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A Hectare of Cerrado. I. General Aspects of the Trees and Thick-Stemmed Shrubs

By

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With 9 Figures

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Summary

SILBERBAUER-GOTTSBERGER I. & EITEN G. 1987. A hectare of cerrado. I. General Aspects of the trees and thick-stemmed shrubs. – Phyton (Austria) 27 (1): 55–91, 9 figures. – English with German summary.

An analysis is presented of a square hectare of cerrado in the middle of São Paulo State, Brazil. When examined it was in a rather dense tree and scrub woodland phase, slowly returning to its original taller and less dense tree woodland form. Its 1180 trees 3–8 m tall, and 3017 shrubs and treelets (scrub), with trunk circumferences of 10 cm or more at 30 cm vertical height, fell into 54 species, of which 42 occurred in both growth forms. *Styrax ferruginea* was the most abundant tree in density, basal area, frequency, and cylindrical volume. *Erythroxylum suberosum* was the most abundant scrub element. A quadrat size of 400 m² gave the most satisfactory size for frequency measurements. Long thin rectangles gave slightly greater frequencies than more equidimensional ones of the same area. Importance curves based on different measures of species quantity of the same complete census had forms varying between the random niche boundary model and the log normal. The trees alone, the scrub elements alone, and the two combined, considering all species together, are slightly clumped on a 10 × 10 m scale. The individual species are also mostly clumped, both on a small and a large scale. All measures of species quantity are strongly correlated with each other. Heights of individuals of different species are correlated with their trunk circumferences on either a linear, logarithmic, or power function regression. Ten percent area samples of density for the hectare, of trees and scrub combined, and

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for the individual species, are not accurate compared to the complete census, nor is a point-quarter sample using 20 points. Cylindrical volume growth over a 3-year period was an average 1985 cm³ per year per surviving individual, or 5.22 m³ per year for the hectare. The average foliage cover above eye level is 41%. A heavy frost decreased the cover but the effect was temporary.

Zusammenfassung

SILBERBAUER-GOTTSBERGER I. & EITEN G. 1987. Ein Hektar Cerrado. I. Allgemeine Aspekte über die Bäume und Zwergbäume. – Phyton (Austria) 27 (1): 55–91, 9 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die vorliegende Arbeit umfaßt die Analyse eines Hektars typischer brasilianischer Cerrado-Vegetation aus dem Zentrum des Staates São Paulo. Zum Zeitpunkt der Untersuchung befand sich die ziemlich dichte Baum-Strauchvegetation in einem Übergangsstadium zu ihrer wahrscheinlich ursprünglichen, höheren und weniger dichten Form. Die 1180 Individuen von 3–8 m hohen Bäumen und 3017 Zwergbäumen, mit einem Stammumfang von mindestens 10 cm, verteilen sich auf 54 Arten, von denen 42 sowohl als Bäume als auch als Zwergbäume vorkommen. 8 Arten machen 50% des Holzbestandes aus. *Styrax ferruginea* war die häufigste Baumart und *Erythroxylum suberosum* die häufigste Zwergbaumart, wenn man die Anzahl der Individuen, ihre Basalfläche, Frequenz und ihr Zylindervolumen berücksichtigt. Um den RAUNKIAERschen Frequenzklassen entsprechende Resultate zu erhalten, erwies sich erst eine Fläche von 400 m² als genügend groß. Lange, schmale Rechtecke gaben eine etwas größere Anzahl von Individuen in den Frequenzklassen, als gleich große von mehr quadratischer Form. „Importance"-Kurven, die auf vollständig erfaßten Daten basieren, variierten für die verschiedenen Größen zwischen dem „Random-Niche-Boundary"-Modell und dem Logarithmus-Modell; man kann daher aus keiner der Kurven auf die Ursachen der Häufigkeit der Arten schließen. Aussagen über die Verteilung der Arten hängen von den in Betracht gezogenen Flächengrößen ab. Auf eine Fläche von 10 m × 10 m bezogen, zeigen die Bäume allein und die Zwergbäume allein sowie beide zusammen immer eine leichte Tendenz zu Gruppierungen. Alle für eine quantitative Aussage über die Arten gemessenen Werte sind stark miteinander korreliert. So sind zum Beispiel die Höhen der Individuen der verschiedenen Arten mit ihren Stammumfängen entweder linear oder logarithmisch oder in Exponentialfunktion korreliert. Eine Minimalfläche von 10% gibt nicht die richtigen Werte für die Individuenzahlen wieder, weder für die Bäume und Zwergbäume als Gruppe, noch für jede einzelne Art. Auch die Resultate aus der „Point-Quarter"-Methode mit 20 Meßpunkten kommen den exakten Werten nicht nahe. Die auf 10% der Fläche gemessene Zunahme des Zylindervolumens innerhalb von 3 Jahren ergab einen Jahresmittelwert von 1985 cm³ für jedes überlebende Individuum oder 5,22 m³ für den gesamten Holzbestand des Hektars. Der Deckungsgrad der Vegetation, errechnet als Mittelwert der Blattdeckung oberhalb der Augenhöhe, war 41%. Ein starker Forst verminderte diesen Wert vorübergehend.

Introduction

Cerrado is the prevailing vegetation of Central Brazil. The woody layer of trees and shrubs that are visually distinct from the ground layer in natural undisturbed stands occurs in all heights and densities, yielding medium tall closed-canopy forest-like forms, open tree-canopy woodlands, closed and open scrubs, and savannas with very scattered trees and shrubs, or this woody layer is absent, yielding forms of cerrado with only a ground layer (EITEN 1972, 1978, 1983). The ground layer is predominantly grassy although it also contains forbs as well as low thin-stemmed semishrubs and shrubs that look like forbs and that do not stand out from the grass-forb layer and so appear to be part of it (EITEN 1984). In the cerrado province, species-rich gallery forests on well drained or swampy soil, or sometimes "veredas" (closed or open stands of buriti palms, *Mauritia vinifera,* in permanent grassy marshes) follow the streams in valley bottoms. Cerrado either contacts the gallery forest directly or is separated from it by a strip of seasonally saturated grassy campo. A very small proportion of the uplands of the cerrado province in Brazil is occupied by evergreen or deciduous forest or non-cerrado campos.

Published quantitative accounts of the cerrado are almost always of scattered quadrats (GIBBS & al. 1983) or point-quarter samples (GOODLAND 1969, 1979) in a large stand. The only other work we know of that attempts to be a complete census of a whole hectare of cerrado is that of HERINGER (1971 a, 1971 b, HERINGER & BARROSO 1968). However, the only information given is the presence of vascular species, without stating in what growth form, in the twenty five 20 × 20 m squares into which the hectare was divided, and even then many of the species present were not mentioned because their specific names had not yet been determined (HERINGER, personal communication).

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Site characteristics

The present paper is a detailed analysis of a single square one-hectare stand of cerrado, situated on slightly sloping ground of a broad shallow valley (Fig. 1) at 550 m altitude, in the Município de Botucatu, 14 km east of the city of São Manuel and 18 km north of the city of Botucatu, at 22°45'S.48°25'W., in the center of São Paulo State. The original vegetation of the region was a mosaic of evergreen broadleaf mesophytic tropical forest and xeromorphic cerrado woodland, both on deep non-stony latosols, the difference in vegetation depending on soil fertility. The forest land is now mostly in cultivation or pasture; the cerrado land is being extensively planted to eucalyptus, or with continual application of limestone and fertilizer, to crops. The hectare when examined in 1971–1975 was in the middle of a preserved area of 700 ha, the remains of a disjunct cerrado that originally covered many tens of square kilometers. This small remnant has since been completely converted to a sugar cane plantation.

Although never clear-cut up to the years it was examined, the cerrado vegetation in and around the hectare had experienced occasional fires and the selective cutting of barbatimão trees (*Stryphnodendron adstringens* (MART.) COVILLE) for their tanniniferous bark. The physiognomy of the hectare was a "low-tree and scrub woodland", although a rather dense one, verging on the "uneven-height closed low-trees and scrub" category (see EITEN 1968 for discussion of physiognomic categories of vegetation). Trees 3–8 m tall formed a slightly uneven-density open layer which admitted abundant light to the treelets, shrubs and ground layer (Figs. 2, 3). Photographs of the site can be found in GOTTSBERGER & SILBERBAUER-GOTTSBERGER 1983 and in SILBERBAUER-GOTTSBERGER & EITEN 1983. There was no real canopy of approximately even height as in a forest or in many arboreal woodlands of open canopy. The total woody plant cover of trees and thick-stemmed shrubs was about 50% (41% above eye level). This physiognomy was probably not the climax form in the hectare. Just upslope was a small grove of taller arboreal cerrado with a closed upper layer forming a more definite canopy which shaded the ground, of trees to 12 m tall; this is the "cerradão" form (Fig. 1) (SILBERBAUER-GOTTSBERGER & GOTTSBERGER 1984). It was nearer to the original state, although the average height of the original cerradão in this spot cannot be ascertained. (The height of undisturbed cerradão depends on the fertility of the soil.) The hectare studied was, then, at a late recovery stage from partial destruction, slowly growing up to cerradão. The propagule dispersal modes of the species of the hectare were discussed by GOTTSBERGER & SILBERBAUER-GOTTSBERGER 1983.

A short preliminary paper in Portuguese on this hectare (SILBERBAUER-GOTTSBERGER & EITEN 1983) has slightly different values for a few of the numbers given here. This is because after that paper was published a few individuals of trees and shrubs were redetermined as to species. The equiva-

