A CHECKLIST OF C_3 AND C_4 GRASSES IN TAIWAN

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Abstract: Nearly half species in the family Gramineae in Taiwan were examined anatomically. The Kranz syndrome based on leaf blade anatomy is characterized by the presence of Kranz sheath, the few number of maximum cells count and short interveinal distance. A preliminary checklist of C_3 and C_4 grasses in Taiwan was presented and determined by the non-Kranz or Kranz syndrome. Of 109 species out of 150 species, were recognized as C_4 and the others were assigned as C_3. Some aspects of the above criteria in related to each subfamily were also described and discussed.

INTRODUCTION

The grass family (Gramineae or Poaceae) is one of the largest family of flowering plants in the world as well as in Taiwan and contains many important cereals, forages and weeds. Their economic significance keeps them as an important group to study (Gould and Shaw, 1983; Hsu, 1975; Jones, 1985). In Agrostology, anatomy has its long term influence in traditional and modern research on grasses (Brown, 1958; Metcalfe, 1960; Decker, 1964; Clayton, 1981; Clifford and Watson, 1977; Hilu and Wright, 1982; Ellis, 1986). Haberlandt described two major types of leaf anatomy in 1882, one with Kranz sheath surounding the vascular tissue. He has predicted that the Kranz may be equipped with some special physiological function (Haberlandt 1914). This prediction was elucidated after the discovery of the C_4 photosynthetic pathway and the extensive studies of the C_4 syndrome (Jones, 1985). The C_4 plants are fundamentally different from the C_3 plants in having C_4 syndrome such as Kranz syndrome of leaf anatomy, C_4 metabolism, high CO_2 compensation point, and low $^{12}C/^{13}C$ ratio etc. (Laetsch, 1974; Brown, 1975). It is clear that C_4 plants are found at least in 20 families of flowering plants, including the Gramineae (Kanai, 1981). The reason to study C_4 grasses is already stated by Jones (1985) and it is also understood that grass family contains both C_3 and C_4 species, C_3-C_4 intermediate species and species with different subtype of C_4 dicarboxylic acid pathway (Gutierrez *et al.*, 1974, 1976; Brown, 1977). Leaf anatomy provides many useful criteria for the prediction of photosynthetic pathway in grasses. These criteria are available merely from the cross section of leaf; including the morphology of bundle sheath, arrangement of mesophyll, interveinal distance, maximum cells count and presence of mestome sheath, and are extensively applied by many authors (Downton and Tregunna, 1968; Brown, 1975; Hattersley and Watson, 1975, 1976; Crookston and Moss, 1974).

Some checklist of C_4 species were compiled from works dealing with various aspects of C_4 photosynthesis (Downton, 1971, 1975). The other work focusing on

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large taxa such as Dicots and/or Monocots was also reported (Welkie and Caldwell, 1970. Rafhavendra and Das, 1978). Among grasses, a lot of work dealing with various C_4 syndrome was noticeable (Brown and Gracen, 1972; Brown, 1974; Hattersley and Watson, 1975; Smith and Brown, 1973). Dealing with the taxa of Taiwan grasses, a total of five subfamilies (excluding bamboos), 27 tribes, 118 genera, 289 species, one subspecies, 39 varieties and 8 forms have been recorded (Hsu, 1971). Here we present a preliminary checklist of C_3 and C_4 grasses in Taiwan based on the Kranz syndrome of leaf anatomy as described above by examine large amount of paraffin sections.

MATERIALS AND METHODS

Fresh materials were fixed in FAA, dehydrated with TBA series and embedded in paraffin. Transverse sections of 10-15 μm thick were cut at the mid-region of mature leaf blades. Permanent preparations were made after staining in Delafield's Hematoxylin. The voucher specimen of materials and the permanent slides are deposited at the herbarium and lab of Department of Biology of National Cheng-Kung University respectively (Table 1). The criteria of leaf anatomy that have been used for predicting the C_3 or C_4 grass by previous authors were followerd, including the type of bundle sheath, the interveinal distance, and the maximum cells count. Besides, the reference dealing with various work of C_4 photosynthesis, the other C_4 syndromes if available, were also cited to each Taiwan grass. A data base file, "Taiwan grass leaf anatomy", was constructed with the File Maker plus package of program running on Macintosh computer. The record of this file contains following fields including species, subfamily, voucher slides, maximum cells count, interveinal distance, Kranz sheath, prediction and reference. Based on the Kranz syndrome of leaf anatomy as described above, a preliminary checklist of C_3 or C_4 grasses in Taiwan was presented (Table 1).

