



Occurrence of C3 and C4 Photosynthetic Pathways in North American Grasses

Item Type	text; Article
Authors	Waller, S. S.; Lewis, J. K.
Citation	Waller, S. S., & Lewis, J. K. (1979). Occurrence of C3 and C4 photosynthetic pathways in North American grasses. <i>Journal of Range Management</i> , 32(1), 12-28.
DOI	10.2307/3897378
Publisher	Society for Range Management
Journal	Journal of Range Management
Rights	Copyright © Society for Range Management.
Download date	24/08/2022 10:05:14
Item License	http://rightsstatements.org/vocab/InC/1.0/
Version	Final published version
Link to Item	http://hdl.handle.net/10150/646540

Occurrence of C₃ and C₄ Photosynthetic Pathways in North American Grasses

S.S. WALLER AND J.K. LEWIS

Abstract

A literature survey was made for the occurrence of C₃ and C₄ photosynthetic pathways in the United States Gramineae. Distinctive characteristics of the two photosynthetic pathways are discussed. Leaf anatomy, CO₂ compensation point, net enhancement of photosynthesis in oxygen-deficient atmosphere, ¹³C 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 C₃ pathways. All tribes within the Eragrostoideae have C₄ 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 C₄ pathways. The subgenus *Dichanthelium* within *Panicum* is C₃ while the *Eupanicum* subgenus contains plants with both C₃ and C₄ photosynthetic pathways.

Plant productivity is dependent on several environmental and biological factors. The most important single factor is photosynthesis. A pathway for carbon dioxide (CO₂) fixation was described by Calvin and Bassham (1962) in which CO₂ 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 (C₃, reductive pentose pathway) was considered the major photosynthetic mechanism for carbon (C) fixation. However, Hatch and Slack (1966) described CO₂ fixation in which labeled CO₂ 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 C₄-dicarboxylic acids in mesophyll cells and subsequent incorporation into the Calvin cycle located in the bundle sheath cells. Plants (C₄ plants) possessing the 4-carbon pathway (also called C₄, dicarboxylic acid, Kranz type, low CO₂ 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 (C₃ plants), especially in relatively sunny, warm, dry climates (Black 1971).

Distinctive characteristics associated with the C₄ pathway prompted intensive research in photosynthetic processes of flowering plants. The most important photosynthetic pathways

are the C₃ and C₄; however, a crassulacean acid pathway (CAM) has been reported in some succulents (Ranson and Thomas 1961; Ting 1971).

The first listing of C₄ plants was prepared in 1970 (Downton 1971). By 1974, the C₄ 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 C₄ 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 CO₂ assimilation, resulting in increased foliage extension and size. Other factors being equal, plants with higher apparent photosynthetic rates (C₄ plants: species having the C₄ pathway, Calvin pathway and Kranz anatomy) have a competitive advantage over those with lower rates (C₃ 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 C₄ photosynthetic pathway are very different from C₃ plants in a variety of characteristics (Black 1971). The net photosynthetic rate is two- to threefold greater; CO₂ compensation points are lower; photosynthesis is not suppressed by oxygen concentration between 1 and 100%; CO₂ is not evolved during illumination; bundle sheath cells contain chloroplasts and starch; discrimination against ¹³C compounds is lower; and CO₂ fixation initially yields 4-C acids as opposed to 3-C acids found in the C₃ 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 ¹⁴C is the only direct method for photosynthetic pathway determination. Hatch et al. (1967) reported that in C₄ 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.

This report was approved for publication by the Director, Agricultural Experiment Station, South Dakota State University, Brookings, as Journal Series No. 1533.

The authors extend appreciation to Dr. D. Kenefick and Dr. C. Chen, South Dakota State University, for their helpful suggestions in manuscript preparation. We also appreciated the aid of Dr. S. Hatch, New Mexico State University, in reviewing the taxonomic classification. We would also like to thank Mrs. Susanne Gardner for typing the manuscript.

Manuscript received January 10, 1978.

exposure to $^{14}\text{CO}_2$ for approximately 1 second. In contrast, early products of the C₃ process were 3-PGA and hexose phosphates.

CO₂ Compensation and Photorespiration

Carbon dioxide compensation point (the point at which photosynthetic CO₂ uptake equals respiratory CO₂ evolution when measured in a closed chamber) is an easily obtainable characteristic. During photosynthesis a light-induced release of CO₂ can occur and is referred to as photorespiration as contrasted to CO₂ released by mitochondria or dark respiration. Plants with the C₄ pathway have a photosynthetic CO₂ 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 C₄ plants. However, since the mesophyll layer surrounds the bundle sheath, the C₄ pathway would rapidly refix any photorespiratory CO₂ and prevent leakage to the atmosphere (Bowes and Ogren 1972). A much higher CO₂ compensation point (37-70 ppm) is characteristic of C₃ plants (Black 1971). Carbon dioxide compensation points provide a convenient means of identifying the type of photosynthetic pathway. The low CO₂ compensation point of C₄ plants indicates an ability to utilize more external CO₂ as compared to C₃ plants.

Oxygen Suppression

Oxygen differentially affects CO₂ exchange in C₃ and C₄ plant species, primarily because of differences in photorespiration. In soybean (*Glycine max*), and probably other C₃ species as well, the total O₂ inhibition consists of two discernible effects. Oxygen substitutes for CO₂ in the carboxylase reaction to yield P-glycolate, a C₃ photorespiratory intermediate. As a result of this substitution, O₂ competitively inhibits the carboxylase with respect to CO₂ (Ogren 1976). During photorespiration glycolate is oxidized, releasing CO₂. Consequently, oxygen depletion will reduce glycolate oxidation thereby increasing photosynthetic CO₂ assimilation by 40 to 50% in species possessing the C₃ pathway, while having no effect on C₄ plants (Downes and Hesketh 1968). The refixation of photorespiratory CO₂ allows C₄ plants to utilize all of the fixed CO₂, thus increasing photosynthetic efficiency.

Chollet (1976) postulated that the enzyme complement of the C₄ pathway increased CO₂ concentration at the site of the C₃ carboxylase, reducing the competitive inhibition of O₂ and minimizing photorespiration. The CO₂ concentration at the site of the C₃ carboxylase coupled with a specialized leaf anatomy, allowing recapture of photorespiratory CO₂, was apparently responsible for the lack of photorespiration and absence of the inhibitory effect of 21% O₂ on net photosynthesis in C₄ plants.

Leaf Anatomy

Leaf anatomy provides an easily distinguished difference between C₃ and C₄ plants. Plants with the C₃ 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 C₄ photosynthetic pathway generally have well-developed parenchymatic bundle sheaths containing high concentrations of chloroplasts and starch. Bundle sheath cells utilize the C₃ photosynthetic process; however, they are surrounded by mesophyll cells containing chloroplasts utilizing the C₄ photosynthetic process which

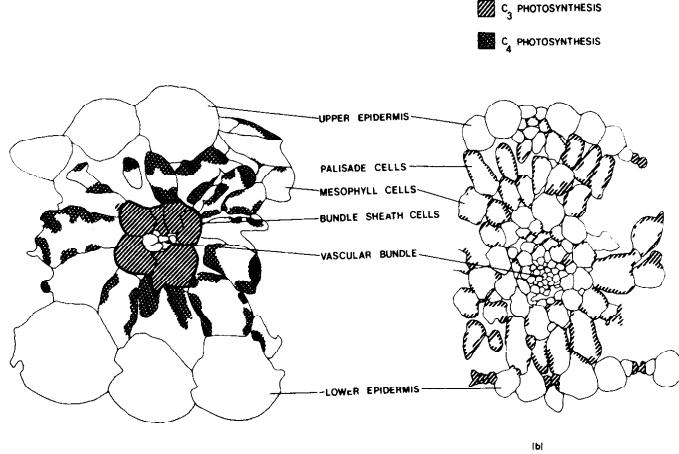


Fig. 1. Comparison of leaf anatomy between plants having C₄ photosynthesis (a) and C₃ photosynthesis (b). The C₄ plant exhibits prominent bundle sheath cells and concentrated photosynthetic activity near the vascular bundles (Adopted from Black 1971).

fix and then supply CO₂ for the C₃ pathway.