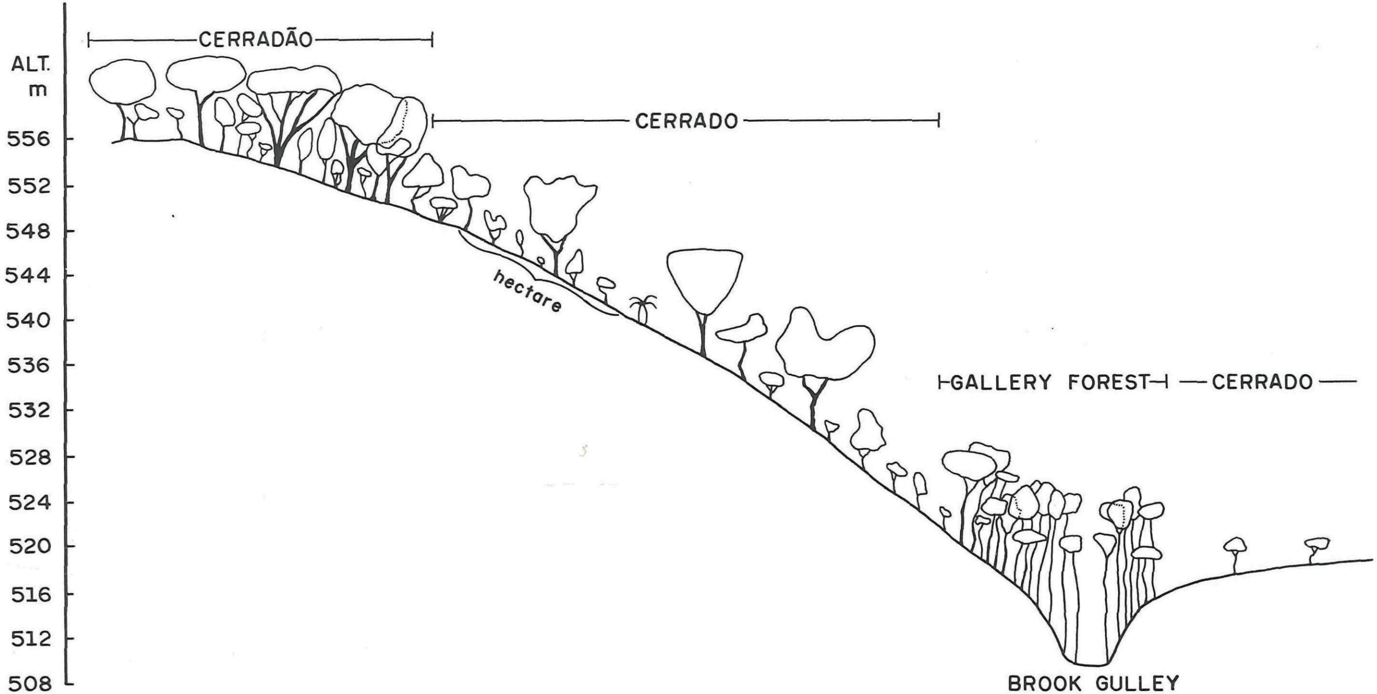


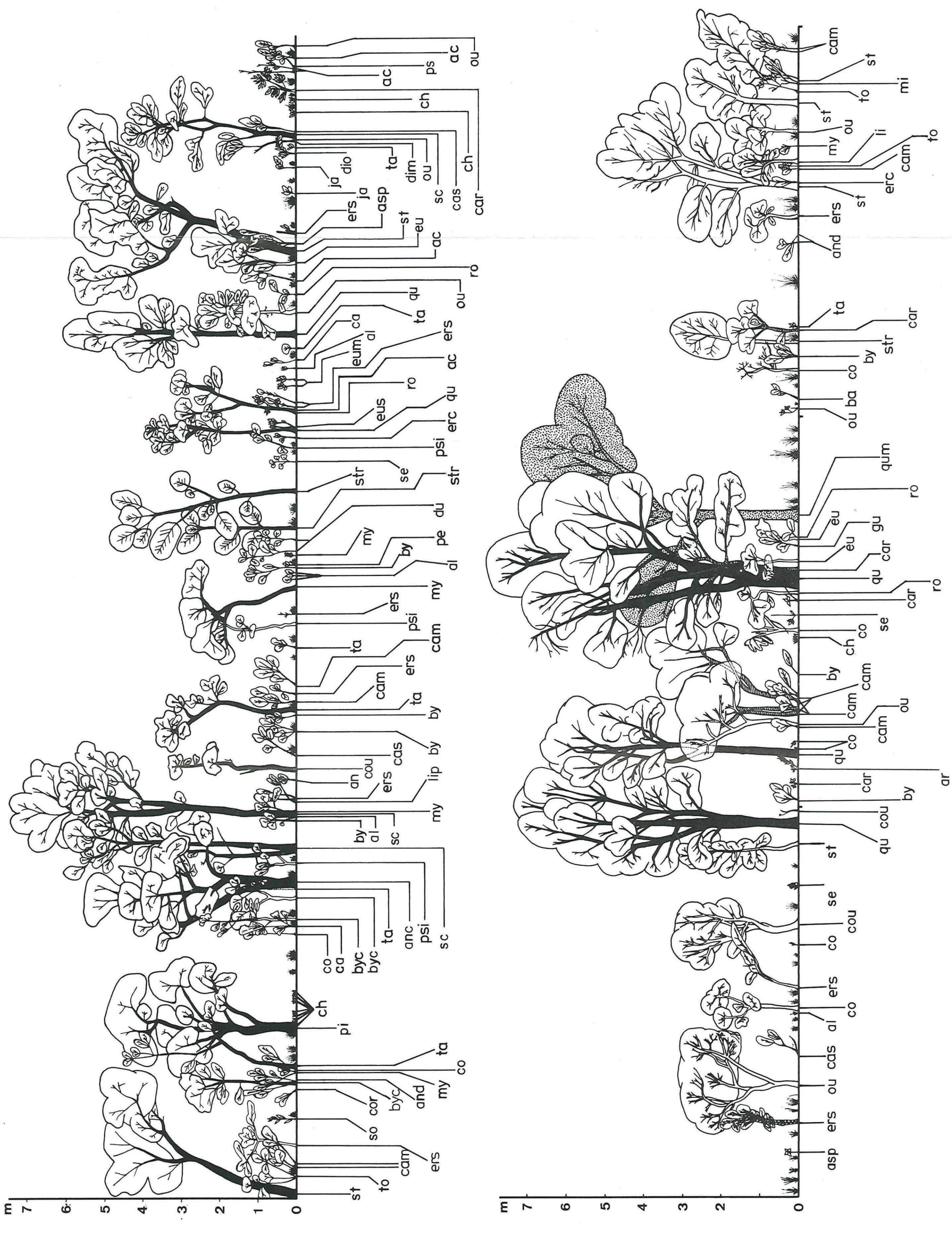
Fig. 1. Diagrammatic profile of the slope on which the cerrado hectare is located. Vertical scale for ground line exaggerated 6.24 times; vertical height of vegetation more exaggerated.

lent numbers differ almost always by only one unit and make no difference in the general conclusions reached.

Climate

The nearest weather station is at Fazenda Edgârdia, 8 km south of the hectare at 520 m alt., almost the same elevation as that of the hectare. The exact altitude is important since in São Paulo rainfall increases considerably with altitude. Also, although the average temperature decreases with altitude, the minimum temperature increases, within the range of altitudes found in this region. Temperature differences probably make a difference within the region only in relation to strong frosts. Only a small proportion of the total cerrado area in Brazil, its southern edge, experiences frosts. Southwestern São Paulo has 1–4 mild frost days a year in the cold season (SETZER 1946). Once every few decades a hard frost occurs which kills most of the coffee plantations and damages a small proportion of native cerrado woody plants (SILBERBAUER-GOTTSBERGER, MORAWETZ & GOTTSBERGER 1977). The tips of the branches, a few whole branches, or rarely the whole above-ground portion of the plant are killed, but in the latter case the plant reshoots from underground parts the next growing season.

Fig. 2, 3. Profiles of cerrado in the hectare where the trees are more evenly spaced and where they are grouped. Band length 30 m, band widths 0.5 m for thin-stemmed shrubs less than 3 m tall, 1.5 m for thick-stemmed shrubs, 4 m for trees in Fig. 2 (top) and 5 m in Fig. 3 (below). All plants drawn to scale. ac. *Acosmium subelegans* (MOHLENBR.) YAK., al *Alibertia obtusa* CHAM., an *Annona cornifolia* ST. HIL., anc *Annona crassiflora* MART., and *Annona dioica* ST. HIL., ar *Arrabidea brachypoda* (DC.) BURM. & K. SCHUM., as *Aspidosperma tomentosum* MART, asp *Aspilia floribunda* BAKER, ba *Banisteriopsis latifolia* (A. JUSS., in ST. HIL.) GATES, by *Byrsonima intermedia* A. JUSS., byc *Byrsonima coccolobifolia* KUNTH, ca *Cassia langsdorfii* KUNTH ex VOG., cam *Campomanesia* sp., car *Caryocar brasiliense* ST. HIL., cas *Cassia rugosa* G. DON, ch *Chrysophyllum soboliferum* RIZZ., co *Connarus suberosus* PLANCH., cor *Cordia truncata* FRESEN. in MART., cou *Couepia grandiflora* (MART. & ZUCC.) BENTH., dim *Dimorphandra mollis* BENTH. & HOOK. f., dio. *Diospyros hispida* A. DC., du *Duguetia furfuracea* (ST. HIL.) BENTH. & HOOK f., erc *Erythroxylum campestre* ST. HIL., ers *Erythroxylum suberosum* ST. HIL., eu *Eugenia aurata* BERG, eum *Eugenia mugiensis* BERG, eus *Eugenia* sp. 1, gu *Guapira noxia* (NETTO) LUNDELL, ja *Jacaranda rufa* MANSO, li *Licania humilis* CHAM. & SCHLECHT., lip *Lippia salviifolia* CHAM., mi *Miconia fallax* DC., my *Myrcia lasiantha* DC., ou *Ouratea spectabilis* (MART.) ENGL., pe *Peritassa campestris* (CAMB.) A. C. SMITH, pi *Piptocarpha rotundifolia* BAKER, ps *Psidium incanescens* MART., ex DC., psi *Psidium* sp., qu *Qualea grandiflora* MART., qum *Qualea multiflora* MART., ro *Roupala montana* AUBL., sc *Sclerolobium aureum* (TUL.) BAIL., se *Serjania erecta* RADLK., so *Solanum lycocarpum* ST. HIL., st *Styrax ferruginea* POHL, str *Stryphnodendron adstringens* COVILLE, ta *Tabebuia ochracea* (CHAM.) STANDLEY, to *Tocoyena formosa* (CHAM. & SCHLECHT.) K. SCHUM. Graminoids shown but not named.



Weather data are available for Edgârdia station for 1971–5. The daily means of temperature through the year ranged from 16.1° to 24.9°, the lowest in July and the highest in February. The yearly average is 20.7°. Precipitation is about 1200 mm per year, but up to 40% departures from the long term average may occur in either direction in a particular year in this part of the state. At Edgârdia, precipitation was 963 mm in 1971, 1649 mm in 1972 and 986 mm in 1973. The driest months are June, July, or August when 0–26 mm falls per month on the average. There is a single wet season; the rainiest months are December or January with 137–441 mm per month. Air humidity varies from 57–75% in the dry season to 82–88% in the wet season between rains. Full sunlight varies from 101 to 287 hours per month.

Soils

Soil samples were taken at various depths in two pits just outside the hectare but within a few meters of its upslope and downslope boundaries (Table 1). Also, a 10 × 10 × 10 cm surface block of soil was taken from the center of each of the one hundred 10 × 10 m squares into which the hectare was divided. Because many of the soil values are extremely small, especially in the deeper layers, some values for a particular character are repeated several times because this is the smallest amount that can be registered and the larger values are multiples of it. The soil is a red latosol (haplustox), very deep and without stones, the most common soil type for cerrado. This particular latosol is very clayey, with (83.4–)86.0–89.4% clay, 0.4–4.2% silt, and (7.6–)9.7–11.8(–15.6%) sand in the 0–10 cm layer, and thus is quite different in granulometry (but not in chemistry) from GOODLAND's 110

Table 1

Soil values in two pits

sample depth	pH (H_2O)	organic matter	available ions, meq/100 g soil			
			Al^{+++}	K^{+}	PO_4^{---}	Ca^{++}
upslope pit						
0– 10 cm	4.6	0.98	0.80	0.030	0.021	0.08
30– 40 cm	4.9	0.36	0.64	0.027	0.008	0.08
60– 70 cm	4.8	0.36	0.72	0.027	0.005	tr
130–140 cm	4.7	0.16	0.64	0.022	0.004	0.08
downslope pit						
0– 10 cm	5.1	0.93	0.80	0.060	0.028	0.24
30– 40 cm	4.9	0.51	0.64	0.020	0.008	0.08
60– 70 cm	4.7	0.36	0.64	0.020	0.004	0.08
130–140 cm	4.7	0.31	0.64	0.025	0.004	0.08

samples of cerrado red latosols from western Minas Gerais (GOODLAND 1969, 1979), which had 70–90% sand. The pH in water of the surface soils in the hectare varies from 4.4 to 4.9 (mode at 4.8) in the hundred samples, a usual acidity of cerrado soils. The pH in 1N KCl varies from 3.6 to 4.1, and the difference between the two measurements in the same soil sample varies from (0.6)0.7 to 0.9(1.0) units. High, medium, and low values for all soil characteristics analyzed are scattered over the hectare; there is no general change across the hectare in any direction, nor do high or low values concentrate in any part of it such as the center or at one corner or edge. In the soil pits the surface soil layer on the upslope side is slightly more acid and that on the downslope side slightly less acid than the deeper layers.

The percent organic matter multiplied by 1.7 gives approximate humus content. In both profiles the humus content is 3–6 times greater in the upper 10 cm (although even there less than 1.7%) than in the deeper layers. Below one meter it drops to one half or one quarter of 1%.

Exchangeable K and Ca is very low in the surface horizon, varying from 0.028 to 0.074 meq and 0.035 to 0.113(–0.212) meq, respectively, per 100 g soil over the hectare. Both elements diminish with depth from slightly less, to a third of their surface values. Available Mg in the surface layer varies over the hectare from proportions of 0.17 to 0.36 of the available Ca in the same sample. (It is not shown for the pit samples.) The most significant macronutrient is phosphorus. Even small differences in trace amounts are associated with changes in the density and physiognomy of cerrado vegetation (SETZER 1966, GOODLAND 1969, 1979, GOODLAND & POLLARD 1973). In the upper 10 cm it varies from 1.3 to 5.3 ppm (0.004 to 0.017 meq) per 100 g soil over the hectare. The surface layer of the pit samples gives larger values, 0.021 and 0.028 meq, perhaps due to differences in the analysis technique (this was also true of carbon content), and these values reduce to a third or a fourth of the surface values at 30–40 cm depth, and to a fifth or seventh of the surface values at lower levels.

There is an appreciable content of available aluminum, (0.11–)0.60–1.04 meq per 100 g soil, over the hectare. This is 4–8 times as much as the other non-hydrogen atoms combined, in the same samples, and it diminishes only slightly with depth. (See GOODLAND 1969, 1971 for discussion of Al in cerrado soils.) Sodium ion concentration is negligable, 0.001–0.009 meq per 100 g soil, over the hectare.

Methods

The hectare was marked on the ground with iron stakes and iron wire as a square divided into 100 10 × 10 m squares, which were consecutively numbered in a sweeping fashion starting with the lower right hand corner when looking upslope.

