TWO

Systematics of California Grasses (Poaceae)

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The grass family (Poaceae or Gramineae) is the fourth largest flowering plant family in the world and contains about 11,000 species in 800 genera worldwide. Twenty-three genera contain 100 or more species or about half of all grass species, and almost half of the 800 genera are monotypic or diatypic, i.e., with only one or two species (Watson and Dallwitz 1992, 1999).

Over the last 150 years the grass flora of California has been the subject of considerable attention by botanists. Bolander (1866) prepared the first comprehensive list, recognizing 112 grasses from California, of which 31 were introductions. Thurber (1880) mentions 175 grasses in California, and Beetle (1947) enumerates 400 known species. It is interesting to note that Crampton (1974) recognized 478 grasses in California, and of these, 175 were introduced and 156 were reported as annuals (we report 152 annuals here).

We recognize 524 grass species in 144 genera; of these, 233 (44.5%) species in 65 genera are introduced (see Appendix 1), and the remaining 291 (55.5%) species in 79 genera are native. Thirty-seven species are endemic to California. One hundred fifty-two grasses in California are annual; of these 101 are introduced and 51 are native. Obviously the grass flora has been altered by humans, especially over the last 300 years since European settlement. The percentage of introduced grasses is perhaps higher in California than in any other state, simply because there are many different habitats (from 212 feet below sea level in Death Valley to 14,496 feet on top of Mount Whitney) available for colonization of weedy species. In addition, many annual species and genera of Mediterranean origins have found suitable habitats in California (see D'Antonio et al., Chapter 6).

To understand the important adaptations within the grasses, a firm grasp of the unique morphological features that define this family is needed. We start this chapter with an introduction to the morphology and ecology of grasses and then discuss the phylogeny (evolutionary relationships among organisms) of the major tribes of California grasses.

Morphology

The most important feature of grasses (Poaceae) is a one-seeded indehiscent fruit (seed coat is fused with the ovary wall), known as a caryopsis or grain (see Figure 2.1; Peterson 2003). The grain endosperm is rich in starch, although it can contain protein and significant quantities of lipids. The embryo is located on the basal portion of the caryopsis and contains high levels of protein, fats, and vitamins. The stems are referred to as culms, and the roots are fibrous and principally adventitious or arising from lower portions of the culms. Silica-bodies are a conspicuous component of the epidermis and are stored in silica short-cells. Many grasses have rhizomes (underground stems) or stolons (horizontal aboveground branches) that allow for vegetative reproduction in perennial grasses. Another important feature of grasses is intercalary meristems; these allow growth well below the apex, typically near the base of the plant. The leaves are parallel-veined and two-ranked with the basal portion forming cylindrical sheaths and the upper portion referred to as a blade. A ligule, located on the upper surface at the junction of the blade and sheath, commonly consists of a flap of tissue or hairs but can be lacking. The primary inflorescence is referred to as a spikelet with one to many two-ranked bracts inserted along the floral axis or rachilla. The lowest two bracts of each spikelet, inserted opposite each other, are called glumes, above which, along the rachilla, are borne pairs of bracts termed florets. Each floret consists of a lemma (lower bract) and palea (upper bract). Within each pair of lemma and palea the highly reduced flowers can be found. Each grass flower usually consists of two or three small scales at the base called lodicules, an ovary with a style and two plumose stigmas, and one to six

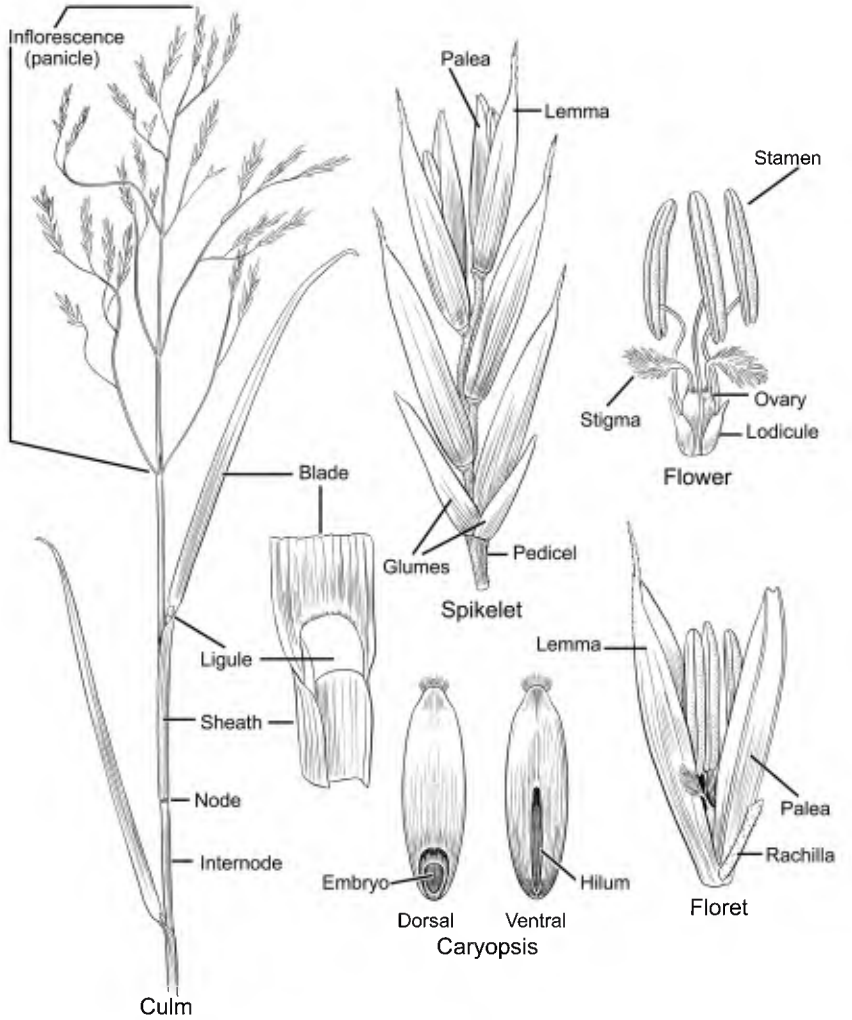

FIGURE 2.1. Diagnostic features of a grass *(Festuca californica)*: caryopsis, culm, floret, flower, and spikelet. Illustrated by Alice R. Tangerini.

(but more commonly three) stamens with basifixed anthers that contain single-pored, wind-dispersed pollen grains. Lodicules function to open the florets during flowering and evidently represent reduced perianth (sepals and petals) segments. Since the morphological features are often cryptic, or occasionally lacking, identification to species is often very difficult and requires a trained specialist.

Ecology

Specializations for open habitats and grazing tolerance, highly reduced floral structure, and wind pollination in the grasses have enabled the family to be extremely successful at planetwide radiation and colonization. One notable feature of grasses and other monocots is intercalary meristems that allow individual culms to resprout once they have been removed. Grasses are well adapted to open, marginal, and frequently disturbed habitats and can be found on every continent, including Antarctica. Two major photosynthetic or carbon dioxide (CO_2) assimilation pathways can be found in the grasses: C_3-fixing CO_2 by ribulose 1,5-biphosphate (Calvin-Benson cycle, found in all vascular plants), and C_4-fixing of CO_2, in which the initial product of photosynthesis is not the C_3 unit 3-phosphoglycerate but a unit with four C atoms (oxaloacetate). This is produced when CO_2 is bound to phosphoenolpyruvate to form four-carbon molecules (oxaloacetate or malate) in the Hatch-Slack cyle. There are corresponding anatomical, physiological, phytogeographical, and ecological differences between these two types. The C_3 grasses are well adapted to temperate climates with winter precipitation, whereas C_4 grasses are well suited to tropical environments with summer/fall precipitation. The evolution of C_4 photosynthesis has allowed grasses to outcompete other plants in warm, tropical and subtropical environments by limiting oxidation (photorespiration) of photosynthetic products (Ehleringer and Monson 1993). All of these features have led to the family's ability to occupy nearly one-quarter of the earth's land surface in various climatic environments as the dominant component of grasslands.