The unique leaf anatomy (Kranz type) of C₄ plants provides several advantages for efficient CO₂ fixation. Surrounding the C₃ bundle sheath cells with C₄ mesophyll cells minimizes the loss of CO₂ from C₃ photorespiration. The presence of two active photosynthetic carboxylases and their associated enzymes in the same leaf of a C₄ plant appears to result in a higher affinity for and more rapid uptake of CO₂. The close proximity of starch formation to the vascular bundles should make photosynthate translocation more efficient.

Carbon Isotope Discrimination

Carbon isotope ratio ($^{13}\text{C}/^{12}\text{C}$) determination in plant tissue is characteristically less than the carbon isotope ratio of atmospheric CO₂, 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 $^{13}\text{C}/^{12}\text{C}$ ratio of the sample relative to a standard and reported as $^{13}\text{C}^{\circ}/\text{oo}$ (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 $^{13}\text{C}^{\circ}/\text{oo}$ values (-24 to -34 $^{\circ}/\text{oo}$) and those with high values (-6 to -19 $^{\circ}/\text{oo}$) (Smith and Epstein 1971). Grasses relatively enriched in ^{13}C have $^{13}\text{C}^{\circ}/\text{oo}$ values in the -6 to -19 $^{\circ}/\text{oo}$ range and are reported to be C₄ while those with relatively low $^{13}\text{C}^{\circ}/\text{oo}$ values are C₃ species (Bender 1971). Troughton et al. (1974) reported a mean $^{13}\text{C}^{\circ}/\text{oo}$ value of -28.11 ± 2.55 for C₃ and -13.46 ± 1.55 for C₄ 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 C₃ and C₄ 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. C₄ plants exhibit continued increase in CO₂ uptake as light intensity increases to nearly full sunlight (approximately 1.5 to 1.8 langleys), while C₃ plants are saturated at 0.2 to 0.4 langleys. Maximum CO₂ assimilation on a leaf area basis at normal atmospheric concentration of CO₂ ranges from 50 to 80 mg CO₂ · dm⁻² · hr⁻¹ for C₄ plants, but only 15 to 35 mg CO₂

$\text{dm}^{-2} \text{ hr}^{-1}$ 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, carboxyldismutase 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 *Oryzopsis*, *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 Arundoideae, Bamboideae, 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 $^{13}\text{C}/\text{o}$ 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 C₃ or C₄ photosynthetic pathway. Occurrence of distinct bundle sheath cells (BS: - = C₃, + = C₄); carbon dioxide compensation point (CO₂:H = C₃, L = C₄); net enhancement of photosynthesis in oxygen deficient atmosphere NE:>+8=C₃<+8=C₄; ¹³C/¹²C ratio (¹³C°/oo:<-22°oo=C₃>-22°oo=C₄); and occurrence of C₄ compounds as initial products in photosynthesis (C₄ cpd: <2%C₃, 2%C₄) 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: Arundinoideae							
TRIBE: Arundineae "Arundo				<-22 ^{21,23}		*	
A. donax L.							
"Cortaderia				<-22 ^{21,23}		*	
C. fulvida (J. Buchanan) Zотов				<-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		*	
"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		*	
"Schismus							
S. barbatus (L.) Thell.				-23 ²¹		*	
Subfamily: Bambusoideae							
TRIBE: Bambuseae							
Arundinaria							
A. tecta (Walt.) Muhl.				-26 ²¹		*	
"Bambusa							
B. eutuloides McClure				-28 ²³			
B. vulgaris Schrad. ex Wendl.				-30 ^{21,22}	0 ^{12,15}	*	
"Phyllostachys							
P. aurea A.				-28 ²¹		*	
P. bambusoides Sieb. and Zucc.				-31 ²³		*	
TRIBE: Phareae							
Pharus							
P. latifolius L.				-30 ²¹		*	
Subfamily: Eragrostoideae							
TRIBE: Aelropodeae							
Distichlis							
D. spicata (L.) Greene	+ ⁴			<8 ³	>-20 ^{1,20,21}		*10
D. stricta (Torr.) Rydb.					>-20 ²		
Monanthochloe					>-20 ^{20,21}		
M. littoralis Engelm.							*
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 ₄ cpd (%)	C ₃	C ₄
<i>Chloris</i>							
<i>C. acicularis</i> Lind. L. in Mitch.		L ¹⁸					*
<i>C. argentina</i> (Hack.) Lillo. and Parodi		L ¹⁸					*
<i>C. canterai</i> Arch.		L ¹⁸					*
<i>C. caribaea</i> Spreng.		L ¹⁸					*
<i>C. cucullata</i> Bisch.				-16 ²¹			* ¹¹
<i>C. distichophylla</i> Lag.		L ¹⁸					* ^{11,6}
<i>C. gayana</i> Kunth	+ ¹²	L ^{5,12,18}	+3 ^{5,8}	-15 ²³	70 ¹⁵		* ^{10,11}
					90 ⁹		
<i>C. inflata</i> Link		L ¹⁸					*
<i>C. pectinata</i> Benth.		L ¹⁸					*
<i>C. petraea</i> Swartz		L ¹⁸					*
<i>C. pilosa</i> Schum. and Thonn.		L ¹⁸					*
<i>C. polydactyla</i> (L.) Sw.		L ¹⁸					*
<i>C. pycnothrix</i> Trin.		L ¹⁸					*
<i>C. radiata</i> (L.) Sw.		L ¹⁸					*
<i>C. submutica</i> H.B.K.		L ¹⁸					*
<i>C. truncata</i> R. Br.		L ¹⁸					*
<i>C. uliginosa</i> Hack.		L ¹⁸					*
<i>C. ventricosa</i> R. Br.				-16 ²³			*
<i>C. virgata</i> Swartz				-14 ²³			*
^a <i>Cynodon</i>							
<i>C. arcuatus</i> F. and C. Presl		L ¹⁸					*
<i>C. dactylon</i> (L.) Pers.		L ^{5,7,12,18}		>-20 ^{1,20,21}			* ^{10,11,6}
<i>Hilaria</i>							
<i>H. belangeri</i> (Steud.) Nash				-14 ²¹			* ¹¹
<i>H. mutica</i> (Buckl.) Benth.	+ ¹⁶						* ^{10,11}
<i>Schedonardus</i>							
<i>S. paniculatus</i> (Nutt.) Trel.	+ ¹⁶						* ^{10,11}
<i>Spartina</i>							
<i>S. alterniflora</i> Loisel.				-13 ^{20,21}			* ¹¹
<i>S. cynosuroides</i> L.				-14 ¹			* ¹¹
<i>S. pectinata</i> Link		L ¹⁸		-13 ¹			* ¹¹
<i>Trichloris</i>							
<i>T. crinita</i> (Lag.) Parodi		L ¹⁸					* ¹⁰
Subfamily: Eragastoideae							
TRIBE:	<i>Eragrostaeae</i>						
<i>Blepharidachne</i> Hack.	+ ¹⁷						
<i>Blepharoneuron</i> Nash	+ ¹⁷						*
<i>Calamovilfa</i> Hack.	+ ¹⁷						*
^a <i>Dactyloctenium</i>							
<i>D. aegyptium</i> (L.) Beauv.		L ⁷					* ¹⁰
<i>D. aegyptiacum</i> Willd.		L ¹⁸		-12 ²¹			* ¹¹
^a <i>Eleusine</i>							
<i>E. compressa</i> Aschers. and Schweinf. ex Christensen.		L ¹⁸					*
<i>E. coracana</i> (L.) Gaertn.		L ^{5,18}	+8 ^{5,8}				* ^{10,11}
<i>E. flagellifera</i> Nees		L ¹⁸					*
<i>E. floccifolia</i> Spreng.		L ¹⁸					*
<i>E. indica</i> (L.) Gaertn.		L ^{7,18}					* ^{10,11}
<i>E. jaegeri</i> Pilger		L ¹⁸					*
<i>E. multiflora</i> Hochst.		L ¹⁸					*
<i>E. tristachya</i> (Lam.) Lam.		L ¹⁸					*
<i>Eragrostis</i>							
<i>E. acutiflora</i> Nees		L ¹⁸					*
<i>E. acutiglumis</i> Parodi		L ¹⁸					*
<i>E. airoides</i> Nees		L ¹⁸					*
<i>E. atherstonei</i> Stapf		L ¹⁸					*
<i>E. bahiensis</i> Schrad.		L ¹⁸					*
<i>E. bicolor</i> Nees		L ¹⁸					*
<i>E. brasiliensis</i> Nees		L ¹⁸					*
<i>E. brownii</i> (Kunth) Nees					97 ¹⁵		* ^{10,11}
<i>E. chalcantha</i> Trin.		L ¹⁸					*
<i>E. charis</i> (Schult.) Hitchc.		L ¹⁸					*
<i>E. chloromelas</i> Steud.		L ^{7,18}	0 ^{5,8}				* ^{10,11}
<i>E. ciliaris</i> (All.) Lutati		L ¹⁸		-20 ^{1,23}			* ¹¹
<i>E. collocarpa</i> K. Schum. ex Engl.		L ¹⁸					*
<i>E. curvula</i> (Schrad.) Nees	+ ¹⁴	L ¹⁸					* ^{10,11,6}
<i>E. denudata</i> Hack. ex Schinz.		L ¹⁸					*
<i>E. dielsii</i> Pilg. ex Diels and Pritz.		L ¹⁸					*