There are two distinctive floras in cerrado vegetation, one composed of thick-stemmed woody plants (stems about 1.5 cm diam. or more at the base) of all heights from 0.3 m up, and the other of thin-stemmed plants (stems almost always less than

1.0 cm diam. at the base), which may be woody, semiwoody, or herbaceous. The thin-stemmed plants make up the ground layer of the cerrado. The thick-stemmed plants make up what is usually considered the "woody layer". The thick-stemmed plants are treated here. These make up about one fifth or one sixth of the total vascular flora in any one hectare of a moderately dense cerrado but in which light is not a limiting factor to the plants of the ground layer. For this paper, all woody plants with trunks of 10 cm circumference (3.18 cm diam.) at 30 cm up from the ground were counted, measured, and identified to species. Those falling into the height class centered on 3 m tall or more are called "trees"; those of lower height are called "thick shrubs". There is a complete intergradation between these two classes and the large majority of the species have mature individuals in both classes. When it was not possible to measure the circumference at exactly 30 cm up because branches or branch stubs were present at that level, or the trunk divided or boughs came out below that level, the measurement was taken as near as possible to 30 cm but below any boughs. This low height was chosen because cerrado trees branch at low levels. Even so, 14.5% of the trees in the hectare had forked trunks or boughs at or below 30 cm, and these belonged to 30 of the 45 tree species present.

In cerrado, most thick shrubs have a single trunk from the ground and therefore are different from the usual conception of a shrub. In the hectare, only 9.9% of the thick shrubs had more than one stem from ground level, or the single stem from the ground divided below 30 cm up into erect branch stems. In these cases there were almost always only 2 stems to measure, rarely 3 to 5. A few shrubs having one or more thick stems also had one to a few erect thin stems from the ground as part of the same individual; the thin stems were not counted in the calculation of basal area.

The height of each individual was recorded in half-meter height classes when less than 3 m tall and in one-meter classes when 4 m or more. Circumferences were measured to the nearest centimeter.

Taxonomic notes

Our plant specimens were determined by many specialists. There is no complete modern flora for São Paulo State or Brazil. Specimens have been deposited in UB, BOTU, NY, GI and other herbaria.

The species given here as *Guapira graciliflora* (MART. ex J. A. SCHMIDT) LUNDELL may really be *G. cafferiana* (CASARETTO) LUNDELL or the two may not be distinct. The second species, *G. noxia* (NETTO) LUNDELL, is considered the variety *psammophila* (MART. ex J. A. SCHMIDT) LUNDELL by Dr. WESTRA, who identified our *Nyctaginaceae*. Our *Banisteriopsis latifolia* (A. JUSS. in ST. HIL.) GATES is var. *paraguariensis* NIEDENZU. We are calling our one *Styrax* species, *S. ferruginea* NEES & MART. Its distinction from *S. camporum* is still to be worked out. Our species of *Schefflera, S. vinosa* (CHAM. & SCHLECHT.) FRODIN, has traditionally been called *Didymopanax vinosum* (CHAM. & SCHLECHT.) MARCH. in MART. *Plenckia populnea* REISS. in MART. has been called *Austroplenckia* (as it is treated here) but recently has been returned to *Plenckia*. Our *Psidium* species has not yet been identified. The *Tocoyena* in the hectare is here called *T. formosa* (CHAM. & SCHLECHT.) K. SCHUM. in MART. The leaf pilosity of *Tocoyena* in the cerrado as a whole varies but all are pilose at least on the undersurface if not on both surfaces. *Tocoyena formosa* is probably a hybrid complex of two species, *T. brasiliensi* and *T. viscidula* (SILBERBAUER-GOTTSBERGER, GOTTSBERGER & EHRENDORFER, unpublished).

Results of the hectare census

The hectare contains 4197 individuals at or above the minimum stem circumference mentioned previously, including 1180 trees and 3017 thick shrubs. This is rather dense for cerrado and is a result of the lack of fire for many years and a sufficient soil fertility (although very low) to yield this density. The tree density per 10 × 10 m square varies from 3 to 25 (average 11.80), thick shrubs 14–51 (av. 30.17), trees plus thick shrubs 23–67 (av. 41.97). The number of tree species per square is 2–16 (av. 7.43), thick shrub species per square 5–18 (av. 12.00), and tree plus thick shrub species 10–23 (av. 16.02). The last average is not equal to the sum of the two preceding averages because most species occur in both growth forms.

The hectare contains 54 species of trees and thick shrubs, of which 3 occur only as trees: one individual each of *Brosimum gaudichaudii* TRÉCUL., *Miconia albicans* (SW.) TRIANA, and *Pouteria torta* (MART.) RADLK. Eight species occur in the hectare only as thick shrubs: *Banisteriopsis latifolia, Byrsonima vacciniifolia* A. JUSS., *Casearia sylvestris* SW., *Cybistax antisyphilitica* MART., *Davilla elliptica* St. HIL., *Hancornia speciosa* Gomez, *Kielmeyera coriacea* MART., and *Tocoyena formosa*. Thus, 43 species, or 80% of the total 54, occur in both growth forms, and in this case, the proportion of the individuals of a species in the hectare that are trees varies, from less than 1%, such as *Erythroxylum suberosum* A. ST. HIL., *Psidium* sp. 1, *Annona coriacea* MART., and *Licania humilis* CHAM. & SCHLECHT., through all values including about 50%, such as *Byrsonima coccolobifolia* (SPR.) KUNTH, *Couepia grandiflora* (MART. & ZUCC.) BENTH., *Eugenia mugiensis* BERG in MART., *Schefflera vinosa, Annona crassiflora* MART., *Eriotheca gracilipes* (K. SCHUM.) A. ROBYNS, and *Erythroxylum tortuosum* MART., up to over 70%, such as *Anadenanthera falcata* (BENTH.) SPEG., *Machaerium acutifolium* VOG., *Plathymenia reticulata* BENTH., and *Qualea multiflora* MART. It appears that among non-forest vegetation types, certain physiognomic forms of cerrado, such as the tree and scrub woodland of our hectare, or cerradões with a dense woody underlayer, have the highest known number of woody species (with thick trunks) per hectare. Only some tropical rainforests have more. The "heath" vegetation of fynbos in s.w. South Africa, and kwongan in s.w. Australia are famous for their rich floras but almost all of the woody species of these vegetations are thin-stemmed.

Styrax ferruginea is the most important tree in the hectare, leading the others in density, basal area and frequency. Among the thick shrubs, however, it is much less important. *Erythroxylum suberosum* is the most important thick shrub, leading the others in all three measurements, but is much less important as a tree. Of the ten tree species and ten thick shrub species with highest density, only *Byrsonima coccolobifolia, Tabebuia ochracea* (CHAM.) STANDLEY, *Ouratea spectabilis* (MART.) ENGL., and *Styrax* *ferruginea* occur on both lists. These four species are also among the five most common on the tree plus thick shrub density list.

Table 2 shows the analytical values for each species (trees and thick shrubs combined). The absolute density (number of individuals in the hectare), absolute basal area of trunk sections at 30 cm up, and frequency (number of 10 × 10 m squares of occurrence) are listed. Density and frequency are exact counts so all digits are significant, but basal area is a measurement of a continuous quantity. Since the circumference was measured to the nearest 1 cm, the basal area is accurate to 0.8 n cm^2 for trunks n cm in circumference.

Table 2 also includes the relative values and the Wisconsin importance percentage (IP) as the average of the three relative values. The species are arranged by IP. The cylindrical volumes (CV), i. e., sum of the basal area × height of each measured stem of the species, are also given, another measure of importance closely related to above-ground biomass. Parabolic or conical volumes are estimates of the volume of a trunk. Since, usually, boughs make up a large proportion of the weight of a cerrado woody plant, or, indeed, it is often difficult to say what is a continuation of a trunk and what is a bough, CV, which is twice parabolic volume and three times conical volume, gives a closer estimate of the true volume, and hence is the best of all the rapidly obtained values that correlate with biomass.

Importance curves

Importance curves or dominance-diversity curves (i. e., made from "ranked abundance lists", PIELOU 1975:20) for density, frequency, CV and IP of the species are shown in Fig. 4, taken from Table 2. In each, the lower curve represents the measures in their percent relative form so as to be comparable, and the upper curve represents the $\log_{10}$ of the percent relative measures. The latter gives more separation among the smaller values. A basal area curve would be intermediate between the density and CV curves and is not shown. The form of the log CV curve shows the closest relationship to that postulated by a log normal distribution of abundances (WHITTAKER 1975: 92, fig. 3.14). This is because CV has a greater amplitude of values than the other measures: the proportion of highest to lowest value is 8615 to 1. The log frequency curve is shorter and more horizontal, approximating that postulated by the random niche-boundary hypothesis of MACARTHUR; the proportion of highest to lowest value is 98 to 1. The density and Wisconsin importance percent curves are intermediate. We therefore have a situation where the ranked abundance curve of one kind of measurement of quantity approaches that postulated for one model of species abundance relationships, and that of another measurement approaches the curve postulated by another model. This shows up another weakness, besides that mentioned by PIELOU 1975: 21, 26–7 (that two different hypoth-

Table 2

Species quantities, absolute and relative, for the 54 species of the hectare (arranged after their importance values).

Species	Density	Basal area, cm2	Fre- quency %	Relative density	Relative basal area	Relative frequency	Importance	Relative cylin. volume	Cylindrical volume dm3
1. Erythroxylum suberosum	860	20113	98	20.49	11.18	6.12	12.60	5.54	3522
2. Styrax ferruginea	250	23779	84	5.96	13.22	5.24	8.14	16.26	10338
3. Qualea grandiflora	183	13795	74	4.36	7.67	4.62	5.55	10.50	6676
4. Byrsonima coccolobifolia	221	10117	84	5.27	5.62	5.24	5.38	5.66	3598
5. Ouratea spectabilis	242	8173	81	5.77	4.54	5.06	5.12	3.05	1943
6. Sclerolobium aureum	147	12909	72	3.50	7.18	4.49	5.06	10.62	6751
7. Tabebuia ochracea	255	7778	72	6.08	4.32	4.49	4.96	3.77	2397
8. Stryphnodendron adstringens	185	8320	64	4.41	4.63	4.00	4.34	4.61	2934
9. Myrcia lasiantha	187	4467	80	4.46	2.48	4.99	3.98	1.57	997
10. Eugenia aurata	183	5174	71	4.36	2.88	4.43	3.89	1.58	1004
11. Couepia grandiflora	122	7803	59	2.91	4.34	3.68	3.64	4.21	2675
12. Annona crassiflora	103	6088	59	2.45	3.38	3.68	3.17	4.16	2648
13. Aspidosperma tomentosum	164	3429	57	3.91	1.91	3.56	3.12	1.51	962
14. Piptocarpha rotundifolia	80	6000	51	1.91	3.34	3.18	2.81	3.11	1981
15. Erythroxylum tortuosum	134	3362	51	3.19	1.87	3.18	2.75	1.06	676
16. Connarus suberosus	107	2402	49	2.55	1.34	3.06	2.31	0.67	429
17. Roupala montana	75	2687	45	1.79	1.49	2.81	2.03	1.58	1005
18. Dimorphandra mollis	54	2253	40	1.29	1.25	2.50	1.68	1.11	703
19. Diospyros hispida	81	1413	29	1.93	0.79	1.81	1.51	0.40	257
20. Caryocar brasiliense	48	2495	30	1.14	1.39	1.87	1.47	1.34	850
21. Licania humilis	44	2542	29	1.05	1.41	1.81	1.42	0.97	618
22. Eriotheca gracilipes	39	3562	20	0.93	1.98	1.25	1.39	2.64	1679
23. Anadenanthera falcata	38	2905	19	0.91	1.62	1.19	1.24	2.17	1379
24. Machaerium acutifolium	29	2085	22	0.69	1.16	1.37	1.07	1.25	795
25. Davilla elliptica	43	535	29	1.02	0.30	1.81	1.04	0.11	70
26. Psidium sp. 1	39	868	26	0.93	0.48	1.62	1.01	0.26	165
27. Byrsonima verbascifolia	37	884	26	0.88	0.49	1.62	1.00	0.26	167
28. Bowdichia virgilioides	26	2013	18	0.62	1.12	1.12	0.95	1.92	1222
29. Acosmium subelegans	29	729	22	0.69	0.41	1.37	0.82	0.30	192
30. Plathymenia reticulata	24	1890	13	0.57	1.05	0.81	0.81	1.41	898
31. Qualea multiflora	12	2933	7	0.29	1.63	0.44	0.78	3.00	1911
32. Strychnos pseudoquina	27	1225	15	0.64	0.68	0.94	0.75	0.66	417
33. Annona coriacea	22	369	19	0.52	0.21	1.19	0.64	0.13	83
34. Tabebuia caraiba	15	823	9	0.36	0.46	0.56	0.46	0.36	231
35. Guapira noxia	10	850	8	0.24	0.47	0.50	0.40	0.40	255
36. Kielmeyera rosea	10	494	8	0.24	0.27	0.50	0.34	0.27	169
37. Tocoyena formosa	11	150	9	0.26	0.08	0.56	0.30	0.04	24
38. Miconia albicans	5	564	5	0.12	0.31	0.31	0.25	0.36	228
39. Aegiphila paraguariensis	7	201	7	0.17	0.11	0.44	0.24	0.09	60
40. Austroplenckia populnea	6	337	5	0.14	0.19	0.31	0.21	0.30	191
41. Xylopia aromatica	7	101	6	0.17	0.06	0.37	0.20	0.04	28
42. Guapira graciliflora	8	280	4	0.19	0.16	0.25	0.20	0.11	73
43. Eugenia mugiensis	4	40	4	0.10	0.02	0.25	0.12	0.02	12
44. Pouteria ramiflora	3	173	3	0.07	0.10	0.19	0.12	0.09	54
45. Pouteria torta	1	446	1	0.02	0.25	0.06	0.11	0.42	268
46. Miconia rubiginosa	3	69	3	0.07	0.04	0.19	0.10	0.02	15
47. Cybistax antisyphilitica	3	48	3	0.07	0.03	0.19	0.10	0.01	9
48. Kielmeyera coriacea	3	29	3	0.07	0.02	0.19	0.09	0.005	3
49. Banisteriopsis latifolia	4	79	2	0.10	0.04	0.12	0.09	0.03	19
50. Schefflera vinosa	2	29	2	0.05	0.02	0.12	0.06	0.01	8
51. Casearia sylvestris	2	23	2	0.05	0.01	0.12	0.06	0.007	5
52. Hancornia speciosa	1	23	1	0.02	0.01	0.06	0.03	0.007	5
53. Brosimum gaudichaudii	1	8	1	0.02	0.004	0.06	0.03	0.005	3
54. Byrsonima vacciniifolia	1	8	1	0.02	0.004	0.06	0.03	0.002	1
SUM	4197	179870	1602	100.00	100.00	100.00	100.00	100.00	63597

