OCCURRENCE OF LEGUMINOUS TREES)

LEGUMES OF THE CERRADO

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ABSTRACT - The Cerrado is a type of savanna vegetation which covers 20% of Brazil. It is an environment with nutrient poor soils. Legumes are one source of nitrogen for agriculture in the Cerrado. There are 59 genera with 548 species of Leguminosae reported to occur in Cerrado vegetation. It is recommended that the search for nitrogen fixing legumes be concentrated in tribes Caesalpinieae and Detarieae and genus Chamaecrista of subfamily Caesalpinioideae, in tribe Mimoseae and genus Enterolobium of subfamily Mimosoideae, and in tribes Dipteryxeae, Dalbergieae, Phaseoleae and Aeschynomene and genera Swartzia, Acosmium and Bowdichia of subfamily Papilinoideae.

Index terms: N₂ fixation, nodules, Rhizobium.

LEGUMINOSAS DO CERRADO

RESUMO - O Cerrado é um tipo de savana que cobre quase 20% do território brasileiro, constituindo-se num ambiente de solos pobres em nutrientes. As leguminosas são uma fonte natural de nitrogênio para a agricultura no Cerrado. Há 59 gêneros e cerca de 548 espécies de leguminosas conhecidas nesta região. A pesquisa sobre leguminosas fixadoras de nitrogênio deve ser concentrada nos seguintes grupos: tribos Caesalpinieae e Detarieae, e no gênero Chamaecrista da subfamília Caesalpinioideae; na tribo Mimoseae e no gênero Enterolobium da subfamília Mimosoideae; nas tribos Dipteryxeae, Dalbergieae, Phaseoleae e Aeschynomene e nos gêneros Swartzia, Acosmium e Bowdichia da subfamília Papilionoideae.

Termos para indexação: Fixação de N₂, nódulos, Rhizobium.

INTRODUCTION

Central Brazil is dominated by a form of savanna vegetation konwn as "Cerrado", sensu lato (s.l.). Within the region other forms of vegetation, such as various types of forests and inundated grasslands, occur, but their presence is a minor element in the area. Due to the Cerrado's dominance, this region is frequently designated as a distinct vegetational province on a world-wide scale, the Cerrado Province (Eiten 1972 and Rizzini 1979).

Recently, there has been renewed interest in agricultural expansion in the Cerrado, s.l., as clearly shown by the estabilishment of the Centro de Pesquisa Agropecuária dos Cerrados near the federal capital, in 1975, and the fourth and fifth Simposia on the Cerrado (Ferri 1977, Marchetti & Machado 1982). This is a logical development following better understanding of conditions in the Cerrado, s.l., region. Adequate light and water combined with the generally excellent physical properties of the soil indicate a large potential for successful agriculture in former areas of Cerrado, s.l., vegetation. The two factors

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most limiting agricultural production in the Cerrado, s.l., are low soil fertility and irregular occurrence of rainfall (Goedert 1982). The former may be overcome by the proper application of various elements including nitrogen (Galvão & Lopes 1982), but the ever increasing costs of these additives will certainly affect agricultural expansion in Central Brazil and the Cerrado, s.l., in the future.

The objective of the present study is to survey the native legume flora of the Cerrado, s.l., vegetation in relation to the probable ability of its members to nodulate and fix nitrogen. This information will facilitate the investigation and use of native legumes in order to improve soil fertility in the Cerrado, s.l., region of Brazil.

CERRADO

Distribution

Cerrado, s.l., vegetation covers approximately 1.8 million square kilometers of Brazil, or about 20% of its land-surface. This is almost the entire state of Goiás, more than half of the states of Minas Gerais, Mato Grosso and Mato Grosso do Sul, and significant portions of the states of Bahia, Maranhão and Piauí. This combined area is approximately 10% greater than the land-surface occupied by the European Economic Community. (Fig. 1).

A portion of the Cerrado, s.l., extends from southern Mato Grosso do Sul into Paraguay, and a detached area of Cerrado, s.l., occurs in Bolivia. Aside from these two relatively insignificant areas of Cerrado, s.l., in Bolivia and Paraguay, Cerrado, s.l., vegetation occurs only in Brazil and nowhere else in the world.

Physionomy and Classification

The overall appearance of Cerrado, s.l., vegetation is highly variable, ranging from open grasslands, with only small, scattered shrubs whose height is equal to or less than that of the grass and forb layer, all the way, to tall, dense forms which are frequently considered as a type of forest. But Cerrado, s.l., is easily distinguished from all other types of savanna by the characteristic features of the woody elements in the vegetation (Warming 1973, Eiten 1972 and Eiten 1982). The trees and shrubs generally have rather large, stiff leaves or large compound leaves with tiny to large leaflets. Soft, hairy or mesomorphic leaves are infrequent. Frequently they have fewer branches and consequently more open crowns than are common in trees and shrubs of tropical mesophytic forests or of temperate forests. Branches are often rather thick right to their tips, and the bark of trunks and branches is usually very thick and furrowed. The characteristic which lends itself to instant recognition of a Cerrado, s.l., is the tortuosity of the trees and shrubs. This tortuosity results from several common aspects of growth: frequent death of the stem and branch apices; assumption of apical growth by a lateral branch; commonly a large angle between the mother axes and their branches; and that the growth of new wood and thick bark obscures the former apices and the fact that the new apices have arisen from lateral branches. (Fig. 2).

The classification and description of Cerrado, s.l., vegetation has traditionally been on a physionomic basis related to the density and height of the woody elements (Eiten 1972, Eiten 1979, Coutinho 1978). Eiten (1972) has summarized much of the confusion in the classification of the Cerrado, s.l., vegetation. The rural inhabitants of Central Brazil have, in my opinion, devised the most satisfactory classification of the Cerrado, s.l., vegetation into five categories: Cerrado, Cerrado, sensus stricto (s.s.);

Campo Cerrado; Campo Sujo; and Campo Limpo. These divisions were used by Goodland (Goodland 1971, Goodland & Ferri 1979) in his now classical phytosociological study of 110 stands of Cerrado, s.l., in western Minas Gerais. Unfortunately, he did not encounter Campo Limpo in that region, and so did not include it in his study. He clearly demonstrated that the Cerrado, s.l., vegetation forms a physionomic gradient which can be conveniently divided into the above five categories based on the characteristics derived from the arboreal element of the vegetation (Table 1). It is clearly evident from Goodland's data that the Cerrado, s.l., forms a continuous gradient often difficult to classify because of its overlapping characteristics. Campo Limpo is defined as a tree-less grassland with only a few, scattered shrubs whose height is equal to or less than that of the grass and forb layer. As a corollary of this definition, Campo Limpo vegetation should give very low or zero values for the characteristics presented in Table 1. (Fig. 3).

TABLE 1. Characteristics of Cerrado, s.l., vegetation in western Minas Gerais, adapted from Goodland (1971).

Category	Cerradão	Cerrado (s.s)	Campo Cerrado	Campo Sujo
Canopy (%)	46	19	3	1
	(15-85)	(1-55)	(0-15)	(0-2)
Tree height (m)	9	6	4	3
	(6-18)	(4-8)	(3-6)	(1-5)
Trees/ha	3215	2253	1408	849
	(1631-4925)	(836-3976)	(335-2928)	(226-2070)
Basal area/ha (cm² x 10³)	312,8	167.6	76.1	29.8
	(202,9-513,3)	(62.2-253.4)	(16.9-141.7)	(9.7-60.0)
Tree species/ha	55	43	36	31
	(40-72)	(26-60)	(18-52)	(19-43)

Species Density

As in many other studies on the Cerrado, s.l., those of species density are few and difficult to compare. In areas of Cerrado, s.s., in the state of São Paulo and near the Federal Capital, Brasília, there were approximately 300 species of vascular plants per ha (Eiten 1982) and 320 (Heringer 1971), respectively. Eiten (1978) has found in only 0.1 ha of Cerrado, s.s., near Brasília 230 species of vascular plants! In a few tens of square km of Cerrado, s.s., the vascular flora may reach as many as 700-800 species (Warming 1973, Eiten 1971). The Cerrado, s.l., vegetation has a very high species diversity which is comparable to that of Amazon forests, consequently a very rich flora. The Leguminosae were the most important family in frequency and species number encountered by Goodland & Ferri (1979) in his study.

Rainfall

The annual rainfall in the Cerrado, s.l., varies from 1,000 to 1,700 mm/year (Goedert 1982). The distribution of the precipitation is strongly seasonal. There is an annual wet season of 6 to 8 months which extends from about October to April, and a dry season of 4 to 6 months which stretches from approximately May to September. The coolest period of the year coincides with the driest.

