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THE CERRADO VEGETATION OF BRAZIL

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I. CERRADO AS A VEGETATIONAL PROVINCE

Centered on the great plateau of Central Brazil and covering a fifth of the whole country, is a characteristic xeromorphic vegetation called "cerrado." Cerrado is often classified in accounts of world vegetation as a "savanna" (Eyre, 1963, pp. 246–7; Hills & Randall, 1968; Schimper, 1903, pp. 373–6; Warming, 1909, pp. 296–7), and in a very wide sense of that much-abused word it is. However, it is found in almost the whole possible range of structural forms: forest (with closed tree canopy), arboreal woodland (with open tree canopy), tree and scrub woodland (trees more scattered and sharing prominence with scrub elements, all woody plants together forming an open layer), closed scrub, open scrub, grassland with scattered trees and shrubs equally prominent, grassland with scattered low shrubs only (the last three "savanna" in the strict structural sense), and grassland without any evidently visible woody plants. All these forms are natural in certain areas; in other areas the lower or more open forms are the result of man-caused degradation of a taller denser form, either by cutting, annual burning, or both. The denser forms predominate. As a rough estimate, in 70% of the total cerrado area today (discounting the up-to-now small fraction deliberately cleared by cutting) the woody plants are too dense to permit a jeep to be driven through. Despite the variation in height and spacing, all cerrado stands possess a certain distinctive appearance because of the contour and morphology of the individual woody plants in it, as described in Part III.

The word "cerrado" is used in Brazil in two senses. In the wide sense, it is a regional large-scale vegetation type that forms both a vegetational and a floristic province. In the strict sense, it refers to a particular range of structural forms of this vegetation, as described below.

This large-scale vegetational province possesses a distinctive flora with a few endemic genera and hundreds of endemic species. It is restricted to a single continental area and is associated with a certain climate, that is, with a certain portion of the geographically changing climatic continuum. It forms a unit that is coordinate to other large-scale vegetation types that also occupy single continental areas with a particular range of climatic conditions and that possess more or less distinctive floras, such as the eastern deciduous forest or the central grasslands of North America, the equatorial hylaea or the open savannas and arboreal woodlands that surround the hylaea in Africa, the Amazon-Orinoco hylaea, the Chaco vegetation or the caatinga in South America, etc.

The word "cerrado" in Portuguese means "dense" or "closed." Originally it was used as an adjective in the term "campo cerrado" to distinguish a campo (field or grassland) in which trees and shrubs are present so as to form a rather open woodland, open scrub, or savanna, from a "campo limpo" ("clean field"), which is a pure or almost pure grassland. In extra-Amazonian Brazil most natural and fire-derived woodlands, open scrubs and savannas belong to a single floristic and vegetational province, so that the term "campo cerrado" came to be restricted to a certain range of structural forms of only this one vegetation type. Eventually, the adjective "cerrado" came to be used as a noun and to refer, when used alone and in its wide sense, to the *whole* range of densities and heights of this vegetation. The older term, "campo cerrado," is still used, however, either in its original sense (the open woodland, open scrub, and savanna forms of this vegetation), or in a sense restricted to the open savanna-like forms only. A full discussion of the confused terminology is given in Part V.

The ecology of the cerrado is taken up in Parts VII and VIII. However, in view of the wide meaning of the term "savanna," of which the cerrado is generally thought to be a part, it should be mentioned here at the outset that cerrado is strictly an upland vegetation (occurring away from the immediate vicinity of streams). It is never inundated and the internal drainage of its soil is almost always excellent, so that the soil does not remain waterlogged for long periods after a rain. In this respect it definitely differs from most natural savannas of northern South America.

II. GEOGRAPHIC LOCATION

The central continuous cerrado region is made up of a core area comprising almost all of Goiás, western Bahia, western Minas Gerais, and all of eastern Mato Grosso (from north to south, but wider in the center and south). The geographic center of the core area lies near the city of Goiás Velho, west of Brasília. From this core area extend great peninsulas of cerrado north into southern Maranhão and northern Piauí, west into central Mato Grosso and southern Rondônia (ex-Guaporé), and southwest into southwestern Mato Grosso and adjacent Paraguay. West of the Pantanal Region in southeastern Bolivia there is a detached area of cerrado. Small outlying disjunct areas of cerrado occur in several places in northeastern Brazil and in São Paulo, and there are also a few tiny atypical areas in northern Paraná. (For the Paraná cerrados, see Maack, 1949; Stellfeld, 1949; Kuhlmann, 1953; Ferri, 1960b; and Coutinho & Ferri, 1960.) Besides the typical cerrado, other disjunct *savanna* areas, large and small, occur north and west of the cerrado region, such as those in eastern Amapá (Guerra, 1954; Azevedo, 1966b); northeastern Roraima Territory (ex-Rio Branco Territory) (Myers, 1936; Guerra, 1956, 1957; Takeuchi, 1960a, 1960b; Rodrigues, 1971); the Guianas (Eden, 1964; van Donselaar, 1965); Venezuela (Blydenstein, 1962; Tamayo, 1964; Sarmiento & Monasterio, 1971) and Colombia (Blydenstein, 1967); in the Amazon region (Sombroek, 1966, pp. 52, 219) as for example at Humaitá (Braun & Ramos, 1959), in Pará along the Rio Trombêtas, north of Alenquer, north of Monte Alegre, and on the Serra do Cachimbo (Soares, 1953, pp. 40–45), and in northern Mato Grosso just west of the main cerrado region on the low interfluves between the Xingu and the Paranatinga (or Teles Pires) rivers (Serra Formosa) and between the Paranatinga and the Arinos (Serra dos Caiabis), etc. The floristic and ecological relationship of these other savanna areas to typical cerrado is yet to be investigated. In this paper, only the central continuous cerrado region and the detached areas in northeastern Brazil and in São Paulo will be considered.

FIG. 1. Vegetation provinces in Brazil. C = cerrado (sens. lat.), CL = southern Brazil campo limpo (napeadic grassland), F = upland mesophytic forest, HAC = high altitude campo, S = Amazonian savanna. Besides those shown, many other smaller disjunct areas of C, CL and HAC occur in the Atlantic forest zone, F in the cerrado, and S and inundated campo in the Amazon forest. The boundaries between provinces run more or less through the middle of the transition zones. The littoral vegetation (beaches, coastal sand dunes, "restinga," mangrove swamps) is too narrow to be shown on a map of this scale.

Within the cerrado region occur gallery forests or gallery palm groves along all brooks and rivers, as well as occasional areas of upland true mesophytic forest on richer soils.

Inadequacy of vegetation maps. No map delimiting the cerrado area in Brazil as a whole is satisfactory and very few are correct even for smaller regions. World vegetation maps found in atlases and geography texts are usually inaccurate for most of Brazil, especially the border between Amazon forest and the central "savanna" region (such as Polunin, 1960; Eyre, 1963; Goode's World Atlas, 1964, etc.). Some recent Brazilian maps of the vegetation of the country are closer to reality in the placement and approximate area of each main type shown, but vary considerably as to exact boundaries. Kuhlmann (1960) shows large tongues of cerrado between the larger northward-flowing rivers in north central Mato Grosso, while in Soares (1953), Magnanini (1961), and Romariz (1964) the same areas are shown as Amazonian forest. Other recent Brazilian maps do not include large areas of cerrado in the core area, but on the other hand do include many Amazonian savannas which are not really cerrados (Lima, 1967; cerrado area from Lima's map copied in Souza Reis, 1971; Ranzani, 1971).

Many maps of smaller areas are incorrect in detail. Magalhães' black-and-white map (1966) is a very rough indication of the extent of cerrado in Minas Gerais based on his travels throughout the state. It is incorrect in several areas, as can be seen by comparison with the distribution of cerrado in the southern end of the state given in the accurate map by Azevedo (1962) based on aerial photographs.

All maps of São Paulo show much less cerrado than actually exists. With two exceptions, none I have seen show any cerrado at all in the whole western half of the state (such as the map in Romariz, 1963, and 1964, p. 497; Lima, 1967; Ranzani, 1971) although there are large areas of cerrado that could be shown at the scale used in Paraguaçu Paulista and Rancharia in the southwest, from northeast of São José do Rio Preto up to the wide forest along the Rio Grande, and vast areas of cerradão in the northwest, as well as many smaller areas scattered throughout the western half of the state.

Veloso's map (1966a) has a sprinkling of cerrado patches in São Paulo, but neither the number of these, their size and shape, nor their placement is very accurate. His outline of the main cerrado region is also rather fanciful. He, too, has included all the Amazon savannas in the cerrado concept.

The nearest approach to a true mapping of cerrado in São Paulo is that of Borgonovi & Chiarini (1965, 1968). This is based on aerial photographs taken in 1962 and distinguishes cerradão, cerrado (including low arboreal, dense scrub, and savanna forms) and campo limpo. However, (1) they purposely do not include areas of cerrado which are cultivated, (2) they have not included some large areas of uncultivated cerrado, such as the large continuous area northeast of São José do Rio Preto, (3) they show an area 10 km wide just north of São Carlos as a break in the continuous cerrado of that region yet my observations of the area in 1961 show no such break, and (4) their concept of "campo" includes at least three unrelated vegetation types, some primary and some secondary, of which one is floristically cerrado and the others are not.

Kuhlmann (1960) presents a map showing most of eastern Mato Grosso covered with cerrado, which is correct. However, he shows a a large area of "vegetação de transição," described in the text as [mesophytic] semideciduous forest, from the Rio das Mortes to 50 km northward (i.e., from the town of Xavantina north), as well as a large area of "floresta tropical" (i.e., non-hylaean mesophytic evergreen forest) from the city of Barra do Garças to 50 km southward. The road from Jataí, through Caiapônia (Goiás), to Barra do Garças, and north to Xavantina and the Serra do Roncador (Mato Grosso), passes through the middle of these two supposed forested regions, yet all I saw along this road, from Jataí to the Serra do Roncador, was one continuous cerrado area, almost all of it of the tree and scrub woodland form.*

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* Physiognomic terms in this paper, such as "forest," "woodland," "tree & scrub woodland," "savanna," etc., are used as strictly and quantitatively defined in Eiten (1968). They do not imply any particular ecological conditions. A brief description is as follows.

"Closed" is a cover of 60% or more; "open," 10% to less than 60%; "sparse," less than 10%. "Tall" trees are 20 m or more; "medium-tall" trees are 7 m to less than 20 m; "low" trees are 3 m to less than 7 m. Tall, medium-tall and low forests and woodlands have canopies which are essentially of the same height limits. Scrub is made up of shrubs or of other plants that are not definitely either trees or herbs, such as acaulescent palms, cacti, agave, yucca, large bromeliads, etc., or if trunked, with total height less than 3 m. The word refers either to a whole stand or to one layer in a stand. "Tall" scrub is 3 m and over; "medium-tall" scrub is 1½ m to less than 3 m; "low" scrub is over ½ m to less than 1½ m; "dwarf" scrub is up to ½ m tall. "Forest' is an arboreal formation of any type with closed tree canopy. In "forest with emergents" (or "closed scrub with emergents") the emergents do not reach 10% cover. "Woodland" is a dominantly arboreal formation with open tree canopy and with the scrub layer absent, sparse or open, but not closed. When a woodland has a closed scrub layer, the form is referred to as "open forest with closed scrub." "Tree and scrub woodland" has the total woody layer open but with that part of the scrub not covered by trees with equal or more cover than the tree crowns (i.e., the trees rather spaced). "Savanna" is scattered trees and/or scrub (10% cover or less) over a non-ephemeral graminoid and/or forb layer (i.e., which lasts more than 3 months of the year on the average, either alive or dead but not decomposed). If the ground layer is ephemeral the savanna is called "sparse woodland," "sparse tree and scrub woodland," or "sparse scrub," as the case may be. Stands without woody plants or persistent scrub elements are tall grassfields or herbfields (if the plants reach 1 m or more during the year), or short grassfields or herbfields (if the plants remain less than 1 m tall all the time), in both cases when the herbaceous cover reaches 10% or more during the year. If it does reach 10% cover it is a sparse grassfield or herbfield.

In the present paper a few further subdivisions are made. Scrub heights are mentioned for those height classes (when appreciable) not covered by taller plants.

The trees present in this cerrado do not form a closed-cover cerradão but on the contrary are scattered over an open scrub layer and could not possibly be mistaken for any kind of forest. Only in rare areas a few hundred meters to a few kilometers along the road did the trees become dense enough to form a cerradão and so could be taken structurally for a forest. True mesophytic forests crossed by the road were only narrow gallery forests and in Mato Grosso several small patches of upland forest each only a few kilometers wide. Toledo's small black-and-white map (1962) for the region north of Barra do Garças is more accurate.

Almeida *et al.* (1962) present a map (made by V. Moreira da Silva) showing a 20–40 km wide belt of forest following the Parnaíba River between Maranhão and Piauí up to its junction with the Rio Balsas. Veloso (1966a) also includes this belt in his map. From a raft trip I made on the river in 1962, which included the stretch from the junction of the Rio Balsas to Floriano, and from what I could see crossing the river at Teresina in 1970, the gallery forest is not more than 100–200 m wide in most places, often less than that, and rarely up to one kilometer. They also show Barra do Corda and Caxias in the middle of "Transitional Forest," although both these Maranhão cities are set in a region of cerradão, with mesophytic forest only as narrow galleries along the streams.

In *Paisagens do Brasil* (Instituto Brasileiro de Geografia, 1968) the chapter on vegetation includes a small colored map called a sketch ("esboço") of the vegetation. A laudable attempt is made to include more vegetation types, such as several types of mesophytic forest, but there are many errors even at the scale used. In Rio Grande do Norte no cerrado is shown although it is the dominant vegetation in the northeastern part of the state (Valverde *et al.*, 1962; Andrade, 1963). Instead, "mata sêca" ("dry forest," the usual Brazilian term for deciduous and semideciduous mesophytic forest) is shown behind a wide continuous humid forest coastal strip (although humid forest only occurs as narrow galleries, now cleared, along the rivers in this state). The "Roraima and Cachimbo Complex" is separated as a distinct category, although the lateritic savannas of Roraima Territory, related to the Guyana Rupununi savanna, are completely different floristically and ecologically from the quartzite lithosol campos and scrubs of the top of the Serra do Cachimbo in Pará. Campo limpo in southern Minas Gerais is put in the same category as the campo limpo of southern Rio Grande do Sul, although the Minas "campo limpo," which occurs mixed over the landscape with scrubs, savannas and upland forests (Azevedo, 1962; Comissão de Solos, 1962), is a form of cerrado or of high-altitude shallow-soil campo, neither having anything to do floristically or ecologically with

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A tree and scrub woodland or savanna is referred to as "low-tree and scrub woodland" and "low-tree and scrub savanna" if essentially all the trees are less than 7 m tall. Savannas are divided into "dense" savanna if the trees and scrub elements total more than 1% cover, and "very open" savanna if less.

the extensive warm-temperate Rio Grande do Sul campos which are related to the pampas of Uruguay.

Magnanini's map (1961) also shows a wide band of forest along the whole east coast of Rio Grande do Norte, directly meeting caatinga, with no intermediate cerrado zone. (He has this coastal forest continuing also along the north coast westwards to Maranhão, almost meeting the Amazon forest.)

Many maps, adapted from Sampaio (1934), including one in Cole (1960), show the States of Maranhão and Piauí completely covered with palm forest. On small scale maps such as these, the implication is that palm forest is the prevailing vegetation of the region. This is incorrect. Two palms are involved, babaçu (*Orbignya barbosiana* Burr.) and carnaúba [*Copernicia prunifera* (Mill.) H. E. Moore]. In reality, only a relatively small percentage of Maranhão, mostly in the north central and northeastern part, has an almost continuous vegetation of babaçu forest. Over a much larger region this palm grows only in narrow gallery forests. Small scattered areas, measured in hectares, in northeastern Maranhão and larger areas in Piauí are covered with carnaúba palm groves as gallery vegetation on deep soil, and the palm also occurs on very small upland areas of shallow soil over rock pavements. The prevailing vegetation in Maranhão is cerrado woodland in the south, Amazon forest in the northwest, and a mosaic of cerrado savanna, cerrado woodland, mesophytic semideciduous forest and babaçu forest in the center and northeast. The prevailing vegetation of Piauí is in the northern half a dense shrub form of cerrado transitional to caatinga and in the southern half caatinga itself.

Galvão (1955) presents a short discussion of the vegetation of Maranhão, as well as a small rough map taken from Lopes (1937). Except for information taken from R. L. de Fróes (in Soares, 1953) concerning the Amazonian vegetation in the northwestern part of the state, and perhaps the part about the mangrove swamps, almost everything else stated in this discussion is incorrect. The map shows the eastern part of the region between the Balsas and Parnaíba Rivers solidly covered with babaçu forest, while in fact, babaçu occurs only as very narrow gallery forests along streams exactly as it does north of the Balsas River where it is not shown at all. The upland between the two rivers, which is over 95% of the land area, is really covered with cerradão. The relatively large areas of babaçu shown on the map just east of Carolina do not exist. A strip of "campina alta," a grassland on plateau tops, is shown along the northeastern border of the state. At least where I crossed this area just west of Timon, no such vegetation exists. The cerrado is divided up in the map into large areas of "chapadas," "tabuleiro" and "tombadores," although there is no essential difference between the three, at least as far as the areas shown are involved. "Tabuleiro" has many meanings in Maranhão; none that I know of is typical cerrado, and one meaning refers to upland carnaúba palm groves, which have nothing to do with cerrado at all. All are relatively small scattered areas of vegetation different from that prevailing in the region in general. The "carrascos altos" of the map are semideciduous mesophytic forests in the transitional region between the Amazon forest and the cerradão; they should be shown extended considerably further south and east.

The discussion in Galvão mentions caatinga in Maranhão. I have not been in any part of the state yet where this vegetation of the northeast occurs. However, it should be remembered that the word "caatinga" is used in several senses in Maranhão for local vegetation types that have nothing to do with the famous northeastern Brazil thorn scrub caatinga. Galvão cites for Maranhão caatingas several species which are typical of cerrado. He also states that the Maranhão cerrados lack *Curatella americana* and *Byrsonima* species, while in fact they are very common in all the cerrados of the state. He cites Sampaio (1934) for the composition of the Maranhão cerrados including the grass "'barba-de-bode' (*Aristida*) . . . faveira (*Pterodon* sp.) . . ." Sampaio took this passage from Fróes Abreu (1931) who appended to the common names what he thought was the scientific name from species that have these common names in southern Brazil. However, in Maranhão, "faveira" is *Parkia platycephala* (also called "fava de bolota" in other parts of the state) and "barba-de-bode," at least in the Loreto region, is *Paspalum ceresia*. I have not seen *Aristida pallens*, the "barba-de-bode" of southern Brazil, in Maranhão.

Magnanini (1961) in a map of the original vegetation of Brazil, has the whole northeastern quarter of Maranhão and all of northern Piauí except the immediate coast covered with caatinga. Actually, the upland vegetation of northeastern Maranhão is cerrado or solid babaçu forest with a few other types occupying only very small areas. The vegetation of northern Piauí is cerrado woodland or a dense scrub transition between cerrado and caatinga, with pure caatinga only along the eastern edge.

He gives tables of areas and percents of each state originally covered with forests, cerrado, caatinga or "campo." There are several serious discrepancies between the map and the table. Thus, the table states that 40% of Piauí was originally covered with cerrado and 40% with caatinga, but the map shows less than 10% covered with cerrado and about 90% with caatinga.

In view of all these sources of error, one must be very careful in accepting statements about vegetation types in Brazil and their extensions as given on maps. Unfortunately, for one who has not actually travelled in the regions concerned to see for himself, it is difficult to know what one *can* accept in the published accounts.

I am well aware of the difficulty of making vegetation maps for the vast area of Brazil, as well as the difficulty of reaching many areas in order to check on the ground the various vegetation types seen on aerial photographs, so the above points are mentioned only to show the necessarily tentative nature of the facts now at our disposal to explain the presence of cerrado.

Since there are areas of vegetation transitional in character between cerrado and the other main vegetation types, part of the discrepancy may be in differences of opinion as to which main vegetation type the transitional forms belong.

III. PHYSIOGNOMIC CHARACTERISTICS OF INDIVIDUAL PLANTS AND FLORISTIC COMPOSITION

Cerrado is a *xeromorphic* vegetation. The trees and shrubs almost always have thick bark (especially as contrasted with the thin bark of the mesophytic forests) and also twisted limbs and trunks, especially where fires are frequent. The ultimate branches, i.e., the twigs, of many of the most common cerrado woody species are relatively thick, 1–3 cm in diameter up to the very tip, giving a characteristic appearance different from forest and caatinga species. The leaves of the trees and shrubs are usually rather large, broad (macrophyll size), thick, and either stiff and glabrous (*Salvertia convallariodora* St. Hil., Fig. 2, *Vochysia, Kielmeyera, Qualea grandiflora* Mart., *Byrsonima coccolobifolia* HBK., etc.) or, more rarely, soft and hairy (*Byrsonima verbascifolia* Rich. ex Juss.). The Bombacaceae have palmately compound leaves; in most species both the leaves and leaflets are large. The leaves of the woody legumes, which plants make up a good part of the vegetation, are also large but are compound, being once or twice pinnate with small or tiny, glabrous or hairy leaflets. The leaflets may be thin and soft (*Dalbergia, Piptadenia*), thickish and soft (*Dimorphandra*), or thick and hard (*Stryphnodendron*). Myrtaceous species, which are common and almost always in shrub form, have small simple leaves, but these are almost always stiff. A cerrado tree usually bears larger and fewer leaves than a forest tree of the same crown size and usually more light enters through the crown. In the open stands, the trees are mostly of the savanna rather than the forest type, i.e., short bole relative to crown height, and the crown rather wide for its height.

Common trees of the cerrado are species of *Aegiphila, Agonandra, Anacardium, Anadenanthera, Andira, Annona, Aspidospermum, Astronium, Bowdichia, Byrsonima, Caryocar, Cassia, Copaifera, Curatella, Dalbergia, Dimorphandra, Diospyros, Dipteryx, Emmotum, Enterolobium, Eriotheca* (formerly *Bombax*), *Esenbeckia, Eugenia, Guazuma, Hancornia, Hymenaea, Kielmeyera, Lofoënsia, Luehea, Machaerium, Magonia, Matayba, Myrcia, Neea, Ouratea, Parkia, Plathymenia, Platypodium, Plenckia, Pouteria, Protium, Pseudobombax* (formerly *Bombax*), *Pterodon, Qualea, Rapanea, Roupala, Rudgea, Salvertia, Sclerolobium, Simarouba, Solanum, Strychnos, Stryphnodendron, Styrax, Sweetia* (the cerrado species recently transferred to *Acrosmium* by Yakovlev, 1970), *Symplocos, Tabebuia* (sometimes the cerrado species are treated as *Tecoma*; recently they have been transferred to a new genus, *Handroan-*

FIG. 2. Young tree of *Salvertia convallariodora* St. Hil. sprouting new leaves at beginning of rainy season in a tree and scrub woodland cerrado on the Serra do Roncador, northeastern Mato Grosso.

thus, by Mattos, 1970), *Terminalia, Vantanea, Virola, Vochysia, Xylopia*, etc.

Common cerrado broadleaf shrubs and semishrubs are species of *Aegiphila, Aeschynomene, Alibertia, Amasonia, Anacardium, Andira, Annona, Arrabidaea, Baccharis, Banisteria, Bauhinia, Brosimum, Byrsonima, Byttneria, Calliandra, Campomanesia, Camptosema, Casearia, Cassia* (very many species), *Cissampelos, Cochlospermum, Combretum, Connarus, Cordia, Crotalaria, Croton, Davilla, Decleuxia, Didymopanax, Diospyros, Duguetia, Eremanthus, Eriosema, Erythroxylum, Eugenia, Eupatorium, Gochnatia, Harpalyce, Helicteres, Heteropteris, Hirtella, Hyptis, Indigofera, Jacaranda, Kielmeyera, Krameria, Lantana, Lippia, Manihot, Miconia, Mimosa, Myrcia* (many species), *Ouratea, Palicourea, Parinari, Peixotoa, Periandra, Piptocarpha, Pisonia, Protium, Psidium, Salacia, Sapium, Sebastiana, Serjania, Solanum, Spiranthera, Stachytarpheta, Symplocos, Tetrapteris, Tibouchina, Tocoyena, Trixis, Vellozia, Vernonia* (very many species), *Virola, Waltheria, Zeyheria*, etc.

Most of the tree species also bloom and fruit in shrub form when kept low by cutting and burning. Therefore, in shrubby cerrados derived from arboreal forms just as many, or even, most, of the shrubs one sees blooming and fruiting are likely to be basically tree species as true shrub species. Besides this, many of the species which are trees in many cerrados never grow beyond a shrub form on especially poor soils even when they are not cut and are burned only infrequently, but flower and fruit normally in the shrub form. It is possible that there are shrub ecotypes adapted to the naturally poorest-soil cerrados which even when planted in richer soils would not grow into trees. On the other hand, tree forms, once cut or burned to the ground, might not be able to grow into trees again but only into shrubs because the soil has been impoverished by the opening and burning of the stand, and they could only grow into trees again when enough nutrients have reaccumulated in the soil by the absence of further disturbance.

Most stands of cerrado contain one to a few species of palms (Fig. 3). These may be acaulescent and up to 1½ m tall, or small tree palms 2–5 m tall. Examples are, in the south: *Alagoptera campestris* (Mart.) O. Ktze. (formerly *Diplothemium campestre* Mart.), *Acanthococos emensis* Toledo, *Butia leiospatha* (Barb. Rodr.) Becc. [perhaps to be included in *B. capitata* (Mart.) Becc.] *Syagrus* spp. such as *S. flexuosa* (Mart.) Becc., and *Attalea* spp. such as *A. ceraensis* Barb. Rodr.; some of the *Attalea* species and the *Alagoptera* may be locally abundant and form dense stands. In the center and north occur *Syagrus* spp. such as *S. comosa* (Mart.), *Astrocaryum campestre* Mart., *Orbignya eichleri* Drude, *Cocos coronata* Mart., etc. Tall palms are apparently absent except in parts of Maranhão and northern Goiás where the tall tree palm, *Orbignya barbosiana* Burr. (formerly *O. speciosa* Barb. Rodr.), which is one of several species of *Orbignya* and *Attalea* known as "babaçu," enters the borders of upland cerrado from its bottomland habitat. In

FIG. 3. Tree and scrub woodland cerrado at the edge of a low lateritic scarp, Serra do Roncador, Mato Grosso. In this stand the low tree-palm "guabiroba" (*Syagrus* sp.) is common. Beginning of rainy season.

northeastern Maranhão, *Copernicia prunifera* (Mill.) H. E. Moore (formerly *C. cerifera* Mart.), occasionally enters upon the upland from its bottomland habitat, although it does so on shallow soil over rock pavements rather than in true deep-soil cerrados. Possibly, tall-tree species of *Attalea* occur in some cerrados in other areas, although they also are basically lowland species.

Although the Velloziaceae are more characteristic of the mountain top rocky campos, some species occur in the usual deep latosol cerrados, such as *Vellozia flavicans* Mart. ex Schult. f. and other species around Brasília (Fig. 4). (Menezes, 1971, has separated some *Vellozia* species into the resurrected genus *Xerophyta*, and some *Barbacenia* species into a new genus, *Aylthonia*.)

Ground or climbing vines, herbaceous or woody, can generally be found in the cerrado, although they are rarely conspicuous in the aspect of the stand. They include species of *Aristolochia, Arrabidaea, Banisteria, Bauhinia, Camptosema, Cayaponia, Centrosema, Cissampelos, Cissus, Clitoria, Davilla, Dioclea, Dioscorea, Ditassa, Eriosema, Evolvulus, Galactia, Ipomoea, Melancium, Merremia, Mikania, Mimosa* (many species), *Passiflora* (many species), *Peixotoa, Rhynchosia, Serjania, Smilax, Strychnos,* etc.

FIG. 4. *Vellozia flavicans* Mart. ex Schult. f. in cerrado in Brasília.

Very few plants in the cerrado are spiny; these are mostly vines and only occur here and there (*Mimosa, Smilax*), but include a few herbaceous and shrubby species of *Solanum* with prickles on the leaves and stems, and bromeliads with hooked spines on the leaf edges.

Cacti are definitely not characteristic of cerrado; they are all but absent. Rocky or lateritic outcrops in the cerrado, or a substrate composed entirely of laterite pebbles, may bear one or two globular or small cylindrical species, but except in some places in the drier northeastern edge of the cerrado region, they are not found on the usual flat sites covered with deep non-stony soil. In southeastern Maranhão, which is part of the drier portion of the cerrado region, the tall, branched, cylindrical, fluted *Cereus peruvianus* Mill. was noted as common as part of the understory in some arboreal cerrado woodlands on flat, deep-soil plateau tops, while in similar woodlands on other plateau tops a few kilometers away, it was completely absent. In the denser arboreal forms of cerrado, epiphytic cacti of the *Phyllocactus* type may occasionally occur.

Terrestrial bromeliads can usually be found in all cerrado areas but only as scattered individuals or rare populations (*Dyckia, Bromelia* and *Ananas* spp., rarely other genera). These occur on the usual deep non-stony soils. A few species are locally abundant, such as *Bromelia antia-*

cantha Bertol. and *Ananas ananassoides* (Baker) L. B. Smith, which may form clumps several to many square meters in area in São Paulo. *Tillandsia usneioides* (L.) L., *T. recurvata* (L.) L. and other species, and *Acanthostachys strobilacea* (Schult. f.) K. in Lk., Kl. & Otto occur as epiphytes, especially in the south, in both arboreal woodland forms of cerrado and in the lower more open forms that have escaped fire for some years. Terrestrial orchids are widespread but rare in individuals. Epiphytic orchid species are extremely rare. Pabst (1971) mentions 48 species of orchids in 10 genera so far known from cerrado, of which *Habenaria* has 19 species and *Cyrtopodium* has nine.

The hemiparasitic Loranthaceae, species of *Psittacanthus, Phoradendron* and *Struthanthus*, occur here and there on trees and shrubs, but in some large regions are rare or absent in cerrado vegetation although present in the gallery forests. The parasite, *Pilostyles*, of the Rafflesiaceae, occurs on the stems of *Mimosa* and some other leguminous cerrado plants. The lauraceous parasitic vine, *Cassytha*, grows on various cerrado plants, as well as *Cuscuta*.

The ground layer of the cerrado is also more or less xeromorphic. Most of the grasses, sedges and forbs have hard, siliceous leaves, although some are soft and densely hairy and a few are purely mesomorphic. There are relatively few microphyllous or ericoid herbs, such as *Vernonia brevifolia* Less., and *Microlicia* spp., and also very few aphyllous herbs in which thin green stems take over the photosynthetic function, such as *Bernardia spartoides* M. Arg., *Crumenaria* spp., *Indigofera gracilis* Bong. ex Benth. and *Rhabdocaulon denudatum* (Benth.) Epling. Squarrose shrubs and herbs, a dominant growth form in the mountain top rocky campos of central Brazil, are rare in typical cerrado.

Common cerrado forbs are species of *Acanthospermum, Achyrocline, Aeschynemone, Alstroemia, Arachis, Aspilia, Baccharis, Bernardia, Bidens, Borreria, Buchnera, Calea, Camarea, Cambessedesia, Cassia* (very many species), *Centrosema, Cleome, Coccosypselum, Commelina, Corchorus, Craniolaria, Crotalaria, Croton, Crumenaria, Cuphea, Deianira, Dalechampia, Desmodium, Dimerostemma, Diodia, Dipladenia, Diplusodon, Dorstenia, Elephantopus, Erechtites, Eremanthus, Eriope, Eriosema, Eryngium, Eupatorium, Euphorbia, Evolvulus, Galactia, Gomphrena, Hibiscus, Hyptis* (many species), *Icthyothere, Ipomoea, Isostigma, Jatropha, Julocroton, Justicia, Lippia, Lupinus, Macrosiphonia, Mandevilla, Manihot* (many species), *Marsypianthus, Microlicia, Mimosa* (many species), *Mitracarpus, Oxalis, Pavonia, Pectis, Peltaea, Peltodon, Pfaffia, Phyllanthus, Piriqueta, Polycarpaea, Polygala, Porophyllum, Rechsteinera, Rhabdocaulon, Rhodocalyx, Richardia, Ruellia, Salvia, Sauvagesia, Sebastiana, Sida, Sisyrinchium, Spilanthes, Stachytarpheta, Staelia, Stevia, Stylosanthes, Trichogonia, Trimezia, Triumfetta, Trixis, Turnera, Vernonia* (very many species), *Wedelia, Zornia*, etc. A few species are occasionally semishrubs or somewhat viny.

In the cerrado there is a complete intergradation between trees and shrubs, between shrubs and semishrubs, and between shrubs or semishrubs and herbs,* in the sense that a large portion of the individuals are hard to classify as one or the other.

Most of the herbs, semishrubs and smaller shrubs possess xylopodia (Rawitscher & Rachid, 1946; Rachid, 1947; Rizzini & Heringer, 1961, 1962b, 1966; Ferri, 1971b).† It is curious to see thin delicate herbs 10 or 20 cm tall attached to a hard woody underground xylopodium as large as a man's fist or forearm.

Almost all cerrado species are perennial. An exception is that many species of *Polygala* are annual herbs. Annual species of other families are a bit more common in the drier northeastern cerrados adjoining the semi-desert thorn scrub caatingas.

Cerrado sedges, which grow in regular well-drained cerrado soil, include many species of *Bulbostylis, Rhynchospora* and *Fimbristylis*, also a few species of *Cyperus, Dichromena* and *Scleria*. Grasses include species of *Andropogon, Aristida, Axonopus, Echinolaena, Eragrostis, Gymnopogon, Ichnanthus, Panicum, Paspalum* (very many species), *Setaria, Trachypogon, Tristachya*, etc. Besides the native cerrado grasses, three species from Africa are common, *Melinus minutiflora* Beauv. (strongly invasive in the southern half of the cerrado region), *Hypharrhenia rufa* (Nees) Stapf, and *Rhyncheletrum repens* (Willd.) Hubb. [= *R. roseum* (Nees) Stapf & Hubb. ex Bews]. The latter is more common in disturbed places and roadsides.

Certain species of *Anemia* and *Polypodium* are the only ferns one usually sees in cerrado. *Adiantum* (such as *A. sinuosum* Gardn.) and a few other genera are occasionally found, especially in shaded spots among rock or laterite block outcrops. Ground or corticolous bryophytes are rare, as well as ground lichens. Corticolous lichens, on the other hand, such as *Parmelia, Anaptychia* and *Usnea*, are common, sometimes thickly covering shrub and tree trunks and branches that have escaped burning for many years, particularly in arboreal forms of cerrado. Although fungi are not as common in cerrado as in forest, bracket fungi and mushrooms such as *Pycnoporus sanguineus* (L. ex Fr.) Murr.,

* Two characteristics are usually given in the definition of a herb, (1) the aerial stem is herbaceous, (2) the aerial stem dies back each unfavorable season to the ground or to a basal rosette. However, some herbs develop some secondary xylem at the stem base but do die completely to the ground each year. In the moist tropics some pure herbs are evergreen. *Andira* (Leguminosae) and *Chrysophyllum* (Sapotaceae) are tree and shrub genera but *Andira humilis* Mart. ex Benth. and *Chrysophyllum soboliferum* Rizz. of the cerrado have no aerial vegetative stems at all but their leaves look like those of woody plants, not like those of herbs. Shrub, semishrub or herb? Even when an individual plant is definitely in one of these categories, the species may belong to 3 or 4 categories, such as *Jacaranda decurrens* Cham. and *J. brasiliana* Pers.

† The word "xylopodium" is preferable to "lignotuber" since it does not imply that the structure must be made of stem tissue only. Also tubers usually form on a rhizome at a distance from the main stem while a xylopodium forms directly under it.

Schizophyllum commune Fr., *Panus crinitus* (L. ex Fr.) Sing., *Pogonomyces hydnoides* (Sw. ex Fr.) Murrill, *Trametes pinsita* (Fr.) O. Fidalgo & M. E. P. K. Fidalgo, and *Phellinus gilvus* (Schw. ex Fr.) Pat. can be found on dead trunks and fallen branches (Fidalgo *et al.*, 1965, and information from my own collections). The *Pycnoporus* almost always occurs on burnt wood. Viégas (1943) describes some leaf fungi from cerrado trees.

Relatively few cerrado species, such as *Andira humilis* Mart. ex Benth. (incl. *A. laurifolia* Benth. in Mart.), *Bowdichia virgiliodes* HBK., *Davilla elliptica* St. Hil., *Magonia pubescens* St. Hil., *Qualea grandiflora* Mart., *Palicourea rigida* HBK., and *Zeyheria digitalis* (Vell.) Hoehne (= *Zeyhera montana* Mart.), occur over the whole cerrado region. Others, such as *Curatella americana* L. occur over all but the southern edge. *Byrsonima verbascifolia* Rich. ex Juss., *Qualea multiflora* Mart. and *Q. parviflora* Mart. occur over the greater part of the region but are missing or rare in some large areas. Most cerrado species are restricted to smaller portions of the cerrado region. Thus, although many of the commonest woody species in a stand are the same all over, giving a false idea of uniformity, there is really a continuous floristic change from one part of the region to another. In areas, say, 1000 km apart only a few percent of the species are identical. This is true, for instance, if one compares the cerrado flora of a local area in São Paulo, in northeastern Mato Grosso, and in southern Maranhão. Neighboring vegetation provinces always contribute a few species to the cerrados adjacent to them but these usually do not penetrate very far.

Many of the most common and widespread cerrado species also occur as co-dominants in the Amazonian and northern South American savannas, such as *Curatella americana* L., *Bowdichia virgilioides*, HBK., *Andira inermis* (W. Wright) DC., *Byrsonima crassifolia* HBK., *B. verbascifolia* Rich. ex Juss., and *Palicourea rigida* HBK. It is probable that the disjunct savannas and campos on deep soils further and further removed north or west from the central continuous cerrado region gradually lose more and more typical cerrado species and acquire more and more savanna species distinctive to their own region. Rocky campo savannas on thin lithosols, however, bordering the cerrado region, such as the quartzite Serra do Cipó in Minas Gerais and other heights of the general Serra do Espinhaço, or not very distant from the edge of the region, such as the quartzite Serra do Cachimbo in southeastern Pará, have completely different and highly endemic floras.

