TRANSACTIONS, ILL. STATE ACAD. SCI.
Vol. 68, No. 2 (1975)

CULM MORPHOLOGY AND GRASS SYSTEMATICS

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ABSTRACT. - The culm characteristics of 194 species of grasses were studied. Characteristics that appear to have some taxonomic significance are the presence or absence of culm and sheath pulvini, whether the culm is hollow or solid, the presence or absence of branches and/or lateral buds at the upper nodes of the stem, and the extent and position of the lateral branches.

During the past 50 years the use of new anatomical, morphological, and cytological criteria have been very significant in the separation of the Gramineae into six distinct subfamilies (Gould, 1968). At the present time some of the most commonly used of these "new" taxonomic characteristics are those concerned with the types of cells in the leaf epidermis, the structure of the vascular bundle sheath and the mesophyll of the leaf, the vascularization and structure of the embryo, the shape and vascularization of the lodicule, and the number and size of the chromosomes. Due to the extensive work of Brown (1958) on the leaf anatomy and the work of Reeder (1957, 1962) on embryo structure in the Gramineae, these two criteria are the most important and reliable of the above mentioned characteristics. In addition several minor characteristics are also being used, and these are also proving to be of some importance in determining phylogenetic relationships in the Gramineae (Stebbins and Crampton, 1961). Among these minor characteristics are certain structures associated with the grass culm. Culm characteristics that appear to have some taxonomic significance are the presence or absence of culm and sheath pulvini, whether the culm is hollow or solid, the presence or absence of branches and/or lateral buds at the upper nodes of the stem, and the extent and position of the lateral branches. The present study was undertaken to determine if these culm characteristics are correlated with the major subfamilies as outlined by Gould (1968).

MATERIALS AND METHODS

Living material of the 194 species of grasses listed in Table 1 were examined for various culm characteristics. Most of the species were collected from natural populations in eastern and central United States; a few cultivars were also examined. For most species more than one population was examined, and in some highly variable species more than 30 populations from widely scattered localities were studied.

The presence or absence of sheath and culm pulvini was determined by splitting the culm longitudinally through the nodal region and examining the sheath and internode base under a dissecting microscope. Usually all the nodes along the culm were examined, but final determination was made from the lower and middle nodes. Many of the species were examined in both flowering and fruiting condition. Internode condition (solid vs. hollow) was determined at the same time.

The presence or absence of lateral buds and branches was determined by removing the leaf sheath from each node of the culm. The nodes were numbered, starting with the first one below the terminal inflorescence, and the presence or absence of buds or branches was recorded for each. Usually between 8 and 15 culms from each population were examined.

More than 200 populations of 98 species of grasses were studied to determine if lateral branch development would be encouraged by the removal of the terminal inflorescence. All populations were from central Illinois and southern Connecticut. In these populations the terminal inflorescence was removed soon after it emerged from the leaf sheath. Three weeks to one month later these decapitated culms were examined and compared with other members of the population to determine the increase in culm branching.

The nomenclature of the species and their arrangement into tribes and subfamilies follows Gould (1968). For species not found in that source the nomenclature follows Hitchcock (1951).

RESULTS

Pulvinus -- Most grasses have a swelling at the base of the leaf sheath (sheath pulvinus), and many also have a swelling at the base of the internode (culm pulvinus). According to Hackel (1890), nearly all grasses have sheath pulvini, at least until the internodes have completed their growth. He also mentions that once growth is completed one of two things can happen. Either the sheath pulvini will remain swollen and capable of functioning, or culm pulvini may develop from 1 to 3 mm above the node, and assume the functions of the sheath pulvini.

Brown, Pratt, and Mobley (1959) apparently were the first to recognize the taxonomic and phylogenetic significance of the culm and sheath pulvini. They found that among the subfamily Festucoideae sheath pulvini are nearly always present while culm pulvini are nearly always absent. In the subfamilies Panicoideae and Eragrostoideae, in contrast, both sheath and culm pulvini are usually present. They also mentioned that in these latter two subfamilies the sheath pulvini are not well developed and often shrivel when the culm pulvini develop.

