Agrostology; An Introduction to the Systematics of Grasses

James P. Smith Jr

Humboldt State University, james.smith@humboldt.edu

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7: GLOSSARY
"Of all things that live and grow upon this earth, grass is the most important." (Donald Culross Peattie. A Prairie Grove. 1938.)

The first word on the title page of this syllabus is an uncommon one. **Agrostology** [Greek, a kind of grass + body of knowledge] is the branch of systematic botany that deals with grasses, especially their identification, classification, and evolution. **Agriculture**, on the other hand, is the applied science that deals with cultivating land, and the raising and breeding of crops and livestock. **Agronomy** is the science of soil management and of crop production. Both terms are derived from the Greek root for fields, soils, and crops.

**WHAT ARE GRASSES?**

All true grasses belong to a single family of flowering plants, Gramineae or Poaceae. I use the phrase "true grasses" because there are many plants that have "grass" as part of their common name that are not, in fact, grasses. Many, but not all, have grass-like leaves that fool the uninformed.

**"GRASSES" THAT ARE NOT GRASSES**

<table>
<thead>
<tr>
<th>Name</th>
<th>Scientific Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alkali-grass</td>
<td>Zigadenus elegans</td>
</tr>
<tr>
<td>Arrow-grass</td>
<td>Triglochin maritima</td>
</tr>
<tr>
<td>Bayonet-grass</td>
<td>Scirpus maritimus</td>
</tr>
<tr>
<td>Bear-grass</td>
<td>Xerophyllum tenax</td>
</tr>
<tr>
<td>Bear-grass</td>
<td>Nolina microcarpa</td>
</tr>
<tr>
<td>Bear-grass</td>
<td>Yucca filamentosa</td>
</tr>
<tr>
<td>Beavertail-grass</td>
<td>Calothractus coerules</td>
</tr>
<tr>
<td>Blue-eyed-grass</td>
<td>Sisyrinchium spp.</td>
</tr>
<tr>
<td>Cotton-grass</td>
<td>Sisyrinchium spp.</td>
</tr>
<tr>
<td>Eel-grass</td>
<td>Zostera marina</td>
</tr>
<tr>
<td>Fish-grass</td>
<td>Cabomba caroliniana</td>
</tr>
<tr>
<td>Gallon-grass</td>
<td>Cannabis sativa</td>
</tr>
<tr>
<td>Golden-eyed-grass</td>
<td>Sisyrinchium spp.</td>
</tr>
<tr>
<td>Goose-grass</td>
<td>Potentilla anserina</td>
</tr>
<tr>
<td>Grass</td>
<td>Cannabis sativa</td>
</tr>
<tr>
<td>Grass-of-Parnassus</td>
<td>Parnassia spp.</td>
</tr>
<tr>
<td>Grass-tree</td>
<td>Xanthorhrea spp.</td>
</tr>
<tr>
<td>Grass-wrack</td>
<td>Zostera marina</td>
</tr>
<tr>
<td>Indian basket-grass</td>
<td>Xerophyllum tenax</td>
</tr>
<tr>
<td>Iron-grass</td>
<td>Carex caryophyllea</td>
</tr>
<tr>
<td>Mat-grass</td>
<td>Phyla nodiflora</td>
</tr>
<tr>
<td>Merlin-grass</td>
<td>Isoetes spp.</td>
</tr>
<tr>
<td>Milk-grass</td>
<td>Valerianella locusta</td>
</tr>
<tr>
<td>Mondo-grass</td>
<td>Ophiopogon japonicum</td>
</tr>
<tr>
<td>Nut-grass</td>
<td>Cyperus esculentus</td>
</tr>
<tr>
<td>Orange-grass</td>
<td>Hypericum gentianoides</td>
</tr>
<tr>
<td>Palm-grass</td>
<td>Cürculigo spp.</td>
</tr>
<tr>
<td>Penny-grass</td>
<td>Thlaspi spp.</td>
</tr>
<tr>
<td>Pepper-grass</td>
<td>Lepidium spp.</td>
</tr>
<tr>
<td>Pigeon-grass</td>
<td>Verbena officinalis</td>
</tr>
<tr>
<td>Pineapple-grass</td>
<td>Astelia spp.</td>
</tr>
<tr>
<td>Pudding-grass</td>
<td>Mentha pulegium</td>
</tr>
<tr>
<td>Pudding-grass</td>
<td>Hedeoma pulegoides</td>
</tr>
<tr>
<td>Purple-eyed-grass</td>
<td>Sisyrinchium spp.</td>
</tr>
<tr>
<td>Ripple-grass</td>
<td>Plantago lanceolata</td>
</tr>
<tr>
<td>Saw-grass</td>
<td>Cladium jamaicense</td>
</tr>
<tr>
<td>Scorpion-grass</td>
<td>Myosotis arvensis</td>
</tr>
<tr>
<td>Sedge-grass</td>
<td>Carex pendula</td>
</tr>
<tr>
<td>Serpent-grass</td>
<td>Polygonum viviparum</td>
</tr>
<tr>
<td>Snake-grass</td>
<td>Equisetum arvense</td>
</tr>
<tr>
<td>Star-grass</td>
<td>Aletris farinosa</td>
</tr>
<tr>
<td>Surf-grass</td>
<td>Phyllospadix spp.</td>
</tr>
<tr>
<td>Tape-grass</td>
<td>Valisneria spp.</td>
</tr>
<tr>
<td>Viper’s-grass</td>
<td>Scorzonera hispanica</td>
</tr>
<tr>
<td>Whitlow-grass</td>
<td>Draba verna</td>
</tr>
<tr>
<td>Widgeon-grass</td>
<td>Ruppia maritima</td>
</tr>
<tr>
<td>Wire-grass</td>
<td>Juncus spp.</td>
</tr>
<tr>
<td>Yellow-eyed-grass</td>
<td>Sisyrinchium spp.</td>
</tr>
<tr>
<td>Yellow-eyed-grass</td>
<td>Xyris spp.</td>
</tr>
</tbody>
</table>

**HOW BIG IS THE FAMILY?**

Grasses, although they do not constitute the largest family of flowering plants, are economically the most important to us and ecologically they are the most dominant form of higher plants. Estimates of the size of the family vary, but ranges of 600-700 genera and about 10,000 species seem reasonable. The family ranks third in number of genera (behind the orchids and sunflowers) and fifth in number of species (after orchids, sunflowers, legumes, and members of the madder family).

**NUMBER OF GENERA & SPECIES**

<table>
<thead>
<tr>
<th>Source</th>
<th># Genera</th>
<th># Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Linnaeus (1771)</td>
<td>43</td>
<td>285</td>
</tr>
<tr>
<td>Trinius (1822)</td>
<td>2457</td>
<td></td>
</tr>
<tr>
<td>Hackel (1887)</td>
<td>313</td>
<td>3500</td>
</tr>
<tr>
<td>Bews (1929)</td>
<td>483</td>
<td>5871</td>
</tr>
<tr>
<td>Pilger (1954)</td>
<td>700</td>
<td>8,000</td>
</tr>
<tr>
<td>Prat (1960)</td>
<td>403</td>
<td>6250</td>
</tr>
<tr>
<td>Dahlgren (1985)</td>
<td>750</td>
<td>10,000</td>
</tr>
</tbody>
</table>
A GLOBAL SUMMARY BY SUBFAMILY

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Genera</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anomalochlooideae</td>
<td>2 (0.3%)</td>
<td>4 (0.1%)</td>
</tr>
<tr>
<td>Pharoideae</td>
<td>3 (0.5%)</td>
<td>12 (0.1%)</td>
</tr>
<tr>
<td>Bambusoideae</td>
<td>65 (9.9%)</td>
<td>965 (9.7%)</td>
</tr>
<tr>
<td>Ehrhartoideae</td>
<td>18 (2.7%)</td>
<td>150 (1.5%)</td>
</tr>
<tr>
<td>Poöideae</td>
<td>154 (23.4%)</td>
<td>3275 (32.8%)</td>
</tr>
<tr>
<td>Arundinoideae</td>
<td>49 (7.4%)</td>
<td>605 (6.1%)</td>
</tr>
<tr>
<td>Danthonioideae</td>
<td>19 (2.9%)</td>
<td>275 (2.8%)</td>
</tr>
<tr>
<td>Aristidoideae</td>
<td>1 (0.1%)</td>
<td>250 (2.5%)</td>
</tr>
<tr>
<td>Centothecoideae</td>
<td>10 (1.5%)</td>
<td>25 (0.2%)</td>
</tr>
<tr>
<td>Panicoidae</td>
<td>207 (31.5%)</td>
<td>3290 (33.0%)</td>
</tr>
<tr>
<td>Totals</td>
<td>658 (100%)</td>
<td>9976 (100%)</td>
</tr>
</tbody>
</table>

[Number of taxa from Thorne, 1999]

THE TWENTY LARGEST GRASS GENERA

<table>
<thead>
<tr>
<th>North America</th>
<th>World-wide</th>
</tr>
</thead>
<tbody>
<tr>
<td>Panicum (113)</td>
<td>Panicum (590)</td>
</tr>
<tr>
<td>Poa (96)</td>
<td>Poa (500)</td>
</tr>
<tr>
<td>Elymus (80)</td>
<td>Festuca (472)</td>
</tr>
<tr>
<td>Muhlenbergia (77)</td>
<td>Eragrostis (350)</td>
</tr>
<tr>
<td>Festuca (63)</td>
<td>Paspalum (330)</td>
</tr>
<tr>
<td>Eragrostis (60)</td>
<td>Stipa (300)</td>
</tr>
<tr>
<td>Bromus (58)</td>
<td>Aristida (290)</td>
</tr>
<tr>
<td>Paspalum (54)</td>
<td>Calamagrostis (230)</td>
</tr>
<tr>
<td>Aristida (51)</td>
<td>Digitaria (230)</td>
</tr>
<tr>
<td>Agrostis (48)</td>
<td>Agrostis (220)</td>
</tr>
<tr>
<td>Calamagrostis (47)</td>
<td>Elymus (221)</td>
</tr>
<tr>
<td>Stipa (43)</td>
<td>Muhlenbergia (160)</td>
</tr>
<tr>
<td>Sporobolus (35)</td>
<td>Sporobolus (160)</td>
</tr>
<tr>
<td>Digitaria (32)</td>
<td>Bromus (150)</td>
</tr>
<tr>
<td>Setaria (28)</td>
<td>Bambusa (150)</td>
</tr>
<tr>
<td>Bouteloua (25)</td>
<td>Axonopus (110)</td>
</tr>
<tr>
<td>Melica (24)</td>
<td>Setaria (110)</td>
</tr>
<tr>
<td>Andropogon (23)</td>
<td>Andropogon (100)</td>
</tr>
<tr>
<td>Glyceria (21)</td>
<td>Brachiaria (100)</td>
</tr>
<tr>
<td>Hordeum (20)</td>
<td>Isachne (100)</td>
</tr>
</tbody>
</table>

DISTRIBUTION

Grasses are the most cosmopolitan of all higher plants, occurring on all continents, including Antarctica. They are also the most frequently encountered vascular plants. There may well be more individual grass plants than there are all other vascular plants combined! They are found from the polar regions to the equator, from mountain tops to seashores. They occur in brackish and freshwater marshes, ponds, streams, rain forests, deserts, tundra, and arid slopes. About one-fourth of the earth's plant cover is grasslands. They are dominant in the vast expanses of the world's prairies, steppes, pampas, paramos, and veldt. A major part of our agricultural lands is devoted to them. Grasses are with us in our cities, either as ornamentals or as weeds along sidewalks and in vacant lots. Grasses are never far away.

ECONOMIC IMPORTANCE

No other plant family, with the possible exception of the legumes and palms, can approach the grasses in direct economic importance to us. Major products include the cereal grains (wheat, rice, maize, barley, rye, sorghum, oats, and millets), hay, pasture, turf grasses, thatching material, timber, paper pulp, sugar (from sugar cane and sorghum), aromatic compounds (e.g., lemon grass and oil of vetiver), brooms, fishing poles, musical instruments, ornamentals, soil binders, starches, edible oils, alcohol, beverages, and food for most of the world's wild and domesticated animals.

We derive a major portion of our calories from cereals. Much of our agricultural land is devoted to the raising of cereals, especially wheat. Still more of the earth's surface is used for pastures for a variety of domesticated animals.

SELECTED REFERENCES


Veldkamp, J. F. Grass literature. [A continuing series of computer disks with ASCII files that are available for purchase or in exchange for herbarium specimens]


1.02 - VEGETATIVE STRUCTURE

"I believe a leaf of grass is no less than the journey-work of the stars." (Walt Whitman)

ROOTS

Most mature grasses have a root system that is fibrous -- finely divided and lacking a dominant one, as in a taproot system. It is also adventitious, in that the primary root system is short-lived and it is soon replaced by roots that are derived from some other node along the embryo axis, rather than developing from the branches of the primary root. The extent and penetration of the grass root system is variable. *Aristida pungens* of North Africa has roots more than 20 m long.

The cells that give rise to root hairs may be equal in length or alternately long and short. There is also a difference in the point of attachment and the angle of insertion of root hairs relative to the basal part of the cell.

The roots are of little direct economic importance to us, although they do retard erosion through the structuring of the soil. Some roots contain aromatic principles, as in oil of vetiver.

STEMS

The erect aerial stem of a grass plant is called a culm. The stem is generally soft and herbaceous in our temperate grasses. Some of the reeds and canes have much tougher culms. Typical bamboos appear to be quite woody, but plant anatomists will argue that what we are seeing is not actually woody tissue. A grass stem may be only a centimeter or so tall to as much as 40 m or so in some of the tropical bamboos. The stem is divided into nodes and internodes. The nodes are regions where leaves are attached; they are typically rather easy to located in grasses because they are swollen. The region between two successive nodes is the internode. It is typically hollow, but we do have several exceptions in some commonly encountered grasses. Some studies suggest that about half of the grasses may have solid internodes. These plants also have a specialized spikelet structure and tend to inhabit arid regions.

Branches of stems arise most commonly from buds at the base of a parent shoot. These basal branches are called innovations. In some crop plants, the innovations are called tillers or suckers. A secondary stem may elongate within a leaf sheath or it may break through it as it develops. We call the former situation intravaginal branching and the latter extravaginal branching. Intravaginal is the more common situation.

Grasses also commonly produce horizontal or repent stems. The two most frequently encountered types are the rhizome and the stolon. A rhizome is a horizontal stem at or below the surface of the ground. It bears reduced, scale-like leaves. Stolons, on the other hand, are horizontal stems running along the surface of the ground and they often bear ordinary foliage leaves.

Both serve as a means of vegetative reproduction. While these definitions sound precise, the distinction between the two is sometimes subtle. Bermuda grass (*Cynodon dactylon*) produces both rhizomes and stolons, depending upon environmental conditions.

Some grasses produce small onion-like bulbs (but without the odor), while others have corms, swollen hard stems surrounded by dry, papery, scale-like leaves, similar to the "bulb" of the gladiola.

The presence of rhizomes, stolons, bulbs, and corms is of taxonomic significance. All grass keys will, sooner or later, ask you whether these structures are present or absent. Make certain that you collect any underground parts of a grass plant when you are doing any serious collecting of grasses for identification or documentation.

Grass stems are very important as sources of building material, hay, forage, and packing material.

LEAVES

Grass leaves are alternate and two-ranked. They are alternate because only one leaf arises from a node. They are two-ranked because if the leaf borne at the first node comes off the left side of the culm, then the leaf at the second node will arise from the right side. Looking down on the stem and leaf system, the points of insertion or attachment are 180° opposite one another.

The leaves are typically composed of a blade or lamina, a sheath, and a ligule. The blade is usually linear -- most grass leaves, after all, do look like grass leaves! -- but it may be thread-like, needle-like, oval, or even arrowhead-shaped. In some of the tropical grasses, the leaf blades closely resemble those of some dicots. The venation is typically parallel, with all of the veins being more or less the same size or with one of them forming a more prominent midrib. Some tropical grasses have pinnate venation.

Some bamboos appear to have petioles, but I suspect they are best considered pseudopetioles. They appear to be nothing more than constrictions of the blade or sheath.

The grass sheath is usually interpreted as a flattened petiole. It is most often rounded, but in some grasses the sheath may be conspicuously flattened. Typically it is open -- the edges of the sheath come together and touch one another or they overlap slightly; but, they are not fused into a cylinder about the nodes. This is a useful character for separating most grasses from most sedges. But beware! Some very common grasses (orchard grass, onion grasses, and bromes) have closed sheaths, in which the edge of the two edges are joined. Wind action and careless use of a dissecting needle can convert closed sheaths to open ones.

The ligule is a membranous flap of tissue or a series of hairs (or both) at the junction of the blade and sheath. Its function may be to prevent water from entering the sheath or to hold the leaf tightly to the
culm. Not all grasses have ligules.

The first leaf of a culm branch or lateral shoot is the prophyllum. It is an unusual leaf, in that it lacks a blade. It protects the immature lateral stem axis and it provides mechanical support. The prophyllum has two prominent strands of vascular tissue running its length.

Grass leaves, especially those of the wheat or barley tribe (Triticeae) have ear- or claw-shaped appendages called auricles. These paired structures arise at the base of the blade in some grasses, but laterally at the sheath apex in others.

The leaf epidermis is an important source of taxonomic information. Typically the upper (adaxial) surface is different from the lower (abaxial) one. Both have cells arranged in columns over the vascular bundles (costal region) or in the zone between adjacent vascular bundles (intercostal zone). The cells are distinguished as long- or short-cells, depending upon their length-width ratio. Long-cells vary in wall thickness and appearance, being sinuous, papillate, or pitted. Those with sinuous walls are called ripple-wall cells.

Short cells occur singly or in pairs. There are two common types, silica cells and cork cells. The former have a silica-body in their lumen. The shape of this deposit determines the type of silica cell -- linear, rounded, irregular, saddle-shaped, dumbbell-shaped, cross-shaped, or double-axhead-shaped. Cork cells have cork in them.

Stomates are arranged in precise columns in the intercostal zone. Each is composed of two guard cells and two subsidiary cells.

An examination of the epidermis may also reveal bulliform cells -- large, colorless cells that are typically present in the intercostal zone of the adaxial surface. They are sometimes called mechanical cells, because they function in the rolling and unrolling (or folding and unfolding) of the leaf blade.

The blade, when seen in cross-section (also referred to as a transverse-section) yields the following features:

- mesophyll: thin-walled parenchyma and chlorenchyma cells
- vascular bundles: composed of xylem and phloem tissue, surrounded by one or two bundle sheaths; the inner one (when present) is termed an endodermis or mesostome sheath by various authors
- sclerenchyma fibers: typically present in clusters in the region between the epidermis and the outer bundle sheath

**TEXTURES**

cartilaginous - resembling cartilage; hard and tough, but flexible
chartaceous - with the texture of writing paper
coriaceous - with the texture of leather
crustaceous - with a brittle texture
hyaline - thin and translucent or transparent
indurate - hard or hardened
membranous - thin, soft, and flexible
pellucid - transparent, clear
scarious - thin, dry, membranous; not green

**COLORS**
cinereous - light gray; ash-colored
ferruginous - rust-colored
fuscous - brownish, dusky
rufous - reddish-brown
stramineous - pale yellow; straw-colored
tawny - pale brown to dirty yellow

**FEATURES OF THE SURFACES OF GRASSES***

- **Surface itself (exclusive of hairs, barbs, etc.)**
  - glabrous - without hairs
  - glaucous - with a whitish, waxy bloom
  - lustrous - shining
  - papillose - warty outgrowths of epidermal cells.
  - pitted - with small depressions, pits, pin-holes, or cavities
  - pruinose - with a waxy, powdery secretion on the surface
  - punctate - dotted with pin-point impressions or translucent dots
  - pustulose - with irregularly raised pimples
  - reticulate - netted with regular, slightly elevated lines
  - rugose - wrinkled
  - scurfy - covered with minute scales
  - smooth - not rough to the touch; not synonymous with glabrous
  - striated - marked with longitudinal lines
  - sulcate - furrowed with longitudinal channels
  - tessellate - marked by square to oblong depressions
  - tuberculate - with small projections; warty
  - verrucose - another way of spelling tuberculate
  - viscid - sticky

- **Projections and depressions from surfaces, margins, and apices**
  - **Hairs branched or forked**
    - stellate - with few- to several branched sessile or stalked hairs
malpighiaceous (dolabriform) - with forked hairs attached at middle

- **Hairs simple, unbranched**
  - **Hooked or barbed**
    - **antrorsely** - with forward or upward directed barbs
    - **retrorsely** - with backward or downward directed barbs
    - **uncinate** - hooked, as in a fish hook
  - **Not hooked nor barbed**
    - **Restricted to apex, base or margins**
    - **ciliate** - with hairs along margins only
    - **fimbriate** - as in ciliate, but hairs coarser and longer
    - **comose** - with a tuft of hairs at apex or base
  - **On surfaces**
    - **Curled, interwoven or entangled**
      - **arachnoid** - with slender, white, loosely tangled hairs
      - **floccose** - with tufts of soft hairs that rub off easily
      - **lanate** - with woolly or cottony hairs
      - **tomentose** - with densely and softly matted hairs
    - **Not curled, interwoven, nor entangled**
      - **bristle** - a stiff slender hair-like appendage
      - **canescent** - with a dense mat of grayish-white hairs
      - **echinate** - with straight, ± large, prickle-like hairs
      - **glabrate** - initially hairy, but becoming glabrous
      - **glandular** - with swollen-tipped hairs; gland-bearing
      - **hirsute** - with rough or coarse, ± erect hairs
      - **hoary** - see canescent
      - **hirsute** - with straight, ± stiff hairs
      - **hirtellous** - minutely hirsute
      - **hispid** - with long, rigid, bristly hairs
      - **hispidulous** - minutely hispid
      - **microhairs** - typically bicellular [rarely multicellular] hairs usually requiring magnification of a compound microscope
      - **macrohairs** - typically one-celled hairs visible within the range of the ordinary dissecting microscope or good handlens;
      - **papillate** - with pimple-like hairs
      - **papillose** - see papillate
      - **pilose** - with sparse, slender, soft hairs
      - **puberulent** - minutely canescent
      - **pubescent** - with short, soft, erect hairs; downy
      - **scabrous** - with coarse, stiff, ascending hairs; rough
      - **sericeous** - with long, fine, appressed hairs; silky
      - **setaceous** - with bristly hairs
      - **setose** - see setaceous
      - **strigose** - with sharp, appressed, rigid, hairs that are often swollen at base
      - **velutinous** - with dense, firm, straight hairs; velvety
      - **villous** - with long, slender, soft (not matted) hairs; shaggy

*[Modified from Smith, J. P. 1977. Vascular plant families]*

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**SELECTED REFERENCES**


1.03 - THE FLOWER, FRUIT, & SEED

FLOWERS

Most of us have never seen grass flowers and we are perhaps not even aware that grasses are flowering plants. The reasons are understandable. Grass flowers are small and hidden away from easy view by a system of reduced leaves (bracts). The brightly-colored sepal and petals that make the somewhat distantly-related lilies and orchids so attractive were lost through the gradual processes of evolutionary reduction. This is another way of saying that grass flowers do not strike most people as being terribly pretty. But, come closer!

All that remains of the grass perianth is two or three microscopic structures called lodicules. They are hygoscopic, swelling in the early morning and thereby forcing apart the bracts that enclose the flower. This process helps to facilitate wind pollination (anemophily). Not all grasses have lodicules.

The reproductive components of the grass flower that have been retained are modified for anemophily. The male part of the flower (androecium) is made up of stamens, each one consisting of a delicate, thread-like supporting stalk called a filament and a sac-like region of pollen-producing tissue, the anther. Most grasses have three stamens; some have two or one; a few have six; bamboo flowers may have hundreds of stamens!

The female portion of the flower (gynoecium) consists of a seed-producing ovary, two styles that are separate to their bases, and a terminal pair of feathery stigmas that trap airborne pollen.

Grass flowers vary in the presence or absence of reproductive parts. A bisexual or perfect flower is one that has both an androecium and a gynoecium. A pistillate flower has only the gynoecium; while the staminate flower has only the complement of stamens. A neuter or sterile flower has no reproductive structures. All grass keys will require you to distinguish among perfect, staminate, pistillate, or neuter flowers. A friendly warning -- what appears so easily defined on this piece of paper is often very difficult to interpret under the dissecting microscope or hand lens. Look at several flowers before reaching your decision. One of the more common causes of error arises when anthers develop early, shed their pollen, shrivel up, and fall from the plant. A quick glance can lead to the mistaken notion that the flower is pistillate. Look carefully for filaments as a clue to the presence of fallen anthers.

FRUIT, SEED, AND EMBRYO

The ovule has a single chamber (locule) and it is one-seeded. In the vast majority of grasses, it will mature into a fruit type known as the caryopsis, in which the seed coat is fused to the ovary wall, except at the funiculus. In a few grasses, the seed is more or less separate from the ovary wall, producing a fruit type called an achene. In some bamboos, the fruit is a large, fleshy, single-seeded berry.

The seed contains endosperm and the embryo itself. Endosperm results from the fusion of two polar nuclei and a sperm nucleus. It provides nourishment to the developing embryo and later to the young seedling. The endosperm is typically solid and starchy in most grasses; in a few it is in a liquid state.

The embryo consists of the embryo axis and its appendages. At the upper end is the shoot or plumule, enclosed in a protective sheath, the coleoptile. At the lower end of the embryo axis is the embryonic root or radicle, also covered by an enveloping cap, the coleorhiza.
The scutellum is the major lateral appendage of the embryo. It is embedded directly in the endosperm, where it enzymatically digests and absorbs the stored food material. This function appears to be unique in the flowering plants. The scutellum is often interpreted as a modified cotyledon. Some grasses have a second appendage, called an epiblast. Its origin is more controversial. It appears as a small outgrowth opposite the scutellum, at a node just above that of the coleorhiza. In some grasses, there is a distinct region, the mesocotyl, between the nodes where the scutellum and the coleoptile are inserted.

SELECTED REFERENCES


# 1.04 - SPIKELET STRUCTURE

## THE BASIC PLAN

Because of their small size, high degree of evolutionary reduction, and lack of easily observed features, grass flowers have not been used extensively as the basis for distinguishing genera and species within the family. Instead, the classification of grasses has been based heavily upon the structure of the bracts that enclose individual grass flowers and that subtend groupings of them.

Grass flowers, the minute stalks that support them, and the bract system associated with them make up the **spikelet**. Some spikelets, especially those containing a single flower, may be quite small. Others may be a few centimeters long and easily seen without magnification. The spikelet, although characteristic of Gramineae, is not its exclusive property. Sedges have spikelets, too. Because their spikelets are superficially similar, it is easy to confuse the two families. Refer back to Table 1 for a comparison of the features of the two families.

All grass spikelets are put together according to the same basic plan. The tiny flowers and bracts are attached either directly or indirectly to an unbranched central spikelet axis called a **rachilla**. At the base of the rachilla are two bracts that are empty or sterile, in that they do not flowers in their axils. Each of the two basal bracts is a **glume**. Careful inspection will show that one bract is inserted slightly below the other. The lower bract is the first glume; the one attached slightly above it is the second glume. The two bracts may be similar in length, width, shape, and texture or they may be significantly different from one another. While most grass spikelets have two glumes, a few have only one, and it appears that in a few species the glumes are completely suppressed.

In addition to glumes, a spikelet contains one or more **florets**, each inserted at its own point of attachment (**node**) on the rachilla. The etymology of floret would suggest to you that the term means “a small flower.” Not so. A floret is not only an individual small flower, but two bracts that enclose it. A floret never has more than one flower in it. The number of florets in a spikelet is of great diagnostic importance. A spikelet with a single floret is said to be one-flowered; one with two florets is two-flowered; and so on.

The two bracts that enclose the flower are the **lemma** and the **palea**. The lemma is typically the more conspicuous bract -- larger and of firmer texture, its edges often partially obscuring the palea. The lemma typically has an odd number of **nerves** or **veins** of vascular tissue running its length. Occasionally it will appear veinless. The number of nerves on the lemma is of great importance in identifying an unknown grass. Counting their number can be a challenge. It is very easy to overlook submarginal veins, those that lie close to the edge of the lemma. In most instances, the nerves of the lemma will converge with one another towards its apex; but in some grasses, they remain parallel to one another. When viewed in cross-section, a lemma often appears to be a rounded bract. Sometimes it is conspicuously flattened or even V-shaped. It may also have a prominent rib (**keel**) running down its center, the term being derived from the structure found on the bottom of a ship or boat. The lemma is attached directly to the rachilla. Usually it has a flower in its axil, in which case it is a **fertile lemma**. If the flower is absent, then it is called a **sterile lemma**.

Unlike the glume or lemma, the palea is not the source of many taxonomic features. It tends to be a delicate, membranous, two-nerved bract. It may be as long as the lemma, but it is usually somewhat shorter. The palea is not inserted directly on the rachilla. You will have to take my word for it, because it is all but impossible to see this level of detail under the dissecting microscope. The palea subtends the flower itself and it is attached to the tiny flower stalk.

The apex of a glume or lemma may bear a short, sharp point called a **mucro**. These bracts may also have a more elongate, substantial, hair-like projection known as an **awn**. It may be a few millimeters to several centimeters long. Awns may be straight, bent (**geniculate**), or twisted. Some, as in oats, function in the self-planting of the seed-like fruits. Some awns are terminal, while others arise from the back of a glume or lemma at about their midpoints. Others come from at or near the base of the bract. While glumes and/or lemmas are commonly awned, it is unusual in temperate grasses to find an awned palea.

The hardened base of a lemma or of a floret is its **callus**. In some instances, the callus is a combination of lemma and rachilla tissue. It may be rounded or sharp-pointed, as in the needle grasses. The callus may lack hairs or it may be clothed in a conspicuous tuft of hairs.

Spikelet parts are homologous with the stems and leaves of a grass plant. The **rachilla** is the homolog of a stem, the glumes and lemmas are homologous with ordinary foliage leaves, and the palea with the specialized first leaf of a side branch, the **prophyllum**.

## COMPRESSION

Spikelets are either round in cross-section (**terete**) or they are flattened (**compressed**). Terete spikelets are relatively uncommon, but they occur in such common plants as the Indian rice-grass. Compressed spikelets come in two models. If the bracts are flattened as though pressure were brought to bear from the sides of the bracts, then the spikelet is **laterally compressed**. If the spikelet is flattened as though pressure were brought to bear from the backs of the bracts, then it is **dorsally compressed**.

Perhaps this distinction between dorsal and lateral compres-sion may be made clearer by drawing on two familiar animals that are flattened. Turtles show dorsal compres-sion, while fish are laterally compressed.

## DISARTICULATION

At maturity, most spikelets will break apart at predeter-mined points of separation. The process is
called **disarticulation** and it occurs in various ways:

- below the first glume, so that the entire spikelet falls from the plant;
- above the glumes and between the florets so that empty glumes are all that remains behind;
- florets may fall separately or in clusters, sometimes with a prominent segment of the rachilla remaining attached.
- between the first and second glume (an unusual situation); or
- above glumes, but lemmas persisting (an unusual situation).

It takes some practice to determine disarticulation. You can force it to occur with a dissection needle, but not necessarily where it would under natural conditions. I recommend that you always observe older inflorescences -- ones that may otherwise look uninviting -- to find bare pedicels or empty glumes.

There is a tendency -- and it is nothing more than that -- for spikelets that are laterally compressed to disarticulate above the glumes and for those that are dorsally compressed to disarticulate below the glumes.

### SEXUALITY

An individual floret or grass plant may be:

- bisexual (perfect or hermaphroditic), if it has both stamens and carpels;
- staminate (male), if it has only male florets;
- pistillate (female), if it has only female florets;
- sterile (neuter or barren), if it lacks either functional carpels or stamens (or, especially in older literature, if a floret were staminate).

There is another level of complexity. In many grasses, the lower florets of a spikelet are typically bisexual, with the upper florets progressively smaller and sterile. Another common situation is the spikelet of panicoid grasses, in which the upper floret is bisexual and the lower is sterile. A less common possibility is the several-flowered spikelet that has both upper and lower florets that are sterile, while those in the middle are fertile.

Grass species, depending on the distribution of their stamens and carpels, may be described as:

- bisexual;
- monoecious, if an individual plant produces both staminate and pistillate spikelets;
- dioecious, if an individual plant produces either staminate or pistillate spikelets;
- various combinations of perfect and unisexual spikelets, on the same or different plants of a species.

### VARIATION ON A THEME

To summarize, a typical grass spikelet consists of two glumes and one or more florets attached to a rachilla. It is laterally or dorsally compressed, or less often terete. The spikelet disarticulates above or below the glumes. The lemmas and/or the glumes may be awned.

While this is the basic plan, the spikelet is subject to a fascinating series of modifications. One of the most important of these is the reduction and loss of spikelet parts. One or both glumes may be missing. In spikelets with more than one floret, the upper one(s) are often smaller than the lower one(s) and they may be sterile. Sometimes the uppermost floret is well-developed and fertile, while the one or two florets below it are reduced. In a few grasses, the middle florets are best developed, while those above and below are reduced or sterile. The palea may be reduced or even absent, as in the bent grasses. This variation can be frustrating at first, but proper interpretation can be more easily assured if you take the time now to learn the basic positional relationships of the spikelet parts.

### SPIKELET FORMULAE

A convenient system for summarizing the number of flower parts characteristic of various plant families is called a **floral formula**. In this system of notation, each of the four floral series is given an abbreviation, such as K (for calyx), C (for corolla), A (for androecium), and G (for gynoecium). Exponents or superscripts indicate the number of sepals, petals, stamens, and carpels. I developed the following little system for describing spikelets.

| G | = glume                  |
| G⁰ | = glumes absent          |
| G¹ | = one glume present      |
| G² | = two similar glumes present |
| G¹⁺¹ | = two dissimilar glumes |
| F | = fertile floret        |
| F²× | = 2 to several fertile florets |
| F⁺ | = awned floret          |
| L | = sterile lemma (of a sterile floret) |
| L⁺ | = 3 to several sterile lemmas |

### SOME SPIKELET MODELS

<table>
<thead>
<tr>
<th>Species</th>
<th>Formula</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agrostis</td>
<td>G² + F</td>
</tr>
<tr>
<td>Andropogon</td>
<td>G² + L¹ + F⁺</td>
</tr>
<tr>
<td>Avena</td>
<td>G² + F²⁻³</td>
</tr>
<tr>
<td>Panicum</td>
<td>G¹⁺¹ + L + F</td>
</tr>
<tr>
<td>Paspalum</td>
<td>G¹ + L + F</td>
</tr>
<tr>
<td>Phalaris</td>
<td>G² + L¹⁻² + F</td>
</tr>
</tbody>
</table>
Poa  
\[ G^2 + F^{2+x} \]

Uniola  
\[ G^2 + L^x + F^y + L^z \]

Zizaniopsis  
\[ G^2 + F \]

**SELECTED REFERENCES**


Grass stems, whether they are the primary culm or a lateral branch, may emerge from their sheaths and bear one to several hundred spikelets. This flowering portion of the grass plant is its inflorescence. A stem may bear only one inflorescence or it may have several of them. If it emerges from the uppermost sheath of a primary stem, it is a terminal inflorescence. If it arises from a lower sheath, it is an axillary or lateral inflorescence.

At first, it may be difficult for you to determine just how much of what you are looking at makes up a single inflorescence. A good rule of thumb is that there are never well-developed foliage leaves within an inflorescence. Whether terminal or axillary, the uppermost or outermost spikelet delimits the top of an inflorescence. The lowest typical foliage leaf marks its base.

The upper portion of the culm that supports the entire inflorescence is the peduncle, while the stalk that supports an individual spikelet is its pedicel. This terminology is not consistent with usage in other plant families. A pedicel is usually the stalk that supports a single flower. The true pedicel of a grass flower is, of course, within the spikelet. This error in terminology goes back about two hundred years to a time when attempts were made by Linnaeus and others to support an individual spikelet is its tissue.

If there is a clearly defined axis within the inflorescence, it is called a rachis. Note that the rachis is the axis of an entire inflorescence of spikelets, while the rachilla is the central axis of an individual spikelet. The rachis may be delicate, wiry, or even thickened with spikelets partially embedded in its tissue.

The exact arrangement of spikelets determines the inflorescence type. You will find this terminology frustrating because it has not been standardized and authors of keys and descriptions vary shamefully in their usage. No scheme is without its problems, but I have found the following one useful.

### SIMPLE INFLORESCENCES

In the spike, the spikelets are inserted directly on an unbranched rachis. Pedicels are, for all practical purposes, absent. The number of spikelets attached at a given node on the rachis is variable. One, two, three, and a cluster of several spikelets per node are common. Many grasses have this inflorescence type.

In the raceme, spikelets are borne on well-developed pedicels arising from an unbranched rachis. Typically spikelets occur in pairs or trios at a given node, infrequently only one spikelet per node, as in the semaphore grasses. It is much less common than the spike. The distinction between the raceme and spike is arbitrary, the degree of pedicel development marking the difference. I use 1 mm as the dividing line.

The rame is a specialized modification of the raceme in which pedicellate and sessile spikelets occur together in pairs or trios. The pedicels are of equal or unequal length. The rame is typical of the barley and bluestem tribes (Triticeae and Andropogoneae). Few authors recognize the rame as distinct from the raceme.

The panicle is probably the most common inflorescence type in the family. Here the spikelets are borne on pedicels that are themselves secondary or tertiary branches of a much-branched system. This means that the spikelets are not attached directly to a central axis as they are in the spike, raceme, or rame. Panicles may be large, open, and very conspicuously branched or it may be so contracted and dense that they appear to be some sort of spike.

An extreme form of the panicle is the solitary spikelet, in which the peduncle bears a single spikelet, as in the poverty oats. In such instances, we believe that the solitary spikelet is the result of evolutionary reduction of a more typical much-branched panicle with multiple spikelets.

In the spike, raceme, or rame, the spikelets may be more or less evenly attached on opposite sides of the rachis so that the inflorescence is balanced, or they may be obviously attached on just one side of the rachis, so that the inflorescence is one-sided. If the spikelets are tightly packed along one side, as in the teeth of a comb, the inflorescence is said to be pectinate. Examples may be seen in grama grass (Bouteloua) and in toothache grass (Ctenium).

### COMPOUND INFLORESCENCES

In many grasses, we see inflorescences composed of unbranched or sparingly branched arms. If we look at any particular branch, it bears a spike of spikelets, a raceme of spikelets, or a rame of spikelets. We may refer to them as compound spikes, compound racemes, and compound rames, respectively. In older literature, these are also considered to be panicles because they are branched inflorescences. In these compound inflorescences, the branches may be clustered at the apex of a peduncle (digitate) or they may be attached at various points along a rachis and be racemose.

### SELECTED REFERENCES


"... grasses break almost all of the rules that many other groups of animals and plants observe...."

**INTRODUCTION**

Pollination is the transfer of pollen from an anther to the surface of a stigma. The term is clearly not synonymous with fertilization, which involves the union of egg and sperm nuclei. In most flowering plants, the two structures are in different flowers and we speak of **cross-pollination**. It offers the selective advantage of yielding new genetic combinations from two different plants. On the other hand, cross-pollination requires a pollinator – insects, birds, water, wind, moths, etc.

In many instances, the stigma of a particular flower is receptive to its own pollen grains or to other flowers on the same plant and **self-pollination** occurs. No pollinator is required. This mechanism obviously is not found in dioecious species, but it may occur in monoecious species, such as maize. Most plants have developed mechanisms that prevent or retard self-pollination.

**WIND POLLINATION**

Grasses are heavily adapted for wind pollination and cross-fertilization. The syndrome of adaptation that we find in the family includes:

- lodicules sensitive to weather;
- elongation of stamen filament;
- new orientation of anthers;
- quick shedding of pollen;
- pollen released with high temperatures and lowered humidity;
- pollen that is light, abundant, easily dispersed;
- light pollen has lowered terminal velocities;
- lower probability of entrapment;
- large, easily exserted stigma;
- inflorescences well-elevated above vegetative plant parts; and
- lack of nectaries.

**INSECT POLLINATION**

Not all grasses are wind pollinated (**anemophilous**). A number of visits by insects have been recorded in the literature. They appear to be looking for food, in the form of pollen grains or various sweet liquids made by the **Claviceps** fungi. Grasses are commonly visited when the inflorescences are in bloom. Insects move from one flower to another and thereby transfer pollen.

**INCOMPATIBILITY**

I have already mentioned that most plants have developed mechanisms that favor cross-pollination, or to put it differently they are self-sterile or self-incompatible. Several possibilities come easily to mind: pollen is produced at a time when the stigmatic surface of that same flower is not receptive; stamens may have short filaments and the styles of the same flower may be very long, thereby physically making self-pollination more difficult. Less obvious are those that may involve genetic incompatibility.

The incompatibility mechanism found in Gramineae is unique. It is referred to as the "**SZ incompatibility system**." Here are the basic elements:

- Compatibility or incompatibility rests on the interaction of two genes, S and Z.
- Both S and Z occur in multi-allelic series, S1, S2, S3, etc.
- In a diploid grass, a haploid pollen grain would contain one S allele and one Z allele. The diploid stigma and style tissue would have nuclei with two of each of them.
- Incompatibility is determined by whether the pollen grain and stigma/style share alleles. If they share none, they are compatible. If they share one, they are compatible. If they share both, they are incompatible.
- Prevents fertilization between genotypes identical in incompatibility alleles.
- Greater the allelic differences -> greater chance that pollen will function.

<table>
<thead>
<tr>
<th>Stigma/Style</th>
<th>Pollen Grain</th>
<th>Outcome</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1S2Z1Z2</td>
<td>S1Z1</td>
<td>Fails</td>
</tr>
<tr>
<td>S1S2Z1Z2</td>
<td>S1Z2</td>
<td>Fails</td>
</tr>
<tr>
<td>S1S2Z1Z2</td>
<td>S2Z1</td>
<td>Fails</td>
</tr>
<tr>
<td>S1S2Z1Z2</td>
<td>S2Z2</td>
<td>Fails</td>
</tr>
<tr>
<td>S1S2Z1Z2</td>
<td>S1Z3</td>
<td>OK</td>
</tr>
<tr>
<td>S1S2Z1Z2</td>
<td>S2Z3</td>
<td>OK</td>
</tr>
</tbody>
</table>

Examples may be found in our temperate grasses, but it is perhaps more common in tropical rain forests where there is little, if any, wind to effect wind pollination.


Neutral stamens and carpels is reproductive structures.

Similarly, a flower, spikelet, or grass plant is sterile if they bear functional carpels. In H & C, they are fertile only if they bear functional stamens and/or carpels. In the classical version of the biological species concept, a plant is fertility if it bears stamens and/or carpels. In H & C, they are fertile only if they bear functional stamens and/or carpels. In the broad sense, a flower, spikelet, or grass plant is sterile if either stamens or carpels, but not both, it is imperfect flowers and spikelets; self-sterility; chasmagamous flowers (ones that are open pollinated); and protandrous flowers, in which the stamens shed their pollen before the stigmas are receptive.

Grasses may be predominantly or exclusively outcrossing or cross-fertilized (allogamous) or they are predominantly self-fertile (autogamous) or they may be outcrossing for some period of time and then switch to selfing at another stage. The taxonomic consequences of crossing and selfing can be both amazing and very frustrating, especially to those who adhere to the classical version of the biological species concept.

The terms 

- fertile
- sterile (barren, neuter, or neutral)

have different meanings, depending on the author. In the broad sense, a flower, spikelet, or grass plant is fertile if it bears stamens and/or carpels. In H & C, they are fertile only if they bear functional carpels.

Similarly, a flower, spikelet, or grass plant is sterile if it lacks functional carpels, even if the stamens are functional! In other words, fertility and sterility are defined by the presence or absence of female reproductive structures.

A flower, a spikelet, or a grass plant that has both stamens and carpels is perfect or bisexual. If it has either stamens or carpels, but not both, it is imperfect or unisexual, and a flower, spikelet, or plant is either male (staminate) or female (pistillate).

A plant that bears both staminate and pistillate flowers or spikelets is monoecious. If male and female flowers or spikelets occur on separate plants, then we have the dioecious condition. These terms do not apply to flowers or spikelets – only to plants or species.

Plants that bear both perfect and imperfect flowers or spikelets are said to be polygamous. Four flavors are recognized:

- ♀ + bisexual on same plant = andromonoecious
- ♂ + bisexual on different plants = androgynoecious
- ♂ + bisexual on same plant = gynomonoeious
- ♂ + bisexual on different plants = gynodioecious

There are basically two kinds of reproduction -- sexual and asexual. Sexual reproduction involves the union of egg and sperm nuclei. Grasses have developed a series of mechanisms that favor outcrossing, so that the gametes that unite come from different plants. These include:

- imperfect flowers and spikelets;
- self-sterility;
- chasmagamous flowers (ones that are open pollinated); and
- protandrous flowers, in which the stamens shed their pollen before the stigmas are receptive.

On the other hand, mechanisms that favor inbreeding or selfing include:

- perfect flowers or spikelets;
- self-fertility; and
- cleistogamous flowers, those that are closed and self-pollinated.

Apomixis is the general term used for all types of asexual reproduction, where there is no union of egg and sperm. The simplest form of apomixis is vegetative reproduction by means of rhizomes, bulbs, corms, bulbets or bulbils (vegetative proliferations that replace flowers), and fragmentation of stems. New plants arise vegetatively because these various structures contain buds that will produce new stems, roots, leaves, and spikelets if suitable moisture and nutrients are available. Many of our most successful weedy grasses have exploited asexual reproduction. Each of those chopped up rhizome segments or bulbs is fully capable of yielding a new, independent plant that is a genetic carbon copy of its mother.

Grasses can be much more subtle about their asexual reproduction. In agamospermy, seeds are produced, but they are not the product of the union of egg and sperm. In adventitious embryony, the embryo develops directly from the diploid tissue of the nucellus or ovule integument. The gametophytic generation has been completely bypassed.

In gametophytic apomixis, alternation of generation occurs, but the gametophytes arise without meiosis having occurred. Five versions are recognized:

- apospory, in which a diploid embryo sac is formed directly from a cell of the nucellus or of the inner integument;
- diplospory, in which a diploid embryo sac is formed from a cell of the archegonium;
- parthenogenesis, in which the embryo forms from a diploid egg cell;
- apogamy, in which the embryo forms from some cell in the embryo sac other than the egg cell; and
- pseudogamy, in which pollination is required to stimulate seed set.

**KEY TO STRATEGIES**

1. Reproduction by means of the union of egg and sperm nuclei (sexual reproduction) → 2
2. Reproduction by means of vegetative tissue only or by means of seeds formed without the union of egg and sperm (asexual reproduction or apomixis)


SOME EXAMPLES


Hidden Cleistogenes: Amphiparca, Andropogon, Aristida, Chloris, Cottea, Danthonia, Dichanthelium, Digitaria, Diplachne, Enneapogon, Leersia, Muhlenbergia, Pappophorum, Paspalum, Pennisetum, Piptochaetium, Sieglingia, Stipa, Triplasis.

Subterranean Cleistogenes: Amphiparca, Chloris, Paspalum

Only Unisexual Florets: Allolepis, Arrhenatherum, Buchloe, Cathesteimum, Coix, Cortadertia, Distichlis, Gynerium, Heteropogon, Luziola, Monanbichloa, Olyra, Opizla, Pharau, Poa, Scleropogon, Tripsacum, Zea, Zizania, Zizaniopsis.

Monoecious: Buchloe, Coix, Distichlis, Luziola, Olyra, Pharau, Scleropogon, Tripsacum, Zea, Zizania, Zizaniopsis.

Dioecious: Allolepis, Buchloe, Cortadertia, Distichlis, Gynerium, Monanbichloa, Opizla, Poa, Scleropogon.


SELECTED REFERENCES

**POLLINATION**


**REPRODUCTION**


1.07 - GENOMES, HYBRIDS, & POLYPLOIDS

GENOMES

A genome is a complete set of chromosomes. In a diploid, it is either of the two sets of chromosomes derived from the parents. In a polyploid, a genome is any of the sets derived from its ancestors. Genomes are usually designated by a single capital letter, as in the B genome of wheat. The number of chromosomes in a genome is often designated by a small letter x, as in x = 7.

In a euploid, the individual, cell, or nucleus contains an exact multiple of x. If x = 10, then 10, 20, 30, 40, etc. would constitute a euploid series. In aneuploids, we have chromosome numbers that are not exact multiples of the base chromosome number. Individual chromosomes have been added or lost. Several kinds of aneuploids are recognized. In the nullisomic, both members of a chromosome pair are missing. In a monosomic, only one member is missing. In a trisomic, one member of a pair is in triplicate. In a tetrasomic, both members of the chromosome pair are duplicated.

We use the small letter n to designate the number of chromosomes found in a sex cell or gamete. The number of chromosomes found in a vegetative cell is shown as 2n, as in 2n = 10. These two conditions are also called the gametic and somatic chromosome numbers, respectively.

A convention has been adopted in plant genetics that tells the chromosome number and ploidy level. According to this scheme the "genetic formula" for bread wheat is 2n = 6x = 42. This means that the vegetative cells contain 42 chromosomes (the 2n indicating a somatic number, rather than a gametic one), and that the plant is a hexaploid (6x). If 6x = 42, then x = 7.

POLYPLOIDY

An individual, a cell, or a nucleus that contains one and only one complete sets of chromosomes is haploid. If it contains two complete sets, it is a diploid. An individual, a cell, or a nucleus that contains three or more complete sets of chromosomes is a polyploid. The combination of the prefixes tri-, tetra-, penta-, hexa-, octa-, etc., and the suffix -ploid, indicates the particular number of complete sets. A hexaploid has six sets.

A polyploid in which all of the chromosome sets are derived from the same genetic lineage, so that a chromosome in one set is capable of pairing with its corresponding number in another set, is an autopoloid or autopolyploid. If, on the other hand, we are dealing with a polyploid in which the chromosome sets are derived from different species, subspecies, or varieties, then we have an allopolyploid. Here the chromosome sets are different enough that pairing of chromosomes is impaired -- slightly to completely. In a segmental allopolyploid, the polyploid appears to be of both auto- and allopolyploid origin. A series of interrelated polyploids, often demonstrating morphological similarities to one another constitute a polyploid complex.

HYBRIDIZATION

C. D. Darlington (1937) defined a hybrid as "a zygote produced by the union of dissimilar gametes." While theoretically acceptable, this definition is too broad for general use. Essentially all sexually reproducing plants and animals would be hybrids. Your classes are filled with hybrid students. We will use the term in a more restricted sense -- the offspring of interbreeding (crossing) between two or more taxa. The process itself is called hybridization. There are hundreds (probably thousands) of crosses between grass species (interspecific hybrids) and a long list of crosses between grass genera (intergeneric hybrids). Here is a long, but incomplete list of the latter.

Aegilops X Elymus
Aegilops X Secale
Aegilops X Triticum
Agropyron X Elymus
Agropyron X Hordeum
Agropyron X Secale
Agropyron X Triticum
Agrostis X Calamagrostis
Agrostis X Polygogon
Ammophila X Calamagrostis
Arctophila X Dupontia
Arrhenatherum X Avena
Arvena X Arrhenatherum
Bothriochloa X Dichanthium
Bromus X Festuca
Calamagrostis X Agrostis
Chloris X Cynodon
Colpodium X Phippsia
Cynodon X Chloris
Danthonia X Sieglingia
Dichanthium X Bothriochloa
Dupontia X Arctophila
Sometimes the offspring of crossing between plants in closely related genera are stable enough to warrant naming, even though they are partially to completely sterile. The following intergeneric hybrids have been named. Not all of them are legal according to the ICBN. It is drawn primarily after Clayton & Renvoize (1986) and Watson & Dallwitz (1992).

**NAMED INTERGENERIC HYBRIDS**

<table>
<thead>
<tr>
<th>Genus 1</th>
<th>Genus 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elymus</td>
<td>Aegilops</td>
</tr>
<tr>
<td>Elymus</td>
<td>Hordeum</td>
</tr>
<tr>
<td>Erianthus</td>
<td>Saccharum</td>
</tr>
<tr>
<td>Festuca</td>
<td>Bromus</td>
</tr>
<tr>
<td>Festuca</td>
<td>Lolium</td>
</tr>
<tr>
<td>Festuca</td>
<td>Vulpia</td>
</tr>
<tr>
<td>Hordeum</td>
<td>Secale</td>
</tr>
<tr>
<td>Hordeum</td>
<td>Triticum</td>
</tr>
<tr>
<td>Imperata</td>
<td>Saccharum</td>
</tr>
<tr>
<td>Koeleria</td>
<td>Trisetum</td>
</tr>
<tr>
<td>Leptochloa</td>
<td>Oryza</td>
</tr>
<tr>
<td>Lolium</td>
<td>Festuca</td>
</tr>
<tr>
<td>Miscanthus</td>
<td>X</td>
</tr>
<tr>
<td>Saccharum</td>
<td>X</td>
</tr>
<tr>
<td>Saccharum</td>
<td>X</td>
</tr>
<tr>
<td>Saccharum</td>
<td>X</td>
</tr>
<tr>
<td>Sacccharum</td>
<td>Sorghum</td>
</tr>
<tr>
<td>Saccharum</td>
<td>X</td>
</tr>
<tr>
<td>Secale</td>
<td>X</td>
</tr>
<tr>
<td>Sieglingia</td>
<td>X</td>
</tr>
<tr>
<td>Sorgum</td>
<td>X</td>
</tr>
<tr>
<td>Soghum</td>
<td>X</td>
</tr>
<tr>
<td>Sphenopholis</td>
<td>X</td>
</tr>
<tr>
<td>Triquetum</td>
<td>X</td>
</tr>
<tr>
<td>Stipa</td>
<td>X</td>
</tr>
<tr>
<td>Tripsacum</td>
<td>X</td>
</tr>
<tr>
<td>Trisetum</td>
<td>X</td>
</tr>
<tr>
<td>Trisetum</td>
<td>X</td>
</tr>
<tr>
<td>X</td>
<td>Koeleria</td>
</tr>
<tr>
<td>X</td>
<td>Trisetum</td>
</tr>
<tr>
<td>X</td>
<td>Sphenopholis</td>
</tr>
<tr>
<td>Triticum</td>
<td>X</td>
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<td>X</td>
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<tr>
<td>Triticum</td>
<td>X</td>
</tr>
<tr>
<td>Tritordeum</td>
<td>X</td>
</tr>
<tr>
<td>Tritordeum</td>
<td>X</td>
</tr>
<tr>
<td>Tritordeum</td>
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</tr>
<tr>
<td>Tritordeum</td>
<td>X</td>
</tr>
<tr>
<td>X</td>
<td>Hordeum</td>
</tr>
</tbody>
</table>

**SELECTED REFERENCES**


SECTION 2 – SYSTEMATICS OF THE GRASSES

2.01 - GRASSES & THEIR RELATIVES

The grass family belongs to a major subgroup of flowering plants called Liliopsida (Monocotyledoneae of earlier systems). Informally called “monocots,” these plants have a single cotyledon, scattered vascular bundles in the stem, a circular pattern of vascular tissue in the roots, parallel venation in the leaf blade, and floral parts in 3’s or multiples of 3. All of these features are usually seen in most grasses, except for the characters of the flower. They are highly reduced and are not easily interpreted. More about them later.

The closest relatives of the grasses belong to little-known tropical and subtropical plant families, such as Flagellariaceae, Centrolepidaceae, and Restionaceae. None of them is represented in the flora of North America. There are, however, two other families whose plants resemble grasses, at least superficially. The rushes (Juncaceae) and sedges (Cyperaceae) occur widely in North America. Rushes are rather easily distinguished from grasses by their 3-parted calyx and corolla and by their fruit, a many-seeded capsule. Sedges require closer inspection. Table 1 presents a comparison of typical members of the two families.

TECHNICAL FAMILY DESCRIPTIONS

GRAMINEAE (THE GRASS FAMILY)

Annual or perennial herbs, sometimes + woody in the canes, reeds, and ornamental bamboos. Roots generally fibrous and adventitious at maturity; rhizomes and stolons frequent, some with bulbs. Stems generally round, sometimes flattened, erect to prostrate; nodes swollen, solid; internodes generally hollow. Leaves alternate, 2-ranked, simple, generally elongate and differentiated into a blade with parallel veins, a sheath (typically open with its edges meeting or overlapping slightly) that encircles the stem, and ligule (a membranous flap or series of hairs at inner apex of sheath). Inflorescence complex, consisting generally of numerous basic units; the spikelets, which are themselves tiny spikes. Spikelets round or flattened (dorsally or laterally) in cross-section; generally consisting of 2 sterile, overlapping, basal bracts (the first and second glume) and one or more florets (flowers and subtending bracts, the palea and lemma); these 2-ranked on an internal axis (the rachilla); glumes equal or unequal in size and shape, awned or awnless; 0 to many-nerved; lemmas similar to glumes in appearance and texture or quite dissimilar, awned or awnless, 0 to many-nerved; palea generally thin, transparent, awnless, 2-nerved, and + enclosed by the lemma; floret base sometimes forming a sharp-pointed and/or hairy callus; breaking apart at maturity either below or above the glumes. Spikelets borne in secondary inflorescences (spikes, spike-like panicles, panicles, etc.), rarely solitary. Flowers generally bisexual, minute, wind-pollinated, the perianth reduced to 2 or 3 microscopic structures (lodicules); stamens [1] 3 [6], anthers generally comparatively large; stigmas generally 2, typically dissected and feather-like; ovary 1-chambered. Fruit a caryopsis (or grain), with the fruit wall + completely fused with the seed coat of the single seed inside. 651 genera; + 10,000 species; cosmopolitan, probably the most frequently encountered flowering plants, found in a wide variety of habitats and on all continents, including Antarctica.

CYPERACEAE (THE SEDGE FAMILY)

Perennial [rarely annual] herbs of wet and marshy sites. Plants often with creeping rhizomes. Stems generally with solid internodes and often 3-sided. Leaves from basal tufts or cauline and 3-ranked; sheaths usually closed; ligule generally absent. Flowers minute, bisexual or unisexual (the species generally monoecious), spirally or distichously arranged in tiny spikes. Each flower is subtended by a small bract (often called a glume). The spike of reduced flowers and subtending bracts form the spikelet, which are themselves arranged in panicles, umbels, or spike-like inflorescences. Perianth of bristles, hairs, scales, or absent. Stamens 3 [rarely 1 or 6]. Carpels 2 or 3, united, 1-ovuled, with as many style-branches as carpels; ovary superior. Fruit an achene or nutlet, lenticular or 3-sided, sometimes enclosed in a membranous sac (perigynium). 90 genera; 4000 species; widespread, particularly in the cool temperate and subarctic regions. Of little economic importance; a few are edible and some are grown as ornamentals.

JUNCACEAE (THE RUSH FAMILY)

Perennial or annual herbs, from erect or horizontal rhizomes. Leaves generally basal, linear, sheathing at base, sheaths generally open; blades sometimes absent. Flowers small, green, actinomorphic, bisexual or unisexual (species dioecious); in heads, panicles, or corymbs. Tepals + 10,000 species of + cosmopolitan. Stamens 6 [rarely 3]. Carpels 3, united, unilocular; placentation axillary or parietal; style 1; stigmas 3, brush-like; ovary superior. Fruit a capsule. 9 genera; 400 species; largely cool temperate and subarctic damp and wet sites. Of no direct economic importance; a few are grown as ornamentals.

CENTROLEPIDACEAE
Annual or perennial grass-like, rush-like, or moss-like herbs. Leaves linear, bristle-like, cauline or in basal rosettes. Flowers tiny, unisexual, in cymose false inflorescences (pseudanthia) of 1 or 2 male flowers and 2-many female flowers. Pseudanthia terminal, spikelike, and subtended by 2-several glume-like bracts. Male flowers reduced to 1 stamen. Female flowers reduced to 1 carpel, the ovary unilocular. Fruit dehiscent or indehiscent, 1-seeded. 5 genera; 30 species; found primarily in New Zealand, Australia, and the southern tip of South America. None occur in North America.

RESTIONACEAE
Perennial, rhizomatous herbs. Stem internodes solid or hollow. Leaves reduced to open sheaths, blades and ligules generally absent. Flowers small, regular, unisexual (species dioecious). Perianth absent or scale-like. Stamens 3 [rarely 1 or 4]. Carpels 1 or 3, united, the ovary superior. Fruit an achene, nut, or capsule. 38 genera; 400 species; found primarily in the southern hemisphere [1 sp. in Viet Nam], especially well-represented in the Cape region of South Africa where 180 ssp. are endemic! Of little economic importance; a few are used for thatch and to make brooms. None occur in North America.

FLAGELLARIACEAE
Glabrous vines. Leaves spirally arranged, blades parallel-veined and terminating in a tendril; ligule absent. Flowers small, regular, bisexual, 3-merous, wind-pollinated, in terminal bracteate panicles. Tepals 3 + 3. Stamens 6. Carpels 3, united; ovary trilocular, superior. Fruit a drupe. 1 genus; 4 species; found primarily in the Old World tropics and islands of the South Pacific. Of little economic importance; one species is used in basket-making in Asia. None occur in North America.

JOINVILLEACEAE
Erect, perennial, rhizomatous herbs. Stem internodes hollow. Leaves grass-like, spirally arranged; ligulate and auriculate. Flowers bisexual, 3-merous, in terminal bracteate panicles. Tepals 3 + 3. Stamens 6. Carpels 3, united; ovary 3-locular, superior. Fruit a drupe. 1 genus; 2 species; restricted to Malaysia and the islands of the Pacific. The family was only recently separated out of Flagellariaceae. Of no economic importance.

A COMPARISON OF GRASSES AND SEDGES

<table>
<thead>
<tr>
<th>Feature</th>
<th>Grasses</th>
<th>Sedges</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stems:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shape in x-section</td>
<td>Round [flat]*</td>
<td>Triangular [round]</td>
</tr>
<tr>
<td>Internodes</td>
<td>Hollow [solid]</td>
<td>Solid</td>
</tr>
<tr>
<td><strong>Leaves:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td># of Ranks</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Sheaths</td>
<td>Present</td>
<td>Open [closed]</td>
</tr>
<tr>
<td>Ligule</td>
<td></td>
<td>Closed</td>
</tr>
<tr>
<td><strong>Spikelets:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bract insertion</td>
<td>Distichous</td>
<td>Distichous, spiral</td>
</tr>
<tr>
<td>Bracts per flower</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td><strong>Flowers:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perianth</td>
<td>2 [3] lodicules</td>
<td>0-6 bristles</td>
</tr>
<tr>
<td>Stamen number</td>
<td>3 [6, 1, many]</td>
<td>1-3</td>
</tr>
<tr>
<td>Anthers</td>
<td>Versatile</td>
<td>Basifixed</td>
</tr>
<tr>
<td>Stigmas</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>Pollen shed as</td>
<td>Monads</td>
<td>Pseudomonads</td>
</tr>
<tr>
<td><strong>Fruit and Seed:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fruit type</td>
<td>Caryopsis</td>
<td>Achene</td>
</tr>
<tr>
<td>Embryo position</td>
<td>Lateral</td>
<td>Central</td>
</tr>
<tr>
<td><strong>Chromosomes:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Centromeres</td>
<td>Monocentric</td>
<td>Diffuse</td>
</tr>
</tbody>
</table>

* Character states in brackets indicate the less typical situation.
SELECTION REFERENCES


"The Grasses are dreadfully difficult and systematically a chaos of imperfect descriptions, erroneous identifications, confused synonymy and imbecile attempts. We have upwards of a century of collections and not an attempt at a classification. Each Botanist in his own country has worked at his sweet will in ignorance of his predecessors' and contemporaries' work, with imperfect materials and often no books -- 'Hinc illae lachrymae.' (Sir Joseph Dalton Hooker)

**********

The purpose of this section is to outline the major attempts in the last four hundred years to classify grasses. While there have been important conceptual advances since Burbidge made his comment of thirty years ago, it still has a ring of truth about it.

Jacob Theodore (Tabernaemontanus) (1590) wrote thirty-five chapters on grasses, including rushes, arrow-grasses, plantains, horsetails, and some caryophylls. His classification was based upon general plant form and a plant's habitat.

Caspari Bauhin (1623) recognized twenty-four groups based upon form of the grass plant. His was an unnatural assemblages of plants, lumping together grasses and cattails.

Joseph Pitton de Tournefort (1694) was the first to present an index to technical and common names. His Class 15 included grasses, chenopods, nettles, smartweeds, sedges, etc. Section 3 was devoted to grasses and it contained 9 "genera" (1-7, cereals; 9, reed grasses; 8, others).

John Ray (1703) urged simplification in classification and the use of easier features. He also encouraged the use of dichotomous keys.

Pier Antonio Micheli (1728) developed a system based upon the completeness of flower and spikelet. He found the "lost petals" of the grass flower (lodicules).

Carolus Linnaeus (1753) recognized thirty-eight genera of grasses (one of them actually a sedge!). They were put into six of his artificial groups.

Robert Brown (1814) was one of England's most influential botanists. He was the first to distinguish the two great groups of grasses: Panicoideae and Pooidae.

Palisot de Beauvois (1812) recognized two "families," divided into tribes and then into sections. He recognized 210 genera based upon glume arrangement and spikelet. His name appears frequently as the author of numerous genera and species of grasses.

Carl Bernard von Trinius (1822) prepared a summary of grass classification and synonymy, in which he listed 2457 species, along with their author and place of publication.

George Bentham (1881) was one of Victorian England's most famous botanists. He often collaborated with Joseph Dalton Hooker. Bentham's system was used by A. S. Hitchcock and others until mid-20th century.

Series A: Paniceae
  Tribe: Paniceae
  Tribe: Maydeae
  Tribe: Oryzeae
  Tribe: Tristegineae
  Tribe: Zosieae
  Tribe: Andropogoneae

Series B: Poaceae
  Tribe: Phalarideae
  Tribe: Agrostideae
  Tribe: Aveneae
  Tribe: Chlorideae
  Tribe: Festuceae
  Tribe: Hordeae
  Tribe: Bambuseae

Eduard Hackel (1887) developed a system much like that of Bentham. He recognized 13 tribes and 313 genera.

George Valentine Nash (1909) wrote major portions of the treatment of Gramineae for the "North American Flora." He recognized 13 tribes, but did not place them in subfamilies.

John Bews was the author of "The World's Grasses: Their Differentiation, Distribution, and Ecology." Although quite dated, it remains a useful reference. In it, he recognized two subfamilies, 15 tribes, 481 genera, and 5871 species.

Subfamily: Pooideae
  Tribe: Maydeae
  Tribe: Andropogoneae
  Tribe: Zosieae
  Tribe: Tristegineae
  Tribe: Paniceae
  Tribe: Oryzeae
  Tribe: Phalarideae
  Tribe: Agrostideae
  Tribe: Aveneae
  Tribe: Festuceae
  Tribe: Chlorideae

Subfamily: Panicoideae
Nikolai Pavlovic Avdulov was a famous Russian botanist. His 1931 cytological examination of Gramineae is considered by many the foundation of the "new agrostology." In it, he listed two series and 13 tribes.

**Series A**
- Tribe: Maydeae
- Tribe: Andropogoneae
- Tribe: Zoysieae
- Tribe: Paniceae
- Tribe: Oryzcea

**Series B**
- Tribe: Phalarideae
- Tribe: Agrostideae
- Tribe: Aveneae
- Tribe: Chlorideae
- Tribe: Festucceae
- Tribe: Hordeae
- Tribe: Bambuseae

Romain Roschevicza, another Soviet botanist, in 1937 recognized two subfamilies (Poatae and Sacchariferae), 5 series, and 28 tribes.

**Subfamily: Poatae**
- Series: Bambusiformes
  - Tribe: Bambuseae
  - Tribe: Phareae
- Series: Phragmitiformes
  - Tribe: Centotheceae
  - Tribe: Arundineae
  - Tribe: Oryzcea
  - Tribe: Stipeae
  - Tribe: Brachypodieae
  - Tribe: Unioleae
- Series: Festuciformes
  - Tribe: Festueae
  - Tribe: Hordeae
  - Tribe: Aveneae
  - Tribe: Phalarideae
  - Tribe: Agrostideae

**Subfamily: Sacchariferae**
- Series: Eragrostiformes
  - Tribe: Eragrosteae
  - Tribe: Pappophoreae
  - Tribe: Chlorideae
  - Tribe: Sporoboleae
- Series: Paniciformes
  - Tribe: Paniceae
  - Tribe: Melinideae
  - Tribe: Zoysieae
  - Tribe: Andropogoneae
  - Tribe: Maydeae

Robert Pilger and Eva Potzal, two eminent German botanists, prepared portions of a world wide treatment of grasses. They recognized nine subfamilies, 34 tribes, and 555 genera. Although the individual generic treatments are still useful, their system is not widely accepted.

Alan Beetle, an American botanist, was one of the first to support more than two subfamilies for our North American material. He recognized:

- Subfamily: Bambusoideae
- Subfamily: Pharoideae
- Subfamily: Festucoidae
- Subfamily: Panicoideae

Tsugo Tateoka is one of Japan's most influential botanists. His system, published in 1957, recognized five subfamilies:

- Subfamily: Pharoideae
- Subfamily: Pooideae
- Subfamily: Eragrostoideae
- Subfamily: Panicoideae
- Subfamily: Arundinoideae

Henri Prat (1960), in his world-wide survey of grasses, recognized six subfamilies, 26 tribes, 403 genera, and 6250 species.

G. Ledyard Stebbins and Beecher Crampton were both professors at the University of California at Davis. In 1961, they published a provisional scheme for North American grasses. It turned out to be very influential.