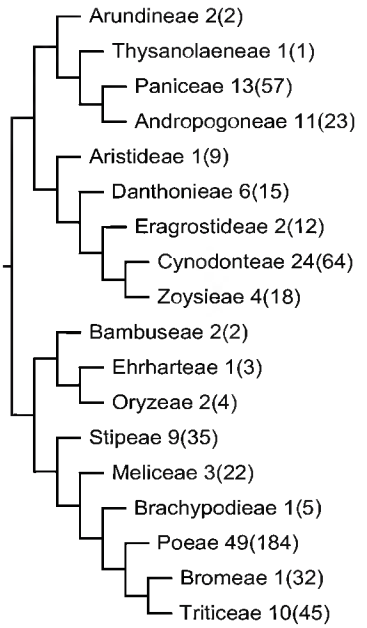

FIGURE 2.2. A hypothetical phylogeny of the grass tribes represented in California based on Soreng et al. 2005. The first numeral indicates the number of genera within a tribe, and the numeral in parentheses () indicates the number of species in California.

A cladogram showing the relationships of the 17 tribes represented in California is given in Figure 2.2. All grasses in the BEP (Bambusoideae, Ehrhartoideae, and Pooideae) clade (all descended from a single common ancestor) and the Californian Danthonioideae are C_3, whereas all grasses in the Aristidoideae and Chloridoideae are C_4. The Panicoideae have C_3, C_4, and C_3-C_4 intermediates, although the majority of the species in California are C_4.

Historically, the grassland biome has been maintained by a myriad of biotic, climatic, and edaphic effects. First, there usually is a dry season in which grasses and adjacent forest border dry out and become flammable (Axelrod 1985). Repeated fires favor grasses over most tree and shrub species, since they very easily resprout from the base. Second, large herbivorous mammals (e.g., bison and antelope) are instrumental at maintaining and further opening up grassland communities (Axelrod 1985). An often overlooked consequence of grazing animals is their effect on soil compaction, which again favors sod-forming grasses over trees and shrubs.

The exact species composition of California's pre-agricultural grasslands is not very well documented. Wester (1981) and Holstein (2001) have presented well-documented accounts based on historical records and current ecological samples of relict vegetation in California. They found these grasslands to be spatially diverse with many different species of the annual or perennial habit. In the San Joaquin Valley, grasslands were apparently dominated by annual species and xerophytic shrubs, and perennial bunchgrasses were common only on well-watered floodplains (Wester 1981).

Phylogeny

Despite variation among grass species in inflorescence structure and vegetative morphology, the grass family was probably characterized as a distinct entity in most early cultures. Three hundred years before the Christian era, Theophrastus, a Greek scholar, recognized the grass family and began to teach his students the concepts of plant morphology. The first scientific subdivision of the family was made by Robert Brown (1814), who recognized two different spikelet types between subfamily Panicoideae and Pooideae (Festucoideae). Bentham (1881) recognized 13 tribes grouped in the two major subfamilies. Hitchcock (1935) and Hitchcock and Chase (1951), in their treatments of the grasses of the United States, recognized 14 tribes in these two major subfamilies. The two-subfamily classification was used by most agrostologists for almost 150 years until more modern syntheses were developed.

With the infusion of molecular data our present concept and classification of the grasses is changing at a rapid rate. In California we currently recognize eight subfamilies: Bambusoideae, Ehrhartoideae, Pooideae, Arundinoideae, Danthonoideae, Aristidoideae, Chloridoideae, and Panicoideae (GPWG 2001; Soreng et al. 2005), and in these subfamilies we recognize 18 tribes and 44 subtribes (Table 1). A cladogram (see Figure 2.2) of these 18 tribes summarizes the most widely accepted concepts regarding the phylogenetic relationships among the tribes and subfamilies represented in California (GPWG 2001, Soreng and Davis 1998, 2000). The tree is rooted between the PACAD and BEP clades. Three numerically small, tropical subfamilies of grasses, not represented in California, diverge below this root point. In the PACAD clade, a clade containing Panicoideae (Andropogoneae, Thysanolaeneae, and Paniceae) and the Arundinoideae (Arundineae) is sister to a clade containing the Chloridoideae (Cynodonteae, Eragrostideae, and Zoysieae), Aristidoideae (Aristideae), and Danthonioideae (Danthonieae). In the BEP clade the Pooideae (Brachypodieae, Bromeae, Meliceae, Poeae, Stipeae, and Triticeae) is sister to a clade of the Ehrhartoideae (Ehrharteae and Oryzeae) and the Bambusoideae (Bambuseae). The BEP clade corresponds, in part, to the old term "festucoid" grasses used by historical agrostologists. The three most diverse subfamilies in California are the Pooideae with 323 (61.6%) species in 73 genera, the Chloridoideae with 94 (17.9%) species in 30 genera, and the Panicoideae with 80 (15.3%) species in 24 genera.

Panicoideae

The Panicoideae are the least diverse of the three major subfamilies represented by the California grasses, and there are no endemic Panicoideae within the state. This paucity of

TABLE 2.1
Classification of the Grasses Found in California

Subfamily Bambusoideae

Tribe Bambuseae

Subtribe Arundinariinae

Pseudosasa

Subtribe Shibataeniae

Phyllostachys

Subfamily Ehrhartoideae (synonym: Oryzoideae)

Tribe Ehrharteae

Ehrharta

Tribe Oryzeae

Subtribe Oryzinae

Leersia, *Oryza*

Subtribe Zizaniinae

Zizania

Subfamily Pooideae

Tribe Stipeae

Subtribe Stipinae

Achnatherum, Hesperostipa, Jarava, Nassella, Piptatherum, Piptochaetium, Ptilagrostis, *Stipa*

Subtribe Ampelodesminae

Ampelodesmos

Tribe Meliceae

Glyceria, Melica, Pleuropogon

Tribe Brachypodieae

Brachypodium

Supertribe Poodae

Tribe Poeae

Subtribe Torreyochloinae

Amphibromus, ***Torreyochloa***

Subtribe Aveninae

Arrhenatherum, Avena, ***Cinna,*** *Gaudinia,* ***Graphephorum, Koeleria,*** *Lagurus, Rostraria,* ***Sphenopholis, Trisetum***

Subtribe Phalaridinae

Anthoxanthum, Phalaris

Subtribe Brizinae

Briza

Subtribe Agrostidinae

Agrostis, *Ammophila, Bromidium,* ***Calamagrostis,*** *Gastridium, Lachnagrostis,* ***Podagrostis, Polypogon***