eses can yield the same curve) in the use of importance curves to hypothesize about what is causing species abundance relationships. The curves are still useful, however, as a purely descriptive measure of the community, like any other, for the purpose of comparing communities.

When the numbers of species that occur in successive classes of abundance values are plotted, we have a "species abundance distribution" (PIELOU 1975: 20). If equal-size classes are used, the classes with small abundances have a relatively large number of species and those with larger abundances have smaller and smaller numbers of species, with many classes having no species at all. Therefore, in this kind of curve a geometric scale of abundances is used, the classes with the higher abundances being progressively wider so as to include more species. The most common method, introduced by PRESTON 1948 is to use doubling classes ("octaves") with each class being twice as wide as the previous class. However, any factor above 1 may be used, such as 1.2, 1.5, 2, 2.3, e (= 2.178...), 3, 4, etc., since the purpose of the grouping is to see if the species have a log normal distribution. We tried several of the above factors, giving differently scaled classes, on our data for density, basal area, frequency, CV, and IP. There is a general tendency for the curves to be irregular, with many ups and downs, and no strong single mode, when the factor used is too small for the total number of species involved. The curve gets smoother and increases to a stronger mode before it decreases, when larger factors are used, but then a smaller number of classes having a non-zero number of species results so that information is lost. Therefore, a compromise must be reached.

The exact shape of the curve (the number of species in each class) for a particular factor of increase of class width, also depends on what number, representing the division between two classes, is used as a starting point (WILLIAMS 1964: 9). For instance, our Wisconsin importance percentages of the 54 species, using × 3 classes, starting with 1/90, gives classes with boundary values of 0.0111..., 0.0333..., 0.1000..., 0.3000..., 0.9000..., 2.7000..., etc. Starting with 1/100 gives class boundaries of 0.010, 0.300, 0.900, 0.270, 0.810, 2.430, 7.290, etc. The first gives species numbers in consecutive classes of 3, 6, 8, 9, 13, 13, 2. The second gives for the same data, 0, 6, 11, 7, 15, 13, 2. Not only are the numbers different but the number of non-zero classes is different. Also note that the first has a flat-topped mode of 13, while the second has a peak mode of 15 and a secondary mode of 11 and so is more irregular.

One can use absolute values of the abundances or relative (percent) values. In the latter case one should use enough decimal places so that a species abundance value falls definitely into one or another class and not on the boundary. If it does fall exactly on a boundary, such as is probable when using absolute numbers of individuals and class division points which are whole numbers, then half the species with the abundance value of the boundary is placed in the lower class and half in the upper class.

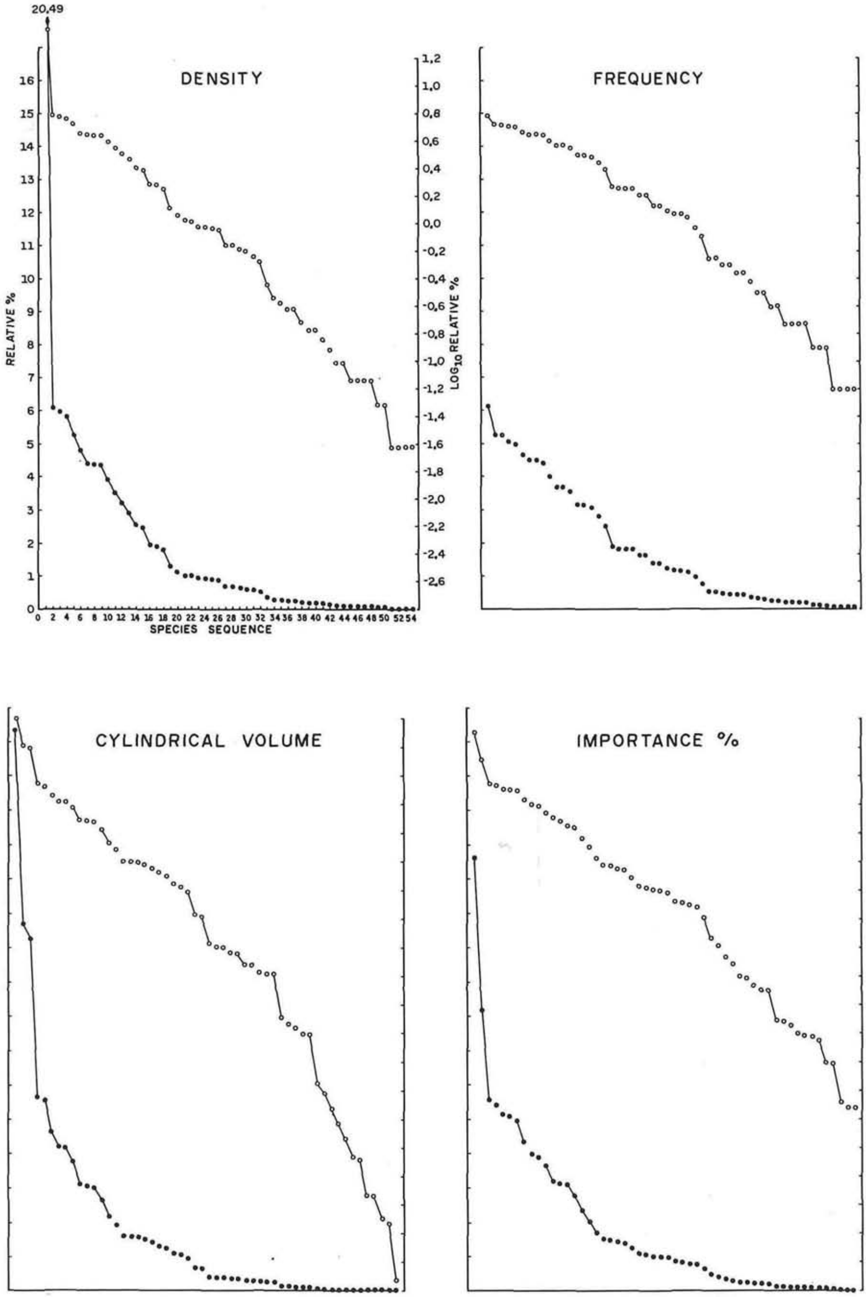


Fig. 4. Relative and $\log_{10}$ relative importance curves for various measures of quantity. Species sequence as in Table 2.

We tested our data, using relative values for comparability, with factors of ×2, ×2.5, ×3, and ×4, and 0.01 as a division point, for the five types of abundance. The smoothest and widest curves for a particular factor of increasing class width was found for CV and basal area (Fig. 5). The curves for CV were usually the widest because this abundance has the largest difference between the smallest und largest values among the species and so is spread over the largest number of classes.

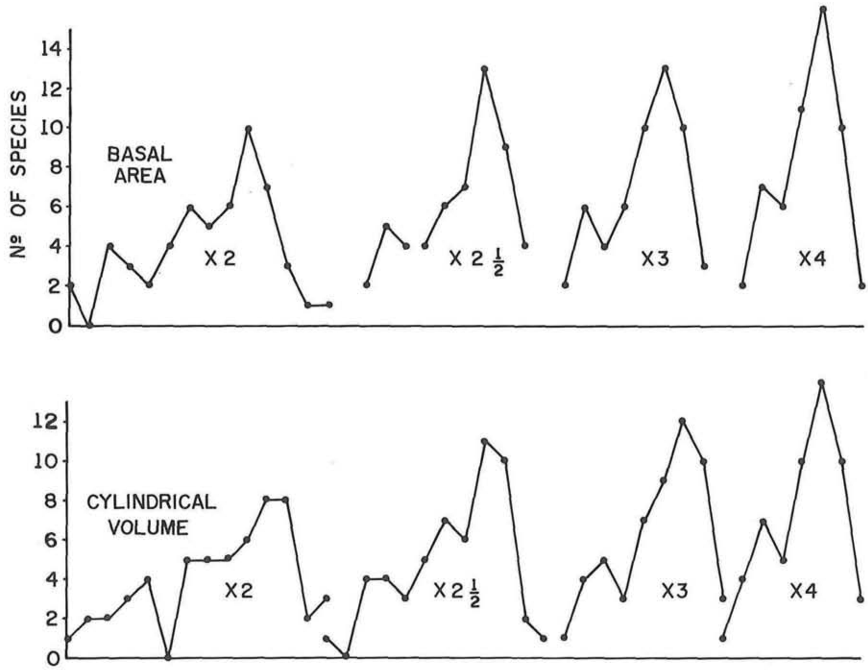


Fig. 5. Species-abundance distribution for basal area and cylindrical volume on log scales with bases of 2, 2.5, 3 and 4.

These two curves, as well as those of density, frequency, and IP, are highly skewed to the left, that is, there are more species in the moderately high abundance classes than in the medium classes. There are more species in the medium classes when one has a truly log normal distribution.

Since our data are not from a random small sample but from a complete census of a small area, there is no sense in using a statistical test to see if our "sample" could have come from a population with a log normal distribution of species abundances. But one could use chi-square sums or Kolmogorov-Smirnov maximum deviations as a measure of the divergence of empirical data from a log normal curve of the same parameters, and thus this could be used to compare different communities (using complete censuses) as to their deviation from a truly log normal distribution of species abundances.

Correlation between the analytic values, by species

The values are not distributed normally so Spearman rank correlations were used. However, the Pearson correlation coefficients have almost the same values when the logarithms of both variables are used. In the following list the Spearman correlation is given first, then the Pearson in parentheses, and then the regression power equations.

BA, cm^2, vs density,	0.851 (0.858),	$y = 71.17525 \times^{1.116588}$
CV, dm^3, vs density,	0.931 (0.920),	$y = 26.148995 \times^{1.098004}$
IP vs density,	0.990 (0.987),	$y = 0.04122 \times^{0.8051105}$
CV, dm^3, vs BA, cm^2,	0.975 (0.986),	$y = 0.7362203 \times^{0.9034422}$
IP vs CV, dm^3,	0.939 (0.931),	$y = 0.0725278 \times^{0.6361105}$
CV, dm^3, vs IP,	0.939 (0.931),	$y = 464.41688 \times^{1.361405}$

The correlations are completely significant for the hectare because they are based on a complete census of the species in it, of the size of plant we are considering. Both CV and IP are good measures of the importance of a species in its community, so it is interesting to see that they correlate well. But four species deviate widely from the regression curve of CV on IP. *Erythroxylum suberosum* is the densist and most frequent species and has the second highest basal area, and is therefore the most important species by IP, but the heights are low and so its CV is well below the regression value calculated from its IP. *Styrax ferruginea, Qualea grandiflora* MART., and *Sclerolobium aureum* (TUL.) BENTH. in MART. are, respectively, the 2nd, 3rd, and 6th highest species in order of IP, for all have high densities, basal areas and frequencies, but their average heights are so much above that of the other species that they have an extra large CV compared to their IP.