**Subfamily: Bambusoideae**
- Tribe: Arundinarieae

**Subfamily: Oryzoideae**
- Tribe: Phareae
- Tribe: Oryzcea
- Tribe: Zizanieae

**Subfamily: Arundinoideae**
- Tribe: Arundineae
- Tribe: Danthonieae
- Tribe: Unioleae
- Tribe: Aristideae

**Subfamily: Festucoidae**
- Tribe: Ampelodesmeae
- Tribe: Stipeae
- Tribe: Brachyelytreae
- Tribe: Hordeae
- Tribe: Aveneae

**Subfamily: Eragrostoideae**
- Tribe: Aeluropideae
- Tribe: Spartineae
Tribe: Pappophoreae
Tribe: Eragrostideae
Tribe: Chlorideae
Tribe: Zoysieae

**Subfamily: Panicoideae**
- Tribe: Paniceae
- Tribe: Andropogoneae

**Subfamily: Centothecoideae**
- Tribe: Centothecaee

**Subfamily: Arundinoideae**
- Tribe: Arundineae
- Tribe: Triticaceae

**Subfamily: Chilorioidae**
- Tribe: Pappophoreae
- Tribe: Orcuttiaee

W. Derek Clayton and Stephen Andrew Renvoize are the authors of one of the two major world-wide surveys to be published in the past few years. The descriptions of genera are relatively brief. The taxa are arranged systematically and keys to tribes and genera are provided.

**Subfamily: Bambusoideae**
- Tribe: Bambuseae
- Tribe: Dendrocalameae

**Subfamily: Pooideae**
- Tribe: Nardeae
- Tribe: Ehrharteae
- Tribe: Bromeae
- Tribe: Phleeae
- Tribe: Meliceae
- Tribe: Diarrheneae
- Tribe: Brachylytreae
- Tribe: Ampelodesmeae
- Tribe: Stipeae
- Tribe: Nardae
- Tribe: Orzyae
- Tribe: Ehrrharteae
- Tribe: Centosteceae
- Tribe: Arundineae
- Tribe: Thyrsanaoleaeae
- Tribe: Aristideae
- Tribe: Cynodonteae
- Tribe: Paniceae
- Tribe: Andropogoneae

**Subfamily: Stipoideae**
- Tribe: Nardeae
- Tribe: Ampelodesmeae
- Tribe: Stipeae
- Tribe: Brachylytreae

**Subfamily: Pooidae**
- Tribe: Triticaceae
Tribe: Brachypodieae
Tribe: Bromeae
Tribe: Aveneae
Tribe: Poeae
Tribe: Meliceae

Subfamily: Bambusoideae
Tribe: Oryzeae
Tribe: Diarrheneae
Tribe: Phareae
Tribe: Bambuseae

Subfamily: Centothecoideae
Tribe: Centotheceae

Subfamily: Arundinoideae
Tribe: Arundineae
Tribe: Danthonieae
Tribe: Aristideae

Subfamily: Chloridoideae
Tribe: Pappophoreae
Tribe: Orcuttieae
Main Chloridoid Assemblage

Subfamily: Panicoideae
Tribe: Paniceae
Tribe: Andropogoneae
Tribe: Maydeae

Grass Phylogeny Working Group. The GPWG is composed of eight individuals located here in the United States, and in South Africa and Switzerland. The system is based on a cladistic analysis of six molecular sequence data sites, chloroplast restriction site data, and more traditional morphological data.

Subfamily: Bambusoideae
Tribe: Bambuseae
Tribe: Oryzeae

Subfamily: Anomochlooideae
Tribe: Streptochaeteae

Subfamily: Pharioideae
Tribe: Phareae

Subfamily: Ehrhartioideae
Tribe: Ehrhartaeae

Subfamily: Centothecoideae
Tribe: Centotheceae

Subfamily: Arundinoideae
Tribe: Arundineae

Subfamily: Chloridoideae
Tribe: Pappophoreae
Tribe: Orcuttieae

Subfamily: Panicoideae
Tribe: Paniceae
Tribe: Andropogoneae

THE SYSTEM-BUILDERS

1880 C. O. Hartz (Germany)
1881 George Bentham (England)
1887 Eduard Hackel (Germany)
1929 John Bews (England)
1931 Nikolai P. Avdulov (Russia)
1934 Charles E. Hubbard (England)
1936 Henri Prat (France)
1946 Romain Roshevitz (Russia)
1954 Robert Pilger (Germany)
1955 Alan Bettle (United States)
1957 Tsugo Tateoka (Japan)
1961 G. Ledyard Stebbins & Beecher Crampton
(United States)
1986 W. Derek Clayton & Stephen A. Renvoize (England)
1988 Leslie Watson & Michael J. Dallwitz (Australia)
1989 Nikolai Tzvelev (Russia)
2001 Grass Phylogeny Working Group

Selected References


Parodi, L. R. 1961. La taxonomia de las gramineas Argentinas a la luz de las investigaciones mas recientes. Recent Advances in Botany 1: 125-130.


The great agrostologists of the past were limited by the instruments and the technology of their period, just as we are today. For the most part, botanists had to rely upon the features that were seen under the light microscope. At first, these devices were relatively crude. You can still see Linnaeus's microscope if you visit his home in Sweden. Workers of the 19th century and the early part of the 20th based their systems of classification primarily on features that could be seen with increasingly better instruments, especially the dissecting microscope. They focused their attention on the morphological details of stems, leaves, the inflorescence, and the spikelet.

By the time A. S. Hitchcock had completed the first edition of "The Manual" in 1935, botanists in various countries around the world had begun using new techniques to understand the relationships in the family and to suggest new systems of subfamilies and tribes. These more modern systems of classification relied heavily upon a series of what we might call microcharacters -- anatomical, cytological, genetic, and chemical traits of grasses. The result is a system of subfamilies, tribes, and genera that is strikingly different from the ones produced by the great figures of the 19th and early 20th centuries. General reviews of these new features upon which the modern classification of the family rests are found in Auquier (1963), Avdulov (1931), Clifford (1969), and Gould & Shaw (1983).

### A CHRONOLOGY

<table>
<thead>
<tr>
<th>Year</th>
<th>Event</th>
</tr>
</thead>
<tbody>
<tr>
<td>1892</td>
<td>Embryo structure</td>
</tr>
<tr>
<td>1926</td>
<td>Chromosome complements</td>
</tr>
<tr>
<td>1931</td>
<td>Chromosome karotypes</td>
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<tr>
<td>1932</td>
<td>Leaf epidermis</td>
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<tr>
<td>1953</td>
<td>Root hair development</td>
</tr>
<tr>
<td>1957</td>
<td>Persistent nucleoli</td>
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<tr>
<td>1957</td>
<td>Shoot apex and meristem activity</td>
</tr>
<tr>
<td>1957</td>
<td>Embryo structure</td>
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<tr>
<td>1958</td>
<td>Germination responses to IPC</td>
</tr>
<tr>
<td>1958</td>
<td>Leaf anatomy</td>
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<tr>
<td>1959</td>
<td>Nodal pulvini and internode structure</td>
</tr>
<tr>
<td>1960</td>
<td>Culm anatomy</td>
</tr>
<tr>
<td>1961</td>
<td>Seedling leaf</td>
</tr>
<tr>
<td>1961</td>
<td>Antigen/antibody reactions</td>
</tr>
<tr>
<td>1962</td>
<td>Starch grains</td>
</tr>
<tr>
<td>1968</td>
<td>Starch versus fructosan accumulation</td>
</tr>
<tr>
<td>1969</td>
<td>Underground seedling organs</td>
</tr>
<tr>
<td>1974</td>
<td>Photosynthetic pathways/leaf anatomy</td>
</tr>
<tr>
<td>1976</td>
<td>Flavonoid patterns</td>
</tr>
<tr>
<td>1978</td>
<td>Stomatal insertion</td>
</tr>
<tr>
<td>1983</td>
<td>Pollen antigens</td>
</tr>
<tr>
<td>1987</td>
<td>Photosynthetic pathways</td>
</tr>
<tr>
<td>1991</td>
<td>Chloroplast DNA analysis</td>
</tr>
<tr>
<td>2000</td>
<td>Phytochrome B</td>
</tr>
</tbody>
</table>

### UNDERGROUND SEEDLING FEATURES

Hoshikawa (1969) recognized six patterns of underground organs of the grass seedling based upon:

- the presence or absence of transitory node roots (TNR);
- whether or not the mesocotyl elongates, and
- the presence or absence of mesocotyl roots (MR).

He also discovered seven patterns of seedling establishment based upon features of the TNR, MR, and crown node roots (CNR). He then used the six patterns of organs and the seven of establishment to characterize various subfamilies and tribes.

### FIRST LEAF

Kuwabara (1960, 1961) investigated the shape, position, and length/width ratio of the first leaf of the grass seedling. He found that in festucohoids the leaf blade was linear, perpendicular, and had a L/W ratio = 10.3-106. In panicoids, the blade was oval to lanceolate, horizontal to ascendent, and L/W = 1.3-12. In eragrostoids, the blade was heterogeneous and L/W = 15.5-25.9.

### ROOT HAIRS

Row & Reeder (1957) and Reeder & von Maltzalen (1953) found two kinds of root hairs in grasses:

Type A, the hairs were made up of alternating long and short cells and the hairs themselves arose from apical end at a 45 angle. Typical of pooid grasses.

Type B, the hairs were composed of cells of equal length and arose from the midpoint at 90° angles. Found more commonly in chloridoid and panicoid taxa.

### LEAF IN TRANSVERSE SECTION

Based upon the studies of Avdulov (1931), Prat (1936), and Brown (1958), we have been able to recognize six different patterns: festucohoid, bambusoid, arundinoid, panicoid, aristidoid, and chloridoid. The characters used to distinguish the six types include those of the vascular bundles, the endodermis, the mestome sheath, the kind and location of plastids, and the pattern of chlorenchyma cells. In leaves of grasses that employ the C₄ photosynthetic pathway, there are specialized cells around the vascular bundles.

### CULM IN TRANSVERSE SECTION

Brown, Harris, & Graham (1959) found that while almost all of the pooid grasses that they examined had hollow internodes, that 49-100% of the chloridoid and panicoid had ± solid internodes. They concluded that there was a positive correlation between the latter condition and hot, arid habitats.
Brown et al. (1959) investigated the presence of leaf sheath pulvini and its correlation with hollow vs. solid culm internodes. Pulvini are meristematic swellings at the base of a leaf sheath. They are sometimes called “motor organs” because they make it possible for a stem that has been trampled or blown down to right itself. They discovered that pooid grasses have pulvini, while most panicoid and chloridoids do not. Therefore, pulvini are correlated with hollow internodes.

**LEAF EPIDERMIS**

Prat (1932, 1936) found that the leaf epidermis was a rich source of useful characters. Based upon the appearance of long cells, short cells, silica bodies, cork cells, stomata, microhairs, macrohairs, prickle-hairs, and papillae, it is possible to recognize four groups: bambooids, pooids, chloridoids, and panicoids.

Tateoka et al. (1959) and Johnston & Watson (1976) have carried out extensive investigations of bicellular microhairs on grass leaf epidermises. Their findings are summarized as follows:

- **Width of hair/length of hair**
  - Panicoids: 0.694
  - Eragrostoids: 2.265
- **Ratio of upper cell to lower cell length**
  - Panicoids: 1.731
  - Eragrostoids: 2.681
- **Angle between axis of hair and shortest line**
  - Panicoids: 2.014
  - Eragrostoids: 0.890
- **Cell wall thickness in upper and lower cells**
  - Type A: about same thickness
  - Type B: intermediate
  - Type C: upper thinner than lower

**TUNICA LAYERS IN SHOOT APEX**

At the apex of a grass shoot is a one- or two-layered tunica layer that covers the main body of cells. Brown et al. (1957) found that grasses always appear to have a two-layered tunica; while Barnard (1964) found that chloridoid and panicooid grasses have only a 1-layered tunica. This is the sort of major controversy that will cause you to toss and turn all night long.

**LODICULE MICROHAIRS**

Tateoka (1967) found that microhairs on lodicules are frequent in bambooids, rare in most subfamilies, and absent in festucoids.

**EMBRYO STRUCTURE**

The grass embryo has been studied intensively for over a century, beginning with Bruns (1892), and continuing with Van Tieghem (1897), Yakovlev (1950), Reeder (1957, 1962), and Kings (1961). John Reeder’s 1957 paper is especially important. He examined four characters:

- whether the vascular trace to the scutellum and coleoptile diverged at the same point [F] or were separated by an internode [P];
- whether the epiblast was present [+] or absent [-];
- whether the scutellum was free from the coleorhiza [P] or fused with it [F]; and
- whether the embryonic leaf margins over-lapped [P] or merely met [F].

Based upon combinations of these character states, Reeder recognized seven embryo types:

- Festucoid: F + F F
- Panicoid: P - P P
- Chloridoid-Eragrostoid: P + P F
- Bambusoid: F + P P
- Oryzoid-Olyroid: F - P P, F + P P, F + F P
- Arundinoid-Danthonioid: P - P F
- Centothecoid: P + P P

**STARCH GRAINS**

For over a century, agrostologists have been studying the starch grains in the grass endosperm, hoping that the variation that they had discovered had some systematic significance. Tateoka (1962) investigated almost 800 taxa and found appreciable variation even within a single species. Although he could not find correlations that held with any subfamilies, he did recognize four different types of starch grains:

- **Type 1**: Triticum-type. Simple grains, broadly elliptic, rounded
- **Type 2**: Panicum-type. Simple grains, angular
- **Type 3**: Miscanthus-type. Simple or of 2-4 granules
- **Type 4**: Festuca-Eragrostis type. Compound grains only.
BASE CHROMOSOME NUMBER

The research carried out by Avdulov (1931) and Carnahan & Hill (1961) provided the breadth of chromosome numbers needed to survey variation in grasses. The range, by the way, is impressive: 2n = 4 to 220. In addition to the numbers reported below, base chromosome numbers of 4, 6, 8, 11, 13, 17, 19, and 23 have been cited.

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Chromosome Numbers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bambusoideae</td>
<td>x = 12</td>
</tr>
<tr>
<td>Pooidae</td>
<td>x = 7</td>
</tr>
<tr>
<td>Arundinoideae</td>
<td>x = 6 or 12</td>
</tr>
<tr>
<td>Ehrhartoideae</td>
<td>x = 12</td>
</tr>
<tr>
<td>Chloridoideae</td>
<td>x = 9 or 10</td>
</tr>
<tr>
<td>Panicoideae</td>
<td>x = 5, 9, or 10</td>
</tr>
</tbody>
</table>

PERSISTENT NUCLEOLI

When the nuclei of somatic cells divide, the nucleolus typically disappears before metaphase. The nucleoli are then reconstituted in the nuclei of daughter cells. Frew & Bowen (1927) and Brown & Emory (1957) found that in certain grasses the nucleolus persists after metaphase. Their studies showed that pooid grasses do not have persistent nucleoli, whereas they do persist in chloridoid and panicoids.

EFFECT OF IPC

Al-Aish & Brown (1958) studied the effect of IPC (isopropyl-n-phenyl carbamate) on grass seed germination. Festucoid seeds are very sensitive to IPC and did not germinate in its presence. Panicoid seeds are able to tolerate it; all seeds germinated.

LOW OXYGEN TENSION

The same authors also investigated the ability of grass seeds to germinate in low oxygen atmospheres. The panicoids tested did germinate; the pooids did not do well. Rice seeds were most successful.

CARBOHYDRATE STORAGE

Grasses are either sacchifers (storing carbohydrates only in the form of starch or sucrose) or laevulifers (storing them not only as starch or sucrose, but also as fructose polymers).

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pooidae</td>
<td>laevulifers</td>
</tr>
<tr>
<td>Chloridoideae</td>
<td>sacchifers</td>
</tr>
<tr>
<td>Panicoideae</td>
<td>sacchifers</td>
</tr>
</tbody>
</table>

HEAT PRODUCTION OF Caryopses

Grasses are just like all other higher plants in having a two-phase photosynthetic process. The light reaction is a photochemical process (photophosphorylation) that occurs in the chloroplasts and chlorenchyma cells of the mesophyll. Adenosine diphosphate (ADP) is converted to adenosine triphosphate (ATP). NADP is also reduced to NADPH. During the dark reaction, CO₂ enters through the stomates and combines with ribulose diphosphate to form a 6-carbon intermediary molecule. It quickly divides into two 3-carbon units, PGA (3-phosphoglyceric acid). These processes occur within the chlorenchyma cells in the mesophyll of the leaf.

About thirty years ago, another version of this dark reaction was discovered that involved 4-carbon units. This alternate pathway is variously known as the Hatch-Slack pathway (after its discoverers) or the kranz-type pathway (from the German word for "ring") an anatomical reference to the arrangement of some specialized leaf cells when seen in cross-section. This second photosynthetic pathway is found in many grasses. Not only are the intermediary compounds different, but the C₄ pathway takes place not only within the chlorenchyma cells of the mesophyll, but also in parenchyma sheath cells (often called kranz cells). Three subtypes of this pathway, based upon the decarboxylating enzymes found in the kranz cells, have been recognized. Smith & Brown (1973), Brown (1975, 1977), and Waller & Lewis (1979) investigated the systematic significance of the two pathways and found the following:

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Subtype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bambusoideae</td>
<td>C3</td>
</tr>
<tr>
<td>Ehrhartoideae</td>
<td>C3</td>
</tr>
<tr>
<td>Pooidae</td>
<td>C3</td>
</tr>
<tr>
<td>Arundinoideae</td>
<td>C3 (mostly) and C4</td>
</tr>
<tr>
<td>Chloridoideae</td>
<td>C4 (mostly) and C3</td>
</tr>
<tr>
<td>Panicoideae</td>
<td>C3 and C4</td>
</tr>
</tbody>
</table>

IMMUNOLOGY AND SEROLOGY

Almost a century ago, two workers in Germany and in England discovered that the combination of antigens and antibodies yielded a visible precipitate and that this phenomenon could be used to investigate how closely related to organisms might be by testing how similar their proteins are to one another. Fairbrothers & Johnson (1961) employed this technique in the grasses and they discovered, for instance, that the Festuceae of George Bentham and later workers was a hodgepodge of unrelated taxa. Their work supported carving out a number of genera and placing them in an entirely different subfamily -- the Chloridoideae. Similar studies of amino acids in various grasses have also been carried out.

Another kind of protein interaction occurs when grass pollen encounters the tissues lining the nasal passages in humans. The taxonomic significance of allergic reactions to grasses has been explored by Watson (1983), and Watson & Knox (1976). Correspondence with Dr. Watson revealed that he and I were both amazed to see that we were allergic to some tribes of grasses, but not to others.

FLAVONOIDs

Flavonoids are secondary metabolites in plants. More specifically, they are kinds of phenolic compounds -- a loose assemblage of chemicals based upon a phenol nucleus. A number of the more unusual plant
pigments are flavonoids. Harborne & Williams (1976, 1987) have studied these pigments in grasses.

**DNA & RNA STUDIES**

When I was a graduate student, chromosomes were the Messiah. Yes, chromosomes had been invented that long ago! Their number, morphology, and behavior during meiosis would provide an objective index for determining whether two plants or two populations of plants belonged to a single species. What a disappointment it was to discover that grasses were not that simple.

More recent techniques focus on genetic information at an even more fundamental level. If chromosomes do not tell us what we need to know, then certainly examining the sequence of base pairs in the genetic material itself ought to do the trick. The earliest attempts to examine nucleic acid sequences involved extracting the total DNA of one plant and comparing it with the total DNA from another. The degree to which the two DNA samples annealed or reassociated was taken as a measure of how closely related the two entities were.

This methodology worked well in microorganisms, but less so in higher plants. Long stretches of repeated DNA sequences and the fact that DNA occurred in chromosomes, mitochondria, and plastids made analysis of these life forms more difficult. Today investigators use only specific sections of DNA that are separated by enzymes (restriction endonucleases) into well defined restriction fragments. These fragments can be separated from one another by gel electrophoresis. These studies rest on the assumption that examination of comparable restriction site fragments of DNA will yield more useful data. One of the more elegant papers on this subject is the work of Jones & Flavell (1982) on rye.

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SECTION 3 - SURVEY OF SUBFAMILIES, TRIBES, & GENERA

3.01 - SUBFAMILY BAMBUSOIDEAE

TECHNICAL DESCRIPTION

**Habit:** Mostly perennial; culms woody or herbaceous; leaf blades often pseudopetiolate

**Root Hairs:** Unequal, arising from the middle of the cell

**Leaf Epidermis:** Bicellular microhairs; short cells paired or in rows; silica-cells cross-, saddle-, or dumbbell-shaped; stomata with dome-shaped subsidiary cells

**Leaf in Cross-section:** Double vascular bundle sheath, the inner with thicker cell walls; large fusoid cells and arm cells present; non-kranz anatomy

**Inflorescence:** Typically paniculate; often subtended by a spathe

**Spikelets:** Bisexual or unisexual; 1- to many-flowered; glumes 2-5; awned or awnless, disarticulation above the glumes and between the florets.

**Flowers:** Lodicules [1] 3 [10]; stamens 3, 6, or more; gynoecium with 1, 2, 3 or more stigmas, tricarpellate

**Fruit:** Caryopsis, nut, berry, or utricle

**Embryo Formula:** F + P P

**Cytology:** x = 10, 11, or 12

**Photosynthetic Pathway:** C₃

**Distribution:** Asia, Africa, the Americas, and the islands of the Pacific and Indian oceans; abundant in the tropics; absent from Europe; mostly in forests, woodlands, and wet places.

Unfortunately, the delimitation of our first subfamily remains controversial. One hint that there is a problem is that these grasses may be treated as one, two or three distinct subfamilies. The most liberal interpretation places the woody and herbaceous bamboos in Bambusoideae, the oryzoid grasses (rice and its relatives) in Ehrhartoideae, and the pharoid grasses (only one species of which is in North America) in Pharoideae. Note how various authors have disposed of our North American bamboos:

- Bentham (1881): Bambuseae
- Roshevits (1937): Bambuseae, Phareae
- Stebbins & Crampton (1961): Bambuseae
- Potzetal (1964): Bambuseae, Arundinariae
- Tzvelev (1989): Bambuseae, Arundinariae
- Clayton & Renvoize (1992): Bambuseae, Olyreae, Phareae, Oryzaeae, Ehrhartaeae, Diarrheneae, Brachyeltyreae

A common error is to assume that any really large grass with what appears to be woody stems must be a bamboo. Look also in Arundinoideae for large bamboo-like grasses, such as the giant reed grass (*Arundo donax*).

**TRIBE: BAMBUSEAE**

Woody perennials from extensive rhizomes. Culms 2-10+ m tall, freely-branched; internodes hollow to solid. Leaves of axillary branches pseudopetiolate, while those of the culm itself typically without blades or those that fall early. Inflorescence usually a large, many-flowered panicle; sometimes reduced to 1 spikelet. Spikelets typically large, several-flowered, bisexual, and disarticulating above the glumes and between the florets. Glumes 2 (the first often reduced), shorter than the lemmas. Lemmas similar to glumes, 5- to many-nerved, usually awnless. Palea often 2-keeled. Lodicules typically 3; stamens usually 6; stigmas usually 3. [= Arundinarieae in older literature].

Bamboos, the tree grasses, are variable in habit. They range from a few centimeters to more than 40 m tall. The culms may be solid or have hollow internodes. Larger bamboos are almost 25 cm in diameter with internodes of up to 1.5 m. Not all bamboos are woody; plants in two of the three tribes represented in the flora of North America are herbaceous. One bamboo is a vine 30 m long.

Rhizome development is extensive. Two types of rhizome systems are recognized. The **pachymorph** rhizome is short and thick, with the lateral buds producing only rhizomes. New culms arise from the apex of the rhizome system. Bamboos of this sort typically, have a “clump” growth form. The **leptomorph** rhizome system is long and slender, with many nodes capable of producing a new culm and adventitious roots. This is the rhizome system.
characteristic of the "running bamboos."

Leaves on the main culm axis are typically bladeless or with blades that fall early. The leaves of lateral branches appear to be petiolate, but they are probably best considered pseudopetiolate. Sheaths and scale leaves have played an important role in the traditional taxonomy of the group.

The inflorescence of many bamboos is a panicle or is reduced to a single spikelet, subtended by a few to several bracts, this combination known as a pseudospikelet. It may be simple or compound.

The flowers are the most monocot-like found in the family. They are composed of three lodicules, 3 or 6 stamens (rarely as many as 120!), and three united carpels. Blooming is erratic. There seems to be three basic patterns. Some bamboos flower gregariously, in regular cycles during which they set tremendous quantities of seeds, and then die within a year or so. Other bamboos are characterized by irregular flowering, during which vegetative growth of the plant is stunted; but, the plants do not die. Still other species flower annually.

It now appears that most of the woody bamboos are probably wind pollinated, but that at least some of the herbaceous bamboos are insect pollinated. Some bear their spikelets beneath the litter of the forest floor; others produce underground fruits, as in the peanut.

The economic uses of bamboos are almost endless -- "No growing things on earth have so many and so varied uses as ... bamboos" (Soderstrom, 1979). They include ornamentals building materials for houses, furniture, ships, aqueducts, carts, umbrella frames, bird cages, tiger cages, chop sticks, musical instruments, springs for carts, food, fibers, cordage, oars, masts, baskets, mats, spear shafts, bows, arrows, knives, ladders, rafts, pails, churns, curtains, tiles for roofs, beehives, fans, fishing poles, medicine ... and several hundred more!

**ARUNDINARIA.** Cane, canebrake, giant cane, switch cane. Rhizomatous perennial. Culms woody, 2-8 m tall. Leaves pseudopetiolate, the blades disarticulating from sheaths. Inflorescence spicate to paniculate; pseudospikelets absent. Spikelets bisexual, large, several-flowered, laterally compressed, disarticulating above the glumes and between the florets. A. gigantea is the only truly woody grass native to N. America and the only commonly occurring native bamboo here. The plants often form dense colonies. The species occurs from Ohio and Illinois into the Southeast. Three subspecies are now recognized.

**PHYLLOSTACHYS.** Fishpole bamboo, madake, timber bamboo, black bamboo, moso bamboo. Shrubby to arborescent perennials. Culms woody, 3-20+ m tall. Leaves pseudopetiolate. Inflorescence spicate-paniculate, often subtended by a spathe. Spikelets large (to 8 cm!), several- to many-flowered, bisexual, disarticulating above the glumes and between the florets. A genus of about 50 eastern Asian species. Of considerable economic importance as a source of handsome ornamentals, fishing rods, walking sticks, furniture, and edible young shoots.

**BAMBUSULA.** Giant bamboo, hedge bamboo, timber bamboo, Oldham's bamboo. Shrubby to arborescent, rhizomatous perennials. Culms 2-35+ m tall. Leaves pseudopetiolate. Inflorescence in panicles or fascicles; pseudospikelets present. Spikelets terete to laterally compressed, large (to 8 cm!), several-flowered, bisexual, disarticulating above the glumes and between the florets. A large genus of about 120 species native to tropical and subtropical areas of the Old and New World. Of considerable economic importance as a source of rods, poles, scaffolding for construction, furniture, fibers for weaving, paper pulp, and edible shoots.

**PSEUDOSASA.** Metake, arrow bamboo. Shrubby, rhizomatous perennial. Culms woody, 2-5 m tall. Leaves pseudopetiolate with auriculate setae. Inflorescence a terminal panicle of bisexual spikelets. A genus of 8 species native to eastern Asia. *P. japonica* is commonly cultivated.

**TRIBE: OLYREAE**

Caespitose perennials. Culms woody, to 3 m. Leaves broad, with asymmetric blades and cordate to sagitate bases. Inflorescence paniculate, the spikelet-bearing branches persistent. Spikelets unisexual (species monoecious), several-flowered, disarticulating above the glumes and between the florets. A tribe of about 18 genera. *Olyra latifolia* occurs in Florida.

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Simmons, J. C. & J. Brandenburg. 1986. The most


**ARUNDINARIA**


**PHYLLOSTACHYS**


3.02 - SUBFAMILY PHAROIDEAE

TECHNICAL DESCRIPTION

**Habit:** Rhizomatous perennial herbs; leaves distichous, pinnately-veined, pseudopetiolate, twisted, the blade resupinate; culms typically solid

**Root Hairs:**

**Leaf Epidermis:** Bicellular microhairs and papillae absent; silica bodies dumbbell-shaped; bulliform cells absent or poorly developed

**Leaf in Cross-section:** Fusoid cells prominent and well-developed; arm cells weakly to moderately well-developed

**Inflorescence:** Open, terminal panicle

**Spikelets:** Unisexual, 1-flowered, the male and female spikelets mostly paired on short branchlets; terete (♀) or laterally compressed (♂); female spikelets covered with uncinate microhairs

**Flowers:** Lodicules 0 or 3 (♂); stamens 6; stigmas 3

**Fruit:** Caryopsis

**Embryo Formula:**

**Cytology:** X = 12

**Photosynthetic Pathway:** C₃

**Distribution:** Pantropical; in New World from Florida southward to Argentina and Uruguay.

SELECTED REFERENCES


SYSTEMATICS

This subfamily was first defined in 1955 by Alan Beetle. It was formally described and published by Clark & Judziewicz in 1996. The subfamily consists of a single tribe of three genera and eleven species. The pharoid grasses are known in North America from a single species collected in Florida.

TRIBE: PHAREAE

Herbaceous perennials. Culms decumbent and rooting at the nodes, the internodes solid. Leaves with broad blades and a twisted, petiole-like constriction above the sheath. Inflorescence a panicle. Spikelets unisexual (species monoecious), 1-flowered, the pistillate sessile and the staminate pedicellate. Glumes 2, shorter than floret, 5- or 7-nerved. Lemmas 5- to 7-nerved, membranous (♂) or indurate (♀). Palea narrow, 2-keeled, 2-nerved.

A tribe of 3 genera. *Pharus lappulaceus* occurs in Florida, based on historic collections. It has probably been extirpated there.
3.03 - SUBFAMILY EHRHARTOIDEAE

TECHNICAL DESCRIPTION

Habit: Herbaceous annuals and perennials
Root Hairs: No studies have been made.
Leaf Epidermis: Bicellular microhairs present; silica cells often broader than long, silica bodies mostly dumbbell-shaped; long cells with rows of papillae, as in the bambusoids
Leaf Anatomy: Arms cells and fusoid cells present, as in the bambusoids; vascular bundles with double sheath, the inner with thicker cell walls; non-kranz
Spikelets: Spikelets 1- or 3-flowered, perfect or unisexual, laterally compressed or terete; glumes reduced or absent; lemma 5- to several-nerved; palea 2- to 3+-nerved
Flowers: Stamens 6, 3, or rarely 1; stigmas 1 or 2
Embryo: F + P F or F + P P
Cytology: x = 12 for most species; x = 15 in Zizania
Photosynthetic Pathway: C₃
Distribution: Marshy and aquatic sites of the tropics and sub tropics.

SYSTEMATICS

Hitchcock and Chase placed the members of this subfamily in three different tribes of their Festucoideae. Until the mid-1990's, the core of this group was rice and its relatives and the subfamily was called Oryzoideae. More recent studies suggest the appropriateness of including Ehrharteae here, which requires a name change.

The ehrhartoid, oryzoid, pharoid, and bambusoid grasses share many features, to the point where many agrostologists combine them into a single subfamily. I have followed that practice for a number of years. However, a number of recent studies, particularly at the molecular level, recognize them as distinct. For nomenclatural reasons that we need not explore, the transfer of Ehrharta into the Oryzoideae (rice subfamily) requires that its name be changed to Ehrhartoideae.

TRIBE: EHRHARTEAE

A small tribe of 4 genera, none of them with native to North America. Our only representative is Ehrharta.

EHRHARTA. Veldt grass. Annual or perennial herbs. Culms (ours) herbaceous, to 1 m tall. Inflorescence racemose to paniculate. Spikelets laterally compressed or terete, 3-flowered (the lower 2 reduced to sterile lemmas), bisexual, disarticulation above the glumes, but not between the florets. Glumes 2, 5-nerved, shorter or much longer than florets; sterile lemmas often transversely wrinkled; fertile lemma 5- to 7-nerved; palea 2-keeled. Lodicules 2; stamens 3, 4, or 6; stigmas 2. A genus of 27 species native to the Old World. E. calycina, E. erecta, and E. longiflora are weedy in California.

TRIBE: ORYZEAE

Annual or perennial herbs. Inflorescence a panicle. Spikelets laterally compressed, bisexual or unisexual, disarticulating above the glumes. Glumes reduced or absent, represented by a cup-like pedicel apex, their place seemingly occupied by sterile lemmas; fertile floret one. A tribe of about 13 genera.

ORYZA. Rice. Annual or perennial herbs. Inflorescence and open to contracted panicle. Spikelets laterally compressed, appearing 1-flowered, bisexual, disarticulating above the glumes. Glumes reduced to a 2-lobed cupule; lemmas 5-nerved, awned or awnless; palea 2-nerved. Lodicules 2; stamens 6; stigmas 2. A genus of about 25 species native to moist, wet, shady regions of the Old and New World; none native to North American. Rice, O. sativa, is one of the principal cereal crops that we consume. It is widely cultivated in flooded fields or on dry land. Another species, O. rufipogon, an Old World weedy species, has recently been found in the U. S.

THE SPECIES OF ORYZA

<table>
<thead>
<tr>
<th>Species</th>
<th>Genome</th>
<th>Native</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diploids [2n= 2x = 24]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>O. australiensis</td>
<td>EE</td>
<td>Australia</td>
</tr>
<tr>
<td>O. barthii</td>
<td>AA</td>
<td>West Africa</td>
</tr>
<tr>
<td>O. brachyantha</td>
<td>FF</td>
<td>West &amp; central Africa</td>
</tr>
<tr>
<td>O. eichingeri</td>
<td>CC</td>
<td>East &amp; central Africa</td>
</tr>
<tr>
<td>O. glaberrima</td>
<td>AA</td>
<td>West Africa</td>
</tr>
<tr>
<td>O. granulata</td>
<td>1</td>
<td>South &amp; Southeast Asia</td>
</tr>
<tr>
<td>O. longisminata</td>
<td>AA</td>
<td>Africa</td>
</tr>
<tr>
<td>O. meyeriana</td>
<td></td>
<td>Southeast Asia, China</td>
</tr>
<tr>
<td>O. nivara</td>
<td>AA</td>
<td>Asia, China, Australia</td>
</tr>
<tr>
<td>O. officinalis</td>
<td>CC</td>
<td>Asia, China, New Guinea</td>
</tr>
<tr>
<td>O. punctata</td>
<td>BB</td>
<td>Africa</td>
</tr>
<tr>
<td>O. rufipogon</td>
<td>AA</td>
<td>Asia and China</td>
</tr>
<tr>
<td>O. sativa</td>
<td>AA</td>
<td>Asia</td>
</tr>
<tr>
<td>O. schlechteri</td>
<td>--</td>
<td>New Guinea</td>
</tr>
<tr>
<td>Tetraploids [2n = 4x = 48]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>O. alta</td>
<td>CCDD</td>
<td>C. &amp; S. America</td>
</tr>
<tr>
<td>O. eichingeri</td>
<td>BBCC</td>
<td>East &amp; central Africa</td>
</tr>
<tr>
<td>O. grandiglumis</td>
<td>CCDD</td>
<td>South America</td>
</tr>
<tr>
<td>O. latifolia</td>
<td>CCDD</td>
<td>C. &amp; S. America</td>
</tr>
<tr>
<td>O. longiglumis</td>
<td>----</td>
<td>New Guinea</td>
</tr>
<tr>
<td>O. minuta</td>
<td>BBCC</td>
<td>Southeast Asia</td>
</tr>
</tbody>
</table>
**LEERSIA.** Cutgrass, rice cutgrass, white grass. Mostly rhizomatous perennials. Inflorescence a panicule. Spikelets laterally compressed, bisexual, 1-flowered, disarticulating below the glumes. Glumes 0; lemmas 5-nerved, usually awnless. Lodules 2; stamens 1-6; stigmas 2. A genre of about 18 species, mostly of moist to wooded sites in the Old and New World; 5 occur in North America. *Leersia oryzoides* is our only California species.

**ZIZANIA.** Wild-rice. Tall, reed-like annuals or perennials. Culms herbaceous, 1-3 m tall. Inflorescence a conspicuous, terminal panicle. Spikelets 1-flowered, unisexual; female spikelets on stiff, erect branches; male spikelets on lower spreading branches. Glumes 0; pistillate lemma 3-nerved, awned; staminate lemma 5-nerved, awn-tipped; pistillate palea 2-nerved; staminate palea 3-nerved. Stamens 6. A genus of 3 species native to North America and Eurasia. *Z. aquatica*, the wild rice of commerce, is native to the eastern half of the United States. A second species, *Z. texana*, occurs only in Texas. The third species ( *Z. latifolia*) is cultivated for its edible shoots.

**ZIZANIOPSIS.** Marsh millet, southern wildrice. Coarse, rhizomatous perennials. Inflorescence a conspicuous, terminal panicle. Spikelets 1-flowered, unisexual (male and female spikelets on the same branch), disarticulating below the glumes. Staminate spikelet: glumes 0; lemma 5-nerved, awnless; palea 3-nerved; pistillate spikelet: glumes 0; lemma 7-nerved, acuminate to awned; palea 3-nerved; stigmas 2. A genus of 3-5 species native to North and South America. *Z. miliacea*, the only species found in North America, grows in wet freshwater and brackish sites from Maryland through the southern states to Texas.

**LUZIOLA.** Southern water grass. Low growing perennials in ponds, marshy sites, and along stream banks. Inflorescences unisexual (♀ terminal and the ♂ axillary). Stamens 6-16. Fruit an achene. As treated here, the genus includes *Hydrocholea*. Three species are found in North America, mostly in the Southeast.

[After Simmonds, 1976]

**SELECTED REFERENCES**


**ORYZA**


**LEERSIA**

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**ZIZANIA**


**ZIZANIOPSIS**


**LUZIOLA**


**TRIBE EHRHARTEAE**


**EHRHARTA**


### TECHNICAL DESCRIPTION

**Habit:** Perennial herbs

**Root Hairs:** No studies have been made.

**Leaf Epidermis:** Bicellular microhairs rodlike to linear; silica cells mostly dumbbell-shaped, confined to the costal region

**Leaf Anatomy:** Vascular bundles with a double sheath, the outer with large, thin-walled parenchyma cells; arm cells present in some species; mesophyll with large intercellular spaces; bulliform cells large, occupying a major portion of the blade in transverse section.

**Spikelets:** Spikelets 2- to many-flowered, with reduction above or below the fertile florets; perfect or unisexual

**Flowers:** Lodicules 2 or 0, many-nerved; stamens 2 or 3; stigmas 2

**Embryo:** P + P P

**Cytology:** x = 12

**Photosynthetic Pathway:** C₃

**Distribution:** Mostly grasses of shaded, warm woodlands and tropical forests of the Americas, Africa, and Asia

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### SYSTEMATICS

The subfamily consists of about 13 genera and only 30 or so species. It is represented in North America by a single tribe containing a single genus, *Chasmanthium*. The subfamily is clearly bambusoid in its affinities and it is merged with Bambusoideae in some modern treatments. Others place the genera in Arundinoideae.

In recent literature, the subfamily and tribe names were sometimes incorrectly spelled Centostecoideae.

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### TRIBE: CENTOTHECEAE

The characters are those of the single genus below.

**CHASMANTHIUM.** Wild oats, spangle grass, broad-leaved uniola. Broad-leaved perennials, often rhizomatous. Culms herbaceous, to 1.5 m tall. Leaf blades broad, flat. Inflorescence an open to contracted panicle. Spikelets 2- to many-flowered (the lower 1-6 sterile), bisexual, laterally compressed, disarticulating above the glumes and between the florets. Glumes 2, 3- to 7-nerved; lemmas 5- to many-nerved, awnless; palea 2-keeled, winged. Lodicules 2; stamens 1 [3]; stigmas 2, red. A genus of 5 or 6 species, of the southeastern and southwestern United States and adjacent Mexico. H & C treated it as part of *Uniola* and placed the genus in their tribe Festuceae. *C. latifolium* is probably the most conspicuous species; it is increasingly popular as an ornamental. Other species may be confused with plants of the genus *Diarrhena*.

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### CHASMANTHIUM AND UNIOLA

<table>
<thead>
<tr>
<th>Feature</th>
<th>Chasmanthium</th>
<th>Uniola</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat</td>
<td>Mesic forests</td>
<td>Coastal sand dunes</td>
</tr>
<tr>
<td>Stamen Number</td>
<td>One</td>
<td>Three</td>
</tr>
<tr>
<td>Spikelet Color</td>
<td>Greenish</td>
<td>Straw-colored</td>
</tr>
<tr>
<td>Disarticulation</td>
<td>Above glumes</td>
<td>Below glumes</td>
</tr>
<tr>
<td>Embryo Type</td>
<td>P + P P</td>
<td>P - P F</td>
</tr>
<tr>
<td>Leaf Anatomy</td>
<td>Bambusoid</td>
<td>Chloridoid</td>
</tr>
<tr>
<td>Chromosomes</td>
<td>x = 12, 24</td>
<td>x = 20</td>
</tr>
</tbody>
</table>

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### SELECTED REFERENCES


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### CHASMANTHIUM


3.05 - SUBFAMILY POÖIDEAE

**TECHNICAL DESCRIPTION**

- **Habit:** Annual or perennial herbs
- **Root Hairs:** Equal
- **Leaf Epidermis:** Relatively simple; bicellular microhairs absent (except in some Stipeae); silica cells round, elliptical, solitary or paired with cork cells; stomata low, dome-shaped or with parallel-sided subsidiary cells
- **Leaf Anatomy:** Vascular bundle sheath usually double; chlorenchyma irregular; non-kranz anatomy
- **Inflorescence:** Typically a panicle, rarely a spike or raceme
- **Spikelets:** Spikelets 1- to many-flowered, laterally compressed or terete; florets 1 to many, the upper usually reduced or aborted; disarticulation usually above the glumes and between the florets; lemmas 5- to many-nerved; palea typically 2-keeled
- **Flowers:** Lodicules 2; stamens usually 3; stigmas 2
- **Embryo:** F + F F
- **Cytology:** x = 7, often relatively large (x = 8, 9 or 10 in Meliceae; x = 7 and 11 in Stipeae); no persistent nucleoli
- **Photosynthetic Pathway:** C₃
- **Distribution:** Herbaceous grasses, primarily of the cool and temperate regions of the world or of the alpine areas of the tropics and subtropics.

**SYSTEMATICS**

This subfamily, called Festucoideae by Hitchcock and Chase, was recognized by all of the classical workers, but in a much broader sense than we see it now defined. The other genera included by H & C now reside in every other subfamily, except Panicoideae.

**FATE OF H & C’S SUBFAMILY?**

**I. Tribes moved to other subfamilies:**
- Bambuseae ➔ Bambusoideae
- Chlorideae ➔ Chloridoideae
- Oryzeae ➔ Oryzoidae
- Zizanieae ➔ Oryzoidae
- Zoysieae ➔ Chloridoideae

**II. Portions of tribes moved:**
- Agrostideae ➔ Arundinoideae
- Agrostideae ➔ Chloridoideae
- Agrostideae ➔ Aristidoideae

**III. Tribes remain more or less intact:**
- Agrostideae = Aveneae: Alopecurinae
- Aveneae = Aveneae: Aveninae
- Hordeae = Aveneae: Triticinae
- Phalarideae = Aveneae: Phalarinae

**IV. New tribes carved out of old ones:**
- Aristideae out of Agrostideae
- Bromeae out of Festuceae
- Danthonieae out of Aveneae
- Melicaceae out of Festuceae
- Nardeae out of Hordeae
- Stipeae out of Agrostideae

**TRIBE: DIARRHENEAE**

The tribe consists of the single genus described below.

**DIARRHENA.** Perennial herbs. Inflorescence a few-flowered panicle, its branches often drooping. Spikelets 3- to 5-flowered, bisexual, disarticulating above the glumes and between the florets. Glumes 2, the first 1-nerved, the second 3-nerved; lemmas 3-nerved, awnless; palea 2-nerved. Lodicules 2; stamens [1] 2 or 3; stigmas 2; fruit a shiny, turgid, beaked achene. The tribe consists of the 5 Old World and New World species of this genus. In North America, we see *Diarrhena americana*, a grass of rich or moist woods in the central and eastern states.

**TRIBE: BRACHYELYTREAE**

This tribe consists of the single genus described below.

**BRACHYELYTRUM.** Perennial, rhizomatous herbs. Culms herbaceous, to 1 m; internodes solid. Inflorescence a few-flowered panicle. Spikelets terete to dorsally compressed, 1-flowered, disarticulating above the glumes. First glume minute to absent; second glume short, awned or awoless. Lemma 5-nerved, awned. Lodicules 2; stamens 3; stigmas 2. This is the only genus in the tribe. It consists of 2 species, one in Japan and Korea; *B. erectum* is native to moist or rocky woods in eastern North America.

**TRIBE: POEAE**

Annual or perennial herbs. Inflorescence a panicle, rarely a raceme or spike. Spikelets 2- to many-flowered, laterally compressed, bisexual [rarely unisexual]. One or both glumes shorter than the lemmas; lemmas 5- to many-nerved, awned or
awlless, its apex variable.

**FESTUCA.** Fescue, fescue grass. Caespitose, rhizomatous, or stoloniferous perennial herbs. Culms to 2 m tall, internodes hollow or solid. Leaves mostly basal; sheaths open. Inflorescence an open to congested panicle. Spikelets 2- to several-flowered, laterally compressed, bisexual, disarticulating above the glumes and between the florets. Glumes 2, unequal, 1- to 3-nerved, shorter than the florets; lemmas similar to glumes in texture or much firmer, typically 3- to 7-nerved, awned from an entire to minutely bifid apex or awnless; palea relatively long, apically notched. Lodicles 2; stamens 3; stigmas 2; flowers open-pollinated.

A genus of about 360+ species of temperate and mountainous regions worldwide. Of economic importance as a source of fodder, lawn grasses, and major weedy species. Common species include *F. ovina* (sheep fescue), *F. arundinacea* (tall or alta fescue), *F. idahoensis* (Idaho fescue), *F. pratensis* (meadow fescue), and *F. rubra* (red fescue).

The annual fescues (*Festuca* sec. Vulpia in H & C) are now most often treated as belonging to the segregate genus *Vulpia*. The table below presents the name changes in the North American species. You will note that several species have disappeared into synonymy.

### ANNUAL FESTUCA TO VULPIA

<table>
<thead>
<tr>
<th>Festuca Sect. Vulpia</th>
<th>Combination in Vulpia</th>
</tr>
</thead>
<tbody>
<tr>
<td>F. arida →</td>
<td>V. microstachys var. m.</td>
</tr>
<tr>
<td>F. confusa →</td>
<td>V. microstachys var. confusa</td>
</tr>
<tr>
<td>F. dertoneis →F.</td>
<td>V. bromoides</td>
</tr>
<tr>
<td>eastwoodiae →F.</td>
<td>V. microstachys var. ciliata</td>
</tr>
<tr>
<td>grayi →</td>
<td>V. microstachys var. ciliata</td>
</tr>
<tr>
<td>F. megalura →F.</td>
<td>V. myuros var. hirsuta</td>
</tr>
<tr>
<td>microstachys →F.</td>
<td>V. microstachys var. m.</td>
</tr>
<tr>
<td>myuros →</td>
<td>V. myuros var. m.</td>
</tr>
<tr>
<td>F. octoflora var. glauca</td>
<td>V. octoflora var. g.</td>
</tr>
<tr>
<td>→ F. octoflora var. hirtella</td>
<td>V. octoflora var. h.</td>
</tr>
<tr>
<td>→ F. octoflora var. octoflora → V. octoflora var. o.</td>
<td></td>
</tr>
<tr>
<td>F. octoflora var. tenella → V. octoflora var. t.</td>
<td></td>
</tr>
<tr>
<td>F. pacifica var. p. → V. microstachys var. pauciflora</td>
<td></td>
</tr>
<tr>
<td>F. pacifica var. simulans → V. m. var. pauciflora</td>
<td></td>
</tr>
<tr>
<td>F. reflexa →</td>
<td>V. microstachys var. pauciflora</td>
</tr>
<tr>
<td>F. sciuere →</td>
<td>V. sciuere</td>
</tr>
<tr>
<td>F. tracyi →</td>
<td>Vl. microstachys var. confusa</td>
</tr>
</tbody>
</table>

**VULPIA.** Annual fescue. Tufted annuals [rarely perennial] herbs. Culms to 9 dm tall, the internodes solid or hollow. Inflorescence a contracted or open spike-like panicle. Spikelets 2- to many-flowered, laterally compressed, bisexual, disarticulating above the glumes and between the florets. Glumes 2, very unequal, 1- to 3-nerved, shorter than the florets; lemmas tapered, firmer than the glumes, 3- to 5-nerved (often inconspicuously so), awned or acuminate; palea relatively long, apically notched. Lodicles 2; anthers 1 [3]; stigmas 2; flowers cleistogamous.

A genus of about 23 species widespread in the temperate regions of the world where they are often weedy. Included in *Festuca* by H & C. Common species include *V. octoflora* (sixweeks fescue), *V. myuros*, and *V. bromoides*. Some agrostologists, myself included, prefer to merge this genus with *Festuca*, but this is not a popular view.

### COMPARISON OF FESTUCA AND VULPIA

<table>
<thead>
<tr>
<th>Festuca</th>
<th>Vulpia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perennial [annual]</td>
<td>Annual [perennial]</td>
</tr>
<tr>
<td>Stamens 3 [1]</td>
<td>1 [3]</td>
</tr>
<tr>
<td>Pollination open [closed]</td>
<td>closed [open]</td>
</tr>
</tbody>
</table>

**LOLIIUM.** Rye grass. Caespitose annuals or perennial from rhizomes or stolons. Culms herbaceous, to 1 m tall, the internodes hollow. Inflorescence a spike (spikelets attached edgewise to rachis). Spikelets several-flowered, laterally compressed, bisexual, disarticulating above the glume and between the florets. Glume 1 (lower missing), except in the uppermost spikelets; lemmas 5- to 9-nerved, awned or awnless; palea relatively long, often ciliolate. Lodicles 2; stamens 3; stigmas 2.

A genus of 8-10 Old World species, especially African and Eurasian. Of economic significance because of fodder, lawn grasses, and common weeds. Formerly placed in Triticeae because of its inflorescence type; *Lolium* now treated as a close relative of *Festuca* because of its interfertility. Recent research suggests it should be merged with that genus. *Lolium perenne* is an important pasture grass; *L. temulentum* (darnel) is commonly toxic because of a fungal infection.

**PUCCINELLIA.** Alkali grass. Annuals or perennials herbs. Culms herbaceous, to 1 m tall. Leaves sheaths open [rarely closed]. Inflorescence an open or congested panicle. Spikelets small, several-flowered, laterally compressed, bisexual, disarticulating above the glumes and between the florets. Glumes 2, very unequal, shorter than the florets, first 1-nerved and the second 3-nerved; lemmas with 5 weak or strong, parallel nerves; palea equalling or exceeding the lemma. Lodicles 2; stamens 3; stigmas 2.

A genus of about 80 species native to the north temperate zone of the Old and New World, especially North America; often of wet or marshy, especially alkaline sites. A few species listed in H & C have been transferred to *Glyceria* and *Torreyochloa* by some workers. *P. airoides* (Nuttall’s alkali grass) is an important forage grass in some areas; otherwise, the genus is of little direct economic importance.

**TORREYOCHELAA.** Stoloniferous or caespitose perennials. Culms herbaceous, to 5 dm tall. Leaf sheaths open. Inflorescence a panicle. Spikelets 3- to 7-flowered, bisexual, laterally compressed, and disarticulating above the glumes and between the florets. Glumes 2, very unequal, 1- or 3-nerved; lemmas 5- to 7-nerved, awnless; palea relatively long. Lodicles 2; stamens 3; stigmas 2.

A genus of 4 species native to northern Asia and North America, often found in wet meadows and aquatic sites. The genus is doubtfully distinct from *Glyceria*.

**POA.** Blue grass, mutton grass. Annuals or perennials, many rhizomatous. Culms herbaceous, to 1.5 m tall, the internodes hollow. Leaf blade with a bow-shaped tip. Inflorescence an open to congested panicle, sometimes reduced to a raceme. Spikelets small, [1-]
2- to 10-flowered, laterally compressed, bisexual or infrequently unisexual (species dioecious), and disarticulating above the glumes and between the florets. Glumes 2, ± equal, 1- or 3-nerved; lemmas typically 5-nerved, keeled, awnless, its base glabrous or with a web of fine, cottony hairs; palea 2-nerved. Lodicules 2; stamens 3; stigmas 2.

A large and notoriously difficult cosmopolitan genus of about 500 species, found typically in grasslands and meadows, but in a variety of other habitats as well; many are weedy. Recent treatments have often resulted in reducing the number of taxa, certainly a step in the right direction. *P. pratensis* (Kentucky bluegrass) may well be the most important perennial pasture grass in North America; *P. fendleriana* (mutton grass) is a very important pasture grass in North America; *P. compressa* (Canada bluegrass) is often used as a lawngrass.

**BRIZA.** Quaking grass, rattlesnake grass. Tufted annuals or perennials. Culms herbaceous, ours to 0.5 m tall. Inflorescence an open panicles, the pedicels slender and often drooping. Spikelets several-flowered (florets crowded and spreading at right angles to the rachilla), bisexual, laterally compressed, and disarticulating above the glumes and between the florets. Glumes 2, ± equal, thin and papery, rounded, 3- to 15-nerved; lemmas similar to glumes in texture, 7- to 15-nerved, awnless; palea 2-nerved. Lodicules 2, stamens 3; stigmas 2.

A genus of about 16-20 species native to Europe, Mexico, and principally South America. Three European species are adventive in North America. They come in three sizes, *B. maxima*, *B. media*, and *B. minor*. The first species is often found as a roadside weed and it is gathered up for dried arrangements.

**DACTYLIS.** Orchard grass. Tall, densely caespitose perennials. Culms herbaceous, to 2 m tall. Leaf sheaths keeled and closed. Inflorescence a panicle, with second spikelets clumped at ends of panicle branches. Spikelets 2- to 5-flowered, bisexual, laterally compressed, and disarticulating above the glumes and between the florets. Glumes 2, shorter than or equaling the florets, 1- or 3-nerved; lemmas 5-nerved, awned or awnless; palea 2-nerved and 2-keeled. Lodicules 2; stamens 3; stigmas 2.

A monotypic genus (or 3-5 species if you are a splitter), native to temperate Eurasia. *D. glomerata* is used as a pasture and fodder grass. It is also a major weed.

**Cynosurus.** Dogtail. Caespitose annuals or perennials. Culms herbaceous, to 1 m tall. Inflorescence a head-like or cylindric, spike-like panicle of two very heteromorphic fertile and sterile spikelets. Fertile spikelets sessile, 1- to 5-flowered, bisexual, laterally compressed, and dis-articulating above the glumes and between the florets. Glumes 2, shorter than or equaling the florets, 1- or 3-nerved; lemmas 5-nerved, awned or awnless; palea 2-nerved and 2-keeled. Lodicules 2; stamens 3; stigmas 2.

A genus of 4-8 species native to Eurasia and Africa. Two species are adventive in North America. *C. echinatus* is an annual weed of disturbed, open ground. *C. cristatus*, also weedy, has been used as a pasture grass.

**Lamarckia.** Goldentop. Caespitose annual. Culms herbaceous, to 2 dm tall. Leaf sheaths keeled and closed for 2/3 their length. Inflorescence a contracted panicle of drooping fascicles of two very heteromorphic fertile and sterile spikelets. Terminal spikelets in each fascicle bisexual (with a single fertile floret and a stipitate rudimentary one), laterally compressed, and disarticulating below the glumes. Glumes 2, ± equal, 1-nerved; lemmas papery, 2-lobed, awned; palea relatively long, 2-nerved. Lodicules 2; stamens 3; stigmas 2. Staminate or sterile spikelets with 3- to 6-flowered, the lemmas awnless.

A monotypic Mediterranean and Asian genus. *L. aurea* is adventive in Texas, Arizona, and California. It is attractive enough to be an ornamental, but I have never seen it offered in nurseries.

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**TRIBE: BROMEAE**

This tribe, traditionally included in Poeae (= Festuceae of older systems), is separated from it on the basis of microcharacters, such as starch grain type and features of the gynoecium. The ovary is hairy, with a conspicuous apical appendage. Our only representative in North America is the genus below.

**Bromus.** Brome grass, rescue grass, chess, ripgut. Annuals or rhizomatous or stoloniferous perennials. Culms herbaceous, to 2 m tall, the internodes hollow (rarely solid). Leaf sheaths closed. Inflorescence an open to contracted panicle, sometimes reduced to a raceme or even 1- to a few spikelets. Spikelets several-flowered, laterally compressed, bisexual, disarticulating above the glumes and between the florets. Glumes 2, typically very unequal, 1- to 5-nerved, usually awnless; lemmas 5- to several-nerved, usually awned from a bifid apex; palea 2-nerved, often adnate to the Caryopsis. Lodicules 2; stamens 1-3; stigmas 2; ovary hairy, with an apical appendage and lateral styles.

A large and complex genus of about 150 species native to a variety of habitats in temperate regions of the Old World and New World, and in cooler, mountainous regions of the tropics and subtropics. It is of economic significance as a source of fodder, hay, and major weedy species. Five sections are recognized. They are sometimes treated as separate genera.

**The Sections of Bromus**

**Ceratochloa.** Native annuals, biennials, and perennials of the Pacific and mountain states; spikelets large, distinctly laterally compressed; glumes and lemmas keeled. *B. carinatus* (California brome), *B. marginatus*, and *B. unioloides* (= *B. catharticus* in H & C) (rescue grass).

**Bromopsis.** Native perennials of woodlands and grass-lands; panicles mostly open, lemmas rounded. *B. inermis* (smooth brome).

**Bromium.** Annual Mediterranean weeds of the grain-fields; glumes and lemmas comparatively broad. *B. meadowgrass* (soft chess), *B. briziformis* (tattlesnake chess), *B. secalinus* (chess), *B. commutatus* (hairy chess), and *B. japonicus* (Japanese brome).

**Bromus** (= *Eubromus* in H & C). Annual
Mediterranean weeds of disturbed sites; glumes and lemmas narrow, long-awned; callus sharp; the ripgut grasses are mechanically injurious to cattle. *B. rubens* (foxtail chess), *B. tectorum* (downy chess), and *B. diandrus* (= *B. rigidus* in H & C) (ripgut).

*Neobromus*. Introduced South American annual; lemmas lanceolate, deeply bifid, the awn twisted and geniculate. *B. berterianus* (Chilean chess) occurs in Oregon, California, and the Southwest.

### EVOLUTION IN BROMUS*

<table>
<thead>
<tr>
<th></th>
<th><strong>Bromopsis</strong></th>
<th><strong>Ceratochloa</strong></th>
<th><strong>Neobromus</strong></th>
</tr>
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<tr>
<td>14</td>
<td>LL</td>
<td>A₁A₁ X B₂B₂</td>
<td>B₃B₃ X B₄B₄</td>
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<tr>
<td></td>
<td><em>B. ciliatus</em></td>
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<td><em>B. anomalus</em></td>
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<td>♀</td>
</tr>
</tbody>
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*After Stebbins (1981)
TRIBE: AVENAE

This group is conceptually difficult. Hitchcock and Chase recognized a relatively large assemblage of grasses characterized by a panicle inflorescence and spikelets with elongate glumes, at least the second one being as long as the lowest lemma. All of the florets were typically fertile, except for the uppermost. The lemmas were usually awned from the base, back, or from a bifid apex. The genera seemed especially arbitrary. Other workers have argued that the group is nothing more than a segment of a larger reduction series involving Phalaris and its relatives with reduced florets below the single fertile one above and Agrostis and its relatives with a single fertile floret.

I have tended to accept the more recent views of the group and to recognize a single large tribe (Aveneae) that included the Aveneae, Phalarideae, and Agrostideae of Hitchcock and Chase. However, recent cluster analysis studies suggest that there is some justification for the view that there are three tribes, but not as described by H & C. The summary below is a compromise, recognizing the three major "lumps" at the subtribal level.

SUBTRIBE: AVENINAE

The subtribe contains most of the genera of H & C’s Aveneae. Typical features include open to contracted panicles of spikelets with 2-several florets whose glumes are as long as or longer than the first floret, often all of them. The lemmas usually have a twisted, geniculate awn arising from the back or apex. The rachilla is often prolonged beyond the upper floret as a slender stalk, sometimes bearing a rudimentary floret.

AVENA. Oats, wild oats. Caespitose annuals. Culms herbaceous, to 1 m tall. Inflorescence an open panicle, the branches capillary and pendulous, sometimes reduced to a raceme or even a solitary spikelet in depauperate material. Spikelets large, typically 2- or 3-flowered, bisexual, laterally compressed, disarticulating above the glumes and between the florets (except in cultivated oats). Glumes 2, ± equal, 3- to 11-nerved, as long as or longer than the florets, awnless; lemmas rounded, 5- to 7-nerved, with a stout, geniculate awn (reduced or absent in cultivated oats); palea 2-nerved. Lodicules 2; stamens 3; stigmas 2.

A genus of 15-30 species native to the Old World. A. fatua var. sativa is cultivated oats; A. fatua var. fatua is one of several important weeds called wild oats.

SUMMARY OF AVENA SPECIES

<table>
<thead>
<tr>
<th>Ploidy: Species</th>
<th>Comment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diploids [2n = 2x = 14]</td>
<td></td>
</tr>
<tr>
<td>A. strigosa (sand oat)</td>
<td>Fodder plant; now weedy</td>
</tr>
<tr>
<td>A. brevis (short oats)</td>
<td>Grown in s. Europe for fodder</td>
</tr>
<tr>
<td>Tetraploids [2n = 4x = 28]</td>
<td></td>
</tr>
<tr>
<td>A. barbata (slender oat)</td>
<td>Weedy</td>
</tr>
</tbody>
</table>

A. abyssinica (Abyssinian oat) Wild/cultivated forms
Hexaploids [2n = 6x = 42]
A. byzantina (red oat) Eaten by livestock and us
A. fatua (wild oats) Pernicious weed
A. nuda (naked oat) Grain crop in China
A. sativa (cultivated oat) Widely cultivated
A. sterilis (animated oat) Fodder and ornamental

ARRHENOTHERUM. Tall oat grass. Caespitose perennials. Culms herbaceous, to 2 m tall; corns sometimes present. Inflorescence a narrow panicle. Spikelets typically 2-flowered (upper perfect, the lower larger and staminate), laterally compressed, bisexual, disarticulating above the glumes (2 florets falling together); rachilla extended as bristle beyond uppermost floret. Glumes 2, very unequal, the first 1-nerved and the second 3-nerved, awnless; lemmas 5- to 9-nerved, awnless or with a dorsal awn; palea relatively long. Lodicules 2; stamens 3; stigmas 2.

A genus of 4-6 species native to Europe and the Mediterranean. A. elatius (tall oat grass) is planted for pasture and has escaped in many areas of North America.

HELICTOTRICHON. Spike-oat, alpine-oat. Caespitose perennials. Culms herbaceous, to 1.5 m tall. Inflorescence a contracted panicle. Spikelets large, 2- to 7-flowered, bisexual, laterally compressed, disarticulating above the glumes and between the florets. Glumes 2, equal to or shorter than the florets, 1- to 5-nerved; lemmas 5- to 7-nerved, apex toothed, with a stout, twisted, geniculate dorsal awn; palea relatively long, 2-nerved. Lodicules 2; stamens 3; stigmas 2.

A genus of about 90 species native to the Old and New World. Two are native to North America (H. hookeri and H. mortonianum); one is introduced from Europe (H. pubescens).

AIRA. Silver hair grass. Delicate, caespitose annuals. Culms herbaceous, to 0.25 m tall. Inflorescence an open or panicle. Spikelets 2-flowered, laterally compressed, bisexual, disarticulating above the glumes and between the florets. Glumes 2, ± equal, as long as or longer than the florets, 1- or 3-nerved; lemmas 5-nerved, a geniculate, hair-like awn arising from below the middle, apex with 2 slender teeth or setae; palea relatively long, 2-nerved. Lodicules 2; stamens 3; stigmas 2.

A genus of 8-10 species native to the northern and southern temperate regions of the Old World. A. caryophyllea, A. elegans, and A. praecox are adventive in North America.

DESCAMPSIA. Hair grass. Mostly caespitose perennials; a few are annuals. Culms herbaceous, to 1 m tall. Inflorescence an open or congested panicle, often with capillary branches. Spikelets small, 2-flowered, laterally compressed, bisexual, disarticulating above the glumes and between the florets, the rachilla hairy and prolonged above the upper floret (sometimes with a rudiment at its apex). Glumes 2, ± equal, the first 1-nerved and the second 3-nerved, as long as or longer than the lower floret; lemmas 5- to 7-nerved (often obscurely so), its apex several toothed or cleft, and with a geniculate awn from or below the middle; palea relatively long. Lodicules 2; stamens 3; stigmas 2.
A genus of about 40 species native to the temperate and cooler portions of the Old and New World. *D. danthonioides*, the only annual species in North America, is common in the West; *D. caespitosa* (tufted hair grass) occurs in mountain meadows in the same region.

**TRISETUM.** Trisetum. Mostly caespitose perennials. Culms herbaceous, to 1.5 m. Inflorescence a contracted panicle. Spikelets 2-flowered [rarely 3- or 4-flowered], laterally compressed, bisexual, disarticulating above or below the glumes, or not disarticulating, the rachilla prolonged above the uppermost floret. Glumes 2, equal or unequal, the first 1- to 3-nerved and the second 1- to 5-nerved; lemmas 5- to 7-nerved, its apex bifid, the teeth awned, with a straight or bent awn from the base of the cleft; palea relatively long, with two apical setae. Lodices 2; stamens 3; stigmas 2.

A genus of about 75-85 species of the temperate and cooler regions of the Old and New World. Of economic importance as a source of pasture and fodder grasses. *T. spicatum* (spike trisetum) occurs in the Rocky Mountains and in the West.

**SPHENOPHOLIS.** Wedgescale. Caespitose annuals and perennials. Culms herbaceous, to 1+ m tall. Inflorescence a contracted panicle. Spikelets 2- or 3-flowered, laterally compressed, bisexual, disarticulating below the glumes. Glumes 2, dimorphic (first narrow and 1- [3-] nerved and the second broad and 3- to 5-nerved); lemmas faintly 5-nerved, awnless or less often awned; palea relatively long. Lodices 2; stamens 3; stigmas 2.

A genus of 4 or 5 species native to North America and the West Indies. *S. obtusata* (prairie wedgescale) is widespread in North America.

**KOELERIA.** June grass. Caespitose annuals or perennials. Culms herbaceous, to 1+ m tall. Inflorescence a spike-like panicle. Spikelets 2- to 4-flowered, laterally compressed, bisexual, disarticulating above the glumes and between the florets, rachilla extended as a bristle beyond the uppermost floret. Glumes 2, ± equal, as long or shorter than the florets, dimorphic (first acute, 1-nerved and the second broader, longer, obscurely 3- to 5-nerved); lemmas 3- to 5-nerved, awnless or awned from a bifid apex; palea relatively long, apically notched, 2-nerved. Lodices 2; stamens 3; stigmas 2.

A genus of about 60 species native to the temperate and cooler regions of the Old and New World. The annual species have been treated as the genus *Lophochloa*. *K. macrantha* (= *K. cristata* in H & C) is native to prairies and wooded areas over much of North America. *K. phleoides* is a small, introduced annual.

**HOLCUS.** Velvet grass. Caespitose perennials. Culms herbaceous, weak, succulent, to 1 m tall. Leaves velvety-pubescent, especially the sheaths. Inflorescence a contracted panicle. Spikelets 2- or 4-flowered (lower perfect, the upper staminate or neuter), laterally compressed, bisexual rachilla prolonged above the uppermost fertile floret, disarticulating below the glumes. Glumes 2, as long as or longer than the florets, the first 1-nerved and the second 3-nerved; lemmas faintly 3- to 5-nerved, the upper one with a short, hooked awn from near its apex; palea relatively long, 2-nerved. Lodices 2; stamens 3; stigmas 2. A genus of 6-8 species native to Eurasia and Africa. *H. lanatus* and *H. mollis* are adventive in North America.

**BECKMANNIA.** Slough grass. Annuals with thick culms. Inflorescence a panicle of pressed or ascending spikes. Spikelets 1- or 2-flowered, ± orbicular, laterally compressed, sessile, disarticulating below the glumes, the rachilla often prolonged. Glumes 2, equal, broad, inflated, 3-nerved, keeled, and apiculate at apex. Lemma ± equal to glumes, narrow, 5-nerved, tapering to a slender tip. Palea narrow, shorter than lemma. Lodices 2; stamens 3; stigmas 2.

A genus of two species native to Eurasia and North America. *Beckmannia syzigachne*, American slough grass, is native to marshes and wet sites over much of the northern and western U. S. It is sometimes frequent enough to use for hay or forage.

**SUBTRIBE: PHALARIDINAE**

As here defined, the subtribe is equivalent to the Phalarideae of H & C. The group is defined by its spikelets with a single fertile floret with 1 or 2 staminate or sterile florets below it, these sometimes reduced to inconspicuous, scale-like rudiments.

**ANTHOXANTHUM.** Sweet vernal grass. Annuals or perennials, pleasantly fragrant because of coumarin. Culms herbaceous, to 1 m tall. Inflorescence a contracted spike-like panicle. Spikelets with a single fertile floret subtended by two sterile ones, laterally compressed, bisexual, disarticulating above the glumes (the three florets falling as a group). Glumes 2, very unequal, the first 1-nerved, the second 3-nerved, longer than the florets; sterile lemma 3-nerved, hairy, awned from a notched apex; fertile lemma 3- to 5-nerved, glabrous except at apex, awnless; palea 1- or 3-nerved. Lodices 0; stamens 2; stigmas 2.

A small genus of about 4 species native to the Old World. Two species, *A. odoratum* (sweet vernal grass) and *A. aristatum* are adventive in North America. The genus is doubtfully distinct from *Hierochloë*.

**HIEROCHLOÉ.** Holy grass, sweet grass. Caespitose or rhizomatous perennials, pleasantly fragrant because of coumarin. Culms herbaceous, to 1+ m tall. Inflorescence an open to contracted panicle. Spikelets with a single fertile floret subtended by two staminate ones, laterally compressed, bisexual, disarticulating above the glumes (the three florets falling as a group). Glumes 2, equal, the first 1- to 5-nerved and the second 3- to 5-nerved, as long as or slightly shorter than the florets; lemmas of stamineate florets awnless or with a short awn from a notched apex, 5-nerved; lemma of fertile floret 3- to 5-nerved, awnless; palea 1- or 3-nerved. Lodices 2; stamens 2 (bisexual florets) or 3 (stamineate florets).