Table 1 continued

Species	BS	CO ₂	NE	¹³ C°/oo	C ₄ cpd (%)	C ₃	C ₄
<i>E. diffusa</i> Buckl.		L ¹⁸				*	
<i>E. ferruginea</i> Beauv.		L ¹⁸				*	
<i>E. flaccida</i> Lindm.		L ¹⁸				*	
<i>E. gummiflua</i> Nees		L ¹⁸				*	
<i>E. heteromera</i> Stapf		L ¹⁸				*	
<i>E. horizontalis</i> Peter.		L ¹⁸				*	
<i>E. intermedia</i> Hitchc.	+ ¹⁶	L ¹⁸		-16 ²¹			* ^{10,11}
<i>E. lappula</i> Nees		L ¹⁸				*	
<i>E. lehmanniana</i> Nees		L ¹⁸				*	
<i>E. margaritacea</i> Stapf		L ¹⁸				*	
<i>E. mexicana</i> (Hornem.) Link		L ^{12,18}					* ^{10,11}
<i>E. nigra</i> Nees. ex Steud.		L ¹⁸				*	
<i>E. obtusa</i> Munro		L ¹⁸				*	
<i>E. oxylepis</i> (Torr.) Torr.		L ¹⁸				*	
<i>E. papposa</i> Steud.		L ¹⁸				*	
<i>E. patentissima</i> Hack. ex Schinz.		L ¹⁸				*	
<i>E. pilosa</i> (L.) Beauv. (<i>E. parviflora</i> Trin.) ^b	+ ¹²	L ^{5,12}		-17 ²³			* ^{10,11}
<i>E. plana</i> Nees		L ¹⁸				*	
<i>E. poaeoides</i> Beauv. ex R. and S.		L ¹⁸				*	
<i>E. polytricha</i> Nees		L ¹⁸				*	
<i>E. rigidior</i> Pilger		L ¹⁸	0 ^a				* ^{10,11}
<i>E. robusta</i> Stent.		L ¹⁸				*	
<i>E. rufescens</i> R. and S.		L ¹⁸				*	
<i>E. secundiflora</i> Presl		L ¹⁸				*	
<i>E. spectabilis</i> (Pursh.) Steud.				-11 ²			*
<i>E. staroselskyi</i> Grossheim.		L ¹⁸				*	
<i>E. stenophylla</i> Hochst.		L ¹⁸				*	
<i>E. superba</i> Pehr.		L ¹⁸				*	
<i>E. tremula</i> Hochst.		L ¹⁸				*	
<i>E. trichodes</i> (Nutt.) Wood		L ¹⁸				*	
<i>E. truncata</i> Hack.		L ¹⁸				*	
<i>E. unioloides</i> (Retz.) Nees		L ¹⁸				*	
<i>E. virescens</i> Presl		L ¹⁸				*	
<i>Gymnopogon</i>							
<i>G. ambiguus</i> (Michx.) B.S.P.				-13 ²¹			* ¹¹
<i>Leptochloa</i>							
<i>L. dubia</i> (H.B.K.) Nees		L ^{7,18}					* ^{10,11}
<i>L. fascicularis</i> (Lam.) A. Gray		L ¹⁸				*	
<i>L. fusca</i> Kunth		L ^{7,18}					* ^{10,11,6}
<i>L. monostachya</i> Roem. and Schult.		L ^{7,18}					* ^{11,6}
<i>Lycurus</i>							
<i>L. phleoides</i> H.B.K.	+ ¹⁷			-14 ²¹			*
<i>Muhlenbergia</i>							
<i>M. emersleyi</i> Vasey				-11 ²¹			* ¹¹
<i>M. lindheimeri</i> Hitchc.				-12 ²¹		* ¹¹	* ¹¹
<i>M. racemosa</i> (Michx.) B.S.P.		L ^{17,18}					* ^{10,11}
<i>M. schreberi</i> Gmel.				-13 ¹			* ¹¹
<i>Sporobolus</i>				-13 ²			
<i>S. asper</i> (Michx.) Kunth							* ¹¹
<i>S. capensis</i> Kunth		L ¹⁸					*
<i>S. contractus</i> Hitchc.		L ¹⁸					*
<i>S. cryptandrus</i> (Torr.) A. Gray.		L ^{17,18}					* ^{10,11}
<i>S. elongatus</i> R. Br.		L ¹⁸		-13 ²³			*
<i>S. fimbriatus</i> Nees		L ¹⁸					*
<i>S. helvola</i> Th. Dur. and Schinz.		L ¹⁸					*
<i>S. heterolepis</i> A. Gray.				-13 ²			*
<i>S. indicus</i> (L.) R. Br.		L ¹⁸					*
(<i>S. jacquemontii</i> Kunth) ^b		L ¹⁸					*
(<i>S. poiretii</i> (R. and S.) Hitchc.) ^b		L ¹⁸					* ^{11,6}
<i>S. ioclados</i> Nees		L ¹⁸					*
<i>S. phyllostichus</i> Hochst.		L ¹⁸					*
<i>S. pyramidatus</i> (Lam.) Hitchc.		L ¹⁸					*
<i>S. spicatus</i> Kunth	+ ¹⁶						*
<i>S. usitatus</i> Stent.		L ¹⁸					* ^{10,11}
<i>S. usitatus</i> Stent.		L ¹⁸					*
<i>S. wrightii</i> Munro. ex Scribn.				12 ²¹			*
<i>Tridens</i>							
<i>T. albescens</i> (Vasey) Woot. and Standl.	+ ¹⁷			-14 ²¹			* ¹¹
<i>T. pilosus</i> (Buckl.) Hitchc.				-13 ²¹			* ¹¹
<i>Vaseyochloa</i>							
<i>V. multinervosa</i> (Vasey) Hitchc.		L ^{17,18}		-15 ²¹			* ^{10,11}