The presence or absence of culm and sheath pulvini for each species examined is recorded in Table 1 (column 1 and 2). In most species the pulvini are definite, easily detected structures, but in some species the pulvini are extremely poorly developed. Such species are listed as having indefinite (I) pulvini. Of the 76 species of the subfamily Festucoideae examined all have a definite sheath pulvinus except for Diarrhena americana Beauv. In this unusual grass no pulvini seem to develop. In all other festucoid grasses the sheath pulvinus is mostly well developed, very obvious, and can usually be observed without cutting a longitudinal section of the stem. The swelling is sometimes more than 1 cm long and twice the normal width of the culm. In only two of the festucoid grasses studied are culm pulvini found. In Brachyelytrum erectum (Schreb.) Beauv. a definite culm pulvinus exists while an indefinite culm pulvinus is present in Oryzopsis racemosa (J.E. Smith) Ricker. Brown, Pratt, and Mobley (1959) reported five species of festucoid grasses with indefinite culm pulvini while 24 lacked culm pulvini. Species of the subfamilies Oryzoideae and Arundinoideae are similar to festucoid grasses in that they usually have well developed sheath pulvini and mostly lack culm pulvini (Table 1).

Of the 60 species of the subfamily Panicoideae examined culm pulvini are present in 45, indefinite in 3, and absent in 12 species. Sheath pulvini are much more common, being present or indefinite in 56 of the 60 species examined (Table 1). Only three species, Leptoloma cognatum (Schult.) Chase, Panicum depauperatum Muhl., and P. linearifolium Scribn., lack culm and sheath pulvini, but all have pulvinus-like regions below most of the nodes. In many of the panicoid species examined the sheath pulvini are not well developed as in festucoid grasses, being nothing more than a slight swelling at the base of the sheath that usually differ in color and texture from the rest of the sheath. Also, the sheath pulvini are usually present in young and early flowering material but shrivel and appear to be non-functional after the culm pulvini develop. It is common for the upper nodes to have well developed sheath pulvini and never develop culm pulvini while the lower nodes have well developed culm pulvini and shriveled, non-functional sheath pulvini. In some species the sheath pulvini do not appear as an external swelling at the base of the sheath, but rather as an internal swelling of the sheath just below the culm pulvini. This was observed in Tripsacum dactyloides (L.) L. and a few other Andropogoneae.

In the subfamily Eragrostoideae the pulvinus condition is highly variable. In the tribes Chlorideae, Eragrosteae, and Unioleae, most of the species have sheath pulvini and lack culm pulvini. One major exception are the species of Muhlenbergia (Eragrosteae) which usually have both sheath and culm pulvini. In the tribe Aristideae, in contrast, the species generally have well developed culm pulvini and lack sheath pulvini. No pulvini are found in Distichlis spicata (L.) Greene, Calamovilfa longifolia (Hook.) Scribn., and Eragrostis spectabilis (Pursh) Steud. The variability of this subfamily in pulvinus condition was also observed by Brown, Pratt, and Mobley (1959). They found that sheath pulvini are usually present, but that the culm pulvini are absent or indefinite in about 65% of the species they examined.

Internode Condition -- The grasses are generally considered to have hollow culms. Canfield (1933,1934) was the first to notice that solid internodes are extremely common in many species of grasses and reported that 74% of the species examined from the Jornada plains in southern New Mexico have solid internodes. He also suggested that the solid-stemmed grasses are better adapted to grazing and to arid conditions than hollow-stemmed species. Brown, Harris, and Graham (1959) were the first to suggest the taxonomic and phylogenetic significance of hollow vs. solid internodes. They found that 54% of the grass species studied have solid internodes and that members of the subfamily Festucoideae usually have hollow internodes (93%) while the majority of the subfamily Panicoideae have solid internodes (68%). They also found a correlation between highly specialized spikelets and/or inflorescences and solid internodes. Brown, Harris, and Graham (1959) also found that a simple distinction of hollow or solid is inadequate to correctly describe grass internodes. They observed that many panicoid species have thick walls and small hollows while most festucoid species have thinner walls and larger hollows. They therefore used the categories hollow, small-hollow, or solid. In the present study it was found that it is very difficult to separate small-hollow from hollow. It is generally true, however, that the panicoid species with hollow internodes have a thicker wall and smaller cavity than that found among festucoid species.