A genus of 20-30 species native to the temperate and cooler regions of both hemispheres. Three species are found in North America. *H. alpina* occurs in from the New England states across Montana; *H. odorata* is found through much of the northern and western states; and *H. occidentale* occurs along the Pacific Coast. Schouten & Veldkamp (1985) proposed merging this genus with *Anthoxanthum*, but their work seems to have gone largely unnoticed.

**PHALARIS.** Canary grass, reed canary grass.
Caespitose annuals or perennials, often from rhizomes. Culms herbaceous, to 2 m tall. Inflorescence typically a spike-like panicle. Spikelets with a single bisexual floret subtended by two reduced (sometimes very tiny!) scale-like florets, laterally compressed, disarticulating above or below the glumes or not disarticulating. Glumes 2, ± equal, as long as or longer than the florets, usually with a winged dorsal keel; sterile lemmas reduced to small scales; fertile lemma 5-nerved, awnless; palea relatively long, 1- or 2-nerved. Lodicules 2; stamens 3; stigmas 2.

A genus of 15 or 16 native to Eurasia, Africa, and the New World. Five are native to North America; four are adventive. Ph. arundinacea (reed canary grass) is an important pasture grass and weed; Ph. canariensis is one of the standard ingredients in commercial birdseed mixtures.

**SUBTRIBE: ALOPECURIINAE**

This subtribe contains some, but by no means all, of the genera of H & C’s Agrostideae. The plants are primarily of the temperate and Arctic regions. The inflorescence is typically a panicle. The spikelets are 1-flowered, small, and mostly laterally compressed. The glumes tend to be longer than the floret. The lemmas are thin, 3- to 5-nerved, and rarely awned.

**AMMOPHILA.** Beach grass, European beach grass. Coarse, rhizomatous perennials. Culms herbaceous, to 1.5 m tall. Inflorescence a dense, spike-like panicle. Spikelets large, 1-flowered, laterally compressed, bisexual, rachilla prolonged as a hairy bristle beyond the floret, disarticulating above the glumes. Glumes 2, ± equal, the first 1-nerved and the second 1- to 3-nerved, as long as or longer than the floret; lemma 5-nerved, awnless, with long hairs at the base; palea relatively long, 4- to several-nerved. Lodicules 2; stamens 3; stigmas 2.

A genus of 2-4 species native to North America and Europe. A. breviligulata (American beach grass) is native to the East Coast and around the Great Lakes; the common name. A. arenaria (European beach grass) was introduced to stabilize sand dunes along the Pacific Coast.

**CALAMAGROSTIS.** Reed grass, bluejoint. Caespitose, rhizomatous, or stoloniferous perennials, often of wet and marshy sites. Culms herbaceous, sometimes reed-like, to 2 m tall. Inflorescence a panicle, typically contracted. Spikelets 1-flowered, laterally compressed, bisexual, disarticulating above the glumes, rachilla often extended beyond the single floret as a slender bristle. Glumes 2, ± equal, longer than the floret, the first 1-nerved and the second 3-nerved; lemma 3- or 5-nerved, its apex notched or toothed, bearing a slender, geniculate dorsal awn; callus long-hairy; palea relatively long, 2-nerved. Lodicules 2; stamens 3; stigmas 2.

A genus of over 230 species native to the temperate and cooler regions of the Old and New World. A number of species reported for North America, all but one of them native. C. canadensis (bluejoint), which occurs throughout much of the northern part of the continent, is an important forage grass. C. purpurascens (purple reedgrass) is found over much of the western United States; C. nutkaensis (Pacific reedgrass) is native along the Pacific coast from Alaska to California; C. inexpansa (northern reedgrass) ranges from Greenland to California.

**AGROSTIS.** Bent grass, bent, redtop, tickle grass. Annuals and caespitose, rhizomatous, or stoloniferous perennials. Culms herbaceous, to 1 m tall. Inflorescence open to contracted panicle. Spikelets small (sometimes distressingly so) 1-flowered, laterally compressed, bisexual, disarticulating above the glumes. Glumes 2, ± equal, the first typically 1-nerved and the second 1- [3-] nerved, as long as or longer than the floret; lemma 3- or 5-nerved, glabrous or hairy at base, awned dorsally from or below the middle or awnless; palea typically small or even absent. Lodicules 2; stamens 3; stigmas 2.

A complex genus of over 200 species native to the temperate and cooler regions of both hemispheres. Several of our North American representatives are of considerable economic importance as forage grasses, lawn grasses, and as the substrate on which some humans use sticks to knock little white balls into small holes in the ground. A number of them are also weedy. A. gigantea (= A. alba in H & C) is redtop; A. hiemalis is winter bentgrass, and A. palustris is the creeping bent used at golf courses.

**CINNA.** Woodreed. Caespitose or rhizomatous perennials, often of wet, shady sites. Culms herbaceous. Inflorescence a congested panicle. Spikelets 1-flowered, laterally compressed, bisexual, disarticulating below the glumes, the rachilla prolonged above the floret as a stub or bristle. Glumes 2, equal or the first shorter, the lower 1-nerved and the upper 1- or 3-nerved; lemmas 3- to 5-nerved, the mid-nerve extended as a short, straight awn; palea about as long as the lemma, 1-nerved. Lodicules 2; stamens 1 or 2 [3]; stigmas 2.

A genus of 3-4 species native to the temperate regions of both hemispheres. C. latifolia (drooping woodreed) is widespread in moist, shaded areas; C. arundinacea (stout woodreed) is found in moist woods in eastern and central North America. C. bolanderi is endemic to California.

**PHLEUM.** Timothy. Caespitose annuals and perennials. Inflorescence an ovoid to cylindrical, spike-like panicle. Culms herbaceous, to 1.5 m tall, the bases sometimes tuberous. Spikelets 1-flowered, strongly laterally compressed, bisexual, disarticulating above or below the glumes. Glumes 2, ± equal, longer than the floret, abruptly narrowed to an awn or mucro, 3-nerved; lemma 5- to 7-nerved, blunt, awnless.

A genus of 10-15 species native to the temperate regions of Eurasia and North America. Ph. alpinum is native in mountainous areas; Ph. pratense (timothy) is perhaps the leading hay grass of the eastern states.

**POLYPOGON.** Rabbitfoot grass. Annuals or perennials. Culms herbaceous, often weak and decumbent and rooting at nodes, to 1 m tall. Inflorescence a soft, dense, contracted panicle. Spikelets 1-flowered, laterally compressed, bisexual, disarticulating above the glumes. Glumes 2, ± equal, longer than the floret, 1-nerved, bearing a long awn from an entire or notched apex; lemma 5-nerved, its apex typically toothed, awned or awnless; palea relatively long, 2-nerved. Lodicules 2; stamens 1 or 3; stigmas 2.

A genus of 10-20 species native mostly to the...
temperate regions of the Old World. Several Eurasian species have been introduced; *P. monspeliensis* (rabbitfoot grass) is a common weed in wet areas across North America. *P. elongatus* is native to Arizona and California.

**Lagurus.** Hare’s tail. Plants annual. Inflorescence a dense, pale, ovoid to oblong capitate panicle. Sheaths and blades pubescent. Spikelets 1-flowered, laterally herbaceous, to 5 dm tall. Inflorescence a dense, pale, ovoid to oblong capitate panicle. Sheaths and blades pubescent. Spikelets 1-flowered, laterally herbaceous, to 5 dm tall. Inflorescence a dense, 

**GASTRIDIUM.** Meadow foxtail. Annuals or caespitose or rhizomatous perennials. Culms herbaceous, to 1 m tall. Inflorescence a dense, spike-like panicle. Spikelets 1-flowered, laterally compressed, bisexual, disarticulating below the glumes. Glumes 2, their lower edges united, ciliate-keeled, equal, 3-nerved, equaling the floret; lemma 5-nerved, its lower margins joined, awned from below the middle; palea relatively long, 2-nerved. Lodicules 0; stamens 3; stigmas 2.

A genus of 25-35 species native to the northern temperate regions of both hemispheres. Of economic significance as a source of fodder, pasture grasses, and weeds. *A. carolinianus*, a native annual, is widely distributed. *A. pratensis* (meadow foxtail), a European pasture grass, is grown in the northern states.

**ALOPECURUS.** Meadow foxtail. Annuals and caespitose or rhizomatous perennials. Culms herbaceous, to 1 m tall. Inflorescence a dense, spike-like panicle. Spikelets 1-flowered, laterally compressed, bisexual, disarticulating below the glumes. Glumes 2, their lower edges united, ciliate-keeled, equal, 3-nerved, equaling the floret; lemma 5-nerved, its lower margins joined, awned from below the middle; palea relatively long, 2-nerved. Lodicules 0; stamens 3; stigmas 2.

A genus of only two species, both native to western Europe and the Mediterranean. *G. ventricosum* (nit grass) is adventive along the Pacific coast and scattered locations in Texas and the East.

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**TRIBE: TRITICEAE**

"Abandon hope all ye who enter here." (Dante Alighieri, writing on an another distressing topic)

Annuals or perennials. Leaf blades usually auriculate. Inflorescence a balanced spike or rame, its axis continuous or breaking apart at maturity. Spikelets commonly 1-3 per node, sometimes as many as 6. Lemmas 5- to 9-nerved, awned from the tip or awnless. Caryopsis free from or adhering to the anthocodium. Hybridization rampant; polyploidy common. $X = 7$. The tribe is more or less equivalent to the Hordeae of H & C.

I am tempted to offer Dante’s admonition about abandoning all hope to those who enter here. Generic delimitations within the tribe are exceedingly difficult, often appearing quite arbitrary, and they remain controversial. To give you some flavor of the difference of opinion as to how to treat this group, some workers recommend recognizing a single genus, *Triticum*. Others, including myself, believe that our North American material can be accommodated in about six genera. The most liberal disposition is that we ought to give generic recognition to each distinct genome or combination of genomes, which yields Avogadro’s number of segregate (and to my way of thinking, useless) genera.

**EVOLVING VIEWS OF TRITICEAE**

**Bentham (1882).** Agropyron, Elymus, Hordeum, Hystrix, Secale, Triticum.

**Neveski (1933).** Aegilops, Agropyron, Brachypodium, Creteisum, Elymus, Elytrigia, Eremopyrum, Hordeum, Psathyrostachys, Secale, Sitanion, Taeniatherum, Triticum,

**Hitchcock (1951).** Aegilops, Agropyron, Elymus, Hordeum, Hystrix, Lolium, Monerma, Nardus, Parapholis, Scriberia, Secale, Sitanion, Triticum.


GENOME-BASED GENERA

Askell Löve and others have argued that the genera of Triticeae should be based on genomes. Here is how that would look.

<table>
<thead>
<tr>
<th>Genome</th>
<th>Genus</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Crithodium</td>
</tr>
<tr>
<td>AB</td>
<td>Gigachilon</td>
</tr>
<tr>
<td>ABD</td>
<td>Triticum</td>
</tr>
<tr>
<td>B</td>
<td>Sitopsis</td>
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<tr>
<td>BU</td>
<td>Aegilemma</td>
</tr>
<tr>
<td>C</td>
<td>Orrhopygium</td>
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<tr>
<td>CD</td>
<td>Cylindropyrum</td>
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<tr>
<td>D</td>
<td>Patropyrum</td>
</tr>
<tr>
<td>DM</td>
<td>Gastropyrum</td>
</tr>
<tr>
<td>DMU</td>
<td>Aegilonearum</td>
</tr>
<tr>
<td>E</td>
<td>Lophopyrum</td>
</tr>
<tr>
<td>EJS</td>
<td>Elytrigia</td>
</tr>
<tr>
<td>F</td>
<td>Eremopyrum</td>
</tr>
<tr>
<td>G</td>
<td>Festucopsis</td>
</tr>
<tr>
<td>H</td>
<td>Critesion</td>
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<td>HJNS</td>
<td>Pascopyrum</td>
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<tr>
<td>HS</td>
<td>Elymus</td>
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<tr>
<td>HT</td>
<td>Hordelymus</td>
</tr>
<tr>
<td>I</td>
<td>Hordeum</td>
</tr>
<tr>
<td>J</td>
<td>Thinopyrum</td>
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<td>JN</td>
<td>Leymus</td>
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<tr>
<td>K</td>
<td>Crithopsis</td>
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<td>L</td>
<td>Chennaipyrum</td>
</tr>
<tr>
<td>M</td>
<td>Comopyrum</td>
</tr>
<tr>
<td>MU</td>
<td>Aegilops</td>
</tr>
<tr>
<td>N</td>
<td>Psathyrostachys</td>
</tr>
<tr>
<td>O</td>
<td>Henrardia</td>
</tr>
<tr>
<td>P</td>
<td>Agropyron</td>
</tr>
<tr>
<td>Q</td>
<td>Heteranthelium</td>
</tr>
<tr>
<td>R</td>
<td>Secale</td>
</tr>
<tr>
<td>S</td>
<td>Psathoroegneria</td>
</tr>
<tr>
<td>T</td>
<td>Taeniatherum</td>
</tr>
<tr>
<td>U</td>
<td>Kharapyrum</td>
</tr>
<tr>
<td>V</td>
<td>Daspyrum</td>
</tr>
<tr>
<td>Z</td>
<td>Amblyopyrum</td>
</tr>
</tbody>
</table>

INTERGENERIC HYBRID

Given the promiscuous nature of the grasses in this group, you will not be surprised to learn that there are many intergeneric hybrids, as seen below.

X Aegilosecale
X Aegilotriticum
X Agroelymus
X Agrohordeum
X Agrositanion
X Agrotrisecale
X Agrotriticum
X Elyhordeum
X Elymordeum
X Elymopyrum
X Elyleymus
X Elysitanion
X Elytesion
X Leytesion
X Pseudelymus
X Sitordeum
X Triticosecale
X Tritordeum

FATE OF H & C’s GENERA

The genera recognized by Hitchcock & Chase (1951) appear in the left column. Their current disposition as per various recent monographs is shown on the right. You will note that the concept of some genera, such as Secale and Triticum, has changed little. Some genera, such as Hystrix, have disappeared. In still other cases, H & C recognized a large genus, such as Elymus, and recent workers also recognize an entity called Elymus, but it is more narrowly defined because one or more species have been transferred to segregate genera.

In a few instances, genera are now seen as members of tribes other than Triticeae. They

Aegilops
Cylindropyrum
Triticum

Agropyron
Elymus

Elymus
Elytrigia

Lophopyrum
Psathyrostachys

Elymus
Elytrigia

Lophopyrum
Psathyrostachys

Elymus
Elytrigia

Lophopyrum
Psathyrostachys

Elymus
Elytrigia

Hordelymus
Thinopyrum

Hordelymus

Elymus

Lophopyrum
Psathyrostachys

Elymus
Elytrigia

Hystrix

Elymus

Lolium

Hymenachne

Elymus

Lolium

Hymenachne

Elymus

Lolium

Hymenachne

Scribneria

Scribneria

Secale

Secale

Sitanion

Sitanion

Elymus

Triticeae

TECHNOLOGY-BASED GENERA

As defined here, the genus consists of about 15 species native to the Mediterranean area and Asia. Our North American representatives are A. cristatum (crested wheatgrass) and A. desertorum (desert
wheatgrass). I follow Stebbins and Gould in placing the other species listed in H & C in the expanded version of *Elymus*. The increasingly popular disposition of these taxa is to place them in a series of segregate genera.

**ELYMUS.** Wild rye. Caespitose or rhizomatous perennials. Culms herbaceous, to 2 m tall. Inflorescence a balanced spike [compound in some species], the rachis continuous. Spikelets typically 1-2 or 3-6 per node; [2-] 3-7 [9-] flowered, laterally compressed, bisexual, disarticulating above the glumes and between the florets. Glumes 2, equal or unequal, 3- to 7-nerved, broad to quite narrow, almost awn-like in some; lemmas 5- to 7-nerved, awn-like to an awn [rarely awnless]; palea relatively long, 2-nerved. Lodicles 2; stamens 3, stigmas 2. A genus of about 150 species widespread in the temperate and cooler regions of both hemispheres. As treated here, the genus includes most of the taxa assigned to *Agropyron* in H & C. Some species are important forage grasses. *E. virginicus* (Virginia wild-rye), *E. canadensis* (Canada wild-rye), *E. glaucus* (blue wild-rye), *E. cinereus*.

Common species transferred from *Agropyron* include *E. smithii* (western wheatgrass), *E. repens* (quack grass), and *E. spicatus* (bluebunch wheatgrass). The genus also includes all of our North American species of *Sitanion* (squirreltail grasses) and *Hystrix* (bottlebrush grasses) that appear in H & C.

**TAENIATHERUM.** Medusa head. Annuals. Culms herbaceous, to 6 dm tall. Inflorescence a bristly, balanced spike; spikelets paired, the rachis continuous. Spikelets 2-flowered (the lower bisexual and the upper rudimentary), dorsally compressed, disarticulating above the glumes. Glumes 2, subulate, indurate, 1- or 3-nerved, joined at base, tapering to a stiff awn; lemma narrow, 5-nerved, with a long, flattened awn; palea about as long as lemma, 2-nerved. Lodicles 2; stamens 3; stigmas 2.

A genus of 2-3 species, doubtfully distinct from *Elymus*, native to Eurasia. *T. caput-medusae* (= *Elymus c.-m.* in H & C) is a serious weed in several of the western states, including California.

**HORDEUM.** Barley, foxtail barley, little barley, squirreltail. Annuals or caespitose perennials. Culms herbaceous, to 1 m tall. Inflorescence a dense, balanced, often bristly spike, continuous or shattering at maturity. Spikelets typically 3 per node, the central sessile and fertile, the laterals often pedicellate and sterile (all three fertile in *H. vulgare*). Central spikelet 1-flowered, the rachilla extended above it and bearing a rudiment, laterally or dorsally compressed, bisexual, disarticulating above the glumes or not disarticulating in cultivars. Glumes 2, narrow, rigid, 1-nerved, subulate or awned; lemma dorsally flattened, 5-nerved (often difficult to distinguish), acuminate to an awn or awn-point; palea about as long as lemma, often adnate to carpel. Lateral spikelets often reduced to awn-like glumes. Lodicles 2; stamens 3; stigmas 2.

A genus of 25-40 species native to the temperate regions of both hemispheres; a number of them are weedy. A dozen or so species are found in North America, most of them native. *H. jubatum* (foxtail barley) is native in the West; *H. brachyantherum* (meadow barley) provides good forage; *H. pusillum* (little barley) is a native annual found over much of North America; *H. vulgare* is cultivated barley, whose grains are eaten and sprouted to make malt for the brewing and distilling industries.

### SUMMARY OF NORTH AMERICAN HORDEUM

<table>
<thead>
<tr>
<th>Ploidy Level: Taxon</th>
<th>Nativity (Duration)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2n = 2x = 14</td>
<td></td>
</tr>
<tr>
<td><em>H. bulbosum</em></td>
<td>Mediterranean (P)</td>
</tr>
<tr>
<td><em>H. californicum</em></td>
<td>Western United States (P)</td>
</tr>
<tr>
<td><em>H. eucalastion</em></td>
<td>South America (A)</td>
</tr>
<tr>
<td><em>H. intercedens</em></td>
<td>Western United States (A)</td>
</tr>
<tr>
<td><em>H. marinum ssp. marinum</em></td>
<td>Mediterranean (A)</td>
</tr>
<tr>
<td><em>H. marinum ssp. gussoneanum</em></td>
<td>Mediterranean (A)</td>
</tr>
<tr>
<td><em>H. murinum ssp. glaucum</em></td>
<td>Mediterranean (A)</td>
</tr>
<tr>
<td><em>H. pusillum</em></td>
<td>North America (A)</td>
</tr>
<tr>
<td><em>H. vulgare ssp. vulgare</em></td>
<td>Cultivated (A)</td>
</tr>
<tr>
<td>2n = 4x = 28</td>
<td></td>
</tr>
<tr>
<td><em>H. brachyantherum</em></td>
<td>West. N. America/East Asia (P)</td>
</tr>
<tr>
<td><em>H. bulbosum</em></td>
<td>Mediterranean (P)</td>
</tr>
<tr>
<td><em>H. depressum</em></td>
<td>Western United States (A)</td>
</tr>
<tr>
<td><em>H. jubatum</em></td>
<td>N. America/East Asia (P)</td>
</tr>
<tr>
<td><em>H. marinum ssp. gussoneanum</em></td>
<td>Mediterranean (A)</td>
</tr>
<tr>
<td><em>H. murinum ssp. murinum</em></td>
<td>Mediterranean (A)</td>
</tr>
<tr>
<td><em>H. murinum ssp. leporinum</em></td>
<td>Mediterranean (A)</td>
</tr>
<tr>
<td><em>H. vulgare ssp. vulgare</em></td>
<td>Cultivated (A)</td>
</tr>
<tr>
<td>2n = 6x = 42</td>
<td></td>
</tr>
<tr>
<td><em>H. arizonicum</em></td>
<td>Southwest United States (A/P)</td>
</tr>
<tr>
<td><em>H. murinum ssp. leporinum</em></td>
<td>Mediterranean (A)</td>
</tr>
</tbody>
</table>

[After R. von Bothmer in Shewry, P. R. (1992)]

**AEGILOPS.** Goat grass. Caespitose or rhizomatous annuals. Culms herbaceous, to 8 dm tall. Inflorescence a single, balanced spike, the spikelets solitary at each node. Spikelets tur- gid or cylindrical, placed flatwise and fitting into the rachis, 2- to 5-flowered, rounded to ± laterally compressed, bisexual, disarticulating above or below the glumes, or not disarticulating. Glumes 2, several-nerved, 1- or 3-awned; lemmas usually 5- to 7-nerved, awnless, mucronate, or 1- or 2-awned; palea relatively long, 2-nerved. Lodicles 2; stamens 3; stigmas 2.

The genus is completely interfertile with *Triticum* and the two genera are often merged. A genus of 20+ species native to the Mediterranean and Asia. *Ae. cylindrica* (jointed goatgrass) is a widespread weed in the central and southern states; *Ae. ovata* and *Ae. triuncialis* are common weeds in California.

**TRITICUM.** Wheat, bread wheat. Caespitose annuals. Culms herbaceous, the internodes hollow or solid, to 1 m tall. Inflorescence a thick, balanced spike, the spikelets solitary at each node and attached flatwise to the rachis. Spikelets 2- to 5-flowered, laterally compressed or rounded, bisexual, disarticulating above or below the glumes, or not disarticulating in cultivars. Glumes 2, ± equal, shorter than the florets, 5- to 11-nerved, mucronate or with 1 or more awns at its apex; lemmas keeled or rounded, glabrous or pubescent, several-nerved, awnless or with 1 or 3 awns.
A genus of about 8 species native to Eurasia. *T. aestivum* (bread wheat) and *T. durum* (durum or macaroni wheat) are the principal economic species.

**SUMMARY OF WHEAT SPECIES**

<table>
<thead>
<tr>
<th>Species (Common Name)</th>
<th>Genome(s)</th>
<th>Species (Common Name)</th>
<th>Genome(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Triticum boeoticum</em> (wild einkorn wheat)</td>
<td>AA</td>
<td><em>Triticum dicoccum</em> (Cultivated emmer wheat)</td>
<td>AABBDD</td>
</tr>
<tr>
<td><em>Triticum monococcum</em> (einkorn wheat)</td>
<td>AA</td>
<td><em>Aegilops speltoides</em> (Goat grass)</td>
<td>AABBDD</td>
</tr>
<tr>
<td><em>Triticum dicoccoides</em> (wild emmer wheat)</td>
<td>AABB</td>
<td>Sterile F&lt;sub&gt;1&lt;/sub&gt; Hybrid</td>
<td>[2n = 3x = 21]</td>
</tr>
<tr>
<td><em>Triticum durum</em> (durum or macaroni wheat)</td>
<td>AABB</td>
<td>Unreduced Gametes</td>
<td>(&quot;Chromosome Doubling&quot;)</td>
</tr>
<tr>
<td><em>Triticum turgidum</em> (poulard or rivet wheat)</td>
<td>AABB</td>
<td>Triticum aestivum (Bread wheat)</td>
<td>[Genomes: AABBDD]</td>
</tr>
<tr>
<td><em>Triticum polonicum</em> (Polish wheat)</td>
<td>AABB</td>
<td>Domestication</td>
<td></td>
</tr>
<tr>
<td><em>Triticum carthlicum</em> (Persian wheat)</td>
<td>AAAGG</td>
<td>Recent domestication</td>
<td></td>
</tr>
<tr>
<td><em>Triticum timopheevii</em></td>
<td>AAGG</td>
<td>Genetic engineering</td>
<td></td>
</tr>
<tr>
<td><em>Triticum araraticum</em></td>
<td>AAGG</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Triticum sphaerococcum</em> (shot wheat)</td>
<td>AABBDD</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Triticum aestivum</em> (bread or common wheat)</td>
<td>AABBDD</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**EVOLUTION OF MODERN HEXAPLOID WHEATS**

**Phase I: Diploid to Tetraploid**

| Triticum boeoticum (Wild einkorn wheat) | [2n = 2x = 14] | Aegilops speltoides (Goat grass) | [2n = 2x = 14] |
| [Genome: AA] | | [Genome: BB] |
| Sterile F<sub>1</sub> Hybrid | [2n = 2x = 14] | | |
| [Genomes: AB] | | | |
| Unreduced Gametes | ("Chromosome Doubling") | | |
| | | | |

**Phase II: Tetraploid to Hexaploid**

| *Triticum dicoccoides* (Wild emmer wheat) | [2n = 4x = 28] | *Aegilops squarrosa* (Goat grass) | [2n = 2x = 14] |
| [Genomes: AABB] | | [Genomes: DD] |

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**SECALE.** Rye. Annuals, sometimes perennials. Culms herbaceous, to 1+ m tall. Inflorescence a balanced spike, the spikelets solitary at the node, and placed flatwise to the rachis. Spikelets typically 2-flowered, laterally compressed, bisexual, disarticulating below the glumes or not disarticulating in cultivars. Glumes 2, narrow, 1-nerved, subulate; lemmas sharply keeled, ciliate on the keels, 5-nerved, tapering to a long awn.

A genus of 5 species native to Eurasia. *S. cereale* (rye) escapes from cultivation.

**X TRITICOSECALE.** Triticale. The hybrid between wheat and rye, combining desirable features from both of these important crop plants. It is the source of triticale berries that you see in the health food markets.
**TRIBE BRACHYPODIEAE**

The characters of the tribe are those of the genus below.

**BRACHYPODIUM.** False brome, purple-brome. Mostly perennial herbs. Inflorescence a series of linear racemes on stiffly erect branches. Spikelets 1 per node, ± sessile, divergent. Spikelets 2- to 20-flowered, ± terete to slightly laterally compressed, disarticulating above the glumes. Glumes 2, 5- to 9-nerved; lemmas herbaceous to thickened at maturity, 7- to 9-nerved, extending into an awn. Lodicules 2; stamens 3; stigmas 2, white.

A genus of 16 species native to the temperate regions of Europe and Asia, especially of woodlands and open grasslands. Two are native to Mexico. *B. distachyon* is a weedy European introduction of scattered sites in the U. S. A.

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**TRIBE: MELICEAE**

A small tribe of grasses often associated with wet sites. Leaf sheaths typically closed. Inflorescence a panicle or raceme. Spikelets several-flowered; disarticulation above or below the glumes. H & C included these genera in their Festucae. See Section 4 for a key to genera.

**MELICA.** Onion grass, melic. Perennials. Culms herbaceous, to 1 m tall, bases often swollen into bulb-like corms. Leaf sheaths closed. Inflorescence an open to contracted panicle. Spikelets several-flowered, rounded to laterally compressed, bisexual, the upper florets sterile, over-lapping, and forming a knob-like cluster, disarticulating above the glumes and between the florets. Glumes 2, 1- to 7-nerved, the margins scarious; lemmas thin, 5- to several-nerved, scarious-margined, awnless; palea present, 2-nerved. Lodicules 2; stamens 3; stigmas 2.

A genus of about 60-80 species native to the temperate regions of both hemispheres; about 20 of them are found in North America. *M. mutica* (two-flowered melic) is native to much of the eastern United States. *M. nitens* and *M. mutica* occur in the eastern states; *M. subulata* (Alaska onion grass) occurs from Alaska to California; *M. porteri* (Porter’s melic) is found in the Southwest.

**GLYCERIA.** Manna grass. Rhizomatous, stoloniferous, or caespitose perennials of wet sites. Culms herbaceous, often decumbent and rooting at the nodes, to 1+ m tall. Inflorescence an open to contracted panicle, sometimes reduced to a raceme. Spikelets fragile, linear, awnless, laterally compressed or almost terete, several-flowered, bisexual, disarticulating above the glumes and between the florets. Glumes 2, unequal, 1- [3-] 7-nerved, shorter than the florets; lemmas broad, with [5] 7 [9] conspicuous, parallel nerves, the apex acute, obtuse, or truncate; palea relatively long, 2-nerved. Lodicules 2; stamens 2 or 3; stigmas 2.

A genus of about 35-40 species native to the temperate regions of the Old and New World; about 15 of them are found in North America. Some species of the genus have been treated under *Puccinellia* and *Torreyochloa* by recent workers. Several species are important sources of food for humans and waterfowl. *G. striata* (fowl manna grass) is probably the most widespread representative of the genus in North America, ranging from Newfoundland to Mexico; *G. borealis* (northern manna grass) occurs from Newfoundland to Washington and south to California; *G. septentrionalis* (eastern manna grass) is found from Canada to Florida, west to Texas.

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**TRIBE: STIPEAE**

Plants of this tribe were placed in the Agrostideae of H & C. They differ in details of spikelet morphology and chromosome number. This group is sometimes placed in the subfamily Arundinoideae; sometimes it is treated as the distinct subfamily Stipoideae. See Section 4 for a key to the North American genera of Stipeae.

**STIPA.** Needle grass, porcupine grass. Caespitose perennials. Culms herbaceous or woody, to 2 m tall. Leaves often in a basal clump; cleistogamous spikelets often present within sheaths. Inflorescence an open to contracted panicle. Spikelets 1-flowered, terete to laterally compressed, bisexual, disarticulating above the glumes. Glumes 2, 1- to 6-nerved, longer than the floret; lemmas long, narrow, firm to indurate at maturity, often tightly wrapped around palea and Caryopsis, terminating in a conspicuous awn; lemma base and rachilla forming a sharp-pointed callus, this usually clothed in stiff hairs; palea relatively long, 2-nerved. Lodicules 3 [2]; stamens 3; stigmas 2-4.

A large genus of about 300 species native to temperate and tropical regions of the Old and New World. Of economic significance as a source of pasture grasses, fibers for cordage and mats, and weeds. The sharp-pointed florets can cause mechanical injury to domesticated and wild animals. *S. spartea* (porcupine grass) occurs in the prairies; *S. pulchra* (purple needle grass) is found in the California Coast Ranges; *S. avenacea* (blackseed needle grass) is native to the eastern and southeastern states. *S. hymenoides* [= *Oryzopsis* h. in H & C] (Indian ricegrass) is an important forage grass in the drier regions of the West. *S. robusta* (sleepy grass) is toxic, especially to horses.

Barkworth (1993) has, for the most part, elevated the sections of *Stipa* (or their equivalent) to the generic level. Our North American material would then fall into the genera *Achnatherum*, *Hesperostipa*, and *Nassella*. If we accept this disposition, which I do not, the new combinations would be as follows:
**STIPA RENT ASUNDER**

<table>
<thead>
<tr>
<th>Stipa (Traditional)</th>
<th>Stipa (Sensu Barkworth)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stipa arida →</td>
<td>Achnatherum aridum</td>
</tr>
<tr>
<td>Stipa x bloomeri →</td>
<td>Achnatherum X bloomeri</td>
</tr>
<tr>
<td>Stipa brachycaeta →</td>
<td>Achnatherum brachycaetum</td>
</tr>
<tr>
<td>Stipa californica →</td>
<td>Achnatherum occidentale</td>
</tr>
<tr>
<td>Stipa cernua →</td>
<td>Nassella cernua</td>
</tr>
<tr>
<td>Stipa comata →</td>
<td>Hesperostipa comata</td>
</tr>
<tr>
<td>Stipa coronata →</td>
<td>Achnatherum coronatum</td>
</tr>
<tr>
<td>Stipa curtiseta →</td>
<td>Hesperostipa curtiseta</td>
</tr>
<tr>
<td>Stipa curvifolia →</td>
<td>Achnatherum curvifolium</td>
</tr>
<tr>
<td>Stipa diegoensis →</td>
<td>Achnatherum diegoense</td>
</tr>
<tr>
<td>Stipa eminens →</td>
<td>Achnatherum eminens</td>
</tr>
<tr>
<td>Stipa formicarum →</td>
<td>Nassella formicarum</td>
</tr>
<tr>
<td>Stipa hymenoides →</td>
<td>Achnatherum hymenoides</td>
</tr>
<tr>
<td>Stipa x latiglumis →</td>
<td>Achnatherum X latiglume</td>
</tr>
<tr>
<td>Stipa lemenoni →</td>
<td>Achnatherum lemenoni</td>
</tr>
<tr>
<td>Stipa lepida →</td>
<td>Nassella lepida</td>
</tr>
<tr>
<td>Stipa lettermanii →</td>
<td>Achnatherum lettermanii</td>
</tr>
<tr>
<td>Stipa leucotricha →</td>
<td>Nassella leucotricha</td>
</tr>
<tr>
<td>Stipa lobata →</td>
<td>Achnatherum lobatum</td>
</tr>
<tr>
<td>Stipa neesiana →</td>
<td>Nassella neesiana</td>
</tr>
<tr>
<td>Stipa nelsonii →</td>
<td>Achnatherum nelsonii</td>
</tr>
<tr>
<td>Stipa neomexicana →</td>
<td>Hesperostipa neomexicana</td>
</tr>
<tr>
<td>Stipa nevadensis →</td>
<td>Achnatherum nevadense</td>
</tr>
<tr>
<td>Stipa occidentalis →</td>
<td>Achnatherum occidentale</td>
</tr>
<tr>
<td>Stipa parishii →</td>
<td>Achnatherum parishii</td>
</tr>
<tr>
<td>Stipa pinetorum →</td>
<td>Achnatherum pinetorum</td>
</tr>
<tr>
<td>Stipa porteri →</td>
<td>Ptilagrostis mongolstep</td>
</tr>
<tr>
<td>Stipa pulchra →</td>
<td>Nassella pulchra</td>
</tr>
<tr>
<td>Stipa richardsonii →</td>
<td>Achnatherum richardsonii</td>
</tr>
<tr>
<td>Stipa robusta →</td>
<td>Achnatherum robustum</td>
</tr>
<tr>
<td>Stipa scribneri →</td>
<td>Achnatherum scribneri</td>
</tr>
<tr>
<td>Stipa spartea →</td>
<td>Hesperostipa spartea</td>
</tr>
<tr>
<td>Stipa speciosa →</td>
<td>Achnatherum speciosum</td>
</tr>
<tr>
<td>Stipa stillmani →</td>
<td>Achnatherum stillmani</td>
</tr>
<tr>
<td>Stipa tenuissima →</td>
<td>Nassella tenuissima</td>
</tr>
<tr>
<td>Stipa thurberiana →</td>
<td>Achnatherum thurberianum</td>
</tr>
<tr>
<td>Stipa viridula →</td>
<td>Nassella viridula</td>
</tr>
<tr>
<td>Stipa webberi →</td>
<td>Achnatherum webberi</td>
</tr>
</tbody>
</table>

**ORYZOPSIS.** Ricegrass. Caespitose perennials. Culms herbaceous, the internodes solid or hollow, to 1-5 dm tall. Inflorescence an open or contracted panicle, the branches sometimes capitillary. Spikelets 1-flowered, terete to dorsally compressed, bisexual, disarticulating above the glumes. Glumes 2, = equal, as long or longer than the floret, 3- to 7-nerved, broad, acuminate to obtuse; lemma 3- to 5-nerved, firm to indurate, with a deciduous awn; callus short and blunt; palea relatively long, similar to lemma in texture and marginally or completely covered by it. Lodicles 2 or 3; stamens 3; stigmas 3.

A genus of 20-35 species native to temperate and sub-tropical regions of both hemispheres. Plants of this genus hybridize freely with *Stipa*. As treated here, *Oryzopsis* includes *Piptatherum*, the latter with an incurved callus, 3 lodicules, marginally covered palea, and free styles. The genus occurs widely in the United States, with species often being locally important as forage. *O. milieaea* (smilo grass) is a weedy Mediterranean grass established on both coasts; *O. micrantha* (little ricegrass) is native in the West from Canada to California; *O. hymenooides* (Indian ricegrass) has been transferred to *Stipa*.

**PIPTOCHAETIUM.** Pinyon ricegrass, blackseed needle grass. Caespitose perennials. Culms herbaceous, stiffly erect, to 1+ m tall. Leaves basal, the blades filiform, usually involute. Inflorescence an open panicle. Spikelets 1-flowered, turged, ± terete, bisexual, disarticulating above the glumes. Glumes 2, = equal, somewhat longer than the floret, 3- to 7-nerved; lemma 5-nerved, dark-pigmented, with a stout, twisted, guniculate awn; palea 2-nerved, 2-kkeeled, with a narrow sulcus between the keels. Lodicles 2 or 3; stamens 3; stigmas 2.

A genus of 20-30 species native to the New World, mostly in South America. *P. fimbriatum* (pinyon ricegrass) is an important forage grass in the Southwest; *P. avenaceum* [= *Stipa a. in H & C] (blackseed needle grass) is native to the wooded areas of the eastern U. S. A few other adventive species have been reported in California.

**TRIBE: HAINARDIEAE**

Grasses of the sea coasts. With their spicate inflorescences, they are similar to *Aegilops*. The spikelets are 1-flowered, disarticulating along with a segment of the rachis. The two genera below were assigned to Hordeae in H & C. See Section 4 for a key to the North American taxa.

**HAINARDIA.** Thintail. Caespitose annuals. Culms herbaceous, the internodes solid, to 5 dm tall. Inflorescence a single spike, spikelets solitary at each node, ± embedded in notches in a thickened, cylindrical rachis. Spikelets 1-flowered, dorsally compressed, bisexual, disarticulating below the glume, with a rachis segment attached. Glume 1, the first absent and the second firm to indurate, acute, 3- to several-nerved, longer than the floret, closing over the cavity in the rachis; lemma 3-nerved, thin, awnless; palea relatively long, hyaline, 2-nerved. Lodicles 2; stamens 1-3; stigmas 2. A monotypic genus native to the Mediterranean area. *H. cylindrica* [= *Monerma c. in H & C] is an introduction in California salt marshes.

**PARAPHOLIS.** Sickle grass. Caespitose annuals. Culms erect to ± spreading, the internodes hollow, to 2 dm tall. Inflorescence a single spike, curved or straight, the spikelets solitary at each node, ± embedded in a thickened rachis, disarticulating below the glumes with a rachis segment attached. Glumes 2, = equal, longer than the floret, 3- or 5-nerved, leathery, their attachment displaced so that they appear side-by-side in front; lemma hyaline, 1-nerved, awnless; palea relatively long, tightly clasped by lemma, 2-nerved. Lodicles 2; stamens 3; stigmas 2.

A genus of 4-6 species native to maritime soils and salt marshes of the Old World; commonly occupying the same habitats as adventives. *P. incurva* is weedy on mud flats and in salt marshes of the Atlantic, Gulf, and Pacific coasts. A second species (*P. strigosus*) is known only from around Humboldt Bay. Its spikes are not curved, as in the other species. It was discovered a few years ago by Thomas Worley, who was an HSU student at the time.
**SCRIBNERIA**. Low, tufted annual. Inflorescence a slender spike; spikelets 1 per node, inserted flatwise against the rachis. Spikelets 1-flowered, disarticulating above the glumes; rachilla extended as a tiny, hairy bristle. Glumes 2, equal, awnless; first 2-nerved and the second 4-nerved. Lemma membranous, minutely bidentate, the midnerve extended as a short, straight awn. Palea about as long as lemma. Stamen 1; stigmas 2. 2n = 36. A monotypic genus. *S. bolanderi* is native from British Columbia to California. H & C placed the genus in their Hordeae.

**SELECTED REFERENCES**


**TRIBE BRACHYELYTREAE**

**BRACHYELYTRUM**


**TRIBE POEAE**


ARCTAGROSTIS


CUTANDIA

Cynosurus


Dactylis


Festuca


**LOLIIUM**


**PHIPPSIA**


**POA**


Soreng, R. J. 1985. *Poa* L. in New Mexico, with a key to middle and southern Rocky Mountain species (Poaceae). Great Basin Nat. 45(3): 395-422.


SCLEROCHLOA


SCLOCHLOA


TORREYOCHLOA


VULPIA


TRIBE BROMEAE

BROMUS


TRIBE AVENEAE


SUBTRIBE AVENINAE

AMPELODESموس


APERA


AVENA


ARRHENATHERUM


BECKMANNIA


CORYNEPHORUS


DESHAMPSIA


DISSANTHELIUM


HELICTOTRICHON


HOLCUS


KOELERIA


SPHENOPHOLIS


TRISETUM


VENETATA

SUBTRIBE PHALARIDINAE

ANTHOXANTHUM

HIEROCHLOÉ
Schouten, Y. & J. F. Veldkamp. 1985. [See citation under Anthoxanthum].

PHALARIS

SUBTRIBE: ALOPECURINAE
ALOPECURUS

AMMOPHILA

CALAMAGROSTIS

AGROSTIS

CINNA

PHLEUM


Jauhar, P. P. & C. F. Crane. 1989. An evaluation of


**AGROPYRON**


**ELYMUS**


**TAENIATHERUM**


Humphries, C. J. 1978. Variation in *Taeniatherum*


**SITANION**


**HORDEUM**


AEGILOPS


TRITICUM


SECALE


Vosa, C. G. 1974. The basic karyotype of rye (Secale cereale) analysed with giemsa and fluorescence methods. Heredity 33: 403-408.

X TRITICOSECALE


EREMOPYRUM

TRIBE MELICEAE


MELICA


GLYCERIA


PLEUROPOGON


SCHIZACHNE


TRIBE STIPEAE


STIPA


Hall, O. And B. L. Johnson. Electrophoretic analysis of the amphiploid of Stipa viridula x Oryzopsis hymenoides and its parent species. Hereditas 48: 530-535.


**ORYZOPSIS**


Johnson, B. L. 1945. Natural hybrids between *Oryzopsis hymenoides* and several species of *Stipa*. American J. Bot. 32: 599-608.


**PTILAGROSTIS**


**PIPTOCHAETIUM**


**TRIBE HAINARDIEAE**

**HAINARDIA**


**PARAPHOLIS**


### TECHNICAL DESCRIPTION

**Habit:** Cane-like, reed-like, or bamboo-like; sometimes perennial herbs

**Root Hairs:** Equal

**Leaf Epidermis:** A combination of festucoid and panicoid features

**Leaf Anatomy:** A combination of festucoid and bambusoid (arm cells present), with a few panicoid features; fusoid cells lacking

**Spikelet:** 1- to several-flowered; upper florets often reduced; in a few lower ones imperfect

**Flower:** Lodicules 2; stamens 3 [rarely 6]; stigmas 2, often densely and minutely plumose; flowers perfect or unisexual

**Embryo:** P - P F

**Cytology:** x = 6, 10, 11, or 12; chromosomes small

**Photosynthetic Pathway:** C₃

**Distribution:** Cosmopolitan, especially southern hemisphere.

### SYSTEMATICS

This subfamily is a mess! It was not recognized by Hitchcock and Chase. Instead, they placed these grasses in their tribes Festuceae and Aveneae. It appears to me that the more we learn from the newer molecular studies, the less tenable our various treatments of Arundinoideae become.

The placement of *Gynerium* remains unsettled. It has been placed in its own tribe; the Grass Phylogeny Working Group left it “incertae sedis,” which translates roughly from the Latin as “we don’t know where the hell it goes.”

### TRIBE: ARUNDINEAE

Tall, coarse, rhizomatous or densely clumped perennials, often of wet sites. Inflorescence a conspicuous terminal panicle. Spikelets few- to several-flowered, often long-hairy, bisexual or unisexual, laterally compressed, disarticulating above the glumes and between the florets. See Section 4 for a new to the genera found in North America.

**ARUNDO.** Giant reed. Rhizomatous perennials. Culms woody, 2-6 m tall. Leaf blades broad, not pseudopetiolate. Inflorescence a terminal, plumose panicle. Spikelets several-flowered, bisexual, laterally compressed, disarticulating above the glumes and between the florets. Glumes 2, ± equal, 3-nerved, tapering to a point, awnless. Lemmas 3-nerved, villous on its lower half, tapering to a point or awn. Palea 2-keeled and 3-nerved. Rachilla glabrous. Lodicules 2; stamens 3; stigmas 2. X = 12; 2n = 60, 72, 110, and 112.

A genus of 3-6 species. *A. donax* is weedy along waterways; it is also grown as an ornamental and its is used in erosion control. It is also one of the sources of material used to make the reeds for certain wind instruments.

**PHRAGMITES.** Reed, common reed. Robust rhizomatous or stoloniferous perennials. Culms herbaceous to woody, to 4 [10] m tall. Leaf blades broad, not pseudopetiolate. Inflorescence a terminal, plumose panicle. Spikelets several-flowered, bisexual, disarticulating above the glumes and between the florets. Glumes 2, pointed, awnless, the first 1-nerved and the second 3-nerved; lemmas 3-nerved, awned or awnless. Rachilla with long, silky hairs. Palea 2-nerved. Lodicules 2; stamens 3; stigmas 2. X = 12; 2n = 36, 44, 46, 48, 49, 50, 51, 52, 54, and 96.

A genus of 3 cosmopolitan species. Our only North American representative is *Ph. australis* (= *Ph. communis* in H & C), often considered the most widely occurring vascular plant. It is found around lakes and along waterways over much of the continent.

**GYNERIUM.** Uva grass, caña brava. Robust, rhizomatous perennials to 10 m tall. Leaf blades to 2 m long; sharply serrulate. Plants dioecious. Inflorescence a conspicuous panicle. Female spikelets with a hairy callus.

A genus of one species, *G. sagittatum*, which is native to streamsides and wet places from Mexico into South America. It has become established in Florida. Stems used for construction, arrow-shafts; leaves for thatch, weaving, and basketry; inflorescences often painted some really tacky color and sold for some outrageous price in “import” shops.

### SELECTED REFERENCES


### TRIBE ARUNDINEAE

#### ARUNDO


#### MOLINIA


#### PHRAGMITES


#### THYSANOLAENA


### TRIBE GYNERIEAE


#### GYNERIUM


3.07 - SUBFAMILY DANTHONIOIDEAE

**TECHNICAL DESCRIPTION**

**Habit:** Caespitose perennials; reed-like in *Cortaderia*

**Root Hairs:**

**Leaf Epidermis:** Panicoid microhairs present; stomates absent or rare; silica bodies various

**Leaf in Cross-section:** Mesophyll non-radiate

**Inflorescence:** Panicle, sometimes reduced to a raceme or solitary spikelet

**Spikelets:** 2- to many-flowered; laterally compressed; disarticulating above the glumes

**Flowers:** Lodicules 2; stamens 3 (0 in unisexual florets); stigmas 2

**Embryo Formula:** P - P F

**Cytology:** x = 9; diploids and tetraploids

**Photosynthetic Pathway:** C₃

**Distribution:** Temperate, especially southern hemi-sphere; only *Danthonia* is native to North America

**SYSTEMATICS**

Hitchcock & Chase placed these grasses in their Festucoideae. More recent workers segregated them out as arundinoids. Recent research has resulted in recognizing seven clades, including the *Cortaderia* clade and the *Danthonia* clade.

**TRIBE: DANTHONIEAE**

Annuals or perennials herbs. Inflorescence a panicle, raceme, or occasionally reduced to a single spikelet. Spikelets few- to several-flowered, bisexual, disarticulating above the glumes and between the florets. Glumes 2, longer than the florets; lemmas bifid or toothed, awned or mucronate.

This tribe of predominantly southern hemisphere grasses is not well represented in North America. Its circumscription remains unsettled. When C. E. Hubbard originally described the group in 1948, he separated out genera of the traditional Aveneae. Agnes Chase retained our few representatives in the Aveneae. The microcharacters of this group combine pooid and panicoid features. See Section 4 for a key to the genera of North American Danthoniaceae.

**CORTADERIA.** Pampas grass. Robust, caespitose perennials. Culms to 4 m tall. Leaves mostly basal, the blades often with harsh, toothed margins. Inflorescence a terminal panicle (conspicuously plumose in female plants). Spikelets 2-3 [5-] flowered, unisexual (the species gynodioecious), laterally compressed, disarticulating above the glumes and between the florets, the rachilla extended beyond the uppermost floret. Glumes 2, ± equal, glabrous, 1- to 3-nerved, aawnless; lemmas 3-nerved, awned or awnless, conspicuously hairy on back and base in pistillate spikelets; palea 2-nerved and keeled. Lodicules 2; stamens 0 or 3; stigmas 0 or 2. X = 9; 2n = 36, 72, 90, and 108.

A genus of 24 species, native to New Zealand and to South America. *C. selloana* is an attractive ornamental that sometimes turns weedy. *Cortaderia jubata* is a pernicious weed of coastal California. You should kill pampas grass where ever it occurs. This will not be easy. You may need a flame thrower or a small nuclear device.

**DANTHONIA.** Poverty-oats. Caespitose perennials. Culms to 1 m tall. Inflorescence a few-flowered panicle or raceme (sometimes reduced to a single spikelet); our North American plants also have cleistogamous spikelets hidden within the leaf sheaths. Spikelets several-flowered, bisexual, disarticulating above the glumes and between the florets. Glumes 2, 3- to 7-nerved, much longer than the florets; lemmas hairy, 7- to many-nerved (often indistinctly so), the apex 2-toothed or -cleft, with a flat, twisted, geniculate awn from its midnerve; palea 2-nerved and -keeled. Lodicules 2; stamens 3; stigmas 2.

A genus of about 20 species of mesophytic to xerophytic habitats. Several are important pasture species. *D. spicata* occurs in much of the U. S., except for the far Southwest. *D. californica* and *D. unispicata* are found over much of the West.

**RYTIDOSPERMA.** Hairy oat grass, hairy-danthonia, poverty grass. Plants perennial, caespitose, spreading, sometimes rhizomatous. Inflorescence a raceme or panicle. Spikelets 3- to several-flowered, bisexual, dis-articulating above the glumes and between the florets. Glumes 2, more or less equal. Lemmas 5- to 9-veined, with 2 more or less complete rows of tufts of hairs (the feature that distinguishes the genus from *Danthonia*). Lodicules 2; stamens 3; stigmas 2.

A genus of about 45 species native to Asia, Oceania, and South America. Three species have been introduced into the United States, all of them along the Pacific coast. Only *R. penicillatum (= Danthonia pilosa in older literature) is well established, especially in northern California and southern Oregon.

**SCHISMUS.** Mediterranean grass. Annual or weak perennials, caespitose or decumbent. Inflorescence a contracted or loosely spicate panicle. Spikelets several-flowered, slightly laterally compressed, disarticulating above or below the glumes, rachilla prolonged beyond uppermost floret. Glumes 2, 3- to 7-nerved, ± equal, shorter than or equaling enclosed florets. Lemmas similar to glumes, apex bifid or marginate, aawnless, mucronate, or awned. Palea 2-nerved, rounded or acute. Lodicules 2; stamens 3; stigmas 2. X = 6.
A genus of 5 species native to Africa, and from the Mediterranean to India. *S. arabicus* (Arabian grass) and *S. barbatus* (Mediterranean grass) have become major weeds in parts of the Southwest and in the deserts of California.

**SELECTED REFERENCES**


**CORTADERIA**


**DANTHONIA**


**RYTIDOSPERMA**


**SCHISMUS**


### TECHNICAL DESCRIPTION

| Habit: | Annual or perennial herbs |
| Root Hairs: | 2-celled panicoid microhairs present; stomates with dome-shaped or triangular subsidiary cells; silica bodies of the festucoid, oryzoid, or panicoid type |
| Leaf Epidermis: | Mesophyll with radiate parenchyma |
| Leaf in Cross-section: | An open to contracted panicle of few to many spikelets |
| Inflorescence: | 1-flowered, cylindric to laterally compressed; typically with a triple or trifid awn (the lateral branches sometimes reduced or absent) |
| Flowers: | Lodicules 2 or 0; stamens 1-3; stigmas 2 (red or brown) |
| Embryo Formula: | C₄ |
| Distribution: | Temperate, subtropical/tropical; often of drier sites; widespread |

### SYSTEMATICS

The genus *Aristida* has always been something of a problem child. Its 1-flowered spikelets led early workers to put it in Agrostideae. A host of microcharacters show that to be untenable. The Grass Phylogeny Working Group has segregated the genus into its own subfamily.

### TRIBE: ARISTIDEAE

The characters of the tribe are those of the single genus that it contains.

**ARISTIDA.** Three-awn grass. Caespitose annuals or perennials. Culms herbaceous, the internodes hollow or solid, to 1 m tall. Inflorescence an open or contracted panicle. Spikelets 1-flowered, terete to laterally compressed, bisexual, disarticulating above the glumes. Glumes 2, thin and narrow, 1-nerved, as long as or longer than the floret; lemmas tough, terete, 3-nerved, with a sharp-pointed callus, tapering gradually to an awn column that usually bears 3 awns (the lateral ones reduced or obsolete in section Streptachne); palea relatively short to reduced, 2-nerved. Lodicules 2 or 0; stamens 1-3; stigmas 2, red or brown pigmented. A genus of almost 300 species native to the temperate and warmer regions of both hemispheres. *A. oligantha* (old field three-awn) is found on open ground, mostly in the eastern half of the country; *A. purpurea* (purple three-awn) and *A. longiseta* (red three-awn) occur on plains and dry hills in the Southwest, especially after they have been disturbed.
3.09 - SUBFAMILY CHLORIDOIDEAE

**TECHNICAL DESCRIPTION**

<table>
<thead>
<tr>
<th>Habit:</th>
<th>Herbaceous; culm internodes hollow or solid</th>
</tr>
</thead>
<tbody>
<tr>
<td>Root Hairs:</td>
<td>Equal</td>
</tr>
<tr>
<td>Leaf Epidermis:</td>
<td>Complex; bicellular microhairs present; silica cells cross- or saddle-shaped; stomata with triangular or dome-shaped subsidiary cells</td>
</tr>
<tr>
<td>Leaf Anatomy:</td>
<td>Vascular bundles with double parenchyma sheath, the outer often with conspicuously radiating cells</td>
</tr>
<tr>
<td>Inflorescence:</td>
<td>Various, often 1-sided racemes or spikes</td>
</tr>
<tr>
<td>Spikelets:</td>
<td>1- to several-flowered; lemmas typically 3-nerved (1-nerved in <em>Sporobolus</em> and <em>Calamovilfa</em>; several-nerved in some grasses in minor tribes)</td>
</tr>
<tr>
<td>Flower:</td>
<td>Lodicules 2; stamens 3; stigmas 2</td>
</tr>
<tr>
<td>Embryo:</td>
<td>P + P F</td>
</tr>
<tr>
<td>Cytology:</td>
<td>X = 9 or 10 (8 in <em>Erioneuron</em>); nucleoli persistent</td>
</tr>
<tr>
<td>Photosynthetic Pathway:</td>
<td>C₄</td>
</tr>
<tr>
<td>Distribution:</td>
<td>Tropical and subtropical regions, especially of the Old World; particularly in arid and semiarid situations where there is high light intensity; best represented on this continent in the American Southwest.</td>
</tr>
</tbody>
</table>

**SYSTEMATICS**

The subfamily has also been called Eragrostoideae in the recent literature, a name that must be rejected for technical reasons. The group was not recognized by Hitchcock and Chase. It is a portion of their Festucoideae. Many of the grasses included here resided in their Festuceae and Chlorideae. The plants are essentially festucoid in spikelet structure and panicoid in many of their microcharacters.

Often there is general agreement as to what makes up the core of a subfamily; the disagreement seems to be mainly about the smaller “fringe groups.” In the chloridoïds, most everyone is satisfied that several smaller tribes belong here. The arguments focus on the core. Several workers recognize two large tribes, Eragrostideae and Cynodonteae (= Chlorideae of H & C); Watson & Dallwitz merge them into a unit they call the “Main Chloridoid Assemblage.”

Here are the various tribes of the subfamily, as viewed by recent authors:

Clayton & Renvoize (1986): Pappophoreae, Orcuttieae, Eragrostideae, Cynodonteae


“The Splitters”: Pappophoreae, Orcuttieae, Eragrostideae, Aeluropodieae, Unioleae, Eriganideae, Sporoboleae, Spartineae, Cynodonteae, Zoysieae

Hilu & Esen (1993): Pappophoreae, Orcuttieae, Eragrostideae


We will use the four tribe model, and also recognize a series of subtribes, each of which has also been viewed as tribes by various agrostologists.

**TRIBE: ERAGROSTIDEAE**

Annuals or perennials. Inflorescence typically a panicle. Spikelets typically few- to many-flowered, the lower florets fertile.

**SUBTRIBE: MONANTHOCHLOINAE**

Mostly grasses of seashores and saline marshy sites. Plants stoloniferous and rhizomatous, mostly dioecious. Inflorescence a condensed panicle or raceme. Leaf epidermis with papillae and sunken bicellular microhairs. These grasses have also been placed in their own tribe, Aeluropodeae.

**DISTICHLIS.** Salt grass. Low, rhizomatous perennial. Culms erect, rigid, the internodes solid, to 2 dm tall. Leaves often distichous. Inflorescence a reduced panicle or racemes. Spikelets several-flowered, laterally compressed, unisexual (species usually dioecious), disarticulating above the glumes and between the florets. Glumes 2, unequal, the first 1- to 5-nerved and the second 4- to 9-nerved, shorter than the florets, awnless; lemmas 9- to 11-nerved, awnless (those of the staminate spikelet thinner in texture); palea relatively long, 2-nerved, 2-keeled, these ± winged. Lodicules 2; stamens 3 or 0; stigmas 2 or 0.

A genus of 1 to a few species native to North America, with one in Australia. Beetle (1955) recognized a number of taxa. I have always found them difficult to distinguish. The treatment put forth by McVaugh (1983) seems reasonable to me. Following this more conservative view, D. spicata occurs along the Atlantic and Pacific coasts and in interior salt flats and marshes. D. texana in H & C has been transferred to the genus *Allolepis*.

**MONANTHOCHLOË.** Shore grass. Mat-forming rhizomatous, stoloniferous perennial. Culms herbaceous, decumbent, much-branched, to 2 dm tall. Leaves tufted, acicular, less than 1 cm long. Inflorescence reduced to a single spikelet ± concealed by upper leaf sheaths. Spikelets few-flowered, laterally compressed to rounded, unisexual (species dioecious), disarticulating below florets. Glumes 0; lemmas several-nerved, awnless; palea relatively
long, 2-keeled. Lodicules 0; stamens 0 or 3; stigmas 2 or 0.

A genus of three species, one in North America and two in South America. *M. littoralis* (shore grass) is found mostly in maritime coastal flats in southern California and in similar habitats in Texas, Louisiana, and Florida.

**SWALLENIA.** Eureka dune grass. Coarse, rhizomatous, perennial. Culms herbaceous to woody, to 1 m tall. Inflorescence a contracted panicle. Spikelets 3 to 7-flowered, laterally compressed, bisexual, persistent on the rachis. Glumes 2, ± equal, the lower 5- to 7-nerved and the upper 7- to 11-nerved; lemmas 5- to 7-nerved, awnless, densely hairy on lower margins; palea relatively long, 2-nerved. Lodicules 2; stamens 3; stigmas 2. A monotypic genus, *S. alexandrae* is known only from sand dunes at two sites in Inyo Co., California. [= *Ectosperma a.* in H & C].

**SUBTRIBE: ERAGROSTINAE**

Annuals or perennials. Inflorescence a panicle, less often 1-sided spikes or racemes. Spikelets with several to many florets, 2 or more of them typically fertile. Glumes shorter than the florets. Lemmas 3-nerved (rarely 1-nerved), these usually conspicuous; awnless or with 1 long awn or 3 short ones. Plants of this subtribe were placed in Festuceae or Chlorideae by H & C.

**ERAGROSTIS.** Lovegrass, stink grass. Caespitose annuals or perennials [rarely stoloniferous]. Culms herbaceous, internodes hollow or solid, to 1 m tall. Inflorescence an open or contracted panicle. Spikelets, few- to many-flowered, the florets usually strongly overlapping, laterally compressed, bisexual [rarely unisexual and the species dioecious], disarticulating above the glumes and between the florets, the paleas persisting on the rachilla. Glumes 2, unequal, shorter than the florets, 1-nerved; lemmas 3-nerved, keeled or rounded, acute or acuminate, awnless; palea usually strongly 2-keeled, often ciliolate. Lodicules 2; stamens 1-3; stigmas 2.

A cosmopolitan genus of about 300 species, often of poorer, sandy sites. A number are weedy. *E. intermedia* (plains love grass) is a forage plant of some importance; *E. curvula* (weeping lovegrass) is an introduced forage grass in the southern states; *E. spectabilis* (purple lovegrass) occurs over much of the central and eastern sections of the United States; *E. ciliaris* (stink grass) is a widespread, malodorous weed. As treated here, the genus includes *Neeragrostis*, a small group of dioecious, mat-forming species.

**TRIDENS.** Purpletop, tridens. Erect, caespitose perennials. Culms herbaceous, to 1 m tall. Inflorescence an open or contracted panicle. Spikelets 3- to 12-flowered, laterally compressed, bisexual, disarticulating above the glumes and between the florets. Glumes 2, ± equal, the first 1-nerved and the second 1- to 3-nerved, shorter than the florets; lemmas broad, 3-nerved, typically hairy below, the apex bidentate, the midnerve usually extending between the teeth as a muro or short awn; palea relatively long, 2-nerved. Lodicules 2; stamens 3; stigmas 2, often red pigmented.

A genus of 16-18 species native to the eastern and southern United States and to adjacent Mexico. In H & C, the genus included a few species that are now assigned to *Erioneuron*. *T. flavus* (purpletop) is common in old fields and in open woods in the eastern half of the country; *T. albescens* (white tridens) of the southwest and south-central states is unusual in having glabrous lemmas; *T. x oklahomensis* is an endemic known only from a wet meadow near Stillwater, OK.

**LEPTOCHLOA.** Sprangletop. Caespitose annuals or perennials, often of marshy or wet sites. Culms herbaceous, to 1+ m tall. Inflorescence variously described as a panicle of racemose, unbranched branches or a compound, race-mose inflorescence whose branches bear spikes or spike-like racemes. Spikelets 2- to several-flowered, often overlapping, rounded to laterally compressed, bisexual, disarticulation above the glumes and between the florets. Glumes 2, equal of unequal, 1-nerved, shorter than the florets; lemmas 3-nerved, often minutely pubescent on the nerves, awnless, mucronate, or awned; palea shorter than lemma, 2-nerved. Lodicules 2; stamens 2 or 3; stigmas 2.

A genus of about 70 species, native to the warmer regions of both hemispheres. As treated here, the genus includes *Diplachne*. See the table below for a comparison. *L. filiformis* (red sprangletop) is a common weed in the Southwest and in the Southeast. *L. dubia* (green sprangletop) is found on dry sites in the Southwest.

**DIPLACHNE VERSUS LEPTOCHLOA**

<table>
<thead>
<tr>
<th>Feature</th>
<th>Diplachne</th>
<th>Leptochloa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spikelets</td>
<td>4-12 mm long</td>
<td>1-4 mm long</td>
</tr>
<tr>
<td>Florets</td>
<td>5-12</td>
<td>2-5 (7)</td>
</tr>
<tr>
<td>Caryopses</td>
<td>elliptical in x-s</td>
<td>triangular in x-s</td>
</tr>
<tr>
<td></td>
<td>not grooved</td>
<td>grooved on one side</td>
</tr>
<tr>
<td>Lemma</td>
<td>rounded</td>
<td>strongly keeled</td>
</tr>
<tr>
<td>lateral nerves</td>
<td>extending to upper margins</td>
<td>lateral nerves</td>
</tr>
<tr>
<td></td>
<td>not extending to upper margins</td>
<td></td>
</tr>
<tr>
<td>Inflorescence</td>
<td>racemose</td>
<td>spicate</td>
</tr>
<tr>
<td></td>
<td>2.5-6 mm wide</td>
<td>0.5-4 mm wide</td>
</tr>
</tbody>
</table>

**REDFIELDIA.** Blowout grass. Rhizomatous perennial to 1 m. Leaf blade involute, with filiform tip. Inflorescence a large, open panicle, 1/3 to ½ length of culms, its branches flexuous. Spikelets [1-] 2- to 6-flowered, dis-articulating above glumes. Glumes 2, acuminate, 1-nerved; lemmas keeled, hairy on margins at base, 3-nerved; callus bearded. Lodicules 2; stamens 3; stigmas 2. One species, *R. flexuosa*, native to the interior sandy hills of the U. S., from SD and OK to CO, AZ.

**SUBTRIBE: ELEUSININAE**

**ELEUSINE.** Goose grass. Low, spreading, annuals. Culms herbaceous, weak, flattened, to 2 dm tall. Inflorescence a series of 2 to several ± digitate branches clumped at the culm apex. Spikelets sessile in 2 rows, 3- to several-flowered, laterally compressed, bisexual, disarticulation above the
glumes and between the florets (except in cultivars). Glumes 2, unequal, the first 1-nerved and the second 3- to 5-nerved, shorter than the florets; lemmas 3-nerved, acute, awnless to mucronate; palea shorter than lemma, apically notched. Lodicules 2; stamens 3; stigmas 2.

A genus of 6-9 species, all but one native to the Old World. E. indica (goose grass) is a common weed over much of the United States; E. coracana (finger millet, ragi) is an important grain crop in the Old World.

**DACTYLOCTENIUM.** Durban grass, crowfoot grass. Annual or perennial herbs, the culms often spreading and rooting at the nodes. Inflorescence a series of paired or digitate racemes; spikelets imbricate in two rows, inserted at right angles to rachis. Spikelets 2- to several-flowered, laterally compressed, disarticulating between the first and second glume. Glumes 2, 1-nerved, the upper with an oblique awn from just below its tip; lemmas 3-nerved, strongly keeled, acute or abruptly narrowed to a short recurved awn. Lodicules 2; stamens 3; stigmas 2.

A genus of about 13 species native to the Old World, especially of dry, sandy sites. *Dactyloctenium aegyptium* is a cosmopolitan weed and is also planted for lawns and playing fields. It occurs in North America from NC to FL and the Pacific coast.

**SUBTRIBE: MUHLENBERGIINAE**

Annuals or perennials with well-developed panicles of small, 1-flowered spikelets. Disarticulation above the glumes. Lemmas 1- or 3-nerved. Plants of this subtribe were placed in Agrostideae by H & C. The group is often recognized as a separate tribe, Sporoboleae.

**SPOROBOLUS.** Dropseed. Caespitose annuals or perennials, a few rhizomatous. Culms herbaceous, internodes usually solid, to 2 m tall. Ligules ciliate (a useful feature in distinguishing the genus from *Muhlenbergia*, with which it is easily confused). Inflorescence an open or contracted panicle. Spikelets small, 1-flowered, rounded to laterally compressed, bisexual, disarticulating above the glumes. Glumes 2, unequal, 1-nerved, shorter than the floret; lemma 1-nerved, awnless; palea relatively long, sometimes splitting at maturity and thereby resembling an extra lemma; pericarp free from the seedcoat, as in *Sporobolus*.

This small genus of 4 species is a favorite of the conservative right because all of them are native to North America. *C. longifolia* and *C. gigantea* are found in sandy habitats in the central and southwestern regions of the country.

**SUBTRIBE: MUNROINAE**

**ERIONEURON.** Fluff grass. Low, tufted, stoloniferous perennials. Culms herbaceous, to 2 dm tall. Leaf blades with cartilaginous margins. Inflorescence a compact, head-like to more open panicle. Spikelets several-flowered spikelets, laterally compressed, bisexual, disarticulating above the glumes and between the florets. Glumes 2, ± equal, 1-nerved; lemmas broad, 3-nerved, with long hairs (at least below), apex bilobed, midnerv extended as a short awn, the lateral ones as a short mucro; palea about as long as lemma, ciliate on the keels, long-hairy below. Lodicules 2; stamens 1-3; stigmas 2, white.

A genus of 5 species native to drier, often rocky sites of the American Southwest and adjacent Mexico. These taxa were included in *Tridens* by H & C. As treated here, the genus includes *Dasyochloa*. *Erioneuron pulchellum* (fluff grass) occurs on mesas, sandy washes, and rocky hills in the Southwest; *E. pilosum* (hairy tridens) is found on plains of the South Central and Southwest regions.

**MUHLENBERGIA.** Muhly, nimblewill. Delicate, caespitose annuals to coarse, rhizomatous, stoloniferous perennials. Culms herbaceous, internodes solid or hollow, to 2 m tall. Ligule membranous. Inflorescence an open to contracted panicle [rarely 2-flowered and rarely keying properly!], laterally compressed, bisexual, disarticulating above the glumes. Glumes 2, equal or unequal, [0-] 1- [3-] nerved, awnless to short-awned; lemmas 3-nerved, typically with a single well-developed awn, occasionally mucronate or awn-less; palea relatively long, 2-nerved. Lodicules 2; stamens 3; stigmas 2.

A large genus of 125-160 species native to diverse habitats of both hemispheres, especially the New World. *M. schreberi* (nimblewill) occurs in damp, shady places in the eastern half of the country; *M. emersleyi* (bull grass) is found in rocky woods and ravines of the Southwest; *M. sylvatica* (forest muhly) is a rhizomatous grass of wooded areas in the eastern and central U. S.; *M. rigens* (deer grass) of southern California was used by Native Americans in basket making.