More than 90% of the total annual precipitation occurs during the wet season which generally begins between the fifteenth of September and the fifteenth of October. The rains are usually of short duration and very intense. Frequently, there occur, during the wet season, periods of 8 to 22 days or more without rain; these periods are very unpredictable, and are called the "veranico".

Soil Fertility

In general, the soils of the Cerrado, s.l., are oxisols of various types, the most frequent of which are the red latosols (Goedert 1982). The soils are deep and well drained with good structure; consequently, they have a low capacity to retain water and are, therefore, highly leached with a low natural fertility. Because of their excellent physical properties, they are well adapted to mechanical cultivation.

The most extensive study of soil characteristics in relation to the categories of Cerrado, s.l., vegetation is that of Lopes & Cox (1977). They sampled the topsoil of 520 sites scattered over approximately one third of the Cerrado, s.l., region. Their results (Table 2) show a high correlation between vegetation type and soil fertility, low stature-low fertility, high stature-high fertility. The physionomic gradient is matched by a fertility gradient.

In general, the Cerrado, s.l., soils have a very low fertility (Table 2). The cation exchange capacity is very low, and consequently the sum of exchangeable bases (K, Ca and Mg) is also low. The acidity is relatively high, and as a result the percent saturation of Al is usually above 50% and the level of P is low. The high acidity and the levels of Al and P may be strongly influenced by the low level of Ca. The results of others (Eiten 1972, Goodland & Ferri 1979, Ribeiro et al. 1981, Haridasan 1982, Miranda et al. 1982) vary considerably from those of Lopes & Cox (1977), but the general correlation of the soil fertility gradient and the physionomic gradient persists. This variation of soil fertility in the Cerrado, s.l., is a natural consequence of the immense area of Cerrado, s.l., and the consequent variation in parent materials.

TABLE 2. Mean topsoil characteristics of four vegetation types of Cerrado, s.l., from 520 sites in central Brazil, adapted from Lopes & Cox (1977).

	Campo Limpo	Campo Cerrado	Cerrado (s.s)	Cerradão
pH (H ₂ O)	4.87	4.94	5.00	5,14
Organic matter (%)	2,21	2.33	2,35	2.32
Exch, Ca (meq/100 ml)	0.20	0.33	0.45	0.69
Exch. Mg (meq/100 ml)	0.06	0.13	0.21	0.38
Exch. K (meg/100 ml)	0.08	0.10	0.11	0.13
Exch. Al (meg/100 ml)	0.74	0.63	0.66	0.61
Eff. CEC (meg/100 ml)	1.08	1.19	1.43	1.81
Al saturation (%)	66	58	54	44
Extr. P	0.50	0.51	0.94	2.10
Extr. Zn	0.58	0.61	0.66	0.67
Extr. Cu	0.60	0.79	0.94	1.32
Extr. Mn	5.40	10,30	15,90	22.90
Extr. Fe	35.70	33.90	33.00	27.10
Clay (%)	33	36	34	34
Silt (%)	20	16	15	16
Sand (%)	46	48	51	53

LEGUMES OF THE CERRADO

In order to determine all the legumes known from the Cerrado, s.l., data were gathered from two sources: the herbarium of the Universidade de Brasília and from the literature. The Universidade de Brasília, with approximately 90,000 specimes in its herbarium, undoubtedly has the most representative herbarium for the Cerrado, s.l., in Brazil. Since the founding of the herbarium in 1963, it has been the central focus of taxonomic research in the Cerrado, s.l. The family *Leguminosae* was examined, and if any species was represented by specimes labeled as coming from Cerrado, s.l., vegetation, then the genus and species were considered to occur in the Cerrado, s.l. Also, any mention of habit was noted.

The principal literature on the Cerrado, s.l., was also searched. There were three useful types: 1) taxonomic check lists (Ferri 1969, Goodland 1970, Eiten 1971, Rizzini 1971, Heringer et al. 1977); 2) taxonomic revisions (Irwin & Barneby 1978, 1982, Ferreira & Costa 1979); and 3) ecological studies (Heringer 1971, Ratter et al. 1973, 1977, Warming 1973, Goodland & Ferri 1979, Cesar 1980, Ratter 1980, Ribeiro et al. 1981).

The genera and species were then compared to the literature on nodulating legumes (Allen & Allen 1981, Halliday & Nakao 1982, University of Hawaii 1983) and lists of recently discovered nitrogen fixing legumes (S.M. Faria, E.M.R. da Silva, A.A. Franco & J. Döbereiner, pers. comm.) to discover which had previously been reported as nodulated. Doubtful and questionable reports were excluded.

Table 3 presents the results of these searches. Seventy two genera and five hundred and twenty seven species of legumes are known or reported from the Cerrado, s.l. 65% of the genera have one or more species reported as nodulators, and 12% of the species are reported as nodulators. Almost none of the species reported to nodulate were examined in the Cerrado, s.l., or Brazil. The majority are either wide spread species which were investigated elsewhere or species under cultivation.

Taxonomic Organization

In 1978, the first International Legume Conference was held under the auspices of the Royal Botanic Gardens, Kew. Two thirds of the results of this conference were published in Advances in Legume Systematics (Polhill & Raven 1981). In the first part, a new classification of the subfamilies, tribes, subtribes and genera of legumes is presented. This classification is a synthesis of the knowledge of 28 of the leading taxonomists now actively working on the systematics of the legumes.

The classification is very similar to and partially based on that of Bentham (1865), as modified by Hutchinson (1964). Generally, most of the changes from the classifications of Bentham and of Hutchinson are minor reorganizations of tribes, subtribes and genera, to reflect recently discovered information in such areas as chemistry and cytology and the latest systematic studies on various scattered taxa within the legumes.

Some of the final decisions did support important existing dispositions or created new fundamental realignments. One of the most basic desicions was to maintain the grouping as a single family, with three subfamilies. Much of the newer evidence over-whelmingly supports this arrangement. Between the subfamilies, the most significant change was the transfer of tribe Swartzieae from subfamily Caesalpinioideae to a basal position in subfamily Papilionoideae. This repositioning is supported by wood anatomy, by nodulation proclivity and by chemistry, as well as various aspects of morphology.

TABLE 3. Genera of Leguminosae known or reported to occur in Cerrado, s.l., vegetation with their total number of species and the number in the Cerrado, s.l., with the number of species reported as positive or negative nodulators and their habit in the Cerrado, s.l. (T = tree; S = shrub; H = herb; V = vine).

	81-	- f C'		Nodu	lation Rep	orts	
Genus		of Species	- Wo	orid	Cerra	do (s.l.)	·
	World	Cerrado (s.l.)	Positive	Negative	Positive	Negative	Habit
Abrus Adans.	17	1	5	-	1	, -	
Acacia Mill.	1200	4	200	11	1	•	TS
Acosmium Schott in Spreng	16	6	1	-	-	-	TS
Aeschynomene L.	150	7	44	•	4	-	HS
Amburana Schwacke & Taub.	1-2	1	•	•	-	-	-
Andira	20	8	4	1	1	-	TS
Arachis L.	60	5	10	•	1	•	HS
Bauhinia L.	250	17	0	27	•	•	TS
Bowdichia Kunth	4	3	1	1	1	1	7
Caesalpinia L.	100	1	•	15	•	1	7
Calliandra Benth,	200	9	12	3		1	TSH
Calopogonium Desv.	8	2	3			•	
Camptosema Hook, & Arn.	12	8					
Cassia L.	30	1					Ì
Cenostigma Tul.	6	2	_	-	_	_	TS
Centrolobium Mart, ex Benth.	6	1	_	_		_	- '`
Centrosema (DC.) Benth.	45	9	8	_	3	-	٠,
Chaetocalyx DC.	12	2		2	-	-	Ĭ
Chamaecrista Moench.	250	137	-	. •	•	•	SHI
Clitoria L.	70	2	8				
Collaea DC.	3	4	0	•	1	•	SH
	25-30	10	-	-	•	-	
Copaifera L. Cratylia Mart. ex Benth.		2	1	1	•	•	TS
-	5 600	18	1 145	-	1	•	S\
Crotalaria L.		• =		•	8	-	SH
Dalbergia L.f.	100	7	15	1	1 -	•	٦
Desmodium Desv.	300	9	76	٠	7	•	SH
Dialium L.	40	1	2	2	1	-	٠.
Dimorphandra Schott in Sprengel	25	3	1	•	-	•	
Dioclea Kunth.	30	6	2	•	•	-	S\
Dipteryx Schreb.	10	2	-	1	•	•]
Diptychandra Tul.	3	2	•	•	•	-	5
Enterolobium Mart,	5	4	3	•	-	•	1
Eriosema (DC.) G.Don	130	26	29	•	3	•	SH
Erythrina L	108	_4	30	•	1	•	٦
Galactia P. Br.	55	21	6	-	•	•	SV
Harpalyce Moc. & Sesse ex DC.	20	4	•	•	-	•	\$
Hymenaea L.	16	4	1	1	1	1	7
Indiofera L.	700	3	193	3	1	0	SH
Inga Mill.	350	3	14	4	-	•	TS
Lonchocarpus Kunth	100	2	11	1	-	•	-
Luetzelburgia Harms	6	1	•	•	•	-	•
Lupinus L.	200	3	56	•	•	•	H
Machaerium Pers.	120	10	5	•	2	•	TS
Mimosa L.	400-450	50	25	3	6	•	
Myrocarpus Allem.	4	1	1	-	•	-	

