Occurrence of C_3 and C_4 Photosynthetic Pathways in North American Grasses

S.S. WALLER AND J.K. LEWIS

Abstract

A literature survey was made for the occurrence of C_3 and C_4 photosynthetic pathways in the United States Gramineae. Distinctive characteristics of the two photosynthetic pathways are discussed. Leaf anatomy, CO_2 compensation point, net enhancement of photosynthesis in oxygen-deficient atmosphere, ^{13}C discrimination, and initial product labeling were criteria selected to evaluate data for 6 subfamilies including 25 tribes, 138 genera, and 632 species. The Arundinoideae, Bambusoideae, Oryzoideae, and Pooideae (Festucoideae) are composed of species with C_3 pathways. All tribes within the Eragrostoideae have C_4 pathways with the exception of Unioleae. Within the Panicoideae, the Andropogoneae and all of the Paniceae, excepting the genera *Sacciolepus, Isachne, Oplismenus, Amphicarpum,* and *Panicum,* have C_4 pathways. The subgenus *Dichanthelium* within *Panicum* is C_3 while the *Eupanicum* subgenus contains plants with both C_3 and C_4 photosynthetic pathways.

Plant productivity is dependent on several environmental and biological factors. The most important single factor is photosynthesis. A pathway for carbon dioxide (CO_2) fixation was described by Calvin and Bassham (1962) in which CO_2 was incorporated into a 6-carbon compound and rapidly converted to a 3-carbon compound, 3-phosphoglyceric acid (3PGA). Previous to discoveries of Kortschalk et al. (1965) and Hatch and Slack (1966), the Calvin cycle (C_3, reductive pentose pathway) was considered the major photosynthetic mechanism for carbon (C) fixation. However, Hatch and Slack (1966) described CO_2 fixation in which labeled CO_2 was first incorporated in 4-carbon compounds (malic, aspartic, or oxaloacetic acid) prior to transfer to sugars by way of 3-phosphoglycerate. The proposed mechanism involved the operation of two interconnected metabolic cycles. Downton (1970) described carbon fixation into C_4-dicarboxylic acids in mesophyll cells and subsequent incorporation into the Calvin cycle located in the bundle sheath cells. Plants (C_4 plants) possessing the 4-carbon pathway (also called C_4, dicarboxylic acid, Kranz type, low CO_2 compensation, tropical, Hatch and Slack, or β carboxylation pathway) were of tropical origin and more efficient. They produced two- to threefold more dry matter than plants possessing the 3-carbon pathway (C_3 plants), especially in relatively sunny, warm, dry climates (Black 1971).

Distinctive characteristics associated with the C_4 pathway prompted intensive research in photosynthetic processes of flowering plants. The most important photosynthetic pathways are the C_3 and C_4; however, a crassulacean acid pathway (CAM) has been reported in some succulents (Ranson and Thomas 1961; Ting 1971).

The first listing of C_4 plants was prepared in 1970 (Downton 1971). By 1974, the C_4 photosynthetic pathway had been identified in 13 families (Aizoaceae, Amaranthaceae, Boraginaceae, Caryophyllaceae, Chenopodiaceae, Compositae, Convolvulaceae, Cyperaceae, Euphorbiaceae, Gramineae, Nyctaginaceae, Portulacaceae and Zygophyllaceae) and 117 genera of the Angiospermae (Downton 1975). Bjorkman (1976) identified three additional families: Acanthaceae, Capparidaceae, and Scrophulariaceae. Many publications have been concerned with identification of the C_4 pathway in individual species.

Knowledge about the photosynthetic pathway allows interpretation of several important ecological characteristics. Black et al. (1969) proposed that competitive ability of plants primarily depended on net capacity of CO_2 assimilation, resulting in increased foliage extension and size. Other factors being equal, plants with higher apparent photosynthetic rates (C_4 plants: species having the C_4 pathway, Calvin pathway and Kranz anatomy) have a competitive advantage over those with lower rates (C_3 plants: species having only the Calvin pathway). Such advantage can help explain aspects of structure and function in terrestrial ecosystems and the importance of warm-season and cool-season plant classification in range management.

The present literature review was undertaken to compile a listing of photosynthetic pathways and related attributes of United States grasses to serve as a reference for range scientists.

Methods of Determining the Photosynthetic Pathway

Plants possessing the C_4 photosynthetic pathway are very different from C_3 plants in a variety of characteristics (Black 1971). The net photosynthetic rate is two- to threefold greater; CO_2 compensation points are lower; photosynthesis is not suppressed by oxygen concentration between 1 and 100%; CO_2 is not evolved during illumination; bundle sheath cells contain chloroplasts and starch; discrimination against ^{13}C compounds is lower; and CO_2 fixation initially yields 4-C acids as opposed to 3-C acids found in the C_3 photosynthetic pathway. Since these distinguishing characteristics are coexistent, various characters have been used as criteria for determining the photosynthetic process. Five characteristics have been widely used to classify the photosynthetic pathway and are discussed below.

Photosynthetic Products

Initial product labeling with ^{14}C is the only direct method for photosynthetic pathway determination. Hatch et al. (1967) reported that in C_4 plants as much as 93% of fixed radioactivity appeared in oxaloacetic, malic, and aspartic acids following

Authors were assistant and associate professor, Animal Science Department, South Dakota State University, Brookings 57007. Senior author is presently Associate Professor, Department of Agronomy, University of Nebraska, Lincoln, Nebr. 68583.

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exposure to $^{14}CO_2$ for approximately 1 second. In contrast, early products of the C_3 process were 3-PGA and hexose phosphates.

CO_2 Compensation and Photorespiration

Carbon dioxide compensation point (the point at which photosynthetic CO_2 uptake equals respiratory CO_2 evolution when measured in a closed chamber) is an easily obtainable characteristic. During photosynthesis a light-induced release of CO_2 can occur and is referred to as photorespiration as contrasted to CO_2 released by mitochondria or dark respiration. Plants with the C_4 pathway have a photosynthetic CO_2 compensation in the range of 0-10 ppm, indicating a lack of significant net photorespiration (Downton and Tregunna 1968). Photorespiration does occur as a normal product of the Calvin cycle within the bundle sheath cells of C_4 plants. However, since the mesophyll layer surrounds the bundle sheath, the C_4 pathway would rapidly refix any photorespiratory CO_2 and prevent leakage to the atmosphere (Bowes and Ogren 1972). A much higher CO_2 compensation point (37-70 ppm) is characteristic of C_3 plants (Black 1971). Carbon dioxide compensation points provide a convenient means of identifying the type of photosynthetic pathway. The low CO_2 compensation point of C_4 plants indicates an ability to utilize more external CO_2 as compared to C_3 plants.

Oxygen Suppression

Oxygen differentially affects CO_2 exchange in C_3 and C_4 plant species, primarily because of differences in photorespiration. In soybean (*Glycine max*), and probably other C_3 species as well, the total O_2 inhibition consists of two discernible effects. Oxygen substitutes for CO_2 in the carboxylase reaction to yield P-glycolate, a C_3 photorespiratory intermediate. As a result of this subsitution, O_2 competitively inhibits the carboxylase with respect to CO_2 (Ogren 1976). During photorespiration glycolate is oxidized, releasing CO_2. Consequently, oxygen depletion will reduce glycolate oxidation thereby increasing photosynthetic CO_2 assimilation by 40 to 50% in species possessing the C_3 pathway, while having no effect on C_4 plants (Downes and Hesketh 1968). The refixation of photorespiratory CO_2 allows C_4 plants to utilize all of the fixed CO_2, thus increasing photosynthetic efficiency.

Chollet (1976) postulated that the enzyme complement of the C_4 pathway increased CO_2 concentration at the site of the C_3 carboxylase, reducing the competitive inhibition of O_2 and minimizing photorespiration. The CO_2 concentration at the site of the C_3 carboxylase coupled with a specialized leaf anatomy, allowing recapture of photorespiratory CO_2, was apparently responsible for the lack of photorespiration and absence of the inhibitory effect of 21% O_2 on net photosynthesis in C_4 plants.