Frequency classes

Table 3 gives the 20% frequency classes for trees and thick shrubs combined, for block sizes of 1 to 5 squares, using shapes as nearly isodiametric as possible and that fit into the 10 × 10 pattern of the hectare so that all squares are used once or an equal number of times. The blocks are made up of 1, 2 × 1, 2 × 1 + 1, 2 × 2, and 2 × 2 + 1 squares, which are, respectively, square, rectangular, L-shaped, square, and L-shaped. For block sizes of 2 and 5 squares, the orientation of the longer axis may be along the contour or along the slope, and there are two ways of fitting the L-shaped 5-square blocks together for each orientation. In these cases, frequencies for all cases of the same area of block were found and averages of the frequency for each species were taken. The L-shaped block of 3 squares fits into a 2 × 2 block with one square not used. Frequencies were found with the non-used block in each of the four positions and averages taken. This method uses each square of the hectare 3 times for block size 3.

Table 3

20% frequency classes at different scales

no. of squares in block	RAUNKIAER's classes, %				
	A	B	C	D	E
1	52	17	13	11	7
2 (av. of 2)	42	13	13	14	18
3 (av. of 4)	35	13	14	11	27
4	31	13	11	15	30
5 (av. of 4)	29	15	5	15	36
RAUNKIAER's averages	53	14	9	8	16
KENOYER's averages	69	12	6	4	9

It can be seen, as has been observed before (CAIN & CASTRO 1959: 157, and many previous workers) that with increasing quadrat size, the proportion of species with small frequencies (class A) constantly diminishes, and that of species with large frequencies (Class E) constantly increases. None of the block sizes give percentages close to either RAUNKIAER's European or KENOYER's American averages. It is necessary to use a block size as large as 4 squares to satisfy RAUNKIAER's rule of inequalities, A>B>C⋚D<E (RAUNKIAER 1918, 1934, KENOYER 1927, GLEASON 1929, ROMELL 1930, PRESTON 1948).

In natural vegetation, individuals of most species are clustered and the clusters of different species are not coterminous but are offset from each other. In this case, long thin rectangles include more species on the average than equidimensional quadrats of the same area, for the former cut across more clusters of different species. Thus, comparing a block size of 5 squares and using all 20 of these that fill out the hectare, the average number of species of trees plus thick shrubs combined per block is 30.45 for the stubby L-shaped block of 2 × 2 + 1 squares, and 31.025 for the long thin block of 5 × 1 squares. For a block size of 10 squares, the 5 × 2 shape has an average of 37.05 species per block, and the 10 × 1 shape an average of 37.40. For a block size of 25 squares, the 5 × 5 shape has an average of 44.25 species, and the 10 × 2 + 5 L-shaped block an average of 44.875. These differences are exact and without sample variation. In each case the longer thinner block has more species. Therefore, when comparing the effect of different size plots on frequency, one should use where possible plots of the same shape.

Spatial pattern of density within the hectare

Figures 6 and 7 give the numbers of individuals of trees of all species, and of trees plus thick shrubs of all species in each 10 × 10 m square. There is no consistent pattern at this scale in the spatial distribution of squares with large and with small numbers of individuals, except for the fact that most of the very low values for trees plus thick shrubs (below 30) are

17	14	20	14	10	6	17	14	16	20
17	5	13	14	15	12	6	12	5	9
14	6	25	10	23	14	4	9	14	11
15	6	15	15	7	5	11	21	9	10
11	9	9	17	5	9	7	16	3	9
16	13	12	19	13	10	9	7	20	15
21	10	13	14	14	9	7	8	11	16
16	11	12	5	4	12	11	15	15	9
7	10	7	5	3	17	16	17	11	14
12	11	13	4	12	16	18	16	3	6

NUMBER OF TREES

67	28	55	36	52	44	45	42	43	44
60	41	50	37	38	52	36	41	33	30
44	28	55	52	48	49	38	48	38	32
42	31	45	57	37	31	43	47	42	34
46	37	42	53	28	47	47	44	30	45
45	42	51	61	29	29	29	26	56	49
54	56	63	44	37	32	24	27	35	49
44	49	30	23	31	34	35	44	41	35
32	41	48	26	39	41	39	43	35	31
29	48	64	28	59	46	61	66	44	39

NUMBER OF TREES & THICK SHRUBS

Fig. 6. (left) Number of individuals of trees (all species combined) in each 10 × 10 m square.

Fig. 7. (right) Number of individuals of trees plus thick-stemmed shrubs (all species combined) in each 10 × 10 m square.

concentrated in the center. When densities at a larger scale are considered, in blocks of 2 × 2 squares, the concentration of very low densities is in the center and slightly below center, while all other values are scattered. The density at an even grosser scale, in blocks of 4 × 4 squares, is lowest in the center and upper right corner, with averages per square of 39.25 and 39.75 respectively, and is highest in the upper left corner, with an average of 45.50. These results show that, whatever may be the reason for spatial differences in density in an area, whether chance, correlation with soil characteristics, or whatever, the strength of the differences and their arrangement depend on the scale used.

There is a tendency for the taller trees in the hectare to occur in the upper half, and the taller the trees the more they are concentrated in the upper half. Thus, the upper half has 50% of the individuals in the 3–8 m height class, 52% of those in the 4–8 m class, 52% of those in the 5–8 m class, 58% of the 6–8 m class, 67% of the 7–8 m class, and 90% of the 8 m class. This may be a vestige of the former disturbance gradient since the taller trees are now concentrated in the part of the hectare closest to the remnant upslope cerradão. However, it should be mentioned that the trees of the 8 m class in the upper half are concentrated in the lower part of it, not near the upper edge.

If individuals were randomly scattered in the hectare, the number of squares with each number of individuals would approximate a Poisson distribution with the same mean. Testing this hypothesis by a chi-square test, we find it is necessary to reject the null hypothesis of random pattern at the 5% level for the trees, for the thick shrubs, and for the two classes together. Most of the chi-square sum is due to there being too many squares with high and with low numbers of individuals, that is, the individuals are clumped at the 10 × 10 m scale. At the 1% level, which allows a greater chi-square sum without rejecting the null hypothesis, we would accept the trees as being distributed at random but not the thick shrubs or the two together.

The variance-mean ratio can be used as a measure of deviation from randomness. In the hectare the value for trees is 1.956, for thick shrubs, 2.411, and for the two together, 2.478. A value of 1.000 is the expected value when individuals are distributed at random and the ratio has higher values when they are clumped and lower values when they are more regularly distributed. In a sample from an infinite population or, in a real case, a sample that makes up a small proportion of a large finite population, there can be sample variation in this value even when the distribution of individuals is random, so that a value of up to about 2 is often taken as an indication of randomness. But our values are based on a complete census of a finite population and so are exact for that population. Their considerable difference from 1.000 then shows that the individuals as a whole are definitely clumped at the scale of 10 × 10 m squares, although slightly less so for the trees alone. This measure, however, is not without pitfalls. For instance, if (n-1)/n of the squares have n individuals each and the other 1/n of the squares are empty, the variance-mean ratio will always equal 1, it making no difference how the occupied squares are arranged; they could be arranged to form one or more evidently visable clumps. The regular number of individuals within the clumps exactly compensates for the presence of the clumps.

The variance-mean ratio shows that in the hectare, the taller individuals tend to be more regularly spaced. The ratio for the individuals in all the height classes together, that is 0.5–8 m, for those in classes 1–8 m, classes 1.5–8, 2–8, 2.5–8, 3–8, 4–8, 5–8, 6–8, 7–8 and 8 m, are, respectively 2.478, 2.443, 2.260, 2.314, 1.804, 1.956, 1.613, 1.225, 1.271, 1.123, and 1.100. Although slightly irregularly, the clumping decreases as we limit ourselves to taller and taller individuals. The tallest trees, those in the 8 m class, are closest to being randomly distributed, but it is possible that the tendency is not to randomness but to regularity, so that if even taller trees were present, the ratio would tend to less than 1.000 for them.

Previous fires and strong frosts probably have repeatedly killed off the above-ground trunks of individuals countless times and these have re-sprouted. This means that the height (and therefore general massiveness) of the above-ground part of the plant is not necessarily strictly correlated with a larger subterranean system that explores more soil volume. But it seems that the correlation is close enough so that, if the stand is undisturbed for a sufficient time, the larger individuals tend to be more regularly spaced in reference to each other, which of course would reduce competition. Since the woody plants are not strongly shading each other, the competition would be mostly in the soil.

That light is not limiting is also shown by the fact that there is no strong correlation between the number of trees and the number of thick shrubs in a square (r = 0.100 for linear–linear, 0.081 for log–log, and 0.112 for Spearman). This is contrary to what WHITTAKER 1956 found in memoral forest in eastern U. S. A., where trees casting deep shade reduce shrub cover, and where the trees are more spaced, the shrub cover is higher.

Spatial pattern of cylindrical volumes

The cylindrical volume for the hectare as a whole is 63597 dm^3, or 63.60 m^3. The lowest value per square is 217 dm^3 and the highest is 1709 dm^3, a proportion of 7.9 to 1. There is no regular pattern of high and low CV per square over the hectare. Neither the very high values (above 1000), the highs (above the mean of 636 but below 1000), the lows (below the mean but above 400), nor the very lows (below 400) are concentrated in any one part of the hectare. Therefore, at this scale, the hectare is "homogenous in its heterogeneity".

At a larger scale, in blocks of 2 × 2 squares, the highest and lowest values are also scattered. On the 4 × 4 block scale CV shows a vague pattern, with the lowest CV in the lower left, second lowest in the center, and the highest in the upper right. Thus the CV pattern is not similar to the density pattern at any scale.

Plant height vs trunk circumference

The statistical distribution of trunk circumferences at 30 cm up from ground level, of all species together, is skewed with a long tail to the higher values. The modal class is 13 cm, close to the minimum of 10 cm. The median is 17 cm and the average circumference is 19.65 cm (6.25 cm diam.). Only 1.8% of the stems exceed 50 cm circ. (16 cm diam.) and only 10 trees have circumferences greater than 75 cm (24 cm diam.). The thickest tree has a circumference of 125 cm (40 cm diam.). Since there are very few trees with very large circumferences, the skewness value is not large.

Figure 8 shows the distribution of individuals in height classes as a histogram since the class widths are not all the same. 28.5% of the individuals are in the modal 2 m class, that is, from 1.75 to 2.24 m tall.

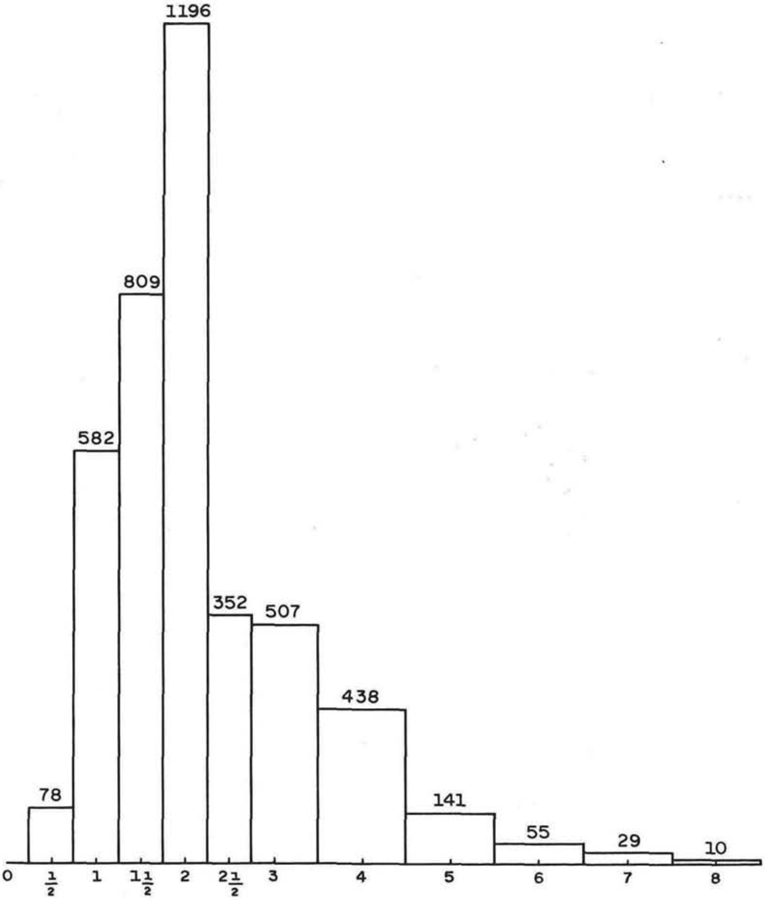


Fig. 8. Histogram of numbers of individuals (trees and thick-stemmed shrubs combined) in the hectare, in height classes.