Table 1 continued

Species	BS	CO ₂	NE	¹³ C°/oo	C ₄ cpd (%)	C ₃	C ₄
TRIBE: Orcuttieae							
Neostapfia							*
<i>N. colusana</i> (Davy.) Davy.				-13 ²¹			* ¹¹
Orcuttia							
<i>O. californica</i> Vasey				-14 ²¹			* ¹¹
TRIBE: Pappophoreae							
Pappophorum							
<i>P. bicolor</i> Fourn.	L ^{17,18}			-13 ²¹			* ^{10,11}
TRIBE: Zoysieae							
"Tragus							
<i>T. australianus</i> S.T. Blake	L ⁸		+2 ⁸				* ^{10,11}
"Zoysia							
<i>Z. japonica</i> Steud.				-15 ²¹			* ^{10,11}
<i>Z. matrella</i> (L.) Merr.				-12 ²¹			* ¹¹
<i>Z. minima</i> (Colenso) Zotov				-14 ²³			*
TRIBE: Unioleae							
Uniola							
<i>U. paniculata</i> L.	+ ¹⁴			-28 ^{20,21}		*	* ^{11,6}
Subfamily: Oryzoideae							
TRIBE: Oryzeae							
Ehrharta							*
<i>E. calycina</i> J.E. Smith			+47 ⁸				*
Hydrochloa							*
<i>H. carolinensis</i> Beauv.				-27 ²¹			*
Leersia							
<i>L. hexandra</i> Swartz					0 ¹⁵		*
<i>L. oryzoides</i> (L.) Swartz	H ¹⁸		-28 ²¹			*	
Luziola					-28 ²¹		*
<i>L. bahiensis</i> (Steud.) Hitchc.							*
"Oryza							
<i>O. rufipogon</i> Griff.			+55 ⁸				*
<i>O. sativa</i> L.	H ^{5,12}		+45 ^{8,5}	-26 ²¹		*	
Zizania							
<i>Z. aquatica</i> L.	H ¹⁸			<-22 ^{1,21}		*	
<i>Z. texana</i> Hitchc.				-27 ²¹		*	
Zizaniopsis					<-22 ^{1,21}		*
<i>Z. miliacea</i> (Michx.) Doell and Aschers.							*
Subfamily: Panicoideae							
TRIBE: Andropogoneae							
Andropogon							
<i>A. gayanus</i> Kunth			-2 ^{5,8}				* ^{10,11}
<i>A. gerardi</i> Vitman	L ¹⁸		-13 ²				*
<i>A. glomeratus</i> (Walt.) B.S.P.			>-20 ²¹				* ¹¹
<i>A. lateralis</i> Nees	L ¹⁸						*
<i>A. papillosum</i> Hochst. ex A. Rich.	L ¹⁸						*
<i>A. selagoanus</i> Hack.	L ¹⁸						*
<i>A. ternatus</i> Nees	L ¹⁸						*
<i>A. virgatus</i> Desv.	L ¹⁸						*
<i>A. virginicus</i> L.	L ⁷						* ^{10,11,6}
"Anthraxon							
<i>A. hispidus</i> (Thunb.) Makino	L ¹⁸						*
Bothriochloa							
<i>B. alta</i> (Hitch.) Henrard	L ¹⁸			-12 ²¹			*
<i>B. barbinodis</i> Herter	L ¹⁸						*
<i>B. decipiens</i> (Hackel) C.E. Hubb.	L ¹⁸						*
<i>B. erwartiana</i> (Domin) C.E. Hubb.	L ¹⁸						*
<i>B. glabra</i> (Rox B.) A. Camus	L ¹⁹						*
<i>B. exaristata</i> (Nash) Henr.							*
(Andropogon hassleri Hack.) ^b	L ¹⁸						
<i>B. insculpta</i> (Hochst.) A. Camus	L ¹⁸						*
<i>B. intermedia</i> (R. Br.) A. Camus	L ¹⁸						*
<i>B. ischaemum</i> (L.) Keng	L ¹⁸						*
<i>B. laguroides</i> (D.C.) Herter	L ¹⁸						*
<i>B. pertusa</i> (Willd.) A. Camus	L ¹⁸						*

Table 1 continued

Species	BS	CO	NE	$^{13}\text{C}^{\circ}/\text{oo}$	Ccpd (%)	C ₃	C ₄
B. saccharoides Swartz (Andropogon saccharoides Swartz) ^b				-12 ²¹			*10
B. springfieldii (Gould) Parodi	L ¹⁸						*
Chrysopogon							
C. gryllus (L.) Trin.	L ¹⁸			-12 ²¹			*11,6
C. montanus Trin.	L ¹⁸						*11
C. serrulatus Trin.	L ¹⁸						*
"Coix							
C. lacryma-jobi L.			0 ⁸				*10,11
"Cymbopogon					-15 ^{20,21}		*11
C. citratus Stapf							*
C. martini (Roxb.) W. Watson	L ¹⁸						
"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						*
"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
"Hyparrhenia							
H. hirta (L.) Stapf	L ¹⁸						*10
H. rufa (Nees) Stapf	L ¹⁸						*
Imperata							
I. arundinacea Cyrill							*10,11
I. chesemanii Hack.							*
I. cylindrica (L.) Beauv.							*
Manisurus							
M. altissima (Poir.) Hitchc.							*11,6
"Miscanthus							
M. sacchariflorus (Maxim.) Hack.							*10
"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
"Sorghum							
S. arundinaceum Stapf		L ¹⁸					*
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. gobicum 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
"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						*	
<i>A. purshii</i> Kunth				-27 ²¹			
Anthaenaria							
<i>A. rufa</i> (Ell.) Schult.				-12 ²¹			* ¹¹
"Anthephora							
<i>A. cristata</i> Hack. ex Wildem. and Th. Dur.	+16						* ^{10,11}
<i>A. elongata</i> Wildem.				-10 ²¹			
<i>A. hermaphrodita</i> O. Ktz (<i>A. elegans</i> Schreb.) ^b				-11 ²¹		*	
<i>A. pubescens</i> Nees		L ^{17,18}		-12 ²¹			* ^{10,11}
Axonopus							
<i>A. affinis</i> Chase				-11 ²¹			* ¹¹
<i>A. compressus</i> (Swartz) Beauv.		L ²²					* ¹⁰
Brachiaria							
<i>B. erucaeformis</i> (J.E. Smith) Griseb.		L ¹⁸					*
<i>B. laeta</i> (Mez) A. Camus		L ¹⁸					*
<i>B. platyphylla</i> (Griseb.) Nash (<i>Paspalum platyphyllum</i> (Griseb.)) ^b		L ¹⁸		-13 ²¹			* ⁶
<i>B. ramosa</i> Stapf		L ¹⁸					*
Cenchrus							
<i>C. biflorus</i> Roxb.		L ¹⁸					*
<i>C. calycatus</i> Cav.				-12 ²³			
<i>C. ciliaris</i> L.		L ¹⁸		-12 ²¹			* ^{10,11,6}
<i>C. echinatus</i> L.		L ⁷					* ¹⁰
<i>C. incertus</i> M.A. Curtis				-12 ²¹			* ¹¹
<i>C. myosuroides</i> H.B.K.	+16	L ¹⁸					* ^{10,11}
<i>C. pauciflorus</i> Benth.		L ¹⁸					*
<i>C. pilosus</i> H.B.K.		L ¹⁸					*
<i>C. setigerus</i> Vahl.		L ¹⁸					*
Dichanthelium ^c (<i>Panicum</i>) ^b							
<i>D. ciliatum</i> Ell.				-26 ²¹			*
<i>D. clandestinum</i> (L.) Gould		H ₅ ^{17,18}		<-22 ^{2,21}			*
<i>D. commutatum</i> (Schult.) Gould		H ⁵		-26 ²¹			*
<i>D. depauperatum</i> (Muhl.) Gould				-25 ²¹			*
<i>D. lancearium</i> Trin.				-27 ²¹			*
<i>D. lanuginosum</i> (Ell.) Gould				-26 ²			*
<i>D. latifolium</i> L.				-25 ²¹			*
<i>D. leibergii</i> (Vasey) Scribn.				-26 ¹			*
<i>D. lindheimeri</i> (Nash) Gould		H ⁵					*
<i>D. linearifolium</i> (Scribn.) Gould				-26 ²¹			
<i>D. meridionale</i> Ashe.				-24 ²¹			*
<i>D. microcarpon</i> Muhl. ex Ell.				-27 ²¹			*
<i>D. nodatum</i> (Hitchc. and Chase) Gould				-28 ²			*
<i>D. oligosanthes</i> (Schult.) Gould		H ^{17,18,19}					*
<i>D. pacificum</i> Hitchc. and Chase	-22	H ^{18,22}		<-22 ^{1,21}	0 ²²		
<i>D. praecocius</i> Hitchc. and Chase		H ^{17,18,19}					*
<i>D. scribnerianum</i> (Nash) Fern.				-32 ¹			*
<i>D. sphaerocarpon</i> (Ell.) Gould				-28 ²			*
<i>D. webberianum</i> Nash				-26 ²¹			*
<i>D. xalapense</i> H.B.K.				-27 ²¹			*
Digitaria							
<i>D. adscendens</i> (H.B.K.) Henrard				-12 ²¹			* ¹¹
<i>D. argyrograpta</i> Stapf		L ¹⁸	0 ⁸				* ^{10,11}
<i>D. biocornis</i> R. and S. ex Loud.		L ¹⁸					*
<i>D. brownii</i> Hughes		L ¹⁸					*
<i>D. californica</i> (Benth.) Henr. (<i>Trichachne californica</i> (Benth.) Chase) ^b		L ^{7,18}		-11 ²¹			* ¹⁰
<i>D. decumbens</i> Stent.							* ^{10,11}
<i>D. diagonalis</i> Stapf		L ¹⁸					*
<i>D. eriantha</i> Steud.		L ¹⁸					*
<i>D. eriostachya</i> Mez.		L ¹⁸					*
<i>D. gazensis</i> Rendle		L ¹⁸					*
<i>D. glauca</i> Stent.		L ¹⁸					*
<i>D. horizontalis</i> Willd.		L ¹⁸					*
<i>D. iburua</i> Stapf		L ¹⁸					*
<i>D. insularis</i> (L.) Mez ex Ekemann (<i>Trichachne insularis</i> (L.) Nees) ^b		L ⁷					*
<i>D. ischaemum</i> (Schreb.) Schreb. ex Muhl.		L ¹⁸					*
<i>D. kilimandscharica</i> Mez.		L ¹⁸					*