Subtribe Puccinelliinae

Puccinellia, *Sclerochloa*

Subtribe Poinae

Apera, ***Dissanthelium, Poa***

Subtribe Alopecurinae

Alopecurus, Beckmannia, Phleum

Subtribe Holcinae

Holcus

Subtribe Airinae

Aira, ***Deschampsia, Vahlodea,*** *Ventenata*

Subtribe Scribneriinae

Scribneria

Subtribe Loliinae

Festuca, Leucopoa, *Lolium, Schedonorus,* ***Vulpia***

Subtribe Dactylidinae

Dactylis, Lamarckia

Subtribe Cynosurinae

Cynosurus

Subtribe Parapholinae

Catapodium, Cutandia, Hainardia, Parapholis

Supertribe Triticoidae

Tribe Bromeae

Bromus

Tribe Triticeae

Subtribe Hordeinae

Agropyron, ***Elymus, Hordeum, Leymus, Pascopyrum, Pseudoroegneria,*** *Secale*

Subtribe Triticinae

Aegilops, Taeniatherum, ***Thinopyrum,*** *Triticum*

TABLE 2.1 (CONTINUED)
Classification of the Grasses Found in California

Subfamily Panicoideae

Tribe Thysanolaeneae

Thysanolaena

Tribe Paniceae

Subtribe Cenchrinae

Cenchrus, *Pennisetum*

Subtribe Digitariinae

Digitaria

Subtribe Melinidinae

Eriochloa, *Melinis,* ***Urochloa***

Subtribe Setariinae

Setaria, *Stenotaphrum*

Subtribe Panicinae

Dichanthelium, Echinochloa, Panicum

Subtribe Paspalinae

Axonopus, ***Paspalum***

Tribe Andropogoneae

Imperata, Miscanthus, Saccharum (Erianthus)

Subtribe Sorghinae

Bothriochloa*, Sorghum*

Subtribe Andropogoninae

Andropogon, Schizachyrium

Subtribe Anthistiriinae

Heteropogon, *Hyparrhenia, Themeda*

Subtribe Tripsacinae

Zea

Subfamily Arundinoideae

Tribe Arundineae

Arundo, ***Phragmites***

Subfamily Aristidoideae

Tribe Aristideae

Aristida

Subfamily Danthonioideae

Tribe Danthonieae

Cortaderia, ***Danthonia,*** *Karroochloa, Rytidosperma, Schismus, Tribolium*

Subfamily Chloridoideae

Tribe Cynodonteae

Acrachne, ***Blepharidachne,*** *Dactyloctenium,* ***Leptochloa, Scleropogon, Swallenia, Tridens***

Subtribe Boutelouinae

Bouteloua

Subtribe Chloridinae

Chloris, *Cynodon, Eustachys*

Subtribe Eleusiniae

Eleusine

Subtribe Hilariinae

Hilaria *(Pleuraphis)*

Subtribe Monanthochloinae

Distichlis, Monanthochloe

Subtribe Muhlenbergiinae

Lycurus, Muhlenbergia, Schedonnardus

Subtribe Munroinae

Dasyochloa, Erioneuron, Munroa

Subtribe Orcuttiinae

Neostapfia, Orcuttia, Tuctoria

Tribe Eragrostideae

Subtribe Cotteinae

Enneapogon

Subtribe Eragrostidinae

Eragrostis

Tribe Zoysieae

Subtribe Sporobolinae

Crypsis, ***Spartina, Sporobolus***

Subtribe Zoysiinae

Zoysia

NOTE: Based on Soreng et al. 2005. Native taxa are **bold**, introduced taxa are lightface type. All genera are *italicized*. A genus is considered native if it includes one or more native species (see Appendix 1 for clarification of native versus introduced species).

species diversity is likely a direct response to the climatic patterns of the past and present, because Panicoideae grasses are best suited to warm and humid environments of tropical and warm temperate zones. The spikelets in this subfamily usually have two glumes and two closely spaced florets; the lower floret is usually sterile, the upper floret without a rachilla extension.

Paniceae

The Paniceae in California contain 57 species in 13 genera and are the sister to the Andropogoneae (Figure 2.2). They are characterized by having two-flowered spikelets with membranous glumes, the lower floret staminate or reduced, membranous, and the upper floret perfect and firm. Even though *Panicum* (10 spp. in California) and *Paspalum* (4 spp. in California) are large genera in the eastern United States and especially in tropical America, they are very poorly represented in the western United States, where the climate is generally dryer, especially in the warmer months.

Andropogoneae

The Andropogoneae are characterized by having fragile racemes of paired spikelets, where there is a sessile and a pedicellate spikelet with differing sexuality. Commonly the pedicellate spikelets are staminate or reduced, and the sessile spikelets are usually perfect or pistillate. Within spikelets, typically the glumes are firm, and the two florets have membranous bracts. The Andropogoneae in California contains 23 species in 11 genera, most of which are uncommon in California grasslands.

Pooideae

There are a few morphological synapomorphies (diagnostic characteristics) delineating the Pooideae. In this subfamily trends include parallel-sided subsidiary cells, nonvascularized lodicules with a membranous margin, an epiblast with no scutellar cleft, and the absence of microhairs.

Stipeae

In California the earliest diverging lineage in the Pooideae clade (Figure 2.2) is the Stipeae. The Stipeae probably arose in Laurasia (37–24 mybp) since a few fossil reports, e.g., *Stipideum* and possibly *Piptochaetium,* are from the Oligocene in North America (Thomasson 1987). Therefore, ancestors of this tribe likely were able to colonize the North American and Eurasian continents before they separated. The Stipeae are characterized as having one-flowered spikelets without rachilla extensions and terete florets that are usually awned near or immediately below the apex and have a well developed, often sharply pointed callus. The Stipeae include three endemics centered in the Sierra Nevada: *Achnatherum latiglume* from the Transverse Ranges and central and southern Sierra Nevada, *A. stillmanii* from the northern Sierra Nevada, and *Ptilagrostis kingii* from the central and southern Sierra Nevada highlands. Members of the Stipeae are well adapted to the steppe vegetation in Eurasia and the Americas, where they are often dominant elements. *Nassella cernua, N. lepida,* and *N. pulchra* are sometimes dominant in parts of the California grasslands.

Meliceae

The next tribe to diverge from the main lineage in the Pooideae clade is Meliceae, also reported as having possible fossils in the Oligocene of North America (Thomasson 1987). The Meliceae have closed sheaths and lemmas that are five- to 13-nerved; short, bushy stigmas; and short, truncate, fleshy lodicules. *Melica torreyana* is an endemic from the northwestern region, the Sierra Nevada, and central western California. Three other varieties of *Melica* are also endemic: *Melica californica* var. *nevadensis* Boyle from northwestern and central western regions, Sierra Nevada foothills, western Transverse Ranges, and the Tehachapi Mountains; *M. geyeri* var. *aristulata* J.T. Howell from the San Francisco Bay Area; and *M. stricta* var. *albicaulis* Boyle from the western Transverse Ranges. The endemics *Pleuropogon californicus* and *P. hooverianus* occur in marshy areas from northwestern California, Cascade Range foothills, and north and central Sierra Nevada foothills; and from the southern North Coast and northern Central Coast regions, respectively.

Poaeae

The largest tribe, Poaeae (184 spp.), includes *Poa* with 34 species. *Poa* has diversified throughout temperate, boreal, and arctic regions around the world and occurs on islands of similar habitats in the tropics (Gillespie and Soreng 2005). The Poeae clade, equivalent to supertribe Poodae, is sandwiched between the ancestral Brachypodieae, with only five introduced species, and the sister supertribe Triticoidae, which includes the Bromeae, with 32 species, and the Triticeae, with 45 species. In California, *Poa* exhibits both high species diversity (34 spp., of these, 28 are native) and a high degree of endemism, with eight species confined to the state (see Appendix 1). *Poa* is characterized as having rather small, multiflowered spikelets; lemmas that are keeled, unawned, usually five-nerved, commonly with weblike hairs from the dorsal side of the callus, caryopses that are firm with lipid and a short hilum; lodicules that are broadly lanceolate, often with a lateral lobe; leaf sheaths closed above the base between 1/20 the entire length and the top; leaf blades that generally have two rows of bulliform cells (one on either side of the midnerve, these appearing like railroad tracks) and no additional rows of bulliform cells; and blades commonly with naviculate (boat-shaped) apices (Soreng 1993; in press a, b). The Poaeae endemics, *Poa kecki, P. stebbinsii,* and *Cinna bolanderi,* have originated on "islands" of arctic habitat in the high Sierra Nevada between 1,800 and 4,000 meters. *Poa atropurpurea* is known only from high-elevation meadows (1,500–2,000 meters) in the Peninsular Ranges and the San Bernardino Mountains. *Poa sierrae* and *P. tenerrima* (known only from serpentine outcrops)