The internode condition (solid vs. hollow) of the grasses studied is recorded in Table 1 (column 3). In most of the species the internode condition is very obvious and constant. Within a population, differences were not observed, and for most species different populations were the same for this characteristic. In the few cases where some populations had solid culms while others had hollow culms, the least common condition is recorded in parenthesis. It is not uncommon for young material to have a solid pith that breaks down when the culm is mature. Also, occasionally the upper internodes may be solid while the remaining internodes are hollow. This is very common in many populations of *Festuca pratensis* Huds., and was sometimes observed in other species. Furthermore, the relatively short basal internodes of the culm may be solid while the fully expanded internodes are hollow. As a result the middle, most expanded internodes on mature fruiting culms were used to determine the internode condition.

Of the 76 species of the subfamily Festucoideae examined all but six were found to have hollow internodes. Of these, *Brachyelytrum erectum* (Schreb.) Beauv. and *Stipa robusta* (Vasey) Scribn. consistently have solid internodes, while in four species this condition varies with different populations. Variation in relative hollowness has been reported in one other festucoid species. Dondlinger (1908) mentioned that the culms of wheat are usually hollow, but that in "some varieties they are quite filled with pith". Also, in *Phleum pratense* L., another commonly cultivated grass, Brown, Harris, and Graham (1959) reported that it had a solid internode while 16 populations studied by the present authors had hollow internodes.

In the subfamily Panicoideae about 40% of the species examined have solid internodes. In this subfamily the more advanced tribe

Andropogoneae (including the Maydeae) has 75% of the species with solid internodes while the more primitive Paniceae has about 35% with solid internodes (Table 1). Brown, Harris, and Graham (1959) reported that 49% of the tribe Paniceae studied have solid internodes. They suggested that Paniceae species of arid regions tend to have solid internodes while those from humid regions often have hollow internodes. The fewer solid-stemmed species found in the present study is undoubtedly due to the high number of species sampled from cool, humid regions. The internode condition in the subfamily Eragrostoideae is similar to that found in the Panicoideae with about 50% of the species examined having solid internodes. The higher percent reported by Brown, Harris, and Graham (1959) may be due to the cool, humid region from which the present sample was made. They found more solid-stemmed species in the tribes Chlorideae, Aristideae, and Sporoboleae.

Culm Branching -- The extend of culm branching and the presence or absence of buds at the nodes for each species is shown in Table 1 (columns 4, 5, and 6). In this table the average number of nodes below the inflorescence that lack buds or branches is recorded in column 4, the percent of the nodes examined which had branches is recorded in column 5, while the position of the branching (whether the branching was from the basal, middle, or upper nodes) is recorded in column 6.

For most of the species examined, the number of nodes below the inflorescence that lacked buds or branches is fairly constant. Some variation does occur, however, with some members of the population having one or rarely two more nodes with or without buds. Occasionally different populations of a species were found in which the number of nodes with or without buds differed consistently from that found in other populations examined. This variation sometimes occurs in grasses that consistently have buds at only the basal nodes of the culm and probably represents a response to habitat conditions. Variation in the number of nodes with or without buds did occur on the upper nodes in eight species. For these species this variation is shown in column 4 where the least common number is reported in parenthesis after the normal condition. In the populations of Agrostis alba L. examined those growing in open areas had buds at all the nodes while those from shaded areas generally lacked buds at the first node below the inflorescence. Populations of Glyceria striata (Lam.) Hitchc. from Georgia, Connecticut, and Illinois consistently averaged five nodes below the inflorescence lacking buds while in one population the average was two nodes. In Panicum virgatum L. all the populations examined from the central United States had only one node below the inflorescence lacking buds, while coastal populations from Connecticut and Florida averaged four nodes lacking buds. Festuca pratensis Huds., Lolium perenne L., and Setaria lutescens (Weigel) Hubb. populations also average one node lacking a bud except for one population which averaged two nodes lacking buds. In Bouteloua curtipendula (Michx.) Torr. the number of nodes lacking buds varied from four in most populations, to two in a population from Kansas, to one in a population from Illinois. The most unusual situation occurred in various populations of Muhlenbergia tenuiflora (Willd.) BSP.

Most of the populations examined had two nodes below the inflorescence lacking buds, while in two populations from Canada, the first eight nodes lacked buds or branches. Also, in a few populations of this species the nodes near the middle of the culm lacked buds, but the nodes above and below had buds present.

