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ANALYSIS OF THE TROPICAL DRY DECIDUOUS FOREST OF THAILAND, II. VEGETATION IN RELATION TO TOPOGRAPHIC AND SOIL GRADIENTS

*Sarayudh Bunyavejchewin**

ABSTRACT

Density, frequency, and basal area cover of tree species and physical environmental characteristics were collected in 40 forest stands. Ordination technique (BRAY & CURTIS, 1957; BEALS, 1960; SWAN & DIX, 1966) was used to analyze canopy structure. A three-dimensional ordination, based on the importance value 300 (CURTIS & MCINTOSH 1951) of the four dominant tree species, was used to illustrate canopy structure, and importance values of the 12 common tree species were demonstrated in the X-Y ordinations. Canopy structure appears to be best described as a continuous pattern in different parts of which individual tree species achieve peak performance.

Topographic and soil parameters including elevation, percentage slope, bulk density, particle density, soil pH, percentage organic matter, cation exchange capacity, available P, total N, and exchangeable K, Ca, Mg and Na, were used for stepwise multiple regression to develop predictive equations for the distribution of tree species. Exchangeable K, Ca and Na, available P, pH, bulk density, particle density and elevation show the greatest predictive ability in these regression equations.

Based on the results from regression analysis, gradients for the eight highest predictive parameters were established. Importance values of the dominant species and frequency of occurrence of the dominance-types were demonstrated along gradients. *Tectona grandis* Linn. f. reaches its ecological optimum at high levels of calcium and phosphorus. In contrast, *Lagerstroemia calyculata* Kurz achieves its optimum at low levels of calcium, phosphorus, and potassium content. The distribution of the two dominance-types, the *Tectona grandis* type and *Lagerstroemia calyculata* type, are similar to the distribution of *Tectona grandis* Linn. f. and *Lagerstroemia calyculata* Kurz.

INTRODUCTION

Although the tropical dry deciduous forest is one of the major forest types of Thailand, only a few studies dealing with environmental relationships have been conducted on this forest type (BUNYAVEJCHEWIN, 1979; SUKWONG & KAITPRANEET, 1975). The present study examines some of the structural and functional aspects of the tropical dry deciduous forest, with emphasis on relating the structure and distribution of vegetation to environmental gradients.

* Silvicultural Research Sub-division, Division of Silviculture, Royal Forest Department, Bangkaen, Bangkok 10900, Thailand.

Gradient analysis seeks to understand vegetation by studying relationships among gradients on three levels—environmental factors, species populations, and community characteristics (WHITTAKER, 1975, 1978).

The objectives were: (1) to determine the canopy structure of the tropical dry deciduous forest, and (2) to determine the relationships of dominant tree species and dominance-types to certain environmental factors.

Field and laboratory methods, and the location, climate, geology and soil of the study area, were described in BUNYAVEJCHEWIN (1983) which is the first paper of this series.

SYNTHESIS OF DATA

Vegetation. Floristic relationships between stands were analyzed by three-dimensional ordination following the method of BRAY & CURTIS (1957) modified by BEALS (1960) and SWAN & DIX (1966). GAUCH & WHITTAKER (1972) and BEALS (1973) recommended this method over other ordination techniques because it gives the best performance with the least distortion. This method demands only simple computation and is clearest for vegetation studies.

In this method the two most dissimilar stands are chosen as the reference stands of the ordination axis. All other stands are projected onto this axis in relation to their relative dissimilarity to the two reference stands. On the second axis, the first reference stand should be a stand that is poorly fitted to the first axis. The closest stand to the first reference stand along the first axis is chosen as the second reference stand, and the other stands are located on the axis. The result is either one, two, or three or more axes.

Vegetation-environment relationships. Stepwise multiple regressions were used to construct predictive equations for plant response to environmental factors. Independent variables consist of bulk density, particle density, percent silt + clay, soil pH, percent organic matter, total nitrogen, available phosphorus, exchangeable potassium, calcium, magnesium and sodium, cation exchange capacity of surface soil (0-15 cm depth), elevation, and percent slope. The general equation is

$$Y = a + b_1X_1 + b_2X_2 + \ldots + b_nX_n \pm SE$$

where Y = dependent variable,
a = Y intercept,
b_i = partial regression coefficient,
X_i = independent variable,
SE = standard error of estimate

RESULTS AND DISCUSSION

Canopy structure

One hundred fifty-one tree species are encountered in the sample stands of the tropical dry deciduous forest of Thailand. Only four species, *Tectona grandis* Linn,f.,*Lagerstroemia calyculata* Kurz, *Xylia kerrii* Craib & Hutch., and *Terminalia mucronata* Craib & Hutch. are dominant species of the canopy and therefore form the basis of the analysis.