Leaf Anatomy

Leaf anatomy provides an easily distinguished difference between C_3 and C_4 plants. Plants with the C_3 photosynthetic capabilities lack well-defined parenchymatic bundle sheaths and starch grains are found mainly within the mesophyll (Bisalputra et al. 1969) (Fig. 1). Plants with the C_4 photosynthetic pathway generally have well-developed parenchymatic bundle sheaths containing high concentrations of chloroplasts and starch. Bundle sheath cells utilize the C_3 photosynthetic process; however, they are surrounded by mesophyll cells containing chloroplasts utilizing the C_4 photosynthetic process which

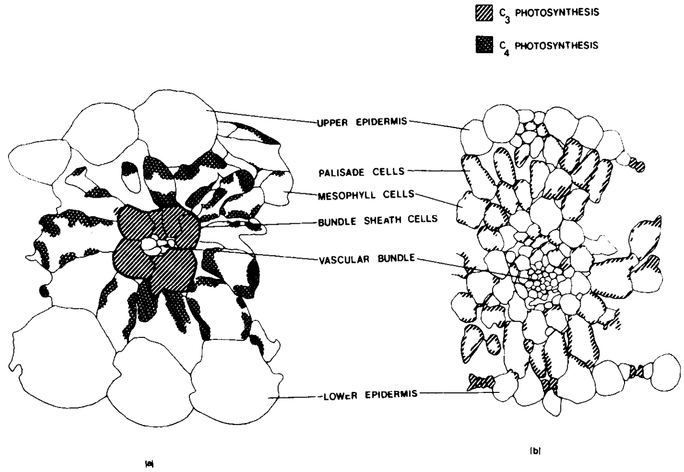

Fig. 1. *Comparison of leaf anatomy between plants having C_4 photosynthesis (a) and C_3 photosynthesis (b). The C_4 plant exhibits prominent bundle sheath cells and concentrated photosynthetic activity near the vascular bundles (Adopted from Black 1971).*

fix and then supply CO_2 for the C_3 pathway.

The unique leaf anatomy (Kranz type) of C_4 plants provides several advantages for efficient CO_2 fixation. Surrounding the C_3 bundle sheath cells with C_4 mesophyll cells minimizes the loss of CO_2 from C_3 photorespiration. The presence of two active photosynthetic carboxylases and their associated enzymes in the same leaf of a C_4 plant appears to result in a higher affinity for and more rapid uptake of CO_2. The close proximity of starch formation to the vascular bundles should make photosynthate translocation more efficient.

Carbon Isotope Discrimination

Carbon isotope ratio ($^{13}C/^{12}C$) determination in plant tissue is characteristically less than the carbon isotope ratio of atmospheric CO_2, indicating that plants preferentially assimilate the lighter of the two isotopes (Troughton et al. 1974). Carbon isotope values are defined as the difference in per mil of the $^{13}C/^{12}C$ ratio of the sample relative to a standard and reported as $^{13}C°/oo$ (Smith and Epstein 1971). Details of the procedure are described elsewhere (Park and Epstein 1960). Higher plants are placed into two categories, those with low $^{13}C°/oo$ values (-24 to $-34°/oo$) and those with high values(-6 to $-19°/oo$ (Smith and Epstein 1971). Grasses relatively enriched in ^{13}C have $^{13}C°/oo$ values in the -6 to $-19°/oo$ range and are reported to be C_4 while those with relatively low $^{13}C°/oo$ values are C_3 species (Bender 1971). Troughton et al. (1974) reported a mean $^{13}C°/oo$ value of -28.11 ± 2.55 for C_3 and -13.46 ± 1.55 for C_4 grasses. The distinctive difference apparently results from differences in affinity of the enzyme systems of the two pathways for the two isotopes of carbon (Whelan et al. 1973). Thus, the carbon isotope technique was cited as a reliable method of distinguishing between C_3 and C_4 plants (Bender 1971).

Other Characteristics Related to Photosynthetic Pathway

Several other physiological characteristics are closely related to photosynthetic pathway, but have not been widely used in plant classification. Light saturation differs in the two pathways. C_4 plants exhibit continued increase in CO_2 uptake as light intensity increases to nearly full sunlight (approximately 1.5 to 1.8 langleys), while C_3 plants are saturated at 0.2 to 0.4 langleys. Maximum CO_2 assimilation on a leaf area basis at normal atmospheric concentration of CO_2 ranges from 50 to 80 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$ for C_4 plants, but only 15 to 35 mg CO_2

dm^{-2} hr^{-1} for C_3 (Black 1971). Consequently, C_4 plants are more efficient in energy conversion at high light intensities.

Optimum temperature for CO_2 uptake by C_4 plants was reported to be 30 to 40°C with uptake decreasing rapidly below 15 to 20°C. In contrast, temperature optima for C_3 plants ranged from 10 to 25°C with usually a sharp decrease above 25°C (Black 1971). Low night temperatures adversely affected chloroplast ultrastructure and chloroplast development in leaves of C_4 plants (Slack et al. 1974). The physiological response of the photosynthetic apparatus to temperature is the probable reason for the observed phenological development of cool-season plants such as western wheatgrass (*Agropyron smithii*) (C_3) and warm-season plants, such as blue grama (*Bouteloua gracilis*) (C_4) (Williams 1974).

Translocation capacity is larger in C_4 than C_3 plants because of a larger cross-sectional area of phloem (Gallaher et al. 1975). Species with the C_4 photosynthetic pathway have fewer cells between leaf vascular bundles than do C_3 species (Crookston and Moss 1974). The closeness of all leaf cells to vascular tissue in C_4 plants suggests greater efficiency in transporting photosynthate. Takeda and Fukuyama (1971) determined an interveinal distance of 25 to 70 μm (micrometers) for C_4 species and 75 to 130 μm for C_3 species.

Enzyme systems differ in plants with the two photosynthate pathways. Significant physical and kinetic differences were reported for phosphoenolpyruvate carboxylase taken from C_4 and C_3 species (Ting and Osmond 1973). However, carboxydismutase activity (ribulose-1, 5-diphosphate carboxylase) was found to be similar in both C_3 and C_4 plants. A low carbonic anhydrase activity appears distinctive of species with low compensation points and high rates of photosynthesis (C_4), while the inverse is true for C_3 plants (Chen et al. 1970; Triolo et al. 1974).

Photoperiod requirements generally differ in the two groups, but not directly. Since C_4 plants are well adapted to tropical regions, it is natural that most would be short-day or day-neutral with respect to flowering. However, C_4 plants growing at higher latitudes have become adapted to long days for flowering. Genetic plasticity therefore apparently exists for selection for adaptation to photoperiod (Evans 1975).

Bender and Smith (1973) have reported a relationship between type of nonstructural polysaccharide (starch or fructosan) accumulated in the lower internodes of grass shoots and carbon isotope determinations. They found that the type of nonstructural polysaccharide was not dependent on the type of photosynthetic pathway. However, data reported by Smith (1968) indicated C_4 plants accumulated starch while C_3 plants generally accumulated fructosans. Selected species of *Oryzopis, Phragmites, Stipa,* and *Panicum* were of the C_3 type but accumulated starch.

Water is a common limiting factor for plant growth throughout western rangelands. Plants which are efficient in water use would have a competitive advantage over less efficient plants during periods of moisture stress. C_4 plants required about half as much water as C_3 plants to produce one unit of dry matter (Black 1971). However, desert biome researchers in the Curlew Valley of northwestern Utah determined that *Atriplex confertifolia* (C_4) and *Ceratoides lanata* (C_3) were about equal in their annual water use while photosynthetic rates were similar (Cox 1977). High photosynthetic rates in C_4 plants did not result in increased transpiration rates compared to C_3 plants (El-Sharkawy and Hesketh 1965).

Taxonomic Classification

Photosynthetic pathway data for 632 species representing 138 genera and 25 tribes of the United States Gramineae were summarized (Table 1). Results were reported for tribes within each of subfamilies (Gould 1968) (Table 2).

Few intermediate values occurred between the identified C_3 and C_4 range of any characteristic utilized for photosynthetic pathway determination. Also, there was little variation within any characteristic from plant to plant within a species. Selected characteristics for photosynthetic pathway determination were consistently in agreement. Thus, in general, knowledge of any one characteristic could be used to predict the presence and level of associated characteristics.

All species studied in the subfamilies Arundinoideae, Bambusoideae, Oryzoideae, and Pooideae (Festucoideae) possessed C_3 characteristics. Within these subfamilies, there is a high probability that all species will possess the C_3 photosynthetic pathway.

Within the subfamilies Eragrostoideae and Panicoideae, both C_3 and C_4 photosynthetic pathways are present. Both subfamilies are predominantly C_4, while the exceptions apparently indicate a need for taxonomic reclassification rather than heterogeneity of photosynthetic pathway within a taxonomic division. In the Eragrostoideae, as defined by Gould (1968), the genus *Uniola* in the tribe Unioleae appears to possess the C_3 photosynthetic pathway as reflected by ^{13}C°/oo percentages. Consequently, *Uniola* was placed in the Oryzoideae by Smith and Brown (1973).