While outlining the numerous criteria that can be used to separate the subfamilies of grasses Stebbins and Crampton (1961) mentioned that the presence or absence of branching may be another potential distinction between the Festucoideae and the other subfamilies. They observed that in festucoid genera the three or four nodes below the inflorescence never bear branches, and these nodes are completely devoid of axillary buds. In most members of the other subfamilies, in contrast, all nodes but the one immediately below the inflorescence either bear branches or can be induced to do so by decapitation, since buds are present in the leaf axil. These observations appear to be fairly accurate. Of the 76 species of the subfamily Festucoideae examined, 52 lack buds or branches on at least the two nodes directly below the inflorescence (Table 1, column 4). In many of these species five or six nodes below the inflorescence are devoid of buds. Of the remaining 24 species 18 lack a bud only at the first node below the inflorescence while in six a bud is found at the first node. Also, branching is not very common in the festucoid species studied (Table 1, column 5 and 6). Sixty nine of these species either lack branches, or branching is restricted to the extreme basal part of the culm.

In the remaining subfamilies the culm usually has extensive branching and all nodes but possibly the one immediately below the inflorescence bears a branch or a bud. In the subfamily Panicoideae of the 60 species examined six have buds at all nodes, and 44 lack a bud at only the node immediately below the inflorescence. Only four species consistently lack buds or branches for more than two nodes below the inflorescence. In the subfamily Eragrostoideae this condition is more variable, but of the 48 species studied nine have buds or branches at all nodes while 18 have buds missing at only the first node below the inflorescence. Though not many species were examined in the subfamilies Oryzoideae and Arundinoideae, these appear to be similar to the panicoid species in that most have buds at all the nodes or the bud is absent only from the node directly below the inflorescence. The amount of branching in these four subfamilies also differs from that commonly found in festucoid grasses. In these subfamilies about 70% of the species have branches at more than 20% of their nodes (column 5), and in some species all of the nodes have a branch. Also, in these subfamilies, branching is common throughout the culm or restricted to the upper and middle nodes (column 6). Rarely do members of these four subfamilies have branching from only the base of the culm.

In most grasses the leaves are arranged alternately in two ranks on the culm with the nodes separated by well developed internodes. In some species, however, there is a suppression of the internode and the resulting development of a compound node. In Chloris verticillata Nutt. most of the culms examined had two or three of these compound nodes separated by internodes of normal length. Each of the

Table 1. Species examined with the pulvinus condition (A-absent, P-present, I-indefinite), the internode condition (H-hollow, S-solid), and the branching pattern (B-basal, M-middle, U-upper, T-throughout).

SPECIES	PULVINI		Internode Condition (3)	BRANCHING			
	Culm (1)	Sheath (2)		Av. # of nodes lacking buds or branches (4)	% of nodes with branches (5)	Position of branches on culm (6)	% of nodes with branches after decapitation (7)
SUBFAMILY 1. FESTUCOIDEAE							
Tribe: AVENEAE							
Agrostis alba	A	P	H	0(1)	0	--	40
A. elliottiana	A	P	H	0	45	U	
A. hiemalis	A	P	H	1	0	--	0
A. perennans	A	P	H	0	0	--	0
A. scabra	A	P	H	1	0	--	
A. stolonifera	A	P	H	1	0	--	
A. tenuis	A	P	H	0	0	--	
Aira caryophyllea	A	P	H	1.5	0	--	
Alopecurus carolinianus	A	P	H	1.3	33	T	40
A. pratensis	A	P	H	3	0	--	0
Ammophila breviligulata	A	P	H	4	20	B	
Anthoxanthum odoratum	A	P	H	1	0	--	0
Arrhenatherum elatius	A	P	H	3	0	--	0
Avena sativa	A	P	H	3	0	--	0
Calamagrostis canadensis	A	P	H	1	20	U	
Cinna arundinacea	A	P	H	5	0	--	0
Deschampsia flexuosa	A	P	H	3	0	--	0
Hierochloë odorata	A	P	H	3	0	--	
Holcus lanatus	A	P	H	2.3	0	--	0
Koeleria cristata	A	P	H	2	0	--	0
Phalaris arundinacea	A	P	H	1	40	M	50
Phleum pratense	A	P	H	3.2	0	--	0
Sphenopholis intermedia	A	P	H	3	0	--	0
S. obtusata	A	P	H	3	0	--	0
Tribe: BRACHYELYTREAE							
Brachyelytrum erectum	P	P	S	5	0	--	0
Tribe: DIARRHENEAE							
Diarrhena americana	A	I	H	4.5	0	--	0
Tribe: FESTUCEAE							
Briza maxima	A	P	H	1	20	M	
Bromus ciliatus	A	P	H	6.5	0	--	
B. commutatus	A	P	H	3	0	--	0
B. inermis	A	P	H	6	0	--	0
B. japonicus	A	P	H	4	0	--	0
B. kalmii	A	P	H	5	0	--	0