TABLE 3. Continuation

			Nodulation Reports		orts		
Genus	No.	of Species	- Wo	orld	Cerra	do (s.l.)	
	World	Cerrado (s.l.)	Positive	Negative	Positive	Negative	Habit
<i>Parkia</i> R. Br.	40	1	5	2	_	•	T
Peltogyne Vogel	23	2	•	1	•	•	Т
Periandra Benth.	6	6	-	-	•		SV
Phaseolus L.	50	17	21	-		•	VSH
Piptadenia Benth.	15	4	1	2	•	•	Ţ
Pithecellobium Mart.	20	2	13	1	-	•	-
Plathymenia Benth.	4	2	•	•	-	•	Т
Platypodium Vogel	1-2	3	•	•	-	•	TS
Poecilanthe Benth.	7	1	-	•	•	•	-
Poiretia Vent.	6	3	•	•	-	•	S
Pterocarpus Jacq.	20	1	14	•	-	•	•
Pterodon Vogel	6	2	-	•	:	•	т
Rhynchosia Lour.	200	4	57	-	1	•	VH
Riedeliella Harms	3	1	-	•	-	•	S
Schranckia Willd.	19	1	2	-	•	•	S
Sclerolobium Vogel	35	4	2	•	1	-	Т
Senna Mill.	240	28					SHT
Strynphnodendron Mart.	20	8	2	-	1	•	TS
Stylosanthes Sw.	25	16	18	•	8	-	SH
Swartzia Schreber	135	8	10	•	1	•	TS
Sweetia Sprengel	1	1	-	•	•	•	•
Tephrosia Pers.	400	4	95	-	1	-	Н
Tipuana (Benth.) Benth.	1	1	1	•	1	•	-
Vatairea Aubl.	7	1	-	-	•	-	Т
Vigna Savi	150	1	46	-	-	-	•
Zornia J.F. Gmel.	80	7	12	•	2	•	HS

The order of presentation of subfamilies, tribes and genera has been drastically altered to agree with the idea that the most primitive member of a taxon should appear first in a linear sequence. So, the subfamilies are presented in the following sequence: Caesalpinioideae, Mimosoideae and Papilionoideae.

Subfamily Caesalpinioideae

Within the Caesalpinioideae, three basic lines have been recognized without any apparent extant connections between them (Polhill et al. 1981). The basal elements of these radiations are the Gladitsia group of genera, subtribe Ceratoniinae of tribe Cassieae and subtribe Cercidinae of tribe Cercideae. Gladitsia and Gymnocladus exhibit a number of primitive characters: functionally unisexual flowers, scarcely differentiated tepals, stigma bilobed and fruit which dehisce like a follicle. These genera are undoubtedly in a basal position on the primary radiation of the family which gave rise to the Mimosoideae and Papilionoideae. (Fig. 4).

TABLE 4. The Cerrado, s.l., genera of subfamily Caesalpinioideae (Leguminosae) in systematic order and numbered according to Polhill & Raven (1981).

1. tribe CAESALPINIEAE 1c. Sclerolobium group Sclerolobium Vogel 1.5 Diptychandra Tul. 1e. Caesalpinia group 1.21 Cenostigma Tull. 1,25 Caesalpinia L. 1h. Dimorphandra group 1.43 Dimorphandra Schott in Sprengel 2. tribe CASSIEAE 2b subtribe Dialijnae IB Dialium L. 2d. subtribe Cassiinae 2.16 Cassia L. emend Gaert. 2,17 Senna Mill. 2.18 Chamaecrista Moench 3. tribe CERCIDEAE subtribe Bauhiniinae 3.4 Bauhinia L. 4. tribe DETARIEAE 4c. Hymenaea group 4.22 Peltyogyne Vogel

Flowers of *Ceratonia* are unisexual, lack petals and have an exposed disc which produces nectar. This genus is in a basal position to the less extensive radiation which gave rise to the assemblage of *Cassia*, s.l. (Polhill et al. 1981).

Cercideae have a calyx tube and a well developed corolla, but their bilobed leaves with palmate nervation and their seeds with the lens above the micropyle rather than below are characteristics encountered nowhere else in the legumes. Also, Cercis is the only genus in the family to have retained the basic chromosome number, n = 7 (Goldblatt 1981). This relatively limited radiation has led to the genus Bauhinia (Polhill et al. 1981).

Tribe Caesalpinieae comes first in the linear order because it has the most primitive genera in the family, Gleditsia and Gymocladus, as members. In the Cerrado, s.l., it is represented by five genera and twelve species (Tables 3 and 4). Two genera, Sclerolobium and Dimorphandra, are reported as nodulators; one, Caesalpinia, as a non-nodulator; and two, Diptychandra and Cenostigma, have not been examined. The most primitive members of the tribe are not present in the Cerrado, s.l., but scattered members of the other major groupings are represented. Sclerolobium and Diptychandra are members of the Sclerolobium group of genera which occupy a central position within the tribe intermediate between subfamily Papilionoideae, the Caesalpinia group and the tribe Detarieae. The Caesalpinia group is repre-

4.23 Hymenaea L.

4.43 Copaifera L.

4e. Detarium group

sented by Cenostigma and Caesalpinia, while the Dimorphandra group is represented only by the genus Dimorphandra. The latter group is important as the connecting link to subfamily Mimosoideae. The tribe is not richly represented by species in the Cerrado, s.l., but all of its various levels of advancement and more important, pivotal generic groups are each sparsely represented.

The next tribe in linear order (Table 4) is Cassieae. This is the radiation which has resulted in Cassia, s.l. Irwin & Barneby (1981) have significantly reorganized the tribe. They created five subtribes which represent the levels of advancement attained within the tribe, and the ultimate subtribe, Cassiinae, is Cassia, s.l., of Bentham (1871), divided into three genera, Cassia L. emend Gaertner, s.s., Senna Mill. and Chamaecrista Moench. Rizzini (1971) has reported that Dialium guianensis (Aubl.) Sandw. is a constituent of Cerrado, s.l., vegetation, but Bentham (1870) reported it to occur only in forests of Amazônia and of coastal Bahia. For this reason, I doubt the report of its occurrence in Cerrado, s.l., vegetation. Consequently, this radiation is represented in the Cerrado, s.l., only by Cassiinae. Its species comprise 31% of the legume flora of the Cerrado, s.l. Irwin and Barneby's generic reorganization (1982), based on floral characters, is significant because the non-nodulators occur in Cassia, s.s., and Senna and the nodulators in Chamaecrista (Corby 1981, Irwin & Barneby 1982); the systematic arrangement, based on morphological characters, corresponds with the ability or lack of it to nodulate. Chamaecrista, with 137 species in the Cerrado, s.l., is dominated by shrubs and herbs with few trees.

Tribe Cercideae is the third major radiation within the Caesalpinoideae. It is even more limited than the Cassieae; two levels of advancement have been recognized within it, subtribe Cercidinae, the more primitive, and subtribe Bauhiniinae, the more advanced (Wunderlin et al. 1981). Bauhinia is the only member of the tribe known in the Cerrado, s.l., but it has been reported to be a non-nodulator.

The final tribe, *Detarieae*, in a linear order with representatives in the Cerrado, s.l., is part of a secondary radiation which has concentrated on co-adaptation with animals and consequently has great variation in its floral structures (Cowan & Polhill 1981). Some the largest, finest legume trees in the Cerrado, s.l., occur in this tribe, species of *Copaifera* and *Hymenaea*. The third Cerrado, s.l., genus of this tribe, *Peltyogyne*, has been reported to be a non-nodulator. The nodulation status of *Copaifera* and *Hymenea* is unclear; *C. officinalis* (Jacq.) L and *H. courbaril* L. have been reported on different occasions to be nondulators or non-nodulators (Allen & Allen 1981).

