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SYSTEMATIC VARIATION IN AMINO ACID COMPOSITIONS OF GRASS CARYOPSES

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Key Word Index—Poaceae; grasses; caryopses; embryos; endosperms; proteins; amino acids; systematic variation.

Abstract—Variation in amino acid patterns of 121 species (72 genera) of grass caryopses is extensively consistent with taxonomic groupings. The patterns of pooids and chloridoids are distinguishable from one another and from those of eu-panicoids and andropogonoids; the bamboos, *Oryza*, Stipeae, *Ehrharta* and *Microlaena*, which share certain morphological and anatomical features, also share a characteristic amino acid profile, while profiles of danthonoioids, *Triodia* and *Aristida* are clearly non-pooid. Caryopsis amino acid patterns vary independently of photosynthetic pathway. Embryos from taxonomically diverse genera all show very similar amino acid profiles, which differ strikingly from those of the endosperms, and the amino acid patterns of whole caryopses are dominated by their endosperms, which are responsible for the taxonomic variation. 'Chemical scores' of the caryopsis proteins, but not total protein contents, correlate to some extent with taxonomic groupings.

INTRODUCTION

Seed proteins from a variety of monocotyledons and dicotyledons have been shown to comprise 4 fractions, namely, albumin, globulin, prolamin and glutelin [1]. Each of these, despite its heterogeneous nature, exhibits a characteristic amino acid pattern [2–10]. The proportions of the different protein fractions differ in seeds from different species; e.g., those of monocotyledons are richer in prolamin and glutelin than are those of dicotyledons [1]. In grasses, all the protein fractions are represented but variation in their quantitative proportions is taxonomically orientated across the family [1, 8, 11]. The total amino acid patterns of grass 'seeds' have also been shown to be taxonomically predictable, and variation appears to involve not only the relative proportions of the 4 protein fractions but also taxonomic patterning in their individual amino acid profiles [1, 8, 11–16]. However, conclusions derived from comparative analyses of compiled data are unsatisfactory, through lack of uniformity in the techniques used [12–16]. Protein hydrolyses carried out at different HCl concentrations, temperatures and hydrolysis times often result in differing degrees of destruction of labile amino acids [17], and amino acid compositions of proteins determined by microbiological assay differ to some extent from those determined by ion-exchange chromatography [18]. Results of amino acid analyses have usually been expressed against total seed nitrogen, and cannot give reliable information on protein amino acid compositions because total nitrogen might involve significant proportions of non-protein sources. Moreover, it is known that lemmas and paleas, which are difficult to separate from the caryopsis in some grasses, are different in amino acid composition from the caryopsis itself, and differences in patterns also occur between immature and mature caryopses [11, 19, 20]. Therefore, absence of information on the preparation of material for analyses compounds the hazards in making detailed comparisons, and in assessing the biological and nutritional significance of the patterns detected in compiled data. Finally, although data exist for more than 80 species of grasses, the coverage remains taxonomically unsatisfactory. For example, in the absence of data on C_3 and C_3–C_4 intermediate eu-panicoid grasses, it is impossible to say whether variation in photosynthetic pathways influences the protein accumulated in the caryopses.

We have tried to determine how far a knowledge of taxonomy is helpful in understanding variation in grass 'seed' proteins. The amino acid compositions of grass caryopses reported here represent 121 species (72 genera) chosen to cover all the main taxonomic groups, with a view to assessing (i) the extent to which amino acid patterns of mature, viable grass caryopses are taxonomically predictable; (ii) whether variation in amino acid patterns is directly related to variation in photosynthetic pathways; (iii) the relative contributions of embryos and endosperms to caryopsis amino acid profiles; and (iv) whether any correlation exists between taxonomy and protein nutritional quality (chemical score).

RESULTS AND DISCUSSION

Taxonomic patterns

Total amino acid compositions of grass caryopses are here assumed to represent protein, since free amino acids have been estimated at less than 5 g % [21–24]. Results for 121 species (72 genera) are presented in Table 1, where the genera are classified into major groupings (≃ subfamilies) and tribes according to current information on taxonomic relationships [25, 26]. Notwithstanding marked variation in the proportions of individual amino acids in certain genera [e.g. *Festuca* spp. (Asx and Pro) and