**CALAMOVILFA.** Sand reedgrass. Coarse, rhizomatous perennials. Culms herbaceous, the internodes solid, to 2 m tall. Inflorescence an open or contracted panicle. Spikelets 1-flowered, laterally compressed, bisexual, disarticulating above the glumes. Glumes 2, unequal, 1-nerved, as long as the floret, lemmas 1-nerved, awnless, the callus bearded; palea reduced, 2-nerved. Lodicules 2; stamens 3; stigmas 2; pericarp free from the seedcoat, as in *Sporobolus*.

This small genus of 4 species is a favorite of the conservative right because all of them are native to North America. *C. longifolia* and *C. gigantea* are found in sandy habitats in the central and southwestern regions of the country.
**ERNIONEURON VERSUS TRIDENS**

<table>
<thead>
<tr>
<th>Feature</th>
<th>Erioneuron</th>
<th>Tridens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Embryo</td>
<td>oval; translucent</td>
<td>reniform; dark brown</td>
</tr>
<tr>
<td>Stigmas</td>
<td>+/- white</td>
<td>dark purple</td>
</tr>
<tr>
<td>Lemmas</td>
<td>2- (3-) lobed</td>
<td>bidentate; not lobed</td>
</tr>
<tr>
<td></td>
<td>hairy near midrib/margins</td>
<td>less pubescent</td>
</tr>
<tr>
<td>Palea long-hairy below</td>
<td>usually glabrous; ciliate on keel</td>
<td>never ciliate</td>
</tr>
<tr>
<td>Habit</td>
<td>low, stoloniferous</td>
<td>tall perennials</td>
</tr>
<tr>
<td>Leaf</td>
<td>white margins</td>
<td>green margins</td>
</tr>
<tr>
<td></td>
<td>cartilaginous</td>
<td>not cartilaginous</td>
</tr>
<tr>
<td>x =</td>
<td>8</td>
<td>10</td>
</tr>
</tbody>
</table>

**CRYPSIS.** Prickle grass, swamp timothy. Prostrate to ascending annuals. Internodes hollow or solid. Inflorescences terminal or axillary, ovoid to capitate, spike-like panicles, often ± enclosed by bract-like sheaths. Spikelets 1-flowered, keeled, strongly laterally compressed, disarticulating above or below the glumes. Glumes 2, acute or short-awned, 0 or 1-nerved; lemma 1-nerved; palea 1- or 2-nerved. Lodicules 0; stamens 2 or 3; stigmas 2, white. Fruit an achene, the seed free from the pericarp, as in *Sporobolus*.

A genus of 8 species, mostly native to the Middle East and Mediterranean; often found on saline soils. Three species occur in the U. S., all of them introduced.

**SUBTRIBE: UNIOLINAE**

**UNIOLA.** Sea-oats. Rhizomatous or stoloniferous perennials. Culms to 2 m tall. Inflorescence a few- to many-flowered panicle. Spikelets several-flowered (the proximal and distal florets sterile), bisexual, laterally compressed, disarticulating below the glumes. Glumes 2, shorter than the florets, 3-nerved, awnless; lemmas 3- to 10-nerved, awnless or mucronate, serratate-keeled; palea 2-keeled, winged, serratate to ciliate. Lodicules 2; stamens 3; stigmas 2.

A small genus of 2 species native to North and South America and the Caribbean. *U. paniculata* is found on coastal sand dunes of Alabama, Florida, and the Gulf Coast. Its large, drooping panicles are popular in dried arrangements, where they are often sprayed some hideous color. The other species, *U. pittieri* is found on the beaches from Mexico to northern South America. As treated by H & C, *Uniola* included several other species now transferred to *Chasmanthium* of the Centostecoideae.

**TRIBE: CYNODONTEAE**

Annuals or perennials. Inflorescence typically a compound spike or raceme, the spikelets often in two rows on one side of the branch. Spikelets 1-flowered or few- to several-flowered, but only one typically fertile. Unisexual spikelets occur in some genera. Disarticulation above the glumes. Lemmas 3-nerved.

**CYNODON.** Bermuda grass. Low, mat-forming, stoloniferous and/or rhizomatous perennials. Culms herbaceous, to 4 dm tall. Inflorescence a series of 2 to several digitate branches, spikelets sessile, in 2 rows on a ± triangular rachis. Spikelets 1-flowered, rachilla extended beyond floret and sometimes bearing a rudiment, laterally compressed, bisexual, disarticulating above the glumes. Glumes 2, ± equal, 1-nerved, the second about as long as the floret; lemmas 3-nerved, hairy on keel and lateral nerves, awnless; palea as long as lemma, 2-nerved. Lodicules 2; stamens 3; stigmas 2, red pigmented.

A genus of 10 species native to the Old World. *C. dactylon* (Bermuda grass) is an important pasture grass, lawn grass, and aggressive weed over most of the warmer parts of North America.

**CHLORIS.** Windmill grass, finger grass. Caespitose annuals or perennials from rhizomes or stolons. Culms herbaceous, internodes hollow or solid. Leaf sheaths keeled. Inflorescence a series of racemose or digitate branches, each bearing 2 rows of sessile spikelets. Spikelets with 1 fertile floret and 1 or more rudimentary ones above it, laterally compressed, disarticulating above the glumes. Glumes 2, equal or unequal, the lower 1-nerved and the upper 1- to 4-nerved; lemmas [1-] 3- [5-] nerved; palea relatively long, strongly 2-nerved. Lodicules 2; stamens 3; stigmas 2.

A genus of about 70 species native to the warmer regions of the Old and New Worlds. As treated here, the genus includes the 2 *Trichloris* species in H & C, but does not include *Chloris* section *Eustachys* in H & C, which is now generally recognized as a distinct genus. *C. gayana* (Rhodes grass) has escaped from cultivation in the southern states; *C. virgata* (feather finger grass) is a common weed; *C. verticillata* (windmill grass) is native to the plains states; *C. cucullata* (hooded windmill grass) is native to the Southwest.

**GYMNOPOGON.** Skeleton grass. Perennials, often rhizomatous. Culms herbaceous, to 1 m tall. Leaf blades stiff, distichous. Inflorescence a series of racemose branches, the spikelets in two rows.
Spikelets 1- to 3-flowered, laterally compressed, bisexual, the rachilla extending beyond the uppermost fertile floret as slender stalk bearing a rudimentary floret, disarticulation above the glumes. Glumes 2, \( \pm \) equal, 1-nerved, the second longer than the florets; lemmas 3-nerved, usually awned; palea relatively long, 2-nerved. Lodicules 2; stamens 3; stigmas 2.

A genus of about 15 species, all but one of them native to the New World. There are four species in North America; \textit{G. ambiguus} is the most commonly encountered species, growing from the Pine Barrens of New Jersey south to Florida and across to Texas and Oklahoma; \textit{G. brevifolius} is native to the southeastern Coastal Plain; two species are endemic to Florida.

\textbf{SPARTINA.} Cord grass, marsh grass. Caespitose, stoloniferous/rhizomatous perennials. Culms herbaceous, internodes solid or hollow, to 2 m tall. Inflorescence a series of few to many short, often appressed, racemose branches. Spikelets 1-flowered, conspicuously laterally compressed, imbricate on one side of rachis, bisexual, disarticulation below the glumes. Glumes 2, unequal, the first 1-nerved and the second 1- to 3-nerved, the second as long or longer than the floret, awned or awnless; lemma 1- or 3-nerved, keeled, awnless; palea relatively long, 2-nerved, with membranous margins. Lodicules 0; stamens 3; stigmas 2.

A genus of 16 species, one native to Europe and the remainder to the New World. \textit{S. pectinata} (prairie cord grass) is common in wet areas over much of the country; \textit{S. foliosa} occurs in salt marshes along the California coast; \textit{S. densiflora}, native to South America, occurs around Humboldt Bay, California; \textit{S. alterniflora} (smooth cord grass) is found in saline marshes along the Atlantic and Gulf coasts.

\textbf{ORIGIN OF SPARTINA X TOWNSENDII}

\textit{Huskins (1931)}

\textit{S. stricta} (2n = 56) \times \textit{S. alterniflora} (2n = 70)

\begin{itemize}
  \item \textit{S. Townsendii} (2n = 126)*
\end{itemize}

\textbf{Marchant (1966)}

\begin{tabular}{ll}
\textit{S. maritima} & \textit{S. alterniflora} \\
AABBC & AAB, B, B, B \\
2n = 60 & 2n = 62 \\
4 long chromosomes & 6 long chromosomes \\
European & American (ballast) \\
Low seed set & Low seed set \\
Good pollen & Poor pollen \\
\end{tabular}

\begin{itemize}
  \item \textit{S. x Townsendii} \\
  \textit{AAB, B, BC} \\
  \textit{Sterile F1 hybrid} \\
  \textit{S. Townsendii} of 1881 description \\
  2n = 62 \\
  10 long chromosomes \\
  Rules out autotetraploidy \\
  Back crosses to \textit{S. a.}
\end{itemize}

* \("\text{S. Townsendii has evidently originated by chromosome doubling, following on interspecific hybridisation. It is an extremely successful new species, having spread widely from its point of origin, and has almost completely eliminated its parent species wherever it has come into competition with them. It seems to be an outstanding example of the significance of allopolyploidy in plant evolution.}"\) (C. L. \textit{Huskins}, 1931)

\textbf{SUBTRIBE: BOUTELOUINAE}

\textbf{BOUTELOUA.} Grama grass. Annuals or caespitose, rhizomatous, or stoloniferous perennials. Culms herbaceous, internodes hollow or solid, to 1 m tall. Inflorescence of 1 to many short, spicate branches that are racemose along a common axis, each bearing sessile spikelets in 2 rows along a flattened or angular rachis. Spikelets with 1 fertile floret and 1-3 rudimentary ones above it, laterally compressed, disarticulation either above the glumes (subgenus \textit{Chondrosum}) or at the base of a branch, the subunit of the inflorescence falling at maturity (subgenus \textit{Bouteloua}). Glumes 2, equal or unequal, 1-nerved, awned or awnless; lemmas 3-nerved, the midnerve often extended as an awn, the lateral ones sometimes also awn-tipped; palea sometimes 2-awned. Lodicules 2; stamens 3; stigmas 2.

A genus of about 40-50 species native to the New World from Canada through South America; the American Southwest is a major center. \textit{B. curtipendula} (sideoats grama) is a valuable forage grass; \textit{B. hirsuta} (hairy grama) occurs on plains and in rocky places in the central United States; \textit{B. gracilis} (blue grama) is found in the plains of the central and western states.

\textbf{BUCHLOË.} Buffalo grass. Low, stoloniferous, mat-forming perennials. Culms herbaceous, internodes solid, to 2 dm tall. Unsexual spikelets in separate inflorescences, typically on different plants, less frequently on the same plant; staminate inflorescence a series of 1-4 spicate branches, each bearing 2 rows of sessile, second spikelets, well-extended above the vegetative portion of the plants; pistillate inflorescence a bur-like head, partially hidden in ± inflated upper leaf sheaths, the outer covering of the bur a combination of thickened rachis and glumes. Staminate spikelets 2-flowered; pistillate spikelet 1-flowered. Glumes 2, the second indurate, with 3 rigid lobes, and enveloping the florets in the pistillate spikelet; lemmas 3-nerved and typically awnless; palea ± equal to lemma, 2-nerved. Lodicules 2 or 0; stamens 3 or 0; stigmas 2 or 0.

A monotypic genus native to open, drier plains of North America. \textit{B. dactyloides}, is a very important...
range grass of the short-grass prairie, where it can be a dominant.

**HILARIA.** Galleta, tobosa, curly-mesquite. Rhizomatous, stoloniferous, or caespitose perennials. Culms herbaceous, stiff, the internodes solid, to 1 m tall. Inflorescence a balanced spike of sessile spikelets inserted in trires in clavate, cup-like depressions along a wavy or zig-zag rachis; disarticulation below the glumes, the trio of spikelets falling as a group. Spikelets of the trio dissimilar, the lateral ones 2- to 4-flowered, staminate; the central one 1-flowered and perfect. Glumes 2, firm, united to form a false involucre, awned on one side from about the middle; lemma 3-nerved, awned or awnless; palea relatively long, 2-nerved. Lodicules 2 or 0; stamens 3; stigmas 2.

A genus of about 10 species native to the New World; five of them are found in North America; *H. belangeri* (curly-mesquite) occurs in the arid and semiarid sites of the Southwest; *H. swallenii* is endemic to western Texas and adjacent Mexico. *H. jamesii* (galleta) is native to dry plains and deserts in the West and Southwest; *H. rigida* (big galleta) is a coarse, ± woody desert grass with a felt-like covering on its culms; *H. mutica* (tobosa) is found on drier sites in the Southwest.

**SUBTRIBE: ZOYSINAE**

This small tribe of introduced grasses. The inflorescence is a contracted raceme of 1-flowered spikelets on short pedicels. Disarticulation is below the glumes. The palea is often reduced or absent. X = 10.

**ZOYSIA.** Zoysia or zoisia. Rhizomatous/stoloniferous perennials. Inflorescence a spike, the spikelets solitary on a zig-zag rachis. Spikelets 1-flowered; disarticulation below the glume. Glume 1 absent; second glume 1-nerved, mucronate or short-awned. Lemma 1-nerved, shorter than second glume and enclosed by it. Palea present or absent. Lodicules 0; stamens 2 or 3; stigmas 2. A genus of about 10 species, native to Southeast Asia and New Zealand. Three species have been introduced into the warmer, southern portions of the United States where they are grown as popular lawn grasses.

**TRAGUS.** Weak-stemmed annuals. Inflorescence a spike-like raceme, the spikelets in bur-like clusters of 2 to 5. Spikelets 1-flowered; disarticulation at the base of a spikelet cluster. Glumes 2, the second one in some spikelets bearing stout, hooked spines. Lemmas 3-nerved, awnless. Lodicules 2; stamens 3; stigmas 2. A genus of 7 species, 6 of them native to Africa. *T. racemosus* and *T. berteronianus* are weedy introductions in the eastern and southwestern portions of the country.

**TRIBE: PAPPOPHOREAE**

This small tribe of warm, dry climate grasses was treated as part of Festuceae by H & C. The inflorescence is a panicle of 3- to several-flowered spikelets. The lower florets are perfect, the upper ones staminate or neuter. Disarticulation above the glumes, the florets separating as a group. Lemmas with 9 or more nerves, the apex divided into 3-many sharp lobes or awns. X = 10. See Section 4 for a key to our North American taxa.

**PAPPOPHORUM.** Pappus grass. Caespitose perennials. Inflorescence a contracted to spike-like panicle. Spikelets 3- to 6-flowered; lower 1 to 3 fertile. Glumes thin, ± equal, 1-nerved, awnless. Lemmas leathery, many-nerved, these extending into unequal awns. Palea about as long as lemma. Lodicules 2; stamens 3; stigmas 2. A genus of 8 species, native to the American Southwest and South America. *Pappophorum bicolor* (pink pappus grass) and *P. mucronulatum* (whiplash pappus grass) are native to North America.

**ENNEAPOGON.** Spike pappus grass. Tufted perennials. Inflorescence a spike-like panicle. Spikelets several-flowered; disarticulation above the glumes. Lemmas ± equal, 5- to many-nerved, awnless. Lemmas much shorter than glumes, firm, 9-nerved, these extending into plumose awns. Lodicules 2; stamens 3; stigmas 2. A genus of about 30 species, mostly of Old World xerophytic sites. *E. desvauxii* (spike pappus grass) is our only New World species. It is found in the Southwest and extends into Mexico.

**COTTEA.** Cottea grass, pelucilla. Tufted perennial. Leaves often pilose. Inflorescence a ± open panicle. Spikes 6- to 10-flowered; disarticulation above the glumes and between the florets. Glumes ± equal, 7- to many-nerved, awned or awnless. Lemmas 9- to 13-nerved, these extending into awns. Palea slightly longer than lemma. Lodicules 2; stamens 3; stigmas 2. A monotypic genus. *C. pappophoroides* is native to Arizona, New Mexico, and Texas. It also occurs in Central and South America.

**TRIBE: ORCUTTIEAE**

This small tribe of California endemics was treated as part of Festuceae by H & C. A peculiar feature of these grasses is that the leaf blade and sheath are not clearly differentiated from one another. The inflorescence is a spike, spike-like raceme, or a panicle. Grasses of this tribe are restricted to mud flats and vernal pools in California and Baja California. All of them are classed as rare and/or endangered. See Section 4 for a key to our North American taxa.

**NEOSTAFFIA.** Colusa grass. Tufted, spreading, aromatic annual. Culm internodes solid. Leaves glandular-viscid, not clearly differentiated into blade and sheath. Inflorescence a dense, cylindric spike-like raceme, often partially enclosed in dilated upper leaf sheaths. Spikelets several-flowered; disarticulation above the glumes. Glumes 0. Lemmas fan-shaped, prominently 7- to 11-veined, awnless. Palea about as long as lemma. Lodicules 2; stamens 3; stigmas 2. A monotypic genus. *N. colusana* is endemic to vernal pool margins in four counties in California.

**ORCUTTIA.** Orcutt grass. Tufted, semiaquatic annuals, erect to prostrate. Leaf blade and sheath not clearly differentiated. Inflorescence a spike-like raceme. Spikelets few- to many-flowered; disarticulation above the glumes and between the florets. Glumes 2, irregularly toothed. Lemmas prominently 5-toothed, awnless. Palea about as long as lemma. Lodicules 0; stamens 3; stigmas 2. A genus of 5 species, endemic to vernal pools in California and Baja California. All taxa are rare and endangered.

**TUCTORIA.** Tufted annuals. Stems ascending to erect, fragile at maturity. Leaf blade and sheath not differentiated. Inflorescence spike-like, often partially
enveloped by upper leaves. Spikelets 5- to many-flowered, spirally inserted; disarticulation above the glumes and between the florets. Glumes 2, ± equal, awnless. Lemmas 11- to 17-veined, the apex entire to minutely toothed. Palea about as long as the lemma. Lodicules 2; stamens 3; stigmas 2. A genus of 3 species, all of them endemic to vernal pools and grasslands in California and Baja California. *T. greenei* and *T. mucronata* are native to a few counties in California.

**SELECTED REFERENCES**


**TRIBE: ERAGROSTIDAE**


**ALLOLEPIS**


**BLEPHARIDACHNE**


**BLEPHARONEURON**


**CALAMOVILFA**


**CRYPSIS**


**DINEBRA**


**DISTICHLIS**


**ELEUSINE**


Hilu, K. W. & J. L. Johnson. 1997. Systematics of
**ERAGROSTIS**


**ERIONEURON**


**LEPTOCHLOA**


**LYCURUS**

Peterson, P. M. & O. Morrone. 1997. Allelic variation in


**MICROCHLOA**


**MONANTHOCHLOÈ**


**MUHLENBERGIA**


**MONROA**


**REDFIELDIA**


**SCLEROPOGON**


**SPOROBOLUS**


Collingwood, Australia. Pp. 184-188.


SWALLENIA


TRIDENS


TRIPLASIS


BOUTELOUA


TRIPLASIS


BOUTELOUA


TRIPLASIS


BOUTELOUA


**CHLORIS**


**CTENIUM**


**EUSTACHYS**


**CYNODON**


**GYMNOPOGON**


**HILARIA**


**SPARTINA**


**TRAGUS**


**WILLKOMMIA**


**ZOYSIA**


**TRIBE PAPPOPHOREAE**

**PAPPOPHORUM**

Chase, A. 1946. *Enneapogon desvauxii* and *Pappophorum wrightii*, an agrostological detective


**ENNEAPOGON**


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**TRIBE ORCUTTIEAE**


**NEOSTAPFIA**

Crampton, B. 1959. The grass genera *Orcuttia* and *Neostapfia*: a study in habitat and morphological specialization. Madroño 15: 97-110.


**ORCUTTIA**

Crampton, B. 1959. The grass genera *Orcuttia* and *Neostapfia*: a study in habitat and morphological specialization. Madroño 15: 97-110.


---


Stagg, C. M. 1977. The distribution of *Orcuttia californica* (Poaceae) in the vernal pools of the Santa Rosa Plateau, River-side County, California. Crossosoma Fall: 10-.

**TUCTORIA**

3.10 - SUBFAMILY PANICOIDEAE

TECHNICAL DESCRIPTION

Habit: Mostly herbaceous grasses; internodes often solid

Root Hairs: Equal

Leaf Epidermis: Complex, needle-shaped bicellular micro-hairs present; silica cells usually dumbbell-shaped, x-shaped, or saddle-shaped; stomata rhombic

Leaf Anatomy: Single sheath of parenchyma around vascular bundles (except in plants with kranz syndrome); chlorenchyma may be more or less radiating

Inflorescence: Panicles, compound racemes, ramos, and spikes

Spikelet: Dorsally compressed, disarticulating below the glumes; 1 terminal perfect floret and a staminate or neuter one below it; glumes 2, 1, or absent

Flower: Lodicules short, truncate, and heavily vasculated; stamens 3; stigmas 2

Embryo: \( P - P P \)

Cytology: \( X = 9, 10 \) (rarely 5 or 8); some with persistent nucleoli

Photosynthetic Pathways: \( C_3 \) and \( C_4 \)

Distribution: Diverse habitats, abundant in the tropics and subtropics; absent from the Arctic.

SYSTEMATICS

This circumscription of this subfamily has changed little in recent years. The principal modifications at the tribal level consists of merging Melinidae with Paniceae. Tripsaceae (Maydeae), here recognized as a distinct tribe, is often merged with Andropogoneae. Many adjustments have occurred at the generic level.

TRIBE PANICEAE

Inflorescence a panicle or a series of racemose or spicate branches that bear racemes or spikes of spikelets. First glume short, sometimes missing; second glume and sterile lemma both membranous and soft; fertile floret indurate or leathery. Spikelets or clusters of them sometimes subtended by bristly or spiny involucres. See Section 4 for a key to our

SUBTRIBE SETARIINAE

The principal distinguishing feature of the subtribe is spikelets with a hard upper lemma. The surface may be granular, wrinkled or highly polished.

PANICUM. Panic grass, panicum. Caespitose, rhizomatous or stoloniferous annuals or perennials. Culms herbaceous or woody, the internodes hollow or solid, to 4 m tall. Inflorescence an open to contracted panicle, either terminal or axillary, rarely a raceme. Spikelets 2-flowered, dorsally compressed, disarticulating below the glumes. Lower floret sterile or sometimes staminate, its lemma similar in size and texture to the second glume. Upper floret fertile, its lemma firm to indurate, awnless, and clasping the palea with its enrolled margins. Fertile lemma and palea of similar texture. Glumes 2, the first much shorter than the second, the first 1- to 7-nerved and the second 3- to 9-nerved; sterile lemma 5- to 9-nerved, awnless, similar to second glume in size and texture; fertile lemma 3- to 11-nerved, awnless, glabrous, firm to indurate at maturity; palea of fertile floret similar to lemma in texture, and tightly clasped by it. Lodicules 2; stamens 3; stigmas 2, red pigmented.

The largest genus of Gramineae with about 500 species, native just about everywhere. Of considerable economic importance as a source of grains, pasture grasses, and weeds. As treated by H & C, the genus consisted of three subgenera: \( \text{Eupanicum}, \text{Dichanthelium}, \) and \( \text{Paurochaetium}. Grasses of subgenus \( \text{Paurochaetium} \) have a point or bristle that subtends the uppermost spikelet and they are now often placed in the genus \( \text{Setaria}. Gould elevated the subgenus \( \text{Dichanthelium} \) to the generic level. That opinion, while followed early on, has been increasingly rejected.

The following key may be helpful in understanding the redefinition of \( \text{Panicum}. \) It is modified from H & C and Gould (1979).

1. Axis of branchlets extending beyond the base of the uppermost spikelet as a point or bristle -> \( \text{Setaria} \) subgenus \( \text{Paurochaetium} \)
2. Plants annual or perennial, without a basal rosette of short, broad blades or a basal tuft of soft, linear blades; panicles open or contracted at maturity, the spikelets long- or short-pediced (in some plants the spikelets sessile and the primary branches spicate); lemma and palea of upper floret smooth or rugose; culms not becoming much-branched in age and with reduced branchlets and panicles; plants flowering from July to November -> \( \text{Panicum} \) subgenus \( \text{Panicum} \)
3. Plants perennial, most species developing a basal rosette of short, broad basal blades in spring or with a tuft of soft, linear blades; panicles of main culms open, the spikelets loosely-spaced, at least some with pedicels much longer than spikelets; lemma and palea of upper floret smooth; culms of several species becoming much-branched in age to produce fascicles of reduced leafy branches and panicles; most species flowering first March to May and then throughout the growing season at irregular intervals \( \text{Panicum} \) subgenus \( \text{Dichanthelium} \)
Important grasses of the subgenus *Panicum* include *P. virgatum* (switch grass), a rhizomatous perennial over much of the United States; *P. capillare* (witch grass), a common plant of open ground and waste places; *P. bulbosum* (bulb panicum), an important forage grass of the Southwest; *P. miliaceum* (proso millet, broomcorn millet), an escape from cultivation; and *P. maximum* (elephant grass, Guinea grass), one of the tropical forage grasses introduced into the southern states.

Hitchcock & Chase recognized over one hundred species in the subgenus *Dichanthelium*, many of them very difficult to distinguish from one another and known only from very localized occurrences. These grasses are especially common in the southeastern states. In their monograph, Gould and Clark performed the heroic and welcomed task of reducing the number of species to 26! *P. oligosanthes*, in the broad sense, is perhaps the most widespread species in the subgenus.

### DICHANTHELIUM VERSUS PANICUM

<table>
<thead>
<tr>
<th>SUBGENUS DICHANTHELIUM</th>
<th>SUBGENUS PANICUM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perennial</td>
<td>Annual or perennial</td>
</tr>
<tr>
<td>Leaf blades rarely ribbed/furrowed</td>
<td>Pronounced ribs/furrows on upper and lower surfaces</td>
</tr>
<tr>
<td>Autumn/winter rosettes present</td>
<td>Rosettes absent</td>
</tr>
<tr>
<td>Cleistogamous lateral inflorescences</td>
<td>Chasmogamous terminal inflorescences</td>
</tr>
<tr>
<td>Diploids (mostly)</td>
<td>Polyploids (mostly)</td>
</tr>
<tr>
<td>$x = 9$</td>
<td>$x = 9$ or $10$</td>
</tr>
<tr>
<td>$2n = 2x = 18$</td>
<td>$2n = 4x = 18, 20, 30, 36, 40, 72 +$ aneuploids</td>
</tr>
<tr>
<td>Embryo relatively small</td>
<td>Embryo relatively large</td>
</tr>
<tr>
<td>Non-kranz anatomy</td>
<td>Kranz anatomy</td>
</tr>
<tr>
<td>$C_3$ [phosphoglyceric acid]</td>
<td>$C_4$ [oxaloacetic acid, malic acid]</td>
</tr>
<tr>
<td>Chlorenchyma irregular</td>
<td>Chlorenchyma radial</td>
</tr>
<tr>
<td>Numerous air spaces</td>
<td>Few air spaces</td>
</tr>
<tr>
<td>Outer sheath without chloroplasts</td>
<td>Large, specialized chloroplasts</td>
</tr>
<tr>
<td>Palea tip with simple papillae</td>
<td>Papillae compound or clustered</td>
</tr>
<tr>
<td>Papillae in regular rows</td>
<td>Papillae irregular</td>
</tr>
<tr>
<td>Double tunica layer</td>
<td>Single tunica layer</td>
</tr>
</tbody>
</table>

Sources:

**GENERAS SEGREGATED FROM PANICUM**

If we look in the "Species Plantarum" of Linnaeus, we will see that He recognized a genus *Panicum*. It included most everything that we now think of as a panicoid grass. Since then, botanists have carved out an impressive list of genera, most of which have stood the test of time.

<table>
<thead>
<tr>
<th>Segregate Genus</th>
<th>Basionym in Panicum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Echinocloa (1812)</td>
<td>Panice crusgalli</td>
</tr>
<tr>
<td>Setaria (1812)</td>
<td>Panicum viride</td>
</tr>
<tr>
<td>Stenotaphrum (1822)</td>
<td>Panicum dimidiatum</td>
</tr>
<tr>
<td>Steinchisma (1830)</td>
<td>Panicum hians</td>
</tr>
<tr>
<td>Brachiaria (1853)</td>
<td>Panicum eruciforme</td>
</tr>
<tr>
<td>Sacciolepis (1901)</td>
<td>Panicum glabrum</td>
</tr>
<tr>
<td>Phananthus (1903)</td>
<td>Panicum gymnacarpum</td>
</tr>
<tr>
<td>Leptoloma (1906)</td>
<td>Panicum cognatum</td>
</tr>
<tr>
<td>Lasiacis (1910)</td>
<td>Panicum divaricatum</td>
</tr>
<tr>
<td>Homolepis (1911)</td>
<td>Panicum aturensis</td>
</tr>
<tr>
<td>Paspalidium (1920)</td>
<td>Panicum geminatum</td>
</tr>
<tr>
<td>Urochloa (1920)</td>
<td>Panicum repans</td>
</tr>
<tr>
<td>Dichanthelium (1974)</td>
<td>Panicum dichotomum</td>
</tr>
</tbody>
</table>

**ERIOCHLOA.** Cup grass. Annuals or perennials, often of moist sites. Culms herbaceous, to 1 m tall. Inflorescence a sparingly branched, contracted panicle. Spikelets 2-flowered (the lower sterile and the upper bisexual), dorsally compressed, disarticulation below the glumes. Glumes 2, the first reduced to minute sheath or strip that is fused to the thickened ring- or cup-like callus; sterile lemma 5-nerved, similar to second glume, longer than fertile floret; sterile lemma 5-nerved, glabrous, indurate, mucronate to awned; palea relatively long, 2-nerved. Lodices 2; stamens 3; stigmas 2. A genus of 25-30 species native to warmer parts of both hemispheres. Of economic significance as a source of minor cereals, grains, pasture grasses, and weeds. *E. contracta* (prairie cup grass) occurs in the central and southwestern portions of the U. S.; *E. sericea* (Texas cup grass) is native to the Great Plains.

**PASPALUM.** Dallis grass, knot grass, bahia grass. Caespitose annuals or perennials, of moist sites. Culms herbaceous, to 1 dm tall. Leaf blades flat, succulent. Inflorescence spike-like, the spikelets embedded in a thickened rachis. Spikelets 2-flowered (the lower staminate or sterile and the upper fertile), dorsally compressed, bisexual, disarticulation below the glumes and falling with a rachis joint. Glumes 2, unequal, the lower nerveless and the upper 5- to 9-nerved; sterile lemma 7- to 9-nerved, as long as the second glume; sterile lemma 3- to 5-nerved, chartaceous, firmer than the glumes; palea relatively long, 2-nerved. Lodices 2; stamens 3; stigmas 2, red or white pigmented. A genus of 6 or 7 species native to the subtropical and tropical regions of the Old and New Worlds. *S. secundatum* (St. Augustine grass) is native to the Southeastern United States. It is a popular lawn grass that also escapes and becomes weedy.

**ECHINOCHLOA.** Barnyard grass, jungle-rice. Coarse, caespitose annuals or perennials. Culms herbaceous, the internodes hollow or solid, often succulent. Leaf sheaths compressed. Inflorescence a contracted to more or less open panicle, the branches simple to rebranched. Spikelets sub sessile, solitary, or in irregular clusters on one side of the branch, 2-flowered (the lower sterile and the staminate or fertile), plano-convex, bisexual, disarticulation below the glumes. Glumes 2, unequal, the lower 0- to 3-nerved and the upper 5- to 7-nerved; sterile lemma similar to second glume, 5-nerved, awned; sterile lemma planoconvex, 5-nerved, smooth and shining, pointed, its margins enrolled below (enclosing the palea at that point), the upper portion flat; palea similar to fertile lemma in texture, tapering to a point that is free from the lemma margins. Lodices 2; stamens 3; stigmas 2, red pigmented. A genus of 20-40 species native to the warmer regions of both hemispheres. Of economic significance as a source of minor cereals, grains, pasture grasses, and weeds. *E. crus-galli* (barnyard grass) and *E. colonia* (jungle-rice) are weedy in the United States.

**AXONOPUS.** Carpet grass, mat grass. Ours stoloniferous or caespitose perennials. Inflorescence a series of 2 to many subdigitate racemes, sometimes inserted on a central axis. Spikelets oblong-elliptical, disarticulating below the glumes. First glume absent; rounded back of fertile lemma indurate, turned away from rachis; palea indurate. Lodices 2; stamens 3; stigmas 2, white. A genus of about 100 species native to the warmer regions of the New World, especially South America. One species is native to Africa. They occur in savannas, in forest clearings, and can become weedy. Some species are used for pasture and for lawns. Three species are native to the United States; *A. affinis*, common carpet grass, is the most frequently encountered.

**SACCIOLEPIS.** Cup scale. Annual or perennial herbs. Inflorescence a contracted [open] panicle. Spikelets laterally compressed, disarticulating below the glumes. Glumes 2, prominently ribbed, the upper one gibbous and inflated; sterile lemma 3- or 5-nerved; upper lemma dorsally compressed; fertile floret smooth, indurate, rounded. Lodices 2; stamens 3; stigmas 2. A genus of about 30 species native to the tropics and...
s

found in wet sites and shallow waters. Only *Setaria*

*Ok* the SE portion of the country.

American cupscale, is native to the U. S., from TX and

North America:

A genus of 110-125 species native to the warmer

3; stigmas 2, white or red pigmented.

one; fertile lemma 1- to 5-nerved, indurate, rounded

bristles (sterile branches), 2-flowered (the lower

sterile and the upper fertile), dorsally compressed,

bisexual, disarticulation below the glumes, but above

the bristle(s). Glumes 2, the first broad, typically

about half the length of the second, second glume and

sterile lemma similar in size and texture; sterile

lemma 5-nerved, as long as or longer than the fertile

one; fertile lemma 1- to 5-nerved, indurate, rounded

at its apex, with fine to coarse transverse wrinkles;

palea relatively long, 2-nerved. Lodicules 2; stamens

3; stigmas 2, white or red pigmented.

A genus of about 300 species native to warmer

regions of both hemispheres. Of economic importance as a source of grains, pasture and lawn grasses, and

weeds. As treated here, the genus includes taxa assigned to *Leptoloma* and *Trichachne* in H & C. *D. sanguinalis* (hairy crab grass) and *D. ischaemum* (smooth crab grass) are major weeds around the country; *D. caespitosa* (Arizona cottontop) [= *Trichachne c.* in H & C] is an important forage grass in the Southwest; *D. cognatum* (fall witchgrass) [= *Leptoloma c.* in H & C] is common in the East.

**SUBTRIBE: CENCHRINAE**

This subtribe is probably the most easily recognized because of the bristles or scales that subdhen the spikelets.

Pennisetum. Fountain grass, feathertop. Caespitose, rhizomatous, stoloniferous perennials; rarely annual. Culms herbaceous, the internodes hollow or solid, to 4 m tall. Inflorescence a dense, spike-like panicle. Spikelets 2-flowered (the lower sterile and the upper fertile), dorsally compressed, bisexual, solitary or in clusters of 2 or 3, subtended by an involucre of bristles (often plumose), these united at their base and falling with the spikelet at disarticulation. Glumes 2, the first small or vestigial, second glume and sterile lemma similar in size and texture; sterile lemma 3- to 9-nerved, less firm than fertile lemma; fertile lemma 5- to 7-nerved, similar to or firmer than glumes in texture; palea relatively long, 2-nerved. Lodicules 2 or 0; stamens 3; stigma 2.

A genus of about 80 species native to the warmer regions of both hemispheres. Of economic importance as a source of grains, pasture and lawn grasses, ornamentals, and weeds. *P. glaucum* (pearl millet) is an important food plant in the tropics. *P. purpureum* (Napier grass, elephant grass) is an important forage plant; *P. clandestinum* (kikuyu grass) is an important pasture grass; *P. villosum* (feathertop) is grown as an ornamental, where it often escapes to become a major pest.

Cenchrus. Sandbur. Annuals or perennials, caespitose, rhizomatous, or stoloniferous. Culms herbaceous, often weak, decumbent, internodes hollow or solid, to 1 m tall. Inflorescence a series of spike-like or racemose burs, these readily disarticulating. Spikelets 2-flowered (lower sterile and the upper fertile), dorsally com-pressed, bisexual,
hidden within burs (involutecres of bristles or spines), the entire structure falling from the plant at maturity. Glumes 2, unequal, the first 1- to 5-nerved and the second 1- to 7-nerved, thin, membranous; sterile lemma 1- to 7-nerved, ± equal to fertile lemma, awnless; fertile lemma 3- to 7-nerved, thin, membranous, its apex acuminate; palea relatively long, 2-nerved. Lodicules 0; stamens 3; stigmas 2.

A genus of about 20 species native to the warmer regions of both hemispheres, but mostly American. *C. incertus* (including *C. pauciflorus* of H & C) is widespread in sandy places over much of the country; *C. myosuroides* (big sandbur) can reach 1.5 m in moist, sandy sites in the Southeast. Transitional species make the distinction between this genus and *Pennisetum* difficult.

**TRIBE: ANDROPOGONEAE**

Inflorescence a series of paired spikelets, evenly or unevenly pedicellate; pedicellate spikelet often reduced (sometimes missing, which can lead to misinterpretation of the inflorescence). Spikelets 2-flowered, the lower sterile or staminate and the upper bisexual, awnless or awned from fertile lemma, the awn often easily disarticulating. Glumes thick, firm, equal in length. Fertile lemma and palea thin.

**SUBTRIBE: SACCHARINAE**

Inflorescence terminal, of solitary, digitate, or paniculate rames. Spikelets paired, similar; one sessile and the other pedicellate or both with pedicels. Clayton & Renvoize view this group as the most primitive because the grasses have unspecialized rachis internodes and both members of the spikelet pair are fertile.

*SACCHARUM*. Sugar cane, plume grass. Robust perennials. Inflorescence a conspicuous, plumose panicle to almost 1 m in length. Spikelets of the pair alike, fertile, awnless, and obscured by a tuft of long, silky hairs attached at the bases. Glumes large and firm. Sterile lemma, fertile lemma (sometimes absent), and palea membranous. *S. officinarum* (sugar cane), one of the earliest plants to be domesticated, is the source of about two-thirds of the sugar used in commerce.

As treated here, the genus includes *Erianthus*, which H & C recognized as a separate genus. These plants, which are found in the Southeast, differ from sugar cane in having a long awn arising from the fertile lemma.

*MISCANTHUS*. Miscanthus, eulalia. Caespitose or rhizomatous perennials, often cane- or reed-like. Culms herbaceous, the internodes solid, to 2 m tall. Inflorescence a fan-shaped panicle. Spikelets unequally pedicellate, silky hairy, 2-flowered, dorsally compressed, bisexual, disarticulation below the glumes. Glumes 2, ± equal, papery to membranous, the first 3- or 4-nerved and the second 1- to 5-nerved; sterile lemma membranous, longer than the fertile one, awnless; fertile lemma membranous, 0- to 3-nerved, with a geniculate and twisted awn or awnless; palea relatively short, nerveless. Lodicules 2; stamens 2 or 3; stigmas 2, red pigmented.

A genus of about 20 species native to the Old World, especially to Asia. *M. sinensis* is grown as an ornamental in this country.

**SUBTRIBE: ANDROPOGONINAE**

Inflorescence of single, paired [digitate] rames, these aggregated into terminal or axillary compound panicles. Spikelets of the pair dissimilar. Grasses of this subtribe have 2-keeled glumes and callus inserted into hollowed tip of the internode.

*ANDROPOGON*. Bluestem, beard grass. Coarse, caespitose or rhizomatous perennials; less frequently annuals. Culms herbaceous, the internodes solid, to 2 m tall. Inflorescence a series of 2- to several rames, the flowering culms much-branched, subtended by a spathic-like sheath in some species. Spikelets 2-flowered (the lower floret sterile, the upper bisexual), dorsally compressed. Sessile spikelet well-developed and fertile, disarticulating with a section of rachis and pedicel; pedicellate spikelet well-developed, reduced, or absent. Glumes 2, ± equal, the first keeled and 1- to several-nerved and the second 1- to 3-nerved, awnless; sterile lemma hyaline, 2-nerved, ± equaling the fertile lemma; fertile lemma hyaline, narrow, 1- to 3-nerved entire or bifid, usually bearing a bent and twisted awn; palea hyaline, reduced or absent, nerveless. Lodicules 2; stamens 1-3; stigmas 2.

A genus of about 100 species native to warmer regions of the Old and New Worlds. We have a number of them in North America, mostly in the southeastern United States. As treated by H & C, *Andropogon* consisted of three subgenera: *Arthrolophis*, *Amphilophis*, and *Schizachyryum*. Each is now recognized as a distinct genus. *Andropogon* [= subgenus *Arthrolophis*] includes such common species as *A. virginicus* (broomsedge), a plant of sandy, sterile soils in the Southeast; *A. gerardii* (big bluestem), a very important forage plant of the tall grass prairie; *A. hallii* (sand bluestem), a close relative of big bluestem that grows in sandy places; and *A. glomeratus* (bushy beard grass), which grows in moist places in the Southeast and Southwest.

*SCHIZACHYRIUM*. Little bluestem. Caespitose or rhizomatous perennials. Culms herbaceous, the internodes hollow or solid. Flowering culms much-branched, each terminating in a single narrow rame. Spikelets as in *Andropogon*, often closely-appressed to the rachis. Sessile spikelet fertile and awned; pedicellate spikelet rudimentary.

A genus of about 60 species native to the warmer regions of north hemispheres. *S. scoparium* (little bluestem) is an important forage plant of the tall grass prairie, where it is one of the dominants.

**SUBTRIBE: ANTHISTRIRIINAE**

According to Clayton & Renvoize (1986: 354), this sub-tribe “... is distinguished from Andropogoninae by a pointed callus applied obliquely to the internode tip, rather than blunt and sunk into it.”

*HYPPARRHENIA*. Thatching grass, jaraguá grass. Caespitose perennials, to 2.5 m tall. Inflorescence an elongate compound panicle, consisting of paired racemes subtended by ± conspicuous bracts. Spikelets paired, the lower pairs sterile and awnless; fertile spikelets 1 to a few on each rame, the lemma bearing a strong geniculate awn.
A genus of about 55 species native to the Old World, mainly to Africa, where they are common in savannas. Introduced in the American tropics, where it has been weedy. Two species, *H. hirta* and *H. rufa*, occur as roadside weeds in the Southwest and Southeast.

**SUBTRIBE: SORGHINAE**

Inflorescence terminal [axillary], of single, digitate, or paniculate rames, sometimes reduced to a trio of spike-lets or a single spikelet. Spikelets paired, dissimilar, the sessile bisexual; pedicellate spikelet male or barren, sometimes much reduced.

**DICHANTHIUM**. Bluestem. Caespitose, rhizomatous or stoloniferous perennials [rarely annual]. Culms herbaceous, the internodes solid, to 2 m tall. Inflorescence similar to *Bothriochloa*, but lacking central groove or membranous area on its pedicels and internodes. The lower pairs of spikelets on each rame are typically sterile and awnless.

A genus of about 16 species native to the Old World tropics. The genus is not included in H & C.

**Bothriochloa**. Bluestem. Caespitose, rhizomatous, or stoloniferous perennials. Culms herbaceous, the internodes solid, to 2 m tall. Inflorescence a series of a few to several rames, as in *Andropogon*. Pedicels and upper rachis branches with a central groove or membranous area. Sessile spikelet fertile and awned, some with a pit (depressed glandular area) on the middle or upper portion of the first glume of the sessile spikelet. Pedicellate spikelet usually well-developed, but stamine or neuter. Spikelets disarticulating with a section of rachis.

A genus of about 30-35 species native to the warmer parts of both hemispheres. This genus was treated as *Andropogon* subgenus *Amphilois* in H & C. *B. saccharoides* (silver beard grass) and *B. barbinodis* (cane bluestem) are important forage grasses.

**SORGHUM**. Sorghum, milo, broomcorn, kaffir. Stout annuals or caespitose, stoloniferous, or rhizomatous perennials. Culms herbaceous, the internodes solid, to 3 m tall. Inflorescence a large, open to contracted panicle. Spikelets in trios at branchlet tips (the lateral ones pedicellate and sterile) or in pairs below (one sessile and the other pedicellate). Sessile spikelets disarticulating with a rachis segment. Glumes 2, ± equal, 3- to several-nerved, leathery, awnless; sterile lemma membranous, 0- 2-nerved, awnless; fertile lemma membranous, 1- to 3-nerved, with a geniculate and twisted awn (deciduous in *S. halepense*); palea relatively long, 2-nerved. Lodicules 2; stamens 3; stigmas 2, red pigmented.

A genus of 30-35 species, only two of them native to the New World (none to North America). The genus is of considerable economic importance as a source of grains, fodder, and weeds. *S. bicolor* (sorghum, milo) [= *S. vulgare* in H & C] is the source of sugary juices for syrups, grain for cattle feed, and brooms from which traditional brooms are made; *S. halepense* (Johnson grass) is a tetraploid, pernicious weed.

**SORGHASTRUM**. Indian grass. Caespitose perennials. Culms herbaceous, to 2 m tall. Inflorescence a terminal panicle of rames. Spikelets paired, the pedicellate greatly reduced (often represented by nothing more than a hairy pedicel). Sessile spikelet disarticulating with rachis segment remaining attached. Glumes 2, ± equal, the lower 9-nerved and the upper 5-nerved, leathery; sterile lemma membranous, 2-nerved, awnless; fertile lemma membranous, 1-nerved (?), with a stout, twisted, geniculate awn; palea often reduced or absent. Lodicules 2; stamens 3; stigmas 2.

A genus of 15-20 species native to the warmer regions of both hemispheres. *S. nutans* (Indian grass) is a native of the tall grass prairie; two other species have more restricted distribution in the Southeast.

**SUBTRIBE: ROTTBOELLINEAE**

Inflorescence cylindrical, spike-like. Spikelets paired, awnless, embedded in cavities or hollow rachis joints, the pedicel often fused to the rachis. Disarticulation occurs as the rachis joints separate from one another at maturity. See Section 4 for a key to our North American taxa.

**ROTTBOELIA**. Itch grass, Kelly grass. Robust annual. Blades to 3 cm wide. Sheaths papillose-hispid, the hairs irritating to some individuals. Inflorescence a subcylindrical raceme, its apex with abortive spikelets only. Spikelets awnless, paired (one sessile and perfect, the other pedicellate and sterile), borne at the nodes of a thickened rachis. Upper rachis joints hollow, the thickened pedicel adnate to it, thereby making the pedicellate spikelet appear sessile. A genus of 3 species native to the Old World tropics. *R. cochinchenensis* (= *R. exaltata* in H & C) is introduced in Florida. It provides fodder.

**ELIONURUS**. Balsamscale. Erect perennials. Inflorescence a single spike-like raceme. Spikelets awnless, paired, one sessile and the other pedicellate, along a discontinuous rachis. The sessile spikelet perfect, appressed to the concave side of the rachis; the pedicellate spikelet stamine. Spikelet pair disarticulating with a segment of the rachis. A genus of about 14 species native to America, Africa, and Australia. Our species are found in the drier areas of the Southeast and in the prairies and pine woods of the Southeast. The spelling *Elyonurus* is used in older literature.

**EREMOCHLOA**. Centipede grass. *Eremochloa ophiuroides*, native to Southeast Asia, has been introduced into Florida and other areas in the Southeast as a popular lawn grass and for erosion control. It is a low, rhizomatous, perennial that forms dense turf. It produces spike-like racemes of paired sessile/pedicellate spikelets on terminal and axillary peduncles. The rachis is not thickened. The first glume of the sessile spikelet is winged at the summit.

**HACKELOCHLOA**. Pitscale grass. Annuals to 1 meter. Sheaths and blades papillose-hirsute. Inflorescence a series of many solitary, spike-like racemes enclosed in spathes. Spikelets awnless, paired, one sessile and the other pedicellate. Rachis joint and pedicel fused, clasped between the edges of the first glume of the sessile spikelet. The rounded, pitted appearance of the first glume is highly diagnostic. A genus of 2 species native to the Old World and New World tropics. *Hackelochloa granularis* has been introduced in the Southwest and in the Southeast. It is a limited source
of forage.

**HEMARTHRIA.** Limpo grass. Mostly perennials. Inflorescence a single flattened, axillary raceme. Spikelets paired, the sessile one sometimes awned, its lower glume slightly winged; pedicel of stalked spikelet fused to internode. A genus of 12 species native to the warmer regions of the Old World, especially of wet sites. *H. altissima* (= *Manisuris* a. in H & C) is adventive in the United States.

**COELORACHIS.** Joint-tail grass. Perennials, often with broad leaf blades. Inflorescence a single cylindrical or flattened raceme. Spikelets paired, less often in trios. Pedicellate spikelet well-developed or vestigial, its stalk free from the rachis. A genus of 20 or so species native to the tropics, especially on damp soils in savannas and grasslands. The four species found in North America were treated as species of *Manisuris* by H & C.

**SUBTRIBE: ZEINAE**

The grasses of this subtribe are characterized by highly modified, unisexual, dimorphic spikelets, borne within the same or in different inflorescences. This group is often treated as a distinct tribe, as in H & C, who called it Tripsaceae [= Maydeae of more recent authors].

If G. L. Stebbins was correct in concluding that grasses are most advanced of the flowering plants, then maize and its relatives may well be the most advanced of the most advanced! That’s why I put them at the end of our survey.

**COIX.** Job’s tears. Annuals or perennials. Culms herbaceous, the internodes solid, to 2 m tall. Leaf blades broad (to 4 cm). Inflorescence a raceme, but not immediately apparent as such. Staminate spikelets 2-flowered, in pairs or trios along a common rachis, protruding from an opening at apex of a very hard, white or drab, beadlike involucre. Pistillate spikelets enclosed within an involucre, typically in groups of 3 (1 fertile and 2 sterile).

A small genus of 4 or 5 species native to tropical Asia. *C. lacryma-jobi* (Job’s tears) is a popular ornamental, its fruit-like involucres used in jewelry and rosaries. It has escaped from cultivation in the South.

**TRIPSACUM.** Gama grass. Robust, rhizomatous, caespitose perennials. Culms herbaceous, to 3+ m tall. Inflorescence a series of [1-] 2-several spike-like branches bearing pistillate spikelets on their lower portions and staminate ones above. Staminate spikelets 2-flowered, paired (1 sessile and 1 pedicellate) on one side of the rachis, disarticulating as a major segment of the inflorescence. Pistillate spikelets solitary and alternately inserted in hollow cavities of a thickened rachis, falling as separate bead-like units. Lodicules 2; stamens 0 or 3; stigmas 2.

A genus of 7-12 species native to warmer parts of the New World. *T. dactyloides* (eastern gama grass) is native to the eastern and central regions; two other species occur in Florida and Arizona.

**ZEA.** Maize, corn, Indian corn, teosinte. Robust annuals or perennials. Culms herbaceous, the internodes solid, to 5 m tall. Staminate spikelets paired, unequally pedicellate, in terminal inflorescences consisting of spike-like branches. Glumes broad, thin; lemma and palea hyaline. Pistillate spikelets paired, in axillary inflorescences, either sunken in cavities of a hardened rachis or sessile on a thickened, almost woody axis, the "cob." Glumes broad, thin, rounded, and much shorter than the mature caryopsis; lemma and palea membranous and hyaline. Lodicules 0; stamens 0 or 3; stigmas 2.

A genus of 5 species native to the New World. As treated here, the genus includes *Euchlaena*. *Z. mays* ssp. *mays* (maize or corn), the only important cereal native to the New World, is unknown in the wild; *Z. mays* ssp. *mexicana* is teosinte (= *Euchlaena* m. in H & C), whose evolution is intertwined with that of maize; *Z. diploperennis* is a recently discovered perennial teosinte endemic to Mexico with great agronomic potential.
## COMPARISON OF NEW WORLD “MAYDEAE”

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* True of Tripsacum dactyloides

[Source: After Mangelsdorf & Reeves, 1939: 205]

## SELECTED REFERENCES


**TRIBE PANICEAE**


**AMPHICARPUM**


**AXONOPUS**


**BRACHIARIA**


**CENCHRUS**


**DIGITARIA**


**ECHINOCHLOA**


**ERIOCHLOA**


LASIACIS


MELINIS


OPLISMENUS


PANICUM


Silveus, W. A. 1942. Grasses: classification and


**PASPALUM**


**PENNISETUM**


**SACCIOLEPIS**


**SETARIA**


Veldekamp, J. F. 1994. Miscellaneous notes on southeast Asia Gramineae. IX. *Setaria* and *Paspalidium*. Blumea


STENOTAPHRUM


UROCHLOA


TRIBE ANDROPOGONEAE


ANDROPOGON


ANTHEPHORA


ARTHRAXON


**BOTHRIOCHLOA**


**COELORACHIS**


**CYMBOPOGON**


**DICHANTHIUM**


**EREMOCHLOA**


**HEMARTHRIA**


**HETEROPOGON**


**IMPERATA**


**MICROSTEGIUM**


**MISCANTHUS**


**ROTBBOELLIA**


**SACCHARUM**


**SCHIZACHYRIUM**


**SORGHASTRUM**


**SORGHUM**


**THEMEDA**


**TRIPSACUM**


**VETIVERIA**


**ZEA**


SECTION 4 - AN OVERVIEW OF U. S. GRASSES

### 4.01 - STATISTICAL SUMMARY

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### 4.02 - SUBFAMILIES, TRIBES, & GENERA OF CONTINENTAL NORTH AMERICA

**SUBFAMILY: ARISTIDOIDEAE**
- Tribe: Aristideae
  - Aristida

**SUBFAMILY: ARUNDINOIDEAE**
- Tribe: Arundineae
  - Arundo
  - Gynerium
  - Hakonechloa
  - Molinia
  - Phragmites
  - Thysanolaena

**SUBFAMILY: BAMBUSOIDEAE**
- Tribe: Bambuseae
  - Arundinaria
  - Bambusa
  - Phyllostachys
  - Pleioblastus
  - Pseudosasa
- Tribe: Olyreae
  - Olyra

**SUBFAMILY: CENTOTHECOIDEAE**
- Tribe: Centothecae
  - Chasmanthium

**SUBFAMILY: CHLORIDOIDEAE**
- Tribe: Cynodonteae
  - Aegopogon
  - Bouteloua
  - Buchloë
  - Chloris
  - Ctenium
  - Cynodon
  - Enteropogon
  - Eustachys
  - Gymnopogon
  - Hilaria
  - Microchloa
  - Opiza
  - Schedonnardus
  - Spartina
  - Tragus
  - Willkommia
  - Zosysia

**SUBFAMILY: ERAGROSTIDOIDEAE**
- Tribe: Eragrostideae
  - Acrachne
  - Allolepis
  - Blepharidachne
  - Blepharoneuron
  - Calamovilfa
  - Cladoraphis
  - Cryopsis

**SUBFAMILY: OLYREAEOIDEAE**
- Tribe: Orcuttieae
  - Neostapfia
  - Orcuttia
  - Tuctoria
- Tribe: Pappophoreae
  - Cottea
  - Enneapogon
SUBFAMILY: DANTHONIOIDEAE

Tribe: Danthonieae
- Cortaderia
- Danthonia
- Rytidosperma
- Schismus

Tribe: Danthonia
- Stenotaphrum
- Urochloa

SUBFAMILY: EHRHARTIOIDEAE

Tribe: Ehrharteae
- Ehrharta

Tribe: Oryzeae
- Leersia
- Luziola
- Oryza
- Zizania
- Zizaniopsis

SUBFAMILY: PANICOIDEAE

Tribe: Andropogoneae
- Andropogon
- Apluda
- Arthroxon
- Bathyrochloa
- Chrysopogon
- Coix
- Coelorachis
- Cymbopogon
- Dichanthium
- Elonurus
- Eremochloa
- Euclasta
- Hackelochloa
- Hemarthria
- Heteropogon
- Hyparrhenia
- Imperata
- Ischaemum
- Microstegium
- Miscanthus
- Polytrias
- Rottboellia
- Saccharum
- Schizachyrium
- Sorghastrum
- Sorghum
- Themeda
- Trachypogon
- Tripsacum
- Zea

Tribe: Paniceae
- Alloteropsis
- Amphicarpum
- Anthaenantia
- Anthephora
- Axonopus
- Brachiaria
- Cenchrus
- Digitaria
- Echinochloa
- Eriochloa
- Hymenachne
- Lasiacis
- Melinis
- Opilsmenus
- Panicum
- Paspalum
- Pennisetum
- Reimarochloa
- Sacciolepis
- Setaria
- Setariopsis
- Schizachne

SUBFAMILY: PHAROIDEAE

Tribe: Phareae
- Pharus

SUBFAMILY: POÖIDEAE

Tribe: Ampelodesmeae
- Ampelodesmos

Tribe: Aveneae
- Agropyron
- Agrostis
- Aira
- Alpecurus
- Avena
- Calamagrostis
- Calamnophila
- Cinna
- Corynephorus
- Deschampsia
- Distylium
- Gastridium
- Gaudinia
- Helictotrichon
- Holcus
- Koeleria
- Lagurus
- Limnodea
- Milimum
- Phalartis
- Phleum
- Polygona
- Sphenopholis
- Trisetum
- Ventenata

Tribe: Brachypodieae
- Brachypodium

Tribe: Brachyelytreae
- Brachyelytrum

Tribe: Triticeae
- Aegilops
- Agropyron
- Dasypryrum
- Elymus
- Eremopyrum
- Hordeum
- Secale
- Triticum

Revised: 10 January 2005
### The 18th Century

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**THE 21ST CENTURY**

... the work continues!
### 4.04 - GRASS GENERA: ALPHABETICAL

The purpose of this section is to provide an alphabetical listing of the genera of North American grasses. The generic name in the left column is the one that I accept, unless you are referred to another name, as in the first entry. The abbreviations in the right column indicate the subfamily and tribe of that genus.

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**NOTES:**

† = presumed to be extinct or extirpated

p. p. = in part

* = found in Alaska and Canada only

Revised: 11 January 2005
**4.05 - GRASS GENERA: SYNOPSIS**

**Acrachne.** One species: *A. racemosa*, adventive in southern California.

**Acroceras.** One species: *A. oryzoides.*

**Aegilops.** Goat grass. Three species: *Ae. cylindrica*, *Ae. ovata*, and *Ae. triuncialis*.

**Aegopogon.** One species: *A. tenellus*.

**X Agropogon.** One species: *X A. littoralis*, an inter-generic hybrid involving *Agrostis stolonifera* and *Polypogon monspeliensis*.

**Agropyron.** Crested wheatgrass. One to three species: (a much smaller genus than in H & C; most species have been transferred to *Elymus*). *A. desertorum*, *A. cristatum*, and *A. pectiniforme*.

**Agrostis.** Bent, bent grass, hair grass, redtop, tickle grass. About 40 species.

**Aira.** Hair grass, tickle grass. Three species: *A. caryophyllea*, *A. elegans*, and *A. praecox*.

**Allolepis.** One species: *A. texana*, native to TX.

**Alloteropsis.** One species: *A. cimicina*. FL.

**Alopecur us.** Foxtail, meadow foxtail. Eleven species.

**Ammophila.** Beach grass, European beach grass. Three species: *A. arenaria* (a European species introduced to control erosion on coastal sand dunes), *A. breviligulata*, and *A. champlainensis* (restricted to the Great Lakes region).

**Ampelodesmos.** Dis grass. One species, *A. mauritanica*, a Mediterranean species sometimes grown as an ornamental has escaped in Napa Co., CA.

**Amphicarpum.** Goober grass. Two species: *A. muhlenbergii* and *A. purshii*, are unusual in having underground cleistogamous spikelets.

**Andropogon.** Bluestem, beard grass, broom-sedge. About 14 species.

**Anthaenantia.** Silky scale. Two species: *A. rufa* and *A. villosa*.

**Anthophora.** One species: *A. hermaphrodit a*.

**Anthoxanthum.** Vernal grass, sweet vernal grass. Two species: *A. aristatum* and *A. odoratum*.

**Apera.** Silky bent grass, wind grass. Two species: *A. spica-venti* and *A. interrupta*.

**Apluda.** Mauritian grass. One species: *A. mutica*, intro-dused in MD where it may not be persisting.

**Arctagrostis.** Polar grass. One species: *A. latifolia*, which is native to AK and Canada, but not found in the conterminous U. S.

**Arctophila.** Pendant grass. One species, *A. fulva*, which is native to AK and elsewhere, but not found in the conterminous U. S.

**Aristida.** Three-awn, arrow feather. Thirty-six species.

**Arrhenatherum.** Oat-grass. One species: *A. elatius*. Eurasia. Some plants have a series of small, bulb-like corms.

**Arthraxon.** One species: *A. hispidus*.

**Arundinaria.** Cane, switch cane. Three species: *A. gigantea*, with two subspecies and a hybrid between them (*A. g. ssp. x macrosperma*) of the eastern and southeastern U. S. are our only native woody bamboos. *A. pumila*, an ornamental bamboo from Japan, is naturalized in CA. *A. simonii* is naturalized in NV.

**Arundo.** Reed, giant reed. One species: *A. donax*. Robust perennial typically found along rivers, streams, and waterways.

**Avena.** Oat, wild oat. Ten species, all native to the Old World.

**Axonopus.** Carpet grass. Three species: *A. affinis*, *A. compressus*, and *A. furcatus*.

**Bambusa.** Hedge bamboo, common bamboo. Two species: *B. glaucens* and *B. vulgaris* have escaped from cultivation and are now established in FL.

**Beckmannia.** Slough grass. One species: *B. syzigachne*.

**Blepharidachne.** Eyelash grass. Two species: *B. bigelovii* and *B. kingii*.

**Blepharoneuron.** Pine dropseed. One species: *B. tricholepis*.

**Bothriochloa.** Silver bluestem. Fifteen species.

**Bouteloua.** Grama grass, sideoats grama. Twenty-two species. Includes *Cathestecum*.

**Brachyelytrum.** Short-husk. Two species: *B. erectum* and *B. septentrionale*.

**Brachypodium.** False brome. Three species (all European): *B. distachyon* occurs widely. *B. sylvaticum* is naturalized in Benton Co., OR. *B. pinnatum* occurs along the California coast.

**Briza.** Quaking grass, rattlesnake grass. Three species: *B. maxima* (often used in dried arrangements), *B. media*, and *B. minor*. European introductions.

**Bromus.** Brome, chess, cheat grass, rescue grass, ripgut, chess. Forty-five species.

**Buchloë.** Buffalo grass. One species: *B. dactyloides*, a native of the short grass and mixed grass prairies.

**Calamagrostis.** Reed grass, reed bent grass, bluejoint. Thirty-seven species.

**X Calamophila.** Reed grass. Two species, hybrids between *Calamagrostis* and *Ammophila*. 

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**Calamovilfa.** Sand reed. Five species.

**Catabrosa.** Brook grass. One species: *C. aquatica*.

**Cenchrus.** Sandbur. Twelve species.

**Chasmanthium.** Wild-oats, spike grass. Five species. The conspicuously flattened spikelets of *C. latifolium* are sometimes used in dried arrangements.

**Chloris.** Finger grass, windmill grass, feather grass, Rhodes grass. Twenty-four species.

**Chrysocephalus.** Beard grass, khus-khus, vetiver grass. Three species: introduced grasses, mostly in the south-eastern U. S.

**Cladoraphis.** Bristly love grass. One species: *C. cyperoides*, adventive in OR. Southern Africa.

**Coelochloris.** Joint grass, joint-tail, thintail. Four species. Treated as *Manisuris* in H & C.

**Coix.** Job’s tears. One species: *C. lacryma-jobi*, established in FL and LA. Its grey-white, seed-like pistillate involucres are found in necklaces, rosaries, and junk jewelry.

**Coleanthus.** One species: *C. subtilis*, adventive in OR and WA.

**Cortaderia.** Pampas grass. Two species: *C. jubata* has become a major pest in northern CA. *C. doloia* is a popular ornamental.

**Corynephorus.** Gray hair grass. One species: *C. canescens*. Europe.

**Cottlea.** One species: *C. pappophoroides*, native from AZ to TX.

**Crypsis.** Swamp timothy, prickle grass. Three species: *C. alopecuroides*, *C. schoenoides*, and *C. vaginiflora*. Eurasia & Africa. [= Heliochloa in H & C].

**Ctenium.** Toothache grass. Two species: *Ct. aromaticum* and *Ct. floridanum*. Grasses of the southeastern U. S., the latter endemic to FL.

**Cutandia.** One species: *C. memphitica*, a Mediterranean introduction naturalized in CA. Doubtfully persisting.

**Cymbopogon.** Citronella grass. Three species: *C. citratus*, *C. nardus*, and *C. refractus*. Source of essential oil used in cooking and perfumes, etc.

**Cynodon.** Bermuda grass, star grass. Five species: *C. dactylon* is a popular lawn grass.

**Cynosurus.** Dogtail. Two species: *C. cristatus* and *C. echinatus*. European weeds.

**Dactylis.** Orchard grass, cocksfoot. One species: *D. glomerata*. Europe.

**Dactyloctenium.** Crowfoot grass. Two species: *D. aegyptium* naturalized along the Gulf and Atlantic coastal plains. *D. radulans*, from Australia, escaped in Tucson, AZ.

**Danthonia.** Poverty-oats, oat-grass. Thirteen species.

**Dasypyrum.** Mosquito grass. One species: *D. villosum*, a Mediterranean introduction.

**Deschampsia.** Hair grass. Seven species: all of them native.

**Desmazeria.** Fern grass. One species: *D. rigida*, a European introduction.

**Diarrhena.** Beak grain. One species: *D. americana*, native to eastern and central states.

**Dichanthium.** Bluestem. Three species: *D. annulatum*, *D. aristatum*, and *D. sericeum*, Old World pasture grasses found in TX and LA.

**Digitaria.** Crab grass, witch grass, Arizona cottontop. About thirty species.

**Dinebra.** Viper grass. One species: *D. retroflexa*, adventive in CA & NC. Tropical Africa and Asia.

**Disanthelium.** One species: *D. californicum*, native to San Clement, Santa Catalina Islands, and Baja California, presumed extinct in the United States (last collected in 1912).

**Distichlis.** Salt grass. One species: *D. spicata*, found typically in saline soils and coastal salt marshes.

**Dupontia.** Tundra grass. One species: *D. fischeri*, native to AK and elsewhere, but not found in the conterminous U. S.

**Echinochloa.** Barnyard grass, jungle-rice, water grass, cockspur. Eight species.

**Ehrharta.** Veldt grass. Three species: *E. calycina*, *E. erecta*, and *E. longiflora* (all from S. Africa) naturalized in CA.

**Eleusine.** Goose grass, African millet, three-spike grass, yard grass. Three species: *E. coracana*, *E. indica* and *E. tristachya* are naturalized in scattered locations.

**Elionurus.** Balsam scale. Two species: *E. barbiculmis* and *E. tripsacoides*.

**X Elyhordeum.** Five species. An intergeneric hybrid between *Elymus* and *Hordeum*.

**Elymus.** Rye grass, wild-rye, quack grass, squirreltail, bottlebrush grass. Genus much larger or much smaller than in H & C, depending upon taxonomic treatment followed. About fifty-five species.

**Enneapogon.** Spike-pappus grass, 9-awned pappus grass. One species: *E. desvauxii*.

**Enteropogon.** Umbrella grass. Three species, two of them introduced from the Old World.

**Eragrostis.** Love grass, stink grass, pony grass. About 56 species.

**Eremochloa.** Centipede grass. One species: *E. ophurooides*, naturalized in TX and LA. Historic collection of *E. ciliaris* from San Francisco bay area.

**Eremopyrum.** Annual wheat grass. Three species: *E. bonepartis* and *E. orientale* are naturalized in NY. *E.
triticeum is naturalized in the western U. S. Old World introductions.

**Eriochloa.** Cup grass. Eleven species.

**Erioneuron.** Fluff grass. Three species: *E. avenaceum, E. pilosum* and *E. pulchellum* are grasses of drier sites in the southwestern U. S.

**Eustachys.** Chickenfoot grass, finger grass, windmill grass. Seven species.

**Festuca.** Fescue, annual fescue, rye grass, darnel. As treated here, genus includes annual species often segregated into *Vulpia, Lolium* and *Festulolium*. About 47 species.

**Festulolium.** Three species, hybrids between *Festuca* and *Lolium*.


**Gastridium.** Nit grass. One species: *G. ventricosum*, a European introduction, widely naturalized.

**Gaudinia.** One species: *G. fragilis*, a European introduction, found only in Sonoma Co., CA.

**Glyceria.** Manna grass, fowl meadow grass. Nineteen species.

**Gymnopogon.** Skeleton grass, beard grass. Three species: mostly eastern half of country; *G. floridana* endemic to FL and adjacent GA.

**Gynerium.** Uva grass. One species: *G. sagittatum*, a popular ornamental in dried arrangements. Escaping in FL.

**Hackelochloa.** One species: *H. granularis*, is naturalized in AZ, NM, and LA.

**Hainardia.** Thintail. One species: *H. cylindrica*, introduced from Europe.

**Hakonechloa.** Hakone grass, Japanese forest grass. One species: *H. macra*, escaped from cultivation in UT.


**Hemarthria.** Limpo grass. One species: *H. altissima*, endemic to TX.

**Heteropogon.** Tanglehead. Two species: *H. contortus* and *H. melanocarpus*, occur in AZ to TX.

**Hilaria.** Tabosa, curly-mesquite, galleta. XXX Two species: *H. jamesii* and *H. rigid* native, mostly from CA to UT, WY, and TX.

**Holcus.** Velvet grass. Two species: *H. mollis* (annual) and *H. lanatus* (perennial). Introduced from Europe and Africa.

**Hordeum.** Barley, squirreltail. Nine species.

**Hymenachne.** One species: *H. amplexicaulis*, found in FL.

**Hyparrhenia.** Thatching grass, jaragua grass. Two species: *H. rufoidea* and *H. hirta*. Neither may persist in North America.

**Imperata.** Cogon grass, satin tail. Three species: *I. cylindrica, I. brasilensis*, and *I. brevifolia*.

**Ischaemum.** Muraina grass. Two species, introduced from Asia.

**Koeleria.** June grass. Two species: *K. macrantha* (a common native perennial) and *K. gerardii* (an introduced annual).