SPECIES	(1)	(2)	(3)	(4)	(5)	(6)	(7)
B. latiglumis	A	P	H	13	0	--	0
B. purgans	A	P	H	5	0	--	0
B. racemosus	A	P	H	4	0	--	
B. tectorum	A	P	H	4	0	--	0
Dactylis glomerata	A	P	H	3	0	--	0
Festuca myuros	A	P	H	1	0	--	
F. obtusa	A	P	H	3	0	--	0
F. ovina	A	P	H	2.3	0	--	0
F. pratensis	A	P	H(S)	1(2)	0	--	0
F. rubra	A	P	H	2.3	0	--	
Lolium multiflorum	A	P	H	1	0	--	20
L. perenne	A	P	H	1(2)	0	--	25
Poa annua	A	P	H	2	20	B	
P. chapmaniana	A	P	H	1	70	T	
P. compressa	A	P	H(S)	1	0	--	0
P. palustris	A	P	H	1	0	--	
P. pratensis	A	P	H	3	0	--	0
P. sylvestris	A	P	H	4	0	--	0
Puccinellia pallida	A	P	H	0	0	--	
Vulpia octoflora	A	P	H	1	40	M	
Tribe: MELICEAE							
Glyceria borealis	A	P	H	1	0	--	
G. canadensis	A	P	H	5	0	--	
G. grandis	A	P	H	4	0	--	
G. striata	A	P	H	5(2)	0	--	0
Melica mutica	A	P	H	3	0	--	
M. nitens	A	P	H	6	0	--	0
Tribe: STIPEAE							
Oryzopsis asperifolia	A	P	H	4	0	--	
O. racemosa	I	P	H	5	0	--	
Stipa columbiana	A	P	H	2	0	--	
S. robusta	A	P	S	3	0	--	
S. spartea	A	P	H	0	0	--	
Tribe: TRITICEAE							
Agropyron cristatum	A	P	H	3	0	--	
A. repens	A	P	H	4	0	--	0
A. smithii	A	P	H	4	0	--	0
Elymus canadensis	A	P	H	6	0	--	0
E. villosus	A	P	S(H)	5	0	--	0
E. virginicus	A	P	H(S)	6.5	0	--	0
Hordeum jubatum	A	P	H	4	0	--	0
H. pusillum	A	P	H	3	0	--	0
Hystrix patula	A	P	H	6	0	--	0
Secale cereale	A	P	H	4	0	--	0
Sitanion hystrix	A	P	H	4	0	--	
Triticum aestivum	A	P	H	3	0	--	0
T. cylindricum	A	P	H	3	0	--	0