Table 1. Amino acid compositions of grass caryopses

Species	Amino acid composition (g % total amino acids)																		Total amino acid (protein content) (g % fr. wt)
	Asx	Thr	Ser	Glx	Pro	Gly	Ala	Cys	Val	Met	Ile	Leu	Tyr	Phe	His	Lys	Trp	Arg	
BAMBOOS																			
Arundinaria sp.	11.4	4.5	5.7	19.6	5.2	4.9	5.9	2.0	4.4	2.8	3.2	7.7	4.7	5.4	2.3	4.6	0.0	5.6	5.4
Dendrocalamus strictus	11.6	3.7	5.1	18.6	5.2	4.4	5.9	1.0	4.9	2.3	3.5	8.2	4.8	5.8	2.3	4.6	0.1	7.8	10.3
Bambusa glaucescens	12.3	4.2	4.9	17.1	5.3	4.7	5.9	1.1	5.4	2.5	3.4	7.5	4.8	5.5	2.8	5.1	0.0	7.4	6.8
ORYZOIDS																			
Oryza sativa cv Baru*	10.3	3.8	5.7	18.6	4.8	4.7	6.1	1.6	5.2	2.2	3.6	9.0	5.6	5.4	2.3	4.6	0.2	6.1	4.6
O. sativa cv Calrose*	10.0	3.7	5.7	18.9	5.0	4.6	6.0	1.5	5.0	2.0	3.6	8.9	5.7	5.4	2.2	5.0	0.1	6.7	4.0
O. sativa cv IR8*	10.0	4.1	5.8	18.6	5.1	4.6	6.0	3.1	4.9	2.8	3.4	8.3	5.5	5.5	2.5	4.7	0.0	5.3	5.0
O. sativa cv 665-24-I*	10.1	4.1	6.0	20.0	4.9	4.4	5.9	1.5	5.1	2.7	3.5	8.6	5.8	5.7	2.3	4.1	0.1	5.2	6.7
POOIDS (Pooideae)																			
Triticeae																			
Agropyron scabrum	5.7	3.4	5.3	32.7	12.7	3.7	3.4	1.9	3.3	1.7	2.5	6.4	3.9	5.4	2.1	3.0	0.0	2.8	16.8
Hordeum leporinum	5.0	3.5	4.9	30.8	13.2	3.5	3.4	1.6	3.3	1.9	2.9	7.3	4.0	6.1	2.1	3.2	0.0	3.3	20.1
*H. vulgare**	5.5	3.1	4.5	28.1	13.0	3.6	3.6	1.7	4.4	1.5	3.2	7.7	4.1	6.0	2.1	3.6	0.2	4.2	13.2
*Secale cereale**	5.6	3.3	4.5	28.6	13.0	3.6	3.7	2.1	4.4	1.5	3.1	7.3	3.9	5.4	2.1	4.0	0.3	3.6	8.6
*Triticum aestivum**	4.8	2.8	5.1	37.0	11.2	3.9	3.3	1.3	3.5	1.5	2.9	6.8	3.7	4.9	2.1	2.8	0.1	2.3	11.2
Bromeae																			
Bromus arenarius	8.0	3.8	4.8	24.5	12.4	4.3	5.0	1.6	3.3	1.7	3.3	6.7	4.1	4.9	2.4	5.3	0.0	3.9	8.2
B. molliformis	7.6	3.7	4.8	26.3	12.3	4.7	4.7	1.3	3.1	1.4	2.7	5.9	4.3	5.6	2.3	4.9	0.0	4.4	10.1
B. rubens	9.7	4.5	6.6	19.1	10.1	4.8	5.9	1.5	3.9	1.8	2.9	6.8	4.2	4.8	2.3	6.0	0.0	4.1	5.8
B. unioloides	6.7	3.8	5.5	26.9	11.6	4.4	4.6	1.5	4.2	1.8	3.2	6.4	4.4	5.1	2.0	4.6	0.2	3.0	9.5
Agrostideae																			
Agrostis avenacea	6.0	3.3	4.8	29.8	7.8	4.1	4.1	2.7	3.7	1.5	2.6	7.8	3.6	8.1	2.2	3.5	0.1	4.3	12.2
A. tenuis	6.4	3.6	5.2	30.0	7.3	3.9	4.5	2.4	3.4	2.1	2.5	7.7	3.7	7.7	2.1	2.8	0.3	4.3	17.8
Aira elegans	8.4	3.2	5.0	24.9	6.4	4.6	5.2	2.5	2.3	2.1	3.1	8.7	4.6	7.7	2.5	3.9	0.3	4.5	15.2
Ammophila arenaria	6.8	4.0	6.0	24.5	5.5	5.0	5.1	2.1	4.4	1.4	2.9	7.5	4.8	7.0	2.4	4.3	0.0	6.3	11.2
Anthoxanthum odoratum	8.7	2.8	4.9	28.3	6.4	4.0	5.0	1.9	3.4	1.6	2.4	9.0	4.2	6.9	2.2	2.8	0.1	5.4	21.0
Deyeuxia gunniana	8.4	3.5	5.1	27.2	6.0	4.0	4.8	1.8	4.5	1.7	3.0	7.8	3.9	7.5	2.0	3.7	0.1	5.0	13.3
D. monticola	8.1	3.0	4.9	27.2	6.4	4.1	4.8	2.6	4.2	1.8	2.9	7.8	4.0	7.2	2.2	3.9	0.0	4.7	13.6
D. quadriseta	8.1	3.2	4.7	25.8	6.2	4.2	4.6	1.8	4.3	1.5	3.3	8.3	4.2	7.7	2.2	3.6	0.1	6.1	17.8
Dichelachne sciurea	4.5	3.7	5.4	27.0	6.4	4.5	5.3	1.9	4.6	1.7	2.9	8.5	4.2	7.3	2.4	4.1	0.1	5.6	14.2
Echinopogon caespitosus	10.9	3.8	6.0	22.7	5.5	4.9	5.1	3.4	3.8	1.6	2.7	7.1	4.3	6.5	2.1	5.2	0.0	4.4	15.5
E. ovatus	11.3	4.0	6.0	22.2	6.0	4.8	5.6	2.4	3.7	1.5	2.7	7.3	4.0	6.4	2.1	5.5	0.0	4.4	11.2
Hierochloe redolens	5.0	3.1	5.7	29.4	5.1	4.6	5.0	2.2	3.6	1.3	2.7	7.5	4.3	8.6	2.4	3.5	0.1	5.8	21.7
Holcus lanatus	8.3	3.3	5.6	26.1	7.1	3.9	5.6	2.0	3.7	1.3	2.9	7.7	3.8	8.6	2.2	3.6	0.0	4.4	11.0
Lagurus ovatus	8.3	3.2	5.4	26.5	6.8	4.3	4.9	2.5	3.4	1.5	2.7	8.1	4.1	6.2	2.1	4.6	0.0	5.4	12.8
Phalaris amethystina	7.2	2.7	5.6	28.6	6.6	3.8	5.3	2.4	4.1	1.6	3.4	8.3	3.4	6.3	2.0	3.5	1.2	4.0	10.6