In the Caesalpinioideae, the genera and species found are the more advanced ones in the tribe. The Cassiinae have undergone explosive radiation in the Cerrado, s.l., and dominate all the other genera with 79% of the Caesalpinoideae species.

Subfamily Mimosoideae

The subfamily Mimosoideae, with approximately one third as many genera as the Caesalpinoideae, is organizationally simpler. There are three principal groups within the Mimosoideae, the tribes Mimoseae, Acacieae and Ingeae (Table 5, Elias 1981). The Mimoseae is the least advanced of the three, with various phenetic links with the Dimorphandra group of Caesalpinioideae. Its members are frequent in the Cerrado, s.l., and commonly trees of low stature. It has been broken up into a series of twelve generic groups based on complexes of characters (Lewis & Elias 1981). The Plathymenia group consists solely of the South American genus Plathymenia which has characteristics in common with the Entada group and links to the Dimorphandra group. The Piptadenia group is also apparently linked more or less directly to the Dimorphandra group. The group is held together by only two characters, compound pollen and a style tip narrowed to a small porate stigma, but is otherwise very diverse in its floral structure and could

TABLE 5. The Cerrado, s.l., genera of subfamily Mimosoideae in systematic order and numbered according to Polhill & Raven (1981).

- 1. tribe PARKIEAE
 - 1.2 Parkia R. Br.
- 3. tribe MIMOSEAE
 - 3g. Plathymenia group
 - 3.14 Plathymenia Benth.
 - 31. Piptadenia group
 - 3.19 Stryphnodendron Mart.
 - 3.21 Piptadenia Benth.
 - 3.27 Mimosa L.
 - 3.28 Schranckia Willd.
- 4. tribe ACACIEAE
 - 4.2 Acacia Mill.
- tribe INGEAE
 - 5.2 Inga Mill.
 - 5.6 Enterolobium Mart.
 - 5.7 Calliandra Benth.
 - 5.8 Pithecellobium Mart.

be divided into two groups based on seed and fruit characters (Lewis & Elias 1981). Stryphnodendron and Piptadenia form a pair of genera with Stryphnodendron, most similar to the Dimorphandra group. Mimosa and Schranckia form a second more advanced pair, with phenetic links between Piptadenia and Mimosa. Stryphnodendron and Schrankia are reported as nodulators, while Piptadenia and Mimosa are reported to have both nodulating and non-nodulating species.

Acacieae and Ingeae are the more advanced groups, and they are closely related, separated only by free filaments in Acacieae and united filaments in the Ingeae. Acacieae consists of but tow genera: Faidherbia A. Chev., which is monotypic and endemic to tropical and subtropical Africa, and Acacia (Vassal 1981). Acacia is pantropical with about 1,200 species of which over half are found in Australia. Acacia is predominately a nodulator, but does have various non-nodulated species. It is represented in the Cerrado, s.l., by only four species.

Tribe Ingeae is a serious taxonomic problem (Nielsen 1981). Generic boundaries within this tribe have fluctuated wildy and are still uncertain for some genera. Three of the Cerrado, s.l., genera, Inga, Calliandra and Pithecellobium, are reported to have nodulating and non-nodulating species. Enterlobium is known so far to have only nodulating species, and is also very similar to Albizia Durazz. where its species could be accommodated easily (Nielsen 1981).

Elias (1981) has pointed out the anomalous character of tribe *Parkieae*. *Pentaclethra* and *Parkia* are joined together in the tribe by their united, imbricated sepals. *Pentaclethra* is one of the most primitive genera in the subfamily, and *Parkia* is one of the most advanced, probably an off-shoot of the *Ingeae* (Elias 1981). One species of *Parkia* occurs in the Cerrado, s.l.

The Mimosoideae has all of its main lines of radiation represented in the Cerrado, s.l. Although its species total is approximately 50% greater than that of the Caesalpinioideae, in the Cerrado, s.l., it only

has 42% as many species as the *Caesalpinioides*. Its larger genera, that is *Acacia* with 1,200 species, *Mimosa* with 400-450 species and *Inga* with approximately 350 species, have not explosively radiated into the Cerrado, s.l., as *Chamaecrista* has.

Subfamily Papilionoideae

The subfamily *Papilionoideae*, with twice as many genera and two and a half times as many species as the *Caesalpinioideae* and *Mimosoideae* combined, has a more complex and ramified radiation. In the last few years, there has been a general grouping of tribes into five main lines: the tribe *Sophoreae*, the genistoide alliance, the galegoid complex, the advanced tropical tribes and the temperate epulvinate series (Polhill et al. 1981, Polhill 1981).

The Sophoreae is the diverse basal group which is linked, via tribe Swartzieae, to the Sclerolobium group of tribe Caesalpinieae (Polhill et al. 1981, Polhill 1981). The Swartzieae, in their flower structure, are equal to the Caesalpinioideae, but their wood anatomy, nodulation and chemistry link them intimately to the Papilionoideae (Cowan 1981, Polhill 1981, Polhill et al. 1981). The Swartzieae and the Sophoreae are the grouping of genera with free stamens. In the Sophoreae, there is a general trend from the Caesalpinioideae androecium and corolla to that typical of the Papilionoideae, with all of the various intermediate grades present.

The Swartzeae are represented only by the genus Swartzia in the Cerrado, s.l. (Table 6). The Sophoreae are reported to be represented by six genera. The Sophoreae can be divided into three general levels of increasing flower specialization (Polhill 1981 a): 1) flowers regular, Cadia group with Acosmium and Myrocarpus in the Cerrado, s.l.; 2) flowers with the vexillum differentiated and the other four petals more or less equal, Myroxylon group with Sweetia, Luetzelburgia and Amburiana; and 3) flowers with progressive differentiation of the wings and keel-petals, Dussia group with Bowdichia.

The huge galegoid complex dominates the center of the subfamily. It is separated from the Sophoreae by union of the stamens, presence of canavanine and general stabilization of the base chromosome number at x = 11 or 10 in the tropical woody members (Polhill et al. 1981). The Cerrado, s.l., members of the complex are from the tribes Dipteryxeae, Dalbergieae and Abreae. Dipteryxeae with Dipteryx and Pterodon in the Cerrado, s.l., and Dalbergieae with nine genera are typical members of the complex. Their genera are important constituents of the arboreal flora and produce some of the finest quality woods for cabinet making. The Abreae with but a single genus, Abrus, are considered to be an outlier of the complex (Polhill 1981 b). The only member of the genus known rarely from the Cerrado, s.l., is A. precatorius L. whose origin is uncertain and often considered as an Asian species introduced into the New World (Bentham 1859-62).

The temperate epulvinate series is easily distinguished by absence of the basal foliar pulvinus, closure of the vascular system and leaves tending to be distichous and with phloem transfer cells (Polhill et al. 1981). As its name indicates, practically all of its members are temperate and also mainly herbaceous. The series is absent from the Cerrado, s.l., and so will not be treated further.

The remainder of the pulvinate series (the advanced tropical tribes) can be subdivided into a core, the *Tephrosieae*, and a series of advanced, mainly tropical tribes which cluster about it. The group as a whole shows increased specialization and variation in floral structure and reduced variation in root nodules, leaves, inflorescences, fruits, seeds and seedlings (Polhill et al. 1981). The *Tephrosieae*, as traditionally

2.

tribe SWARTZIEAE

1.2 Swartzia Schreber

tribe SOPHOREAE

TABLE 6. The Cerrado, s.l., genera of subfamily Papilionoideae (Leguminosae) in systematic order and numbered according to Polhill & Raven (1981).