Table 1 continued

Species	BS	CO ₂	NE	¹³ C°/oo	C _{4cpd} (%)	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		-18			*
D. smutsii Stent.		L ¹⁸					* 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 ^f		L ¹⁸					*
E. holubii Stapf		L ¹⁸					*
E. pyramidalis Hitchc. and Chase		L ¹⁸					*
E. spiralis Vasinger		L ¹⁸					*
E. stagnina Beauv.		L ⁵		-35, 8			* 10
Eriochloa							
E. lemmoni Vasey and Scribn.							* 11, 6
(E. gracilis (Fourn) Hitchc.) ^b							
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					* 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}					* 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					*
P. laevifolium Hack.		L ^{17, 18, 19}					* 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}					* 10, 11, 6
P. miliooides Nees ex Trin.	- 14	L ¹⁸					* 10
P. obtusum H.B.K.		L ^{17, 18, 19}		-13 ²¹	90 ⁹		* 10, 11
P. philadelphicum Bernh. ex Trin.		L ^{17, 18, 19}					* 10, 11
(P. minus Nash) ^b		L ^{17, 18, 19}					* 10, 11
P. plenum Hitchc. and Chase		L ^{17, 18, 19}		-12 ²¹	85 ⁹		* 10, 11
P. polygonatum Schrad.		L ^{17, 18}					* 10, 11
P. prolutum F. Muell.		L ^{17, 18, 19}					* 10, 11
					93 ⁹		

Table 1 continued

Species	BS	CO ₂	NE	¹³ C°/oo	C ₄ cpd (%)	C ₃	C ₄
P. purascens Raddi				-11 ²¹			* ¹¹
P. queenslandicum Domin.		L ¹⁸		-11 ²¹			*
P. reptans L.				-11 ²¹			* ¹¹
P. staphianum Fourc.		L ¹⁸		-11 ²¹			* ^{10,11}
P. tenerum Beyer.				-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. alnum 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. paspaloides 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. purnilum 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					*
"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. macrorhynchum 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					*
Reimarochoa							
R. acuta Hitchc.				-12 ²¹			* ¹¹
"Rhynchospora							
R. repens (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		L ¹⁸					*
(Panicum firmulum Hitchc. and Chase) ^b							*
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 ₁ cpd (%)	C ₃	C ₄
<i>S. lutescens</i> (Weigel) Hubb.	+ ¹²	L ^{12,18}				* ^{10,11,6}	
<i>S. neglecta</i> de Wit.		L ¹⁸				*	
<i>S. pallidifusca</i> Stapf and C.E. Hubb.		L ¹⁸				*	
<i>S. palmifolia</i> (Koen.) Stapf		L ¹⁸				*	
<i>S. phanerococcra</i> Stapf		L ¹⁸				*	
<i>S. reverchonii</i> Vasey (<i>Panicum reverchonii</i> Vasey) ^b		L ^{17,18}		-12 ²¹		*	
<i>S. scheelei</i> (Steud.) Hitchc.				-13 ²¹		*	
<i>S. sphacelata</i> (Schum.) Stapf and C.E. Hubb.	L ¹⁸	0 ⁸		-14 ²³		* ^{10,11,6}	
<i>S. verticillata</i> (L.) Beauv.	L ¹⁸					*	
<i>S. viridis</i> (L.) Beauv.	L ^{7,18}			-13 ²³		* ^{10,11}	
<i>Stenotaphrum</i>							
<i>S. secundatum</i> (Walt.) Kuntze				-16 ^{20,21}		* ^{11,6}	
Subfamily: Pooideae							
TRIBE: Aveneae							
<i>Agrostis</i>							
<i>A. alba</i> L.	H ^{5,12,18}	+42 ⁸		-28 ²		*	
<i>A. castellana</i> Boiss and Reut.		+45 ⁸				*	
<i>A. hiemalis</i> (Walt.) B.S.P.	H ¹⁸			-28 ²¹		*	
<i>A. perennans</i> (Walt.) Tuckerm.				-30 ¹		*	
<i>S. scabra</i> Willd.				-29 ¹		*	
<i>A. tenuis</i> (Sibth.)				-28 ²¹		*	
<i>Alopecurus</i>							
<i>A. pratensis</i> L.	H ¹⁸			<-22 ^{2,23}		*	
<i>Ammophila</i>							
<i>A. breviligulata</i> Fern.				-28 ¹		*	
" <i>Anthoxanthum</i>						.	
<i>A. odoratum</i> L.	H ¹²			-28 ²¹		*	
" <i>Arrhenatherum</i>							
<i>A. elatius</i> (L.) Presl	H ^{12,18}			<-22 ^{2,23}		*	
" <i>Avena</i>							
<i>A. abyssinica</i> Hochst. ex A. Rich	H ¹⁸					*	
<i>A. alba</i> Vahl.		+50 ⁸				*	
<i>A. barbata</i> Brot.	H ¹⁸					*	
<i>A. clauda</i> Dur. in Duch.	H ¹⁸					*	
<i>A. fatua</i> L.	H ¹⁸					*	
<i>A. longiglumis</i> Dur. in Duch.	H ¹⁸					*	
<i>A. pilosa</i> Bieb.	H ¹⁸					*	
<i>A. sativa</i> L.	H ^{5,12,18}			-24 ²¹	2 ¹⁵	*	
<i>A. semipervirens</i> Will.		+51 ⁸				*	
<i>A. sterilis</i> L.	H ¹⁸					*	
<i>A. strigosa</i> Schreb.	H ¹⁸					*	
<i>A. ventricosa</i> Balansa	H ¹⁸					*	
<i>Beckmannia</i>							
<i>B. syzigachne</i> (Steud.) Fernald.	H ¹²			-25 ²¹		*	
<i>Calamagrostis</i>							
<i>C. canadensis</i> (Michx.) Beauv.	H ¹⁸			<-22 ^{2,21}		*	
<i>Cinna</i>							
<i>C. latifolia</i> (Trevir.) Griseb.	H ¹²			-25 ²¹		*	
<i>Deschampsia</i>							
<i>D. caespitosa</i> (L.) Beauv.	H ¹⁸					*	
<i>D. chapmani</i> Petrie				-27 ²³		*	
<i>D. flexuosa</i> (L.) Trin.				-24 ²¹		*	
<i>Helictotrichon</i>							
<i>H. hookeri</i> (Scribn.) Henr.	H ¹⁸					*	
<i>Hierochloe</i>							
<i>H. odarata</i> (L.) Beauv.				-23 ²¹		*	
<i>H. redolens</i> Roem. and Schult.				-29 ²³		*	
" <i>Holcus</i>							
<i>H. lanatus</i> L.				-31 ²³		*	
<i>Koeleria</i>							
<i>K. cristata</i> (L.) Pers.	H ¹⁸					*	
<i>K. phleoides</i> (Vill.) Pers.	H ¹⁸					*	
<i>K. setacea</i> D.C.	H ¹⁸					*	
<i>K. valesiaca</i> Gaud.	H ¹⁸					*	
<i>Limnodea</i>							
<i>L. arkansana</i> (Nutt.) L.H. Dewey				-28 ²¹		*	
<i>Milium</i>							
<i>M. effusum</i> L.				<-22 ^{21,23}		*	