P. arundinacea	7.4	3.1	5.7	29.7	6.4	4.1	5.1	2.6	3.8	2.1	3.0	7.9	3.7	5.9	3.4	2.1	0.9	3.0	12.2
P. brachystachya	5.9	3.0	5.1	28.8	7.1	3.3	4.8	1.5	5.1	2.0	4.4	9.0	3.7	7.2	2.3	3.1	0.2	3.4	11.1
P. coerulescens	7.1	2.8	5.2	29.8	6.7	3.7	4.8	2.3	3.8	1.6	3.3	8.4	3.7	6.4	2.2	3.0	1.7	3.6	16.0
P. californica	8.4	3.5	6.0	25.7	5.8	4.9	5.3	2.2	4.1	1.5	3.1	7.6	4.3	6.4	2.2	4.5	0.6	4.0	7.8
P. canariensis	5.8	2.8	5.3	31.5	7.1	3.2	4.8	3.0	3.7	1.8	3.1	8.3	3.2	6.6	2.2	2.7	1.4	3.4	11.1
P. minor	6.5	2.8	5.3	30.4	6.8	3.6	4.8	2.0	3.9	1.8	3.3	8.3	3.6	6.1	2.2	3.1	1.5	4.1	13.4
P. paradoxa	6.7	2.6	5.1	31.1	6.6	3.5	4.7	2.6	3.6	1.7	3.2	8.2	3.5	6.3	2.3	2.7	1.9	3.8	17.7
P. truncata	7.2	3.0	5.2	28.1	6.4	3.8	5.0	2.4	3.7	1.7	3.1	8.4	3.7	6.1	2.1	3.6	1.6	4.9	15.1
P. tuberosa	7.3	3.2	5.6	29.1	6.9	4.1	5.1	1.3	3.7	1.8	3.5	8.0	4.0	5.9	2.1	3.4	1.4	3.7	7.9
Polypogon monspeliensis	8.0	3.4	5.1	28.2	6.8	4.3	4.2	3.0	3.6	1.4	2.9	7.6	3.9	8.2	2.4	3.4	0.0	4.7	12.9
Aveneae																			
Amphibromus neesii	9.6	3.5	5.8	24.9	6.0	4.7	4.9	2.4	3.6	1.4	2.9	7.4	4.4	6.6	2.3	4.1	0.0	5.6	8.5
Arrhenatherum elatius	10.8	4.0	5.6	21.0	5.5	4.4	4.1	4.8	3.7	1.6	3.2	8.2	4.5	5.4	2.3	4.6	1.2	5.1	6.8
Avena fatua	9.1	3.7	5.8	23.8	5.7	4.9	4.9	2.6	4.1	1.8	3.2	8.0	4.7	5.8	2.3	4.6	0.0	5.1	13.3
*A. sativa**	9.0	3.9	6.2	22.7	5.8	5.4	5.1	2.2	4.5	1.9	3.4	8.3	4.6	5.6	2.1	5.0	0.2	3.8	7.5
Meliceae																			
Glyceria declinata	11.1	4.0	6.4	20.2	5.0	4.7	6.4	1.2	3.8	2.5	3.0	8.1	4.9	5.3	2.2	4.7	0.1	6.3	7.6
Melica californica	8.7	4.1	5.7	20.3	5.1	4.0	6.8	1.9	5.0	2.6	3.7	9.1	5.3	4.9	2.2	4.0	0.1	6.5	9.3
Poeae																			
Briza maxima	9.0	3.5	6.3	22.3	5.9	5.7	4.8	3.2	4.5	1.3	3.4	7.7	5.0	5.6	2.2	4.0	0.2	5.3	12.8
B. minor	9.4	3.4	5.4	25.8	5.8	4.3	5.3	1.8	3.6	1.6	2.7	7.9	3.9	8.1	2.4	3.9	0.1	4.6	18.4
Cynosurus echinatus	9.1	3.7	6.5	23.6	5.9	6.0	5.2	1.5	3.7	1.7	2.7	7.2	4.2	5.7	2.5	4.8	0.1	6.0	6.1
Dactylis glomerata	10.1	3.3	6.3	24.2	6.0	4.9	4.9	1.8	4.0	1.5	2.7	7.3	4.1	7.4	2.5	3.7	0.0	5.2	11.4
Festuca arundinacea	7.8	3.7	5.0	25.6	9.3	5.0	4.7	2.2	3.1	1.7	2.7	7.2	4.3	7.1	2.4	4.9	0.0	3.5	11.4
F. hookerana	10.4	3.5	4.8	23.6	5.0	4.3	4.4	1.9	4.7	1.6	3.5	7.3	4.4	7.1	2.8	4.7	0.1	5.9	27.5
F. rubra	5.5	3.1	4.4	27.8	11.2	5.3	4.2	2.7	3.6	1.6	2.9	6.8	3.3	8.1	2.2	3.8	0.2	3.2	10.7
Lolium perenne	6.6	3.7	4.5	24.0	9.8	5.4	4.6	2.4	4.0	1.6	3.2	7.6	4.3	7.0	2.2	4.6	0.2	4.2	6.0
Monerma cylindrica	8.4	3.1	6.1	27.0	6.5	4.9	4.2	2.1	3.5	1.5	2.8	7.2	4.1	7.9	2.3	3.3	0.1	4.4	22.8
Poa helmsii	5.3	3.8	5.3	29.3	7.2	4.3	4.1	2.6	4.3	1.6	3.0	7.5	3.9	8.4	2.2	3.2	0.1	4.2	10.7
P. labillardieri	6.6	3.4	5.6	32.0	7.0	3.8	4.3	1.9	3.8	1.8	2.9	6.9	3.7	8.1	2.0	2.8	0.0	3.6	13.9
P. pratensis	5.5	3.5	4.9	30.6	7.1	3.8	4.0	2.2	3.6	2.0	2.9	7.7	4.1	8.5	2.2	3.1	0.0	4.2	12.4
P. sieberana	5.7	3.8	5.2	27.4	7.3	4.3	4.4	4.3	4.1	2.0	3.2	7.7	3.8	8.5	2.1	3.0	0.0	3.2	8.5
Psilurus incurvus	4.9	3.1	4.1	29.9	12.3	4.7	4.1	2.1	2.9	1.7	2.4	6.6	3.5	9.1	2.4	3.8	0.0	2.5	12.3
Puccinellia pseudodistans	10.4	3.7	5.6	24.2	5.6	4.6	5.1	2.0	4.1	1.8	2.9	7.5	4.3	6.5	2.1	4.6	0.0	5.1	8.9
Vulpia myuros	4.9	3.1	3.8	29.1	13.0	4.7	3.7	2.4	3.2	1.7	2.6	6.7	3.6	8.8	2.2	3.6	0.0	3.0	14.4
DANTHONIOIDS (Danthonieae)																			
Danthonia bipartita	7.5	3.2	5.6	24.4	6.4	2.6	9.0	1.6	4.7	3.3	3.7	11.9	4.2	5.5	2.1	1.8	0.2	2.3	25.0
D. pallida	6.5	3.5	6.2	28.8	7.3	2.6	7.1	1.4	4.0	2.4	3.3	9.8	5.4	5.3	2.2	2.1	0.0	2.0	16.6
D. penicillata	6.6	3.3	5.9	29.9	7.1	2.6	6.8	1.6	4.7	1.8	3.5	9.5	5.0	5.1	2.1	2.1	0.0	2.3	16.8
Eriachne ovata †	8.1	4.0	7.3	23.2	6.1	3.7	8.9	2.3	4.6	2.0	3.2	8.4	4.3	5.7	2.3	3.2	0.0	2.8	6.7
Triraphis mollis †	5.3	3.6	3.8	31.0	6.4	3.2	6.1	1.1	4.4	4.4	3.4	9.4	5.0	5.7	2.1	2.4	0.1	2.8	10.1
CHLORIDOIDS																			
Chloris gayana †	6.9	3.9	5.1	30.5	5.8	3.0	5.9	1.7	4.8	3.6	3.7	8.3	3.7	6.0	2.0	3.1	0.2	2.0	13.9
C. truncata †	6.2	4.2	5.2	32.8	6.2	2.5	5.6	1.2	4.1	3.8	3.4	8.8	3.8	6.5	1.9	2.0	0.0	2.0	17.8
*Eleusine coracana** †	6.6	4.5	6.1	22.8	7.2	3.5	6.6	1.5	5.3	3.5	3.6	10.5	4.6	5.9	2.3	3.3	0.2	2.0	5.8

