areas than are now known botanically. At present, knowledge of them comes for the most part from Mendocino County where the largest and most southerly (Rigg, 1933) of the bogs occurs.

Unlike the endemic species of the Great Valley to be considered of recent derivation from typically California genera, *Agrostis longiligula* and *Calamagrostis bolanderi* are representatives of cosmopolitan genera and are possibly relics. Bog soceties are more common northward in North America and are closely related to similar societies in Eurasia (Transeau, 1903). According to Transeau:

> Present bog habitats are continuations of similar habitats which existed in early postglacial times, when tundra conditions and tundra vegetation were dominant . . . [and] the temperature phenomena of undrained depressions, containing deposits of peat are favorable to the preservation of these types [that is, relics].

The more recently formed bogs tend to have a characteristic flora consisting of *Calamagrostis bolanderi, C. breweri, C. inexpansa, Glyceria pauciflora,* and *Deschampsia caespitosa.*

OTHER CALIFORNIA GRASSES

In addition, the grass family is represented in California by the bamboos, cereals, a few lawn grasses (*Opizia stolonifera, Axonopus compressus, Stenotaphrum secundatum,* and *Eremochloa ophiuroides*), and a few ornamentals (for example, *Cortaderia selloana* and *Ampelodesmos mauritanicus*), which are usually found only under cultivation. A partial list of introduced grasses and their histories is given by Robbins (1940); for additions see Beetle (1943, *b*).

CONCLUSION

Some of the foregoing material is available in floras of California and all of it could be. The application of this enlarged focus however, prepares the way for a new viewpoint in conservation work. The practical application of the present study in the field of agronomy centers around efforts to improve rangeland, a natural resource no less important than forest or wildlife, which has been found to require a program of planned management if its value is to be maintained undiminished (Jones and Love, 1945). The natural areas defined by the known ranges of grass species are the areas within which any given program of management will be practical.

In the search for better range grasses, the regions from which introductions might be presumed to be successful could be chosen on the evidence of: (1) incidence of successful introductions in the past; and (2) failure of unsuccessful introductions in the past, regardless of whether they have been brought in by nature before man or subsequently either purposely or accidentally by man. This is the type of evidence that should control the choice of native range plants for selection improvement or the choice of species and areas in reseeding programs.

In the larger and more general ecological picture, the evidence given by the detailed study of the grass family may now be correlated with the known facts concerning the migration of whole floras. Then greater confidence may be placed in the indicator value of grasses in studies of plant succession and range management. In addition, herein is basic evidence bearing on the question of grassland as a climax or subclimax.

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