Within the subfamily Panicoideae, the genera *Oplismenus, Sacciolepis, Amphicarpum,* and *Isachne* are C_3. The genus *Panicum* contains species with both C_3 and C_4 pathways. The subgenus *Paurochaetium* C_4) was reclassified as *Sertaria* by Gould (1968). The subgenus *Dichanthelium* contained only C_3 species, while *Eupanicum* contained species with both C_3 and C_4 pathways. Further evaluation of the subgenus *Dichanthelium* has been reported by Brown and Smith (1975).

Adaptation and Competition

The function of the C_4 pathway is, in effect, to concentrate CO_2 in the bundle sheath cells, permitting the Calvin cycle to operate at more favorable concentrations of this rate-limiting substrate. This provides a more efficient mechanism for CO_2 fixation at low CO_2 concentrations in the intercellular spaces than does C_3 photosynthesis. Thus, the advantage of C_4 photosynthesis is maximal when photosynthesis is operating at high light intensities and temperature, and especially when stomatal conductance to gas exchange is low. In the case of low temperatures and light intensities the advantage would at most be marginal (Bjorkman 1976).

This adaptation correlates well with the historical concept of warm- and cool-season plants used by range scientists, verifying the ecological importance of such a classification. Brown (1978) reported that C_4 plants have a greater nitrogen (N) use efficiency compared to C_3 plants, which may give them an adaptive advantage, particularly on sites low in N. This is probably one of the factors responsible for the greater abundance of C_4 species in range soils lower in fertility (White 1961). It appears probable that the growing season of the species with the C_3 pathway would coincide with the cool, moist months, while the physiological traits of C_4 plants allow them to grow during the hotter, drier months. This would allow many species to occupy the same site with minimal interspecific competition (Williams and Markley 1973). The C_4 pathway is an important adaptive mechanism in hot environments, but it does not necessarily provide a significant advantage in cool, moist environments (Bjorkman et al. 1974).

Table 1. Identification of taxa within the United States Gramineae possessing the C_3 or C_4 photosynthetic pathway. Occurrence of distinct bundle sheath cells (BS: $-=C_3$, $+=C_4$); carbon dioxide compensation point (CO_2: H=C_3, L=C_4); net enhancement of photosynthesis in oxygen deficient atmosphere NE: $>+8=C_3$ $<+8=C_4$); $^{13}C/^{12}C$ ratio (^{13}C°/oo: <-22°oo=C_3 >-22°/oo=C_4); and occurrence of C_4 compounds as initial products in photosynthesis (C_4 cpd: $<2\%C_3$ $2\%C_4$) were characteristics used to evaluate photosynthetic pathway. Taxonomic classification follows that of Gould 1968, 1975)

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
			Subfamily: Arundionoideae				
TRIBE: Arundineae							
[a]Arundo							
A. donax L.				<−22[21,23]		*	
[a]Cortaderia							
C. fulvida (J. Buchanan) Zotov				<−22[21,23]		*	
C. selloana (Schult.) Aschers. and Graebn.		H[12]		<−22[21,23]		*	
Phragmites							
P. communis Trin				<−22[1,21,23]		*	
(P. australis (Cav.) Trin. ex. Steud.)[b]				−27[21]		*	
[a]Molinia							
M. caerulea (L.) Moench				−27[21]		*	
TRIBE: Centotheceae							
Chasmanthium latifolium (Michx.) Yates							
(Uniola latifolia Michx.)[b]				−29[21]		*	
TRIBE: Danthonieae							
Danthonia							
D. montevidensis Hack. and Arech.		H[18]				*	
D. pilosa R. Br.		H[18]				*	
D. spicata (L.) Beauv. ex Roem. and Schult.				−26[21]		*	
[a]Schismus							
S. barbatus (L.) Thell.				−23[21]		*	
			Subfamily: Bambusoideae				
TRIBE: Bambuseae							
Arundinaria							
A. tecta (Walt.) Muhl.				−26[21]		*	
[a]Bambusa							
B. eutuloides McClure				−28[23]			
B. vulgaris Schrad. ex Wendl.				−30[21,22]	0[12,15]	*	
[a]Phyllostachys							
P. aurea A.				−28[21]		*	
P. bambusoides Sieb. and Zucc.				−31[23]		*	
TRIBE: Phareae							
Pharus							
P. latifolius L.				−30[21]		*	
			Subfamily: Eragrostoideae				
TRIBE: Aeluropodeae							
Distichlis							
D. spicata (L.) Greene	+[4]		<8[4]	>−20[1,20,21]			*[10]
D. stricta (Torr.) Rydb.				>−20[2]			
Monanthochloe							
M. littoralis Engelm.				>−20[20,21]			*
TRIBE: Aristideae							
Aristida							
A. adscensionis L.		L[3]	<8[3]				*[10,11]
A. armata Henrard				−14[23]			*
A. glauca (Nees) Walp.				−13[21]			*[1]
A. longiseta Steud.	+[16]						*[10,11]
A. purpurea Nutt.				−14[21]			*[11]
A. ternipes Cav.	+[16]						*[10,11]
A. uniplumis Lichtst in Roem. and Schult.		L[22]					*[10,11]
TRIBE: Chlorideae							
Bouteloua							
B. curtipendula (Michx.) Torr.		L[18]	+8[8]	>−20[1,21]			*[10,11]
B. filiformis (Fourn.) Griffiths.		L[18]		−13[21]			*[11]
B. gracilis (H.B.K.) Lag.		L[24]		−13[1]			*[11]
B. hirsuta Lag.		L[18]					*
Buchloe							
B. dactyloides (Nutt.) Engelm.		L[18,24]		>−20[1,21]			*[10,11]

Table 1 Continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4cpd (%)	C_3	C_4
Chloris							
C. acicularis Lind. L. in Mitch.		L[18]					*
C. argentina (Hack.) Lillo. and Parodi		L[18]					*
C. canterai Arech.		L[18]					*
C. caribaea Spreng.		L[18]					*
C. cucullata Bisch.				−16[21]			*[11]
C. distichophylla Lag.		L[18]					*[11,6]
C. gayana Kunth	+[12]	L[5,12,18]	+3[5,8]	−15[23]	70[15] 90[9]		*[10,11]
C. inflata Link		L[18]					*
C. pectinata Benth.		L[18]					*
C. petraea Swartz		L[18]					*
C. pilosa Schum. and Thonn.		L[18]					*
C. polydactyla (L.) Sw.		L[18]					*
C. pycnothrix Trin.		L[18]					*
C. radiata (L.) Sw.		L[18]					*
C. submutica H.B.K.		L[18]					*
C. truncata R. Br.		L[18]					*
C. uliginosa Hack.		L[18]					*
C. ventricosa R. Br.				−16[23]			*
C. virgata Swartz				−14[23]			*
[a]Cynodon							
C. arcuatus F. and C. Presl		L[18]					*
C. dactylon (L.) Pers.		L[5,7,12,18]		>−20[1,20,21]			*[10,11,6]
Hilaria							
H. belangeri (Steud.) Nash				−14[21]			*[11]
H. mutica (Buckl.) Benth.	+[16]						*[10,11]
Schedonnardus							
S. paniculatus (Nutt.) Trel.	+[16]						*[10,11]
Spartina							
S. alterniflora Loisel.				−13[20,21]			*[11]
S. cynosuroides L.				−14[1]			*[11]
S. pectinata Link		L[18]		−13[1]			*[11]
Trichloris							
T. crinita (Lag.) Parodi		L[18]					*[10]
			Subfamily: Eragrostoideae				
TRIBE: Eragrosteae							
Blepharidachne Hack.	+[17]						
Blepharoneuron Nash	+[17]						*
Calamovilfa Hack.	+[17]						*
[a]Dactyloctenium							
D. aegyptium (L.) Beauv.		L[7]					*[10]
D. aegyptiacum Willd.		L[18]		−12[21]			*[11]
[a]Eleusine							
E. compressa Aschers. and Schweinf. ex Christensen.		L[18]					*
E. coracana (L.) Gaertn.		L[5,18]	+8[5,8]				*[10,11]
E. flagellifera Nees		L[18]					*
E. floccifolia Spreng.		L[18]					*
E. indica (L.) Gaertn.		L[7,18]					*[10,11]
E. jaegeri Pilger		L[18]					*
E. multiflora Hochst.		L[18]					*
E. tristachya (Lam.) Lam.		L[18]					*
Eragrostis							
E. acutiflora Nees		L[18]					*
E. acutiglumis Parodi		L[18]					*
E. airoides Nees		L[18]					*
E. atherstonei Stapf		L[18]					*
E. bahiensis Schrad.		L[18]					*
E. bicolor Nees		L[18]					*
E. brasiliensis Nees		L[18]					*
E. brownei (Kunth) Nees					97[15]		*[10,11]
E. chalcantha Trin.		L[18]					*
E. chariis (Schult.) Hitchc.		L[18]					*
E. chloromelas Steud.		L[7,18]	0[5,8]				*[10,11]
E. cilianensis (All.) Lutati		L[18]		>−20[1,23]			*[11]
E. collocarpa K. Schum. ex Engl.		L[18]					*
E. curvula (Schrad.) Nees	+[14]	L[18]					*[10,11,6]
E. denudata Hack. ex Schinz.		L[18]					*
E. dielsii Pilg. ex Diels and Pritz.		L[18]					*