Table 1. *Continued*

Species	Amino acid composition (g % total amino acids)																		Total amino acid (protein content, g % fr. wt)
	Asx	Thr	Ser	Glx	Pro	Gly	Ala	Cys	Val	Met	Ile	Leu	Tyr	Phe	His	Lys	Trp	Arg	
E. indica †	7.3	4.5	5.8	24.3	6.8	3.4	6.5	1.0	5.2	3.5	3.7	9.9	4.4	5.9	2.3	3.7	0.0	2.9	7.9
Enneapogon nigricans †	6.6	3.1	4.8	35.5	6.1	2.6	6.2	1.6	3.8	3.2	3.0	7.6	3.6	5.4	1.9	2.6	0.1	2.2	17.4
E. acicularis †	5.7	3.9	5.1	29.6	7.3	3.3	6.4	1.1	4.7	2.8	3.8	8.7	4.3	6.8	2.0	2.2	0.2	2.0	15.9
Eragrostis benthamii †	6.7	3.9	5.7	27.0	6.6	2.9	6.2	2.7	4.4	4.5	3.2	8.3	5.3	6.0	2.0	2.3	0.1	2.3	10.2
E. chloromelas †	6.8	4.1	6.3	24.7	6.7	3.6	6.4	1.8	3.8	5.4	3.2	8.3	5.2	5.8	2.2	3.0	0.0	2.5	8.1
E. cilianensis †	6.0	3.4	5.5	31.4	6.2	2.6	6.1	1.2	4.0	3.9	3.4	8.6	5.6	6.5	1.9	1.8	0.0	1.7	11.1
E. dielsii †	5.6	3.6	4.5	36.0	5.1	3.2	5.0	1.2	4.9	2.8	3.4	8.5	4.9	4.9	1.9	2.1	0.1	2.4	9.7
Sporobolus australasicus †	7.5	3.4	5.7	27.3	6.3	3.6	6.6	0.8	4.6	4.2	3.8	9.9	4.9	5.8	1.7	2.0	0.1	1.8	10.6
S. virginicus †	9.9	4.3	6.5	22.9	7.3	2.6	7.1	1.0	3.9	2.3	3.3	9.2	4.6	7.9	1.9	2.5	0.0	2.6	9.1
Zoysia macrantha †	9.0	3.9	5.8	27.3	6.8	2.1	7.4	1.4	5.3	1.7	3.2	9.5	4.7	6.3	1.6	2.0	0.0	2.1	15.7
PANICOIDS *sensu lato*																			
Eu-panicoids																			
Axonopus affinis †	6.9	3.2	5.4	22.2	7.6	2.3	8.2	5.8	4.2	2.6	2.9	11.6	4.6	6.3	1.8	1.9	0.0	2.2	15.2
Cenchrus longispinus †	7.7	3.6	6.8	27.3	8.8	2.1	11.0	1.3	4.9	2.4	3.7	5.2	3.8	5.1	2.5	1.4	0.0	2.2	14.9
Digitaria sanguinalis †	6.1	3.7	6.0	23.8	7.5	2.7	9.2	0.9	4.5	3.7	3.6	11.7	4.2	6.1	2.0	2.2	0.1	1.9	11.0
Echinochloa crus-galli †	6.7	3.6	5.5	22.8	7.2	3.2	9.4	1.7	4.4	2.7	3.7	10.6	4.5	6.4	2.1	2.7	0.1	2.7	7.2
Entolasia marginata	6.6	3.3	6.2	22.7	8.9	2.1	9.7	0.8	4.5	2.2	3.0	13.2	5.0	6.2	2.1	1.7	0.0	2.0	10.2
E. stricta	7.5	3.3	6.2	21.6	9.0	2.1	9.6	0.9	4.5	2.1	3.2	12.7	5.1	6.3	2.1	1.9	0.0	1.9	9.9
Eriochloa pseudoacrotricha †	7.3	3.6	5.8	23.7	7.7	2.5	8.7	1.0	4.1	2.4	3.5	12.5	4.2	6.2	1.9	2.3	0.0	2.4	15.6
Oplismenus aemulus	6.7	3.1	6.3	18.8	10.0	3.3	9.0	0.9	3.8	2.4	3.9	14.8	6.1	6.5	2.0	1.6	0.0	1.8	14.1
Panicum antidotale †	7.5	3.8	5.8	22.1	7.8	2.5	8.5	1.5	4.7	2.3	3.9	13.4	3.9	5.4	2.0	2.2	0.7	2.0	14.6
P. hians	6.8	3.0	5.8	23.5	8.4	1.9	9.5	0.9	4.4	3.6	3.8	12.4	4.6	6.1	2.1	1.5	0.0	1.8	16.1
P. milioides	6.6	2.9	5.7	23.3	8.5	2.1	9.5	0.9	4.5	3.5	3.6	12.6	4.8	6.0	2.1	1.6	0.0	1.9	13.2
Paspalum dilatatum †	6.8	3.1	5.6	22.7	7.3	2.2	10.0	1.0	4.8	2.0	3.0	9.3	7.1	8.1	1.8	2.1	0.2	2.8	12.0
P. distichum †	7.3	3.7	5.7	21.8	6.8	2.9	9.0	0.7	4.9	2.4	3.7	9.7	6.0	6.9	2.2	3.1	0.0	3.3	7.4
Pennisetum alopecuroides †	9.5	3.4	5.1	23.9	7.1	2.7	8.9	1.3	4.2	1.9	2.7	13.1	3.3	5.2	1.9	2.7	0.1	3.0	22.0
Setaria geniculata †	7.2	3.5	6.6	23.1	8.6	2.0	9.2	1.1	4.4	2.6	3.2	12.9	3.7	6.2	1.9	1.6	0.1	2.1	13.5
S. verticillata †	6.8	3.7	5.5	23.5	8.2	2.0	8.9	0.5	4.9	2.4	3.9	14.7	4.0	5.8	1.9	1.4	0.3	1.7	17.7
Spinifex hirsutus †	7.7	2.5	6.7	24.3	8.5	2.1	12.4	1.1	4.1	1.7	2.4	9.3	4.9	5.5	2.6	1.5	0.1	2.6	12.6