2.	tribe 5	OPHOREAE
		2a. <i>Cadia</i> group
	2.2	Acosmium Schott in Sprengel
	2.3	Myrocarpus Allem
		2b. Myroxylon group
	2.10	Sweetia Sprengel
	2,11	
		Luetzelburgia Harms
	2.13	Amburana Schwacke & Taub.
		2g. Dussia group
	2.34	Bowdichia Kunth
3.	tribe D	IPTERYXEAE
	3.1	Dipteryx Schreb.
	3.3	Pterodon Vogel
4.	tribe D	ALBERGIEAE
.,	4.1	Andira A.L. Juss.
	4.3	Vatairea Aubl.
	4.5	
		Machaerium Pers.
	4.6	Dalbergia Linn, f.
	4.8	Centrolobium Mart, ex Benth.
	4.10	Pterocarpus Jacq.
	4.11	Tipuana (Benth.) Benth.
	4.12	Platypodium Vogel
	4.17	Riedeliella Harms
5.	tribe A	BREAE
	5.1	Abrus Adans.
6.	triba T	EPHROSIEAE
	11106 1	
٥.	ti ibe i	Lonchocarpus Kunth.
.	tinge i	Lonchocarpus Kunth.
.	tibe i	Poecilanthe Benth.
.		<u>=</u> '
8.		Poecilanthe Benth.
		Poecilanthe Benth. Tephrosia Pers.
8.	tribe IN 8,2	Poecilanthe Benth. Tephrosia Pers. IDIGOFEREAE Indigofera L.
	tribe IN 8,2	Poecilanthe Benth. Tephrosia Pers. IDIGOFEREAE
8.	tribe IN 8.2 tribe D	Poecilanthe Benth. Tephrosia Pers. IDIGOFEREAE Indigofera L.
8.	tribe IN 8,2	Poecilanthe Benth. Tephrosia Pers. IDIGOFEREAE Indigofera L. ESMODIEAE
8.	tribe IN 8.2 tribe D	Poecilanthe Benth. Tephrosia Pers. IDIGOFEREAE Indigofera L. ESMODIEAE subtribe Desmodiinae
8.	tribe IN 8.2 tribe D	Poecilanthe Benth. Tephrosia Pers. IDIGOFEREAE Indigofera L. ESMODIEAE subtribe Desmodiinae Desmodium Desv.
8.	tribe IN 8.2 tribe D 9.9 tribe Pl	Poecilanthe Benth. Tephrosia Pers. IDIGOFEREAE Indigofera L. ESMODIEAE subtribe Desmodiinae Desmodium Desv. HASEOLEAE 10a. subtribe Erythrininae
8.	tribe IN 8.2 tribe D	Poecilanthe Benth. Tephrosia Pers. NDIGOFEREAE Indigofera L. ESMODIEAE subtribe Desmodiinae Desmodium Desv. HASEOLEAE 10a. subtribe Erythrininae Erythrina L.
8.	tribe IN 8.2 tribe D 9.9 tribe Pl	Poecilanthe Benth. Tephrosia Pers. IDIGOFEREAE Indigofera L. ESMODIEAE subtribe Desmodiinae Desmodium Desv. HASEOLEAE 10a. subtribe Erythrininae Erythrina L. 10b. subtribe Diocleinae
8.	tribe IN 8.2 tribe D 9.9 tribe Pl 10.1	Poecilanthe Benth. Tephrosia Pers. NDIGOFEREAE Indigofera L. ESMODIEAE subtribe Desmodiinae Desmodium Desv. HASEOLEAE 10a. subtribe Erythrininae Erythrina L. 10b. subtribe Diocleinae Dioclea Kunth
8.	tribe IN 8.2 tribe D 9.9 tribe Pl 10.1 10.10 10.17	Poecilanthe Benth. Tephrosia Pers. IDIGOFEREAE Indigofera L. ESMODIEAE subtribe Desmodiinae Desmodium Desv. HASEOLEAE 10a. subtribe Erythrininae Erythrina L. 10b. subtribe Diocleinae Dioclea Kunth Camptosema Hook, & Arn,
8.	tribe IN 8.2 tribe D 9.9 tribe Pl 10.1 10.10 10.17 10.18	Poecilanthe Benth. Tephrosia Pers. IDIGOFEREAE Indigofera L. ESMODIEAE subtribe Desmodiinae Desmodium Desv. HASEOLEAE 10a. subtribe Erythrininae Erythrina L. 10b. subtribe Diocleinae Dioclea Kunth Camptosema Hook. & Arn. Cratylia Mart. ex Benth.
8.	tribe IN 8.2 tribe D 9.9 tribe Pl 10.1 10.10 10.17 10.18 10.19	Poecilanthe Benth. Tephrosia Pers. IDIGOFEREAE Indigofera L. ESMODIEAE subtribe Desmodiinae Desmodium Desv. HASEOLEAE 10a. subtribe Erythrininae Erythrina L. 10b. subtribe Diocleinae Dioclea Kunth Camptosema Hook. & Arn. Cratylia Mart. ex Benth. Collaea DC.
8.	tribe IN 8.2 tribe D 9.9 tribe Pl 10.1 10.10 10.17 10.18	Poecilanthe Benth. Tephrosia Pers. IDIGOFEREAE Indigofera L. ESMODIEAE subtribe Desmodiinae Desmodium Desv. HASEOLEAE 10a. subtribe Erythrininae Erythrina L. 10b. subtribe Diocleinae Dioclea Kunth Camptosema Hook. & Arn. Cratylia Mart. ex Benth.

10.21 Calopogonium Desv.

10f. subtribe Clitoriinae

10.45 Centrosema (DC.) Benth.

10.46 Periandra Benth.

10.47 Clitoria L.

10g. subtribe Phaseolinae

10.65 Vigna Savi

10.71 Phaseolus L.

10h. subtribe Cajaninae

10.81 Rhynchosia Lour.

10,82 Eriosema (DC.) G. Don

14. tribe AESCHYNOMENEAE

14a, subtribe Ormocarpinae

14.6 Chaetocalyx DC.

14b, subtribe Aeschynomeninae

14.8 Aeschynomene L.
14d. subtribe Poiretiinae

14.19 Poiretia Vent.

14.20 Zornia J.F. Gmel.

14e. subtribe Stylosanthinae

14.24 Stylosanthes Swartz

14.25 Arachis L.

24. tribe BRONGNIARTIEAE

24.2 Harpalyce Moc. & Sesse ex DC.

29. tribe CROTALARIEAE

29.6 Crotalaria L.

32. tribe GENISTEAE

32a. subtribe Lupininae

32.1 Lupinus L.

organized into genera, have a number a inseparable genera (Geesink 1981), and their reorganization is continuing. Around the Tephrosieae are various advanced tribes of which five are found in the Cerrado, s.l.: Indigofereae, Desmodieae, Phaseoleae, Aeschynomeneae and Brongniartieae. These are principally New World tribes except for Phaseoleae that is pantropical. Of the five tribes, it has the most representatives in the Cerrado, s.l., with fourteen genera which are either vines, shrubs or herbs except Erythrina which is reported to have four arboreal species. Next in importance in the Cerrado, s.l., is the Aeschynomeneae with six genera. There is special emphasis on members of this tribe in the Brazilian agricultural research because some genera, especially Stylosanthes, offer promise in pasture improvement and because the center of diversity of Arachis is in the drier areas of Brazil. The Indigofereae and Desmodieae are represented in the Cerrado, s.l., by only their type genera, both of which are large, diverse and pantropical. Polhill (1981) has suggested that the Brongniartieae have tribal status only because they have a straight radicle combined with a relatively advanced flower, and inferred that the tribe could easily be accomodated within the Tephrosieae. It is represented in the Cerrado, s.l., by four species of Harpalyce, all shrubs.

The genistoid alliance is a lateral group which has evolved in areas of Mediterranean climate all over the world, with two main lines: one in the southern hemisphere and another in the northern hemis-

phere (Polhill et al. 1981, Polhill 1981). Many of the specializations of other groups are brought together here, but the trends do not seem to resemble those of the other groups. Crotalaria of the Crotalarieae and Lupinus of the Lupinineae are encountered in the Cerrado, s.l. These are two of the most advanced genera in the alliance which suggest that the Cerrado, s.l., is not a major center of development for the alliance and that only its most advanced members have come into the Cerrado, s.l., after they had undergone evolution and dispersal.

The Papilionoideae is represented in the Cerrado, s.l., by all of the major tropical radiations which are present in the New World. The genistoid alliance is represented by its most advanced members which were probably the results of later introductions. The temperate epulvinate series is not represented at all. Like the Mimosoideae, no one genus in the Papilionoideae has adapted and radiated explosively as has Chamaecrista. Consequently, the Papilionoideae has just 252 species in the Cerrado, s.l., which is only 19% more than the Caesalpinioideae, altough there are six times as many species in Papilionoideae than in Caesalpinioideae.

RECOMMENDATIONS

In the subfamily Caesalpinioideae, special effort to determine nodulation capacity should be concentrated on members of the tribe Caesalpinieae, the genus Chamaecrista and the tribe Detarieae. Caesalpinieae has some fine arboreal species, such as those of Sclerolobium and Dimorphandra, which are very frequent in the Cerrado, s.l. Chamaecrista, with 137 species reported from the Cerrado, s.l., has the greatest variation of any legume genus, and with the recent excellent revision of Irwin & Barneby (1978, 1982) will be easy to work with. Detarieae has some of the finest Cerrado, s.l., trees in the genera Hymenea and Copaifera, but so far the nodulation reports for these genera are conflicting and need clarification.