OBSERVATIONS AND DISCUSSION

Observation on the presence, size and distribution of the chloroplast in the bundle sheath cells is the criteria most often used to predict the pattern of photosynthesis. (Downton, 1971; Brown, 1977). In general, C_4 plants have Kranz type arrangement of leaf anatomy in which the vascular bundles are surround by a chlorenchymatous sheath of large thick-walled bundle cells with chloroplast larger than that in mesophyll. Comparing with previous works, this Kranz sheath shows definite correlation with other C_4 syndrome (Table 1). This result reveals that this traditional method is still valuable in predicting the photosynthetic pathway in Taiwan grasses. The other criterion is to count the number of chlorenchyma cells of mesophyll located between two adjacent bundle sheath. This criterion, the maximum cell count, has been extensively used by Hattersely and Watson (1975). In Taiwan grasses examined, this data were fairly correlated to the Kranz sheath. As Hattersely and Watson (1975) have already stated that the C_3 grasses have the maximum cell count of more than 4 and the C_4 grasses ranging from 2-4. The following subfamilies including Oryzoiedeae, Arundinoideae and Festucoideae were all with the maximum cell count more than seven. In Eragrostoideae this number ranges from two to four. It shows great variation in the subfamily Panicoideae as follows: two to four in tribe Andropogoneae, four to ten in the

Table 1. The checklist of C_3 and C_4 grasses in Taiwan

Species	Voucher[1]	Kranz[2]	Reference(s)[3]
Alloteropsis semialata (R. Br.) Hitchc.	g18 43 g379	K	r+/2
Apluds mutica L.	g76 g211	K	
Arthraxon hispidus (Thunb.) Makino	g162 g193 g168 g316 g340	K	cl/9
Arundinella hirta (Thunb.) Tanaka	g376	K	cl/9
Arundinella setosa Trin.	29 g68 g112 g124 g229	K	
Axonopus affinis Chase	g161	K	r+/12
Axonopus compressus (Sw.) P. Beauv.	t9	K	
Bothriochloa glabra (Roxb.) A. Camus	g136	K	cl/9
Bothriochloa intermedia (R. Br.) A. Camus	g4 g74	K	cl/9
Bothriochloa ischaemum (L.) Keng	g34	K	cl/9
Brachiaria mutica (Forsk.) Stapf	6 g84 g345	K	m4/7
Brachiaria subquadripara (Trin.) Hitchc.	g9 g147 g260	K	
Capillipedium assimile (Steud.) A. Camus	g77	K	
Cenchrus echinatus L.	B, g127	K	
Chloris barbata Sw.	g13 g33 U G g222	K	cl/11, o−/10
Chrysopogon aciculatus (Retz.) Trin.	g66 22	K	
Coix lacryma-jobi L.	g174	K	o−/3
Cymbopogon citratus (DC.) Stapf	g205	K	r+/12
Cymbopogon tortilis (Presl) A. Camus	g67 g104 49 R, g115	K	
Cymbopogon winterianus Jowitt	g204	K	
Cynodon dactylon (L.) Pers.	g10 g143 g85	K	p−/5, r+/12
Dactyloctenium aegyptium (L.) Beauv.	g58	K	cl/9, r+/12
Dichanthium annulatum (Forsk.) Stapf	g3 g135	K	cl/9
Dichanthium aristatum (Poir.) C. E. Hubb.	g142	K	
Digitaria heterantha (Hook. f.) Merr.	g2 g141 g227 g257	K	
Digitaria radicosa (Presl.) Miq.	g23 g144 g350	K	
Digitaria radicosa (Presl.) Miq. var. *hirsuta* (Honda) C. Hsu	g144 g145	K	
Digitaria sericea (Honda) Honda	g32	K	
Digitaria setigera Roem. & Schult.	g22 g28 t23 g164 g170 g173 g221	K	
Digitaria violascens Link	g118 g156	K	
Diplachne fusca (L.) Beauv.	g25 g188	K	
Echinochloa colonum (L.) Link	t10	K	m4/8
Echinochloa crus-galli (L.) Beauv.	g41 g83 g165 K1 g346 g347	K	cl/9, 10, m4/8, o−/10, r+/12
Eleusine indica (L.) Gaertn.	g14 g21	K	cl/9, m4/6
Enteropogon dolichostachyus (Lag.) Keng	g5 g86	K	
Enteropogon gracilior Rendle	g148	K	
Eragrostis amabilis (L.) Wight & Am. ex Nees	g12 g27 t25 g132	K	
Erograstis ciliaris (L.) R. Br.	g250	K	cl/11, o−/10
Eragrostis cumingii Steud.	t37 t38 g120	K	
Eragrostis curvula	g341	K	
Eragrostis ferruginea (Thunb.) Beauv.	46 g178	K	cl/9
Eragrostis nevinii Hance	t36	K	
Eragrostis pilosissima Link	g258	K	
Eragrostis unioloides (Retz.) Nees ex Steud.	g65f	K	cl/9
Eremochloa ophiuroides (Munro) Hack.	t26	K	r+/12

