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Robert W. Kiger

THE KRANZ SYNDROME AND ITS SUBTYPES IN GRASS SYSTEMATICS

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[1] *Memoirs* 23 (2), containing the paper by Robert R. Kowal entitled "Systematics of *Senecio aureus* and allied species on the Gaspé Peninsula, Quebec," was published on August 22, 1975.

THE KRANZ SYNDROME AND ITS SUBTYPES IN GRASS SYSTEMATICS

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THE KRANZ SYNDROME AND ITS SUBTYPES IN GRASS SYSTEMATICS[1],[2]

The classification of the Gramineae based upon morphological (mostly spikelet) characters that developed during the 19th Century culminated in the treatments of Bentham and Hooker (1883) and Hackel (1887). This general system persisted during the first half of the 20th Century (Hitchcock, 1920, 1950; Stapf, 1920; Bews, 1929; and others). However, new characters were discovered starting in 1875 with the report by Duval-Jouve that there are two basic types of grass leaf anatomy.

During the past hundred years numerous studies of grass leaf anatomy were published. Schwendener (1890) examined the mestome sheath in numerous taxa. Holm (1890–1901) examined the leaf anatomy of many species in numerous tribes, and first reported the "double" parenchyma sheath condition in *Aristida*. Pée-Laby (1898) pointed out the concentration of chlorophyll in the parenchyma sheath cells. Lohauss (1905) studied general leaf anatomy and noted that some tribes, especially the classical Festuceae, contain among their genera both anatomical types. Avdulow (1931), however, first successfully utilized basic leaf anatomy (called "festucoid" or "panicoid") in an attempt to construct a better classification of the family. He also employed basic chromosome number, chromosome size, nucleolus characters, starch grain type, first seedling leaf characters, etc. as criteria. Hubbard (1948), Potztal (1952), de Wet (1956), Stebbins (1956), Brown (1958) and others continued the study of leaf anatomy in relation to the systematics of the Gramineae. Stebbins (1956) proposed four different leaf anatomical types and Brown (1958) recognized six.

Between 1900 and the present, other non-morphological characters were discovered and applied to grass systematics. Prat (1932, 1936) studied the peculiar bicellular hairs and silica cells of the leaf epidermis and utilized their characters, along with those employed by Avdulow (1931), in an attempt at taxonomic clarification. He separated from the Festuceae and Agrostideae those genera having panicoid leaf anatomy. Tateoka, Inoue, and Kawano (1959), and Tateoka and Takagi (1967) have added data and quantified the subject of bicellular hairs, the presence or absence of which is now a major character in grass systematics.

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[1] This paper is dedicated to Joseph Duval-Jouve on the hundredth anniversary of his 1875 publication reporting that there are two basic contrasting types of leaf anatomy within the grass family. During the subsequent century numerous studies have confirmed his discovery, and recognition of these basic types has been instrumental in the development of new systematic treatments of the family.

[2] Terms and notation used throughout are listed and defined under "Terminology and notation."

Reeder (1957, 1961, 1962), Decker (1964), and Tateoka (1969a) investigated the taxonomic application of embryo characteristics first revealed by van Tieghem (1897): vascular pattern, presence or absence of a cleft between the coleoptile and coleorhiza, and width of the first true leaf. Embryo vascularization is now of major importance in grass systematics.

Chromosome number and size have been significant in placement of many species and genera, and a few tribes. There has been some change from the conclusions of Avdulow, based on the increased importance accorded basic chromosome numbers (Tateoka, 1961a).

Characters of lodicules (Stebbins, 1956; Tateoka, 1967; Hsu, 1965) and root hairs (Reeder and von Maltzahn, 1953; Row and Reeder, 1957), persistence of nucleoli (Brown and Emery, 1958), and many other non-morphological characters have been found useful in grass systematics. Stebbins (1956) discussed some of these newer characters and related them to systematics. Stebbins and Crampton (1961), Prat (1960), Metcalfe (1960), Jacques-Felix (1962), and Auquier (1963) have listed and described most or all of them in considerable detail. Auquier listed a total of 67 characters of all sorts, some more significant than others, useful at various taxonomic levels. It is remarkable how these characters are correlated. As a result, conclusions based upon one character can be tested by numerous others.

Prat's and Auquier's reviews detailed these characters adequately and summarized knowledge of the subject up to 1963. They were published just at the time development of electron microscopy (Brown and Johnson, 1962; Johnson, 1964) and discovery of C_4 photosynthesis (Kortschak, Hartt, and Burr, 1965; Hatch and Slack, 1966) stimulated a resurgence of interest in leaf anatomy and its systematic significance. Subsequent investigations have revealed correlations between subtypes of C_4 photosynthesis and subtypes of Kranz anatomy.

In 1875, Duval-Jouve reported that there are two basic types of leaf anatomy among grass taxa. By 1920, these two sorts had been reported additionally in nine other angiosperm families. Occasionally these contrasting states were employed in systematics (Avdulow, 1931). In one state there are no specialized cells around the vascular bundles. That is the common type of leaf anatomy in angiosperms, now called non-Kranz. The other type, which is much less common, is usually characterized by a ring or wreath (in German, a "Kranz") of specialized cells around the vascular bundles. The latter was called the Kranz type by Haberlandt (1884). Thus, reference to Kranz cells specifies those of this unique sheath or tissue, and taxa characterized by such a tissue are referred to as Kranz species, genera, families, etc. (Brown, 1975). There are hundreds of Kranz species, in perhaps 200 genera, but only 12 Kranz families.

The earliest method of characterizing plants as Kranz or non-Kranz was by examination of stained mechanically cut or unstained freehand leaf cross sections. A second method was by observing the veins of whole leaves, living or dead, of such dicotyledons as *Atriplex* (Moser, 1934). Such observation of non-Kranz dicotyledonous leaves by transmitted light at low magnification reveals a solid green or brown background and thin, usually translucent veins. If the leaf has Kranz veination (not "venation"), thick, dark, sheath-covered veins are observed, with small, irregularly-shaped, translucent spots among them. If a leaf is too thick to reveal the type of veination otherwise, boiling in water for about 30 seconds will make it obvious (Brown and Smith, 1974b). This is an excellent and quick method for screening large numbers of specimens. There are, of course, some dicotyledonous leaves that can be difficult to classify by this method, such as narrow leaves or leaf lobes that have nearly parallel veins. Linear glands may produce an appearance like Kranz veination. This method is unusable with grasses or sedges.

Brown (1974) demonstrated that the M.S. subtype of Kranz anatomy, as determined from paradermal leaf sections, is almost always correlated with Kranz cells that are elongated parallel to the vein and are about twice as long as wide. In marked contrast, P.S. anatomy is correlated with Kranz cells oriented perpendicular to the vein and usually from twice as wide as long to about square. These correlations, which hold throughout the Panicoideae and Eragrostoideae, are made from paradermal views and enable a check of determinations made from cross sections. Often, paradermal views are critical to accurate determination.

Hattersley and Watson (1975, 1976) recently examined many grass species for Kranz anatomical subtypes, employing their own symbolic representations. They demonstrated that all examined non-Kranz species have more than four (usually about seven) chlorophyll-containing mesophyll cells between adjacent parenchyma sheaths, whereas all examined Kranz grass species have no more than two to four such mesophyll cells between adjacent Kranz cells. Their work updates that on the "intervascular interval" by Lommasson (1961) and the observations of Prat (1936), Takeda and Fukuyama (1971), and Kanai and Kashiwagi (1975), who also saw taxonomic correlation with "interveinal distance." They considered this to be the best character for distinguishing between Kranz and non-Kranz in grasses, and I agree that it is at least as reliable as any other. For example, it indicates that the intermediates *Panicum milioides* and *P. hians* should be C_3 species, which they are according to $\delta^{13}C$ ratios. This anatomical difference emphasizes that during, preceding, or following the evolution of the Kranz syndrome, additional intercalary veins have always evolved, possibly to increase the volume of Kranz tissue relative to mesophyll tissue and thus achieve a proper proportion for maximum efficiency of C_4 photosynthesis (see also the discussion of distinctive cells under "The small tribes of the Panicoideae").

In 1965, Kortschak, Hartt, and Burr, and, soon after, others (Hatch and Slack, 1966, 1970) discovered and characterized a new biochemical pathway of photosynthetic CO_2 fixation which is called C_4 photosynthesis. Almost immediately, C_3 photosynthesis was related to non-Kranz anatomy and C_4 to Kranz (Hatch, Slack, and Johnson, 1967; Downes and Hesketh, 1968; Downton and Tregunna, 1968; Johnson and Hatch, 1968; Laetsch, 1968). Aside from some hybrids between Kranz and non-Kranz species of *Atriplex* (Björkman, et al., 1971), Kranz anatomy has been reported for all plants characterized as C_4 and non-Kranz for essentially all C_3 plants. Therefore, C_4 photosynthesis must require Kranz anatomy without exception, though the crassulacean acid metabolism (CAM) of some succulents is similar to C_4 photosynthesis but is correlated with non-Kranz anatomy. There are a few taxa *(Mollugo verticillata,* Kennedy and Laetsch, 1974; *Panicum milioides* and *P. hians,* Brown and Brown, 1975; and a few plants of *Alloteropsis semialata)* which, essentially, have Kranz anatomy but C_3 photosynthesis. Although some of their photosynthetic enzymes have intermediate activities, these are closer to C_3 than C_4 (Kanai, Ryuzi, and Kashiwagi, in press; Ku, Edwards, and Kanai, in press).

Because there are a number of detectable differences between C_4 Kranz and C_3 non-Kranz plants, the totality of character states unique and common to all C_4 Kranz plants has been designated as the Kranz syndrome. Brown (1975) has proposed that the single, simple, unambiguous term "Kranz" be used to include and imply all these anatomical and physiological characteristics of the syndrome.

Since the Kranz syndrome consists of a group of correlated characteristics, each distinct from the corresponding state in non-Kranz species, it follows, and has been demonstrated, that determination of any one of them predicts the presence of the others (Tregunna, et al., 1970; Laetsch, 1974). Each such characteristic is either necessary for C_4 photosynthesis or else a result of that process.

Biochemically, C_4 species have much the same enzymes as C_3 species, but in the former these enzymes may be separated, some in the mesophyll and others in the Kranz cells of the sheath. Furthermore, the activities of certain photosynthetic enzymes may be higher in either the mesophyll or Kranz tissue of C_4 plants than in C_3 plants. Notably, C_4 plants possess the enzyme pyruvate P_i dikinase not found generally in C_3 plants.

Simply stated, in C_4 plants the CO_2 enters the leaf and is combined with phosphoenolpyruvate by the enzyme phosphoenolpyruvate carboxylase (PEP-Case) to form, in the mesophyll, the 4-carbon molecule oxaloacetate. This is then converted, mostly to malate in the so-called malate formers and mostly (or entirely, Das and Rathnam, 1974) to aspartate in the aspartate formers. Malate or aspartate is then transported inward from the mesophyll cells to the Kranz cells through plasmodesmata in the cell walls. There the malate is decarboxylated by NADP-malic enzyme (NADP-me), or the aspartate (or derivative) is decarboxylated by NAD-malic enzyme (NAD-me) or by PEP-carboxykinase enzyme (PEP-ck) (Edwards, Kanai, and Black, 1971), liberating a molecule of CO_2 and pyruvate. The CO_2, now in the Kranz cells, is incorporated into 3-phosphoglyceric acid by ribulose diphosphate carboxylase (RuDP-Case) of the well-known Calvin-Benson cycle. The pyruvate (or alanine, Hatch, et al., 1975) returns to the mesophyll to pick up more CO_2. Thus, sugar and starch are formed mainly within the chloroplasts of the Kranz cells, whereas in C_3 species the starch is formed within mesophyll cells.

The above Hatch-Slack biochemical cycle, which has three known variations for which corresponding biochemical pathways have been proposed (Hatch, Kagawa, and Craig, 1974), absolutely requires two distinct tissues: the mesophyll and the Kranz tissue. Therefore, all C_4 plants must have Kranz anatomy, characterized at least by having a Kranz tissue internal to the mesophyll (Brown, 1975). Kranz cells have thicker walls (an apparent structural requirement) than do mesophyll cells, and these contain numerous pits and plasmodesmata.

Biochemically, C_4 photosynthesis can be detected (as it was originally) by determination that the first molecules containing the ^{14}C from $^{14}CO_2$ are of the 4-carbon types oxaloacetate, malate, and aspartate. This photosynthetic type, as well as its three subtypes, can also be determined by the relative activities of NADP-me, NAD-me, and PEP-ck present (Gutierrez, Gracen, and Edwards, 1974; Hatch, et al., 1975). Tables 1 and 2 list most taxa known to have been characterized both enzymatically and anatomically.

TABLE 1. *Photosynthetic and anatomical subtypes reported by others for Kranz species of the Gramineae, arranged by tribes and genera.*

	Phot.	Anat.	Author[1]
PANICEAE			
Axonopus			
compressus	NADP-me	M.S.	2
Brachiaria			
brizantha	PEP-ck	P.S.	2
ciliatissima	PEP-ck	P.S.	2
dictyoneura	PEP-ck	P.S.	2
erucaeformis	PEP-ck		2
plantaginea	PEP-ck	P.S.	2
platyphylla	PEP-ck	P.S.	2
ramosa	PEP-ck	P.S.	2
xantholeuca	PEP-ck		2
Cenchrus			
pauciflorus	NADP-me	M.S.	3
Digitaria			
decumbens	NADP-me	M.S.	6
sanguinalis	NADP-me	M.S.	5
Echinochloa			
crus-galli	NADP-me	M.S.	3
colonum	NADP-me	M.S.	3
Eriochloa			
borumensis	PEP-ck	P.S.	2
crebra	PEP-ck		2
Setaria			
faberi	NADP-me	M.S.	3
italica	NADP-me	M.S.	3
lutescens	NADP-me	M.S.	3
verticillata	NADP-me	M.S.	3
viridis	NADP-me	M.S.	3
Urochloa			
bolbodes	PEP-ck	P.S.	2
mosambicensis	PEP-ck	P.S.	2
panicoides	PEP-ck	P.S.	3
pullulans	PEP-ck	P.S.	2
Panicum			
agrostoides	NADP-me	M.S.	2
antidotale	NADP-me	M.S.	1
bergii	NAD-me	P.S.	3
capillare	NAD-me	P.S.	3
coloratum	NAD-me	P.S.	3
decompositum	NAD-me	P.S.	3
fasciculatum	PEP-ck	P.S.	2
hallii	NAD-me	P.S.	3
makarikariense	NAD-me	P.S.	3
maximum	PEP-ck	P.S.	6

Table 1 continued.

	Phot.	Anat.	Author[1]		Phot.	Anat.	Author
gracilis	PEP-ck	P.S.	2	*miliaceum*	NAD-me	P.S.	5
pseudoacrotricha	PEP-ck		2	*molle*	PEP-ck	P.S.	3
punctata	PEP-ck	P.S.	2	*obtusum*	NADP-me	M.S.	2
sericea	PEP-ck	P.S.	2	*stapfianum*	NAD-me	P.S.	3
Paspalum				*texanum*	PEP-ck	P.S.	3
notatum	NADP-me	M.S.	3	*turgidum*	NAD-me	P.S.	3
Pennisetum				*Pseudobrachiaria*			
purpureum	NADP-me	M.S.	1	*deflexa*	PEP-ck	P.S.	2
typhoides	NADP-me	M.S.	6				
ANDROPOGONEAE							
Andropogon				*Sorghastrum*			
gerardi	NADP-me	M.S.	3	*nutans*	NADP-me	M.S.	3
virginicus	NADP-me	M.S.	6	*Sorghum*			
Euchlaena				*bicolor*	NADP-me	M.S.	3
mexicana	NADP-me	M.S.	3	*sudanense*	NADP-me	M.S.	3
Microstegium				*vulgare*	NADP-me	M.S.	4
vimineum	NADP-me	M.S.	2	*Zea*			
Saccharum				*mays*	NADP-me	M.S.	4
officinarum	NADP-me	M.S.	3	*Schizachyrium*			
				scoparium	NADP-me	M.S.	3
CHLORIDEAE							
Bouteloua				*Eleusine*			
gracilis	NAD-me	P.S.	3	*indica*	NAD-me	P.S.	3
curtipendula	PEP-ck	P.S.	3	*Enteropogon*			
Buchloë				2 species			2
dactyloides	NAD-me	P.S.	2	*Eustachys*			
Chloris				6 species			2
distichophylla	NAD-me	P.S.	3	*Leptochloa*			
gayana	PEP-ck	P.S.	5	*dubia*	NAD-me	P.S.	3
17 species			2	*monostachya*	NAD-me	P.S.	3
ERAGROSTEAE							
Eragrostis				*curvula*	NAD-me	P.S.	3, 5
cilianensis	NAD-me	P.S.	3	*superba*	NAD-me	P.S.	2
SPOROBOLEAE							
Muhlenbergia				*cryptandrus*	NAD-me	P.S.	3
schreberi	PEP-ck	P.S.	3	*fimbriata*	PEP-ck		5
Sporobolus				*poiretii*	PEP-ck	P.S.	3
airoides	NAD-me	P.S.	3				

Table 1 continued.

	Phot.	Anat.	Author[1]		Phot.	Anat.	Author
			ZOYSIEAE				
Zoysia japonica	PEP-ck	P.S.	3	*Hilaria belangeri*	PEP-ck	P.S.	2
			ARISTIDEAE				
Aristida purpurea	NADP-me	D.S.	3				

Totals: 80 species; NADP-me, 29; NAD-me, 21; PEP-ck, 30[2].

[1] Authors:
1) Brown and Gracen, 1972
2) Gutierrez, Edwards, and Brown, 1976; and Gutierrez and Edwards, unpublished
3) Gutierrez, et al., 1974
4) Hatch and Kagawa, 1974a
5) Hatch and Kagawa, 1974b
6) Kanai and Black, 1972

[2] Number of PEP-ck species is disproportionately large because of deliberate search for them in *Brachiaria*, *Eriochloa*, and *Urochloa*. *Panicum fasciculatum*, *P. molle*, and *P. texanum* have previously been transferred to *Brachiaria*.

TABLE 2. C_4 *photosynthetic subtypes reported by others for a sedge and some dicotyledonous species, arranged by families.*

	CYPERACEAE	
Cyperus rotundus	NADP-me	(Chen, et al., 1974)
	AIZOACEAE	
Mollugo cerviana	aspartate	(Kennedy and Laetsch, 1974)
M. nudicaulis	aspartate	(Rathnam, et al., 1976[1])
Gisekia pharnacoides	aspartate	(Rathnam, et al., 1976)
Trianthema portulacastrum	malate	(Rathnam, et al., 1976)
	AMARANTHACEAE	
Alternanthera pungens	aspartate	(Rathnam, et al., 1976)
Amaranthus edulis	NAD-me	(Hatch, et al., 1975)
A. hybridus	NAD-me	(Gutierrez, et al., 1974)
A. palmeri	NAD-me	(Hatch, et al., 1975)

A. retroflexus	NAD-me	(Gutierrez, et al., 1974)
A. tricolor	NAD-me	(Gutierrez, et al., 1974)
A. viridis	aspartate	(Rathnam, et al., 1976)
Froelichia gracilis	NADP-me	(Gutierrez, et al., 1974)
Gomphrena celosoides	NADP-me	(Hatch, et al., 1975)
G. globosa	NADP-me	(Gutierrez, et al., 1974)
G. globosa	malate?	(Rathnam, et al., 1976)
Tidestromia oblongifolia	NADP-me	(Björkman, et al., 1975)
	BORAGINACEAE	
Heliotropium scabrum	malate	(Rathnam, et al., 1976)
	CARYOPHYLLACEAE	
Polycarpaea corymbosa	aspartate	(Rathnam, et al., 1976)
	CHENOPODIACEAE	
Atriplex rosea	aspartate	(Pearcy and Björkman, 1971[2])
A. sabulosa	NAD-me	(Björkman, et al., 1975)
A. spongiosa	NAD-me	(Hatch, et al., 1975)
Bassia hyssopifolia	NADP-me	(Downton, 1970)
Kochia childsii	NADP-me	(Gutierrez, et al., 1974)
K. scoparia	NADP-me	(Gutierrez, et al., 1974)
Salsola kali	NADP-me	(Gutierrez, et al., 1974)
	EUPHORBIACEAE	
Chamaesyce hirta	malate	(Rathnam, et al., 1976)
C. maculata	NADP-me	(Gutierrez, et al., 1974)
C. supina	NADP-me	(Gutierrez, et al., 1974)
	NYCTAGINACEAE	
Boerhaavia diffusa	aspartate	(Rathnam, et al., 1976)
	PORTULACACEAE	
Portulaca oleracea	NAD-me	(Hatch, et al., 1975)
Portulaca oleracea	NAD-me	(Gutierrez, et al., 1974)
Portulaca oleracea	malate	(Rathnam, et al., 1976)
P. grandiflora	NADP-me	(Gutierrez, et al., 1974)
	ZYGOPHYLLACEAE	
Tribulus terrestris	aspartate	(Rathnam, et al., 1976)

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[1] Rathnam, C. K. M., A.S. Raghavendra, and V. S. Rama Das. 1976. Z. Pflanzenphysiol. 77:283–291.

[2] Pearcy, F. W. and O. Björkman. 1971. Carnegie Inst. Wash. Year Book 69:632–639.

The chloroplasts of the Kranz cells are more or less restricted in some species to the inner or centripetal regions, and in other species to the outer or centrifugal regions of the cells (Brown, 1960; Gutierrez, Gracen, and Edwards, 1974). After long exposure to light these chloroplasts contain starch grains, whereas those of mesophyll cells usually do not. Therefore, iodine staining of thin cross sections of living leaves produces blue mesophyll if from a C_3 plant, but a blue ring of Kranz tissue if from a C_4 plant. Under the electron microscope, chloroplasts that lie in the centrifugal regions of Kranz cells are observed to be of the NADP-me type in some species and of the PEP-ck type in others. The former contain few or no grana (Johnson, 1964; Laetsch, 1974; Bragnon, 1973; Kirchanski, 1975), whereas the latter contain large grana. Chloroplasts in the centripetal regions of Kranz cells are of the NAD-me type and have many large grana (Laetsch, 1974). They also have many associated mitochondria (Laetsch, 1974, for review), even in such intermediates as *Panicum milioides* (R. H. Brown, unpublished; Ku, et al., in press) and *Mollugo verticillata* (Kennedy and Laetsch, 1974).

It is often stated that the walls of Kranz cells are thicker than those of mesophyll cells (Downton, 1971b; Laetsch, 1974), and that is true. But it is also true that there is great variation in Kranz cell wall thickness itself. Among the Kranz grasses some such walls are five or six times as thick as others. Furthermore, considerable range in thickness occurs within tribes and genera as well as within the anatomical and enzymatic subtypes. Among the Kranz dicotyledons the walls of Kranz cells are almost without exception very thin, often only about twice as thick as those of the mesophyll cells, and no suberized layer has been observed in them (Laetsch, 1974; personal observation).

The models of C_4 photosynthesis (Hatch, et al., 1975) propose that the Kranz cell wall is a barrier separating the PEP-carboxylase reaction in the mesophyll cells from the decarboxylating and RuDP-carboxylase reactions that occur within the Kranz cells. It has also been proposed that in grasses an impervious suberized layer on the outer tangential and radial wall surfaces of the Kranz cells provides or adds to the barrier effect of the thick walls (Laetsch, 1974). Transport pathways between mesophyll and Kranz protoplasts are provided by numerous plasmodesmata that penetrate the thick Kranz cell walls (Johnson, 1964; Laetsch, 1974).

In C_4 species, CO_2 incorporation by PEP-carboxylase does not discriminate against the ^{13}C atoms of CO_2 as does that by ribulose diphosphate carboxylase in C_3 species (Whelan, Sackett, and Benedict, 1973). As a result, the organic matter of Kranz plants has a $^{13}C/^{12}C$ ratio not much different from that of CO_2 in the air. The organic matter of non-Kranz species is, on the other hand, much lower in ^{13}C. As expressed in the literature, relative to the PDB carbonate standard, C_4 species have high negative ratios (between -9 and -18 ‰), whereas C_3 plants have low ratios (between -22 and -38 ‰) (Bender, 1968; Smith and Brown, 1973; Troughton, et al., 1974). Such ratios are probably the best evidence obtainable for indicating whether an angiospermous plant is Kranz or non-Kranz, provided it is neither aquatic nor succulent.

Also, because of the different responses of ribulose diphosphate carboxylase and PEP-carboxylase to oxygen, non-Kranz plants have increasingly greater photosynthetic activity as the oxygen concentration in the ambient atmosphere is lowered from the 21 percent of air to about 2 percent. Kranz plants, however, function with constant efficiency throughout this range (Brown and Gracen, 1972; Brown and Brown, 1975).

C_3 plants carry on a process called photorespiration; C_4 plants may also, but if so it is undetectable. As a result, non-Kranz plants in a closed system can only reduce the CO_2 concentration from the 320 ppm of air to about 50 ppm. Kranz plants, on the other hand, are able to reduce the CO_2 concentration to about zero. These limits are called CO_2 compensation points (Krenzer and Moss, 1969), determination of which permits rather rapid survey of species in large numbers to determine whether C_3 or C_4 (Krenzer, Moss, and Crookston, 1975). Uniquely, *Panicum milioides* and *P. hians* are definitely intermediate (15–20 ppm) in CO_2 compensation point and oxygen effect (Brown and Brown, 1975; R. H. Brown, unpublished).

The photorespiration of non-Kranz plants produces a burst of CO_2 just after removal from light to dark. This is called the CO_2 postillumination burst or PIB. There are also, however, some Kranz plants, the aspartate formers, that show a PIB of sorts (Brown and Gracen, 1972).

Since 1965, all these differences between non-Kranz and Kranz states have been used as criteria for assigning plants to one or the other category. Until then, leaf anatomy was the only character known, or adequately enough known, for such use.

The Kranz syndrome has been found: only in terrestrial angiosperms; in no trees or bushes except some woody species of *Atriplex*, *Heliotropium*, and *Euphorbia (Chamaesyce)* in Hawaii (Percy and Troughton, 1974); only between latitudes 45° N and 45° S; usually in plants of bright sunny habitats; and, in temperate zones, in plants growing only during the hot season. So far it has been reported: in twelve families of angiosperms; in a large number of genera in the Gramineae, Cyperaceae, and Chenopodiaceae; and in smaller numbers of genera (often only in one or part of one genus) in the Amaranthaceae, Compositae, Euphorbiaceae, Nyctaginaceae, Portulacaceae, Molluginaceae, Zygophyllaceae, Boraginaceae, and Caryophyllaceae. No family is all Kranz and many genera contain both Kranz and non-Kranz species. Kranz species range in habitat from very wet (some species of *Cyperus*, some grasses, some Hawaiian species of *Chamaesyce*, etc.) to very arid (*Atriplex*, *Kallstroemia*, *Tidestromia*, and some grasses), but are almost always found in bright sunlight and usually in hot regions (Kawanabe, 1968; Björkman, et al., 1972; Troughton, et al., 1974).

It has long been recognized that certain taxa (genera, tribes, and subfamilies) are entirely either Kranz or non-Kranz. Realization that some taxa are anatomically heterogeneous developed slowly: Holm (1901) and de Winter (1965) for Aristideae; Potztal (1952) and Tateoka (1957) for Panicoideae and Paniceae; de

Wet (1954) for Danthonieae; Brown (1958) for *Panicum*. During the 1960's numerous studies confirmed that the Paniceae and *Panicum* contain both Kranz and non-Kranz taxa. This was made very evident in a survey of the family by $^{13}C/^{12}C$ ratios (Smith and Brown, 1973).

The primary intent of this investigation was to survey as many genera and species of the Paniceae as possible, and many sections and species of *Panicum*. Though each of these taxa was known to contain both Kranz and non-Kranz species, only a minority had actually been characterized by any of the techniques known to differentiate the two states. The anatomical and physiological data acquired were to be analyzed for taxonomic significance at the generic and sectional levels.

In addition, selected species from other tribes of the Panicoideae as well as from other subfamilies, especially the Danthonieae, Aristideae, and Eragrostoideae, were to be studied similarly.

As originally planned, the investigation was to be of $^{13}C/^{12}C$ ratios; study of leaf anatomy came later. The latter soon became the more significant as it revealed relationships between Kranz anatomical subtypes and C_4 biochemical subtypes. The overall investigation promoted studies, some quite extensive, of the Cyperaceae and certain dicotyledonous families (Webster, Brown, and Smith, 1975, of the Euphorbiaceae; Smith and Turner, 1975, of the Compositae; and others now underway).

MATERIALS AND METHODS

Nearly all the materials examined were from herbarium specimens. Such material is as good as living for determining $^{13}C/^{12}C$ ratios, and for most of the anatomical study it was quite adequate, excepting a few species. Specimens were borrowed from herbaria with permission to remove samples. The herbaria providing them are listed, with their abbreviations, under "Terminology and notation." Each specimen tested was ticketed, stating the $^{13}C/^{12}C$ ratio and/or the type of leaf anatomy (N for non-Kranz; K, M.S. for the M.S. subtype of Kranz anatomy; or K, P.S. for the P.S. subtype of Kranz anatomy).

Pieces of leaves for anatomical study were boiled a few minutes and then freehand cross sections were cut with a sharp razor blade in water under a dissecting microscope. The sections were examined in water under a cover glass with a compound microscope. A second procedure was also followed for Kranz species and for those difficult to characterize as Kranz or non-Kranz from cross sections. A boiled piece was positioned in water, flat on the stage of the dissecting microscope, adaxial (upper) side up. It was then repeatedly scraped parallel to the stage with a razor blade until some lower epidermis became visible. In water under a cover glass, the paradermal appearance of the bundle sheath and Kranz cells was then observed with a compound microscope (Brown, 1974, 1975).

$^{13}C/^{12}C$ ratios (or $\delta^{13}C$ ‰ numbers) were determined as follows. Dried tissue (5–10 mg) was burned at 800° C in an excess of oxygen, and isotope ratios of the CO_2 evolved were measured on a Nier-type mass spectrometer modified according to McKinney, et al. (1950). Results are reported relative to a carbonate standard in terms of $\delta^{13}C$, calculated according to the formula

$$\delta^{13}C\ ‰ = 1000\ [(R\ sample/R\ standard) - 1]$$

where R = mass 45/mass 44 of sample or standard CO_2. The standard used was carbonate from the fossil skeleton of *Belemnitella americana* from the Peedee formation of South Carolina (the PDB standard). Sample replication was ± 0.2 ‰, but different samples of a species taken from different locations can vary by a few parts per thousand. For this work it is meaningful only whether a ratio falls in the high, C_4 range (−9 to −18 ‰) or in the low, C_3 range (−22 to −36 ‰). As far as known there is always a gap of at least 4 ‰ between high and low ranges in grasses, which makes this a very reliable method of characterizing a sample as C_3 or C_4 (Smith and Epstein, 1971).