Andropogonoids																			
Bothriochloa macra †	7.8	3.5	4.9	22.0	10.3	2.7	8.8	0.7	3.8	2.1	3.0	13.6	4.0	5.2	2.3	2.9	0.0	2.4	21.4
Cymbopogon refractus †	9.0	3.0	4.9	20.5	11.2	2.8	8.9	1.5	4.5	1.5	3.5	12.7	3.5	5.0	2.3	2.8	0.0	2.3	24.2
Hemarthria uncinata †	4.8	3.5	5.7	23.3	8.2	3.0	9.8	1.3	4.0	1.9	2.7	13.0	3.5	8.0	2.4	2.5	0.0	2.5	16.3
Heteropogon contortus †	8.8	2.8	5.3	18.4	15.9	2.9	14.7	1.1	4.0	3.3	3.4	5.8	2.6	5.3	2.2	1.4	0.6	1.6	23.0
Themeda australis †	8.6	2.5	5.3	22.5	14.5	2.7	13.8	0.9	3.8	3.0	3.4	5.5	3.5	5.2	2.4	1.1	0.2	1.3	21.3
*Sorghum vulgare** †	7.3	3.5	5.3	21.5	8.5	3.2	9.4	1.7	4.1	1.9	3.1	13.6	4.6	5.2	2.1	2.7	0.2	2.2	6.7
*Zea mays** †	5.9	3.2	5.6	22.9	9.5	2.6	8.1	1.5	3.5	2.3	3.7	16.0	5.0	5.5	2.1	1.9	0.0	1.8	12.4
Isolated genera, and small groups of doubtful affinities																			
Aristideae																			
Aristida browniana †	4.5	2.9	4.3	30.9	9.2	1.9	7.1	0.7	4.2	4.0	3.5	12.9	4.2	4.7	1.6	1.2	0.3	2.0	22.5
A. obscura †	4.8	3.0	4.8	29.5	11.9	2.6	5.9	1.3	3.8	3.4	2.9	10.1	4.3	4.7	1.9	2.3	0.6	2.3	17.5
A. ramosa †	5.5	2.9	5.0	29.7	11.1	2.5	6.5	1.6	4.1	3.4	2.6	10.8	4.1	5.2	1.5	1.6	0.0	1.9	22.2
A. vagans †	6.0	2.7	4.8	30.7	11.4	2.4	6.5	1.5	4.1	2.3	2.5	10.4	4.5	5.0	1.6	1.6	0.0	1.9	20.0
Stipeae																			
Anisopogon avenaceus	12.0	3.3	5.8	22.8	5.1	4.3	5.8	1.4	4.0	2.4	2.5	7.7	5.0	5.9	2.3	3.7	0.2	6.0	10.1
Nassella trichotoma	11.0	4.0	5.5	21.3	5.3	4.6	5.9	1.4	3.7	1.9	2.9	8.5	5.1	5.7	2.2	4.4	0.0	6.4	7.1
Stipa falcata	11.1	4.4	5.4	20.8	5.2	4.6	5.8	1.7	3.4	2.4	3.2	8.2	5.1	5.4	2.5	4.9	0.1	6.0	18.4
S. mollis	11.1	3.9	5.4	22.5	5.0	4.6	5.8	1.4	3.9	1.7	2.7	8.1	5.4	5.8	2.3	3.7	0.1	6.6	15.2
S. neesiana	11.9	4.0	5.3	21.4	5.1	4.8	5.7	1.6	3.4	2.1	2.8	8.1	5.3	5.4	2.5	4.0	0.1	6.3	16.7
S. nitida	8.6	4.0	4.6	21.9	5.8	4.7	5.7	1.3	4.9	2.1	3.6	9.0	5.4	5.5	2.3	3.5	0.3	7.0	13.5
S. platychaeta	9.3	4.3	4.8	20.3	5.1	4.4	5.7	2.1	4.8	2.4	3.5	8.3	5.2	5.7	2.4	4.5	0.3	6.8	8.6
S. pubescens	10.2	3.7	5.9	22.2	5.2	4.6	5.8	1.8	4.2	2.2	2.5	8.4	5.1	5.6	2.5	3.5	0.0	6.6	16.0
Triodieae																			
Triodia basedowii †	6.1	3.2	4.2	33.4	4.9	2.5	6.0	1.6	4.9	4.2	3.5	10.2	4.1	4.8	1.9	1.9	0.2	2.4	20.7
'Oddments'																			
Ehrharta calycina	12.1	4.4	5.8	16.5	5.4	4.9	6.4	1.6	4.4	2.4	3.4	8.3	4.5	5.7	2.5	5.6	0.0	6.1	7.6
E. erecta	11.8	4.3	6.1	18.2	5.8	4.7	6.3	1.7	4.2	2.0	3.2	8.4	4.4	6.2	2.3	5.1	0.0	5.2	11.0
Microlaena stipoides	11.3	4.3	5.5	18.4	5.3	4.8	6.5	2.4	4.5	2.1	3.1	7.7	4.4	6.1	2.6	5.2	0.0	5.8	7.8

C_4 species are indicated by a †, and those cultivated as cereals by an asterisk. Material analysed consisted of complete, mature, viable caryopses, stripped of other spikelet parts and flower remnants; except in *Eleusine* spp. and *Sporobolus* spp., where the free seeds were used in lieu of caryopses. Classification of grass genera after Watson and Clifford (updated) and MacFarlane (for Pooideae) [25,26].

Phalaris spp. (Asx, Glx and Lys)], it is apparent that the overall amino acid patterns of different species from the same genus tend to be closely comparable. Furthermore, the data now available re-affirm and greatly expand upon the existence of clear taxonomic patterns in the amino acid profiles, which may now be confidently attributed to systematically orientated variations in caryopsis proteins. The amino acid pattern characteristics of taxonomic groupings referred to in what follows are readily verifiable from Table 1 in terms of graphs and statistical analyses, which it would be tedious and unnecessary to reproduce here.

Considering first the four largest major grass groupings, namely, the pooids, chloridoids, eu-panicoids and andropogonoids, it is clear from the information given in Table 1 and summarized in Table 2 that the genera of pooids are distinguishable from eu-panicoids and andropogonoids by their consistently higher Gly, Lys and Arg, and consistently lower Ala, Met and Leu. Even the less obvious differences in Glx, Cys and Phe are also statistically significant (s.e. of difference > twice s.e.). On the other hand, the relatively close relationship between eu-panicoids and andropogonoids postulated by taxonomists (e.g. the 'Panicoids *sensu lato*' [25]) is re-affirmed by their closely similar amino acid profiles, which are characterized by high Ala and Leu, and low Glx. The eu-panicoids, however, seem to bridge the gap between the chloridoids (see below) and andropogonoids in terms of Glx and Pro. Among the andropogonoids, the genera *Heteropogon* and *Themeda* are especially closely related, both being referred to the same minor generic group of the subtribe Themedastrae [27]; and it is noticeable that the *Heteropogon* and *Themeda* species in the present sample have yielded an almost identical amino acid pattern which differs somewhat from those of the rest (high Pro and Ala, and low Lys and Arg). The chloridoids, which morphologically and anatomically occupy a somewhat intermediate position between the pooids and eu-panicoids, as reflected in taxonomic systems, are higher in Glx and Met, and lower in Pro, Ala and Leu than are the eu-panicoids and andropogonoids. Their Glx levels fall within the pooid range, but they occupy an intermediate range (i.e. with respect to pooids and Panicoids *sensu lato*) in terms of Ala, Leu and Lys, and some of them (e.g., *Eragrostis benthamii*, *E. chloromelas* and *Sporobolus australasicus*) exhibit Met levels which are very high in the context of the family as a whole.

Referring to the smaller high-level taxonomic groupings, the bamboos sampled exhibit Ser, Gly, Leu and His levels comparable with pooids, with which they appear in other respects to have closer, albeit distant, taxonomic affinities. They are outstanding in the sample as a whole for their high levels of Asx, Thr, Ala, Val, Met, Ile, Tyr, Lys and Arg, and low levels of Glx, Pro and Phe. Interestingly, a strikingly similar amino acid profile to that of bamboos is shown by *Oryza*, whose taxonomic affinities with them are indicated by features of floret morphology (e.g. stamen number) and leaf anatomy (e.g. arm cells), and by certain other genera showing such bambusoid/oryzoid features as 3 lodicules (Stipeae), stamens in excess of 3 and reduced glumes (*Ehrharta* and *Microlaena*).