SPECIES	(1)	(2)	(3)	(4)	(5)	(6)	(7)
SUBFAMILY 2. PANICOIDEAE							
Tribe: ANDROPOGONEAE							
Andropogon elliottii	P	P	S	1	50	U&M	
A. gerardii	P	P	S	1	32	U	40
A. virginicus	P	P	S	1	70	U&M	
Arthraxon hispidus	P	P	H	1	90	T	
Erianthus alopecuroides	A	P	S	4	0	--	
E. ravennae	A	P	S	2	0	--	
Manisuris rugosa	P	P	S	1	65	U&M	
Microstegium vimineum	P	P	H	0	60	U&M	
Miscanthus sinensis	A	I	S	11	0	--	0
Schizachyrium scoparium	P	P	S	1	57	U&M	65
Sorghastrum elliottii	P	P	H	4	0	--	
S. nutans	P	P	H	2	0	--	0
Sorghum halepense	P	P	S	1	22	U	50
S. vulgare	I	P	S	1	5	U	
Tripsacum dactyloides	P	P	S	1	25	U	25
Zea mays	P	P	S	5	16	M	
Tribe: PANICEAE							
Cenchrus pauciflorus	P	P	H(S)	1	66	T	75
Digitaria filiformis	P	P	H	1	50	T	
D. ischaemum	P	P	H	1	55	T	75
D. sanguinalis	P	P	H	1	75	T	75
Echinochloa crusgalli	P	P	S	1	50	T	65
Leptoloma cognatum	A	A	H	1	60	T	
Panicum agrostoides	P	P	H	0	45	U&M	
P. anceps	P	P	H	0	45	U&M	
P. boscii	P	P	S(H)	1	20	U	20
P. capillare	P	P	H	1	40	U&M	50
P. clandestinum	P	P	H	0	35	U&M	45
P. columbianum	P	P	S	1	25	U	
P. depauperatum	A	A	H	1	35	U	
P. dichotomiflorum	P	P	H	1	80	T	80
P. dichotomum	P	P	H	1	20	U	
P. huachucae	P	P	S	1	35	U&M	50
P. lanuginosum	P	P	S(H)	1	0	--	
P. latifolium	P	P	H	1	60	U&M	70
P. linearifolium	A	A	H	1	75	T	
P. mattamuskeetense	P	I	H	1	25	M	
P. meridionale	P	P	S	1	15	U	
P. microcarpon	P	P	H	1	60	U&M	
P. oligosanthes	I	P	H	1	50	U&M	
P. perlongum	P	I	H	1	45	U&M	
P. polyanthes	P	P	H	1	5	U	
P. scribnerianum	P	P	H	1	42	U&M	
P. virgatum	A	P	H	1(4)	0	--	0
P. xalapense	P	P	H(S)	1	40	U&M	
Paspalum blodgettii	A	P	S	0	40	U	
P. ciliatifolium	A	P	S	0	40	U&M	40
P. circulare	A	P	H	1	0	--	
P. dilatatum	P	P	H	1	45	U&M	

SPECIES	(1)	(2)	(3)	(4)	(5)	(6)	(7)
P. floridanum	P	P	H	2	10	U	
P. fluitans	A	P	H	1	75	T	
P. pubiflorum	P	P	H(S)	2	55	T	55
P. urvillei	A	P	H	1	10	M	
Pennisetum alopecuroides	P	P	H	1	20	B	
Setaria faberii	P	P	S	1	70	M&B	80
S. italica	P	A	H	1	25	B	
S. lutescens	P	P	S(H)	1 (2)	50	T	70
S. macrostachya	P	P	S	1	80	T	
S. magna	P	P	H	1	26	U&B	
S. verticillata	P	P	S	1	43	T	
S. viridis	P	P	S	1	35	M&B	80
SUBFAMILY 3. ERAGROSTOIDEAE							
Tribe: AELUROPODEAE							
Distichlis spicata	A	A	S	3.5	19	M	
Tribe: ARISTIDEAE							
Aristida dichotoma	P	A	H	0	84	T	
A. divaricata	P	A	S	1	20	B	
A. fendleriana	P	A	S	2	20	B	
A. intermedia	P	A	H	0	53	T	
A. longespica	A	P	H	1	24	M	
A. oligantha	P	A	H(S)	1	65	T	
A. purpurascens	P	A	S	1	0	--	
A. ramosissima	P	A	H	1	47	T	
A. tuberculosa	P	A	S	1	75	T	
Tribe: CHLORIDEAE							
Bouteloua curtipendula	A	P	S	**	0	--	0
B. gracilis	A	P	S	4	0	--	
B. hirsuta	A	P	S	1	0	--	
Buchloë dactyloides	A	P	S	2	43	M&B	
Chloris verticillata	A	P	S	2.5	30	B	
C. virgata	A	P	S	2	25	B	
Cynodon dactylon	P	P	H	3	22	M&B	
Eleusine indica	A	P	S	2	20	M	20
Hilaria jamesii	A	P	S	3	30	B	
Leptochloa fascicularis	A	[illegible]	H	1	30	U	
L. filiformis	A	P	H	2	70	M&B	
Spartina patens	A	P	H	7	0	--	
S. pectinata	A	P	H	4	0	--	0
Tribe: ERAGROSTEAE							
Calamovilfa longifolia	A	A	S	13	0	--	0
Eragrostis cilianensis	A	P	H	1.2	33	U&M	40
E. frankii	A	P	H	1	75	T	80
E. hypnoides	P	P	H	1	50	T	60
E. oxylepis	A	P	H	1	0	--	
E. pectinacea	A	P	H(S)	1	80	T	80
E. spectabilis	A	A	H	4	0	--	0
E. trichodes	A	[illegible]	H	1	0	--	0