TERMINOLOGY AND NOTATION

N or Non-Kranz—Having no specialized Kranz tissue in the leaves, an anatomical condition correlated with C_3 photosynthesis. For description see text.

K or Kranz—Having specialized Kranz tissue in the leaves, an anatomical condition correlated with C_4 photosynthesis. For description see text.

Subscripts of N or K:
  a—Determined by anatomical examination.
  r—Inferred from determination of photosynthetic type by $^{13}C/^{12}C$ ratio.
  c—Inferred from determination of photosynthetic type by CO_2 compensation point.
  e—Determined by electron microscopic examination.

M.S.—That subtype of Kranz anatomy in which the Kranz sheath has evolved from a mestome sheath. For description see text.

P.S.—That subtype of Kranz anatomy in which the Kranz sheath has evolved from a parenchyma sheath. For description see text.

D.S.—That subtype of Kranz anatomy in which a double Kranz sheath is present; limited to *Aristida*. For description see text.

$\delta^{13}C$—$^{13}C/^{12}C$ ratio: −9 to −18 ‰ = C_4 photosynthesis (Kranz); −22 to −35 ‰ = C_3 photosynthesis (non-Kranz).

C_3—Having the Calvin (Calvin-Benson) type of photosynthetic dark reaction. For description see text.

C_4—Having the Hatch-Slack type of photosynthetic dark reaction. For description see text.

NADP-me—That subtype of C_4 photosynthesis in which NADP-malic enzyme is the dominant decarboxylase in the Kranz tissue.

NAD-me—That subtype of C_4 photosynthesis in which NAD-malic enzyme is the dominant decarboxylase in the Kranz tissue.

PEP-ck—That subtype of C_4 photosynthesis in which PEP-carboxykinase is the dominant decarboxylase in the Kranz tissue.

Herbaria:
  K—Royal Botanic Gardens, Kew, England.
  NSW—National Herbarium, Sydney, Australia.
  P—Laboratoire de Phanerogamie, Muséum National d'Histoire Naturelle, Paris, France.
  PRE—National Herbarium, Pretoria, Republic of South Africa.
  TEX—University of Texas, Austin.
  US—U. S. National Herbarium, Smithsonian Institution, Washington, D. C.

THE PANICEAE

The significant early contribution of leaf anatomy to grass systematics was the belief that major taxa (subfamilies, tribes, subtribes, and genera) uniformly had either Kranz or non-Kranz anatomy. For example, all taxa of the subfamily Panicoideae were reported to have Kranz anatomy, hence the term "panicoid" for that type of leaf anatomy (Hubbard, 1948). Many Kranz genera and subtribes of the putatively non-Kranz Festucoideae were transferred to the Panicoideae on this basis, but that produced the need for a second Kranz subfamily, the Eragrostoideae.

During the 1950's it became evident (in

retrospect) that some Panicoideae did not have panicoid leaf anatomy. Potztal (1952) reported "festucoid" leaf anatomy in the small tribe Isachneae of the Panicoideae. Tateoka (1956a) and Brown (1958) observed the same in a few genera of the Paniceae, including *Panicum*. Smith and Brown (1973), Ellis (1974a), and others during recent years have reported festucoid anatomy in additional species of *Panicum* and other genera of Paniceae. This inconsistency in terms has led to the use of "non-Kranz" for "festucoid" and "Kranz" for "panicoid" leaf anatomy (Brown, 1975).

Throughout the remainder of the text it is assumed that all species having M.S. anatomy are NADP-me, those with P.S. anatomy and centripetal chloroplasts are NAD-me, and those with P.S. anatomy and centrifugal chloroplasts are PEP-ck. These are presently acceptable generalizations which will be treated as facts.

The methods used and materials available permitted examination of at least one (and usually more) species in each of essentially all genera of the Paniceae. Often, more than one specimen of a species was examined to confirm observations. Little attempt was made to check the validity of the names found on specimen sheets. Therefore, some names reported may be incorrect.

As Hsu (1965) discovered, it is impossible to discuss the rest of the Paniceae separately from the genus *Panicum*. This is true partly because *Panicum* constitutes a large part of the tribe. Furthermore, the transfer of many species and sections out of *Panicum* by some agrostologists but not by others requires balanced consideration. And the two taxa are further entangled because all the discussed variations found in the tribe are also found within the genus. Such extreme diversity in putatively fundamental taxonomic characters, leaf anatomy and photosynthesis types, within one genus indicates a peculiar relationship to the higher inclusive taxon. The two have been treated here in separate sections for simplicity and clarity. However, throughout the discussion of each, references to the other are numerous.

Table 3 reports data for 297 species of 86 genera examined. Excluded are species of *Panicum* and *Dichanthelium*, which are treated separately. Numbers in parentheses following specific names indicate the numbers of specimens examined for $\delta\,^{13}C$ and/or anatomy. Table 4 summarizes data for 90 genera of Paniceae, including *Panicum* and *Dichanthelium*.

This survey of the Paniceae is very complete for genera. Bews (1929) listed about 60 genera now considered to belong in Paniceae. Pilger (1954) listed 79 genera as constituting the tribe. The 86 genera covered here do not include five listed by Pilger, but do include a number of presently recognized or tentative genera not listed by him (such as *Psilochloa*, *Paraneurachne*, *Thyridolepis*, *Pseudobrachiaria*, and *Dichanthelium*). About eight genera of Paniceae are lacking along with other genera included by some but excluded by Pilger and the author (such as *Anthephora* and *Trachys*). The small panicoid tribes recognized by Pilger (Anthephoreae, Arthropogoneae, Arundinelleae, Cyphochlaeneae, Lecomtelleae, Melinideae, and Trachyeae) are also excluded from Paniceae here and treated separately.

TABLE 3. *Species of Paniceae (less* Panicum*) examined, arranged by genera: anatomical and photosynthetic characters, provenances, and voucher herbaria; with new combinations under* Steinchisma.

	$\delta^{13}C$	Anat.	Prov.	Herb.
Acroceras amplectans	−21.1	Nr	Africa	US
basicladum	−27.3	Nr	Africa	US
macrum	−26.1	Nr	Africa	US
munroanum	−28.8	Nr	Asia	US
paucispicatum (see text)	−11.6	P.S.	S. Am.	TEX
pilgerana (see *Psilochloa*)				
tonkinensis (see Neohusnotia)				
zizanioides (4)	−29.8	Nar	S. Am.	TEX
Acritochaete volkensii	−30.7	Nr	Africa	US
Alloteropsis angusta (2)	−12.2	M.S.	Africa	PRE
cimicina (see *Coridochloa*)				
gwebiensis (2)	−11.9	M.S.	Africa	PRE
paniculata (see *Coridochloa*)				
quintasii (see *Coridochloa*)				
semialata (17)	ca. −11	M.S.	various	many
var. *eckloniana* (8)	ca. −26	Nar	Africa	PRE
Amphicarpum purshii	−26.7	Nar	U.S.A.	TEX
muhlenbergianum	−28.1	Nar	U.S.A.	TEX
Ancistrachne uncinulata	−24.4	Nr	Aust.	US
Anthaenantia rufa	−12.2	M.S.	U.S.A.	TEX
villosa	−15.3	M.S.	U.S.A.	TEX
Anthaenantiopsis rajasiana	−12.3	M.S.	S. Am.	US
perforata	−12.0	M.S.	S. Am.	US
Axonopus affinis	−10.6	M.S.	U.S.A.	TEX
appendiculatus		M.S.	S. Am.	TEX
deludens		M.S.	S. Am.	TEX
scoparius	−10.8	M.S.	S. Am.	TEX
Beckeropsis procera	−18.1	M.S.	Africa	US
uniseta		M.S.	Africa	TEX
Bracheria brizantha		P.S.	Africa	TEX
ciliatissima		P.S.	U.S.A.	TEX
decumbens		P.S.	Africa	TEX
echinulatum		P.S.	S. Am.	TEX
eruciformis		P.S.	Aust.	TEX
foliosa		P.S.	Aust.	TEX
leucantha		P.S.	Africa	TEX
mutica		P.S.	Africa	TEX
marlothii		P.S.	Africa	TEX
negropedata		P.S.	Africa	TEX
ophryodes		P.S.	Mexico	TEX
plantaginea		P.S.	Mexico	TEX
platyphylla	−12.7	P.S.	U.S.A.	TEX

Table 3 continued.

	$\delta^{13}C$	Anat.	Prov.	Herb.
poaeoides	−13.2	P.S.	Africa	US
ramosa		P.S.	India	TEX
reptans	−11.4	P.S.	World	TEX
ruzizensis		P.S.	Africa	TEX
scalaris		P.S.	Africa	TEX
serrata		P.S.	Africa	TEX
xantholeuca		P.S.	Africa	TEX
Calyptochloa gracillima	−25.1	Nr	Aust.	US
Cenchrus ciliaris (2)	−11.3	M.S.	U.S.A.	TEX
incertus	−11.5	M.S.	U.S.A.	TEX
myosuroides	−11.9	M.S.	U.S.A.	TEX
palmeri		M.S.	Mexico	TEX
tribuloides		M.S.	U.S.A.	TEX
Centrochloa singularis	−13.1	M.S.	S. Am.	US
Chaetium bromoides (3)	−12.2	P.S.	Mexico	TEX
cubanum (3)	−12.4	M.S.	Cuba	US, TEX
festucoides (2)	−12.5	M.S.	S. Am.	US, TEX
Chamaeraphis hordeacea	−12.2	M.S.	Aust.	US
Cleistochloa subjuncea	−23.8	Nr	Aust.	TEX
sclerachne	−26.6	Nr	Aust.	US
Chloachne oplismenoides	−29.6	Nr	Africa	PRE
Commelinidium gabunensis	−32.6	Nr	Africa	US
meyumbense	−27.9	Nr	Africa	US
nervosum	−31.0	Nr	Africa	US
Coridochloa cimicina (5)	ca. −13	P.S.	various	PRE
quintasii (2)	−12.9	P.S.	Africa	PRE
paniculata	−13.0	P.S.	Africa	PRE
Cymbosetaria sagittifolia	−12.1	M.S.	Africa	PRE
Cyrtococcum accrescens	−29.1	Nr	Africa	US
chaetophoron	−31.7	Nr	Africa	US
oxyphyllum	−28.8	Nr	Aust.	US
patens	−28.6	Nr	Africa	US
trigonum	−31.6	Nr	Asia	US
Dichanthelium (73 species, all)		Nar	Amer.	TEX, US
Digitaria adscendens	−11.6	Kr	U.S.A.	TEX
decumbens		M.S.	Africa	TEX
longifolia	−13.7	M.S.	Africa	US
perrottetii		M.S.	Africa	US
sanguinalis	−12.7	M.S.	U.S.A.	TEX
smutsii		M.S.	Africa	TEX
zeyheri	−11.2	M.S.	Africa	US
Dimorphochloa rigida	−25.6	Nar	Aust.	NSW
Dissochondrus biflorus	−13.1	M.S.	Hawaii	TEX
Echinochloa colonum		M.S.	U.S.A.	TEX
crusgalli	−11.4	M.S.	U.S.A.	TEX

Table 3 continued.

	$\delta^{13}C$	Anat.	Prov.	Herb.
cruspavonis		M.S.	U.S.A.	TEX
haploclada	−11.6	M.S.	Africa	US
holciformis		M.S.	Africa	TEX
lulubii		M.S.	Africa	US
oplismenoides	−15.3		S. Am.	TEX
paludigena		M.S.	U.S.A.	TEX
polystachya		M.S.	U.S.A.	TEX
pyramidalis		M.S.	Africa	TEX
walteri		M.S.	U.S.A.	TEX
zelayensis	−12.3	M.S.	Aust.	US
Echinolaena gracilis	−29.5	Nr	S. Am.	US
inflexa	−26.2	Nr	S. Am.	US
madagascariensis	−29.6	Nr	Madag.	US
Entolasia imbricata	−27.3	Nr	Africa	PRE
marginata	−27.3	Nr	Aust.	NSW
stricta	−24.2	Nr	Aust.	NSW
Eriochloa aristata	−12.8	P.S.	U.S.A.	TEX
borumensis		P.S.	Africa	TEX
contracta		P.S.	U.S.A.	TEX
distachya		P.S.	S. Am.	TEX
gracilis		P.S.	U.S.A.	TEX
lemmonii		P.S.	Mexico	TEX
michauxii	−11.9	P.S.	U.S.A.	TEX
nelsonii		P.S.	Mexico	TEX
nubica (2)		P.S.	Africa	TEX
platystachya		P.S.	S. Am.	TEX
punctata	−11.8	P.S.	U.S.A.	TEX
ramosa		P.S.	S. Am.	TEX
sericea	−16.3	P.S.	U.S.A.	TEX
villosa (2)		P.S.	Asia	TEX
Holcolemma caniculatum	−11.7	M.S.	Asia	US
Homolepis aturensis (2)	−27.6	Nr	S. Am.	TEX
isocalycia	−28.4	Nr	S. Am.	US
Homopholis belsonii	−23.9	Nr	Aust.	US
Hymenachne acutigluma	−27.1	Nr	Asia	US
amplexicaulis (3)	ca. −28	Nr	S. Am.	US
assamica		Na	Asia	US
donacifolia	−28.3	Nr	S. Am.	TEX
hemitonom (see text)	−25.2	Nr	U.S.A.	TEX
pseudo-interrupta	−25.8	Nr	Asia	US
Ichnanthus australiensis (2)	−13.0	Kar	Aust.	NSW, US
bambusiflorus	−27.7	Nr	S. Am.	US
brevivaginatus	−32.4	Nr	S. Am.	US
candicans	−29.1	Nr	S. Am.	TEX
camporum	−29.0	Nr	S. Am.	US

Table 3 continued.

	$\delta^{13}C$	Anat.	Prov.	Herb.
confertus	−29.9	Nr	S. Am.	US
foliolosus	−12.0	Kr	Asia	KEW
latifolius	−29.6	Nr	S. Am.	US
nemorosus	−26.3	Nr	S. Am.	US
pallens (3)	ca. −31	Nr	S. Am.	TEX
pauciflorus	−11.8	Kr	Aust.	US
procurrens		Na	S. Am.	US
trinii	−25.3	Nr	S. Am.	US
venezuelanus	−28.8	Nr	S. Am.	US
vicinus	−29.3	Nr	S. Am.	US
Ixophorus unisetus (3)	−12.3	M.S.	Mexico	US, TEX
Lasiacis divaricata	−25.6	Nar	S. Am.	TEX
grisebachii	−27.5	Nar	S. Am.	US
linearis		Na	S. Am.	US
procerrima	−25.8	Nr	S. Am.	TEX
rugelii		Na	S. Am.	US
ruscifolia	−24.4	Nr	S. Am.	TEX
sloanei		Na	S. Am.	US
Leptocorypheum lanatum	−11.0	M.S.	S. Am.	TEX
Leptoloma arenicola		M.S.	U.S.A.	TEX
cognatum	−12.2	M.S.	U.S.A.	TEX
Leptasaccharum filiforme	−11.0	M.S.	S. Am.	US
Leucophrys glomerata (2)		P.S.	Africa	US, TEX
mesocoma (Ellis)		P.S.	Africa	PRE
Megaloprotachne albescens	−12.0	M.S.	Africa	PRE
Mesosetum filifolium	−12.3	M.S.	S. Am.	US
loliiforme	−12.3	M.S.	S. Am.	US
pittieri	−12.5	M.S.	S. Am.	TEX
Microcalamus aspidistrula	−33.6	Nr	Africa	PRE
Neohusnotia tonkinensis	−29.4	Nr	Asia	US
Neurachne munroi (3)	−13.3	M.S.	Aust.	NSW
Odontelytrum abyssinicum	−13.5	M.S.	Africa	PRE
Oplismenopsis najada	−26.9	Nr	S. Am.	US
Oplismenus burmannii	−27.5	Nr	S. Am.	TEX
hirtellus (2)	−31.0	Nar	Mexico	TEX
rariflorus		Na	S. Am.	TEX
setarius	−26.2	Nr	U.S.A.	TEX
Oryzidium barnardii	−12.8	P.S.	Africa	PRE, US
Otachyrium inaequale	−26.8	Nar	S. Am.	US
pterigodium	−27.2	Nar	S. Am.	US
versicolor	−25.3	Nar	S. Am.	US
Ottochloa arnottiana	−26.6	Nar	Africa	US
fusca	−26.0	Nr	Asia	US
gracillima	−30.4	Nr	Aust.	US
nodosa	−27.1	Nar	Asia	US

Table 3 continued.

	$\delta^{13}C$	Anat.	Prov.	Herb.
Panicum (241 spp. of all sorts.)				
Paractaenum novae-hollandiae	−12.3	M.S.	Aust.	US
Paraneurachne muelleri (3)	ca. −12	M.S.	Aust.	TEX, US
(Jacobs)	Ka		Aust.	NSW
Paratheria prostrata	−11.0	M.S.	Africa	PRE
Paspalidium constrictum	−14.6	M.S.	Aust.	NSW
flavidum		M.S.	Aust.	NSW
geminatum (2)	−11.3	M.S.	Aust.	NSW, TEX
jubiflorum (2)	−11.9	M.S.	Aust.	US
paludivagum	−12.8	M.S.	U.S.A.	TEX
punctatum	−11.9	M.S.	Asia	US
Paspalum decumbens		M.S.	S. Am.	US
distichum		M.S.	U.S.A.	TEX
fimbriatum	−12.5	M.S.	S. Am.	US
floridanum		M.S.	U.S.A.	TEX
inaequivalve		M.S.	S. Am.	US
langei		M.S.	U.S.A.	TEX
lineispatha		M.S.	S. Am.	US
longicuspe		M.S.	Mexico	TEX
macrophyllum		M.S.	S. Am.	US
monostachyum		M.S.	U.S.A.	TEX
notatum (Bender, 1968)	(−13.2)	M.S.	U.S.A.	
publiflorum	−12.6	M.S.	U.S.A.	TEX
repens		M.S.	S. Am.	US
saccharoides	−11.6	M.S.	S. Am.	US
sericatum		M.S.	S. Am.	US
sodiroanum		M.S.	S. Am.	US
stellatum	−11.8	M.S.	S. Am.	US
urvillei	−13.3		U.S.A.	TEX
vaginatum		M.S.	S. Am.	US
Pennisetum purpureum (2)		M.S.	C. Am.	TEX
setosum (2)	−14.7	M.S.	S. Am.	TEX
villosum		M.S.	U.S.A.	TEX
Phanopyrum gymnocarpon (2)	−29.1	Nar	U.S.A.	TEX
Plagiosetum refractum	−12.3	M.S.	Aust.	US
Poecilostachys festucaceus	−31.5	Nr	Africa	PRE
Pseudechinolaena polystachya	−30.4	Nr	World	TEX
madagascariensis	−29.9	Nr	Madag.	P
Pseudobrachiaria deflexa (3)	−12.2	P.S.	Africa	PRE, TEX
Pseudochaetochloa australiensis	−11.4	M.S.	Aust.	US
Pseudoraphis paradoxa	−12.0	M.S.	Asia	US
spinescens	−10.8	M.S.	Asia	US
Psilochloa pilgerana	−11.9	P.S.	Africa	PRE
Reimarochloa acuta (2)	−12.2	M.S.	S. Am.	TEX

Table 3 continued.

	$\delta^{13}C$	Anat.	Prov.	Herb.
Sacciolepis africana	−26.5	Nr	Africa	TEX
campestris	−24.5	Nr	S. Am.	TEX
curvata (2)	−26.3	Nr	Africa	PRE, TEX
delicatula	−25.9	Nr	Madag.	US
glaucescens	−24.7	Nr	Africa	US
indica	−26.1	Nr	India	US
micrococca	−26.4	Nr	Africa	US
myuros	−24.9	Nr	S. Am.	TEX
interrupta	−24.3	Nr	Africa	US
striata	−27.1	Nr	U.S.A.	TEX
strumosa	−24.9	Nr	S. Am.	TEX
transbarbata	−25.9	Nr	Africa	US
Scutachne amphistemon	− 9.2	P.S.	W. Ind.	US
dura	−15.7	P.S.	W. Ind.	US
Setaria barbata	−10.8	M.S.	S. Am.	US
chevalieri		M.S.	Africa	TEX
globulifera	−12.5	M.S.	S. Am.	US
italica	−13.8	M.S.	cult.	TEX
leiantha		M.S.	S. Am.	US
leucopila		M.S.	U.S.A.	TEX
magna		M.S.	U.S.A.	TEX
membranifolia	−12.0	M.S.	S. Am.	US
palmifolia		M.S.	S. Am.	TEX
paniculifera (3)		M.S.	S. Am.	TEX
poiretiana	−11.2	M.S.	S. Am.	US
scandens	−12.1	M.S.	S. Am.	US
scheelei	−12.6	M.S.	U.S.A.	TEX
viridis (Bender, 1968)	(−13.3)	M.S.	U.S.A.	TEX
Paurochaetium (subgenus)				
chapmanii (2)		M.S.	Cuba	TEX
distantiflorum		M.S.	Cuba	TEX
firmulum		M.S.	U.S.A.	TEX
leonis		M.S.	Cuba	TEX
ophiticola		M.S.	Cuba	TEX
ramisetum	−11.7	M.S.	U.S.A.	TEX
reverchonii	−11.9	M.S.	U.S.A.	TEX
utowaneum		M.S.	W. Ind.	TEX
Setariopsis auriculata		M.S.	Mexico	TEX
latiglumis	−12.2	M.S.	Mexico	TEX
Spheneria kegelii (2)	−11.9	M.S.	S. Am.	US, TEX
Spinifex littoreus	−12.2	P.S.	Asia	US
Steinchisma (see text)				
cuprea[1] (2)	−26.9	Nr	S. Am.	US, TEX
decipiens[2]	−26.7	Nr	S. Am.	US
exiguiflora[3] (2)	−28.1	Nr	S. Am.	US, TEX

Table 3 continued

	$\delta^{13}C$	Anat.	Prov.	Herb.
hians (3)	−26.0	Nr	U.S.A.	TEX
milioides (10)	ca. −26	Nar	S. Am.	TEX
Stenotaphrum secundatum	−15.7	M.S.	world	TEX
Stereochlaena cameronii	−10.8	M.S.	Africa	US
Streptolophus sagittifolius	−11.6	M.S.	Africa	US
Streptostachys asperifolium	−27.0	Nr	S. Am.	US
Tarigidia aequiglumis	−11.3	M.S.	Africa	PRE
Thrasya campylostachya	−12.0	M.S.	S. Am.	US
petrosa	−12.2	M.S.	C. Am.	US
trinitensis		M.S.	S. Am.	TEX
Thrasyopsis cinerascens	−11.0	M.S.	S. Am.	US
repandum	−11.1	M.S.	S. Am.	US
Thuarea involuta (2)	−12.2	P.S.	Asia	US
Thyridolepsis alopecuroides (2)	−26.1	Nar	Aust.	US, NSW
mitchelliana (2)	−25.3	Nar	Aust.	NSW
multiculmis (Jacobs)		Na	Aust.	NSW
xerophila (Jacobs)		Na	Aust.	NSW
Trichachne californica	−11.2	M.S.	U.S.A.	TEX
hitchcockii		M.S.	Mexico	TEX
insularis		M.S.	U.S.A.	TEX
sacchariflora		M.S.	Mexico	TEX
Triscenia ovina (2)	−31.6	Nr	Cuba	US, TEX
Uranthoecium truncatum (2)	−11.7	M.S.	Aust.	US
Urochloa bolbodes		P.S.	Africa	TEX
helopus	−10.8	P.S.	Africa	US
mosambicensis	−12.1	P.S.	Africa	TEX
panicoides	−11.5	P.S.	Africa	US
pullulans		P.S.	Africa	TEX
Xerochloa barbata	−12.1	M.S.	Aust.	US
cheribon	−11.0	M.S.	Aust.	US
laniflora	−12.2	M.S.	Aust.	NSW
Zygochloa paradoxa	−14.2	M.S.	Aust.	US

[1] ***Steinchisma cuprea, comb. nov.:*** *Panicum cupreum* Hitchcock & Chase, Contr. U.S. Natl. Herb. 15:120. 1910.

[2] ***Steinchisma decipiens, comb. nov.:*** *Panicum decipiens* Nees, Agrost. Bras., 193; in Martius, Flora Bras. 2. 1829.

[3] ***Steinchisma exiguiflora, comb. nov.:*** *Panicum exiguiflorum* Griseb., Cat. Pl. Cuba, 234. 1866.

The coverage of species is much less complete, especially for large genera such as *Digitaria*, *Setaria*, *Sacciolepis*, *Ichnanthus*, *Paspalum*, *Axonopus*, *Brachiaria*, and *Pennisetum*. Nevertheless, these large genera were deliberately surveyed for unusual subgeneric types and, in combination with other data on leaf anatomy accumulated during the past hundred years, I believe this was adequate to characterize them quite reliably. The species of Paniceae examined, including those of *Dichanthelium* (72) and *Panicum* (241) treated separately, total 610, or more than one third of the tribe.

As summarized in Table 4, the Paniceae include many genera (33) that are non-Kranz, nearly 38 percent, and more (57) that are Kranz, about 62 percent. The Kranz genera are of two subtypes: M.S., 44 genera, about 78 percent; and P.S., 13 genera, about 22 percent.

TABLE 4. *Genera of Paniceae examined, arranged according to types of leaf anatomy and photosynthesis.*[1] *Approximate total numbers of species per genus (Hubbard, 1973) given in parentheses.*

NON-KRANZ	KRANZ	
	M.S., NADP-me	*P.S., NAD-me and PEP-ck*
Acroceras (15)	*Anthaenantia* (2)	*Brachiaria* (PEP-ck) (60)
Acritochaete (1)	*Anthaenantiopsis* (1)	*Eriochloa* (PEP-ck) (20)
Alloteropsis (1)	*Alloteropsis* (4)	*Coridochloa* (3)
Amphicarpum (2)	*Axonopus* (35)	*Leucophrys* (2)
Ancistrachne (2)	*Beckeropsis* (6)	*Oryzidium* (1)
Calyptochloa (1)	*Cenchrus* (25)	*Pseudobrachiaria* (PEP-ck) (1)
Chloachne (2)	*Centrochloa* (1)	*Psilochloa* (1)
Cleistochloa (2)	*Chaetium* (2)	*Chaetium* (1)
Commelinidium (3)	*Chamaeraphis* (1)	*Scutachne* (2)
Cyrtococcum (12)	*Cymbosetaria jl(l)*	*Thuarea* (2)
Homopholis (1)	*Digitaria* (380)	*Urochloa* (PEP-ck) (25)
Panicum (100+)	*Panicum* (20+)	*Panicum* (NAD-me) (117+)
Dichanthelium (120)	*Dissochondrus* (1)	*Spinifex* (3)
Dimorphochloa (1)	*Echinochloa* (30)	
Echinolaena (6)	*Holocolemma* (2)	
Entolasia (5)	*Ixophorus* (3)	
Homolepis (3)	*Leptocorypheum* (1)	
Hymenachne (8)	*Leptoloma* (2)	
Ichnanthus (26)	*Leptosaccharum* (1)	
Lasiacis (30)	*Megaloprotachne* (1)	
Microcalamus (4)	*Mesosetum* (35)	
Thyridolepis (4)	*Neurachne* (5)	
Neohusnotia (4)	*Odontelytrum* (1)	
Oplismenopsis (1)	*Paractaenum* (1)	
Oplismenus (15)	*Paratheria* (2)	
Otachyrium (4)	*Paspalidium* (20)	
Ottochloa (6)	*Paspalum* (250)	
Phanopyrum (1)	*Pennisetum* (130)	
Poecilostachys (20)	*Plagiosetum* (1)	
Pseudechinolaena (2)	*Pseudchaetochloa* (1)	

Table 4 continued.

NON-KRANZ	KRANZ		
	M.S., NADP-me	*P.S., NAD-me and PEP-ck*	
Sacciolepis (30)	*Pseudoraphis* (7)		
Steinchisma (4)	*Reimarochloa* (5)		
Triscenia (1)	*Setaria* (140)		
	Setariopsis (2)		
	Stenotaphrum (7)		
	Stereochlaena (1)		
	Streptolophus (1)		
	Tarigidia (1)		
	Thrasya (15)		
	Thrasyopsis (2)		
	Trichachne (15)		
	Uranthoecium (1)		
	Xerochloa (4)		
	Zygochloa (1)		
Genera 33 Species 433+	Genera 44 Species 1170+	Genera 13 Species 237+	Total 86 Total 1,840

[1] *Alloteropsis*, *Chaetium*, and *Panicum* are listed in more than one column.

In general, any particular grass genus is either entirely Kranz or entirely non-Kranz. The only known exceptions are the very large genus *Panicum* and the small Old World genus *Alloteropsis*. For *Panicum*, it can be proposed that the genus is artificial and that the only true *Panicum* species are those which are Kranz P.S., NAD-me. In *Alloteropsis*, on the other hand, the only non-Kranz taxon is the South African variety *eckloniana* of the widespread *A. semialata*. If that variety is retained in its present status, this is the only angiosperm species presently known to contain both Kranz and non-Kranz elements.

As previously constituted, only three Kranz genera contain both M.S. and P.S. taxa: *Alloteropsis* (s. lat.); the small American genus *Chaetium;* and *Panicum*. In *Alloteropsis*, the P.S. taxa are here segregated as the revived genus *Coridochloa*. In *Panicum*, the P.S., PEP-ck taxa are removed to the *Urochloa-Brachiaria-Eriochloa* complex, and the very few M.S. taxa (Table 8) are candidates for new generic status. In *Chaetium*, the problem has not yet been resolved, but future taxonomic changes may result.

Two other cases of Kranz/non-Kranz distinction between similar genera exist: the Australian genus *Homopholis* is like a primitive, non-Kranz *Digitaria* (Dr. S. Jacobs, pers. comm.); and non-Kranz *Thyridolepis* is closely related to Kranz *Neurachne*. Jacobs also reports that a third genus, *Paraneurachne*, belongs in this latter Australian complex and that it has Kranz anatomy. Thus, within the group "Neurachneae" Blake there are two Kranz and one non-Kranz genera, among which, according to Jacobs, *Neurachne* seems to be the least specialized.

From the present sample of Paniceae, it seems evident that the tribe is heterogeneous; no other tribe or subfamily contains such large proportions of taxa representing each of the various types of photosynthetic biochemistry and leaf anatomy.

Some comments about a few other genera seem appropriate here.