**Lagurus.** Hare's tail. One species, *L. ovatus*, a Mediterranean introduction. Sometimes used in dried arrangements.

**Lamarckia.** Golden top. One species: *L. aurea*, introduced from the Mediterranean.

**Lasiacis.** Small cane, tibisee. Two species: *L. divaricata* and *L. rusci folia* (both restricted to FL).

**Leersia.** Cutgrass, white grass, catchfly grass. Five species. Grasses of moist woods and stream banks.

**Leptochloa.** Sprangletop. Twelve species.

**Limnodea.** Ozark grass. One species, *L. arkansana*. This genus endemic to North America.

**Lolium.** Rye grass, darnel. Six species, all introduced.

**Luziola.** Southern water grass. Three species: *L. bahiensis, L. carolinensis*, and *L. peruviana*. Aquatic grasses found mostly in Southeast.

**Lycurus.** Wolf tail, Texas timothy. One species: *L. phleoides*, of drier sites in Southwest.

**Melica.** Onion grass, melic. Eighteen species. Some have small, onion-like bulbs.

**Melinis.** Two species: *M. minutiflora* (molasses grass) a Brazilian introduction; *M. repens* (ruby grass, Natal grass), an African introduction, from CA to TX. Includes taxa traditionally assigned to *Rhynchelytrum*.

**Mibora.** Early sand grass. One species: *M. minima*, a European introduction naturalized in MA.

**Microchloa.** Small grass. One species: *M. kunthii*, endemic to Cochise Co., AZ.

**Microstegium.** One species: *M. vimineum*, an Asian introduction.

**Milium.** Wood-millet. One species: *M. effusum*, a Eurasian introduction.

**Miscanthus.** Eulalia, plume grass, zebra grass. Four species: all Old World introductions, have become naturalized. Popular ornamentals.

**Molinia.** Moor grass. One species: *M. caerulea*, a Eurasian introduction.

**Monanthochloë.** Shore grass, key grass. One species: *M. littoralis*, Atlantic, Gulf, and California coasts. Its needle-like leaves are unique among N. American grasses.

**Monroa.** False buffalo grass. One species: *M. squarrosa*, native from California across Great Plains.
**Muhlenbergia.** Muhly, scratch grass, hair grass, nimble will, bull grass, satin grass, deer grass, ararejo grass. Seventy-three species.

**Nardus.** Moor mat grass. One species: *N. stricta*, a European introduction.

**Neostaphia.** Colusa grass. One species: *N. colusana*, endemic to vernal pools in California.

**Neyraudia.** Burma-reed. Two species: *N. arundinacea* and **XXX introduced in CA and FL.**

**Olyra.** One species: *O. latifolia*, known only in N. America from questionable historic collection from Tampa Bay area, FL.

**Opizia.** One species: *O. stolonifera*, occurs in Florida.

**Oplismenus.** Basket grass, wood grass. One species: *O. hirtellus*, naturalized in TX and LA.

**Orcuttia.** Orcutt grass. Five species: all endemic to vernal pools in California; one variety in Baja California. Other species cited in H & C are now in Tuctoria.

**Oryza.** Rice. Two species: *O. sativa* (cultivated rice), persists around paddies in CA, AR, MS, LA and FL. *O. rufipogon* naturalized in CA and FL.

**Oryzopsis.** Rice-grass, mountain-rice. Eleven species. Some species cited in H & C are now placed in Stipa.

**Panicum.** Panic grass, witch grass, millet, vine-mesquite, maiden cane. The largest genus of grasses in North America, which alone makes for a grand challenge.

**Pappophorum.** Pappus grass. Two species: *P. bicolor* and *P. mucronulatum* found in AZ and TX.

**Parapholis.** Sickle grass, hard grass. Two species: *P. incurva* and *P. strigosa* (known in N. America from recent collections around Humboldt Bay, in Humboldt Co., CA).

**Paspalum.** Knot grass, dallis grass, Vasey grass, paspalam, bahia grass. Forty-four species.

**Pennisetum.** Fountain grass, feather grass, buffel grass, Napier grass, elephant grass, kikuyu grass, pearl millet. Thirteen species. Pernicious weeds and grass. **Forty-four species.**

**Phalaris.** Canary grass, reed canary grass, May grass. Eleven species.

**Pharus.** Creeping leafstalk grass. One species: *Ph. lap-pulaceus*; FL.

**Phippisia.** Ice grass, snow grass. One species: *Ph. algida*; native to CO, WY, and MT.

**Phleum.** Timothy. Six species: *Ph. pratense*, a Eurasian pasture grass now occurs widely in N. America. *Ph. alpinum* native to mid- and high altitude grasslands. Three other species naturalized locally, especially in OR.

**Phragmites.** Common reed, carrizo. One species: *Ph. australis*, common along water ways. Some authors suggest this species the most widely occurring vascular plant.

**Phyllostachys.** Bamboo. Two species: *Ph. aurea* (golden bamboo, fishpole bamboo) and *Ph. bambusoides* (timber bamboo, madake) escaped from cultivation in CA, NM, LA, and FL.

**Piptochaetium.** Piñon rice grass, needle grass. Six species: native species occur mostly in FL and Southwest.

**Pleiolepis.** Dwarf bamboo. Two species: *P. humilis* and *P. simonii* are escaped Japanese bamboos.

**Pleuropus.** Semaphore grass. Five species: mostly grasses of Pacific coast; two endemic to CA.

**Poa.** Blue grass, winter grass, spear grass, mutton grass. About 80 species.

**Pogonarthria.** Herringbone grass. One species: *P. squarrosa*, introduced in AZ.

**Polypogon.** Beard grass, rabbitfoot grass, water bent grass. Five species: two native.

**Polytrias.** One species: *P. praemorsa*, introduced from Java.

**Pseudosasa.** Arrow bamboo, metake. One species: *P. japonica*, naturalized in FL.

**Ptilagrostis.** Porter's needle grass. One subspecies, *P. mongholica ssp. porteri*, endemic to CO.

**Puccinellia.** Alkali grass. Thirty-two species.

**Redfieldia.** Blowout grass. One species: *R. flexuosa*, native to sandy sites.

**Reimarochloa.** Florida reimar grass. One species: *R. cochinchen-sis*, naturalized in TX, LA and FL.

**Rottboellia.** Itch grass. One species: *R. cochinchen-sis*, naturalized in TX, LA and FL.

**Rytyosperma.** Hairy oat grass, hairy danthonia. Three introduced species.

**Saccharum.** Sugar cane, noble cane. Ten species: *S. saccharum* persists around sugar cane fields in FL. *S. spontaneum* (wild Asian sugar cane) also naturalized in FL. Includes *Erianthus*.

**Sacciolepis.** Cupscale. Two species: *S. striata* (native) and *S. indica*, naturalized in TX and perhaps in GA.

**Schedonnardus.** Wire grass, tumble grass, Texas crab grass. One species: *S. paniculatus*.

**Schismus.** Mediterranean grass. Two species: *S. arabicus* and *S. barbatus*, Old World introductions in CA and AZ.

**Schizachne.** False melic. One species, *S. purpurascens*, native.

**Schizachyrium.** Bluestem. Eleven species.

**Sclerochloa.** Hard grass. One species: *S. dura*, a European introduction.

**Scleropogon.** Burro grass. One species: *S. brevifolius*, native to CA to CO and TX.
Scolochloa. Marsh grass, prickly grass. One species: *S. festucacea*.

Scribneria. Scribner's grass. One species: *S. bolanderi*, native along Pacific coast from BC to CA.


Setaria. Foxtail, millet, bristle grass. Twenty-seven species.

Setariopsis. One species: *S. auriculata*, naturalized in AZ.

Sorghastrum. Indian grass, wood grass. Four species: *S. apalachicolense*, endemic to FL; *S. nutans*, dominant of tall grass prairie.

Sorghum. Sorghum, sorgo, sorgho, Kafir-corn, Johnson grass, Sudan grass, chicken-corn, broom-corn. Two species: *S. bicolor*, source of important forage and seed crops; *S. halepense* (Johnson grass), a pernicious weed, especially in agricultural areas.


Sphenopholis. Wedge grass, bunch grass. Five species: all native.

Sporobolus. Dropseed, smut grass, sacaton, poverty grass. Twenty-eight species.

Stenotaphrum. St. Augustine grass. One species: *S. secundatum*, popular lawn grass of Atlantic and Gulf coastal states, where it escapes.

Stipa. Needle grass, porcupine grass, winter grass, sleepy grass. Thirty-eight species.

Swallenia. Eureka Valley Dune grass. One species: *S. alexanderae*, endemic to sand dunes in Inyo Co., CA.

Themeda. Kangaroo grass. One species: *T. quadrivalvis* naturalized in LA.


Torreyochloa. XXX

Trachypogon. Crinkle awn. Two species: *T. montufari* and *T. secundus*, the latter indigenous from AZ to TX.

Tragus. Bur grass. Two species: *T. berteronianus* and *T. racemosus* (Old World introductions), naturalized in AZ, NM, and TX.

Trichoneura. Silveus grass. One species: *T. elegans*, native to TX.

Tridens. Purpletop, redtop, tridens. Twelve species. Some species in H & C now in *Erioneuron*.

Triplasis. Sand grass. Two species: *T. americana* and *T. purpurea*.

Tripogon. One species: *T. spicatus*, native to TX.

Tripsacum. Gama grass. Four species: *T. dacyloides* grows in prairies; *T. floridanum* endemic to FL.

Triraphis. Purpleheads. One species: *T. mollis*, naturalized in TX.

Trisetum. Yellow-oats. Thirteen species: all but one native.

Triticum. Wheat. One species: *T. aestivum* established around agricultural fields.

Tuctoria. Tuctoria. Two species: *T. greenei* and *T. mucronata*, endemic to a few counties in CA.


Urochloa. Signal grass, Guinea grass, brown-top millet, panicum, Pará grass. Fifteen species.

Vaseyochloa. Texas grass. One species: *V. multinervosa*, endemic to TX.

Ventenata. One species: *V. dubia*, Eurasian introduction naturalized in OR and CA.

Willkommia. One species: *W. texana*, endemic to San Patricio and Kleberg counties in TX.


Zizaniopsis. Water-millet, Texas wild-rice, marsh millet, southern wild-rice. One species: *Z. miliacea*, aquatic grass of southern U. S.


Revised: 10 January 2005
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Sorghum bicolor
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Coelorrachis spp.
Arthraxon hispidus
Coelorrachis spp.
Echinocloa colona
Sorghum bicolor
Themeda quadrivalvis
Bouteloua kayii
Rottboellia cochinchenesis
Monanthochloë littoralis
Chrysopogon zizanioides
Chrysopogon zizanioides
Pennisetum clandestinum
Dichanthium annulatum
Poa pratensis
Koeleria spp.
Muhlenbergia spp.
Panicum rigidulum
Ischaemum spp.
Poa fendleriana
Pennisetum purpureum
Cymbopogon nardus
Melinis repens
Bouteloua spp.
Piptochaetium spp.
Aristida spp.
Stipa comata
Muhlenbergia schreberi
Gastriodium ventricosum
Saccharum officinarum
Ventenata dubia
Avena spp.
Trisetum spp.
Piptochaetium spp.
Arrhenatherum spp.
Leersia lenticularis
Cymbopogon iwarancusa
Hainardia cylindrica
Melica spp.
Ctenium aromaticum
Dactylis glomerata
Sorghum bicolor
Pennisetum polystachyon
Melinis minitiflora
Molinia caerulea
Nardus strictus
Dasyphyrum villosum
Coleanthus subtilis
Festuca arizonica
Stipa webberi
Orzyopsis spp.
Muhlenbergia spp.
Panicum rigidulum
Ischaemum spp.
Poa fendleriana
Pennisetum purpureum
Melinis repens
Bouteloua spp.
Piptochaetium spp.
Aristida spp.
Stipa comata
Muhlenbergia schreberi
Gastriodium ventricosum
Saccharum officinarum
Ventenata dubia
Urochloa spp.
Argena spp.
Setaria palmifolia
Cortaderia spp.
Digitaria decumbens
 Panicum spp.
Steinchisma hians
Urochloa spp.
Panicum spp.
Enneapogon desvauxii
Pappophorum spp.
Urochloa mutica
Setaria spp.
Paspalum quadribracteatum
Urochloa brizantha
Setaria palmifolia
Cortaderia spp.
Digitaria decumbens
Panicum spp.
Steinchisma hians
Urochloa spp.
Panicum spp.
Enneapogon desvauxii
Pappophorum spp.
Urochloa mutica
Setaria spp.
Paspalum spp.
Bucholeo dactyloides
Cynodon dactylon
Chloris cucullata
Amphicarpum purshii
Pennisetum americanum
Arctophila fulva
Setaria pumila
Heteropogon contortus
Festuca arizonica
Calamagrostis spp.
Hackelochloa granulatiss
Hackelochloa granulatiss
Miscanthus spp.
Saccharum spp.
Chloris radiata
Lolium temulentum
Arctagrostis latifolia
pony grass Eragrostis hypnoides
popotillo Andropogon spp.
popotillo colorado Schizachyrium scoparium
popotillo del pinar Blepharoneuron tricholepis
porcupine grass Stipa spp.
Porter's needle grass Ptilagrostis porteri
poverty grass Sporobolus spp.
povotillo Andropogon spp.
povotillo colorado Schizachyrium scoparium
povotillo del pinar Blepharoneuron tricholepis
prose millet Panicum miliaceum
pull-and-be-damned Paspalum lividum
puna grass Stipa brachychaeta
puny needle grass Triraphis mollis
purple heads Tridens flavus
purpletop
quack grass Elymus repens
quack grass Elyhordeum spp.
quaking grass Briza spp.
quail grass Elymus repens
quitch grass Elymus repens
rabbit foot grass Polypogon monspeliensis
ragi Eleusine corocana
rat's tail Sporobolus jacquemontii
rattlesnake chess Bromus briziformis
rattlesnake grass Briza maxima
Rhodes grass Chloris spp.
sacaton Sporobolus spp.
sabina Eremopoa persica
salt and pepper grass Deschampsia caespitosa
salt grass Allotropis texana
salt grass Distichlis spp.
salt meadow grass Sporobolus airoides
sand bunt grass Leptochloa panicea
sand burr(s) Centrurus spp.
sand grass Sporobolus spp.
sand reed Calamovilfa spp.
sandbur grass Centrurus spp.
sandspur grass Mibora minima
satina Imperata spp.
satin tail Schismus spp.
schismus
scraper grass Muhlenbergia asperifolia
scrub grass Scriberia bolanderi
tiger grass Elymus mollis
torrid meadow grass Distichlis spp.
unpalpitate Uniola paniculata
v拉丁weed Paspalum lividum
wheat grass Brachypodium spp.
weedy grass Elymus ararun
whorly grass Elymus maximum
wild oat grass Elymus torreyi
wheat grass Elymus ararun
| Texas grass                   | Vaseyochloa multinervosa                      | winter grass                   | Stipa spp.                  |
| Texas millet                 | Urochloa texana                              | wire grass                     | Eleusine indica             |
| Texas wild-rice              | Zizaniopsis miliacea                         | wire grass                     | Schedonnardus paniculatus   |
| Texas winter grass           | Stipa leucotricha                            | wire stem                      | Muhlenbergia mexicana       |
| Texas-panicum                | Urochloa texana                              | witch grass                    | Digitaria spp.              |
| Texas-timothy                | Lycurus philoides                            | witch grass                    | Panicum spp.                |
| thatch grass                 | Hyparrhenia hirta                            | wolf tail                      | Lycium philoides            |
| thatching grass              | Hyparrhenia spp.                             | wood grass                     | Opilismenus hirtellus       |
| thimble grass                | Fingerhuthia africana                        | wood grass                     | Sorghastrum spp.            |
| thintail grass               | Coelorachis spp.                             | wood-grass                     | Cinna spp.                  |
| thintail grass               | Hainardia cylindrlica                        | wood-millet                    | Milium effusum              |
| Thompson grass               | Paspalum distichum                           | wood-oats                      | Chasmanthium spp.           |
| three-awn grass              | Aristida spp.                                | woolly grass                   | Erioneuron spp.             |
| three-spike grass            | Eleusine tristachya                           | yard grass                     | Eroses tsetum spp.          |
| tibisee                      | Lasiacis spp.                                | yellow-oat                     | Holcus lanatus              |
| tick grass                   | Eragrostis echioloide                         | Yorkshire fog                  |                           |
| tickle grass                 | Agrostis spp.                                |                               |                             |
| tiger grass                  | Thysanolaena latifolia                       |                               |                             |
| timothy                      | Phleum spp.                                  |                               |                             |
| tobossa                      | Hilaria mutica                               |                               |                             |
| tobosa menudo                | Hilaria belangeri                            |                               |                             |
| toothache grass              | Ctenium spp.                                 |                               |                             |
| torpedo grass                | Panicum repens                               |                               |                             |
| tres barbas                  | Aristida oligantha                           |                               |                             |
| tridens                      | Tridens spp.                                 |                               |                             |
| tridens                      | Erioneuron spp.                              |                               |                             |
| trisetum                     | Trisetum spp.                                |                               |                             |
| triticele                    | Triticosecale rimpaul                        |                               |                             |
| trompetilla                  | Hymenachne amplexicaulis                     |                               |                             |
| tuctoria                     | Tuctoria spp.                                |                               |                             |
| tumble grass                 | Schedonnardus paniculatus                    |                               |                             |
| tumble grass                 | Eragrostis spectabilis                       |                               |                             |
| tundra grass                 | Dupontia fischeri                            |                               |                             |
| tussock grass                | Stipa neessiana                              |                               |                             |
| umbrella grass               | Enteropogon spp.                             |                               |                             |
| uniola                       | Chasmanthium spp.                            |                               |                             |
| uva (grass)                  | Gynerium sagittatum                          |                               |                             |
| vanilla grass                | Anthoxanthum spp.                            |                               |                             |
| Vasey grass                  | Paspalum urvillei                            |                               |                             |
| veldt grass                  | Ehrharta spp.                                |                               |                             |
| velvet grass                 | Holcus spp.                                  |                               |                             |
| vernal grass                 | Anthoxanthum spp.                            |                               |                             |
| vetiver grass                | Chrysopogon zizianoides                      |                               |                             |
| vine-mesquite                | Panicum obtusum                              |                               |                             |
| viper grass                  | Dinebra retroflexa                           |                               |                             |
| wallaby grass                | Rytidosperema spp.                           |                               |                             |
| wallaby grass                | Danthonia spp.                               |                               |                             |
| water grass                  | Echinchoioa spp.                             |                               |                             |
| water grass                  | Luziola spp.                                 |                               |                             |
| water millet                 | Zizaniopsis miliacea                         |                               |                             |
| water-rice                   | Zizania spp.                                 |                               |                             |
| waterside-reed               | Pennisetum macrowum                          |                               |                             |
| wedge grass                  | Sphenopholis spp.                            |                               |                             |
| weeping grass                | Ehrharta calvina                             |                               |                             |
| West Indian marsh grass      | Hymenachne amplexicaulis                     |                               |                             |
| wheat                        | Triticum spp.                                |                               |                             |
| wheat grass                  | Agropyron spp.                               |                               |                             |
| wheat grass                  | Elymus spp.                                  |                               |                             |
| white grass                  | Leersia virginica                            |                               |                             |
| whorl grass                  | Catabrosa aquatica                           |                               |                             |
| wild cane                    | Gynerium sagittatum                          |                               |                             |
| wild rye                     | X Elyhordeum hirta                           |                               |                             |
| wild rye                     | Elymus spp.                                  |                               |                             |
| wild-oats                    | Chasmanthium spp.                            |                               |                             |
| wild-rice                    | Zizania spp.                                 |                               |                             |
| wild-timothy                 | Muhlenbergia glomerata                       |                               |                             |
| wind grass                   | Apera interrupta                             |                               |                             |
| windmill grass               | Eustachys spp.                               |                               |                             |
| windmill grass               | Choris spp.                                  |                               |                             |
| winter grass                 | Poa annua                                    |                               |                             |

* (grass) indicates that the word grass is sometimes used as part of the common name.

Revised: 12 January 2005
Why are we using a book that first appeared in 1935 and then revised in 1951? Half a century is a long time, even in systematics! The answer is amazingly simple -- nothing has come along to take its place. Hitchcock & Chase remains the only comprehensive treatment of the grasses of the United States. The late Frank Gould, John Kartesz, and I have compiled checklists for the United States and for North America, but they are nothing more than that.

But, help is on the way! In 2003, Oxford University Press published the first of a two-volume treatment of the grasses of North America. It will be part of the larger "Flora of North America" project. The FNA is a first-class operation. The other volume is scheduled to appear in 2006. Now the bad news. The volumes will cost about $100 each! There is a chance that a one volume, scaled-down version may become available.

Just how out-of-date are the names of subfamilies, tribes, genera, and individual grasses? In this section of the syllabus you will see a comparison of the subfamilies, tribes, and genera used in The Manual (left entry) versus today's version of the truth (right entry). You will also have access to a notebook in the lab that will permit you to look up any species name used in The Manual to see if it is still current. Of course, I am the person who compiled this list and other experts would not always agree with me.

### TWO VERY DIFFERENT VIEWS

#### HITCHCOCK & CHASE
(The Old Testament)

**Subfamily: Festucoideae**
- Tribe: Bambuseae
- Tribe: Festuceae
- Tribe: Hordeae
- Tribe: Aveneae
- Tribe: Agrostideae
- Tribe: Zoysieae
- Tribe: Chlorideae
- Tribe: Phalarideae
- Tribe: Oryzaeae
- Tribe: Zizanieae

**Subfamily: Panicoideae**
- Tribe: Melinideae
- Tribe: Paniceae
- Tribe: Andropogoneae
- Tribe: Tripsaceae

#### GRASS PHYLOGENY GROUP
(The New Testament)

**Subfamily: Bambusoideae**
- Tribe: Bambuseae
- Tribe: Olyreae

**Subfamily: Pharioideae**
- Tribe: Phareae

**Subfamily: Ehrhartioideae**
- Tribe: Oryzaeae
- Tribe: Ehrhartae

**Subfamily: Centothecoideae**
- Tribe: Centothecoae

### SUBFAMILIES

As you will see from the table below, the subfamily Panicoideae of H & C came through unscathed, but look at what happened to their Festucoideae. One large subfamily became nine.

<table>
<thead>
<tr>
<th>Festucoideae</th>
<th>Pooideae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pharoideae</td>
<td>Bambusoideae</td>
</tr>
<tr>
<td>Erhartoideae</td>
<td>Centothecoideae</td>
</tr>
<tr>
<td>Chloridoideae</td>
<td>Aristidoideae</td>
</tr>
<tr>
<td>Arundinoideae</td>
<td>Danthonioidae</td>
</tr>
</tbody>
</table>

**Panicoideae**
- Pooideae

#### TRIBES

At the tribe level, three things have happened. Some have been merged (Melinidae with Paniceae), some have been split into smaller tribes (look at Festuceae!), and some are again unchanged.

<table>
<thead>
<tr>
<th>Agrostideae</th>
<th>Aveneae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stipeae</td>
<td>-</td>
</tr>
<tr>
<td>Brachyphylloideae</td>
<td>-</td>
</tr>
<tr>
<td>Aristideae</td>
<td>-</td>
</tr>
<tr>
<td>Andropogoneae</td>
<td>Andropogoneae</td>
</tr>
<tr>
<td>Aveneae</td>
<td>-</td>
</tr>
<tr>
<td>Bambuseae</td>
<td>-</td>
</tr>
<tr>
<td>Chloridoideae</td>
<td>-</td>
</tr>
<tr>
<td>Eragrostideae</td>
<td>-</td>
</tr>
<tr>
<td>Poeae</td>
<td>-</td>
</tr>
<tr>
<td>Eragrostideae</td>
<td>-</td>
</tr>
</tbody>
</table>
The genera below are arranged as they are in H & C. The entry in the right-hand column tells you whether the genus is still recognized and its taxonomic position.

### AVENEAE
- **Aira** Unchanged
- **Arrhenatherum** Unchanged
- **Avena** Unchanged
- **Corynephorus** Unchanged
- **Danthonia** Unchanged
- **Deschampsia** Unchanged
- **Helictotrichon** Unchanged
- **Holcus** Unchanged
- **Koeleria** Unchanged
- **Schismus** Unchanged
- **Sieglingia** Unchanged
- **Sphenopholis** Unchanged
- **Trisetum** Unchanged

### BAMBUSEAE
- **Arundinaria** Bambusoideae: Bambuseae

### FESTUCAEAE
- **Ampelodesmos** Unchanged
- **Blepharidachne** Unchanged
- **Brachypodium** Unchanged
- **Briza** Unchanged
- **Bromus** Unchanged
- **Catabrosa** Unchanged
- **Cortaderia** Unchanged
- **Cottea** Unchanged
- **Cutandia** Unchanged
- **Cynodon** Unchanged
- **Dactylis** Unchanged
- **Desmazeria** Unchanged
- **Diarrhena** Unchanged
- **Dissanthelium** Unchanged
- **Distichlis** Unchanged
- **Enneapogon** Unchanged
- **Eragrostis** Unchanged
- **Festuca** Unchanged
- **Glyceria** Unchanged
- **Hesperochloa** Unchanged
- **Lamarckia** Unchanged
- **Melica** Unchanged
- **Molinia** Unchanged
- **Monanthochloa** Unchanged
- **Monroa** Unchanged
- **Neostaphia** Unchanged
- **Neyraudia** Unchanged
- **Orcuttia** Unchanged
- **Pappophorum** Unchanged
- **Phragmites** Unchanged
- **PleuroEGINA** Unchanged
- **Poa** Unchanged
- **Puccinellia** Unchanged
- **Redfieldia** Unchanged
- **Schizachne** Unchanged
- **Sclerochloa** Unchanged
- **Scleropyrum** Unchanged
- **Scleropogon** Unchanged
- **Schoenoplectus** Unchanged
- **Swallenia** Unchanged
- **Tridens** Unchanged
- **Triplasis** Unchanged
- **Uniola** Unchanged
- **Vaseyochloa** Unchanged

### AGROSTIDEAE
- **Agrostis** Unchanged
- **Alopecurus** Unchanged
- **Ammophila** Unchanged
- **Apera** Unchanged
- **Aristida** Aristidoideae: Aristideae
- **Blepharoneuron** Chloridoideae: Eragrostideae
- **Brachyelytrum** Pooidae: Brachyelytrae
- **Calamagrostis** Unchanged
- **Calamovilfa** Unchanged
- **Cinna** Unchanged
- **Coleanthus** Chloridoideae: Eragrostideae
- **Crypsis** Chloridoideae: Eragrostideae
- **Gaetria** Chloridoideae: Eragrostideae
- **Heleiocnthus** Chloridoideae: Eragrostideae
- **Haplochloa** Chloridoideae: Eragrostideae
- **Lagurus** Unchanged
- **Limnodia** Unchanged
- **Lycurus** Unchanged
- **Milium** Unchanged
- **Muhlenbergia** Unchanged
- **Oryzopsis** Unchanged
- **Phippsia** Unchanged
- **Phileum** Unchanged
- **Piptochaetium** Unchanged
- **Polygonon** Unchanged
- **Sporobolus** Chloridoideae: Eragrostideae
- **Stipa** Chloridoideae: Eragrostideae

### ANDROPOGONEAE
- **Arthraxon** Unchanged
- **Chrysocephalus** Unchanged
- **Elyonurus** Unchanged
- **Erianthus** Unchanged
- **Hackelochloa** Unchanged
- **Heteropogon** Unchanged
- **Hyparrhenia** Unchanged
- **Imperata** Unchanged
- **Manisurus** Unchanged
- **Microstegium** Unchanged
- **Miscanthus** Unchanged
- **Rotboelia** Unchanged
- **Saccharum** Unchanged
- **Sorghastrum** Unchanged
- **Sorghum** Unchanged
- **Trachypogon** Unchanged

###期权
- **Neostaphia** Chloridoideae: Eragrostideae
- **Elyonurus** Unchanged
- **Saccharum** Unchanged
- **Sorghastrum** Unchanged
- **Sorghum** Unchanged
- **Trachypogon** Unchanged
<table>
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<th>Chlorideae</th>
<th>Phalaris</th>
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</thead>
<tbody>
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<td>Beckmannia</td>
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<tr>
<td>Bouteloua</td>
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<td>Cynodon</td>
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<tr>
<td>Dactyloctenium</td>
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<td>Microchloa</td>
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<td>Munroa</td>
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<table>
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<tr>
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<tr>
<td>Lolium</td>
<td>Pooidae: Poeae</td>
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<tr>
<td>Monerma</td>
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<tr>
<td>Parapholis</td>
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<tr>
<td>Scribneria</td>
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<td>Sitonion</td>
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<table>
<thead>
<tr>
<th>Melinidae</th>
<th>Paniceae</th>
</tr>
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<tbody>
<tr>
<td>Melinis</td>
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<table>
<thead>
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<tbody>
<tr>
<td>Leersia</td>
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</tr>
<tr>
<td>Oryza</td>
<td>Erhartoideae: Oryzeae</td>
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<table>
<thead>
<tr>
<th>Paniceae</th>
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<tbody>
<tr>
<td>Amphicarpum</td>
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</tr>
<tr>
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</tr>
<tr>
<td>Axonopus</td>
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</tr>
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<td>Brachiaria</td>
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</tr>
<tr>
<td>Cenchrus</td>
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</tr>
<tr>
<td>Digitaria</td>
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</tr>
<tr>
<td>Echinochloa</td>
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<tr>
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<td>Lasiacis</td>
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<tr>
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<td>Opismenus</td>
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<tr>
<td>Panicum</td>
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</tr>
<tr>
<td>Paspalum</td>
<td>Unchanged</td>
</tr>
<tr>
<td>Pennisetum</td>
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</tr>
<tr>
<td>Reimarochloa</td>
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</tr>
<tr>
<td>Rhyncheleyrum</td>
<td>Melinis</td>
</tr>
<tr>
<td>Sacciolepis</td>
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<tr>
<td>Setaria</td>
<td>Unchanged</td>
</tr>
<tr>
<td>Stenotaphrum</td>
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</tr>
<tr>
<td>Trichachne</td>
<td>Digitaria</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Phalarideae</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Anthoxanthum</td>
<td>Aveneae</td>
</tr>
<tr>
<td>Hierochloe</td>
<td>Anthoxanthum</td>
</tr>
</tbody>
</table>
There is another vastly important group of grasses -- those that we feed to our domesticated animals, especially horses, dairy cattle, and beef cattle. Forage is the general term for plants consumed by livestock. In the broad sense, the term includes pasture and browse plants, straw, hay, and silage. Another way of looking at it is that we use dairy and beef cattle to transform plants into meat, milk, and other dairy products. In the United States alone, forage crops constitute a multibillion dollar industry. It is estimated that more than half of the earth's land surface is devoted to pastures and meadows used for grazing by farm animals.

The high cellulose levels of grass stems and leaves make these tissues relatively difficult for most animals to digest. However, the bacteria that inhabit the intestinal tracts of both ruminants and nonruminants carry out a fermentation process that reduces the cellulose to simpler compounds. We also create an environment in which anaerobic fermentation can occur when we put silage into a silo. For all practical purposes, chopped up plant material is pickled by being bathed in organic acids that are produced by the bacteria. If done properly, silage can be stored for years. It certainly doesn't sound very appetizing, does it? Do you like sauerkraut? How is it prepared?

Although literally thousands of plant species can provide palatable food for our domesticated animals, all of the important forage plants are either grasses or legumes. Most of them are Old World introductions, especially from Europe and Africa.

**SELECTED REFERENCES**

### FORAGE GRASSES

<table>
<thead>
<tr>
<th>Grass Type</th>
<th>Scientific Name</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bahia grass</td>
<td><em>Paspalum notatum</em></td>
<td>Used especially in the southeastern U. S.</td>
</tr>
<tr>
<td>Bent grass</td>
<td><em>Agrostis spp.</em></td>
<td>Excellent forage; common in western states</td>
</tr>
<tr>
<td>Bermuda grass</td>
<td><em>Cynodon dactylon</em></td>
<td>Also an aggressive weed and lawn grass</td>
</tr>
<tr>
<td>Big bluestem</td>
<td><em>Andropogon gerardii</em></td>
<td>Provides excellent forage</td>
</tr>
<tr>
<td>Black grama</td>
<td><em>Bouteloua eriopoda</em></td>
<td>Important southwestern species</td>
</tr>
<tr>
<td>Blue grama grass</td>
<td><em>Bouteloua gracilis</em></td>
<td>Best while immature</td>
</tr>
<tr>
<td>Brome grasses</td>
<td><em>Bromus spp.</em></td>
<td>Very important in dry, cool regions</td>
</tr>
<tr>
<td>Buffalo grass</td>
<td><em>Buchloë dactyloides</em></td>
<td>Native grass of cool, dry prairies</td>
</tr>
<tr>
<td>Bush muhly</td>
<td><em>Muhlenbergia porteri</em></td>
<td>Native southwestern species</td>
</tr>
<tr>
<td>Crested wheat grass</td>
<td><em>Agropyron cristatum</em></td>
<td>Good in cool, dry areas</td>
</tr>
<tr>
<td>Dallis grass</td>
<td><em>Paspalum dilatatum</em></td>
<td>Well adapted to Cotton Belt states and California’s C. Valley</td>
</tr>
<tr>
<td>Fescues</td>
<td><em>Festuca spp.</em></td>
<td>Well adapted to warm summers</td>
</tr>
<tr>
<td>Gama grass</td>
<td><em>Tripsacum dactyloides</em></td>
<td>Excellent forage; southeastern states</td>
</tr>
<tr>
<td>Hair grass</td>
<td><em>Deschampsia cespitosa</em></td>
<td>Used in northern and western states</td>
</tr>
<tr>
<td>Harding grass</td>
<td><em>Phalaris aquatica</em></td>
<td>Across the southern states</td>
</tr>
<tr>
<td>Indian grass</td>
<td><em>Sorghastrum nutans</em></td>
<td>Excellent forage; eastern and central states</td>
</tr>
<tr>
<td>June grass</td>
<td><em>Koeleria macrantha</em></td>
<td>Commonly used, except in the Southeast</td>
</tr>
<tr>
<td>Little bluestem</td>
<td><em>Schizachyrium scoparium</em></td>
<td>One of the best and most palatable</td>
</tr>
<tr>
<td>Love grasses</td>
<td><em>Eragrostis spp.</em></td>
<td>Best when immature</td>
</tr>
<tr>
<td>Maiden cane</td>
<td><em>Panicum hemitomon</em></td>
<td>Widely used in southern Great Plains</td>
</tr>
<tr>
<td>Onion grass</td>
<td><em>Melica bulbosa</em></td>
<td>Native grass of the Southeast coastal plain</td>
</tr>
<tr>
<td>Orchard grass</td>
<td><em>Dactylis glomerata</em></td>
<td>Used especially in Northwestern states; native</td>
</tr>
<tr>
<td>Pangola grass</td>
<td><em>Digitaria decumbens</em></td>
<td>Does well in cool, humid regions</td>
</tr>
<tr>
<td>Pearl millet</td>
<td><em>Pennisetum americanum</em></td>
<td>Popular in Florida; native to Africa</td>
</tr>
<tr>
<td>Redtop</td>
<td><em>Agrostis stolonifera</em></td>
<td>Also a major human food in Africa and India</td>
</tr>
<tr>
<td>Reed canary grass</td>
<td><em>Phalaris arundinacea</em></td>
<td>One of the best wetland forage grasses</td>
</tr>
<tr>
<td>Rye grasses</td>
<td><em>Lolium spp.</em></td>
<td>Well adapted to wet areas</td>
</tr>
<tr>
<td>Sideoats grama</td>
<td><em>Bouteloua curtipendula</em></td>
<td>Winter/irrigated pasture in southern states and California</td>
</tr>
<tr>
<td>Sorghum</td>
<td><em>Sorghum bicolor</em></td>
<td>Provides forage over much of the country</td>
</tr>
<tr>
<td>Spike trisetum</td>
<td><em>Trisetum spicatum</em></td>
<td>Also used for grain, silage, and syrup</td>
</tr>
<tr>
<td>Sudan grass</td>
<td><em>Sorghum sudanense</em></td>
<td>Used in the West and in the Northeast</td>
</tr>
<tr>
<td>Timothy</td>
<td><em>Phleum pratense</em></td>
<td>Hybrids with sorghum widely used</td>
</tr>
<tr>
<td>Wheat grasses</td>
<td><em>Agropyron spp.</em></td>
<td>Eurasian; widely planted</td>
</tr>
<tr>
<td>Wild oats</td>
<td><em>Avena fatua</em></td>
<td>Good in cool, dry areas</td>
</tr>
<tr>
<td>Wild ryes</td>
<td><em>Elymus spp.</em></td>
<td>Commonly used, except in southeastern states</td>
</tr>
</tbody>
</table>

[With thanks to Prof. K. O. Fulgham for his assistance.]
"What is a weed? A plant whose virtues have not yet been discovered." (Ralph Waldo Emerson)

Weeds are of great economic importance, mostly in the negative sense. It is estimated that weeds cost the American farmer several billion dollars each year by reducing both the quantity and the quality of crops produced. Their damage causes a loss as large as insect injury and disease combined. Another reason for studying weeds is their intimate association with our own species. Many of them are essentially our wards and they would perish without our encouragement. As Edgar Anderson said, "... the history of weeds is the history of man."

**A DEFINITION**

There are many definitions of a weed. Inherent in most of them is the idea that a plant is a weed if it is growing where we do not wish it to be. The picture of a well-manicured lawn dotted with dandelions comes easily to mind. There are problems with this approach. If I am growing irises, then a rose that appears in my garden is a weed. Bermuda grass is a highly prized lawn grass in much of the southern United States. Elsewhere it tends to live in disturbed areas. Is Bermuda grass a weed?

A good botanical definition of a weed is that of Herbert Baker, a botanist at the University of California at Berkeley. A plant is a weed, "... if, in any specified geographical area, its populations grow entirely or predominately in situations markedly disturbed by man (without, of course, being deliberately cultivated plants).

Remember that disturbed sites include not only relatively undesirable vacant lots and roadsides, but also our prime agricultural lands. Some weeds invade one or the other; some live in both.

Weeds are such a problem in the agricultural states that there is legislation against them. Many states have weed laws that require the farmer to use varying degrees of control against weedy plants. The "primary noxious weeds" are considered so bad that the land owner is required to destroy them if he discovers them on his property.

**CHARACTERISTICS**

There are certain biological features that many weedy plants have. Many grasses are excellent weeds because they:

- can persist from year to year in an area;
- reproduce vegetatively, by such means as rhizomes or stolons that allow the plants to spread quickly and efficiently;
- have seeds that can germinate in many different environments;
- have high seed production;
- set seed in a wide variety of conditions;
- have rapid seedling growth;
- have a "general purpose" set of genes that will enable the plants to compete very effectively against native plants when they are competing on disturbed sites;
- often contain multiple genomes derived through hybridization;
- are self-pollinated or substitute some asexual means of reproduction for a sexual one; and
- may be unpalatable or even toxic to livestock or herbivores.

If we were to construct the "perfect weedy grass," it would:

- be physically attractive
- mimic a crop
- be a perennial
- reproduce both sexually and asexually
- have long-lived seeds
- produce numerous seeds over a long period
- germinate its seeds early in the growing season
- germinate its seeds in many environments
- have rapid seedling growth
- be unpalatable to livestock
- have chemical/physical defense mechanisms
- thrive in disturbed habitats.

Can we say anything positive about weeds? Certainly! In ruined and abandoned areas, weeds make up much of the flora. Many of the more attractive plants that city folks see these days are weeds. They also retard or prevent erosion along many of our roadsides.

**NOXIOUS GRASSES & SEDGES OF CALIFORNIA**

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aegilops cylindrica</td>
<td>Jointed goat grass</td>
</tr>
<tr>
<td>Aegilops ovata</td>
<td>Ovate goat grass</td>
</tr>
<tr>
<td>Aegilops triuncialis</td>
<td>Barb goat grass</td>
</tr>
<tr>
<td>Elymus caput-medusae</td>
<td>Medusa head grass</td>
</tr>
<tr>
<td>Elymus repens</td>
<td>Quack grass</td>
</tr>
<tr>
<td>Cenchrus echinatus</td>
<td>Southern sand bur</td>
</tr>
<tr>
<td>Cenchrus incertus</td>
<td>Coast sand bur</td>
</tr>
<tr>
<td>Cenchrus longispinus</td>
<td>Mat sand bur</td>
</tr>
<tr>
<td>Cynodon</td>
<td>Bermuda grass</td>
</tr>
<tr>
<td>Cyperus esculentus</td>
<td>Yellow nut grass</td>
</tr>
<tr>
<td>Cyperus rotundus</td>
<td>Purple nut grass</td>
</tr>
<tr>
<td>Heteropogon contortus</td>
<td>Tanglehead</td>
</tr>
<tr>
<td>Imperata cylindrica</td>
<td>Satintail</td>
</tr>
<tr>
<td>Muhlenbergia schreberi</td>
<td>Nimblewill</td>
</tr>
<tr>
<td>Oryza rufipogon</td>
<td>Perennial wild red rice</td>
</tr>
<tr>
<td>Panicum antidotale</td>
<td>Blue panic grass</td>
</tr>
<tr>
<td>Pennisetum clandestinum</td>
<td>Kikuyu grass</td>
</tr>
<tr>
<td>Setaria faberi</td>
<td>Giant foxtail</td>
</tr>
<tr>
<td>Sorghum halepense</td>
<td>Johnson grass</td>
</tr>
<tr>
<td>Stipa brachychaeta</td>
<td>Puna grass</td>
</tr>
</tbody>
</table>
Ratings:
A = Subject to state enforced action involving eradication, quarantine, containment, rejection, or other holding action at state or county level
B = Subject to eradication, containment, control, or other holding action at the discretion of the county commissioner
C = Not subject to state enforced action, except to retard spread

[Source: California Dept. of Food & Agriculture]

**GRASSES: EXOTIC PEST PLANT LIST**

**A. Pest Plants of Greatest Ecological Concern:**
- *Aegilops triuncialis* (barbed goat grass)
- *Avena barbata* (slender wild oat)
- *Avena fatua* var. *fatua* (wild oat)
- *Brachypodium distachyon* (false brome)
- *Bromus diandrus* (ripgut brome)
- *Lolium multiflorum* (Italian ryegrass)
- *Schismus arabicus* (Mediterranean grass)
- *Schismus barbatus* (Mediterranean grass)

**B. Potential to Spread Explosively:**
- *Spartina anglica* (cord grass)
- *Spartina densiflora* (dense-flowered cord grass)
- *Spartina patens* (salt-meadow cord grass)

**C. Most Invasive Pest Plants (Widespread):**
- *Ammophila arenaria* (European beach grass)
- *Arundo donax* (giant reed)
- *Bromus tectorum* (cheat grass)
- *Cortaderia jubata* (Andean pampas grass)
- *Cortaderia selloana* (pampas grass)
- *Elymus caput-medusae* (medusa head)
- *Pennisetum setaceum* (fountain grass)

**D. Most Invasive Pest Plants (Regional):**
- *Bromus rubens* (red brome)
- *Ehrharta calycina* (veldt grass)
- *Spartina alterniflora* (smooth cord grass)

**E. Wildland Plants of Lesser Invasiveness:**
- *Ehrharta erecta* (veldt grass)
- *Festuca arundinacea* (tall fescue)
- *Holcus lanatus* (velvet grass)
- *Phalaris aquatica* (Harding grass)

[Source: California Exotic Pest Council]

**FEDERALLY LISTED GRASSES**
[Listed as of 08 September 2000]

- *Avena sterilis* (animated oat)
- *Chrysopogon aciculatus* (pilipiliula)
- *Digitaria abyssinica* (African couch grass)
- *Digitaria velutina* (velvet finger grass)
- *Imperata brasiliensis* (Brazilian satintail)
- *Imperata cylindrica* (cogon grass)
A CHECKLIST OF WEEDY GRASSES OF THE UNITED STATES

Aegilops cylindrica  
Aegilops geniculata  
Aegilops triuncialis  
Agropyron cristatum  
Agrostis canina  
Agrostis gigantea  
Agrostis stolonifera  
Alopecurus aequalis  
Alopecurus geniculatus  
Alopecurus myosuroides  
Alopecurus rendlei  
Andropogon gerardii  
Andropogon glomeratus  
Andropogon ternarius  
Andropogon virginicus  
Anthoxanthum aristatum  
Anthoxanthum odoratum  
Apera spica-venti  
Aristida adscensionis  
Aristida longiseta  
Aristida oligantha  
Arrhenatherum elatius  
Arundo donax  
Avena barbata  
Avena fatua  
Avena sterilis  
Axonopus affinis  
Axonopus compressus  
Bothriochloa saccharoides  
Bouteloua aristidoides  
Bouteloua gracilis  
Brachiaria fasciculata  
Brachiaria mutica  
Brachiaria plantaginea  
Brachiaria platyphylla  
Brachiaria repans  
Brachiaria texana  
Brachypodium distachyon  
Briza maxima  
Briza media  
Briza minor  
Bromus arvensis  
Bromus catharticus  
Bromus commutatus  
Bromus diandrus  
Bromus erectus  
Bromus hordeaceus  
Bromus inermis  
Bromus japonicus  
Bromus lanceolatus  
Bromus rigidus  
Bromus rubens  
Bromus secalinus  
Bromus sterilis  
Bromus tectorum  
Catapodium rigidum  
Cenchrus biflorus  
Cenchrus brownii  
Cenchrus ciliaris  
Cenchrus echinatus  
Cenchrus incertus  
Cenchrus longispinus  
Cenchrus myosuroides  
Cenchrus pauciflorus  
Cenchrus tribuloides  
Chloris gayana  
Chloris polydactylon  
Chloris virgata  
Coix lacryma-jobi  
Cynodon dactylon  
Cynosurus echinatus  
Dactylocenium aegyptium  
Deschampsia caespitosa  
Deschampsia flexuosa  
 Dichanthium annulatum  
Dichanthium aristatum  
Digitaria ciliaris  
Digitaria filiformis  
Digitaria horizontalis  
Digitaria ischaene  
Digitaria longiflora  
Digitaria sanguinialis  
Digitaria violacea  
Echinochloa colona  
Echinochloa crus-galli  
Echinochloa crus-pavonis  
Eleusine indica  
Elymus caninus  
Elymus caput-medusae  
Elymus repens  
Eragrostis barrelieri  
Eragrostis ciliensis  
Eragrostis curvula  
Eragrostis mexicana  
Eragrostis minor  
Eragrostis pectinacea  
Eragrostis pilosa  
Eragrostis tenella  
Eragrostis unioloides  
Eriochloa brachiata  
Eriochloa punctata  
Festuca arundinacea  
Festuca ovina  
Festuca rubra  
Heteropogon contortus  
Holcus lanatus  
Holcus mollis  
Hordeum jubatum  
Hordeum leporinum  
Hordeum murinum  
Hordeum pusillum  
Imperata brasiliensis  
Imperata cylindrica  
Koeleria phleoides  
Koeleria pyramidata  
Lagurus ovatus  
Lamarckia aurea  
Leersia hexandra  
Leersia oryzoides  
Leptochloa fascicularis  
Leptochloa filiformis  
Leptochloa scabra  
Leptochloa uniflora  
Leptochloa virgata  
Lolium multiflorum  
Lolium perenne  
Lolium persicum  
Lolium remotum  
Lolium temulentum  
Melinis repens  
Microstegium vimineum  
Miscanthus floridus  
Muhlenbergia schreberi  
Oplismenus hirtellus  
Oryza rufipogon  
Oryzopsis miliacea  
Paniceum antidotale  
Paniceum capillare  
Paniceum clandestinum  
Paniceum dichotomiflorum  
Paniceum dichotomiflorum  
Paniceum gattingeri  
Paniceum maximum  
Paniceum miliaceum  
Paniceum obtusum  
Paniceum repens  
Paniceum trichoides  
Paniceum virgatum  
Paspalidium geminatum  
Paspalum ciliatifolium  
Paspalum conjugatum  
Paspalum dilatatum  
Paspalum distichum  
Paspalum fluitans  
Paspalum laeve  
Paspalum lividum  
Paspalum notatum  
Paspalum paspaloides  
Paspalum picatum  
Paspalum scrobiculatum  
Paspalum urvillei  
Paspalum vaginatum  
Paspalum virgatum  
Pennisetum americanum  
Pennisetum clandestinum  
Pennisetum polystachyon  
Pennisetum purpureum  
Pennisetum villosum  
Phalaris aquatica
Phalaris arundinacea
Phalaris brachystachya
Phalaris canariensis
Phalaris minor
Phalaris phalaroides
Phragmites australis
Poa annua
Poa bulbosa
Poa compressa
Poa pratensis
Poa trivialis
Polygopon monspeliensis
Polygopon viridis
Rottboellia cochinchinensis
Schizachyrium scoparium
Setaria barbata
Setaria faber i
Setaria glauca
Setaria gracilis
Setaria italica
Setaria lutescens
Setaria palmitaria
Setaria sphacelata
Setaria verticillata
Setaria viridis
Sorghum bicolor
Sorghum halepense
Sporobolus airoides
Sporobolus juncea
Sporobolus neglectus
Sporobolus pyramidalis
Sporobolus vaginiflorus
Sporobolus virgincus
Stenotaphrum secundatum
Tragus berteronianus
Tragus racemosus
Vulpia bromoides
Vulpia myuros
Zoysia matrella

MAJOR WEEDY GRASSES OF THE WORLD

Arundinoideae

Arundineae
Phragmites australis
Phragmites karka

Chloridoideae

Cynodonteae
Cynodon dactylon

Eragrostideae
Dactyloctenium aegyptium
Eleusine indica
Leptochloa chinensis
Leptochloa panicea

Ehrhartoideae

Oryzeae
Leersia hexandra

Panicoideae

Paniceae
Axonopus compressus
Brachiaria mutica
Cenchrus echinatus
Digitaria abysinnica
Digitaria ciliaris
Digitaria sanguinalis
Echinochloa colona
Echinochloa crus-galli
Imperata cylindrica
Ischaemum rugosum
Panicum maximum
Panicum repens
Paspalum conjugatum
Paspalum dilatatum
Pennisetum clandestinum
Pennisetum pedicellatum
Pennisetum polystachion
Pennisetum purpureum
Rottboellia cochinchinensis
Setaria verticillata
Setaria viridis
Sorghum halepense

Pooideae

Avenae
Avena fatua
Poeae
Lolium temulentum

[Source: Chapman & Peat, 1992: 86]

SELECTED REFERENCES

GENERAL REFERENCES


Häfliger, E. & H. Scholz. 1981. Grass weeds 2: weeds of the sub-families Chloridoideae, Pooideae,
PARTICULAR GRASSES


Grasses have, of course, long been used for lawns. Less appreciated has been their use as more showy ornamentals. You may have noticed how many more grasses are now being offered for landscaping purposes and that there are now a number of books on ornamental grasses available.

### HERBACEOUS ORNAMENTALS

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agrostis nebulosa</td>
<td>cloud grass</td>
</tr>
<tr>
<td>Alopecurus lanatus</td>
<td>wooly foxtail grass</td>
</tr>
<tr>
<td>Calamagrostis spicata</td>
<td>(dis) grass</td>
</tr>
<tr>
<td>Andropogon gerardii</td>
<td>big bluestem</td>
</tr>
<tr>
<td>Andropogon glomeratus</td>
<td>(bushy) bluestem</td>
</tr>
<tr>
<td>Anthoxanthum odoratum</td>
<td>(velvet) grass</td>
</tr>
<tr>
<td>Apera spica-venti</td>
<td>(silky) bent</td>
</tr>
<tr>
<td>Alopecurus pratensis</td>
<td>(purple three-awn) grass</td>
</tr>
<tr>
<td>Bromus brizaeformis</td>
<td>(cloud) grass</td>
</tr>
<tr>
<td>Bromus ramosus</td>
<td>(woody) brome</td>
</tr>
<tr>
<td>Calamagrostis acutiflora</td>
<td>(feather reed) grass</td>
</tr>
<tr>
<td>Calamagrostis arundinacea</td>
<td>(fall-blooming) reed grass</td>
</tr>
<tr>
<td>Calamagrostis canescens</td>
<td>(purple) small reed</td>
</tr>
<tr>
<td>Calamagrostis epigejos</td>
<td>(bush) grass</td>
</tr>
<tr>
<td>Chasmanthium latifolium</td>
<td>(wild-oats) grass</td>
</tr>
<tr>
<td>Chloris virgata</td>
<td>(finger) grass</td>
</tr>
<tr>
<td>Coix lacryma-jobi</td>
<td>(Job's tears)</td>
</tr>
<tr>
<td>Cortaderia selloana</td>
<td>(pampas) grass</td>
</tr>
<tr>
<td>Cortaderia jubata</td>
<td>(purple) pampas grass</td>
</tr>
<tr>
<td>Dactylis glomerata</td>
<td>(orchard) grass</td>
</tr>
<tr>
<td>Deschampsia caespitosa</td>
<td>(tufted) hair grass</td>
</tr>
<tr>
<td>Deschampsia flexuosa</td>
<td>(crinkled) hair grass</td>
</tr>
<tr>
<td>Elymus ramosus</td>
<td>(blue) lyme grass</td>
</tr>
<tr>
<td>Elymus repens</td>
<td>(bent) awn plume grass</td>
</tr>
<tr>
<td>Elymus canadensis</td>
<td>(weeping) love grass</td>
</tr>
<tr>
<td>Eragrostis curvula</td>
<td>(purple) love grass</td>
</tr>
<tr>
<td>Eragrostis spectabilis</td>
<td>(teff)</td>
</tr>
<tr>
<td>Eragrostis trichodes</td>
<td>(sand) love grass</td>
</tr>
<tr>
<td>Eriachne contortus</td>
<td>(bent awn) plume grass</td>
</tr>
<tr>
<td>Eriachne gigantea</td>
<td>(sugar cane) plume grass</td>
</tr>
<tr>
<td>Eriachne ravennae</td>
<td>(ravena) grass</td>
</tr>
<tr>
<td>Festuca ovina</td>
<td>(giant) fescue</td>
</tr>
<tr>
<td>Festuca gigantea</td>
<td>(sheep) fescue</td>
</tr>
<tr>
<td>Glyceria maxima</td>
<td>(reed) meadow grass</td>
</tr>
<tr>
<td>Gladiolus communis</td>
<td>(adobe) grass</td>
</tr>
<tr>
<td>Gynura sagittatam</td>
<td>(uva) grass</td>
</tr>
<tr>
<td>Helictotrichon sempervirens</td>
<td>(blue) oat grass</td>
</tr>
<tr>
<td>Holcus mollis</td>
<td>(velvet) grass</td>
</tr>
<tr>
<td>Hordeum jubatum</td>
<td>(foxtail) barley, (squirrel) tail</td>
</tr>
<tr>
<td>Koeleria brevis</td>
<td>(blue) hair grass</td>
</tr>
<tr>
<td>Koeleria poiretiana</td>
<td>(large blue) hair grass</td>
</tr>
<tr>
<td>Lagurus ovatus</td>
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<tr>
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<td>Sesleria caerulea</td>
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<td>Spardina pectinata</td>
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Stipa calamagrostis  
Stipa capillata  
Stipa gigantea  
Stipa hymenoides  
Stipa ichu  
Stipa pennata  
Stipa ramosissima  
Stipa splendens  
Stipa tenacissima  
Themenia triandra  
Thysanolaena maxima  
Tripsacum dactyloides  
Uniola latifolia  
Zea mays  
Zizania aquatica

**ORNAMENTAL BAMBOOS**

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<td>Bambusa glaucescens</td>
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<td>Bambusa oldhami</td>
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<td>Bambusa ventricosa</td>
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**LAWN GRASSES**

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<th><strong>Species</strong></th>
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<tr>
<td>Agrostis palustris</td>
<td>(creeping bent grass)</td>
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<td>Agrostis tenuis</td>
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<td>Cynodon dactylon</td>
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<td>Eremochloa ophiuroides</td>
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<td>Festuca longifolia</td>
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<td>Festuca rubra</td>
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<td>Lolium multiflorum</td>
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<td>Lolium perenne</td>
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<td>(Kentucky blue grass)</td>
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<td>Poa trivialis</td>
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<td>Stenotaphrum secundatum</td>
<td>(St. Augustine grass)</td>
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<tr>
<td>Zoysia matrella</td>
<td>(zoysia)</td>
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**SELECTED REFERENCES**


4.11 - ENDEMIC GRASSES

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<tr>
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<td>Agrostis ampla</td>
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<td>Agrostis aristiglumis</td>
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<td>Agrostis clivicola var. punta-reyesensis</td>
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<td>Agrostis exarata var. minor</td>
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<td>Agrostis hallii</td>
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<td>Amphicarpum muelenbergianum</td>
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<td>Andropogon glomeratus var. glaucopsis</td>
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<td>Andropogon gyrans var. stenophyllum</td>
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<td>Andropogon liebmanni</td>
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<td>Andropogon ternarius var. cabanisii</td>
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<td>Aristida rhizomorpha (Florida three-awn)</td>
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<td>Calamagrostis scopulorum (Jones’ reed grass)</td>
<td>western U. S.</td>
<td></td>
</tr>
<tr>
<td>Calamagrostis tweedyi (Tweedy’s reed grass)</td>
<td>WA, MT, ID</td>
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</tr>
<tr>
<td>Calamophila don-hensonii (Henson’s reed grass)</td>
<td>MI</td>
<td></td>
</tr>
<tr>
<td>Calamovilfa arcuata (Cumberland sand reed)</td>
<td>OK, AR, AL, TN</td>
<td></td>
</tr>
<tr>
<td>Calamovilfa brevipilis var. brevipilis (pine barren sand reed)</td>
<td>NJ to SC</td>
<td></td>
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<tr>
<td>Calamovilfa brevipilis var. calvipes</td>
<td>VA</td>
<td></td>
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<tr>
<td>Calamovilfa curtissii (Florida sand reed)</td>
<td>FL</td>
<td></td>
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<tr>
<td>Calamovilfa gigantea (big sand reed)</td>
<td>southeast &amp; southwestern U. S.</td>
<td></td>
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<tr>
<td>Chasmanthium laxum var. laxum (spike grass)</td>
<td>southeastern U. S.</td>
<td></td>
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</tbody>
</table>
**Chasmanthium laxum** var. **sessiliflorum** (long leaf uniola) southeastern U. S.

**Chasmanthium nitidum** (shiny uniola) southeastern U. S.

**Chasmanthium ornithorhynchum** (bird bill uniola) southeastern U. S.

**Chloris x subdolichostachya** (short-spike windmill grass) AZ to KS, LA

**Chloris texensis** (Texas windmill grass) TX

**Cinna bolanderi** (Bolander’s reed grass) CA

**Coelorachis cylindrica** (Carolina joint-tail) southeastern U. S.

**Coelorachis rugosa** (wrinkled joint-tail) southeastern U. S.

**Coelorachis tesselata** (lattice joint-tail) LA to FL

**Coelorachis tuberculosa** (Florida joint-tail) southeastern U. S.

**Ctenium aromaticum** (toothache grass) VA to FL, LA

**Ctenium floridanum** (Florida toothache grass) GA, FL

**Danthonia epilis** (Carolina oat grass) southeastern U. S.

**Danthonia sericea** (downy oat grass) eastern U. S.

**Digitaria arenicola** (sand witch grass) TX

**Digitaria cognata** (fall witch grass) eastern & central U. S.

**Digitaria filiformis** var. **filiformis** (Caribbean crab grass) southeastern U. S.

**Digitaria floridana** (Florida crab grass) Hernando Co., FL

**Digitaria horizontalis** (Jamaica crab grass) southeastern U. S. ???

**Digitaria leucocoma** Lake Co., FL

**Digitaria pauciflora** (two-spike finger grass) Dade Co., FL

**Digitaria pubiflora** (western witch grass) southwestern U. S.

**Digitaria simpsonii** (Simpson’s)

**Dissanthelium californicum** (Catalina grass) CA (CFP)

**Elyhordeum callifornicum** ???

**Elyhordeum iowense** (Iowa barley) MT, ND, NB, IA

**Elyhordeum piperi** (Piper’s barley) WA

**Elyhordeum stebbinsianum** (Stebbins’ barley) WA, OR, CA

**Elymus ambiguus** var. **ambiguus** (Rocky Mountain lyme grass) UT, MT to NM

**Elymus arenicola** (sand lyme grass) WA, OR, MT, ID

**Elymus arizonicus** (Arizona wild rye) CA, AZ, NM, TX

**Elymus californicus** (California bottlebrush) CA

**Elymus elymoides** ssp. **hordeoides** (western squirreltail) WA, OR, ID, CA, NV

**Elymus flavescens** (sand lyme grass) WA, OR, ID, SD

**Elymus laevis** (California wild rye) CA

**Elymus x multiflorus** CA, CFP ?

**Elymus multisetus** (big wild rye) western U. S.

**Elymus pacificus** (Pacific wild rye) CA

**Elymus salinus** ssp. **mojavensis** (Salina wild rye) CA, AZ

**Elymus salinus** ssp. **salinus** (Salina wild rye) western U. S.

**Elymus sierrae** (Sierra wild rye) CA, NV

**Elymus simplex** (smooth wild rye) western U. S.

**Elymus stebbinsii** ssp. **septentrionalis** (Stebbins’ wild rye) CA

**Elymus stebbinsii** ssp. **stebbinsii** (Stebbins’ wild rye) CA

**Elymus trachycaulus** ssp. **sierrus** Source ??

**Elymus villosus** var. **arkansanus** (hairy wild rye) central & eastern U. S.

**Eragrostis bahiensis** (bahia love grass) LA, AL, FL

**Eragrostis lutescens** (six week’s love grass) WA, CA, NV, CO, AZ, NM

**Eragrostis pectinacea** var. **miserrima** (desert love grass) TX to FL

**Eragrostis pectinacea** var. **tracyi** (Tracy’s love grass) FL

**Eragrostis refracta** (coastal love grass) southeastern U. S.

**Eragrostis swallenii** (Swallen’s love grass) TX

**Eragrostis trichodes** (sand love grass) central & eastern U. S.

**Eriochloa michauxii** var. **michauxii** (long leaf cup grass) southeastern U. S.

**Eriochloa michauxii** var. **simpsonii** (Simpson’s cup grass) FL

**Eustachys floridana** (Florida finger grass) AL, GA, FL

**Eustachys glauca** (salt marsh windmill grass) southeastern U. S.

**Eustachys neglecta** (four-spoke windmill grass) FL

**Festuca arizonica** (Arizona fescue) AZ, CO, NM, TX

**Festuca brachyphylla** ssp. **coloradensis** (alpine fescue) western U. S.
Festuca californica var. californica (California fescue) OR, CA
Festuca calligera (southwestern fescue) southwestern U. S.
Festuca dasyclada (Utah fescue) UT, CO
Festuca elliotae (squirrel-tail six-weeks grass) south-central & southeastern U. S.
Festuca elmeri (Elmer's fescue) WA, OR, CA
Festuca howellii (Howell's fescue) WA, OR, CA
Festuca kingii (spiked fescue) western U. S.
Festuca ligulata (Guadalupe fescue) TX
Festuca minutiflora (small-flowered fescue) southwestern U. S.
Festuca occidentalis (western fescue) western U. S.
Festuca paradoxa (clustered fescue) central & eastern U. S.
Festuca parishii (California fescue) CA
Festuca proliferà (proliferous fescue) ME, NM (Canada only ??)
Festuca rubra ssp. arctica (red fescue) NH (+ ?)
Festuca rubra ssp. deniuscula (red fescue) OR, CA
Festuca sororia (ravine fescue) AZ, CO, UT, NM
Festuca thurberi (Thurber's fescue) AZ, NM, CO, UT, WY
Festuca viridula (green leaf fescue) western U. S.
Glyceria acutiflora (creeping manna grass) eastern U. S.
Glyceria septentrionalis var. arctistis (Arkansas manna grass) OK, TX, southeastern U. S.
Gymnopogon brevifolius (slim skeleton grass) south-central & southeastern U. S.
Gymnopogon chapmanianus (Chapman's skeleton grass) GA, FL
Helictotrichon mortonianum (Morton's alpine-oat) UT, CO, NM
Hilaria jamesii (galleta) western U. S.
Hordeum arizonicum (Arizona barley) CA, AZ, NM
Hordeum brachyantherum ssp. californicum (California barley) OR, CA, NV
Leersia hexandra (Southern sweet grass) southeastern U. S.
Leersia lenticularis (catchfly grass) eastern U. S.
Melica aristata (awned melic) WA, OR, CA, NV, KT
Melica bulbosa var. inflata WA, CA
Melica californica var. californica (California melic) OR, CA
Melica californica var. nevadensis (California melic) CA
Melica fugax (little onion grass) WA, OR, CA, ID, NV
Melica geyeri var. aristatura (Geyer's onion grass) CA
Melica geyeri var. geyerii (Geyer's onion grass) OR, CA, NV
Melica imperfecta (coast range melic) CA (CFP)
Melica mutica (two-flowered melic) eastern U. S.
Melica porteri var. laxa (Porter's melic) AZ, NM, TX
Melica porteri var. porteri (Porter's melic) UT, CO, AZ, NM, TX
Melica stricta var. albiculalis (nodding onion grass) CA
Melica stricta var. stricta (nodding onion grass) OR, CA, NV, UT
Melica subulata var. pammelii (Pammel's onion grass) ID, MT, WY
Melica torreyana (Torrey's melic) CA
Muhlenbergia bushii (nodding muhly) central & eastern U. S.
Muhlenbergia californica (California muhly) CA [extinct]
Muhlenbergia expansa (cutover muhly) southeastern U. S.
Muhlenbergia filiculmis (slim stem muhly) southwestern U. S.
Muhlenbergia jonesii (Modoc muhly) CA
Muhlenbergia pungens (sandhill muhly) western & central U. S.
Muhlenbergia reverchonii (see p. 129) OK, TX
Muhlenbergia sericea (dune hair muhly) southeastern U. S.
Muhlenbergia thurberi (Thurber's muhly) NV, UT, CO, AZ, NM
Muhlenbergia torreyana (New Jersey muhly) northeastern U. S.
Muhlenbergia villiflora var. villosa (hairly muhly) NM, TX
Muhlenbergia virescens (screw-leaf muhly) AZ, NM
Neostephanus colusana (Colusa grass) CA
Orcuttia californica (California orcutt grass) CA (CFP)
Orcuttia inaequalis (San Joaquin Valley orcutt grass) CA
<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
<th>Location</th>
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<tbody>
<tr>
<td>Orcuttia pilosa</td>
<td>hairy Orcutt grass</td>
<td>CA</td>
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<tr>
<td>Orcuttia tenuis</td>
<td>slender Orcutt grass</td>
<td>CA</td>
</tr>
<tr>
<td>Orcuttia viscida</td>
<td>(Sacramento Orcutt grass)</td>
<td>Sacramento Co., CA</td>
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<tr>
<td>Oryzopsis contracta</td>
<td>(contracted rice grass)</td>
<td>MT, WY, CO</td>
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<tr>
<td>Oryzopsis hederonii</td>
<td>(Henderson’s rice grass)</td>
<td>WA, OR, ID</td>
</tr>
<tr>
<td>Orcuttia tenuis</td>
<td>CA</td>
<td></td>
</tr>
<tr>
<td>Orcuttia viscida</td>
<td>CA</td>
<td></td>
</tr>
<tr>
<td>Oryzopsis contracta</td>
<td>(contracted rice grass)</td>
<td>MT, WY, CO</td>
</tr>
<tr>
<td>Oryzopsis hederonii</td>
<td>(Henderson’s rice grass)</td>
<td>WA, OR, ID</td>
</tr>
<tr>
<td>Panicum acuminatum var. columbiae</td>
<td>(blood panic grass)</td>
<td>southeastern U. S.</td>
</tr>
<tr>
<td>Panicum acuminatum var. sericeum</td>
<td>(blood panic grass)</td>
<td>western U. S.</td>
</tr>
<tr>
<td>Panicum anceps var. anceps</td>
<td>(beaked panic grass)</td>
<td>south-central &amp; southeastern U. S.</td>
</tr>
<tr>
<td>Panicum anceps var. rhizomatum</td>
<td>(beaked panic grass)</td>
<td>southeastern U. S.</td>
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<tr>
<td>Panicum bosci</td>
<td>(Bosc's panic grass)</td>
<td>eastern U. S.</td>
</tr>
<tr>
<td>Panicum brachyantherum</td>
<td>(pimple panic grass)</td>
<td>OK, TX, AR, LA, MS</td>
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<tr>
<td>Panicum capillare var. hillmanii</td>
<td>(Hillman’s panic grass)</td>
<td>CA, IA, south-central U. S.</td>
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<tr>
<td>Panicum chamaeleonche var. breve</td>
<td>(beaked panic grass)</td>
<td>FL</td>
</tr>
<tr>
<td>Panicum consanguineum</td>
<td>Kunth’s panic grass</td>
<td>southeastern U. S.</td>
</tr>
<tr>
<td>Panicum dichotomiflorum var. puritanorum</td>
<td>(fall panic grass)</td>
<td>eastern U. S.</td>
</tr>
<tr>
<td>Panicum dichotomum var. glabrofolium</td>
<td>(fall panic grass)</td>
<td>eastern &amp; southeastern U. S.</td>
</tr>
<tr>
<td>Panicum dichotomum var. lucidum</td>
<td>(fall panic grass)</td>
<td>MA to FL</td>
</tr>
<tr>
<td>Panicum dichotomum var. mattamuskeetense</td>
<td>(fall panic grass)</td>
<td>FL</td>
</tr>
<tr>
<td>Panicum dichotomum var. nitidum</td>
<td>(fall panic grass)</td>
<td>southeastern U. S.</td>
</tr>
<tr>
<td>Panicum ensifolium var. curtifolium</td>
<td>(cut throat panic grass)</td>
<td>southeastern U. S.</td>
</tr>
<tr>
<td>Panicum ensifolium var. breve</td>
<td>(cut throat panic grass)</td>
<td>FL</td>
</tr>
<tr>
<td>Panicum gymnocarpon</td>
<td>(savanna)</td>
<td>southeastern U. S.</td>
</tr>
<tr>
<td>Panicum malacophyllum</td>
<td>(soft-leaved panic grass)</td>
<td>central &amp; eastern U. S.</td>
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<tr>
<td>Panicum mohavense</td>
<td>(Mohave panic grass)</td>
<td>AZ, NM</td>
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<tr>
<td>Panicum philadelphicum ssp. lithophilum</td>
<td>(Philadelphia panic grass)</td>
<td>GA, NC, SC</td>
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<tr>
<td>Panicum philadelphicum ssp. philadelphia</td>
<td>(Philadelphia panic grass)</td>
<td>eastern U. S.</td>
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<tr>
<td>Panicum ovale var. pseudopubescent</td>
<td>(egg-leaf panic grass)</td>
<td>central &amp; eastern U. S.</td>
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<tr>
<td>Panicum perlongum</td>
<td>(long-sheath panic grass)</td>
<td>central U. S.</td>
</tr>
<tr>
<td>Panicum ravenelii</td>
<td>(Ravenell's panic grass)</td>
<td>eastern &amp; southeastern U. S.</td>
</tr>
<tr>
<td>Panicum rigidulum var. abscissum</td>
<td>(cut throat panic grass)</td>
<td>FL</td>
</tr>
<tr>
<td>Panicum rigidulum var. combsii</td>
<td>(Comb’s panic grass)</td>
<td>southeastern U. S.</td>
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<tr>
<td>Panicum rigidulum var. elongatum</td>
<td>(Comb’s panic grass)</td>
<td>eastern U. S.</td>
</tr>
<tr>
<td>Panicum rigidulum var. pubescens</td>
<td>(Comb’s panic grass)</td>
<td>southeastern U. S.</td>
</tr>
<tr>
<td>Panicum rigidulum var. rigidulum</td>
<td>(redtop panic grass)</td>
<td>CA, OR, eastern U. S.</td>
</tr>
<tr>
<td>Panicum scabriusculum</td>
<td>(tall swamp panic grass)</td>
<td>southeastern U. S.</td>
</tr>
<tr>
<td>Paspalum bifidum</td>
<td>(pitchfork paspalum)</td>
<td>southeastern U. S.</td>
</tr>
<tr>
<td>Paspalum distichum (knot grass)</td>
<td>(knot grass)</td>
<td>western, south-central, eastern U. S. ??</td>
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<tr>
<td>Paspalum floridanum var. floridanum</td>
<td>(Florida paspalum)</td>
<td>eastern U. S.</td>
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<tr>
<td>Paspalum laeve</td>
<td>(field paspalum)</td>
<td>eastern U. S.</td>
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<tr>
<td>Paspalum lividum</td>
<td>(longtom)</td>
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<tr>
<td>Paspalum separatum</td>
<td>(field paspalum)</td>
<td>TX ???</td>
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<tr>
<td>Paspalum setaceum var. longepedunculatum</td>
<td>(bare stem paspalum)</td>
<td>southeastern U. S.</td>
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<tr>
<td>Paspalum setaceum var. muhlenbergii</td>
<td>(barred stem paspalum)</td>
<td>central &amp; eastern U. S.</td>
</tr>
<tr>
<td>Paspalum setaceum var. psammophila</td>
<td>(sand paspalum)</td>
<td>eastern U. S.</td>
</tr>
<tr>
<td>Paspalum setaceum var. supinum</td>
<td>(supine paspalum)</td>
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<tr>
<td>Phalaris californica</td>
<td>(California canary grass)</td>
<td>OR, CA (CFP)</td>
</tr>
<tr>
<td>Phalaris lemmonei</td>
<td>(Lemon’s canary grass)</td>
<td>CA</td>
</tr>
<tr>
<td>Piptochaetium avenacioides</td>
<td>(Florida needle grass)</td>
<td>FL</td>
</tr>
<tr>
<td>Pleuropogon californicus var. californicus</td>
<td>(California semaphore grass)</td>
<td>CA</td>
</tr>
<tr>
<td>Pleuropogon californicum var. davyi</td>
<td>(Davy’s semaphore grass)</td>
<td>CA</td>
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<tr>
<td>Pleuropogon hooverianus</td>
<td>(Hoover’s semaphore grass)</td>
<td>CA</td>
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<tr>
<td>Pleuropogon oreganus</td>
<td>(Oregon semaphore grass)</td>
<td>OR</td>
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<tr>
<td>Poa arctica ssp. aperta (arctic blue grass)</td>
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<td>CO, WY, NM</td>
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<tr>
<td>Poa arctica ssp. grayana (Gray’s blue grass)</td>
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<td>MT to NM, UT</td>
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<tr>
<td>Poa arrowiae (Arrow’s blue grass)</td>
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<td>ID, UT</td>
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</tbody>
</table>
Poa atropurpurea (San Bernardino blue grass) CA
Poa autumnalis (autumn blue grass) OK, TX
Poa bolanderi (Bolander’s blue grass) WA, OR, CA, ID, UT
Poa chambersii (Chambers’ blue grass) Lane Co., OR
Poa chapmaniana (Chapman’s blue grass) central & eastern U. S.