Table 1 continued

Species	BS	CO2	NE	13C°/oo	C4 cpd (%)	C3	C4
E. diffusa Buckl.		L[18]					*
E. ferruginea Beauv.		L[18]					*
E. flaccida Lindm.		L[18]					*
E. gummiflua Nees		L[18]					*
E. heteromera Stapf		L[18]					*
E. horizontalis Peter.		L[18]					*
E. intermedia Hitchc.	+[16]	L[18]		−16[21]			*[10,11]
E. lappula Nees		L[18]					*
E. lehmanniana Nees		L[18]					*
E. margaritacea Stapf		L[18]					*
E. mexicana (Hornem.) Link		L[12,18]					*[10,11]
E. nigra Nees. ex Steud.		L[18]					*
E. obtusa Munro		L[18]					*
E. oxylepis (Torr.) Torr.		L[18]					*
E. papposa Steud.		L[18]					*
E. patentissima Hack. ex Schinz.		L[18]					*
E. pilosa (L.) Beauv.		L[5,12]					*[10,11]
(E. parviflora Trin.)[b]	+[12]			−17[23]			*
E. plana Nees		L[18]					*
E. poaeoides Beauv. ex R. and S.		L[18]					*
E. polytricha Nees		L[18]					*
E. rigidior Pilger		L[18]	0[8]				*[10,11]
E. robusta Stent.		L[18]					*
E. rufescens R. and S.		L[18]					*
E. secundiflora Presl		L[18]					*
E. spectabilis (Pursh.) Steud.				−11[2]			*
E. starosselskyi Grossheim.		L[18]					*
E. stenophylla Hochst.		L[18]					*
E. superba Peyr.		L[18]					*
E. tremula Hochst.		L[18]					*
E. trichodes (Nutt.) Wood		L[18]					*
E. truncata Hack.		L[18]					*
E. unioloides (Retz.) Nees		L[18]					*
E. virescens Presl		L[18]					*
Gymnopogon							
G. ambiguus (Michx.) B.S.P.				−13[21]			*[11]
Leptochloa							
L. dubia (H.B.K.) Nees		L[7,18]					*[10,11]
L. fascicularis (Lam.) A. Gray		L[18]					*
L. fusca Kunth		L[7,18]					*[10,11,6]
L. monostachya Roem. and Schult.		L[7,18]					*[11,6]
Lycurus							
L. phleoides H.B.K.	+[17]			−14[21]			*
Muhlenbergia							
M. emersleyi Vasey				−11[21]			*[11]
M. lindheimeri Hitchc.				−12[21]		*[11]	*[11]
M. racemosa (Michx.) B.S.P.		L[17,18]					*[10,11]
M. schreberi Gmel.				−13[1]			*[11]
Sporobolus							
S. asper (Michx.) Kunth				−13[2]			*[11]
S. capensis Kunth		L[18]					*
S. contractus Hitchc.		L[18]					*
S. cryptandrus (Torr.) A. Gray.		L[17,18]					*[10,11]
S. elongatus R. Br.		L[18]		−13[23]			*
S. fimbriatus Nees		L[18]					*
S. helvola Th. Dur. and Schinz.		L[18]					*
S. heterolepsis A. Gray.				−13[2]			*
S. indicus (L.) R. Br.		L[18]					*
(S. jacquemontii Kunth)[b]		L[18]					*
(S. poiretii (R. and S.) Hitchc.)[b]		L[18]					* [11,6]
S. iocladus Nees		L[18]					*
S. phyllotrichus Hochst.		L[18]					*
S. pyramidatus (Lam.) Hitchc.		L[18]					*
S. spicatus Kunth	+[16]						*
S. usitatus Stent.		L[18]					*[10,11]
S. usitatus Stent.		L[18]					*
S. wrightii Munro. ex Scribn.				12[21]			*
Tridens							
T. albescens (Vasey) Woot. and Standl.	+[17]			−14[21]			*[11]
T. pilosus (Buckl.) Hitchc.				−13[21]			*[11]
Vaseyochloa							
V. multinervosa (Vasey) Hitchc.		L[17,18]		−15[21]			*[10,11]

Table 1 continued

Species	BS	CO_2	NE	^{13}C‰	C_4 cpd (%)	C_3	C_4
TRIBE: Orcuttieae							
Neostapfia							
N. colusana (Davy.) Davy.				−13[21]			*[11]
Orcuttia							
O. californica Vasey				−14[21]			*[11]
TRIBE: Pappophoreae							
Pappophorum							
P. bicolor Fourn.		L[17,18]		−13[21]			*[10,11]
TRIBE: Zoysieae							
[a]Tragus							
T. australianus S.T. Blake		L[8]	+2[8]				*[10,11]
[a]Zoysia							
Z. japonica Steud.				−15[21]			*[10,11]
Z. matrella (L.) Merr.				−12[21]			*[11]
Z. minima (Colenso) Zotov				−14[23]			*
TRIBE: Unioleae							
Uniola							
U. paniculata L.	+[14]			−28[20,21]		*	*[11,6]
Subfamily: Oryzoideae							
TRIBE: Oryzeae							
Ehrharta							
E. calycina J.E. Smith			+47[8]			*	
Hydrochloa							
H. carolinensis Beauv.				−27[21]		*	
Leersia							
L. hexandra Swartz					0[15]	*	
L. oryzoides (L.) Swartz		H[18]		−28[21]		*	
Luziola							
L. bahiensis (Steud.) Hitchc.				−28[21]		*	
[a]Oryza							
O. rufipogon Griff.			+55[8]			*	
O. sativa L.		H[5,12]	+45[8,5]	−26[21]		*	
Zizania							
Z. aquatica L.		H[18]		<−22[1,21]		*	
Z. texana Hitchc.				−27[21]		*	
Zizaniopsis							
Z. miliacea (Michx.) Doell and Aschers.				<−22[1,21]		*	
Subfamily: Panicoideae							
TRIBE: Andropogoneae							
Andropogon							
A. gayanus Kunth			−2[5,8]				*[10,11]
A. gerardi Vitman		L[18]		−13[2]			*
A. glomeratus (Walt.) B.S.P.				>−20[21]			*[11]
A. lateralis Nees		L[18]					*
A. papillosus Hochst. ex A. Rich.		L[18]					*
A. selloanus Hack.		L[18]					*
A. ternatus Nees		L[18]					*
A. virgatus Desv.		L[18]					*
A. virginicus L.		L[7]					*[10,11,6]
[a]Anthraxon							
A. hispidus (Thunb.) Makino		L[18]					*
Bothriochloa							
B. alta (Hitch.) Henrard		L[18]		−12[21]			*
B. barbinodis Herter		L[18]					*
B. decipiens (Hackel) C.E. Hubb.		L[18]					*
B. ewartiana (Domin) C.E. Hubb.		L[18]					*
B. glabra (Rox B.) A. Camus		L[19]					*
B. exaristata (Nash) Henr.							*
(Andropogon hassleri Hack.)[b]		L[18]					
B. insculpta (Hochst.) A. Camus		L[18]					*
B. intermedia (R. Br.) A. Camus		L[18]					*
B. ischaemum (L.) Keng		L[18]					*
B. laguroides (D.C.) Herter		L[18]					*
B. pertusa (Willd.) A. Camus		L[18]					*