Table 1. The checklist of C_3 and C_4 grasses in Taiwan (Continued)

Species	Voucher[1]	Kranz[2]	Reference(s)[3]
Eriochloa procera (Retz.) C. E. Hubb.	g8 g126 202 g216 g219	K	
Hackelochloa granularis (L.) Ktze.	g121	K	
Hemarthria compressa (L. f.) R. Br.	g130	K	
Heteropogon contortus (L.) Beauv. ex Roem. & Schult.	g1 g226	K	c1/9, o−/3
Imperata cylindrica (L.) Beauv.	g17 g213	K	
Ischaemum barbarum Retz. var. *gibbum* (Trin.) Ohwi	t48 g116	K	
Ischaemum indicum (Houtt.) Merr.	g6 t34 t36 g152 g179	K	
Leptochloa chinensis (L.) Nees	g348 g312	K	
Leptochloa panicea (Retz.) Ohwi	g133 g290	K	
Lepturus repens (G. Forst.) R. Br.	g138 g251	K	r+/12
Microstegium ciliatum (Trin.) A. Camus	g129 g146 g150 g171	K	
Microstegium dilatatum Koidz.	g46 g74 g190	K	
Microstegium fauriei Honda	g184 g195	K	
Microstegium vimineum (Trin.) A. Camus	g177 g46 g74 g190	K	
Miscanthus floridulus (Labill.) Warb. ex Schum. & Laut.	g43 g187	K	
Miscanthus sinensis Anders.	g73	K	
Miscanthus transmorrisonensis Hayata	g157 g196 g292	K	
Muhlenbergia longistolon Ohwi	g192 g245	K	
Panicum dichotomiflorum Michx.	g286 g287	K	c1/9, r+/12
Panicum maximum Jacq.	t5 t8	K	c1/9, m4/6, 7, 8, r+/12
Panicum paludosum Roxb.	t3 t4 g238 g239 g370	K	
Panichum repens L.	A t7 t21 L t 17	K	c1/11, o−/10
Pasparum commersonii Lam.	t66	K	
Paspalum conjugatum Berg.	g94 t18 t73	K	c1/9
Paspalum dilatatum Poir.	t11 t65 g119 g155 g274	K	c1/4, 9
Paspalum distichum L.	g57 t39 t70	K	c1/4, 9
Paspalum longifolium Roxb.	101 53	K	
Paspalum notatum	g137 g322	K	
Paspalum orbiculare Forst.	g19 35 68	K	
Paspalum plicatum	g134	K	
Paspalum scrobiculatum L.	g297	K	
Paspalum thunbergii Kunth ex Steud.	t67 g163	K	
Paspalum urvillei Steud.	t64 t102 g325	K	c1/9, 10, o−/10, r+/12
Pennisetum alopecuroides (L.) Spreng.	g159 g358	K	
Pennisetum cladestinum Hochst. ex Chiov.	g242	K	
Pennisetum purpureum Schumach.	g100	K	m4/8
Pennisetum setosum (Sw.) L. C. Rich.	g180	K	
Pogonatherum crinitum (Thunb.) Kunth	g88 t28	K	
Rhynchelytrum repens (Willd.) C. E. Hubb.	g29	K	
Rottboellia exaltata L. f.	g326	K	
Saccharum officinarum L.	g200	K	c1/4, 9, m4/8, r+/12
Saccharum sinensis Roxb.	g103	K	
Saccharum spontaneum L.	t44	K	
Schizachyrium brevifolium (Sw.) Nees ex Buse	52 33s	K	
Setaria geniculata (Lam.) Beauv.	t57 g30 g64 g169	K	