In subfamily Mimosoideae, special study should be concentrated on tribe Mimoseae and the genus Enterolobium. Within Mimoseae occur several genera of high frequency, such as Stryphnodendron and the genus Mimosa, which with 50 species or more is the second largest legume genus in the Cerrado, s.l., and is also very variable. Enterolobium is a frequent arboreal element in the Cerrado, s.l.

In subfamily Papilionoideae, effort should be concentrated on tribes Dipteryxeae, Dalbergieae, Phaseoleae and Aeschynomene, and on the genera Swartzia, Acosmium and Bowdichia. Dipteryxeae and Dalbergieae have the majority of the arboreal species in the subfamily and produce some of the finest cabinet woods found in the Cerrado, s.l. Phaseoleae and Aeschynomeneae are now the focci of intense research into pasture management and improvement. The genera Swartzia, Acosmium and Bowdichia contain arboreal species of significant stature and high frequency in the Cerrado, s.l.

ACKNOWLEDGEMENTS

I thank Drs. Johanna Döbereiner and H.D.L. Corby for generously sharing their unpublished data, and the Interamerican Institute for Cooperation on Agriculture for their financial support.

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APPENDIX

Check list of the species of Leguminosae known or reported from the Cerrado, s.l.

Abrus Adans.

precatorius L.a

Acacia Mill.

adhaerens Benth.^a, farnesiana (L.) Willd.^a, paniculata Willd.^a, plumosa Lowe^a, p

Acosmium Schott in Sprengel

brachystachyum (Benth.) Yakovl.^{a, p}, dasycarpum (Vog.) Yakovl.^{a, p}, elegans (Vog.) Yakovl.^p, glabrifolium (Tul.) Yakovl.^p, nitens (Vog.) Yakovl.^a, pseudoelegans Yakovl.^e

Aeschynomene L.

brasiliana (Poir.) DC.^a, falcata (Poir.) DC.^a, q, histrix Poir.^a, marginata Benth.^a, oroboides Benth.^a, paniculata Willd.^a, p, paucifolia Vog.^a, g

Amburana Schwacke & Taub.

cearense (Allem.) A.C. Smith^g

Andira A.L. Juss.

cuyabensis Benth.^{a, p}, humilis Mart. ex Benth.^{a, p}, inermis H.B.X.^p, laurifolia Benth.^p, paniculata Benth.^{a, l}, pisonis Mart.^a, stipulacea Benth.^m, vermifuga Mart.^a, p

Arachis L.

glabrata Benth.^I, marginata Gardn.^I, lutescens Krap. & Rigoni^I, prostrata Benth.^A, tuberosa Benth.^I Bauhinia L.

bongardi Steud.^{a, p}, burchellii Benth.^{a, f}, caloneura Malme^p, cheilantha (Bong.) Benth.^{a, i}, cunamensis H.B.K.^{a, p}, cupulata Benth.^{a, n}, curvula Benth.^a, depauperata Glaz.^a, dumosa Benth.^{a, b}, goyazensis Harms^{a, m}, holophylla Steud.^p, leiopetala Glaz.^a, nitida Benth.^{a, e}, pulchella Mart.^p, rubiginosa Bong.^a, rufa (Bong.) Steud.^{a, p}, tenella Benth.^{a, f}, h

Bowdichia Kunth

major (Mart.) Benth. p, virgilioides H.B.K.a, p

Caesalpinia L.

pulcherrima (L.) Sw.a

Calliandra Benth.

axillaris Benth.^a, dysantha Benth.^a, longipes Benth.^a, macrocephala Benth.^a, microphylla Benth.^a, parviflora Benth.^a, pavciflora Griseb.^a, virgata Benth.^a

Calopogonium Desv.

caerulescens Hemsl.^q, sericeum Benth.^a

Camptosema Hook. & Arn.

coccineum Benth.^a, coriaceum (Nees. & Mart.) Benth.^a, p, goiasana Cowan^a, isopetala (Lam.) Benth.^c, nobile Lindm.^p, pedicellatum Benth.^a, scarlatinum (Mart. ex Benth.) Burk.^a, tomentosum Benth.^a, p

Cassia L. emend Gaert.

ferruginea (Schrader) DC. var. ferrugineaa, K

Cenostigma Tul.

gardnerianum Tul.a, p, macrophyllum Tul.a

Centrolobium Mart. ex Benth.

tomentosum Benth.P

Centrosema (DC.) Benth.

angustifolium (H.B.X.) Benth.^{a, q}, bifidum Benth.^a, bracteosum Benth.^{a, c}, brasilianum Benth.^{a, q}, coriaceum Benth.^a, dasyanthum Benth. ^q, hastatum Benth. ^q, pascuorum Mart.^a, venosum Mart.^a

Pesq. agropec. bras., Brasília, 19 s/n: 23-46, jun. 1984.

Chaetocalyx DC.

brasiliens (Vog.) Benth.^a, hebecarpa Benth.^a

Chamecrista Moench

acosmifolia (Benth.) IB^a, j, k, adenophora (Harms) IB^a, j, k, adenophylla (Taub.) IB^a, amambaya (IB) IB^j, k, apoucouita (Aubl.) IB^a, astrochiton (IB) IB^a, j, k, auris-zerdae (IB) IB^j, k, aurivilla (Benth.) IB^a, j, k, azulana (IB) IB^j, k, basifolia (Vog.) IB^a, j, k, benthami (Ghesquiere) IB^j, k, benthamiana (Harms) IB^a, j, k, bifoliola (Harms) IB^a, j, k, brachyblepharis (Harms) IB^j, k, brachyrachis (Harms) IB^a, j, k, bracteolata (Vog.) IB^a, brevicalyx (Benth.) IB^a, j, k, burchellii (Benth.) IB^j, k, caespitosa (Benth.) IB^a, j, k, caiapo (IB) IB^j, k, calycioides (Coll.) Greene^a, j, k, campestris IB^j, k, campicola (Harms) IB^a, j, k, cardiostegia IB^a, k, cathartica (Mart.) IB^a, j, k, catiarae (IB) IB^j, k, cavalcantina (IB) IB^a, j, k, celiae (IB) IB^a, j, k, centiflora (IB) IB^j, k, chaetostegia (IB) IB^a, j, k, choriophylla (Vog.) IB^a, j, k, ciliolata (Benth.) IB^a, j, k, cipoana (IB) IB^a, j, k, clausseni (Benth.) IB^a, j, k, constinted (Be continifolia (G. Don) IBa, j, k, crenulata (Benth.) IBa, cristalinae (IB) IBa, j, k, crommyotricha (Harms) IB^{a, j, k}, cytisoides (Coll.)IB^{a, j, k}, dalbergiifolia (Benth.) IB^a, dawsonii (Cowan) IB^{a, j, k} debilis (Vog.) IBa, decrescens (Benth.) IBa, decumbens (Benth.) IBa, j, k, densifolia (Benth.) debilis (Vog.) IB^a , decrescens (Benth.) IB^a , decumbens (Benth.) IB^a , J, K, densifolia (Benth.) IB^a , J, K, dentata (Vog.) IB^a , J, K, desertorum (Benth.) IB^a , J, K, desvauxii (Coll.) Killip^a, J, K, diphylla (L.) Greene^a, J, K, distichoclada (Benth.) IB^a , J, K, dumalis (Hoehne) IB^a , J, K, elachistophylla (Harms) IB^J , K, exsudans (Benth.) IB^J , K, fagonioides (Vog.) IB^a , J, K, fasciculata (Mich.) Greene^a, J, K, feliciana (IB) IB^a , J, K, filicifolia (Benth.) IB^a , J, K, flexuosa (L.) Greene^a, J, K, foederalis (IB) IB^a , J, K, fragilis (IB) IB^a , J, K, geminata (Benth.) IB^a , J, K, gilliesii (Harms) IB^J , K, gonoclada (Benth.) IB^J , K, gymonothyrsa (IB) IB^a , J, K, hedysaroides (Vog.) IB^a , J, K, huntii (IB) IB^a , J, K, imbricans (IB) IB^a , J, K, incurvata (Benth.) IB^a , isidorea (Benth.) IB^a , J, K, itambana (Benth.) IB^J , K, ixodes (IB) IB^J , K, juruenensis (Hoehne) IB^a , J, K, kunthiana (Schlect. & Cham.) IB^a , J, K, labouriaeae (IB) IB^J , K, lamprosperma (Benth.) IB^J , K, lavradioides (Benth.) IB^a , J, K, lentiscifolia (Benth.) IB^J , K, leucopilis (Harms) IB^a , lomatopoda (Benth.) IB^a , hundii (Benth.) IB^a , J, K, multiseta (Benth.) IB^a , J, KIB^a, j, k, mollicaulis (Harms) IB^a, j, k, multinervia (Benth.) IB^j, k, multiseta (Benth.) IB^a, j, k, neesiana (Benth.) IB^a, j, k, nictitans (L.) Moench^a, j, k, nummulariifolia (Benth.) IB^a, j, k, obtecta (Benth.) IB^a, j, k, ochnoacea (Vog.) IB^a, j, k, ochrosperma (IB) IB^j, k, oligosperma (Benth.) IB^a, j, k, orbiculata (Benth.) IB^a, j, k, pachyclada (Harms) IB^a, j, k, paniculata (Benth.) IB^a, j, k, paraunana (IB) IB^a, j, k, parvistipula (Benth.) IB^a, j, k, pascuorum (Benth.) IB^a, j, k, philippi (IB) IB^j, k, pilosa (L.) Greene^a, j, k, planaltoana (Harms) IB^a, j, k, pohliana (Benth.) IB^a, j, k, polita (IB) IB^a, j, k, ramosa (Vog.) IB^a, j, k, repens (Vog.) IB^a, j, k, rigidifolia (Benth.) IB^a, j, k, rigidifolia (B roncadorensis (IB) IB^a, j, k, roraimae (Benth.) Gleason^a, j, k, rugosula (Benth.) IB^j, k, rotundata (Vog.) IB^a, j, k, rotundifolia (Pers.) Greene^a, j, k, scabra (Benth.) IB^a, secunda (Benth.) IB^j, k, serpens (L.) Greene^a, j, k, seticrenata (IB) IB^j, k, setosa (Vog.) IB^a, j, k, sophoroides (Benth.) IB^a, j, k, souzana (IB) IB^j, k, spirulosa (IB) IB^a, stillifera (IB) IB^a, strictula (IB) IB^a, j, k, subdecrescens (IB) IBa, j, k, supplex (Benth.) Britton & Rose ex Britton & Killipa, j, k, tephrosiifolia (Benth.) IB^j, k, tragacanthoides (Benth.) IB^a, j, k, trichopoda (Benth.) Britton & Rose ex Britton & Killip^a, j, k, urophyllidia (IB) IB^a, j, k, ursina (Benth.) IB^a, j, k, venatoria (Benth.) IB^a, j, k, venulosa (Benth.) IB^j, k, viscosa (H.B.K.) IB^a, j, k, xanthadena (Benth.) IB^j, k, zygophylloides (Taub.) IBa, j, k