Triodia and *Aristida* represent groupings small in genera but distinctive, and taxonomically isolated in the family as a whole. They differ sharply from one another in their Asx, Ser, Glx, Pro, Val and Met levels, but both show greater similarity to chloridoids (high Glx and Met, and low Ala) than to eu-panicoids or andropogonoids. However, their profiles come closer to the latter than to the pooids (high Ala, Met and Leu, and low Gly, Lys, Phe and Arg). The danthoniods also provide manifestly non-pooid amino acid profiles (high Ala, Met and Leu, and low Gly, Phe, Lys and Arg). In this context, it is worth noting that the amino acid pattern of the monotypic Australian genus, *Anisopogon*, is indistinguishable from those of Stipeae, whereas it differs noticeably from those of the danthonioids in Asx, Glx, Pro, Gly, Ala, Leu, Lys and Arg. *Anisopogon* was referred to the danthonioids by Watson and Clifford [25], although their decision was a marginal one on the basis of the information then available. Study of fresh material (Watson, L., unpublished) has since revealed that the flowers of *Anisopogon* have 3 lodicules—a feature not uncommon among Stipeae, bamboos etc., but unknown among danthonioids. This, in addition to the evidence from amino acid patterns, forcibly suggests that the genus really belongs in the Stipeae.

The large pooid tribes, Agrostideae and Poeae seem indistinguishable in their amino acid profiles, which mostly exhibit high Phe and (within this context) large variation in Asp and Glu. Nevertheless, even within the rather homogeneous subfamily Pooideae, some taxonomic pattern is detectable. The caryopses of Aveneae differ somewhat from the rest, notably in their relatively high Asx, Ser, Leu and Tyr, and low Glx. Some taxonomists have preferred to follow Stebbins and Crampton [28] in sinking the Agrostideae in the Aveneae, but this difference supports MacFarlane's [26] action in maintaining them as separate tribes. The Triticeae and *Bromus* (i.e., Bromeae) differ from one another in Asx, Glx, Gly, Ala and Lys, but in the context of Pooideae as a whole they share outstandingly high Pro and low Cys and Arg levels; and to this extent the amino acid profiles afford a degree of independent support for MacFarlane's proposal to distinguish Triticeae and Bromeae from the rest of the Pooideae at supertribal level. The amino acid patterns of 2 representatives of the rather distinct tribe Meliceae show closer affinity with those of the Aveneae (high Asx, Ser, Leu, Tyr, Lys and Arg, and low Glx and Pro) than with those of the Agrostideae or Poeae. However, the Meliceae patterns also bear some resemblance to those of the Triticeae and Bromeae (i.e. Triticanae, low Cys and Phe), hinting perhaps at an intermediate taxonomic position between Poanae and Triticanae.

Photosynthetic pathways and caryopsis amino acid patterns

Variation in caryopsis amino acid patterns is superficially correlated with differences in photosynthetic pathway; i.e., those of bamboos, *Oryza*, Pooids, Stipeae (C_3 grasses) can be distinguished statistically as a group from those of chloridoids, C_4 eu-panicoids and andropogonoids (C_4 grasses). However, it is now apparent that this merely reflects the fact that caryopsis amino acid profiles, and photosynthetic pathways, are independently correlated with taxonomy. Table 1 shows that C_3 danthonioids have yielded patterns closer to those of C_4 andropogonoids and eu-panicoids than to those of the C_3 pooids; and in particular, the eu-panicoids, which include C_3, C_4 and intermediate types, have yielded a characteristic eu-panicoid pattern irrespective of photosynthetic pathway. Likewise, the caryopsis amino acid patterns of

Table 2. Amino acid compositions of grass caryopses: taxonomic group means of data in Table 1

Major groups/tribes (no. spp./no. genera)	Amino acid composition (g% total amino acids)																	
	Asx	Thr	Ser	Glx	Pro	Gly	Ala	Cys	Val	Met	Ile	Leu	Tyr	Phe	His	Lys	Trp	Arg
BAMBOOS (3/3)	11.8	4.1	5.2	18.4	5.2	4.7	5.9	1.4	4.9	2.5	3.4	7.8	4.8	5.6	2.5	4.8	0.0	6.9
ORYZOIDS (4/1)	10.1	3.9	5.8	19.0	5.0	4.6	6.0	2.0	5.1	2.4	3.5	8.7	5.7	5.5	2.3	4.6	0.1	5.8
POOIDS	7.6	3.4	5.3	26.9	7.7	4.3	4.7	2.2	3.8	1.7	3.0	7.7	4.1	6.7	2.3	3.9	0.4	4.4
Triticeae (5/4)	5.3	3.2	4.9	31.4	12.7	3.7	3.5	1.7	3.8	1.6	2.9	7.1	3.9	5.6	2.1	3.3	0.1	3.2
Bromeae (4/1)	8.0	3.9	5.4	24.4	11.6	4.6	5.1	1.5	3.6	1.7	3.0	6.5	4.3	5.1	2.3	5.2	0.1	3.8
Agrostideae (25/12)	7.5	3.2	5.4	27.7	6.5	4.1	4.9	2.3	3.8	1.7	3.0	8.0	4.0	7.0	2.3	3.6	0.7	4.5
Aveneae (4/3)	9.6	3.8	5.9	23.1	5.8	4.9	4.8	3.0	4.0	1.7	3.2	8.0	4.6	5.9	2.3	4.6	0.4	4.9
Meliceae (2/2)	9.9	4.1	6.1	20.3	5.1	4.4	6.6	1.6	4.2	2.6	3.4	8.6	5.1	5.1	2.2	4.4	0.1	6.4
Poaceae (16/10)	7.5	3.5	5.2	26.6	7.8	4.7	4.5	2.3	3.8	1.7	2.9	7.3	4.0	7.3	2.3	3.9	0.1	4.3
DANTHONIOIDS (5/3)	6.8	3.5	5.8	27.5	6.7	2.9	7.6	1.6	4.5	2.8	3.4	9.8	4.8	5.5	2.2	2.3	0.1	2.4
CHLORIDOIDS (13/7)	7.0	3.9	5.5	28.6	6.5	3.0	6.3	1.4	4.5	3.5	3.4	8.9	4.6	6.1	2.0	2.5	0.1	2.2
PANICOIDS *sensu lato*																		
Eu-panicoids (17/12)	7.2	3.4	5.9	23.0	8.1	2.4	9.5	1.3	4.5	2.5	3.4	11.7	4.7	6.1	2.1	2.0	0.1	2.3
Andropogonoids (7/7)	7.4	3.1	5.3	21.3	11.2	2.9	10.5	1.3	3.9	2.3	3.0	11.2	3.8	5.6	2.2	2.2	0.1	2.0
Isolated genera, and small groups of doubtful affinities																		
Aristideae (4/1)	5.2	2.9	4.7	30.2	10.9	2.4	6.5	1.3	4.0	3.3	2.9	11.1	4.3	4.9	1.7	1.7	0.2	2.1
Stipeae (8/3)	10.6	4.0	5.3	21.6	5.2	4.6	5.8	1.6	4.0	2.2	3.0	8.3	5.2	5.6	2.4	4.0	0.1	6.5
Triodieae (1/1)	6.1	3.3	4.2	33.5	4.9	2.1	6.1	1.6	4.9	4.3	3.5	10.2	4.1	4.8	1.9	1.9	0.2	2.4
'Oddments' (3/2)	11.7	4.3	5.8	17.7	5.5	4.8	6.4	1.9	4.4	2.2	3.2	8.1	4.4	6.0	2.5	5.3	0.0	5.7

C_4 danthonioids, *Eriachne ovata* and *Tiraphis mollis*, are similar to those of their C_3 relatives.