Table 1 continued

Species	BS	CO ₂	NE	¹³ C°/oo	C ₄ cpd (%)	C ₃	C ₄
Phalaris							
<i>P. californica</i> Hook and Arn. (<i>P. amethystina</i> Trin.)				+60 ⁸		*	
<i>P. arundinacea</i> L.		H ^{5,7,12,18}	+45 ^{5,8}	<-22 ^{2,21}		*	
<i>P. brachystachys</i> Link				-25 ²¹		*	
<i>P. canariensis</i> L.		H ⁷		<-22 ^{23,21}		*	
<i>P. minor</i> Retz.				-28 ²³			
<i>P. tuberosa</i> L.			+39 ⁸			*	
Phleum							
<i>P. alpinum</i> L.			+40 ⁸			*	
<i>P. nodosum</i> L.			+45 ⁸			*	
<i>P. phleoides</i> Simenkaia				-30 ²³		*	
<i>P. pratense</i> L.		H ¹⁸		-27 ²		*	
Polypogon							
<i>P. monspeliensis</i> (L.) Desf.				-28 ²³		*	
Sphenopholis							
<i>S. obtusata</i> (Michx.) Scribn.				-29 ²¹		*	
Trisetum							
<i>T. flavescens</i> (L.) Beauv.		H ¹⁸				*	
TRIBE: Brachelytreae							
Brachelytrum							
<i>B. erectum</i> (Schreb.) Beauv.				-27 ²¹		*	
TRIBE: Diarrheneae							
Diarrhena							
<i>D. americana</i> Beauv.				-30 ²¹		*	
TRIBE: Meliceae							
Glyceria							
<i>G. grandis</i> S. Wats.				-24 ²¹		*	
<i>G. striata</i> (Lam.) Hitchc.				-25 ²¹		*	
Melica							
<i>M. altissima</i> L.				-28 ²³		*	
<i>M. mutica</i> Walt.		H ⁷		-26 ²¹		*	
Schizachne							
<i>S. purpurascens</i> (Torr.) Swallen				-28 ²¹		*	
TRIBE: Monermeae							
^a Parapholis							
<i>P. incurva</i> (L.) C.E. Hubb.				-26 ²¹		*	
<i>P. pannonica</i> Kunth				-25 ²¹		*	
TRIBE: Nardeae							
^a Nardus							
<i>N. stricta</i> L.				-26 ²¹		*	
TRIBE: Poeae							
^a Brachypodium							
<i>B. phoenicoides</i> Roem. and Schult.				-26 ²³		*	
^a Briza							
<i>B. maxima</i> L.				-29 ²³		*	
<i>B. minor</i> L.				-30 ²³		*	
<i>B. rotundata</i> Steud.				-27 ²¹		*	
Bromus							
<i>B. albidus</i> M.B.							
(<i>B. biebersteinii</i> R. and S.) ^b		H ¹⁸				*	
<i>B. coloratus</i> Steud.			+40 ⁸			*	
<i>B. commutatus</i> Schrad.					-28 ²¹	*	
<i>B. diandrus</i> Roth.							
(<i>B. rigidus</i> Roth.) ^b		H ¹⁸				*	
<i>B. hankeanus</i> (Presl) Kunth			+49 ⁸			*	
<i>B. inermis</i> Leyss.		H ^{12,18}		<22 ^{2,21}		*	
<i>B. kalmii</i> A. Gray				-30 ¹		*	
<i>B. purgans</i> L.				-25 ²¹		*	
<i>B. tectorum</i> L.		H ^{12,18}		<-22 ²³		*	
<i>B. unioloides</i> (Willd.) H.B.K.							
(<i>B. catharticus</i> Vahl.) ^b		H ¹⁸		<-22 ^{1,23}		*	
^a Dactylis							
<i>D. aschersoniana</i> Graebn.			+25 ⁸			*	
<i>D. glomerata</i> L.	+14	H ^{5,12,18}	+46 ^{5,8}	<-22 ^{2,21}		* ⁶	
Festuca							
<i>F. ampla</i> 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}	*		
"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			*		
"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. holiformis (MB) Rich.			+45 ⁸		*		
O. hymenoides (Roem. and Schult.) Ricker				-28 ¹	*		
O. miliacea (L.) Benth. and Hook. ex Aschers. and Schweinf.					*		
O. racemosa (J.E. Smith) Ricker		H ¹²		-30 ²³	*		
Stipa							
S. columbiana Macoun				-24 ^{20,21}	*		
S. comata Trin. and Rupr.				-25 ¹	*		
S. leucotricha Trin. and Rupr.				-27 ²¹	*		
S. nitida Sprague and Summerh.			+40 ⁸		*		
S. robusta (Vasey) Scribn.				-25 ²¹	*		
S. Sparteo Trin.				-28 ¹	*		
S. tenuissima Trin.				-25 ²¹	*		
S. viridula Trin.				-27 ²	*		
TRIBE: Triticeae							
"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. ligistica (Savign.) Coss		H ¹⁸			*		
A. longissima Schw. et. Musch.		H ¹³			*		
A. ovata L.		H ¹³			*		
A. pergrina (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
<i>A. littorale</i> Dum.		H ¹⁸				*	
<i>A. loloides</i> (Karel. and Kir.)		H ¹⁸				*	
<i>A. obtusiusculum</i> Lange P. Candargy		H ¹⁸				*	
<i>A. orientale</i> R. and S.		H ¹⁸				*	
<i>A. panormitanum</i> Parl. ex Boiss.		H ¹⁸					
<i>A. pectiniforme</i> R. and S.		H ¹⁸				*	
<i>A. pseudorepens</i> Scribn. and Smith		H ¹⁸				*	
<i>A. pungens</i> (Pers.) R. and S.		H ¹⁸				*	
<i>A. repens</i> (L.) Beauv.		H ⁸		< -22 ^{2,21}		*	
<i>A. rigidum</i> Beauv.		H ¹⁸				*	
<i>A. scabriglume</i> (Hack.) Parodi		H ¹⁸				*	
<i>A. semicostatum</i> (Steud.) Ness ex Boiss		H ¹⁸				*	
<i>A. sibiricum</i> (Willd.) Beauv.		H ^{18,24}		-28 ²		*	
<i>A. Smithii</i>		H ^{18,24}		-28 ²		*	
<i>A. spicatum</i> (Pursh) Scribn. and Smith		H ¹⁸		-27 ²¹		*	
<i>A. striatum</i> (Steud.) P. Candargy		H ¹⁸				*	
<i>A. subulatum</i> R. and S.		H ¹⁸				*	
<i>A. tenerum</i> Vasey		H ¹⁸				*	
<i>A. trachycaulum</i> (Link) Steud.				-28 ²		*	
<i>A. trichophorum</i> (Link) Richt.		H ¹⁸				*	
<i>A. violaceum</i> Vasey		H ¹⁸				*	
Elymus							
<i>E. agropyroides</i> Presl		H ¹⁸				*	
<i>E. angustus</i> Trin. ex Ledeb.		H ¹⁸				*	
<i>E. antarcticus</i> Hook.		H ¹⁸				*	
<i>E. arenarius</i> L.		H ¹⁸				*	
<i>E. canadensis</i> L.		H ¹⁸		-27 ²		*	
<i>E. carolinianus</i> Walt.		H ¹⁸				*	
<i>E. cinereus</i> Scribn. and Merr.		H ¹⁸				*	
<i>E. crinitus</i> Schreb.		H ¹⁸				*	
<i>E. dahuricus</i> Turcz.		H ¹⁸				*	
<i>E. glaucus</i> Buckl.		H ¹⁸				*	
<i>E. innovatus</i> Beal		H ¹⁸				*	
<i>E. junceus</i> Fisch.		H ¹⁸		-26 ²		*	
<i>E. mollis</i> Trin.	-4		7 + 8, 4	-28 ¹		*	
<i>E. paboanus</i> Claus		H ¹⁸				*	
<i>E. virginicus</i> L.		H ¹⁸		-27 ²¹		*	
Hordeum							
<i>H. bogdani</i> Wilensky		H ¹⁸				*	
<i>H. brevisubulatum</i> Link		H ¹⁸				*	
<i>H. bulbosum</i> L.		H ¹⁸	+47 ⁸			*	
<i>H. chilense</i> Roem. and Schult.			+34 ⁸			*	
<i>H. comosum</i> Presl		H ¹⁸				*	
<i>H. compressum</i> Griseb.		H ¹⁸				*	
<i>H. hystrich Roth.</i>		H ¹⁸				*	
<i>H. jubatum</i> L.		H ¹⁸	-29 ²			*	
<i>H. marinum</i> Huds.		H ¹⁸				*	
<i>H. pusillum</i> Nutt.			-27 ²¹			*	
<i>H. spontaneum</i> Koch		H ¹⁸				*	
<i>H. stebbinsii</i> Covas		H ¹⁸				*	
<i>H. vulgare</i> L.		H ^{5,12,13,18}				*	
^a Secale							
<i>S. ancestrale</i> Zhuk.			+48 ⁸			*	
<i>S. cereale</i> L.		H ¹⁸	+37 ⁸			*	
<i>S. montanum</i> Guss.		H ¹⁸				*	
<i>S. vavilovii</i> Grossheim		H ¹⁸				*	
Sitanion							
<i>S. hystrich</i> (Nutt.) J.G. Smith							
^a Triticum							
<i>T. aestivum</i> L.	-22					* ⁶	
(<i>T. sativum</i> Lam.) ^b		H ¹²			0 ¹⁵	*	
(<i>T. vulgare</i> Vill.) ^b		H ¹⁸				*	
<i>T. baeticum</i> Boiss. et. Schiem.		H ¹³				*	
<i>T. compactum</i> Host.		H ¹³				*	
<i>T. dicoccoides</i> Korn.		H ¹³				*	
<i>T. dicoccum</i> Schrank		H ¹⁸				*	
<i>T. durum</i> Desf.		H ¹⁸	+50 ⁸			*	
<i>T. monococcum</i> L.		H ^{18,13}				*	
<i>T. persicum</i> Vav.		H ¹³				*	
<i>T. polonicum</i> L.		H ¹³				*	
<i>T. spelta</i> L.		H ¹³				*	
<i>T. sphaerococcum</i> Perc.		H ¹³				*	
<i>T. timopheevi</i> Zhukov		H ¹³				*	