Clitoria L.

densiflora (Benth.) Benth.^q, guianensis Benth.^a, g

Collaea DC.

decumbens Benth. q, glaucescens (H.B.K.) Benth. q, macrophylla Benth. q, neesii (DC.) Benth. a

Copaifera L.

cordifolia Hayne^a, coriacea Mart.^p, elliptica Mart.^a, langsdorffii Desf.^a, ^p, luetzelburghii Harms^a, malmei Harms^a, ^p, martii Hayne^a, ^p, nana Rizz.^a, oblongifolia Mart.^a, ^p, trapezifolia Hayne^a

Cratylia Mart. ex Benth.

argentea Desv.^a, floribunda Benth.^a

Crotalaria L.

anagyroides H.B.K.^{a, p}, breviflora DC.^q, depauperata Mart.^c, flavicoma Benth.^{a, q}, incana L.^a, juncea L.^a, leptophylla Benth.^c, maypurensis H.B.K.^c, nitens H.B.K.^a, paulina Schrank.^a, pohliana Benth.^q, pterocaulon Desv.^{a, q}, retusa L.^f, stipularis Desv.^{a, q}, unifoliata Benth.^{a, h}, velutina Benth.^{a, q}, vespertilio Benth.^a

Dalbergia Linn. f.

ferrugineo-tomentosa Hoehne^p, glandulosa Benth.^a, gracilis Benth.^a, hiemalis Malme^p, miscolobium Benth.^a, spruceana Benth.^p, violacea (Vog.) Malme^a, p

Desmodium Desv.

asperum (Desv.) Poir.^a, barbatum (L.) Benth.^a, canum (Gmel.) Schinz. & Thell.^c, discolor Vog.^a, leiocarpum D. Don^a, pachyrhizum Vog.^q, platycarpum Benth.^a, q, procumbens (Mill.) Hitch^a, sclerophyllum Benth.^a

Dialium L.

guianense (Aubl.) Sandw.P

Dimorphandra Schott in Sprengel

biretusa Tul.^a, gardneriana Tul.^a, p, mollis Benth.^a, p

Dioclea Kunth

bicolor Benth.^a, coriacea Benth.^a, erecta Hoehne^p, latifolia Benth.^a, paraguayensis Benth.^a, virgata (Rich.) Amsh.^a

Dipteryx Schreb.

alata Vog.a, p, odorata (Aubl.) Willd.a

Diptychandra Tul.

aurantica Tul.a, p, glabra Benth.a, p

Enterolobium Mart.

contortisiliquum (Vell.) Morong^p, ellipticum Benth.^{a, p}, incuriale (Vell.) Kuhlm.^p, gummiferum (Mart.) MacBr.ⁱ

Eriosema (DC.) G. Don

benthamianum Mart. ex Benth.^a, ^q, brachyrhachis Harms^a, brevipes Grear^a, campestris Benth.^h, congestum Benth.^a, ¹, crinitum (H.B.K) Don^a, ^c, cupreum Harms^a, defoliolatum Benth.^h, floribundum Benth.^a, glabrum Mart. ex Benth.^a, glaziovii Harms^a, heterophyllum Benth.^a, ^c, irwinii Grear^a, lagoense Micheli^q, longiflorum Benth.^a, longifolium Benth.^q, prorepens Benth.^a, pycnanthum Benth.^a, ^q, rigidum Benth.^a, ¹, rufum (H.B.K.) G. Don^a, ^q, simplicifolium (H.B.K.) G. Don^a, ^q, stipulare Benth.^a, strictum Benth.^q

Erythrina L.

dominguezzi Hasseler^a, falcata Benth.^p, mulungu Mart.^p, velutina Willd.^p

Galactia P. Browne

benthamiana Micheli^q, boavista (Vell.) Burk.^a, crassifolia (Benth.) Taub.^a, ¹, decumbens (Benth.) Hoehne^a, ^c, dimorpha Burk.^a, eriosematoides Harms^a, glaucesens H.B.K.^a, ^p, greweiaefolia (Benth.) Taub.^a, ^h, heringerii Burk.^a, hoehnei Burk.^a, irwinii Cowan^a, martii Benth.^a, nana Burk.^a, neesii DC.^a, peduncularis (Benth.) Burk.^a, ¹, previaefolia (Benth.) Taub.^b, rhynchosoides Benth.^a, speciosa (DC.) Brit.^a, stereophylla Harms^a, ^b

Harpalyce Moc. & Sesse ex DC.

brasiliana Benth. 2, p. lepidota Taub. 2, parvifolia Irwin & Arroyo 2, robusta Irwin & Arroyo 2

Hvmenaea L.

courbaril L.^{a, p}, martiana Hayne^{a, p}, stigonocarpa Mart.^{a, p}, stilbocarpa Hayne^g

Indiogofera L.

gracilis Bong. a, g, lespedezioides H.B.K. a, q, suffruticosa Mill. a, c

Inga Mill.

affinis DC.2, p, fagifolia Willd.2, p, umbellifera (Vahl) Steud.2

Lonchocarpus Kunth

campestris Mart.p, spruceanus Benth.p

Luetzelburgia Harms

praecox (Harms) Malmeh, p

Lupinus L.

crotalarioides Mart. ex Benth. q, vaginans Benth. a, velutinus Benth. b

Machaerium Pers.

aculeatum Raddi^a, ^p, acutifolium Vog.^a, ^p, amplum Benth.^a, ^p, angustifolium Vog.ⁱ, eriocarpum Benth.^p, lanatum Tul.^p, mucronulatum Mart.^a, oblongifolia Vog.^a, opacum Vog.^a, ^p, villosum Vog.^p

Mimosa L.