occur in the Sierra Nevada canyons and foothills. *Poa napensis* is known only from mineralized soils around hot springs in the North Coast Ranges, *P. kelloggii* is known only from the North and Central Coast Redwood forests (not found in Oregon), *P. douglasii* is known only from the South Coast sand dunes, and *P. diabolii* is known only from coastal soft scrub over Edna shale in the South Coast. These species of *Poa* belong to three subgenera and four sections. *Poa kelloggii* belongs to the earliest-diverging lineage in the genus, *Sylvestres*, a subgenus that, so far as is known, is endemic and principally confined to rich forests of North America. *Poa napensis* and *P. tenerrima* belong to subgenus *Stenopoa* section *Secundae* and are closely related to *P. secunda*, which is perhaps the most common native grass across California, occurring in a wide range of habitats from coast range low-elevation sites to high-elevation Sierra Nevada meadows and Great Basin grasslands. *Poa keckii* belongs to a complex of short-anthered species of the western cordillera of North America (Beringia), placed in subgenus *Stenopoa* section *Abbreviatae*. *Poa atropurpurea, P. douglasii,* and *P. diaboli* are members of the diclinous *Poa* subgenus *Poa* section *Madropoa*, which is centered in and mostly endemic to western North America. Several other species of *Poa* section *Madropoa* are nearly confined to California; *P. piperi, P. pringlei,* and *P. rhizomata* extend into SW Oregon on serpentine, volcanic, and peridotite substrates, respectively.

Other endemic species in the Poeae, subtribe Agrostidinae include *Agrostis blasdalei, A. hooveri, Calamagrostis ophitidis,* and *C. foliosa*, all from the North and South Coast Ranges, and *Dissanthelium californicum* (subtribe Poinae), which was previously thought to be extinct but was recently re-collected on Santa Catalina Island. *Scribneria bolanderi,* the sole species of subtribe Scribneriinae, is endemic to vernal pool habitats in the California Floristic Province, although it also reaches Oregon. The generic relationship between *Agrostis* and *Calamagrostis* is somewhat controversial since both are morphologically similar and have one-flowered spikelets. Species of *Calamagrostis* have rachilla extensions (usually hairy), a callus with hairs, and membranous to chartaceous lemmas, whereas species of *Agrostis* do not have rachilla extensions, have a callus that is usually glabrous, and have hyaline to membranous lemmas (Peterson and Saarela in press). Current research on *Dissanthelium* indicates that species in this genus should be subsumed within *Poa* (Gillespie and Soreng 2005; Refulio Rodriguez, personal communication). *Puccinellia howellii* (Puccinelliinae), another endemic, is known only from mineral springs in the Yolla Bolly Mountains and the Klamath Range.

Bromeae

The Bromeae are characterized as having closed sheaths, lemmas that are bifid or toothed with a subapical awn, hairy apically bilabiate appendages of the ovary, and simple starch grains. In California, *Bromus* (Bromeae) consists of 32 species; of these, 17 are native. *Bromus* can be distinguished from other grasses by having connate leaf sheath margins, subapically inserted awns, hairy apical bilabiate appendages of the ovary, and simple starch grains (Wagnon 1952; Saarela and Peterson in press). This genus is widely distributed in temperate and mountainous regions of the Northern and Southern Hemispheres, and several species are important native forage grasses in California [*B. ciliatus, B. richardsonii, B. suksdorfii*] (Peterson et al. 2002). Endemics within California include *Bromus grandis* and *B. hallii* from the southern Sierra Nevada, Transverse and Peninsular ranges; and *B. pseudolaevipes* from the San Francisco Bay Area, Outer South Coast Ranges, South Coast, Channel Islands, Western Transverse Ranges, and the Peninsular Ranges (Saarela and Peterson in press). All three of these species were included in Wagnon's (1952) Pacific Slope Group of *Bromus* section *Bromopsis,* where he mentions that *B. grandis and B. hallii* perhaps share a common origin with *B. orcuttianus*. *Bromus carinatus* is a widespread native that occurs in many habitats mostly below 3500 meters.

The genus *Bromus* contains 15 introduced species; many of these are invasive in California grasslands. *Bromus diandrus* and *B. hordeaceus* are widespread and dominant or codominant throughout coastal and valley grasslands (see D'Antonio et al., Chapter 6). *Bromus tectorum* and *B. madritensis* subsp. *rubens* (L.) Husn. are more common in the California deserts. These four species of *Bromus* are listed by the California Invasive Plant Council (Cal-IPC at http://www.cal-ipc.org) as invasive pest plants of concern to wildland habitat.

Triticeae

The Triticeae (sister to the Bromeae), or wheat grass tribe, in California includes 45 species in 10 genera. The tribe is characterized by having a true spike inflorescence where all the spikelets are sessile and aligned singly or in groups of two or three along the central rachis; coriaceous glumes and lemmas; ovaries with densely hairy apices; and caryopses with simple starch grains and long hilums. The evolutionary history of this tribe is fairly well known since wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), and rye (*Secale cereale*) are members. The tribe is thought to have originated in Eurasia, possibly during the Miocene, and then radiated to the New World (Blattner 2006). Two species, *Elymus californicus* and *Leymus pacificus*, are endemic to coastal California. The former species is known from the North and Central Coast prairies, North Coast Ranges, and San Francisco Bay Area, and the latter is known from the North and Central Coast and the Channel Islands. *Leymus condensatus* is also a conspicuous associate (culms 1.5–3.5 meters tall) of the chaparral and coastal sage scrub in California and Baja California, Mexico, and *L. triticoides* was perhaps historically dominant on heavier soils in valleys and hillslopes of Central California (Gould and Moran 1981; Holstein 2001).

Chloridoideae

The core species in this subfamily share two morphological synapomorphies. All exhibit "Kranz" or C_4 leaf anatomy (except *Eragrostis walteri* Pilg. from South Africa) and most

have chloridoid bicellular microhairs (broad, short terminal cell the same thickness as the basal cell) present on leaf surfaces (Peterson et al. in press). Other character trends in the chloridoids include a base chromosome number of $x = 10$ (a pleisiomorphy or ancestral characteristic), embryos with nonlinear hilums that are usually punctiform or small with elongate mesocotyl internodes, and two fleshy, vascularized, truncate lodicules (GPWG 2001; Soreng and Davis 1998). However, most of these character trends are seen in sister subfamilies: Aristidoideae, Arundinoideae, Danthonioideae, and Panicoideae.

The Eragrostideae is considered the earliest diverging tribal lineage of the chloridoids and is sister to a clade that contains the Zoysieae and the Cynodonteae (Figure 2.2). Character combinations in the Eragrostideae include spikelets with many florets, lemmas with 3 to 13 nerves, and many species adapted to xeric habitats. At this point we have no clear idea as to the relationships among the seven Cynodonteae subtribes (see Table 1). However, we do have good molecular support for maintaining the tribe Cynodonteae and morphological support for all of the seven subtribes (Peterson et al. in press). There are no definitive morphological characters that differentiate the Cynodonteae from the Eragrostideae and/or Zoysieae; the Cynodonteae essentially includes most of the variation present in the entire subfamily.