Acroceras (type species, *A. zizanioides* Dandy) has included species with characters that warrant their removal. Hsu (1965) supported the transfer of *A. tonkinensis*, *A. amplectans*, and *A. macer* to *Neohusnotia* A. Camus. *Acroceras pilgerana* Schweick has recently been segregated as *Psilochloa pilgerana* (Schweick) Launert (1970). I find *P. pilgerana* to be Kranz whereas *Acroceras* and *Neohusnotia* are non-Kranz. Therefore, the erection of *Psilochloa* is supported. A southern South American species, *A. paucispicatum* (Morong) Henrard has Kranz P.S. anatomy, C_4 photosynthesis, racemose inflorescences, and transversely rugose lemmas. Since *Acroceras* (s. str.) is non-Kranz and has essentially smooth lemmas, *A. paucispicatum* is placed in the *Brachiaria* group (see later) for the present. However, it may deserve generic rank.

Most species with laterally compressed glume and lemma tips, by which *Acroceras* was considered distinguishable, were included in that genus. But now, with *Psilochloa* and *Neohusnotia* separated and *A. paucispicatum* removed from *Acroceras*, and in view of the fact that some species of *Mesosetum* also exhibit such compression (Chase, 1911), it becomes obvious that this characteristic is not of generic value. The laterally compressed tips may be the early stage of the evolution of awns. Among these taxa, the compression is most extreme in *A. paucispicatum*, here allied with *Brachiaria* and *Eriochloa*, some species of which do have awned glumes and/or lemmas.

Chase (1911) considered *Alloteropsis cimicina* of the Old World to be generically distinct from *A. semialata* and so retained it as *Coridochloa cimicina* (L.) Nees ex Jacks. Because the Kranz species of *Alloteropsis* have M.S. leaf anatomy whereas *Coridochloa* species are P.S., Ellis (in litt.) and I retain *Coridochloa* for the common Old World *C. cimicina* and the African *C. quintasii* (Mez) Pilger and *C. paniculata* (Benth.) Stapf.

Most of the Kranz P.S. genera listed in Table 4 seem to form two natural and related groups, one of which can be called the *Brachiaria* group. In general, genera of this P.S. group have racemose inflorescences and rough (papillate to rugose) fertile lemmas, although in *Brachiaria* and some other genera there are species with smooth lemmas. This group also includes certain taxa often included in *Panicum* (groups "Fasciculata" and "Purpurascentia," *P. reptans* L., etc.). Hsu (1965) and Stapf (1920) placed these in *Brachiaria* whereas Pilger (1940) included them in his subgenus *Urochloides* of *Panicum*. That this *Brachiaria* group is a natural one is supported by the biochemical evidence that *Brachiaria*, *Eriochloa*, *Urochloa*, and "Fasciculata" are, uniquely and rather uniformly, PEP-ck (Gutierrez, Edwards, and Brown, 1976). Therefore, all species in *Panicum* that are P.S., PEP-ck should be removed and placed either in *Brachiaria* or elsewhere in that group.

Dichanthelium has recently been elevated to generic rank (Gould, 1974). An extensive survey of 72 species has shown it to be a completely non-Kranz taxon (Brown and Smith, 1975) and therefore distinct from typical *Panicum*. Its transfer is also supported by this study and by the scanning electron microscope study of Clark and Gould (1975).

A large number of *Echinochloa* species was studied because Hsu (1965) placed that taxon among the unspecialized (non-Kranz) genera. Also, Clark and Gould (1975) reported a marked difference between it and typical *Panicum* in palea surface character. However, the whole genus seems to be Kranz M.S., the subtype typical of the tribe.

Under the non-Kranz genus *Ichnanthus* are listed three species that are Kranz. These, at least the Australian *I. australiensis* and *I. pauciflorus*, are actually neither *Panicum* nor *Ichnanthus* (Lazarides, 1959), but have not been reassigned yet. *Panicum majusculum* and *P. muelleri* (Table 6), both also Kranz species from Australia, present problems of placement along with *I. foliolosus*, a Kranz species from Burma. Stieber (1975) considers that these five Kranz species form a taxon distinct from both *Ichnanthus* and *Panicum*, leaving *I. vicinus* the sole Asiatic-African species in that genus, one closely related to the American *I. pallens*. Present evidence thus indicates that *Ichnanthus* is a completely non-Kranz genus.

Phanopyrum Nash has been retained for the unusual, non-Kranz American species usually treated as *Panicum gymnocarpon* Ell.

Within the large genus *Setaria* two problems were examined. It has already been established that some "typical" species of that genus are Kranz (Smith and Brown, 1973). However, it also includes a number of wide- and plicate-leaved, shade-tolerant or shade-requiring species, the subgenus *Ptychophyllum*. Such species might be expected to be non-Kranz, but those examined (*S. barbata, S. chevalieri, S. membranifolia, S. palmifolia, S. paniculifera,* and *S. poiretiana)* are all Kranz. A very unusual shade-requiring genus, *Microstegium*, of the wholly Kranz Andropogoneae is also typically Kranz M.S., and *M. vimineum* is NADP-me and C_4. Thus, as far as known, shade-requiring species of typically Kranz taxa remain Kranz. (See Table 11 and further discussion under "The Andropogoneae").

The second problem in *Setaria* involves the subgenus *Paurochaetium* of *Panicum*. In 1910, Hitchcock and Chase proposed this subgenus for 8 to 10 American species that have transversely rugose, apiculate lemmas, a bristle below the terminal spikelet on most branchlets of the panicles, few-flowered slender inflorescences, and narrow leaves, and that are xerophytes of bright sunlight. Pilger (1940), Rominger (1962), and Hsu (1965) considered these to be species of *Setaria*. The present study supports that transfer because: groups of Kranz *Panicum* species with rough lemmas seem better included in other genera, and most *Setaria* species have rugose lemmas; and the few groups in *Panicum* that have M.S. anatomy ("Agrostoidea," "Tenera," and "Plena") are otherwise very distinct from *Paurochaetium*, whereas *Setaria*, like most genera of Paniceae, is also M.S. The only other alternative is to raise *Paurochaetium* to generic rank.

Steinchisma Raf. was proposed for the single North American species generally designated as *Panicum hians* Elliott. Hitchcock and Chase (1910) proposed the informal group "Laxa" for 13 or more American species of *Panicum* usually characterized by spectacular enlargement of lower sterile floret paleas. This group included *P. hians* and *P. milioides* (the latter from southern South America) of recent scientific prominence. Study of these two species (Brown and Brown, 1975) prompted a detailed investigation of that group.

Hsu (1965) noted differences between *Panicum hians* and some other species of the group, notably that the fertile lemma is roughened by longitudinal rows of papillae, as illustrated by Clark and Gould (1975) for the palea. It is also true that two different sorts of inflorescence are present in the group. Condensed to open panicles are found in *P. hians*, *P. milioides*, *P. cupreum*, *P. exiguiflorum*, and *P. decipiens*, whereas *P. laxum* and most of the other species have spikelets borne on essentially unilateral racemes. Correlated with the paniculate type are fertile florets with rows of papillae; with the unilaterally racemose type, smooth fertile florets. Since these are characters given very high priority in the Paniceae, I propose to segregate the *P. hians* assemblage in the genus *Steinchisma* (Table 3) and leave the *P. laxum* assemblage in *Panicum* as the group "Laxa" (Tables 6, 7, and 8).

These two taxa also differ in habit and habitat. *Steinchisma* comprises basically erect plants usually growing in full sunlight, whereas "Laxa" contains mostly prostrate plants growing in partial to heavy shade.

It has recently been demonstrated that *Steinchisma milioides* and *S. hians* have character states intermediate between those usually associated with C_3 and C_4 plants. Brown and Brown (1975) and Brown (in press) have shown that these species have intermediate leaf anatomy, mostly centripetal chloroplasts with numerous associated mitochondria, and intermediate photorespiratory effects. Ku, Edwards, and Kanai (in press), and Kanai and Kashiwagi (1975) have shown that they are intermediate in anatomy and biochemical activities of numerous C_4 photosynthetic enzymes. Actually, *S. hians* (Ell.) Nash ex Small and *S. milioides* are conspecific (as Arechavaleta, 1894, proposed) on the basis of habit, spikelet and inflorescence characters, photosynthetic intermediacy, and flavonoids (author, unpublished). When the two are merged, the correct name under *Steinchisma* is *S. hians*.

Leaf anatomy of the Mexican species *Steinchisma cuprea* seems to be typically non-Kranz, at least by the criteria of Hattersley and Watson (1976). That of *S. exiguiflora* from Cuba and Haiti appears to be Kranz-like based on observation of embedded, stained sections, except that the walls of the "Kranz cells" are relatively thin. Details of the leaf anatomy of *S. decipiens* have not been studied. However, $^{13}C/^{12}C$ ratios of all species of the genus are within the C_3 range. It can be concluded, therefore, that *S. exiguiflora* should be intermediate between C_3 and C_4 types as is *S. hians*, but that *S. cuprea* can be expected to be rather typically C_3.

The monotypic *Tarigidia aequiglumis* Gossens may be a bigeneric hybrid of *Anthephora pubescens* Nees and a *Digitaria* species (Loxton, 1974).

The work reported here complements that of Hsu (1965), who examined quite different characters—of lodicules, style bases, leaf epidermis, and especially fertile lemma epidermis—in about 40 genera of Paniceae, including 96 species of *Panicum* (including *Dichanthelium*). From his data he worked out a "specialization index" based upon two or three alternative states for each character and upon assumptions as to which are most specialized (his Table 2). He then arranged the various genera accordingly (his Figure 11). The main vertical separation was: on the left, florets papillate or rugose; on the right, florets smooth or silicate. The main horizontal separation was: above, style bases united and lemmas thinner; below, style bases distinct and lemmas firmer. Thus, his figure has four quarters as well as some minor subdivisions. Table 5 is a modification of Hsu's figure but maintains his basic plan.

When the genera treated by Hsu are designated Kranz or non-Kranz, as determined in this study, nearly all of those he placed in the lower right quarter and in the lower third of the lower left quarter are non-Kranz. If subgenus *Panicum* and the genus *Echinochloa* are removed from his lower right quarter (they are both Kranz), and non-Kranz *Hymenachne* is brought down from the upper right to the lower right quarter, all non-Kranz genera of Paniceae, including the subgenera *Sarmentosum* and *Megathyrsum* of *Panicum*, occupy the lower right quarter and the bottom of the lower left quarter. A line can then be drawn around all the non-Kranz genera leaving all the Kranz genera outside and above.

According to Hsu's scheme, the non-Kranz, C_3 genera are thus the least specialized. He considered this group of genera with low specialization indices as the origin of the variously more specialized groups. That implies, therefore, that the Kranz genera probably evolved from this non-Kranz group. However, some Kranz groups in *Panicum* and the Kranz genus *Echinochloa* have Hsu specialization indices as low as those of any C_3 genera.

Evolutionary theory would also predict that the uncommon, biochemically and anatomically specialized Kranz condition has evolved from the very common and less specialized non-Kranz state.

The correlation between my results and those of Hsu, based upon very different and unrelated criteria, is excellent and

TABLE 5. *Genera of Paniceae, arranged according to a modification of Hsu's (1965) scheme. Numbers in parentheses are Hsu's specialization indices for the taxa he studied.*

<table>
<tr><th colspan="2">Lemmas rough</th><th>Lemmas smooth</th></tr>
<tr><td colspan="2">C_4, M.S., NADP-me
Digitaria, *Anthaenantia*, *Trichachne*, *Leptoloma* (7–8), *Leptocoryphium*, *Leptosaccharum*, *Stereochlaena*.</td><td>C_4, M.S. and P.S.
Cenchrus, *Pennisetum*, *Zygochloa*, *Thuarea*, *Beckeropsis*, *Spinifex*, *Stenotaphrum*, *Trachys*, *Pseudoraphis*, (5–8).</td></tr>
<tr><td colspan="3">Style bases united; lemmas thinner</td></tr>
<tr><td colspan="3">Style bases free; lemmas firmer</td></tr>
<tr><td>Lemmas rugose</td><td>Lemmas papillate</td><td></td></tr>
<tr><td colspan="2">C_4, M.S., NADP-me</td><td rowspan="2">C_4, M.S., NADP-me
Echinochloa (2), *Paratheria*, *Odontelytrum*, *Panicum* —a few American groups</td></tr>
<tr><td>*Ixophorus* (7)
Setaria (4–5)
Setariopsis (4)
Paspalidium (4)</td><td>*Alloteropsis* (5)
Paspalum (4–5)
Axonopus (4)
Holcolemma
Streptolophus</td></tr>
<tr><td colspan="2">C_4, P.S., PEP-ck</td><td rowspan="2">C_4, P.S., NAD-me
Panicum, subgenus *Panicum*. (1)</td></tr>
<tr><td>*Urochloa* (4)
Brachiaria (4)
Pseudobrachiaria
Psilochloa
Panicum, section *Fasciculatum*</td><td>*Chaetium* (6)
Eriochloa (4)
Coridochloa
Leucophrys
Oryzidium
Scutachne</td></tr>
<tr><td></td><td>C_3
Ottochloa (4)
Amphicarpum (4)
Panicum, subgenus *Megathyrsus* (4)
Neohusnotia (3)
Cyrtococcum (3)
Entolasia
Steinchisma</td><td>C_3
Hymenachne (6)
Pseudechinolaena (6)
Dichanthelium (5–7)
Panicum, subgenus *Sarmentosa* (3–4)
Sacciolepis (3)
Oplismenus (2)
Ichnanthus (2)
Acroceras (2)
Commelinidium (1)
Lasiacis (1)
Acritochaete
Chloachne
Microcalamus</td></tr>
</table>

greatly strengthens his assumptions as to which conditions are to be considered unspecialized and which specialized. It can be proposed, therefore, that non-Kranz genera having style bases free and firm lemmas are the least specialized of the Paniceae.

Another character Hsu considered significant in the Paniceae is the outer surface condition of the fertile florets, whether rough or smooth. The two alternatives seem equally represented among both Kranz and non-Kranz types. If this character is highly significant, if one state has rarely evolved into the other, then it can be proposed that there are two parallel lines of evolution within the Paniceae, one with smooth and one with rough fertile florets.

Most Kranz genera of Paniceae with less specialized inflorescences have style bases distinct and rough fertile florets, and are placed in Hsu's lower left quarter. Those with obvious specializations in the inflorescence (e.g., *Stenotaphrum, Spinifex, Cenchrus, Anthephora, Thuarea, Trachys,* and *Zygochloa*) have style bases united and smooth fertile florets, and appear in the upper right quarter. Perhaps, then, with inflorescence specialization fertile florets have become smooth and style bases have become united.

The few genera in Hsu's upper left quarter, genera characterized by united style bases, thin fertile lemmas that are not inrolled, and rough fertile florets, are the clearly related *Digitaria, Trichachne, Leptoloma, Anthaenantia, Leptocoryphium,* etc. (Stapf's subtribe *Digitarianinae* emended).

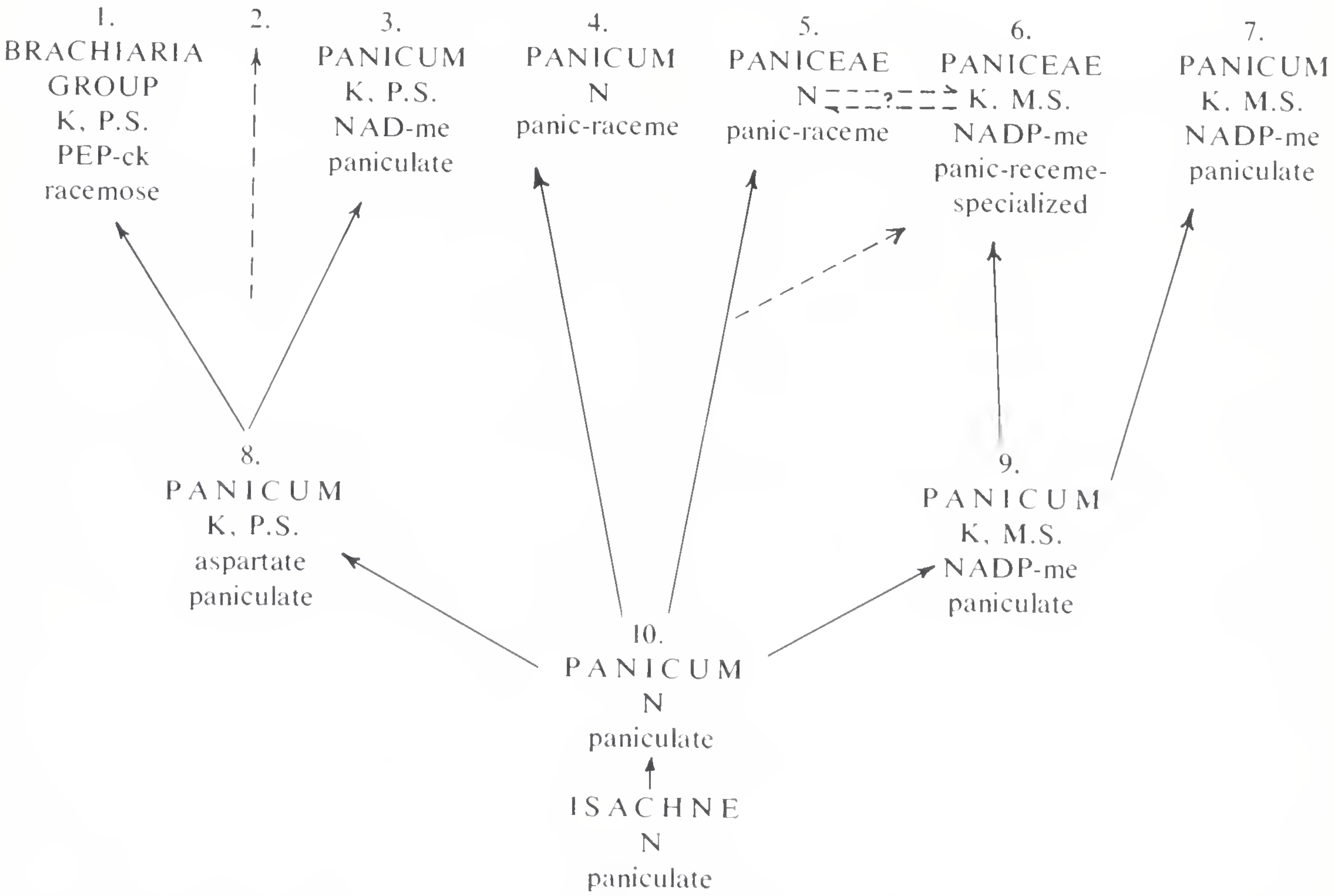
Almost all P.S. genera occupy the middle of Hsu's lower left quarter (*Urochloa, Brachiaria, Eriochloa,* and *Chaetium,* studied by Hsu and me, as well as *Coridochloa, Psilochloa, Leucophrys, Oryzidium, Scutachne, Pseudobrachiaria,* and some sections of *Panicum,* studied by me). These genera are similar morphologically, anatomically, and by Hsu's specialization index. The highly specialized P.S. genera *Spinifex* and *Thuarea* were placed by Hsu in the upper right quarter, and the P.S., NAD-me species of *Panicum* are distinct (Figure 1).

Figure 1 is an evolutionary scheme embodying major changes in arrangement of the Paniceae, based upon data from this study and the following assumptions. As generally accepted by agrostologists, racemose and more highly specialized inflorescences have evolved from the diffuse panicle, and the evolutionary tendency within the spikelet is from numerous florets toward one per spikelet. Evolution in leaf anatomy is from the general non-Kranz to the unusual and more complex Kranz types. Evolution progresses from the simple, common, Calvin-Benson (C_3) type of carboxylation to the biochemically unusual and more complex C_4 types. Of apparent necessity, these anatomical and biochemical characters have evolved together. There is no good evidence that evolution from C_4 to C_3, Kranz to non-Kranz has ever occurred. In general, evolution of the Kranz syndrome in the Gramineae occurred a few times fairly early in the history of the family. This assumption is based on the fact that *wholly* Kranz grass taxa are often large, such as the Andropogoneae, many genera of Paniceae, and the Eragrostoideae. Recent evolution of the syndrome would produce isolated species or genera that are partially Kranz and partially non-Kranz, such as *Chamaesyce* (Webster, Brown, and Smith, 1975), *Kallstroemia*, *Flaveria* (Smith and Turner, 1975), *Alternanthera*, *Mollugo*, and in grasses, *Alloteropsis semialata* and the group "Grandia" of *Panicum*.

The tropical, non-Kranz, panicoid tribe Isachneae is characterized by having two similar, seed-producing, indurated florets per spikelet. Such a condition is assumed to have been the evolutionary precursor of that found in the Paniceae. The latter typically have a single fertile floret per spikelet, a condition which probably evolved rapidly to produce the original, tropical, paniculate, non-Kranz *Panicum* (Figure 1, number 10), undergoing only minor subsequent alteration. Like *Isachne*, these were species of moist, shady habitats, of tropical forests and forest borders. They probably existed before the separation of Africa and South America and must have occurred in both areas.

It has already been remarked (Chase, 1911) that some species of *Isachne* resemble the American genus *Dichanthelium*, which may have evolved rather recently from some American species of the former, long after wide separation of the New and Old Worlds.

FIGURE 1. *Evolutionary scheme of the Paniceae.*



At some later time, some species of *Panicum* living in bright light evolved the Kranz syndrome with the M.S. type of leaf anatomy and the correlated NADP-me type of C_4 photosynthesis (number 9). This M.S. type is the common subsyndrome among the Kranz genera of Paniceae (Table 4) and occurs in all Andropogoneae. From a paniculate *Panicum* of this type the various modern genera of M.S. Paniceae have evolved (number 6). There are a few small groups of *Panicum* in America having this subsyndrome also (number 7), and the two lines might be combined.

Of course, there also must have been evolution from a non-Kranz *Panicum* type (number 10) to produce the numerous extant non-Kranz genera of Paniceae (number 5 and Table 4). A line of evolution was also maintained leading to extant non-Kranz *Panicum* (number 4), which perhaps should be combined with the other non-Kranz Paniceae as one general "line" of evolution.

At some time, in the evolutionary line of non-Kranz *Panicum*, some species evolved the P.S. type of anatomy and the associated aspartate type of C_4 photosynthesis (number 8). From such a paniculate *Panicum* have evolved, probably not at the same time, the typical modern NAD-me species of *Panicum* (number 3) and also the genera of the *Brachiaria* group that are characterized by PEP-ck photosynthesis and usually racemose inflorescences (number 1). Number 2 in Figure 1 designates any non-Panicum genera having P.S. anatomy and NAD-me photosynthesis, such as, possibly, *Oryzidium*, *Chaetium*, *Scutachne*, *Thuarea*, and *Spinifex* (Table 4).

This scheme suggests that the obviously heterogeneous *Panicum* is artificial and that all C_3 taxa (number 4) and all Kranz M.S., NADP-me taxa (number 7) should be removed because the type species, *P. miliaceum* L., is Kranz P.S., NAD-me. It also suggests the transfer of any PEP-ck species, the group "Fasciculata" for example, to the *Brachiaria* group (number 1). The latter and *Panicum* (number 3) have morphological intermediates, Stapf's section *Eriochloideae (P. meyeranum)*, *Pseudobrachiaria*, and "Fasciculata," but their type of C_4 photosynthesis is distinctive. When these taxa are placed in the *Brachiaria* group on that basis, the latter and *Panicum* become distinct and homogeneous.

If the tribe is to be divided phylogenetically into subtribes, it should be according to the foregoing scheme, assuming that leaf anatomy and photosynthesis types are indeed the best criteria for such subdivision. The following subtribal divisions (paralleling Table 4 and Figure 1) can be proposed.

Subtribe 1. Paniculate mostly, Kranz M.S., C_4 NADP-me. This taxon contains the largest number of genera and species (numbers 6 and 7, Figure 1; middle column, Table 4).

Subtribe 2. Non-Kranz, C_3 (numbers 4 and 5, Figure 1; first column, Table 4). This is the second largest subtribe.

Subtribe 3. Brachiariinae Butzin. Racemose, Kranz P.S., C_4 PEP-ck. A smaller but substantial and widespread group of genera allied to *Brachiaria* (number 1, Figure 1; part of third column, Table 4).

Subtribe 4. Panicinae Stapf. Paniculate, Kranz P.S., C_4 NAD-me. As here circumscribed, this subtribe includes only the numerous species of *Panicum* allied to *P. miliaceum*, its type species (number 3, Figure 1). It should perhaps also include a few genera from the third column of Table 4, those excluded from Subtribe 3 (number 2, Figure 1).

Subtribes 1 and 2 are very distinct from one another and from the others on these criteria. Subtribes 3 and 4 are, however, less distinct from each other. Both are aspartate formers and have the same basic anatomy. It does seem likely that they differ generally in chloroplast location within the Kranz cells. In *Panicum* the chloroplasts are centripetal, whereas in the *Brachiaria* group they are centrifugal (Gutierrez, Gracen, and Edwards, 1974). These same two types of aspartate former have been reported in the Eragrostoideae, also wholly P.S. At this time it is not known how fundamental or trivial is the difference between the NAD-me and PEP-ck types of C_4 photosynthesis.

As discussed earlier, there are a few possible exceptions to this scheme, one which assumes evolution of the Kranz syndrome two or three times during the early history of the tribe. The Australian non-Kranz *Thyridolepis* seems to be closely related to the Australian Kranz *Neurachne* and *Paraneurachne*, and the Australian non-Kranz *Homopholis* to the widespread Kranz *Digitaria*. These may represent two cases of more recent and independent evolution of the Kranz syndrome. Even more suggestive that evolution of the syndrome may have occurred very recently, in addition to early in the history of the tribe, is the previously discussed case of *Alloteropsis semialata/A. eckloniana*, in which both the Kranz and non-Kranz types are morphologically almost indistinguishable and possible intermediates occur in South Africa (Ellis, 1974b). There are also two other possible cases of recent evolution from non-Kranz to Kranz, within the "Grandia" group of *Panicum* and the Australian genus *Neurachne*. Nevertheless, in spite of such expected exceptions, the assumption that the Kranz syndrome did evolve a few times during the early evolution of the tribe remains acceptable.

Because the only grasses with M.S. leaf anatomy are the Andropogoneae and most of the Kranz Paniceae, and because these two tribes are related by spikelet characteristics, it seems evident that the recent Andropogoneae (Hartley, 1958a) evolved from some ancient M.S. Paniceae or, at least, Panicoideae.

It has been stated (Downton, 1971b) that the Kranz syndrome is an evolutionary adaptation to arid environments. There are, of course, Kranz species in arid regions, but there are many more in mesic areas. Among the Paniceae it is probably true that some Kranz species occupy drier habitats than do any non-Kranz species. But there are numerous Kranz species which grow in very wet places (in *Echinochloa*, *Paspalum*, *Axonopus*, *Oryzidium*, and *Paspalidium*), and there are non-Kranz species of dry habitats (in *Cleistochloa*, *Dichanthelium*, *Dimorphochloa*, *Thyridolepis*, and *Ichnanthus*).

The generalization that Kranz species are tropical has often been made, with the implication that non-Kranz species are not. Among the Paniceae both types extend over approximately the same latitudinal range, from about 45° N to 45° S. In North America, though both non-Kranz (*Dichanthelium*) and Kranz (*Panicum, Echinochloa, Paspalum, Setaria*, etc.) types extend about equally far north, many more Kranz species do so.

Full sunlight seems to be necessary for most Kranz species, except some in *Chamaesyce (Euphorbia)* and *Setaria*, and all of *Microstegium* (Andropogoneae). On the other hand, non-Kranz species tolerate light intensities ranging from deep shade in tropical forests to full sunlight in open tropical and subtropical habitats.

Of course, non-Kranz species of the Festuceae, etc. range into arctic and alpine regions where no Kranz species occur, and some species of Bambuseae, Oryzeae, etc. do grow in full tropical sunlight.

In warm temperate regions where the ground does not freeze during the winter, the non-Kranz festucoid grasses grow during the winter and early spring, whereas in late summer and early fall nearly all growing grasses are Kranz or else are non-Kranz species of subfamilies represented mainly in hot regions (Panicoideae, Eragrostoideae, Oryzoideae). That is, C_3 grasses of high latitude origins can and do grow during the winter in warm temperate regions, whereas C_3 *and* C_4 grasses of low latitude origins seem unable to do so. The climatic restrictions are thus independent of C_3/C_4 character.

PANICUM

It has been well established that within the genus *Panicum* all basic types of leaf anatomy and correlated types of photosynthetic systems occur (Downton, Berry, and Tregunna, 1969; Smith and Brown, 1973; Guteirrez, Gracen, and Edwards, 1974), just as they all occur among the rest of Paniceae. Because basic type of leaf anatomy, Kranz or non-Kranz, was the major basis for systematic revision elsewhere in the Gramineae between 1931 (Avdulow, 1931) and 1961 (Stebbins and Crampton, 1961), it seems likely that this criterion might be equally significant in the systematics of *Panicum*.

Accepting the assumptions previously discussed, these types characterize four distinct groups of related species within *Panicum*. However, if C_3 to C_4 evolution took place long ago and a number of times within the Gramineae, as seems likely, it is also possible that there is something about grasses that predisposes them to evolution of the Kranz syndrome. Therefore, less ancient and even quite recent evolution of C_4 photosynthesis cannot be ruled out. There exists also the possibility of reverse evolution, from C_4 to C_3. However, rigorous proof that evolution did indeed go in that direction is demanded.

Hsu (1965) employed quite different characters in his study and classifications of the Paniceae and *Panicum*. Perhaps the most meaningful character he used was the cellular appearance of the fertile lemma surfaces as seen under high magnification of a compound microscope. The nearest the present study approached Hsu's was examination of fertile lemma surfaces under high power of a dissecting microscope, as utilized routinely by taxonomists. The only species examined in this way were those of unknown sections and a few others. Hsu grouped sections within subgenera at least in part on this character. Of course it is well known that within genera (e.g., *Setaria*, *Brachiaria*) these surfaces can range from very rugose to smooth, so this character should be utilized in systematics with caution, though it must certainly be employed in such studies.

Throughout its taxonomic history genera have constantly been removed from *Panicum*, and yet it remains very large and heterogeneous. Since about 1900, taxonomists have erected many new genera and subdivided what remains of *Panicum* into groups or sections of apparently related species. Hitchcock and Chase (1910) divided the North American species into a number of informal groups. Stapf (1920) subdivided the species of tropical Africa into formal sections. Pilger (1940) treated the genus on a world-wide scale, subdividing it into formal sections. Hsu (1965) sampled a few species each from most of the accepted sections for selected characters—of lodicules, fertile lemma surface, styles, etc.—and arranged the sections according to level of "specialization index". His treatment was about the only one of these that implied an evolutionary scheme.