Table 1 continued

Species	BS	CO	NE	^{13}C°/oo	C4cpd (%)	C3	C4
B. saccharoides Swartz (Andropogon saccharoides Swartz)[b]				−12[21]			*[10]
B. springfieldii (Gould) Parodi		L[18]					*
Chrysopogon							
C. gryllus (L.) Trin.							*[11,6]
C. montanus Trin.		L[18]		−12[21]			*[11]
C. serrulatus Trin.		L[18]					*
[a]Coix							
C. lacryma jobi L.			0[8]				*[10,11]
[a]Cymbopogon							
C. citratus Stapf				−15[20,21]			*[11]
C. martini (Roxb.) W. Watson		L[18]					*
[a]Dichanthium							
D. annulatum Stapf		L[18]					*
D. aristatum (Poir.) C.E. Hubb.			0[8]				*[10]
D. sericeum A. Camus		L[18]					*
D. superciliatum A. Camus		L[18]					*
[a]Eremochloa							
E. ophiuroides (Munro) Hack.	+[16]			−11[21]			*[10,11,6]
Erianthus							
E. maximus Brongn.					84[15]		*[10,11]
Heteropogon							
H. contortus (L.) Beauv.		L[7,18]	0[8]				*[11,6]
[a]Hyparrhenia							
H. hirta (L.) Stapf		L[18]					*[10]
H. rufa (Nees) Stapf		L[18]					*
Imperata							
I. arundinacea Cyrilli							*[10,11]
I. chesemanii Hack.				−13[23]			*
I. cylindrica (L.) Beauv.				−12[23]			*
Manisuris							
M. altissima (Poir.) Hitchc.							*[11,6]
[a]Miscanthus							
M. sacchariflorus (Maxim.) Hack.							*[10]
[a]Saccharum							
S. officinarum L.		L[5,18]		>−20[21,15]	65,86[9,15]		*[10,11,6]
S. robustum Brandes and Fesw.							*[10,11]
S. sinense Roxb.					63[15]		*[10,11]
S. spontaneum L.					65[15]		*[10,11]
Schizachyrium							
S. cirratus Hack.		L[18]					*
S. condensatus H.B.K.		L[18]					*
S. hirtiflorus (Nees) Kunth		L[18]					*
S. scoparium Michx.							*
(Andropogon scoparius Michx.)[b]		L[7]		−14[2]			*[10,6]
Sorghastrum							
S. nutans (L.) Nash	+[16]	L[18]		−12[2]			*[10,11]
S. pellitum Parodi		L[18]					*[6,11]
[a]Sorghum							
S. arundinaceum Stapf		L[18]					*[11]
S. bicolor (L.) Moench		L[7,18]			94[9]		*[10,11,6]
S. caffrorum Beauv.		L[18]					*
S. caudatum Stapf		L[18]					*
S. controversum (Steud.) Snowden		L[18]					*
S. dochna (Forsk.) Snowden		L[18]					*
S. drummondii Nees		L[18]					*
S. gambicum Snowden		L[18]					*
S. halepense (L.) Pers.		L[7,18]		−12[23]	64[15]		*[10,11]
S. japonicum (Hackel) Roshev.		L[18]					*
S. nigricans Hort. ex R. and S.		L[18]					*
S. propinquum (Kunth) Hitchc.							*[10,11]
S. saccharatum Moench		L[18]					*
S. sudanense Stapf	+12[3]	L[3,12,18]	−10[8]		88[9]		*[10,11]
S. technicum (Koern.) Battand and Trab.		L[18]					*
S. verticilliflorum Stapf		L[18]					*[11]
S. virgatum (Hack.) Stapf		L[18]					*
S. vulgare Pers.		L[12]	+4[5,8]	−14[21]			*[10,11]
Tripsacum							
T. dactyloides L.		L[7]		−12[21]			*[10,11]
[a]Zea							
Z. mays L.	+[4,12,22]	L[7,22,13,12,18]	0-6,[4,5,8]	>20[21,22,23,20]	86[9,15,22]	*[10,11,6]	

Table 1 continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
TRIBE: Paniceae							
Amphicarpum							
A. purshii Kunth				−27[21]		*	
Anthaenantia							
A. rufa (Ell.) Schult.				−12[21]			*[11]
[a]Anthephora							
A. cristata Hack. ex Wildem. and Th. Dur.	+16						*[10,11]
A. elongata Wildem.				−10[21]			*[11]
A. hermaphrodita O. Ktz							
(A. elegans Schreb.)[b]				−11[21]			*
A. pubescens Nees		L[17,18]		−12[21]			*[10,11]
Axonopus							
A. affinis Chase				−11[21]			*[11]
A. compressus (Swartz) Beauv.		L[22]					*[10]
Brachiaria							
B. erucaeformis (J.E. Smith) Griseb.		L[18]					*
B. laeta (Mez) A. Camus		L[18]					*
B. platyphylla (Griseb.) Nash				−13[21]			*[6]
(Paspalum platyphyllum (Griseb.)[b]		L[18]					*[11]
B. ramosa Stapf		L[18]					*
Cenchrus							
C. biflorus Roxb.		L[18]					*
C. calycalatus Cav.				−12[23]			*
C. ciliaris L.		L[18]		−12[21]			*[10,11,6]
C. echinatus L.		L[7]					*[10]
C. incertus M.A. Curtis				−12[21]			*[11]
C. myosuroides H.B.K.	+16	L[18]					*[10,11]
C. pauciflorus Benth.		L[18]					*
C. pilosus H.B.K.		L[18]					*
C. setigerus Vahl.		L[18]					*
Dichanthelium[c]							
(Panicum)[b]							
D. ciliatum Ell.				−26[21]		*	
D. clandestinum (L.) Gould		H5[17,18]		<−22[2,21]		*	
D. commutatum (Schult.) Gould		H[5]		−26[21]		*	
D. depauperatum (Muhl.) Gould				−25[21]		*	
D. lancearium Trin.				−27[21]		*	
D. lanuginosum (Ell.) Gould				−26[2]		*	
D. latifolium L.				−25[21]		*	
D. leibergii (Vasey) Scribn.				−26[1]		*	
D. lindheimeri (Nash) Gould		H[5]				*	
D. linearifolium (Scribn.) Gould				−26[21]			
D. meridionale Ashe.				−24[21]		*	
D. microcarpon Muhl. ex Ell.				−27[21]		*	
D. nodatum (Hitchc. and Chase) Gould				−28[2]		*	
D. oligosanthes (Schult.) Gould		H[17,18,19]				*	
D. pacificum Hitchc. and Chase	−[22]	H[18,22]		<−22[1,21]	0[22]		
D. praecocius Hitch. and Chase		H[17,18,19]				*	
D. scribnerianum (Nash) Fern.				−32[1]		*	
D. sphaerocarpon (Ell.) Gould				−28[2]		*	
D. webberianum Nash				−26[21]		*	
D. xalapense H.B.K.				−27[21]		*	
Digitaria							
D. adscendens (H.B.K.) Henrard				−12[21]			*[11]
D. argyrograpta Stapf		L[18]	0[8]				*[10,11]
D. biocornis R. and S. ex Loud.		L[18]					*
D. brownei Hughes		L[18]					*
D. californica (Benth.) Henr.							*[10]
(Trichachne californica (Benth.) Chase[b]		L[7,18]		−11[21]			*
D. decumbens Stent.							*[10,11]
D. diagonalis Stapf		L[18]					*
D. eriantha Steud.		L[18]					*
D. eriostachya Mez.		L[18]					*
D. gazensis Rendle		L[18]					*
D. glauca Stent.		L[18]					*
D. horizontalis Willd.		L[18]					*
D. iburua Stapf		L[18]					*
D. insularis (L.) Mez ex Ekmann							
(Trichachne insularis (L.) Nees)[b]		L[7]					*
D. ischaemum (Schreb.) Schreb. ex Muhl.		L[18]					*
D. kilimandscharica Mez.		L[18]					*