The floristics of the cerrado is still in its infancy. No relatively complete list of cerrado species has ever been made. Many large cerrado areas have never been collected in at all and others only superficially. One of the difficulties in using herbarium material is that in over 90% of the specimens, especially old ones, no habitat at all is given, and for those in which the vegetation is mentioned, a large percent that were collected in cerrado say only "campo." Since there are many kinds of both natural and derived "campo" in Brazil, some being part of cerrado in the wide sense and many being completely different vegetation types, one cannot tell whether the specimen was collected in cerrado or not. One must also be careful of expressions like "wet places in cerrado," "cerrado seep," "wet meadow on cerrado slope," "marshy cerrado," etc., on some modern labels. These refer to seasonally soaking areas of grassy campo limpo within a general cerrado landscape but which do not bear a cerrado flora and are not part of the cerrado vegetation.* Rocky places in cerrado bear both local deep soil cerrado species and also species which otherwise grow only in other rocky vegetation types which are not cerrado. For instance, the tree composite, *Wunderlichia crulsiana* Taub., otherwise encountered only in mountain top rocky campos, grows on some small quartzite outcrops in cerrados in Brasília, along with typical cerrado species. A cylindrical species of "xique-xique" cactus of the *Cereus* tribe, otherwise known only from the caatinga, grows on sandstone outcrops in the midlde of the cerrado in southeastern Maranhão but does not occur in the deep soil cerrado itself. Another difficulty in cerrado floristics, of course, is that many cerrado

* Some herbarium specimens from the Serra do Cipó made by various modern collectors are marked as from "cerrado." From the species involved, altitudes and road distances given, and mention of "sandstone" outcrops, it is clear that the specimens are neither from the lower part of the west slope (where cerrado from the adjacent lower land intergrades to the planalto vegetation) nor from an exceptional very small area of true cerrado (on red deep latosol without outcrops, situated over a true sandstone bedrock) on the planalto itself, but rather from the very different and highly endemic "rocky campo" vegetation on gray lithosol over itacolomite quartzite, which is the almost universal plant cover of the planalto. This planalto vegetation consists of (1) natural grassy meadows on level upland sites, (2) open campo slopes with stony soil and rock slab outcrops, some portions of which are moist for long periods during the rainy season (because they are situated in or next to drainage rills) but completely dry in the dry season, and other portions of which are always well-drained, (3) small areas of closed scrub of shrubs and small trees on rocky outcrops, (4) cliffside vegetation. There are also narrow gallery scrubs and low forests along the streams. Some modern collectors of Serra do Cipó plants call the open rocky campo slopes "cerrado," although, as stated, it is not really this vegetation. Since the word "cerrado" in general Portuguese means "dense," it is sometimes used by other collectors to refer to the dense upland scrub groves of this non-cerrado planalto vegetation. Prof. E. P. Heringer, who has collected extensively in central Brazil, tells me his collections marked as "Serra do Cipó, M. G. Cerrado" come from this dense scrub. His non-Serra do Cipó collections marked "cerrado" come from the regular cerrado vegetation as recognized in this paper, with one possible exception as follows. Some rivers in central Brazil flowing through flat cerrado-covered terrain (particularly the Rio Araguaia) do not have distinct gallery forests along part of their course. The cerrado on flat land comes right to the edge of the channel and on the few-meters-wide steep slope to the water itself occurs an open- to closed-cover scrub or arboreal vegetation, semideciduous like the cerrado, and which may contain some cerrado species. Such riverside slopes also contain, or indeed may be made up only of, forest species, so that the decision as to whether it is really mesophytic forest or not is sometimes difficult to make. Prof. Heringer, in his collections from such sites, has used expressions like "cerrado, margem do rio," etc.

species, like those of other vegetation types in tropical America, belong to species complexes whose taxonomy and nomenclature have not yet been worked out.

A partial review of the floristic literature mentioning cerrado plants now follows, emphasizing the more recent Brazilian contributions.

Martius (1824, 1950) mentions some common species for Minas Gerais cerrados (referred to as "campo" and "tabuleiro"). Warming (1892, 1908) gives a very complete list of species of the cerrado (which he calls "campo") for an area of about 150 sq. km around Lagoa Santa, Minas Gerais. Ule (1895) mentions several dozen species for Goiás cerrados under the heading "Chapadas." He also refers to the cerrados as "taboleiros cobertos" or "cerrados." Lindman (1914) mentions about 100 common species of the cerrados of Mato Grosso. Malme (1924) gives a list of 27 leguminous cerrado trees from a small area of Mato Grosso. (He also includes *Andira humilis,* a dwarf shrub, but he is probably applying this name to the tree species, *A. inermis.*) Ferri (1944), Rachid (1947), Rawitscher (1948), and Ferri & Coutinho (1958) give a list of most of the species, based on collected specimens, of an area of 4–5 hectares of cerrado at Emas, near Piraçununga, São Paulo.

Ferri & Coutinho (1958) also list some of the common species in a small area of cerrado near Goiânia, Goiás, and in another small area near Campo Grande, Mato Grosso. Of 55 common species at Emas, São Paulo, 48 also occur commonly in the Goiânia cerrado (plus four more not found at Emas) and 36 occur commonly in the Campo Grande cerrado (plus two more not found at Emas).

Sick (1955) mentions a few common species for the cerrados around Xavantina, Mato Grosso, under his vegetation types "cerrado" and "cerradão." Although he classifies them separately from cerrado, his types, "descampado com núcleos de cupim" and "campo limpo pedregoso" are also forms of that vegetation; some of the species of his "capão sêco" are also cerrado species.

Mello Barreto (1956) gives common species for the Minas Gerais open cerrados under his vegetation type, "campos baixos" and for cerradão under his "caatanduva" or "mata campestre."

Rizzini (1963b) gives a long, although still very incomplete, list of woody species of the cerrado in general. Eiten (1963) gives a list of 210 cerrado species, woody and herbaceous, from a cerrado area of several square kilometers in eastern São Paulo. Although still very incomplete for the area, it is based entirely on collected and identified specimens, and the physiognomy of the stand in which each was collected is stated. (A second part with further species is in preparation.) Rennó (1960) published a mimeographed list of species in the herbarium of the Instituto Agronômico at Belo Horizonte, most of whose specimens are from Minas Gerais, and gave the habitat of each, of which "cerrado," "cerrado sujo," and probably most cases of "campo arenoso," "campo sujo" and "campo" belong to the cerrado vegetation. In 1965 the same author published a mimeographed list of Minas Gerais cerrado species, a very partial account of the rich cerrado flora of that state.

Labouriau *et al.* (1964b), in a paper on nocturnal stomate opening, give a list of 50 species of common cerrado plants used (all except two being woody). These were mostly from Paraopeba, Minas Gerais, plus a few from Brasília, D.F. Although this list is not meant to be a complete account of the species occurring at Paraopeba, it is interesting to note that of 32 woody species in genera which have also been determined to species for the cerrado at Emas, São Paulo, 16 also occur on the Emas list; of the other 16, some do not grow as far south as São Paulo while others grow in cerrados in São Paulo other than Emas.

In a paper on seed germination under natural conditions in the southern part of the cerrado region, Labouriau *et al.* (1964a) give a long list of cerrado plants found germinating in the field, of which 50 were determined to species.

Descriptions and drawings of seeds of cerrado grasses have appeared in Sendulsky (1965, 1966). Pinho (1966, 1969) has published on the wood anatomy of some cerrado trees, Beiguelman (1962a) on the anatomy of tension wood, and Massa & Arens (1971) on the periderm.

Ferri in 1969 published a handsome book with full page line drawings of 79 common species of the São Paulo cerrados, mostly made from material collected at Emas. Goodland (1969, 1970a) treated 600 cerrado species found in his phytosociological study of 110 stands in the Triângulo Mineiro region of western Minas Gerais. Of these, 350 were identified to species. Included were 219 woody species with trunks at base over 10 cm circumference (135 of these determined to species). Cerradão is included in the conception of cerrado (sens. lat.) in this work, which is not always true of other lists of cerrado species. Although a large number of herbaceous species are listed, since the survey was made in the dry season, most of the herbaceous species, which appear only in the rainy season, could not, of course, be included.

Cerrado is extremely rich in the number of vascular species occurring in a stand. Very few studies of this type have been made since it is necessary to observe the same stand every few days the year round. Heringer & Barroso (1968) and Heringer (1971) found over 300 species in a single square hectare of original, relatively undisturbed, low-tree & scrub woodland cerrado on the University of Brasília campus. Of these, 288 were determined to species. Included were nine species of *Eupatorium*, eight of *Myrcia*, seven each of *Mimosa* and *Cassia*, and five each of *Baccharis* and *Hyptis*. It is interesting to note that of the twenty five 20 × 20 meter plots into which the hectare was divided, no species was found in all plots. The most common species occurred in only 22 plots; the number of species per plot varied from 52 to 117.

Rizzini (1971a) published a list of 73 cerrado species, stating for each its habit; type of fruit; the months in which fruit appears; number of seeds per fruit; form, dimensions and color of seed or endosperm;

aspect and consistency of seed testa; weight per 100 seeds; and percent found eaten by insects in various gatherings.

Rizzini's manual of Brazilian lumber trees (1971b) includes a few cerrado and cerradão species.

Rizzini (1971c) presented a new list of cerrado woody species and a short list of vicarious species in cerrado and mesophytic forest.

A good beginning in studies of pollen grains of cerrado plants has been made, mostly in the Instituto de Botânica of São Paulo. These include: Barth, 1966 (three of the species of *Caryocar* treated are from cerrado: *C. brasiliense*, *C. coriaceum* and *C. cuneatum*); Campos, 1962; Campos & Salgado-Labouriau, 1962; Felippe & Salgado-Labouriau, 1964; Ferreira & Salgado-Labouriau, 1966; Handro, 1965; Marques & Melhem, 1966; Matos & Melhem, 1966; Melhem, 1964, 1966a, 1966b, 1966c, 1968, 1971; Melhem & Salgado Labouriau, 1963; Melhem & Paula, 1966; Melhem & Campos, 1969; Melhem, Moura & Lieu, 1971; Salgado Labouriau, 1961, 1967; Salgado Labouriau & Barth, 1962; Salgado-Labouriau, Carvalho & Cavalcante, 1969; Salgado-Labouriau & Gusman, 1967; Salgado-Labouriau & Morhy, 1969; Salgado-Labouriau & Válio, 1964; Salgado Labouriau, Vanzolini & Melhem, 1965; Válio & Salgado Labouriau, 1964. In addition, Salgado-Labouriau has written a general article on palynology (1962) and on palynology of the cerrado (1966). Her doctorate thesis (1971, University of São Paulo) contains a general key for identifying pollen grains of cerrado plants, with descriptions and illustrations of the pollen types. It must be mentioned that in this pollen work, the species to be included were based on published lists of cerrado species, but the actual specimen from which pollen was taken did not always come from a cerrado. Some came from a forest, or an open field or pasture derived from forest, or in many cases, no habitat information at all was provided by the original collector on the label. There might possibly be some slight quantitative differences in pollen of the same species growing in forest and in cerrado, perhaps due to incipient ectotype differentiation. One case has in fact already been found, in *Dorstenia brasiliensis* (Melhem, 1966a).

IV. TORTUOSITY OF CERRADO TREES AND SHRUBS

As a general rule among the woody plants in the cerrados, a particular stem axis, either the main stem or a branch, gives out over one or more years one to several branches and then dies at its tip, a terminal or a subterminal branch then taking over the main growth. Usually only one, sometimes two, rarely more, of these branches survive. Thus a few-branched sympodial axis develops and since each branch generally grows out at a wide angle to the axis from which it arises, or even reverses its direction, the sympodium is jagged rather than straight. Further thickening then occurs, covering the dead tips of the several branch orders, and new bark forms an uninterrupted surface, covering over the previously visible junctions of branches with their mother axes, thus hiding the fact that the single axis is sympodial and not monopodial. The thickening also reduces the sharpness of the angles at the branch junctions and turns the axis from zig-zag to strongly curving and twisted. The trunks of most cerrado trees, therefore, do not represent a single axis. (L. T. Eiten, personal communication.)

A similar process also occurs in forest trees and shrubs but (1) the trunk of a tree is usually a single axis, (2) more branches along a single monopodial portion of an axis usually survive, producing a much more branched system, (3) the sympodial axes that arise, when they thicken, are straighter or more gently curved, not so strongly zig-zag, (4) those axes that are zig-zag remain thin-stemmed. The visual effect, therefore, is very different.

In the cerrado it was noted that branch tips died even when not burned. Whole sympodial trunks or large branches developed during periods of several years without fire, and these were usually jagged also. Thus, the tortuosity of cerrado woody plants does not depend on fire. But since fire often kills a stem tip that might have continued to grow further before it died naturally, the effect of fire would be to shorten the average length to which an axis grows before its tip dies and a branch takes over, thereby *increasing* the tortuosity.

The following example from a cerrado on the Serra do Roncador, Mato Grosso, illustrates the process.

Figure 5A is a drawing of a shrub of *Curatella americana* about 2 m tall made in the rainy season (December). A fire during the previous dry season had charred the trunk except the top portion. It is not known whether any of the burned branches on the trunk were alive when the trunk was burned. The uncharred branch tips on the upper part of the trunk died naturally (as could be noted also in other stands unburned for several years) although some may have been killed by the heat without charring. The branch tips did not seem to be insect-eaten. The tip of branch order 2 bore an inflorescence so its growth would have stopped anyway. The heat evidently did not kill the third-order branch to the right, for from its base a fourth-order branch grew during the present rainy season, the only branch now alive on this shrub.

During the growth of the shrub the first-order stem from the ground stopped growing and a terminal branch from it of the second order continued the main growth giving off third order branches and terminat-

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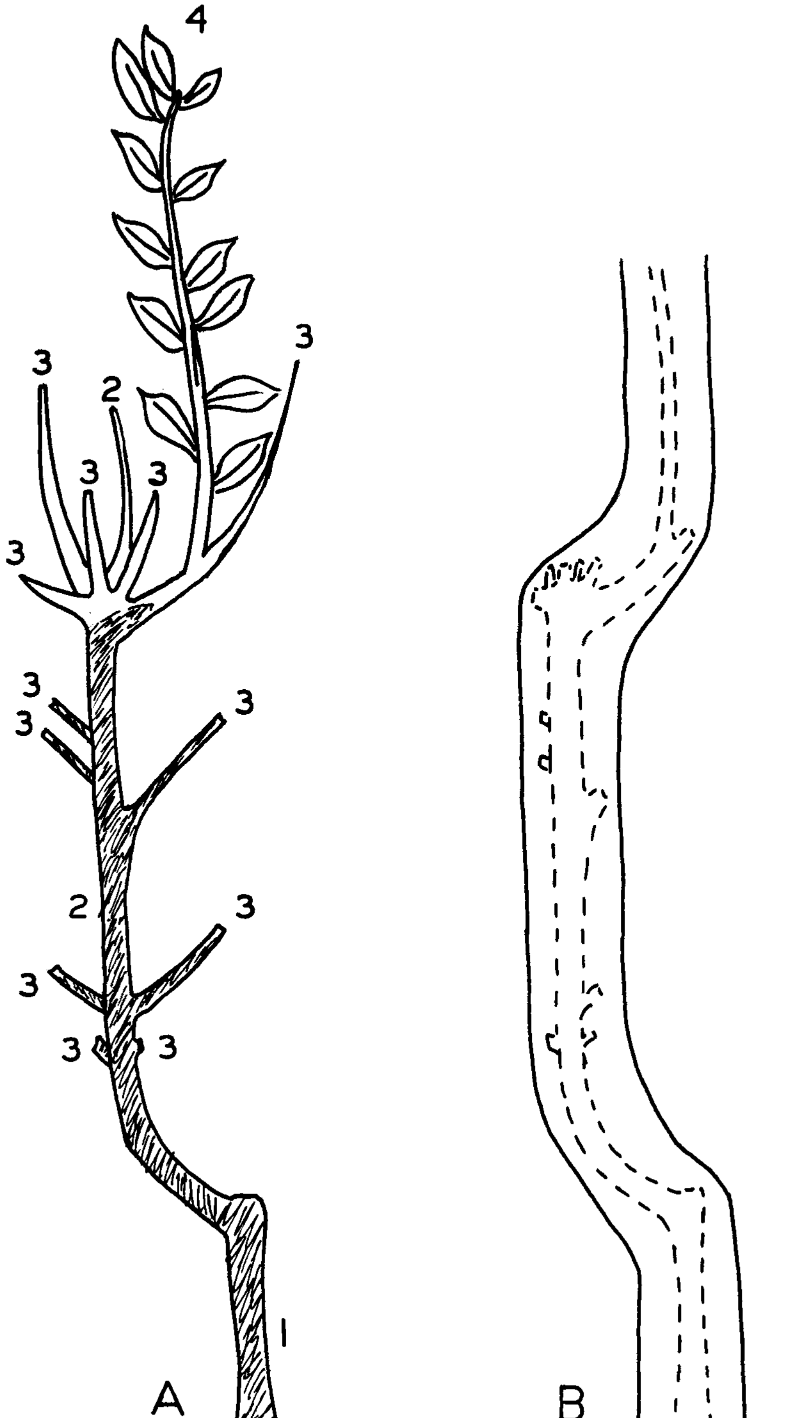
FIG. 5. A) *Curatella americana* L. 2 m tall. Burned trunk and branches shown shaded. Branch order 4 is growth of current season. Unburned branch tips of 3rd order died naturally. Tip of branch order 2 bore an inflorescence which stopped further growth of that axis. B) Hypothetical future thickening to form a single twisted trunk, which, up to the point shown, consists of 4 branch orders. The dead branch tips have been reduced in length by decay and fall and covered over by the growth of new wood and bark. The original younger stage is shown in dotted outline.


4
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A
B

ing in an inflorescence. One of the third order branches from near its tip, that shown to the right, continued the growth, but the end of it died and a fourth order branch from its base continued alive. The branches, arising at wide angles, make for a jagged effect.

Figure 5B shows the hypothetical future thickening of these stem axes which would cover the dead branch tips and form a single twisted trunk.

While working at the Instituto de Botânica at São Paulo, Dr. L. G. Labouriau planted various species of cerrado trees and shrubs in the soil of recently cleared secondary forest on the Instituto's grounds. These provide a valuable comparison with cerrado plants growing in their native habitat. Visited after several years, it was noted that the typical cerrado plant, *Stryphnodendron barbadetimam*, now 2½ m tall, grew with a single straight main axis from the ground, either with no branches at all, or with a few thin branches only a few centimeters long at the very tip of the trunk. The trunk therefore was straight, monopodial, and unbranched or essentially so, a condition rarely met with in the cerrado in this species. When a monopodial trunk does occur in the cerrado in this species it always bears several long thick branches. The other planted cerrado species also were considerably less twisted.

Three causes could be brought forward for the lack of tortuosity of a typical cerrado woody plant grown on forest soil in the city of São Paulo. (1) No fire ever passed through the planted stand. But in cerrados where fire had not occurred for many years the new woody growth that formed during that period was still rather twisted, that is, jagged sympodial axes formed. (2) The total rainfall in different parts of the city of São Paulo varies from slightly over 1300 mm to about 1500 mm average per year. This is at the higher end of the rainfall range in which cerrado occurs in the state. The dry season in the city is on the average only slightly less strong than that in the main part of the cerrado area. But since a certain proportion of typical cerrado occurs in the state under a rainfall regime like that of the city of São Paulo, as well as in the city itself and nearby on certain substrate types (Ab' Saber, 1970a, 1970b), the rainfall regime probably is not the reason for the difference in tortuosity. (3) The forest soil of the Instituto's grounds is deep like that of the cerrado, and although nutritionally rather poor is not so poor as cerrado soils in general. The possibility remains then that by some mechanism not yet known poor soil nutrient level may be a factor in the tortuosity of cerrado plants, either by its effect in evolutionarily producing genotypes that grow in this manner or, as is possibly the case here, by its direct effect on individual ontogeny.

The formation of jagged sympodial axes with each branch leaving the preceding branch at a wide angle is how the cerrado produces its twisted trunks and boughs, but why practically all the trees and taller shrubs of this vegetation evolved this manner of growth is still an open question. Poor soils in other tropical regions with about the same rainfall, a comparable dry period, and presumably the same susceptibility to natural fires, such as in Africa, Asia and Australia, have not produced a vegetation like the cerrado in the peculiar visual aspect of its individual woody plants.

V. STRUCTURAL FORMS AND TERMINOLOGY

Cerrado in the wide sense occurs in almost all possible structural forms, that is, with different heights and densities of the various layers. The physiognomic peculiarities of the individual plants, mentioned above, impress a certain visual unity on stands of cerrado and serve to distinguish this vegetation wherever it occurs from woodland, scrub, and savanna structural forms of other vegetation types even if the characteristic cerrado species are not immediately recognized. Except for certain small regions of intergradation, one can usually distinguish any of the structural forms of cerrado from mesophytic forest and its successional stages, and also from the many forms of caatinga, these being the two main large-scale vegetation types with which the cerrado region is in contact. (The cerrado also adjoins the Chaco vegetation in southwestern Mato Grosso along a narrow front, but I do not know enough about the latter to list its distinguishing physiognomic characteristics.)

In reading authors who have written on the cerrado, it is necessary to know what terms they have used for it in the wide sense and for its various structural forms. Unfortunately, there is no uniformity. Two authors may use the same term for two different concepts (of which one may partially or completely include the other), or use two different terms for the same concept.

Of these various usages, it is most important to know how the current generation of Brazilian geographers and students of vegetation use the terms, for most of the literature being published about local geographic distribution of cerrado and other vegetation in Brazil, as well as vegetation maps, is prepared by the federal government's Instituto Brasileiro de Geografia e Estatística and printed in its several publications: Revista Brasileira de Geografia, Boletim Geográfico, and separate books such as Conselho Nacional de Geografia, 1959, 1960, 1962, 1963a, 1963b, 1965; Instituto de Geografia, 1968; Instituto Brasileiro de Geografia e Estatística, 1957–1964, 1960; Valverde & Dias, 1967; all with many photographs and colored maps. For comparison, the savanna areas of the Territories of Amapá and Roraima are treated briefly in Guerra (1954, 1957), Azevedo (1967) and Takeuchi (1960a, 1960b).

These geographers recognize the following vegetation types in Brazil for purposes of discussion and mapping.

1. *Equatorial Forest*: the Amazonian hylaea.

2. *"Tropical Forest"*: broadleaf mesophytic forest in galleries (evergreen) and small detached upland areas (evergreen or semideciduous, rarely deciduous) within the cerrado region.

3. *"Transitional Vegetation"*: tall, broadleaf, mesophytic semideciduous forest forming a belt on the eastern and southern edge of the hylaea. One of the forms of forest commonly called "mata sêca."

4. *Atlantic Coastal Forest*: broadleaf evergreen (interior portion semideciduous or occasionally deciduous in local areas), from Rio Grande do Norte to Rio Grande do Sul. (Sometimes, from southern Bahia south, the wetter forests of the slope and crest that form the seaward edge of the central plateau are distinguished from the drier forests of the interior on the plateau surface.)

5. *Caatinga*: deciduous (in some small areas semideciduous) thorn-scrub, sometimes thorn-forest, in northeastern Brazil behind the coastal forest belt.

6. *Cerrado*: central Brazil, with outliers in São Paulo and the Northeast. The Amapá and Roraima savannas are sometimes included, and occasionally even the small Amazon savannas.

7. *Palm Forest* ("Cocais"): *Orbignya barbosiana* (= *O. speciosa*) and *Copernicia prunifera* (= *O. cerifera*) forests and woodlands in the northeast; *Copernicia alba* (= *C. australis*) forest in the southwestern Mato Grosso Pantanal.

8. *"Campo Limpo"*: more or less pure grassland of any vegetation type on non-inundated terrain, when this is the predominant vegetation of the region.

9. *Inundated Campos*: periodically indundated sedge-grassland ("campo de várzea"), mapped only for Marajó Island and Amapá although they occur on a smaller scale along the Middle Amazon and in many other regions.

10. *Araucaria Forest*: large areas extending from northern Rio Grande do Sul to Paraná, as well as scattered small areas in São Paulo and southern Minas Gerais at high altitudes.

11. *Pantanal Complex*: southwestern Mato Grosso.

12. *Chaco Vegetation*: a small area in southwestern Mato Grosso extending from Paraguay.

13. *Littoral Vegetation*: (a) evergreen broadleaf mesophytic forest and scrub on coastal plain sands ("restinga") and associated sea-level lacustrine and alluvial clays; (b) vegetation of beaches and of seaside dunes; (c) mangrove swamps. Sometimes the dune areas or the mangrove areas are extensive enough so that they are mapped separately from the rest of the littoral vegetation.

This is an adequate large-scale primary analysis, being more detailed than Martius' division of Brazilian vegetation into five series. However, besides the inevitable transitions between the delimited types, it must be recognized that they are not all really coordinate to each other nor are they all mutually exclusive. (1) The Pantanal Complex, for instance, includes many of the other types mentioned, such as non-inundated campos limpos, inundated campos, cerrado (all forms), evergreen mesophytic forest, palm forest, Chaco vegetation, marshes, etc. (2) Pantanal itself, in the strict sense of seasonally inundated sedge-grassland with scattered trees, or with small groves of trees on raised earth mounds associated with termite nests, occurs in the Pantanal Complex of southwestern Mato Grosso, but also in an area hundreds of kilometers wide in northeastern Mato Grosso and adjacent Goiás (it can be seen when flying from Brasília to Manaus) between the cerrado and the edge of the Amazonian hylaea. This extensive northeastern Mato Grosso-Goiás pantanal has not been marked as such on published maps but is included in the cerrado region, despite the fact that the cerrado is never inundated. (3) What is called "campo limpo" on the maps, as the name for a regional vegetation, includes areas that fall into several different vegetation provinces. Thus, it is used (a) for the southern Brazil grassland (Paraná and south), (b) for areas in southern Minas Gerais and in southern Mato Grosso (Campos da Vacaria) which are floristically cerrado, and (c) for a narrow north-south band of grassland ("campina" or "gerais") along a flat water divide that follows the Goiás-Bahia border and which is an extremely impoverished form of cerrado due to continuous soil weathering and leaching since the Mesozoic.

It is necessary to mention these other vegetation types in Brazil, and how they have been mapped, in order to point out that there are areas not marked as cerrado (in the wide sense) on the maps that certainly well may be included in that concept, and that some of the regions marked as cerrado are not really that vegetation.

Within the true cerrado vegetation as a whole, Brazilian geographers distinguish four structural types.

(1) *Cerradão*: the medium-tall arboreal form with a closed or semi-open canopy (down to about 30–40% tree crown cover) (Fig. 6).

(2) *Cerrado* (restricted sense): includes several forms with the total woody plant cover closed or down to about 30–40%, such as (a) closed or semi-open *low arboreal* forms (canopy generally less than about 7 m tall) (Fig. 7), (b) closed or semi-open *scrub* forms (canopy generally less than about 3 m tall), the elements of which may be definitely shrubby, arboriform, or the two mixed, (c) closed or semi-open *scrub mixed with scattered trees* of various heights. The trees may be emergents and form a single upper layer or, usually, rise to varying heights along with varying heights of scrub elements so that the upper surface of the vegetation is "hilly" (Figs. 8 & 9).

(3) *Campo Cerrado*: includes several forms with the total woody plant cover rather open or sparse, that is, less than 30–40% cover, such as (a) quite open scrub, (b) low arboreal quite open woodland, and (c) true physiognomic savanna, i.e., *scattered* medium-tall or low trees, or shrubs (Fig. 10), or usually both trees and shrubs intermixed (Fig. 11), over a continuous or slightly open layer of grasses, herbs, dwarf shrubs and semishrubs.

FIG. 6. Cerradão arboreal woodland (locally called "chapada") in southeastern Maranhão. Beginning of dry season.

FIG. 7. Low woodland cerrado in Brasília at beginning of dry season. The trees are too low for the stand to be called a cerradão. Note shrub layer definitely subordinate in aspect to tree layer.

FIG. 8. Cerrado tree and scrub woodland in São José dos Campos, São Paulo. The total woody vegetation forms an open layer with the shrubs prominent in the aspect. This is probably a derived form due to disturbance and recuperation from the original cerradão at this locality.

FIG. 9. Cerrado low-tree and scrub woodland on the Serra do Roncador, Mato Grosso. This physiognomy is natural here, not due to disturbance. Note that the vegetation is more open than in Fig. 8.

FIG. 10. Cerrado scrub savanna, probably derived from cerradão, São José dos Campos, São Paulo. The soil on this slope is deep and not stony. The scrub elements are almost all less than 3 m tall, although arboriform.

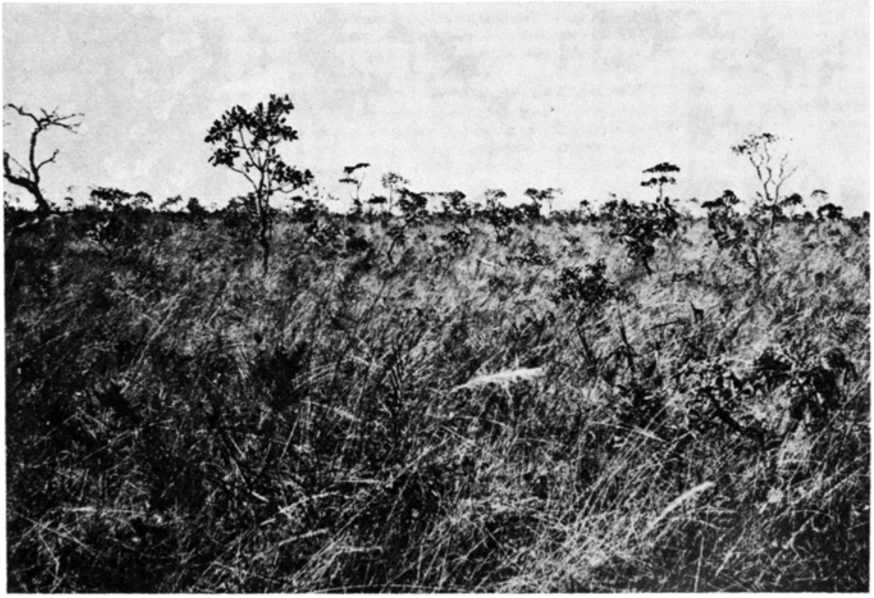

FIG. 11. Cerrado low-tree and scrub savanna in Brasília at beginning of dry season. It is difficult to say if this form is natural here or derived by burning from the more common tree and scrub woodland form.

(4) *Campo Limpo*: grassland with taller visible woody plants essentially absent, and whose flora is made up of practically the same species as the ground layer of campo cerrado. (Note that the use of "campo limpo" here is for a variation of the *cerrado* flora.) Sometimes, when a cerrado grassland has a few, very scattered, low but conspicuous shrubs or acaulescent palms it is distinguished as "campo sujo."

In this classification three grades of density are distinguished (four if campo sujo is included), while the height of the woody layer makes a difference only in the densest grade.

In many parts of Brazil, farmers, stock raisers and woodsmen use these terms (including "campo sujo"). Although the exact boundaries of the meaning of each term may vary from person to person, they are fairly consistent. In other regions completely different terminologies are used by the people for the cerrado in general and for its several forms.

The word "campo," without qualifying adjective, is often used in Brazil in everyday language for any vegetation that is not closed forest or dense scrub, i.e., any open vegetation, cerrado or not, with enough herbaceous growth that it can be grazed.* When speaking about cerrado vegetation, some geographers may informally use "campo" in this sense as a general structural term for the combined concepts of "campo cerrado," "campo sujo" and "campo limpo." Other geographers would include in the general "campo" concept also the dense scrub form or even the semi-open tree-and-scrub woodland, that is, all cerrado forms that are not definitely forest-like.

The main thing to note here is that the word "cerrado" itself is currently used in the technical literature in two senses: (1) for the whole large-scale vegetation type or province with all its structural forms, and (2) for a certain partial range of the continuous structural variation of this vegetation type. This is unfortunate but, as there is apparently no other available word for the lower more or less closed form, "cerrado" will probably continue to be employed in both senses, and it is necessary each time to see how it is being used.

The range of structural forms in cerrado is completely continuous in the sense that stands can be found in any region which may be ranged in a series from arboreal, through all grades of scrub and structural savanna, to (usually) pure grassland of the cerrado type. This continuity was recognized by many of the early travelers and particularly emphasized by Smith (1885). In some regions some or all of these forms are natural; in other regions only cerradão is natural (although it may originally have been of different heights depending on soil fer-

* Such as: (1) periodically inundated tallgrass stands in Amazonia, the "campos de várzea"; (2) the pure grasslands of the southern states, Paraná, Santa Catarina and Rio Grande do Sul (where they often have other local names); (3) pastures derived from forests may also be called "campos," as well as (4) cultivated fields ("campos de cultura"). Natural and derived grasslands on dry or wet soil also have other local names: "resfriado," "invernada," "potreiro," etc.

TABLE I
AVERAGE AND RANGE OF CHARACTERISTICS OF TRIÂNGULO MINEIRO CERRADOS.
(GOODLAND, 1969)

	Cerradão	Cerrado	Campo Cerrado	Campo Sujo
% canopy cover	46 (15–85)	19 (1–55)	3 (0–15)	1 (0–2)
General height of stand, m.	9 (6–18)	6 (4–8)	4 (3–6)	3 (1–5)
Number of trees per hectare	3200 (1631–4925)	2250 (836–3976)	1400 (335–2928)	850 (266–2070)
Basal area of trees per hectare (thousands of cm^2)	313 (203–513)	168 (62–253)	76 (17–142)	30 (10–60)
Number of species of trees noted per stand	55 (40–72)	43 (26–60)	36 (18–52)	31 (19–43)

tility) and all the lower, more open forms are due to cutting and/or burning. A quantitative measure of this continuity is given in the recent work of Goodland (1969, 1971b). Working in the cerrados of the Triângulo Mineiro (a western extension of Minas Gerais interposed between São Paulo and Goiás), he was the first to apply gradient analysis to Brazilian vegetation. He examined 110 stands over a wide area, counting 80 trees in each stand by the point quarter method. Since trees intergrade to shrubs in cerrado, he defined a "tree" as any plant with a woody stem 10 cm or more in circumference at the base, above any root swellings but below any branches. Defined this way, many shrubs or arboriform scrub elements were included in the concept of "tree." In each stand he estimated the general height of the trees and at 20 points estimated the canopy cover above eye level. Each stand was classified before measurement as either "cerradão," "cerrado" (strict sense), "campo cerrado" or "campo sujo," using the help of a Brazilian companion who knew cerrado intimately. (The "campo limpo" form of cerrado does not occur in the region.) Approximately equal numbers of each form were examined. Thus he was able to give quantitative limits to the various structural characteristics of the four forms as usually interpreted by the people. These are reproduced in Table I.

We may now turn to the varied cerrado terminology of other authors. One of the earliest was that of Martius (1824; Portuguese translation, 1950). Speaking of the terminology used at that time for the campos of Minas Gerais, he states that there are two general kinds, campo limpo on the one hand and campo fechado or campo cerrado on the other. When the tree and shrub clumps of these campos are so close that it is difficult to get through, it is called "campo acarrascado" [that is, campo verging to "carrasco," which in Martius' use is a type of dense scrub].

When the shrubs lose their leaves in the dry season, it is "campo acatingado" [that is, campo verging to caatinga]. When the campos are more definitely dominated by trees with twisted and extended boughs, thick bark and relatively sapless gray-green leaves [i.e., typical cerrado trees], the vegetation is called "tabuleiro." When these tree crowns touch, it is "tabuleiro coberto," and when there is dense scrub between the trees, it is "tabuleiro cerrado." All these terms refer to vegetation at moderate altitudes, and from the appended species mentioned are types of cerrado. Martius distinguishes these from the higher-altitude mountain top campos.

Table II attempts to show the range of senses in which certain subsequent authors have used the various Brazilian terms. From this table and the appended notes we see that most workers recognize cerradão (under some name or other) as a type of *forest* in the structural sense although recognizing the floristic affinity of its trees with the taller woody plants of the lower more open forms of cerrado. However, the IBGE publications map cerradão correctly as part of the broad cerrado vegetation type, contrasting the cerrado as a whole with caatinga, Atlantic forest, Amazonian forest, etc. This difference in treatment of cerradão depends upon whether one is thinking primarily of the structure or of the species composition.

It is in the lower and more open forms of cerrado, forms 2–5, that there is the greatest variation in the meaning of the terms used. Note that the terms "campo" (even restricting its use only to cerrado vegetation), "campo cerrado," "cerrado" and "campo limpo" have different extensions of meaning among the different authors cited or even in different papers of the same author. Often only a close analysis will reveal how an author is using a particular term. "Campo sujo," where used at all, seems to be the only term besides "cerradão" that means about the same thing all the time.

Hills & Randall (1968) present a table (their Fig. 4) which correlates various usages of terms for different structural forms of "savanna" (sensu latissimo). In their book the word "savanna" is not used as I would use it, to refer to a particular restricted range of structural forms of *any* vegetation type, namely, a grassland or herb-covered area with scattered trees or shrubs or both, or with the woody plants grouped into scattered small groves. From the examples given in the book, "savanna" is used as a general term for any terrestrial tropical vegetation (or at least low-altitude tropical vegetation) which is not closed evergreen broadleaf mesophytic forest or desert. Included as "savannas" are graminoid marshes, herbaceous swamps with scattered trees, pure grasslands, grasslands with scattered trees and/or shrubs, scrubs of all densities, arboreal woodlands, and dry-season semideciduous or deciduous forest, both xeromorphic and mesomorphic. This is a very broad spectrum, both structural and ecological, to fit into the single concept, "savanna."