A number of model curves were tested to fit the hight-circumference values of the 4197 individuals. (When an individual had more than one measured stem, that with the largest circumference was used.) Although height of woody plants does not theoretically increase linearly with stem thickness, a linear model could give a closer fit with a particular set of values than the logarithmic or power curve models, which flatten out but continue to rise slowly. The log curve had the best fit but is only marginally better than the linear, while the power curve had the poorest fit. The Pearson correlation coefficients are 0.815, 0.810, and 0.771 respectively. The Spearman rank coefficient is 0.777.

Another theoretical possibility is that the woody plants assymptotically approach a limiting average height which they do not surpass no matter

Table 4

Correlations of plant height-trunk circumference for each species with more than 50 individuals in the hectare.

Species	no. ind. in ha	Spearman rho	best Pears. r	model for best corr.	estimated av. ht. in m by model for 60 cm circ.	largest circ., cm	largest height class, m
Annona crassiflora	103	0.87	0.89	log	5.9	84	8
Aspidosperma tomentosum	164	0.73	0.85	log	5.9	40	5
Byrsonima coccolobifolia	221	0.85	0.85	log	5.2	62	5
Connarus suberosus	107	0.69	0.67	lin	5.4	30	4
Couepia grandiflora	122	0.84	0.83	log	4.7	100	5
Dimorphandra mollis	54	0.83	0.78	power	5.0	40	5
Diospyros hispida	81	0.62	0.71	lin	5.8	26	3
Erythroxylum suberosum	860	0.60	0.58	log	3.3	44	4
Erythroxylum tortuosum	134	0.73	0.69	log	3.9	37	3
Eugenia aurata	183	0.71	0.73	lin	5.3	35	4
Myrcia lasiantha	187	0.69	0.71	lin	6.3	42	4
Ouratea spectabilis	242	0.74	0.76	log	4.0	63	4
Piptocarpha rotundifolia	80	0.77	0.76	power	5.0	61	5
Qualea grandiflora	183	0.87	0.86	log	6.1	96	8
Roupala montana	75	0.77	0.85	lin	7.3	51	7
Sclerolobium aureum	147	0.92	0.88	log	6.1	125	8
Stryphnodendron adstringens	185	0.77	0.80	power	7.5	43	5
Styrax ferruginea	250	0.87	0.89	lin	6.0	70	8
Tabebuia ochracea	255	0.76	0.82	lin	8.5	55	7

how thick the trunk becomes. Seven model functions were tested, two of these exponential and constrained to rise from the origin, two exponential and not so constrained, two hyperbolic and constrained to rise from the origin and one hyperbolic not so constrained. These were, respectively, $y = a - ab^{-x}$, $y = a - ab^{-cx}$, $y = a - ab^{-x} + d$, $y = a - ab^{-cx} + d$, $y = a - b/(x + b/a)$, $y = a - b/(cx + b/a)$, and $y = a - b/x$. An iterative computer program gave convergences in some cases, but the results were not consistent and so are not considered further. By visual estimate of the graph of points (which had considerable dispersion), when the circumference was 60 cm, the average height was about 6 m.

Linear, log, and power model functions were also fitted to height-circumference values for all species individually that have over 50 individuals in the hectare. Table 4 gives for each of these species, the Spearman rank and Pearson correlation coefficients, and the type of model curve that gave the highest Pearson correlation. It also gives the largest circumference and tallest height class for each species. (These were not necessarily from the same individual.) Not all species had individuals that reached 60 cm circ., but for comparison, the estimated height is given for 60 cm circ. for each species. The estimated heights at this circumference varied from 3.3 to 8.5 m, showing that the rate of increase of height with circumference varies between the species.

It is of value to find the closeness of fit of height-circumference values of a species to a theoretical curve, for when the dispersion of values around the curve is slight, height and therefore CV can be estimated from circumference alone.

Species in height classes

Figure 9 is a histogram of numbers of species in each height class. The height classes centered on 1.0, 1.5, 2.0, 2.5, 3 and 4 m each contain a large number of species, between 34–47 of the 54 present. The shortest class, with individuals under 0.75 m, has 15 spp., while the tallest class, centered on 8 m, has 6. The number of species in the consecutive height classes increases to the modal 2 m, then decreases. Some species, even with medium to large numbers of individuals in the hectare, do not reach the taller classes. The 860 individuals of *Erythroxylum suberosum,* the 29 of *Acosmium subelegans,* the 37 of *Byrsonima verbascifolia,* the 107 of *Connarus suberosus,* the 183 of *Eugenia aurata,* the 44 of *Licania humilis,* the 187 of *Myrcia lasiantha,* and the 242 of *Ouratea spectabilis* are all less than 4.5 m tall. All the 81 individuals of *Diospyros hispida,* the 134 of *Erythroxylum tortuosum,* and the 39 of *Psidium* sp. 1, are under 3.5 m tall, and all the 43 individuals of *Davilla elliptica* are less than 2.5 m tall. The canopy is sufficiently open and the ground layer is at most semishaded, so that no individual was suppressed because of lack of light. Even as little as 20% of

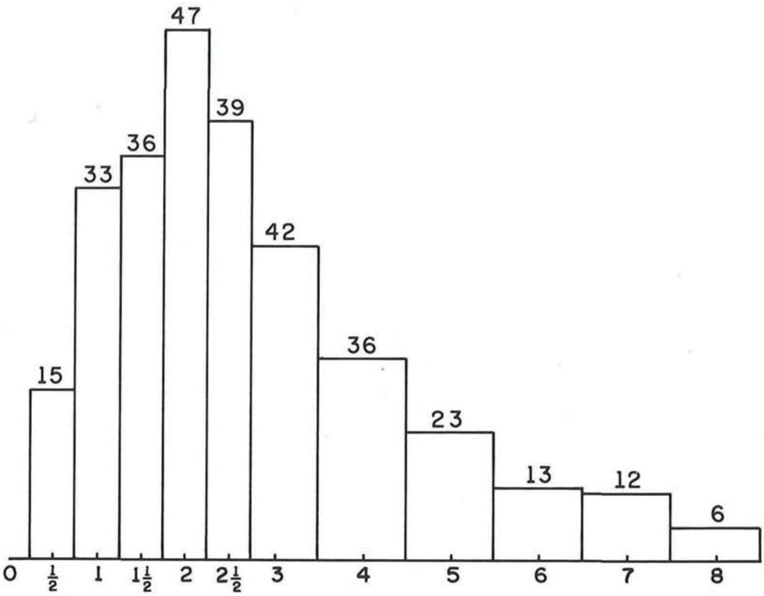


Fig. 9. Histogram of numbers of species (of trees and thick-stemmed shrubs combined) in the hectare, in height classes.

full sunlight enables complete photosynthesis to occur in heliophilic species (HORN 1971). It is not probable that root competition for scarce nutrients in this crowded stand is causing these species to remain short since they rarely grow taller in any cerrado. In fact, on the average, the more open the woody layer of undisturbed cerrado, the shorter the trees and shrubs are.

Relation of samples to the complete census

It is of interest for investigating large areas of cerrado to know how representative small areas are in relation to larger areas so that samples of the larger areas may be made as small as possible. One of the larger size samples that seems useful for trees and shrubs is a 10% area sample of a hectare. This may be drawn from the hectare in several ways, of which the following were used.

1) A single strip 100 × 10 m along the contour. There are ten of these in the hectare.

2) A single strip 100 × 10 m up and down the slope. There are ten of these in the hectare.

3) Ten 10 × 10 m squares randomly selected. Ten samples of ten squares each were chosen.

4) A single block of 50 × 20 m. There are ten of these with the long axis along the contour and ten with the long axis up and down the slope.

Table 5

Number of individuals in each species, of trees and thick-stemmed shrubs combined, in three groups of 10 samples each. Species arranged after their number of individuals.