Table 1 continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4^{cpd} (%)	C_3	C_4
D. milanjiana Stapf		L[18]					*
D. pentzii Stent.		L[7,18]					*[10,11]
D. phaeothrix Parodi		L[18]					*
D. sanguinalis (L.) Scop.		L[5,12,18]		−15[23]			*[10,11,6]
D. seriata Stapf		L[18]					*
D. smutsii Stent.		L[18]	−1[8]				*[10,11]
D. swazilandensis Stent.		L[18]					*
D. valida Stent.		L[18]					*
Echinochloa							
E. colonum (L.) Link		L[4]					*[10,6,11]
E. crusgalli (L.) Beauv		L[5,7,12,13,18]		>-20[1,21,23]			*[10,6,11]
E. frumentacea (Roxb.) W.F. Wight		L[18]		−15[23]			*
E. haploclada Stapf		L[18]					*
E. holubii Stapf		L[18]					*
E. pyramidalis Hitchc. and Chase		L[18]					*
E. spiralis Vasinger		L[18]					*
E. stagnina Beauv.		L[5]	−3[5,8]				*[10]
Eriochloa							
E. lemmoni Vasey and Scribn. (E. gracilis (Fourn) Hitchc.)[b]							*[11,6]
E. michauxii (Poir) Hitchc. (Panicum molle Michx.)[b]		L[18]					*
[a]Isachne							
I. globosa Kuntze				−28[23]		*	
Leptoloma							
L. cognatum (Schult.) Chase				>−20[2,21]			*[11]
[a]Melinis							
M. minutiflora Beauv.			0[8]	−13[21]			*[10,11]
[a]Oplismenus							
O. burmanni (Retz.) Beauv.				−28[21]		*	
O. hirtellus (L.) Beauv.				−31[21]		*	
O. undulatifolius Beauv. (O. imbecillus Roem. and Schult.)[b]				−27[23]		*	
Panicum							
P. bisulcatum Thunb.		H[17,18,19]				*[6]	
P. gymnocarpon Ell.				−29[21]		*	
P. hemitomon Schult.		H[18]		−25[21]		*	
P. hians Ell.				−26[21]		*	
P. trichanthum Nees		H[18]				*	
P. verrucosum Muhl.				−26[21]		*	
P. wilcoxianum Vasey		H[17,18]		−26[21]		*	
P. amarulum Hitchc. and Chase		L[18]		−13[1]		*	*[11]
P. anceps Michx.		L[17,18,19]		−12[21]			*[11]
P. antidotale Retz.		L[17,18,19]		−14[21]	84[9]		*[10,11]
P. bergii Arech.		L[18]					*[11,6]
P. bulbosum H.B.K.		L[5]			87[9]		*[10',11]
P. capillare L.	+[12,22]	L[5,7,12,17,18,19,22]		−14[21]	89[9]		*[10,11,6]
P. coloratum Cav. (Walt.)		L[17,18,19]		−12[23]			*[10,11]
P. cymbiforme D.K. Hughes		L[17,18]					*[11,6]
P. decompositum R. Br.		L[17,18]					*[11,6]
P. deustum Thunb.		L[17,18]					*[11]
P. dichotomiflorum Michx.		L[17,18,19]		>20[1,21]			*[10,11]
P. effusum R. Br.		L[18]					*
P. filipes Scribn.	+[16]						*[10,11]
P. geminatum Forsk.				−11[21]			*[11]
P. hallii Vasey		L[17,18,19]		−13[21]	93[9]		*[10,11]
P. havardii Vasey		L[18]			96[9]		*
P. laevifolium Hack.		L[17,18,19]			97[9]		*[10,11]
P. lanipes Mez.		L[18]					*
P. larcomianum D.K. Hughes		L[18]					*
P. longijubatum Stapf		L[18]					*
P. makarikariense (Van Rensb.) Gooss		L[17,18]					*[11]
P. maximum Jacq.		L[7,17,18,19]		−13[21]	99[9]		*[10,11,6]
P. miliaceum L.		L[5,12,17,18,19]			96[9]		*[10,11,6]
P. milioides Nees ex Trin.	−[14]	L[18]				*[6]	*[10]
P. obtusum H.B.K.		L[17,18,19]		−13[21]	90[9]		*[10,11]
P. philadelphicum Bernh. ex Trin.							*[10,11]
(P. minus Nash)[b]		L[17,18,19]			93[9]		*[10,11]
P. plenum Hitchc. and Chase		L[17,18,19]		−12[21]	85[9]		
P. polygonatum Schrad.		L[17,18]					*[10,11]
P. prolutum F. Muell.		L[17,18,19]			93[9]		*[10,11]

Table 1 continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
P. purpurascens Raddi				—11[21]			*[11]
P. queenslandicum Domin.		L[18]					*
P. reptans. L.				−11[21]			*[11]
P. stapfianum Fourc.		L[18]					*[10,11]
P. tenerum Beyr.				−11[21]			*[11]
P. texanum Buckl.		L[17,18]			97[9]		*[10,11,6]
P. trachyrahachis Benth.		L[18]					*
P. turgidum Forsk.		L[17,18,19]			94[9]		*[10,11,6]
P. urvilleanum Kunth				−12[21]			*[11]
P. virgatum L.		L[7,17,18,19]		>−20[1,21]	97[9]		*[10,11]
P. whitei J.M. Black		L[18]					*
Paspalidium							
P. geminiflorum Steud. (Paspalum geminiflorum Steud.)[b]		L[18]					*
Paspalum							
P. almum Chase		L[18]					*
P. boscianum Fluegge		L[18]					*
P. brunneum Mez.		L[18]					*
P. ciliatifolium Michx.		L[18]					*
P. conjugatum Bergius		L[18]					*[11]
P. dilatatum Poir.		L[7,12,18]		−13[23]	66[15]		*[10,11]
P. distichum L.	+[4]	L[5,12,18]	−8[4]	−14[23]			*[10,11]
P. hartwegianum Fourn.	+[16]						*[10,11]
P. intermedium Munro ex Morong		L[18]					*
P. juegensii Hack.		L[18]					*
P. mandiocanum Trin.		L[18]					*
P. nicorae Parodi		L[18]					*
P. notatum Fluegge		L[5,7,18]	+2[5,8]	−12[23]			*[10,11,6]
P. paniculatum L.		L[18]					*
P. paspaliodes Scribn.				−13[23]			*
P. paucispicatum Vasey		L[18]					*
P. plicatulum Michx.		L[18]					*
P. polystachyum Kuntze		L[18]					*
P. pubiflorum Rupr. ex Fourn.		L[18]		−13[21]			*[11]
P. pumilum Nees		L[18]		−12[23]			*
P. quadrifarium Lam.		L[18]					*
P. rojasii Hack.		L[18]					*
P. scrobiculatum L.		L[18]					*
P. umbrosum Trin.		L[18]					*
P. urvillei Steud.		L[18]		−11[21]			*[11]
P. virgatum L.		L[18]					*
P. yaguaronense Henr.		L[18]					*
[a]Pennisetum							
P. ciliare (L.) Link		L[18]		−11[21]			*[11]
P. flaccidum Griseb. in Goett.		L[18]					*
P. glaucum (L.) R. Br.		L[12,18]	−3[8]				*[10,11]
P. macrourum Trin.		L[18]		−12[23]			*
P. massaicum Stapf		L[18]					*
P. orientale Rich.		L[18]					*
P. pedicellatum Trin.		L[18]	0[8]				*[10,11]
P. polystachyum Schult.		L[18]					*
P. purpureum Schum.		L[7]					*[10,7,11]
P. spicatum R. & S.		L[18]					*
P. typhoideum Rich.		L[18]					*
Reimarochloa							
R. acuta Hitchc.				−12[21]			*[11]
[a]Rhynchelytrum							
R. repends (Willd.) C.F. Hubbard (R. roseum (Nees) Stapf and Hubb.)[b]				−13[21]			*[11]
Sacciolepis							
S. striata (L.) Nash				−27[21]		*	
Setaria							
S. adhaerens (Forsk.) Chiov.		L[18]					*
S. almaspicata de Wit.		L[18]					*
S. argentina Herrm.		L[18]					*
S. faberri Herrm		L[18]					*[11]
S. firmulum Hitchc. and Chase (Panicum firmulum Hitchc. and Chase)[b]		L[18]					*
S. glauca (L.) Beauv.		L[5,13,18]					*[11]
S. holstii Herrm.		L[18]					*
S. italica (L.) Beauv.		L[7,12,18]	0[8]	−14[23]			*[10,6]

Table 1 continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
S. lutescens (Weigel) Hubb.	+[12]	L[12,18]					*[10,11,6]
S. neglecta de Wit.		L[18]					*
S. pallidifusca Stapf and C.E. Hubb.		L[18]					*
S. palmifolia (Koen.) Stapf		L[18]					*
S. phanerococca Stapf		L[18]					*
S. reverchoni Vasey				−12[21]			*
(Panicum reverchoni Vasey)[b]		L[17,18]					*[11]
S. scheelei (Steud.) Hitchc.				−13[21]			*
S. sphacelata (Schum.) Stapf and C.E. Hubb.		L[18]	0[8]	−14[23]			*[10,11,6]
S. verticillata (L.) Beauv.		L[18]					*
S. viridis (L.) Beauv.		L[7,18]		−13[23]			*[10,11]
Stenotaphrum							
S. secundatum (Walt.) Kuntze				−16[20,21]			*[11,6]
Subfamily: Pooideae							
TRIBE: Aveneae							
Agrostis							
A. alba L.		H[5,12,18]	+42[8]	−28[2]		*	
A. castellana Boiss and Reut.			+45[8]			*	
A. hiemalis (Walt.) B.S.P.		H[18]		−28[21]		*	
A. perennans (Walt.) Tuckerm.				−30[1]		*	
S. scabra Willd.				−29[1]		*	
A. tenuis (Sibth.)				−28[21]		*	
Alopecurus							
A. pratensis L.		H[18]		<−22[2,23]		*	
Ammophila							
A. breviligulata Fern.				−28[1]		*	
[a]Anthoxanthum							
A. odoratum L.		H[12]		−28[21]		*	
[a]Arrhenatherum							
A. elatius (L.) Presl		H[12,18]		<−22[2,23]		*	
[a]Avena							
A. abyssinica Hochst. ex A. Rich		H[18]				*	
A. alba Vahl.			+50[8]			*	
A. barbata Brot.		H[18]				*	
A. clauda Dur. in Duch.		H[18]				*	
A. fatua L.		H[18]				*	
A. longiglumis Dur. in Duch.		H[18]				*	
A. pilosa Bieb.		H[18]				*	
A. sativa L.		H[5,12,18]		−24[21]	2[15]	*	
A. semipervirens Will.			+51[8]			*	
A. sterilis L.		H[18]				*	
A. strigosa Schreb.		H[18]				*	
A. ventricosa Balansa		H[18]				*	
Beckmannia							
B. syzigachne (Steud.) Fernald.		H[12]		−25[21]		*	
Calamagrostis							
C. canadensis (Michx.) Beauv.		H[18]		<−22[2,21]		*	
Cinna							
C. latifolia (Trevir.) Griseb.		H[12]		−25[21]		*	
Deschampsia							
D. caespitosa (L.) Beauv.		H[18]				*	
D. chapmani Petrie				−27[23]		*	
D. flexuosa (L.) Trin.				−24[21]		*	
Helictotrichon							
H. hookeri (Scribn.) Henr.		H[18]				*	
Hierochloe							
H. odarata (L.) Beauv.				−23[21]		*	
H. redolens Roem. and Schult.				−29[23]		*	
[a]Holcus							
H. lanatus L.				−31[23]		*	
Koeleria							
K. cristata (L.) Pers.		H[18]				*	
K. phleoides (Vill.) Pers.		H[18]				*	
K. setacea D.C.		H[18]				*	
K. valesiaca Gaud.		H[18]				*	
Limnodea							
L. arkansana (Nutt.) L.H. Dewey				−28[21]		*	
Milium							
M. effusum L.				<−22[21,23]		*	