Table II.
Cerrado terminology of various authors*

C E R R A D O
(wide sense)

IBGE publications[a]	1 CERRADÃO	2 CERRADO (strict sense)	3 CAMPO CERRADO	4 CAMPO SUJO	5 CAMPO LIMPO
Description	xeromorphic forest or arboreal woodland	xeromorphic low forest, low arboreal woodland, closed scrub, or slightly open scrub	xeromorphic well-open low woodland, well-open scrub, arboreal savanna, tree-and-scrub savanna, or scrub savanna	xeromorphic very open scrub savanna (very scattered but definitely visible shrubs and tree-like scrub elements up to 2 (-3) m tall; ground layer as in 5	xeromorphic grassland (pure grassfield or grassfield with herbs; dwarf shrubs and semishrubs, if present, generally hidden in the grasses
Warming 1892, 1907[b]	caatanduva or mata campestre	c a m p o campo cerrado (or cerrado)		campo limpo (or campo descoberto)	
Löfgren 1898[c]	caatanduva, cerradão capão	cerrado	caatininga, campo cerrado	campo limpo (campo sujo ?), campo	
Warming 1909		c a m p o campo cerrado (denser extreme)			
Luetzelburg 1923[d]	agreste				
Rawitscher 1946[e]		as used: campo cerrado (or cerrado) as defined: cerrado	campo cerrado	campo sujo	
Waibel 1948	cerradão (or mata de terceira classe)	campo (informal general sense) campo cerrado (or cerrado)		campo sujo campo limpo	
Mello Barreto 1956[f]	mata campestre or caatanduva	campo baixo or cerrado			
Aubreville 1959[g]	cerradão	cerrado	campo cerrado		campo limpo
Rizzini & Heringer 1962[h]	cerradão (or floresta xeromorpha semidecídua)	campo (general sense) 1. campo cerrado cerrado (denser taller extreme)		campo sujo (lower open extreme) 2. campos gerais 3. campo limpo (or "campo" in restricted sense)	
Rizzini 1963a[i]	floresta xeromorfa (or cerradão or caatanduva)	"savana central" (or cerrado, etc.)			
Rizzini 1963b[j], 1964	cerradão (or floresta xeromorfa)	cerrado		campo (or campo limpo)	
Eyre 1963[k]	cerradão	campos or campos savannas	campo cerrado	campo sujo	
Borgonovi & Chiarini 1965[l]	cerradão	cerrado			campo
Lima 1966[m]	cerradão	cerrados			
Hueck 1966[n]	cerradão	campo cerrado (or cerrado)		campo sujo	campo limpo

* See Notes for Table II, p. 235–238.

* NOTES FOR TABLE II

This table gives the senses in which the five Brazilian terms given at the head of the columns, as well as other terms, are defined or used by various authors when discussing cerrado vegetation. Sometimes an author defines a term in a certain way but then uses it both in the defined sense and in other senses. Sometimes an author uses more than one term in the same paper to refer to the same structural form of cerrado.

Besides using the Brazilian terms, each author also has his own ideas of what a "savanna" is and applies this word to some of the above forms and not others.

[a] Publications of the Instituto Brasilerior de Geografia e Estatística. All authors writing on vegetation in these publications use the five terms more or less consistently, except that in some cases, "campo sujo" is not distinguished as separate from campo cerrado. Goodland (1969) also uses the five terms in the same sense.

[b] Warming uses the word "campo" as the general term for forms 2 to 5 and contrasts it with forest ("mata"), which for the Lagoa Santa region is all mesophytic (either evergreen, or on limestone outcrops, deciduous). He did not describe cerradão for this region, but in quoting from Lund, he mentions "caatanduva" and "mata campestre," Lund's terms for the cerradões of São Paulo. Under the general term "campo," he distinguishes "campo cerrado" (or just "cerrado") as the denser form, that is, what would be equivalent to our forms 2 and 3, and "campo limpo" (or "campo descoberto") as the open form, what would be equivalent to our forms 4 and 5. Warming incorrectly spells the word "cerrado" as "serrado," and this spelling was also used in his "Oecology."

[c] Löfgren's use of "Caapão" is for an isolated grove of cerradão surrounded by lower more open vegetation of the cerrado flora. However, in Brazil in general, capão (the modern spelling) refers to an isolated grove of closed or semiclosed trees or tall shrubs of any vegetation at all. Most cases of its use are for mesophytic forest, whether the groves are isolated naturally or are remnants of a formerly continuous forest. His use of the term "caatininga" (not "caatinga") for campo cerrado has not been taken up by any other author so far as I know.

[d] Luetzelburg, in his Estudos Botanicos do Nordeste, uses the word "agreste" for what is clearly cerradão, according to his description of its location, physiognomy, and component species. He probably picked up this local usage in the Serra do Araripe first and then applied it whenever he encountered cerradão again as in southern Maranhão (where it is called "chapada"). He does not mention the fact that "agreste" is used in the eastern part of the Northeast in a completely different sense. Thus, from northern Bahia to Rio Grande do Norte there is a coastal forest zone and an interior dry caatinga zone. Between them is a middle zone which has a moist type of caatinga vegetation in the dry lowlands and evergreen mesophytic forest on the mountain tops (which catch more rain). This middle zone as a whole is the "agreste" of the eastern, or most populated part, of northeastern Brazil and has nothing to do with any form of cerrado or cerradão. (As an adjective, the word "agreste" means "wild" or "rude," and may be used in this sense for any vegetation in literary descriptions.) In northeastern Brazil, behind the forest zone on certain geological formations, small areas of low cerrados do occur. In this region they are called "tabuleiros."

In vol. 3 of his work, Luetzelburg mentions "campos cerrados," "cerrados" and "cerradões." In his travels he did not come across vegetation types to which he gave these names, but takes the terms from the literature. However, when he tries to characterize them, most of the information he gives is incorrect, such as the spacing of the woody plants given on page 37, and the statement that they always contain abundant Velloziaceae and Eriocaulonaceae. (These two families are characteristic of the "campos rupestres" or non-cerrado rocky fields on mountain and ridge tops.) Luetzelburg did not realize that his "agreste" and the "cerradão" of the literature are the same thing.

[e] Rawitscher in this paper uses "campo cerrado" in a general sense. As subdivisions of this concept he defines "cerrado" in a footnote as the form with dense shrubs, "campo cerrado" (restricted sense) as savanna-like (no density mentioned), and "campo sujo" as the form in which "there are shrubs and some small trees." He seems to imply that the woody layer of the "campo sujo" is more open than that of "campo cerrado" but the descriptive phrase quoted does not distinguish it as anything different from a savanna. In one place he uses "cerrado" as a synonym for his general sense "campo cerrado," as in the summing up where he says "the true climax, at least at Emas, is not the cerrado vegetation but one of a more forest-like character." Rawitscher does not mention cerradão but says there occur "woodlands with a continuous forest-like cover."

The use of "campo cerrado" for all cerrado forms except cerradão and pure campo limpo is rather widespread among many agronomists in São Paulo. This usage carries the implication that either cerradão and campo limpo are not part of the same vegetation type or the relation of these latter forms to "campo cerrado" is not considered at all.

[f] Mello Barreto, in classifying the vegetation of Minas Gerais, puts "campos" as a coordinate category to forest, caatinga, etc. He then divides the campos into the lower-level cerrados, which he usually calls "campos baixos" and the mountain top "campos altos" (referred to in the present paper as high-altitude rocky campo) and gives characteristic species for both types. Thus, his distinction between the cerrados and the mountain top campos is less fundamental than that between the campos in general and the forest or caatinga.

[g] Aubreville uses "cerrado" as a general term. In a restricted sense he defines "cerrado" as a densely shrubby, treed savanna. "Campo cerrado" is a treed savanna with the trees open to very open. "Cerradão" is a dry, very low dense forest with the crowns touching, sparser grass carpet, and fire does not enter [sic!]. Cerradão is probably climax and cerrado [sens. strict.] is a degraded facies caused by fire, grazing and cutting. Campo cerrado is a still more degraded facies. Campo limpo is a herbaceous savanna without trees or shrubs. Frequently the latter occupies the sides of the slightly rolling planaltos with cerrado ("chapadão") on top. The edaphic origin of these cerrado-type campos limpos is certain but whether it is the nature of the soil or the annual water regime is yet to be determined. In other cases the campo limpo is abandoned pasture derived from dense humid forest [this, of course, not belonging to the cerrado vegetation]. Thus, with the exception of certain types of campo limpo, Aubreville believes that only cerradão is natural, the other cerrado forms being degradation phases caused by man.

[h] These authors use the word "campo" formally in a wide general sense for all the non-cerradão forms of cerrado, contrasting this with cerradão, which they consider a type of forest ("floresta xeromorfa semidecídua"). Their usage of the other terms is extremely confusing. They divide the general concept of "campo" into: (1) "campos cerrados," with the taller denser form of this called "cerrado," and the lower more open form of it called "campo sujo," (2) "campos gerais," a pure grassland with well-spaced shrubs, i.e., really a campo sujo also, (3) "campos limpos" (also referred to simply as "campo" in a restricted sense of this word), a pure grassland, or grassland with scattered low trees, i.e., the later really a type of campo sujo also. Thus the authors in this one paper use two specific names for the campo sujo form, as well as three more general names which include this form among others —five names for the same form.

Also note that, as the general term including forms 2 and 3, Rizzini uses "campo cerrado" in his 1962 paper and "cerrado" in his 1963b and 1964 papers.

[i] In this paper, Rizzini calls the cerradão "floresta xeromorfa" (and considers it definitely as a kind of forest) but says that the people call it "cerradão" or "catanduva." He calls the rest of the cerrado "savana central," and says it is known as "cerrado and campo cerrado," with other names being "campo coberto," "campo

firme," "chapada," "tabuleiro coberto," "savana arborizada." These terms seem to restrict the meaning of his "savana central" to stands with visible woody plants and so excludes pure grassland. In another part of this paper he himself uses the term "cerrado" as a synonym for "savana central."

[j] Here Rizzini gives a list of woody species for the Brazilian cerrados in general and analyses the floristic relations of the "cerrado" with other vegetation types. "Cerrado" in this paper seems to mean only forms 2 and 3, for he contrasts its woody flora with cerradão, with "campo" (sometimes called here "campo limpo"), and with the Atlantic and Amazonian forests. As he makes a comparison between the *woody* flora of the "cerrado" and the "campo," the word "campo" here must include at least campo sujo since the true campo limpo has no obviously visible woody plants. (The "campo" referred to in this paper is the grassland form of the cerrado vegetation. "Campo" forms of other Brazilian vegetation types are not involved although this is not made explicit.)

Rizzini confuses the issue by using "campo" and its adjective form "campestre" to refer not only to a vegetation form but also to low woody species in general (subshrubs and shrubs) within the whole range cerradão-cerrado-campo. Also, he uses "cerradão" and the adjective form of forest ("florestal") to refer both to a vegetation form and to tall woody plants in general (trees and taller shrubs) within the whole range of structural forms. Since both cerradão and his "campo" as vegetation forms contain both low and tall woody plants, it is difficult to know exactly what he is comparing with what.

[k] Eyre, who probably took his terminology from Cole (1960) whom he cites, includes cerradão in the concept of campos. "Interesting questions arise when one examines the structures and composition of the campos savannas however. These are by no means homogenous; they grade from almost closed-canopy, semi-evergreen woodland (cerradão), through a treed savanna (campo cerrado) to a very grassy savanna in which trees and shrubs are few and scattered (campo sujo)." He does not give a term for cerrado in the strict sense, unless he means his "cerradão" to include that form also, although cerrado in the strict sense is necessarily included in the gradation of forms from cerradão to campo sujo. He does not mention the campo limpo form of cerrado.

[l] The authors give a map of the distribution of "cerradão," "cerrado" and "campo" in São Paulo as of 1962. They show photographs of different forms of what they include under the term "cerrado." Included are a low-arboreal cerrado, too low to be called "cerradão"; a dense scrub form; and a very open low-shrub savanna, i.e., the campo sujo form. Their "campo" category is illustrated by photographs of the pure campo limpo of Campos do Jordão (which is not a cerrado flora), but from its distribution on the map seems to be mostly campo limpo forms of cerrado (plus perhaps some cases of true campos limpos of the southern Brazil type), plus some small areas near the coast that most likely were derived from forest.

This terminology, which refers to form 1 as "cerradão," forms 2, 3 and 4 as "cerrado," and form 5 as "campo," is also that generally used by the people in São Paulo, Mato Grosso and Goiás in referring to cerrado vegetation in the broad sense, when they do not wish to enter more into detail as to density of the woody plants. The terms refer, respectively, to the forest-like form, all other forms with conspicuous woody plants, and pure grassland.

[m] Lima divides the vegetation of Brazil into two "formations types": "forest formations" and "campos (grassland) formations." He then divides each into floristic-geographic communities. He includes cerradão in the forest formation type and characterizes it as "xeromorphic sub-deciduous seasonal tropical forest," ". . . the most developed stage of the 'cerrados' type formations in Brazil." He states that it is called "agrestes" in the Araripe plateau [southern Ceará-northwestern Pernambuco].

Lima places "cerrados" among the campos formations. "Differences in size and density of the trees, give place to various designations or sub-types of 'cerrados' which, still not well defined, are disregarded in this paper. On the other hand, the 'cerrados' of certain areas of Brazil receive particular common names, as 'tabuleiros' in the Eastern-Northeast and 'cobertos' in Pará." Apparently, the pure grassland form of the cerrado flora is not included in Lima's "cerrado" and it does not appear elsewhere in his classification.

[n] Hueck uses "campo sujo" and "campo limpo" as special terms for the scattered low shrub and pure grassland variations, respectively, of the general vegetation he refers to either as "campo cerrado" or "cerrado" indiscriminately. However, he uses "campo limpo" and "campo sujo" not only for the low open forms of what is truly cerrado vegetation but also for a different natural vegetation occurring in small areas on mountain tops of moderate altitude in central Brazil, the "campo rupestre" ("rocky field"). Hueck regards the campo rupestre as part of the general cerrado vegetation but although there are some campos rupestres with an appreciable number of species which are also typical of cerrado (Rizzo, 1970) they are essentially different from the cerrado in flora and physiognomy and completely different in soils and ecology.

In their table, the authors equate various English, French and Spanish expressions, as well as Brazilian cerrado terms (contributed by A. P. Camargo of Campinas, São Paulo), to Hills' seven-fold savanna classification and to Cole's five-fold classification. Since this book is an important contribution to savanna literature, some comments may be made on the authors' use of the Brazilian terms.

1. *Cerradão* is equated to Hills' expression, "forest type savanna" and to Cole's "savanna woodland." (Cole uses "woodland" in a different sense from Hills.) Cerradão is indeed equivalent to "forest" if "forest" is taken as having a closed *or* a slightly open canopy, and is equivalent to "woodland" if this is used in the sense of a closed or somewhat open *arboreal* formation.

2. *Campo limpo* is equated to Hills' "grassland type savanna" and to Cole's "savanna grassland." The terms are, indeed, equivalent.*

3. *Campo coberto* is equated to Hills' "parkland type savanna" and to Cole's "savanna parkland." From the two photographs given of this type it is evident that this "parkland" is what I would call "woodland," i.e., an open arboreal formation in which shrubs are few or absent. In Hills use, "parkland type savanna" also seems to include the denser phases of what I would call "arboreal savanna."

As for the Portuguese term, "campo coberto," I am not acquainted with the modern-day use of this expression in Brazil, as I have never heard it used by the people in any of the parts of Brazil in which I have traveled nor seen it employed in recent Brazilian literature. It was occasionally mentioned in older literature for what are apparently forms 2 and 3 of Table II and not necessarily only for the "parkland" form. Most Brazilian geographers would call the parkland form simply "cerrado" in the wide sense if it consisted of trees of this vegetation type or an arboreal form of "campo cerrado" in a stricter sense, since it is too open to be called "cerradão." The structure is sufficiently distinct, however, being purely arboreal, from other uses of the term "campo cerrado" to merit a special name, since campo cerrado practically always contains abundant shrubs. When the parkland form occurs in other vegetation types, such as in stands of babaçu or carnaúba palms, the special terms referring to stands of these palms are used, "babaçual" or "cocal," and "carnaubal."

4. *Campo cerrado* is equated to Hills' "woodland type savanna" (note different use of "woodland" here from Cole's usage above). Cole's "savanna woodland" is repeated here as a synonym but I believe this is an error since her "savanna woodland" is a rather closed *arboreal* formation ("cerradão") and cannot be used for the present form. The photo-

* Although "campo limpo" is used for, and I think should be restricted in its technical sense to, physiognomically pure grasslands (and herbfields), it should be recognized that the term is sometimes popularly used for grasslands with extremely scattered single *trees*, as in parts of Rio Grande do Sul. The point is that these trees do not hinder absolutely free passage and no not incommode one in any way.

graph given as an example of Hills' "woodland type savanna" shows a Venezuelan example of what in Brazil would indeed be called "campo cerrado," a low-tree-and-scrub savanna in my sense, and is equivalent to what Cole would really call a "low tree and shrub savanna."

5. *Campo sujo* is equated to Hills' "shrub type savanna" and to Cole's "low tree and shrub savanna." The equivalence to Hills' term is correct as shown by the photograph given. "Campo sujo" is usually used in Brazil, where used at all, for a grassland with very scattered rather low shrubs or tree-like shrubs, that is, what I would call, structurally, a "very open scrub savanna," the scrub being "dwarf" to "medium-tall" (up to 2, or rarely 3 m). "Campo sujo," like "campo limpo," is a purely structural term and may be used for similar physiognomies of different vegetation types, such as cerrado, southern Brazil natural grassland, pastures derived from forest, etc.

6. *Caatinga*, in the usage of the table, is the thorn scrub of northeastern Brazil. It is not a structural form of cerrado, but a different, coordinate large-scale vegetation type with a completely different flora. In the table it is equated to Hills' "scrub type savanna" and to Cole's "thicket and scrub." Apparently, a closed scrub is meant. Although closed scrub is the commonest form of caatinga, this vegetation type also occurs in many other structures, all natural in some regions: forest, arboreal woodland, closed scrub (mostly of definite shrubs 2–5 m tall), closed scrub with emergent low trees, open scrub (mostly of definite shrubs 1½–3 m tall), scrub savanna (scattered low trees and/or shrubs over a closed shortgrass layer, the "seridó" form), etc. Many of the shrubs and trees are spiny. Cacti are almost always present, such as tree cacti of the *Cereus* tribe, low clumps of globular and cylindrical species, and *Opuntia*. Terrestrial species of bromeliads are very abundant in most caatingas.

7. *"Savanna with forest inliers,"* Hills' term, is a mosaic form that, as far as I know, does not occur as a natural form in cerrado or caatinga. It does occur as a natural structure in the southern Brazil grassland. The nearest approach to it in the cerrado region is the "pantanal" (strict sense), with cerrado trees and shrubs forming scattered circular groves from several meters to a few tens of meters in diameter on raised ground (each with a termite mound) in periodically flooded or otherwise saturated grassland areas. (The surface of these raised earth platforms generally does not become covered with water.) This landscape as a whole, however, cannot be included in "cerrado" even under the widest sense of this term since the grassland portion is made up of species which are not of the cerrado flora but rather those adapted to flooded and saturated soil. The Brazilian word "capão" is given in Hills' table as an equivalent to "savanna with forest inliers." However, "capão" means only *one* of the isolated forest groves or "inliers," not the whole vegetational mosaic of grassland-with-groves.

VI. STRUCTURAL FORM AND FLORISTIC COMPOSITION

After two years of plant collecting in cerrado stands of various densities and heights within a restricted area in São Paulo, I stated (Eiten, 1963): "What seems to be the case from a cursory examination, and which should be verified statistically, is that the species composition of cerrado vegetation changes from the open "campo" form, through "campo cerrado," the denser "cerrado" (sens. strict.), to "cerradão," but that this change is gradual, and especially in the tree layer a rather slight one." Goodland's data (1969) have now given this impression a quantitative basis. In his Triângulo Mineiro study he shows how the average importance of a particular species changes along the structural gradient. For trees, the importance value was calculated as the sum of percents of relative density, relative frequency and relative basal cross-sectional area of trunk (possible variation 0–300). For herbs and shrubs the percent relative frequency was used (possible variation 0–100).

The average importance value of most tree species more or less constantly either increases or decreases along the structural gradient; only a few species definitely peak in one of the two middle forms. The *rate* of change also varies among species from steep to slight. For example, in average importance value along the gradient cerradão-cerrado-campo cerrado-campo sujo, *Erythroxylum suberosum* rises rapidly (4, 15, 35, 38), *Piptocarpha rotundifolia* rises moderately fast (2, 3, 8, 17), and *Connarus suberosus* rises slowly (3, 4, 4, 7). *Qualea grandiflora* falls rapidly (33, 28, 8, 8) and *Roupala montana* falls slowly (8, 5, 3, 1). *Lafoënsia densiflora* (6, 14, 4, 0) and *Sweetia elegans* (3, 2, 19, 9) peak rather strongly in the middle of the gradient, while *Bysonima coccolobifolia* (4, 7, 9, 5) peaks slightly. *Annona crassiflora* (5, 6, 5, 5) remains constant, *Caryocar brasiliense* (12, 11, 10, 3) falls very slowly or perhaps remains steady in the first three forms, then falls rapidly in the most open form.

In the ground layer, the frequency of *Trachypogon mollis* (3, 13, 32, 36) and of *Tristachya chrysothrix* (3, 23, 26, 38) rises rapidly, and that of *Echinolaena inflexa* (32, 32, 42, 42) and *Andira humilis* (1, 3, 8, 9) rises less rapidly. *Melinus minutiflora*, an introduced grass (42, 28, 14, 2) and *Serjania grandiflora* (27, 2, 0, 0) fall rapidly, *Elephantopus mollis* (12, 5, 2, 1) falls less rapidly, and *Cassia rugosa* (8, 6, 5, 5) falls slowly. *Axonopus pressus* (15, 33, 14, 13) peaks rather strongly in the middle, while *Borreria latifolia* (6, 12, 5, 7) and *Aristida pallens* (8, 14, 18, 15) peak moderately in the middle. *Salacia campestris* (4, 5, 5, 4) remains constant.

Another measure of species change along the structural gradient is percent presence in stands of each density. In determining presence the probability of a species being noted in the stand increases with the area surveyed, with the intensity with which the investigator tries to note the species, and with the time spent. Naturally, conspicuous species or those in flower will be noted more easily. Percent presence, therefore, is less accurate in that the ground surveyed is less minutely searched than in frequency counts where the quadrats are exhaustively examined or in the plotless methods for trees where each individual chosen is identified. On the other hand much more ground is covered. In general, Goodland's percent presence data (25–28 stands for each of the four forms) showed the same pattern of rise and fall for a species as the importance value or frequency. Of 152 tree species, 92 definitely increased or definitely decreased and only 13 definitely changed in some other fashion, such as peaking in the middle, or at both ends, or irregularly. Of the remaining species, a few appeared with more or less the same presence in all four forms; the rest appeared only once or twice in the 110 stands. Of 420 species found in the dry season in the ground layer, 141 definitely increased or decreased, and 76 changed in some other fashion. A few maintained themselves constant and the rest only occurred once or twice.

In the quotation given above, I had noted that the change in the tree layer was less than in the ground layer. That is, I had the impression that a higher proportion of cerradão ground layer species than cerradão trees were lacking in the more open cerrados, and conversely, a higher proportion of open cerrado ground species than of trees were lacking in the shade of the cerradão. The presence data in Goodland's lists show just that: of those ground layer species that increased or decreased regularly from cerradão to campo sujo, 38% were lacking (i.e., not noted) at one end or the other of the range of forms, while this was true for only 26% of the tree species.

VII. CLIMATE

The main continuous cerrado region is that part of the continent where this vegetation type is dominant in the landscape, covering by far the major portion of the land area. *Within the region* also occur (1) gallery and valley forests (these only directly along the stream, or covering a wider valley floor, or also extending partly or entirely up the valley sides); (2) permanent or seasonal valley-floor or valley-side marshes; (3) some areas of mesophytic forest on upland richer deep-soil areas. Where rock peaks and ridges outcrop or rock or laterite pavements occur near the surface, may be found (4) rocky-field campos at the higher altitudes or (5) low-herbaceous swards on the resulting shallow lithosols, or (6) forests on rocks in which trees can root such as limestone, as well as (7) scattered herbs and scrub in clefts on steep bare rock outcrops. The total area of these non-cerrado types in the cerrado region is small. *At the borders to neighboring vegetation provinces*, such as to the continuous upland Amazonian or Atlantic-coast forest or to the caatinga, either the cerrado (1) meets the other type directly, or (2) is separated from it only by a stream with its attendant gallery forest, or (3) there is an ecotone several kilometers to 200 km wide of intermediate vegetation grading from one main type to the other, or (4) there is an ecotonal zone consisting of a mosaic of vegetation types, those of the two main provinces and also special types belonging to neither, or (5) within a variable-width belt along the border the cerrado occurs as small patches or tongues in a matrix of the neighboring type, and to a smaller extent, the neighboring type occurs in tongues and patches in the cerrado matrix.

Clues as to what characteristics of its environment "cause" cerrado, or allow it to exist in the face of competition from neighboring vegetation types, can be found by examining (1) the location of the main cerrado region (and its outliers) within the continent and (2) the factors associated with the presence of other vegetation types within the main cerrado region.

Since the cerrado occurs over a large number of geologic formations, types of topography, and at altitudes from almost sea level to over 1300 m, the placement of the main region of this vegetation in the continent, *as a whole*, in relation to neighboring types must be due to the macroclimate since this is the only factor which is consistently different from the region of one large-scale vegetation type to another. We note that: (1) the main cerrado region is in the *tropical zone*, and as defined here almost wholly south of the equator, and (2) it has an *intermediate rainfall.*

Temperature. The cerrado is a *tropical* vegetation like its neighbors, the Amazon hylaea, the caatinga, the Atlantic coastal forest and the Chaco vegetation, but unlike the warm temperate to subtropical "napeadic" vegetation of broadleaf forests, araucaria forests and natural grasslands of southern Brazil.* The average annual temperature of the cerrado region is 20–26°C. In southern São Paulo it may be as little as 18°C. Extremes of minimum temperature vary from 14°C (or 18°C in northern Piauí) to -4°C in parts of São Paulo. The average variation in temperature extremes within a year is from 22°C in northern Piauí and 26° in central Maranhão to 44°C in southern São Paulo.

That part of the very southern edge of the cerrado that occurs at moderately high altitudes (800–1000 m) in southwestern São Paulo (Itararé) bordering the southern Brazil napeadic region occasionally

* Martius designated the "Napeas" vegetation of Brazil as that of the "extra-tropical valleys," that is, the subtropical broadleaf forests and araucaria forests of the southern Brazil highlands (which usually occur in valley bottoms and sides), and excluded both the southern highland grasslands (which occur on the divides and plateau tops), and the lower-level tropical coastal forest. The Atlantic coastal forest as a whole he called the Dryades vegetation province, and the subtropical grasslands he included in the Oreades vegetation province of central Brazil, along with the cerrados and the mountain top rocky campos. However, since each of his other vegetation provinces is associated with a separate large geographic region and is, therefore, based on climate, it would be better if we dissociated the southern grasslands from the Oreades vegetation (from which they are floristically distinct anyway) and associate them with the subtropical forests of the same climatic province. These southern grasslands or campos limpos may then be called "napeadic grasslands" as distinguished from the cerrado-type campos limpos which may then be called "oreadic grasslands."

experiences frosts, 1–2(–4) frost days per year on the average due to rapid radiation of heat to the sky at night in the cold season. Cerrados in the rest of São Paulo and even in southern Minas Gerais at the higher altitudes may experience a very slight frost once every few years. The rest of the cerrado region practically never has frosts. Regular frosts occur only in a very small fraction of one percent of the total cerrado area of Brazil and have not caused any essential change in the appearance of the vegetation, although they are undoubtedly associated with some differences in species composition. The cerrados of southwestern São Paulo are mostly predominantly grassy (campo limpo) or with only low scattered woody growth (campo sujo), but this restriction of the naturally low open types to this cool part of São Paulo is almost certainly due at least partially to soil effects and not frost alone since the usual woody forms of cerrado also occur in the same region, although to a smaller extent. At the same altitude and with the same rainfall, geological formation, and relative geographic position in relation to the coast, but slightly further south in Paraná where the average temperature is cooler and frosts more frequent, the cerrado gives way to the southern Brazil (napeadic) grasslands.

Rainfall. If we compare in broad outlines on a map the presence of cerrado with the rainfall regime within the climatically tropical portion of the continent east of the Andes, we find that this vegetation as a whole occupies an *intermediate pluviometric position.* Cerrado occurs in regions with a yearly average ranging from 750–800 mm of rainfall on the dry side to (north of São Paulo) 2000 mm on the wet side. The region drier than this on the northeastern side of the cerrado region supports semidesert thorn scrub caatinga as the main vegetation, and the drier region on the southwestern side supports the Chaco vegetation of Paraguay, southeastern Bolivia and adjacent Argentina. Regions wetter than the cerrado, with over 2000 mm of rainfall per year, support continuous mesophytic forest (almost all evergreen), that is, the Amazon forest and the Atlantic coastal forest. (Rainfall data from maps in Serra, 1956; Torres, 1948; Enciclopédia dos Municípios Brasileiros; Conselho Nacional de Geografia, 1959, 1960, 1962, 1963a, 1965; Santos, 1962; Setzer, 1946, 1966; Garcia Blanco & Godoy, 1967; Figueiredo Monteiro, 1951.)*

* Although cerrado is practically restricted to regions with between 750–2000 mm of rainfall per year, its actual presence depends on the correct soil type, depth and drainage as explained below. For caatinga can still occur, although rarely, as the main vegetation in regions with up to almost 1000 mm a year, and mesophytic forest as the main vegetation can occur in any region wetter than this.

At present the rainfall limits of the region in which cerrado can occur must be regarded as approximate. This is due both to inexactness of rainfall data for large areas and incomplete knowledge of the geographical limits of cerrado vegetation. Due to sparsity of meteorological stations around the edges of the cerrado region (except for São Paulo and southern Minas), the rainfall values for areas usually shown on maps for a particular place may be as much as several hundred millimeters different from one map to the other. Secondly, with almost no exceptions, I cannot

In São Paulo the cerrado is restricted to that part of the state which has less than 1500 mm of average yearly rainfall. Most cerrado in the state, in fact, occurs in regions with less than 1300 mm. Forest also occurs in the same region, depending on soils. That part of the state with more than 1500 mm supports only continuous evergreen forest, now mostly destroyed. The fact that over 1500 mm of rainfall per year in São Paulo is enough for forest to exclude cerrado while north of São Paulo 2000 mm is needed may be due to the fact that São Paulo, being at the southern end of the cerrado region, has slightly cooler temperatures on the average so that evaporation is less and the rain that does fall is more effective.

Outside the rainfall limits given above, small areas of cerrado do occur. The limits given are minimum error limits, that is drawn at such a point, albeit roughly, that outside the limits there exists the smallest total area of cerrado, and inside the limits there exists the smallest total area of other vegetation types on sites and soils that should support cerrado.

Thus, summing up, in the tropical portion of South America east of the Andes and south of the Amazon River, cerrado occupies a central interior geographic position in relation to the vegetation types that surround it, and possesses an intermediate rainfall range. To its northeast is the drier caatinga, to its southwest is the drier Chaco vegetation, to its west and northwest is the moister Amazon forest, and to its southeast is the moister coastal forest. If the amount of rainfall is represented as a saddle-surface over this region, cerrado occupies the area around the saddle-point (Fig. 12).

Average annual rainfall is only one measure of the dryness of a climate. The length and severity of the dry season is another. In Brazil, the two aspects go together: the lower the total annual rainfall, in general, the longer and drier is the dry season. The cerrado region has a single dry period. The driest month (July or August) in a region whose main vegetation is typical cerrado may have as much as 40 mm of rain on the average or as little as 5 mm or even less. Over most of the cerrado region the average rainfall for the driest month is 10–30 mm. Near its border with the northeastern caatinga, the cerrado has a climate which is transitional to a typical caatinga climate of the moister type in that five months may pass with no rain at all in some years (May–September) or with only a few millimeters in August, although in compensation, more rain falls during the rainy season here than in the caatinga.

Another very important point is that the rains come every year in the cerrado region while in the caatinga the variation from year to year

agree with any published map I have seen of cerrado vegetation in the wide sense for regions I am acquainted with, and this includes recent maps presumably based on aerial photographs (see Part II).

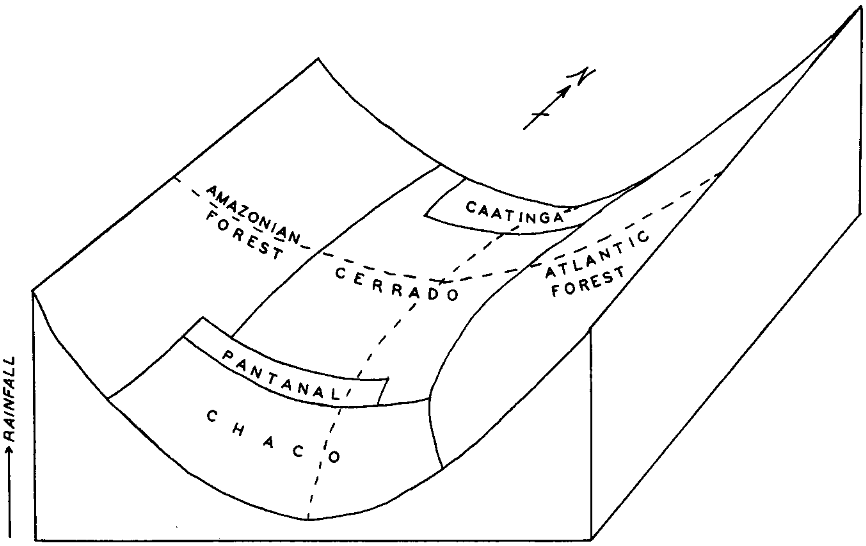

FIG. 12. Saddle surface of rainfall values (generalized) showing intermediate position of main cerrado region geographically and in relation to rainfall. The Pantanal region of southwestern Mato Grosso and adjacent Bolivia and Paraguay is due to seasonal ill-drainage while the position of the other vegetation regions shown is due to climate.

is considerable and sometimes more than a year may pass with no rain at all. Also, parts of the caatinga region have the rainy period broken into two parts by a short dry season.

Other measures of climatic dryness also show the intermediate nature of the cerrado region as compared to caatinga and to forest, such as number of rainy days per year, number of consecutive "dry" days in the dry season, potential evapotranspiration, ratio of rainfall to potential evapotranspiration during the whole year or during the dry season, de Martonne's dryness index, Thornthwaite's index of precipitation effectiveness and index of humidity, Mohl's index, etc. However, for central Brazil their values are not more strongly correlated with the distribution of the cerrado region than simple average annual rainfall and its correlated length and severity of the dry season (Table III).

In northern tropical America natural savannas occur within a much larger rainfall range, namely, regimes of 500 mm with 7 drought months to over 2500 mm with a negligible dry season. However, in most cases the savannas occur on ground seasonally saturated for long periods due to flooding of nearby streams or to a perched water table due to impeded drainage (Beard, 1953; Blydenstein, 1962).

It should be noted that climatic indices correlating well with the vegetation are not necessarily those that best correlate with areas of strong periodic drought. In northeastern Brazil, because of their social implications, droughts and the climate in general have been much studied. An index that distinguishes areas with strong drought years from those with the same average rainfall or rainfall-evaporation indices but a lesser incidence of drought years has been developed (Becker, 1968).

One measure of climatic dryness based on the usual meteorological data that does correspond very well with the distribution of large-scale vegetation types in Brazil is Gaussen's xerothermic index as applied to Brazil by Galvão (1967). The dry season is defined as the sequence of months in which the average monthly precipitation in millimeters is less than or equal to double the average monthly temperature in degrees centigrade. (There may be one or two dry seasons in the year.) In cooler areas, therefore, there may be a definite moderate dry season without this being counted as a dry season in Gaussen's sense. Within the effective dry season(s) the average number of rainless days is counted. This number is reduced by multiplying by a coefficient which varies from 0.65 to 1.0 depending on relative humidity. Rainless days in the dry season which have dew or mist are counted as half rainy days, and the average number of these (over the years) is subtracted from the above. Thus, relative humidity, mist, and dew are taken into account as attenuating the effect of a rainless day. The number of rainless days in the dry season, reduced by these considerations, is the xerothermic index. "Bioclimates" are defined, each covering a certain range of the index, and further subdivided by whether there are one or two dry seasons and by the temperature of the coldest month.

In subtropical Brazil, a region of campo limpo, araucaria forest and subtropical broadleaf forest, there is no dry season in Gaussen's sense, i.e., the X. I. is zero, and the temperature of the coldest month is between 10–15°C. (In a small area of highland in northeastern Rio Grande do Sul and adjacent southeastern Santa Catarina the coldest month is between 0–10°C.) This subtropical region includes Rio Grande do Sul (except its northeastern coast) and Santa Catarina and Paraná except for their lower-altitude coastal strip. North of Paraná there are small areas of subtropical climate (coldest month less than 15°C) in São Paulo and Minas Gerais at the highest elevations. Of these there is no effective dry season on the Campos do Jordão plateau, with its campo limpo and araucaria forests, and in a narrow east-west strip in southern São Paulo from Itararé at the Paraná border to the city of São Paulo. This latter strip includes natural grassy campos limpos, araucaria forests and a few small cerrado areas, but is mostly broadleaf tropical forest. A slight dry season (X. I. 0–40) occurs on the plateau of southeastern Minas Gerais, an area generally forested but also including the very southeast edge of the cerrado region.

The rest of the country can be considered to have a fully tropical climate and it is here that there is a very good correlation between forest, cerrado and caatinga regions and the xerothermic index.

TABLE III

COMPARISON OF THE MAIN ECOLOGICAL FEATURES OF UPLAND FOREST, CERRADO, AND CAATINGA (TROPICAL BRAZIL).