The behaviours of the four dominant species are expressed on the three dimensional ordination (X-Y, X-Z, and Y-Z axis pairs) by their importance value (Fig. 1). The importance value 300 (CURTIS & McINTOSH, 1951) is selected as the principal phytosociological measure of species performance. This value is the sum of relative density, relative frequency, and relative basal area. The importance value 300 is divided into five classes and a different circle size assigned to each (Fig. 1). For each species, importance value classes are represented in each ordination.

Figure 1 shows that *Tectona grandis* achieves maximum values at the middle right of the X-Y and X-Z diagrams. *Lagerstroemia calyculata* achieves its greatest performance at the lower center and center of the X-Y and X-Z diagrams, respectively. In the Y-Z ordination, *Tectona grandis* reaches its highest importance at the center of the diagram while *Lagerstroemia calyculata* is most important slightly upper-left of center. *Xylia kerrii* is evenly distributed thoughout the diagram. *Terminalia mucronata* has a pattern which overlaps *Tectona grandis* and *Lagerstroemia calyculata*. The other species which occur in the upper canopy are represented in the X-Y diagram (Fig. 2). Most of them have importance values lower than 25 and overlap with both *Tectona grandis* and *Lagerstroemia calyculata*, except *Terminalia alata* Heyne ex Roth which shows a high correlation with *Tectona grandis*. Such patterns do not represent a distribution by chance alone, a fact that lends support to the value of the ordination as a basis for explaining canopy structure.

Species relationships are obtained by plotting the different levels of their importance values on the ordination (Fig. 3). Figure 3 shows the relationships of the four dominant species on the X-Y ordination for importance value levels of IV $\geqq$ 25, IV $\geqq$ 50, and IV $\geqq$ 100.

Figure 3A shows that all dominant tree species except *Terminalia mucronata* are found in stands with importance values above 100. However, *Lagerstroemia calyculata* occurs in two stands and *Xylia kerrii* in one stand only. In Figure 3B, *Tectona grandis* and *Lagerstroemia calyculata* occupy only a limited part of the ordination and little overlap of pattern is indicated. *Xylia kerrii* and *Terminalia mucronata* occur in only a few stands. A species having an importance value above 50 in a stand is considered the major contributor to the canopy. Figure 3B indicates that 28 stands from 40 sample stands are almost dominated by one tree species. All species cover greater area when the importance value is 25 or greater (Fig. 3C). At this level each species is linked to the others but none is completely associated with any other.