SPECIES	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Muhlenbergia frondosa	P	P	H	0	100	T	100
M. mexicana	P	P	H	2	60	U&M	
M. schreberi	P	P	S	1	26	U&B	40
M. sobolifera	P	P	H	1	13	U	25
M. sylvatica	P	P	H	0	70	U&M	
M. tenuiflora	P	P	H	2 (8)	0	--	0
Sporobolus asper	A	P	S	0	30	U	45
S. clandestinus	A	P	S	0	40	U	
S. cryptandrus	A	P	S	1	45	U	
S. heterolepis	A	P	S	3	0	--	0
S. neglectus	P	P	S(H)	0	70	U&M	
S. poiretii	A	P	S	1	0	--	
S. vaginiflorus	P	P	S	0	80	U&M	
S. wrightii	A	P	H	3	0	--	
Tridens flavus	A	P	H	2.5	0	--	0
Triplasis purpurea	A	P	S	0	90	T	
Tribe: UNIOLEAE							
Uniola paniculata	T	P	H	3	0	--	
SUBFAMILY 4. ORYZOIDEAE							
Tribe: ORYZEAE							
Leersia lenticularis	A	P	H	1.5	13	B	
L. oryzoides	A	P	H	1	50	T	
L. virginica	A	P	H	1	60	T	75
Oryza sativa	A	P	H	1	20	B	
SUBFAMILY 5. ARUNDINOIDEAE							
Tribe: ARUNDINEAE							
Arundo donax	A	A	H	3	17	M	
Phragmites communis	T	A	H	6	0	--	
Tribe: CENTOTHECEAE							
Chasmanthium latifolium	T	P	H	6	0	--	0
Tribe: DANTHONIEAE							
Danthonia compressa	A	P	S	0	61	U&M	
D. sericea	A	P	H	0	45	U	
D. spicata	A	P	H	0	45	U	45

** see text

compound nodes is composed of three or four nodes grouped together with each having a well developed leaf and a bud or branch in the leaf axil. The same type of compound nodes are found in *Aristida oligantha* Michx. and *A. tuberculosa* Nutt., particularly on the upper part of the culm. An almost idential type of development is found in *Eleusine indica* (L.) Gaertn. where the culms usually have two compound nodes separated by a normal internode. Each of the compound nodes is composed of two or three nodes, each with a well developed leaf and usually a bud or branch in the axil of each leaf. Occasionally the upper node of a compound node will lack a bud or branch.

Hackel (1890) reported the existence of "tufts" on the upper nodes and runners in species of *Sporobolus*, *Cynodon*, *Aeluropus*, and *Chloris*, which were caused "through the non-development of the internodes". Bogdan (1952) also mentioned the existance of compound nodes on the stolons and culms of 18 species of grasses from Kenya, while more recently Rawal and Harlan (1971) found the same condition in *Cynodon dactylon* (L.) Pers. They reported that the culms of this species have two leaves at each node, with only the lower subtending a lateral bud. Similar results were obtained during the present study. This type of compound node also occurs in *Eragrostis hypnoides* (Lam.) BSP., where usually only the lower leaf of a compound node will subtend a bud or branch. Rarely, in this latter species both of the leaves of a compound node subtend a bud or branch. Occasionally compound nodes are also found near the upper part of the culm of *Arundo donax* L., and near the middle of the culm of *Uniola paniculata* L. In both species, the leaves of the compound nodes may or may not have buds present. In these two species usually there is only one compound node on the culm with the remaining internodes well developed.