	FOREST ("MATA") (mesophytic; on drained soil)	CERRADO (xeromorphic; incl. arboreal "cerradão" and lower more open forms)	CAATINGA (semi-desert; deciduous broadleaf and succulents)
1. Geographic region where this form is the main vegetation	Atlantic coast, Amazon valley	Central Brazil Plateau	northeast Brazil (behind coastal forest)
2. Surface relief of main part of region	Atlantic coast: mountainous with rounded contours Amazon: alluvial plain; low plateau; rolling terrain in south; hilly in north; (tabular sandstone topography in n.w. Maranhão)	tabular topography (plateaus with steep sides separated by flat-bottomed valleys); large tablelands with long gently-sloped sides to lower levels	intermontane and inter-plateau slightly dissected pediplain with inselbergs (tops and sides of sandstone plateaus in Piauí and n.w. Pernambuco)
3. Main underlying rock types	Rich sandstones (micaceous or calcareous), basalt and gabbro; some shales, granite, gneiss, limestone, etc., in drier climate; on almost any rock type if soil is deep enough in wetter climate	under young soils: poor sandstones (siliceous, ferrugineous, clayey); under old soils: almost any rock type but very rare on basic rocks like basalt, diabase and gabbro	limestone; calcareous sandstone; granite, schist, gabbro and other crystallines (non-calcareous sandstone in Piauí)
4. Soils (in undisturbed vegetation)	mineral portion *poor to rich*, acidic, abundant humus	mineral portion *very poor* (low cation exchange capacity and low base exchange), acidic; small amount of humus in cerradão, less in open forms	mineral portion *poor to relatively rich*, circum-neutral to slightly alkaline; some humus to almost none
5. Effective soil depth	shallow to very deep	almost always very deep	shallow to deep

TABLE III (Continued)

	FOREST ("MATA") (mesophytic; on drained soil)	CERRADO (xeromorphic; incl. arboreal "cerradão" and lower more open forms)	CAATINGA (semi-desert; deciduous broadleaf and succulents)
6. Average rainfall per year, mm.	1000–4500 (forest only, without cerrado, generally occurs in regions with over 2000, or in São Paulo, over 1500)	750–2000 (in São Paulo, 1000–1300 (–1500))	300 in small areas inside region to 750–800 at western limit where joins cerrado, or to 1000 at eastern and southern limits where it joins forest
7. Average rainfall of driest month, mm.	(10–) 40–200	(5–) 10–30 (–40)	0–10
8. Gaussen's xerothermic index (and number of months of effective dry season)	0 or between 0 and 40 (0–2 months)	40–100 (3–4 months)	100–250 (5–8 (–11) months)
9. Average annual evaporation, mm.	from less than 600 to 1200 (Amazon) 600 to 1000 (Atlantic coast)	600 to 1400	1000 at boundary with Atlantic forest and 1400 at boundary with cerrado, going on to higher values within caatinga region
10. Rainfall/evaporation quotient	more than 2.5 at boundary of Amazon forest with cerrado more than 1.0 at boundary of Atlantic forest with caatinga	0.5 to 2.5 (the latter value at cerrado-Amazon forest boundary)	less than 0.5
11. Martonne's index of aridity	40 and over	10 at boundary with caatinga, to 40 or over at boundary with forest	from less than 10 inside caatinga region to 10 at boundary with cerrado, or to 40 at boundary with Atlantic forest

TABLE III (Continued)

	FOREST ("MATA") (mesophytic; on drained soil)	CERRADO (xeromorphic; incl. arboreal "cerradão" and lower more open forms)	CAATINGA (semi-desert; deciduous broadleaf and succulents)
12. Knoche's index of aridity	from more than 20 up to 60 along boundary of Atlantic forest with caatinga; up to more than 100 within Amazon forest	20 at boundary with caatinga, to 100 at boundary with forest	less than 20 inside caatinga region and at cerrado boundary; 20 to 60 at boundary with Atlantic forest
13. Main Köppen climate	Am, Af, As	Aw (Cw at southern edge)	B (several varieties)
14. Depth of permanent water table on uplands	shallow to deep	(3–) 6–30 (–more than 50) m	usually none (perhaps present and deep in some sandstone plateaus in Piauí)
15. Soil water storage over dry season in typical conditions	in *evergreen* forests, soils moist to surface; in *semideciduous* forests, upper layer more or less dries out but lower layers within reach of some tree roots stay moist; in *deciduous* forests on shallow soils, usually whole profile to bed rock dries out completely for short time	upper layer (to about 2 m deep) dries out; lower layers remain moist, with several years rainfall stored in soil above permanent water table	on shallow soils whole profile to bedrock dries out completely and stays dry during long dry season; on deep soils dries out completely in upper layers within reach of roots; (probably deeper layers remain moist on some sandstone plateaus in Piauí where there is semideciduous caatinga)
16. Structure of non-disturbed vegetation	closed-canopy arboreal; canopy tall, (15–) 20–35 m (emergents may exceed 40 m)	closed- to open-canopy arboreal, medium-tall (7–20 m); tree-and-scrub woodland, the trees medium-tall (7–15 m) to low (3–7 m); open scrub or closed scrub (all heights); medium-tall (1½–3 m) to low (½–1½ m) scrub savanna; pure grassland or grass-herb field	closed- to open-canopy low to medium-tall arboreal; medium-tall to tall (us. 2–5 m) closed scrub, often with emergent low trees (to 7 or 8 m); medium-tall open scrub; scrub savanna

TABLE III (Continued)

	FOREST ("MATA") (mesophytic; on drained soil)	CERRADO (xeromorphic; incl. arboreal "cerradão" and lower more open forms)	CAATINGA (semi-desert; deciduous broadleaf and succulents)
17. Deciduousness of stands	mostly *evergreen*, sometimes *semideciduous*; (rarely completely deciduous, and then usually on very shallow soils)	*semideciduous* (cerradão rarely evergreen; scrub forms very rarely completely deciduous)	completely *deciduous* (semideciduous on some sandstone plateau tops in Piauí)
18. Characteristic growth forms other than broadleaf trees and shrubs	canopy and undergrowth tree-palms; lianas; vascular epiphytes (orchids, bromeliads, aroids, ferns) especially dense in high rainfall areas; undergrowth bamboo in some areas	acaulescent and low-tree palms	cacti in all forms, incl. arboreal; terrestrial bromeliads; many shrubs thorny; acaulescent and low-tree palms in some areas; barrel-trunked trees in some areas
19. Leaf consistency of upper-layer broadleaf plants	mesomorphic to slightly coriaceous	xeromorphic, stiff and siliceous or coriaceous; (sometimes soft and densely hairy)	mesomorphic, thin, soft
20. Xeromorphic anatomical characters of leaves of plants exposed to the regional climate	rare (when present, occurs in canopy trees, especially in secondary stands, and in epiphytes)	very frequent (in canopy trees in cerradão; in all trees and shrubs and in many herbs in open forms)	rare
21. Stomate activity in dry periods during the day for most canopy species	close *relatively rapidly* (observed in high rainfall area on crest of Serra do Mar, São Paulo)	*very slow*; stomates are open over long periods even in dry season; restriction of transpiration rare (observed in several areas in center and south of cerrado region)	*rapid*; stomates open only for short periods even in rainy season; restriction of transpiration frequent even in rainy season (observed in northern Bahia)

The two forest regions have an X. I. of less than 40. In fact, most of the Atlantic coastal forest, as well as western Amazonia, have an index of zero, that is, no effective dry season in Gaussen's sense, even though there is a period of the year when the rainfall is less. The caatinga area has an X. I. of more than 100, that is, a strong effective dry season, and the type of caatinga varies well with the exact value. In general, caatinga is a closed or open thorn scrub, or in some places, arboreal. The two separate driest areas (X. I. over 200) coincide well with the two areas of the driest, most open caatinga, the natural thorn-shrub savanna form, "seridó."

The cerrado region is practically coterminous with the region having an X. I. of 40–100, that is, intermediate. This climate covers all of central Brazil and extends as large tongues into Rondônia and Maranhão just as the cerrado does, as well as pushing a short tongue southward to cover the cerrados of eastern São Paulo. The X. I. 40 line falls very close to the long western boundary of the cerrado region, where it adjoins the Amazon forest, and reasonably close to the short southeastern boundary where it adjoins the Atlantic forest in Minas Gerais. The X. I. 100 line falls very close to the eastern boundary of the cerrado region where it adjoins the caatinga in Piauí and northern Bahia, and reasonably close in northern Minas Gerias.

Only a small part of the cerrado region (less than 5%) has an X. I. less than 40 (but greater than zero), that is, more functionally humid than the main part of the region. This is at the southern edge, in southeastern Mato Grosso and western São Paulo, regions where cerrado areas are mixed with continuous upland forest areas.

There is a certain correlation in Brazil between large-scale climatic regions, geomorphological provinces, and large-scale vegetation types. Where these three features coincide, they demark a "core area" characterized by a certain uniformity in the environment and landscape, with the different core areas quite distinct from each other (Ab' Sáber, 1963, 1967, 1971). These core areas correspond remarkably well with Martius' five large-scale vegetation series or provinces.

VIII. SUBSTRATE

A further clue as to the causes of cerrado is to be found in the fact that this vegetation does not occur in all parts of the region where the climate is suitable, and that the places where it is found have special characteristics. These characteristics can be divided into three broad categories and in general all must be satisfied for typical cerrado to appear rather than some other vegetation type.

Soil depth. The soil material must be deep for typical woodland and scrub cerrados to occur, usually at least three meters and probably much more. In by far the major portion of its area, soil material under cerrado is, in fact, several tens of meters deep.

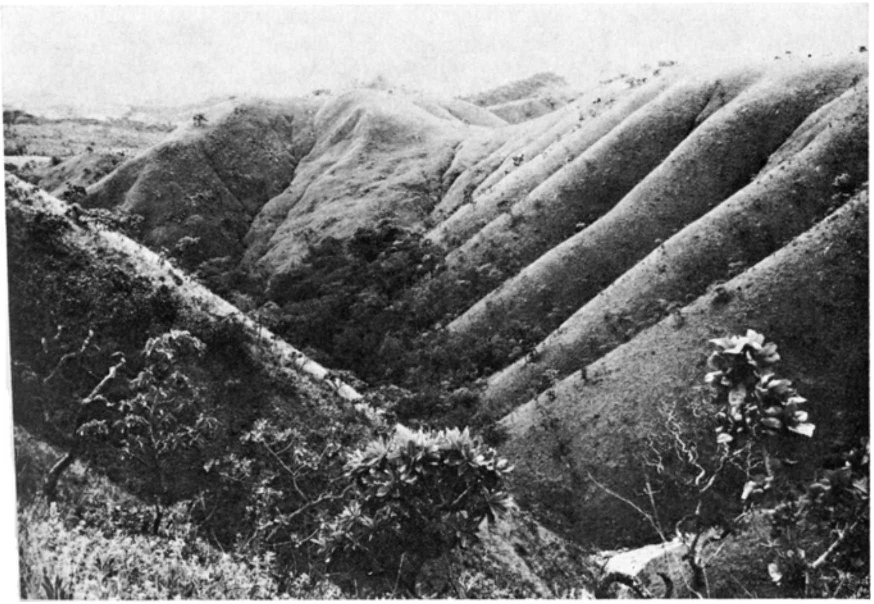

FIG. 13. Valley northwest of Sobradinho, near Brasília. Note gallery forest at bottom of valley, and slopes covered with cerrado dwarf to low scrub very open savanna on very shallow slate lithosol.

Typical cerrados do not usually develop on lithosols, that is, soils which are appreciably less than 1 m deep over solid bedrock or over a solid laterite pavement. In this case a cerrado on deep soil may be suddenly replaced by another vegetation on the shallow soil, such as forest, non-cerrado herb-grassfield, or low dense shrubbery of special species. Or a modified lower cerrado vegetation may occur, it being difficult sometimes to say whether this modified vegetation should really be included within the broad concept of cerrado or not. In determining soil depth it must be remembered that although the bedrock or laterite layer may approach or reach the surface, if it contains numerous cracks or other openings into which roots can penetrate it will not offer an obstacle to development of the usual cerrado height and density of the region. Five examples of lithosol modification of cerrado may be mentioned.

The Brasília region is a slightly dissected peneplain over highly tilted and folded sedimentary rocks. The soil is usually several to many meters deep so that typical cerrado of various heights and densities develops. Cerradão is rare, but open scrub and tree-and-scrub woodland forms are common. Just northwest of Sobradinho, a deep, wide, steep-walled valley has been cut into the prevailing peneplain (Fig. 13). The valley sides have a very thin stony soil, 0–20 cm deep over the highly weathered slate bedrock. Normally, the usual conspicuous cerrado woody plants do not grow in soil so shallow but cerrado herbs, graminoids, and scattered very small shrubs and subshrubs to about 2 dm tall can do so, forming a natural "campo limpo." However, since the slate layers are inclined to the surface and have weathered considerably, some of the thin layers have become as soft as clay while others have remained hard rock. This is sufficient for a few shrubs here and there to push their roots directly into the exposed soft clayey layers or through cracked hard layers into a soft layer and gain a foothold. The results is a "campo sujo" or dwarf to low scrub savanna form of cerrado on the slope. Nearby, on the more level top of the plateau where roadcuts showed the soil to be a meter or more thick, the usual medium-tall open scrub form of Brasília cerrado occurred, while where it was 3 m thick, as determined in a brook gully, a low-tree woodland form developed.

In the Furnas region of south central Minas Gerais (Comissão de Solos, 1962), the underlying rock outcrops at altitudes of 900–1300 m. Cerrado occurs on some deep soils but small areas of it may occur on thinner soils. In this region there is no sandstone, but rather limestone, quartz, quartzite, granite, shale and several forms of gneiss. The limestone outcrops usually bear a deciduous forest, probably because tree roots can penetrate its cracks, but the thin soil formed on the other more solid rock types where the soil is not too steep bears a high-altitude grass-herb field ("campo de altitude"). Since in such thin soils the bedrock outcrops in places, these campos are also called "campos rupestres." They bear a non-cerrado flora. Where cerrado rather than forest occurs downslope on deep soil it may continue upslope to where the soil is only 1½–2 m deep. In such cases, it is of the open savanna form, "campo cerrado," not the arboreal woodland or dense scrub form. Where the soil is still shallower, some of the low cerrado shrubs may continue to grow but the herbaceous species change to those of the rocky campo flora, a different vegetation type. Finally, further upslope, where the lithosol is only a few decimeters deep even the few cerrado shrubs disappear and only the typical rocky field low shrubs and herbs (or only the herbs) occur.

At the eastern edge of southern Maranhão and adjacent Piauí, around the city of Floriano, the underlying shale or sandstone in some areas approaches the surface and forms level pavements with a very thin soil. (These areas are locally called "tabuleiros.") The prevalent vegetation of the region, cerradão woodland (locally called "chapada") on the usual deep soils here gives way to a lower and more open vegetation. Where the soil over the pavement is only up to about 15 cm deep it is covered with a shortgrass layer with a carpeting *Mimosa* herb, or if a large water puddle can accumulate, with submerged and floating aquatics during the rainy season. A slightly deeper soil allows a few scattered shrubs (usually cerrado species) and the non-cerrado carnaúba palm (*Copernicia prunifera*) also to take hold, forming a type of savanna. Where the soil is still thicker, the shrub layer becomes denser. Thus as the soil becomes thinner there is a gradual change in the vegetation, a thinning-out and lowering of the woody plants (except for the palm, which retains its usual height) as well as a change in species composition of the ground layer, and although the pure shortgrass-and-herb field should be excluded from cerrado, it is difficult to say without a detailed floristic analysis up to which point before this the cerrado concept should extend.

In northern Goiás, such as at the city of Paraíso do Norte de Goiás along the Belém-Brasília road, small areas occur of 1-few hectares each, of level, solid laterite pavements with practically no soil. Low-arboreal cerrado woodland is the general vegetation of the usual deep soils here, which may or may not contain laterite blocks and pebbles, but the woodland stops short at the edge of the solid pavement, which is covered only with short grasses, sedges and forbs (including a similar carpeting *Mimosa*) 10–15 cm tall. In this case there is no series of intergrading forms. The herbaceous carpet can be considered as not a part of the cerrado since its species do not occur or are very rare in the undisturbed woodland.

This herbaceous carpet depends on the fact that there is practically no soil above the pavement, not on the fact that the pavement is made of laterite. Fifty kilometers south of Paraíso granite outcrops. The same herbaceous carpet with the same species occurs on level and slightly sloping granite pavements covering a few-centimeters thick soil.

The very narrow, north-south ridge-like mountain range, Serra do Cipó, in Minas Gerais (part of the more extensive serra do Espinhaço) separates the cerrado region to the west from the forest region to the east. Its more or less flat-topped crest, of shallow light gray soil 1–3 dm thick over quartzite, supports a highly endemic rocky campo flora. But one small area on the crest, only 200 m wide, bears a red latosol which the roadcut shows to be at least 2 m thick over sandstone bedrock. This soil supports typical, non-endemic, open scrub cerrado, completely different in aspect and flora from the surrounding lithosol campo.

Thus, adjacent to usual deep-soil cerrados may occur (1) soil only about 1 m thick, or (2) an even shallower lithosol over the same bedrock or over a laterite pavement, or (3) a lithosol on a radically different bedrock. These support, respectively, a modification of the cerrado (1) to a lower more open form of the same vegetation, (2) to a lower and usually more open form of a vegetation grading away from cerrado or to a short-herb carpet, depending on the exact depth of the thin soil, and (3) to a lower and more open form of a completely different vegetation. The areal extent of any vegetation in Brazil on lithosols is very small, and the proportion of cerrado on thin soils is only a very small fraction of 1% of its total area. In general, cerrado occurs on very deep latosols, sometimes with quartz or laterite stones or pebbles mixed in, or in a few areas on very deep sandy regosols derived from siliceous-cemented sandstones. The general relation of rainfall and soil depth

TABLE IV

MAIN UPLAND VEGETATION TYPES AND DEGREE OF DECIDUOUSNESS IN RELATION TO RAINFALL AND SOIL DEPTH IN TROPICAL BRAZIL.

Total average annual rainfall	Average length and intensity of dry season	Soil deep	Soil shallow (less than 1 m)
		EVERGREEN MESOPHYTIC FOREST	EVERGREEN MESOPHYTIC FOREST
High	short (1–3 mo.); weakly to slightly dry	EVERGREEN SCRUB FOREST or SAVANNA (on podsolized white sands in Amazonia; ground layer evergreen)	EVERGREEN SAVANNA, or ROCKY CAMPO (on ridges and plateau tops in Amazonia, especially quartzite; ground layer usually seasonal)
		EVERGREEN TO SEMIDECIDUOUS MESOPHYTIC FOREST (on richer soils)	DECIDUOUS MESOPHYTIC FOREST (especially on limestone outcrops)
Intermediate	intermediate length (4–5 mo.) slightly (to strongly) dry	SEMIDECIDUOUS XEROMORPHIC FOREST (sens. lat.) (on poorer soils; ground layer seasonal)	SEMI-DECIDUOUS OR EVERGREEN ROCKY CAMPO (at high altitudes, 900–1500 m, on quartzite, iron ore, etc.; ground layer seasonal
		DECIDUOUS MESOPHYTIC FOREST ("Mata de cipo") (in caatinga-coastal forest transition)	
Low	long (5–8 (–11) mo.); strongly dry	DECIDUOUS CAATINGA (or SEMIDECIDUOUS in some of the higher rainfall areas on deep soil)	DECIDUOUS CAATINGA

on type and deciduousness of vegetation in tropical Brazil is shown in Table IV.

I have never seen cerrado on soil showing a "hogwallow" surface, an irregular configuration of curving hummocks and channels with a surface relief of up to about 3 dm, such as occur in some northern South American savannas (Beard, 1953; van Donselaar, 1965). Also I have never seen cerrados with trees whose roots grow for long horizontal distances in a shallow soil layer unable to penetrate a dense lateritic hardpan, such as are described for some Venezuelan savannas by Foldats & Rutkin (1965, 1969).

Drainage. Typical cerrado requires a well-drained soil.

(a) There must be no long-term accumulation of water at the surface during the rainy season. This means: (1) the site must never be inundated by a rise in a neighboring watercourse; (2) the internal drainage of the soil must be free so that rainwater does not accumulate at the surface forming pools that take days or weeks to drain away or evaporate after the rain stops (temporary perched water table); (3) the site must not be a hillside marsh where water flushes out and saturates the soil permanently or for long periods.

In sum, *typical cerrado cannot tolerate a water-logged site*, not even temporarily. Note that this is exactly the opposite of the conditions often asserted to be necessary for the appearance of "savanna" in Tropical America (Beard, 1953; Fuson, 1963).

This is well shown by several examples. In all cases to be mentioned the soil is deep so that the complication of a lithosol does not enter, only drainage factors. In parts of the Pantanal Region of Mato Grosso (an area climatically part of the cerrado region) the landscape consists of a gently rolling terrain of only a few meters relief with circular depressions. The yearly rise of the Paraná river and its tributaries floods a large portion of the area and as the river lowers during the dry season the depressions gradually dry out, the deeper ones taking longer and some of the very deepest remaining with permanent water over the whole dry season. Or, without the land being generally flooded from the streams, rainwater accumulates in the depressions in the wet season and there gradually dries out. On this terrain, therefore, there is a gradient in the amount of time that the soil remains saturated. The typical cerrado in this region, the woodland or dense scrub form, only occurs on the higher levels which practically never become covered with water.

In São José dos Campo, São Paulo, there are a few localities in the cerrado-covered area that have shallow depressions without an outlet. Water tends to accumulate in the soil at the base of the depressions keeping it moister for a longer time. The soil there has more clay and more humus. There the cerrado gives way to a marshlike vegetation although it is dry most of the year. Where the soil in the bottom of a depression remains saturated for a shorter time, cerrado vegetation, including a few of the shrubs, covers it but there is a slight increase in the number of sedge species typical of wet soil. Therefore intermediate conditions can occur which are reflected in the species composition but they take up a miniscule area in comparison to that occupied by typical cerrado.

In northeastern Mato Grosso, north of Barra do Garças, the gently rolling topography still bears its pre-settlement arboreal woodland or scrub forms of cerrado on the level uplands, and gallery forests along the streams on the shallow valley floors. But the gallery forest is separated from the cerrado by a bordering strip of moist or marshy grassy meadow that covers the slope, the meadow soil becoming seasonally (rarely permanently) saturated from soil water flushing from higher terrain (Fig. 16). Most of these valley-side moist campos bear scattered circular raised earth platforms a few meters in diameter, each with a termite nest on top. The platform was probably raised by the termites to provide a non-saturated base for their nest. These platforms are covered with cerrado scrub and small trees so that they look like wooded island-like groves in the grassy marshes, similar to the Florida Everglades hammocks, a "pantanal" landscape in the strict sense. While the latosols of the upland cerrados are yellowish or reddish, the valley-side soil is invariably light gray from gleying, or further downslope where moister the subsoil is light gray and the upper few decimeters are black with humus. The earth platform and the termite nest, formed from the subsoil, are therefore light gray also. The fact that cerrado plants grow on these platforms shows that it is not the different chemical composition of the soil (reduction of ferric hydroxides to ferrous form) that prevents the cerrado from moving downslope, but the temporary to permanent saturation of the soil, for as soon as this same soil is raised high enough (3 dm or more) the cerrado flora invades it.

These examples show that cerrado is on well-drained terrain and stops or changes when the soil becomes flooded or saturated for any appreciable period in the rainy season. My experience is the opposite of that of Cole (1958) who states that as a general rule cerrados on the "chapadões" (extensive flat plateau-like uplands) have a subsurface laterite layer and are ill-drained in the rainy season (presumably because of this layer). By far the greater part of the cerrado area I have seen, including many chapadões, do not have a subsurface laterite layer, and in all those I have seen which do there is no difficulty in drainage, not even *during* rainstorms. On the contrary, the drainage is very rapid. Therefore, although there might be some chapadão surfaces which do have very temporary surface flooding during rains, it is certainly not the general rule.

As will be mentioned in Part IX, some relatively small stands of scrub or arboreal cerrado on flat interfluves in the northern half of the cerrado region have a "clean" grassy ground layer with the usual dwarf and low shrubs and coarse herbs of the ground layer very rare or absent. It *may* be that this variation is due to a slight subterranean saturation for short periods in the rainy season due to relatively poor soil drainage. Some of these stands of "clean" grassy cerrado have light gray soil suggesting temporary waterlogging, but other stands have the usual reddish or yellowish-brown soil. This subterranean saturation, if it occurs, does not cause free water to appear at the surface.

The extensive flat interfluves of the Espigão Mestre divide along the Goiás-Bahia boundary may have temporary flooding of a day or so after rains. The cerrado here is of the pure grassland (campo limpo) form or dwarf scrub very open savanna (campo sujo). How much this openness is due to the short period of flooding and how much to soil poverty from the original bedrock and continuous leaching and latosolization over geological ages remains to be seen.

(b) For cerrado to occur the upper few meters of the soil must be able to *dry out thoroughly in the dry season.* This means: (1) The site must be such that the permanent water table is not near the surface. Usually the water table in cerrado (noted in open wells dug entirely in deep soil) is 10–20 m or more deep although I have seen cerrado on sites where the water table is only 3 m deep or more than 30 m. (2) The site must not be the sloping side of a valley through whose surface, subsoil water from the higher terrain continues to flow out during the dry season as a long-term flush, that is, the site must not be a permanent or temporary hillside marsh (as in the example given in (a)). In fact, cerrado cannot even occupy a position of the slope slightly above this level, where the flush is underground but near enough to the surface so that the upper soil layer does not dry out sufficiently in the dry season.

Thus cerrado is always an *upland* vegetation, never being found on bottomlands along streams. (An apparent exception is that in a few areas, the head of a brook gully may rapidly cut its way into an upland cerrado, and mesophytic gallery forest or scrub has not yet formed along its banks, so that the cerrado does directly adjoin the steep-sided gully. But this is a case where the brook gully has invaded the upland and there is no valley bottom. Further downstream, where a valley forms, mesophytic gallery forest or scrub always appears.)

Soil fertility. For cerrado to occur the soil must be *poor in nutrients,* that is, in those available cations and anions necessary for plant growth. In the cerrado region this may come about in two ways.

(a) In relatively *young soils,* i.e., immature, slightly weathered and leached, the character of the underlying rock type (or previously transported soil material) is of great importance. In this case, cerrados are over rocks like poor sandstones and shales which yield a soil whose *mineral portion* contains only a small quantity of available potassium, calcium, magnesium, phosphorus, sulfur, etc., while mesophytic upland forest in the same region occurs over richer, more basic rocks like gabbro, basalt, gneiss with dark minerals (biotite, hornblende, etc.), limestone, calcareous or micaceous sandstone, etc.

(b) In *old soils* on level sites, the same soil particles stay in place for millions of years, or only move a very slight distance downslope but remain in the same conditions, and thus become highly weathered and leached. In a tropical climate with sufficient rainfall, whether or not there is a short or moderate dry season, and under the usual moderately acid conditions, this has six effects.

(1) Ions released by weathering of clay-forming minerals leach out in the order: Cl^-, SO_4^{--}, Ca^{++}, Na^+, Mg^{++}, K^+, because of low retention

and are carried away in the streams. The leaching order is not exactly the same, but is related to, the force with which ions are held on the surface and edges of clay minerals. The more strongly an ion is held the further along it is in the replaceability series. The exact replacement order depends on the particular clay mineral under consideration. With certain exceptions, the higher the valence, the larger the ionic size, and the less the degree of hydration, the more tightly the ions are held.

(2) The strong leaching of bases, together with the leaching of colloidal silica which in time also occurs, causes the higher cation exchange capacity 2:1 lattice type secondary clay minerals (montmorillonite, vermiculite) to change to the lower cation exchange capacity 1:1 lattice type clay minerals (kaolinite). This results in fewer exchange sites for holding the cations necessary for plant growth.

Thus, montmorillonite has a cation exchange capacity of 80–150 milliequivalents per 100 gm of mineral, vermiculite, 100–150, and kaolinite only 3–15, at pH 7. The following discussion is taken from data in Grim (1953).

2:1 clay minerals have the structure of a stack of sandwiches. Each "sandwich" is made up of two layers of silica (silicon oxide-hydroxide) tetrahedrons separated by a layer of alumina (aluminum oxide-hydroxide) octahedrons. The tetrahedrons and octahedrons within layers and the different layers are united by sharing certain oxygen atoms. In the ideal state, electrical balance is maintained by only two-thirds of the octahedrons being filled with aluminum ions, the rest being empty, and by the extra bond of non-shared oxygens being balanced by hydrogen (that is, these corners are hydroxyl groups rather than oxygen atoms alone). In the actual mineral, however, there is a small degree of substitution of aluminum for silicon in the tetrahedron sheets and there can be any degree of substitution of magnesium, iron and other metals for aluminum in the octahedron sheets. In these lattice substitutions the entrance of cations with smaller positive charge leaves the 3-layer unit with an excess negative charge. This can be partially compensated within the lattice. Thus, substitutions of Al^{3+} for Si^{4+} in the tetrahedron layer may be partially compensated by filling slightly more than two-thirds of the octahedron positions with cations. But there is always an excess negative charge which is balanced by adsorption of cations on the surface, that is, between one 2:1 unit and another. Montmorillonite and vermiculite are expandable, that is, water and other polar molecules can enter between the 2:1 units and separate them. The exact distance that adsorbed cations are held at the surface depends on the amount of water present in the clay.

Cations are also held at the edges of the units on "broken bonds." This is mostly replacement by the cations of the hydrogens of hydroxyl ions exposed at the edges. In montmorillonite and vermiculite about 80% of the cation exchange capacity is on the flat surfaces and 20% at the edges.

The illite minerals also have the same 2:1 structure as montmorillonite. Some silicon is always replaced by aluminum and the resulting charge is balanced by potassium ions. These hold the 2:1 units tightly together so that water cannot enter; the mineral is non-expandable. In well-crystallized muscovite mica the structure is nearest the ideal form. In biotite mica most of the aluminum in the octahedron layer is replaced by magnesium and iron. In both micas the stacking of the 2:1 unit layers is regular. In the illite clay minerals the bonding K^+ ions may be partially replaced by Ca^{++}, Mg^{++} and H^+. There is some randomness in the stacking of the 2:1 unit layers, and the particle size is very small. Because the unit layers are held tightly together, the bonding cations are not available and there is substantially no cation exchange capacity on the surface of the units, only at the edges. The exchange capacity is therefore small, 10–40 meq/100 gm.

The 1:1 clay minerals, such as kaolinite and halloysite, are made up of one layer of silica tetrahedrons and one layer of alumina octahedrons. The charges within the lattice are balanced. There is very little substitution of other ions within the lattice so that there is almost no cation exchange capacity on the surface of the unit, only at the edges, and the total is therefore small, 3–15 meq/100 gm for kaolinite and 5–50 for halloysite. In kaolinite the 1:1 unit layers are held tightly together in a regular stacking order. In halloysite the stacking position of successive 1:1 layers is more or less at random. A layer of water molecules can enter between the unit layers forming the hydrated form of this mineral.

Anions are held by clay minerals by the anions replacing whole hydroxyl ions at the edges of the units. Another possible method of connection for anions like phosphates and borates which are of about the same size and shape as silica tetrahedrons is to hook on to the silica tetrahedrons at the edges of the units in such a way as to extend the lattice in the same plane.

Desilicification of clay minerals consists of the removal of the silica layer. This changes a 2 : 1 mineral to a 1 : 1 mineral. Desilicification of the latter leaves the free alumina octahedron layer. When pure, this is the mineral gibbsite.

Iron cannot enter the kaolinite lattice and so forms oxides which color the soil red.

With continued strong leaching more silica is removed, the kaolinite, a hydrated aluminum silicate, breaks down, and "all the constituents released by silicate hydrolysis are removed in dilute solution as quickly as they are weathered except iron and aluminum which readily form very insoluble hydrous oxides." (Crompton, 1967). This leaves the soil with still fewer nutrient ions and an even lower capacity to hold them. Aluminum sesquioxide (gibbsite) and iron sesquioxides (goethite, hematite) accumulate. These oxides come directly from the breakdown of the primary minerals or in some cases from desilicification of the clay minerals. In some areas, probably formerly with higher rainfall, the gibbsite or its less dehydrated form, boehmite, or a mixture of both, accumulate, forming the deposits known as bauxite.

The usual clay minerals and oxides in cerrado soils are kaolinite, gibbsite, goethite, hematite, and illite, all with very small exchange capacity.

The relation molecular SiO_2/Al_2O_3, or *ki*, expresses the degree of silica loss and aluminum sesquioxide accumulation, that is, the degree of latosolization* or maturity of the soil under tropical moist conditions.** Soils with $ki = 1.8$ or lower are usually considered latosols. Soils with the same *ki*, however, may have different amounts of exchange capacity and base saturation depending on the substrate rock. Basic rocks develop clays which start out with high exchange capacity and base saturation and continue to be fertile even when reaching low *ki* values, such as basalt giving rise to "terra roxa legítima." Therefore, among soils taken from different rock types there is no correlation between *ki* or *kr* and fertility (Pavageau, 1952) but among soils with different degrees of weathering from the same rock type, there is.

Soils developing from siliceous sandstones (those not containing mica and in which the cement binding the sand particles is also silica and not clayey or calcareous) do not contain any appreciable clay or minerals which can weather to clay. These rocks can only develop an an almost pure sandy profile, which when deep, because of lack of horizonation, is a very sandy regosol. They contain from less than 1% to perhaps 5% clay. In the cerrado region, when not kept moist by ground water, regosols support cerrado, such as those around São Carlos, Itirapina and Brotas in central São Paulo.

(3) The soils are acid, at least in the upper layers, either because of the rock type or because of the long weathering or both, and under these conditions in the moist or semi-moist tropics, exchangeable aluminum ions, which are continually being produced from clay decomposition and from substitution of other metals for aluminum in the clay lattice, come to occupy an increasing proportion of the exchange sites. The increased aluminum saturation of the exchange complex may have a direct effect on the vegetation (Goodland, 1969, 1971a). Thus the ability of cerrado to compete with forest on poor upland soils in a climate where

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* Since the development of a latosol and the development of soft or hard laterite (plinthite) are two separate processes, it would be well if the names of these processes were different. Therefore, the development of a latosol should be called "latosolization" (or "ferralitization"), leaving the word "laterization" for the development of laterite. For the confusion that has arisen from latosols being called laterites, see Hamming (1968).

** The ratio *kr*, or molecular $SiO_2/Fe_2O_3 + Al_2O_3$, may also be used; both accumulate together. Since the presence of iron oxides is so characteristic of tropical soils this ratio may even be a better one (Pavageau, 1952).

The best method of testing soil maturity is X-ray analysis of the clay minerals to see what proportion of the different forms along the weathering sequence are present. This is expensive, however, so for routine analysis the *ki* or *kr* ratios are used.

both can occur may possibly be due in some cases not only to the fact that the cerrado flora has evolved to endure a lower level of nutrients than forest, but also because it can stand higher absolute levels of available aluminum, or rather higher saturation of the exchange complex by that element. Aluminum is probably somewhat poisonous to the forest flora.

(4) Under the acid conditions prevailing, phosphorus as phosphate combines with the large amounts of iron and aluminum oxides present in old soils as occluded iron-aluminum phosphate, thus becoming unavailable to plants.

(5) Tropical weathering under moist conditions (i.e., with sufficient rain to carry leachates away) produces a very deep soil on slopes that are not too steep, as Rawitscher (1944) has stressed. Whatever the rock type the pH is usually highest at the soil mantle-bedrock interface. It is here that most of the colloidal silica is leached out since it is more soluble in alkaline conditions.

The less weathered, more fertile soil directly above bedrock soon passes beyond the reach of the deepest roots so that the relatively large quantities of bases released and not yet leached out at this level can no longer be absorbed by the plants and redeposited on the surface by leaf fall.

(6) The resulting poor soil can support only a more open vegetation with less leaf mass per unit area of ground and leaves with a lower proportion of bases than is true for forests. The total amount of organic matter returned to the soil is less and mineralizes rapidly, producing a constant low humus content. Only a very low level of nitrogen and sulfur compounds can accumulate in the soil.

In sum, the longer the weathering a particular soil has suffered, with the same soil particles or most of them remaining in place and not carried away from the site, the poorer the *mineral portion* of the soil will be in nutrients, and the less influence will the underlying rock type have on vegetation (Denevan, p. 48, in Hills & Randall, 1968). The surface of the flat undissected uplands between the major northward-flowing rivers in the cerrado region is estimated to have existed from the Early Cenozoic, Cretaceous, or even Jurassic.

Camargo (1965) describes Brazilian latosols as follows:

"Soils well, or very well drained, deep, friable, porous, coloration varying from red to dark yellow or brown, intensively meteorized and lixiviated, with a very small reserve of meteorizable materials, typical profiles with indistinctive differentiation of horizons and with a lack of sub-superficial horizon and [lack of] evidence of significant accumulation of clay. The silt content is very low and the clay fraction comprises kaolinite and high contents of iron oxid, being relevant the thin firm aggregation which is responsible for the great permeability, in spite of the high clay contents they may present. The base content, oxid content, organic matter content and color vary."

In central and southeast Brazil the dominant cerrado soils are dark-red latosol and red-yellow latosol, both having phases with high and with low clay content.

Up to now we have been discussing the fertility of the mineral portion of the soil, that is, the nutrient ions bound to the clay colloidal complex. But nutrient ions are also bound to, and available from, the organic colloidal complex (humus), as well as from colloidal complexes that are formed of both organic and mineral components. A soil may be relatively fertile, therefore, if it contains enough humus, even when the nutrient ions supplied by the clay are few, for what the clay does supply or what is set free by decay of original minerals and of plant and animal remains (the latter important for nitrogen and sulfur) will be held available and not leached away so quickly but remain to be reabsorbed and recycled. But whereas the clay component originates from parent rock minerals or transported soil material, the humus can only originate from the remains of plants already growing on the soil and the animals associated with these plants (besides the small amount of organic material that settles from the air). Some vegetation types, like broadleaf mesophytic forest, by the chemical composition of their tissues, particularly the leaves, and by the fact that they shade the soil, allow more humus to accumulate than an open scrub or savanna. The organic component of the soil, therefore, is, under a particular set of drainage conditions, dependent on the type of vegetation that covers the ground. *Once present*, a forest builds up humus, shades the ground, etc., and therefore the forest flora seeds that fall on this soil have a competitive advantage over any cerrado seeds that may enter. Conversely, if a cerrado is present, its microclimate and the small humus content of its soil competitively favor cerrado seed establishment over forest seed. Long-term climatic changes such as a general increase in rainfall can cause forest to invade cerrado, but for the short term, each of these two vegetation types produces conditions that maintain itself against the other.

The question then is what causes cerrado in the first place, or forest, to establish itself in a moderately dry climate and on upland deep drained soils where both *can* occur? Tropical mesophytic forest is undoubtedly older, evolutionarily speaking, than the cerrado, and at least a dry semideciduous form of mesophytic forest probably originally covered the central Brazilian plateau. As the level soil weathered over geological eras the cerrado flora evolved, adapted to survive on these soils that were becoming nutritionally poorer and poorer, while the forest continued to inhabit the moist valleys and also a few upland areas where a basic rock type kept the soil rich even under high latosolization. As long as man did not appear on the scene, fires in the intermediate rainfall region were relatively few and did not materially affect the course of soil evolution. When a cerrado burned there was a temporary release of nutrients to be washed away, but by the next rainy season the grasses were all back in full thickness and within a few more years the original low-shrub density was reattained. One could hypothesize that under pre-human conditions, some areas of mesophytic forest in and just outside the main cerrado region would be able to maintain themselves, if only in a semideciduous form, on some soils whose mineral colloids had through geological time become nutritionally poor by leaching and latosolization, because the humus in the upper layers continued to hold enough available nutrient ions to favor the continuation of the forest over the establishment of a cerrado and these ions were continually cycled through the humus layer. These forests, with the mineral-nutrient portion of their soils leached out from under them, would gradually find themselves in an unstable equilibrium. When man suddenly appeared on the scene, the greater frequency of fires would open up the forest soil to the sun and allow the humus to be oxidized, and would even directly burn the humus itself, as well as volatize nitrogen and sulfur compounds, without giving enough time for the forest to establish the original conditions before the next fire arrived. The soil would become poorer in available nutrients. Cerrado seeds, which had always been coming in from nearby cerrados, would now be at a competitive advantage and could establish themselves, creating microclimate and soil conditions in which they were more and more at an advantage and the forest seeds at a disadvantage. When European settlement arrived, fires became annual, thus destroying other forests that had continued to be stable under the lesser burning frequency of Indian occupation.