Table 1 continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
Phalaris							
P. californica Hook and Arn.							
(P. amethystina Trin.)			+60[8]			*	
P. arundinacea L.		H[5,7,12,18]	+45[5,8]	<−22[2,21]		*	
P. brachystachys Link				−25[21]		*	
P. canariensis L.		H[7]		<−22[23,21]		*	
P. minor Retz.				−28[23]			
P. tuberosa L.			+39[8]			*	
Phleum							
P. alpinum L.			+40[8]			*	
P. nodosum L.			+45[8]			*	
P. phleoides Simenkai				−30[23]		*	
P. pratense L.		H[18]		−27[2]		*	
Polypogon							
P. monspeliensis (L.) Desf.				−28[23]		*	
Sphenopholis							
S. obtusata (Michx.) Scribn.				−29[21]		*	
Trisetum							
T. flavescens (L.) Beauv.		H[18]				*	
TRIBE: Brachyelytreae							
Brachyelytrum							
B. erectum (Schreb.) Beauv.				−27[21]		*	
TRIBE: Diarrheneae							
Diarrhena							
D. americana Beauv.				−30[21]		*	
TRIBE: Meliceae							
Glyceria							
G. grandis S. Wats.				−24[21]		*	
G. striata (Lam.) Hitchc.				−25[21]		*	
Melica						*	
M. altissima L.				−28[23]		*	
M. mutica Walt.		H[7]		−26[21]		*	
Schizachne				−28[21]		*	
S. purpurascens (Torr.) Swallen							
TRIBE: Monermeae							
[a]Parapholis							
P. incurva (L.) C.E. Hubb.				−26[21]		*	
P. pannonica Kunth				−25[21]		*	
TRIBE: Nardeae							
[a]Nardus							
N. stricta L.				−26[21]		*	
TRIBE: Poeae							
[a]Brachypodium							
B. phoenicoides Roem. and Schult.				−26[23]		*	
[a]Briza							
B. maxima L.				−29[23]		*	
B. minor L.				−30[23]		*	
B. rotundata Steud.				−27[21]		*	
Bromus							
B. albidus M.B.							
(B. biebersteinii R. and S.)[b]		H[18]				*	
B. coloratus Steud.			+40[8]			*	
B. commutatus Schrad.				−28[21]		*	
B. diandrus Roth.							
(B. rigidus Roth.)[b]		H[18]				*	
B. hankeanus (Presl) Kunth			+49[8]			*	
B. inermis Leyss.		H[12,18]		<22[2,21]		*	
B. kalmii A. Gray				−30[1]		*	
B. purgans L.				−25[21]		*	
B. tectorum L.		H[12,18]		<−22[23]		*	
B. unioloides (Willd.) H.B.K.							
(B. catharticus Vahl.)[b]		H[18]		<−22[1,23]		*	
[a]Dactylis							
D. aschersoniana Graebn.			+25[8]			*	
D. glomerata L.	+[14]	H[5,12,18]	+46[5,8]	<−22[2,21]		*[6]	
Festuca							
F. ampla Hack			+53[8]			*	

Table 1 continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
F. arundinacea Schreb.		H[7]		<−22[2,23]		*[6]	
F. pratensis Huds.						*	
(F. elatior C.)[b]		H[12,18]		−29[2]		*	
F. rubra L.				−27[1,2]		*	
[a]Lolium							
L. gaudinii Parl.			+49[8]			*	
L. multiflorum Lam.		H[7,18]	+50[5,8]			*	
L. perenne L.		H[18]		−29[2]		*	
L. persicum Boiss. and Hohen.		H[18]				*	
L. rigidum Gaud.		H[18]				*	
L. strictum Presl		H[18]				*	
L. temulentum L.		H[18]				*	
[a]Lamarckia							
L. aurea (L.) Moench				−30[23]		*	
Poa							
P. ampla Merr.			+40[8]			*	
P. annua L.		H[18]				*	
P. compressa L.		H[12]		−22[2,21]		*	
P. pratensis L.		H[18]	+37[5,8]	−27[2]		*	
P. trivialis L.		H[18]				*	
P. secunda Presl				−28[20,21]		*	
Puccinellia							
P. distans (L.) Pal.				−28[23]		*	
Vulpia							
V. myuros (L.) K.C. Gremlin							
(F. megalura Nutt.)[b]		H[18]				*	
TRIBE: Stipeae							
Oryzopsis							
O. hol iformis (MB) Rich.			+45[8]			*	
O. hymenoides (Roem. and Schult.) Ricker				−28[1]		*	
O. miliacea (L.) Benth. and Hook. ex Aschers. and Schweinf.				−30[23]		*	
O. racemosa (J.E. Smith) Ricker		H[12]				*	
Stipa							
S. columbiana Macoun				−24[20,21]		*	
S. comata Trin. and Rupr.				−25[1]		*	
S. leucotricha Trin. and Rupr.				−27[21]		*	
S. nitida Spraque and Summerh.			+40[8]			*	
S. robusta (Vasey) Scribn.				−25[21]			
S. Spartea Trin.				−28[1]			
S. tenuissima Trin.				−25[21]		*	
S. viridula Trin.				−27[2]		*	
TRIBE: Triticeae							
[a]Aegilops							
A. bicornis Jakub et. Sp.		H[13]				*	
A. biuncinalis Vis.		H[13]				*	
A. caudata L.		H[13,18]				*	
A. columnaris Zhukov		H[13,18]				*	
A. comosa Sibth. et. Sm.		H[13]				*	
A. crassa Boiss		H[13,18]				*	
A. cylindrica Host.		H[13,18]	+42[8]			*	
A. heldreichii Holzm.		H[18]				*	
A. ligustica (Savign.) Coss		H[18]				*	
A. longissima Schw. et. Musch.		H[13]				*	
A. ovata L.		H[13]				*	
A. perigrina (Hack.) Eig.			+40[8]			*	
A. sharonensis Eig.		H[13]				*	
A. speltoides Tausch		H[18]				*	
A. squarrosa L.		H[13,18]		−34[23]		*	
A. triaristata Willd.		H[13,18]				*	
A. triuncialis L.		H[13,18]				*	
A. umbellulata Zhukov.		H[13,18]				*	
A. uniaristata Vis.		H[13]				*	
A. variabilis Eig.		H[13]				*	
A. ventricosa Tausch		H[13]				*	
Agropyron							
A. glaucum R. and S.		H[18]				*	
A. inerme (Scribn. and Smith) Rydb.		H[18]				*	
A. intermedium (Host) Beauv.		H[18]		<−22[1,21,23]		*	
A. junceum (L.) Beauv.		H[18]				*	
A. kosanini Nabelek		H[18]				*	
A. latiglume (Scribn. and Smith) Rydb.		H[18]				*	
A. leptourum (Nevski) Grossheim		H[18]				*	