Because of its heterogeneity and its interrelationships with other genera, *Panicum* can hardly be treated apart from the tribe (Hsu, 1965) (Figure 1). Therefore, this study included an almost complete survey of the genera of the tribe and examination of about half the species of *Panicum*, representing all proposed groups and sections except a small (three species) section of Pilger's (1940), *Pseudolasiacis*, from Madagascar.

TABLE 6. *Species of* Panicum *examined, arranged alphabetically: anatomical and photosynthetic characters, provenances, and voucher herbaria. Numbers in parentheses indicate numbers of specimens examined if more than one.*

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
abscissum (2)	Ka		M.S.	U.S.A.	TEX
adenophorum	Nar	−22.4		Africa	US
adspersum	Ka		P.S.	S. Am.	TEX
aequinerve	Nr	−26.7		Africa	PRE
afzelii	Ka		P.S.	Africa	US
agrostoides	Kar	−14.1	M.S.	U.S.A.	TEX
altum	Ka		P.S.	Mexico	TEX
amarulum (4)	Kar	−11.4	P.S.	U.S.A.	TEX
anceps	Kar	−11.8	M.S.	U.S.A.	TEX
andringitrense	Na			Africa	US
antidotale (8)	Kar	−14.1	M.S.	India	TEX
aphanoneurum (2)	Ka		P.S.	Africa	US, TEX

Table 6 continued.

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
aquaticum (3)	Kar	−12.2	P.S.	S. Am.	TEX
arcurameum	Ka		P.S.	Africa	US
arizonicum	Kar	−11.5	P.S.	U.S.A.	TEX
arbusculum	Ka		P.S.	Africa	PRE
atrosanguineum (3)	Ka		P.S.	Africa	US
auritum	Nr	−27.7		Asia	US
australiensis (2)	Kar	−13.0	P.S.	Aust.	NSW, TEX
bartlettii (2)	Nr	−28.3		C. Am.	TEX
bartowense	Kar	−14.4	P.S.	U.S.A.	TEX
beccabunga	Na			Africa	US
beecheyi	Kar	−12.7	P.S.	Hawaii	US
bergii	Kar	−12.2	P.S.	U.S.A.	TEX
biglandulare (2)	Nr	−27.4		S. Am.	US, TEX
bisulcatum	Nr	−24.3		Asia	TEX
boliviense (2)	Nr	−26.2		S. Am.	US, TEX
brachyanthum	Nr	−28.3		U.S.A.	TEX
brevifolium	Na			Africa	US
bulbosum	Ka		M.S.	U.S.A.	TEX
buncei (3)	Kar	−13.1	P.S.	Aust.	NSW, TEX
calvum (2)	Na			Africa	US, TEX
cambogiensis	Ka		P.S.	Asia	US
capillare	Ka		P.S.	U.S.A.	TEX
capillarioides	Ka		P.S.	Mexico	TEX
capillipes	Ka		P.S.	Aust.	TEX
caricoides	Kar	−14.0	M.S.	Cuba	TEX
caudiglume	Na			Africa	US
cayennense	Ka		P.S.	Mexico	TEX
cervicatum	Kar	−13.6	P.S.	S. Am.	US
chasei	Ka		P.S.	S. Am.	TEX
chionachne	Na			Africa	TEX
chusqueoides	Kar	−13.6	P.S.	Africa	PRE
cinereum	Kar	−11.4	P.S.	Hawaii	US
colliei	Kar	−12.1	P.S.	Hawaii	US
coloratum (3)	Ka		P.S.	Africa	TEX
cupressifolium	Nar	−27.6		Madag.	US
cyanescens	Nar	−27.6		S. Am.	US
cynodon	Nar	−25.9		Hawaii	US
cyrtococcoides	Nr	−29.8		Africa	US
decolorans (2)	Kar	−12.7	P.S.	Mexico	TEX
decompositum (2)	Kar	−12.2	P.S.	Aust.	NSW, TEX
deustum (2)	Kar	−11.9	P.S.	Africa	PRE, TEX
dichotomiflorum (3)	Kar	−14.1	P.S.	U.S.A.	TEX
diffusum	Ka		P.S.	Mexico	TEX
discrepans (5)	Kar	−13.5	M.S.	Cuba	US, TEX
dregeanum	Kar	−12.3	P.S.	Africa	PRE
echinulatum	Ka		P.S.	S. Am.	TEX

Table 6 continued.

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
ecklonii	Nar	−24.4		Africa	PRE
effusum	Kar	−12.6	P.S.	Aust.	NSW
elephantipes (3)	Kar	−14.2	P.S.	S. Am.	US, TEX
exiguum	Ka		P.S.	S. Am.	TEX
fasciculatum	Kar	−13.0	P.S.	U.S.A.	TEX
fauriei	Kar	−10.9	P.S.	Hawaii	US
filipes	Ka		P.S.	U.S.A.	TEX
flexile	Ka		P.S.	U.S.A.	TEX
fluviicola	Ka		P.S.	Africa	US
foliolosum	Kr	−12.0		Asia	KEW
foliosum	Ka		P.S.	Aust.	TEX
frederici	Nr	−24.6		Africa	US
frondescens (2)	Nar	−32.4		S. Am.	US, TEX
fulgens	Na			Africa	US
fulgidum (2)	Kar	−12.1	P.S.	Aust.	NSW, TEX
gardneri	Nr	−31.4		S. Am.	US
gattingeri	Ka		P.S.	U.S.A.	TEX
genuflexum	Ka		P.S.	Africa	US
ghiesbregtii (3)	Ka		P.S.	Mexico	TEX
glabrescens (2)	Ka		P.S.	Africa	PRE, TEX
glabripes	Ka		P.S.	S. Am.	TEX
glutinosum (2)	Nar	−26.8		S. Am.	US, TEX
gouini	Ka		P.S.	Mexico	TEX
gracilicaule	Nr	−29.6		Africa	US
griffonii (2)	Ka		P.S.	Africa	TEX
grande (2)	Nar	−28.3		S. Am.	US, TEX
grumosum (2)	Nr	−25.6		S. Am.	US, TEX
gymnocarpon (3)	Nar	−29.1		U.S.A.	TEX
guianense	Nr	−24.0		S. Am.	US
haenkeanum (2)	Nar	−28.0		S. Am.	US, TEX
hallii	Kar	−13.4	P.S.	U.S.A.	TEX
havardii	Ka		P.S.	U.S.A.	TEX
helobium (2)	Nar	−27.9		S. Am.	TEX
heterostachyum (2)	Nr	−30.5		Africa	PRE, TEX
hillmanii	Ka		P.S.	U.S.A.	TEX
hippothrix (2)	Ka		P.S.	Africa	US, TEX
hirsutum	Ka		P.S.	S. Am.	TEX
hirticaule (2)	Ka		P.S.	Mexico, Texas	TEX
hirtum (3)	Nar	−30.7		W. Indies	US, TEX
hochstetteri (2)	Na			Africa	US, TEX
humile	Kar	− 9.5	P.S.	Asia	US
hygrocharis	Ka		P.S.	Africa	US
hymeniochilum	Nr	−26.8		Africa	PRE
hystrix	Na			Africa	US
ianthum	Na			Africa	US

Table 6 continued.

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
ichnanthoides	Ka		P.S.	S. Am.	TEX
infestum	Ka		P.S.	Africa	US
kaalense	Ka		P.S.	Hawaii	TEX
kalahariense	Kar	−13.8	P.S.	Africa	PRE
kerstingii (2)	Ka		P.S.	Africa	US, TEX
koolauense	Na			Hawaii	TEX
lachnophyllum (2)	Nar	−23.3		Aust.	NSW, TEX
laetum	Ka		P.S.	Africa	US
laevifolium (2)	Kar	−12.1	P.S.	Africa	PRE, TEX
lacustre	Ka		P.S.	Cuba	TEX
laxum (2)	Nar	−25.8		Mexico	TEX
lepidulum	Ka		P.S.	Mexico	TEX
leium	Na			C. Am.	TEX
lineatum	Nar	−29.5		Africa	US
longijubatum	Ka		P.S.	Africa	US
longum	Nr	−27.9		S. Am.	US
lundellii	Ka		P.S.	Mexico	TEX
longifolium	Ka		M.S.	U.S.A.	TEX
majusculum (2)	Kar	−12.0	P.S.	Aust.	NSW, US
maximum (3)	Kar	−13.3	P.S.	Africa	TEX
mertensii (2)	Nr	−29.5		C. Am.	US, TEX
meyerianum	Kar	−12.3	P.S.	Africa	PRE
microthyrsum	Na			Africa	US
miliaceum (3)	Kar	−16.0	P.S.	India	US, TEX
micranthum	Na			W. Indies	TEX
milleflorum (2)	Nr	−27.1		S. Am.	US, TEX
mindansense	Kar	−10.6	P.S.	Aust.	NSW
molle (2)	Ka		P.S.	Mexico	TEX
monticolum (2)	Nar	−31.1		Africa	PRE, TEX
montanum	Na			India	TEX
muelleri	Kr	−13.2		Aust.	US
natalense	Nar	−23.8		Africa	PRE
neglectum (2)	Kar	−12.4	P.S.	Africa	US, TEX
nephelophilum (2)	Kar	−11.4	P.S.	Hawaii	US, TEX
nervosum	Na			W. Indies	TEX
novemnerve (2)	Kar	−11.5	P.S.	Africa	PRE, TEX
nubigenum	Ka		P.S.	Hawaii	TEX
obseptum	Kar	−17.5	P.S.	Aust.	NSW
obtusum	Kar	−12.7	M.S.	U.S.A.	TEX
ovaliferum	Na			S. Am.	TEX
paludosum (8)	Kar	−12.8	P.S.	Aust., As.	NSW, US
pampinosum	Ka		P.S.	U.S.A.	TEX
pantrichum	Nr	−30.4		Mexico	US
parcum	Ka		P.S.	Mexico	TEX

Table 6 continued.

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
parvifolium (2)	Nar	−31.1		Africa, S. Am.	PRE, TEX
parviglume (2)	Nar	−29.2		S. Am.	US, TEX
pauciflorum	Kr	−11.8		Aust.	US
paucispicatum	Kar	−11.6	P.S.	S. Am.	TEX
pectinatum	Nr	−26.4		Africa	US
pectinellum	Na			Africa	US
pellitum	Kar	−12.8	P.S.	Hawaii	US
penicillatum	Na			S. Am.	TEX
petersonii (2)	Kar	−17.0	M.S.	Cuba	TEX
philadelphicum	Ka		P.S.	U.S.A.	TEX
pilcomayense	Ka		P.S.	S. Am.	TEX
pilosum (4)	Nar	−28.1		S. Am.	TEX
pinifolium	Kar	−12.4	P.S.	Africa	TEX, US
plenum (2)	Kar	−11.9	M.S.	U.S.A.	TEX
polygonatum (3)	Nar	−28.5		C. Am.	TEX
porphyrrhizos (2)	Ka		P.S.	Africa	US, TEX
prialtum	Na			Africa	US
prionitis	Kar	−12.0	M.S.	S. Am.	US
procurrens (2)	Nar	−28.7		S. Am.	US, TEX
prolutum	Nar	−25.9		Aust.	NSW
psilopodium	Ka			India	TEX
pterigodium	Na			S. Am.	TEX
pubiglume	Nr	−27.0		Africa	US
pulchellum (3)	Nar	−30.4		Mexico	US, TEX
pusillum (2)	Nar	−26.8		Africa	US, TEX
pygmaeum (3)	Nar	−29.7		Aust.	NSW, TEX
pyrularium	Nr	−29.4		S. Am.	US
quadriglume	Ka		P.S.	S. Am.	TEX
queenslandicum	Kar	−12.0	P.S.	Aust.	NSW
racemosum (2)	Kar	−11.3	P.S.	S. Am.	US, TEX
rectissimum	Na			S. Am.	TEX
repens (2)	Kar	−12.3	P.S.	America	TEX
rhizomatum	Kar	−12.9	M.S.	U.S.A.	TEX
rigidulum (2)	Ka		M.S.	U.S.A.	TEX
rivulare	Na			S. Am.	TEX
robynsii	Na			Africa	US
rowlandii	Ka		P.S.	Africa	US
rudgei (2)	Kar	−14.5	P.S.	S. Am.	US, TEX
rugulosum (5)	Nar	−29.0		S. Am.	TEX
schiffneri (3)	Nar	−28.6		S. Am.	US, TEX
schinzii	Ka		P.S.	Africa	US
schmitzii (2)	Nar	−26.8		S. Am.	US, TEX
sciurotis (2)	Nar	−27.9		S. Am.	US, TEX
sellowii (2)	Nr	−28.1		S. Am.	US, TEX
seminudum	Kar	−12.3	P.S.	Aust.	NSW

Table 6 continued.

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
snowdenii	Na			Africa	US
sonorum	Ka		P.S.	Mexico	TEX
spathellosum	Nar			S. Am.	TEX
spergulifolium	Na			Africa	US
stagnatile (4)	Na			C. Am.	TEX
stapfianum (2)	Ka		P.S.	Africa	PRE, TEX
stenodes (2)	Kar	−11.6	M.S.	S. Am.	TEX
stenodoides	Ka		M.S.	C. Am.	TEX
stevensianum (2)	Nar	−25.2		S. Am.	US, TEX
stipitatum	Ka		M.S.	U.S.A.	TEX
stoloniferum (3)	Nar	−36.7		S. Am.	US, TEX
stramineum	Ka		P.S.	Mexico	TEX
subalbidum	Kar	−11.4	P.S.	Africa	US
subflabellatum	Ka		P.S.	Africa	US
sublaetum	Nr	−25.6		Africa	US
sucosum	Ka		P.S.	Mexico	TEX
subxerophilum	Nar	−25.8		Aust.	NSW
tamaulipense	Ka		P.S.	Mexico	TEX
tenerum (3)	Kar	−11.4	M.S.	U.S.A.	TEX
tenuifolium (2)	Kar	−11.5	P.S.	Hawaii	US, TEX
texanum	Ka		P.S.	U.S.A.	TEX
torridum (2)	Kar	−12.1	P.S.	Hawaii	US, TEX
trachyrachis	Kar	−13.3	P.S.	Aust.	NSW
transiens	Na			Mexico	TEX
transvenulosum	Na			Africa	US
trichanthum (2)	Nar	−28.4		C. Am.	TEX
trichocladum (3)	Ka		P.S.	Africa	US, TEX
tricholaenoides	Ka		P.S.	S. Am.	TEX
trichoides (3)	Nar	−25.3		World	TEX
trigonum	Na			Asia	TEX
tuckermani	Ka		P.S.	U.S.A.	TEX
tuerckheimii (3)	Kar	−13.5	M.S.	C. Am.	US, TEX
turgidum	Kar	−12.7	P.S.	Africa	US
umbellatum	Kar	−10.7	P.S.	Africa	US
urvilleanum (3)	Kar	−12.1	P.S.	U.S.A.	TEX
uvulatum	Nr	−28.6		Madag.	US
vaseyanum	Ka		P.S.	Mexico	TEX
venezuelae	Na			Cuba	TEX
verrucosum	Nr	−25.6		U.S.A.	TEX
virgatum	Kar	−11.7	P.S.	U.S.A.	TEX
virgultorum (2)	Na			Mexico	TEX
voeltzkowii	Kar	−12.6	P.S.	Madag.	US
whitei	Kar	−13.3	P.S.	Aust.	NSW
xerophilum	Ka		P.S.	Hawaii	TEX
yavitaense	Nr	−30.1		S. Am.	US

Totals: N=100; P.S.=117; M.S.=20.

Table 6 lists alphabetically the 241 species examined from the world distribution of the genus, but mostly from tropical Africa and America, the regions of greatest abundance (Hartley, 1958b). The selection of species was determined in part by an attempt to sample all previously proposed groups and sections, in part by availability, and in part by an effort to find non-Kranz species. This large world-wide sample seems to be representative enough for sound general conclusions about the genus.

Of the species examined, 104 are non-Kranz and 137 are Kranz. This list does not include 72 species of *Dichanthelium* usually included in *Panicum*, all of which are non-Kranz (Brown and Smith, 1975) and have been segregated from it (Gould, 1974). Of this sample, 57 percent are Kranz and 43 percent are non-Kranz. Thus, probably, somewhat more than 50 percent of all *Panicum* species are Kranz.

It is also evident from Table 6 that the Kranz species fall in both the M.S. and P.S. classes of leaf anatomy, with P.S. species being by far the more numerous. Furthermore, all the M.S. species are American except the Asiatic *Panicum antidotale*. Whereas the majority of Kranz species of *Panicum* are P.S., a majority of Kranz Paniceae are M.S. (Table 4).

A deliberate attempt was made to examine species from all groups and sections of Hitchcock and Chase (1910), Stapf (1920), Pilger (1940), and Hsu (1965). When all examined species were assigned as far as possible to their proper taxa, it became evident that nearly all such named groups are homogeneously Kranz or non-Kranz, P.S. or M.S. Section *Clavelligera* Stapf is all non-Kranz except for *Panicum deustum*. Group "Maxima" Hitch. and Chase, as treated by Hsu (1965), is obviously artificial, according to these criteria, by inclusion of non-Kranz *P. trichocladum*, Kranz M.S. *P. bulbosum* and *P. plenum*, and *P. maximum* that is Kranz P.S. and PEP-ck. And *P. antidotale*, which is Kranz M.S., is out of place among the non-Kranz species of section *Sarmentosa* Pilger. Table 7 reflects an effort to make all sections and groups homogeneous for these characters. As used here these taxa are tentative, in the sense of Hitchcock and Chase (1910). Some of them deserve formal recognition but others do not. Those not already named formally should remain informal until a detailed study of all species of the world is completed, employing all available evidence.

It is assumed that leaf anatomical characters are, in general, more fundamental and conservative than the morphological ones (other than the very conservative basic spikelet plan of the Paniceae). I thus propose to modify any sections or groups that are heterogeneous, making each uniformly Kranz or non-Kranz. Furthermore, among the Kranz taxa it is proposed to make each uniformly M.S. or P.S., and among the Kranz P.S. species to segregate where possible the few known to be PEP-ck and their obvious allies from the NAD-me species at the subgeneric or generic level. All non-Kranz taxa are also segregated in separate subgenera or genera.

The wholly non-Kranz subgenus *Dichanthelium* (Brown and Smith, 1975) has been raised to generic rank (Gould,

1974) and that change is supported by Clark and Gould (1975) and by this study.

Species of that genus are not included in Tables 6, 7, or 8.

TABLE 7. *Species of* Panicum *examined, arranged by supraspecific taxa: anatomical and photosynthetic characters, provenances, voucher herbaria, and basic chromosome numbers, if known.*

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
I. Subgenus *PANICUM* (x=9)					
1. Section *Panicum* (x=9)					
altum	Ka		P.S.	C. Am.	TEX
amarulum	Ka		P.S.	U.S.A.	TEX
arcurameum	Ka		P.S.	Africa	US
atrosanguineum	Ka		P.S.	Africa	US
beecheyi	Kar	−12.7	P.S.	Hawaii	US
cambogiense	Ka		P.S.	Asia	US
capillare	Kar	−14.3	P.S.	U.S.A.	TEX
cayennense	Ka		P.S.	Mexico	TEX
cinereum	Kar	−11.4	P.S.	Hawaii	US
colliei	Kar	−12.1	P.S.	Hawaii	US
decolorans	Kar	−12.7	P.S.	Mexico	TEX
effusum	Kar	−12.6	P.S.	Aust.	NSW
fauriei	Kar	−10.9	P.S.	Hawaii	US
flexile	Ka		P.S.	U.S.A.	TEX
gattingeri	Ka		P.S.	U.S.A.	TEX
havardii	Ka		P.S.	U.S.A.	TEX
hillmanii	Ka		P.S.	U.S.A.	TEX
hippothrix	Ka		P.S.	Africa	US
hirticaule	Ka		P.S.	U.S.A.	TEX
humile	Kar	− 9.5	P.S.	Asia	US
ichnanthoides	Ka		P.S.	C. Am.	TEX
kaalense (2)	Ka		P.S.	Hawaii	TEX
kerstingii (2)	Ka		P.S.	Africa	US, TEX
laetum	Ka		P.S.	Africa	US
lundellii	Ka		P.S.	C. Am.	TEX
miliaceum (3)	Kar	−16.0	P.S.	Asia	US, TEX
nephelophilum (2)	Kar	−11.4	P.S.	Hawaii	US, TEX
novemnerve	Kar	−11.5	P.S.	Africa	PRE
nubigenum (2)	Kar	−11.7	P.S.	Hawaii	US, TEX
pampinosum	Ka		P.S.	U.S.A.	TEX
parcum (2)	Ka		P.S.	Mexico	US, TEX
pellitum	Kar	−12.8	P.S.	Hawaii	US
philadelphicum	Ka		P.S.	U.S.A.	TEX
sonorum	Ka		P.S.	Mexico	TEX
stramineum	Ka		P.S.	Mexico	TEX

Table 7 continued.

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
tenuifolium (2)	Kar	−11.5	P.S.	Hawaii	US, TEX
torridum (2)	Kar	−12.1	P.S.	Hawaii	US, TEX
trachyrachis	Ka		P.S.	Aust.	NSW
tuckermani	Ka		P.S.	U.S.A.	TEX
virgatum	Kar	−11.7	P.S.	U.S.A.	TEX
2. Group "Dichotomiflora" (x=9)					
bartowense	Kar	−14.4	P.S.	U.S.A.	TEX
coloratum	Ka		P.S.	Africa	TEX
dichotomiflorum	Kar	−14.1	P.S.	U.S.A.	TEX
hygrocharis	Ka		P.S.	Africa	US
kalahariense	Kar	−13.8	P.S.	Africa	PRE
laevifolium (2)	Kar	−12.1	P.S.	Africa	PRE, TEX
longijubatum	Ka		P.S.	Africa	US
porphyrrhizos (2)	Ka		P.S.	Africa	US, TEX
schinzii	Ka		P.S.	Africa	US
stapfianum	Ka		P.S.	Africa	TEX
sabalbidum	Kar	−11.4	P.S.	Africa	US
sucosum	Ka		P.S.	Mexico	TEX
vaseyanum	Ka		P.S.	Mexico	TEX
3. Section *Repentia* (x=9)					
aquaticum (2)	Kar	−12.2	P.S.	S. Am.	TEX
decompositum	Kar	−12.2	P.S.	Aust.	US
gouini (2)	Ka		P.S.	Mexico	TEX
lacustre	Ka		P.S.	Cuba	TEX
paludosum (8)	Kar	−16.6	P.S.	As, Aust.	NSW, US
pinifolium	Kar	−12.4	P.S.	Africa	US
repens (3)	Kar	−12.3	P.S.	World	TEX
subflabellatum	Ka		P.S.	Africa	US
4. Group "Diffusa" (x=9)					
afzelii	Ka		P.S.	Africa	US
aphanoneurum	Ka		P.S.	Africa	US
bergii	Kar	−12.3	P.S.	S. Am.	TEX
capillarioides	Ka		P.S.	Mexico	TEX
chasei	Ka		P.S.	S. Am.	TEX
diffusum	Ka		P.S.	Mexico	TEX
dregeanum	Kar	−12.3	P.S.	Africa	PRE
filipes	Ka		P.S.	U.S.A.	TEX
fluviicola	Ka		P.S.	Africa	US
genuflexum	Ka		P.S.	Africa	US
ghiesbregtii (3)	Ka		P.S.	Mexico	TEX
griffonii	Ka		P.S.	Africa	US
hallii	Kar	−13.4	P.S.	U.S.A.	TEX
hirsutum	Ka		P.S.	C. Am.	TEX
lepidulum	Ka		P.S.	Mexico	TEX

Table 7 continued.

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
pilcomayense (2)	Ka		P.S.	S. N. Am.	TEX
rowlandii	Ka		P.S.	Africa	US
quadriglume	Ka		P.S.	S. Am.	TEX
tamaulipense	Ka		P.S.	Mexico	TEX
5. Group "Rudgeana" (x=9)					
rudgei	Kar	−14.5	P.S.	S. Am.	US, TEX
6. Section *Dura* (x=9)					
neglectum (2)	Kar	−12.4	P.S.	Africa	US, TEX
racemosum	Kar	−11.3	P.S.	S. Am.	US
turgidum	Kar	−12.7	P.S.	Africa	US
urvilleanum	Kar	−12.1	P.S.	America	TEX
Miscellaneous "true" panicums.					
arbusculum	Ka		P.S.	Africa	PRE
buncei (3)	Kar	−13.1	P.S.	Aust.	NSW, TEX
cervicatum	Kar	−13.6	P.S.	S. Am.	US
exiguum	Ka		P.S.	S. Am.	TEX
fulgidum (2)	Kar	−12.1	P.S.	Aust.	NSW, TEX
glabripes	Ka		P.S.	S. Am.	TEX
nubigenum	Ka		P.S.	Hawaii	TEX
obseptum	Kar	−17.5	P.S.	Aust.	NSW
psilopodium	Ka		P.S.	India	TEX
queenslandicum	Kar	−12.0	P.S.	Aust.	NSW
seminudum	Kar	−12.3	P.S.	Aust.	NSW
tricholaenoides	Ka		P.S.	S. Am.	TEX
voeltzkowii	Kar	−12.6	P.S.	Madag.	US
whitei (2)	Kar	−13.3	P.S.	Aust.	NSW, TEX
xerophilum	Ka		P.S.	Hawaii	TEX
P.S. species of doubtful position or not *Panicum*					
deustum (2)	Kar	−11.9	P.S.	Africa	PRE, TEX
elephantipes (3)	Kar	−14.2	P.S.	S. Am.	US, TEX
glabrescens (2)	Ka		P.S.	Africa	PRE, TEX
trichocladum (3)	Ka		P.S.	Africa	US, TEX
umbellatum	Kar	−10.7	P.S.	Africa	US
chusqueoides (like *Brachiaria*)			P.S.	Africa	PRE
echinulatum = *Brachiaria echinulata* (Mez) Parodi				S. Am.	TEX
infestum (like *Brachiaria*)			P.S.	Africa	US
maximum (like *Brachiaria*)			P.S.	Africa	TEX
meyerianum (2) = *Eriochloa meyeriana* (Nees) Pilger			P.S.	Africa	PRE, TEX
Group "Fasciculata" (All *Brachiaria*)					
adspersa (Trin.) Parodi			P.S.	S. Am.	TEX
arizonica (S. and M.) S. T. Blake				U.S.A.	TEX

Table 7 continued.

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
fasciculata (Sw.) Parodi			P.S.	U.S.A.	TEX
mollis (Sw.) Parodi			P.S.	C. Am.	TEX
ramosa Stapf			P.S.	Asia	TEX
reptans (L) Gardn. and Hubb.			P.S.	World	TEX
texana (Buckl.) S. T. Blake			P.S.	U.S.A.	TEX.
Ichnanthoid group					
australiensis (2)		−13.0	P.S.	Aust.	TEX, NSW
foliosum	Kr	−12.0	P.S.	Asia	K
majusculum (2)	Kar	−12.0	P.S.	Aust.	NSW, US
muelleri	Kr	−13.2		Aust.	US
pauciflorum	Kr	−11.8		Aust.	US
II. Miscellaneous M.S. Assemblage (x=9,10)					
7. Group "Agrostoidea" (x=9)					
abscissum	Ka		M.S.	U.S.A.	TEX
agrostoides	Kar	−14.1	M.S.	U.S.A.	TEX
anceps	Kar	−11.8	M.S.	U.S.A.	TEX
longifolium	Ka		M.S.	U.S.A.	TEX
rhizomatum	Kar	−12.2	M.S.	U.S.A.	TEX
rigidulum	Ka		M.S.	U.S.A.	TEX
stipitatum	Ka		M.S.	U.S.A.	TEX
8. Group "Tenera" (x=10)					
caricoides	Ka	−14.0	M.S.	Cuba	TEX
stenodes	Kar	−11.6	M.S.	S. Am.	TEX
stenodoides	Ka		M.S.	C. Am.	TEX
tenerum	Kar	−11.4	M.S.	U.S.A.	TEX
9. Group "Plena" (x=9)					
antidotale (3)	Kar	−14.1	M.S.	India	TEX
bulbosum	Ka		M.S.	U.S.A.	TEX
plenum (2)	Kar	−11.9	M.S.	U.S.A.	TEX
10. Group "Obtusa" (x=10)					
obtusum	Kar	−12.7	M.S.	U.S.A.	TEX
11. Group "Discrepantia" (x=?)					
discrepans (5)	Kar	−13.5	M.S.	S. Am.	US, TEX
12. Group "Tuerckheimiana" (x=?)					
tuerckheimii (2)	Kar	−13.5	M.S.	S. Am.	US, TEX
21. Group "Grandia" (pars) (x=10)					
petersonii (2)	Ka		M.S.	Cuba	TEX
prionitis	Kar	−12.0	M.S.	S. Am.	US

Table 7 continued.

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
III. Subgenus *SARMENTOSUM* (x=9,10)					
13. Group "Haenkeana" (x=10)					
haenkeanum (2)	Nar	−28.0		C. Am.	US, TEX
14. Group "Megista" (x=10)					
mertensii (2)	Nar	−29.5		S. Am.	US, TEX
15. Group "Parviglumia" (x=9)					
parviglume	Nr	−29.2		S. Am.	US
schiffneri	Nr	−28.6		S. Am.	US
schmitzii (2)	Nar	−26.8		S. Am.	US, TEX
virgultorum	Na			Mexico	TEX
16. Group "Parvifolia" (x=9)					
cyanescens	Nar	−27.6		S. Am.	US
nervosa	Na			S. Am.	TEX
parvifolium (2)	Nar	−31.1		Africa	PRE, TEX
17. Section *Pusilla* (x=?)					
beccabunga	Na			Africa	US
pusillum (2)	Nar	−26.8		Africa	US, TEX
18. Section *Sarmentosa* (x=9)					
bisulcatum	Nr	−24.3		Asia	TEX
glutinosum	Nar	−26.8		S. Am.	US
montanum	Na			India	TEX
rugulosum (5)	Nar	−27.2		S. Am.	TEX
sellowii (2)	Nar	−28.1		S. Am.	US, TEX
19. Group "Stolonifera" (x=10)					
biglandulare	Nr	−27.4		S. Am.	US
frondescens	Nr	−32.4		S. Am.	US
pulchellum	Nr	−30.4		Mexico	US
stoloniferum	Nr	−36.7		S. Am.	US
20. Section *Trinerves* (x=?)					
caudiglume	Na			Africa	US
microthyrsum	Na			Africa	US
21. Group "Grandia" (pars) (x = 10)					
grande (2)	Nar	−28.3		S. Am.	US, TEX
grumosum (2)	Nar	−25.6		S. Am.	US, TEX
rivulare	Na			S. Am.	TEX
stagnatile (4)	Na			S. Am.	TEX
Miscellaneous					
andringitrense	Na			Africa	US
auritum	Nr	−27.7		Asia	US
cyanescens	Nar	−27.6		S. Am.	US
cynodon	Nar	−25.9		Hawaii	US

Table 7 continued.