Thus Setzer (1967) mentions forest soil analyses he made on the upper Xingu, just west of the main cerrado region where the rainfall is 2200 mm per year on the average, with a moderately strong dry season. He shows that the original soil fertility of the virgin forest is all in the upper humic layers. Therefore, once the forest is cut the humus will rapidly disappear and with it the original fertility.*

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* Intensive agriculture in the tropics, giving high yields in a small area, can only be carried on under one or another of the following conditions, assuming sufficient water is present as rainfall or by irrigation:

(1) the underlying rock type is one that yields soils with a mineral portion of high nutrient value, such as volcanic rocks (Java), limestones, etc.;

(2) a floodplain situation, where periodic rises of water level leave constantly renewed, relatively rich soil sediments (Amazon várzeas, floodplain and delta of the Nile, Ganges, Irrawady, etc.);

(3) small areas of naturally poor soil kept fertile by heavy appilcations of organic manures (São Félix, Bahia, *vide* Waibel, 1958, pp. 303–305);

(4) application of chemical fertilizers.

The last requires modern techniques and transportation facilities and relatively heavy outlays of capital to be economical. Traditional tropical areas of high population density are usually based on the first two situations.

In Brazil, except for small floodplain areas, the soil is relatively poor. Even the best upland soil, "terra roxa" from basalt, loses its fertility after several years of cultivation if fertilizer is not applied. In poorer soils the loss is even more rapid; only one or two crops can be obtained before it has to be abandoned. This is

TABLE V

CHARACTERISTICS OF CERRADO SOILS.

pH	4.1 -7.0 (usually 4.5-5.5)
N%	0.01-0.2 (-0.3)
C%	0.1 -3.2 (-4.6)
Organic matter % (humus)	0.2 -5.0
Ca me/100 gm	0.2 to rarely more than 1.0
K me/100 gm	0.04-1.25 (mean ca. 0.1)
Available P me /100 gm	0.02 to usually less than 1.0
Al me/100 gm	0.0 -2.0 (3.5)
Cation exchange capacity me/100 gm	2-4 (-20)
Base saturation %	2-44 (very rarely to 100 in top dm)
Sum of exch. bases	0.3 -2.3 (rarely more than 1.0)
Available water capacity[a] %	1-10 (-30)

[a] Weight of water held between ½-15 atm to dry weight of soil.

However, in spite of this reasoning, it must be emphasized that although clearing the forest reduces soil fertility, the proportion of the original forest area which has become *cerrado* seems to be extremely small. There is no evidence at all, contrary to what several writers have maintained, that large areas of cerrado today were forests before man appeared, or especially, before European settlement. This is true even in São Paulo and southern Minas, where in some regions forest has been cleared for over a century. When the soil became too poor for cultivation and was turned to pasture or when forest was cut directly to pasture, this was burned almost every year. The pasture remained grassland, with a *non-cerrado flora* even when near original cerrado areas, and except perhaps in a few small spots, did not become cerrado vegetation, although in some cases a few cerrado species may have entered.

Table V presents ranges of soil values from the top 1 or 2 dm layer from several hundred analyses of soils under cerrado vegetation of all heights and densities from the southern half of the cerrado region and from the disjunct northeastern cerrados. The data is taken from Setzer,

because the nutrient level of the mineral colloids of the soil was low to start with, most of the nutrient ions being held by the organic portion. And it is precisely the organic colloids, the humus, which is rapidly reduced by cultivation and burning.

Thus we see the precarious nature of upland mesophytic forests and of cerradão in Brazil. While they are not disturbed most of the carbon content of the soil-plus-plant layer is in the plant layer, and the small proportion in the soil is mostly in the upper few decimeters, deposited by constant leaf, branch and trunk fall, and its decomposition and incorporation into the soil. A much smaller proportion reaches lower levels due to decay of deep roots or the activities of burrowing animals.

1949; Pavageau, 1952; Comissão de Solos, 1960; Braun, 1962; Ranzani, 1963, 1971; Benemma, 1964; Goodland, 1969, and 1971c. The nutrient levels shown are very low, even considering that these upper levels have the greatest amount of humus in the profile.

The humus is calculated in the usual way as 1.7 times carbon content.* Open cerrados rarely have more than 2% humus. Among open cerrados, those at higher altitudes and those with more clay generally have higher humus content (Benemma, 1964; Ranzani, 1963). Ranzani (1963) shows a positive correlation between clay content and N and between clay content and C in soils under cerrado from a large part of the country. This can be expected because of the positive correlation between greater clay content and greater absolute cation exchange capacity (if we assume that the distribution in the soils tested of degree of latosolization of the clay is the same among soils with low and with high clay content). The more clayey soils would then tend to attract or allow to develop a taller denser cerrado and this would supply and allow the soil to retain more humus, that is, C content. The greater clay content and the greater humus content would then hold more nitrogen available as well as other ions.

Although this may be true in general, it is not necessarily true in a small area. Goodland (1969, 1971c) working in the Triâangulo Mineiro, found no significant correlation between clay-plus-silt content (almost all of this being clay) and the four classes of cerrado density into which he divided his 110 stands. He did show a strong positive correlation between cerrado density and several nutrients such as N, P and K, and his work is the first on a large scale which has shown the relation between nutrient level and density *within* cerrado vegetation rather than between cerrado and other vegetation types.** His highest density class, cerradão, the arboreal form, is of course a primitive form, and the second densest class, cerrado sens. strict., a rather dense tall scrub, is probably original also in the region investigated, at least in part, because it is by far the

* This method may lead to higher values for humus than really exist due to the presence of wood ashes. Charred bark when sloughed off, or the charred parts of stems and trunks fallen to the ground break into small pieces. These then get smaller until they are the size of sand particles. Rain washing over the surface concentrates these carbon particles into small patches on bare soil areas between the grass clumps. Percolating water and animal activities carry them down into the upper soil layers.

** Camargo & Arens (1967) present single soil analyses for adjacent stands of "cerradão" (dense woody vegetation 4–12 m tall), "cerrado" (more open woody layer with individuals to 3 m), and "campo limpo" (abandoned cultivated field on cerrado soil, really a campo sujo since some woody species are mentioned) in a reserved area near Rio Claro, São Paulo. The organic material content of the soils is 2.4%, 1.0 % and 0.8% respectively, and N, P, and K content are in general diminished in the same order. The "campo limpo" is of course due to disturbance and it is highly probable that the difference in density and height between the "cerrado" and "cerradão" is also due to previous differences in the degree of disturbance and recuperation. The present soil fertilities then are due to the humus that the vegetation has been able to accumulate and are not a cause of the difference in height and density.

most common form.* The distribution of these two forms, then, is probably caused by original nutrient level differences in their soils. The two most open forms, campo cerrado and campo sujo (savannas with scattered scrub elements) are undoubtedly due to excessive fires. The region has been sparsely occupied by European culture since last century and intensively occupied by cattle raisers for over 30 years. In these two most open forms then, the lower nutrient level of their soils was probably caused by the excessive fires, which both opened the vegetation creating these physiognomies, and burned the humus directly as well as opening the soil to the sun which also destroyed more humus and so reduced the soil fertility. Thus although correlation between density and nutrient level can be shown, the interpretation as to which is cause and which effect, or whether both are effects of some other cause, can be different for each part of the values being correlated.

Laterite. Since laterite (hard plinthite) is a soil phenomenon that may occur in latosols but not necessarily, it is of interest to know if its presence affects vegetation or not. My observations show that hard laterite has an obvious effect only if it is compact and at the surface. The size of the concretions, the depth and distribution may vary considerably in the same region as in the following example.

The Serra do Roncador in northeastern Mato Grosso, runs north and south. The northern part is covered with Amazonian forest; the southern half lies in the cerrado region. The gently rounded crest of the southern portion bears, on the uplands, cerrado vegetation exclusively. Over 90% of the upland area consists of the tree-and-scrub woodland or low-tree-and-scrub woodland forms. The other forms occupy smaller areas, such as "closed low-trees-and-scrub" (a low-tree-and-scrub woodland in which the low scrub layer has become closed due to lack of recent fires), closed scrub, open scrub, or, where the crest reaches its highest altitude, scrub savanna or low-tree-and-scrub savanna. All these forms occur on flat to gently sloped terrain, and the soil on by far the greatest portion is reddish or yellowish-tan deep latosols without stones or laterite concretions. In some restricted areas, on scarp sides or on flat land near the edge of a scarp descent, there is a hard fossil laterite layer 3–5 dm thick within a few decimeters of the surface or exposed at the surface. This layer is not solid but composed of irregular blocks 5–20 cm long, and does not restrict drainage. These scarp slopes or the upper part of them may bear a campo limpo form of cerrado, that is, a grassfield with or without a few scattered shrubs and whose floristic composition is a restricted number of the ground layer species that grow in the adjacent

* If it were not an original form we would expect it to be rather uncommon since those cerrados which *are* burned are fired almost every year, and a stand opened by fire would need a period of absence of fire or of very few fires to be able to grow back to a taller denser form. We would not expect this to have happened so uniformly over so large an area.

more developed cerrados, plus a very few species not found in the latter, such as a globular cactus and special bromeliad species. The grasses and herbs that do grow here grow to the same height as they do in the woodland cerrados. Other scarps bear the usual scrub or woodland cerrados over their whole slope.

Some level areas far from any scarps have a substrate that is purely of laterite pebbles 1–2 cm long (not cemented together) with only about 1% by volume of fine soil, and these pebbles occupy at least the upper meter or so (which was as far as soil pits were dug). The pebble layer does not offer any difficulty in drainage. Most of the time the pebble areas bear the usual woodland form of cerrado, showing that tree root penetration is not hindered either. But in one restricted region (the same higher-altitude portion of the crest where the savanna form is the principal vegetation and occurs on deep soils without concretions) there occur scattered areas, 10–30 m long or so, on level or very slightly sloping ground, with an upper dense laterite layer, pebbly at the surface. Here, instead of woodland or scrub or the grassfield type mentioned above for scarps, occurs a continuous short-herbaceous layer, only 10–15 cm tall, of short grasses, sedges and scattered herbs growing in an appressed herbaceous legume carpet (*Arachis* sp.) very similar in appearance to herbaceous carpets on solid laterite or rock pavements in Goiás and Maranhão-Piauí (where the carpeting legume is *Mimosa* sp.). Possibly here, drainage and tree rooting through the laterite layer are difficult. Thus, on the Serra do Roncador the presence of laterite concretions has no consistent effects on the vegetation, the variations in physiognomy and species content of the stands they underlie probably having to do with the exact degree of compactness as this affects drainage and ability of tree roots to penetrate.

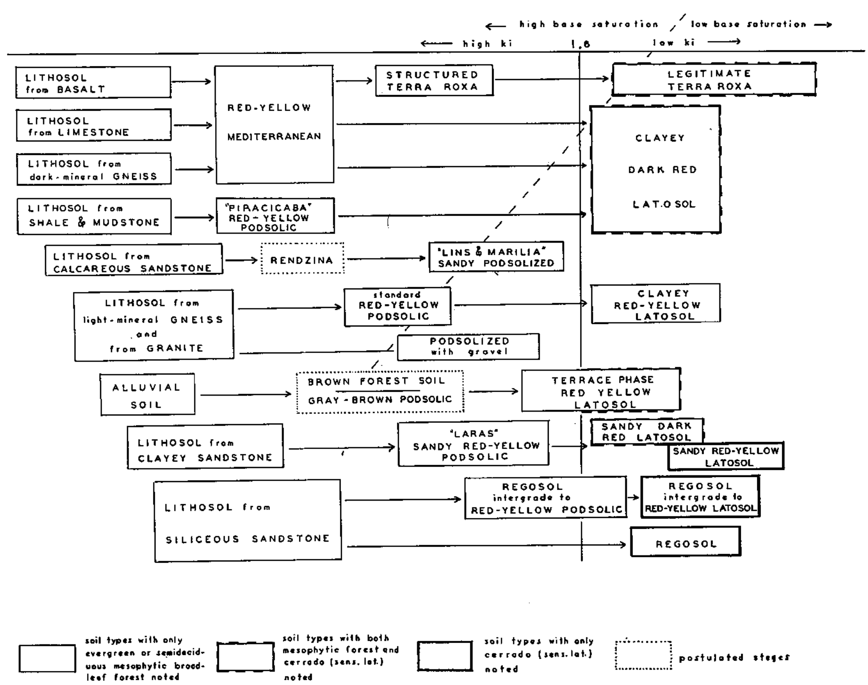
It should be mentioned that the formation of hard laterite crusts can occur not only in open-vegetation areas where on the uplands it is undoubtedly fossil, but also under dense equatorial forests where in some cases it is probably currently active. Meters-thick crusts of nodules so compact that roots cannot penetrate support forests on a soil layer only 10 cm thick above it in Rondônia (Guerra, 1953). In this case the vegetation rapidly cycles minerals, the proportion in the soil at any time being small because of the small volume of soil.

According to current theory (Sombroek, 1966), soft laterite (soft plinthite) seems to form in latosols under a fluctuating water table within a few meters of the surface. It has a grayish or whitish color, is usually clayey, and is mottled with yellowish, reddish or purplish spots forming a pattern. The center of the spots may be indurated. The spots turn to hard laterite concretions under certain conditions of exposure or near-exposure of the soft laterite layer. The concretions may increase in size and form a layer above the soft laterite. If much iron is present the concretions may cement together forming a carapace. The unlaterized soil layer above the concretionary layer may then be worn away, exposing the hard concretions. Exposed hard laterite may then disintegrate again, forming a fine soil layer above. In road cuts the laterite would then appear as a stone line. Where the concretions can be carried away by water or by gravity downslope, as occurred in many parts of the inner Amazon valley, they may be deposited on soil which did not originally contain concretions, forming a layer at the surface, or if then covered by soil, appearing as a stone line in cuts. Several cycles of hard laterite formation and denudation can occur in the same soil. Since the water table in cerrado is almost always very deep, and without a temporary perched water table near the surface, lateritic concretions in cerrado soil probably formed in the past under other climatic or geomorphologic conditions, that is, the laterite layer is now a fossil one. The hard laterite layers I have seen on interfluves in the cerrado are not underlain by soft laterite, so these concretions were probably transported to their present position under conditions very different from the present ones. Laterite is definitely not typical of cerrado although common in certain areas, and where it does occur is probably almost all fossil.

Soil types and vegetation. The relation of soil types to cerrado in the State of São Paulo is shown in Table VI. This includes only those soils on which cerrado *could* occur in the state, that is, that are well-drained, with a deep water table, and occur in a climate with less than 1500 mm rainfall per year with a well-defined dry season. These soil types make up more than 90% of the area of the state. The soils in the table have been arranged in presumed maturity sequences (*ki* ratio decreasing, or degree of latosolization increasing, from left to right), with the sequences arranged from top to bottom according to richness in nutrient ions that the original rock types can produce on first weathering. Cerrado in any of its forms was noted in the soil survey only on those soils with *ki* in general less than 1.8 in the top meter or so. These are all latosols except for the rich "terra roxa legítima" (which, although highly latosolized, might by some be excluded from the concept of latosol) and the clay-poor regosol. Since only relatively few profiles per soil type were examined in this preliminary survey, it is possible that cerrado occurs on some of the types not shown as supporting it, such as clayey red-yellow latosol and possibly the "Lins & Marília" sandy posolized. Note that almost any soil with *ki* less than 1.8 *may* support cerrado, while of these, those with the lowest nutrient status (sandy red-yellow latosol, regosol, and intermediates between these two) bear *only* cerrado and not forest as far as noticed.

Within any one maturity sequence, that is, among soils derived from any one rock type, low *ki* (ratio of molecular SiO_2 to Al_2O_3, taken as a measure of latosolization) is associated with low nutrient status, i.e., low absolute amount of exchangeable bases. But when the rock source is of a rich type, one that yields a high concentration of nutrient ions, its residual soils may reach a low *ki* (silica leached, aluminum oxides increased) but still maintain a relatively high concentration of nutrient

TABLE VI. Maturity sequences of mid-altitude, well-drained, planalto soils under less than 1500 mm average annual rainfall in the State of São Paulo. Soil types are placed along the *ki* scale according to where the bulk of their *ki* values fall. In some cases the actual range is greater. The soil types furthest to the left reach *ki* 3.8, and those furthest to the right reach *ki* 0.3. The table is modified from Fig. 8 in Comissão de Solos, Bol. 12, 1960, according to data provided in that publication. Not shown on the table is Humic Red-yellow Latosol. This has most of its area in a continuously humid climate, arises from granite-gneiss, and is covered with forest. A small portion (less than 1% of the area of the state) of this soil type occurs in a dry-season climate near Campinas (underlying rock not known) and is covered with cerrado. The supposition that the "Laras" Sandy Red-yellow Podsolic is an intermediate stage on the sequence between the clayey sandstone lithosol and the sandy latosols is that of the author of the present paper, not the source. Rendzina does not occur in São Paulo, but a similar type is postulated as a stage in the maturity sequence shown. Legitimate terra roxa covers 15% of the state, "Lins & Marília" Sandy Podsolic covers 19%, Sandy Dark Red Latosol, 20%, and Sandy Red-yellow Latosol, 5%. The other soil types each cover less than 5% of the state.



ions, as is the case of virgin legitimate terra roxa.* Therefore, low *ki* in itself does not necessarily mean low nutrient status. Apparently, cerrado

* "Terra roxa" ("purple soil" in Portuguese) is a different kind of soil from "terra rossa" ("red soil" in Italian).

in São Paulo occurs on deep soils (not on lithosols) of poor nutrient status if the *ki* is low enough. Note also that sandy regosols support cerrado only. They are nutritionally poor because the clay content is very small. For that very reason the absolute available aluminum content is also low although its saturation of the poor exchange complex may be high. Low *ki* values mean high absolute available aluminum content only when there is enough clay to start with.

The data suggest that some function based upon both nutrient status and *ki* would be the soil characteristic that most closely correlates with vegetation type, whether forest or cerrado, on these soils.

Table VII gives soil values for non-waterlogged soils in a high-altitude region (750–1300 m) in south central Minas Gerais, that around the Furnas dam. Besides soil types, the actual values of *ki*, aluminum and nutrients are given for each of the vegetation types distinguished in the region. The cerrado was divided into two density forms in the field. The two campo vegetations are non-cerrado grassfields differing floristically from each other and in their altitudes, soils and underlying rock. The forest types include those on both deep and shallow soils. The table has been constructed from data given in Comissão de Solos, Bol. 13, 1962. For simplicity, soil intergrades and vegetation intergrades mentioned in that work are not given here.

In general, the soils of the two forms of cerrado have lower levels of exchangeable bases, lower base saturation, and more available aluminum than the forest soils. Also, cerrado soils reach slightly lower *ki* values (probably not significant from this sample) and in general, do not reach such high values as some forest soils do. This agrees with results in São Paulo. The difference between the denser and the more open cerrados is that the former occurs in deep soils and the latter on more shallow soils but there is no consistent difference in the other values as far as these data go. The two campo forms, which grow on different soil types, also have soils of low nutrient status but differ from cerrado soils in other respects such as being shallow and, as we would expect in lithosols over rocks (rather than over laterite crusts), having higher *ki* values, that is less latosolization.

Pavageau (1952) tested 25 upland soils from Central Brazil, each sampled at several levels up to 2 m deep. The soils came from a variety of rocks: sandstone, shale, diorite and diabase, as well as colluvium and alluvium. Thirteen soils came from cerrado (including cerradão) and the rest from forest. In three-quarters of the samples the top 15 cm had less than 4% of humus; cerrado and forest had approximately equal amounts of humus on the average but cerrado soils reached lower values (0.2%) and the forest soils higher values (7.6%). Pavageau contrived a fertility scale based on available Ca, Mg, K, P, total P and N, cation exchange capacity, humus, pore volume, moisture equivalent and pH, and found that this correlated well with the vegetation. With two exceptions the 13 cerrado soils had a lower fertility index than 11 of the

TABLE VII

SOIL CHARACTERISTICS OF THE FURNAS REGION, SOUTH CENTRAL MINAS GERAIS, AS RELATED TO VEGETATION.

Vegetation	Main rock types	Soils	Soil depth	Soil layer	Ki	Available Al me/100 gm	Available P me/100 gm	Sum of exch. bases me/100 gm	% Base saturation
broadleaf forest (evergreen and semideciduous)	limestone, gneiss, shale	red-yellow latosol, dark red latosol, dark red humic latosol, red-yellow podsolic, structured terra roxa. red-yellow mediterranean, lithosol from gneiss	shallow (< 1 m) to usually deep (2– > 4m)	A	1.1–2.2(–3.0)	0.08–0.4(–2.0)	0.4–1.4(1.7)	0.5–6(–12)	(5–)20–70
				B	1.0–2.2	0.17–0.4	0.1–0.3(–0.7)	0.5–4(–11)	(5–) 8–85
				C	1.7–2.5	1.8	0.1–0.3(0.5)	0.5–3(–16)	15–90
cerrado (tree-&-scrub woodland)	gneiss, shale	dark red latosol, red-yellow latosol	deep (2– > 4m)	A	1.0–1.2	1.2–2.1	0.1–0.5	(0.3–)0.5–1.5	6–16
				B	0.9–1.3	0.2–0.3	0.1	0.4–0.6	8–17
				C	2.0	2.3	0.1	0.4	9–14
campo cerrado (scrub savanna)	gneiss, shale, sericitic quartzite	Alpinópolis podsolized; lithosols from shale, schist and gneiss	medium shallow (1½-2 m)	A	0.9–1.6(–2.3)	0.9–1.0	0.3–0.7(–5.2)	0.4–0.6(–1.7)	9–21
				B	0.9–1.8	0.2–0.9	0.1–0.2	—	11–15
				C	0.9–1.9	0.2	0.1–0.6	0.4	16
campos gerais (grassfield)	shale	acid brown soil, lithosol from shale	shallow (to 1 m)	A	1.8	2.3–4.0	0.2–0.8	0.4–0.6	6–7
				B	1.8–2.1	} 0.5–2.3 (B–C)	} 0.1 (B–C)	0.4	6–14
				C	2.3			0.3	9–15
high-altitude campo (grassfield)	sericitic quartzite, sericitic schist	Alpinópolis podsolized; lithosols from quartzite and schist	shallow (to 1 m)	A	1.3–3.6	(0.2–)0.5–1.1	0.4–1.5	0.3–0.6	11–16
				B	1.1–1.2	0.4–0.5	0.4–0.5	0.3	7–13
				C	2.4	0.2	0.8	0.3	16

12 forest soils. (One alluvial-soil forest had a fertility index within the cerrado range.) There was no correlation between fertility and *ki* or *kr* due to the variety of parent materials.

Thus, low fertility of the soil is one of the most important factors associated with the existence of cerrado within its proper climatic region.* On the other hand, the physical qualities of the soil (assuming no hardpan is present) are less important. Medina & Grohmann (1966) have shown that the range of variation in soil texture and water retention is the same in cerrado soils as in agricultural soils (derived from forest land) in São Paulo.

Although presence of cerrado is correlated with lower soil fertility in the present arrangement of cerrado and forest over the landscape, this does not mean that the lower fertility is what *causes* the cerrado to occur where it does rather than forest, for the forest, once present, enriches its soil. Thus at the cerrado-upland forest border on the Serra do Roncador crest, a region of virgin vegetation, the soil under both vegetation types is of the same kind from sandstone. But that under the forest has more clay, probably from the underlying sandstone containing more mica. Surface soil samples and those in the C layer down to 4 meters show significantly more extractable and total phosphorus in the forest than in the cerrado. If this difference in phosphorus content is an original contribution of the different bedrocks and has lasted down to the present degree of latosolization, it may be the cause of the present distribution of cerrado and upland forest in this region. However, since there is also more organic carbon in the forest soils than in the cerrado soils (2 to 2.5 times more even in the C layer), and neither phosphorus nor carbon decreases much with depth, the phosphorus content may

* In the Anais of the XX Congresso Nacional de Botânica held in Goiânia (published in 1970), there is an article entitled "Uma nova teoria que tenta elucidar a origem do cerrado" ["A new theory which attempts to elucidate the origin of the cerrado"] by J. D. de Beltrão. Unfortunately, no light is thrown on the subject. The reasoning of the author is of the following type. He states that magnesium is a constituent of chlorophyll, chlorophyll is necessary for photosynthesis, cerrado plants photosynthesize strongly, ergo, there cannot be any lack of magnesium in cerrado soils. Phosphorus is a constituent of the adenosine phosphates, these compounds are necessary for respiration, cerrado plants have no difficulty respiring, ergo, there is no lack of phosphorus in cerrado soils. Potassium and calcium are necessary for root growth, subterranean parts of cerrado plants are highly developed, ergo, there is no lack of K and Ca in cerrado soils, etc. The author, an agronomist, apparently makes no distinction between what a vegetation evolutionarily adapted to poor soil can do and what crop plants grown at economically dense spacing can do. He also states that since cerrados generally grow on more or less level ground and at tropical latitudes, they therefore receive strong radiation; strong light destroys plant hormones, hormones cause plant growth, therefore the cerrado is a low vegetation. The author does not explain why tall forests can grow, also on level ground, at the same latitudes as cerrado. The author makes some amazing statements, such as that there are no herbaceous plants in the cerrado, and gives reasons for this! Also ". . . we know that 49% of the species of the flora of the cerrado are highly woody. . ." Where this "49%" came from is not explained.

be linked with the carbon content and thus be a secondary effect determined mainly by the vegetation type which is present due to some other reason (Askew *et al.*, 1970b, 1971). The authors suggest that the greater water-retaining capacity of the more clayey soil may be enough to swing the delicate balance and enable the forest to hold this soil against the cerrado, and, once present, the forest enriches the topsoil. On the sandier soil the opposite would be true; cerrado wins out and does not enrich the topsoil so much. So the original "cause" of cerrado here may be the lesser water-retention of its soil and not its lower fertility. Rizzini (1970) also warns against assuming that the *deeper* soil layers under cerrado are always necessarily poorer in nutrients than those under forest. In most cases it might be difficult to assign the exact responsibility of water-retention and of original soil fertility in determining whether a cerrado or a mesophytic forest occupies an upland drained site. However, since many cerrado soils have much clay and are therefore quite retentive of water, the fact that they bear cerrado would seem to show that in their case original low soil fertility was the cause.

It was previously stated that there are floristic, and in most cases, also climatic differences between cerrado and the scattered small disjunct savannas within the Amazon forest region. There is also a large difference in the soils. Cerrado is typically on regular latosols while most of the Amazon savannas are on shallow lithosols, ground water laterite soils, or in the case of the Rio Negro "caatingas," on ground water podsols with a very deep white sand A_2 horizon simulating a sandy regosol (Sombroek, 1966). The soil differences support the position adopted here that it is best not to treat these Amazon savannas as part of the cerrado vegetation, even though in some cases they may visually resemble cerrado, as when they contain much *Curatella americana.* Including the Amazon savannas as part of the cerrado concept reduces the possibility of finding significant correlations between true cerrado and the climate and soils.

IX. DISTRIBUTION OF CERRADO VEGETATION OVER THE LANDSCAPE

By far the greater part of the cerrado region of central Brazil consists of flat to gently rolling land with cerrado covering the interfluves and with gallery forests along the streams. The gallery forests may be bordered or not by marshy campo strips. This is the prevalent pattern in east central and northeastern Mato Grosso, in Goiás, in southern Maranhão, and in parts of Minas and São Paulo, and occurs over a large series of rock types. However, other patterns of distribution occur, in which cerrado is mixed with upland forests, with non-cerrado campos, and with marshes. The extent to which the lowland forests climb the valley sides also varies, as well as whether they contain or are made up mostly of palms. This variation in upland and lowland vegetation is associated with topography, rock type and drainage conditions, but the extent to which these factors affect the vegetation varies with the geographic region. A few examples will be given.

The first is repeated from Eiten (1970) and is based on vegetation mapping being carried on by Sr. Luiz Guimarães de Azevedo. In northwestern São Paulo, he found four types of distribution.

(1) Dry forest (semideciduous mesophytic) on the interfluves and slopes of the gently rolling terrain, with narrow moist gallery forest (evergreen mesophytic or hygrophytic) along the streams.

(2) Moist forest (evergreen mesophytic) on the highest parts of the terrain, dry forest on the slopes, and moist gallery forest or *Typha* marsh along streams.

(3) Moist forest covering the whole topographic profile.

(4) Region with horizontal layers of sandstone of two types. The upper layers occurs in scattered remnants forming the higher parts of the terrain. It yields a relatively rich soil type and is covered with moist forest. The lower sandstone yields a poorer soil. Where the lower sandstone is exposed, the more or less flat top of this layer is covered with dry forest, while its gentle slopes are covered with cerradão. The cerradão continues to the streams where it meets gallery forest or *Typha* marsh.

A series of examples provided by Branco (1964) for southern and central Minas Gerais now follow.

Along the Brasília-Belo Horizonte road, to João Pinheiro. Most of the region is metamorphic rock plateau, mainly sericitic-quartzose schists, whose tops are an erosion surface, supposedly Cretaceous, at ca. 900 m altitude. Their soils are strongly latosolized and rich in aluminum. Some samples have 41% Al_2O_3, almost bauxite. These plateau tops are covered with cerrado. The stream valleys cut into these surfaces, with younger richer soils, bear gallery forests.

Same road, east of Paracatu, descending to the Paracatu and Prata Rivers. At ca. 700 m, the schists give way to the Bambuí Series of rocks, alternate layers of chloritic slatelike shales and limestone. The shales yield a poor soil generally with cerrado and open cerrado-type campos. The limestones have a karst topography with lakes, and are covered with forest but with areas and bands of cerrado. On parts of the outer river terraces at 600 m are non-consolidated sandstones (possibly Pleistocene) yielding sands and kaolinite clays covered with cerrado. On the east side of the river valley, limestone outcrops bearing deciduous forest ("mata sêca"), then higher up occurs a sandstone layer at 800–900 m that covers much of the central eastern part of Minas Gerais. It is covered with cerrado, possibly primatively cerradão. Gallery forests occur along the streams. Where the deeper valleys cut into lower level shales and siltites, water flowing over these impermeable layers through the permeable sandstone above them flushes out from the latter on both sides of the valley, forming valley-side marshes.

Chapada de Andrequicé to Felixlândia. The highland is a plateau capped with Bauru sandstone over ferruginous chloritic siltites of the Bambuí Series. The sandstone soils are generally covered with cerrado while the siltite soils, which are extremely poor in all bases except magnesium, have practically pure campo limpo. The streams have buriti palm galleries (*Mauritia vinifera*) with the usual valley-side marshy strips separating the buriti from the upland cerrados. The lower-level land to the southeast is underlain by calcareous siltites with limestone lenses. The siltite is covered with cerradão, a better developed cerrado form than on the sandstone plateau. Where the limestone lenses outcrop there are mesophytic forest groves.

Near Patos de Minas. Here is a sandstone surface above 1000 m altitude with strongly latosolized soil covered with cerrados and campos limpos, and with gallery forests along the streams. Near Patos and Salitre, however, some areas of this surface are covered with tuffs or alkaline rocks which yield a richer soil with more available bases and montmorillonite clays and are covered with exuberant forests. To the southeast of Patos the valley of the Rio Paranaíba exposes an underlayer of slate covered with cerrados and campos.

Triângulo Mineiro. The Mesozoic sandstone exposed over most of the region supports cerrado, and where basalt comes to the surface are mesophytic forests. However, in some areas where the basalt is exposed on the upland, it yields a very old deep dark red latosol rich in sesquioxides of aluminum and iron. This soil supports cerrado just as the sandstone soils do. The sides of the valleys cut into this basalt give rise to younger richer soils which support forest (now cleared for cultivation).

Central Minas Gerais. Surfaces with soils derived from slate support cerrado or campo limpo. A 200 m thick limestone layer underlies the slate and where this forms the surface further southeast, the residual soils are very old and deep, yellowish or reddish, rich in sesquioxides and poor in calcium. That is, even though they arise from limestone they have been so leached as to form latosols. They support the cerrados (probably primitively cerradões) of the Rio das Velhas region, Sete Lagoas and Lagoa Santa.* In some of the places where the limestone rock itself outcrops, the soils are not so deep and not so leached. These small areas support mesophytic forest which is evergreen where the soil has a certain minimum thickness and deciduous where the forest grows on the practically bare rock, rooting in the crevices.

Some observations of my own now follow.

São Carlos. In São Paulo, the city of São Carlos occupies a plateau made up of flat alternate layers of sandstone and basalt. The basalt sur-

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* The topography here is of rounded hills with convex sides which are quite steep on the lower part of the slope. Forest fills the valleys and reaches part way up the slope; in the Rio das Velhas valley, the forest occupies the whole slope to the top. These are not exactly "gallery" forests; perhaps they should be called "valley forests."

face at 900 m was covered with mesophytic forest (some almost virgin remnants still exist). Going down the north slope of the plateau an underlayer of sandstone outcrops and the forest remnants suddenly change to cerrado. Further downslope, another layer of basalt outcrops and secondary forest reappears. Further downslope, the sandstone appears again at 500 m and extends in a level plain from there north; this sandstone is covered with cerrado. All the cerrados of the region were originally cerradão; the lower plain is a cerradão 7–8 m tall, and except where cleared is very dense. In fact, it looks very much like "capoeira" or low secondary forest. The plateau top has 1200 mm rainfall per year on the average, the plain at the base of its northern side a somewhat lower figure. But the exact correlation of forest with basalt and cerrado with sandstone at all levels shows the overriding influence of the underlying rock type, through the residual soil it produces, in a climate where both forms can occur.

Belém-Brasília highway. The city of Anápolis, west of Brasília and at the southern end of the highway, lies in a valley in an area underlain by mica schist. It is surrounded by forest (now mostly cleared for cultivation). The uplands bear cerrado. At Hinterlândia, several kilometers north, the underlying rock changes to gneiss, which forms a mountainous terrain. With this change of rock the vegetation changes to continuous forest (on both uplands and in valleys) on a more fertile soil. This forest has been cleared for the most part for pasture and cultivation. Further north, the rock changes to mica schist again; however, cerrado does not reappear on the upland. Instead, continuous forest remains until north of Ceres, although there are some areas of cerrado scrub savanna on some slopes. North of Ceres continuous forest stops and cerrado again appears as the dominant vegetation of the region. This is probably associated with a rock change. The cerrado here is mostly in the form of open-canopy arboreal woodland (cerradão) and tree-and-scrub woodland, although there are small areas of closed-canopy cerradão and uneven closed trees-and-scrub. As usual, gallery forests occur along the streams. Further north, particularly from a little south of Santa Teresa up to Gurupi, there are many cerrados of the scrub savanna form on level or very gently sloped ground on interfluves. In these savannas there is a tendency for the usual dwarf shrubs and coarse herbs to be reduced in number, producing a "clean" grassy ground layer. These savanna cerrados are of two forms, non-hydromorphic and hydromorphic. The non-hydromorphic scrub savanna has its shrub individuals scattered over a grass layer on a reddish latosol. The hydromorphic scrub savanna has some of its shrubs scattered individually and others grouped in small round clusters a few meters in diameter, or only in clusters. The clusters are on soil platforms raised a few centimeters above the general soil surface, and always contain a small termite nest. The subsoil is light gray, the latosol having been gleyed. These gray soil campos occur in this region not only on some shallow valley sides bordering a gallery forest where we may suppose the water flushes at or close to the surface (ground water gleying), but also on the very flat uplands between stream courses, or in slight depressions at the heads of valleys containing gallery forest further downstream, in which case we may posit poor internal drainage that allows the soil to remain saturated somewhat longer than usual, too long for the more closed cerrados to form, although the water does not remain standing over the surface (tendency to surface-water gleying). If there is any subsurface water-logging it must be rather temporary, for the day after a heavy rain a deep road cut through one of these savannas did not show any water seepage. Thus there are intermediate cases between well-drained typical upland cerrados and definite valley-side marshes with scattered cerrado groves on raised soil platforms. In some cases, in fact, in this region, it was difficult to tell if a cerrado savanna was hydromorphic or not.

To the north the cerrado continues as the dominant vegetation, although the rock type changes several times. Thus, at Gurupi it is mica schist. North of Gurupi gneiss appears. Here the lower level flat land has cerrado of the same heights and densities as just to the south. The gneiss ridges, however, bear mesophytic forest. North of Roselândia, the underlying rock changes to granite. (This outcrops a bit further north as the Serra do Serrote.) The granite supports cerrado. North of Campo Maior the granite changes to quartzite but the cerrado continues. North of Paraíso granite appears again. Here the cerrado continues on flat land, but the mountain slopes bear either continuous forest, scrub savanna cerrado and forest side by side, or scrub savanna cerrado on the gently sloped descending ridges on the mountain face with forest filling the shallow valleys between these ridges. The scrub savanna in this region was noted in one roadcut to be growing on a 1½ m deep soil over a crumbly weathered granite bedrock. Further north along the road the underlying rock becomes shale, afterwards sandstone, then shale again. Cerrado continues as the sole upland vegetation over all these rocks.

Several kilometers south of Araguaína to 30 km north of it, basalt and diabase become the underlying rocks. Here the cerrado stops and these more basic rocks support continuous mesophytic forest, with babaçu palm forest in many of the valleys.

Thirty kilometers north of Araguaína sandstone appears again and with it the cerrado. This continues until 20 km before reaching the Tocantins River where basalt appears. The cerrado stops with the basalt and is replaced by a rich, tall mesophytic forest (which I saw in its virgin state in 1963 but which is now completely cleared for pasture as far as one can see from the road). On the east side of the river, in Maranhão, from the village of Estreito north, cerrado appears again and continues to Imperatriz, mixed with babaçu forests in the valleys.

From Imperatriz northwards there is a 15 km wide transition zone in which babaçu palm forest is the main vegetation both on uplands and in the valleys. This leads to the Amazon forest edge (which is now also cleared for pasture as far as one can see from the road).

Summing up: cerrado occurs along the Belém-Brasília road over sandstone, shale, granite, gneiss, and mica schist. Variations in cerrado density are due to soil fertility and drainage, and in some cases on slopes, perhaps to shallow soil depth. Gallery forests occur along all streams. In the Anápolis-Ceres region, continuous forest occurs on gneiss and mica schist; around Araguaína, on basalt and diabase; and on the west side of the Tocantins River near Estreito, on basalt, all these forests on deep, well-drained soils.