Poa curtifolia (Little Mountain blue grass) WA
Poa cusickii ssp. cusickii (Cusick’s blue grass) WA, OR, CA, MT, ID, NV
Poa cuspidata (early blue grass) southeastern U. S.
Poa douglasii (sand dune blue grass) CA
Poa x fibrata ???

Poa hartzii ssp. alaskana (Hartz’s blue grass) AK
Poa keckii (Keck’s blue grass) CA
Poa liebergii (Leiberg’s blue grass) WA, OR, ID
Poa macroclada ID, MT, CO
Poa x multnomae (Multnomah Falls blue grass) OR

Poa napensis (Napa blue grass) Napa Co., CA
Poa occidentalis (New Mexico blue grass) AZ, CO, NM, TX
Poa paludigena (bog blue grass) northeastern U. S.
Poa piperi (Piper’s blue grass) OR, CA
Poa pringlei (Pringle’s blue grass) OR, CA

Poa reflexa (nodding blue grass) western U. S.
Poa rhizomata (timber blue grass) OR, CA
Poa sierrae (Sierra blue grass) CA
Poa stebbinsii (Stebbins’ blue grass) CA
Poa tenerirma (delicate blue grass) CA

Poa tracyi (Tracy’s blue grass) CO, NM
Poa unilateralis ssp. pachypholis WA
Poa wolfii (Wolf’s blue grass) eastern U. S.
Puccinellia howellii (Howell’s alkali grass) Shasta Co., CA
Puccinellia parishii (Parish’s alkali grass) CA, AZ, NM

Puccinellia simplex (little alkali grass) CA, UT
Puccinellia sublaevis (smooth alkali grass) AK
Redfieldia flexuosa (blowout grass) western & central U. S.
Saccharum alopecuroides (silver plume grass) southeastern U. S.
Saccharum baldwinii (narrow-plume plume grass) southeastern U. S.

Saccharum brevibarbe var. brevibarbe south-central & southeastern U. S.
Saccharum brevibarbe var. contortum (bent-awn plume grass) central & southeastern U. S.
Saccharum coarctum (bunched plume grass) southeastern U. S.
Schizachyrium maritimum (seashore false bluestem) LA, AL, MS, FL
Schizachyrium niveum (pine scrub false bluestem) FL

Schizachyrium rhizomatum (Florida false bluestem) FL
Schizachyrium scoparium var. divergens (little bluestem) south-central & southeastern U. S.
Schizachyrium scoparium var. neomexicanum (little bluestem) AZ, NM, TX
Schizachyrium scoparium var. stoloniferum (little bluestem) southeastern U. S.
Schizachyrium sericatum (little bluestem)

Scribneria bolanderi (Scribner’s grass) WA, OR, CA
Setaria reverchonii ssp. firmula [ssp. not in K & M] TX ???
Sorghastrum eliottii (slender Indian grass) south-central & southeastern U. S.
Sorghastrum secundum (lop-sided Indian grass) southeastern U. S.
Spartina bakeri (sand cord grass) TX, GA, SC, FL

Spartina cynosuroides (big cord grass) MA to TX gulf coast
Sphenopholis filiformis (long-leaf wedge grass) southeastern U. S.
Sphenopholis longiflora (Texas wedge grass) TX, AR, LA
Sphenopholis x pallens (wedge grass) eastern U. S.
Sphenopholis pensylvanica (swamp wedge grass) eastern & southeastern U. S.

Sporobolus clandestinus (hidden dropseed) central & eastern U. S.
Sporobolus compositus var. drummondii (meadow dropseed) central & southeastern U. S.
Sporobolus compositus var. macer (Mississippi dropseed) southwestern U. S.
Sporobolus coromandelianus (whorled dropseed) southwestern, central, & eastern U. S.
Sporobolus floridanus (Florida dropseed) AL, GA, SC, FL

Sporobolus interruptus (black dropseed) AZ
4.12 - INTRODUCED GRASSES WITH LIMITED DISTRIBUTION*

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acrachne racemosa (goose grass)</td>
<td>Riverside Co., CA</td>
</tr>
<tr>
<td>Aegilops crassa (Persian goat grass)</td>
<td>NY</td>
</tr>
<tr>
<td>Aegilops geniculata (ovate goat grass)</td>
<td>CA, VA, NY</td>
</tr>
<tr>
<td>Aegopogon cenchroides (Guatemalan fragile grass)</td>
<td>CA</td>
</tr>
<tr>
<td>Agropyron orientale (oriental wheat grass)</td>
<td>NY</td>
</tr>
<tr>
<td>Agropyron squarrosum</td>
<td>NY</td>
</tr>
<tr>
<td>Agrostis tandilensis (Argentine bent grass)</td>
<td>CA</td>
</tr>
<tr>
<td>Alba caryophyllea var. cupiana (silver hair grass)</td>
<td>CA</td>
</tr>
<tr>
<td>Allotrois cimicina (bug seed grass)</td>
<td>MD, FL</td>
</tr>
<tr>
<td>Alopecurus creticus (Cretan meadow foxtail)</td>
<td>PA (historic)</td>
</tr>
<tr>
<td>Scientific Name</td>
<td>Common Name</td>
</tr>
<tr>
<td>-----------------------------------------------------</td>
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<tr>
<td>Alopecurus rendlei</td>
<td>Rendle’s meadow foxtail</td>
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<tr>
<td>Ampelodesmos mauritanica</td>
<td>(dis grass ... or it is dat grass?)</td>
</tr>
<tr>
<td>Amphibromus neesii</td>
<td>(wallaby grass)</td>
</tr>
<tr>
<td>Amphibromus scabrivalvis</td>
<td>(swamp wallaby grass)</td>
</tr>
<tr>
<td>Andropogon bicornis</td>
<td>(barbas de indio)</td>
</tr>
<tr>
<td>Anaphphora hermaphrodita</td>
<td>(old field grass)</td>
</tr>
<tr>
<td>Apluda mutica</td>
<td>(Mauritian grass)</td>
</tr>
<tr>
<td>Avena occidentalis</td>
<td>(western oat)</td>
</tr>
<tr>
<td>Avena strigosa</td>
<td>(black oat)</td>
</tr>
<tr>
<td>Bambusa multiplex</td>
<td>(hedge bamboo)</td>
</tr>
<tr>
<td>Bambusa oldhamii</td>
<td>(Oldham’s bamboo)</td>
</tr>
<tr>
<td>Bambusa vulgaris</td>
<td>(common bamboo)</td>
</tr>
<tr>
<td>Brachypodium caespitatum</td>
<td>(false brome)</td>
</tr>
<tr>
<td>Brachypodium phoenicoides</td>
<td>(Mediterranean false brome)</td>
</tr>
<tr>
<td>Brachypodium sylvaticum</td>
<td>(slender false brome)</td>
</tr>
<tr>
<td>Bromus alopecuros</td>
<td>Source ??</td>
</tr>
<tr>
<td>Bromus hordeaceus ssp. pseudothominei</td>
<td>(soft brome)</td>
</tr>
<tr>
<td>Bromus lepidus</td>
<td>(slender soft brome)</td>
</tr>
<tr>
<td>Chenicurus biflorus</td>
<td>(Indian sandbur)</td>
</tr>
<tr>
<td>Chloris barbata</td>
<td>(swollen finger grass)</td>
</tr>
<tr>
<td>Chloris elata</td>
<td>(many-flowered windmill grass)</td>
</tr>
<tr>
<td>Chloris pectinata</td>
<td>(comb windmill grass)</td>
</tr>
<tr>
<td>Chloris radiata</td>
<td>(radiate windmill grass)</td>
</tr>
<tr>
<td>Chloris truncata</td>
<td>(Australian finger grass)</td>
</tr>
<tr>
<td>Chloris ventricosa</td>
<td>(plump windmill grass)</td>
</tr>
<tr>
<td>Chrysopogon fulvus</td>
<td>(red false beard grass)</td>
</tr>
<tr>
<td>Chrysopogon pauciflorus</td>
<td>(Florida rhaphis)</td>
</tr>
<tr>
<td>Chrysopogon zizanioides</td>
<td>(khus-khus)</td>
</tr>
<tr>
<td>Cladoraphis cyperoides</td>
<td>(bristly love grass)</td>
</tr>
<tr>
<td>Coleanthus subtilis</td>
<td>(moss grass)</td>
</tr>
<tr>
<td>Cortaderia jubata</td>
<td>(purple pampas grass)</td>
</tr>
<tr>
<td>Crypsis alopecuroides</td>
<td>(foxtail prickle grass)</td>
</tr>
<tr>
<td>Crypsis schoenoides</td>
<td>(swamp prickle grass)</td>
</tr>
<tr>
<td>Crypsis vaginiflora</td>
<td>(modest prickle grass)</td>
</tr>
<tr>
<td>Cutandia memphitica</td>
<td>(Memphis grass)</td>
</tr>
<tr>
<td>Chrysochogon iwarancusa</td>
<td>(oil grass)</td>
</tr>
<tr>
<td>Chrysochogon nardus</td>
<td>(citronella grass)</td>
</tr>
<tr>
<td>Cynodon aethiopicus</td>
<td>(Ethiopian dogtooth grass)</td>
</tr>
<tr>
<td>Cynodon dactylon var. aridus</td>
<td>(couch grass)</td>
</tr>
<tr>
<td>Cynodon dactylon var. x magennisii</td>
<td>(Magennis’ Bermuda grass)</td>
</tr>
<tr>
<td>Cynodon aristiglumis</td>
<td>Source ??</td>
</tr>
<tr>
<td>Cynodon nlemfuensis var. nlemfuensis</td>
<td>(African Bermuda grass)</td>
</tr>
<tr>
<td>Cynodon nlemfuensis var. robustus</td>
<td>(African Bermuda grass)</td>
</tr>
<tr>
<td>Cynodon plectostachyus</td>
<td>(star grass)</td>
</tr>
<tr>
<td>Dactylis glomerata var. aschersoniana</td>
<td>(orchard grass)</td>
</tr>
<tr>
<td>Dactyloctenium radulans</td>
<td>(button grass)</td>
</tr>
<tr>
<td>Dasystyrum villosum</td>
<td>(mosquito grass)</td>
</tr>
<tr>
<td>Dendrocalamus latiflorus</td>
<td>(giant bamboo)</td>
</tr>
<tr>
<td>Dichanthium annulatum</td>
<td>(Kleberg bluestem)</td>
</tr>
<tr>
<td>Dichanthium sericeum</td>
<td>(Queensland bluestem)</td>
</tr>
<tr>
<td>Digitaria longiflora</td>
<td>(Indian crab grass)</td>
</tr>
<tr>
<td>Digitaria milanjiana</td>
<td>(Madagascar finger grass)</td>
</tr>
<tr>
<td>Digitaria nuda</td>
<td>(naked crab grass)</td>
</tr>
<tr>
<td>Digitaria setigera</td>
<td>(East Indian crab grass)</td>
</tr>
<tr>
<td>Dinebra retroflexa</td>
<td>(viper grass)</td>
</tr>
<tr>
<td>Echinochloa crusgalli ssp. spiralis</td>
<td>(barnyard grass)</td>
</tr>
<tr>
<td>Echinochloa esculenta</td>
<td>(Japanese millet)</td>
</tr>
<tr>
<td>Echinochloa oryzicola</td>
<td>(late barnyard grass)</td>
</tr>
<tr>
<td>Echinochloa oryzoides</td>
<td>(early barnyard grass)</td>
</tr>
<tr>
<td>Echinochloa utilis</td>
<td>Source ??</td>
</tr>
<tr>
<td>Ehrharta calyicina</td>
<td>(weeping veldt grass)</td>
</tr>
<tr>
<td>Scientific Name</td>
<td>Location(s)</td>
</tr>
<tr>
<td>-----------------------------------------------------</td>
<td>-------------</td>
</tr>
<tr>
<td><em>Ehrharta erecta</em> (panic veldt grass)</td>
<td>CA</td>
</tr>
<tr>
<td><em>Ehrharta longiflora</em> (long-flowered veldt grass)</td>
<td>CA</td>
</tr>
<tr>
<td><em>Eleusine coracana</em> ssp. <em>africana</em> (finger millet, ragi)</td>
<td>SC</td>
</tr>
<tr>
<td><em>Elyhordeum atlanticus</em> (Russian quack grass)</td>
<td>OR, CA</td>
</tr>
<tr>
<td><em>Elymus pycnanthus</em> (tick grass)</td>
<td>WA, OR, TX</td>
</tr>
<tr>
<td><em>Elymus racemosus</em> (giant wild rye)</td>
<td>AZ</td>
</tr>
<tr>
<td><em>Enneapogon cenchroides</em> (soft feather pappus grass)</td>
<td>AZ</td>
</tr>
<tr>
<td><em>Enneapogon mollis</em> (soft feather pappus grass)</td>
<td>AZ</td>
</tr>
<tr>
<td><em>Enteropogon dolichostachyus</em></td>
<td>SC</td>
</tr>
<tr>
<td><em>Enteropogon prieurii</em> (Prieuri's umbrella grass)</td>
<td>NC, AL</td>
</tr>
<tr>
<td><em>Eragrostis airoides</em> (darnel love grass)</td>
<td>Brazos Co., TX</td>
</tr>
<tr>
<td><em>Eragrostis atrovirens</em> (thalia love grass)</td>
<td>FL</td>
</tr>
<tr>
<td><em>Eragrostis ciliaris</em> var. <em>laxa</em> (gopher tail love grass)</td>
<td>FL</td>
</tr>
<tr>
<td><em>Eragrostis cylindriflora</em> (tube-flowered love grass)</td>
<td>MD</td>
</tr>
<tr>
<td><em>Eragrostis echinochloidea</em> (African love grass)</td>
<td>AZ, MD</td>
</tr>
<tr>
<td><em>Eragrostis elongata</em> (long love grass)</td>
<td>DC, SC, FL</td>
</tr>
<tr>
<td><em>Eragrostis gangetica</em> (slim-flowered love grass)</td>
<td>LA, MS, FL</td>
</tr>
<tr>
<td><em>Eragrostis plana</em> (South African love grass)</td>
<td>SC</td>
</tr>
<tr>
<td><em>Eragrostis scaligera</em> (tender love grass)</td>
<td>FL</td>
</tr>
<tr>
<td><em>Eriochloa fatmensis</em> (vernal cup grass)</td>
<td>TX, MS, FL</td>
</tr>
<tr>
<td><em>Eriochloa polystachya</em> (Carib grass)</td>
<td>TX, MS, FL</td>
</tr>
<tr>
<td><em>Eustachys distichophylla</em> (weeping love grass)</td>
<td>CA, TX, FL</td>
</tr>
<tr>
<td><em>Eustachys paspaloides</em> var. <em>caribaea</em></td>
<td>Source ???</td>
</tr>
<tr>
<td><em>Festuca arvernensis</em> (blue fescue)</td>
<td>CA (?), NM</td>
</tr>
<tr>
<td><em>Festuca ciliata</em> (fringed six-weeks grass)</td>
<td>PA</td>
</tr>
<tr>
<td><em>Festuca gigantea</em> (giant fescue)</td>
<td>MI, CT, NY</td>
</tr>
<tr>
<td><em>Festuca heteromalla</em> (spreading fescue)</td>
<td>WI</td>
</tr>
<tr>
<td><em>Festuca rigescens</em></td>
<td>AZ (historic)</td>
</tr>
<tr>
<td><em>Festulolium loliiaceum</em></td>
<td>NY, SC</td>
</tr>
<tr>
<td><em>Fingerhuthia africana</em> (zulu-fescue)</td>
<td>CA</td>
</tr>
<tr>
<td><em>Gaudinia fragilis</em> (fragile-oat)</td>
<td>Sonoma Co., CA</td>
</tr>
<tr>
<td><em>Glyceria declinata</em> (waxy manna grass)</td>
<td>CA, LA, NY</td>
</tr>
<tr>
<td><em>Gynerium sagittatum</em> (uva grass, wild cane)</td>
<td>FL</td>
</tr>
<tr>
<td><em>Hakonechloa macra</em> (Hakone grass, Japanese forest grass)</td>
<td>UT</td>
</tr>
<tr>
<td><em>Hemarthria altissima</em> (limpo grass)</td>
<td>TX, FL</td>
</tr>
<tr>
<td><em>Hordeum bulbosum</em> (bulbous barley)</td>
<td>CA</td>
</tr>
<tr>
<td><em>Hyparrhenia hirta</em> (thatch grass)</td>
<td>CA, TX, FL</td>
</tr>
<tr>
<td><em>Hyparrhenia rufula</em> (jaragua grass)</td>
<td>FL</td>
</tr>
<tr>
<td><em>Ischaemum indicum</em> (Indian muraina grass)</td>
<td>MD</td>
</tr>
<tr>
<td><em>Ischaemum rugosum</em> (ribbed muraina grass)</td>
<td>TX, MD</td>
</tr>
<tr>
<td><em>Lamarckia aurea</em> (goldentop)</td>
<td>CA, AZ, TX</td>
</tr>
<tr>
<td><em>Leptochloa chloridiformis</em> (Argentine sprangletop)</td>
<td>TX (historic)</td>
</tr>
<tr>
<td><em>Leptochloa digitata</em> (cane sprangletop)</td>
<td>SC</td>
</tr>
<tr>
<td><em>Lolium temulentum</em> ssp. <em>remotum</em> (poison darnel)</td>
<td>ND (historic)</td>
</tr>
<tr>
<td><em>Mibora minima</em> (early sand grass)</td>
<td>NY, MA</td>
</tr>
<tr>
<td><em>Milium vernale</em> (spring millet grass)</td>
<td>ID</td>
</tr>
<tr>
<td><em>Miscanthus floridulus</em> (giant Chinese silver grass)</td>
<td>MO, AR</td>
</tr>
<tr>
<td><em>Muhlenbergia diversiglumis</em></td>
<td>Galveston Co., TX</td>
</tr>
<tr>
<td><em>Neyraudia arundinacea</em> (Madagascar grass)</td>
<td>CA (unverified)</td>
</tr>
<tr>
<td><em>Neyraudia reynaudiana</em> (Burma reed)</td>
<td>FL</td>
</tr>
<tr>
<td><em>Opizia stolonifera</em> (Acapulco grass)</td>
<td>FL</td>
</tr>
<tr>
<td><em>Oplismenus hirtellus</em> var. <em>hirtellus</em> (wood grass)</td>
<td>FL</td>
</tr>
<tr>
<td><em>Oplismenus hirtellus</em> var. <em>undulatifolius</em> (basket grass)</td>
<td>MD</td>
</tr>
<tr>
<td><em>Oryza rufipogon</em> (wild red rice)</td>
<td>CA, FL</td>
</tr>
<tr>
<td><em>Oryza sativa</em> var. <em>fatua</em> (rice)</td>
<td>FL</td>
</tr>
<tr>
<td><em>Panicum alatum</em> var. <em>alatum</em> (winged panic grass)</td>
<td>CA, AZ</td>
</tr>
</tbody>
</table>
Panicum alatum var. longiflorum (winged panic grass) CA
Panicum bergii (Berg’s panic grass) TX, GA, AL
Panicum napaliense (Napal panic grass) NM
Panicum paludosum (aquatic panic grass) MD
Pappophorum pappiferum (limestone pappus grass) (Peterson et al. 2001: 179)
Parapholis strigosa (hard grass) Humboldt Co., CA
Paspalum almum (Comb’s crown grass) TX, LA
Paspalum coryphaeum (emperor crown grass) FL
Paspalum fimbriatum (fringed crown grass) FL
Paspalum malacophyllum (ribbed crown grass) TX
Paspalum modestum (water paspalum) TX, LA
Paspalum noctatum var. latiflorum TX (Source ????)
Paspalum wrightii (Wright’s paspalum) TX
Pennisetum advena (purple feather grass) CA, TX
Pennisetum clandestinum (kikuyu grass) CA, AZ
Pennisetum flaccidum (Himalayan fountain grass) TX
Pennisetum latifolium (Uruguay fountain grass) CA
Pennisetum macrourum (African feather grass) CA
Pennisetum nervosum (bent-spike fountain grass) CA, TX
Pennisetum orientale (laurisa grass) TX
Pennisetum pedicellatum ssp. unispicum (kyasuma grass) FL
Pennisetum petiolare (petioled fountain grass) IA
Pennisetum polystachyon ssp. setosum (West Indian pennisetum) AZ, NV, FL
Pennisetum purpureum (Napier grass, elephant grass) CA, TX, FL
Phalaris aquatica (Harding grass) OR, CA
Phalaris coerulescens CA
Phleum arenarium (sand timothy) OR, MA, NY
Phleum paniculatum (British timothy) OR, NY
Phleum subulatum (Italian timothy) OR, MA, PA
Phragmites karka (tall reed) TX
Phyllostachys dulcis (sweet shoot bamboo) MA
Phyllostachys flexuosa (zig-zag bamboo) MD
Phyllostachys meyeri (Meyer’s bamboo) MD
Phyllostachys viridiglaucens (green-wax golden bamboo) NJ
Piptochaetium setosum (bristly spear grass) CA
Piptochaetium stipoides var. purpurascens CA
Poa chaixii (Chaix’s spear grass) MN, NY
Pogonarthria squarrosa (herringbone grass) Cochise Co., CA
Polypogon australis (Chilean beard grass) WA, CA, NM
Polypogon imberbis (bear grass) CA
Polytrias amaura (Java grass) FL
Puccinellia rupestris (British alkali grass) WA, PA, NY
Rytidodisperma biannulare (wallaby grass) OR, CA
Rytidodisperma penicillatum (hairy wallaby grass) OR, CA
Rytidodisperma racemosum (wallaby grass) CA
Rytidodisperma semiannulare (wallaby grass) CA
Saccharum bengalense (wild sugar cane) Zuloaga et al. 2003: 551
Saccharum spontaneum (wild Asian sugar cane) FL
Schizachyrium sanguineum var. sanguineum (crimson false bluestem) AL, FL
Secale montanum (wild rye) WA, CA
Setaria barbata (Mary grass) MS, FL
Setaria megaphylla (big leaf bristle grass) LA, FL
Setaria nigrirostris (black bristle grass) OR (historic)
Setaria pumila ssp. pallidefusca (yellow bristle grass) OR, LA
Setaria rariflora (Brazilian bristle grass) AL, FL
Setaria setosa (West Indian bristle grass) NJ, AL, FL
Setaria sphacelata (golden-timothy) CA, AL, FL
Setariopsis auriculata  Pima Co., AZ
Sorghum bicolor ssp. arundinaceum (wild sorghum)  CA, FL

Sporobolus creber  Glenn Co., CA
Stipa capensis (Mediterranean needle grass)  CA
Stipa manicata (Ecuador needle grass)  CA
Stipa neesiana (Uruguayan tussock grass)  AL
Stipa papposa (false rice grass)  ???

Stipa plumosa (South American rice grass)  CA
Themeda arguens (Christmas grass)  VA, MD
Themeda quadrivalvis var. helferi (kangaroo grass)  KS
Themeda quadrivalvis var. quadrivalvis (grader grass)  CA, LA, FL
Themeda triandra (rooi grass)  TX

Thysanolaena latifolia (tiger grass)  ???
Tragus australianus (Australian bur grass)  SC
Tragus berteronianus (spike bur grass)  AZ, NM, TX
Tragus heptaneuron (Kenyan bur grass)  SC
Tribolium obliterum (cape grass)  Monterey Co., CA

Triraphis mollis (purple heads)  TX
Trisetum aureum (golden false oat)  NJ (historic)
Triticum spelta (spelt wheat)  KT, VT
Triticum turgidum (rivet wheat)  NY
Urochloa arrecta (African signal grass)  FL

Urochloa brizantha (palisade signal grass)  TX
Urochloa mosambicensis (sabi grass)  TX
Urochloa oligobrachiata (few-bracted liverseed grass)  FL
Urochloa piligera (hairy signal grass)  FL
Urochloa platytaenia  Source ???

Urochloa subquadripapra (two-fingered guinea grass)  FL
Urochloa villosa (two-ranked liverseed grass)  MD, VA
Zea mays ssp. parviglumis (teosinte)  FL
Zea perennis (Mexican teosinte)  SC
Zoysia matrella var. matrella (Manila temple grass)  AL, GA, FL
Zoysia tenuifolia (Mascarene grass)  LA, FL

* I define limited distribution as those grasses found in no more than three states. This is, of course, an entirely arbitrary decision. You can easily see which ones are found in only one or two states, if you should prefer a narrower limit.

Revised: 02 January 2005
The principal reason for collecting is to provide permanent, representative specimens of plants for future study. In the case of smaller vascular plants, such as annual herbs, the specimen often consists of one to several complete individuals. In larger plants, such as trees or shrubs, a specimen usually consists of representative portions of vegetative and reproductive material.

Many specimens collected by students in university botany classes or by the serious amateur will eventually become housed in an herbarium, a permanent collection of pressed and dried plant specimens. Here the plants will be examined by botanists interested in such matters as distribution, verification of determinations, blooming and fruiting times, general morphological features, and anatomical details. Herbarium specimens are frequently loaned among herbaria.

A major problem facing the inexperienced collector is what constitutes enough plant material to make an acceptable specimen. In the case of small annuals, a specimen is not a single plant, but a few to many, depending upon their size. A single larger annual or smaller perennial is usually sufficient. With experience comes the almost unconscious habit of deciding that a particular plant will make a suitable specimen because it will fit on an herbarium sheet of 12" X 18". However, many larger herbs and most woody plants are too large to accommodate within these limits. Special techniques are used here. These will be discussed later.

The following items are useful: field press, plant press, plastic bags, digger, clippers, pocket knife, compass, altimeter, coin envelopes, pickling fluids, camera, and notebook. While none of them is absolutely essential, each is helpful in collecting and preparing specimens. Here the plants will be examined by botanists interested in such matters as distribution, verification of determinations, blooming and fruiting times, general morphological features, and anatomical details. Herbarium specimens are frequently loaned among herbaria.

COLLECTING SPECIMENS

You should be guided by one overriding consideration, to collect and prepare a permanent specimen that is as much like the living plant as possible, given the constraints of the pressing and drying techniques. Flower color may fade or change and three dimensional forms are flattened, but a wealth of scientific information and even a certain aesthetic quality remain intact.

Always keep in mind that the specimen that you collect must be determined eventually. Most keys and descriptions rely heavily upon the structure of the flower and fruit. Collecting herbaceous plants in the vegetative state is probably futile. I suggest that you collect extra flowering and fruiting material for use during the identification process. In this way the specimen itself can remain intact. This additional material should be submitted as a part of the specimen. It will be placed in a fragment folder and mounted on the herbarium sheet along with the plant. As you become more familiar with the genera, you will learn what plant features are critical for accurate determination.

With herbaceous plants, it is also standard practice to gather underground parts. The nature of the root system or subterranean stems may be critical. "Top-snatching" is a dreadful habit. Roots and other underground plant parts should be cleaned carefully to remove soil or mud.

A standard plant press (12" X 18") is too bulky and heavy to carry about in the field. Although you can construct your own, most of them are purchased, usually at great price, from one of the biological supply houses. A regular plant press has wooden or light metal end pieces called frames. Between the two frames is a series of blotters, and corrugates or ventilators arranged in a particular sequence. Two common arrangements are repeating units made up of corrugate-blotters-blotter-corrugate, and corrugate-blotters-blotters-blotters-corrugate. In the first plan, a specimen in a single fold of newspaper is inserted between the two blotters (corrugate-blotters-specimen-corrugate). In the second option, two specimens are inserted (corrugate-blotters-specimen-blotters-specimen-corrugate). An empty plant press has about a foot or so of pressing material in it.

The following items are useful: field press, plant press, plastic bags, digger, clippers, pocket knife, compass, altimeter, coin envelopes, pickling fluids, camera, and notebook. While none of them is absolutely essential, having the proper collecting gear close at hand can result in greater efficiency and better specimens. By a "digger," I mean any of a variety of implements, such as a geologist's pick, a dandelion digger, a gardener's trowel or even a large screwdriver.

Although specimens may be stored temporarily in plastic bags or other containers, they should be pressed as soon as possible. Pressing flattens the plants so that they do not curl or wrinkle and it also brings the plant parts into direct contact with newspapers and indirectly with blotters and corrugates, thereby beginning the drying process. There are two types of plant presses. One is the temporary field press. It is usually small, light-weight, and easy to carry in a pack. You do not buy a field press; you make your own out of cardboard or press-board end pieces, newspapers, and perhaps a few blotters, the whole thing being bound up by a strap or belt. Those of you who are backers will find that you can accommodate an amazing number of plants in a field press. Specimens will last for a few days in such a temporary press until you can transfer them to a regular press.

The principal reason for collecting is to provide permanent, representative specimens of plants for future study. In the case of smaller vascular plants, such as annual herbs, the specimen often consists of one to several complete individuals. In larger plants, such as trees or shrubs, a specimen usually consists of representative portions of vegetative and reproductive material.

Many specimens collected by students in university botany classes or by the serious amateur will eventually become housed in an herbarium, a permanent collection of pressed and dried plant specimens. Here the plants will be examined by botanists interested in such matters as distribution, verification of determinations, blooming and fruiting times, general morphological features, and anatomical details. Herbarium specimens are frequently loaned among herbaria.
PRESSING SPECIMENS

Plants are first placed in a single fold of newsprint. One of the most common errors is to assume that if a single fold of newspaper is good, then an entire section will be just that much better. All you accomplish is retarding the drying process by having several layers of wet newspaper. Tabloid newspaper, such as "The National Inquirer" or "The Lumberjack" are just the right size. If you use a full-sized newspaper, then tear it down the middle to yield two single fold sections of about 11" X 15". Do not exceed this size or the plant specimens may not fit on the herbarium sheet. Do not use slick, clay-finish newprint from magazines or catalogues. It will not absorb moisture from the specimen.

Annuals and small perennials fit nicely in the newspaper and present no particular problem. But, some herbs are too tall and/or broad to be accommodated properly. If the problem is mainly one of height, consider folding the plant. This works well if it is no more than about a half meter tall. Fold the plant in such a way that the parts do not obscure one another. Too much bulk may also impair proper drying. Make sharp bends, not gently rounded ones. These may be held in place during the drying process by using flexostats. You make your own by cutting and index card or computer card into segments about 4 cm x 8 cm. Cut a slit about 3 cm long in each and slip the "knee" of the plant through the opening. After the plant has dried, remove the flexostat and reuse it. Still larger plants may be subdivided into two or more sections. Such a suite of specimens is often the most practical method of collecting larger herbaceous plants.

It is important that you put only one kind of plant inside the newspaper. The collection number (see below) for that particular plant should be written prominently along one margin. This will assist you later in sorting material and in finding a particular specimen. Some arranging of plant parts and trimming can now be done. Leaves and stems should be positioned so that they do not overlap unnecessarily. Leaf blades should be turned so that some of them have the upper surface exposed, while in others the lower surface may be seen in the final specimen. Specimen quality can often be improved by some judicious pruning of excess bulk. If parts are removed, leave a short stub so that it is evident what has occurred. This is also a good time to get rid of the dirt or mud trapped in the roots. It can ruin the specimen and label if allowed to remain.

This process of putting specimens in a single fold of newspaper, trimming and arranging, and assigning collection numbers (see below) is done until the press is filled or you have run out of plants. The plant press is now closed by tightening the straps, belts or ropes. It must be cinched tight enough to flatten the specimens and bring them into firm contact with the pressing materials. Presses will loosen as the plant dries. Tighten the straps from time to time.

FIELD DATA

At the same time that it is vital to collect and prepare adequate plant specimens, it is just as critical to take down the necessary field data. Without them, the specimens are scientifically worthless. Data may be recorded in permanent notebooks carried into the field or written in temporary pocket notebooks. Either method has its advantages and disadvantages. The important point is, however, to write down your field data, rather than relying on your memory.

The collection site is probably the single most important bit of data. This should be as precise as possible. I suggest the following sequence:

1) state
2) county or parish
3) quadrangle name
4) tier, range, and section (or latitude and longitude)
5) reference to a more or less permanent location, such as towns, highways, rivers, particularly those that can be found on ordinary highway maps

Quadrangle names, tier, range and section coordinates, and latitude/longitude are found on topographic maps available from the United States Geological Survey. Some of this information may also be found on U.S. Forest Service and Bureau of Land Management maps. The new hand-held GPS devices allow for very accurate site data.

Other data that you should enter in your records include:

1) habitat information (vegetation type, associated species, geology of the site, soil type, etc.)
2) elevation
3) remarks on the frequency of the plant at that site
4) remarks on the plant itself (size, color, odor, etc.)
5) collection date
6) personal collection number for that plant specimen

The personal collection number is the number that you assign to this particular specimen. A different collection number is given to each different collection of a particular kind of plant that you make during your career as a field botanist. Your first collection bears the number "1". You will now use a different number anytime you collect a new plant at this site, anytime you move from one location to another, or anytime you collect on a different day. Perhaps a few illustrations will help to clarify this matter.

1) If I collect ten different kinds of plants at a certain site, I will have ten collection numbers.
2) If I collected each of the ten plants in duplicate or triplicate, I would still have only ten collection numbers, each in duplicate or triplicate. This is the only situation in which a collection number is used more than once.
3) If I move to a second site and collect five more plants, I will have five more collection numbers. This is true whether or not any or all of the five plants duplicate species collected at the first site. New numbers are assigned because this is a different collection site.
4) If I should return to any of these sites at a later date, all of the plant collections made at that time would get new numbers.

It is not uncommon to be unsure whether two plants belong to the same or different species or varieties. If
in doubt, assign them different numbers. Should they later turn out to be the same thing, combine them under the first collection number. If what you thought in the field to be duplicates are later determined as two or more different taxa, then call one of them 682 and the other 682A or 682A and 682B.

**DRYING SPECIMENS**

Once plants have been put into the plant press, they must be dried. Presses may be left out in the sunlight or they may be strapped into rooftop racks on automobiles, much to the curiosity of fellow motorists. But the usual method is to put the plant press in an electric or steam drier. These are found on most college campuses.

How long should plants remain in the drier? Until the plants are dry and no longer. The length of time will depend upon the kind of drier, the types of plants collected, the arrangement of pressing materials in the press, and how many other presses are in the drier. While 48 hours is often sufficient for most plants, it is critical to check the presses. Are the labels and newspapers still slightly damp? Does the plant still feel and smell wet? Will your thumbnail leave an impression in a stem or petiole? If the answer is "yes" to any of these questions, then the plant needs to remain in the drier. If you take them out too soon, the plants will mold. If, however, they are dried too long, they will discolor badly and become very brittle. Remember to check the straps periodically. Presses will loosen during the drying process and curling of plant parts can occur.

**LABELS**

If specimens are to be deposited in an herbarium or submitted as part of a class requirement, they must be accompanied by a label that gives the pertinent collection data for that plant. Labels should be made from high quality paper, preferably 100% rag content bond paper. Most herbaria supply them to collectors. Label information should be typed. Permanent ink is an acceptable alternative. Do not use ballpoint pen or soft lead pencil. Labels should provide at least the following information:

1) scientific name of the plant
2) location data
3) location date
4) your name
5) collection number for the specimen

The scientific name, for purposes of completeness and accuracy, must include the authority. Location data has already been discussed. Dates should be presented as 12 March 1979 or March 12, 1979, not 3-12-79. In the last example, the date may be read in at least four different ways. Use your first name or initials, not just your last name, unless you are Carolus Linnaeus, Willis Lynn Jepson, Asa Gray, or some other equally famous dead botanist. Put the collection number beside your name.

In addition to these essential elements, you may also wish to provide habitat data, along with commentary on the plant itself. A series of sample labels is appended to this handout. Once completed, the labels are slipped inside the newspaper with the plant specimen. Do not glue, tape, or staple either the plant or the label to the newspaper. Both will eventually be removed and mounted on an herbarium sheet for permanent reference.

**THE ETHICS OF PLANT COLLECTING**

While there are certainly valid educational and scientific reasons for plant collecting, important questions should be considered before taking specimens. Will the collecting of this plant contribute to educational or scientific advancement? What will be the impact on the population of the removal of this plant?

In 1993, California Native Plant Society adopted a set of guidelines regarding plant collecting for educational/scientific purposes. The following points are based on that statement.

- It is illegal to collect plants along a highway right-of-way, in national parks, national monuments or national forests, state parks, or most local parks without a collecting permit, which may be obtained from the appropriate supervising agency.
- It is legal and permissible to collect plants on private lands, provided that permission of the landowner is obtained.
- It is the responsibility of an instructor to ensure that students are made aware of rare plants that are endemic to the area in which collecting is to take place, and to caution students against collecting these plants.
- Collecting should be limited to the taking of as little plant material as necessary to allow identification.
- Collecting should be done inconspicuously. Casual observers may not understand the reasons for such activities and may feel they can do likewise.
- The Society encourages all botany instructors to use common plants, especially weedy or garden species, for demonstrating collecting techniques, structures, and taxonomic features.
- The primary justification for collecting plants for herbaria is that they contribute to increased knowledge of the California flora. Repeated collecting in well known areas may serve no useful purpose. While it is important to document the distribution of plants, including rare species, it is critical to evaluate the impact of collecting.
- A key to ensuring preservation of California’s diverse flora and fauna is to develop a public informed of their value. For this reason, CNPS encourages limited and discriminating collection of plants as part of the educational process.

**SOME FAMOUS LAST WORDS**

"No, let's not stop here. There will be lots more of them down the road."

"No reason to collect this. It's just a weed."

"I really shouldn't take the last one, but ...."
"This stuff lasts forever in a plastic bag. We'll press all these plants when we get back to campus."

"Sure, dump everything in the same plastic bag. We can sort them out later."

"Are you kidding? Why number them now? We'll never get these specimens mixed up."

"Let's not take the time. We'll be able to find all of these locations on the maps when we get back home."

"No, this plant press isn't too high."

"Why anchor this stuff down? There's no wind."

"Oh well, you probably didn't need the rhizome anyway."

"Get that one. It will fit in the press!"

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**SELDITED REFERENCES**


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5.02 - GRASS FLORAS & CHECKLISTS

**GRASS NAMES**

(Authors, Where Published, Synonyms, etc.)


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**GENERAL REFERENCES**


UNITED STATES (REGIONAL)


UNITED STATES (BY STATE)

ALABAMA


ALASKA


**ARIZONA**


**ARKANSAS**


**CALIFORNIA**


**COLORADO**


**FLORIDA**


**GEORGIA**


**HAWAI'I**


**IDAHO**


**ILLINOIS**


**INDIANA**


**IOWA**


**KANSAS**


**KENTUCKY**


**LOUISIANA**


**MAINE**


**MARYLAND**


**MASSACHUSETTS**


**MICHIGAN**


**MINNESOTA**


**MISSISSIPPI**


**MISSOURI**


**MONTANA**


**NEBRASKA**


NEVADA


NEVADA

NEVADA

NEVADA

NEW HAMPSHIRE


NEW JERSEY


NEW MEXICO


NEW YORK


NORTH CAROLINA


NORTH DAKOTA


OHIO


OKLAHOMA


Oregon

Pennsylvania

Rhode Island

South Carolina

South Dakota

Tennessee

Texas

Utah

Vermont
VIRGINIA

WASHINGTON

WEST VIRGINIA

WISCONSIN

WYOMING

MEXICO, CENTRAL AMERICA & THE CARIBBEAN


Renvoize, S. A. 1998. Gramineas de Bolivia. Royal


**GREAT BRITAIN & EUROPE**


**AFRICA**


ASIA


Stapleton, C. M. A. 1994. The bamboos of Nepal and


AUSTRALIA & OCEANIA


### 5.03 - DICHOTOMOUS KEYS

#### INTRODUCTION

A key is a logical device that assists you in the identification -- not the classification -- of an unknown organism. The keys used in botany usually take the form of a series of paired statements that describe various aspects of the plants treated therein. Each statement is called a lead; the two leads together constitute a couplet. The leads of a couplet are written in such a way that they are contrasting or contradictory propositions, as in:

1. Florets 1 . . . . . . .  Agrostis
2. Florets 2 or more . . . Festuca

You must decide in each case which of the two statements best describes the unknown plant. These decisions then determine a somewhat serpentine pathway through a series of subsequent couplets. Because you are presented with a series of paired statements, the key is called a dichotomous key (Greek, in two + to cut).

#### TYPES OF KEYS

Dichotomous keys may be simple or complex, long or short, utilize a wide combination of floral and vegetative features or be restricted to statements relating to a particular aspect of the plants, such as leaf features. A key is termed natural if it is constructed in such a way that it shows evolutionary affinities or artificial if there is no concern shown for relationships. Most modern keys are artificial ones.

Two types of keys are recognized on the basis of their mechanical structure. In the bracket key the leads of a couplet are always together. Each statement ends in the name of a taxon or in the number or letter of the next couplet that is to be read, as in the example below. The "Key to the U. S. Species of Spartina" in this syllabus is an example of a bracket key.

In the indented key or yoked key a subordinate lead is indented beneath the statement preceding it. Each type of key has its advantages. The indented key is easier to follow and allows the user to more easily grasp the subgroupings and logic of the key. The bracket key is preferred by editors and publishers because it is easier to set up and requires less space. The keys in Hitchcock & Chase are examples of indented keys.

#### WRITING A DICHOTOMOUS KEY

I suggest the following steps be done when you are attempting to write a dichotomous key.

- Carefully define the taxa to be included. If nothing else, make a checklist of the plants that you must consider.
- Give the key a descriptive title, such as "A Key to the Grasses of Humboldt County, California". This will immediately alert the potential user of the appropriateness of the key.
- Examine the plants to be treated. Determine a series of "key characters" that will discriminate among the taxa. Remember that you are primarily interested in how the plants are different from one another. These traits should be stable, easily observed features that are usually present through much of the year. Most keys employ macroscopic features or those that are visible under low magnification. Try to minimize the use of ephemeral traits.
- Prepare a comparison chart, putting the taxa to be keyed along one axis and the characters along the other. A particular feature that looked promising may not be that useful once this chart is completed. During the writing of the key statements, you may have to return to this comparison chart and add additional columns of features before all taxa can be distinguished.
- Examine the comparison chart to discover a trait that will divide the plants into two groups of about the same size. There may be several possible characters that you can use. With experience you will learn to weigh the relative merits of characters. Once this feature is chosen, it is defined in terms to two opposing character states. This will be the first couplet of the key. This process of selecting features continues until all of the taxa have been incorporated into the key.
- It is critical that the key be strictly dichotomous. For each statement there can be only one alternative lead.
- Select the key format (indented or bracket) that you wish to use. Do not attempt to hybridize these two structures. The internal logic of the key must be maintained consistently through the entire series of statements.
- Select key characters that are in opposition to one another and that are mutually exclusive. The
unknown plant should fit under one, and only one, of the contradictory propositions.

- Use parallel construction within a couplet. If the first lead describes leaf shape, then so must the other lead of the pair.
- The initial word of each lead should be the name of the plant part being described. This is followed by the adjective, as in "Plants annual" or "Leaves hairy," rather than "Annual plants" or "Leaves hairy."
- Omit verbs. They are not necessary. Although it will look a bit awkward at first, you will quickly get use to it.
- The statements in a key may be numbered or lettered to make it easier to find the other member of a couplet. This is seldom a problem in shorter keys, but can become a frustration in longer keys that run to several pages. Once you have used a number or letter for a particular couplet, do not reuse it.
- Whenever possible, phrase the leads in a positive form. Avoid the use of "not as above" as the contrasting statement of a couplet. It provides no information about the plants falling on that side of the dichotomy.
- Avoid ill-defined characters. What is meant by the terms "tall," broad," and "rough?" Use precise botanical terminology.
- It is often useful to include measurements. Avoid overlapping limits in variation, as in "Leaves 3-7 cm long" vs. "Leaves 5-12 cm long". Under which lead is a plant with a leaf 7 cm long?
- The simplest keys usually contrast one feature in a statement. Better keys employ two or more features, separated by semicolons, as in:
  1. Inflorescence a panicle; glumes awned
  1. Inflorescence a spike; glumes awnless
- Sometimes it may be necessary to bring a plant out in more than one place in a key if it has two or more character states for a particular trait.

### SOME HINTS IN USING KEYS

- Make sure that you are using the right key. It is both a waste of time and an embarrassment to spend several hours attempting to identify a plant in the wrong key.
- Read the key very carefully. If it is a good key, the author has spent a great deal of time selecting the right words. Much frustration results from misreading. There is a world of difference in the meaning of "and" and "or." They are not interchangeable.
- Watch for weasel words, such as "mostly" and "usually." Most of us who write keys use these words as avenues of escape when we do not want to be pinned down.
- Read both leads of the couplet before making your decision. The first lead may sound pretty good, but the second half may be perfect.
- Do not base your decision on a single observation, particularly when you are being asked about measurements.
- If neither lead seems to make any sense at all, you have probably made an error in keying and should not be in that section. Go back a step or two and check yourself.
- Check to see if there is a glossary at the back of the key. Authors vary in their use of certain terms and you will have to get use to the eccentricities of the writer.
- Do not assume that a key says something that it does not. In the second lead below, the author has not said that the leaves are alternate.
  1. Plant annual; leaves opposite
  1. Plants perennial
- If you are not confident about which lead to take, try both of them. One pathway should get you into difficulty fairly quickly.
- If one side of a dichotomy will take you to a relatively small number of plants, check out their descriptions or look at drawings. This additional knowledge may be helpful to you. Also, as you gain more knowledge of the flora you will be able to eliminate certain leads because they will take you to plants that you know.
- Learn to weigh the relative values of characters used in keys. Features of flower and fruit tend to be more important than those of plant height, for instance.
- When you have arrived at a determination, you should check it against a technical description, illustration, or specimen.

### FEATURES USED IN GRASS KEYS

#### Growth Form (Habit)
- Annual
- Herbaceous perennial
- Woody perennial
- Tufted
- Caespitose
- Rhizomatous
- Stoloniferous
- Bulbous

#### Culms
- Round or flattened
- Solid or hollow
- Erect or decumbent

#### Leaves
- Blades
  - Flat
  - Rolled
  - Bow-shaped tips
- Nature of margins
  - Rounded
  - Flattened
Auricles
  Present
  Absent

Inflorescence
  Terminal or axillary
  Open or contracted
  Included or exserted
  Balanced or 1-sided
  Involucre present or absent
Type
  Panicle
  Raceme
  Spike
  Digitate
  Solitary

Rachis
  Intact at maturity (continuous)
  Shattering at maturity (discontinuous)

Spikelets
  Similar or dissimilar
  Number per node
    1, 2, 3, etc.
  Fascicles
  Position relative to rachis
    Inserted edgewise
    Inserted flatwise
    Sunken in corky or fleshy rachis
  Covered by involucre
  Subtended by spines/bristles
Compression
  Lateral
  Dorsal
  Terete
Disarticulation
  Above glumes
  Below glumes
  Falling singly
  Falling in groups
  Falling with rachis segment

Glumes
  Number (2, 1, 0)
  United or separate
  Size relative to one another
  Size relative to lemma(s)
  Glabrous or variously hairy
  Nerve number
  Nature of apex
  Awned or awnless

Floret
  Number
  Sexuality
    Perfect
    Pistillate
    Staminate
  Degree of reduction
    All ± similar
    Upper reduced
    Lower reduced
    Upper and lower reduced

Lemma
  Size relative to glumes
  Size relative to palea
  Texture
    Membranous
    Papery
    Indurate
  Nerve number
  Nerves converging or parallel

Glabrous or variously hairy
Nature of apex
  Acute
  Rounded
  Bifid
  Truncate
Sterile or fertile
Awned or awnless
Awn attachment
  Nature of callus
    Glabrous
    Bearded
    Cobwebby

Palea
  Present or absent
  Texture
  Size relative to lemma
  Nerve number
  Awn absent or present
  Wings present or absent

Rachilla
  Extension
    Beyond uppermost floret
    Not extended
  Rudiments
    Ending in rudiment
    Not ending in rudiment
  Glabrous or variously hairy

Glabrous or variously hairy
Nature of apex
  Acute
  Rounded
  Bifid
  Truncate
Sterile or fertile
Awned or awnless
Awn attachment
  Nature of callus
    Glabrous
    Bearded
    Cobwebby
Grasses often have two names. One is a common name used by most of us in everyday circumstances when we make reference to a weed growing in the yard, an ornamental, or to one of the widely grown cereal crops. Grasses also have scientific names (or Latin names, as they are sometimes called) used by scientists and by the "serious" amateur. In this course, you and I will be using both common names and scientific names. You will need to be able to communicate with more than one audience.

**COMMON NAMES**

It would be foolish for me to maintain that common names have no value. They are the only names known to most of us. These names are often simple, easy to remember, descriptive, colorful, pleasing to the ear, and easy to pronounce. Given this impressive list of advantages, why do we not simply use common names for grasses and be done with it? There are several reasons why scientists do not use them.

- A grass may have more than one common name. *Stipa hymenoides* is commonly called Indian ricegrass, Indian millet, silk grass, and sand bunch grass.
- The same common name may be used for more than one plant. We all know corn when we see it. You may be surprised to learn that in other English-speaking countries, their corn is what we call wheat.
- Many common names are confusing and misleading. Kentucky bluegrass is not blue, nor is it native to Kentucky. Broomcorn is not a kind of corn, but a variety of sorghum. The heavenly-bamboo is not a kind of bamboo, but a member of the barberry family.
- Because there are no universally accepted rules for giving common names to grasses, we cannot say that a particular one is the correct common name.
- Common names do not provide an indication of close relationship among the plants that share the name. Sour-grass, arrow-grass, blue-eyed grass, grass (marijuana), and China-grass are not kinds of grasses, nor are they related to one another.
- Probably the most serious difficulty is that most grasses do not have common names. We have used only a small portion of the half million or so kinds of plants to the extent that common names have been applied to them. This is a problem for authors of field guides, for consultants who write environmental impact statements, and for staff members in various state and federal agencies who must prepare material for general consumption. Authors have attempted to compensate for this lack of common names by inventing them, usually by translating the scientific name into English. The advantage of Orcutt's brome over *Bromus orcuttianus* or the spicate trisetum over *Trisetum spicatum* is not immediately apparent to me.

A word or two about the spelling of the common names of grasses. You will notice inconsistencies from one text to another. For instance, *Stipa comata* is variously called needle and thread, needle and thread grass, needle-and-thread grass, and needleandthread grass. The last spelling seems terribly awkward. Some Floras list needlegrass; others, needle grass. Some authors capitalize common names (Giant Needle Grass); others do not (giant needle grass). *Sorghum halepense* is Johnson grass, but *Tuctoria greenei* is Greene's tuctoria. Apostrophes come and go.

**SCIENTIFIC NAMES**

Although scientific names may cause you some discomfort, their advantages to the botanist are compelling.

- There is a single, universally recognized name for each plant. Because they are used by botanists all over the world, scientific names facilitate the free transfer of ideas and information. Consider the difficulties that would arise if the botanists in the United States, England, Germany, Russia, China, etc. each had their own independent set of names for the plants of their countries.
- The same scientific name may not be used for more than one kind of plant. Once it has been published, that name cannot be used again for any other plant.
- Scientific names are given according to an "International Code of Botanical Nomenclature.” These regulations are reviewed every four years at International Botanical Congresses. There is, therefore, a legally correct scientific name.
- Inherent in our system of scientific names is the concept of evolutionary or genetic relationship. When we place einkorn wheat, emmer wheat, and bread wheat in the same genus (*Triticum*), we do so because we have concluded that the morphological, anatomical, genetic, and chemical traits that they share suggest that they are closely related. Because there is a set of features associated with the name, it has predictive value. The better we have circumscribed the taxa, the higher the value.

There are some difficulties with scientific names. They can be difficult to pronounce, especially if you did not
learn to divide words into syllables early on in your education. You might note, however, that such familiar and easily pronounced common names as aster, rhododendron, magnolia, chrysanthemum, petunia, and begonia are also the first part of the scientific names of these plants. My own experience in teaching undergraduates to use scientific names is that once you get past the psychological barrier that these are terribly long words that only those who have had a strong background in Latin and Greek can pronounce, then you will become much more comfortable with them and begin using them rather easily.

WHY ALL THE NAME CHANGES?

One of the more frustrating features of scientific names, especially for someone who is just learning about them, is that they are changed from time to time. Just when you think that you have become familiar with the scientific names for a particular group of plants, someone will publish a new revision of the group and you discover that some of the names have been changed. These changes come about for several reasons. As new information about the anatomy, chemistry, and genetics of plants becomes known, it may cause botanists to rethink the evolutionary relationships among the plants being studied. These changes may require us to revise the scientific names to reflect the new level of information now available to us. Sometimes names are changed, not for biological reasons, but because someone studying a group may discover that the name given to a particular plant has to be rejected because it violated some provision of the International Code of Botanical Nomenclature. For example, the name may not have been properly published in a scientific journal. One 19th century botanist was a public school principal who handed out printed copies of his newly described plants to his students at graduation each spring. This is not exactly legal.

Examples point out one of the important operating principles in plant classification. As new information becomes available and as errors are discovered, we make adjustments and corrections. What appears to be a fine scheme of classification today may be modified drastically or even discarded completely at some point in the future.

COMPONENTS

If we examine the botanical works of the 15th and 16th centuries, we see that the name of a plant was often a polynomial, a lengthy series of descriptive words, typically in Latin, as in "Convolvulus argenteateus folliis ovatis divisis basi truncatis: lacinis intermediis duplo longioribus." These phrase names became increasingly awkward because the discovery of a new kind of plant required that the existing polynomial be slightly modified so that it could be distinguished from the older one.

A new way of naming plants was developed over two centuries ago to replace the polynomials. It was popularized by Carolus Linnaeus, the leading botanist of his time. This system was based upon the principle that each plant (or animal for that matter, because they are named according to the same scheme) is given a scientific name that consists of two components, both of them parts of the taxonomic hierarchy mentioned above. The first element of the scientific name is the genus (or generic name), as in *Triticum*, the genus of wheat. The plural of genus is genera, not genuses. The second element is the specific epithet, as in *aestivum*, the particular kind of wheat called bread wheat. This second element of the scientific name is often incorrectly called the "species." It is the genus and specific epithet together that form the species name. *Triticum aestivum* is the species name of bread wheat. Because the name of a plant or animal is the combination of these two words, the scientific name is called a *binomial* and we call this scheme of giving technical names to organisms the Binomial System of Nomenclature.

The binomial, for reasons of completeness and accuracy, is followed by the name (typically abbreviated) of the person or persons who first published that name for the plant. For example, in the scientific name *Zea mays* L., the "L." stands for Linnaeus. This part of the scientific name is the authority.

It is sometimes necessary to move the name of a plant from one genus to another, usually because more recent research has demonstrated that the plant was incorrectly assigned to a particular genus. For instance, in 1753 Linnaeus published the name *Panicum dactylon* for the plant that we now call Bermuda grass. In 1805, Christian Persoon transferred the epithet (or "moved the species," as we say more informally) from *Panicum* to the new genus *Cynodon*. The scientific name of Bermuda grass then becomes *Cynodon dactylon* (L.) Persoon. The person whose name is in the parentheses first published the specific epithet for the plant. The name after the parentheses is that of the person who transferred it into the genus where it now resides.

It is often useful to recognize and to name variation below the species level. The two most widely used are the *subspecies* (abbreviated ssp.) and the *variety* (abbreviated var.). These names also have authorities, as in *Bromus vulgaris* (Hook.) Shear var. *robustus* Shear. If the subspecies or varietal name is a repeat of the specific epithet, then the authority is not repeated, as in *Zea mays* L. ssp. *mays*.

An additional explanation is needed for the term variety. For reasons that are obvious, we have developed many different cultivated strains of a particular crop plant or ornamental. There are literally thousands of different kinds of rice. There are probably hundreds of different kinds of tuberous begonias. In general parlance, we often call these varieties. However, for purposes of formal nomenclature, these variations are considered too minor and often too short-lived to warrant giving them a separate scientific name. The variety of botanical nomenclature is not used in these instances. Instead, we employ the term *cultivar* (abbreviated cv.). A kind of sorghum used to make molasses in the Southwest by American Indians is *Sorghum bicolor* cv. 'Apache Red Cane.'

Many of our economic plants are of hybrid origin, that is they result from the accidental or purposeful crossing of two closely related plants. This can be reflected in the scientific name of the plant by inserting an "X." If the X occurs before the generic name, then the plant is considered the result of a cross between two plants in different genera. *X Agropogon* is an intergeneric hybrid between *Agrostis* and *Polypogon*. If the X occurs between the generic
name and the specific epithet, then the plant is the product of a cross between two species in the same genus, as in *Tridenis x oklahomensis*.

**THE ORIGIN OF NAMES**

Most of the words that make up scientific names are derived from Latin or Greek, although there is no requirement that they must be. Modern names and even nonsensical ones have been used. Many students, however, believe that there must be some requirement that scientific names be as long and unpronounceable as possible. This reveals a certain lack of scholarship. Even a rudimentary knowledge of etymology is very helpful in understanding the composition of scientific names. The following examples may be helpful.

**Commemorative Names:** Lamarckia, Scribneria, and Orcuttia are named after J. B. A. P. Monnet de Lamarck (the famous French naturalist), Frank L. Scribner (a noted American agrostologist), and Charles Russell Orcutt (a San Diego botanist). Agnesia is named after Agnes Chase.

**Classical/Aboriginal Names:** Agrostis, Bromus, Festuca, and Poa are all ancient Latin names for grasses.

**Geographical Names:** anglicus (from England), galicus (from France), canadensis (from Canada), australis (southern)

**Habitat:** arenarius (growing in sand), campestris (of the fields), fluviatilis (of the rivers), riparius (of the river banks), sativus (cultivated), litoralis (of the seashore).

**Growth Form:** arboresus (tree), repens (creeping), scandens (climbing), pusillus (insignificant).

**Structural Feature:** amabilis (lovely in appearance), bulbosum (having a swollen part), gracilis (slender), mollis (soft hairy), scoparius (broom-like).