Table 1. The checklist of C_3 and C_4 grasses in Taiwan (Continued)

Species	Voucher[1]	Kranz[2]	Reference(s)[3]
Setaria pallide-fusca (Schumach.) Stapf & G. E. Hubb.	g158	K	cl/9
Setaria palmifolia (Koen.) Stapf	g40 g95 24 g172	K	cl/9
Setaria plicata (Lam.) T. Cooke	g149 g240	K	
Setaria verticillata (L.) Beauv.	g30	K	cl/9, m4/6
Setaria vilidis (L.) Beauv.	g31	K	cl/9, m4/6
Sorghum bicolor (L.) Moench	g201	K	cl/9, m4/6
Sorghum halepense (L.) Pers.	g82	K	cl/4, 9
Spinifex littoreus (Burm. f.) Merr.	g101	K	
Spodiopogon tainanensis Hayata	g72 g125	K	
Sporobolus diander (Retz.) Beauv.	t33 g176	K	
Sporobolus fertilis (Steud.) W. D. Clayton	g11 g20 t19 g113 g349	K	
Sporobolus hancei Rendle	g372	K	
Sporobolus virginicus (L.) Kunth	g36 g105	K	
Stenotaphrum secundatum (Walt.) Kuntze	g198	K	
Themada japonica (Willd.) C. Tanaka	g128	K	
Themeda caudata (Nees) A. Camus	g128	K	
Thuarea involuta (Forst.) R. Br. ex Roem. & Schult.	g56 g139	K	
Zea mays L.	g102	K	cl/4, 9, m4/6, 7, o−/3, p−/5, r+/12
Zoysia sinica Hance	g35	K	
Agrostis arisan-montana Ohwi	g51 g53 ag59 g183	N	
Agrostis clavata Trin.	g111	N	
Agrostis fukuyamae Ohwi	g60 g59b	N	
Alopecurus aequalis Sobol. var. *amurensis* (Komar.) Ohwi	g197	N	
Arundo donax L.	g80	N	r−/12
Arundo formosana Hack.	g38 g70 g97	N	
Avena sativa L.	g203	N	r−/12, ch/4, 9
Brachypodium sylvaticum (Huds.) Beauv.	g62 g107 g186	N	
Bromus catharticus Vahl.	g93	N	r−12, ch/9
Cyrtococcum accrescens (Trin.) Stapf	g44 g55a	N	
Cyrtococcum patens (L.) A. Camus	g99 54 51 S	N	r−12
Deschampsia caespitosa (L.) Beauv. var. *festucaefolia* Honda	g106	N	ch/9
Deschampsia flexuosa (L.) Trin.	g50	N	r−12
Festuca takasagoensis Ohwi	g109	N	
Ichnanthus vicinus (F. M. Bail.) Merr.	58	N	
Isachne albens Trin.	g108 g194	N	
Isachne globosa (Thunb.) Ktze.	27 g7 g151 g185	N	
Isachne kunthiana (Weight. & Arn.) Nees ex Steud.	g153	N	
Isachne nipponensis Ohwi	g154	N	
Leersia hexandra Sw.	g117	N	r−/12
Lophatherum gracile Brongn.	17	N	
Oplismenus compositus (L.) Beauv.	g92 g167	N	
Oryza sativa L.	42	N	o+/3
Panicum brevifolium L.	g55b	N	
Panicum incomtum Trin.	47 g75	N	
Panicum notatum Retz.	g75 g42 g131	N	
Phalaris canariensis	g54	N	

Table 1. The checklist of C_3 and C_4 grasses in Taiwan (Continued)