Brasília. The following account is taken from Feuer (1956), Servico de Documentação (1956), and my own observations. The region is underlain by folded sedimentary rocks and was peneplained. The upper or first erosion surface is at 1300 m altitude and contains a few monadnocks. Erosion of this surface has produced a second erosion surface of wide gently sloped valley sides. Laterite pebbles occur only at the edges of the peneplain where the second erosion surface starts. (The laterite probably formed in the past when a fluctuating water table approached the peneplain surface at these valley edges. The water table at present is very much deeper.) The first and second surfaces have soils which are at least a few meters deep if not more and are covered with cerrado, which I noted varies from tree-and-scrub woodland, low-tree-and-scrub woodland and open scrub to scrub savanna. Cerradão is rare. A suddenly more rapid period of downcutting produced a third erosion surface of 20–30° slope or more. This formed a deeper central valley in the shallow second-surface valleys and also produced narrow subsequent valleys that cut into the second-surface valley sides. The heads of these third-surface valleys also cut directly into the first-surface peneplain in some areas. These third-surface valleys are filled up to their top edges with the gallery forests of the region, an extremely dense layer of thin-trunked rather low trees. Recent more active downcutting has sunk the stream beds in gullies in the floor of the third-surface valleys in some areas, producing a fourth erosion surface. Where not too steep this is covered with the inner part of the gallery forest. A fifth surface is the deposited alluvium in some stream beds. I noticed in a few areas, marshy strips just outside the gallery forests. The third erosion surface is not invariably covered with gallery forest, however. As mentioned in Part VIII above, near the city of Sobradinho there is a very steep-walled valley, several kilometers wide across the top. The valley is cut directly into the peneplain and its steep third-surface sides bear campo limpo and sujo of the cerrado flora. Only at the very bottom of this slope is found a gallery or valley-bottom forest (Fig. 13). Third-surface valleys are filled completely with gallery forest only when they are narrow.

The distribution of cerrado, gallery forest and valley-side marshy campos on the southern half of the crest of the Serra do Roncador in northeastern Mato Grosso has already been mentioned.

Southeastern Maranhão—Loreto. The vegetation of this region will be made the subject of a future paper but a resumé may be given here. Maranhão and Piauí comprise a vast sedimentary basin, mostly of sandstones, and the horizontal layers have produced a typical tabular topography. South of the city of Loreto, between the Balsas and Parnaíba Rivers, occur two main horizontal rock strata, a lower-layer whitish or varicolored, hard, fine-grained siltic sandstone, which outcrops only in the central part of the region, and an upper-layer coarse red sandstone. (These are probably the Pastos Bons and Sambaíba strata, respectively, of the petroleum geologists. See Campbell *et al.*, 1949.) The red sandstone is more resistant to erosion, and until it is worn away it protects the more rapidly eroding layer beneath it. Four forms of cerrado occur on the uplands here. (The vegetation of the region is still mostly essentially undisturbed by man.) The flat plateau tops, of red sandstone, bear a very deep non-stony latosol supporting cerradão (locally called "chapada"). This is a medium-tall semideciduous (occasionally evergreen) arboreal woodland form of cerrado with an open tree canopy of many species, a sparse to open shrub layer, and a tallgrass ground layer 1–2 m tall in flower. The steep plateau sides, with stony soil, bear "costaneira," a semideciduous cerrado of somewhat different composition and usually much fewer species, varying from low arboreal woodland to open scrub savanna with a grassy layer about 1 m tall in flower. Wide, flat valley floors between plateaus and on the same red sandstone also bear chapada woodland. Where the lower whitish rock layer is newly exposed at the side of the plateaus, forming a small fringing area of steep hills with stony soil, it supports "morraria," a completely different deciduous low-arboreal woodland or open scrub form of cerrado with a somewhat different proportion of species. Most of this exposed lower rock layer, further from the plateaus, forms a lower-level slightly rolling terrain with "tabuleiro," a low to medium-tall arboreal woodland with its own distinctive group of a small number of cerrado tree species, and with a sparse to open shrub layer and a shortgrass ground layer. Over much of the tabuleiro the woody plants are absent, only the shortgrass layer remaining to form rolling grassy pastures. How much this absence of woody plants is natural and how much due to excessive fires is impossible to determine. (All the local names for vegetation types given above are used for completely different vegetation types in other parts of Brazil.) Thus, although all these four upland types in the Loreto region are cerrado, the dry climate has allowed several forms of it to evolve in relation to rock type and to steepness of slope. They are all "climax" and one does not change to another in autogenic succession; they change only as a result of geomorphologic processes changing their substrates. Each has its own range of species proportions and each has a different visual aspect relating to spacing, trunk thickness, crown proportions, trunk leaning and twistedness of boughs.

The valleys have gallery forests of several degrees of tree canopy spacing related to degree of water-logging in the wet season and possibly also to rock type. Similar to the case in Brasília, narrow steep-sided valleys cut into the red sandstone plateau sides bear forest over their whole profile, while wide steep-sided valleys, more than about half a kilometer across at the top, bear the constaneira form of cerrado on their sides and gallery forest only on the valley floor along the brook gulley. The vegetation type thus keeps pace with the geomorphological evolution of the landscape. Cerrado (chapada type) is the original and oldest vegetation of the region, occupying the tops of the residual plateaus. The sides of a narrow valley that cuts into the plateau bear gallery forest. As the valley gets wider (i.e., as the plateaus recede one from the other), the forest on its slope changes gradually back again to cerrado (costaneira type), all of this on the same red sandstone. If the finer-grained sandstone is present below and is exposed by the deepening of the valley, this lower part of the slope bears cerrado also but of a different type (morraria).

Southeastern Maranhão—Pastos Bons. This region is 250 km east of Loreto. The city lies in a valley several kilometers wide cut into the regional sandstone layers. Narrow lateral valleys run into the main valley. The flat plateau top is covered with semideciduous cerradão ("chapada"), a medium-tall arboreal woodland with open tree canopy on deep non-stony soil. The shrub layer may be open to dense. (Where dense, the stand becomes, structurally, "open forest with closed scrub.") Where this plateau top grades very gradually down to a stream, it is covered with the same chapada with open shrub layer, but where the valley cuts deep and has steep sides, as near the city of Pastos Bons, a different situation occurs. The upper half of the slope bears "costaneira" on stony soil, an open- to closed-canopy semideciduous cerradão woodland of somewhat different tree composition from the chapada of the plateau top. The lower half of the slope (in this region called "caatinga" although it has nothing to do with the thorn-scrub caatinga of northeastern Brazil) bears a similar-looking medium-tall somewhat more deciduous woodland on non-stony soil. The tree component of this "caatinga" has many of the same species as the costaneira of the upper slope but in different proportions and lacks others of its species. Also it contains some species of the valley floor forests. Thus it is hard to say whether it is cerradão or a type of mesophytic forest. The line of division between the two valley-side vegetation types is very sharp.

The valley floor contains babaçu palm forest ("cocal") nearest the stream, with semideciduous "mata" (mesophytic forest) of dicotyledonous trees flanking it on the outer valley floor. The soil is not stony. The valley floor forest has, besides the babaçu and other tree palms, many tree species not present at all in the other communities. Further up the heads of the narrow lateral valleys, the babaçu stops and only the dicot forest fills the valley floor. At the very heads of the lateral valleys where they just start to carve into the plateau top, the forest (which by now is a mixture of mata and costaneira species) may give way to a chapada woodland which grades into that of the plateau top. Several tree species are confined to only one of the four arboreal vegetation types mentioned, as can be seen when they are in flower. The valley floor (cocal and mata), and to a much lesser degree and only recently, the lower half of the steep valley sides ("caatinga") have been cleared and cultivated in part; the upper valley sides (costaneira) and the top of the plateau (chapada) are never cultivated. The same two sandstone strata are involved here as in Loreto in causing the distinctions in vegetation type and soil fertility. The difference in degree of deciduousness between the two valley-side vegetation types, each on one of the strata, and the sharp boundary between them are strikingly apparent in the dry season.

The situation in southeastern Maranhão, then, is not the simple restriction of cerrado to flat plateau tops and mesophytic forest to valley sides and floors that Cole (1960) describes for Central Brazil.

Espigão Mestre, Goiás-Bahia border. This is a region of high-altitude flat to very gently rolling land on the north-south divide between the Tocantins and São Francisco Rivers. The interfluves are wide flat areas separated by wide, very gentle valleys of the parallel streams. The interfluves are sandy and after heavy rains may have a few centimeters of water above the surface for about a day or so, but no longer. They are covered with "campina" vegetation, which is either a campo limpo (short-grass plains) or campo sujo (dwarf shrub very open savanna) of cerrado vegetation. On nearing the border of a valley, with the water table somewhat nearer the surface, the shrubs gradually become denser and taller, the vegetation changing to campo cerrado (scrub savanna), then to cerrado (sens. strict.) (open scrub or low-tree and scrub woodland), then to cerradão (medium-tall arboreal woodland). This stops short at the border of the valley-side marshy strips that border the narrow gallery forests along the streams. This change in cerrado physiognomy from low and open to taller and denser *which then stops at the wet campo border* (rather than joining directly with the gallery forest in the absence of a wet campo) is a phenomenon which seems to be restricted to the Espigão Mestre.

Certain extensive non-forest rocky areas within the general cerrado region, at elevations of about 1000 m or more, bear high-altitude rocky campos, a vegetation type that should be distinguished from cerrado. Such an area is the Chapada dos Veadeiros, in Goiás north of Brasília. Hills and ridges with rocky slopes are separated by flat grassy meadows. The slopes bear an open savanna with scattered shrubs and very low trees and an open to sparse herbaceous ground cover. Some of the woody plants have twisted trunks and boughs like those of the cerrado, but in general the flora is a special one, highly endemic like that of all high-altitude rocky campos of central Brazil. The slope soil is shallow and humusy, with stones and bedrock showing. The flat meadows are not cerrado either. They bear waist-high grasses and sedges with practically no woody plants at all. The soil is black with much humus, and is soaking from water accumulation for months at a time during the rainy season but dries out during the dry season. The flora is related to that of the valley-side flush marshes (wet campos) with similar physiognomy that occur in other parts of the cerrado region.*

X. TRANSITIONS TO OTHER VEGETATION PROVINCES

In almost every region the details of the transition from the main cerrado region to neighboring large-scale vegetation provinces are different. A few examples follow.

Transition to Amazonian forest.

Northeastern Mato Grosso, upper Xingu region. Setzer (1967) gives a description of a virgin region just west of the Serra do Roncador, therefore essentially inside the Amazon forest region but near its border with the cerrado region of central Brazil. His area has an average rainfall (calculated by extrapolation) of 2200 mm per year, just slightly above the 2000 mm calculated here as being the general value along the eastern border of the Amazon forest. The terrain varies in altitude from 300 m in the 20–40 km wide floodplains to 400 m on the flat interfluves. Most of the wide floodplains are covered with water for all or almost all of the year. The full floodplain forests are not over 5 m tall. On the edge of the floodplain where flooding is rarer, the bottomland forests can reach 10 m tall. Just outside the floodplain where the ground rises and is never flooded ("terra firme") the rainforest is 20–25 m tall with trunks up to 1 m in diameter. Here, the water table is 5–8 m deep on the average, with a minimum of perhaps 2 m at the end of a very rainy season. As the ground rises the water table becomes deeper and the vegetation becomes lower. Thus, the evergreen forest continues up the slope to where the water table averages 10 m, and gets lower in height as it does so. From that point it intergrades to a tall dense cerrado upslope where the water table is about 15 m deep, and this to a lower more open cerrado where the water table is 20 or more meters deep. The soil forms a catena also, a sandy clay, with the sand becoming coarser upslope. There

* I would like to thank Dr. Howard Irwin of the New York Botanical Garden for information about the Espigão Mestre and the Chapada dos Veadeiros, and Sra. Arraes and Dr. L. G. Labouriau of the University of Brasília for information about the Serra do Araripe. Dr. Labouriau took the photograph shown in Fig. 14. (The rest of the photographs were taken by the author.)

Finally, I wish to thank my wife, Liene T. Eiten; the driver, Ziro Matsui; and our general adjutant, José Angelo Corrêa, for aid and companionship during the long trips we took together through the Brazilian cerrados. Most of the work on which this paper is based was done while the author was at the Instituto de Botânica, São Paulo.

is no surface runoff. During the rainy season there is a temporary perched but subsurface water table in the B layer of the terra firme tall forest due to precipitated clay. The perched water table disappears between rains. The terra firme forest then can stand a certain amount of temporary waterlogging in the upper layer but not in the deeper layers, which would produce swamp forest.*

Setzer's analysis of the tall terra firme forest soil after one year of cultivation shows a pH of 6.8 and 2.7% humus, with high available Ca and Mg but low K and no available Al. Soils of the lower-height forests further upslope have less fertility and in some cases a lower pH, less humus, and a small amount of aluminum. The soil fertility then is a reflection of the vegetation, as the latter is of the water table. The clay is characteristic of latosol and does not hold much nutrients, these ions being held available mostly in the humus which is stabilized by the high calcium content. The cerrado soils of this region that were tested have a pH of 5.2 or 5.3, a humus content about equal to the forest soils but much less P, Ca and Mg, much less cation exchange capacity and base saturation and much more available Al. The soil of the taller cerrado is slightly more like forest soil than that of the lower more open cerrado. Thus the same soil differences between cerrado and forest and their different heights and densities, on non-inundated ground, are apparent just outside the continuous cerrado region as inside it. The greater total rainfall of this region means that a greater proportion of the landscape is covered with forest than with cerrado until, further west, it becomes so high that no true cerrado can be found, although savanna of other kinds may still occur for edaphic reasons other than latosolization, such as poor drainage, podsolization, thin soil, etc.

In the region referred to, Setzer believes that the cerrados on the interfluves are due to Indian burning of what was formerly forest (he saw from the air burnt areas several kilometers wide resulting from fires set for hunting purposes) for he believes that original cerrado only occurs under an average rainfall of less than 1500 mm per year. This is true for São Paulo, where Setzer did most of his work, but it is not true further north. In central Brazil, inside the continuous cerrado region where there is no doubt that the cerrado is original, there are large areas with average yearly rainfall between 1500 and 2000 mm. Probably this is because the higher temperatures in central Brazil than in São Paulo, along with these higher rainfalls, have promoted stronger latosolization so that cerrado can still occur as the main vegetation under somewhat higher rainfall regimes than in São Paulo. Once the rainfall passes a certain point, however, and the dry period becomes shorter and weaker,

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* Egler (1964) explains a similar case for some Amazon forests on alluvial soils. A few meters below the surface occurs a layer of laterite concretions which temporarily holds up drainage and also forces most tree root growth to occur laterally above it. He thinks this is advantageous in slowing down leaching.

even strong latosolization is not enough to favor cerrado over forest because, besides poor soil, cerrado needs a definite dry season. In the region under consideration there are three consecutive months with an average of 20 mm of rain or less.

The fact that a very sparse population of primitive Indians could burn such large stretches means there was a vegetation there in the first place that could be burned. That means an original cerrado with its dense, seasonally-dry grassy layer, not evergreen forest and not even mesophytic semideciduous forest, for neither of these has a tall dense grass layer. This fact is well shown on the Serra do Roncador crest, for example, where the open cerrado region changes to the semideciduous mesophytic forest of the Amazon forest edge. Here there is a few-kilometers wide transition belt of cerradão. I noticed that the fires that the Indians had set in the open cerrado before the road was built and any Brazilians had entered the region, did not even enter the cerradão transition belt, much less the dry mesophytic forest further on. The latter two formations had no marks of fire at all, even though the open cerrado which was continuous with it had been burned 3–4 years previously and many times before that. If this is true where the dry forest is bordered by burnable cerrado, then it is unlikely that a few Indians were able to destroy by burning a vast area of original plateau forest and convert it to cerrado, and this in an even wetter region than the Serra do Roncador. There is no doubt that the plateau top cerrados in the region Setzer visited are natural, and if examined would probably reveal several endemic species, a sure mark that this vegetation existed there before man.

Eastern Pará-northern Goiás. The case just mentioned shows one kind of transition, from a region with cerrados covering all uplands, with thin gallery forests along the streams and wider ones along the larger rivers (this defined as the main cerrado region) to a region with cerrado occurring only on some parts of the uplands, with evergreen or semideciduous mesophytic forest covering most of the area (this defined as part of the forest region). Soares (1953) gives a full discussion of this transition in his attempt to draw a line that would best show on a geographical scale the limit of the Amazon forest in Brazil. It must be understood that in the transitional region the change from cerrado to definite forest may be sharp or there may occur all kinds of intermediate vegetation types with different heights, spacing, and degree of deciduousness. Thus in eastern Pará, at the latitude of 6°50′, intermediate types of vegetation occur. When Soares made his observations here practically all of this vegetation was virgin. There occur [translated]: "a) *matas frondosas* [mesophytic evergreen forests], in the bottoms of the valleys, on the river plains (flooded or not), in depressions of rolling terrain, and on the lower parts of the mountain sides, ranges and plateau [slopes]; b) *matas secas* [dry forests], made up of cerradões, cerrados, 'charravascais' or 'chavascais' [cerrado shrubs joined together by a dense growth of *Smilax*, *Scleria*, etc., forming an impenetrable tangle], 'bamburrais' [thin forests] and 'catanduvas' [a somewhat rachitic forest], all these growing on the flat tops of the plateaus, in the stream valleys that cut these plateau surfaces, and on the upper part of the mountain sides and crests. As a whole, this transitional area is about 50% [mesophytic] forest." On the other hand, the changeover may be from definite mesophytic forest to definite cerrado:

"In Pará the Amazonian forest commonly comes up to the Araguaia River, passing it to form a narrow band with extremely irregular outline on the Goiás side. In some places on the Pará side the Amazonian forest does not reach the Araguaia, being separated from its margin by large areas of campos cerrados which the forest penetrates as wide gallery forests or large disjunct groves, as in the region west of the Araguaia between the cities of Conceicão do Araguaia and Araguacema."

Both on the Pará side and in northern Goiás and Maranhão, the transitional region possesses large areas of mesophytic forest with deciduous dicot trees mixed with babaçu palms, both on uplands and lowlands. Babaçu is characteristic of this transition zone.

Serra do Roncador, northeastern Mato Grosso. The change to Amazon forest on the crest of this narrow, gently rounded highland is as follows. (Observations on the virgin vegetation were made in 1968 and 1969.) The open cerrados in the main cerrado region vary from tree-and-scrub woodlands to open scrubs. At the transition, the taller trees start to get closer together until the stand forms an open canopy arboreal woodland, i.e., a cerradão. Going north, this tree canopy starts to close and gets slightly taller and at the same time the tree species start changing gradually, the cerrado species dropping out and species of the Amazonian mesophytic dry forest edge coming in. Within a few kilometers, but with some irregularities due to topographic position on the very gently rolling terrain, the change from strongly semideciduous open cerrado to slightly semideciduous mesophytic forest is completed.

In a few places the change from the cerrado region to the continuous forest is different. A woodland cerrado continues up to a shallow brook valley. There it stops short and the usual valley-side marshy campo suddenly takes its place, giving way to an evergreen forest directly along the brook gully. But instead of the forest then stopping on the other side of the brook, to change again to valley-side campo and then cerrado on the upland, as it has been doing up to now in the cerrado region, the mesophytic forest continues solidly over the terrain from there on, only differing by turning semideciduous on the upland. These two kinds of transitions form a lobed front of continuous forest running roughly NE-SW.

Maranhão. The Amazon forest comes into the northeastern third of the state, its border following an east-west line about at the latitude of Imperatriz and then turning north to follow the Mearim River. The southern portion of the state is part of the general cerrado region, with cerradão being the main form. Between the two is a wide transition zone. Except at Imperatriz, I did not see the actual N-S transition from cerrado to hylaea but observation along the transition zone from west to east, that is, from a little south of Imperatriz to Montes Altos, Sítio Nôvo do Grajaú, Grajaú, Barra do Corda, Presidente Dutra and Codó, presents a mosaic of different primary vegetation types. (So far the vegetation has been very little disturbed.) From west to east occur regions with the main vegetation as follows: (1) low arboreal cerrado, (2) cerrado low-tree-and-scrub savanna with a short grass-sedge layer, (3) cerradão arboreal woodland, with lower scrub layer sometimes open (in which case the vegetation is locally called "chapada"), sometimes closed (in which case the vegetation is locally called "carrasco," Fig. 15), (4) upland strongly semideciduous mesophytic forest with lower scrub layer open or with a closed scrub layer of shrubs or bamboo (also locally called "carrasco"), (5) cerradão with dense scrub layer, (6) upland semi-deciduous forest again, (7) babaçu forest region where this palm grows thickly over the whole topography except for the tops of low peak-like plateaus. This is a simplified version of the mosaic of upland vegetation types found in the transition zone. Actually the forms mentioned are more thoroughly mixed and each has many variations. East and south of Codó, in Caxias and Timon, we enter a northern tongue of the general cerrado region. Here there are various heights and densities of cerrado and cerradão on the uplands with gallery forests along the streams, the latter of babaçu palms, less often of dicot trees, or where the ground is actually soaking, of buriti palms.

Transition to caatinga.

I observed this transition only in Piauí, from Floriano east to Picos, and from Floriano south southeast to São Raimundo Nonato.

From Floriano eastward. Cerradão, the arboreal woodland form of cerrado, covers southern Maranhão, with gallery forest in the valleys. The regular transition from cerradão eastward to caatinga in Piauí is broken for several kilometers east of Floriano by outcrops of rock pavements with thin soil that form lithosol compos as mentioned above. When deep soils occur again the transition continues on the same topography as in Maranhão, consisting of flat plateau tops separated by shallow valleys. But now, instead of the cerradão with open undergrowth typical of southern Maranhão right up to the limit with Piauí, the vegetation here is a very dense shrubbery with the taller trees forming a more open canopy above the shrub layer than they do in Maranhão. The transition zone has started. Further on east, the trees emerging from the shrub layer form a canopy varying in density from open to sparse, with the sparse condition becoming more and more frequent. The trees are species all of which occur in the southern Maranhão cerradão, but in this transition region in Piauí there occur much fewer species. The shrubs at first also are species that occur in the Maranhão cerradão but instead of having the large number of species in one stand characteristic of cerradão, there are only about half a dozen, and these are all species that are not characteristic of the whole stretch of Maranhão cerradão but that only started to appear in it as rare individuals near its eastern border. Further east in this Piauí transition zone new shrub species replace them. Therefore, in general, there is a lessening in number of tree species, but not a replacement to new ones, while there is a lessening in number of shrub species but also a replacement to new ones, practically all of these latter being spiny legumes.

At first the shrub layer is about 5 m tall. This gradually gets lower to the east although irregularly so due to variations in topography. About halfway to Picos, terrestrial bromeliads and small cacti start to appear beneath the shrubbery, best seen in the dry season. All this time the trees above the shrub layer have been getting more and more spaced until finally there are long stretches with only shrubs, but once in a while, especially on valley sides, some low overtopping trees appear again. Coming into Picos there is a long descent to a flat valley floor and east of the city the dense shrubbery, now 3–4 m tall, continues but without overtopping trees. At the eastern end of the state the shrubbery lowers to about 2 m tall and stretches in which the shrub layer itself opens slightly (naturally, not due to disturbance) become more common. This transition across Piauí from cerradão to typical caatinga is extremely gradual and there is no one place where one can say the transition belt has stopped and the pure caatinga has begun, although I would say that from Picos east, that is, once off the plateau top and on the valley floor, there is typical caatinga of the east central Piauí facies. This would make the transition belt 150 km wide.

A wide gradual transition in flora and physiognomy such as this one, between two vegetation provinces (without a mosaic of the two pure forms, and without the appearance of special "buffer" vegetations) is a pattern not included in Ab' Sáber's provisional list (1971) of models of transition and contact between core areas in Brazil.

Floriano southward. Instead of going east from Floriano, if we go south to Canto do Buriti, a completely different type of transition to caatinga takes place. The cerradão first continues (with many stretches that have been cleared in 1963). Then patches of shrubby caatinga appear intermixed in the cerradão matrix. At the same time the cerradão starts to lose its xeromorphic aspect and takes on more and more the character of a deciduous mesophytic forest-like woodland. That is, the bark becomes thinner and the boughs not so twisted. The stretches of caatinga become larger and more frequent. Continuing south of Canto do Buriti, to São Raimundo Nonato, no more cerrado is seen. One crosses an immense flat-topped sandstone plateau covered with white sandy soil and a *semideciduous* dense caatinga scrub about 3 m tall. South of this plateau there are a series of rocky ravines between low plateaus. The ravines are filled with the same type of deciduous forest mentioned above. Finally, near the Bahian border, one passes out of the sandstone area onto crystalline rocks and the caatinga becomes a completely deciduous medium-tall open shrubbery.

Ceará-Piauí. Ferri (1955) quotes Löfgren (1910) concerning the transition from caatinga to cerrado. Speaking of the caatinga-covered plateau in the region of Viçosa, São Benedito, etc., in Ceará, Löfgren states (translated): "Part of the center of this plateau and certain other places, mainly on the slope towards Piauí, are very sandy and there developed a special vegetation in which enter many of the characteristic species of the general cerrados of Brazil. We find there *Stryphnodendron barbatimao, Byrsonima verbascifolia, Piptadenia rigida,* several species of *Heteropteris* and *Smilax.* There is even *Eremanthus sphaerocephalus, Psychotria rigida, Miconia albicans,* an *Escallonia* and a *Styrax,* all inhabitants of the Minas and São Paulo cerrados. Our lists give a better idea of this semi-oreadic [i.e., semi-cerrado] flora in which the hamadryadic [i.e., caatinga] species of juremas [*Mimosa*], caatingueiros [*Cassia*], sabiás [*Mimosa*], and others introduce a note of veritable confusion."

Northwestern Minas Gerais. Most of the border between the cerrado and the caatinga regions occurs in western Bahia and northwestern Minas Gerais. From Goiás eastward the climate gets drier until it reaches a range of rainfall where cerrado and caatinga can both occur, and there the decision is made by the rock type and the soil this produces. In the region around Januária in the valley of the Rio São Francisco, for instance, outside of the periodically inundated valley floor, there is a very strong correlation between the presence of sandstone with cerrado (mostly the open scrub form), and limestone with caatinga. In the latter case, limestone itself supports the arboreal form of caatinga, while non-inundated calcareous clay-sand Pleistocene deposits of the ancient river bed support lower shrub forms of caatinga (Azevedo, 1966).

Transition to Atlantic coastal forest.

Most of the cerrado is separated from the coastal forest by the caatinga region,* and meets the coastal forest directly only in southern

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* The caatinga itself on its eastern side is separated from the Atlantic coastal forest from about the latitude of Salvador, Bahia, south, by an ecotonal zone, a narrow north-south belt of dense deciduous "mata de cipó" (literally "liana forest"). The mata de cipó is 7 m tall in its northern part and gradually becomes 10 to 15 m tall in its southern part in northern Minas Gerais. It is more closely related to caatinga in the north since, when destroyed, its secondary scrub is almost identical to the local caatinga. In its southern portion it gradually changes into regular evergreen tall coastal forest, and its secondary scrub becomes less caatinga-like and more "capoeira"-like, the capoeira being the secondary scrub and low-tree regeneration stages of true mesophytic forest.

This gradual north-south change in the mata de cipó is broken only at the Bahia-Minas boundary where, on a long stretch of flat granite plateau top over

Minas Gerais and São Paulo. Here each form keeps its identity well distinct, the cerrado having its arboreal, scrub, savanna and grassland forms, and the forest its semideciduous and evergreen forms (occasionally deciduous on limestone outcrops) and its secondary stages. Within the border of a continuous cerrado matrix, forest occurs only as galleries or small upland patches in a few areas. Beyond this border, cerrado occurs as large to small areas and patches in a forest matrix in the still dryish climates and disappears altogether nearer the coast where the rainfall increases.

Transition to southern Brazil grasslands.

As mentioned before, in southwestern São Paulo, the cerrado patches acquire more species of the southern Brazil campos limpos (napeadic grasslands) and change to that vegetation type rather rapidly at the Paraná border.

Transition to Chaco vegetation.

I am not acquainted with the details of this transition. It occurs only on a narrow front between the forests of western Paraná on the east and the low flooded Pantanal Complex on the west. A small finger of Chaco vegetation from Paraguay enters the extreme southwestern corner of Mato Grosso near Pôrto Murtinho (Hueck, 1955).

XI. THE DISJUNCT CERRADOS OF NORTHEASTERN BRAZIL

Scattered through the caatinga region are several sandstone plateaus and tablelands of the Barreiras formation, pediplained to the Velhas surface, and bearing cerrado. Those near the coast are today referred to in the technical literature as "coastal tabuleiros." Examples are northeastern Rio Grande do Norte behind the narrow strip of littoral vegetation, the area of Goiana in Pernambuco, a north-south series of areas in northeastern Bahia just east of Tucano and west of Cícero Dantas, the eastern half of the Serra do Araripe, etc. Cole (1960) maintains that the existence of these cerrados is due to these particular geological formations and erosion surfaces. This is true but only in a background sense. The immediate reason is that the climatic and soil requirements have been met. That is, that combination of environmental conditions that is predominant in central Brazil here occurs in small disjunct areas in northeastern Brazil.

The northeastern cerrado areas occur where (1) the underlying rock is sandstone or some other that yields a poor soil (Ranzani *et al.*, 1962, 1963; Ranzani, 1963), (2) the surface is level and of sufficient age so

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1000 m high, the mata de cipó reduces to a 2–3 m tall dense deciduous scrub, which should probably be separated out as a distinctive minor vegetation type making up part of the transition zone between caatinga and coastal forest.

that the soil stays in place and has had time to become senile, (3) most important, all of these areas are in the correct intermediate rainfall range. Laroche (1963, 1967) states that all the coastal tabuleiros from south of Touros in northern Rio Grande do Norte south to Bahia have average rainfalls between 700–2100 mm per year, which as we saw is almost exactly the range of rainfall in the general cerrado region of central Brazil. Most of the disjunct cerrado areas occur between the coastal forest and the caatinga, where the rainfall is less than that which supports forest and more than that which supports caatinga *on this kind of substrate.* The rainfall must be in the correct range for cerrado to occur. If it is not, then even with the other requirements met, cerrado will not appear.

This is plainly shown on the Serra do Araripe, a narrow plateau about 180 km long from east to west, separating northwestern Pernambuco from southern Ceará. The western end extends slightly into Piauí. Its surface is a stratum of soft sandstone and varies somewhat in altitude in places along the north and south edges, but in the center is almost flat for the whole east-west length at an altitude of 750 m, which is 400 m above the lower-level caatinga on crystalline rocks which surround the plateau on all sides (Anjos, 1967). It is elevated high enough above the surrounding country to catch the moist east winds from the ocean. These deposit some rain on the eastern end of the plateau top but this rainfall diminishes along the plateau top to the west. The lower elevations on the south side of the plateau have much less rainfall and longer dry seasons than the lower elevations on the north side. Certain low elevations on the north side in fact may have about the same average rainfall or even slightly more than the plateau top itself (approx. 1000 mm per year) but on the plateau top the variation in rainfall from year to year is less and the dry season is somewhat shorter on the average and not often so strong (Nimer, Filho & Amador, 1971).

The excess rainfall on the plateau top drains away because of a very slight dip in the strata to the northeast, to re-emerge on the northeastern slope. There it appears in a series of springs which are the sources of rivers, and it also moistens the soil sufficiently and continuously, even over the long dry season, to sustain the tall (30 m) liana-filled, evergreen mesophytic forests near Crato, Ceará. The forests extend from the base of the plateau to the top edge on that side. The plateau top itself has a deep porous soil with almost no water courses. At the eastern end of the plateau, from north to south on the plateau top, there occur the following vegetation types: (1) a zone about 12 km wide of low (15 m tall) evergreen mesophytic forest with closed tree canopy ("orla da serra"), (2) a zone about 10 km wide of a 10-meter tall semideciduous arboreal woodland with a semi-open tree canopy, almost purely of *Caryocar coriaceum* Wittr. trees with some *Hancornia speciosa* Gomez ("zona dos piquizeiros"), (3) a zone of the Araripe "agreste" vegetation which covers most of the eastern half of the plateau top. Where undisturbed, the agreste is a 2–3 tall very dense scrub with interlacing branches, of species

FIG. 14. Serra do Araripe "agreste" vegetation. Overtopping tree is *Parkia platycephala.* Southern Ceará.

of many families, overtopped with scattered medium-tall trees of mostly *Parkia platycephala* Benth. and *Caryocar coriaceum* and low trees of *Stryphnodendron rotundifolium* Mart., *Styrax camporum* Pohl, species of *Vochysia, Qualea* and *Callisthene,* and a few other species (Fig. 14). The tree canopy is open to sparse above the dense scrub layer. Both the scrub and the tree layer are slightly semideciduous. The southern edge of the eastern part of the plateau top used to have a band of evergreen mesophytic forest like the northern edge but today is a mixture of dry grassfields and secondary scrubs due to disturbance. (Vegetation details from Arraes, 1969 and personal communication; Labouriau, personal communication.*)

* The confused account of the vegetation of the Serra do Araripe given by Luetzelburg (1923, vol. 2, pp. 62–69, and vol. 3, pp. 24–31) is somewhat different. He describes a vegetation called "lacre" which forms a few-kilometer wide band on the north and south edges of the eastern end of the plateau top but which physiognomically is not forest but is like what we have here called "agreste." Covering most of the plateau top in his account is what he calls "agreste," which from the description and photographs (vol. 2, fig. 43; vol. 3, fig. 13) is plainly cerradão with an open shrubby layer. This usual type of cerradão was not encountered by Arraes or by Labouriau in their visits to the region in the last few years, but it may still occur in the portion east of Crato. Luetzelburg shows a photograph of the plateau top further west (vol. 2, fig. 42) with a vegetation with the typical physiognomy of "agreste" in our sense but he calls it "agreste mixed with carrasco," that is, scattered

FIG. 15. Cerradão-like vegetation in central Maranhão east of Grajaú. Sparse to open canopy tree layer overtopping a very dense 3–4 m tall scrub layer. Note similar physiognomy to Fig. 14.

From the species composition, physiognomy and deciduousness, it is apparent that the *Caryocar* zone and the agreste zone of Araripe are forms of cerrado in the wide sense. As has been mentioned, the peculiar physiognomy of the Araripe agreste also occurs in the cerrado-hylaea transition zone in central Maranhão (Fig. 15) and in the cerrado-caatinga transition zone in central Piauí. In both cases, as on Araripe, *Parkia platycephala* is an important overtopping tree, and the vegetation is on deep soil of flat-topped sandstone plateaus. This physiognomic form of cerrado, although occurring occasionally in small areas in central Brazil, seems to be a characteristic feature of the edge of the cerrado province in northeastern Brazil. The Araripe agreste is simply a disjunct portion of it in the middle of the caatinga province where correct rainfall and soil conditions occur.

Going west along the Araripe plateau top, the agreste continues to the central portion of the plateau, then gradually changes its floristic composition, becoming more and more caatinga-like until at the western end it is pure caatinga. (The vegetation of the central portion of the

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cerradão trees (his "agreste") overtopping a scrub layer (his "carrasco"). Luetzelburg uses the word "carrasco" generally for any open or closed dry scrub, generally on stony ground, which is neither definitely what he considers to be caatinga (although some of his examples are really of caatinga in the wide sense) nor a secondary successional stage to mesophytic forest, but covers certain types of dense interlaced cerrado scrubs and also open to closed scrubs of mountain top rocky campos.

plateau top is now considerably destroyed due to cultivation.) This change from what is essentially cerrado to typical caatinga is correlated with the diminished rainfall westwards and takes place on an identical geological formation and erosion surface and at about the same elevation. It is thus a perfect example of the necessity for *all* environmental requirements to be met for cerrado to occur.

XII. WATER RELATIONS AND LEAF XEROMORPHISM

Cerrado is characteristically a xeromorphic vegetation. During the dry season the upper layers of the soil dry out, usually below the wilting point, particularly the upper two meters or so. In consequence the herbaceous vegetation is seasonal, that is, it dries up to a large extent, forming a layer of "hay on the stem." The aerial parts of most of the herbaceous plants, which are practically all perennials, dry up. The dead leaves of many of the forbs disintegrate and disappear during the dry season. Those of other forbs and all the graminoids remain attached, although dead, over the whole dry season if they are not burned. New graminoid leaves appear in the middle of the clumps and push the old leaves aside, and new forb tops grow from underground parts, either towards the end of the dry season before the rains start or just afterwards. This new growth starts earlier and is more evident if the ground has been burned. When not burned off, the old leaves rot away after the rains. Thus the herbaceous plants may be regarded as drought-evading (Rachid, 1947).*

The woody plants, however, are only partially drought-evading, namely in the fact that practically all cerrado is semideciduous. The individuals of some species in a stand lose all their leaves so that they remain bare for a certain part of the dry season. Individuals of other species lose only some of their leaves before new ones grow. The mass of the woody vegetation, therefore, contains only a fraction of the live leaves that were present in the wet season, the proportion varying from stand to stand, and in one stand, from week to week during the dry season. In many species new leaves sprout during this season, before the rains start again.

Those leaves which do remain on the trees and shrubs through the dry season, or which newly appear and mature during this season, are, surprisingly, freely transpiring through open stomates, and in fact, the

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* Lund (in Warming, 1909, p. 99) and Ferri in various papers have commented on the rarity of seed germination in cerrados. There are certainly fewer germinating seeds per unit area in cerrados than in forests, but if one looks hard enough seedlings can be found of many woody and herbaceous species (Labouriau *et al.*, 1963, 1964a; Válio & Morães, 1966). It is not known how important seed germination is in maintaining a cerrado (as compared to forest and caatinga), that is, what proportion of plants that newly appear above the ground each year in a more or less constant cover and go on to mature arise from seeds rather than from permanent underground parts.

ability of the stomates to close with water stress is lacking or limited and cuticular transpiration is high (Ferri, 1944; Coutinho & Ferri, 1956; Ferri & Coutinho, 1958; Válio *et al.*, 1966a, 1966b, 1966c; Handro, 1969; Grisi, 1971). Some species in fact keep their stomates open also at night, even in the dry season (Labouriau *et al.*, 1964). Therefore, the woody layer is not xerophytic. The leaves are able to transpire freely because the plants have very long roots that tap the moist soil above a deep water table (Rawitscher, Ferri & Rachid, 1943; Rawitscher, 1944; Ferri, 1944; Ferri & Coutinho, 1958). Almost all cerrado is on deep soil material, at least several meters deep and usually several tens of meters deep. Depth of water in open wells in upland cerrado is usually 10–30 m, occasionally less; at Lagoa Santa it may be over 50 m (Rennó, 1971). There is a rather small variation in depth during the year, and frequently because of lag the water table may be higher in the dry season (Schubart & Rawitscher, 1950; Schubart, 1959; Rizzini, 1970).