adenocarpa Benth.^a, albida H. & B.^c, angusta Benth.^a, arachnoides Taub.^c, asperata L.^a, barbigera Benth.^a, brachycarpa Benth.^a, brachycaulis Harms^l, calycina Benth.^q, capillipes Benth.^c, h, claussenii Benth.^a, b, conferta Benth.^a, i, debilis Mart.^a, densa Benth.^a, h, distans Benth.^q, dumetorum St.-Hil.^a, gardneri Benth.^a, goyazensis Benth.^a, gracilis Benth.^a, b, hapaloclada Malme^p, imbricata Benth.^a, h, invisa Mart.^a, q, lanata Benth.^a, h, lanuginosa Glaz. ex Burk.^a, b, lasiocarpa Benth.^q, laticifera Rizz. & Mattos^a, p, microcarpa Benth.^a, nervosa Bong.^q, neurolema Benth.^c, obovata Benth.^a, paludosa Benth.^a, paucifolia Benth.^h, pigra L.^a, pithecolobioides Benth.^a, platyphylla Benth.^p, polycarpa Benth.¹, pteridifolia Benth.^a, radula Benth.^a, 1, rixosa Mart.^a, c, sensitiva L.^q, setosa Benth.^a, h, somnians H. & B.^a, stipularis Bong.^a, subsericea Benth.^c, viscosa^a, xanthocentra Mart.^q

Myrocarpus Allem

fastigiatus Allem.P

Parkia R. Br.

platycephala Benth.a, p

Peltogyne Vog.

confertiflora (Hayne) Benth. a, i, maranhensis Duckea

Periandra Benth

acutifolia Benth.^a, densiflora Benth.^a, dulcis Mart.^b, ^g, heterophylla Benth.^a, ^q, mediterranea (Vell.) Taub.^a, ^b, ^g

Phaseolus L.

brachycalyx Hasseler^a, bracteolatus Nees & Mart.^a, candidus Vell.^h, clitorioides Mart.^a, erythoroloma Mart. ex Benth.^q, firmulus Mart.^a, ^q, linearis H.B.K.^b, longifolius Benth.^a, longipedunculatus Mart. ex Benth.^a, monophyllus Benth.^q, obliquifolius Mart. ex Benth.^q, peduncularis H.B.K.^a, pius Mart. ex Benth.^q, prostratus Benth.^c, semierectus L.^a, truxillensis H.B.K.^q

Piptadenia Benth,

falcata Benth.^p, macrocarpa Benth.^p, peregrina (L.) Benth.ⁱ, rigida Benth.^a

Pithecolobium Mart.

campestre Spruce^p, multiflorum (H.B.K.) Benth.^p

Plathymenia Benth. foliolosa Benth. a, reticulata Benth. a, p Platypodium Vog. elegans Vog.a, p, grandiflorum Benth.a, n, viride Vog.a Poecilanthe Benth. subcordata Benth.P Poiretia Vent. angustifolia Vog. a, h, latifolia Vog. a, q, psoralioides DC. q Pterocarpus Jacq. rohrii (H.B.K.) Vahl^p Pterodon Vog. polygaliflorus Benth. a, p, pubescens Benth. a, p Rhynchosia Lour. clausseni Benth.^{a, q}, edulis Griseb.^a, melanocarpa Grear^a, phaseoloides (SW.) DC.^a Riedeliella Harms graciliflora Harms^{a, p} Schrankia Willd. Unidentified specimen in the herbarium of the Universidade de Brasília. Sclerolobium Vog. aureum (Tul.) Benth. a, p, beaurepairei Harms a, paniculatum Vog. a, p, rugosum Mart. P Senna Mill. alata (L.) Roxb.^a, bicapsularis (L.) Roxb.^a, cana (Nees. & Mart.) IB^a, ^k, cernua (Balbis) IB^k, chrysocarpa (Desv.) IB^a, corifolia (Benth.) IB^a, ^k, hirsuta (L.) IB^k, kuhlmannii Hoehne^k, macranthera (Coll.) IB^a, ^k, mucronifera (Benth.) IB^a, ^k, obtusifolia (L.) IB^a, occidentalis (L.) Link.^k, pendula (Willd.) IB^a, ^k, pentagonia (P. Miller) IB^k, pilifera (Vog.) IB^a, ^k, reniformis (G. Don) IB^k, rizzinii IB^k, rostrata (Mart.) IB^k, nugosa (G. Don) IB^a, ^k, septemtrionalis (Viviani) IB^k, silvestris (Vell.) IB^a, ^k, spectabilis (DC.) IB^a, ^k, splendida (Vog.) IB^k, tapajozensis (Ducke) IB^k, trachypus (Benth.) IBⁱ, uniflora (P. Miller) IB^k, velutina (Vog.) IB^a, ^k Stryphnodendron Mart. adstringens (Mart.) Coville^{a, c}, confertum Rizz. & Her. a, coriaceum Mart. p, cristalinae Her. a obovatum Benth.2, P, platyspicum Rizz. & Her.2, polyphyllum Benth.P, rotundifolium Mart.2, P Stylosanthes Sw. acuminata Ferr. & Costa^d, bracteata Vog.^d, ^q, capitata Vog.^d, ^h, debilis Ferr. & Costa^d, gracilis H.B.K.^a, ^d, grandifolia Ferr. & Costa^d, guyanensis (Aubl.) Sw.^a, ^d, hippocampoides Mohlenbr.^d, humilis H.B.K.^d, leiocarpa Vog.^d, ^q, linearifolia Ferr. & Costa^d, macrocephala Ferr. & Costa^d, montevidensis Vog.^a, ^d, ^g, scabra Vog.^a, ^c, ^d, viscosa Sw.^c, ^d Swartzia Schreber auriculata Poepp.a, flaemingii Raddia, grazielana Rizz.a, P, leptopetala Benth.a, macrostachya Benth. a, p, multijuga Vog. a, p, pilulifera Benth. p Sweetia Sprengel fruticosa Sprengel^p Tephrosia Pers. adunca Benth. a, q, leptostachya DC. a, q, nitens Benth. a, rufescens St. Hil. c Tipuana (Benth.) Benth. cinerascens (Benth.) Malmep

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macrocarpa (Benth.) Duckep

Vatairea Aubl.

Vigna Savi

paraguensis Benth.^C

Zornia J.F. Gmel.

brasiliensis Vog.^q, diphylla Pers.^g, latifolia Sm^{a, c}, reticulata Sm.^{a, c}, ulei Harms^a, vestita Mohlenbr.^a, virgata Moric.^a, q

a Represented by a specimen in the herbarium of the Universidade de Brasília.

Reported to be found in the Cerrado, s.l., from the following literature: b) Cesar 1980; c) Eiten 1971; d) Ferreira & Costa 1979; e) Ferri 1969; f) Goodland 1970; g) Goodland & Ferri 1979; h) Heringer 1971; i) Heringer et al. 1977; j) Irwin & Barneby 1978; k) Irwin & Barneby 1982; l) Ratter 1980; m) Ratter et al. 1973; n) Ratter et al. 1977; o) Ribeiro et al. 1981; p) Rizzini 1971; q) Warming 1973.

^r José Valls, personal communication.

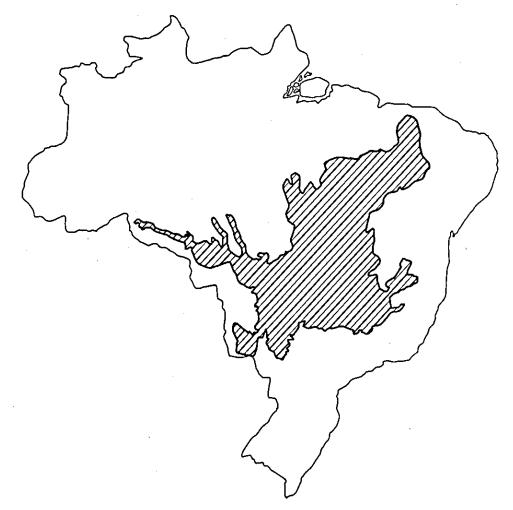


FIG. 1. The area of Cerrado, s.l., vegetation in Brazil, adapted from Azevedo and Caser (1982).



FIG. 2. Cerrado, s.s., on the Chapada da Contagem near Brasília showing the tortuosity of the trees and shrubs; courtesy of George Eiten.

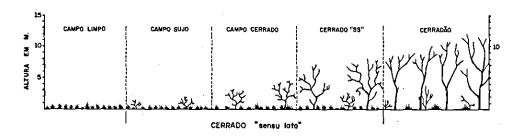


FIG. 3. Stylized profiles of the five categories of Cerrado, s.l., vegetation, edapted from Coutinho (1978).

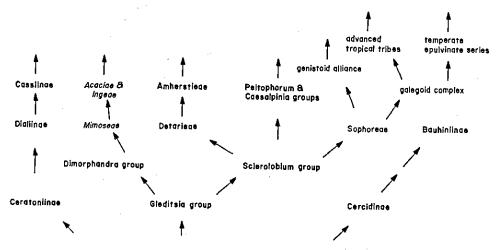


FIG. 4. The main evolutionary radiations in the Leguminosae, from Polhill et al. (1981).