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
hymeniochilum	Nr	−26.8		Africa	PRE
koolanense	Na			Hawaii	TEX
leium	Na			C. Am.	TEX
miranthum	Na			W. Ind.	TEX
prolutum	Nar	−25.9		Aust.	NSW
pterigodium	Na			S. Am.	TEX
pygmaeum (3)	Nar	−29.7		Aust.	NSW, TEX
rectissimum	Na			S. Am.	TEX
sciurotis	Nr	−27.9		S. Am.	US
transiens	Na			Mexico	TEX
transvenulosum	Na			Africa	US
uvulatum	Nr	−28.6		Madag.	US
venezuelae	Na			Cuba	TEX
yavitaense	Nr	−30.1		S. Am.	US
22. Group "Laxa" (x=10)					
boliviense	Nr	−26.2		S. Am.	TEX
guianense	Nr	−24.0		S. Am.	US
laxum	Nr	−24.0		C. Am.	US
longum	Nr	−27.9		S. Am.	US
milleflorum	Nr	−27.1		S. Am.	US
pilosum (2)	Nar	−27.8		S. Am.	US, TEX
polygonatum (2)	Nar	−28.4		S. Am.	US, TEX
stevensianum	Nr	−25.2		S. Am.	US
IV. Subgenus *MEGATHYRSUS* (x=9,10)					
23. Section *Clavelligera* (x=?)					
adenophorum	Nr	−22.4		Africa	US
lineatum	Nar	−29.4		Africa	US
24. Section *Pectinata* (x=9)					
ecklonii	Nr	−24.4		Africa	US, PRE
pectinatum	Nr	−26.4		Africa	US
pectinellum	Na			Africa	US
25. Section *Monticola* (x=9 and/or 10)					
calvum (2)	Na			Africa	US
hochstetteri	Na			Africa	US
monticolum	Nar	−31.1		Africa	PRE, US
natalense	Nr	−23.8		Africa	PRE
26 Group "Trichoidea" (x=9)					
aequinerve	Nr	−26.7		Africa	PRE
brevifolium	Na			S. Am.	US
chionachne	Na			S. Am.	US
cyrtococcoides	Nr	−29.8		Africa	US
gardneri	Nr	−31.4		S. Am.	US

Table 7 continued.

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
helobium (2)	Nar	−27.9		S. Am.	US, TEX
heterostachyum	Nr	−30.5		Africa	PRE, US
pyrularium	Nr	−29.4		S. Am.	US
robynsii	Na			Africa	US
snowdenii	Na			Africa	US
trichanthum (2)	Nar	−28.4		S. Am.	US, TEX
trichoides (3)	Nar	−29.9		World	NSW, US
27. Group "Depauperata" (x=?)					
cupressifolium	Nr	−27.6		Madag.	US
spergulifolium	Na			Madag.	US
28. Group "Verrucosa" (x=9)					
brachyanthum	Nr	−28.3		U.S.A.	TEX
verrucosum	Nr	−25.6		U.S.A.	TEX
29. Section *Verruculosa* (x=?)					
frederici	Nr	−24.6		Africa	US
fulgens	Na			Africa	US
gracilicaule	Nr	−29.6		Africa	US
hystrix	Na			Africa	US
ianthum	Na			Africa	US
prialtum	Na			Africa	US
pubiglume	Nr	−27.0		Africa	US
sublaetum	Nr	−25.6		Africa	US
Miscellaneous					
bartlettii	Nr	−28.3		C. Am.	TEX
hirtum (3)	Nar	−30.7		C. Am.	US, TEX
ovaliferum	Na			S. Am.	TEX
pantrichum	Nr	−30.4		Mexico	US
penicillatum	Na			S. Am.	TEX
spathellosum	N			S. Am.	TEX
subxerophilum	Nar	−25.8		Aust.	NSW
trigonum	Na			Asia	TEX

With the removal of *Steinchisma* (see previous section), the wholly American group "Laxa" of Hitchcock and Chase (1910) seems to be a typical, tropical, non-Kranz taxon both anatomically and biochemically (by $\delta^{13}C$ ratios), except for a few C_4 enzymes in *Panicum laxum* (Medina, Bifana, and Delgado, in litt.). Their proposal that *P. laxum* may be a C_3 species derived from some C_4 ancestor, because it grows in wet places and has senescent plastids in parenchyma sheath cells, is probably based upon incorrect assumptions. These are that C_4 taxa all evolved in arid regions and might evolve back to C_3 species in wet habitats, and that unusual chloroplasts in parenchyma sheath cells may indicate degenerate Kranz cells. Rather, the habitat and unusual chloroplasts in parenchyma sheath cells of *P. laxum* are not unusual among non-Kranz grasses. The "Laxa" group is non-Kranz with smooth fertile lemmas and, therefore, is included in the subgenus *Sarmentosum* (Table 8).

It is proposed to revive *Phanopyrum gymnocarpon* Nash for that monotypic American species usually designated as *Panicum gymnocarpon* Ell., because it is morphologically distinctive and is non-Kranz. The *Panicum* subgenus *Phanopyrum* of Pilger (1940) and Hsu (1965), containing sections *Gymnocarpa* and *Dura* and groups "Megista" and "Obtusa," is too heterogeneous for acceptance (Tables 6 and 7).

Group "Fasciculata" of *Panicum* was transferred to *Brachiaria* by Pilger (1940) and Hsu (1965). That transfer, based upon morphological characters, is supported by this and other studies (Gutierrez, Edwards, and Brown, 1976). Both "Fasciculata" and *Brachiaria* have, uniquely in the Paniceae, PEP-ck photosynthesis and transversely rugose fertile lemmas. Whether *P. texanum, P. fasciculatum,* etc., which constitute "Fasciculata, should all be transferred to *Brachiaria,* as has been done, or, like *P. deflexa,* which now constitutes *Pseudobrachiaria,* become one or more new genera, is not indicated by this work. Old World agrostologists place the Asiatic species *P. ramosum* L. in *Brachiaria* (Bor, 1960), whereas Hitchcock (1950) included it in "Fasciculata." A comparison of Asiatic *B. ramosa* (L.) Stapf, American *P. fasciculatum* Swartz, South African *P. chusqueoides* Hack., and South African *B. (Pseudobrachiaria) deflexa* (Schum.) C. E. Hubb. ex Robyns demonstrates great similarity among them. Chippindall (1955) remarked about the last species (p. 378), "Some botanists treat the group to which *B. deflexa* belongs as species of *Panicum.* If the grass in question is retained as a species of *Brachiaria,* then *Panicum chusqueoides* should probably be referred to *Brachiaria.*" And on p. 326, about *P. chusqueoides,* "This species should possibly be referred to *Brachiaria,* for it is hardly separable from the section of that genus to which *B. deflexa* belongs." For the present, at least, all these P.S., PEP-ck species having usually transversely rugose fertile lemmas and more or less racemose inflorescences should be transferred to *Brachiaria.*

Henrard's (1940) transfer of non-Kranz *Panicum venezuelae* to *Brachiaria* is not supported by leaf anatomy or surface character of the fertile lemma.

The species often called *Panicum purpurascens* Raddi in the United States, of group "Purpurascentia," is clearly *Brachiaria mutica* Stapf., and *P. reptans* L. clearly belongs in the *Brachiaria* group as *Urochloa reptans* (L.) Stapf. or *B. reptans* (L.) Gard. and C. E. Hubb.

Panicum paucispicatum Morong of Paraguay and Bolivia was transferred to *Acroceras* by Henrard (1940). However, *Acroceras* is a non-Kranz genus with nearly smooth fertile lemmas, whereas *P. paucispicatum* is Kranz and has rugose lemmas. The latter probably belongs in the *Brachiaria* group, possibly as a monotypic genus.

Panicum maximum and other species,

placed in section *Maxima* by Hsu (1965) and others, present problems in relationship. *Panicum maximum* is Kranz P.S. and PEP-ck (Table 1), so should be placed in the *Brachiaria* group; *P. bulbosum* and *P. plenum* are Kranz M.S., and doubtlessly NADP-me. They can best be included in a group of M.S. taxa that are exclusively American except for *P. antidotale* Retz., which is native to India. *Panicum transvenulosum*, being non-Kranz, should certainly not be associated with *P. maximum* or *P. bulbosum*. The other species included by Stapf (1920) in the group with rough lemmas are P.S., but whether PEP-ck or NAD-me is not known. If PEP-ck, like *P. maximum*, they should also be transferred to the *Brachiaria* group. It is likely that *P. trichocladum* and *P. spongiosum*, with smooth and polished fertile lemmas, are not PEP-ck species.

The M.S. paniculate species *Panicum bulbosum*, *P. plenum*, and *P. antidotale* are associated as the group "Plena" although they may have had separate origins. *Panicum plenum* and *P. bulbosum* may be conspecific.

The other, all American, M.S. groups of *Panicum* ("Agrostoidea," "Tenera," "Obtusa," "Discrepantia," "Tuerckheimiana," and at least two species of "Grandia;" Table 7) seem out of place among the non-Kranz and Kranz P.S. taxa of the genus. Anatomically they resemble more closely the bulk of Kranz genera of Paniceae. It seems likely that they have evolved completely independently of P.S. *Panicum*. Possibly they are more closely allied to other M.S. Paniceae, or they may be more or less recent derivatives of non-Kranz Paniceae. In either case, they could be considered as distinct genera.

Panicum discrepans Doell, for example, has Kranz cells with unusually thick walls around the small veins, but the inner and lateral walls of the Kranz cells around larger veins are very thick, as thick as the walls of mestome sheath cells in non-Kranz species. Much the same is true of *P. petersonii*. I propose that such anatomy indicates recent evolution of the Kranz syndrome and of the M.S. Kranz sheath from the mestome sheath.

It is not proposed that the M.S. groups of *Panicum* be associated as an interrelated assembly but rather as more or less unrelated taxa. Some may represent rather recent and independent evolutions of the M.S. subsyndrome. Certainly the Kranz M.S. species of the group "Grandia" appear to be products of such a recent evolution. It is tentatively proposed that "Grandia" is more closely related to the unusual genus *Steinchisma* than to non-Kranz *Panicum*.

Of the three species examined from section *Clavelligera*, two are non-Kranz and one, *Panicum deustum*, is Kranz. Although it is possible to have two closely related species be Kranz and non-Kranz, it is not likely in this group. Therefore, I propose to remove the Kranz species, *P. deustum*, and leave the section a non-Kranz taxon. Its remaining species are most closely related to the two non-Kranz sections *Monticola* and *Pectinata* (Hsu, 1965).

Section *Sarmentosa* becomes a non-Kranz taxon with the removal of *Panicum antidotale*. The placement of that species in M.S. "Plena" has been discussed above.

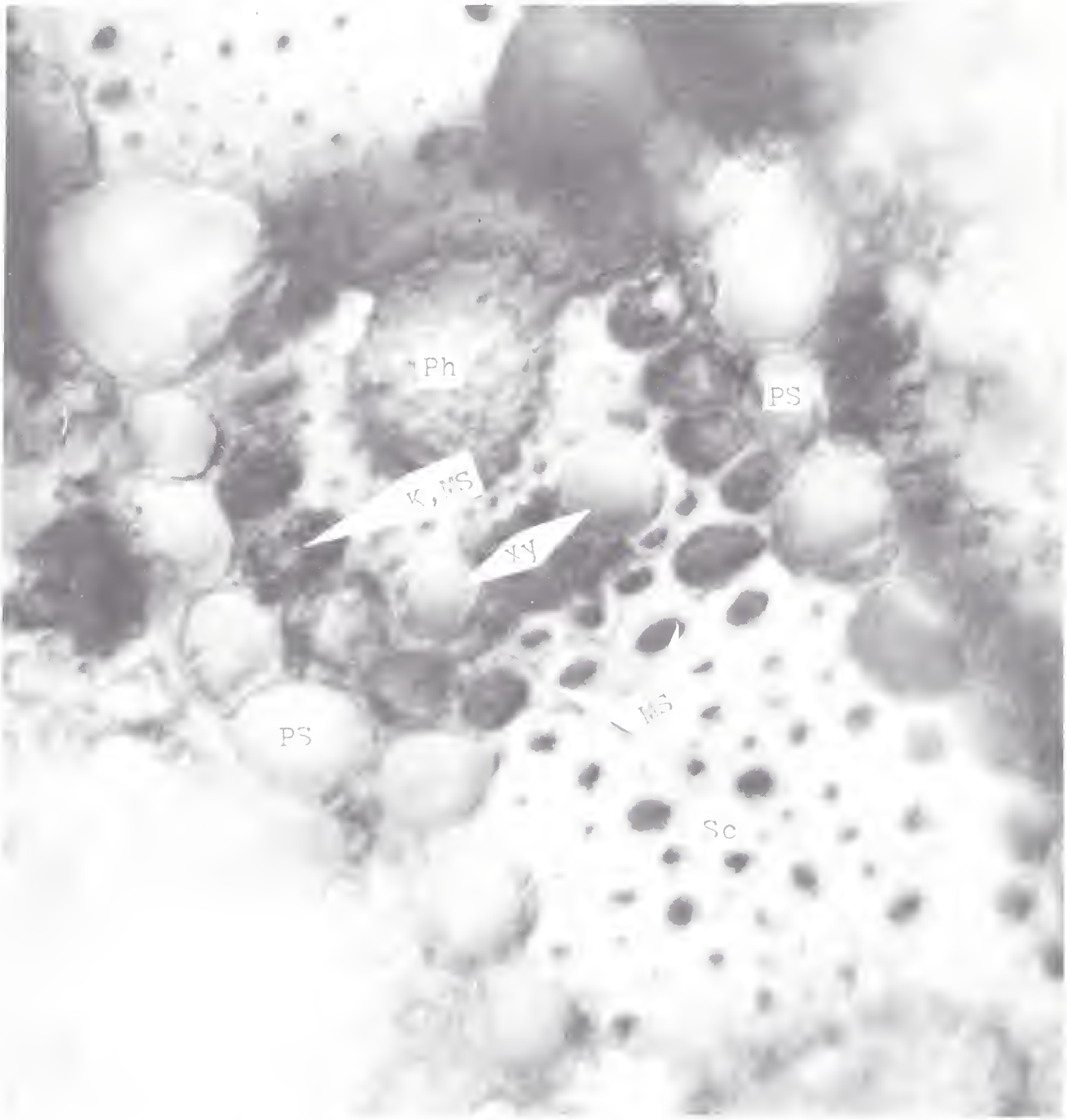


FIGURE 2. *Photomicrograph of a partial midrib cross section showing M.S. anatomy with a parenchyma sheath present in* Panicum petersonii. *One bundle (center) and part of another (lower right) are shown. The mestome sheath cells (K, M.S.) contain chlorophyll, but over the xylem (Xy) they are very thick-walled (M.S.). The cells of the parenchyma sheath (P.S.) are large and empty of chlorophyll, and the sheath is continuous over the sclerenchyma (Sc) between the two bundles. The phloem (Ph) of both bundles is visible. The lower bundle is closer to the surface of the midrib, which constitutes nearly all of the blade in this Cuban species. See text for discussion. ca. 800X.*

The group "Grandia" is unique because it appears to contain both Kranz and non-Kranz species. Hitchcock (1915) stated that *Panicum grande* is morphologically close to *P. grumosum*, *P. rivulare*, and *P. prionitis;* that *P. stagnatile* is close to *P. rivulare;* and (1936) that *P. petersonii* is close to *P. prionitis*. Thus, the group seems to be composed of related species. On the other hand, four species are non-Kranz, whereas *P. prionitis* and *P. petersonii* have Kranz M.S. anatomy.

The anatomy of the latter two species is unique and, in a sense, is intermediate between non-Kranz and Kranz. The M.S. Kranz cells are, for Kranz cells, very thick-walled and, in fact, part of the sheath may be composed of typical, very thick-walled, non-Kranz-like mestome sheath cells (Figure 2). This is especially common where the sheath surrounds the inner bundle when two are radially arranged in the midrib, which essentially constitutes the blade in these species. Thus the Kranz sheath is obviously derived from the mestome sheath. Furthermore, the parenchyma sheath is still obvious, composed of not enlarged, thin-walled, apparently empty cells. The only other known examples of M.S. species having parenchyma sheaths are in *Alloteropsis* (Africa to Australia) and two species of *Neurachne* (Australia). They, too, are closely related to non-Kranz taxa, *A. semialata* var. *eckloniana* (Ellis, in press) and *Thyridolepis*. It is proposed that these three cases are examples of recently evolved Kranz syndrome. The mestome sheath cells are still small and the walls are excessively thick for Kranz cells. The parenchyma sheath, which is lost in all other M.S. species, persists.

Rather than divide these apparently related species between subgenus *Sarmentosum* (non-Kranz) and the M.S. groups (Kranz), it seems preferable, temporarily, to maintain "Grandia" separate from both (Table 8).

It is interesting that this recent evolution of the Kranz syndrome in *Panicum* yielded the M.S. anatomy characteristic of Kranz Paniceae in general, rather than the P.S. subtype of typical *Panicum*. It can be proposed that in the Paniceae generally, evolution of the Kranz syndrome is almost always via the M.S. subtype. Perhaps only once has the Kranz syndrome evolved via the P.S. subtype, to yield the P.S., NAD-me species of subgenus *Panicum* (Tables 7 and 8). The P.S., PEP-ck species, though excluded from *Panicum* (the *Brachiaria* group), may have been derived from the same evolution of the P.S. subtype that yielded the subgenus *Panicum*. Certainly, taxonomic treatments of the past indicate considerable similarity between subgenus *Panicum* and the *Brachiaria* group (*Brachiaria*, *Eriochloa*, *Urochloa*, etc.), so a common ancestry seems likely (Figure 1).

Group "Hemitoma" Hitchcock, sometimes included in *Panicum*, has been transferred by Hsu (1965) to *Hymenachne*. Since *P. hemitomon* Schult. is non-Kranz, as is *Hymenachne*, this study, if anything, supports its transfer. Pohl and Lersten (1975), however, excluded *P. hemitomon* from *Hymenachne* because of its hollow internodes and staminate lower florets.

Thus, from *Panicum* as constituted by Hitchcock (1950), the following have been transferred:

Subgenus *Paurochaetium* to *Setaria*.
Subgenus *Dichanthelium* to genus *Dichanthelium*.
Group "Hemitoma" to *Hymenachne?*
Group "Geminata" to *Paspalidium*.
Group "Purpurascentia" to *Brachiaria*.
Group "Fasciculata" to the *Brachiaria* group.
Group "Laxa" in part to genus *Steinchisma*.
Group "Gymnocarpa" to genus *Phanopyrum*.

Even with these transfers the genus remains a large and heterogeneous assemblage of non-Kranz and Kranz, P.S. and M.S., NADP-me and NAD-me taxa.

With these modifications among the sections and groups, the application of leaf anatomy at the subgeneric level deserves consideration. It is evident that, with the Kranz P.S., PEP-ck species transferred out of *Panicum* to the *Brachiaria* group, four general types remain (Table 8). There are two types of non-Kranz taxa (Hsu, 1965), those with smooth and those with rough fertile lemmas, and two types of Kranz taxa, P.S. and M.S. The rough-lemma, C_3 taxa can be included in Subgenus *Megathyrsum* Pilger, and the smooth lemma, C_3 ones in subgenus *Sarmentosum* Hsu. The corresponding Kranz taxa are subgenus *Panicum* with P.S. leaf anatomy, and a new informal assemblage of groups with M.S. leaf anatomy (Table 7).

Subgenus *Panicum* is very homogeneous (P.S., smooth and shining fertile lemmas) and the taxa included here correspond quite well with those included by Hsu (1965).

The M.S. groups have little in common except that subtype of leaf anatomy. Because the M.S. condition is typical of most Kranz Paniceae except the *Brachiaria* group and subgenus *Panicum*, it is possible that the M.S. groups would best be treated as distinct genera, perhaps of recent origins along with "Grandia."

The two non-Kranz subgenera are not homogeneous. Some groups are related, such as "Parvifolia," "Parviglumia," and "Stolonifera," but others, such as "Megista," section *Depauperata*, and "Verrucosa," are individually unlike any others. It can be concluded that each subgenus includes present-day termini of a number of evolutionary lines, many of which have been distinct for a long time.

Type of leaf anatomy is assumed to be the best available character for delimiting subgenera, and character of the fertile lemma surface seems to be equally good at the next lower level of classification. Utilization of these characters has not greatly modified the groups and sections as based upon morphological characters, but has grouped them at the subgeneric level. If leaf anatomy and correlated biochemistry are as significant in systematics as is assumed here, it follows that the genus *Panicum* might be conceived as limited to the homogeneous subgenus *Panicum*. That may be achieved eventually, but should not be attempted until a very detailed acquaintance with all the species of the genus has been acquired.

Chromosome counts for species of *Panicum* are now numerous. It is evident that there are two basic chromosome numbers within the genus, 9 and 10. Of these, 9 is the more common. When available numbers were assigned to the species listed in Table 7, it became evident that most groups and sections are uniform for one or the other basic number. Furthermore, the whole subgenus *Panicum* is characterized by the basic number 9, reflecting the general uniformity of that taxon. The three other subgenera each contain both x = 9 and x = 10 taxa, which parallels their morphological heterogeneity.

TABLE 8. *Supraspecific taxa of* Panicum, *arranged according to types of leaf anatomy, photosynthesis, and fertile lemma surface.*

Non-Kranz, C_3	Kranz, C_4
Fertile lemmas rough **Subgenus *Megathyrsum* Hsu**	P.S., NAD-me fertile lemmas smooth **Subgenus *Panicum***
section *Clavelligera* Stapf section *Depauperata* Pilger section *Monticola* Stapf section *Pectinata* Stapf group "Trichoidea" Hitchc. section *Trinerves* Stapf group "Verrucosa" H. and C. section *Verruculosa* Stapf	section *Panicum* group "Dichotomiflora" H. and C. group "Diffusa" H. and C. section *Repentia* Stapf section *Dura* Stapf group "Rudgeana" Hitchc.
	P.S., PEP-ck fertile lemmas rough **Questionably "true" panicums**
Fertile lemmas smooth **Subgenus *Sarmentosum* Hsu**	M.S., NADP-me **Miscellaneous Assemblage**
group "Laxa" H. and C. group "Parvifolia" H. and C. group "Parviglumia" H. and C. group "Stolonifera" H. and C. group "Megista" Hitchc. section *Sarmentosa* Pilger group "Haenkeana" Hitchc.	group "Agrostoidea" H. and C. group "Obtusa" H. and C. group "Plena" W. V. Brown group "Tenera" H. and C. group "Discrepantia" W.V. Brown group "Tuerckheimiana" Hitchc.
group "Grandia" Hitchc. (pars)--------	----- group "Grandia" (pars)

There are a few transfers of species indicated by basic chromosome numbers. Both *Panicum elephantipes* of tropical America and *P. glabrescens* of Africa appear to have x = 10 but P.S. anatomy. They have been removed tentatively from subgenus *Panicum*. *Panicum glutinosum* (x = 10) has been removed from section *Sarmentosa*, which seems to have a basic number of 9. Section *Monticola* has one species reported as x = 9 and one reported as x = 10, so no generalization as to basic number is possible now.

Panicum maximum seems to be characterized by the unusual chromosome number 2n = 32. It is interesting that *P. trichocladum*, which Stapf (1920) put in the same section with *P. maximum*, also appears to have 2n = 32. These two appear to be the only species of *Panicum* with a basic number other than 9 or 10. Neglecting apomictic species, which often have aneuploid numbers, there are species in other genera, such as in *Pennisetum* and such as *Brachiaria (Panicum) reptans* L., with n = 7. The apparent x = 8 of *P. maximum* and *P. trichocladum* may further relate these two species to the *Brachiaria* group of PEP-ck genera.

The chromosome numbers of *Panicum* species have been determined by many investigators and for this analysis were extracted from the standard published lists of chromosome numbers, especially the annual "Index to plant chromosome numbers," (Regnum Vegetabile, Volumes 90, 91, and earlier).

THE SMALL TRIBES OF THE PANICOIDEAE

In addition to the large tribes Andropogoneae and Paniceae, there are up to nine small tribes of Panicoideae. The present study provides evidence for maintaining these taxa as distinct tribes (Pilger, 1954) rather than for incorporating some of them in the Paniceae. They have been sampled in order to make this survey as complete as possible and are discussed as tribes. Among them are non-Kranz, Kranz M.S., and Kranz P.S. taxa, but each tribe is homogeneous for leaf anatomical type.

CYPHOCHLAENEAE. This includes two or three very small genera endemic to Madagascar and adjacent islands (Pilger, 1954). They have greatly modified spikelets and are non-Kranz (Table 9). They doubtless represent end lines of a group that has evolved in isolation for a long time.

LECOMTELLEAE. This is a monotypic tribe of Madagascar. *Lecomtella madagascarensis* is non-Kranz and, like the species of the Cyphochlaeneae, has evolved in isolation.

ISACHNEAE. This is a considerably larger tribe than the two above, but like them is all non-Kranz. *Coelachne*, *Heteranthoecia*, *Limnopoa*, and *Sphaerocaryum* are small and geographically restricted genera. *Isachne*, on the other hand, is pantropical (Potztal, 1952) (Table 9). It differs from non-Kranz Paniceae by having two hardened, usually fertile florets per spikelet, the lemmas of which have thread-like microhairs on their surfaces (Hsu, 1965). However, numerous species of *Isachne* have sterile lower florets, and a few Paniceae, such as the Hawaiian *Dissochondrus*, have fertile ones. Thus, the difference between *Isachne* and Paniceae is not great.

It is assumed by agrostologists that the original grasses had spikelets of numerous florets, so that taxa having spikelets of one or two florets are somewhat advanced. Therefore, it is likely that evolution leading to the typical spikelet of the Paniceae (two florets, of which the lower does not have lemma and palea indurated and is sterile or staminate) probably passed through a stage having two fertile and specialized florets, as occurs in the Isachneae. It can be proposed that the Isachneae represent modern descendants of that two-fertile-floret, non-Kranz, pre-Paniceae stage of evolution. It has already been stated that Chase (1911) saw similarities between *Isachne* and *Dichanthelium*.

The remaining small tribes all have Kranz leaf anatomy.

TABLE 9. *Species of the small panicoid tribes examined, arranged by tribes and genera: anatomical and photosynthetic characters, provenances, and voucher herbaria.*

	Syndrome	Anatomy	$\delta^{13}C$	Provenance	Herbaria
	BOIVINELLEAE				
Cyphochlaena					
madagascariensis	Nr		−32.5	Madag.	P, US
	LECOMTELLEAE				
Lecomtella					
madagascariensis	Nr		−26.5	Madag.	P
	ISACHNEAE				
Coelachne					
africana	Nr		−27.2	Africa	US
4 other spp. (Potztal, 1952)	Na			Old World	
Heteranthoecia					
isachnoides (Potztal, 1952)	Na			Africa	
Isachne					
albens	Na			India	US
confusa	Na			Asia	US
disperma	Nr		−27.1	S. Am.	TEX
distichophylla	Nr		−25.6	S. Am.	TEX
kunthiana	Na			Asia	US
polygonoides	Na			C. Am.	TEX
pubescens	Nr		−26.0	C. Am.	TEX
pulchella	Nr		−27.7	India	TEX
rigidifolia	Nr		−25.8	W. Ind.	TEX
saxicola	Na			Asia	US
scabrosa	Na			Asia	US
23 more spp. (Potztal. 1952)	Na				

Table 9 continued.

	Syndrome	Anatomy	$\delta^{13}C$	Provenance	Herbaria
Limnopoa					
meeboldii (Potztal, 1952)	Na			India	
Sphaerocaryum					
malaccense (Potztal, 1952)	Na			Asia	
ANTHEPHOREAE					
Anthephora					
cristata	Ka	M.S.		Africa	TEX
hermaphrodita (2)	Kar	M.S.	−11.1	America	TEX
pubescens	Kar	M.S.	−12.5	Africa	TEX
hochstetteri (Günzel, 1912)	Ka				
undulatifolia (Günzel, 1912)	Ka				
TRACHYEAE					
Trachys					
muricata	Kr	M.S.	−11.6	India	US
MELINIDEAE					
Melinis					
minutiflora	Kar	P.S.	−12.7	S. Am.	TEX
Rhynchelytrum					
repens	Kar	P.S.	−12.7	Africa	TEX
Tricholaena					
capensis	Ka	P.S.		Africa	TEX
monachne	Kar	P.S.	−11.9	Africa	PRE, TEX
teneriffae	Ka	P.S.		India	TEX
Neyraudia					
reynaudiana (Tateoka, 1956)	Ka	P.S.			
ARTHROPOGONEAE					
Achlaena					
piptostachya	Ka	M.S.		Cuba	TEX
Arthropogon					
scaber (Tateoka, 1963b)	Ka	P.S.!			US
villosus	Ka	M.S.	−13.3		US
xerachne (Tateoka, 1963b)	Ka	P.S.!			US
Reynaudia					
filiformis	Ka	M.S.	−11.6	W. Ind.	TEX, US
Snowdenia					
polystachya			−13.5		US
ARUNDINELLEAE					
Arundinella					
berteroniana	Kr	M.S.	−14.5	C. Am.	TEX

Table 9 continued.