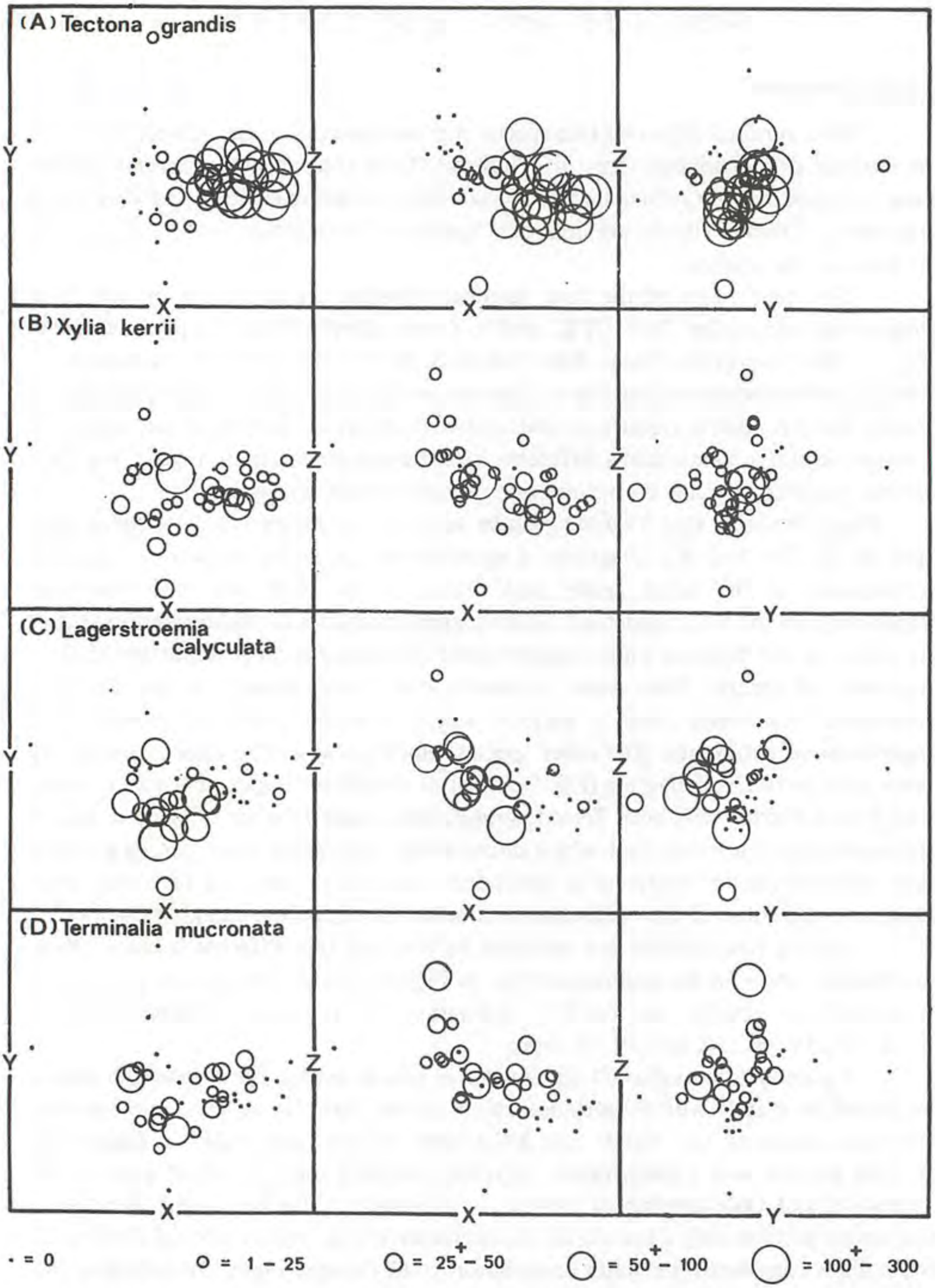

Figure 1. The importance value distribution of (A) *Tectona grandis;* (B) *Xylia kerrii;* (C) *Lagerstroemia calyculata;* and (D) *Terminalia mucronata* on the three dimensional ordination. Various sizes of circles represent five classes of importance values as shown below.