Table 1 continued

Species	BS	CO ₂	NE	¹³ C/oo	C ₄ cpd (%)	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 <i>Dichanthelium</i> to the generic level. This change was made for all species in the <i>Dichanthelium</i> 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 Gauth (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 C₄ plants are generally inferior food sources for herbivores, primarily insects, and are often avoided by them relative to C₃ plants. Caswell and Reed (1975) determined that the grasshopper (*Melanoplus confusus*) was capable of digesting C₃ grass material, but was unable to totally digest the thick-walled bundle sheath cells of C₄ grasses. Further research with 10 species of grasshoppers indicated that the large quantities of nutritional material in the bundle sheath cell of C₄ plants was at least partially unavailable (Caswell and Reed 1976). Plants with the C₄ photosynthetic pathway are also generally lower in total digestible nutrients for cattle and sheep

than C₃ 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 (C₄) 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 (C₃) 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 (C₄) (*Andropogon gerardii*) and little bluestem (C₄) (*Schizachyrium scoparium*) had a significant positive preference by grazing cattle wherever they occurred, while preference for western wheatgrass (C₃) (*Agropyron smithii*) varied with site. This indicates that a generalization concerning lower palatability of C₄ species compared to C₃ may not apply to all herbivores.

Table 2. A summary of C₃ and C₄ photosynthetic pathway in the United States. Taxonomic classification follows that of Gould (1968).

Subfamily	Tribe	Number			
		Genera	Species	C ₃	C ₄
Arundinoideae	Arundineae	4	5	* ¹	
	Centotheceae	1	1	*	
	Danthoniaeae	2	4	*	
Bambusoideae	Bambuseae	3	5	*	
	Phareae	1	1	*	
Eragrostoideae	Aelropodaeae	2	3	*	
	Aristideae	1	7	*	
	Chlorideae	13	49	*	
	Eragrostaeae	9	72	*	
	Orcuttiaeae	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	*	
	Brachelytreae	1	1	*	
	Diarrhenacae	1	1	*	
	Meliceae	3	5	*	
	Monermeae	1	2	*	
	Nardeae	1	1	*	
	Poeae	10	36	*	
	Stipeae	2	12	*	
	Triticaceae	7	97	*	
		138	632		

* indicates presence of either C₃ or C₄ 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.

Literature Cited

- Akin, D.E., and D. Burdick. 1977. Rumen microbial degradation of starch-containing bundle sheath cells in warm-season grasses. Crop Sci. 17:529-533.
- Bender, M.M. 1971. Variations in the ¹³C/¹²C ratios of plants in relations to the pathway of photosynthetic carbon dioxide fixation. Phytochemistry 10:1239-1244.
- Bender, M.M., and D. Smith. 1973. Classification of starch-and fructosan-accumulating grasses as C-3 or C-4 species by carbon isotope analysis. J. Brit. Grassl. Soc. 28:97-100.