	Syndrome	Anatomy	$\delta^{13}C$	Provenance	Herbaria
confinis	Ka	M.S.		Mexico	TEX
deppeana	Kr		−11.7	C. Am.	TEX
hirta (Tateoka, 1956, etc.)	Kace	M.S.		Asia	
hispida	Ka	M.S.		India	TEX
leptochloa	Ka	M.S.		India	TEX
martinicensis	Ka	M.S.		W. Ind.	TEX
metzii	Ka	M.S.		India	TEX
nepalensis (Tateoka, 1958)	Kace	P.S.!		India	
palmeri	Ka	M.S.		Mexico	TEX
11 other spp. (Tateoka, 1958)					
Danthoniopsis					
dinteri	Ka	M.S.	−12.5	Africa	PRE
Gilgiochloa					
indurata	Ka	M.S.	−12.7	Africa	PRE
Loudetia					
kagerensis	Ka	M.S.		Africa	TEX
pedicellata (de Wet, 1960)	Ka			Africa	
rogerensis	Kr		−11.9	Africa	US
simplex	Kar	M.S.	−11.4	Africa	US, TEX
sp.	Ka	M.S.		Africa	TEX
Trichopteryx					
dregeana	Kar	M.S.	−13.3	Africa	PRE
simplex	Kar	M.S.	−11.4	Africa	PRE
stolziana	Ka	M.S.		Africa	TEX
Tristachya					
avenacea	Ka	M.S.		Mexico	TEX
biseriata	Ka	M.S.		Africa	TEX
hispida	Kar	M.S.	−11.4	Africa	PRE
GARNOTIEAE					
Garnotia					
acutigluma	Kar	M.S.	−10.7	China	US
arundinacea	Kar	M.S.	−11.5	India	US
stricta	Kar	M.S.	− 9.5	India	TEX
triseta	Ka	M.S.		China	TEX
10 other spp. (Tateoka, 1958)					
TRACHYEAE					
Trachys					
muricata	Kar	M.S.	−11.6	India	US

TRACHYEAE. This possibly distinct tribe (Pilger, 1954; Potztal, 1957) is constituted by the single Indian species *Trachys muricata*. Hsu (1965) included the genus in the Paniceae. Smith and Brown (1973) recorded it as having a C_4 $\delta^{13}C$ ratio. Its leaf anatomy is M.S., which contributes nothing to clarifying its placement, however.

MELINIDEAE. This mostly African tribe of about four genera is unique among these small tribes of Panicoideae in having P.S. leaf anatomy (Table 9). Hsu (1965) maintained it as a distinct tribe and the leaf anatomy supports that decision. The only other Panicoideae having P.S. leaf anatomy are the *Brachiaria* group of genera and the typical subgenus of *Panicum*. Spikelet comparison between these taxa of Paniceae and the Melinideae suggests a relationship at the tribal level.

ANTHEPHOREAE. This taxon comprising one genus and about 20 species can be considered as merely a highly specialized genus of Paniceae (Reeder, 1960; Stebbins and Crampton, 1961; Hsu, 1965), as possibly crossable with *Digitaria* (Loxton, 1974), or as different enough from Paniceae to warrant status as a distinct tribe (Pilger, 1940; Tateoka, 1957). No modern grass systematist places *Anthephora* anywhere except in the Panicoideae.

Reeder (1960) reviewed the placement of *Anthephora* historically and compared one species, *A. hermaphrodita*, to some Zoysieae and Paniceae. By all the usual characters (silica cells, bicellular hairs, chromosome size and basic number, and embryos) *Anthephora* is similar to Paniceae and all Kranz Panicoideae. The only character Reeder discussed that might help settle its placement was spikelet morphology, a subject of disagreement for 200 years. But he presented no new evidence except a detailed comparison of internal "bur" structures in *A. hermaphrodita* with *Cenchrus*.

Anthephora has leaf anatomy typical of most Kranz Panicoideae, the M.S. subtype. However, the presence of "distinctive cells" in at least *A. cristata* is a recently discovered characteristic differentiating the genus (Johnson, 1964). Distinctive cells (see later) have been reported in no grass taxa except a few of these small tribes of Panicoideae. Their presence plus the specialized spikelets and inflorescences suggest retention of the tribe Anthephoreae.

ARTHROPOGONEAE. This is a tribe of four small genera, three American and one African (Table 9). Tateoka (1963b) and this study have demonstrated that all species are Kranz and that many possess distinctive cells. Tateoka reported the P.S. subtype of Kranz anatomy but I found the M.S. subtype in those same species. For uniformity of comparison with other Kranz taxa, the Arthopogoneae are here treated categorically as being M.S. Although the African genus *Snowdenia* is Kranz (Smith and Brown, 1973), its type of leaf anatomy was not determined. Its relationship to the American genera is somewhat questionable (Tateoka, 1963b).

Since it is assumed here that the presence or absence of distinctive cells is a significant character in grass systematics, it is suggested that the genera of this group are distinct enough from all other taxa except Anthephoreae, Arundinelleae, and Garnotieae to justify maintenance of the tribe Arthropogoneae.

ARUNDINELLEAE. This tribe of about six genera is centered in southern Africa except for the pantropical genus *Arundinella*. Hsu (1965) treated *Arundinella* as probably distinct from the Paniceae. Tateoka (1958) supported the concept of the tribe Arundinelleae and related it to the Garnotieae. The genera of Arundinelleae are Kranz M.S. (Conert, 1957; Metcalfe, 1960) (Table 9), although Tateoka (1958) described them as P.S.

Tateoka (1958) and Hsu (1965) placed the Arundinelleae in the Panicoideae, but Pilger (1954) placed the tribe in the Festucoideae which, by most modern concepts, would be a very unnatural association. According to such modern criteria as silica cell, bicellular hair, and embryo characters, cytology, and leaf anatomy, the Arundinelleae belong in the Panicoideae. Spikelet structure indicates a relationship to the Paniceae or Danthonieae.

Distinctive cells have been reported in numerous species of *Arundinella* (Tateoka, 1956a and b, 1958; Brown, 1958; Crookston and Moss, 1973) and in *Loudetia* and *Trichopteryx*. If presence of distinctive cells indicates phylogenetic relationship, as Tateoka (1958) and I assume, then the Anthephoreae, Arthropogoneae, Arundinelleae, and Garnotieae are set off from all other tribes as a related group, possibly a single tribe.

Spikelets of Arundinelleae have similarities to some of the two-floreted Danthonieae of South Africa, such as some species of *Danthonia* and all species of *Pentameris* and *Pentaschistis*. De Wet (1954) stated that, "These . . . genera [*Tristachya* and *Loudetia*] and also the *Danthonia* species group including *D. forskalii* are closely related to the tribe Arundinelleae." Furthermore, silica cells of some Danthonieae and bicellular hairs of most are similar to those of Arundinelleae and, in fact, all Panicoideae. Chromosome numbers within *Arundinella* itself and related genera are now known to show a "lack of uniformity" (Li, Lubke, and Phipps, 1966) (n = 6 or 12, 7, 8, 9, 10). The Panicoideae, aside from apomictic species, which are common (Brown and Emery, 1958), are characterized by the basic numbers 5 or 10, and 9. In the Danthonieae, however, basic numbers of 6, 7, and 9 have been reported (de Wet, 1954; Brock and Brown, 1961). Thus the variable basic numbers of the Arundinelleae are matched by similar variability in the Danthonieae.

Leaf anatomy favors relationship to the Panicoideae. In the latter subfamily the Kranz species are mostly M.S. also (Table 9). The Kranz Danthonieae, *Asthenatherum* and *Alloeochaete* of South Africa (de Wet, 1954) and *Pheidochloa* of Australia, have P.S. leaf anatomy. Therefore, any relationship of Arundinelleae to Danthonieae should not be to the known Kranz genera of Danthonieae.

For the present, a position intermediate between the Danthonieae and the Paniceae seems appropriate.

GARNOTIEAE. This comprises one genus of about 30 species from southeastern Asia and southeastward (Tateoka, 1958; Gould, 1972).

Pilger (1954) assigned *Garnotia* to a

monogeneric subtribe of the Eragrosteae. Tateoka (1958) placed it as a monogeneric tribe in the Panicoideae on anatomical and epidermal leaf characters, and Gould (1972) agreed with that placement. It has M.S. leaf anatomy, unknown in the Eragrostoideae but typical of the Panicoideae, and bicellular hairs quite unlike those of the Eragrostoideae. Tateoka and Gould considered it to be perhaps distantly related to the Arundinelleae. Like the latter and some other small Kranz panicoid tribes, some species of *Garnotia* have distinctive cells (Tateoka, 1958). Therefore, inclusion of *Garnotia* in the Panicoideae seems adequately justified.

Examination of transverse and longitudinal views of distinctive cells and rows of such cells leads to the interpretation that the longitudinal rows are remnants of Kranz sheaths of the small bundles which have no vascular tissue, as indicated by Tateoka (1958). Crookston and Moss (1973) observed in part that the (evident) vascular bundles of such a leaf are as far apart as in most non-Kranz species. If the rows of distinctive cells are vascular bundle sheath remnants, then they should be closely spaced, as they are, like the small bundles of typical Kranz leaves (Hattersley and Watson, in press). Furthermore, lateral bundles do interconnect the true bundles and rows of distinctive cells, just as though the latter were small bundles. In species of *Loudetia* and *Trichopteryx* there are multicellular strands of distinctive cells intermediate in appearance between typical Kranz sheaths and single rows of distinctive cells, as also observed in *Arundinella* and *Garnotia* by Tateoka (1958).

In Kranz species, ribulose diphosphate carboxylase (RuDP-Case) is mostly restricted to Kranz cells. That distinctive cells are indeed Kranz cells has been further indicated recently (Hattersley, et al., in press). Leaf sections were treated with antiserum to RuDP-Case carrying a fluorescent dye to reveal the sites of RuDP-Case in the leaf. The chloroplasts of the distinctive cells fluoresced as brilliantly as did those of the Kranz sheath cells in the species *Arundinella nepalensis*.

It has been established, therefore, from studies of various species, that distinctive cells are quite certainly Kranz cells. They are similar for large agranal chloroplasts, storage of starch, thickness of walls with an electron-opaque band between such cells (Crookston and Moss, 1973), and now for presence of RuDP-Case.

It is always possible to read evolutionary change in either direction. Therefore, rows of single or multicellular distinctive cells may be stages in the evolution of the intercalary, closely-spaced, small bundles typical of Kranz grasses. Certainly, intercalary bundles have always evolved in grasses along with Kranz anatomy, and such closely-spaced bundles with Kranz sheaths do occur in some species of most or all genera reported to have distinctive cells.

On the other hand, if Kranz cells not associated with vascular tissues (distinctive cells) work well enough in C_4 photosynthesis, perhaps rows of distinctive cells are developmentally modified intercalary bundles (degenerate bundles) rather than formative stages. This seems most likely and I propose it as a working hypothesis, although it is difficult to account for such occurrence in only some species of most genera of only these four small tribes.

Because distinctive cells have been observed in no other Kranz genera of grasses, it is assumed that this is a unique qualitative characteristic sufficient to indicate phylogenetic relationship among the small Kranz panicoid tribes Arundinelleae, Arthropogoneae, Garnotieae, and Anthephoreae, as stated in part by Tateoka (1958, 1963b). This justifies their maintenance as four distinct but related tribes or as one inclusive tribe.

Tateoka (1958, 1963b) concluded that the numerous species he examined of Arundinelleae, Garnotieae, and Arthropogoneae have a mestome sheath surrounded by a Kranz parenchyma sheath, P.S. leaf anatomy. After careful examination and reexamination of numerous species of these tribes against a background of experience with hundreds of Kranz grass species, I am certain that these are M.S. taxa. I cannot explain this difference of opinion over something so simple. At least they are M.S. according to my criterion for recognizing that subtype, which is that in cross sections of larger veins, Kranz sheath cells are in contact tangentially with the large metaxylem vessels.

The non-Kranz tribes Cyphochlaeneae, Lecomtelleae, and Isachneae can be related to the non-Kranz genera of Paniceae, and to the non-Kranz subgenera of *Panicum*. It is likely that the Cyphochlaeneae and Lecomtelleae have evolved certain spikelet specializations while the Isachneae have maintained the pre-panicoid condition (two fertile florets). Certainly these non-Kranz tribes have less specialized leaf anatomy and photosynthesis than do the Kranz tribes.

Of the six Kranz tribes, the Melinideae are unusual in having P.S. leaf anatomy. They could be related by leaf anatomy to Eragrostoideae, P.S. *Panicum*, P.S. Paniceae, *Stipagrostis* of the Aristideae, or Kranz Danthonieae. Of these, the Eragrostoideae can be eliminated especially because of their club-shaped bicellular hair cells. The P.S. Paniceae (the *Brachiaria* group) and P.S. *Panicum* (the typical panicums) seem to be recent advanced types quite unlike the Melinideae. *Stipagrostis* also is a specialized type quite distinct from Melinideae. Therefore, the most likely relationship of the latter is to the Danthonieae or Panicoideae.

If M.S. leaf anatomy does indicate supertribal relationship, the Arundinelleae, Arthropogoneae, Anthephoreae, and Garnotieae seem closest to the M.S. Paniceae and Andropogoneae as, perhaps, a third offshoot from some common ancestor. The presence of distinctive cells, however, does help to set them off from all other tribes of Gramineae.

THE ANDROPOGONEAE

Previous studies of leaf anatomy and photosynthesis have, without exception, reported species of the Andropogoneae to be Kranz (Table 10; 60 genera and 181 species), M.S. (Brown, 1975), and NADP-me (Table 1). This uniformity indicates that no other subtypes should be expected, except possibly in *Microstegium*. The latter, a small genus occurring from southern Asia eastward and to South Africa, is characterized by growing in, and possibly requiring, dense shade.

It has been well established that Kranz species are, with few exceptions, restricted to bright light. Therefore, species of otherwise Kranz taxa that seem to require low light intensity might be expected to have non-Kranz leaf anatomy and/or biochemistry. If so, they would be examples of reverse evolution, from Kranz to non-Kranz. Taxa examined to check this possibility included four species of *Microsteigum* (Andropogoneae), six species of *Setaria* subgenus *Ptychophyllum* (Paniceae), and some

TABLE 10. *Genera of Andropogoneae examined for Kranz characters by various investigators, arranged alphabetically. All species examined (numbers per genus as indicated) are Kranz. Among them, all those characterized as to anatomical and/or photosynthetic subtypes are M.S. and NADP-me.*

Amphilophis	3
Andropogon	22
Apluda	1
Arthraxon	4
Bothriochloa	8
Chasmopodium	1
Chrysopogon	6
Coelorhachis	1
Cymbopogon	6
Dichanthium	7
Diectomis	1
Dimeria	1
Eccoilopus	1
Elyonurus	4
Eremochloa	2
Eremopogon	1
Erianthus	5
Eriochrysis	1
Eulalia	5
Eulaliopus	1
Germainia	1
Hackelochloa	1
Hemarthria	4
Heteropogon	2
Hyparrhenia	6
Hypogynium	1
Imperata	3
Ischaemum	10
Iseilema	1
Jardinea	2
Lasiurus	2
Manisuris	3
Microstegium	4
Miscanthus	3
Monocymbium	1
Miscanthidium	1
Pogonatherum	1
Phacelurus	1
Pseudopogonatherum	1
Rattraya	1
Raphis	1
Rhytachne	2
Rottboellia	2
Saccharum	5
Schizachyrium	4
Sehima	1
Sorghastrum	1
Sorghum	11
Spodiopogon	1
Themeda	6
Trachypogon	2
Urelytrum	2
Vetiveria	5
Vossia	2
Chionachne	1
Coix	1
Euchlaena	2
Polytoca	1
Tripsacum	1
Zea	1

Totals: 60 genera; 181 species.

species of *Muhlenbergia* (Eragrostoideae).

The four species of *Microstegium* and all species of *Ptychophyllum* have Kranz M.S. leaf anatomy, and *M. vimineum* has a $^{13}C/^{12}C$ ratio of −13.8 and is NADP-me (Gutierrez and Edwards, unpublished) (Table 11). It is true that the leaves of these species are thin for Kranz leaves.

There are also some species of typically xerophytic *Muhlenbergia* that usually grow in the shade of moist woods or thickets and are found as far north as southern Canada (Hitchcock, 1950). These species, like all others of the genus, have Kranz leaf anatomy and/or $\delta^{13}C$ ratios (Table 11). In the northern extremes of their ranges they grow under conditions of low light intensity, low temperature, and high soil moisture, quite unlike those usually considered essential for, or characteristic of, Kranz species.

TABLE 11. *Some shade-tolerant species of* Microstegium *(Andropogoneae),* Setaria *(Paniceae), and* Muhlenbergia *(Sporoboleae): anatomical and photosynthetic characters, provenances, and voucher herbaria.*

	Synd.	$\delta^{13}C$	Anat.	Prov.	Herb.
Microstegium					
ciliatum	Ka		M.S.	India	TEX
glabratum	Ka		M.S.	Fiji	TEX
nudum	Ka		M.S.	India	TEX
vimineum	Kaer	−13.8	M.S.	U.S.A. (intro.)	TEX
Setaria, subgenus *Ptychophyllum*					
barbata	Kar	−10.8	M.S.	S. Am.	US
chevalieri	Ka		M.S.	Africa	TEX
membranifolia	Kar	−12.0	M.S.	S. Am.	US
palmifolia	Ka		M.S.	Asia	TEX
paniculifera (3)	Ka		M.S.	S. Am.	TEX
poiretiana	Kar	−11.2	M.S.	S. Am.	US
Muhlenbergia					
frondosa (Pohl)	Ka		P.S.	U.S.A.	TEX
glabriflora (Pohl)	Ka		P.S.	U.S.A.	TEX
mexicana	Kar	−13.4	P.S.	U.S.A.	TEX
schreberi	Kar	−15.0	P.S.	U.S.A.	TEX
sobolifera (Holm)	Ka		P.S.	U.S.A.	TEX
sylvatica	Kar	−13.2	P.S.	U.S.A.	TEX
tenuiflora	Ka		P.S.	U.S.A.	TEX

The only Kranz dicotyledonous species known to require dense shade occur in *Chamaesyce* (Euphorbiaceae) (Pearcy and Troughton, 1974). In Hawaii there are a few species of this genus that are restricted to the dense shade of rain forests. Nevertheless, they are definitely C_4 according to the $^{13}C/^{12}C$ ratios reported. They are also rare examples of woody Kranz species.

There are also species of the grass genus *Brachiaria*, such as *B. miliiformis*, *B. remota*, and *B. setigera* of India and Ceylon (Bor, 1960), that at least sometimes grow in rather dense shade. These and *Muhlenbergia (M. schreberi*, Table 1) are or should be PEP-ck, whereas *Microstegium*, *Setaria* (Table 1), and *Chamaesyce* (Table 2) are or should be NADP-me. Thus, reversion of Kranz taxa to shade-tolerance or shade-requirement is not correlated with taxonomy or photosynthetic biochemistry.

All known shade-requiring species of otherwise Kranz taxa are themselves Kranz. There is no evidence that reverse evolution (Kranz to non-Kranz) has ever occurred, although it has been invoked in the attempt to reconcile Kranz/-non-Kranz patterns with taxonomic and phylogenetic schemes (Carolin, Jacobs, and Vesk, 1975).

These results indicate that when Kranz species adapt to shade they conserve the Kranz anatomy, C_4 photosynthesis, and perhaps the biochemical subtype of their high-light-requiring ancestors. Nevertheless, it seems likely that in some aspects their photosynthesis and/or photorespiration might differ from those of related Kranz species that require full sunlight.

The complete uniformity of the Andropogoneae for the Kranz syndrome can be interpreted as indicating its origin rather recently from some Kranz panicoid grass. A relatively recent origin of the tribe in tropical Africa and/or Asia has already been proposed (Hartley, 1958a; Whyte, 1973). It is possible that those tribes of the Panicoideae (excluding the Paniceae and Melinideae at least) that have Kranz M.S. leaf anatomy, a basic chromosome number of 10, and delicate, often awned, fertile lemmas might have had a common origin. This would relate the Andropogoneae to the Arudinelleae, Arthropogoneae, Anthephoreae, and Garnotieae.

THE DANTHONIEAE

The tribe Danthonieae may well represent a central group in the evolution of the Gramineae. As more and more is learned about the leaf and other characters now assumed to be most significant in the systematics of the family, increasing numbers of tribes and genera seem to show possible relationships to the Danthonieae. And the Danthonieae themselves show considerable variation in such basic characters as chromosome number, spikelet morphology, floret number, silica cell form, and leaf anatomy. The number of generic segregates from southern African and Australian *Danthonia* during the past decades has been large. Previous studies by de Wet (1954, 1956) demonstrated this variability and pointed out that two genera segregated from non-Kranz *Danthonia*, *Asthenatherum* and *Alloeochaete*, by Nevski (1934) and

Hubbard (1940) respectively, are Kranz. The tribe deserves extensive and intensive study, and a survey of all available genera was therefore undertaken, including examination of leaf anatomy and/or $^{13}C/^{12}C$ ratios, and the literature (Table 12).

TABLE 12. *Species of Danthonieae examined for Kranz characters by various investigators, arranged by genera: anatomical and photosynthetic characters, provenances, and voucher herbaria. Data from this study unless otherwise attributed.*

		Synd.	Anat.	$\delta^{13}C$	Prov.	Herb.
Afrachneria						
ampla	(de Wet, 1956)	Na		−29.3	Africa	US
aurea	(de Wet, 1956)	Na			Africa	PRE
capensis	(de Wet, 1956)	Na		−24.5	Africa	US
capillaris	(de Wet, 1956)	Na			Africa	PRE
ecklonii	(de Wet, 1956)	Na			Africa	PRE
microphylla	(de Wet, 1956)	Na			Africa	PRE
Alloeochaete						
namuliensis	(de Wet, 1956)	Ka			Africa	PRE
Amphibromus						
neesii		Na			Aust.	US
quadridentulus		Na			S. Am.	US
Amphipogon						
caricinus (2)		Na		−25.9	Aust.	NSW, US
turbinatus		Na		−24.5	Aust.	US
Anisopogon						
avenaceus		Na		−27.6	Aust.	NSW
Asthenatherum						
forskalii	(de Wet, 1954)	Ka			Africa	PRE
glaucum	(de Wet, 1954)	Ka	P.S.	−12.7	Africa	PRE
mossamedensis (2)	(de Wet, 1954)	Ka	P.S.	−12.6	Africa	PRE, TEX
pumila	(de Wet, 1954)	Na?			Africa	PRE
Chaetobromus						
dregeanus	(de Wet, 1956)	Na			Africa	PRE
involucratus	(de Wet, 1956)	Na			Africa	PRE
schraderi	(de Wet, 1956)	Na			Africa	PRE
Chionochloa						
australis	(de Wet, 1956)	Na			N. Z.	PRE
conspicua	(C. J. V., 1973)	Nae			Aust.	NSW
crassiuscula	(de Wet, 1956)	Na			N. Z.	PRE
oreophila	(de Wet, 1956)	Na			Aust.	PRE
Danthonia						
californica		Nar		−27.4	U.S.A.	TEX
disticha		Nar		−25.4	U.S.A.	TEX
intermedia		Nr		−25.6	U.S.A.	TEX
monticola	(C.J.V., 1973)	Nae			Aust.	NSW

Table 12 continued.

		Synd.	Anat.	$\delta^{13}C$	Prov.	Herb.
pallida	(C.J.V., 1973)	Nae			Aust.	NSW
purpurea (2)	(de Wet, 1954)	Nar		−25.9	Africa	PRE, TEX
purpurascens[1]		Na			Aust.	NSW
semiannularis (2)	(de Wet, 1954)	Nar		−27.3	Africa	PRE, TEX
spicata (2)	(de Wet, 1954)	Nar		−26.4	U.S.A.	TEX, PRE
vickeryi[2]		Na			Aust.	NSW
37 more spp.	(de Wet, 1954)	Na			Africa	US
Diplopogon						
setaceus (2)		Nar		−24.8	Aust.	NSW, US
Monachather						
paradoxus (2)		Na			Aust.	NSW, TEX
Monostachya						
oreoboloides		Na			N. Guin.	NSW
Notochloe sp.	(Decker, 1964)	Na			Aust.	
Pentamaris						
dregeana	(de Wet, 1956)	Na			Africa	PRE
longiglumis	(de Wet, 1956)	Na			Africa	PRE
macrocalycina (2)	(de Wet, 1956)	Nar		−24.9	Africa	PRE, US
obtusifolia	(de Wet, 1956)	Na			Africa	PRE
thuarii	(de Wet, 1956)	Na			Africa	PRE
Pentaschistis						
macrantha		Nr		−25.5	Africa	US
31 more spp.	(de Wet, 1956)	Na			Africa	PRE
Pheidochloa						
gracilis		Kar	P.S.	−12.5	Aust.	NSW
Plagiochloa						
uniolae	(de Wet, 1960)	Na			Africa	
Poagrostis						
pusilla (2)	(de Wet, 1956)	Nar		−26.8	Africa	PRE, US
Prionathium						
ecklonii	(de Wet, 1956)	Na			Africa	PRE
Schismus						
aristulatus	(de Wet, 1956)	Na			Africa	PRE
barbatus (2)	(de Wet, 1956)	Nar		−22.7	Africa	PRE, US
barbatus (2)	(C.J.V., 1973)	Nae			Aust.	NSW
inermis	(de Wet, 1956)	Na			Africa	PRE
Sieglingia						
decumbens	(Tateoka, 1956)	Na				

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[1] *Danthonia purpurascens* J. Vickery is now *Notodanthonia tenuior* (Steud.) S. T. Blake (Blake, 1972).

[2] *Danthonia vickeryi* Hubb. is now *Plinthanthesis urvillei* Steud. (Blake, 1972).

Pilger (1954) included *Amphipogon* and *Diplopogon* in the Aristideae. Most treatments place these Australian genera in the Danthonieae along with Kranz

Pheidochloa. If the Aristideae are very close to some Danthonieae, then tribal assignment becomes a matter of arbitrary definition. For the present it seems best to restrict the Aristideae to species with one floret per spikelet.

It is evident that most genera of Danthonieae are non-Kranz. The Kranz genera are *Alloeochaete* and *Asthenatherum* of southern Africa and *Pheidochloa* of Australia. No species of *Alloeochaete* were examined, but de Wet (1956) stated that the genus has panicoid (Kranz) leaf anatomy. *Asthenatherum* and *Pheidochloa* (and possibly *Alloeochaete*) are P.S. In that they resemble Eragrostoideae, *Stipagrostis* of the Aristideae, *Eriachne*, Melinideae, and some Paniceae. Of these, the Eragrostoideae are least like them on the basis of silica cells and bicellular hairs. The P.S. Paniceae seem more likely to be recent derivatives of non-Kranz Paniceae than of Kranz Danthonieae. In most characters the Aristideae are similar to the Danthonieae and might be considered as specialized, single-floreted Danthonieae, just as *Pheidochloa* is like a two-floreted *Aristida*. *Eriachne* also is much like a two-floreted *Aristida*, but differs from all tribes in some characters (see later).

It is also typical of all these P.S. taxa, except the Eragrostoideae, to have the walls of the mestome sheath cells, at least over the xylem, much thinner than is typical in non-Kranz tribes.

Another characteristic shared by these P.S. genera is Kranz cells that, in paradermal view, are longer than wide, somewhat like those of the M.S. subtype (Brown, 1974). In contrast, Kranz cells of Eragrostoideae and subgenus *Panicum* are short and radially wide (Brown, 1974). Such elongate P.S. Kranz cells are found in Melinideae, Paniceae except subgenus *Panicum*, *Stipagrostis*, *Eriachne*, *Pheidochloa*, and *Asthenatherum*. Actually, these genera have Kranz cells statistically longer than those in the *Eragrostoideae* and subgenus *Panicum*, and statistically somewhat shorter than Kranz cells of M.S. genera.

As indicated in Figure 3, the Aristideae may have evolved from ancient Danthonieae, probably in Africa, where the non-Kranz genus of Aristideae, *Sartidia*, and most of the more abundant *Stipagrostis* occur. The Danthonieae may represent the ancient grasses which first evolved the mesocotyl, and the very ancient transition to the subfamilies Arundinoideae, Panicoideae, and Eragrostoideae (Figure 4).

THE ARISTIDEAE

It has been known since about 1900 (Holm, 1901) that *Aristida* is all Kranz but has two sorts of leaf anatomy. Some species have one Kranz sheath, the parenchyma sheath, whereas others have two sheaths that are both considered to be Kranz sheaths.

More recently, the presence of two sheaths in *Aristida* has been confirmed at both the light microscope level (Henrard, 1929; Lommasson, 1957; Brown, 1958; Cáceres, 1961; Bourreil, 1962) and that of the electron microscope (Johnson, 1964; Johnson and Brown, 1973; Carolin, Jacobs, and Vesk, 1973). The latter

TABLE 13. *Species of Aristideae examined for Kranz characters by various investigators, arranged by sections and genera: anatomical and photosynthetic characters, provenances, and voucher herbaria. Data from this study unless otherwise attributed.*

	$\delta^{13}C$	Anat.	Prov.	Herb.
ARISTIDA				
Section *Adscensiones*				
longispica	−12.2	D.S.	U.S.A.	TEX
oligantha	−12.0	D.S.	U.S.A.	TEX
Section *Arthratherum*				
californica	−12.7	D.S.	U.S.A.	TEX
browniana		D.S.	Aust.	NSW
desmantha	−12.6	D.S.	U.S.A.	TEX
meridionalis	−12.6	D.S.	Africa	PRE
Section Chaetaria				
armata		D.A.	Aust.	NSW
canescens	−12.2	D.S.	Africa	PRE
ramosa		D.S.	Aust.	NSW
Section *Dichotoma*				
basiramea	−12.0	D.S.	U.S.A.	TEX
dichotoma	−12.6	D.S.	U.S.A.	TEX
Section *Divaricata*				
divaricata	−12.0	D.S.	U.S.A.	TEX
pansa	−14.0	D.S.	U.S.A.	TEX
Section *Pseudoarthratheum*				
congesta	−12.1	D.S.	Africa	PRE
Section *Pseudochaetaria*				
hordeacea (2)	−12.8	D.S.	Africa	PRE
Section *Purpurea*				
fendleriana	−12.4	D.S.	U.S.A.	TEX
tenuispica	−12.5	D.S.	U.S.A.	TEX
glauca	−13.4	D.S.	U.S.A.	TEX
purpurea	−13.8	D.S.	U.S.A.	TEX
wrightii	−13.0	D.S.	U.S.A.	TEX
Section *Schizachne*				
parvula	−12.8	D.S.	Africa	PRE
Section *Streptachne*				
orcuttiana	−12.7	D.S.	U.S.A.	TEX
schiedeana	−13.2	D.S.	C. Am.	TEX
ternipes (2)	−12.7	D.S.	U.S.A.	TEX
utilis		D.S.	Aust.	NSW
72 more spp. by various authors				
STIPAGROSTIS				
acutifolia		P.S.	(Holm, 1901; Bourreil, 1962)	

Table 13 continued.