The evolutionary history of the chloridoids as a whole is even more obscure. Thomasson's et al. (1986) identification of Kranz anatomy in a fossil from a Miocene Ogallala formation in Kansas is the first definitive record. Since more than half of the genera within the Chloridoideae reside in Africa and all larger tribes and subtribes, excluding Muhlenbergiinae, have centers of diversity in Africa, Hartley and Slater (1960) concluded that the subfamily probably originated on the African continent (perhaps during the Oligocene) and spread from that region to other parts of the world.

Cynodonteae

The Boutelouinae, Hilariinae, Muhlenbergiinae, and Orcuttinae are clearly North American subtribes, but how their ancestor(s) arrived there is obscure. These subtribes probably ultimately descended from a Laurasian ancestor, given the distribution of *Muhlenbergia,* i.e., predominantly from the southwestern United States and northern Mexico, and also with six species in China (Peterson 2000; Peterson and Ortíz-Diaz 1998; Peterson et al. in press; Wu and Peterson 2006). Since the Chloridinae are most species-rich in South America, it seems likely that they originated in that continent and spread northward, although we have no genetic evidence for this. It is very difficult to determine any directional signal from the Monanthochloinae and Munroinae, although these two subtribes are slightly more species-rich in South America, suggesting a southern derivation. The Eragrostideae and Zoysinae are more likely west Gondwanaland groups, although the exact timing and routes of migration to both North America and South America are unknown.

The Muhlenbergiinae are characterized by having spikelets perfect, staminate, or sterile; occasionally with cleistogenes in the leaf sheaths; inflorescence paniculate of spicate main branches or a single raceme; spikelet-bearing axis disarticulating (falling entire) or persistent; spikelets solitary, rarely paired or in triplets, occasionally secund; glumes awned or unawned; lemmas three-nerved, awned or unawned; and a base chromosome number of $x = 8–10$ (Peterson 2000). The largest genus, *Muhlenbergia,* has 18 species in California with a single introduced species *(Muhlenbergia schreberi).* Two species, *M. californica* and *M. jonesii,* are endemic to California, the former occurring in the South Coast and Transverse Ranges and the latter known only from the northern Sierra Nevada and the Klamath and High Cascade ranges (Peterson 1993, in press).

Seven species *(Neostapfia colusana, Orcuttia inaequalis, O. pilosa, O. tenuis, O. viscida, Tuctoria greenei,* and *T. mucronata)* of the eight species in the Orcuttiinae are endemic to California. Unlike most Chloridoideae, which are adapted to summer rains, these annual species are well adapted to winter rains and summer drought. They occur in the western part of the state in vernal pools, an endangered habitat. This subtribe is a unique lineage in the Cynodonteae and is exclusively restricted to the California biome [*Orcuttia californica* and *Tuctoria fragilis* (Swallen) J. Reeder extend into Baja California, Mexico].

Introductions

There are 43 introduced grass species currently included in the Cal-IPC Invasive Plant Inventory (Cal-IPC), and 28 species in 20 genera do not share any native congeners (species belonging to the same genus). Two of these genera, *Brachypodium* with five species and *Ehrharta* with three species, represent introduced tribes, the Brachypodieae and Ehrharteae.

Strauss et al. (2006) compared three groups: introduced species that are harmful to California ecosystem, native species, and introduced species that cause relatively little harm to California ecosystems. They demonstrated that the harmful introduced species are more distant phylogenetically from the native species than the benign introduced species are. This is an interesting conclusion, since it implies that Darwin's naturalization hypothesis and the "the escape from natural enemies" hypothesis are valid; species that are more distantly related to the native community are more likely to become noxious invasive weeds (Strauss et al. 2006).

The following grasses are currently on the alert category (species that appear to be expanding their range or species showing signs of being invasive in some areas) published by the Cal-IPC: *Brachypodium sylvaticum, Ehrharta longiflora, Spartina alterniflora, S. anglica, S. densiflora,* and *Stipa capensis. Aegilops triuncialis, Ammophila arenaria, Arundo donax, Ehrharta calycina,* and *Taeniatherum caput-medusae* are reported on the

Cal-IPC list as having a high rating (species that have severe ecological impacts, have moderate to high rates of dispersal, and are widely distributed).

Evolution toward Specialization

We can see several overarching patterns in the distribution of native and endemic species. There were repeated specializations to narrowly distributed habitats or restricted edaphic or climate settings: (1) isolated wetlands, including (a) vernal pools, mostly of the Central Valley and adjacent foothills (Orcuttiinae, *Scribneria, Phalaris lemmonii, Pleuropogon californicus, Puccinellia simplex* [now introduced in Utah]), (b) saline springs (*Puccinellia howellii* and the rare *P. parishii*, which is sporadic across the southwestern states) and mineralized soils around springs *(Poa napensis)*, (c) freshwater wetlands and moist mountain meadows *(Pleuropogon hooverianus, Poa atropurpurea, P. stebbinsii, Ptilagrostis kingii)*; (2) sand dunes *(Agrostis blasdalii, Calamagrostis bolanderi, Leymus pacificus, Poa douglasii, Swallenia alexandrae)*; 3) ultramafic substrates *(Calamagrostis ophitidis, Poa piperi, P. rhizomata, P. tenerrima)* and isolated shales *(P. diaboli)*; (4) alpine and peaks *(Alopecurus aequalis, A. geniculatus, Calamagrostis muiriana, Cinna bolanderi, Festuca brachyphylla, Koeleria macrantha, Poa glauca* ssp. *rupicola* (Nash) W.A. Weber, *P. keckii, P. pringlei)*; (5) the California Floristic Province *(Achantherum latiglume, A. stillmannii, A. diegoense, A. coronatum)*; (6) central and south coastal grasslands *(Melica imperfecta, Nassella cernua, N. lepida, N. pulchra, Aristida hamulosa, Leymus condensatus, Muhlenbergia microsperma, M. rigens)*; (7) southern coastal mountains/chaparral and forests *(Achnatherum parishii, Elymus stebbinsii, Melica frutescens, M. torreyana, Phalaris californica, P. lemmonii)*. Many of these species of limited distribution have evolved from more widespread congeners and belong to genera that are species-rich and well established in California.

Appendix 1: A List of the Grass Species Known to Occur in California

Intraspecific categories are not included. **Bolded** names are native, and those marked with an asterisk (*) are endemic. All other species are introduced and naturalized. This list was prepared using the *Catalogue of New World Grasses* (Soreng et al. 2005), PLANTS (USDA, NRCS 2006), and the Grass Manual on the Web (Barkworth et al. 2006). Also consulted but not completely followed were The Grasses of California (Smith 2006), A Synthesis of the North American Flora (Kartesz and Meacham 2006), and the Jepson Online Interchange for California floristics (JOI 2006). We have not done an extensive evaluation for all possible introductions, since these are continually being added as reports are published.