Amino acid profiles of embryos and endosperms

Bamboos, oryzoids, pooids, Stipeae and some danthonioids have smaller embryos than do the eu-panicoids and andropogonoids [25]. This embryo/endosperm relationship is there quantified in terms of weights and protein contents for a small but diverse sample of grasses (Table 3). The bamboos, *Triticum aestivum*, *Bromus unioloides* and *Avena sativa* have yielded weight ratios between 1:32 and 1:117 and the contribution of their embryos to the overall caryopsis amino acid patterns is evidently negligible. For caryopses representing 'large embryo' groupings the ratios are much lower, with an extreme of 1:5 in *Zea mays*; and it therefore seemed desirable to assess the contribution of embryos to caryopsis amino acid profiles. In the event, Table 4 shows all the embryos sharing a characteristic amino acid profile (high Asx, Thr, Gly, His and Lys, and low Glx, Pro and Phe), which is very different from those representing the rest of the caryopsis (whose pattern is presumably dominated by endosperm). However, comparisons between these results and those of whole caryopsis analyses (cf. Tables 1 and 4) show that the amino acid patterns of endosperms dominate those of the embryos. This is true even in caryopses where large embryos are involved, although there the influence of the embryo's contribution is detectable when the figures are plotted on graphs. For example, the whole caryopsis profile of *Sorghum* is then seen to be closely similar to that of the endosperm, but slightly shifted towards that of the embryo.

Taxonomy and nutritional aspects

Successful cereal crops are characterized by many essential attributes, in addition to their seed protein content and amino acid composition. Nevertheless, the nutritional status of the protein is presumably relevant in searching for potential new crops, and data on seed protein composition allied with taxonomy might help in locating potential donors of useful genes for existing crops.

The protein contents for the present sample of grass caryopses range from 4.0 g % in *Oryza sativa* cv Calrose to 27.5 g % in *Festuca hookerana* (Table 1). In some genera (e.g. *Phalaris*, *Festuca*, *Stipa* and *Danthonia*), the variation is evidently large, while in others (e.g. *Aristida*, *Eleusine* and *Eragrostis*) the variation, at least as manifested in this small sample, is slight. Nevertheless, bamboos, *Oryza*, *Bromus*, Aveneae, Meliceae and 'Oddments' tend to give values of less than 10 g %, while Triticeae, Agrostideae, Poeae, Danthonieae, chloridoids and eu-panicoids range between 10 and 15 g % and *Triodia*, *Aristida* and andropogonoids often exceed 15 g %.

Since amino acid patterns in grass caryopsis proteins are taxonomically predictable, and since the nutritional status of the protein as assessed by nutritionists depends on the essential amino acids [29], it is worth inquiring whether the nutritional quality of the grass caryopsis proteins is also correlated with taxonomic groupings. Table 5 presents the chemical scores derived via two different procedures, the first based on comparisons of essential amino acids with the provisional amino acid scoring pattern of WHO 1973 [29] and the second based on comparisons of A/T ratio (essential amino acids): A/T ratio (egg protein reference) [11]. Except for the sequence of the limiting amino acids, the correlation between the two methods is good. Both procedures indicate that Lys would be the most limiting amino acid in the caryopsis proteins of the danthonioids, *Triodia*, *Aristida*, chloridoids, eu-panicoids and andropogonoids, and the chemical scores are generally low (31–45 % by WHO 1973 reference; 38–57 % by egg reference. Based on the WHO 1973 scoring pattern, Lys is also the limiting amino acid in the *Oryza*, Triticeae, Agrostideae, Meliceae, Poeae and Stipeae, but here the chemical scores are higher (60–84 %); Ile is limiting in bamboos, Aveneae and 'Oddments' (78–85 %), and Val is limiting in *Bromus* (72 %). However, with egg protein as reference, Ile is the most limiting amino acid in caryopses of bamboos, *Oryza*, pooids, Stipeae and 'Oddments' (60–68 %). Thus, insofar as protein quality is concerned, caryopses of danthonioids, *Triodia*, *Aristida*, chloridoids, eu-panicoids and andropogonoids are nutritionally poorer than those of bamboos, *Oryza*, pooids, Stipeae and 'Oddments'.

Caryopses of several non-cereals, some of which grow in arid regions hopelessly unsuitable for existing cereal crops and which have not been subjected to human selection and genetic improvement, have protein contents, amino acid compositions and chemical scores (i.e., nutritional status) similar to, or better than, many of the cultivated cereals [30, 31]. For example, *Bromus* spp.,

Table 3. Embryo/endosperm relationships for some grass caryopses

Species	Weight ratio embryo: endosperm	Protein content (g % fr. wt.) Embryo	Endosperm	Protein contribution by embryo (%)
Bambusa glaucescens	1:32	14.0	5.4	7
Triticum aestivum	1:53	23.6	10.6	4
Bromus unioloides	1:117	28.4	11.1	2
Avena sativa	1:42	24.6	8.6	6
Pennisetum alopecuroides	1:7	12.5	22.3	7
Sorghum vulgare	1:10	13.9	11.0	11
Zea mays	1:5	10.2	10.7	17