		$\delta^{13}C$	Anat.	Prov.	Herb.
amabilis		−13.3	P.S.	(deWinter, 1965)	
anomala		−12.6	P.S.	(deWinter, 1965)	
brachyathera			P.S.	(Holm, 1901; Bourreil, 1962)	
brevifolia			P.S.	(deWinter, 1965)	
ciliatum			P.S.	(Holm, 1901; de Winter, 1965)	
damarensis			P.S.	(deWinter, 1965)	
dinteri			P.S.	(deWinter, 1965)	
dregeanum			P.S.	(deWinter, 1965)	
fastigiata			P.S.	(deWinter, 1965)	
foexiana			P.S.	(Bourreil, 1962)	
garubensis			P.S.	(deWinter, 1965)	
geminifolia		−12.0	P.S.	(deWinter, 1965)	
gonatostachya			P.S.	(deWinter, 1965)	
hermannii		−14.1	P.S.	(deWinter, 1965)	
hirtigluma			P.S.	(deWinter, 1965)	
hochstetteriana			P.S.	(deWinter, 1965)	
lanipes			P.S.	(deWinter, 1965)	
lutescens			P.S.	(deWinter, 1965)	
namaquensis			P.S.	(deWinter, 1965)	
namibensis			P.S.	(deWinter, 1965)	
obtusa			P.S.	(deWinter, 1965)	
papposa			P.S.	(deWinter, 1965)	
pennata			P.S.	(Holm, 1901)	
plumosa			P.S.	(Holm, 1901, Bourreil, 1962)	
proxima			P.S.	(deWinter, 1965)	
pungens			P.S.	(Holm, 1901; Bourreil, 1962)	
raddiana			P.S.	(Bourreil, 1962)	
ramulosa			P.S.	(deWinter, 1965)	
sabulicola			P.S.	(deWinter, 1965)	
sahelica			P.S.	(Bourreil, 1962)	
schaeferi			P.S.	(deWinter, 1965)	
subacaulis			P.S.	(deWinter, 1965)	
uniplumis		−12.1	P.S.	(deWinter, 1965)	
zeyheri			P.S.	(deWinter, 1965)	
		SARTIDIA			
angolensis (2)	−23.9	−26.6	Nar	(deWinter, 1965)	
jacunda (2)	−21.5	−24.4	Nar	(deWinter, 1965)	
vanderijstii (2)	−25.3	−26.5	Nar	(deWinter, 1965)	
sp.		−26.4	Nr		

studies have revealed that the cell walls of the inner sheath are very thick for Kranz cells, and that the chloroplasts are nearly agranal and lie in the centrifugal regions of the cells. There are large pits in the thick walls between these cells and between them and the cells of the outer sheath. The cell walls of the outer sheath are quite thin, and the chloroplasts are granal and lie in the centripetal regions of the cells.

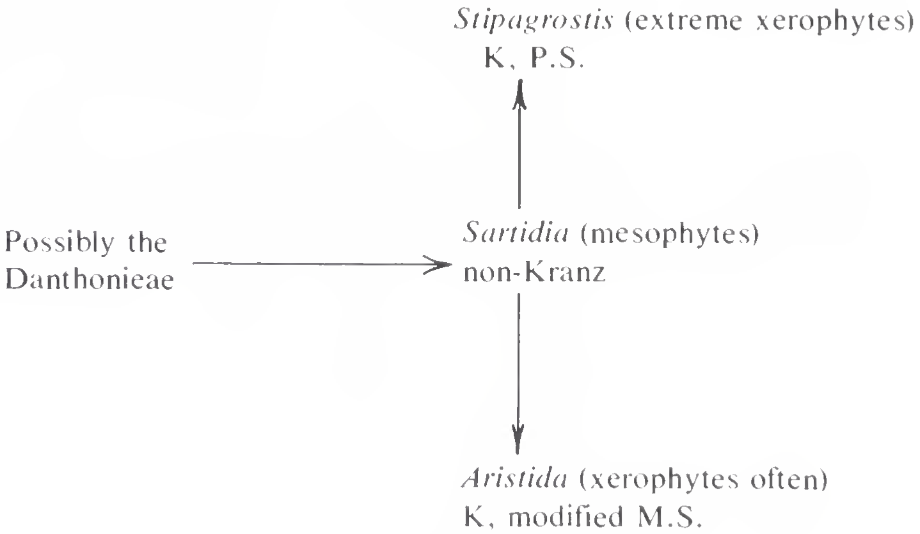
Recently Hattersley, et al. (in press) treated leaf sections of three species of *Aristida* with RuDP-Case antiserum carrying a fluorescent dye. Such a complex combines with RuDP-Case and reveals its location by fluorescence. The chloroplasts in both sheaths of *Aristida* were thus shown to contain RuDP-Case, thereby indicating that both sheaths consist of Kranz or at least Kranz-like cells.

De Winter (1965) demonstrated from a study of leaf anatomy that there are really three genera involved. *Aristida* has two Kranz sheaths; *Stipagrostis* has one Kranz sheath, the parenchyma sheath, as well as a mestome sheath of quite thick-walled cells; and *Sartidia* is non-Kranz with typical mestome and parenchyma sheaths. These three genera constitute the tribe Aristideae.

The ^{13}C/^{12}C ratios determined in this study confirm that *Aristida* and *Stipagrostis* are C$_4$ and that *Sartidia* is C$_3$ (Table 13), as predicted from leaf anatomy. Because *Stipagrostis* is P.S., it is predicted to be NAD-me. And because in *Aristida* the mestome sheath consists of large Kranz cells with nearly agranal, centrifugal chloroplasts, whereas the presumed Kranz cells of its parenchyma sheath are small, it is predicted to be NADP-me. Gutierrez, et al. (unpubl.) have determined that one species, *A. purpurea,* is indeed of that subtype.

Sartidia, with three or four species, grows in mesic, subtropical, southern Africa. *Stipagrostis* occurs in very arid southern and northern Africa and eastward to Afghanistan. *Aristida* is reported from arid to mesic, tropical to warm temperate regions around the world.

FIGURE 3. *Evolutionary scheme of the Aristideae.*



I propose that *Sartidia* represents the original non-Kranz Aristideae of mesic origin in southern Africa. (Figure 3). Because of the significant anatomical and biochemical differences between *Stipagrostis* and *Aristida*, it seems likely that the Kranz syndrome originated twice among C_3 Aristideae in southern Africa, once to produce the P.S. type *(Stipagrostis)* and once to produce the modified M.S., the D.S., type (*Aristida*). In most M.S. taxa the parenchyma sheath has been lost, but in *Aristida* it too became a Kranz sheath, although apparently one of minor functional significance.

TABLE 14. *Comparison of various grass taxa by significant morphological, anatomical, and cytological characters.*

Character	Eragrostoideae	Paniceae	Aristideae	Danthonieae	*Eriachne*
embryos[1]	P + PF	P − PP	P − FF and P−PF	P − PF	?
lodicules	truncate	truncate	elongate	truncate	truncate to elongate
leaf anatomy	P.S.	N, P.S., M.S.	N, P.S., D.S.	N, P.S.	P.S.
K cells l/w[2]	wide	wide to long$^-$	long$^+$	wide to long$^-$	long$^+$
K plastids[3]	Cp, Cf	Cp, Cf	Cf + Cp		?
bicell. hairs	club	linear	linear	linear	linear
on leaves	7.2[4]	2.7	3.2	3.4	3.2 (estimate)
on lodicules	absent	absent	absent	present	?
silica cells	kidney to double ax	dumbbell	dumbbell, to circular	dumbbell, various	transversely saddle
hila	basal, punctate	basal, punctate	linear	short to ½ grain	?
chromosome base no.	9, 10	9, 10	11	6(12), 7	?

[1] Symbolism of Reeder (1957)—1st: *P* = mesocotyl present; 2nd: + = epiblast present; 3rd: P = scutellum separated from coleorhiza, F = these not separated; 4th: F = first seedling leaf narrow and not overlapping, P = first seedling leaf wide and overlapping.

[2] Kranz cells length/width ratios in longitudinal view (Brown, 1974).

[3] Kranz cell plastids: Cp = located centripetally, Cf = located centrifugally (Brown, 1960).

[4] Numbers from Tateoka, et al. (1959): high numbers, apical cell is short and wide; low numbers, apical cell is long and narrow.

The Aristideae have no evident relationship to any of the Eragrostoideae (Table 14). They are closer to the Paniceae and/or the Danthonieae. *Eriachne* and *Pheidochloa*, possibly belonging in the Danthonieae, are very much like a hypothetical two-floreted, single-awned *Aristida*. *Eriachne*, *Pheidochloa*, *Asthenatherum*, *Alloeochaete*, and *Stipagrostis* are entirely P.S. with large glumes and similar bicellular hairs and silica cells (Cáceres, 1961; de Winter, 1965), and they, along with non-Kranz *Sartidia* (de Winter, 1965), have rather thin-walled mestome sheath cells. Furthermore, in *Aristida* (Lommasson, 1957; this study), as in *Eriachne*, the sheath cells are very, almost uniquely, long and are parallel to the bundle. Overall, the Aristideae seem related to the Danthonieae.

ERIACHNE

This genus of about 35 mostly Australian species has been variously placed in different systems proposed for the Gramineae, or it has remained unplaced because of its peculiarities. Tateoka (1961b) examined the leaf anatomy and epidermal characters of most species and concluded only that, "the affinity of *Eriachne* ought to be sought in some panicoid or danthonioid group." He did demonstrate that *Eriachne* is a genus of Kranz species that have thread-like bicellular hairs. The Panicoideae, Danthonieae, and Aristideae have species possessing these characters. That the species of *Eriachne* are P.S., as reported by Tateoka, has been confirmed (Table 15). However, unlike the Kranz cells of most P.S. grasses, which tend to be wider radially than long (Brown, 1974), the Kranz cells in *Eriachne* are somewhat longer than wide. This tends to relate *Eriachne* to the P.S. Danthonieae and Aristideae rather than to the Paniceae.

Tateoka (1961b) considered the transversely elongate, saddle-shaped silica cells of *Eriachne* to be "panicoid," but he was using the term in a broad sense, as contrasted with the "festucoid" character of the Aveneae in this case. It is now well established that within the Panicoideae the silica cells are characteristically dumbbell-shaped, with the long axis of the cells parallel to the long

TABLE 15. *Species of* Eriachne *examined for Kranz characters by various investigators: anatomical and photosynthetic characters, and voucher herbaria. Data not attributed are from this study.*

	$\delta^{13}C$	Anatomy	Herbarium	
anomala	−12.0	P.S.	US	(Tateoka, 1961)
aristidea	−15.0	P.S.	US	(Tateoka, 1961)
armitii	−12.5	P.S.	US	(Tateoka, 1961)
glabrata		P.S.	TEX	(Tateoka, 1961)
mucronata		P.S.	NSW	(Tateoka, 1961) (C.J.V., 1973)
obtusa		P.S.	TEX	(Tateoka, 1961)
pallens	−11.5	P.S.	US	
pulchella		P.S.	NSW	(Tateoka, 1961)
stipacea		P.S.	NSW	
triodoides		P.S.	TEX	(Tateoka, 1966)
triseta		P.S.	NSW	(Tateoka, 1961)
16 other species		P.S.	(mostly US)	(Tateoka, 1961)

axis of the leaf. Dumbbell-shaped and saddle-shaped silica cells are very different, so, in this respect, *Eriachne* is very different from the Panicoideae. The shapes of silica cells in the Danthonieae are too various to be characterized by a single term, and the silica cell type of *Eriachne* can certainly be matched somewhere among the Danthonieae. Since the Aristideae have dumbbell-shaped or spherical silica cells (de Winter, 1965), this character does not seem to relate *Eriachne* to that tribe (Table 14).

The cuneate lodicules of *Eriachne* are quite different from the more lanceolate ones of Aristideae (Tateoka, 1967) and are more like those of the Eragrostoideae than any other group (Tateoka, 1960).

In its long glumes, *Eriachne* resembles the Danthonieae and Aristideae; in lemma and palea induration, the Aristideae and Paniceae; and in lemma awning, the Danthonieae and Aristideae more than the Paniceae. In fact, the spikelets of some species of *Eriachne* look very much the same as two-floreted spikelets of *Aristida* might look. *Pheidochloa* (see "The Danthonieae") also has such spikelets, but its silica cells are undulate-rectangular, quite different from those of Aristideae or most *Eriachne*.

Eriachne is P.S., like Kranz Eragrostoideae, Danthonieae, and *Stipagrostis* of the Aristideae (Table 15). In contrast, the Paniceae are basically M.S. (Tables 3 and 4). The P.S. Paniceae seem to be rather recently evolved taxa (Hartley, 1958b).

I conclude that *Eriachne* is derived from a xeric offshoot of the Danthonieae close to but separate from the origin of the Aristideae. I assume that the Kranz syndrome evolved at the beginning of generic evolution, probably in Australia.

THE ERAGROSTOIDEAE

The subfamily Eragrostoideae is, so far as known, entirely Kranz. The present sample (Table 16) includes 327 species from 68 genera and all eight tribes. Available evidence, dating back to Schwendener (1890), also indicates that all species are P.S. (Brown, 1975). However, some are reported to be PEP-ck, whereas most of those examined are NAD-me (Brown, 1960; Gutierrez, Gracen, and Edwards, 1974; Hatch and Kagawa, 1974), which adds interest to this otherwise apparently uniform group.

NAD-me biochemistry seems to be correlated with centripetal chloroplast location and PEP-ck with centrifugal, although rather few species have been examined for either character, especially the biochemical one. Whereas the correlation seems to be phylogenetically significant in the Paniceae (Table 4), its import in the Eragrostoideae, if any, is obscure at this time. That is, some species within the same genus (*Bouteloua*,

TABLE 16. *Genera of Eragrostoideae containing species reported as P.S. by others, arranged by tribes.*

	no. spp.		no. spp.
Aeluropideae		*Leptochloöpsis*	2
Aeluropus	3	*Lintonia*	1
Allolepis	1	*Munroa*	1
Distichlis	3	*Plectrachne*	2
Jouvea	2	*Scleropogon*	2
Monanthochloë	1	*Tetrachne*	1
Reederochloa	1	*Tridens*	16
Vaseyochloa	1	*Triodia*	23
Chlorideae		*Uniola*	2
Acrachne	2	*Viguierella*	1
Astrebla	3		
Bouteloua	11	Lepureae	
Buchloë	1	*Ichnurus*	1
Chloris	9	*Lepturus*	2
Ctenium	2		
Cynodon	2	Pappophoreae	
Dactyloctenium	1	*Blepharidachne*	1
Dinebra	1	*Enneapogon*	1
Eleusine	2	*Neostapfia*	1
Enteropogon	1	*Orcuttia*	1
Eustachys	3	*Pappophorum*	8
Fingerhuthia	2	*Schmidtia*	2
Gouinia	12		
Gymnopogon	1	Spartineae	
Leptochloa	4	*Spartina*	9
Lepturidium	1		
Melanocenchris	1	Sporoboleae	
Microchloa	1	*Blepharoneuron*	1
Oropetium	2	*Calamovilfa*	4
Pogonathria	1	*Crypsis*	3
Rendlia	1	*Heleochloa*	1
Schedonnardus	1	*Lycurus*	1
Trichloris	2	*Muhlenbergia*	71
Tripogon	1	*Sporobolus*	30
		Urochondra	1
Eragrosteae			
Apochiton	1	Zoysieae	
Cleistogenes	1	*Hilaria*	2
Diplachne	1	*Mosdenia*	1
Eragrostis	40	*Perotis*	2
Erioneuron	5	*Tragus*	3
		Zoysia	3

Totals: 8 tribes, 69 genera, 328 species.

Sporobolus, *Muhlenbergia*, *Chloris*, *Eragrostis*, and *Tridens*) are NAD-me whereas others are, or seem to be, PEP-ck (Table 1 and unpubl.). In *Chloris*, the difference is largely correlated with taxonomy; most species are PEP-ck, but those of subgenus *Eustachys* (Anderson, 1974) are NAD-me. Subgeneric correlation may also occur within *Bouteloua*.

Complete correlation of C_4 photosynthesis and Kranz anatomy is further supported by evidence reported here (Table 17). Reasons for selection of the particular species examined varied considerably and are given in the discussions of individual genera.

Uniola. Brown and Smith (1974a) determined the $^{13}C/^{12}C$ ratios of most species in the small tribe Unioleae. Their results confirmed Yates' (1966) conclusion that the genus must be divided into two or three genera of two distinct types. *Uniola* (type species, *U. paniculata* L.) and *Leptochloöpsis* are Kranz genera with characters quite typical of the Eragrosteae. The non-Kranz species are included in *Chasmanthium*. Since the tribe Unioleae was based almost completely on *C. latifolium*, the former tribal designation is abandoned and *Chasmanthium* is included in the centostecoid group after Soderstrom and Decker (1973).

Aeluropus. This halophytic Kranz genus was investigated because Ilan and Waisel (1973) reported that *A. litoralis* responds to salt concentration around the root system by increasing concentrations of both RuDP-Case and PEP-Case. Plants in no NaCl had PEP-Case too low to be measured. If confirmed, this would be the only species known to have Kranz anatomy but C_3 photosynthesis, when growing in low salt soil.

Acrachne (Chlorideae), ***Lintonia*** (Eragrosteae), and ***Tretrachne*** (Chlorideae) are here reported to be Kranz for the first time.

TABLE 17. *Species of Eragrostoideae examined, arranged by tribes and genera: anatomical and photosynthetic characters, provenances, and voucher herbaria. Data from this study unless otherwise attributed.*

	$\delta^{13}C$	Anat.	Prov.	Herb.
AELUROPIDEAE				
Aeluropus lagopoides	−14.3	P.S.	Asia	TEX
Allolepis texana		P.S.	U.S.A.	TEX
Distichlis spicata (Bender and Smith, 1973)	−13.3			
Jouvea pilosa	−11.4	P.S.	Mexico	TEX
Monanthochloë littoralis	−14.1	P.S.	U.S.A.	TEX
Vaseyochloa multinervosa	−14.6	P.S.	U.S.A.	TEX
CHLORIDEAE				
Acrachne racemosa	−19.3	P.S.	Africa	PRE

Table 17 continued.

	$\delta^{13}C$	Anat.	Prov.	Herb.
A. verticillata	−13.1	P.S.	Africa	PRE
Bouteloua aristidoides		P.S.	U.S.A.	TEX
B. chondrosioides		P.S.	U.S.A.	TEX
B. curtipendula	−12.5	P.S.	U.S.A.	TEX
B. eriopoda		P.S.	U.S.A.	TEX
B. filiformis		P.S.	U.S.A.	TEX
B. gracilis		P.S.	U.S.A.	TEX
B. rigidiseta		P.S.	U.S.A.	TEX
B. trifida		P.S.	U.S.A.	TEX
Buchloë dactyloides	−14.3	P.S.	U.S.A.	TEX
Chloris andropogonoides		P.S.	U.S.A.	TEX
C. cuculata	−15.9	P.S.	U.S.A.	TEX
Cynodon dactylon	−15.3	P.S.	U.S.A.	TEX
Dactyloctenium aegyptium	−12.2	P.S.	U.S.A.	TEX
Eustachys distichophylla		P.S.	U.S.A.	TEX
E. petraea		P.S.	U.S.A.	TEX
Gymnopogon ambiguus	−13.4	P.S.	U.S.A.	TEX
Leptochloa dubia		P.S.	U.S.A.	TEX
Schedonnardus paniculatus		P.S.	U.S.A.	TEX
Trichloris pluriflorus		P.S.	U.S.A.	TEX
Tripogon spicatus		P.S.	U.S.A.	TEX
ERAGROSTEAE				
Eragrostis cilianensis		P.S.	U.S.A.	TEX
E. curtipedicellata		P.S.	U.S.A.	TEX
E. intermedia	−15.6	P.S.	U.S.A.	TEX
E. oxylepis		P.S.	U.S.A.	TEX
E. spectabilis (Bender and Smith, 1973)	−11.0			
E. trichodes		P.S.	U.S.A.	TEX
Erioneuron pilosa	−13.4	P.S.	U.S.A.	TEX
E. pulchellum		P.S.	U.S.A.	TEX
Leptochloöpsis condensata	−13.3	P.S.	America	US
L. virgata	−12.8	P.S.	America	US
Lintonia nutans	−12.4	P.S.	Africa	TEX
Munroa squarrosa		P.S.	U.S.A.	TEX
Plectrachne pungens (Jacobs, 1971)		P.S.	Aust.	NSW
P. schinzii (Jacobs, 1971)		P.S.	Aust.	NSW
Scleropogon brevifolius		P.S.	U.S.A.	TEX
Tetrachne dregii		P.S.	Africa	US
Tridens albescens	−13.5	P.S.	U.S.A.	TEX
T. elongatus		P.S.	U.S.A.	TEX
T. flavus		P.S.	U.S.A.	TEX
T. muticus		P.S.	U.S.A.	TEX
Triodia basedowii	−17.1	P.S.	Aust.	NSW

Table 17 continued.

	$\delta^{13}C$	Anat.	Prov.	Herb.
T. clelandii		P.S.	Aust.	NSW
T. hostilis	−13.2	P.S.	Aust.	NSW
Uniola paniculata (5)	ca. −12.5	P.S.	U.S.A.	TEX
U. pittieri	−13.4	P.S.	C. Am.	TEX
LEPTUREAE				
Ischnurus (Hanson and Potztal, 1954)		P.S.		
Lepturus radicans (Tateoka, 1959)		P.S.		
L. repens	−12.7	P.S.	Pacific	TEX
PAPPOPHOREAE				
Blepharidachne bigelovii		P.S.	U.S.A.	TEX
Enneapogon desvauxii		P.S.	U.S.A.	TEX
Neostapfia colusana	−13.3		U.S.A.	TEX
Orcuttia californica	−13.6		U.S.A.	TEX
Pappophorum bicolor	−13.4	P.S.	U.S.A.	TEX
P. mucronulatum		P.S.	U.S.A.	TEX
Schmidtia bulbosa (Günzel, 1912) Ka				
S. pappophoroides (Günzel, 1912) Ka				
SPARTINEAE				
Spartina alternifolia	−13.1	P.S.	U.S.A.	TEX
S. cynosuroides (Bender, 1971)	−14.4			
S. pectinacea (Bender, 1971)	−13.4			
S. spartinae (Johnson, 1964) Ke				
SPOROBOLEAE				
Blepharoneuron tricholepis		P.S.	U.S.A.	TEX
Calamovilfa brevipilis		P.S.	U.S.A.	TEX
C. curtissii		P.S.	U.S.A.	TEX
C. gigantea		P.S.	U.S.A.	TEX
C. longifolia		P.S.	U.S.A.	TEX
Lycurus phleoides	−13.8	P.S.	U.S.A.	TEX
Muhlenbergia capillaris	−13.2	P.S.	U.S.A.	TEX
M. emersleyi	−11.0	P.S.	U.S.A.	TEX
M. fragilis	−13.5	P.S.	U.S.A.	TEX
M. involuta		P.S.	U.S.A.	TEX
M. lindheimeri	−12.4	P.S.	U.S.A.	TEX
M. mexicana	−13.4	P.S.	U.S.A.	TEX
M. minutissima	−11.8	P.S.	U.S.A.	TEX
M. montana	−13.4	P.S.	U.S.A.	TEX
M. porteri	−14.3	P.S.	U.S.A.	TEX
M. reverchoni		P.S.	U.S.A.	TEX

Table 17 continued.

	$\delta^{13}C$	Anat.	Prov.	Herb.
M. schreberi	−15.0	P.S.	U.S.A.	TEX
M. sylvatica	−13.2	P.S.	U.S.A.	TEX
M. utilis		P.S.	U.S.A.	TEX
M. wolfii	−12.5	P.S.	U.S.A.	TEX
Sporobolus airoides		P.S.	U.S.A.	TEX
S. asper (Bender and Smith, 1973)	−13.4			
S. cryptandrus		P.S.	U.S.A.	TEX
S. heterolepis (Bender and Smith, 1973)	−12.7			
S. neglectus		P.S.	U.S.A.	TEX
S. poiretii (Bender, 1971)	−13.7			
S. wrightii	−12.3	P.S.	U.S.A.	TEX
Urochondra setulosa (Hubbard, 1947) Ka				
ZOYSIEAE				
Hilaria belangeri	−13.8	P.S.	U.S.A.	TEX
H. mutica		P.S.	U.S.A.	TEX
Mosdenia phleoides (Tateoka, 1957) Ka				
Perotis patens (deWet, 1960) Ka				
Tragus berteronianus		P.S.	U.S.A.	TEX
Zoysia japonica	−14.7	P.S.	Japan	TEX
Z. matrella	−12.3	P.S.	Japan	TEX

Muhlenbergia. Numerous studies of this genus (Soderstrom, 1967; Pohl, 1969) have demonstrated that all species have Kranz anatomy. The $^{13}C/^{12}C$ ratios of annuals, perennials, xerophytes, mesophytes, and northern species demonstrate that all are C_4 also (Table 17). Because *Muhlenbergia* is related to *Sporobolus* and because there are both NAD-me and PEP-ck species in the latter (see below), *Muhlenbergia* is being examined biochemically (by Edwards and Gutierrez) to determine whether it too has both subtypes.

Sporobolus. It has now been adequately demonstrated that there are both NAD-me and PEP-ck species in this genus (Gutierrez, Gracen, and Edwards, 1974; Hatch, Kagawa, and Craig, 1975) (Table 1). The survey is inadequate at present to determine whether the two subtypes are correlated with distinct subgeneric taxa or not. The presence of both within single genera suggests that perhaps they may be interconvertable during evolution.

Bouteloua. This is another genus that contains both NAD-me and PEP-ck species. The available evidence does not suggest that the two subgenera presently recognized are differentially correlated with the two subtypes, because *B. curtipendula* is PEP-ck but *B. rigidiseta* may be NAD-me and both are in subgenus *Antheropogon*. All species of subgenus *Chondrosium* so far examined are NAD-me.

Chloris. This is a fourth genus of the subfamily that probably contains both NAD-me and PEP-ck species. At present, the few species of typical *Chloris* that have been examined biochemically are PEP-ck, whereas one species of subgenus *Eustachys, C. distichophylla,* is NAD-me (Table 1). This distinction supports separate generic status for *Eustachys,* as proposed by Anderson (1974).

Eragrostis. In this genus also, both C_4 subtypes may occur (Table 1). The Old World species *E. cilianensis, E. curvula,* and *E. superba* are NAD-me. However, the American *E. intermedia* and *E. trichodes* apparently have centrifugal Kranz cell chloroplasts, so they may be PEP-ck.

Tridens. For this genus only cytological observations are available. Whereas *T. flavus* apparently has centrifugal Kranz cell chloroplasts, those of the other species are centripetal.

Triodia. In his recent examination of 23 *Triodia* species, Jacobs (1971) clarified their anatomical status, after the earlier vagueness of Burbidge (1946). He concluded that all species have Kranz anatomy of a rather peculiar form, and further that they "could perhaps be considered as primitive representatives of the tribe Eragrosteae." He also included data on first seedling leaf morphology, silica cells, bicellular microhairs, iodine staining, lodicule shape, chlorenchyma, starch grains, and chromosome number and size. McWilliam and Mison (1974) have determined that *T. irritans* is C_4, according to PEP-Case level and leaf anatomy. The present study confirms that this genus is Kranz P.S.

Plectrachne. Jacobs (1971) also examined two species of this genus, which is very close to *Triodia.* Everything stated about *Triodia* as a Kranz genus of the Eragrosteae applies equally to *Plectrachne.*

Hilaria. Two species of this American genus have been studied: *H. belangeri,* a small stoloniferous species which has Kranz anatomy, centripetal Kranz cell chloroplasts, and a $^{13}C/^{12}C$ ratio of -13.8; and *H. mutica,* which also has Kranz anatomy but Kranz cell chloroplasts which change position according, presumably, to light intensity! In low light (about 1,000 foot-candles, in a greenhouse) the chloroplasts are dispersed through the cell evenly, but in bright sunlight (4,000 to 8,000 foot-candles, and other out-of-doors conditions) they are concentrated in the centripetal regions of the Kranz cells, as in typical NAD-me species. Thus, there seem to be three chloroplast location conditions in Kranz cells of P.S. species.

Gutierrez, Gracen, and Edwards (1974, p. 292) stated that the chloroplasts in Kranz cells of *Panicum virgatum* are "evenly distributed" throughout the cell. Much the same was reported for *P. laevifolium, P. dichotomiflorum,* and *Muhlenbergia lindheimeri.* In this study I found it also in species of *Eragrostis* and *Tridens,* and in *Hilaria mutica.* All of these species should be NAD-me, and the movable chloroplasts of *H. mutica* indicate that "chloroplasts evenly distributed" is a modification of the centripetal rather than of the centrifugal condition, which it somewhat resembles.

The Eragrostoideae are all Kranz P.S. The rather scanty biochemical and cytological evidence indicates that the subfamily is typically NAD-me with centripetal Kranz cell chloroplasts. It appears that in some genera the PEP-ck subtype has evolved, with accompanying change in chloroplast location. The precise significance of the apparent correlation between biochemical subtype and chloroplast location within Kranz cells is unknown. Nevertheless, variation in the latter can be ascribed to some functional difference.

This taxon is quite distinct from other subfamilies, with diagnostically different silica cell and bicellular hair types. Nevertheless, within the large genus *Eragrostis* there is considerable variation in many of the characters useful in modern grass systematics.

MISCELLANEOUS GRASS TAXA

Although my original intent was a thorough study of *Panicum*, the Paniceae, and related tribes, ensuing involvement with anatomical derivations of the Kranz sheaths (Brown, 1975) and with the subtypes of C_4 photosynthesis prompted some diversions into taxa from other subfamilies. Such investigations in the Danthonieae, Aristideae, *Eriachne*, Eragrostoideae, and Andropogoneae have already been discussed, and a study of *Uniola* has been published (Brown and Smith, 1974a). Table 18 presents data on the remainder studied, as well as some on other such species from Smith and Brown (1973), Tateoka (1963), and Carolin, Jacobs, and Vesk (1973).

TABLE 18. *Species of other grass tribes examined for Kranz characters by various investigators, arranged by tribes and genera: anatomical and photosynthetic characters, provenances, and voucher herbaria. Data from this study unless otherwise attributed.*

	$\delta^{13}C$ or Synd.	Provenance	Herbarium
	OLYREAE		
Cryptochloa varians	−31.1	C. Am.	TEX
Lithachne pauciflora	−29.7	C. Am.	TEX
Mniochloa strephioides	−33.3	Cuba	US
Olyra latifolia	−29.5	Africa	PRE
O. yucatana	−29.8	C. Am.	TEX
	PARIANEAE		
Pariana bicolor	−30.3	S. Am.	TEX
20 other species (Tateoka, 1961c)	Na	S. Am.	US
	PHAREAE		
Leptaspis cochleata	−31.1	Africa	PRE
Pharus latifolius	−29.6	C. Am.	TEX

Table 18 continued.