**Use:** esculentus (edible), officinalis (recognized as medically important), textilis (having useful fibers)

**DERIVATION OF GENERIC NAMES OF GRASSES**

<table>
<thead>
<tr>
<th>Species</th>
<th>Origin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Achnatherum</td>
<td>[Gk., awned scale]</td>
</tr>
<tr>
<td>Aegilops</td>
<td>[L., ancient name for wheat]</td>
</tr>
<tr>
<td>Aegopogon</td>
<td>[Gk., goat + beard]</td>
</tr>
<tr>
<td>Agropyron</td>
<td>[Gk., wild + wheat]</td>
</tr>
<tr>
<td>Agrostis</td>
<td>[Gk., a kind of grass, pasture]</td>
</tr>
<tr>
<td>Alopecurus</td>
<td>[Gk., fox + tail]</td>
</tr>
<tr>
<td>Ammophila</td>
<td>[Gk., sand + loving]</td>
</tr>
<tr>
<td>Ampelodesmos</td>
<td>[Gk., grape leaves + to tie together]</td>
</tr>
<tr>
<td>Amphicarpum</td>
<td>[Gk., double + fruit-bearing]</td>
</tr>
<tr>
<td>Anthogon</td>
<td>[Gk., man + beard]</td>
</tr>
<tr>
<td>Anthaenantia</td>
<td>[Gk., flower + contrary]</td>
</tr>
<tr>
<td>Antheaphora</td>
<td>[Gk., flower + to bear]</td>
</tr>
<tr>
<td>Anthoxanthum</td>
<td>[Gk., yellow + flower]</td>
</tr>
<tr>
<td>Apera</td>
<td>[Gk., not maimed]</td>
</tr>
<tr>
<td>Aptluda</td>
<td>[L., chaff]</td>
</tr>
<tr>
<td>Arctagrostis</td>
<td>[L., arctic + a kind of grass]</td>
</tr>
<tr>
<td>Arctophila</td>
<td>[L., arctic + G., to love]</td>
</tr>
<tr>
<td>Aristida</td>
<td>[Gk., a stout hair, awn]</td>
</tr>
<tr>
<td>Arrhenatherum</td>
<td>[Gk., male + awn]</td>
</tr>
<tr>
<td>Arthroxan</td>
<td>[Gk., joint + axis]</td>
</tr>
<tr>
<td>Arundo</td>
<td>[L., a reed grass]</td>
</tr>
<tr>
<td>Avena</td>
<td>[L., oats]</td>
</tr>
<tr>
<td>Axonopus</td>
<td>[Gk., axis + foot]</td>
</tr>
<tr>
<td>Beckmannia</td>
<td>[J. Beckmann, German botanist]</td>
</tr>
<tr>
<td>Blepharidachne</td>
<td>[Gk., eyelash + chaff]</td>
</tr>
<tr>
<td>Blepharoneuron</td>
<td>[Gk., eyelashes + nerve]</td>
</tr>
<tr>
<td>Bothriochloa</td>
<td>[Gk., pit + grass]</td>
</tr>
<tr>
<td>Bouteloua</td>
<td>[C. and E. Boutelou, Spanish botanists]</td>
</tr>
<tr>
<td>Brachiarzia</td>
<td>[L., arm]</td>
</tr>
<tr>
<td>Brachyelytrum</td>
<td>[Gk., short + husk]</td>
</tr>
<tr>
<td>Brachypodium</td>
<td>[Gk., thick + foot]</td>
</tr>
<tr>
<td>Briza</td>
<td>[Gk., a kind of nodding grain]</td>
</tr>
<tr>
<td>Bromus</td>
<td>[Gk., food, ancient name for oats]</td>
</tr>
<tr>
<td>Buchloe</td>
<td>[Gk., buffalo + grass]</td>
</tr>
<tr>
<td>Calamagrostis</td>
<td>[Gk., a reed grass]</td>
</tr>
<tr>
<td>Calamovilla</td>
<td>[Gk., reed + Vilfo, a grass genus]</td>
</tr>
<tr>
<td>Catabrosa</td>
<td>[Gk., devouring]</td>
</tr>
<tr>
<td>Cathes tucem</td>
<td>[Gk., an ancient name]</td>
</tr>
<tr>
<td>Chloris</td>
<td>[Gk., Goddess of flowers]</td>
</tr>
<tr>
<td>Chrysopogon</td>
<td>[Gk., golden + beard]</td>
</tr>
<tr>
<td>Cinna</td>
<td>[Gk., a kind of grass]</td>
</tr>
<tr>
<td>Coix</td>
<td>[Gk., a kind of palm]</td>
</tr>
<tr>
<td>Coleanthus</td>
<td>[Gk., sheath + flower]</td>
</tr>
<tr>
<td>Cortaderia</td>
<td>[Sp., cutting]</td>
</tr>
<tr>
<td>Corynephorus</td>
<td>[Gk., club-bearing]</td>
</tr>
<tr>
<td>Crypsis</td>
<td>[Gk., hidden]</td>
</tr>
<tr>
<td>Ctenium</td>
<td>[Gk., a small comb]</td>
</tr>
<tr>
<td>Cymbopogon</td>
<td>[Gk., boat + beard]</td>
</tr>
<tr>
<td>Cynodon</td>
<td>[Gk., dog + tooth]</td>
</tr>
<tr>
<td>Cynosurus</td>
<td>[Gk., dog + tail]</td>
</tr>
<tr>
<td>Dactylis</td>
<td>[Gk., finger]</td>
</tr>
<tr>
<td>Dactylolcinium</td>
<td>[Gk., finger + small comb]</td>
</tr>
<tr>
<td>Danthonia</td>
<td>[E. Danthion, French botanist]</td>
</tr>
<tr>
<td>Dasyachloa</td>
<td>[Gk., hairy + grass]</td>
</tr>
<tr>
<td>Deschampsia</td>
<td>[J. Deslongchamps, French botanist]</td>
</tr>
<tr>
<td>Desmazeria</td>
<td>[J. B. Desmazeriers, French botanist]</td>
</tr>
<tr>
<td>Diarrhena</td>
<td>[Gk., twice + male]</td>
</tr>
<tr>
<td>Dichanthelium</td>
<td>[Gk., twice + flowering]</td>
</tr>
<tr>
<td>Digitaria</td>
<td>[L., finger]</td>
</tr>
<tr>
<td>Dinebra</td>
<td>[Arabic, little tail]</td>
</tr>
<tr>
<td>Dissantherium</td>
<td>[Gk., two + small flower]</td>
</tr>
<tr>
<td>Dupontia</td>
<td>XXX</td>
</tr>
<tr>
<td>Distichlis</td>
<td>[Gk., two-ranked]</td>
</tr>
<tr>
<td>Echinochloa</td>
<td>[Gk., hedgehog + grass]</td>
</tr>
<tr>
<td>Ehrharta</td>
<td>[J. F. Ehrhart, German botanist]</td>
</tr>
<tr>
<td>Eleusine</td>
<td>[Gk., Eleusis, an ancient town]</td>
</tr>
<tr>
<td>Eleonurus</td>
<td>[Gk., to roll + tail]</td>
</tr>
<tr>
<td>Elymus</td>
<td>[Gk., a kind of millet]</td>
</tr>
<tr>
<td>Elytrigia</td>
<td>[Gk., nine + beard]</td>
</tr>
<tr>
<td>Eneapogon</td>
<td>[G., intestine + beard]</td>
</tr>
<tr>
<td>Enteropogon</td>
<td>[Gk., love + grass]</td>
</tr>
<tr>
<td>Ergrodis</td>
<td>[Gk., centipedes + grass]</td>
</tr>
<tr>
<td>Erianthus</td>
<td>[Gk., wool + flower]</td>
</tr>
<tr>
<td>Eriochloa</td>
<td>[L., woolly + grass]</td>
</tr>
<tr>
<td>Eriocystis</td>
<td>[Gk., woolly + nerve]</td>
</tr>
<tr>
<td>Eucharis</td>
<td>[Gk., true or well + cloak]</td>
</tr>
<tr>
<td>Festuca</td>
<td>[L., classical name for a weedy grass]</td>
</tr>
<tr>
<td>Fingerhuthia</td>
<td>[K. A. Fingerhuth, German botanist]</td>
</tr>
<tr>
<td>Gastridium</td>
<td>[Gk., a small pouch or sac]</td>
</tr>
<tr>
<td>Gaudinia</td>
<td>[J. F. G. Gaudin, French botanist]</td>
</tr>
<tr>
<td>Glycera</td>
<td>[Gk., sweet]</td>
</tr>
<tr>
<td>Gymnopogon</td>
<td>[Gk., naked + beard]</td>
</tr>
</tbody>
</table>
Gyneryium [Gk., female + wool]  Polygopon [Gk., many + beard]
Hackelochoa [E. Hackel + Gk., grass]  Pseudoroegneria [Gk., false + a name for Elymus]
Hainardia [P. Hainard, Swiss phytogeographer]  Ptilagrostis [Gk., feather + grass]
Hakonechloa [Mt. Hakon (in Japan) + Gk., grass]  Puccinellia [B. Puccinelli, Italian botanist]
Helictotrichon [Gk., twisted + bristle]  Redfieldia [J. H. Redfield, Philadelphia businessman]
Hemarthria [Gk., blood (?)+ joint]  Reimarochloa [J. A. H. Reimarus + Gk., grass]
Hesperostipa [Gk., western + tow]  Rhynchochloa [L., beard + scale]
Heteropogon [Gk., different + beard]  Rottboellia [C. F. Rottbohl, Danish botanist]
Hierochloe [Gk., holy + grass]  Saccharum [L., sugar]
Hilaria [A. de St. Hilaire, French botanist]  Sacciolepis [Gk., small bag + scale]
Hordeum [L., classical name for barley]  Schedonardus [Gk., near + Nardus, a grass genus]
Holcus [L., a kind of grass]  Schismus [Gk., split]
Hydrochloa [Gk., water + grass]  Schizachne [Gk., split + chaff]
Hyparrhenia [Gk., below + male]  Schizachyrium [Gk., split + chaff]
Hystrix [Gk., porcupine]  Sclerochloa [Gk., hard + beard]
Imperata [F. Imperato, Italian naturalist]  Scleropogon [Gk., hard + beard]
Ischaemum [G., hip-socket joint]  Scolochloa [Gk., prickle + grass]
Koeleria [G. L. Koeler, German botanist]  Scriberia [F. L. Scribner, American botanist]
Lagurus [Gk., hair + tail]  Secale [L., classical name for rye]
Lamarckia [J. B. Lamarck, French naturalist]  Setaria [L., bristle]
Lasiacis [Gk., woolly + point]  Setariopsis [L., Setaria + resembling]
Leersia [J. D. Leers, German apothecary]  Sieglingia [Siegling, German botanist]
Leptochloa [Gk., slender + grass]  Sorghastrum [Sorghum + L., a poor imitation of]
Leptoloma [Gk., thin + bore]  Sorghum [It., sorgho]
Leymus [Anagram of Elymus]  Spartina [Gk., cord]
Limnoda [Alteration of Limnas, a grass genus]  Sporobolus [Gk., seed + to throw]
Lolium [L., classical name for darel]  Stenotaphrum [Gk., narrow + trench]
Luziola [Luzula, a genus of sedges + resembling]  Stipa [L., tow]
Lycurus [Gk., wolf + tail]  Swallenia [J. Swallen, American botanist]
Manisuris [Gk., necklace + tail]  Taeniatherum [Gk., ribbon + awn]
Melica [L., honey]  Themeda [Arabian name for this grass]
Melinis [Gk., a kind of millet]  Thysanolaena [Gk., fringe + cloak]
Microchloa [Gk., small + grass]  Torreyochloa [J. Torrey, American botanist + grass]
Microstegium [Gk., small + cover]  Trachypogon [Gk., rough + beard]
Miscanthus [Gk., stalk + flower]  Tragus [Gk., he-goat]
Molinia [J. I. Molina, Jesuit missionary-botanist]  Tribolium [L., three + fiery arrow]
Monanthochloe [Gk., one + flower + grass]  Trichachne [Gk., hair + chaff]
Monocera [Gk., one + support]  Trichloris [Gk., three + Chloris, a grass genus]
Monroa [W. Munro, English botanist]  Trichachne [Gk., one + chaff]
Muhlenbergia [H. L. E. Muhlenberg, Penn. botanist]  Tridens [L., three + tooth]
Nassella [L., a kind of basket]  Triplasis [Gk., three + awn]
Neostapfia [Gk., new + O. Stapf, British botanist]  Tripogon [Gk., three + beard]
Neyraudia [Anagram of Reynaudia]  Tripsacum [Uncertain: perhaps Gk., to rub]
Olyra [Gk., an ancient name for a kind of grain]  Trisetum [L., three + bristle]
Oplismenues [Gk., armed]  Tuctoria [Anagram of Orcutta]
Orcuttia [C. Orcutt, California botanist]  Uniola [L., a kind of grass]
Oryza [Gk., classical name for rice]  Urophila [Gk., tail + grass]
Oryzopsis [Gk., rice + resembling]  Vaseyochloa [G. Vasey, American botanist + grass]
Oryza [Gk., new + O. Stapf, British botanist]  Venetana [P. Venenat, French botanist]
Panicum [L., ancient name for common millet]  Vetiveria [Tamil name for this grass]
Pappophorum [Gk., pappus + bearing]  Vulpia [J. S. Vulpius, German botanist]
Parapholus [Gk., beside + scale]  Willkommia [H. M. Willkomm, German botanist]
Paschopyrum [L., pasture + Gk., wheat]  Zea [Gk., a kind of grain]
Passalum [Gk., a kind of grass]  Zizania [Gk., a weed of grain fields]
Pennisetum [L., feather + bristle]  Zizaniopsis [Gk., Zizania + resembling]
Pilmatrichon [Gk., twisted + bristle]  Zoysia [K. von Zois, German botanist]
Phalaris [Gk., a grass with shiny spikelets]  "Pseudoroegneria" [G., false + a name for Elymus]
Pharus [Gk., mantle or cloth]  "Ptilagrostis" [G., feather + grass]
Phlachne [C. J. Phipps]  "Puccinellia" [B. Puccinelli, Italian botanist]
Phiphoa [Gk., marsh reed]  "Redfieldia" [J. H. Redfield, Philadelphia businessman]
Phragmites [Gk., growing in hedges along streams]  "Reimarochloa" [J. A. H. Reimarus + Gk., grass]
Piptatherum [Gk., falling + bristle]  "Rhynchochloa" [L., beard + scale]
Piptochlaetum [Gk., falling + hair]  "Rottboellia" [C. F. Rottbohl, Danish botanist]
Pleuraphis [Gk., side + needle]  "Sacciolepis" [Gk., small bag + scale]
Pleuropogon [Gk., side + beard]  "Schedonardus" [Gk., near + Nardus, a grass genus]
Poa [Gk., ancient name]  "Sclerochloa" [Gk., hard + beard]
Pogonarthria [G., beard + a joint]  "Scleropogon" [Gk., hard + beard]

PRONUNCIATION

The International Code of Botanical Nomenclature states that scientific names of plants are to be treated as Latin words, regardless of their origin. A few of the more scholastically inclined botanists will argue,
therefore, that we ought to pronounce scientific names according to the strict rules of the sounds of vowels and consonants in Latin and that great care should be taken in accenting the proper syllable. But, there are traditional English, reformed academic, and Church Latin versions of Latin to choose from, each with its own set of rules for pronunciation.

Most American botanists pronounce the scientific names of plants as though they were English words. Some of us follow the rules in Latin for determining which syllable is accented; most of us do not. Many of us pronounce scientific names the way we were taught as undergraduates (if any formal discussion occurred) or more commonly we imitate the way our professors said them when we took their classes. These become the familiar and "correct" way to pronounce the scientific names of plants.

The following is an attempt on my part to present a basic guide to pronouncing vowels, consonants, and diphthongs, together with some of the rules for accenting syllables.

- The letters of the Latin alphabet are basically the same as ours, except that J, U, and W did not occur in the classical version.

- Each syllable will contain a vowel or a double vowel combination (ae, au, ei, oe, or ui). The latter are called diphthongs.

- Pronounce all of the syllables. Secale is "see-kale-e," not "see-kale."

- Final vowels are long, with the exception of a. If a word ends in two vowels (unless they are a diphthong), they are sounded separately. The epithet angustifolia is pronounced "an-gust-i-fo-li-ah."

- The diphthongs "ae" and "oe" have the sound "e," as in beat; "au" has the sound of "aw," as in the word awful; "ei" usually has the sound "i," as in sile; "eu" has the sound of "u," as in neuter; and "ui" has the ui-sound in the word ruin.

- The "oi" in the ending "-oides" is treated as a diphthong by most American botanists and we give it the sound that "oi" has in the word oil. This habit is considered close to barbaric by English and Europeans who are much more persnickety about such matters. Because these two vowels do not form a diphthong, they should be pronounced separately, so that the ending "-oides" has the sound "-o-e-deez."

- A single consonant is placed with the following vowel, as in "pa-ter." Double consonants are separated, as in "am-mi." If there are two or more consonants, the first one is usually put with the preceding vowel, as in "an-gli-cus."

- B, d, f, h, l, m, n, p, qu, and z are pronounced the same in Latin and English.

- The consonants c and g are soft (that is, have the sounds of "s" and "j") if they are followed by ae, e, i, oe, or y. Otherwise, the c is pronounced like a "k" and the g is also hard, as in "go." The s is always pronounced as it is in the word "so," not as a "z." An initial x is pronounced as a "z," not "ek-zer-kle." Xerochloa is pronounced "zero-o-chlo-a," not "ek-zero-chlo-a."

- The first letter is silent in words beginning with cn, ct, gn, mn, pn, ps, pt, and tm.

Accenting the proper syllable can be tricky. Sometimes the author of a flora or other manual may provide assistance by including an accent mark. Most do not. If included, they are for the convenience of the reader and they are not part of the scientific name itself. If you must determine which syllable to accent, the following rules may be helpful.

Words of two syllables are always accented on the first syllable. The genus of Kentucky bluegrass is "Po-a." In words of three or more syllables, the last syllable is never accented. The stress will fall either on the next to the last syllable (the penultimate syllable), as in "ar-ven-sis," or on the third from the last syllable (antepenultimate), as in "an-gli-cus."

No matter how long the word, the accent can never be to the left of the antepenultimate syllable. Deciding between these two options is a difficult choice. Accent the penultimate syllable if it ends in a consonant, diphthong, or in a long vowel.

Commemorative names (patronyms) present a special problem because giving them the proper accenting can render the person's name unrecognizable. The epithet jamesii should be pronounced "ja-me-se-i," not "jamz-e-i." Most American botanists ignore this rule.

There is a somewhat less scholarly approach that you might find useful.

- Pronounce all of the syllables.
- Say them as you would any English syllables.
- Put the accent where you think it sounds best.
- Try to be consistent.

### A LITTLE ETYMOLOGY

#### PREFIXES

<table>
<thead>
<tr>
<th>Prefix</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>a-</td>
<td>without</td>
</tr>
<tr>
<td>angusti-</td>
<td>narrow</td>
</tr>
<tr>
<td>apo-</td>
<td>separate</td>
</tr>
<tr>
<td>bi-</td>
<td>two</td>
</tr>
<tr>
<td>brachy-</td>
<td>short</td>
</tr>
<tr>
<td>brevi-</td>
<td>short</td>
</tr>
<tr>
<td>chori-</td>
<td>separate</td>
</tr>
<tr>
<td>cleisto-</td>
<td>closed, hidden</td>
</tr>
<tr>
<td>con-</td>
<td>with</td>
</tr>
<tr>
<td>echino-</td>
<td>spiny</td>
</tr>
<tr>
<td>eu-</td>
<td>true, typical, good</td>
</tr>
<tr>
<td>ex-</td>
<td>without</td>
</tr>
<tr>
<td>gyno-</td>
<td>female</td>
</tr>
<tr>
<td>halo-</td>
<td>salt</td>
</tr>
<tr>
<td>homo-</td>
<td>the same</td>
</tr>
<tr>
<td>hyper-</td>
<td>above</td>
</tr>
<tr>
<td>hypo-</td>
<td>below</td>
</tr>
<tr>
<td>in-</td>
<td>in, within</td>
</tr>
<tr>
<td>inter-</td>
<td>between</td>
</tr>
<tr>
<td>lati-</td>
<td>broad, wide</td>
</tr>
<tr>
<td>longi-</td>
<td>long</td>
</tr>
<tr>
<td>macro-</td>
<td>large, great</td>
</tr>
<tr>
<td>meso-</td>
<td>in the middle</td>
</tr>
<tr>
<td>micro-</td>
<td>small</td>
</tr>
<tr>
<td>mono-</td>
<td>one</td>
</tr>
</tbody>
</table>
There are a few simple rules that must be followed in writing scientific names. The genus is always capitalized; the specific epithet should not be. The rules of nomenclature allow them to be if they are commemorative, as in Elymus smithii (a relative, no doubt) or if the epithet was once itself a generic name, as in Arundo Donax, the giant reed grass. Even in such instances, however, the rules discourage capitalization.

The generic name and specific epithet are underlined when they appear in handwritten or typed material. They are put in italics or bold-face in printed text. The authority is always capitalized, but it is not underlined or otherwise set off from the remainder of the text.

**THE TAXONOMIC HIERARCHY**

The taxonomic hierarchy is the series of categories that have been arranged in a particular sequence to show relationships with one another. The names of these categories and their sequence are set by the ICBN. It is the official list of groups into which plants are classified. Any one of these categories, at any level, is called a taxon (plural, taxa). The sequence of taxa and their standard endings is as follows:

<table>
<thead>
<tr>
<th>Category</th>
<th>Ending</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>Division or Phylum</td>
<td>-phyta</td>
<td>Magnoliophyta</td>
</tr>
<tr>
<td>Class</td>
<td>-opsida</td>
<td>Liliopsida</td>
</tr>
<tr>
<td>Subclass</td>
<td>-idae</td>
<td>Commelinidae</td>
</tr>
<tr>
<td>Order</td>
<td>-ales</td>
<td>Poales</td>
</tr>
<tr>
<td>Family-aceae</td>
<td>-oideae</td>
<td>Poaceae</td>
</tr>
<tr>
<td>Subfamily</td>
<td>-oideae</td>
<td>Panicoideae</td>
</tr>
<tr>
<td>Tribe</td>
<td>-eae</td>
<td>Andropogoneae</td>
</tr>
<tr>
<td>Subtribe</td>
<td>-inae</td>
<td>Tripsacinae</td>
</tr>
<tr>
<td>Genus*</td>
<td></td>
<td>Zea</td>
</tr>
<tr>
<td>Subgenus</td>
<td>*</td>
<td>Zea</td>
</tr>
<tr>
<td>Section</td>
<td>*</td>
<td>Zea</td>
</tr>
<tr>
<td>Species</td>
<td>*</td>
<td>Zea mays</td>
</tr>
<tr>
<td>Subspecies</td>
<td>*</td>
<td>mexicana</td>
</tr>
<tr>
<td>Variety</td>
<td>*</td>
<td>mexicana</td>
</tr>
</tbody>
</table>

* No standard ending

There are no standardized endings for taxa at or below the rank of genus. There are, however, grammatical considerations. Their terminations must agree in gender and in number. This explains why Tridens pulchellus becomes Erioneuron pulchellum when the epithet is transferred from one genus to the other.

My reason for including this brief discussion of the taxonomic hierarchy is that the generic and species names are two levels of this hierarchy. In this course, we will use the names of subfamilies, tribes, genera, and species frequently.

**GRAMINEAE VERSUS POACEAE**

Before leaving the subject of the naming of grasses, an explanation of the family name of the true grasses is in order. In older references, grasses seem to belong to a family called Gramineae, while in more recent publications the family name is Poaceae. This might suggest that the "old name" Gramineae has been replaced by the "new name" Poaceae, probably because Poaceae is considered the correct name and Gramineae is now incorrect for some reason.

One of the basic principles of botanical nomenclature is that we are to use the first validly and effectively published name for a plant or group of plants (genus,
family, etc.). The name Gramineae was published by A. L. Jussieu in 1789; Poaceae by Barnhart in 1895. Therefore, following this principle of priority of publication, Gramineae is the correct name for the grass family.

The problem arises because another section of the International Code of Botanical Nomenclature (ICBN) requires that family names end in the suffix -aceae, which Gramineae obviously does not. Nor do Compositae, Cruciferae, Labiatae, Leguminosae, Umbelliferae, and Palmae. What do all of these families have in common? They are among our best known, most easily recognized, and most economically important plant families. These names were in use long before we had any international rules to govern such matters.

Which name, Gramineae or Poaceae, is correct? They are both correct and they may be used interchangeably. The ICBN makes an exception in these cases and allows two valid names for the same group. Article 18.5 of the ICBN states, "The following names, sanctioned by long usage, are treated as validly published: ... Gramineae (Poaceae; type Poa L.),...." Article 18.6 then goes on to say that, "The use, as alternatives, of the names in parentheses in Art. 18.5 is authorized."

The same holds for these first published family names and their equivalents with an -aceae ending:

- Compositae/Asteraceae
- Cruciferae/Brassicaceae
- Guttiferae/Clusiaceae
- Labiatae/Lamiaceae
- Leguminosae/Fabaceae
- Umbelliferae(Apiaceae
- Palmae/Arecaceae.

My personal preference is to use Gramineae. It was the first name to be legally published for the family. It is the name used in the Code itself. Poaceae is the alternate name for Gramineae, and not the other way around.

**SELECTED REFERENCES**


### 6.02 - GREAT MOMENTS IN AGROSTOLOGY

<table>
<thead>
<tr>
<th>Year</th>
<th>Event</th>
<th>Author/Contributor</th>
</tr>
</thead>
<tbody>
<tr>
<td>1703</td>
<td>J. Ray publishes <em>Methodus Graminum, Juncorum et Cyperorum Specialis</em></td>
<td></td>
</tr>
<tr>
<td>1709</td>
<td>J. Scheuchzer publishes <em>Agrostographiae Helveticae Prodromus</em></td>
<td></td>
</tr>
<tr>
<td>1737</td>
<td>C. Linnaeus publishes <em>Genera Plantarum</em></td>
<td></td>
</tr>
<tr>
<td>1753</td>
<td>C. Linnaeus publishes <em>Species Plantarum</em></td>
<td></td>
</tr>
<tr>
<td>1811</td>
<td>A. J. Gaudin publishes <em>Agrostologia Helvetica</em></td>
<td></td>
</tr>
<tr>
<td>1812</td>
<td>P. de Beauvois publishes <em>Essai d'une Nouvelle Agrostographie</em></td>
<td></td>
</tr>
<tr>
<td>1822</td>
<td>C. B. Trinius publishes <em>Clavis Agrostographiae</em></td>
<td></td>
</tr>
<tr>
<td>1829</td>
<td>C. G. Nees von Esenbeck publishes <em>Agrostologia Brasiliensis</em></td>
<td></td>
</tr>
<tr>
<td>1835</td>
<td>C. S. Kunth publishes <em>Distribution Methodique de la Famille des Graminees.</em></td>
<td></td>
</tr>
<tr>
<td>1855</td>
<td>Charles Darwin identifies his first grass!</td>
<td></td>
</tr>
<tr>
<td>1855</td>
<td>E. G. Steudel publishes <em>Synopsis Plantarum Glumacearum</em></td>
<td></td>
</tr>
<tr>
<td>1881</td>
<td>G. Bentham publishes &quot;Notes on Gramineae&quot;</td>
<td></td>
</tr>
<tr>
<td>1881</td>
<td>E. Hackel publishes &quot;Untersuchungen über die Lodiculae der Gräser&quot;</td>
<td></td>
</tr>
<tr>
<td>1883</td>
<td>C. S. Kunth publishes <em>Agrostographia...</em></td>
<td></td>
</tr>
<tr>
<td>1883</td>
<td>G. Vasey publishes <em>Grasses of the United States</em></td>
<td></td>
</tr>
<tr>
<td>1883</td>
<td>G. Bentham publishes treatment of Gramineae in <em>Genera Plantarum</em></td>
<td></td>
</tr>
<tr>
<td>1884</td>
<td>G. Vasey publishes <em>Agricultural Grasses of the United States</em></td>
<td></td>
</tr>
<tr>
<td>1887</td>
<td>W. J. Beal publishes <em>Grasses of North America</em></td>
<td></td>
</tr>
<tr>
<td>1887</td>
<td>E. Hackel publishes treatment of Gramineae in <em>Engler &amp; Prantl's Die Natürlichen Pflanzenfamilien</em></td>
<td></td>
</tr>
<tr>
<td>1891</td>
<td>G. Vasey publishes <em>Grasses of the Southwest</em></td>
<td></td>
</tr>
<tr>
<td>1892</td>
<td>G. Vasey publishes <em>Grasses of the Pacific Slope</em></td>
<td></td>
</tr>
<tr>
<td>1892</td>
<td>G. Vasey publishes <em>Monograph of the Grasses of the United States and British America</em></td>
<td></td>
</tr>
<tr>
<td>1892</td>
<td>E. Bruns publishes &quot;Der Grasembryo&quot;</td>
<td></td>
</tr>
<tr>
<td>1896</td>
<td>W. J. Beal publishes <em>Grasses of North America, Vol. II</em></td>
<td></td>
</tr>
<tr>
<td>1896</td>
<td>A. Grob publishes <em>Beträge zur Anatomie der Epidermis der Gramineenblätter</em></td>
<td></td>
</tr>
<tr>
<td>1897</td>
<td>F. Scribner publishes <em>American Grasses</em></td>
<td></td>
</tr>
<tr>
<td>1903</td>
<td>G. V. Nash publishes treatment of Gramineae in <em>J. K. Small's Flora of the Southeastern United States</em></td>
<td></td>
</tr>
<tr>
<td>1910</td>
<td>A. S. Hitchcock &amp; A. Chase publish &quot;The North American Species of Panicum&quot;</td>
<td></td>
</tr>
<tr>
<td>1913</td>
<td>E.-G. Camus publishes <em>Les Bambusées</em></td>
<td></td>
</tr>
<tr>
<td>1917</td>
<td>E. A. Bessey publishes &quot;Phylogeny of the Grasses&quot;</td>
<td></td>
</tr>
<tr>
<td>1917</td>
<td>O. Stapf publishes first installment of Gramineae in <em>Flora of Tropical Africa</em></td>
<td></td>
</tr>
<tr>
<td>1922</td>
<td>A. Chase publishes <em>First Book of Grasses</em></td>
<td></td>
</tr>
<tr>
<td>1927</td>
<td>C. Niles publishes <em>Beauvois’ Agrostographie</em></td>
<td></td>
</tr>
<tr>
<td>1929</td>
<td>J. W. Bews publishes <em>The World's Grasses</em></td>
<td></td>
</tr>
<tr>
<td>1931</td>
<td>N. P. Avdulov publishes &quot;Kariosistematicheskoye Issledovaniye Semeystva Zlakov&quot;</td>
<td></td>
</tr>
<tr>
<td>1932</td>
<td>H. Prat publishes &quot;L' épiderme des Graminees...&quot;</td>
<td></td>
</tr>
<tr>
<td>1932</td>
<td>M. K. Elias publishes &quot;Grasses and Other Plants from the Tertiary Rocks of Kansas and Colorado&quot;</td>
<td></td>
</tr>
<tr>
<td>1934</td>
<td>A. Arber publishes <em>The Gramineae</em></td>
<td></td>
</tr>
<tr>
<td>1935</td>
<td>P. Weatherwax publishes &quot;Phylogeny of Maize&quot;</td>
<td></td>
</tr>
<tr>
<td>1935</td>
<td>A. S. Hitchcock publishes <em>Manual of the Grasses of the United States</em></td>
<td></td>
</tr>
<tr>
<td>1936</td>
<td>H. Prat publishes &quot;La Systématique des Graminées&quot;</td>
<td></td>
</tr>
<tr>
<td>1939</td>
<td>P. Mangelsdorf &amp; R. G. Reeves publish <em>The Origin of Indian Corn and Its Relatives</em></td>
<td></td>
</tr>
<tr>
<td>1939</td>
<td>G. W. Beadle publishes &quot;Teosinte and the Origin of Maize&quot;</td>
<td></td>
</tr>
<tr>
<td>1939</td>
<td>R. Pilger publishes &quot;Zur Morphologie des Ahrchens der Gramineen&quot;</td>
<td></td>
</tr>
<tr>
<td>1951</td>
<td>A. Chase publishes revised edition of <em>Manual of the Grasses</em></td>
<td></td>
</tr>
<tr>
<td>1954</td>
<td>R. Pilger publishes &quot;Das System der Gramineae&quot;</td>
<td></td>
</tr>
<tr>
<td>1954</td>
<td>T. Tateoka publishes &quot;On the Systematic Significance of Starch Grains of Seeds in Poaceae&quot;</td>
<td></td>
</tr>
<tr>
<td>1955</td>
<td>A. Beetle publishes &quot;The Four Subfamilies of the Gramineae&quot;</td>
<td></td>
</tr>
<tr>
<td>1956</td>
<td>G. L. Stebbins publishes &quot;Cytogenetics and Evolution of the Grass Family&quot;</td>
<td></td>
</tr>
<tr>
<td>1956</td>
<td>G. L. Stebbins publishes &quot;Taxonomy and Evolution of Genera, with Special References to the Family Gramineae&quot;</td>
<td></td>
</tr>
<tr>
<td>1958</td>
<td>W. V. Brown publishes &quot;Leaf Anatomy in Grass States&quot;</td>
<td></td>
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</tbody>
</table>

1960 H. Prat publishes "Vers une Classification Naturelle des Graminées"

1960 W. V. Brown publishes "The Morphology of the Grass Embryo"


1960 N. L. Bor publishes *Grasses of Burma, Ceylon, India and Pakistan*


1961 H. T. Clifford publishes "Floral Evolution in the Family Gramineae"

1961 H. J. Conert publishes *Die Systematik und Anatomie der Arundineae*

1962 Agnes Chase & Cornelia Niles publish *Index to Grass Species*

1966 F. A. McClure publishes *The Bamboos: a Fresh Perspective*

1968 F. W. Gould publishes *Grass Systematics*

1972 G. L. Stebbins publishes "The Evolution of the Grass Family"

1973 F. A. McClure publishes "Genera of Bamboos Native to the New World..."

1975 F. W. Gould publishes *The Grasses of Texas*

1976 N. N. Tsvelev publishes *Zlaki SSSR*

1978 F. W. Gould & C. A. Clark publish "*Dichanthelium (Poaceae) in the United States and Canada*"

1978 R. W. Pohl publishes *How to Know the Grasses*

1979 H. E. Conner publishes "Breeding Systems in the Grasses: a Survey"

1979 H. H. Iltis et al. publish "*Zea diploperennis* (Gramineae): a new Teosinte from Mexico"


1980 R. W. Pohl publishes treatment of Gramineae in *Flora Costaricensis*


1983 H. H. Iltis publishes "The Catastrophic Sexual Transmutation Theory..."

1986 Derek Clayton & S. Renvoize publish *Genera Graminum: Grasses of the World*

1987 Thomas Soderstrom et al. publish *Grass Systematics and Evolution*

1989 N. N. Tsvelev publishes *The System of Grasses and Their Evolution*

1992 L. Watson & M. J. Dallwitz publish *The Grass Genera of the World*


1998 R. J. Soreng & J. I. Davis publish *Phylogenetics and Character Evolution in the Grass Family*

1999 E. J. Rudziewicz et al. publish *American Bamboos*

2000 Jacobs & Everett publish *Grass Systematics and Evolution*

2001 Grass Phylogeny Working Group publishes new system of subfamilies and tribes

2003 Second volume of the treatment of Gramineae published in *Flora of North America north of Mexico*
Albert Spear Hitchcock was born in Michigan in 1865, grew up in Kansas and Nebraska, and went to Iowa State Agricultural College (now Iowa State University), where he graduated in 1884. [1865 to 1884 = 19 years!] While there he studied under the eminent American botanist, Charles Edwin Bessey. He was then a faculty or staff member at Iowa State, the State University of Iowa, the Missouri Botanical Garden, Washington University, and Kansas State Agricultural College (now Kansas State University). In 1901 he moved to Washington, D. C. as the Assistant Chief of the Division of Agrostology in the U. S. Department of Agriculture. He would spend the remainder of his career working there, becoming the head of the grass collection of the United States National Herbarium, and one of this country’s most respected systematic botanists. Willis Lynn Jepson, the distinguished University of California botanist and pre-eminent expert on the state’s flora, once inscribed a book to Dr. Hitchcock, calling him an “eager explorer, far-seeing botanist, and wise promoter of scientific research in America.” Dr. Hitchcock died in 1935, on board a ship returning from an International Botanical Congress in Europe.

His best known work, the “Manual of the Grasses of the United States,” was published only months before his death. The first printing sold out in a matter of weeks. I have been told that the two editions of The Manual are the top-selling government publications in history. The U. S. Government Printing Office finally had to give up on reprinting the second edition because the plates had worn out! The comprehensive nature of the work, its keys and illustrations, made it the “Bible” for people needing to know about grasses. Its system of subfamilies and tribes, and the names of individual grasses, would dominate regional and state floras for decades.

One year after A. S. Hitchcock moved to Washington, D. C., so did Mary Agnes Chase, as a scientific illustrator for the Department of Agriculture. In 1905, she started to work for Dr. Hitchcock. Being a person of great intelligence and sensitivity, she fell in love with grasses. She became Hitchcock’s scientific collaborator and was a major force behind the publication of The Manual in 1935. She retired as Senior Botanist at the Smithsonian in 1939, having become the successor to A. S. Hitchcock. She stayed on as an unsalaried research scientist until her death in 1963. One of her greatest accomplishments was the revision of The Manual, which appeared in 1951. Many of us, wanting to give her the recognition that she richly deserved, always call it “Hitchcock and Chase.”

In her later years, Mrs. Chase could have been the type specimen of the little old granny. But as a young woman she was an activist for women’s causes – not at all the shy and retiring lady botanist. On one or two occasions she was put in jail for her political beliefs.

**ALBERT SPEAR HITCHCOCK**


1929. Hitchcock, A. S. Grasses of Canton and


MARY AGNES CHASE


1937. Chase, A. Arthraxon hispidus var. cryptatherus (Hack.) Honda in Pennsylvania. Rhodora 39:


**SELECTED REFERENCES**


"In my opinion, the climax of flowering-plant evolution is represented by the grasses." (G. Ledyard Stebbins)

**6.04 - EVOLUTION OF GRASSES**

**EVOLUTIONARY TRENDS IN THE GRASSES**

### VEGETATIVE FEATURES

<table>
<thead>
<tr>
<th>Habit: perennial</th>
<th>annual</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elongate rhizome: absent</td>
<td>present</td>
</tr>
<tr>
<td>Seedling leaves: short</td>
<td>elongate</td>
</tr>
<tr>
<td>Ligule: membranous</td>
<td>Pseudopetiole: hairs</td>
</tr>
<tr>
<td>Bicellular hairs: present</td>
<td>absent</td>
</tr>
<tr>
<td>Silica cells: quadrate/elongate</td>
<td>dumbbell-shaped oblong</td>
</tr>
<tr>
<td>Stomates: lozenge-shaped</td>
<td>Kranz anatomy: absent</td>
</tr>
</tbody>
</table>

### SPIKELET AND INFLORESCENCE

<table>
<thead>
<tr>
<th>Panicle branches: single</th>
<th>pairs, trios, clusters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peduncle: well developed</td>
<td>Florets short/absent per spikelet: several</td>
</tr>
<tr>
<td>Disarticulation below glumes: no</td>
<td>yes</td>
</tr>
<tr>
<td>Glumes: awnless</td>
<td>awned</td>
</tr>
<tr>
<td>Glumes: shorter or equal to longer than lemmas</td>
<td>Sterile basal lemmas: absent</td>
</tr>
<tr>
<td>Lemma callus: blunt</td>
<td>Lemma elongate, pointed</td>
</tr>
<tr>
<td>Texture: similar</td>
<td>Dissimilar</td>
</tr>
<tr>
<td>Lemmas: awned</td>
<td>Awned</td>
</tr>
<tr>
<td>Awn: straight, single</td>
<td>bent, twisted or trifid</td>
</tr>
<tr>
<td>Awn: terminal</td>
<td>dorsal or basal</td>
</tr>
<tr>
<td>Lemma apex: tapering</td>
<td>notched, bilobed, toothed</td>
</tr>
<tr>
<td>Lemma veins: convergent</td>
<td>Parallel</td>
</tr>
</tbody>
</table>

### FLORET AND CARYOPSIS

<table>
<thead>
<tr>
<th>Florets: bisexual/mixed</th>
<th>unisexual</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palea: 1-partite</td>
<td>2-partite</td>
</tr>
<tr>
<td>Lodicule number: 3</td>
<td>2 nonvascular</td>
</tr>
<tr>
<td>Lodicule apex: thin</td>
<td>thick, truncate</td>
</tr>
<tr>
<td>Stamen number: six</td>
<td>three</td>
</tr>
<tr>
<td>Style branches: three</td>
<td>two</td>
</tr>
<tr>
<td>Stigmas: elevated</td>
<td>sessile</td>
</tr>
<tr>
<td>Embryo/caryopsis ratio: &lt;1/3</td>
<td>&gt;1/3</td>
</tr>
<tr>
<td>Embryo internode: short</td>
<td>elongate/absent</td>
</tr>
<tr>
<td>Starch grains: compound</td>
<td>simple</td>
</tr>
</tbody>
</table>

### NUMBER OF ADVANCED CHARACTER STATES IN REPRESENTATIVE GRASSES

<table>
<thead>
<tr>
<th>Tribe</th>
<th>Genus</th>
<th># Advanced States</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bambuseae</td>
<td><em>Bambusa</em></td>
<td>02</td>
</tr>
<tr>
<td>Streptochaetae</td>
<td><em>Streptochaeta</em></td>
<td>04</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Tribe</th>
<th>Genus</th>
<th># Advanced States</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oryzeae</td>
<td><em>Oryza</em></td>
<td>09</td>
</tr>
<tr>
<td>Ampelodesmeae</td>
<td><em>Ampelodesmos</em></td>
<td>11</td>
</tr>
<tr>
<td>Eragrosteeae</td>
<td><em>Eragrostis</em></td>
<td>11</td>
</tr>
<tr>
<td>Ehrharteae</td>
<td><em>Ehrharta</em></td>
<td>11</td>
</tr>
<tr>
<td>Danthonieae</td>
<td><em>Danthonia</em></td>
<td>12</td>
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<tr>
<td>Poeae</td>
<td><em>Festuca</em></td>
<td>12</td>
</tr>
<tr>
<td>Arundineae</td>
<td><em>Arundo</em></td>
<td>13</td>
</tr>
<tr>
<td>Chlorideae</td>
<td><em>Chloris</em></td>
<td>14</td>
</tr>
<tr>
<td>Olyreae</td>
<td><em>Olyra</em></td>
<td>16</td>
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<td>Stipeae</td>
<td><em>Stipa</em></td>
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<tr>
<td>Triticeae</td>
<td><em>Hordeum</em></td>
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<td>Paniceae</td>
<td><em>Panicum</em></td>
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<tr>
<td>Aveneae</td>
<td><em>Avena</em></td>
<td>18</td>
</tr>
<tr>
<td>Agrostideae</td>
<td><em>Agrostis</em></td>
<td>18</td>
</tr>
<tr>
<td>Andropogoneae</td>
<td><em>Schizachyrium</em></td>
<td>19</td>
</tr>
</tbody>
</table>


### MAJOR CLADES

Evidence is presented to support the recognition of several major clades within the family:

- **Streptochaeta & Phareae** (early-diverging lineage)
- **PACC clade** (Panicoideae, Arundinoideae, Chloridoideae, Centothecoideae)
- **BOP clade** (Bambusoideae, Oryzoideae, Pooidae)

[Source: Grass Phylogeny Working Group, 2000]

### SELECTED REFERENCES


The great civilizations, both past and present, have been based upon agriculture. These agricultural systems, in turn, have been founded upon a handful of cereals or grains. The great civilizations of the Near and Middle East, notably those of Greece, Rome, and Egypt, were based primarily on wheat; as were those of Europe and later North America. The well-developed agriculture of the Maya, Aztecs, and Incas rested on maize. The great societies of China, India, and the Far East were based upon rice. While all of the great civilizations cultivated many different kinds of plants for a variety of purposes, it is almost impossible to overestimate the importance of the cereals. We devote 70% of our farmland to growing cereals and we derive about 50% of our calories from them. As a group they are, without question, the most important source of our food and they have been throughout our entire cultural history.

All of the true cereals belong to Gramineae. It is common to recognize maize (corn), rice, and wheat as the major cereals. Barley, rye, and oats are the best known of the minor cereals. In addition to the true cereals is an artificial group of plants called the false cereals. They are characterized by small, grain-like fruits. Sunflower and buckwheat "seeds" are perhaps the best known examples.

There are several features of cereals that make them useful to us. They are annuals, which means that we can rely on getting a crop in a relatively short time. They are also adaptable and efficient producers of food. Cereals are very nutritious. Grains can be easily harvested, cleaned, and processed.

The most important part of the cereal plant is its fruit, the seed-like caryopsis. It is more commonly known as a grain or a berry. It contains a single seed whose outer coat is fused to the inner wall of the fruit. The outer layer of the grain (ovary wall and seed coat) are often called bran; the embryo within the grain is the germ.

**THE PROCESS OF DOMESTICATION**

The monumental event that is often called the single most significant occurrence in human cultural evolution happened a scant 10,000 years ago. That event is the domestication of plants and animals. To emphasize how recent this was in the scheme of things, I will switch time scales. Assume that the entire history of the universe can be collapsed into a single year.

<table>
<thead>
<tr>
<th>Year</th>
<th>Event</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan. 01</td>
<td>Creation of the Universe</td>
</tr>
<tr>
<td>Sep. 25</td>
<td>Origin of life on earth</td>
</tr>
<tr>
<td>Dec. 20</td>
<td>Plants colonize the land</td>
</tr>
<tr>
<td>Dec. 28</td>
<td>First flowering plants appear</td>
</tr>
<tr>
<td>Dec. 31: 10:30 p.m.</td>
<td>First humans</td>
</tr>
<tr>
<td>Dec. 31: 11:00 p.m.</td>
<td>Use of tools</td>
</tr>
<tr>
<td>Dec. 31: 11:59 p.m.</td>
<td>Domestication (agriculture)</td>
</tr>
</tbody>
</table>

Domestication is really directed evolution, which in turn is based upon two basic phenomena: variation, the concept that not all individuals are the same and that some are better adapted for survival than others, and natural selection, the view that nature selects for those individuals that are best adapted to reproduce the species. Natural selection has been largely replaced by artificial selection -- by people selecting those individuals that we want to preserve. This has been done consciously and unconsciously.

Domestication involves three important steps:

- moving seeds, grains, etc. from their native habitats and planting them in new areas;
- removing selective pressures and thereby allowing more variants to survive; and
- selecting for characteristics that are useful to us, but not necessarily for the plant under its natural conditions.

**THE CHANGES**

Some changes in plants that have occurred as a result of domestication include:

- spread into a greater diversity of environments and a wider geographic range;
- flowering and fruiting simultaneously;
- reduction or loss of dispersal mechanisms;
- conversion from perennials to annuals;
- absence of normal pollinators;
- loss of defense mechanisms (thorns, awns, etc.).
- increased palatability;
- development of seedless fruits;
- reproduction by vegetative means;
- increase or decrease in plant size;
- change in chromosome number;
- increased susceptibility to disease;
- loss of seed dormancy;
- loss of photoperiod controls;
- change from self-incompatability to self-
  compatability
- conversion of flower parts from one series to
  another.

WHERE DID IT OCCUR?

The Near East Complex

<table>
<thead>
<tr>
<th>Crop Name</th>
<th>Scientific Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avena sativa</td>
<td>oats</td>
</tr>
<tr>
<td>Hordeum vulgare</td>
<td>barley</td>
</tr>
<tr>
<td>Secale cereale</td>
<td>rye</td>
</tr>
<tr>
<td>Triticum aestivum</td>
<td>bread wheat</td>
</tr>
<tr>
<td>Triticum monococcum</td>
<td>einkorn wheat</td>
</tr>
<tr>
<td>Triticum turgidum</td>
<td>emmer wheat</td>
</tr>
</tbody>
</table>

The Asian Complex

<table>
<thead>
<tr>
<th>Crop Name</th>
<th>Scientific Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brachiaria ramosa</td>
<td>anda horra</td>
</tr>
<tr>
<td>Coix lacryma-jobi</td>
<td>Job's tears</td>
</tr>
<tr>
<td>Digitaria cruciata</td>
<td>raishan</td>
</tr>
<tr>
<td>Digitaria sanguinalis</td>
<td>manna</td>
</tr>
<tr>
<td>Echinochloa colona</td>
<td>shama</td>
</tr>
<tr>
<td>Echinochloa frumentacea</td>
<td>Japanese millet</td>
</tr>
<tr>
<td>Oryza sativa</td>
<td>rice</td>
</tr>
<tr>
<td>Panicum miliaceum</td>
<td>Proso millet</td>
</tr>
<tr>
<td>Panicum sumatrense</td>
<td>sawan</td>
</tr>
<tr>
<td>Paspalum scrobiculatum</td>
<td>khodo millet</td>
</tr>
<tr>
<td>Setaria glauca</td>
<td>korali</td>
</tr>
<tr>
<td>Setaria italica</td>
<td>foxtail millet</td>
</tr>
</tbody>
</table>

The African Complex

<table>
<thead>
<tr>
<th>Crop Name</th>
<th>Scientific Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brachiaria deflexa</td>
<td>animal fonio</td>
</tr>
<tr>
<td>Digitaria exilis</td>
<td>fonio</td>
</tr>
<tr>
<td>Digitaria iburua</td>
<td>black fonio</td>
</tr>
<tr>
<td>Eleusine coracana</td>
<td>finger millet</td>
</tr>
<tr>
<td>Eragrostis tef</td>
<td>teff</td>
</tr>
<tr>
<td>Oryza glaberrima</td>
<td>African rice</td>
</tr>
<tr>
<td>Pennisetum americanum</td>
<td>pearl millet</td>
</tr>
<tr>
<td>Sorghum bicolor</td>
<td>sorghum</td>
</tr>
</tbody>
</table>

The New World Complex

<table>
<thead>
<tr>
<th>Crop Name</th>
<th>Scientific Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bromus mango</td>
<td>mango</td>
</tr>
<tr>
<td>Bromus unioloides</td>
<td>tuca</td>
</tr>
<tr>
<td>Panicum sonorim</td>
<td>sauwi</td>
</tr>
<tr>
<td>Setaria geniculata</td>
<td>brittle grass</td>
</tr>
<tr>
<td>Zea mays</td>
<td>maize (corn)</td>
</tr>
</tbody>
</table>

When Were They Domesticated?

<table>
<thead>
<tr>
<th>Year</th>
<th>Crop</th>
</tr>
</thead>
<tbody>
<tr>
<td>9000</td>
<td>Barley</td>
</tr>
<tr>
<td>9000</td>
<td>Emmer wheat</td>
</tr>
<tr>
<td>7500</td>
<td>Rice</td>
</tr>
<tr>
<td>7500</td>
<td>Rye</td>
</tr>
<tr>
<td>7000</td>
<td>Einkorn wheat</td>
</tr>
<tr>
<td>7000</td>
<td>Sugar cane</td>
</tr>
<tr>
<td>7000</td>
<td>Durum wheat</td>
</tr>
<tr>
<td>6000</td>
<td>Bread wheat</td>
</tr>
<tr>
<td>6000</td>
<td>Finger millet</td>
</tr>
<tr>
<td>5500</td>
<td>Maize</td>
</tr>
<tr>
<td>5500</td>
<td>Foxtail millet</td>
</tr>
<tr>
<td>4500</td>
<td>Sorghum</td>
</tr>
<tr>
<td>1500</td>
<td>African rice</td>
</tr>
<tr>
<td>1000</td>
<td>Millets</td>
</tr>
<tr>
<td>1000</td>
<td>Oats</td>
</tr>
<tr>
<td>1000</td>
<td>Maize (larger ears)</td>
</tr>
<tr>
<td>1972</td>
<td>Wild rice</td>
</tr>
</tbody>
</table>

Why Did It Take So Long?

The overriding question about the domestication of plants is why did it take so long for us to make so simple a "discovery" or to take this step. A number of theories have been put forth:

- While we lived by hunting, fishing, and gathering we had too little time for such cultural luxuries.
- Domestication became a necessity after dramatic shifts in climate.
- For thousands of years, we would be satisfied just to meet our basic needs for food, shelter, and clothing. Domestication occurred as the culmination of an ever increasing differentiation and specialization of human communities.
- Some plants and animals may have been domesticated as parts of religious ceremonies.
- No particular motive or advance was required; only the revelation that seeds can be sown to produce plants when and where desired ("The Eureka! Model").
- There is no single explanation; all of them have contributed to our understanding of the problem ("The No-Model Model").

The Worst Mistake in History?

You should be aware that not everyone is convinced that the domestication of plants and animals has been such a fine thing. But certainly we are now better off than the people in the Middle Ages? The cavemen? The apes? Jared Diamond (1987) argues the following:
We are now much more dependent upon a few high carbohydrate crops, such as rice and the potato.

We are more susceptible to famine and crop failure.

Studies show an increase in tooth enamel defects associated with malnutrition, an increase in iron-deficiency anemia, an increase in bone lesions, and until recently a decrease in life expectancy.

The population densities that are now possible with agriculture encourage the spread of parasites and infectious disease.

Agriculture and led to deep class divisions and accentuated the inequality of the sexes.

**SELECTED REFERENCES**


First, a short detour into the field of economic botany. There is a convention of long standing that calls for recognizing two groups of cereals – true and false. **True cereals** are the grains derived from plants of Gramineae. All others, such as buckwheat, sunflower, grains-of-paradise, etc., are **false cereals** or **pseudocereals**. We will ignore the false cereals.

It is also customary to distinguish two groups of true cereals – major and minor. The **major cereals** are wheat, rice, and maize (corn). The **minor cereals** are all of the remaining true cereals such as barley, oats, and rye.

### WHEAT

This is the most widely cultivated crop plant and also one of our oldest. Archeological remains dating to 6700 B. P. have been found in Jarmo, Iraq. These were relatively primitive wheats. But, even the advanced bread wheat is known from 5000 B. C. from the Nile Valley. Wheat was brought to the New World by the Spanish in 1529. It has been in cultivated in the United States since about 1602.

There are about 14-16 commonly recognized species of wheat. They fall easily into three groups, differing in chromosome number and morphology. In *Triticum*, x = 7. Two of the wheats are diploid (2x = 14); eight are tetraploids (4x = 28); and six are hexaploids (6x = 42). A more detailed summary is presented below. The diploid and tetraploid wheats are of little economic importance; it is the hexaploids that we use. The evolution of these 6X wheats is a fascinating story of hybridization between primitive wheats and weedy relatives (goat grasses of the genus *Aegilops*), followed by what was described for many years as a "spontaneous doubling of chromosome number". It always seemed to me that there was something mystical in that phrase. Most researchers now believe that the change from diploid to tetraploid came about through the union of unreduced gametes. This process occurred without our assistance. We just took advantage of the results. I will go into this in more detail in lecture.

Today there are many different cultivars of wheat available. They are classified in several ways. The **winter wheats** are planted in the fall, remain dormant during the winter, and then mature in the early summer. Winter wheats are grown from Texas to South Dakota. **Spring wheat** is planted in the spring and matures that same summer. It is adapted for growing seasons as short as 90 days. Spring wheat is used in the northern regions of the U. S. and Canada.

Wheat is the most important cereal for bread making because of the nature of the protein in its grains. Glutenin and gladin are sticky proteins that can hold a paste or dough together in a mass. Together they form gluten. If a mixture of wheat flour and water is exposed to the air for any length of time, it will become infected by naturally occurring microorganisms, including yeasts. They produce gases as part of their life cycle. The proteins in wheat flour have the ability to trap these gas bubbles within the dough. The result is leavened bread.

#### WILD AND DOMESTICATED WHEATS

<table>
<thead>
<tr>
<th>Ploidy: Scientific Name</th>
<th>Genome(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Diploids [2n = 2x = 14]</strong></td>
<td></td>
</tr>
<tr>
<td><em>Triticum boeoticum</em> (wild einkorn)</td>
<td>AA</td>
</tr>
<tr>
<td><em>Triticum monococcum</em> (einkorn)</td>
<td>AA</td>
</tr>
<tr>
<td><strong>Tetraploids [2n = 4x = 28]</strong></td>
<td></td>
</tr>
<tr>
<td><em>Triticum dicoccoides</em> (wild emmer wheat)</td>
<td>AABB</td>
</tr>
<tr>
<td><em>Triticum dicoccon</em> (emmer wheat)</td>
<td>AABB</td>
</tr>
<tr>
<td><em>Triticum durum</em> (durum or macaroni)</td>
<td>AABB</td>
</tr>
<tr>
<td><em>Triticum turgidum</em> (poulard or rivet)</td>
<td>AABB</td>
</tr>
<tr>
<td><em>Triticum polonicum</em> (Polish wheat)</td>
<td>AABB</td>
</tr>
<tr>
<td><em>Triticum carthlicum</em> (Persian wheat)</td>
<td>AABB</td>
</tr>
<tr>
<td><em>Triticum timopheevii</em></td>
<td>AAGG</td>
</tr>
<tr>
<td><em>Triticum araraticum</em></td>
<td>AAGG</td>
</tr>
<tr>
<td><strong>Hexaploids [2n = 6x = 42]</strong></td>
<td></td>
</tr>
<tr>
<td><em>Triticum spelta</em> (spelt wheat)</td>
<td>AABBD</td>
</tr>
<tr>
<td><em>Triticum macha</em> (macha wheat)</td>
<td>AABBD</td>
</tr>
<tr>
<td><em>Triticum vavilovii</em> (Vavilo's wheat)</td>
<td>AABBD</td>
</tr>
<tr>
<td><em>Triticum compactum</em> (club wheat)</td>
<td>AABBD</td>
</tr>
<tr>
<td><em>Triticum sphaerococcum</em> (shot wheat)</td>
<td>AABBD</td>
</tr>
<tr>
<td><em>Triticum aestivum</em> (bread wheat)</td>
<td>AABBD</td>
</tr>
</tbody>
</table>


#### EVOLUTION OF MODERN HEXAPLOID WHEATS

**PHASE I: DIPLOID TO TETRAPLOID**

| Triticum boeoticum (Wild einkorn wheat) | Aegilops speltoides (Goat grass) |
| [2n = 2x = 14] | [2n = 2x = 14] |
| [Genome: AA] | [Genome: BB] |
Sterile F₁ Hybrid
[2n = 2x = 14]
[Genomes: AB]

Unreduced Gametes
("Chromosome Doubling")

Triticum dicoccoides
(Wild emmer wheat)
[2n = 4x = 28]
[Genomes: AABB]

Domestication

Triticum dicoccum
(Cultivated emmer wheat)
[2n = 4x = 28]
[Genomes: AABB]

PHASE II: TETRAPLOID TO HEXAPLOID

Triticum dicoccum
(Cultivated emmer wheat)
[2n = 4x = 28]
[Genomes: AABB] X [Genomes: DD]

Sterile Hybrid
[2n = 3x = 21]
[Genomes: ABD]

Unreduced Gametes
("Chromosome Doubling")

Triticum aestivum
(Bread wheat)
[2n = 6x = 42]
[Genomes: AABBD]

Domestication

Hulled/Free-threshing cultivars

Recent domestication/genetic engineering

RICE

Rice is the principal food for about 60% of the world’s population. It has been cultivated in southeast Asia for at least 5000 years. Literally thousands of cultivars have been developed, 8000 of them in India alone. Rice was introduced into America in 1647.

Unlike wheat, most kinds of rice are diploid (2n = 2x = 24). It is usually grown in a swampy field known as a paddy. This helps to explain why so much rice is raised in the monsoon belt where heavy seasonal rainfall is used. In most instances, rice seeds are not planted directly in the paddies. Instead there are nurseries where seedlings are started and then transferred. The seedlings are planted in small bunches, each clump about 4-16” from the next one. Most cultivated strains require flooding, this being accomplished by taking advantage of the monsoons and by the skillful manipulation of dikes in the paddies.

At maturity, most rice plants are 4-6 ft. tall. In the Mekong Valley, some deep water varieties reach 20 ft. Once the plants have flowered, the water level is reduced and finally the supply is shut off entirely and the fields allowed to dry. When the plants begin to wither, it is time to harvest the crop. In the Old World, the harvesting and threshing processes are done by hand. In the U.S. and other technologically advanced countries, much of this is done by machine. In this country, Arkansas, Louisiana, and California are the main rice growing states.

THE PROCESS

Oryza rufipogon
Wild: Asia
Perennial
2n = 2x = 24
Genome: AA

Oryza nivara
Wild: India, Asia, Oceania
Annual
2n = 2x = 24
Genome: AA

Domestication

Oryza sativa
Cultivated: widespread
Annual
2n = 2x = 24
Genome: AA
We commonly recognize three types of rice based upon the length of the grain:

- **long**: tropical rices; not too soft nor starchy; grains 7-8 mm long, the length prized by the connoisseur
- **medium**: commonly grown in the U. S.; somewhat softer; grains averaging about 6.6 mm long
- **short**: grown in the more northern climates, often planted in Japan; even more starchy; grains averaging about 5.5 mm long

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### MAIZE

First, a word about the common name of *Zea mays*. In this country, we usually call this plant corn or Indian corn. Maize is a better common name (and a perfectly legitimate one) because corn is used by English-speaking peoples around the world for several other cereals.

There are three features of maize that make it different from wheat, rice, or any other cereal. It is the only important cereal that is native to the New World. Second, maize as we know it today is considerably different in appearance from its wild ancestors. The progenitors of the other cereals are basically the same in general appearance as their modern derivatives. Maize is strikingly distinct. And third, maize is unique among the major cereals in having separate male and female flowers borne on entirely different parts of the plant. The male flowers are found on the branches of the tassel, while the female flowers are clustered in the ear, the complex fruiting structure that bears an even number of rows of caryopses, or kernels as they are commonly called.

There are six main types of maize in use today:

- **flint**: kernel made of hard starch; in use by Native Americans at the time of Columbus; widely used in the northern corn belt;
- **dent**: kernel of hard starch, capped by soft starch that dries to leave a small depression in the top of the grain; economically the most important maize; much used in the corn belt;
- **flour**: kernel consists almost entirely of soft starch; used by the Native Americans of the Southwest and those in South America for hand grinding;
- **sweet**: kernels with high sugar content, consumed while immature; most widely grown for human consumption here and in Europe;
- **pop**: kernels lacking soft starch, cells burst upon heating because of high water content of central cells; related in flint corn;
- **pod**: peculiar type with comparatively little economic importance; kernel enclosed by bracts; considered by some to be the ancestor of modern maize.

Maize has many uses. About 90% of the crop goes into livestock food. In this country, maize is relatively unimportant as a food for humans. This is not the case in many other areas of the world, especially Africa. It is inferior to wheat and to some other cereals in its protein content. This means that maize flour products are less tasty than those made from rye or wheat. Maize flour, however, has been the mainstay of many peoples in Central and South America. Other important products from maize include corn starch, corn oil, alcoholic beverages, and silage.

### HYBRID MAIZE

One of the great developments in modern agricultural genetics is hybrid corn. The basic principle involved is that stable inbred lines can be crossed with one another to produce uniform plants with higher yields that combined the desirable features of the two parental lines. Modern hybrid corn involves a double crossing. During the first year, inbred line A is crossed with line B. Self-pollination is prevented during these crosses by removing the male flowers from one strain (dettasseling), thereby rendering the plants effectively female. The manual emasculation of plants, once a common summer job for young people living in the Corn Belt, has all but disappeared because of another important advance -- genetically controlled male sterility in maize. In separate fields, lines C and D are similarly crossed. The seeds from the A x B and from the C x D crosses are planted. These mature into AB and CD individuals. These are then crossed during the second year, yielding the double cross ABCD hybrid seed. It is planted the third year to produce tremendous yields of high-quality seed. The ABCD seed is not true-breeding and must, therefore, be purchased regularly.

### CYTOPLASMIC MALE STERILITY

In 1938, Paul Mangelsdorf, a Harvard botanist who devoted his life to the study of maize, discovered a sweet corn variety in Texas that was male sterile. The male flowers of its tassel had shriveled anthers that did not produce fertile pollen grains. Investigation of this plant revealed that the sterility was under genetic control, as opposed to some short-lived environmental problem, such as drought. Sterile sex cells typically result from chromosomal abnormalities, either in their number or structure. However, in this case the corn plant produced sterile pollen when a sterility factor [S] in the cytoplasm of the cell was present at the same time that it had a double recessive gene [rf] in its nucleus. This same kind of phenomenon was first found in onions, and is now known to occur in several crop plants. One possible explanation is that the cytoplasmic sterility is caused by viruses that can survive only if the rf rf condition exists. If the gene is...
traits were passed from parent to offspring through the egg. To summarize:

\[
\begin{align*}
S \, rf \, rf &= \text{male sterile plants} \\
S \, Rf \, rf &= \text{male fertile plants} \\
S \, Rf \, Rf &= \text{male fertile plants} \\
N \, rf \, rf &= \text{male fertile plants} \\
N \, rf \, rf &= \text{male fertile plants}
\end{align*}
\]

Therefore, by using an inbred line that contains the \( S \, rf \, rf \) genetic combination, male sterile plants are produced. The corn plants are rendered functionally female. The difficulty in finding enough workers and their cost made the male-sterile strains a very attractive alternative to manual detasseling. Within twenty years, practically all of the maize grown in the United States incorporated the male sterility factor first found in the Texas corn plants. Once again we had made one of our major crop plants more genetically similar to one another, with all of the advantages and disadvantages associated with that uniformity. The bill came due in the summer of 1970. Our corn fields were invaded by a fungus \( (\text{Helminthosporium maydis}) \), which causes the southern leaf blight. The disease spread rapidly, moving from Florida northward at about 150 km per day. By the end of the summer, the blight had covered much of the eastern and central United States. It devastated the Texas male-sterile hybrids, causing more than a $1 billion loss in the corn crop. Today’s maize cultivars are based upon normal cytoplasm and are detasseled by hand.

**"Jumping Genes"**

James Watson, who shared the Nobel Prize with Francis Crick for their discovery of the structure of DNA, said, "There are really three main figures in the history of genetics -- the three M’s: Mendel, Morgan, and McClintock." Gregor Johann Mendel (1822-1884), an Austrian monk, is often called the father of genetics. His work on the changes that he observed from one generation to the next in pea plants that he grew in the monastery garden is well known -- a standard fixture in all high school and college texts in biology and genetics. Thomas Hunt Morgan (1866-1945), of Columbia University, along with his wife (Lillian) and his students did his research on the fruit fly \( (\text{Drosophila melanogaster}) \). His lab was the first to demonstrate that genes were located on chromosomes in the cell nucleus, that genes were located at specific sites on a chromosome, and that traits were passed from parent to offspring through genes. Morgan won the Nobel Prize in 1933 for these fundamental discoveries.

The third "M" is Barbara McClintock (1902-1992). She earned her bachelor’s degree in botany from Cornell University, where she was also awarded her master’s and doctorate. In 1931, McClintock identified the ten chromosomes of maize, and she co-authored with Harriet Creighton the first paper to describe the genetic phenomenon of crossing-over. In 1944, McClintock identified the seven chromosomes of the bread mold, \( \text{Neurospora} \), and began her research on mobile genes and controlling elements in maize. She had observed that some plants have leaves with different patterns of pigment in them. In maize, some kernels were white, some solid purple, and some had speckles of purple on otherwise white kernels.

After years of detailed study, McClintock developed a theory to explain what she had seen. The differences in pigmentation of corn kernels was caused by some genes moving from one site on a chromosome to another location, or from one chromosome to another. Further, it appeared to her that other genes acted as switches that turn a gene on and off during plant development. McClintock presented the results of her work in 1951 at a Cold Spring Harbor Symposium. The reaction was mixed. Most of her colleagues failed to understand her work, others rejected it outright, and others thought that poor Barbara had been out in the sun too long playing her corn plants. One said, that "...he had never heard anything as ridiculous." Another, "I understand that you’re doing something that’s very strange. I don’t want to hear a word about it.” At the other end of the spectrum, the distinguished Caltech geneticist Alfred Sturtevant said, "I didn’t understand one word she said, but if she says it is so, it must be so!"

What Barbara McClintock had proposed was heresy! Everyone knew that a chromosome was like a necklace and the beads were genes. This bead is always next to that bead in a necklace; this gene is always next to that gene on a chromosome. And she was saying that it ain’t necessarily so. In her now classic paper, McClintock concluded that the best explanation for what she was seeing was that a gene did, in fact, actually move from one site on a chromosome to the site of the gene that controlled pigment color. She called it \( Ds \), the dissociator gene. \( Ds \) would instruct the color gene. The \( Ds \) gene, in turn, was controlled by an activator, \( Ac \).

McClintock called these mobile genetic units \textbf{transposons}. Time Magazine called them “jumping genes.” It explained McClintock’s theory in terms of three characters -- a painter, a boss, and a policeman. The painter is the structural gene that makes a kernel have a particular color. The boss (\( Ds \) or dissociator gene) can tell the painter to paint or not to paint. The boss must follow the directions of the police officer (\( Ac \) or activator gene), who can tell the boss to let the painter do his job or not. The officer can tell the boss to have the painter stop and then later resume painting. Depending on the interaction of the painter, boss, and policeman, the kernel will be pigmented, speckled, or colorless.

On 10 October 1983, McClintock learned from the radio that she had won the Nobel Prize in Physiology.
or Medicine. The folks in Stockholm had tried to call her at home, but she didn’t have a telephone. She, Marie Curie in 1911, and Dorothy Hodgkin in 1964 are the only three women to receive an unshared Nobel in any field.

McClintock’s long-time friend and champion, Marcus Rhoades, said of her work:

“One of the remarkable things about Barbara McClintock’s surpassingly beautiful investigations is that they came solely from her own labors. Without technical help of any kind she has by virtue of her boundless energy, her complete devotion to science, her originality and ingenuity, and her quick and high intelligence made a series of significant discoveries unparalleled in the history of cytogenetics. A skilled experimentalist, a master at interpreting cytological detail, a brilliant theoretician, she has had an illuminating and pervasive role in the development of cytology and genetics.”

Transposable elements have since been found in many plants and animals. They are best known in maize, fruit flies, yeasts, and humans.

**MAIZE RELATIVES**

It is also important not to over emphasize the uniqueness and remoteness of maize. It does have close relatives, although you might not recognize them as such on casual inspection.

**Gama grass (Tripsacum ssp.).** There are about seven species of gama grasses found from the central United States to southern Brazil. All of them are perennials. The male and female flowers are separated from one another, but do not occur in the tassel/ear configuration in corn.

**Teosinte.** There are three kinds of teosinte, all occurring in Mexico and Central America. Traditionally, teosinte has been placed in its own genus (*Euchlaena*), but in more recent works the species have been put in *Zea*. The male flowers are borne in a tassel at the top of the plant; the female flowers are borne on a spike on the lower parts of the plant.

**POSSIBLE ANCESTORS**

A great deal of research and speculation has been focused on the ancestor or ancestors of modern maize. Here are the major players.

**Corn Grass.** This plant is an anomalous grass with numerous slender leaves, numerous tillers, and small ears. There is a long spathe, more characteristic of *Coix* than of maize. These differences are supposedly the result of a single dominant gene. The plant really does not look like maize, but it was once proposed as an ancestor. It has few, if any, proponents these days.

**Teosinte.** When first proposed by Ascherson, the hypothesis was that maize was a domesticated form of teosinte. The theory was later modified by Harshberger and Collins to say that one parent of maize was teosinte, but that it had a second parent of unknown identity. George Beadle discovered that teosinte kernels will pop; a reason to preserve it as a food plant. The polystichous nature of the maize ear could be the result of fusion of teosinte spikes. The advocates of teosinte provided the only real challenge to the pod corn theory as the leading explanation of corn’s ancestor.

Common Ancestry. According to this theory, maize originated from a perennial, wild, maize-like ancestor. This plant is now extinct. The pre-maize, in turn, had an ancestor in common with both teosinte and gama grass. That grandparent is also now extinct. This theory is largely untestable because the principal players are extinct. They cannot be tested or measured.

Pod Corn. This theory was developed about sixty years ago by Paul Mangelsdorf and R. G. Reeves, two of the great names in this area. Pod corn is still very much with us today. It is a peculiar, primitive looking maize with well-developed papery bracts surrounding the individual kernels. We grow it in this country as a curiosity; in South America it remains a food plant of limited importance. The pod corn theory has three basic premises:

- Modern maize originated from a wild form of pod corn indigenous to the lowlands of Central or South America;
- Teosinte is the product of natural hybridization between maize and gama grass; and
- Many of the strains of maize that we see today are the result of past hybridization between *Zea* and *Tripsacum*.

**NATURE OF EVIDENCE**

Archeological/ethnobotanical remains. Although archeological remains of maize are fairly common in the New World, they have never been found in the Old World. This fact helps us to conclude that maize is indigenous to the New World. Several of the important digs are:

Bat Cave (New Mexico). The floor of this cave is littered with six feet of garbage, coprolites (fossil poop), debris, and tiny cobs of maize about 5600 years old. The cobs are 2-3 cm long, with kernels partly enclosed by bracts. Anatomically, it is a pod corn or a pop corn.

Swallow Cave (New Mexico). At the lowest levels are tiny cobs similar to those in the Bat Cave. The prehistoric context of the cobs indicates their great age.
Coxcatlán Cave (Tehuacán Valley of Mexico). The cave system consists of 28 superimposed levels. The upper 14 have well-preserved cobs. The cave was occupied from 10,000 to 2300 B.C. and then again from 900 B.C. to A.D. 1500. The cave faces a broad alluvial plain where wild and cultivated maize could have grown. The oldest remains bridge the gap between wild maize and the earliest stages of domesticated maize.

La Perra Cave (Tamaulipas, Mexico). The oldest remains are from about 2500 B.C. They show the signs of crossing with gama grass at the lower levels, but show "tripsacoid" features at the upper levels.

Purron Cave (Tehuacán Valley of Mexico). This cave was inhabited from about 200 B.C. to A.D. 1500. The surrounding soils are fertile and there was an abundance of water.

Pollen. During the excavations required for a new office building in Mexico City, grass pollen was discovered in cores taken at a depth of about 70 meters. The pollen was about 80,000 years old. Detailed studies made by Elso Barghoorn, a paleobotanist at Harvard University, showed that the pollen was that of maize. Above the six meter level was copious pollen of modern, cultivated maize. Barghoorn's work again provides support for the New World origin of maize. The plants that produced this pollen were alive and well thousands of years before we migrated into the Valley of Mexico. Second, this discovery tended to support the pod corn theory of Mangelsdorf and Reeves. The ancestor of modern maize as a more primitive kind of maize.

Genetic. On the fourth longest chromosome of pod corn is a gene designated Tu. In pure pod corn the gene is present in the homozygous recessive state (tt) and it is homozygous recessive (ttu) in modern maize. The change from Tu to tutu is associated with many changes in pod corn, including a number that have made the plant much more useful to us. These have also rendered it unable to live in the wild. The changes include:

- reduction in prominence of the tassel;
- increase in the development of the ear;
- changing the tassel from principally female to male;
- decrease in the length and weight of the bracts surround the kernels; and
- increase in the size and weight of the axis of the ear.

Walter Galinat (1983, 1985) reports that the gene Tr controls the two- versus four-ranked ears. The gene Pd controls single versus paired spikelets. Ab determines the presence or absence of abscission layers in the ear. The gene Tu codes for soft outer glumes and a soft rachis.

Molecular. John Doebley of the Univ. of Minnesota has studied isozyme variation in maize and teosinte. He has looked at 13 enzyme systems encoded by 21 loci. If teosinte were the ancestor of maize, we would expect to find considerable similarity at the molecular level. His studies show that maize and teosinte are indistinguishable.

**TEOSINTE VERSUS MAIZE**

- In teosinte the female spikelets are solitary; they are paired in maize;
- In teosinte the central spike of the female inflorescence is two-ranked; it is many-ranked in maize;
- In teosinte the rachis shatters at maturity; it is non-shattering in maize;
- The caryopsis is encased in teosinte; naked in maize.

At first, the differences seem striking. As Paul Mangelsdorf noted, "If maize has originated from teosinte, it represents the widest departure of a cultivated plant from its wild ancestor which still comes within man's purview...

However, according to Doebley (1990), perhaps as few as five genes account for 50-80% of the differences between maize and teosinte. "If you took those five regions from maize and put them into teosinte, the thing you'd have in front of you would be called maize." He estimates that these dramatic changes could have occurred in less than 1000 years.

An alternative explanation, wonderfully entitled the "Cataclysmic Sexual Transmutation Theory," was advanced by Hugh Iltis of the Univ. of Wisconsin. He thinks of an ear of corn as "... that magnificently monstrous enigmatic anomaly...." His argument builds on the fact that the maize ear and the central spike of the maize tassel are homologous. Both are polystichous and both are governed by the same genes. The central spike of the tassel is often feminized into an ear by abnormal environments or by disease, such as corn smut. Iltis argues that the maize ear is a feminized tassel reduced to its terminal spike. Therefore, the teosinte tassel could be transformed into a maize ear in one giant step. This would explain the lack of connecting links in the archaeological record.