Achnatherum altum (Swallen) Hoge & Barkworth
Achnatherum aridum (M.E. Jones) Barkworth
Achnatherum coronatum (Thurb.) Barkworth
Achnatherum diegoense (Swallen) Barkworth
Achnatherum hymenoides (Roem. & Schult.) Barkworth
****Achnatherum latiglume*** (Swallen) Barkworth
Achnatherum lemmonii (Vasey) Barkworth
Achnatherum lettermanii (Vasey) Barkworth
Achnatherum nelsonii (Scribn.) Barkworth
Achnatherum nevadense (B.L. Johnson) Barkworth
Achnatherum occidentale (Thurb. ex S. Watson) Barkworth
Achnatherum parishii (Vasey) Barkworth
Achnatherum pinetorum (M.E. Jones) Barkworth
****Achnatherum stillmanii*** (Bol.) Barkworth
Achnatherum thurberianum (Piper) Barkworth
Achnatherum webberi (Thurb.) Barkworth
Acrachne racemosa (B. Heyne ex Roem. & Schult.) Ohwi
Aegilops cylindrica Host
Aegilops geniculata Roth
Aegilops tauschii Coss.
Aegilops triuncialis L.
Agropyron cristatum (L.) Gaertn.
Agropyron desertorum (Fisch. ex Link) Schult.
Agropyron fragile (Roth) P. Candargy
****Agrostis blasdalei*** Hitchc.
Agrostis capillaris L.
Agrostis densiflora Vasey
Agrostis elliottiana Schult.
Agrostis exarata Trin.
Agrostis gigantea Roth
Agrostis hallii Vasey
Agrostis hendersonii Hitchc.
****Agrostis hooveri*** Swallen
Agrostis idahoensis Nash
Agrostis microphylla Steud.
Agrostis oregonensis Vasey
Agrostis pallens Trin.
Agrostis scabra Willd.
Agrostis stolonifera L.
Agrostis variabilis Rydb.
Aira caryophyllea L.
Aira elegantissima Schur
Aira praecox L.
Alopecurus aequalis Sobol.
Alopecurus carolinianus Walter
Alopecurus geniculatus L.
Alopecurus myosuroides Huds.
Alopecurus pratensis L.
Alopecurus saccatus Vasey
Ammophila arenaria (L.) Link
Ammophila breviligulata Fernald
Ampelodesmos mauritanicus (Poir.) T. Durand & Schinz
Amphibromus neesii Steud.
Andropogon glomeratus (Walter) Britton, Sterns & Poggenb.
Andropogon virginicus L.
Anthoxanthum aristatum Boiss.

Anthoxanthum nitens (Weber) Y. Schouten & Veldkamp
Anthoxanthum occidentale (Buckley) Veldkamp
Anthoxanthum odoratum L.
Apera interrupta (L.) P. Beauv.
Apera spica-venti (L.) P. Beauv.
Aristida adscensionis L.
Aristida californica Thurb.
Aristida dichotoma Michx.
Aristida divaricata Humb. & Bonpl. ex Willd.
Aristida hamulosa Henrard
Aristida oligantha Michx.
Aristida purpurea Nutt.
Aristida schiedeana Trin. & Rupr.
Aristida ternipes Cav.
Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl
Arundo donax L.
Avena barbata Pott ex Link
Avena fatua L.
Avena occidentalis Durieu
Avena sativa L.
Avena sterilis L.
Avena strigosa Schreb.
Axonopus fissifolius (Raddi) Kuhlm.
Beckmannia syzigachne (Steud.) Fernald
Blepharidachne kingii (S. Watson) Hack.
Bothriochloa barbinodis (Lag.) Herter
Bothriochloa ischaemum (L.) Keng
Bothriochloa laguroides (DC.) Herter
Bouteloua aristidoides (Kunth) Griseb.
Bouteloua barbata Lag.
Bouteloua curtipendula (Michx.) Torr.
Bouteloua eriopoda (Torr.) Torr.
Bouteloua gracilis (Kunth) Lag. ex Griffiths
Bouteloua trifida Thurb.
Brachypodium distachyon (L.) P. Beauv.
Brachypodium phoenicoides (L.) P. Beauv. ex Roem. & Schult.
Brachypodium pinnatum (L.) P. Beauv.
Brachypodium rupestre (Host) Roem. & Schult.
Brachypodium sylvaticum (Huds.) P. Beauv.
Briza maxima L.
Briza media L.
Briza minor L.
Bromidium tandilense (Kuntze) Rúgolo
Bromus alopecuros Poir.
Bromus arenarius Labill.
Bromus arizonicus (Shear) Stebbins
Bromus berteroanus Colla
Bromus briziformis Fisch. & C.A. Mey.
Bromus carinatus Hook. & Arn.
Bromus catharticus Vahl
Bromus cebadilla Steud.
Bromus ciliatus L.
Bromus commutatus Schrad.
Bromus diandrus Roth
****Bromus grandis*** (Shear) Hitchc.
****Bromus hallii*** (Hitchc.) Saarela & P.M. Peterson
Bromus hordeaceus L.
Bromus inermis Leyss.
Bromus japonicus Thunb.
Bromus laevipes Shear
Bromus madritensis L.
Bromus marginatus Nees ex Steud.
Bromus maritimus (Piper) Hitchc.
Bromus orcuttianus Vasey
Bromus polyanthus Scribn. ex Shear
Bromus porteri (J.M. Coult.) Nash
****Bromus pseudolaevipes*** Wagnon
Bromus racemosus L.
Bromus richardsonii Link
Bromus secalinus L.
Bromus sitchensis Trin.
Bromus sterilis L.
Bromus suksdorfii Vasey
Bromus tectorum L.
Bromus vulgaris (Hook.) Shear
Calamagrostis bolanderi Thurb.
Calamagrostis breweri Thurb.
Calamagrostis canadensis (Michx.) P. Beauv.
****Calamagrostis foliosa*** Kearney
Calamagrostis koelerioides Vasey
Calamagrostis muiriana B.L. Wilson & Sami Gray
Calamagrostis nutkaensis (J. Presl) J. Presl ex Steud.
****Calamagrostis ophitidis*** (J.T. Howell) Nygren
Calamagrostis purpurascens R. Br.
Calamagrostis rubescens Buckley
Calamagrostis stricta (Timm) Koeler
Catapodium rigidum (L.) Dony
Cenchrus ciliaris L.
Cenchrus echinatus L.
Cenchrus incertus M.A. Curtis
Cenchrus longispinus (Hack.) Fernald
Chloris gayana Kunth
Chloris truncata R. Br.
Chloris verticillata Nutt.
Chloris virgata Sw.
****Cinna bolanderi*** Scribn.
Cinna latifolia (Trevir. ex Go|2pp.) Griseb.
Cortaderia jubata (Lemoine) Stapf
Cortaderia selloana (Schult. & Schult. f.) Asch. & Graebn.
Crypsis alopecuroides (Piller & Mitterp.) Schrad.
Crypsis schoenoides (L.) Lam.
Crypsis vaginiflora (Forssk.) Opiz
Cutandia memphitica (Spreng.) K. Richt.
Cynodon dactylon (L.) Pers.
Cynodon plectostachyus (K. Schum.) Pilg.
Cynodon transvaalensis Burtt Davy
Cynosurus cristatus L.
Cynosurus echinatus L.
Dactylis glomerata L.
Dactyloctenium aegyptium (L.) Willd.
Danthonia californica Bol.
Danthonia decumbens (L.) DC.