A very unusual type of branching is found in *Triplasis purpurea* (Walt.) Chapm. and the three species of *Danthonia* examined. In the axils of most of the culm leaves are elongated spikelets. These spikelets usually consist of one to five widely separated florets with the slender rachilla joints as long or longer than the individual florets. The entire structure is enclosed by the leaf sheath and is strikingly different from the normal spikelets borne on the terminal inflorescence. These cleistogamous spikelets were first reported by Chase (1908) in *Triplasis purpurea* (Walt.) Chapm. and later in 12 species of *Danthonia* (Chase, 1918). For the purpose of this study these spikelets are treated as branches (Table 1).

Stebbins and Crampton (1961) suggested that branching could be increased in many grasses by removing the terminal inflorescence. To determine the extent to which branching could be increased, individuals in populations of 89 different species of grasses were decapitated as the terminal inflorescence emerged from the leaf sheath (Table 1, column 7). Of the 47 species of the subfamily Festucoideae that were decapitated, only five developed any branches. In two of these the controls also branched, while in the remaining three (*Agrostis alba* L. and two species of *Lolium*), the controls

Table 2. The pulvinus condition, the internode condition, and the bud and branching pattern that is most commonly found in each of the subfamilies of grasses. The percentage of the species studied that have the commonly encountered characteristics is also included for each trait.

	FESTUCOIDEAE (75 species)	PANICOIDEAE (60 species)	ERAGROSTOIDEAE (48 species)	ORYZOIDEAE (4 species)	ARUNDINOIDEAE (6 species)
Culm Pulvinus	ABSENT in 97% of the species studied	PRESENT in 75% of the species studied	ABSENT in 60% of the species studied	ABSENT in 100% of the species studied	ABSENT in 66% of the species studied
Sheath Pulvinus	PRESENT in 99% of the species studied	PRESENT in 87% of the species studied	PRESENT in 75% of the species studied	PRESENT in 100% of the species studied	PRESENT in 66% of the species studied
Internode Condition	HOLLOW in 97% of the species studied	HOLLOW in 63% of the species studied	HOLLOW in 54% of the species studied	HOLLOW in 100% of the species studied	HOLLOW in 83% of the species studied
Average number of nodes lacking buds or branches (from top of culm)	Upper 3 or more nodes lack buds in 61% of the species studied	Upper 1 or 2 nodes have buds present in 93% of the species studied	Upper 1 or 2 nodes have buds present in 70% of the species studied	Upper 1 or 2 nodes have buds present in 100% of the species studied	Upper 3 or more nodes lack buds in 50% of the species studied
Branching	ABSENT in 88% of the species studied	PRESENT in 87% of the species studied	PRESENT in 67% of the species studied	PRESENT in 100% of the species studied	PRESENT in 66% of the species studied

did not branch. In the other festucoid species tested, even the buds near the base of the culm did not develop into branches, though there was increased tillering from the rhizomes of some of the species. In the remaining subfamilies, it was found that if the culms normally branched, then branching could usually be increased to some extent by decapitation, but species that normally did not branch could not be induced to do so.

CONCLUSIONS

Culm characteristics such as the presence or absence of sheath and culm pulvini, solid vs. hollow internodes, and the extent and position of axillary buds and/or branches are of some taxonomic value in the Gramineae. Furthermore, some of these characteristics can be used as an additional aid in separating the subfamilies as they are now recognized in most modern systems of grass classification (Table 2). The species studied in the subfamily Festucoideae are very consistent in their culm characteristics with nearly all lacking culm pulvini, having sheath pulvini, having hollow internodes, and lacking lateral branches. Also, the majority of the species lack buds at the upper three or more nodes of the culm. The Panicoideae and Eragrostoideae species are more variable in pulvini and internode condition, but the majority have both culm and sheath pulvini. These two subfamilies, however, can usually be separated from the Festucoideae since most of the species have branching culms and buds, or branches present at all but the upper one or two nodes of the culm (Table 2).

The present study also indicated that the internode condition (solid vs. hollow) is the result of environmental adaptation. Solid stemmed species are more common in arid regions while hollow internodes are more common in species from cool humid regions.

ACKNOWLEDGEMENTS

We wish to express our appreciation to the Connecticut Agricultural Experiment Station which provided space and equipment for four months to examine and collect material, and to Mr. Loy Rich Phillippe (University of Tennessee -Knoxville) who supplied us with living material of 25 species of grasses.

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