**PUTTING IT ALL TOGETHER**

The salient points appear to be:

- Maize is native to the New World, probably Mexico or Central America.
The direct ancestor of maize is teosinte.

"... teosinte is not a hybrid of maize and *Tripsacum*. Perhaps I may be permitted to enjoy some degree of satisfaction in the fact that it is colleagues and not my critics who have shown that this part of our tripartite hypothesis is no longer tenable." (Paul Mangelsdorf, 1974)

The transformation of teosinte into maize began about 8000 B. P.

Archaeological evidence suggests that we first began to cultivate maize about 5200-3400 B. C.

"The mystery of maize is not such a mystery after all, and the romance has been exaggerated." (Jack Harlan, 1992)

Early Native Americans discovered that they could accelerate the forces of natural selection by physical separation of selected plant types.

Use of irrigated garden plots or isolated plots meant that these forms would not be genetically swamped by wild populations.

They selected the most useful variants out of large populations of teosinte.

"... American Indians had already developed two or three hundred races of corn, essentially all we have today. Theirs was the most extraordinary achievement in plant breeding in all of man's existence, including his most recent history.... Perhaps most remarkable of all were the earliest steps when man (or, more likely, woman) first began to influence the evolution of what I believe to be the wild ancestor of corn." (George W. Beadle, 1972)

**THE MINOR CEREALS**

**BARLEY**

*Hordeum vulgare* ranks number fourth in terms of world-wide annual production. Along with wheat, it was one of the first plants that we domesticated. All of the cultivated species are diploids (2n = 2x = 14). Barley differs from wheat, maize, and rice in having three spikelets per node. If all three develop, the spike has the appearance of having six rows of grains (the 6-rowed barleys); if the two lateral spikelets are rudimentary, then the spike appears to have two rows of spikelets (the 2-rowed barleys). The two bracts immediately surrounding the grain are fused to it. The grain is pearled, rubbed against abrasive disks to remove the hulls and some of the outer layers of the grain, during the processing for human consumption. The chief use of barley is as animal food. It is a relatively unimportant food for humans. About one-third of the crop is used for making malt used in brewing, flavoring, cereals, icings, coffee substitutes, infant foods, flours, medicinal syrups, candies, and industrial fermentations.

**RYE**

*Secale cereale* is a plant of cool, non-humid regions. It is grown chiefly in northern Europe. In the United States, North and South Dakota and Nebraska grow...
the most rye. The species is diploid \((2n = 2x = 14)\). It is now unknown in the wild. Most rye is fed to cattle. We use it to make flour for "rye bread" or the famous black bread (Schwartz brot) of Germany, Poland, and Russia. Most of our U. S. rye bread has a very high wheat flour content. Rye is also used to make whisky and industrial alcohol. Ergot \((Claviceps purpurea)\) is an important fungal parasite of rye. It causes tremendous crop losses and poisoning in both cattle and humans. Consumption of contaminated grain over a period of time leads to a gangrenous loss of tissues because of constriction of blood vessels, especially in the extremities of the body. Larger doses can have pronounced effects on the central nervous system.

### THE PROCESS

<table>
<thead>
<tr>
<th>Secale montanum</th>
<th>×</th>
<th>Secale ancestrale</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wild rye</td>
<td></td>
<td>Wild rye</td>
</tr>
<tr>
<td>S. Europe/SW Asia</td>
<td></td>
<td>Anatolia/Armenia</td>
</tr>
</tbody>
</table>

\[ Secale cereale \]

### OATS

The origin of oats \((Avena spp.)\) is obscure. There are few references to it in the ancient literature; none, for instance, in the Old Testament. It may have become domesticated in the cultivated fields of barley or of some other crop. It is now grown in temperate regions, chiefly Europe and North America.

As in wheat, there are diploid, tetraploid, and hexaploid oats. We use the hexaploids more than the others. The diploids include \(A. brevis\) (slender oats), \(A. strigosa\) (sand oats), \(A. wiestii\) (desert oats), and \(A. nudibrevis\). The tetraploids are \(A. barbata\) (slender oats) and \(A. abyssinica\) (Abyssinian oats). The hexaploids include \(A. fatua\) var. \(fatua\) (wild oats), \(A. fatua\) var. \(sativa\) (cultivated oats), \(A. sterilis\) (wild red oats), \(A. byzantina\) (red oats), and \(A. nuda\) (naked oats).

Until quite recently, oats were not widely appreciated, even though they are very nutritious (protein content of 13.8%). Oats are used to make flour, rolled oats, and even as a beverage (avena). The crop is often rotated with corn. Iowa is the leading U. S. producer.

### SORGHUM

The U. S. is the leading producer of sorghum \((Sorghum bicolor + other spp.)\). Annual world-wide production now stands at 57 million metric tons of this increasingly popular grain. The species are believed to be Asian or African in origin. Sorghum was introduced into the U. S. in the mid-1800's. The grains are small and difficult to process. We use the various species mostly for forage and silage, but in the Old World the grains are often eaten like rice or made into an unleavened bread. All of the species are diploids \((2n = 2x = 40)\), except for Johnson grass, a very aggressive tetraploid weed.

There are four commonly recognized groups of sorghum species, based upon their use:

- syrup or sorgos, whose stem juices are abundant and sweet;
- broomcorn, used to make old-style commercial brooms;
- grain sorghums, such as kaffir, milo, and durra; and
- grass sorghums, such as Sudan grass, Tunis grass, and Johnson grass, grown for forage and silage.

### WILD RICE

\(Zizania aquatica\) is native to North America. The common name is confusing, because it is not really a kind of rice \((Oryza)\). The plants are robust aquatics. As in maize, the two sexes are found in separate spikelets on different parts of the plant. Native Americans gathered the grains by boat. Until recently, wild rice has eluded cultivation with most of the crop coming from Minnesota. It is now being cultivated, including in some of our northern California counties.

### T’ EF OR TEFF

This popular grain, derived from \(Eragrostis abyssinica\), is native to northeastern Africa. Its major production site is Ethiopia, where it is more popular than all other cereal grains combined. The very small grains (1/32 in. in diameter) are typically fermented for a day or so and then made into pancakes. Teff has become popular among natural food enthusiasts in this country in recent years. The plants are also an excellent source of fodder.

### JOB’S TEARS

Although native to southeastern Asia, \(Coix lacryma-jobi\), named after the righteous sufferer in the Old Testament parable, is now very common through all of the tropical and subtropical regions of the world where its grains are used as food. It is not highly regarded, even though it has a very high protein content. Many of you will have seen these grains because they are also used to make rosaries and tourist trinkets.

### MILLETS

This is a group name for an artificial assemblage of grasses that have very small grains. Most of the common ones belong to the genera \(Pennisetum, Setaria, Panicum,\) and \(Eleusine\). For the most part, the various species are native to tropical and subtropical areas of the Old World. They are especially well
adapted to poorer soils. Most of us in Europe or North America have never eaten any of the millets (unless, of course, we frequent hippie cooperative food stores) and probably do not appreciate the role that they play in the diet of about one-third of the world's people. We see millet relatives as roadside weeds or as constituents in bird seed mix. They are also used for forage.

**TRITICALE**

Both its common name and generic name (X *Triticosecale*) suggest the origin of this cereal. It is a human-mediated hybrid between wheat (*Triticum*) and rye (*Secale*). Natural hybrids had been known for many years, but their offspring were usually sterile. Genetic work began in the late 1930's to produce a synthetic hybrid that would combine the useful features of these two important cereals. In 1965, the Centro Internacional de Mejoramiento de Maize y Trigo launched a major effort to make triticale a major food crop. It is the only artificial cereal to date that has had a major impact.

**THE PROCESS**

<table>
<thead>
<tr>
<th><em>Secale cereale</em></th>
<th>X</th>
<th><em>Triticum durum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Rye</td>
<td></td>
<td>Durum wheat</td>
</tr>
<tr>
<td>RR</td>
<td></td>
<td>AABB</td>
</tr>
<tr>
<td>(\downarrow)</td>
<td></td>
<td><em>Triticosecale</em></td>
</tr>
<tr>
<td></td>
<td>ABR</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><em>Secale cereale</em></th>
<th>X</th>
<th><em>Triticum aestivum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Rye</td>
<td></td>
<td>Breadwheat</td>
</tr>
<tr>
<td>RR</td>
<td></td>
<td>AABBCC</td>
</tr>
<tr>
<td>(\downarrow)</td>
<td></td>
<td><em>Triticosecale</em></td>
</tr>
<tr>
<td></td>
<td>ABCR</td>
<td></td>
</tr>
</tbody>
</table>
# THE MINOR CEREALS

<table>
<thead>
<tr>
<th>Common Name [Scientific Name]</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>acha [Digitaria exilis]</td>
<td>African; quite palatable and nutritious</td>
</tr>
<tr>
<td>Adlay [Coix lacryma-jobi]</td>
<td>Widely used in China, India, and Africa</td>
</tr>
<tr>
<td>African millet [Eleusine coracana]</td>
<td>Old World; one of the ancient cereals</td>
</tr>
<tr>
<td>barley [Hordeum vulgare]</td>
<td>Known to us also as an agricultural weed</td>
</tr>
<tr>
<td>barnyard grass [Echinochloa crus-galli]</td>
<td></td>
</tr>
<tr>
<td>broom millet [Panicum miliaceum]</td>
<td>Cultivated especially in the Old World</td>
</tr>
<tr>
<td>browntop [Brachiaria ramosa]</td>
<td>A relative of the Panicum cereals</td>
</tr>
<tr>
<td>bulrush millet [Pennisetum americanum]</td>
<td>A relative of elephant and Napier grass</td>
</tr>
<tr>
<td>channel millet [Echinochloa turnerianum]</td>
<td>A relative of our barnyard grass</td>
</tr>
<tr>
<td>club wheat [Triticum compactum]</td>
<td>Grown mostly in Chile, USA, and India</td>
</tr>
<tr>
<td>common millet [Panicum miliaceum]</td>
<td>In use since prehistoric times; Eurasia</td>
</tr>
<tr>
<td>durum wheat [Triticum durum]</td>
<td>High in gluten; used to make spaghetti</td>
</tr>
<tr>
<td>einkorn wheat [Triticum monococcum]</td>
<td>Primitive diploid, 1-seeded wheat</td>
</tr>
<tr>
<td>emmer wheat [Triticum dicoccon]</td>
<td>Ancient Mediterranean wheat; still used</td>
</tr>
<tr>
<td>finger millet [Eleusine coracana]</td>
<td>Important cereal in Africa and India</td>
</tr>
<tr>
<td>fonio [Digitaria exilis]</td>
<td>Used in tropical Africa</td>
</tr>
<tr>
<td>foxtail millet [Setaria italica]</td>
<td>Native to India; Near East &amp; China</td>
</tr>
<tr>
<td>German millet [Setaria italica]</td>
<td>See foxtail millet</td>
</tr>
<tr>
<td>guinea grass [Panicum maximum]</td>
<td>A perennial grass of tropical areas</td>
</tr>
<tr>
<td>hog millet [Panicum miliaceum]</td>
<td>See common millet</td>
</tr>
<tr>
<td>Hungarian millet [Setaria italica]</td>
<td>Old World; now widely cultivated</td>
</tr>
<tr>
<td>Hungry-rice [Digitaria eximis]</td>
<td>West Africa; now unknown in wild</td>
</tr>
<tr>
<td>Italian millet [Setaria italica]</td>
<td>See Hungarian millet</td>
</tr>
<tr>
<td>Japanese millet [Echinochloa crusgalli]</td>
<td>See barnyard grass</td>
</tr>
<tr>
<td>Job's tears [Coix lacryma-jobi]</td>
<td>SE Asia; ornamental use in jewelry</td>
</tr>
<tr>
<td>kans [Saccharum spontaneum]</td>
<td>Sugar cane relative grown in Africa</td>
</tr>
<tr>
<td>koda millet [Paspalum commersonii]</td>
<td>Old World; relative of Dallis and bahia grass</td>
</tr>
<tr>
<td>little millet [Panicum sumatrense]</td>
<td>Grown extensively in India</td>
</tr>
<tr>
<td>manna grass [Glyceria spp.]</td>
<td>Used especially in North America</td>
</tr>
<tr>
<td>naked oats [Avena nuda]</td>
<td>Upland regions of China</td>
</tr>
<tr>
<td>oats [Avena spp.]</td>
<td>Hexaploids most important</td>
</tr>
<tr>
<td>pearl millet [Pennisetum glaucum]</td>
<td>Highly nutritious; hybrids grown in USA</td>
</tr>
<tr>
<td>perennial teosinte [Zea mays ssp. diploperennis]</td>
<td>Recently discovered in Mexico</td>
</tr>
<tr>
<td>Polish wheat [Triticum polonicum]</td>
<td>S. Europe and n. Africa, not Poland</td>
</tr>
<tr>
<td>proso millet [Panicum miliaceum]</td>
<td>Ancient; grown mostly in USSR and Asia</td>
</tr>
<tr>
<td>ragi [Eleusine coracana]</td>
<td>See finger millet</td>
</tr>
<tr>
<td>rye [Secale cereale]</td>
<td>Probably native to southeast Asia</td>
</tr>
<tr>
<td>sanwa millet [Echinochloa frumentacea]</td>
<td>Used primarily as cereal in Far East</td>
</tr>
<tr>
<td>shama millet [Echinochloa colona]</td>
<td>Old World; now also a widespread</td>
</tr>
<tr>
<td>sorghum [Sorghum bicolor]</td>
<td>Ancient cereal of Asia and Africa</td>
</tr>
<tr>
<td>tartarian oats [Avena orientalis]</td>
<td>One-sided spikelet clusters</td>
</tr>
<tr>
<td>teff [Eragrostis abyssinica]</td>
<td>Ethiopia and African highlands</td>
</tr>
<tr>
<td>teosinte [Zea mays ssp. mexicana]</td>
<td>A close relative of maize</td>
</tr>
<tr>
<td>triticale [Triticosecale spp.]</td>
<td>Artificial wheat/rye hybrid</td>
</tr>
<tr>
<td>wild rice [Zizania spp.]</td>
<td>Native to North America; recently domesticated</td>
</tr>
</tbody>
</table>

Revised: 07 July 2002
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RICE


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**MAIZE**


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Weatherwax, P. 1955. History and origin of corn. I.


**MINOR CEREALS**


Grasslands are plant communities in which grasses are dominant. Major grassland areas occur in North America, South America, Africa, Asia, and Australia. Most of them are associations with more than one dominant species. Grasslands are often found in the interior of continents, where rain falls mainly in the summer months. The distribution of grasslands is dependent upon certain climatic, edaphic, and human-generated factors.

There are three major kinds of grasslands, with many subdivisions and transitional types:

- **Savannas** are dominated by high, coarse grasses and more or less widely scattered, low trees. Turf is seldom formed. They are often found in the tropical and subtropical regions, often in areas characterized by a short dry season. Typical examples include the llano of Venezuela, the Campo of Brazil, and the vast grasslands of much of Africa.

- **Steppes** are treeless grasslands of low relief. They may be arid or semi-arid and occur in warm or cool climates. Steppes are dominated by sod-forming grasses, tufted tall grasses, or short grass vegetation. They are characterized by a protracted cold season. Typical examples include the grasslands of the southern republics of the former Soviet Union and the Great Plains east of the Rocky Mts. in the United States.

- **Prairies** are treeless grasslands of low relief, climatically and vegetationally intermediate between savannas and short-grass steppes. Prairies are less humid than savannas and are less arid than steppes. They are usually absent from tropical/subtropical regions. Their deep, dark soils are covered with sod-forming tall-grasses. Typical examples include the Trans-Mississippi Valley in the United States, the Black Earth Belt of Russia, and the Pampa of Argentina.

---

**THE EARTH’S COVER (mi²)**

<table>
<thead>
<tr>
<th>Water</th>
<th>139,150,000</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ice caps</td>
<td>5,830,000</td>
</tr>
</tbody>
</table>

**Forests:**

- Tropical Rain Forest | 3,800,000 |
- Temperate Rain Forest | 550,000 |
- Deciduous Forest | 6,500,000 |
- Coniferous Forest | 7,600,000 |
- Dry or Monsoon Forest | 2,000,000 |
- Thorn Forest | 340,000 |
- Sclerophyll Brushland | 1,180,000 |
- Total | 21,970,000 |

**Deserts:**

- Desert Shrub/Grass | 10,600,000 |
- Salt Desert | 30,000 |
- Desert (Hot & Dry) | 2,400,000 |
- Tundra (Cold) | 4,400,000 |
- Total | 17,430,000 |

**Grasslands:**

- High Grass Savanna | 2,800,000 |
- Tall Grass Savanna | 3,900,000 |
- Tall Grass | 1,580,000 |
- Short Grass | 1,200,000 |
- Desert Grass Savanna | 2,300,000 |
- Total | 12,570,000 |

---

[After Shantz, 1954]

Forests are 42% of the earth’s vegetation cover, deserts are 34%, and grasslands are 24%. With adjustments to recognize the extent of grasslands in forests and deserts: forests = 40%; grasslands = 27%; and deserts = 33%.
GRASSLANDS OF NORTH AMERICA

<table>
<thead>
<tr>
<th>Grassland Type</th>
<th>%</th>
<th>Hectares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tallgrass Prairie</td>
<td>19</td>
<td>57,351,100</td>
</tr>
<tr>
<td>Mixed-grass Prairie</td>
<td>19</td>
<td>56,617,400</td>
</tr>
<tr>
<td>Shortgrass Prairie</td>
<td>21</td>
<td>61,522,300</td>
</tr>
<tr>
<td>Coastal Prairie</td>
<td>01</td>
<td>3,800,000</td>
</tr>
<tr>
<td>California Grassland</td>
<td>03</td>
<td>9,200,000</td>
</tr>
<tr>
<td>Palouse Prairie</td>
<td>22</td>
<td>64,471,600</td>
</tr>
<tr>
<td>Fescue Prairie</td>
<td>08</td>
<td>25,500,000</td>
</tr>
<tr>
<td>Desert Grassland</td>
<td>07</td>
<td>20,756,500</td>
</tr>
<tr>
<td>Total</td>
<td>29</td>
<td>299,222,900</td>
</tr>
</tbody>
</table>

The Sandhills of Nebraska is a recognizably distinct component, characterized by:

- Redfieldia flexuosa  Blowout grass
- Stipa hymenoides    Indian rice grass
- Eragrostis trichoides Sand love grass
- Stipa comata        Porcupine needle grass
- Calamovilfa longifolia Prairie sandreed
- Schizachyrium scoparium Little bluestem
- Andropogon hallii    Sand bluestem
- Muhlenbergia pungens Sandhill muhly

TALL GRASS PRAIRIE

The Tall Grass Prairie, True Prairie, or Bluestem Prairie occurs at the eastern edge of the grassland formation, from southern Manitoba to south-central and eastern Texas, and eastward into Ohio. Characteristic grasses include:

- Andropogon gerardii  Big bluestem
- Sorghastrum nutans   Indian grass
- Panicum virgatum     Switch grass
- Schizachyrium scoparium Little bluestem
- Spartina pectinata   Prairie cord grass
- Sporobolus heterolepis Prairie dropseed
- Koeleria macrantha   June grass
- Bouteloua curtipendula Sideoats grama
- Bouteloua gracilis   Blue grama
- Bouteloua hirsuta    Hairy grama
- Stipa spartea        Porcupine needle grass

MIXED GRASS PRAIRIE

The Mixed Grass Prairie or Mixed Prairie is the largest grassland association. It occurs from Canada to south-central Texas; from western Nebraska to the Rocky Mountains. Rainfall (10-27") comes mainly in the spring and in the early summer. A summer drought is expected periodically. The characteristic grasses include:

- Elymus smithii       Western wheat grass
- Elymus dasystachys    Thickspike wheat grass
- Schizachyrium scoparium Little bluestem
- Stipa spartea        Porcupine needle grass
- Stipa comata         Needle-and-thread grass

DESSERT GRASSLAND

The Desert Grassland occurs in the American Southwest and in adjacent north-central Mexico. It is the hottest, driest of our grasslands, receiving 11-17" of precipitation each year. Snow is a factor at higher elevations. Characteristic low-elevation grasses include:

- Bouteloua eriopoda   Black grama
- Hilaria mutica       Tobosa
- Aristida divaricata  Poverty three-awn
- Aristida purpurea    Purple three-awn
- Muhlenbergia porteri Bush muhly
- Sporobolus cryptandrus Sand dropseed

At higher elevations:

- Hilaria belangeri    Curly mesquite
- Bouteloua gracilis   Blue grama
- Bouteloua hirsuta    Hairy grama
- Bouteloua eriopoda   Black grama
- Hilaria mutica       Tobosa
- Stipa neomexicana    New Mexico feather grass
- Bouteloua curtipendula Sideoats grama
CALIFORNIA PRAIRIE

The California Prairie or Pacific Prairie covers about 10 million hectares in California and Baja California. It occurs as open grassland and as an understory. It consists of two elements – one occurring along the North Coast at medium and higher elevations and the other in the Great Central Valley, southern Coast Range, and extending into Mexico.

Northern Component: pre-European settlement

Danthonia californica  California oat grass
Deschampsia cespitosa  Tufted hair grass
Festuca occidentalis  Western fescue
Festuca idahoensis  Idaho fescue
Festuca rubra  Red fescue
Calamagrostis nutkaensis  Pacific reed grass

Northern Component: post-European settlement

Festuca arundinacea  Tall fescue
Holcus lanatus  Velvet grass
Anthoxanthum occidentale  Sweet vernal grass
Lolium multiflorum  Italian rye grass
Arrhenatherum elatius  Tall oat grass
Dactylis glomerata  Orchard grass

Central Valley: pre-European settlement

Stipa pulchra  Purple needle grass
Stipa cernua  Nodding needle grass
Elymus glaucus  Blue wild rye
Poa scabrella  Pine bluegrass
Muhlenbergia rigens  Deer grass

Central Valley: post-European settlement

Avena fatua var. fatua  Wild oat
Avena barbata  Slaender oat
Bromus mollis  Soft cheat grass
Bromus diandrus  Ripgut grass
Bromus rubens  Foxtail brome
Hordeum murinum  Mouse barley
Hordeum pusillum  Little barley
Festuca myuros  Foxtail fescue
Festuca megarura  Foxtail fescue

Erodium cicutarium  Filaree
Erodium botrys  Filaree

FESCUE PRAIRIE

The Fescue Prairie is found on the northern and northwestern sides of the Mixed Grass Prairie, from central Saskatchewan into Alberta and southward into northern Montana. Its sole dominant is Festuca scabrella, which can account for 50% or more of the vegetative cover. It is richer in forbs than is the adjacent Mixed Grass Prairie. Characteristic grasses include:

Festuca scabrella  Rough fescue
Elymus subsecundus  Bearded wheat grass
Danthonia intermedia  Timber oat grass
Helictotrichon hookeri  Spike-oat
Stipa  Porcupine needle grass
Festuca idahoensis  Idaho fescue

COASTAL PRAIRIE

The Coastal Prairie occurs along the Gulf of Mexico, from southwestern Louisiana through Texas, into northeastern Mexico. It is a region of high humidity and rainfall (26-34”). The mild climate and long growing season favor the growth of subtropical grasses. There has also been an influx of taxa from the Short Grass Prairie. Characteristic grasses include:

Bothriochloa saccharoides  Silver blustem
Stipa leucotricha  Texas needle grass
Schizachyrium scoparium var. littorale  Seacoast bluestem
Andropogon gerardii  Big bluestem
Heteropogon contortus  Tanglehead
Sorghastrum nutans  Indian grass
Paspalum plicatulum  Brownseed paspalum
Spartina spartinae  Gulf cord grass

THE KÜCHLER CLASSIFICATION

A. W. Küchler (1964) drew a distinction between real vegetation, which comprised all of the types of vegetation present at the time observations were made and potential natural vegetation, which he defined as "the vegetation that would exist today if man were removed from the scene and if the resulting plant succession were telescoped into a single moment." He recognized 116 vegetation types in the conterminous United States (i. e., the lower 48 states). The following contain one or more grasses as dominants.


**Shinnery.** Dominants: Schizachyrium scoparium, Quercus mohriana. Other components: Acacia, Andropogon halii, Aristida, Artemisia, Bouteloua gracilis, Bouteloua hirsuta, Buchlœo dactyloides, Celtis, Cenchrus, Eriogonum, Juniperus, Prosopis, Prunus, Quercus, Rhus, Sorghastrum nutans, Sporobolus cryptandrus, Yucca. Occurrence: Panhandle of Texas and adjacent parts of New Mexico and Oklahoma.


Occurrence: Coastal plains of Texas and Louisiana.

**Southern Cordgrass Prairie.** Dominants: *Spartina alterniflora*. Other components: *Carex, Distichlis spicata, Juncus, Mariscus, Panicum hemitomon, Panicum repens, Phragmites australis, Sagittaria, Scirpus, Spartina cynosuroides, Spartina patens, Spartina spartinae, Typha, Zizaniopsis miliacea.* Occurrence: Southeastern Texas and southern Louisiana.

**Palmetto Prairie.** Dominants: *Aristida stricta, Serenoa repens*. Other components: *Andropogon, Aristida spiciformis, Axonopus compressus, Axonopus furcatus, Lyonia, Paspalum distichum, Sabal, Vaccinium.* Occurrence: Southeastern Texas and southern Louisiana.

**Oak Savanna.** Dominants: *Andropogon gerardii, Schiza-chyrium scoparium, Quercus macrocarpa*. Other components: *Amphicarpa bracteata, Calamovilfa longifolia, Carya, Comandra, Euphorbia, Fraxinus, Monarda, Panicum leibergii, Quercus, Rosa, Sorghastrum nutans, Sporobolus heterolepis, Stipa spartea.* Occurrence: Central Florida.

**Cedar Glades.** Dominants: *Celtis laevigata, Juniperus virginiana, Quercus stellata, Sporobolus neglectus, Sporobolus vaginiflorus, Ulmus alata*. Other components: *Andropogon gerardii, Arenaria, Bouteloua curtipendula, Bumelia, Carya, Celtis, Cercis, Cheilanthes, Croton, Forestiera, Leavenworthia, Palafoxia, Dalea, Pleurochae, Psonalea, Quercus, Rhus, Schizachyrium scoparium, Sedum, Symphoricarpos.* Occurrence: Tennessee, Alabama, Missouri, and Arkansas.

**Cross Timbers.** Dominants: *Schizachyrium scoparium, Quercus marilandica, Quercus stellata*. Other components: *Andropogon gerardii, Bouteloua curtipendula, Bouteloua hirsuta, Carya, Celtis, Elymus canadensis, Eragrostis spectabilis, Eragrostis trichodes, Panicum scribnerianum, Panicum virgatum, Sorghastrum nutans, Sporobolus asper, Stipa leucotricha, Ulmus.* Occurrence: Wisconsin, Minnesota, North Dakota.

**Mesquite-Buffalo Grass.** Dominants: *Buchloë dactyloides, Prosopis juliflora*. Other components: *Acacia, Aristida purpurea, Aristida roemeriana, Bouteloua gracilis, Bouteloua hirsuta, Bouteloua trifida, Cordalia, Juniperus, Quercus, Schedonnardus paniculatus, Yucca.* Occurrence: Texas to Kansas.

**Mesquite-Oak Savanna.** Dominants: *Schizachyrium scoparium, Prosopis juliflora, Quercus*. Other components: *Aloysia, Andropogon barbinodis, Aristida intermedia, Aristida purpurea, Bouteloua curtipendula, Bouteloua hirsuta, Bouteloua rigidiseta, Brayodendron, Buchloë dactyloides, Juniperus, Quercus, Ulmus.* Occurrence: Central Texas.

**Fayette Prairie.** Dominants: *Schizachyrium scoparium, Buchloë dactyloides*. Other components: *Aristida purpurea, Aristida roemeriana, Bothriochloa saccharoides, Bothriochloa tenerium, Paspalum dilatum, Paspalum plicatum, Stipa leucotricha.* Occurrence: Southern Texas.

**Live Oak-Sea Oats.** Dominants: *Quercus virginiana var. maritima, Uniola paniculata*. Other components: *Baccharis, Cenchrus tribuloides, Croton, Ilex, Iva, Juncus, Myrica, Opuntia, Panicum amarum, Sabal, Salsola, Serenoa, Spartina alterniflora, Spartina patens, Yucca.* Occurrence: Eastern and Gulf coasts from North Carolina to Alabama.

**Cypress Savanna.** Dominants: *Aristida affinis, Aristida patula, Taxodium distichum*. Other components: *Acer, Annona, Blechnum, Cyperus, Hypericum, Ilex, Leersia hexandra, Magnolia, Mariscus, Myrica, Persea, Rhychnospora, Salix, Saururus, Spartina bakeri, Stillingia aquatica, Taxodium, Tillandsia, Utricularia.* Occurrence: Southwestern Florida.

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**Mesquite-Oak Savanna.** Dominants: *Schizachyrium scoparium, Juniperus ashei, Quercus virginiana*. Other components: *Baccharis, Cenchrus tribuloides, Croton, Ilex, Iva, Juncus, Myrica, Opuntia, Panicum amarum, Sabal, Salsola, Serenoa, Spartina alterniflora, Spartina patens, Yucca.* Occurrence: Eastern and Gulf coasts from North Carolina to Alabama.

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**NATIONAL GRASSLANDS**

**California:**
- Butte Valley National Grassland 18,000 acres Macdoel, CA

**Colorado:**
- Comanche National Grassland 435,028 acres Springfield, CO
- Pawnee National Grassland 193,060 acres Greeley, CO

**Idaho:**
- Curlew National Grassland 47,749 acres Malad, ID

**Kansas:**
- Cimarron National Grassland 108,175 acres Elkhart, KS

**Nebraska:**
- Oglala National Grassland 94,316 acres Chadron, NE

**New Mexico:**
- Kiowa/Rita Blanca National Grasslands 136,417 acres Clayton, NM

**North Dakota:**
- Little Missouri National Grassland 525,000 acres
Grasses cover about 20% of the continent. Two very different kinds of grasslands are present. The high-grass savanna is characterized by tall grasses and low trees. It occurs next to the tropical rain forests centered in the Congo Basin. Common grasses include Andropogon schimperi, Hyparrhenia rufa, Pennisetum benthamii, Imperata cylindrica, and Pennisetum purpurascens. Sorghum, millets, and rice are also widely cultivated in the region. The tall grass savanna is characterized by tall grasses and various species of Acacia, a shrubby legume. The grasses are about 1-2 m tall; the trees are scattered. It occurs in the eastern and southern parts of the continent. Common grasses include various species of Andropogon, Hyparrhenia, Themeda, and on the drier sites Aristida, Chloris, Melinis, and Digitaria are found.

**GRASSLANDS OF SOUTH AMERICA**

Grasslands cover about 2 million sq. mi. (or about one-third) of the continent. There are three well-defined and separate regions. The llano and savanna of the Orinoco Basin occur mostly in Venezuela and in the Guianas. The common grasses include Andropogon condensatus, Cymbopogon rufus, Sporobolus junceus, Trachypogon plumosus, Panicum maximum, and Aristida spp. The campo and savanna of upland Brazil is a region of extreme wet and dry seasons. The grasses are typically tall and coarse. Common species include Melinis minutiflora, Panicum maximum, and Hyparrhenia spp. The pampa and prairies of Uruguay and Argentina are broad, level plains and plateaus. The regions may be subhumid, semiarid, or arid. The grass flora is rich. Various species of Stipa, Poa, Sporobolus, Bromus, Paspalum, Bothriochloa, Panicum, Aristida, Hordeum, Melica, Eragrostis, Briza, Axonopus, and Cortaderia are typical.

**SELECTED REFERENCES**


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Humphrey, R. R. 1953. The desert grassland, past and present. J. Range Mgt. 6: 159-164.


6.08 - TOXIC GRASSES

Because the grass family is the source of so many important food plants, it may come as a surprise to learn that it is also the source of a number of poisonous plants. The victims of grass toxicity are wild and domesticated animals, humans, and even other plants. Symptoms range from those that are mildly irritating to death. Mechanisms of poisoning include:

- plant parts that cause mechanical injury;
- absorption of toxins from the soils where grasses are growing;
- manufacture of one or more toxins by the grass itself;
- acting as a host to a fungus that makes the toxins.

**MECHANICALLY INJURIOUS**

Some grasses are toxic only in the broadest sense because they are armed with stout awns that can cause mechanical injury. The sites of penetration, often around the eyes, snout, or the soft parts of the mouth cavity, can become infected and then further complications may occur. Such grasses do not actually produce toxic substances.

<table>
<thead>
<tr>
<th>Scientific (Common) Name</th>
<th>Cause</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aristida spp. (three-awns)</td>
<td>awns</td>
</tr>
<tr>
<td>Avena fatua (wild oat)</td>
<td>awns</td>
</tr>
<tr>
<td>Bromus spp. (bromes)</td>
<td>awns</td>
</tr>
<tr>
<td>Cenchrus spp. (sand burs)</td>
<td>spines</td>
</tr>
<tr>
<td>Hordeum spp. (barleys)</td>
<td>awns</td>
</tr>
<tr>
<td>Leersia spp. (cut grasses)</td>
<td>leaf margins</td>
</tr>
<tr>
<td>Setaria spp. (foxtails, bristle grasses)</td>
<td>awns</td>
</tr>
<tr>
<td>Spartina spp. (cord grasses)</td>
<td>leaf margins</td>
</tr>
<tr>
<td>Stipa spp. (needle grasses)</td>
<td>awns</td>
</tr>
</tbody>
</table>

**NITRATE/NITRITE INTOXICATION**

Others species, especially cereal crops and agricultural weeds are toxic not because they contain a poison, but because they absorb it from fertilizer-rich soils and then sequester in the plant body.
<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avena sativa</td>
<td>Oat</td>
</tr>
<tr>
<td>Cynodon spp.</td>
<td>Bermuda grasses</td>
</tr>
<tr>
<td>Echinochloa frumentacea</td>
<td>Sanwa millet</td>
</tr>
<tr>
<td>Hordeum jubatum</td>
<td>Foxtail barley</td>
</tr>
<tr>
<td>Hordeum vulgare</td>
<td>Barley</td>
</tr>
<tr>
<td>Lolium spp.</td>
<td>Rye grasses</td>
</tr>
<tr>
<td>Pennisetum glaucum</td>
<td>Pearl millet</td>
</tr>
<tr>
<td>Sorghum spp.</td>
<td>Sorghums</td>
</tr>
<tr>
<td>Triticum aestivum</td>
<td>Bread wheat</td>
</tr>
<tr>
<td>Zea mays</td>
<td>Maize, corn</td>
</tr>
<tr>
<td>Leersia hexandra</td>
<td>Clubhead cutgrass</td>
</tr>
<tr>
<td>Leptochloa dubia</td>
<td>Green sprangletop</td>
</tr>
<tr>
<td>Lollum perenne</td>
<td>Perennial rye grass</td>
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<tr>
<td>Melica altissima</td>
<td>Onion grass</td>
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<tr>
<td>Molinia caerulea</td>
<td>Purple moor grass</td>
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<tr>
<td>Oryza sativa</td>
<td>Rice</td>
</tr>
<tr>
<td>Panicum maximum</td>
<td>Guinea grass</td>
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<tr>
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<td>Para grass</td>
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<tr>
<td>Poa pratensis</td>
<td>Kentucky bluegrass</td>
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<tr>
<td>Secale cereale</td>
<td>Rye</td>
</tr>
<tr>
<td>Sorghastrum nutans</td>
<td>Indian grass</td>
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<tr>
<td>Sorghum x alimum</td>
<td>Columbus grass</td>
</tr>
<tr>
<td>Sorghum bicolor</td>
<td>Sorghum, Sudan grass</td>
</tr>
<tr>
<td>Sorghum halepense</td>
<td>Johnson grass</td>
</tr>
<tr>
<td>Stipa robusta</td>
<td>Sleepy grass</td>
</tr>
<tr>
<td>Tridens flavus</td>
<td>Purpletop</td>
</tr>
<tr>
<td>Triticum aestivum</td>
<td>Bread wheat</td>
</tr>
<tr>
<td>Zea mays</td>
<td>Maize, corn</td>
</tr>
</tbody>
</table>

**CYANOCYTIC GLYCOSIDES***

- General Features:
  - Found widely in plant kingdom
  - Common in roses, grasses, legumes, spurges
  - HCN glycoside (sugar + toxic component)
  - Activated by chewing, crushing, freezing, etc.
  - Pure HCN very toxic
  - Readily absorbed on skin; dangerous when inhaled

- Symptoms:
  - Acts at cellular level
  - Blocks release of oxygen from red blood cells
  - Instantaneous collapse (large doses)
  - Weakness, giddiness, headache
  - Nausea & vomiting
  - Coma
  - Death from cellular asphyxiation

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agrostis stolonifera</td>
<td>Creeping bent grass</td>
</tr>
<tr>
<td>Andropogon spp.</td>
<td>Bluestems</td>
</tr>
<tr>
<td>Avena sativa</td>
<td>Oat</td>
</tr>
<tr>
<td>Bambusa spp.</td>
<td>Bamboo</td>
</tr>
<tr>
<td>Bothriochloa spp.</td>
<td>Old World bluestems</td>
</tr>
<tr>
<td>Bouteloua gracilis</td>
<td>Blue grama</td>
</tr>
<tr>
<td>Bouteloua hirsuta</td>
<td>Hairy grama</td>
</tr>
<tr>
<td>Briza spp.</td>
<td>Quaking grasses</td>
</tr>
<tr>
<td>Catabrosa aquatica</td>
<td>Brook grass</td>
</tr>
<tr>
<td>Chloris truncata</td>
<td>Australian finger grass</td>
</tr>
<tr>
<td>Cortaderia spp.</td>
<td>Pampas grasses</td>
</tr>
<tr>
<td>Cymbopogon spp.</td>
<td>Lemon grasses</td>
</tr>
<tr>
<td>Cynodon spp.</td>
<td>Bermuda grass, star grasses</td>
</tr>
<tr>
<td>Dactylctenium aegyptium</td>
<td>Egyptian crowfoot</td>
</tr>
<tr>
<td>Danthonia semiannularis</td>
<td>Oat grass</td>
</tr>
<tr>
<td>Eleusine coracana</td>
<td>African millet</td>
</tr>
<tr>
<td>Eleusine indica</td>
<td>Goose grass</td>
</tr>
<tr>
<td>Elymus spp.</td>
<td>Wild ryes</td>
</tr>
<tr>
<td>Festuca spp.</td>
<td>Fescues</td>
</tr>
<tr>
<td>Glyceria canadensis</td>
<td>Canadian manna grass</td>
</tr>
<tr>
<td>Glyceria grandis</td>
<td>American manna grass</td>
</tr>
<tr>
<td>Glyceria septentrionalis</td>
<td>Eastern manna grass</td>
</tr>
<tr>
<td>Holcus lanatus</td>
<td>Velvet grass</td>
</tr>
<tr>
<td>Hordeum vulgare</td>
<td>Barley</td>
</tr>
<tr>
<td>Lagurus ovatus</td>
<td>Hare’s-tail grass</td>
</tr>
<tr>
<td>Larnarckia aurea</td>
<td>Goldentop</td>
</tr>
<tr>
<td>Leersia hexandra</td>
<td>Clubhead cutgrass</td>
</tr>
<tr>
<td>Leptochloa dubia</td>
<td>Green sprangletop</td>
</tr>
<tr>
<td>Lollum perenne</td>
<td>Perennial rye grass</td>
</tr>
<tr>
<td>Melica altissima</td>
<td>Onion grass</td>
</tr>
<tr>
<td>Molinia caerulea</td>
<td>Purple moor grass</td>
</tr>
<tr>
<td>Oryza sativa</td>
<td>Rice</td>
</tr>
<tr>
<td>Panicum maximum</td>
<td>Guinea grass</td>
</tr>
<tr>
<td>Panicum muticum</td>
<td>Para grass</td>
</tr>
<tr>
<td>Poa pratensis</td>
<td>Kentucky bluegrass</td>
</tr>
<tr>
<td>Secale cereale</td>
<td>Rye</td>
</tr>
<tr>
<td>Sorghastrum nutans</td>
<td>Indian grass</td>
</tr>
<tr>
<td>Sorghum x alimum</td>
<td>Columbus grass</td>
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<tr>
<td>Sorghum bicolor</td>
<td>Sorghum, Sudan grass</td>
</tr>
<tr>
<td>Sorghum halepense</td>
<td>Johnson grass</td>
</tr>
<tr>
<td>Stipa robusta</td>
<td>Sleepy grass</td>
</tr>
<tr>
<td>Tridens flavus</td>
<td>Purpletop</td>
</tr>
<tr>
<td>Triticum aestivum</td>
<td>Bread wheat</td>
</tr>
<tr>
<td>Zea mays</td>
<td>Maize, corn</td>
</tr>
</tbody>
</table>

**PHOTOSENSITIZATION***

Several grasses are implicated in this syndrome. Sensitive animals are poisoned when they eat grasses that contain certain pigments that react with sunlight to form toxins that can cause damage to their skin and underlying tissues. Probably the best known example of this phenomenon is found in our local weedy Klamath weed or St. John’s wort (Hypericum perforatum), a member of Guttiferae.

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<thead>
<tr>
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<tbody>
<tr>
<td>Avena sativa</td>
<td>Oat</td>
</tr>
<tr>
<td>Cenchrus incertus</td>
<td>Southern sandbur</td>
</tr>
<tr>
<td>Echinochloa crusgalli</td>
<td>Barnyard grass</td>
</tr>
<tr>
<td>Eriochloa contracta</td>
<td>Prairie cup grass</td>
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<tr>
<td>Hordeum murinum</td>
<td>Wall barley</td>
</tr>
<tr>
<td>Hordeum vulgare</td>
<td>Barley</td>
</tr>
<tr>
<td>Secale cereale</td>
<td>Annual rye</td>
</tr>
<tr>
<td>Setaria italica</td>
<td>Foxtail millet</td>
</tr>
<tr>
<td>Sorghum spp.</td>
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</tr>
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**GRASS TETANY***

Also known as grass staggers, this syndrome appears to be associated with ionic imbalances in the blood serum after eating large amounts of lush growth. Low magnesium levels are typical. Animals suffering from grass tetany first show signs of excitement, poor coordination, and anorexia, followed by cardiovascular involvement, convulsions, coma, and death.

<table>
<thead>
<tr>
<th>Scientific Name</th>
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<tbody>
<tr>
<td>Agropyron spp.</td>
<td>Wheat grasses</td>
</tr>
<tr>
<td>Avena sativa</td>
<td>Oat</td>
</tr>
<tr>
<td>Bromus spp.</td>
<td>Bermes</td>
</tr>
<tr>
<td>Dactylis glomerata</td>
<td>Orchard grass</td>
</tr>
<tr>
<td>Elymus spp.</td>
<td>Wild ryes</td>
</tr>
<tr>
<td>Festuca spp.</td>
<td>Fescues</td>
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<td>Hordeum vulgare</td>
<td>Barleys</td>
</tr>
<tr>
<td>Lolium perenne</td>
<td>Perennial rye grass</td>
</tr>
<tr>
<td>Phalaris spp.</td>
<td>Canary grasses</td>
</tr>
<tr>
<td>Phleum pratense</td>
<td>Timothy</td>
</tr>
<tr>
<td>Secale cereale</td>
<td>Annual rye</td>
</tr>
</tbody>
</table>
**ERGOTISM***

✓ **Chronic or Gangrenous Ergotism**
  - Small amounts over long period of time
  - Constriction of blood vessels
  - Death of tissues
  - Loss of extremities

✓ **Acute or Convulsive Ergotism**
  - Larger amounts quickly consumed
  - Central nervous system
  - Crawling sensation on skin
  - Tingling of skin; fingers
  - Tinnitus aurium
  - Headache
  - Vertigo
  - Vomiting & diarrhea
  - Hallucinations
  - Painful muscular contractions
  - Epileptiform seizures

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<td>Manna grasses</td>
</tr>
<tr>
<td>Holcus spp.</td>
<td>Velvet grasses</td>
</tr>
<tr>
<td>Hilaria spp.</td>
<td>Tobosas, galletas</td>
</tr>
<tr>
<td>Hystrix spp.</td>
<td>Bottlebrush grasses</td>
</tr>
<tr>
<td>Lolium spp.</td>
<td>Rye grasses</td>
</tr>
<tr>
<td>Paspalum spp.</td>
<td>Paspalum, water grasses</td>
</tr>
<tr>
<td>Poa spp.</td>
<td>Bluegrasses</td>
</tr>
<tr>
<td>Sphenopholis spp.</td>
<td>Wedgescales</td>
</tr>
</tbody>
</table>

Interestingly, the best known cases of poisoning from ingesting grasses are caused by parasitic fungi that live on the plants. It is the fungus that makes the toxin, not the grass. The so-called endophytic fungi are the subject of much recent research, particularly those that infect fescue grasses. The following grasses have been found to serve as hosts to such fungi.

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**ALLERGIC REACTIONS**


abaxial: the side of a structure facing away from an axis

achene: a dry, single-seeded indehiscent fruit whose seed coat and fruit wall separate from one another, as in the sedges

acicular: needle-shaped, as in the leaves of Monanthochloë

acuminate: gradually tapering to an extended point

acute: sharp-pointed

adaxial: the side of a structure facing toward an axis

adnate: the fusion of unlike parts

adventitious: originating from mature tissues rather than meristematic ones, as in aerial roots that arise from a location other than the primary root system or aerial bulbs

adventitious embryony: a type of apomixis (q. v.) in which the embryo arises in the nucellus or in the integument, rather than within the embryo sac

adventive: a plant that is introduced accidentally

aerial: growing above ground, rather than in the soil

agamospermy: the production of seed without the prior fusion of gametes

aleurone: the outermost protein-rich layer(s) of endosperm

allopolyploid: a type of polyploid that contains genomes that are different from one another, often from two or more species

amphiploid: an allopolyploid that behaves as though it were a diploid

androecium: the male portion of a flower, consisting of one or more stamens

andromonoecious: the condition of having both bisexual and male flowers in the same inflorescence, as in most panicoïd spikelets

anemophily: wind-mediated pollination

aneuploid: the condition of having a chromosome number that is not an exact multiple of the base number for that organism

annual: living for a single growing season

anther: the sac-like, pollen-producing part of a stamen

anthesis: the phase during which a flower is fully opened and pollination occurs

anthoecium: the collective term for the lemma and palea

antrorse: directed upwards, as in barbs on an awn

apex: the upper or distal end of a structure; plural, apices

aphylloptic: the condition of having bladeless lower leaves, as in some sedges

apiculate: an apex that bears a short, typically flexible point

apomixis: a type of reproduction that involves the organs and processes typically associated with sexual reproduction, but which does not involve the actual fusion of egg and sperm nuclei; used more loosely as a synonym for asexual reproduction

apospor: a type of apomixis in which the embryo sac is derived from a cell of the inner integument

appressed: lying against a surface or, in the case of inflorescence branches, against a central or principal axis

arista: an awn or beard

aristate: an apex that tapers to a very narrow, elongate, bristle-like point; awned

arm cell: a leaf mesophyll cell type, characteristic of bambusoid grasses, in which the internal partitions or septae are incomplete

ascending: growing upward, obliquely at first and then erect, as in certain grass stems

asexual: any form of reproduction that does not involve the union of egg and sperm

attenuate: gradually narrowed to a slender point

auricles: the paired, ear-shaped appendages at the apex of the sheath in some grasses

autopolyploid: an organism with three or more chromosome sets that are ± identical to one another; often the result of doubling of chromosomes or through unreduced gametes

awl-shaped: the leaf or bract shape characterized by a gradual taper from the base to a sharp point

awn: a substantial hair or bristle that arises from the apex or back of glumes or lemmas [very rarely paleas]; awned, having awns

axile: the interior angle formed by a stem and the petiole or pedicel that it bears

axillary inflorescence: an inflorescence that arises from a lateral position on a culm, as opposed to one that is terminal
axis: the central stem of an inflorescence

balanced: having spikelets ± equally inserted on both sides of a central axis

basifixed: said of an anther that is attached to a filament by its base, as opposed to being attached at its midpoint

beak: a prominent sterile elongation of a caryopsis

beard: a line or tuft of hairs

beautiful: of or pertaining to grasses, especially native ones

berry: a multi-seeded, indehiscent fruit in which the fruit wall is fleshy throughout; common examples include the tomato and grape; in the grass family, berries are found in certain bamboos

bifid: two-cleft or two-lobed, as in the apex of a lemma or glume

bisexual: a flower, floret, or spikelet that bears both male and female reproductive structures; the term perfect is also used for this condition

blade: the flattened, expanded portion of a leaf

body: the portion of a glume, lemma, or palea, exclusive of awns or teeth

B. P.: Before Present

bract: a reduced leaf; glumes, lemmas, and paleas are all considered bracts

bractlet: a small bract

bran: the outer layers of a cereal grain that are removed during the grinding process

bristle: a short, stiff hair; a sterile branch

bulb: an underground plant structure consisting of a series of overlapping leaf bases attached to a much-reduced stem axis; many bulbs are actually corms (q. v.)

bulbils: small axillary bulbs that replace more typical florets or spikelets, as in Poa bulbosa

bulblet: a small bulb

bulliform cells: the comparatively large, thin-walled, colorless epidermal cells of the intercostal zone of the grass leaf blade

bundle sheath: the layer of tissue that surrounds the vascular bundle; not all grasses have bundle sheaths

- C -

c, grasses: those grasses, often found in the cooler, temperate regions, whose photosynthetic pathway has a 3-carbon compound (3-phosphoglycerate) as its first detectable sugar precursor

c, grasses: those grasses, often subtropical and tropical, whose photosynthetic pathway has a 4-
complex: a group of closely related, difficult to differentiate, taxa, as in the *Festuca microstachys* complex

compound raceme: an inflorescence in which the peduncle bears two or more branches, each bearing a raceme of spikelets

compound rame: an inflorescence type in which the peduncle bears two or more branches, each bearing a rame of spikelets

compound spike: an inflorescence type in which the peduncle bears two or more branches, each bearing a spike of spikelets

compressed: flattened, as if pressure had been applied to a structure from the back or sides

continuous: not breaking apart; remaining intact, as in the central axis of an inflorescence at maturity

contracted: narrowed, as opposed to open or spreading

convolute: rolled longitudinally, with one edge completely within the other, as in a rolled up leaf blade

cordate: heart-shaped, as in the shape of certain leaf bases

coriaceous: leathery, as in the texture of certain lemmas or glumes

corm: a dense, vertical, underground stem surrounded by dry, papery leaf bases; often loosely called a bulb

corrugated: wrinkled

cosmopolitan: common to all or to most of the world

costal: the region on a grass leaf that is above the strands of vascular tissue (nerves)
culm: the stem of a grass plant

cultivar: a cultivated variety; a cultivated strain of a crop plant or of an ornamental
cuneate: wedge-shaped
cv.: cultivar

- D -
deciduous: falling from a plant at the end of a season
decumbent: said of stems that lie on the ground, but whose ends are upturned
denticulate: minutely toothed
depauperate: not fully developed, stunted; often the result of growing on an impoverished site
diaspore: from the Greek word for dispersion, a unit of plant dispersal; examples include caryopses, grains with husks remaining attached, groups of spikelets, etc.
diffuse: widely or loosely spreading, as in inflorescence branches
digitate: having parts that radiate from a central point, as do the fingers of a hand
dimorphic: having two different shapes, as in the glumes of *Koeleria*
dioecious: a species in which staminate and pistillate flowers or spikelets occur on separate plants, as in buffalo grass
diploid: the chromosome complement found in vegetative cells of the plant body; typically expressed in terms of "2n," as in 2n = 14
disarticulation: the separating or disjoining of spikelet parts from one another or of portions of an inflorescence axis from one another
distal: at the end opposite the point of attachment, as opposed to proximal (q. v.)
distichous: attached in two vertical rows, as in leaves on a stem or spikelet bracts on a rachilla
divaricate: spread very far apart, as in inflorescence branches
divergent: spread apart from one another, as in divaricate, but less so
dorsal: relating to or attached to the back of an organ, the side that is turned away from the axis
dorsally compressed: flattened, as if pressure had been brought to bear on the back of bract

e -
elliptical: in the form of a flattened circle
emarginate: a leaf or bract with a shallow notch at its apex
endemic: confined to a particular region, applied especially when the area is relatively small
endosperm: the nutritive tissue within the seed that originates from the fusion of polar nuclei and sperm nucleus
entire: said of a margin of a leaf or bract that lacks lobes or teeth
entomophily: insect-mediated pollination
epiblast: the small, nonvasculated flap of tissue that occurs on the side opposite the scutellum in some, but not all, grass embryos
erose: said of a margin that appears to have been gnawed or worn away
euploid: having a chromosome number that is an exact multiple of the base chromosome number
exserted: protruding beyond or out of another structure, as in an inflorescence from a sheath
extirpate: to eliminate or destroy; literally, to pull up by the roots
extravaginal branching: a type of branching in which the shoot breaks through the leaf sheath
fascicle: a tight cluster or clump, as in leaves, axillary stems, or spikelets

fertile lemma: a lemma that encloses a flower

filament: the delicate stalk that supports an anther

filiform: thread-like

fimbriate: fringed, as in a bract margin

flabellate: fan-shaped

floret: a subunit of a spikelet, consisting of a lemma, palea, and flower; sometimes incorrectly defined as only the flower itself

forb: any herbaceous plant that is not a grass or does not appear grass-like

fusoid cells: the large, colorless mesophyll cells found in the leaves of most bambusoid grasses

gamete: a sex cell; the egg or sperm

gametophytic apomixis: a kind of reproduction in which a diploid embryo sac is produced because reduction division did not occur during the meiotic cycle

geniculate: said of structure that is bent sharply, as in certain grass stems and awns

genome: all of the genetic information found in a single complete set of chromosomes in an organism

genus: a group of related species; the first component of a scientific name

gibbous: having a pouch-like enlargement on one side of a structure, as at the base of a glume

glabrous: without hairs

gland: a secretory structure; used more broadly for any warty protuberance; glandular, having or bearing glands

glaucous: having a blue-gray or sea-green color; also used for a whitish waxy covering that can be easily rubbed off

globose: almost spherical

glume: a sterile bract at the base of a spikelet; most grasses have two such structures, some have one, a few have none

glutinous: covered with a sticky exudate

grain: the fruit of the grass family; see caryopsis

graminoid: grass-like

gynoecium: the female portion of a flower, consisting of the seed-producing components (carpels)

habit: the general appearance of a plant

haploid: the chromosome complement found in the nuclei of gametes; often expressed by the letter n, as in n = 7

herb: an annual, biennial, or perennial plant whose stems die back to the ground at the end of the growing season because they lack the firmness of sufficient secondary growth

herbaceous: having the features of an herb

hirsute: having coarse, ± erect hairs

hispid: having long, rigid, bristly hairs; hispidulous, minutely hispid

hulls: the bracts of the grass spikelet, especially the lemma and palea

hyaline: having a colorless, thin, translucent or transparent texture

hybrid: a plant or animal that is the offspring of a cross between two or more strains, breeds, varieties, species, or genera; hybrids occur spontaneously in nature and they are created in the garden and laboratory

hybridization: the natural or artificial methods by which hybrids are created

hygroscopic: absorbing or attracting water; water sensitive, as in the grass lodicules

imbricate: overlapping one another, as in bracts of the spikelet

included: occurring within, as opposed to protruding from

indigenous: native to a region

indurate: hard, as in texture

inflorescence: the flowering portion of a grass plant; the arrangement of spikelets on a culm

innovation: a basal, typically vigorous offshoot

inserted: joined to or placed on, as in leaves on a stem or bracts on the spikelet axis

intercostal: the region between the nerves or veins of vascular tissue on a leaf or bract

introduced: purposefully brought into a region, as in the case of a crop plant or an ornamental

involucre: an organized set of bracts or of branchlets that surrounds or forms a series or set beneath a spikelet, group of spikelets, or floret
involute: with both edges rolled longitudinally inward toward the midpoint of a leaf or bract

- J -

joint: the node of a grass stem; a point where articulation or disarticulation occurs

- K -

keel: a prominent ridge or rib, as seen in some glumes, lemmas, or paleas

krankz syndrome: the set of anatomical and physiological traits that are found in those plants that have the C\textsubscript{4} photosynthetic pathway

- L -

lanceolate: a leaf blade or bract that is narrow and tapers on both ends and that is widest above the middle; not to be confused with Lancelot, the most famous of King Arthur's knights

laterally compressed: flattened, as if pressure had been brought to bear on the sides of a bract, as opposed to the back (dorsally compressed)

lemma: one of the two bracts enclosing the grass flower, the other being the palea; the lemma is typically the larger bract

lenticular: lens-shaped, as in the appearance of certain seeds or fruits

leptomorph rhizome: the type of slender rhizome found in certain bamboos, in which each node as a bud and a whorl of roots

lignified: woody

ligule: the membranous flap or series of hairs at the junction of the sheath and blade of the grass leaf

linear: several to many times longer than wide, as in the typical blade of a grass leaf

lodicule: the reduced perianth of the grass flower; these tiny, mitten-shaped structures are all that remains of the calyx

- M -

macrohair: any of the larger, easily seen surface hairs on a plant structure

malt: germinated cereal grain, often barley, used as an enzyme source in brewing and distilling

membranous: soft, thin, and pliable, as in the texture of a glume or lemma

meristem: the region of actively dividing cells of the stem or root apex; the meristematic region of the grass leaf occurs at its base, thereby permitting the plants to survive grazing, fires, and lawn mowers

mesocotyl: that portion of the grass embryo axis that occurs between the node where the scutellum and the coleoptile are attached

metabolically challenged: dead

microhair: any of the more or less microscopic hairs that occur on the surface of plant parts; in the grasses, they are of diagnostic significance

midrib: the central rib of a leaf or bract

minute: small, as in the size of your vocabulary if you had to use the glossary for this term

monoecious: said of a species in which the staminate and pistillate flowers or spikelets occur on the same plant, as in maize or Job's tears

monotypic genus: a genus of only one species

mucro: a short, sharp point or extension, as seen at the tip of lemma or glume; mucronate: bearing a mucro

muricate: a surface characterized by short, hard, tubercular outgrowths

- N -

n: the chromosome number found in the nuclei of sex cells; in diploid organisms \(n\) equals the haploid chromosome number

native: originating naturally in a particular region; occurring in an area before the arrival of humans, especially European explorers, traders, etc.

naturalized: not native to a particular area, but now well established and maintaining itself without our assistance

nerve: a vein or strand of vascular tissue, appearing as ridges on the surface of glumes, lemmas, or paleas

neuter: lacking reproductive structures; sterile

node: the point or region on a stem where a leaf or bract is attached

nut: a dry, hard, indehiscent, 1-seeded fruit

- O -

oblique: slanting or unequal-sided

oblong: much longer than broad, with the sides \(\pm\) parallel, as in the shape of certain leaf blades

obovate: of the shape of an inverted egg

obtuse: blunt in form; also dull in perception or intellect, as in the people who find grasses ugly and boring

oides: a suffix meaning resembling

open sheath: a sheath in which the two edges touch one another or overlap, but are not fused to form a collar or cylinder

ovary: the seed-bearing portion of a flower

- P -

pachymorph rhizome: the short, thick type of rhizome found in some bamboos, in which lateral buds typically produce only additional rhizomes

palea: one of two bracts enclosing the grass flower, the other being the lemma; typically the smaller and more delicate of the two
pampas: the vast open grasslands of South America, especially those in Argentina and Uruguay, dominated by taller bunch grasses in the east and by shorter grasses and shrubs in the drier southern and western portions

panicle: an elongate or rounded, much-branched inflorescence in which the spikelets are attached on the outermost branchlets

papillate: bearing small pimple- or nipple-like protuber-ances; also papillose

parallel: extending in the same direction and equidistant, as in the veins of most grass blades

parthenogenesis: meaning "virgin birth," a kind of apomixis in which the embryo develops from an egg cell that was not fertilized

pearl: to remove the outer layer(s) of a grain by exposing them to abrasive surfaces that grind away the tissues

pectinate: having units, such as spikelets, closely inserted next to one another, as in the teeth of a comb

pedicel: the stalk that supports a spikelet; see also peduncle

pedicellate: borne on a stalk (pedicel)

peduncle: the stalk that supports an inflorescence of spikelets; see also pedicel

pendent: hanging down

perennial: living for several to many years, often blooming and dying back at the end of each growing season; see also annual

perfect: a flower, floret, or spikelet that bears both male and female reproductive structures; the term bisexual is also used for this condition

pericarp: the fruit wall

perigynium: the membranous sac or sheath that surrounds the gynoecium or achene in some sedges

persistent: not breaking apart, as in an inflorescence axis or rachilla that remains intact at maturity

petiole: the stalk that supports a leaf blade

plano-convex: a structure that is flat on one side and rounded on the other, as in the fertile floret of certain panicoid grasses

Pohlstoffe: a distilled water, methanol, detergent (Aerosol OT) mixture used to soften dried plant specimens to facilitate their being examined; named after the late R. W. Pohl, the eminent and eccentric American agrostologist

pilose: covered with soft distinct hairs

pistillate: a flower, floret, spikelet, or plant that bears only female reproductive structures

pitted: having small cavities or depressions; also referred to as punctate

dicate: folded into pleats, typically lengthwise

dumose: feather-like, as in the awn of certain needle-grasses with prominent hairs

polygamous: a plant that bears both bisexual and unisexual flowers or spikelets

polyploid: an organism whose nuclei contain three or more sets of chromosomes

p. p.: the abbreviation of the Latin phrase pro parte, meaning "in part;" often used to mean some, but not all species in a genus, as in Panicum p. p.

prairie: the extensive level or somewhat undulating grasslands of central North America, characterized by rich soils and tall, sod-forming grasses

prophylum: the first leaf of a lateral branch; also spelled prophyll

proliferated: the term applied to a spikelet or an inflorescence when some portion has been modified into bulblets or other vegetative structures

prop roots: the aerial roots at the base of a maize plant that provide mechanical support for the stem

prostrate: lying flat on the ground

pseudogamy: a kind of apomixis in which the embryo develops without the egg cell being fertilized, but which requires sperm nuclei to fertilize the polar nuclei for the embryo and the endosperm to develop

pseudospikelet: literally a "false spikelet," it is the structure found in some bamboos in which a single true spikelet is subtended by several bracts

puberulent: minutely pubescent; downy, the hairs soft, straight, and erect

pubescent: said of any plant structure that is hairy, especially if the hairs are short and soft

pulvinus: the swollen or enlarged base of a leaf sheath or of an inflorescence branch in some grasses; pulvini are associated with the movement of these structures

- Q -

q. v.: the abbreviation of a Latin phrase meaning "which see," which is the author's way of telling you that the word or topic is explained elsewhere in the text

- R -

raceme: an elongate arrangement of stalked spikelets attached along an unbranched central axis

rachilla: the unbranched central axis of a spikelet; not the central axis of an inflorescence of spikelets; rachilla is the English spelling

rachilla extension: the portion of a rachilla that extends beyond the insertion of the uppermost floret; often appearing as a bristle

rachis: the unbranched central axis of a spike, raceme, or rame; the primary axis of a panicle
rame: an elongate arrangement of stalked and unstalked spikelets borne in repeating pairs or trios along an unbranched axis; the inflorescence type characteristic of the bluestem grasses and their relatives

rank: a vertical row, as seen when looking down on a plant; often expressed in terms of 2-ranked, 3-ranked, etc., which would indicate the number of rows

reflexed: turned or bent abruptly downward or backward

reptent: creeping or sprawling plants or stems, often rooting at the nodes; also referred to as trailing; when the accent is placed on the other syllable, you feel sorry or contrite about a past action

retrorse: directed backward or downward, as in barbs on a bristle

rhizomatous: rhizome-bearing

rhizome: an underground, horizontal stem that bears reduced, scaly leaves

rosette: a dense, circular cluster of basal leaves

rudiment: a small, very poorly developed floret

rugose: wrinkled, as in the surface of a bract

runner: a stolon (q. v.), especially a slender one

savanna(h): a type of subtropical or tropical grassland characterized by coarse grasses and scattered trees

scabrous: covered with short, stiff hairs, so as to be rough to the touch

scarious: thin, dry, membranous, and non-green, as in margins of certain leaves and bracts

scutellum: the organ of the grass embryo that is located between the endosperm and the embryo axis; it is often interpreted as the grass cotyledon

secund: with florets or spikelets turned toward one side only, usually as a result of torsion along an axis

segmental allopolyploid: a polyploid of hybrid origin in which the chromosome sets of the parents are not identical, nor are they that different from one another, such that the plants sometimes behave as though they are autopolyploids and sometimes as allopolyploids

sessile: not stalked; seated on or attached directly to another plant part

seta: a bristle; setaceous means bristle-like

sheath: the lower portion of a grass leaf that surrounds the stem

silica bodies: crystals of silicon dioxide that occur in specialized epidermal cells of the grass leaf; their shape is of diagnostic significance

silica cells: the shorter epidermal cells of the grass leaf and stem that contain silica deposits

s. l.: the abbreviation of the Latin phrase sensu lato, meaning "in the broad sense"

somatic cells: the vegetative cells of the plant body, as opposed to the gametes or sex cells

sp.: species, in the singular

spathulate: having a large bract that is attached beneath and that often ± surrounds an inflorescence, as in the bracts of certain bluestems

species: a kind of plant or animal whose distinctiveness is seen in morphological, anatomical, cytological, chemical, and genetic discontinuities presumably brought about by reproductive isolation; thought by many zoologists to be real biological entities and by many botanists to be convenient constructs of the human mind

species name: a binomial consisting of the genus and the specific epithet, as in Zea mays

specific epithet: the second element of a binomial (the mays of Zea mays)

spike: an elongate arrangement of sessile spikelets borne on an unbranched central axis

spikelet: the basic unit of the grass inflorescence, typically consisting of two glumes and one or more florets

spp.: species, in the plural

spreading: oriented outward and more or less diverging from the point of origin

s. s.: the abbreviation of the Latin phrase sensu stricto, meaning "in the narrow or restricted sense"

ssp.: abbreviation for subspecies; sspp., plural

stamen: the pollen-producing organ of a flower, consisting of an anther and a filament

staminate: said of a flower, floret, spikelet, or plant that bears only stamens

stem: the plant axis that bears leaves, flowers, and fruits; principally aerial, but sometimes subterranean in the form of rhizomes, bulbs, etc.

steppe: any of the extensive, often tree-less, semi-arid grasslands of Eurasia, Africa, and the Americas dominated by short bunch grasses

sterile: lacking reproductive parts

sterile lemma: a lemma that does not enclose a flower; often all that remains of a reduced floret

stigma: the region of the female reproductive structure (carpel) that is receptive to pollen; in grasses, the feathery portion that sits atop the ovary

stipe: a stalk

stipitate: stalked, as in the florets of certain grasses

stolon: an aerial, horizontal stem, often rooting at the nodes, that bears ordinary foliage leaves, as in Bermuda grass; often called runners
stoloniferous: stolon-bearing
striate: marked with fine, longitudinal, parallel lines, grooves, or ridges
strict: close together, straight, and upright, as in certain stems
strigose: characterized by short, stiff, appressed hairs
sub: Latin prefix, meaning below, inferior to, almost, or somewhat
subglobose: almost spherical, as in the shape of a floret or a grain
suborbicular: almost circular in outline
subtend: to be below another plant part in point of attachment, as in a set of bracts attached beneath a spikelet
sucker: a vegetative shoot that originates from below ground

- T -
tabashir: silica deposits within the culms of certain bamboos; the term is little known outside the world of crossword puzzles
tawny: dull brownish-yellow
taxon: a taxonomic group of any rank; plural, taxa
terete: round, as seen in cross-section; spherical is not a synonym
terminal: uppermost, as in a floret in a spikelet or an inflorescence on a stem
tetraploid: a cell or an organism in which the nuclei contain four sets of chromosomes
throat: the adaxial surface at the junction of the sheath and blade of the grass leaf
tiller: a ± erect basal branch or sucker shoot
tomentose: covered by dense, soft, woolly hairs
transverse: in a cross-wise direction, as across the face or surface of a plant part
trichome: any hair-like outgrowth of the epidermis
truncate: with a squared-off or chopped-off apex or base, as in the appearance of certain leaves or bracts
tubercule: a warty protuberance
tufted: in bunches or clumps, as in the stems of a grass plant
turgid: swollen

- U -
uncinate: hooked, as in certain hairs
unilateral: one-sided; situated on one side only
unisexual: a flower, spikelet, or plant that bears either stamens or carpels, but not both
utricle: an indehiscent, 1-seeded, bladdery fruit; found in certain bamboos

- V -
var.: variety
vein: a strand of vascular tissue in a leaf or bract, seen as a ridge on the surface; in the grasses, veins are also called nerves
veld: a type of tree-less grassland best developed in southern Africa
venation: the arrangement of veins on a leaf or bract
ventral: pertaining to or attached to the inner side of an organ; the side that faces toward a central axis
verrucose: a surface, as on a lemma, covered by warty protuberances
versatile: said of an anther that is attached at its midpoint, such that it moves freely on the apex of the filament
verticil: a whorl or circular arrangement of parts around a central axis; verticillate, whorled
vestigial: rudimentary, poorly developed, much-reduced in size
vestiture: any surface feature on a plant, such as hairs, spines, scales, wax, etc.
villous: covered with shaggy, soft, but unmatted hairs
vivipary: in grasses, the term is restricted to a form of asexual reproduction in which bracts of the spikelet are modified into leafy or tailed bulb-like structures, as in certain blue grasses, fescues, and wheat grasses
viscid: sticky, gummy

- W -
wanting: lacking, missing
weed: an undesirable, worthless, aggressive kind of plant that has a set of biological features that often allows it to out-compete native species and crop plants in a particular area
winged: having a wing, a membranous lateral extension of an organ, as in a winged glume or inflorescence branch

- X -
x: the designation of the number of chromosomes that constitutes the basic set for a particular organism, as in $x = 5$

- Z -
zygote: the fertilized egg
SOURCES


[Revised 24 December 2004]