Table 4. Amino acid compositions of grass embryos and endosperms

	Amino acid composition (g % total amino acids)																	
	Asx	Thr	Ser	Glx	Pro	Gly	Ala	Cys	Val	Met	Ile	Leu	Tyr	Phe	His	Lys	Trp	Arg
Embryos																		
Bambusa glaucescens	11.9	4.7	4.9	14.8	5.7	5.4	6.5	0.0	5.7	2.0	3.8	7.8	4.5	4.1	4.2	7.3	0.3	6.5
Triticum aestivum	11.5	5.0	5.0	14.7	4.9	6.1	6.9	0.0	5.2	2.3	3.3	7.4	3.7	4.1	3.0	8.8	0.2	7.9
Bromus unioloides	11.6	5.0	5.4	16.0	5.4	6.0	6.5	0.0	5.2	2.3	3.1	7.3	3.8	4.2	3.6	7.2	0.3	7.0
Avena sativa	10.5	4.8	5.3	15.3	4.6	6.1	6.4	0.0	5.3	2.3	3.2	7.2	3.7	4.1	6.1	8.5	0.1	6.6
Pennisetum alopecuroides	10.6	4.2	5.6	16.8	5.4	5.6	6.3	0.0	4.9	2.1	2.8	7.4	3.9	4.1	4.3	6.2	0.3	9.5
Sorghum vulgare	11.6	4.2	5.6	16.7	5.2	5.8	6.3	0.0	5.2	2.0	2.8	7.1	3.7	4.2	3.5	7.2	0.0	8.9
Zea mays	10.6	4.7	5.7	16.0	5.5	5.8	6.9	0.1	5.5	2.3	3.1	7.5	3.8	4.6	3.6	7.4	0.0	7.0
Endosperms																		
Bambusa glaucescens	11.8	4.5	5.0	17.1	5.5	4.9	5.9	0.0	5.4	3.1	3.6	7.7	5.0	5.3	2.7	5.3	0.0	7.2
Triticum aestivum	5.4	3.2	5.0	33.9	11.7	3.5	3.3	0.0	4.4	1.9	3.2	7.1	3.6	5.0	2.4	2.5	0.0	3.9
Bromus unioloides	6.4	3.8	5.2	28.6	12.6	3.9	4.2	0.0	4.7	1.8	3.4	6.3	4.3	4.9	2.1	3.9	0.0	4.0
Avena sativa	9.3	3.6	5.6	23.8	6.7	4.8	5.3	0.0	4.9	2.0	3.7	7.9	4.7	5.5	2.3	4.3	0.0	5.5
Pennisetum alopecuroides	9.7	4.1	5.3	25.1	9.2	2.2	10.6	0.0	5.8	2.3	4.4	4.8	3.7	6.4	2.1	1.7	0.0	2.6
Sorghum vulgare	6.6	3.1	4.5	25.1	9.4	2.0	9.2	0.0	4.5	1.7	3.6	15.2	4.7	5.4	2.0	1.1	0.0	1.9
Zea mays	7.5	3.7	5.0	20.9	10.2	3.1	3.7	0.0	4.6	2.2	3.3	14.0	4.9	5.2	2.8	2.4	0.0	2.9

Table 5. Limiting essential amino acids and protein chemical scores for grass caryopses. Values are based on the mean from Table 1

Grass tribes (no. spp./no. genera)	Limiting amino acids (chemical scores %)	
	WHO 1973*	Egg reference†
BAMBOOS (3/3)	Ile (85)	Ile (63)
	Lys (87)	Val (83)
	Val (98)	Met + Cys (87)
ORYZOIDS (4/1)	Lys (84)	Ile (66)
	Ile (88)	Val (87)
	Thr (98)	Lys (89)
POOIDS (Pooideae)		
Triticeae (5/4)	Lys (60)	Ile (68)
	Ile (67)	Lys (80)
	Val (76)	Val (82)
Bromeae (4/1)	Val (72)	Ile (67)
	Ile (75)	Val (73)
	Met + Cys (91)	Met + Cys (76)
Agrostideae (25/12)	Lys (65)	Ile (64)
	Ile (75)	Val (74)
	Val (76)	Lys (79)
Aveneae (4/3)	Ile (78)	Ile (61)
	Lys (82)	Val (74)
	Val (82)	Lys (92)
Meliceae (2/2)	Lys (80)	Ile (67)
	Ile (85)	Val (79)
	Val (88)	Lys (90)
Poeae (16/10)	Lys (71)	Ile (60)
	Ile (73)	Val (72)
	Val (76)	Lys (84)
DANTHONIOIDS (Danthonieae) (5/3)	Lys (38)	Lys (44)
	Thr (85)	Ile (71)
	Ile/Val (88)	Val (82)
CHLORIDOIDS (13/7)	Lys (45)	Lys (57)
	Ile (85)	Ile (68)
	Val (90)	Val (82)
PANICOIDS *sensu lato*		
Eu-panicoids (17/12)	Lys (36)	Lys (41)
	Ile (85)	Ile (67)
	Thr (85)	Val (81)
Andropogonoids (7/7)	Lys (40)	Lys (49)
	Ile (75)	Ile (64)
	Thr/Val (78)	Val (76)
Isolated genera, and small groups of doubtful affinities		
Aristideae (4/1)	Lys (31)	Lys (38)
	Ile (73)	Ile (62)
	Thr (73)	Val (79)
Stipeae (8/3)	Lys (73)	Ile (61)
	Ile (75)	Val (75)
	Val (80)	Lys (85)
Triodieae (1/1)	Lys (35)	Lys (39)
	Thr (80)	Ile (71)
	Ile (88)	Thr (84)
'Oddments' (3/2)	Ile (80)	Ile (62)
	Val (88)	Val (78)
	Lys (96)	Met + Cys (96)

* With reference to WHO 1973 provisional scoring pattern.

† With reference to egg composition.

Stipa spp., *Nassella trichotoma*, *Anisopogon avenaceus*, *Ehrharta erecta*, *E. calycina* and *Microlaena stipoides* have protein contents that are equivalent to those of cultivated cereals (Table 1). Furthermore, their amino acid compositions and chemical scores are as good as those of the commercial rice and oat varieties, and surpass those of the wheat, barley, rye, *Sorghum* and maize varieties analysed here (Table 1 and 5).

The embryos of grass caryopses, unlike those of the endosperm, have high Lys content (6.2–8.8 g %). In terms of protein chemical score, all grass embryos are probably far superior to the whole caryopses but unfortunately, the embryos occupy small proportions of the caryopses. However, with a better understanding of the physiological and genetic aspects of seed development, it may be possible and useful to transfer the expression of genes for the high Lys protein(s) of embryos to the endosperms [32, 33]. This may be less improbable than it appears at first sight, since some grasses (i.e. bamboos with non-endospermic seeds) may have transferred the endosperm function to the embryo in the natural course of evolution [34].

EXPERIMENTAL

Plant materials. Grass fruits were obtained from CSIRO Australia, or collected from the field. Only mature fruits were analysed, and most of the samples used have subsequently been shown to contain viable seeds. All identities were conscientiously checked with references to appropriate floras.

Preparation for amino acid analysis. Caryopses were individually dissected out to remove glumes, lemmas, paleas and flower remnants. In the case of *Eleusine* spp. and *Sporobolus* spp. which have a flimsy, loose pericarp, the free seeds were used in lieu of caryopses. 5–10 mg samples of caryopses, embryos and caryopses minus embryos, were hydrolysed in 0.15 ml 3N mercaptoethanesulfonic acid in a sealed tube at 110° for 22 hr [35]. After hydrolysis, samples were neutralized with 0.15 ml 2N NaOH, diluted with 2 ml dist. H_2O filtered to remove any residues, then eluted through a 1.5 × 4 cm column of Bio-Rad AG-50W-X2 (100–200 mesh) cation-exchange resin. The column was eluted wih 12 ml dist. H_2O, followed by 12 ml 10 % (w/w) NH_3, soln. The NH_3 soln fraction was collected and evapd to dryness in a rotary evaporator. The sample was recovered in 1.0 ml 2N Na citrate pH 2.2 and 0.1 ml was analysed on a Beckman 119CL amino acid analyser.

Protein content. Protein contents were calculated from total amino acid values, and expressed as g % fr. wt sample.

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