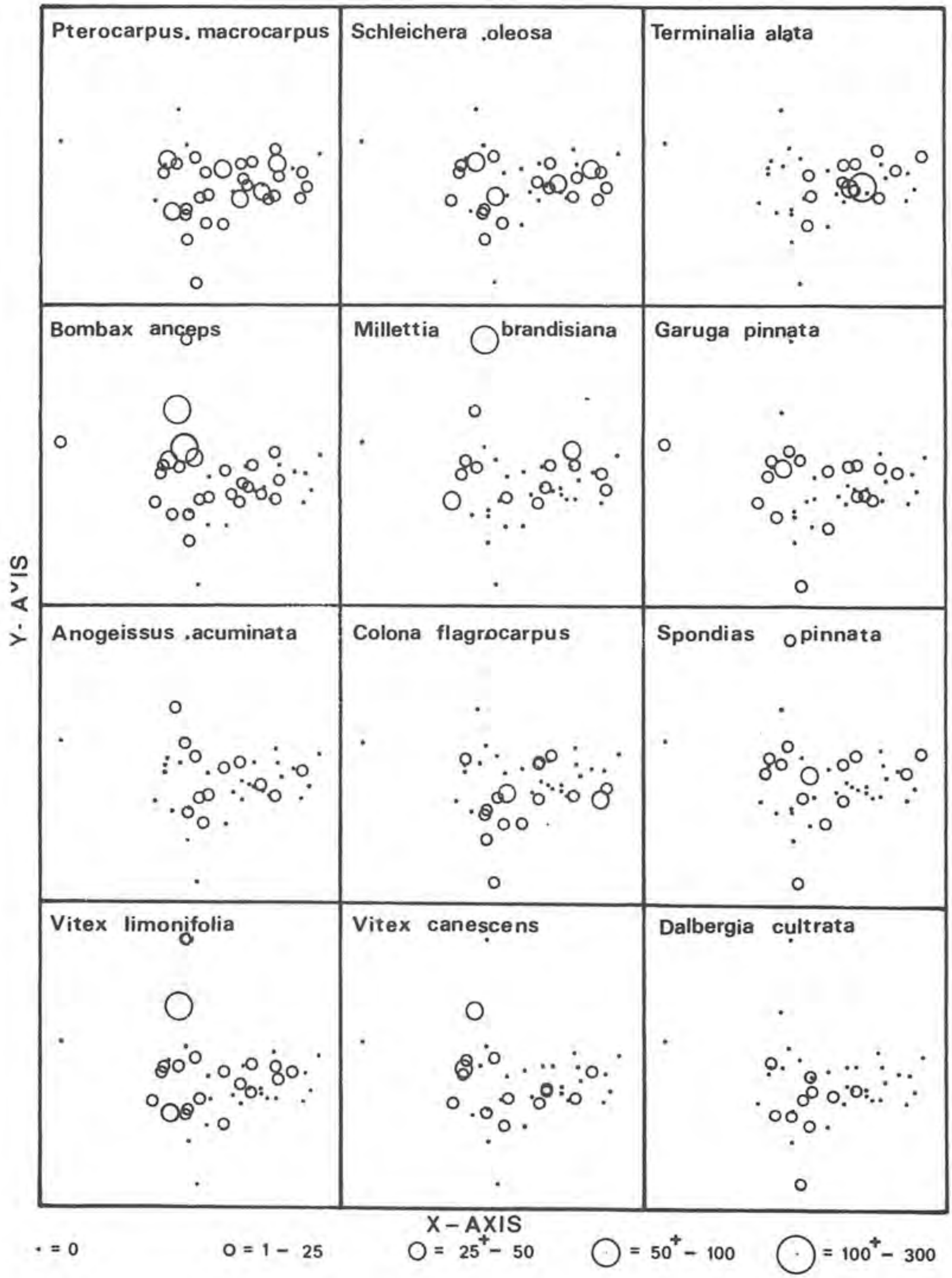

Figure 2. The importance value distribution of twelve tree species on the X—Y ordination. Various sizes of circles represent five classes of importance values as shown below.