Species	Voucher[1]	Kranz[2]	Reference(s)[3]
Phragmites communis (L.) Trin.	g189	N	r−/12
Phragmites karka (Retz.) Trin. ex Steud.	g166	N	
Poa acroleuca Steud.	g52 g26 g110	N	
Poa annua L.	g63	N	ch/9
Poa sphondyodes Trin. var. *kelungensis* (Ohwi) Ohwi	g37	N	
Poa takasagomontana Ohwi	g61	N	
Polypogon fugax Nees	g49 g191 g181	N	
Polypogon monspeliensis (L.) Desf.	g207	N	
Sacciolepis indica (L.) Chase	t20 t40	N	
Sphaerocaryum malaccense (Trin.) Pilger	g160	N	
Thysanolaena maxima (Roxb.) Ktze.	g39 g87	N	
Trisetum bifidum (Thunb.) Ohwi	g53b g182	N	
Triticum aestivum L.	g202	N	ch/1, 9, o+/3, m3/6, p+/5
Zizania latifolia (Griseb.) Stapf	g199	N	

Notes:

1. Voucher(s) of paraffin sections.
2. K—show Kranz syndrome; N—show non-Kranz syndrome.
3. Each reference was cited as the following format "symbol/reference(s)". [e.g. r+/2, cl/9, 10]

Symbols:

r, determined by isotopic ratio; r+—high ratio, r—low ratio.
c, determined by CO_2 compensation point; ch—high, cl—low.
m, determined by metabolism; m_3—C_3, m_4—C_4.
o, determined by oxygen effect on photosynthesis; o+—inhibited, o—uninhibited.
p, determined by photorespiration; p+—high, p—low.

References:

1. Bisalputra, T., Downton, W. J. S. and Tregunna, E. B. 1969. The distribution and ultrastructure of chloroplasts in leaves differing in photosynthetic carbon metabolism. I. Wheat, Sorghum, and Aristida (Gramineae). Can. J. Bot. **47**: 15-21.
2. Brown, W. V. 1975. Variations in anatomy, associations, and origins of Kranz tissue. Amer. J. Bot. **62**: 395-402.
3. Downes, R. W. and Hesketh, J. D. 1968. Enhanced photosynthesis at low oxygen concentrations: differential response of temperate and tropical grasses. Planta **78**: 79-84.
4. Downton, W. J. S. and Tregunna, E. B. 1968. Carbon dioxide compensation—its relation to photosynthetic carboxylation reactions, systematics of the Gramineae, and leaf anatomy. Can. J. Bot. **46**: 207-215.
5. Fredick, S. E. and Newcombs, E. H. 1971. Ultrastructure and distribution of microbodies in leaves of grasses with and without CO_2 photorespiration. Planta, **96**: 152-174.
6. Gutierrez, M., Edwards, G. E. and Brown W. V. 1976. PEP carboxykinase containing species in the Brachiaria group of the subfamily Panicoideae. biochemical systematics and ecology, **4**: 47-49.
7. Gutierrez, M., Gracen, V. E. and Edwards, G. E. 1974. Biochemical and cytological relationships in C_4 plants. Planta **119**: 279-300.
8. Hatch, M. D., Kagawa, T. and Craig C. 1975. Subdivision of C_4-pathway species base on differing C_4 acid decarboxylating systems and ultrastructural features. Aust. J. Plant Physiol.
9. Krenzer, E. G. Jr., Moss, D. N. and Crookstoon, R. K. 1975. Carbon dioxide compensation points of flowering plants. Plant Physiol. **56**: 194-206.
10. Morgan, J. A. and Brown, R. H. 1979. Photosynthesis in grass species differing in carbon dioxide fixation pathways. Plant Physiol. **64**: 257-262.
11. Raghavendra, A. S. and Das, V. S. R. 1976. Distribution of the C_4 dicarboxylic acid pathway of photosynthesis in local monocotyledonous plants and its taxonomic significance.
12. Smith, B. N. and Brown, W. V. 1973. The Kranz syndrome in the Gramineae as indicated by carbon isotopic ratios. Amer. J. Bot. **60**(6): 505-513.