There is a gradient in root depth among species, the herbaceous species having roots that go only 10 or 15 cm deep, or to 30 cm, or more rarely to about 1 m. With few exceptions their leaves die during the dry season, for the soil dries out each year to further down than their roots reach. But at the end of the rainy season, as rains become less frequent and dry spells increase, it is advantageous to be able to restrict transpiration by physiological means such as rapid stomate closing, for then the herbs can continue to function when the air and soil is moist again until the upper soil becomes too dry for too long. And in general, the more shallow-rooted the herb species are, the more rapid is their stomate closing with water stress (Rachid, 1947). Similarly, shallow-rooted seedlings of species which when adult have deep roots, also show rapid stomate closing with water stress (Handro, 1969, for *Andira humilis*). There are some herbs however which act like adult woody plants (Andrade, Rachid Edwards & Ferri, 1957).

The woody plants also form a gradient in root depth. Some shrubs, even though many years old, never reach down more than about one meter. Some of these, like *Cochlospermum regium* (Mart. & Schr.) Pilger, regularly lose all their leaves in the dry season. Other species reach increasingly greater depths. Below about two meters there is sufficient water in the soil over the dry season (in the conditions of Emas, São Paulo, with 1300 mm average yearly rainfall and 5 consecutive months with less than 20 mm each) (Rawitscher, Ferri & Rachid, 1943; Rachid, 1947). There is no correlation of aerial height with root depth in the woody species. Some of the smallest permanent plants, like *Andira humilis*, only 20–30 cm tall, have roots that have been found to reach 18 m. In the West African savannas, on the other hand, the taller woody plants have the deeper roots (Hopkins, 1962).

The fact that the cerrado woody layer has a large proportion of its leaves functioning in the dry season obviously is advantageous, since it allows the plants to continue assimilating, in contrast to the deciduous caatinga vegetation. Its ability to do this depends on the fact that the plants grow in a deep soil with a permanent water table and which in the continuously moist soil above the water table holds the equivalent of several years rainfall, and on the fact that they possess deep roots that can tap this water. The plants are in effect semi-phreatophytes and those whose roots actually reach to the water table are full phreatophytes.

Some woody species common in cerrado, such as *Solanum lycocarpum* St. Hil., a shrub or small tree, do restrict their transpiration during the day even when there is some water in the soil (Matos *et al.*, 1968b). This atypical response may be because this species, although found in the cerrado today, has not really evolved as part of the cerrado flora. It is a common roadside weed in cleared forest land while typical cerrado species are not. Forest trees whose water balance has been investigated, like *Hymenaea stilbocarpa* Hayne, which also grows in cerradão but not in open cerrado (Goodland, 1969), also more or less strongly restrict transpiration during the warm hours of the day, whether growing in forest or transplanted to cerrado, when the soil is fully or partially dry (Válio *et al.*, 1966b; Matos *et al.*, 1968a) but not in the middle of the rainy season (Válio *et al.*, 1966d). Ability to restrict transpiration during a water stress seems to be the typical response of forest trees in distinction to cerrado trees (Coutinho, 1962). The native cerrado vicariant of *H. stilbocarpa*, namely *H. stigonocarpa* Mart., *slightly* restricts its transpiration in the dry season during the warm hours of the day (Válio *et al.*, 1966b).

There seems to be a relation between soil fertility and thus the concentration of nutrient ions in the leaf tissue, and the ability to close stomates rapidly under water stress. Arens, Ferri & Coutinho (1958) supplied dilute nutrient solution to cerrado plants through a branch or directly onto the leaves in the evening and noticed less transpiration the next day, with the stomates able to close more rapidly, than in controls.

Although many or most individual woody plants in a cerrado stand can continually tap water even during the dry season, this does not mean that devices to *slow down* water loss or reduce the harmful effects of a temporary water stress would not be useful, particularly since the stomates remain open or close only very slowly under lack of water. Undoubtedly, the cerrado woody plants as a whole cannot draw as much water, or so fast, in the dry season as they can in the wet season when the upper soil layers are moist also. This seems obvious from the fact that some leaves do fall. There is some water stress, therefore, and we may expect to find features which reduce water loss in the leaves which remain.

Cerrado woody plants have developed to a high degree xeromorphic leaf structures, which would be of value when leaves remain functioning over the dry season, either by helping to reduce transpiration or by supporting leaf tissue during a water stress. These structures include a dense network of veins, water storage tissue, hairiness, thick cell walls, lignified bundle sheaths and lignified girder tissue extending from the bundles to the epidermis, long supporting sclereids, silica impregnation, thick cuticle, stomates in pits, fewer stomates per unit area or stomates lacking on one surface, etc., as well as the chemical character of essential oils which might lower transpiration by creating a vapor film over the leaf. Naturally, these features only have value when the leaves are present over the dry season and help to reinforce other leaf adaptations to dryness such as fast stomate closing or rolling up. The presence of one of these characters does not necessarily mean it really acts to protect the leaf against water loss or the harmful effects of a temporary water loss in every case. This must be investigated for each species under each condition. Each character should be considered in isolation, that is, it can be imagined to be useful in some circumstances, all other things being equal. Often xeromorphic leaves are found to transpire more water than mesomorphic leaves. This, however, does not prove that xeromorphic characters do not restrict transpiration. In that particular leaf the transpiration might be even higher without these structures. Drought resistance and survival, which collectively is something different from being able to restrict transpiration, probably depends more on physiological reactions such as increase in osmotic pressure (which reduces cell membrane permeability to water) and modification in the protoplasm (which increases water holding capacity and ability to survive with less water content) (Maximov, 1929, 1931; Shields, 1950).

The leaves of almost all cerrado woody plants have a thick cuticle (or thick cutinized outer epidermal wall), stomates only on the lower surface (or in a few species, much more frequent on the lower surface than the upper), thick fiber bundle completely surrounding the midvein and usually also the side veins, and a solid parenchyma layer without chloroplasts above and below the midvein extending to the epidemises. Very frequent also are silica bodies and silicification of the cell walls, a fiber bundle running along the edge of the leaf, a colorless parenchyma strand running along the edge of the leaf, the stomates in pits, hairy leaves, and essential oils. Less frequent but still characteristic are fiber bundle extensions from the side veins to the upper and lower epidermises (girder tissue), stomates grouped in clusters, and long sclereids forming a "brushpile" skeleton in the mesophyll. The latter, for instance, is present in *Annona coriacea* Mart. and *Ouratea spectabilis* (Mart.) Engler.

Each cerrado woody species has many xeromorphic leaf features. Of 30 common woody species from São Paulo, two thirds have half or more of a selected list of 13 independent characters (calculated from description and drawings in Ferri, 1944; Morretes & Ferri, 1959; Beiguelman, 1962b, 1962–3, 1963–4a, 1963–4b; Morretes, 1967, 1969). These species also have other xeromorphic characters besides the 13 counted.

Herbaceous cerrado species in general have somewhat less leaf xeromorphy than the woody species as might be expected from the fact that the leaves function only or mainly during the wet season.

Other authors treating cerrado leaf anatomy have concentrated more on venation pattern as an aid in taxonomy, particularly so that the information could be used in future identification of fossil remains (Handro, 1964, 1967; Felippe & Alencastro, 1966; Válio *et al.*, 1966a; Carvalho, 1967; Chacur, 1968; Ferreira, 1968; Matos *et al.*, 1968b; Matos, 1969; Campos & Labouriau, 1970; Figueiredo & Handro, 1971b).

Silica bodies, both in the sense of structures formed inside the cells and remains of silica impregnation of the cell walls when plant tissue is incinerated, have been reported on for cerrado grasses by Sendulsky & Labouriau (1966), Campos & Labouriau (1969), Teixeira da Silva & Labouriau (1970), Söndahl & Labouriau (1970) and Figueiredo & Handro (1971a) with a view to the use of this information in future soil studies to identify the vegetation that previously grew in an area.

The xeromorphic features of cerrado woody plants contrast with the evergreen leaves of primary rainforest canopy trees. These usually do not have many strong xeromorphic features. Secondary evergreen trees have more, such as a higher percent of species with hairy leaves, thicker cuticles and some mechanical tissue. As may be expected because they are so subject to drying out even in short dry spells, rainforest epiphytes are more xeromorphic, often having scales to trap rainwater, mist and dew, and thick water storage tissues to hold it, usually the upper hypodermis. Compared to cerrado leaves, rainforest leaves have on the average a smaller number of palisade layers, more total air space, and smaller epidermal cells (Coutinho, 1962).

Cerrado leaves also contrast with leaves of caatinga species. The latter are structurally mesomorphic. The cuticle is almost always thin and stomates are not sunken. Other xeromorphic features are very much less in evidence than in cerrado plants (Ferri, 1955a).

Ferri (1961a, 1961b) sums up the situation, comparing the water balance and leaf xeromorphism of the cerrado, the dry northeast Brazil caatinga, and a third vegetation investigated, the evermoist scrubby evergreen "caatinga" forest on white sand in the Rio Negro region of Amazonia. He states that the occasional periods of slight water stress that cerrado and evergreen Amazon "caatinga" plants may be subject to can be reduced by possessing a permanent xeromorphic leaf anatomy which slightly conserves water, and this does no harm because even if it reduces photosynthesis slightly by reducing gas exchange, this is made up for by the fact that photosynthesis can occur all year round. This slight protection against water loss would not do for the non-succulent northeast Brazil caatinga plants during their long strong dry season; they must lose their leaves. But dry spells also occur in the rainy season and during the warmest hours of the day. Physiological reactions, i.e., rapid stomate closing, can then protect the plant during these periods and the stomates can open rapidly when the air is humid again or a rain provides soil water. For caatinga non-succulents it would be disadvantageous to have xeromorphic leaf structure causing a permanent low gas-diffusion rate for this would prevent the rapid rates of photosynthesis necessary during the short periods of satisfactory moisture conditions in that part of the year when the plant has leaves. In the cerrado there was no selection stress for developing physiological mechanisms of protection against water loss in the permanent plants. In general, Ferri accepts Arens' theory on the causes of cerrado leaf xeromorphism (see below).

These are the characteristics of cerrado and of dry caatinga in general. In some areas there are exceptions. In a disjunct area of cerrado (locally called "tabuleiro") in northeast Brazil, near Goiana, Pernambuco, Ferri & Lamberti (1960) found in three common woody species a certain restriction in transpiration, relatively rapid stomate closure when the leaves were excised and low cuticular transpiration, that is, a tendency towards the mesophytic reactions of evergreen rainforest and dry caatinga species. Since this cerrado has an average rainfall of almost 2000 mm per year, which is near the upper limit for this type of vegetation, the authors find the necessity for restriction of transpiration baffling. They state that there is a subsurface hard laterite layer which, however, is not continuous, and although it might slow up drainage somewhat, deep roots can reach lower soil layers. The water table is almost 30 m deep.

Another exception to regular cerrado conditions was noted by Ferri (1960b) and Coutinho & Ferri (1960). They examined the water balance of a few woody species in one of the southernmost cerrados in Brazil, a small disjunct stand in Campo Mourão in northern Paraná surrounded by araucaria forest. They found the transpiration and stomate behavior similar to that in cerrados in São Paulo and in central Brazil. But they found an abundance of cerrado species seedlings in the locale and therefore believed that the cerrado is recently invading this area, perhaps due to deforestation of the araucaria. This conclusion is contrary to that of Maack (1949) who believes that forest has been invading areas previously covered with cerrado and southern Brazil campo limpo (when not prevented by man) due to a geologically recent long-term increase in rainfall in this region, and that the cerrado of Campo Mourão is therefore a relict.

Up to now we have been considering leaf xeromorphism as something that evolved because of its value in some conditions of slightly reducing water loss and the harmful effects of water loss by morphological means. But this may not be its only value. One could imagine that if only the necessity to reduce water loss slightly were involved this could be obtained by merely having a smaller number of stomates or these being of smaller size openings and that all the other xeromorphic characters except those supporting the leaf tissue during periods of non-turgidity would not be necessary. I suggested in 1963 that perhaps another value of leaf xeromorphism was protection of the leaves against fire. Since a large percent of the leaves are present in the dry season which is when most fires would occur under natural conditions even if they occurred rarely, any characters which helped protect the leaves against fire would be useful. Naturally, the lower-level leaves would mostly be killed by the grass fires but of those somewhat further up the tree a larger percent might survive when protected by dense hairs, thick cuticles, and silica-impregnated tissues than leaves without these features. Stomates would be more protected when sunken or surrounded by hair tufts than when exposed on the surface. This would be useful if we imagine that it is more necessary to protect stomates than the other epidermal cells.

Arens (1958a) explains leaf scleromorphism as caused by an excess of carbohydrates not used in protein synthesis, i.e., growth. This excess may be caused by either lack of water as in evergreen mediterranean and desert plants, or by low levels of nutrients such as nitrogen in non-insectivorous bog plants. He cites many studies which show that lack of water or lack of nutrients reduces growth more than it reduces photosynthesis (it may even increase photosynthesis) so that an excess of carbohydrates builds up which is then "excreted" in the form of scleromorphic structures such as thicker cell walls and cuticles, more fibers, veins and ligneous structures in general. In a companion paper (Arens, 1958b) and again later on (Arens, 1963) he applied this idea to the cerrado. Since cerrado woody plants are always in contact with water they keep on photosynthesizing. But the carbohydrates produced cannot be used in growth since production of protoplasm also needs nitrogen, phosphorus and other nutrients in short supply in cerrado soils. Therefore the excess carbohydrates are used in building up the scleromorphic structures. While this is a suggestive theory, there are several weaknesses:

(1) It does not account for xeromorphic characters having to do with silica deposition, very common in cerrado plants, since silica is not formed from carbohydrates as is cutin, cellulose and lignin. It would have to be shown that excess carbohydrates somehow also cause greater silica deposition in leaves.

(2) Mediterranean climate shrubs and trees are the classical examples for leaf xeromorphism but very often occur on fertile limestone soils. Water is not always lacking in the dry season in all mediterranean vegetation especially if we consider how much could have been stored in the originally deeper soils upon which this vegetation evolved before man caused the soil to be washed away by overgrazing and cropping.

(3) Even if it is true that the low level of soil nutrient ions in cerrado conditions allows carbohydrates to build up in excess of what can be used in ordinary growth, this merely supplies the building material; it does not explain why the material is used as it is. Why are the excess carbohydrates used specifically to build up xeromorphic leaf characters instead of being used in other ways? There must be some selective value in these characters. They are not cancerous growths; they have definite

structures which could only have evolved under natural selection. And if they *are* important it would seem that they would have been produced even if the soil were fertile.

(4) In general, the herbaceous plants of the cerrado have a less pronounced xeromorphy, which is explainable on the fact that the leaves function only during the wet season or only for a short time into the dry season, but not so easily explained on the soil fertility theory since they grow in the same soil as the woody plants. While it is true that the shallow-rooted herbs exploit the upper soil layer which has the most humus and therefore might be expected to be the most fertile part, the upper layer is in fact not always the most fertile part as soil analyses have shown, and anyway, the whole profile is extremely infertile. Besides this, many woody plants, besides having deep roots, also have shallow ones in the upper soil layer so that the difference in fertility of the soil they tap as compared to the herbs is insignificant or none.

The question is still open. That leaf xeromorphism is often associated with soil poverty is shown by the temperate bog shrubs Arens cites, also by correlation of minor element lack with some Australian sclerophyll scrub and by the fact that the Rio Negro "caatinga," a scrubby evergreen forest in Amazonas, also shows a large measure of leaf xeromorphism. (The latter vegetation, which has nothing to do, floristically, physiologically or ecologically, with the northeast Brazil thorn scrub caatinga, occurs under an extremely high rainfall, up to 4000 mm per year, with no month with less than 100 mm, and on highly podsolized white sand, extremely poor in nutrients. Its transpiration and stomate movement is similar to that of the carrado (Ferri, 1959, 1960a, 1961b). Aubreville (1962) discusses this vegetation under the names, "campina," "carrasco" and "pseudo-caatinga," and Sombroek (1966) under "Amazonian caatinga.")

The plants of the "campos rupestres," also called "campos de altitude" (IBGE publications), "campos serranos" (Kuhlmann, 1956) and "campos montanos" (Eiten, 1970), rocky natural openfield vegetation of some mountain tops and high plateaus in central Brazil, also have strong xeromorphic features (Handro, Mello Campos & Oliveira, 1970). But here the case is complicated by the fact that, besides being nutritionally poor, the soils are thin lithosols which dry out in the dry season, so that here both soil poverty and drought may be acting in the same direction in producing leaf xeromorphy.

Handro (1966) raised the amaranthaceous cerrado herb, *Gomphrena prostrata*, in pots in its original nutrient-poor cerrado soil and in this soil enriched with a complete nutrient solution. Additional nutrients did not diminish the amount of lignification of the bundle sheaths in the leaves, which is one particular xeromorphic character, and thus seems to be evidence against Arens theory. The experiment tests only the phenotypic modificability of the species but is an indication of the careful experiments that will have to be made before Arens' theory can be accepted.

Recently, Goodland (1969, 1971a) has hypothesized that the high aluminum saturation of the base exchange complex in cerrado soils may be responsible for the scleromorphism of cerrado plants along with the low level of necessary nutrient ions. He mentions evidence that certain plant groups with high importance value in cerrado, such as the Vochysiaceae, are not only tolerant to aluminum but are aluminum accumulators. Forest soils in general, even highly latosolized ones like terra roxa, usually have less available aluminum than cerrado soils in the same region and they particularly have less aluminum saturation of the base exchange complex. This interesting hypothesis should certainly be tested.

XIII. MAN'S INFLUENCE ON THE CERRADO

Fire. Before man appeared on the scene, it is highly probable that fire passed through cerrado vegetation with enough frequency that, as a whole, the vegetation became adapted to it. In this way it is comparable to the North American prairies, to the southeastern United States coastal plain pine forests, and to certain natural grasslands, savannas and open woodlands in other continents. In the cerrado these adaptations are the following.

(1) The grasses, sedges, herbs and low shrubs have the ability to grow back vigorously immediately after a fire either before the new rains start or just after. The perennating parts of the graminoids are in the center of the clumps; these are protected from fire by an insulating layer of fibrous or hairy bases of the old leaves ("tunic graminoids"). A similar result is obtained in certain *Anemia* species where the rhizome and petiole base in these ferns is covered with dense hairs. Forbs, low shrubs and semishrubs almost always have thick woody subterranean xylopodia, which besides being proof against fire also provide stored food and water for new growth. Illustrations of grass and sedge clumps, fern rhizomes and of xylopodia of herbs and semishrubs of cerrado species may be found in Warming, 1892, 1908; Rachid, 1947, 1956; Rizzini, 1965; and Rizzini & Heringer, 1961, 1962b, 1966.

(2) Trees burned or cut to the ground but which manage to sprout again from the base of their trunks have the ability to flower and fruit while still small, often while less than 1 m tall. In this respect they are like certain scrub oaks in eastern United States.

(3) The stems of the taller shrubs and low trees have the ability to remain alive though completely charred by fire, protected by their thick corky bark, and to sprout again from these burned trunks and branches. The contrast between a new green shoot and the black charcoal-covered branch from which it sprouts is striking.

For these reasons, even severe annual fires over many years will not destroy a cerrado. Such fires may lower and open out the woody layer but hardly affect the herbaceous cover except perhaps for relative species composition. No matter how frequent the fires the herbaceous cover is not weakened any more than it would be in a virgin North American prairie. No other vegetation will enter. In fact, if only fires occur but no heavy grazing there will not even be an invasion of exotic weeds.

Indian occupation of the cerrados caused fires to be more frequent. The Indians fired the cerrados, usually in the dry season when it was easiest, in order to drive game and to provide burnt areas where deer would be attracted to lick the ashes for minerals and to browse on the new grass shoots which were tenderer and more abundant than in non-burned areas and which were not mixed with the last season's dead tough dry leaves. The frequency of fires must have varied according to how close the cerrado was to the Indians' dwelling places or hunting routes.

For instance, in the Serra do Roncador in northeastern Mato Grosso a new road was recently built along the crest. Before the road there was no settlement on the crest of the range, which is essentially flat. The local Xavante Indians live along the larger rivers but they crossed the crest in the dry season while hunting. I examined the cerrados in the dry season of 1968 in an area where only one previous dry season had passed since the road was opened. Settlement was very sparse, an average of one house every few tens of kilometers along the road and practically none off it. Temporary shelters of the Indians could be seen in a few places. Small areas of the cerrado had been burned immediately around the houses of the settlers but the burning did not extend far. More than one or two kilometers from the houses very few stretches had been burned the present or previous dry season. All areas of cerrado had signs of previous burning but not for 4–5 years, or in some cases 3 years. We may take 3–5 years then as the smallest average time that had passed between fires in this region under Indian occupation.

The number of years since the last fire could be told from the number of branch orders of unburned boughs growing out of burned trunks (or unburned branches growing out of burned boughs) in those species which usually grow one branch order per year. Also the number of years since the last fire could be told by the general density and height of the low thin-stemmed shrubs since these are mostly wiped out in a single fire. If a fire had occurred during the present dry season this was evident of course. If it was being viewed in the wet season and a fire had occurred during the previous dry season this was recognized by the presence of ashes, generally bare soil due to fallen leaves and old leaves on grass and sedge clumps having been burned away, killed low shrubs, and burnt foliage at low levels still present on trees and taller shrubs.

It is probable that before Indian occupation fires caused by lightning, etc., were not more frequent than once every few decades on the average, but that they definitely did occur.

When a cerrado region is settled it is used only for cattle raising and is burned every year, almost always during the dry season. However, a fire once started does not burn indefinitely but stops after a few hundred meters or a few kilometers or tens of kilometers due to barriers such as roads and paths, gallery forests, rocky or lateritic areas with little grass growth, etc., or even for no apparent reason perhaps due to a change in the wind. Therefore, there will always be patches that are not burned in any one year. My experience has been that the recently burned areas of cerrado average about half the total cerrado area in a relatively long-settled region of continuous uncultivated cerrado such as northern Goiás or Maranhão. Therefore, any one spot is burned on the average once every two years.

The effect of fire on the physiognomy of the cerrado varies from region to region and even from stand to stand in the same region. In the Serra do Roncador the new road gave an opportunity to see the effect of *one* fire on a cerrado that had not been burned for several years, for in certain places there had occurred a fire on one side of the road but this had not extended to the other side. The cerrado had the same basic physiognomy on both sides of the road before the fire. It was noted that one fire killed off, and therefore thinned out, only shrubs up to about 1 m tall, occasionally to 1½ m, presumably because these had the thinnest stems and because all of their foliage was reached by the flames. Charred foliage on the trees showed that the flames usually reach to 2 m up, rarely higher. The main fuel is of course the dried grass clumps 1–1¼ m tall. The taller shrubs and the trees were not affected by one fire and since these form the basic skeleton of the physiognomy, this was not changed. When several years now pass without fire the low shrubs grow back to their original height and density, and the tall shrubs and trees, some of which may have been weakened although not killed by the fire, now have a chance to regain their vigor.

However, when the region is settled and the fires become more frequent, passing through a stand every 1 or 2 years on the average, there is no chance for low shrubs to grow back so thickly or for many of the weakened trees to recuperate. Many of these trees then are eventually killed by one of the fires. They may remain erect at first, leafless and dead, or immediately fall over. They are finally consumed by the same fire that killed them or in subsequent fires, lying on the ground with their trunks glowing at one end like a cigarette and leaving a line of ashes that marks their branches. Under this same burning frequency the younger trees have no chance to grow to their complete heights before they too are weakened and eventually fall over. Therefore, excessive burnings generally lower and open out the woody vegetation of the cerrado. (Live unburned trees also fall from time to time.)

However, the resulting changed physiognomy varies from place to place depending on (1) the vigor with which the plants can grow back between fires, (2) the degree of protection the individual trees and shrubs have to the local fires, (3) the amount of fuel (i.e., grass) that can grow, dry, and accumulate between fires. Some arboreal woodland cerradões, for instance, may lose all their tall trees after one or a few fires and turn to a campo cerrado (scrub savanna) as in São Paulo and the Triângulo Mineiro, while other cerradões may retain most of their trees but lose most of their shrubs. The latter has occurred in may places in southern Maranhão, forming beautiful semi-open arboreal woodlands with a grass layer, and so clear beneath the tree canopy that one can see for one or two hundred meters or more.

Although as a general rule repeated fires keep woody growth more sparse, apparently the opposite occurs in a few places. Barros (1952) mentions a campo in which repeated burning caused invasion of cerrado shrubs while less burning kept the campo more purely grassy. This is the only observation of this type I have come across.

Summing up then, we may say that the effect of fire on the physiognomy of the cerrado depends on its frequency, only producing a long time change if occurring every 1–2 years.

Is cerrado a derived vegetation? It is now necessary to enter a very controversial question, whether fire has converted large areas of former mesophytic forest to cerrado. I will say here and now I see no reason to believe this at all. My impression is that except perhaps for a very few areas, measured in hectares or a few square kilometers, in long-settled regions where cerrado meets upland forest such as in São Paulo, and where historical records or accounts of old residents tell of a change from forest to cerrado, that all present-day cerrado areas always were cerrado, at least during recent geological periods. Repeatedly burned former forest land in the climatic region where cerrado can occur and which is not now cultivated is grassy pasture, *but not of the cerrado flora and appearance.* When fire becomes less frequent this pasture, even if it has been burned every year for half a century, starts a secondary succession to forest, passing through a closed shrub and low forest stage composed of typical mesophytic secondary forest succession species, a flora completely different from that of the cerrado in species and in appearance.

Cerrado always occurs, in its climatic region, on certain geological formations and resulting soils. If large areas of cerrado were formerly forest this correlation to geology would be less evident. The acid test is that cerrados protected from fire show not the slightest indication of invasion by forest species. A small area of cerrado in Emas, São Paulo, was held as a study area by the Department of Botany of the University of São Paulo unburned for nearly three decades. A small patch of forest occurs nearby and more extensive forest within several kilometers, but no forest plants invaded the cerrado all this time. (It should be mentioned that seedlings of the native cerrado species were not found either. In the later years molassas grass invaded and formed a thick layer where fire was excluded, but this cannot be what prevented forest seeds from establishing, for pasture on former forest land in São Paulo, also thickly covered with molassas grass, soon starts its succession to secondary forest when fire is stopped.) Many other small areas of cerrado in São Paulo and Minas have been prevented from burning for several to many years because they were not set fire to and because fires from outside did not reach them since they were surrounded by open fields and roads. And it has just been recounted that large areas of cerrado in the Serra do Roncador were not burned for up to 5 years or more. In all these cases no forest species at all started to appear although forests exist nearby. This is in direct contrast to the Derived Savanna in West Africa, which was originally a dry deciduous mesophytic forest, and which even with 1 or 2 years of fire protection is immediately filled with secondary forest shrubs and tree saplings (Clayton, 1958; Hopkins, 1962).* In the true West African savannas further north in a drier climate this does not occur. The cerrado situation is also in contrast with the former prairies and open oak woodlands along a large portion of the eastern edge of the prairie region of North America which had been maintained as prairies or open woodlands by fires set by the Indians, and which after settlement and suppression of fire grew up to closed oak forest (Curtis, 1959).

It cannot be alleged that protected cerrado areas do not show a change to forest because the original forest soil has been irreversibly changed. If this were true one would think that at least a few of the many cerrado areas that have been protected for a few to many years from fire would show at least a partial invasion of forest species due to a soil that has

* "The term *derived savanna* with its genetic connotation . . . refers to the forest-savanna vegetation complex. This term applies especially well to the vegetation of Africa, where many excellent studies have documented the effects of fire on forest vegetation. Numerous experimental studies also indicate that when protection from fire and human activities is provided, grasses of the forest-savanna mosaic are quickly invaded by brush as a pioneer stage leading to forest." (Batchelder & Hirt, 1966). None of this has to do with cerrado.

It may be mentioned that in other areas of Africa such as Zambia the miambo woodland, whose grass layer is burned every year and which has an open tree cover, if protected from fire for many years forms a closed tree cover and so can be called a type of forest. Although in this forest many of the undergrowth species are different from those in the open woodland, being more shade-tolerant and more sensitive to fire, *most of the canopy species are the same* (W. C. Verboom, 1970, personal communication). Therefore, there is a question as to how much the miambo woodland, a fire disclimax (at least in some places), is really a different vegetation type from the dry forest it replaces when the latter is burned. It does not seem in this this case that a forest has been turned by fire into what is really a different vegetation, a "savanna woodland" of different composition.

Cerradão also occurs in open- and closed-canopy phases but is always considered the same vegetation. The difference from miambo woodland is that open-canopy cerradão in most places where it occurs does not close its tree canopy on protection from fire (although the shrubs may become denser). Closed-canopy cerradão may open its tree canopy with fire or it may be so much opened and lowered that it is no longer considered a cerradão.

been less impoverished, but so far as I know this has never happened. Cerrado remains cerrado unless the climate changes.

Several authors have considered the Brazilian cerrados in total or in large part as derived from forest by man's activities. I will present their arguments and give reasons against their views.

Batchelder & Hirt (1966), citing Hardy (without date), state:

"Indiscriminate and widespread burning can initiate change in vegetation cover which is non-reversable. Few authors consider the *campo cerrado* of Brazil [the term used here for the cerrado in general, although perhaps excluding cerradão] to have been derived from an extensive forest, but there is ample evidence that many areas now in low brush and grass were once forested. Hardy (n.d.) in studying the *campo cerrado* of south-east Brazil, concluded that burning contributed greatly to the rapid degeneration of soils after the forest had been felled. This was especially evident in areas where repeated burning took place. Not only was organic residue in the soil lost, but rapid mineralization and loss of nutrients by leaching was accompanied by soil erosion. Accordingly, the edaphic environment was completely altered and forest is prevented from regenerating. Hardy noted that soils supporting *campo cerrado* are extremely low in nutrients and have all the characteristics of senile soils in transition between kaolinite and the gibbsite-hematite stages of weathering. He concludes, therefore, that *campo cerrado* is a "deflected" climax, that is, the *campo cerrado* is an edaphic savanna, supporting low brush and grass as an edaphic climax produced by forest clearing and fire."

All the facts mentioned are true but the conclusion does not follow. Because cerrado occurs on poor soils and burning forests improverishes the soil does not mean that cerrado is derived from forest by burning. It is perfectly true that "many areas now in low brush and grass were once forested"; the point is (1) whether that brush and grass is *cerrado* or the totally different flora of cleared mesophytic forest land kept low by repeated burnings, and (2) if the low brush and grass *is* cerrado, whether the "forest" that historical evidence once showed was there was mesophytic forest or closed cerradão. Closed cerradão is structurally forest, but being cerrado floristically, gives lower more open cerrados on burning. Mesophytic forest does not yield cerrado on burning.*

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* Corner (1964) shows an aerial photograph (n° 37) of an open woodland cerrado with gallery forest in Amapá, in an area without signs of human occupation, with the statement that the upland had been deforested and burned and trees were now re-invading. Presumably then, it would be forest trees that were re-invading. However, the color (gray, not the black of forest trees, corresponding to cerrado gray-green and forest deep green) and spacing of the upland trees is typical of cerrado such as was present before human occupation, and present for the same reasons it exists in central Brazil: rainfall low enough to permit cerrado and highly leached soils which favored it over forest. Usually, continuous forest land cleared for pasture is burned every year and so does not return to trees, but if not burned, forest does not re-invade in the manner shown. A dense closed shrub layer forms first, which

Dawson (1957), working in the center of the cerrado region in east central Goiás north of Brasília, also thought that the cerrado is secondary vegetation due to long-term burning by Indians and later by Brazilians.

"As a result of these destructive practices the stature of the vegetation has steadily been reduced and the scrubby *cerrado* extended at the expense of heavier forest which has been pushed back to the margins of streams and swamps in many areas. Thus, the *cerrado* is surely not a climax vegetation, for it does not seem to represent the maximum vegetation that the ecological conditions can maintain. Indeed, one sees in areas of especially severe and frequent burning the deterioration of even the scrubby, fire-resistent *cerrado* to produce *campo sujo* or clean grasslands (campo limpo) in which trees and shrubs are all but eradicated. On the other hand, one can find occasional small areas that have been protected in some way for several years from the fires. In these the *cerrado* vegetation has become tall and dense (known as *cerradão*), and there is evidence that continued protection would give rise to the development of the *mato de segunda classe* or second class forest described by Waibel, such as now persists along most of the streams and rivers of the Planalto."

There are two points to be made about Dawson's argument: (1) many areas of cerrado seem lower and more open than the ecological conditions supposedly can maintain, (2) cerradão in undisturbed conditions will in time turn to "second class forest." As to the first point, the maximum vegetation that the ecological conditions can maintain on the Planalto depends on the exact conditions of the soil and site. Dawson collected in the region in the late 1940's when there was very little settlement or in some areas none at all, so that fire probably did not occur in a given spot every year. From observations along the Serra do Roncador in Mato Grosso, in a similar settlement and fire frequency stage, it was observed that up to that time fire had modified the structure of the cerrado very little. Certainly in no case had it wiped out any cerradão or other tall dense cerrado and changed it to campo limpo or even to the savanna form, campo cerrado or campo sujo. Also there was a great deal of local variation in soil type and distribution of laterite associated with differences in the cerrado structure. Therefore, it seems unlikely that in the region well north of Brasília, on more or less similar

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then more or less evenly grows higher to scrub and then forest. The forest does not re-enter a former forest land in Brazil in the form of well-separated trees with clear spaces around them as shown in the photograph. This physiognomy is typical of cerrado woodlands and open scrubs.

His photograph n° 40 shows a grassland with gallery forest along the streams in Goiás. Again, Corner says that the upland was deforested. Although this area is settled (a few houses and trails appear), it is highly unlikely that it was continuous forest. Goiás is the state that has the largest percent of its area in cerrado, and all its upland forest regions still have forest remnants, some of which would undoubtedly show in an area as large as that pictured. The photograph is that typical of a landscape of the campo limpo (or campo sujo) form of cerrado with gallery forests.

rock types to that of the Serra do Roncador and in an even drier climate, that mesophytic forest or even cerradão was the prevalent upland vegetation before man and had been destroyed by fire to small vestiges. It may be remarked that in the "Mato Grosso de Goiás," a continuous upland forest region between Anápolis and Ceres in Goiás due to exposure of a richer rock type, many pastured areas have been cut from the forest and burned for 20–30 years and there is no indication of invasion by cerrado species. The variations in cerrado density in the region Dawson explored were most probably mostly due to variations in soil fertility and laterite compactness (and the marshy campo limpos in the valleys due to water-logging) although fire may have caused a minor degree of opening here and there.

As for the second point, I have never seen any evidence that cerradão is a subclimax stage in a secondary succession leading to "second class forest," which by Waibel's description is mesophytic semideciduous forest. A cerradão is climax and remains cerradão if not destroyed by man. Only if the climate becomes appreciably more rainy does a cerradão turn to mesophytic forest by the invasion of species of this forest type. On the other hand, in the same climate and on a more or less flat site, the opposite can occur: the gradual impoverishment of the soil over millions of years can cause semideciduous mesophytic forest to turn to cerradão and if continued can cause the cerradão to change to a lower more open form of cerrado. But these are changes in the climax, not in a primary or secondary succession. Incidentally, Waibel's "second class forest" is an *upland* mesophytic forest and is semideciduous. The gallery forests of the Planalto are by definition lowland forests and (except for some near the border of the caatinga region) are always evergreen. The planalto gallery forests then cannot be equated with Waibel's second class forests.

Ferri (1943) states that the cerrados of Lagoa Santa, Minas Gerais, and of Emas, São Paulo, both of which he studied, are secondary due to the original forests having been destroyed by agencies like burning, cutting, grazing, cattle stamping, etc. Certainly these and practically all other cerrados show signs of burning. But this does not indicate by any means that there was originally forest on those sites and these were destroyed by burning. Ferri mentions fruit trees planted and thriving on unfertilized, unirrigated cerrado soils both in Emas and Lagoa Santa and affirms that the fact these can grow there is because they are protected from fire, the ax and animals, and that the soil obviously *can* support trees. But this is no proof that forest was the original vegetation. Many forest trees can grow in cerrado soil if planted and protected from competition by the cerrado vegetation, which it would be of course when the cerrado is cleared for an orchard. The fact is not whether forest trees can grow in cerrado soil if planted but whether a forest vegetation as a whole can take or maintain possession of a site against the competition of the cerrado vegetation as a whole under natural conditions. Street, farmhouse and shelterbelt trees planted in the pampas of Argentina and in the shortgrass plains of North America also do very well even though in both cases, areas of this kind of vegetation protected for many years from grazing, fire and cutting show no tendency to start a secondary succession to forest.

Ferri states (translated): "It is not necessary to maintain that fire has produced permanent changes. Leave the cerrado free from devastation and it can cover itself with forest! An indication of this can be noted in the locale where Lund is buried. This was sufficient to permit a Caryocar Brasiliense [tree] to develop considerably, forming a wide and vigorous crown, and this in a species which in the open cerrado [i.e., not protected against fire] does not achieve such a conspicuous development."

However, this is no indication that a forest, in the sense of a mesophytic forest, will form. *Caryocar brasiliense* is not a mesophytic forest tree; it occurs in all cerrados, open and low to closed and arboreal (cerradão). Thus the protection shows that the low scrub cerrado outside the wall can develop into *cerradão* when undisturbed; it does not prove it will develop into mesophytic forest. Although Warming does not mention tall arboreal cerrado around Lagoa Santa this well could have been the original form of cerrado in the region. Even today patches of rather dense, low-arboreal cerrado occur near the city, just a little too low to be called cerradão.

On the other hand, Ferri further states: "But even if cultivated plants do not prove anything, there is one more fact which clearly demonstrates that many campos owe their desolation [i.e., lack of trees] only to accidental causes: in a campo limpo, once in a while, one can observe a tree. This tree can grow even on top of a ridge, which by its nature excludes the possibility of an excessive accumulation of water. On the outskirts of Lagoa Santa such a tree is in general a palm (Acrocomia sclerocarpa) or a Copaiba (Copaifera Langsdorfii and other species). These plants clearly indicate that the soil should contain sufficient water to permit their development. If one tree can grow why not a forest? It is because the forest is cut down, only a few species being left by man for better use."

In this case, from the species mentioned, if they were not planted, there was probably a forest originally on their site, not cerrado, since all species of *Acrocomia* that I have ever seen in Brazil in more or less natural vegetation have been in forest, never in cerrado. *Copaifera langsdorfii* Desf. grows in both forest and cerrados in southern Minas and São Paulo, so at least it is not an indication against forest having been originally present. Forest does grow in the Lagoa Santa region up the whole valley side to the ridges when the valley surrounds a large body of water. Photographs in Warming (1892, 1908) show forest covering the whole slope above the lake to the highest point (in the direction photographed) and the same can be seen today in the relatively large valley of the Rio das Velhas north of Lagoa Santa. These trees therefore are remnants of forests and the campo limpo in which they grow is typical pasture derived from forest land such as is common all over Brazil. Therefore it is no proof that the cerrados of Lagoa Santa are secondary.