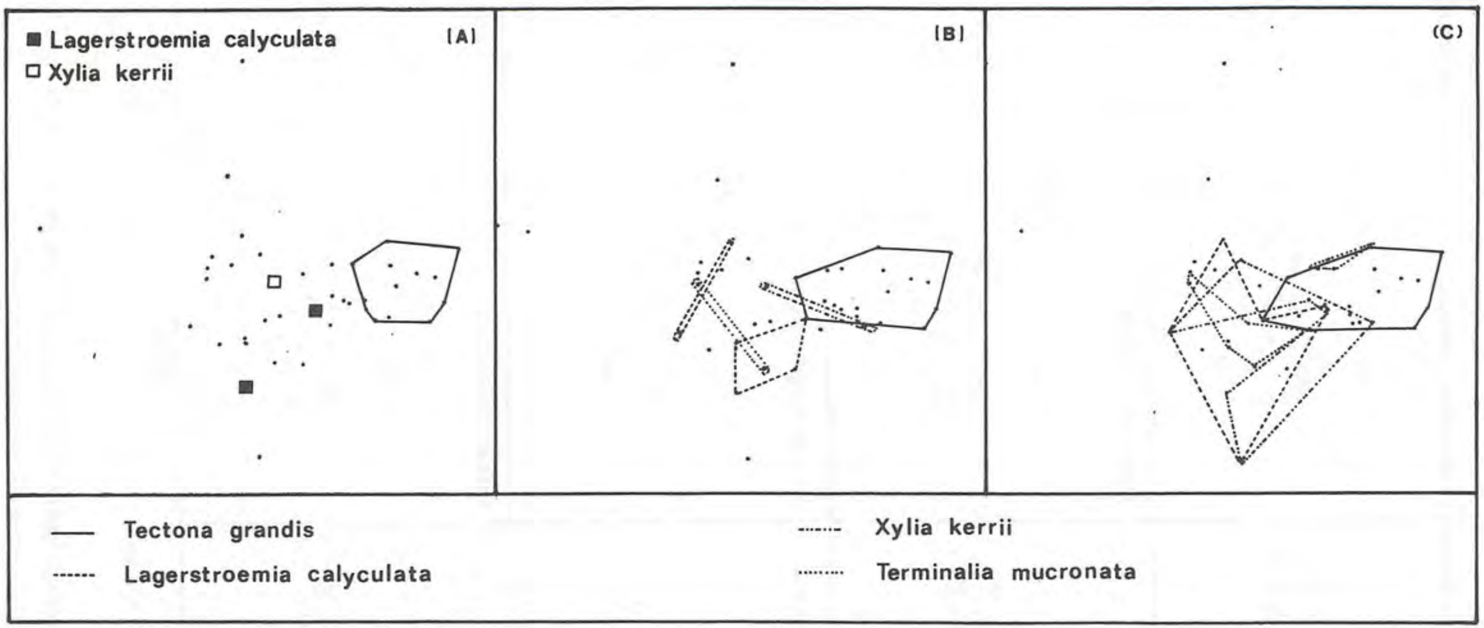

Figure 3. Distributions of four dominant species at selected importance value levels on the X-Y ordination. (A) Importance values of 100 or greater; (B) values of 50 or greater; and (C) values of 25 or greater.

This analysis shows that patterns are more distinct above an importance value of 50. The degree of overlap is increased by a decrease in importance value. This may indicate that the canopy structure can be separated into two groups, one dominated by *Tectona grandis* and another by *Lagerstroemia calyculata*. Each group has the other three species as the associated species. This analysis supports the classification of the tropical dry deciduous forest by BUNYAVEJCHEWIN (1983).

Vegetation-environment relationships

Of the initial 20 tree species used for multiple regression analysis, five common species including two dominant species of the upper canopy, *Lagerstroemia calyculata* and *Terminalia mucronata*, failed to yield any independent variables with statistical significance. The regressions of importance value of those species on environmental factors are summarized in Table 1. The coefficient of determination (R^2) of the selected equations range from 0.550 for *Xylia kerrii* to 0.990 for *Dillenia parviflora* Griff. The coefficient of determination represents the percentage of variance accounted for by multiple regression. Thus, all regression equations present account for 55 percent or more of the variation in importance value and are statistically significant.

Each of the environmental variables is retained within the regressions, although some occur more frequently than others. Table 2 shows the frequency of occurrence of the environmental variables in the regression models. The complete regression equations show four non-nutrient parameters occurring most frequently. These include particle density, bulk density, pH and elevation. The nutrient parameters frequently retained by regression analysis are exchangeable K, Ca, Na, and available P. Further analysis of the equations shows that exchangeable K, Ca, and available P appear with positive regression coefficients in 77.8, 22.2 and 12.5 percent of the regressions respectively. The frequent occurrence of negative regression coefficients for these three nutrients may be related to annual fire. ZINKE *et al.* (1978) reported that potassium, calcium and phosphorus contents are higher in the surface soils following burning. The regression equations also indicate that *Tectona grandis* and *Terminalia alata* are calcium-favouring species.

Distribution of species along the gradients

Based on the frequency of occurrence of the environmental factors which were retained in the multiple equations, the eight environmental factors: exchangeable K, Ca and Na, available P, pH, particle density, bulk density, and elevation, were used to establish environmental gradients (Tables 3 to 10). Each gradient was subdivided into five classes and each class was assigned an index number from 1 to 5 according to its position along the gradient. The 40 stands were divided into five groups of eight each; but this was not always possible because of a lack of natural breaks at these precise intervals. Diagrams of the distribution of selected species along the gradients are shown in Figures 4 and 5, which show autecological optima and the

Table 1. Predictive multiple regression equations based on importance values of the selected species along environmental parameters.