Table 1 (continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
A. littorale Dum.		H[18]				*	
A. loliodes (Karel. and Kir.)		H[18]				*	
A. obtusiusculum Lange P. Candargy		H[18]				*	
A. orientale R. and S.		H[18]				*	
A. panormitanum Parl. ex Boiss.		H[18]					
A. pectiniforme R. and S.		H[18]				*	
A. pseudorepens Scribn. and Smith		H[18]				*	
A. pungens (Pers.) R. and S.		H[18]				*	
A. repens (L.) Beauv.		H[8]		<−22[2,21]		*	
A. rigidum Beauv.		H[18]				*	
A. scabriglume (Hack.) Parodi		H[18]				*	
A. semicostatum (Steud.) Ness ex Boiss		H[18]				*	
A. sibiricum (Willd.) Beauv.		H[18,24]		−28[2]		*	
A. Smithii		H[18,24]		−28[2]		*	
A. spicatum (Pursh) Scribn. and Smith		H[18]		−27[21]		*	
A. striatum (Steud.) P. Candargy		H[18]				*	
A. subulatum R. and S.		H[18]				*	
A. tenerum Vasey		H[18]				*	
A. trachycaulum (Link) Steud.				−28[2]		*	
A. trichophorum (Link) Richt.		H[18]				*	
A. violaceum Vasey		H[18]				*	
Elymus							
E. agropyroides Presl		H[18]				*	
E. angustus Trin. ex Ledeb.		H[18]				*	
E. antarcticus Hook.		H[18]				*	
E. arenarius L.		H[18]				*	
E. canadensis L.		H[18]		−27[2]		*	
E. carolinianus Walt.		H[18]				*	
E. cinereus Scribn. and Merr.		H[18]				*	
E. crinitus Schreb.		H[18]				*	
E. dahuricus Turcz.		H[18]				*	
E. glaucus Buckl.		H[18]				*	
E. innovatus Beal		H[18]				*	
E. junceus Fisch.		H[18]		−26[2]		*	
E. mollis Trin.	−[4]		7+[8,4]	−28[1]		*	
E. paboanus Claus		H[18]				*	
E. virginicus L.		H[18]		−27[21]		*	
Hordeum							
H. bogdani Wilensky		H[18]				*	
H. brevisubulatum Link		H[18]				*	
H. bulbosum L.		H[18]	+47[8]			*	
H. chilense Roem. and Schult.			+34[8]			*	
H. comosum Presl		H[18]				*	
H. compressum Griseb.		H[18]				*	
H. hystrix Roth.		H[18]				*	
H. jubatum L.		H[18]		−29[2]		*	
H. marinum Huds.		H[18]				*	
H. pusillum Nutt.				−27[21]		*	
H. spontaneum Koch		H[18]				*	
H. stebbinsii Covas		H[18]				*	
H. vulgare L.		H[5,12,13,18]				*	
[a]Secale							
S. ancestrale Zhuk.			+48[8]			*	
S. cereale L.		H[18]	+37[8]			*	
S. montanum Guss.		H[18]				*	
S. vavilovii Grossheim		H[18]				*	
Sitanion							
S. hystrix (Nutt.) J.G. Smith							
[a]Triticum							
T. aestivum L.	−[22]	H[5,22,3,18,13]	+23[8], +50[5]	<−22[20,22,23]		*[6]	
(T. sativum Lam.)[b]		H[12]			0[15]	*	
(T. vulgare Vill.)[b]		H[18]				*	
T. baeoticum Boiss. et. Schiem.		H[13]				*	
T. compactum Host.		H[13]				*	
T. dicoccoides Korn.		H[13]				*	
T. dicoccum Schrank		H[18]				*	
T. durum Desf.		H[18]	+50[8]			*	
T. monococcum L.		H[18,13]				*	
T. persicum Vav.		H[13]				*	
T. polonicum L.		H[13]				*	
T. spelta L.		H[13]				*	
T. sphaerococcum Perc.		H[13]				*	
T. timopheevi Zhukov		H[13]				*	

Table 1 continued

Species	BS	CO_2	NE	$^{13}C°/oo$	C_4cpd (%)	C_3	C_4
T. turanicum Jakubz.		H[13]				*	
T. turgidum L.		H[13]				*	
T. vavilovii Tuman		H[13]				*	

[a]= genera represented by introduced or adventive species only
[b]= indicates synonym of preceding taxa
[c]=Recent interpretations have elevated the subgenus *Dichanthelium* to the generic level. This change was made for all species in the *Dichanthelium* subgenus, regardless of the publication of a current authority.

[1]Bender (1971)
[2]Bender and Smith (1973)
[3]Bisalputra et al. (1969)
[4]Bjorkman and Gauhl (1969)
[5]Black et al. (1969)
[6]Brown and Gracen (1972)
[7]Chen et al. (1970)
[8]Downes and Hesketh (1968)
[9]Downton (1970)
[10]Downton (1971)
[11]Downton (1975)
[12]Downton and Tregunna (1968)
[13]Dvorak and Natr (1971)
[14]Gracen et al. (1972)
[15]Hatch et al. (1967)
[16]Johnson (1964)
[17]Krenzer and Moss (1969)
[18]Krenzer et al. (1975)
[19]Moss et al. (1969)
[20]Smith and Epstein (1971)
[21]Smith and Brown (1973)
[22]Tregunna et al. (1970)
[23]Troughton et al. (1974)
[24]Williams and Markley (1973)

Caswell et al. (1973) proposed that C_4 plants are generally inferior food sources for herbivores, primarily insects, and are often avoided by them relative to C_3 plants. Caswell and Reed (1975) determined that the grasshopper (*Melanoplus confusus*) was capable of digesting C_3 grass material, but was unable to totally digest the thick-walled bundle sheath cells of C_4 grasses. Further research with 10 species of grasshoppers indicated that the large quantities of nutritional material in the bundle sheath cell of C_4 plants was at least partially unavailable (Caswell and Reed 1976). Plants with the C_4 photosynthetic pathway are also generally lower in total digestible nutrients for cattle and sheep than C_3 plants at the same stage of maturity (Crampton and Harris 1969). Akin and Burdick (1977) reported that the large amount of potential nutrients in the parenchyma bundle sheath of selected warm-season (C_4) grasses may not be readily available because of slow degradation of the sheath cell wall by rumen bacteria. They hypothesized that the "sheath barrier" to utilization of starch and other nutrients in these cells may be a factor responsible for the lower nutritive value to ruminants of some warm-season grasses compared to cool-season (C_3) species. However, many factors interact to determine both herbivore preference and digestibility (Stoddart et al. 1975). Rogler (1944) reported that warm-season grasses were, in general, more highly relished by steers than cool-season grasses. Tomanek et al. (1958) determined that big bluestem (C_4) (*Andropogon gerardii*) and little bluestem (C_4) (*Schizachyrium scoparium*) had a significant positive preference by grazing cattle wherever they occurred, while preference for western wheatgrass (C_3) (*Agropyron smithii*) varied with site. This indicates that a generalization concerning lower palatability of C_4 species compared to C_3 may not apply to all herbivores.

Table 2. A summary of C_3 and C_4 photosynthetic pathway in the United States. Taxonomic classification follows that of Gould (1968).

Subfamily	Tribe	Number: Genera	Number: Species	C_3	C_4
Arundinoideae	Arundineae	4	5	*[1]	
	Centotheceae	1	1	*	
	Danthonieae	2	4	*	
Bambusoideae	Bambuseae	3	5	*	
	Phareae	1	1	*	
Eragrostoideae	Aeluropodeae	2	3		*
	Aristideae	1	7		*
	Chlorideae	13	49		*
	Eragrosteae	9	72		*
	Orcuttieae	2	2		*
	Pappophoreae	1	1		*
	Zoysieae	1	3		*
	Unioleae	1	1	*	
Oryzoideae	Oryzeae	7	10	*	
Panicoideae	Andropogoneae	20	73		*
	Paniceae	23	189	*	*
Pooideae	Aveneae	21	51	*	
	Brachyelytreae	1	1	*	
	Diarrheneae	1	1	*	
	Meliceae	3	5	*	
	Monermeae	1	2	*	
	Nardeae	1	1	*	
	Poeae	10	36	*	
	Stipeae	2	12	*	
	Triticeae	7	97	*	
		138	632		

[1]* indicates presence of either C_3 or C_4 photosynthetic pathway.

Significance of the Photosynthetic Pathway for Range

Knowledge of the photosynthetic pathway is an important tool in plant classification and will be useful to plant breeders in developing improved species and varieties of forage (Downton and Tregunna 1968). However, the greatest value of this knowledge in range management will be the better understanding of the reasons for the patterning of range vegetation along environmental gradients, including those produced by man. Better understanding of the structure and function of range ecosystems should lead to wiser management decisions for optimum utilization of the most extensive of our terrestrial ecosystems.

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