Danthonia intermedia Vasey
Danthonia unispicata (Thurb.) Munro ex Macoun
Dasyochloa pulchella (Kunth) Willd. ex Rydb.
Deschampsia cespitosa (L.) P. Beauv.
Deschampsia danthonioides (Trin.) Munro
Deschampsia elongata (Hook.) Munro
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark
Dichanthelium oligosanthes (Schult.) Gould
Digitaria bicornis
Digitaria ciliaris (Retz.) Koeler
Digitaria eriantha Steud.
Digitaria ischaemum (Schreb.) Schreb. ex Muhl.
Digitaria sanguinalis (L.) Scop.
****Dissanthelium californicum*** (Nutt.) Benth.
Distichlis spicata (L.) Greene
Echinochloa colona (L.) Link
Echinochloa crus-galli (L.) P. Beauv.
Echinochloa crus-pavonis (Kunth) Schult.
Echinochloa muricata (P. Beauv.) Fernald
Echinochloa oryzoides (Ard.) Fritsch
Echinochloa phyllopogon (Stapf) Stapf ex Kossenko
Ehrharta calycina Sm.
Ehrharta erecta Lam.
Ehrharta longiflora Sm.
Eleusine indica (L.) Gaertn.
Eleusine tristachya (Lam.) Lam.
Elymus arizonicus (Scribn. & J.G. Sm.) Gould
****Elymus californicus*** (Bol. ex Thurb.) Gould
Elymus canadensis L.
Elymus elymoides (Raf.) Swezey
Elymus glaucus Buckley
Elymus lanceolatus (Scribn. & J.G. Sm.) Gould
Elymus multisetus (J.G. Sm.) Burtt Davy
Elymus repens (L.) Gould
Elymus scribneri (Vasey) M.E. Jones
Elymus sierrae Gould
****Elymus stebbinsii*** Gould
Elymus trachycaulus (Link) Gould ex Shinners
Enneapogon desvauxii P. Beauv.
Eragrostis barrelieri Daveau
Eragrostis cilianensis (All.) Vignolo ex Janch.
Eragrostis curvula (Schrad.) Nees
Eragrostis hypnoides (Lam.) Britton, Sterns & Poggenb.
Eragrostis lehmanniana Nees
Eragrostis lutescens
Eragrostis mexicana (Hornem.) Link
Eragrostis minor Host
Eragrostis pectinacea (Michx.) Nees
Eragrostis pilosa (L.) P. Beauv.
Eragrostis superba Peyr.
Eriochloa acuminata (J. Presl) Kunth
Eriochloa aristata Vasey
Eriochloa contracta Hitchc.
Eriochloa fatmensis (Hochst. & Steud.) Clayton
Eriochloa villosa (Thunb.) Kunth
Erioneuron pilosum (Buckley) Nash
Eustachys distichophylla (Lag.) Nees
Festuca ammobia Pavlick
Festuca arvernensis Auquier, Kergue|4len & Markgr.-Dann.
Festuca brachyphylla Schult. & Schult. f.
Festuca californica Vasey
Festuca elmeri Scribn. & Merr.
Festuca idahoensis Elmer
Festuca minutiflora Rydb.
Festuca occidentalis Hook.
Festuca roemeri (Pavlick) E.B. Alexeev
Festuca rubra L.
Festuca saximontana Rydb.
Festuca sororia Piper
Festuca subulata Trin.
Festuca subuliflora Scribn.
Festuca trachyphylla (Hack.) Krajina
Festuca viridula Vasey
Gastridium phleoides (Nees & Meyen) C.E. Hubb.
Gaudinia fragilis (L.) P. Beauv.
Glyceria borealis (Nash) Batch.
Glyceria elata (Nash) M.E. Jones
Glyceria fluitans (L.) R. Br.
Glyceria grandis S. Watson
Glyceria leptostachya Buckley
Glyceria occidentalis (Piper) J.C. Nelson
Glyceria striata (Lam.) Hitchc.
Graphephorum wolfii (Vasey) Vasey ex Coult.
Hainardia cylindrica (Willd.) Greuter
Hesperostipa comata (Trin. & Rupr.) Barkworth
Heteropogon contortus (L.) P. Beauv. ex Roem. & Schult.
Hilaria jamesii (Torr.) Benth.
Hilaria mutica (Buckley) Benth.
Hilaria rigida (Thurb.) Benth. ex Scribn.
Holcus lanatus L.
Holcus mollis L.
Hordeum arizonicum Covas
Hordeum brachyantherum Nevski
Hordeum bulbosum L.
Hordeum depressum (Scribn. & J.G. Sm.) Rydb.
Hordeum intercedens Nevski
Hordeum jubatum L.
Hordeum marinum Huds.
Hordeum murinum L.
Hordeum pusillum Nutt.
Hordeum vulgare L.
Hyparrhenia hirta (L.) Stapf
Imperata brevifolia Vasey
Jarava brachychaeta (Godr.) Peñailillo
Jarava ichu Ruiz & Pav.
Jarava plumosa (Spreng.) S.W.L. Jacobs & J. Everett
Jarava speciosa (Trin. & Rupr.) Peñailillo
Karroochloa purpurea (L. f.) Conert & Türpe
Koeleria macrantha (Ledeb.) Schult.
Lachnagrostis filiformis (G. Forst.) Trin.
Lagurus ovatus L.
Lamarckia aurea (L.) Moench

Leersia oryzoides (L.) Sw.
Leptochloa dubia (Kunth) Nees
Leptochloa fusca (L.) Kunth
Leptochloa panicea (Retz.) Ohwi
Leptochloa viscida (Scribn.) Beal
Leucopoa kingii (S. Watson) W.A. Weber
Leymus cinereus (Scribn. & Merr.) Á. Löve
Leymus condensatus (J. Presl) Á. Löve
Leymus mollis (Trin.) Pilg.
* ***Leymus pacificus*** (Gould) D.R. Dewey
Leymus salinus (M.E. Jones) Á. Löve
Leymus triticoides (Buckley) Pilg.
Lolium multiflorum Lam.
Lolium perenne L.
Lolium rigidum Gaudin
Lolium temulentum L.
Lycurus setosus (Nutt.) C. Reeder
Megathyrsus maximus (Jacq.) B.K. Simon & S.W.L. Jacobs
Melica aristata Thurb. ex Bol.
Melica bulbosa Geyer ex Porter & Coult.
Melica californica Scribn.
Melica frutescens Scribn.
Melica fugax Bol.
Melica geyeri Munro
Melica harfordii Bol.
Melica imperfecta Trin.
Melica spectabilis Scribn.
Melica stricta Bol.
Melica subulata (Griseb.) Scribn.
* ***Melica torreyana*** Scribn.
Melinis repens (Willd.) Zizka
Miscanthus sinensis Andersson
Monanthochloe littoralis Engelm.
Muhlenbergia andina (Nutt.) Hitchc.
Muhlenbergia appressa C.O. Goodd.
Muhlenbergia arsenei Hitchc.
Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi
****Muhlenbergia californica*** Vasey
Muhlenbergia filiformis (Thurb. ex S. Watson) Rydb.
Muhlenbergia fragilis Swallen
****Muhlenbergia jonesii*** (Vasey) Hitchc.
Muhlenbergia mexicana (L.) Trin.
Muhlenbergia microsperma (DC.) Kunth
Muhlenbergia minutissima (Steud.) Swallen
Muhlenbergia montana (Nutt.) Hitchc.
Muhlenbergia pauciflora Buckley
Muhlenbergia porteri Scribn. ex Beal
Muhlenbergia richardsonis (Trin.) Rydb.
Muhlenbergia rigens (Benth.) Hitchc.
Muhlenbergia schreberi J.F. Gmel.
Muhlenbergia utilis (Torr.) Hitchc.
Munroa squarrosa (Nutt.) Torr.
Nassella cernua (Stebbins & Love) Barkworth
Nassella lepida (Hitchc.) Barkworth
Nassella manicata (E. Desv.) Barkworth
Nassella pulchra (Hitchc.) Barkworth
Nassella tenuissima (Trin.) Barkworth
Nassella viridula (Trin.) Barkworth
****Neostapfia colusana*** (Burtt Davy) Burtt Davy
Orcuttia californica Vasey
****Orcuttia inaequalis*** Hoover
****Orcuttia pilosa*** Hoover
****Orcuttia tenuis*** Hitchc.
****Orcuttia viscida*** (Hoover) Reeder
Oryza rufipogon Griff.
Oryza sativa L.
Panicum alatum Zuloaga & Morrone
Panicum antidotale Retz.
Panicum capillare L.
Panicum dichotomiflorum Michx.
Panicum hillmanii Chase
Panicum hirticaule J. Presl
Panicum miliaceum L.
Panicum repens L.
Panicum rigidulum Bosc ex Nees
Panicum urvilleanum Kunth
Parapholis incurva (L.) C.E. Hubb.
Parapholis strigosa (Dumort.) C.E. Hubb.
Pascopyrum smithii (Rydb.) Barkworth & D.R. Dewey
Paspalum dilatatum Poir.
Paspalum distichum L.
Paspalum notatum Flüggé
Paspalum urvillei Steud.
Pennisetum clandestinum Hochst. ex Chiov.
Pennisetum glaucum (L.) R. Br.
Pennisetum latifolium Spreng.
Pennisetum macrourum Trin.
Pennisetum nervosum (Nees) Trin.
Pennisetum purpureum Schumach.
Pennisetum setaceum (Forssk.) Chiov.
Pennisetum villosum R. Br. ex Fresen.
Phalaris angusta Nees ex Trin.
Phalaris aquatica L.
Phalaris arundinacea L.
Phalaris brachystachys Link
Phalaris californica Hook. & Arn.
Phalaris canariensis L.
Phalaris caroliniana Walter
Phalaris coerulescens Desf.
Phalaris lemmonii Vasey
Phalaris minor Retz.
Phalaris paradoxa L.
Phleum alpinum L.
Phleum pratense L.
Phragmites australis (Cav.) Steud.
Phyllostachys bambusoides Siebold & Zucc.
Phyllostachys nigra (Lodd. ex Lindl.) Munro
Piptatherum exiguum (Thurb.) Dorn
Piptatherum micranthum (Trin. & Rupr.) Barkworth
Piptatherum miliaceum (L.) Coss.
Piptochaetium setosum (Trin.) Arechav.