- Bisalputra, T., W.J.S. Downton, and E.B. Tregunna.** 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.
- Bjorkman, O.** 1976. Adaptive and genetic aspects of C₄ photosynthesis. p. 287-309. In: R.H. Burris, and C.C. Black. (Eds.) CO₂ metabolism and plant productivity. University Park Press, Baltimore, Md.
- Bjorkman, O., and E. Gauhl.** 1969. Carboxyldismutase activity in plants with and without β -Carboxylation photosynthesis. *Planta* 88:197-203.
- Bjorkman, O., B. Mahall, M. Nobs, W. Ward, F. Nicholson, and H. Mooney.** 1974. An analysis of the temperature dependence of growth under controlled conditions. p. 757-767. In: S.A. McGough, (Ed.). Carnegie Institution of Washington, Yearbook 73. J.D. Lucas Printing Co., Baltimore, Md.
- Black, C.C.** 1971. Ecological implications of dividing plants into groups with distinct photosynthetic production capacities. p. 87-114. In: J.B. Cragg, (Ed.) Advances in Ecological Research. Academic Press, New York, N.Y.
- Black, C.C., T.M. Chen, and R.H. Brown.** 1969. Biochemical basis for plant competition. *Weed Sci.* 17:338-344.
- Bowes, G., and W.L. Ogren.** 1972. Oxygen inhibition and other properties of soybean ribulose 1, 5-diphosphate carboxylase. *J. Bio. Chem.* 247:2171-2176.
- Brown, R.H.** 1978. A difference in N use efficiency in C₃ and C₄ plants and its implications in adaptation and evolution. *Crop Sci.* 18:93-98.
- Brown, R.H., and V.E. Gracen.** 1972. Distribution of the postillumination CO₂ burst among grasses. *Crop Sci.* 12:30-33.
- Brown, W.V., and B.N. Smith.** 1975. The genus *Dichanthelium* (Gramineae). *Bull. Torrey Bot. Club* 102:10-13.
- Calvin, M., and J.A. Bassham.** 1962. The Photosynthesis of Carbon Compounds. W.A. Benjamin, New York, N.Y. 127 p.
- Caswell, H., and F.C. Reed.** 1975. Indigestibility of C₄ bundle sheath cells by the grasshopper, *Melanoplus confusus*. *Ann. Entomol. Soc. Amer.* 68:686-688.
- Caswell, H., and F.C. Reed.** 1976. Plant-herbivore interactions: the indigestibility of C₄ bundle sheath cells by grasshoppers. *Oecologia (BERL)* 26:151-156.
- Caswell, H., F.C. Reed, S.N. Stephenson, and P. Werner.** 1973. Photosynthetic pathways and selective herbivory: a hypothesis. *Amer. Natur.* 107:465-480.
- Chen, T.M., R.H. Brown, and C.C. Black.** 1970. CO₂ compensation concentration, rate of photosynthesis, and carbonic anhydrase activity of plants. *Weed Sci.* 18:399-403.
- Chollet, R.** 1976. C₄ control of photorespiration: studies with isolated mesophyll cells and bundle sheath strands. p. 327-341. In: R.H. Burris and C.C. Black, (Eds.) CO₂ Metabolism and Plant Productivity. University Park Press, Baltimore, Md.
- Cox, L.M.** 1977. Asking questions of desert shrubs. *Utah Sci.* 38:71-74.
- Crampton, E.W., and L.E. Harris.** 1969. Applied Animal Nutrition. W.H. Freeman and Co. San Francisco, Calif. 753 p.
- Crookston, R.K., and D.N. Moss.** 1974. Interveinal distance for carbohydrate transport in leaves of C₃ and C₄ grasses. *Crop Sci.* 14:123-125.
- Downes, R.W., and J.D. Hesketh.** 1968. Enhanced photosynthesis at low oxygen concentrations: differential response of temperate and tropical grasses. *Planta* 78:79-84.
- Downton, W.J.S.** 1970. Preferential C₄ -dicarboxylic acid synthesis, the postillumination CO₂ burst, carboxyl transfer step, and grana configurations in plants with C₄ —photosynthesis. *Can. J. Bot.* 48:1795-1800.
- Downton, W.J.S.** 1971. Check list of C₄ species, p. 554-558. In: M.D. Hatch, C.B. Osmond, and R.O. Slayter, (Eds.). Photosynthesis and Respiration. Wiley Interscience, New York, N.Y.
- Downton, W.J.S.** 1975. The occurrence of C₄ photosynthesis among plants. *Photosynthetica* 9:96-105.
- 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.
- Dvorak, J., and L. Natr.** 1971. Carbon dioxide compensation points of *Triticum* and *Aegilops* species. *Photosynthetica* 5:1-5.
- El-Sharkaway, M., and J.D. Hesketh.** 1965. Photosynthesis among species in relation to characteristics of leaf anatomy and CO₂ diffusion resistances. *Crop Sci.* 5:517-521.
- Evans, L.T.** 1975. Photoperiodism and photosynthetic pathways. *Can. J. Bot.* 53:590-591.
- Gallaher, R.N., D.A. Ashley, and R.H. Brown.** 1975. ¹⁴C photosynthate translocation in C₃ and C₄ plants as related to leaf anatomy. *Crop Sci.* 15:55-59.
- Gould, F.W.** 1968. Grass Systematics. McGraw-Hill Book Co., New York, N.Y. 382 p.
- Gould, F.W.** 1975. The Grasses of Texas. Texas A&M University Press, College Station, Tex. 653 p.
- Gracen, V.E. Jr., J.H. Hilliard, R.H. Brown, and S.H. West.** 1972. Peripheral reticulum in chloroplasts of plants differing in CO₂ fixation pathways and photorespiration. *Planta* 107:189-204.
- Hatch, M.D., and C.R. Slack.** 1966. Photosynthesis by sugar-cane leaves. A new carboxylation reaction and the pathway of sugar formation. *Biochem. J.* 101:103-111.
- Hatch, M.D., C.R. Slack, and H.S. Johnson.** 1967. Further studies on a new pathway of photosynthetic carbon dioxide fixation in sugar-cane and its occurrence in other plant species. *Biochem. J.* 102:417-422.
- Johnson, M.C. Sr.** 1964. An electron microscope study of the photosynthetic apparatus in plants with special reference to Gramineae. PhD Thesis, Univ. of Texas, Austin. 264 p.
- Kortschalk, H.P., C.E. Hartt, and G.O. Burr.** 1965. Carbon dioxide fixation in sugar-cane leaves. *Plant Physiol.* 40:209-213.
- Krenzer, E.G. Jr., and D.N. Moss.** 1969. Carbon dioxide compensation in grasses. *Crop Sci.* 9:619-621.
- Krenzer, E.G. Jr., D.N. Moss, and R.K. Crookston.** 1975. Carbon dioxide compensation points of flowering plants. *Plant Physiol.* 56:194-206.
- Moss, D.N., E.G. Krenzer, and W.A. Brun.** 1969. Carbon dioxide compensation points in related plant species. *Science* 164:187-189.
- Ogren, W.L.** 1976. Search for higher plants with modifications of the reductive pentose phosphate pathway of CO₂ assimilation. p. 19-29. In: R.H. Burris and C.C. Black, (Eds.) CO₂ Metabolism and Plant Productivity. University Park Press, Baltimore, Md.
- Park, R., and S. Epstein.** 1960. Carbon isotope fractionation during photosynthesis. *Geochim. Cosmochim. Acta* 21:110-126.
- Ranson, S.C., and M. Thomas.** 1961. Crassulacean acid metabolism. *Annu. Rev. Plant Physiol.* 11:81-110.
- Rogler, G.A.** 1944. Relative palatabilities of grasses under cultivation on the Northern Great Plains. *J. Amer. Soc. Agron.* 36:487-496.
- Slack, C.R., P.G. Roughan, and H.C.M. Bassett.** 1974. Selective inhibition of mesophyll chloroplast development in some C₄—pathway species by low night temperature. *Planta* 118:57-73.
- Smith, B.N., and S. Epstein.** 1971. Two categories of ¹³C/¹²C ratios for higher plants. *Plant Physiol.* 47:380-384.
- Smith, B.N., and W.V. Brown.** 1973. The Kranz syndrome in the Gramineae as indicated by carbon isotopic ratios. *Amer. J. Bot.* 60:505-513.
- Smith, D.** 1968. Classification of several native North American grasses as starch or fructosan accumulators in relation to taxonomy. *J. Brit. Grassl. Soc.* 23:306-309.
- Stoddart, L.A., A.D. Smith, and T.W. Box.** 1975. Range management. McGraw Hill Book Co., Inc., New York, N.Y. 532 p.
- Takeda, T., and M. Fukuyama.** 1971. Studies on the photosynthesis of the Gramineae. I. Differences in photosynthesis among subfamilies and their relations with the systematics of the Gramineae (in Japanese, English summary). *Crop Sci. Soc. Japan, Proc.* 40:12-19.
- Ting, I.P.** 1971. Non autotrophic CO₂ fixation and crassulacean acid metabolism. p. 169-185. In: M.D. Hatch, C.B. Osmond, and R.O. Slayter (Eds.), Photosynthesis and Photorespiration. Wiley Interscience, New York, N.Y.
- Ting, I.P., and C.B. Osmond.** 1973. Photosynthetic phosphoenol-pyruvate carboxylases, characteristics of alloenzymes from leaves of C₃ and C₄ plants. *Plant Physiol.* 51:439-447.
- Tomanek, G.W., E.P. Martin, and F.W. Albertson.** 1958. Grazing preference comparisons of six native grasses in the Mixed Prairie. *J. Range Manage.* 11:191-193.
- Tregunna, E.B., B.N. Smith, J.A. Berry, and W.J.S. Downton.** 1970. Some methods for studying the photosynthetic taxonomy of the angiosperms. *Can. J. Bot.* 48:1209-1214.
- Triolo, L., D. Bagnara, L. Anselmi, and C. Bassanelli.** 1974. Carbonic anhydrase activity and localization in some plant species. *Physiol. Plant.* 31:86-89.
- Troughton, J.H., K.A. Card, and C.H. Hendy.** 1974. Photosynthetic pathways and carbon isotope discrimination by plants. p. 768-780. In: S.A. McGough, (Ed.). Carnegie Institution of Washington, Yearbook 73. J.D. Lucas Printing Co., Baltimore, Md.
- Whelan, T., W.M. Sackett, and C.R. Benedict.** 1973. Enzymatic fractionation of carbon isotopes by phosphoenolpyruvate carboxylase from C₄ plants. *Plant Physiol.* 51:1051-1054.
- White, E.M.** 1961. A possible relationship of little bluestem distribution to soils. *J. Range Manage.* 14:243-247.
- Williams, G.J. III.** 1974. Photosynthetic adaptation to temperature in C₃ and C₄ grasses. *Plant Physiol.* 54:709-711.
- Williams, J. III., and J.L. Markley.** 1973. The photosynthetic pathway type of North American shortgrass prairie species and some ecological implications. *Photosynthetica* 7:262-270.