tribe Isachneae and one to ten in the tribe Paniceae. In Isachneae, with the exception of *Isachue albens* shows a C_3 grasses with the count lesser than 4. In Panieceae, only the following C_3 grasses *Cyrtococum accrescens, C. patens, Oplismenus compositus, Panicum bisulcatum, P. brevifolium, P. incomtum, P. notatum* and *Sacciolepis indicum* have the maximum cell count more than 4. The data of the counts of interveinal distance were frequently presented in the report on productivity of agricultural plant. There are some general counclusion that the plant with shorter interveinal distance may have higher net photosynthetic productivity, lower CO_2 compensation point and oxygen insensitive than that with longer one (Takeda and Fukuyama, 1971; Crookston, R. K. and D. N. Moss, 1974; Morgan and Brown, 1979). Apparently it is a convenient criterion for predicting the presence of C_4 syndrome. In the present observation, we found that this distance varies from 50-450 μm. A considerable variation also occurs in the subfamily Panicoideae, uniformly less than 150 μm in tribe Andropogoneae, with higher value more than 200 μm in the tribe Isachneae and with diversity in the tribe Panicae. In general, most species with other Kranz syndrome also have short distance less than 150 μm. There were a few exceptions in Eragrostoideae, only *Eleusine indica* has slightly higher measurement of 190 μm and in Arundioideae and Festucoideae, *Arundo donax, Arundo formosana* and *Poa takasagomontana* have short distance less than 150 μm. This data were compatible to both of Crookston and Moss (1974) and Morgan and Brown (1979), but quite different from that of Takeda and Fukuyama (1971). As we can realize that the parallel venation of grass usually turns to become narrower both basipetally and acropetally. Takeda and Fukuyama (1971) examined and measured this distance at the base of blade and they stated the higher CO_2 compensation point grasses (C_3 grasses) still have a very short distance between 75-130 μm. However this difference and some exceptions should not be ignored, we should be careful to use this criterion as a Kranz syndrome. According to the variable aspects of the above criteria in related to each subfamily, we would like agree with the suggestion made by Ellis (1986) that high priority should be given to the studies of the Panicoideae.

LITERATURE CITED

BROWN, R. H. and V. E. GRACEN 1972. Distribution of post-illumination CO_2 burst among grasses. Crop Science **12**: 30-33.

BROWN, W. V. 1958. Leaf anatomy in grass systematics. Bot. Garz. **119**: 170-178.

BROWN, W. V. 1974. Another cytological difference among the Kranz subfamilies of the Gramineae. Bull. Torrey Bot. Club. 101: 120-124.

BROWN, W. V. 1975. Variations in anatomy, associations, and origins of Kranz tissue. Amer. J. Bot. **62**: 395-402.

BROWN, W. V. 1977. The Kranz syndrome and its subtypes in grass systematics. Memoirs of the Torrey Bot. Club. **23**(3): 1-97.

CLAYTON 1981. Evolution and distribution of grasses. Ann. Missouri Bot. Gar. **68**: 5-14.

CLIFFORD, H. T. and L. WATSON, 1977. Identifying grasses: data, methods and illustrations. Univ. of Queensland Press. 146 pp.

CROOKSTON, R. K. and D. N. MOSS 1974. Intervenial distance for carbohydrate transport in leaves of C_3 and C_4 grasses. Crop. Sci. **14**: 123-125.

DECKER, H. F. 1964. An anatomic-systematic study of the classical tribe Festuceae (Gramineae). Amer. Journ. Bot. **51**: 453-463.

DOWNTON W. J. S. and E. B. TREGUNNA 1968. Carbon dioxide compensation—its relation to photosynthetic carboxylation reactions, systematics of the Gramineae, and leaf anatomy. Can. J. Bot. **46**: 207–215.

DOWNTON W. J. S. 1971. Checklist of C_4 species. *In* photosynthesis and photorespiration. ed. M. D. Hatch, C. B. Osmand and R. O. Slatyer, pp. 554–8. (Wiley-Inter Science, N. Y.).

DOWNTON W. J. S. 1975. The occurrence of C_4 photosynthesis among plants. Photosynthetica **9**(1): 96–105.