Species	Regression equations
Tectona grandis Linn. f.	Y = 399.718 + 4.690 Ca* − 0.249 elev.* + 1.838 S+C* − 1103.652 N* + 34.276 OM* + 87.710 Na* − 194.327 PD* + 70.587 K* − 0.373 P* ± 47.472 (R^2 = .648)
Xylia kerrii Craib & Hutch.	Y = −407.125 + 1.049 S+C + 160.338 PD − 1.413 Ca + 25.468 K − 0.338 P + 9.276 pH + .023 elev. + 64.547 N ± 17.128 (R^2 = .550)
Pterocarpus macrocarpus Kurz	Y = 83.949 + 1.199 Mg* + .656 CEC* − .492 S+C + .160 Ca + 3.772 OM − .048 elev. − 11.999 pH + 21.118 K ± 9.502 (R^2 = .553)
Millettia brandisiana Kurz	Y = 175.410 − 1.222 S+C + 69.207 Na − 2.845 Mg − 91.701 K − 2.203 PD + 7.944 OM − 12.734 pH + .166 P − 26.417 BD* ± 6.879 (R^2 = .940)
Terminalia alata Heyne ex Roth	Y = 96.639 + 6.328 Ca − 1.987 pH − 31.486 Mg + 1.877 K − 50.068 BD − 15.364 CEC + 3.760 N − 91.671 P ± 3.546 (R^2 = .981)
Bombax anceps Pierre	Y = −73.776 − .601 S+C + 49.041 Na + 180.423 N − .422 P + 17.406 pH − .943 CEC + .168 slope* − 1.188 Ca ± 12.247 (R^2 = .639)
Garuga pinnata Roxb.	Y = 47.218 + 7.027 OM − .042 elev. − 12.375 K − .630 Mg − 18.287 PD − .259 Ca ± 7.684 (R^2 = .643)
Vitex limonifolia Wall.	Y = −34.393 + 64.953 N + 85.706 K − .259 BD + 30.218 Na − .169 P + .156 slope − 1.697 Ca − .033 elev. ± 7.890 (R^2 = .829)

Table 1. (Continued)

Species			Regression equations
Vitex canescens Kurz	Y	=	98.888 − 30.552 BD − .051 elev. + 11.005 Na − .329 P + 28.830 K − 10.666 pH + 2.409 OM ± 5.332 (R^2 = .901)
Spondias pinnata Kurz	Y	=	−70.253 + .056 slope − .405 Ca + 4.160 OM + 32.885 PD + 11.162 Na ± 3.972 (R^2 = .711)
Anogeissus acuminata Wall. var. *lanceolata* Clarke	Y	=	−6.713 + 18.202 CEC − .250 Mg + .028 elev. + .174 slope − 1.288 S+C ± 4.218 (R^2 = .805)
Dillenia parviflora Griff	Y	=	15.364 + 237.096 Na − .719 slope − 16.032 BD − .009 elev. + .888 CEC − .123 Mg ± 2.879 (R^2 = .990)
Terminalia bellerica Roxb.	Y	=	−137.216 + 123.372 PD + 262.384 K − 77.212 BD − 10.271 Ca ± 1.603 (R^2 = .982)
Terminalia nigrovenulosa Pierre ex Laness	Y	=	244.496 − 60.724 BD − 1.056 CEC − 75.272 PD − 1.062 pH ± 2.048 (R^2 = .977)
Berria mollis Wall. ex Kurz	Y	=	90.933 + 30.756 Na − 25.274 BD − .436 P − 29.467 PD − 51.107 N ± .473 (R^2 = .971)

* For abbreviation codes, see Table 2.

Table 2. Frequency of occurrence of the 14 independent variables retained in 15 multiple regressions.

Independent variables	Frequency
Exchangeable potassium (K)	9
Exchangeable calcium (Ca)	9
Exchangeable sodium (Na)	8
Available phosphorus (P)	8
Elevation (elev.)	8
Particle density (PD)	8
Bulk density (BD)	8
pH	7
Percent silt + clay (S + C)	6
Cation exchange capacity (CEC)	6
Exchangeable magnesium (Mg)	6
Total nitrogen (N)	6
Percent organic matter (OM)	6
Percent slope (Slope)	5

Table 3. Characteristics of the exchangeable calcium gradient.