Rawitscher (1948, 1949) maintains that the cerrado at Emas, and those of São Paulo in general, are secondary since there is enough water permanently in the subsoil to support forest, while the true cerrado region is in a much drier part of the country. Thus (translated):

"The abundance of water encountered through the year in the deeper part of the soil, together with the fact that the transpiration even in the driest time of the rainless period is not greatly diminished, leads to the conclusion that indeed the true climax, at least at Emas, is not the cerrado vegetation but one of a more forest-like character. This agrees with the fact that even in the drier interior of the State of São Paulo there exist continuous virgin forests of a rather hygrophilic character . . . These forests never use up entirely the water stored in the soil, so that rivers and streams here flow throughout the year. This is different in the drier parts of Brazil. Already in northern Minas the still hygrophilous forests consume in the dry period all their water reserves, streams and rivers drying up annually. Progressing from here to the still drier north and northeast we come to the region where the cerrado is at its best and where it must be considered as a climax. We must suppose that migrating from here it has invaded the clearings opened by deforestation."

In the first place the question is not how much water there is in the subsoil that determines whether cerrado or forest will develop but (1) whether the *upper* soil layer can also remain moist over the dry season even without a closed tree canopy over it, and (2) the soil fertility. When the first requirement is met, as in moist ground next to a permanent stream, a gallery forest forms *even on very poor soil.* On the upland, however, within the climate that permits cerrado, the upper soil layer does dry out in the dry season as the investigations of Rawitscher himself showed for Emas and as is evident by the drying of the cerrado herb layer in general. This surface drying combined with the low level of soil nutrients is enough to support cerrado over forest. Now this low level of nutrients may be original or may be due to deforestation by man and subsequent leaching during many years in which repeated burnings prevented the return of forest. However, the fact that forest species did not invade the Emas cerrado *at all* while it was protected for nearly 30 years from fire, as well as Emas being in a geological region containing rocks known to produce poor soil even in the first weathering stages and which support extensive cerrados, make it more probable than not that this area always was part of the many natural cerrado areas of the state. Surveys of immense virgin areas in São Paulo made at the end of last century and the beginning of this one (Loefgren, 1890; Sampaio, 1890, Edwall, 1913) showed large areas of cerrado of all heights and densities all over the state, especially cerradão.

Much of this still exists today. Cerradão when burned gives low open cerrados; mesophytic forest does not. If by "more forest-like character" Rawitscher meant Emas was originally cerradão, there is no disputing, but not that it was mesophytic forest.

But there is another part of Rawitscher's statement that must be commented on. He states that cerrado is at its best and is climax north and northeast of northern Minas Gerais. However, this direction is the caatinga region of northeast Brazil, not the cerrado. The center of the cerrado region is to the west at that latitude, in Goiás and adjacent eastern Mato Grosso. The cerrado here *is* certainly climax. The northeastern edge of this central cerrado region is only now beginning to be settled and disturbed. But Goiás is no drier than Emas, and the northeastern edge of the central cerrado region even has a considerably *higher* rainfall than Emas or the interior of São Paulo in general. The cerrado ground layer in much of Goiás and northern Mato Grosso is much more floriferous and less dried out in the dry season than that of the cerrados of São Paulo. Therefore, it is not correct to say that the cerrados of Central Brazil are climax because they are in a drier region and those of São Paulo must be secondary because the climate is moister.

Dansereau (1947, 1948) states that the campos cerrados (his general term for cerrado vegetation) of central Goiás, western Minas Gerais and eastern Mato Grosso is almost certainly climax. In many marginal areas its advance is probably from fires and cutting of forests. In São Paulo it appears to be disclimax by fire or at most pre-climax remains. The same objections can be raised to this similar view that cerrado in areas marginal to central Brazil are fire disclimaxes. Under the view that the cerrado patches in São Paulo were once more continuous and have retreated to their relic positions due to a geologically recent increase in rainfall in southern Brazil, then Dansereau's second choice is true. they are "pre-climax remains."

Schnell (1961) takes up the question of the origin of the cerrado but comes to no definite conclusion. He mentions Aubreville's view that cerradão is natural and all cerrados with lower more open woody growth come from cerradões that have suffered degradation by human action. Schnell includes the small scattered Amazon savannas under the concept of cerrado, although these are really a different vegetation type in a different climate and on a different kind of soil.

Hueck (1957a, 1957b) explains that by last century and the beginning of the present century, large areas of forest in southern Brazil had already been cleared, producing uniform homogenous campos. He says that Schimper, Wettstein and others thought these were natural formations [or at least wrote in such a way as not to make plain that they considered them secondary]. Later this impression was corrected and now we know these areas are secondary. But the same idea was then unjustifiably applied to the very different cerrado-type campos. No doubt the theory that the cerrados are secondary was fortified by the results of fire protection of certain savanna areas in Africa yielding successions to forest. However, the cerrado as a whole is certainly primitive, being practically the sole vegetation over immense areas of central Brazil where no European has settled and where the Indian population is extremely sparse. Hueck goes on to say that characteristic cerrado woody species can be found in disjunct "cerrados" in the Amazon region where they are known as "campinas." Cerrados [the disjunct ones beyond the main cerrado region] have practically the same composition whether they are in a region of tropical forest, subtropical forest or other vegetation type.* Except for the few errors here mentioned in the footnote, I agree with Hueck's thesis that the cerrados, including those in southern Brazil (São Paulo) are primitive, only stating that in spite of several conspicuous cerrado species occurring in almost all cerrados, the bulk of the flora of cerrados very distant from each other is composed of different species.

Why the cerrado does *not* generally enter destroyed forests is a question that is still open. Cerrado is adapted to poor soils, and when a mesophytic forest is cleared and the soil cultivated or burned for several years the fertility is rapidly reduced. One would think that if the land were then abandoned and if a cerrado were nearby as a seed source it should be able to occupy the land, competing against a return to forest, especially if the land is burned over every year. But perhaps the cerrado to be successful in competition with mesophytic forest needs not only a poor soil but also one rich in available aluminum. While the former forest soil rapidly loses nutrients on clearing and burning, it does not rapidly gain aluminum; this only comes about over geological time with changes in the type of clay produced by weathering. Goodland (1969, 1971a) has shown that cerrado soils in general are poor in nutrients and rich in available aluminum and has used the high aluminum content to explain the scleromorphism of cerrado plants, but he has not emphasized so much its possible role in cerrado competition with forest. Low aluminum content then may be the reason cerrado does not generally invade exhausted upland forest soils. It should be emphasized that high available aluminum may be needed for cerrado to establish itself *in competition* against forest; cerrado plants can grow very well in cleared forest soils if planted.

Fire is the most widespread disturbance that the cerrado suffers. As mentioned before, it is probable that infrequent burnings were part of the normal environment in which the cerrado evolved, but annual

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* Hueck shows a photograph of a campina near Manaus in the Amazon region with the implication that this is a stand of cerrado. However, while some savanna areas in Amazonia are cerrados, most are not. The "campinas" or "caatingas" near Manaus definitely are not but are a completely different flora and vegetation on highly podsolized white sands. In this paper, Hueck also records several small campo areas in São Paulo south of the general cerrado region and states that these are disjunct cerrados. Those for São José dos Campos and Atibaia are indeed cerrados, but the Butantã and Cunha campos definitely are not.

burnings over long periods of years definitely were not. However, adaptations to the infrequent burnings as well as adaptations to poor soil, and in the case of herbs and small shrubs, the presence of xylopodia, acted as pre-adaptations to a regime of annual burnings, enabling the cerrado to continue, although perhaps in a lower and less dense form, against invasion by any other vegetation type as long as the climate stayed about the same.

It is necessary to make a distinction between a vegetation (1) *originated* by fire, (2) *maintained* by fire, and (3) *affected* by fire. It is also necessary to distinguish between fire causing a different vegetation type to appear, such as oak forest to prairie in temperate North America, tropical mesophytic forest to cerrado in Brazil, hardwood forest to pine forest in southeastern United States, and fire causing a different physiognomic variation of the same vegetation type to appear.

"Originated" has two senses, the evolutionary sense and the secondary successional sense. In certain types of vegetation and climate, lightning-caused fire was undoubtedly frequent enough so that features of individual species were evolved in response to it, such as among plants, closed-cone pines that open only by fire heat; pines of open- or closed-cone type that can germinate only on mineral soil and thus only when fire has burned away leaf duff and the upper organic fermentation layer; fibrous tunics of grass and sedge leaf bases, etc. Animals associated with a particular vegetation type are often abundant only in certain fire-modified forms of it, such as in burn openings, or under more open canopy cover, or in ecotones between closed vegetation and burn openings ("edge effects"), etc. Fire cannot be said to have evolutionarily originated these biomes as a whole although it seems to have caused certain features of it to evolve.

More commonly the sense of "originated" is that fire has caused a lower successional stage of a vegetation to appear in a particular local area, such as pine forest stands in the eastern U.S. coastal plain where there formally was a hardwood forest, aspen stands in the North American boreal forest, herbaceous and shrubby burn openings in a forest, etc. Or fire has caused a geographically neighboring vegetation type to appear, such as prairie in repeatedly burned oak forest on the prairie edge, "derived savanna" in the dry deciduous northern border of the forest zone of West Africa, etc. In all these cases, once the non-climax vegetation has entered it is *maintained* by repeated fires.

Many natural vegetation types are merely *affected* by fires without changing to another type: natural prairie (not fire-maintained), natural woodlands and savannas, etc. In these cases the physiognomy remains more or less the same whatever the fire frequency, as in the prairie and other pure grasslands, or may become lower and more open as in woodlands and savannas. The floristic composition may also remain more or less constant if it has already reached equilibrium with the burning frequency, or be changed to a composition of more fire-resistent species if it has not.

I maintain that the relation of fire to cerrado (in the wide sense) is the third case: it is affected by fire without having been originated by it or even maintained by it. It is affected in its structure by fire perhaps more than most "savanna" types because in by far the greatest part of its area its "natural" physiognomy (caused by substrate and not essentially modified under the slight frequency of non-man-made fires) is rather dense so that frequent man-made fires can lower and open it and have done so over large areas.

Thus, concerning the origin of the cerrado, I agree with Alvim (1954) (translated):

"The biotic theory [of savanna formation, i.e., disturbance of forest by man causing its transformation to savanna] has recently been strongly defended by Rawitscher and his associates of the Faculty of Philosophy of the University of São Paulo. In Rawitscher's opinion, the cerrado is a product of man and results from frequent burnings by cattle raisers, done to 'clean the range' during the dry period in order to 'stimulate herbaceous shoots' in the rainy season. This theory, like that of Warming [that the climate with its strong dry period is the cause] does not explain the sudden changes in the vegetation that can be seen in the campo cerrado region [cerrado and forest side by side on the uplands]. It is a faulty explanation also because the [cerrado] region never was economically used for agriculture [i.e., crop-raising] and because one does not find cerrados in the populous and most agriculturally exploited zones (naturally of richer soils) where fire has also been, as in all Brazil, the common system of cleaning the fields. Warming considered the fire theory as 'totally inadmissable.'

"Of the theories proposed to explain the formation of the campos cerrados, the only one which is based on experimental evidence is that of the chemical composition of the soil [*vide* Alvim & Araujo, 1952]. Without doubt, the climate exercises a pronounced effect on the vegetation and on the soil formation itself, but within the climatic zone of the cerrado the quality of the soil appears to be the factor which determines the type of vegetation of a particular area. This quality of the soil is a function mainly of its geologic origin.

"The frequent burnings naturally have modified the flora and the physiognomic characteristics of the cerrado, but the majority of authors consider fire as a secondary factor, concluding that typical cerrado—already susceptable by nature to burn easily—arose first, in consequence of the soil. Beard's theory [of American tropical savanna formation by] bad drainage conditions does not hold for the cerrados of the Central Plateau of Brazil."

Ab' Sáber & Costa Junior also noted the primitiveness of the cerrado by taking a wide geologic, topographic and climatic view. After referring to Paiva (1932) and other writers, they state (translated):

". . . a large part of the central planaltos of Brazil were entirely occupied by a vegetation of 'cerrados' and 'cerradões' until the installation [in this region] of the tropical humid climates of the Atlantic coast. The advent of humid climates from the east, besides the great reactivation of down-cutting in the sedimentary lands of the west, implied an invasion of the forest cover from east to west. The climax area of cerrados and cerradões in Goiás and Mato Grosso thus became isolated between the south Amazon and Atlantic forest areas, occupying preferentially the interfluvial platforms of the tabular plateaus. The penetration of the forest extended along the wide valleys in the form of gallery forests while the ancient vegetation restricted itself to the flat tops.

"According to this view, the cerradão is perhaps the form most related to the primitive botanical complex, from which the principal components of the present campos flora of Brazil have been derived by a selection imposed by pedologic, geo-hydrographic, topographic and altimetric conditions.

"Historic man with his pastoral activities and systematic burning contributed still more to modify the ancient picture, transforming cerradões into cerrados and 'cerradinhos' ['little,' i.e., lower, cerrados], as well as [transforming larger areas of forest into] isolated remnants, [all these being] degraded types of vegetation."

In 1932, Paiva had already noted (translated):

"This vegetation evolution from the water divide to the thalweg is interesting, so much is it in accord with the geology, presenting favorable evidence for the original pre-existence of the campos as botanical formations, and in absolute discordance with affirmations of some authors who imagine [the campos] always as remains of forests destroyed by fire."

Beiguelman (1963) also admits the possibility that cerrado is an original vegetation, a climax of primary succession, due, however, not to dryness of climate or site, but to low nutrient level of the soil. He also states that present day cerrados, whether primary or having replaced former forests due to man's destruction of the latter, would not return to forest if cutting and burning were stopped, because of the poor soil conditions.

Summing up, we may conclude that the Brazilian cerrado is an original vegetation due to certain climatic and edaphic causes. It is not due to the destruction of mesophytic forests by burning. Both in its central position in the country and on its margins where it contacts other vegetation provinces, it is an original primitive vegetation.

Grazing. Grazing in the cerrado is extensive but not intensive. Except for local areas near ranch houses and in fenced fields, the herbaceous layer of the cerrado does not usually appear cropped. It is doubtful if the usual light grazing has modified the cerrado much in general, either physiognomically or floristically. In the few small heavily grazed areas it has undoubtedly changed the native floristic composition and introduced some weeds. Weeds in cerrado seem to be due more to the soil disturbance consequent on heavy grazing and nearness to weed sources than to light grazing in itself. For instance, the exotic weeds, *Melinis minutiflora* (molassas grass) and *Rhyncheletrum repans*, were found in the virgin area of the crest of the Serra do Roncador extremely rarely and then almost exclusively in the disturbed soil of the new roadside where the seeds were undoubtedly brought in by vehicles. In Fazenda Campininha in São Paulo, in a region long cultivated, a small disjunct area of cerrado which had previously been grazed contained almost no weeds, even along the dirt roadsides when these were distant from habitations; weeds grew on the roadsides only near houses. In this respect the cerrado is like certain sandy parts of the eastern U.S. coastal plain, such as the New Jersey Pine Barrens. On the other hand, a cerrado scrub seen in Brasília changed its ground layer from native grasses and herbs to solid molassas grass (present on a nearby roadside) within a few months when it began to be heavily grazed.

Cultivation. Very little of the cerrado has been cleared up to now for cultivation. In a few areas plots of cerradão (which has the richest cerrado soil) have been cleared, as in São Paulo, Minas Gerais and southern Goiás. The lower cerrados are only now starting to be cultivated but are being destroyed rapidly. Since they generally occur on level ground it is economical to use machinery. This, plus the large outlay of capital necessary for limestone and fertilizers, means that farming in the cerrado is usually an industrial operation carried on by rich farmers, agricultural companies and cooperatives, and the government. It is not worth the effort of poor subsistence farmers to clear and plant it. In the greater part of the cerrado area of central Brazil there are no railroads to bring in fertilizer cheaply, and local limestone sources have not been much developed yet.

Cutting. Much larger areas of cerradão and lower dense cerrados have been cut over and burned to make unsown pasture than have been cultivated. This turns it into the more open savanna form (campo cerrado and campo sujo) so as to increase grass growth for grazing. This has been done in the southern part of the cerrado region where cerradão and other primitive cerrado forms are generally rather dense, shade the ground and have little grass growth. In southern Maranhão, on the other hand, the prevailing cerradões and lower arboreal cerrados with few exceptions have a more open tree canopy so that plenty of light reaches the ground and grass growth is thick. "Capim agreste" (*Trachypogon plumosus* Nees), the dominant grass here, reaches 1–2 (–3) m tall in flower with the leaves rising to half this height and grows densely so there is no need to cut the trees.

A great area of both forest and cerradão in São Paulo and southern Minas Gerais used to be cut to supply wood for the wood-burning locomotives of the railroads. The locomotives now are practically all diesels. However, large areas of forest and cerradão were and are rapidly being cut to supply charcoal for the iron foundries of São Paulo, Minas and the State of Rio, since Brazil has little coal (Oliveira, 1970). Every time a new road was built in a cerradão or forest area relatively near to large population centers, the charcoal makers immediately moved in and in less than a year almost all the arboreal vegetation was gone as far as could be seen from the road. Coke is also imported for the foundries and some siderugical companies grow eucalyptus for charcoal but only after all the cerradões within economic transporting distance are cut. In a few places, textile factories used firewood for generating steam power and cerradão within several tens of kilometers around the city was cut, such as in Caxias, Maranhão. Since the local rural population in the cerrado region has been small up to now, charcoal and firewood for home use has not caused much cutting of the cerrado; enough dead fallen wood can usually be found close by. Around villages and cities the demand is greater so more has been cut.

Where cerradão has been cut over, lower forms of cerrado of course take its place and these are usually burned often so that they have not generally regained their original heights.

Utilization. With the clearing of practically all the Atlantic coastal forest for agriculture, attention is now being turned to a more intensive utilization of the cerrado. Up to now it has been used only as a supply of charcoal and for open-range cattle raising. The large level topography and excellent physical condition of the soil make mechanized farming economical once limestone and mineral fertilizers are added.* Many articles in the popular Brazilian agricultural magazines are now being published on this aspect.

The transfer of the capital of Brazil from coastal Rio de Janeiro to Brasília, in the middle of the cerrado region, and the present gradual populating of this vast and relatively empty demographic space, has also turned attention to a more efficient exploitation of its vegetation and soil. Several symposia on the cerrado have been held, with papers on its botany, ecology, soils, zoology, geology, climate, phytochemistry and agricultural possibilities (Ferri, ed., 1963, 1971b; Serviço de Informacão

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* Agricultural grasses and legumes were grown in pot tests with cerrado soils from São Paulo and from Anápolis, Goiás, by McClung *et al.* (1958). Comparing growth when given complete nutrient solution with complete solution minus one element, they showed that lack of added phosphorus produced the poorest growth, particularly if lime was also not added. (Lack of lime itself had small depressing effect when the other elements were present.) Lack of nitrogen alone had small effect and lack of potassium none. Lack of an added mixture of micro-nutrients also significantly depressed growth. Later, McClung & Freitas (1959) showed that the lack of sulfur among the minor nutrients was responsible for the poor growth (when enough phosphorus was present) rather than lack of Mo, Cu, Zn, Fe, and B. The sulfur might be low because of burning of the cerrado. They concluded that phosphorus and sulfur are the elements most lacking for agricultural plants in the cerrado soils tested.

Miyasaka *et al.* (1964), in field tests, also found that phosphorus significantly increased bean and soybean yields on cerrado soils, while N and K had small effect. They did not test minor elements.

Agrícola, 1964; Labouriau, ed., 1966). There is increasing interest in cerrado land for growing trees, not only eucalyptus and pine but also cerradão species (Ferri, 1955c; Rizzini & Heringer, 1962a; Rizzini, 1970; Oliveira, 1970). Ferri (1963, 1964), Labouriau (1963, 1966), and Goodland (1969, 1970b) have presented summaries of research on cerrado vegetation, plants, soils, and ecology, and Labouriau's papers, as well as Labouriau & Vanzolini (1964), suggest further lines of research.

XIV. CERRADO AND THE SAVANNA CONCEPT

"Savanna" is usually defined and used in a wide sense, physiognomically, floristically and ecologically. In Africa it sometimes refers to all upland vegetation between evergreen rainforest and desert, including semideciduous and deciduous forests and woodlands, grasslands with scattered trees and/or shrubs, and pure grasslands of various types. Often high-altitude grasslands (alpine meadows) are excluded, but on the other hand, certain marshes may be included.

In Australia, "savanna" is more often restricted to grassland with scattered trees and/or shrubs.

In northern tropical America the "savanna" includes a number of different associations on seasonally wet and permanently dry white sands, and on wet and dry heavier soils. The physiognomy is that of pure grassfield or grassfield with scattered trees and shrubs or with scattered small groves of these (Beard, 1947; Blydenstein, 1962; Van Donselaar, 1965; Van Donselaar-Ten Bokkel Huinink, 1966). Dense scrubs and taller dry forests are often included in the concept by being referred to as "savanna scrub" and "savanna forest" (Van Donselaar, 1965). The water table approaches or reaches the surface seasonally, almost always to within 2 m or less. On sites where the top of the capillary water layer above the water table stays permanently more than a few decimeters below the soil surface and rain penetration from the surface does not reach the capillary layer, a permanent dry zone remains sandwiched between the two moist layers which may inhibit root growth vertically (Van Donselaar-Ten Bokkel Huinink, 1966). Laterite or clay hardpans may also be present and inhibit root growth. These savannas mostly suffer an alternation of long periods of soaking and of strong drying out.

From what has been said about the cerrado, it is obvious that the ecology of the northern tropical American savannas is very different from that of the cerrado. In fact, if a savanna concept ecologically and physiognomically as wide as that used in northern tropical America (lowland Columbia and Venezuela, the Guianas, Trinidad) were to be applied to Brazil, one would have to include as "savanna" not only the cerrado in all its forms but also (1) the valley-side grassy marshy campos that border the gallery forests in the cerrado region, (2) the scrubs and meadows of the rocky campos of the central Brazil mountain tops, (3) the periodically inundated pantanal grasslands, (4) a number of deciduous forests on special substrates, and (5) practically all the edaphic grasslands, savannas (sens. strict.), scrubs, and low forests, both upland and lowland, scattered within the Amazon tall forest (Sombroek, 1966). Among Brazilian vegetation, only tall evergreen forest, some mesophytic semideciduous forests, the thorn scrub caatinga, permanent marshes and beach and dune vegetation would be excluded from this wide sense of "savanna." Some European authors would even include the caatinga in the "savanna" concept (Cole, 1958, 1960).

The cerrado, even with all its permissable edaphic variants, is a much narrower concept; typical cerrado is narrower still. Its prevalent combination of deep, non-stony, non-lateritic latosols, with a permanent very deep water table, does not seem to be duplicated in savannas in northern tropical America.

XV. THE CERRADO AS CLIMAX

In view of the present exposition we can see that cerrado is a climax vegetation, that is, it is not a stage or a disclimax in either a primary or secondary succession to a forest or to any other vegetation type. However, the kind of climax it is should be made more explicit.

Let us consider the cerrado first as a type of vegetation in the wide sense distinct from the neighboring and included mesophytic forests, marshes, non-cerrado grasslands and various types of lithosol campos. One recognizes the cerrado in any one of its structural forms and successional or disturbance stages by its high proportion of distinctive species (most of which do not occur in the other vegetation types) and by the distinctive morphological peculiarities of these species: thick bark, twisted boughs, leaning and twisted trunks, thick twigs, large leaves, sclerophylly, etc. In practice, this is how a stand of cerrado is recognized. Since essentially undisturbed cerrado in its closest approach to "virgin" conditions occurs in every possible structural form, and since species composition varies considerably from stand to stand in the same region, even among stands with the same structure on similar topographic positions and with similar soils, neither structure (physiognomy, formation type, life form of visual dominants) nor narrow floristic "associations" in the Clementsian or Braun-Blanquet sense can be used to define the cerrado. Thus, a third criterion for recognizing a community to be called climax, namely, a distinctive morphology of the individual plants independent of their height and spacing, must be added to the two mentioned by Whittaker (1953), which were "growth-forms" or "physiognomy" (i.e., structure) and "populations" (i.e., associations).

Still considering undisturbed cerrado in the wide sense, is it a climatic, topographic (physiographic), edaphic (lithologic and pedologic), biotic, fire, or some other climax? Since we are now speaking about cerrado as undisturbed by man, fire would enter only as natural lightning-caused fire. We saw that this almost certainly occurred but was infrequent and from present-day evidence did not essentially change the basic physiognomy. There is no evidence for non-human biotic control of cerrado. Termites and ants do not make any essential difference when they are present in large numbers or small (as testified by the frequency of their nests). There are and were no large herds of native grazing mammals, such as the bison that maintained a shortgrass natural disclimax in the midgrass plains of North America.

The first four factors, climate, topographic position, underlying rock and soil, do, together, "cause" cerrado. In the first place, the monoclimax view does not hold here; in the same climate, on deep upland soils, evergreen mesophytic forest, semideciduous mesophytic forest, or cerrado in any of its forms can occur depending on soil fertility. There is no autogenic successional convergence to one of these vegetations in this environment. Yet climate does control cerrado in the sense that outside of a certain climatic range which can be defined, cerrado does not occur. Topography also controls cerrado. Within a climate favorable for cerrado, this vegetation will not grow on slopes so steep that soil cannot stay in place, nor in places where water accumulates or flushes out so as to soak the soil, and this is true whatever the fertility of the soil. Lithology and soil also control cerrado. Within the climatically favorable region, on suitable drained topographic sites, typical cerrado forms occur only where a deep soil can build up. The nature of the underlying rock (or in some cases transported soil material) and the length of time this has been subjected to weathering determine whether cerrado or mesophytic forest will occur. Rock type and time act together to produce the final result. If the rock type or transported soil material is already poor in the minerals that yield nutrients on weathering, the soil will be poor even when recently formed. If the rock type is richer but the residual soil it has produced has weathered for a long enough time, the soil will also be poor, and in both cases supports cerrado over forest.

Thus the cerrado is *at the same time* a climatic, topographic, and edaphic climax.

Structural variations within virgin cerrado are due to edaphic differences of soil fertility and latosolization among more or less level deep-soil stands. Less frequently variations are due to shallowness of soils or to differences in upland topographic position (level ground compared to scarp, ridge or hillside). Each of these different structures of cerrado is also climax for it lasts through geologic epochs and changes only with geomorphologic change of the topography or with the slow rate of soil latosolization, assuming during this time period that the climate does not change so much that cerrado disappears from the region.

Floristic variation in virgin cerrados is correlated with stand structure, both of these being correlated with the environmental factors just mentioned. But the same structure in a single small region can have differences in composition. How much this is due to chance effects is unknown. Thus any floristic "associations" or arbitrary portions of a floristic continuum within undisturbed cerrado vegetation would be edaphic climaxes when compared one with the other. Since the cerrado extends over a large geographic region, differences in species composition in cerrados far apart are also due to the limited range of individual species.

Human disturbance of the cerrado is mostly in the form of a much increased frequency of burning. In some regions there is extensive cutting of cerradão for charcoal for industrial purposes or to make pasture. Grazing by domestic animals in uncut cerrado probably also has some effect. Clear cutting or complete destruction of the trees by burning would introduce a secondary succession, at least in reference to the trees. But probably most disturbance has caused only a partial structural regression to a lower more open phase of the woody layer. These continually disturbed cerrados are at various stages of recuperation from the periodic partial destruction, but no studies have been made on secondary succession.

Cerradão is the tallest form of cerrado and where present is undoubtedly climax. Lower, more open forms are caused by a variety of factors: (1) soil poverty, (2) water-logging, (3) thinness of soil, (4) "excess" fires, (5) cutting, (6) over-grazing by domestic animals, trampling, soil erosion, etc. Factors 1, 2 and 3 are natural, not due to man except indirectly in some cases; 4 is a more intense occurrence of a naturally occurring factor; 5 and 6 are not present in the absence of man except for some rare soil erosion on very steep deep-soil slopes.

Whittaker's climax pattern idea (1953) is the most useful approach for cerrado, as for any other vegetation, for relating the stable vegetation communities of a region. It shares with the polyclimax view the realization that there is no one single cause for a climax, such as the climate, and that all vegetation in a region does not necessarily converge to one type of community. On the other hand, it does not assume the existence of definite "associations" but rather different terminal species compositions that fit different environmental conditions, and with chance variations in composition among sites that are environmentally similar. I only wish to point out that along some gradually changing environmental gradients, such as soil fertility, the vegetation may also change gradually, such as in cerrado structure and floristic composition, or as in the change from cerradão to mesophytic forest, while along other gradually changing environmental gradients the vegetation may change suddenly, such as the change from cerrado scrub or woodland to valley-side non-cerrado grassy campo at a certain point in the gradual approach of the water table to the surface (Fig. 16). Daubenmire (1968, p. 18) gives other examples of this type of change.

The environmental gradients involved among primitive vegetation types in the climatic region of the cerrado province are: (1) total soil fertility, mineral and organic, possibly with associated aluminum toxicity, (2) accumulation of water along drainage lines, (3) periodicity in soil soaking, (4) soil depth. The first two gradients are shown in Table VIII.

FIG. 16. Very gentle valley side on the Serra do Roncador, Mato Grosso. Virgin vegetation of cerrado woodland on left (over deep water table) and mesophytic gallery forest on right (over shallow water table). Between the two woody communities is a belt of grassland on seasonally moist soil.

The classes represent stages in a continuous sequence and are meant to show relative position, not exact absolute values. The soil fertility gradient is fully expressed only on completely drained deep soils. The drainage gradient shown holds only for those parts of the cerrado region where valley-side marshy campos are not present. In this case, low open cerrados on uplands grade to gallery forest through a narrow

TABLE VIII

TWO DIMENSIONAL GRADIENT OF CLIMAX VEGETATION IN THE CERRADO REGION ON DEEP NON-STORY SOILS.

Drainage		Soil Fertility (mineral and organic): high ←					→ low
good ↑	Well-drained uplands (deep water table)	Mesophytic evergreen forest (mata)	Mesophytic semideciduous forest (mata sêca)	Xeromorphic semideciduous forest or woodland (cerradão)	Xeromorphic tree and scrub woodland or closed to slightly open scrub (cerrado, strict sense)	Xeromorphic tree and scrub savanna or scrub savanna (campo cerrado)	Xeromorphic very open low shrub savanna (campo sujo)
Drainage	Water accumulates but does not inundate surface (shallow water table)	Mesophytic gallery forest (mata galeria)			cerradão ecotone	cerrado (s.s.) ecotone	campo cerrado ecotone
↓ poor	water accumulates with seasonal to permanent inundation	Gallery swamp forest (mata pantanosa)					

TABLE IX

TWO DIMENSIONAL GRADIENT OF CLIMAX VEGETATION IN THE CERRADO REGION ON UPLAND SOILS.

<table>
<tr><td rowspan="5">deep
↑
Effective soil depth
↓
shallow</td><td>several to many meters</td><td>Mesophytic evergreen forest
(mata)</td><td rowspan="3">Mesophytic semideciduous forest
(mata sêca)</td><td>Xeromorphic semideciduous forest or woodland
(cerradão)</td><td colspan="2">Xeromorphic tree and scrub woodland or closed to slightly open scrub
(cerrado strict sense)</td><td>Xeromorphic tree and scrub savanna or scrub savanna
(campo cerrado)</td><td>Xeromorphic very open shrub savanna
(campo sujo of cerrado flora)</td></tr>
<tr><td rowspan="2">several decimeters to ca. 2m</td><td rowspan="2">Mesophytic deciduous forest on limestone (rooted in soil or cracks in rock) (mata sêca)</td><td colspan="2" rowspan="2">campo cerrado</td><td colspan="3">campo sujo
(of cerrado flora)</td></tr>
<tr><td colspan="3">campo limpo
(of cerrado flora)</td></tr>
<tr><td rowspan="2">none to a few decimeters</td><td colspan="6">rocky campos (grassy or shrubby)
(campos rupestres campos de altitude)</td><td rowspan="2">low herbaceous carpet over solid surface of laterite pavement</td></tr>
<tr><td colspan="6">low herbaceous carpets over bedrock
(occasionally with shrubs or carnaúba palms in n.e. Brazil)</td></tr>
<tr><td></td><td></td><td colspan="7">high ← Soil Fertility (mineral and organic) → low</td></tr>
</table>

ecotone of taller denser cerrado, then cerradão. This is due to the greater soil fertility caused by increasing water accumulation, the same water accumulation that ultimately causes a gallery forest to form. (We are here dealing with the case where the same rock type is exposed over the whole valley profile. When a deeper richer rock layer is exposed, the richer residual soil adds its effects to the greater water accumulation.) This cerrado ecotone to gallery forest has been indicated in the table on the middle level and is shown as compressed zones shifted to the left, that is, more soil water produces the same vegetational effect as a soil with an originally richer mineral component.

Where valley-side marshy campos are present the case is more complicated. Since they invariably occur between well-drained upland cerrado and gallery forest, they probably evolved to fit alternating seasonal conditions of water flush and dryness at the soil surface on the poor soils that originally supported cerrado before the valley formed. Once evolved, they could compete with gallery forest in some cases, holding their own against forest or buriti palm grove on lower slopes which are continually moist. This gradient in the habitat, in some regions such as eastern Mato Grosso, southwestern Goiás, the Triângulo Mineiro and parts of western São Paulo, does not cause a gradient in the total vegetation but rather the placement along it of sharply distinct vegetation forms. *Within* each of the distinct vegetation forms there is a floristic gradient correlated with the environmental gradient. In other regions, such as northern Goiás and central Maranhão, the "clean grassy ground layer" cerrados, which are possibly a subsurface drainage phenomenon, span the gap between the usual cerrados and pantanal grassy marshes, thus producing a continuous vegetational gradient also.

The fourth gradient, soil depth, is shown in relation to soil fertility in Table IX. The classes here also represent stages in a continuous sequence. *Effective* soil depth is meant, that is, the depth to which the roots can actually penetrate and exploit. Rocks or laterite blocks exposed at the surface have no effect if tree roots can easily penetrate between them to lower soil levels. A highly weathered rock or a dense layer of small closely-fitting laterite blocks and pebbles exposed at the surface may be penetrated in its cracks to 1 or 2 m so that the effective soil depth is deeper than appears. On the other hand, this penetration may be accomplished by relatively few individuals of woody plants so that a lower more open vegetation results than if the same depth were pure soil.

The campo limpo of southern Mato Grosso (Campos da Vacaria) is not included in these tables. I do not know if its soil is less fertile than that of the surrounding wooded cerrados. Its climate, related to its position at the southern edge of the cerrado region, is probably involved as well as soil fertility, perhaps in a similar fashion to that of the cerrado-type campos limpos of São Paulo. Drainage factors may also be acting.

Most cerrado is on more or less level ground with deep infertile soil. This type covers by far the greatest part of the ground surface of the total cerrado region, probably over 80%. Only a small proportion of the cerrado region is covered with fertile soil, shallow soil, laterite, steep slopes or soaking ground. Therefore, most investigation of the relation of cerrado to its environment will naturally be on level deep-soil sites. Here differences in structure and floristic composition are due to original differences in soil fertility; superimposed on this variation is the further variation due to human disturbance. This disturbance has in itself reduced soil fertility even more from its originally low level, so that the attainment of the climax condition upon protection from further disturbance would take a long time since the soil would have to build up its former fertility.

The cerrado is a large-scale vegetation type, a whole floristic province. Although variations in species composition can be noted from place to place associated with different structures or among stands of the same structure, the changes are gradual. Very little quantitative sociology has yet been done in cerrado. A very large proportion of it has never even been botanized to know the species present, much less their quantitative relations. Careful studies such as those of Ratter (1971) distinguishing two floristic types of primary cerradão within a small area of the Serra do Roncador in Mato Grosso are almost unique. Therefore, it seems extremely premature to distinguish floristic climax types of the cerrado as a whole at present, even in a vague way, and worse yet, to map them, as has been done by Veloso (1966b).

XVI. SUMMARY

The cerrado is a semideciduous xeromorphic vegetation dominant in central Brazil, occupying about 20% of the whole country or 40% of the non-Amazonian part. It forms a floristic province with a rather

distinct flora on the species level although much less distinct on the genus level. It has a unique appearance. Its taller woody plants are characterized by thick bark, leaning and twisted trunks, twisted jagged boughs, thick twigs, open crowns, large hard or soft-hairy simple leaves or large palmate or pinnate compound leaves. It occurs in every possible structure from closed forest-like forms, through arboreal woodlands, tree and scrub woodlands, closed or open scrubs, dense to very open tree and scrub savannas or scrub savannas, to pure grasslands. In different parts of the cerrado region different ones of these structures are the prevalent native forms, but annual burnings and cutting-over have lowered and/or opened the woody layer of much of the taller denser cerrados. The ground layer is seasonal, predominantly grassy, with some xerophytic sedge species and many herbs, and a variable density of low shrubs, semishrubs, and a few herbaceous to woody or subwoody ground and climbing thin-stemmed vines. Both woody and herbaceous species have a high degree of leaf xeromorphism, and the forbs, low shrubs and semishrubs generally have xylopodia.

The cerrado occurs within an intermediate rainfall region, and only its southern edge may occasionally experience frosts. To the west and southeast, where rainfall is higher and the dry period less strong, the cerrado gives way to continuous mesophytic forest provinces, respectively, the Amazon forest and the Atlantic coastal forest. To the northeast and southwest, where the rainfall is lower and the dry season stronger, the cerrado gives way respectively to caatinga and to the Chaco vegetation. Within its own climatic region, the cerrado is adapted to poor, well-drained, senile soils with low nutrient-ion content and high available aluminum and aluminum saturation (latosols). These soils cover the major proportion of the area. Richer upland soils from more basic rocks in this climatic region occupy only a relatively small area and are covered by mesophytic forest. Where cerrado covers the upland, gallery forests follow the streams.

Up to now the cerrado region has been sparsely inhabited and used almost only for extensive cattle raising. It is now beginning to be cultivated (with the addition of limestone and mineral fertilizers) in the more populated southern portion where there is no more uncleared forest land available.

The cerrado is a climax vegetation dependent upon the correct range of climate, topographic position and soil. Its secondary and regressive stages due to human disturbance are also part of the same vegetation type, and most of the species of the secondary stages are the same as those of the climax stage.

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