	$\delta^{13}C$ or Synd.	Provenance	Herbarium
PHYLLORACHIEAE			
Humbertochloa bambusiuscula	−30.9	Africa	PRE
Phyllorhachis sagittata	−26.0	Africa	PRE
THYSANOLAENEAE			
Thysanolaena maxima	−27.4	Africa	PRE
CENTOTHECEAE			
Centosteca lappacea	−30.9	Africa	TEX
Megatachya mucronata	−26.2	Africa	PRE
Zeugites pittieri	−23.6	S. Am.	TEX
PHAENOSPERMEAE			
Diarrhena americana	−29.5	U.S.A.	TEX
Phaenosperma fauriei (Tateoka, 1957)	Na	Asia	
P. japonica (Tateoka, 1957)	Na	Asia	
P. globosa	−28.7	Asia	US
EHRHARTEAE			
Ehrharta erecta	−26.5	Africa	TEX
19 other spp. (Tateoka, 1963)	Na		
Microlaena stipoides (CJV[1])	Nae	Aust.	NSW
5 other spp. (Tateoka, 1963)	Na		
Petriella colensoi (Tateoka, 1963)	Na		
P. thomsonii			
Tetrarrhena			
3 spp. (Tateoka, 1963)	Na		
AGROSTIDEAE			
Agrostis bergiana	−26.4	South Africa	PRE
A. natalensis	−27.7	South Africa	PRE

[1] Carolin, Jacobs, and Vesk, 1973.

These data augment evidence that the tribes represented are all non-Kranz. Most are tropical forest grasses, and such shade-requiring species, with few exceptions, are non-Kranz. The Ehrharteae are not forest species but, as Tateoka (1963a) reported, they have non-Kranz leaf anatomy. Prat (1936) reported bicellular microhairs in *Ehrharta* and *Microlaena*, and the tribe is characterized by festucoid embryo vascularization (Reeder, 1957; Tateoka, 1963a). These characters and its

African-Australian distribution make placement of the Ehrharteae difficult. Assignment to the Oryzoideae (Stebbins and Crampton, 1961) or to Group II (see later and Figure 4) seems as logical as any for the present.

The non-Kranz $\delta^{13}C$ ratios of *Agrostis bergina* and *A. natalensis* support the inclusion of these South African species in the Festucoideae.

Though this study contributes no data useful in placing these miscellaneous genera and tribes sampled, it does provide further evidence that they are non-Kranz taxa.

DISCUSSION

By 1960, the new characters used in the "new systematics" of the Gramineae had reached the point of treatment in general reviews (Jacques-Felix, 1962; Prat, 1960; Stebbins and Crampton, 1961; Auquier, 1963). These were initiated by the 1959 symposium, "The Natural Classification of the Gramineae" (Recent Advances in Botany, 1961) and paralleled a resurgence of interest in grass leaf interiors.

Rhoades and Carvalho (1944) had reported that the Kranz cells of *Zea mays* contain, compared to mesophyll cells, large specialized plastids that store starch.

Kortschak and coworkers in Hawaii had been building toward the discovery of C_4 photosynthesis in sugarcane (Burr, et al., 1957).

Hodge, Mclean, and Mercer (1955) had examined the chloroplasts of *Zea mays* by electron microscopy and reported that those of the Kranz cells lack grana.

Badenhuizen, Bartlett, and Gude (1958) had attempted to determine enzymatic differences between the mesophyll and sheath cells of *Cynodon dactylon* (Eragrostoideae) with respect to starch synthesis, which normally occurs only in the Kranz cells.

Brown (1960) observed differences in chloroplast location within Kranz cells.

Johnson (1964) examined leaf chloroplasts of numerous grass species by electron microscopy and found essentially agranal Kranz cell chloroplasts in Andropogoneae and most Paniceae but large grana in chloroplasts of Kranz cells in Eragrostoideae.

Meanwhile, techniques for determining $^{13}C/^{12}C$ ratio (Wickman, 1952; Park and Epstein, 1961), postillumination CO_2 burst (Decker, 1959), and CO_2 compensation point (Moss, 1962) were developed.

Between 1965 and 1970, models of C_4 photosynthesis were developed (Hatch and Slack, 1970) and that condition was correlated with Kranz leaf anatomy in the 10 angiosperm families known to be Kranz since 1920.

Between 1970 and 1975, three subtypes of C_4 photosynthesis were characterized (NADP-me, NAD-me, and PEP-ck) (Hatch and Kagawa, 1974; Gutierrez, Gracen, and Edwards, 1974; Hatch, Kagawa, and Craig, 1975). A preliminary survey of $^{13}C/^{12}C$ ratios in the Gramineae (Smith and Brown, 1973) demonstrated many C_3 species of Paniceae. And Brown (1975) characterized two anatomical subtypes of Kranz anatomy, the P.S. type having the Kranz tissue derived from the parenchyma sheath, and the M.S. type with the Kranz tissue evolved from the mestome sheath of non-Kranz grasses. Brown and Gracen (1972) and Gutierrez, Gracen, and Edwards (1974) related NADP-me and PEP-ck photosynthesis to centrifugal chloroplast position within Kranz cells, and NAD-me to centripetal. Thus, the three subtypes of C_4 photosynthesis were correlated with three subtypes of Kranz leaf anatomy and cytology.

Brown (1958) had characterized the Panicoideae as having some species with and some without an endodermis (mestome sheath), and the Eragrostoideae as always having a mestome sheath. Now, the evolutionary and phylogenetic significance of those observations is accentuated by the discovery of correlations between anatomical and C_4 photosynthetic subtypes. This is particularly germane to analysis of the Paniceae, a tribe that contains non-Kranz genera, subgenera, sections, groups, and species, as well as all three Kranz subtypes. Also amenable to such analysis are the genus *Panicum* itself (s. lat.), which also contains all four conditions, and the tribes Danthonieae and Aristideae, which contain both non-Kranz and Kranz genera.

The data accumulated in this work especially, but other scattered observations also, demonstrate that C_3 photosynthesis is indeed always associated with non-Kranz anatomy and C_4 always with Kranz. The only exceptions are the *Atriplex* hybrids (Björkman, et al., 1971) and the unknown condition in the South African grass *Alloteropsis semialata* (s. lat.). The only reported "intermediates" between C_3 and C_4, *Mollugo verticellata* (Kennedy and Laetsch, 1974) and *Steinchisma hians* (Brown and Brown, 1975), are C_4-like C_3 species.

It seems evident that no species contains both Kranz and non-Kranz subspecies, although many genera contain species of both types. This, then, is a specific but not necessarily a generic difference. I assume that it takes at least as long for the Kranz condition to evolve from the non-Kranz as for any other "good" specific characteristic to evolve. Though intermediates are known (*Mollugo verticellata, Steinchisma hians*, and evidently *Chamaesyce acuta*), in such cases the condition appears to be uniform throughout the species. It can be concluded, therefore, that non-Kranz/Kranz status is a very good character for specific differentiation.

The implications of this study for the various tribes and for *Panicum* have already been discussed. Here, evolution of the Kranz syndrome within the Gramineae and major events in the evolution of the family are considered.

Figure 5 presents conclusions on the evolution of the Kranz syndrome in the Gramineae. Figure 4 presents an evolutionary scheme for the family itself. I shall discuss the latter first because the Kranz syndrome, regardless of how often it has evolved within the family, is limited to the most advanced subfamilies.

During the past 45 years many nonmorphological characters have been found useful in grass systematics (Stebbins and Crampton, 1961; Prat, 1960; Auquier, 1963), but some are useful only within subfamilies or tribes and some are too variable to be considered major guides to the evolution of the family. It is my considered opinion that the most significant evolutionary changes, in order, may have been as follows.

The original grasses, like all angio-

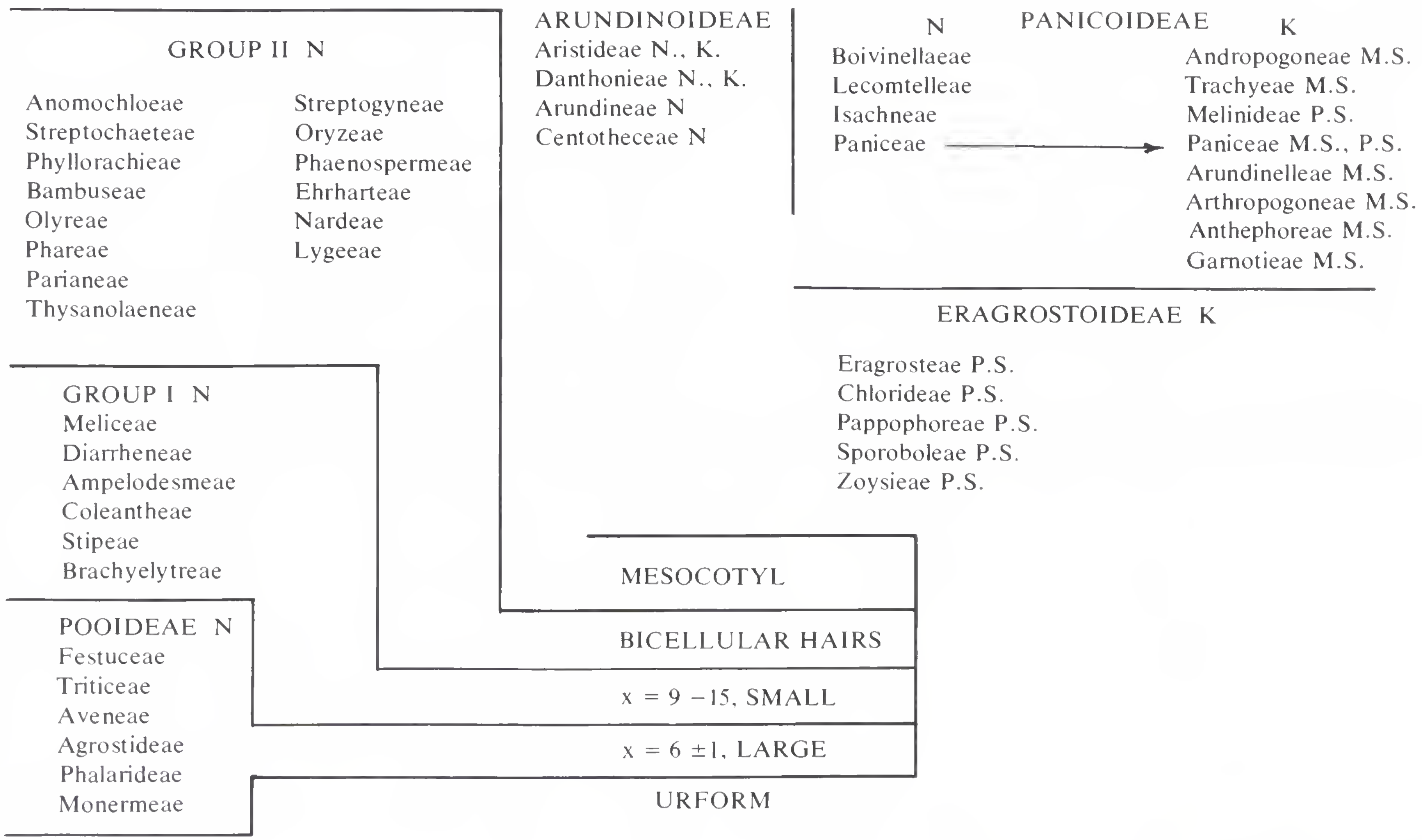


FIGURE 4. *Evolutionary scheme of the Gramineae.*

sperms probably (Ehrendorfer, et al., 1968), had a basic chromosome number of 6 ± 1 and the chromosomes were relatively large. The extant subfamily with these characteristics is the Pooideae. The taxa of this subfamily generally grow in mesic, cool to cold regions or seasons (cold, temperate, arctic, alpine, and wet cool winters).

The first major evolutionary change was the establishment at the tetraploid level of a new range of basic chromosome numbers, x = 9–15, and the chromosomes were small. This characterizes all other grass subfamilies. The group of tribes with these characteristics, but otherwise much like the Pooideae, I have designated as Group I.

The second major change was the acquisition of bicellular microhairs. All subsequent subfamilies possess these unique structures, on the leaf epidermis at least. Correlated with this change was invasion of the tropics, especially the tropical forests. The extant taxa exhibiting such additional changes, the miscellaneous tribes constituting Group II of Figure 4, have been variously treated by systematists (Tateoka, 1957b; Stebbins and Crampton, 1961; Parodi, 1961; Calderón and Soderstrom, 1973; Stebbins, 1972; Soderstrom and Decker, 1973; Hubbard, 1973). I lump them merely because they possess bicellular hairs but not the next evolutionary acquisition.

The third major change was development of a mesocotyl (Reeder, 1957, 1961, 1962). The three preceding groups do not have this structure; the three subsequent subfamilies do. It is only among the latter that the Kranz syndrome has evolved, either in all three subfamilies or else only in two if the Eragrostoideae originated as Kranz grasses.

The Arundinoideae are usually considered to be a primitive group. Of these, the temperate tribe Danthonieae may be most like those grasses in which the embryonic mesocotyl evolved. In numerous characters, such as silica cell and lodicule shapes, the Danthonieae resemble the Panicoideae and Eragrostoideae, and spikelet character trends lead from Danthonieae to Arundinelleae in the Panicoideae (Table 14).

This scheme (Figure 4) is based almost entirely upon a sequence of what can be considered the most significant and conservative evolutionary changes from simple to complex. Some previous proposals have assumed that the Arundinoideae (Stebbins, 1956, 1972; Prat, 1960) or some tribes of Group II (Tateoka, 1957b) may most nearly represent the ancient forms of Gramineae. But in order to derive the Pooideae from the Arundinoideae, reduction by loss of the mesocotyl and bicellular hairs, reduction in basic chromosome number, and significant increase in chromosome size would have to be proposed. Thus, the Group II tribes would be the oldest or next most ancient, and the Group I tribes more ancient than the Pooideae. That scheme would also permit some Panicoideae to represent more ancient grass types.

There is considerable merit for considering the Arundinoideae to represent the most primitive type of Gramineae. Certainly most tribes of Groups I and II and some Panicoideae do seem to be remnants of ancient taxa, and the Pooideae can be interpreted as recently-evolved, greatly reduced taxa which have occupied recent cool and cold, mostly northern hemisphere environments.

Such schemes are interesting but all are largely hypothetical and based mostly on comparison of extant taxa. Without numerous early Tertiary or late Cretaceous fossils, which are almost completely lacking, the early forms of grasses and the actual evolutionary sequences in the family may never be known with certainty (Stebbins, 1972).

FIGURE 5. *Evolutionary scheme of the Kranz syndrome in the Gramineae.*

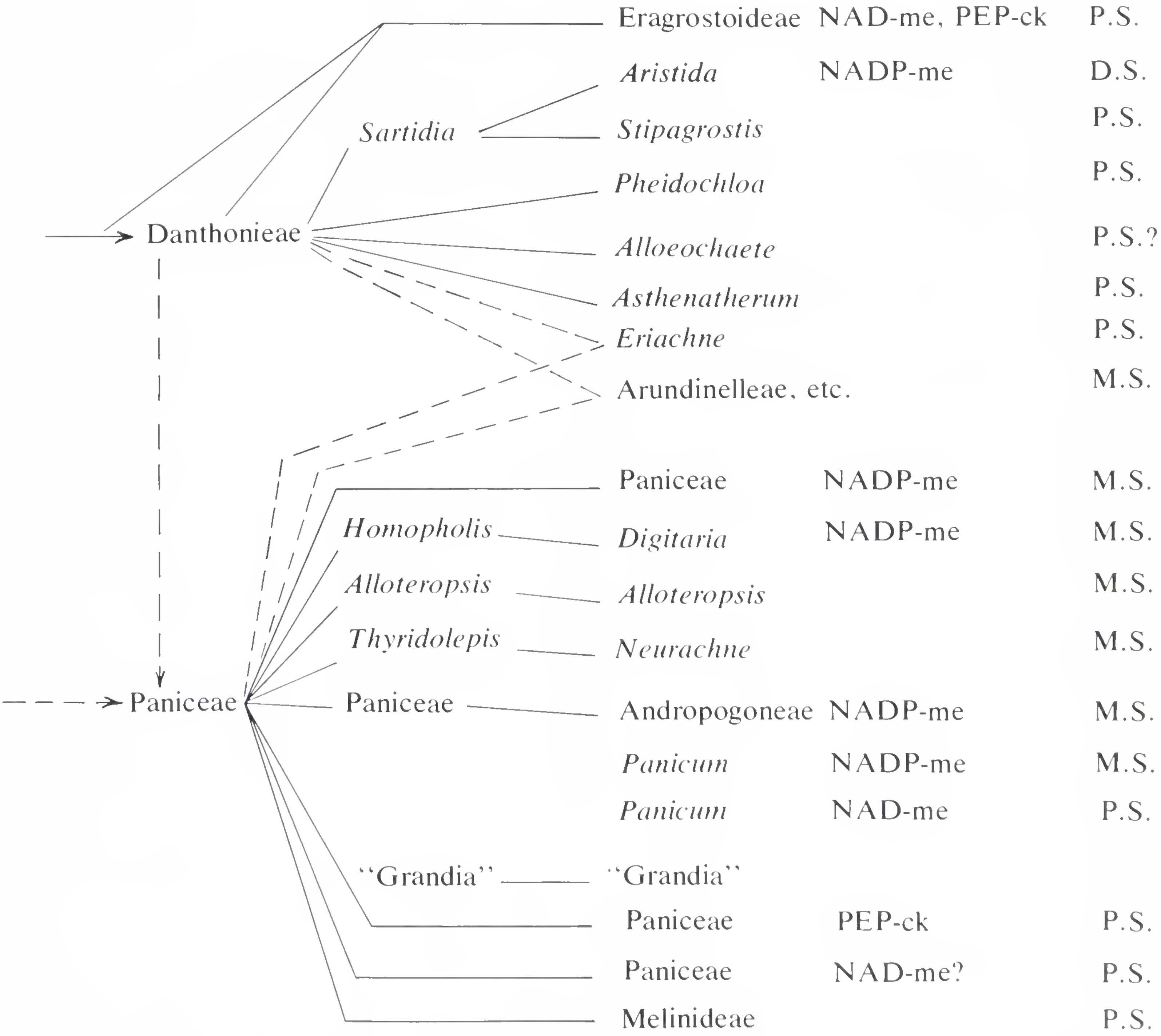


Figure 5 reflects the conclusion that the Kranz syndrome has evolved several different times during the histories of the subfamilies having an embryonic mesocotyl.

Because all the Eragrostoideae are Kranz P.S. (Table 17), it can be assumed that the original eragrostoid grasses were already Kranz and that the subfamily must have evolved long ago in order to have permitted subsequent evolution of its constituent tribes.

More recently, the non-Kranz African genus *Sartidia* (Aristideae) probably evolved from non-Kranz Danthonieae. From *Sartidia, Stipagrostis* evolved as a desert genus with Kranz P.S. anatomy. But *Aristida* originated separately. Mainly Kranz M.S., it also includes species with a double Kranz sheath unique to that genus. Since the one species of *Aristida* examined has the NADP-me subtype of C_4 photosynthesis, which correlates with the M.S. subtype of Kranz anatomy, *Aristida* and *Stipagrostis* seem to represent two distinct evolutions of the Kranz syndrome (Figure 3).

The danthonioid genera *Pheidochloa* of Australia and *Alloeochate* and *Asthenatherum* of South Africa are all P.S. and may represent one, two, or three separate evolutions of the Kranz syndrome.

Within the Panicoideae there are non-Kranz as well as Kranz tribes. The non-Kranz genera of Paniceae are of various sorts; most are hydrophytes or forest plants. The latter are very similar to the numerous non-Kranz species of *Panicum*. From Kranz M.S. Paniceae, or from some common ancestor, evolved the completely Kranz Andropogoneae, which Hartley (1958a) considered to be the most recently evolved tribe of the Gramineae.

The Melinideae are Kranz P.S. and may represent a distinct evolution of the Kranz syndrome. Or they may be closely related to the typical NAD-me sections of *Panicum*, and perhaps to any other NAD-me genera of Paniceae.

The PEP-ck, P.S. Paniceae (the *Brachiaria* group) either represent a distinct evolution of the Kranz syndrome or else were derived recently from NAD-me, P.S. Paniceae such as occur in *Panicum* (Table 4 and Figure 1).

It seems likely that very recent evolutions of the M.S. subtype have occurred in South America within the group "Grandia" of *Panicum*. Most other Kranz genera of Paniceae are M.S. and must represent an early evolution of the syndrome. However, the Australian genus *Homopholis* may represent the non-Kranz ancestor of the worldwide genus *Digitaria*, and the Australian non-Kranz genus *Thyridolepis* may represent an ancestral form of the Australian Kranz genera *Neurachne* and *Paraneurachne* (Figure 5 and see later).

It is quite clear that the non-Kranz and Kranz forms of *Alloteropsis semialata* in South Africa are very closely related; they are almost indistinguishable morphologically. At this time it can be hypothesized that the Kranz syndrome evolved recently in the South African non-Kranz population, though long enough ago for the Kranz form to spread to China and Australia. It is possible, of course, that reverse evolution occurred and that in South Africa the non-Kranz form evolved from the Kranz form, or that the two forms are not closely related but reflect convergent evolution.

Both the Eragrostoideae and Andropogoneae seem to be uniform in leaf anatomy, P.S. and M.S. respectively. But, whereas the Andropogoneae seem to be uniformly NADP-me, the Eragrostoideae contain both NAD-me and PEP-ck species. This could be interpreted as indicating the biochemical and anatomical isolation of M.S., NADP-me taxa, and the close relationship of P.S., NAD-me and P.S., PEP-ck taxa. In the Eragrostoideae most species seem to be NAD-me, so that the few PEP-ck species seem to be derived from some recent or extant NAD-me ancestors (Table 1). Therefore, it can be proposed that the P.S., NAD-me subgenus of *Panicum* and the P.S., PEP-ck genera of Paniceae may also have had some common, NAD-me ancestor (Figure 1).

On the other hand, Hatch, Kagawa, and Craig (1975) have proposed biochemical schemes which seem to indicate that the NAD-me subtype is more complex than the PEP-ck (their PCK-type). At least, the former exhibits, within the Kranz cell mitochondria, biochemical reactions that seem to occur outside the plastids and mitochondria in PEP-ck species. However, the PEP-ck subtype may be, in fact, a biochemical derivative of the NAD-me subtype, as it certainly seems to be from evolutionary considerations.

How many times has the Kranz syndrome evolved within the Gramineae? The M.S. Panicoideae probably had at least one evolution of the Kranz syndrome long ago. But *Alloteropsis*, *Neurachne*, and the group "Grandia" of *Panicum* indicate three apparently recent and independent evolutions of the syndrome. It seems likely that *Steinchisma* (*S. hians*/*S. milioides* at least) may be in some middle stage of evolving from non-Kranz to Kranz.

The P.S., NAD-me condition in Panicoideae may have had a single ancient origin. Whether the P.S., PEP-ck type is derived from the NAD-me type or evolved separately in non-Kranz Paniceae is presently unknown.

In the Danthonieae, the Kranz syndrome evolved at least once to produce the genera *Asthenatherum*, *Alloeochaete*, and *Pheidochloa*.

In the Aristideae, *Aristida* and *Stipagrostis* seem to be the results of two evolutions of the syndrome.

The Eragrostoideae probably all derive from one ancient evolution of the syndrome, perhaps the first in the family, and possibly among ancestors in common with the Danthonieae.

Thus, within the Gramineae it can be proposed that there have been at least seven separate evolutions of the Kranz syndrome. The actual number may be considerably higher.

It has often been stated (Downton, 1974b) that the Kranz syndrome is an adaptation to more xeric habitats (high temperatures, high insolation, and low soil moisture). Although there are certainly many cases in which this is debatable, in the Gramineae it seems to be generally true. There are, however, xerophytic non-Kranz genera (*Cleistochloa*, *Dimorphochloa*, *Thyridolepis*, etc.) and emergent aquatic Kranz species (in *Oryzidium*, *Paspalum*, etc.) in the family.

It is now possible to address the further question: Is any subtype of the Kranz syndrome in the Gramineae more successful as an adaptation to xeric conditions than the others? The grass taxa containing the species and genera native to the most xeric environments are the Eragrostoideae, the Aristideae, and, among the Paniceae, the subgenus *Panicum*.

In the Aristideae, non-Kranz *Sartidia* is mesophytic. Kranz *Aristida* seems to be basically a modified M.S., NADP-me taxon, the species of which range from mesic to xeric habitats. The third genus, *Stipagrostis*, is P.S. and is native to very arid regions of Africa and southern Asia.

It is well known (Hartley and Slater, 1960) that the Eragrostoideae include most of the grass species of very arid regions. They are all P.S. and mostly NAD-me, although PEP-ck species are known (Table 1).

Most Paniceae are M.S., doubtlessly NADP-me, and mesophytic (Hartley, 1958b). Probably the most xerophytic species of the genus are in section *Dura* of the P.S. subgenus *Panicum*. These are true desert species and probably NAD-me. Numerous other species of the subgenus are also found in rather arid environments.

Therefore, it can be proposed that among the Gramineae those species occupying the most arid regions and growing during the hot dry season have the P.S. subtype of Kranz leaf anatomy and the NAD-me subtype of C_4 photosynthesis.

In 1958 I proposed six types of grass leaf anatomy, three non-Kranz and three Kranz. There is now reason for modifying the designations of the non-Kranz types because some of them occur within the Panicoideae, but that will not be attempted here. The designations of the Kranz types (chloridoid, panicoid, and aristidoid) also deserve reconsideration in light of recent studies. I propose to change from taxon-based terms to descriptive and evolutionary ones because the former have erroneous implications.

Chloridoid (or eragrostoid) anatomy, typical of all species of the Eragrostoideae, should be referred to as the P.S. type, whether occurring in that subfamily, the Panicoideae, or the Arundinoideae. Panicoid anatomy should be referred to as the M.S. type, even though it is, so far as known, restricted to the Panicoideae. Within the Panicoideae, a wide variety of anatomical types occur: perhaps more than one non-Kranz type, as well as Kranz M.S. and two types of P.S. Aristidoid anatomy is restricted to the genus *Aristida* as presently delimited (de Winter, 1965). However, non-Kranz and the P.S. types also occur within the tribe Aristideae. Therefore, I suggest that this Kranz type, as it occurs in *Aristida*, be designated the D.S. (for "double sheath") type, parallelling M.S. and P.S. Other subtypes of Kranz leaf anatomy occur in other families and have been named (Johnson and Brown, 1973; Brown, 1975).

The anatomical evolutionary steps from non-Kranz to the M.S. type now seem clear. Brown (1975) reported that a Kranz sheath can evolve from the mestome sheath of non-Kranz grasses. Now, with closely related non-Kranz and Kranz taxa known in *Alloteropsis*, *Panicum* (group "Grandia"), and

Thyridolepis/Neurachne, the sequence of anatomical changes is evident. First the mestome sheath cells become larger, thinner walled, and acquire chloroplasts. Then C_4 photosynthesis evolves, as in *Alloteropsis semialata* and *Panicum petersonii,* with slight modification of the parenchyma sheath. At about this same time there is evolution (perhaps in a rapid, single step) of the closely-spaced intercalary bundles typical of all Kranz grasses. This change seems to be necessary to increase the amount of Kranz tissue relative to mesophyll for biochemical balance of the two steps in C_4 photosynthesis. Distinctive cells do not represent an intermediate step in the evolution of intercalary bundles because they occur in taxa which must be derivatives of an ancient evolution of the Kranz syndrome.

The persisting parenchyma sheath, as it occurs in *Alloteropsis semialata* and *Panicum petersonii,* would inhibit the circulation of molecules between mesophyll and Kranz tissue. In *Neurachne munroi* and *N. muelleri,* the parenchyma sheath cells seem to be greatly reduced in size. Finally, as is true in nearly all M.S. species, the parenchyma sheath is lost completely, so that mesophyll and Kranz cells are in direct contact.

It can be concluded, therefore, that any Kranz M.S. taxon which is closely related to a non-Kranz taxon and has a persisting parenchyma sheath is an example of recent evolution of the Kranz syndrome.

Among Kranz P.S. taxa there is no such anatomical marker known that might indicate recently evolved taxa. *Steinchisma (Panicum) hians/S. milioides* is C_3 although intermediate in a number of characters. It has not evolved the intercalary bundles. What is known seems to indicate that anatomical changes toward Kranz anatomy precede biochemical changes toward C_4 photosynthesis.

Taxonomically, the difference between the Kranz syndrome and the non-Kranz condition is at the least a specific one. There is no known species containing both Kranz and non-Kranz subspecies *(Alloteropsis semialata* and its variety *eckloniana* are actually at least specifically distinct; Ellis, 1974b). Even the known intermediates between C_3 and C_4 are specifically distinct *(Mollugo verticillata, Steinchisma hians, Chamaesyce acuta).* On the other hand, the difference is not necessarily a generic one; there are too many genera and sections containing both sorts, especially among dicotyledons.

This degree of taxonomic distinction would seem at least commensurate with that of what are recognized as interspecific differences in more traditional characters. Ten genetic changes or more are necessary to achieve the cytological, anatomical, and physiological transformation from non-Kranz to Kranz. Furthermore, the amount of time required to achieve such an evolutionary change must be at least as great as that needed for interspecific differentiation in more traditional characters.

It has recently been demonstrated among a few species of dicotyledons (Björkman, et al., 1975) that Kranz species are not exactly alike in temperature optima for maximum growth, and that such differences also exist between (various) Kranz and (one) non-Kranz species. Photosynthetic membrane characteristics seem to be most critical in these differences. One Kranz species, *Tidestromia oblongifolia*, has photosynthetic membranes highly specialized for extremely high temperatures, whereas two Kranz species of *Atriplex* have membranes less extremely specialized. The latter can, therefore, grow much better than *T. oblongifolia* at somewhat lower temperatures. It seems likely that Kranz grass species with wide climatic ranges, such as *Panicum virgatum, P. capillare, Setaria lutescens, Digitaria sanguinalis*, and *Schizachyrium scoparium*, have photosynthetic membranes of the less specialized type. On the other hand, species of the desert section *Dura* of *Panicum* may have photosynthetic membranes specialized for very high temperatures.

It is likely that such differences in photosynthetic membranes also exist among non-Kranz grass taxa. If so, that could explain restriction of the Pooideae and the Group I tribes of Figure 4 to cool growing seasons, but of certain other non-Kranz groups such as the Bambusoideae and Oryzoideae (most tribes of Group II in Figure 4) to warm growing seasons. It is assumed that photosynthetic membranes adapted for high temperature efficiency (but of low efficiency in cool temperatures) are typical of certain non-Kranz as well as most Kranz taxa.

It also seems likely that some Kranz taxa have evolved photosynthetic membranes adapted for efficiency in cool temperatures and/or in dense shade (see discussion under ''The Andropogoneae'').

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