			CONTOUR STRIPS										SLOPING STRIPS										RANDOM										
			1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	1-100	2-99	3-98	4-97	5-96	6-95	7-94	8-93	9-92	10-91	1	2	3	4	5	6	7	8	9	10	AV.
	NUMBER OF INDIVIDUALS	HA. 4197	484	375	366	421	417	419	409	432	418	456	388	397	428	397	405	398	417	503	401	463	410	394	438	435	468	348	431	386	458	437	420.5
RANK	NUMBER OF SPECIES	HA. 54	38	38	36	34	34	36	41	43	40	39	36	35	34	39	33	35	39	40	40	38	41	35	39	39	42	34	41	38	38	36	38.3
1	ERYTHROXYLUM SUBEROSUM	860	121	68	70	79	89	73	72	103	98	87	76	92	106	98	104	73	91	86	71	63	82	74	93	73	92	62	106	61	108	71	82.2
2	TABEBUIA OCHRACEA	255	5	4	10	17	13	19	29	51	60	47	25	12	8	21	34	33	27	39	38	18	21	20	26	23	17	5	21	24	28	25	21.0
3	STYRAX FERRUGINEA	250	30	27	23	25	16	19	26	23	24	37	20	35	23	22	22	24	27	35	10	32	28	26	35	17	28	19	31	16	30	22	25.2
4	OURATEA SPECTABILIS	242	22	16	13	24	29	48	23	24	18	25	26	37	27	20	20	14	23	23	20	32	12	24	22	26	19	22	20	22	18	18	20.3
5	BYRSONIMA COCCOLOBIFOLIA	221	28	23	25	20	25	23	14	15	24	24	21	15	16	21	19	31	24	25	19	30	31	21	29	23	28	19	19	31	34	33	26.8
6	MYRCIA LASIANTHA	187	36	22	21	29	11	14	17	14	9	14	13	8	17	14	19	12	20	38	17	29	12	25	18	23	22	23	8	20	16	18	18.5
7	STRYPHNODENDRON ADSTRINGENS	185	8	18	28	22	33	23	3	22	11	17	26	13	16	11	21	20	20	16	19	23	13	17	7	26	20	25	14	30	26	13	19.1
8	EUGENIA AURATA	183	22	19	21	33	15	13	22	11	12	15	9	14	27	19	13	20	18	27	14	22	19	11	20	28	41	17	22	11	22	26	21.7
9	QUALEA GRANDIFLORA	183	21	18	20	29	30	10	12	18	14	11	23	32	27	26	10	9	9	14	13	20	24	24	14	16	17	18	14	16	17	12	17.2
10	ASPIDOSPERMA TOMENTOSUM	164	2	14	6	3	22	23	43	17	12	22	9	8	14	17	5	23	26	24	25	13	19	12	22	32	14	5	29	11	14	25	18.3
11	SCLEROLOBIUM AUREUM	147	16	14	17	12	16	23	12	13	14	10	14	8	11	14	19	20	18	16	11	16	12	15	15	12	13	15	15	19	6	13	13.5
12	ERYTHROXYLUM TORTUOSUM	134	25	12	12	14	10	9	13	12	8	19	9	26	25	18	7	10	9	8	14	8	10	10	16	5	6	8	11	6	11	7	9.0
13	COUEPIA GRANDIFLORA	122	27	15	9	13	9	15	12	5	8	9	3	5	17	6	14	8	11	26	21	11	8	14	6	16	10	14	6	6	10	22	11.2
14	CONNARUS SUBEROSUS	107	4	4	6	9	8	31	27	9	7	2	8	11	11	11	8	13	12	10	9	14	11	6	20	6	17	8	24	9	7	11	11.9
15	ANNONA CRASSIFLORA	103	13	8	9	14	5	6	14	9	13	12	10	6	15	12	15	9	7	7	7	15	11	13	12	18	15	9	10	10	12	9	11.9
16	DIOSPYROS HISPIDA	81	26	16	7	2	14	7	2	1	4	2	26	0	0	1	1	4	7	14	21	7	13	18	3	8	16	10	1	12	10	19	11.0
17	PIPTOCARPHA ROTUNDIFOLIA	80	7	6	12	6	9	6	9	7	13	5	4	9	4	12	6	7	5	8	12	13	9	6	9	18	16	7	11	10	6	12	10.4
18	ROUPALA MONTANA	75	12	7	5	13	9	5	10	5	1	8	5	5	6	5	8	4	5	11	7	19	6	4	4	9	10	10	8	8	7	14	8.0
19	DIMORPHANDRA MOLLIS	54	12	3	2	8	8	4	2	3	8	4	11	1	6	4	2	5	5	5	11	4	6	8	5	2	5	4	7	4	8	9	5.8
20	CARYOCAR BRASILIENSE	48	8	9	11	6	5	4	2	1	2	0	4	4	12	7	5	2	1	2	4	7	4	6	3	11	6	11	2	11	4	3	6.1
21	LICANIA HUMILIS	44	4	4	8	2	4	2	4	7	4	5	1	7	12	6	5	3	2	3	2	3	1	3	4	10	3	4	6	4	6	2	4.3
22	DAVILLA ELLIPTICA	43	6	4	2	1	3	7	8	7	4	1	5	11	2	4	8	5	3	1	0	4	2	9	4	3	6	2	6	2	3	0	3.7
23	ERIOTHECA GRACILIPES	39	4	6	0	1	5	0	7	5	3	8	10	3	2	1	6	9	2	4	2	0	10	3	6	2	1	1	6	0	10	5	4.4
24	PSIDIUM SP.1	39	3	5	2	11	3	4	1	2	3	5	3	4	1	2	4	6	3	8	3	5	3	4	5	2	3	4	1	3	4	5	3.4
25	ANADENANTHERA FALCATA	38	0	0	0	0	0	3	1	4	6	24	2	3	1	2	2	2	5	11	2	8	5	1	2	3	4	0	5	0	3	1	2.4
26	BYRSONIMA VERBASCIFOLIA	37	6	1	2	1	5	4	3	7	6	2	2	4	3	3	7	11	2	1	0	4	6	0	8	2	6	1	3	5	9	5	4.5
27	ACOSMIUM SUBELEGANS	29	1	2	2	6	4	1	2	6	4	1	0	1	1	5	7	3	6	1	1	4	1	5	4	1	3	4	2	3	2	5	3.0
28	MACHAERIUM ACUTIFOLIUM	29	1	2	3	5	2	0	2	4	1	9	3	5	6	0	3	2	0	7	2	1	2	4	2	0	5	2	4	2	6	0	2.7
29	STRYCHNOS PSEUDOQUINA	27	2	6	8	1	0	6	1	2	1	0	1	0	0	3	4	4	7	5	3	0	2	2	5	0	0	9	1	6	1	3	2.9
30	BOWDICHIA VIRGILIOIDES	26	1	4	2	4	0	2	1	4	3	5	1	1	2	1	0	1	6	8	5	1	8	1	1	1	5	1	3	4	2	7	3.3
31	PLATHYMENIA RETICULATA	24	1	0	1	6	6	2	2	2	1	3	0	0	0	0	1	0	0	3	3	17	1	1	1	2	1	1	2	6	0	6	2.1
32	ANNONA CORIACEA	22	1	4	2	2	1	2	2	1	4	3	2	4	2	2	0	0	2	4	1	5	3	0	4	4	4	4	1	3	2	5	3.0
33	TABEBUIA CARAIBA	15	1	2	2	0	1	2	2	0	4	1	5	0	0	0	0	7	0	0	0	3	4	2	1	0	2	0	0	1	1	1	1.2
34	QUALEA MULTIFLORA	12	0	0	0	0	0	0	1	1	2	8	4	2	4	1	0	0	1	0	0	0	2	0	2	1	2	0	3	1	7	1	1.9
35	TOCOYENA FORMOSA	11	2	2	1	0	0	0	0	2	3	1	0	3	0	0	0	0	1	2	2	3	1	0	0	3	2	2	1	3	0	4	1.6
36	GUAPIRA NOXIA	10	2	0	0	1	4	0	1	1	1	0	0	4	1	0	0	1	0	1	0	3	0	2	0	1	1	0	1	0	1	0	0.6
37	KIELMEYERA ROSEA	10	0	0	0	0	0	0	0	2	5	3	4	0	0	1	0	0	2	1	1	1	1	1	0	2	1	0	1	2	2	2	1.2
38	GUAPIRA GRACILIFLORA	8	0	5	1	0	0	2	0	0	0	0	0	1	0	1	0	0	0	4	2	0	0	0	4	1	0	0	0	0	0	2	0.7
39	AEGIPHILA PARAGUARIENSIS	7	1	1	1	0	0	0	1	2	0	1	0	2	0	1	2	0	1	0	1	0	0	1	1	0	1	0	1	0	0	0	0.4
40	XYLOPIA AROMATICA	7	0	0	0	0	0	3	2	1	0	1	0	0	0	1	0	0	3	0	2	1	1	0	1	2	1	0	2	1	0	0	0.8
41	AUSTROPLENCKIA POPULNEA	6	0	0	0	0	0	0	0	5	1	0	0	0	0	1	3	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0.1
42	MICONIA ALBICANS	5	0	1	0	0	0	2	0	1	1	0	0	0	1	0	0	0	0	1	1	2	1	0	0	1	1	1	0	1	0	1	0.6
43	BANISTERIOPSIS LATIFOLIA	4	0	0	0	0	1	0	0	0	0	3	0	0	0	0	0	0	3	0	1	0	3	0	3	0	0	0	1	0	3	0	1.0
44	EUGENIA MURGIENSIS	4	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	2	1	0	0	0	0	0	2	0	1	0	1	0	0.2
45	CYBISTAX ANTISYPHILITICA	3	0	0	1	0	0	0	1	0	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0.2
46	KIELMEYERA CORIACEA	3	0	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0.1
47	MICONIA RUBIGINOSA	3	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0.2
48	POUTERIA RAMIFLORA	3	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0.2
49	CASEARIA SILVESTRIS	2	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0.1
50	SCHEFFLERA VINOSA	2	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0.3
51	BROSIMUM GAUDICHAUDII	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0.1
52	BYRSONIMA VACCINIIFOLIA	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
53	HANCORNIA SPECIOSA	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
54	POUTERIA TORTA	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
	PROPORTION OF INDIVIDUALS %		11.5	8.9	8.7	10.0	9.9	10.0	9.7	10.3	10.0	10.9	9.2	9.5	10.2	9.5	9.7	9.5	9.9	12.0	9.6	11.0	9.8	9.4	10.4	10.4	11.2	8.3	10.3	9.2	10.9	10.4	10.0
	PROPORTION OF SPECIES %		70.4	70.4	66.7	63.0	63.0	66.7	75.9	79.6	74.1	72.2	66.7	64.8	63.0	72.2	61.1	64.8	72.2	74.1	74.1	70.4	75.9	64.8	72.2	72.2	77.8	63.0	75.9	70.4	70.4	66.7	70.9
			AV. DENSITY = 10.0% AV. SPECIES = 70.2%										AV. DENSITY = 10.0% AV. SPECIES = 68.3%										AV. DENSITY = 10.0% AV. SPECIES = 70.9%										

5) The single sample composed of ten parallel 100 × 1 m strips running along the contour and equally spaced along a 100 m base line.

Table 5 presents the number of individuals of trees and thick shrubs combined of each of the included species in ten samples each of the first three types of sample. For each sample the total number and percent are given. The same results for trees alone or for thick shrubs alone would be similar but more variable because of the smaller numbers involved. (In the table the strips are indicated by the numbers of their end-point squares. The "1–10" strip is that along the lower edge of the hectare; the "1–100" strip is that along the right edge.)

The ten 10%-area strip samples, contour or sloping, are not independent of each other since the sum must be 4197, the percent densities must add up to 100% and the average percent density must be exactly 10% (with a possible small discrepancy due to the rounding off of decimal places). The ten random samples are of course independent. Among these ten random samples of ten squares each it happened that 34 of the 100 squares in the hectare were not included in any sample, while those squares which were included entered into 1–2(–5) samples each.

In general, the 10%-area samples are relatively constant for density. The number of individuals for single species varies more because of the smaller numbers involved. Multiplying by 10 gives an estimate for the hectare. Thus, based on a single contour strip, the estimated number of *Tabebuia ochracea* individuals in the hectare varies from 40 to 600; based on a single sloping strip, from 80 to 390; and based on a single 10-square random sample, from 50 to 280. The true value is 255. Thus, neither a 10% strip nor a 10% random sample of squares is accurate for estimating the density of individual species. The estimate of total density of all species together, based on single 10%-area samples of these shapes, range among the ten samples for the same three methods between 3660–4840, 3880–5030, and 3400–4680, whereas the true number is 4197. Here the ten random samples have a slightly greater range than the strips. Another set of ten random samples, however, had a smaller range than the strips.

We may examine the absolute deviations from the ten-sample average, using percent values for comparability, of each series of samples. (Absolute deviations are used instead of standard deviations since no statistical tests are being made and the absolute values have the advantage that, in calculating the average, each deviation, contributes according to its magnitude and not according to the square of its magnitude as is the case for standard deviation.) In the contour strips there is a slight tendency for the middle-level strips (the 5th and the 6th) to have smaller deviations from the ideal 10% than the upper or lower strips. The three lower strips have deviations of 1.1 or more, the upper strips (except for the 9th) have deviations of 0.3 to 0.9, while the two middle strips have deviations of only 0.1 or zero. In the sloping strips there is no definite pattern, nor, naturally, is there one in the random samples. This particular set of ten random samples has the largest average absolute deviation from its mean of 10.0%, namely, 0.69; the average is 0.67 for the sloping strips and 0.55 for the contour strips. We would expect a sample of randomly scattered subsamples to be more representative of the whole hectare than the same size sample with its subsamples arranged in a single file. However, when the number of subsamples is small, here only ten, there may be great fluctuation. Another set of ten random samples had a smaller average deviation than the strip samples. Also, in real vegetation, where the individuals of almost all species are clumped, when the single file is taken through the middle of the hectare, its deviation from the true average is usually smaller than when taken through any other part, since the similarity of two plots falls off with distance, and the middle has the smallest sum of distances to the other parts of the hectare. The deviation of a median strip from the true average can be even smaller than that of a random sample. And this is what happened here. The absolute deviations of the two middle contour strips are 0.1 and zero, which are smaller than any of the deviations of the random samples. The deviations of the two middle sloping strips, 0.7 and 0.5, however, are of average size. A single medianly placed strip is much less trouble to lay out on the ground, and to find again if this should be necessary, than a number of scattered squares. It is true that a 10%-area sample made up of a larger number of subplots, say 20 or 40, would probably give more accurate results but is even more trouble to lay out.

The results based on 50 × 20 m samples are similar to the 100 × 10 m strips except that they are slightly more variable due to the fact that a more equidimensional sample area falls more often more wholly in or out of a clump and so shows greater variation.

The fifth type of 10% sample is that of the ten equally spaced 100 × 1 m strips running along the contour. The number of individuals multiplied by ten, 4040, is as close to the true value, 4197, as that of many of the 100 × 10 m strips. In general, we would expect an estimate of a statistic to be closer to the true value for this type of sample which is more cut up and spread over the hectare than that of any single 100 × 10 m strip, even a middle one. However, there might be more inaccuracy due to the ten times greater edge effect (ten times more decisions must be made as to whether an individual on the border of the plot is included in the sample or not). For the species taken individually, we do find this ten-strip 10% sample to be more accurate. The average absolute deviation among the species of the sample relative percentage of density from their true relative values in the complete census, was 0.43 for the thin-strip sample, 0.61 for the fifth 100 × 10 m contour strip and 0.69 for the sixth contour strip. The fifth and sixth sloping strips gave 0.64 and 0.62. The thin-strip sample gave results closer to the true values but we do not feel that they are so much more accurate as to compensate for the considerably greater amount of work necessary in laying out this complex sample, at least if only the thick-stemmed woody plants are involved.

The sample results for proportion of included species is somewhat different than that for density. The thirty 10% samples given in Table 5 include 33–43 species per sample (av. 37.7) or 61–80% (av. 70.0%) of the 54 species in the hectare. Here there is no tendency in the contour strips for the lowest absolute deviations to be in the middle strips. In fact, the deviations there are among the highest for these two strips include a lower number of species than the average. This is probably because a few species are present only in the upper or lower part of the hectare and absent in the middle. Because of the large number of species with few individuals, the inclusion of a species in a sample of this size is more haphazard than the proportion of individuals. Thus, a 10%-area sample should have a higher probability of including a number of individuals close to 10% of the total, that is 420, than it would to include a number of species close to the value for that area on the species-area curve, that is, about 38. On the average, the absolute deviations, using percent values, of species inclusion are on the order of 6.5 times greater than those for density.