Piptochaetium stipoides (Trin. & Rupr.) Hack. ex Arechav.
Pleuropogon californicus (Nees) Benth. ex Vasey
Pleuropogon hooverianus (L.D. Benson) J.T. Howell
Pleuropogon refractus (A. Gray) Benth.
Poa abbreviata R. Br.
Poa annua L.
Poa atropurpurea Scribn.
Poa bigelovii Vasey & Scribn.
Poa bolanderi Vasey
Poa bulbosa L.
Poa compressa L.
Poa confinis Vasey
Poa cusickii Vasey
Poa diaboli Soreng & D.J. Keil
Poa douglasii Nees
Poa fendleriana (Steud.) Vasey
Poa glauca Vahl
Poa howellii Vasey & Scribn.
Poa infirma Kunth
Poa keckii Soreng
Poa kelloggii Vasey
Poa leptocoma Trin.
Poa lettermanii Vasey
Poa macrantha Vasey
Poa napensis Beetle
Poa nemoralis L.
Poa palustris L.
Poa piperi Hitchc.
Poa pratensis L.
Poa pringlei Scribn.
Poa rhizomata Hitchc.
Poa secunda J. Presl
Poa sierrae J.T. Howell
Poa stebbinsii Soreng
Poa tenerrima Scribn.
Poa trivialis L.
Poa unilateralis Scribn. ex Vasey
Poa wheeleri Vasey
Podagrostis humilis (Vasey) Björkman
Podagrostis thurberiana (Hitchc.) Hultén
Polypogon australis Brongn.
Polypogon elongatus Kunth
Polypogon imberbis (Phil.) Johow
Polypogon interruptus Kunth
Polypogon maritimus Willd.
Polypogon monspeliensis (L.) Desf.
Polypogon viridis (Gouan) Breistr.
Pseudoroegneria spicata (Pursh) Á. Löve
Pseudosasa japonica (Siebold & Zucc. ex Steud.) Makino ex Nakai
Ptilagrostis kingii (Bol.) Barkworth
Puccinellia distans (Jacq.) Parl.
Puccinellia howellii J.I. Davis
Puccinellia lemmonii (Vasey) Scribn.
Puccinellia maritima (Huds.) Parl.
Puccinellia nutkaensis (J. Presl) Fernald & Weath.
Puccinellia nuttalliana (Schult.) Hitchc.
Puccinellia parishii Hitchc.
Puccinellia pumila (Vasey) Hitchc.
Puccinellia simplex Scribn.
Rostraria cristata (L.) Tzvelev
Rytidosperma biannulare (Zotov) Connor & Edgar
Rytidosperma caespitosum (Gaudich.) Connor & Edgar
Rytidosperma penicillatum (Labill.) Connor & Edgar
Rytidosperma racemosum (R. Br.) Connor & Edgar
Rytidosperma richardsonii (Cashmore) Connor & Edgar
Saccharum ravennae (L.) L.
Schedonnardus paniculatus (Nutt.) Branner & Coville
Schedonorus arundinaceus (Schreb.) Dumort.
Schedonorus pratensis (Huds.) P. Beauv.
Schismus arabicus Nees
Schismus barbatus (L.) Thell.
Schizachyrium cirratum (Hack.) Wooton & Standl.
Schizachyrium scoparium (Michx.) Nash
Sclerochloa dura (L.) P. Beauv.
Scleropogon brevifolius Phil.
Scribneria bolanderi (Thurb.) Hack.
Secale cereale L.
Setaria faberi R.A.W. Herrm.
Setaria italica (L.) P. Beauv.
Setaria parviflora (Poir.) Kerguélen
Setaria pumila (Poir.) Roem. & Schult.
Setaria sphacelata
Setaria verticillata (L.) P. Beauv.
Setaria viridis (L.) P. Beauv.
Sorghum bicolor (L.) Moench
Sorghum halepense (L.) Pers.
Spartina alterniflora Loisel.
Spartina anglica C.E. Hubb.
Spartina densiflora Brongn.
Spartina foliosa Trin.
Spartina gracilis Trin.
Spartina patens (Aiton) Muhl.
Sphenopholis obtusata (Michx.) Scribn.
Sporobolus airoides (Torr.) Torr.
Sporobolus contractus Hitchc.
Sporobolus creber De Nardi
Sporobolus cryptandrus (Torr.) A. Gray
Sporobolus flexuosus (Thurb. ex Vasey) Rydb.
Sporobolus indicus (L.) R. Br.
Sporobolus vaginiflorus (Torr. ex A. Gray) Alph. Wood
Sporobolus wrightii Munro ex Scribn.
Stenotaphrum secundatum (Walter) Kuntze
Stipa capensis Thunb.
Swallenia alexandrae (Swallen) Soderstr. & H.F. Decker
Taeniatherum caput-medusae (L.) Nevski
Themeda quadrivalvis (L.) Kuntze
Thinopyrum intermedium (Host) Barkworth & D.R. Dewey
Thinopyrum junceum (L.) Á. Löve
Thinopyrum ponticum (Podp.) Barkworth & D.R. Dewey
Thinopyrum pycnanthum (Godr.) Barkworth
Thysanolaena latifolia (Roxb. ex Hornem.) Honda

Torreyochloa erecta (Hitchc.) G.L. Church
Torreyochloa pallida (Torr.) G.L. Church
Tribolium obliterum (Hemsl.) Renvoize
Tridens flavus (L.) Hitchc.
Tridens muticus (Torr.) Nash
Trisetum cernuum Trin.
Trisetum flavescens (L.) P. Beauv.
Trisetum spicatum (L.) K. Richt.
Triticum aestivum L.
****Tuctoria greenei*** (Vasey) Reeder
****Tuctoria mucronata*** (Crampton) Reeder
Urochloa arizonica (Scribn. & Merr.) Morrone & Zuloaga
Urochloa texana (Buckley) R.D. Webster
Vahlodea atropurpurea (Wahlenb.) Fr. ex Hartm.
Ventenata dubia (Leers) Coss.
Vulpia bromoides (L.) Gray
Vulpia microstachys (Nutt.) Munro
Vulpia myuros (L.) C.C. Gmel.
Vulpia octoflora (Walter) Rydb.
Zea mays L.
Zizania palustris L.
Zoysia japonica Steud.

California Grasslands

ECOLOGY AND MANAGEMENT

Edited by

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