ELLIS R. P. 1986. A review of comparative leaf anatomy in the systematics of the Poaceae: The past twenty-five years. *In* T. R. Soderstrom, M. E. Barkworth, C. S. Campbell and K. W. Hilu [eds.], Grass systematics and evolution, 3-10. Smithonian Institution Press, Washington, DC. Proceedings of the International Symposium on Grass Systematics and Evolution, Washington, DC. 27-31 July 1986.

GOULD, F. W. and R. B. SHAW 1983. Grass systematics. 2nd ed. Texas A & M University press.

GUTIERREZ M., V. E. GRACEN and G. E. EDWARDS 1974. Biochemical and cytological relationships in C_4 plants. Planta **119**: 279–300.

GUTIERREZ, M., G. E. EDWARDS and W. V. BROWN 1976. PEP carboxykinase containing species in the Brachiaria group of the subfamily Panicoideae. Biochemical Systematics and Ecology, **4**: 47–49.

HABERLANDT, G. 1914. Physiological plant anatomy. MacMillan and Co., London.

HABERLANDT, G. 1882. Vergleichende anatomie des assimilatorischen gewebesystems der Pflanzen. Pringshiem Jahrb. Wiss. Bot. Bd. 13.

HATTERSLEY, P. W. and L. WATSON 1975. Anatomical parameters for predicting photosynthetic pathways of grass leaves: the 'maximum lateral cell count' and the 'maximum cell distant count'. Phytomorphology **25**: 325–333.

HATTERSLEY, P. W. and L. WATSON 1976. C_4 grasses: an anatomical criterion for distinguishing between NADP-enzyme species and PCK or NAD-enzyme species. Aust. J. Bot. **24**: 297–308.

HILU, K. W. and K. WRIGHT 1982. Systematics of Gramineae: A cluster analysis study. Taxon **31**(1): 9–36.

HSU, C. C. 1971. A guide to the Taiwan grass, with keys to subfamilies, genera and species. Taiwania **16**: 199–341.

HSU, C. C. 1975. Taiwan Grasses. Taiwan Prov. Educ. Ass. Taipei, Taiwan. published. [in Chinese]

JONES, C. A. 1985. C_4 grasses and cereas-growth, development and stress response. John Wiley and Sons, Inc. New York.

KANAI 1981. Plant physiology. Chapter 4. 1. C_4 photosynthesis. p. 162–181. Asakura Book Store [in Japanese]

LAETSCH, W. M. 1974. The C_4 syndrome: a structural analysis. Annu. Rev. Plant Physiol. **25**: 27–52.

METCALFE, C. R. 1960. Anatomy of the Monocotyledons. I. Gramineae. Oxford, U. K.

MORGAN, J. A. and BROWN, R. H. 1979. Photosynthesis in grass species differing in carbon dioxide fixation pathways. Plant Pysiol. **64**: 257–262.

RAGHAVENDRA, A. S. and V. S. R. DAS 1978. The occurrence of C_4 photosynthesis: a supplementary list of C_4 plants reported during late 1974- mid 1977. Photosynthetica **12**: 200–208.

SMITH, B. N. and W. V. BROWN 1973. The Kranz syndrome in the Gramineae as indicated by carbon isotopic ratios. Amer. J. Bot. **60**(6): 505–513.

TAKEDA, T. and FUKUYAMA, M. 1971. Studies on the photosynthesis among subfamilies and their relations with the systematic of the Gramineae. Proc. Crop Sci. Japan **40**: 12–19.

WELKIE G. W. and M. CALDWELL 1970. Leaf anatomy of species in some dicotyledon families as related to the C_3 and C_4 pathways of carbon fixation. Can. J. Bot. **48**: 2135–2146.

臺灣產 C_3 和 C_4 禾草名錄

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摘要

經由解剖鏡檢近半數以上的臺灣產禾本科植物。根據葉片解剖所觀察到的顆綠環綜合特徵；包括顆綠環束鞘之存在，具較小的脈間細胞數最大值及較短的脈間距。由此綜合特徵預測臺灣產禾草光合作用型式，並初步列出 C_3 和 C_4 禾草名錄。於檢視的 150 種中，有 109 種爲 C_4 型，其它 41 種爲 C_3 型。此外，各亞科在顆綠環綜合特徵方面的若干特性也隨文討論。