A sixth type of sample, a 1% area sample of one hundred 1 × 1 m quadrats each, was not set up for sampling woody plants of the size we are considering, but for sampling the ground flora. However, for completeness, we may mention the results that this sampling method gave for the tree plus thick shrub category. Two independent sets of 100 quadrats each were used. The estimate of the number of individuals of all species together is 4900 for the first series and 4800 for the second series. This overestimation may be due to chance, but the fact that both series gave nearly the same large estimate may be due to a tendency to include too many individuals on the borders of the quadrats. In the estimation of numbers of individuals of each species separately there are very wide discrepancies from the true values. A sample of such small total area is not accurate for plants of the size we are considering, even when the sample is considerably split up and scattered over the hectare.

The first series includes 18 of the 54 species and the second series, 22. This may be compared with the single squares of the same total 100 m², which have 10–23 species, average 16.02. Thus, the same size sample area split up and scattered over the hectare includes more species than are usually found in a single block, which is what we would expect.

Point-quarter sampling

GOODLAND 1969 has applied the Wisconsin school point-quarter method of sampling to cerrado vegetation of western Minas Gerais. For each sample he chose an area of 6–8 ha of more or less uniform physiognomy. His

20 points were chosen by walking in a zig-zag line through the stand and stopping each time after a predetermined number of paces. In order to test the accuracy of this sampling method, we randomly chose 20 of the 25 midpoints (already marked with stakes) of the twenty five 20 × 20 m squares into which the hectare could be divided. Since each of these consists of four adjacent 10 × 10 m squares, these were used as the four quadrants. The nearest tree or thick shrub to the point was chosen in each quadrant. The plant size category is the same as that used by GOODLAND. The point to plant distance was measured and used to calculate total density and density for each species included in the sample. The frequency (proportion of the 20 points at which a species occurred) and the basal area already known were used with the density estimates to calculate Wisconsin importance values. In comparison with the complete census, the sample of 80 individuals included 26 of the 54 species present in the hectare. It gave an estimated total of 3585 plants per hectare. For individual species the relative densities were (0.25–)0.6 to 3.5(–6.5) times the true values, the estimated relative frequencies were (0.25)0.4 to 2.6(4.2) times the true values (although based on a different method), and the estimated relative basal areas were 0.25 to 5.45 times the true values. The importance values ranged from (0.3)0.6 to 2.7(4.25) times the true values. For these four statistics, 6 to 8 of the 26 species had estimated values between 0.8 to 1.2 times their true values, that is, within 20%, and 13 to 19 of the species had estimated values between 0.5 to 1.5 times their true values (within 50%). The fact that the estimated importance values of the individual species were from less than a third to more than 4 times their true values (even though half were within 50% of the true values), as well as the fact that only half of the species were included, shows that the point-quarter method counting 80 plants is not an accurate sample of thick-stemmed woody plants of a woodland cerrado. If the sample had been taken from a 6–8 ha area, as was the case in GOODLAND's investigation, rather than from 1 ha as in our comparison, the results would be even further off. Also, estimation of density using the point-quarter method assumes that the individuals of all the species together are randomly spaced, while we saw that this is not true of our hectare. (It is also not true for several cerrados of various densities in Brasília tested by the second author.) GOODLAND was successful in using this method because, although far from accurate for single stands, it is accurate enough for showing significant correlations between species composition and woody plant density when a large number of stands is counted over a large range of densities. GOODLAND counted 110 stands ranging from an estimated 1.00 to 5.13 m^2 of trunk basal area per hectare. The lack of randomness was not sufficiently serious to prejudice predictions based on its assumption when averages of so many stands were used.

The fact that 26 species were included in a sample of 80 individuals is interesting in view of the fact that, from the species-area relationship to be presented in a future paper, on the average about 300 m^2 (three contiguous 10×10 m squares) would be needed to contain 26 species. Yet an area of this size contains on the average 126 individuals. (The range in number of individuals among the thirty three 30×10 m rectangles which can fit into the hectare is 87–162.) The reason why in the point-quarter method only 80 individuals are needed to include 26 species is undoubtedly because these 80 are chosen from over the whole hectare. Many species are present only in certain parts of the hectare so that when a particular number of individuals is chosen from a restricted area, the species that could be selected are fewer than when the same number of individuals are chosen from over a larger area.

The 26 species in the sample included the first 15 species in order of density in the complete census, but by chance also included a species as rare as *Tocoyena formosa,* the 35th in order of density, with only 0.26% relative density.

Standard error (SE) can also be used for calculating the amounts by which a statistic of a sample of a finite population is likely to be in error. The SE of the relative density of a sample of size n is equal to the standard deviation (SD) of the relative density divided by $\sqrt{n}$. The random variable here has the value 1 with a probability p = number of individuals of the species concerned divided by the total number of individuals of all species, N, and has the value 0 with probability 1–p. The SD = $\sqrt{(\Sigma \text{ dev}^2/N)}$ = $\sqrt{[p(1-p)]}$. The sample relative densities are asymptotically normally distributed around the true value of the population, so that the true relative density ± SE gives the range of estimates in which about 2/3 of the sample values will fall. The SE divided by the true relative density is a measure of the amount by which a sample estimate is likely to be off the true value. Thus, in a random sample of 80 drawn from a population of 4197 individuals, the estimated density is likely to be off by up to 0.22 times the true value for the most abundant species in the sample, *Erythroxylum suberosum,* with 860 individuals in the hectare, and is likely to be off by up to 2.18 times the true value of *Tocoyena formosa,* the rarest species in the sample, with 11 individuals in the hectare.

As mentioned above, the estimated relative densities given by the point-quarter sample ranged from 0.25 (for *Erythroxylum)* to 6.5 (for *Tocoyena*) times the true relative densities for the 26 species. The standard error method is thus reasonably accurate for the more common species and less so for the uncommon ones, as one would expect.

For species with one individual in the hectare, the standard error method says that a sample of 80 from 4197 would yield an estimate of relative density that can be up to 7.1 times the true value.

Sampling by the point-quarter method is not exactly a random sample of the individuals in the population, for individuals in patches of lesser density are more likely to be chosen than those inside the denser clumps. The clumps in question are those of individuals of all species taken together. The amount of clumping shown by the individuals of all species together of trees and thick shrubs in cerrados in general seems simply to add a bit more variation to sample statistics which are based on an assumption of random sampling, but unfortunately there is no way of telling how much more variation it adds.

Growth in 3 years

When the trees and shrubs were originally counted in 1971 there was no intention to measure growth changes, only what was present in that particular year. Therefore, individual plants were not labelled for future reference. But in 1974 the heights and circumferences of trees and shrubs of ten randomly chosen 10 × 10 m squares were remeasured. No fire had passed through the stand during those years nor was any cutting done. In almost all cases it was possible to identify the same individuals as had been measured previously in each square, by the species and by the new heights and circumferences as compared to the old. Undoubtedly, in some squares new individuals (or new above-ground stems attached by rhizomes to old individuals) had appeared, or if they were previously present were now large enough to be included in the counts. Also, some individuals had doubtless disappeared, or if still present their former aerial stems were gone and new ones had not yet grown large enough to be included. When there were many individuals of the same species in a square, that were similar in size, it was not always easy to match all the individuals of the old count with those of the new. Two kinds of change can be measured: 1) size increase in the same individual, 2) increase of above-ground growth in general in a square as approximated by measurements of changes in basal area and height. For the first kind of change only individuals which we are certain are the same in both counts are included. For the second, all individuals are counted.

Since the bark of many species is thick and with large ridges, and the position and size of the ridges changes greatly from year to year (and indeed, even within the same growing season) at the same height, it is possible for a circumference measurement of the same stem to be less by up to a few cm in a later measurement. This fact had to be taken into account when matching individuals from one count to the other, and for this a limit of 2 cm reduction was allowed. In such a case of a later slightly smaller circumference for the same individual, the circumference of the later measurement is used for both years when basal area is calculated. (One individual of *Erythroxylum tortuosum*, the only one in its square, had a circumference of 18 cm in 1971 and 12 in 1974. In this case undoubtedly the whole stem had died and a new one had grown in its place. Dead stems are frequent in the cerrado, even without fire; they may die during the growing season or during the dry season.) By the same token, an increase of a few cm may not be a real increase but only a fluctuating increase that may disappear later. Since we are considering the circumference the same when it became slightly smaller but always including the increase when it became larger, our measurement of increase in basal area is probably greater than it should be, although certainly not more than a few percent.

Because half meter height classes were used, an increase of as little as 1 cm, for instance, could be counted as a 0.5 m increase, such as from 2.24 to 2.25 m, where the former would have been recorded as 2 m and the latter as 2.5 m. By the same token, some increases of up to 49 cm, such as from 1.75 to 2.24 m, would not be counted as an increase, since both would be recorded as 2 m. When the height class widths are 1 m this variation in the heights that fall into one class or the other is even more. There are more ways for a change to be recorded in the next higher class than for it to remain in the same class, but the average quantity of change in height per plant is the same, whatever the height class width is (in relation to a smaller class width that could have been chosen). Therefore, in a large enough sample the errors involved in using a grosser class width tend to cancel out.

In the first count, 347 individuals of 39 species were found in the ten squares, and in the second count of the same squares 345 individuals of 40 species were found. (*Palicourea rigida* HBK., not recorded for the hectare previously, was the new species found, represented by a single small individual.) For various reasons, 23 individuals of one or another year were discounted. Of the rest, in three years 53 individuals had disappeared from the 10% sample (i. e., had died, or the aerial part had died and any new above-ground stem was still too small to be counted), and 60 new individuals were recorded; 319 individuals were present in both counts. When a plant had more than one trunk, only the widest, that which usually bore the tallest foliage, was used to measure change. During the three year period, 24% of the 319 individuals present in both counts did not increase their circumference, in 52% the circumferences increased by 1–3 cm, and in the rest by 4–21 cm. Over half the individuals did not increase their height enough to enter the next height class, a quarter increased their height enough to be placed in the next 0.5 m class, and most of the rest enough to be placed in height classes of 1.0–2.5 m more. But in 7% of the individuals there was a reduction in height, presumably due to the uppermost stem dying off somewhat (this can be observed in cerrado trees and thick shrubs), or the whole aerial stem had died and new growth had not yet reached the previous level. Of course it is possible that in some plants the branch producing the uppermost foliage died and a lower branch grew up to above the former height, so that this growth would be recorded as an increase, but not as much as if the original branch had persisted and grown.

Of the 319 plants present in both counts, 133 increased in both circumference and height classes, 87 (including representatives of almost all the species) increased in circumference but not enough in height to fall into a higher class, 31 increased in height but not in circumference, and 38 did not increase in either the circumference or height classes. In 30 cases there was a reduction in height as already mentioned.

The 289 individuals in which circumference and heights were maintained or increased had an average circumference of 19.73 cm and an average height of 2.34 m in 1971, and an average circumference of 22.31 cm and an average height of 2.73 in 1974. Therefore, the circumference of an average individual increased by 2.58 cm (diameter by 0.81 cm and basal area by 8.45 cm^2), and the height by 0.39 m. A closer estimate of biomass is obtained by using cylindrical volume. Calculating this as the sum of the cylindrical volumes of the 289 individuals, it increased from 4.50 m^3 to 6.22 m^3, an increase of 1.72 m^3 for the 10% sample, or 1985 cm^3 CV growth per individual per year among those which increased or remained the same.

If we consider the whole growth increase between 1971 and 1974 (including plants which remained, which died, and which newly appeared at the second date), we have a CV of 5.30 m^3 in 1971 and 6.86 m^3 in 1974 for the ten squares, an increase of 1.56 m^3. For the whole hectare the estimate would be 15.66 m^3, or 5.22 m^3 per year. This is a reasonable increase per year for a cerrado that is growing up to cerradão.

Another aspect of growth is cover. Unfortunately, detailed cover values were not recorded when the plot was laid out in 1971. On Jan 1975, in the middle of the rainy season, an estimate to the nearest 5% was made of the cover above eye level (within an imaginary circle centered at the zenith and whose edges diverged about 5° from the zenith) at 200 random points in the hectare. The type of cover considered was real cover, the area of sky actually blocked by leaves and branches.

In Jan 1975 the true cover for the hectare ranged from 0% (which occurred in 24% of the positions) to 100%. The average was 41.26%. (The average cover for positions which had non-zero cover was 54.33%.) Since the cerrado is growing taller and denser, one would expect the cover to increase each year. However, there was a rare severe frost in July 1975 and branches of most species of trees and shrubs were killed as already mentioned. By Jan 1976 the mature foliage had grown out again, but on the 17th of that month a re-estimate of the cover over the same 200 points showed an average decrease of 8.43% due to the frost damage. This temporary decrease would be made up, however, in future years without severe frosts. Photographs of the increase in density of a cerrado in São Paulo that had been taken almost every year for a long time and then allowed to grow up without fire for three decades towards its original cerradão form may be found in FERRI 1973, 1977 and 1979.

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