Class	Class limits of calcium gradient	Average of the class	No. plots in the class
1	1.91 - 3.95	3.17	8
2	3.96 - 5.25	4.80	8
3	5.26 - 8.00	6.94	8
4	8.01 - 12.45	11.17	8
5	12.46 - 47.00	18.80	8

Table 4. Characteristics of the exchangeable potassium gradient.

Class	Class limits of potassium gradient	Average of the class	No. plots in the class
1	.18 - .30	.23	7
2	.31 - .44	.39	9
3	.45 - .50	.47	8
4	.51 - .64	.57	8
5	.65 - .98	.76	8

Table 5. Characteristics of the available phosphorus gradient.

Class	Class limits of phosphorus gradient	Average of the class	No. plots in the class
1	2.10 - 3.45	2.82	8
2	3.55 - 4.60	4.25	8
3	4.61 - 6.25	5.68	8
4	6.26 - 9.50	8.41	8
5	9.51 - 67.00	34.39	8

Table 6. Characteristics of the exchangeable sodium gradient.

Class	Class limits of sodium gradient	Average of the class	No. plots in the class
1	.10 - .37	.30	8
2	.38 - .48	.44	8
3	.49 - .55	.53	8
4	.56 - .73	.64	8
5	.74 - 1.06	.92	8

Table 7. Characteristics of the particle density gradient.

Class	Class limits of particle density gradient	Average of the class	No. plots in the class
1	1.714 - 1.853	1.796	8
2	1.854 - 1.930	1.910	8
3	1.931 - 1.982	1.964	7
4	1.983 - 2.029	2.006	8
5	2.030 - 2.138	2.088	9

Table 8. Characteristics of the bulk density gradient.

Class	Class limits of bulk density gradient	Average of the class	No. plots in the class
1	.80 - 1.05	.92	8
2	1.06 - 1.13	1.10	7
3	1.14 - 1.19	1.17	8
4	1.20 - 1.33	1.26	9
5	1.34 - 1.54	1.40	8

Table 9. Characteristics of the elevation gradient.

Class	Class limits of elevation gradient	Average of the class	No. plots in the class
1	180 - 280	236.11	9
2	281 - 345	321.25	8
3	346 - 430	395.00	8
4	431 - 520	489.38	8
5	521 - 850	612.14	7

Table 10. Characteristics of the pH gradient.

Class	Class limits of pH gradient	Average of the class	No. plots in the class
1	4.55 - 5.05	4.88	8
2	5.06 - 5.35	5.25	8
3	5.36 - 5.60	5.50	8
4	5.61 - 5.85	5.81	9
5	5.86 - 7.65	6.39	7

amplitude of tolerance of each species. The ecological optimum adopted by WARING & MAJOR (1964), and WIKUM & WALI (1974) is the point at which the maximum importance value of each species occurs along an environmental gradient.

Figures 4 and 5 and Tables 3 to 10 suggest that *Tectona grandis* succeeds well on slightly acidic soil with high exchangeable calcium and slightly high levels of available P, bulk density, and particle density, at elevations ranging from 430 to 520 m. In contrast, *Lagerstroemia calyculata* grows well at low elevations of 180 to 280 m, with acidic soils of low exchangeable K, available P, and slightly low exchangeable Ca and Na.

The highest elevation sites of the study area, 540 to 850 m, with high levels of exchangeable K and Na, are occupied by *Xylia kerrii. Terminalia mucronata* is well developed at elevations between 345 and 430 m but soils under *Terminalia mucronata* have high exchangeable K, Na and Ca.

Results of this study show that the distributions of the dominant tree species along the environmental gradients occur in a continuous, overlapping, and nondiscrete fashion. This supports Gleason's and Remensky's individualistic hypothesis (WHITTAKER, 1962) and the continuum concept described by CURTIS & McINTOSH (1951).

Distribution of dominance-types along the gradients

According to BUNYAVEJCHEWIN (1983). The tropical dry deciduous forest is divided into two dominance-types— *Tectona grandis* type and *Lagerstroemia calyculata* type. The eight environmental parameters used for illustrating species distribution along environmental gradients were also used to evaluate the distribution of dominance-types. Frequency of occurrence of dominance-types were plotted along each gradient (Fig. 6).

The *Lagerstroemia calyculata* type has its distribution on low elevation sites.

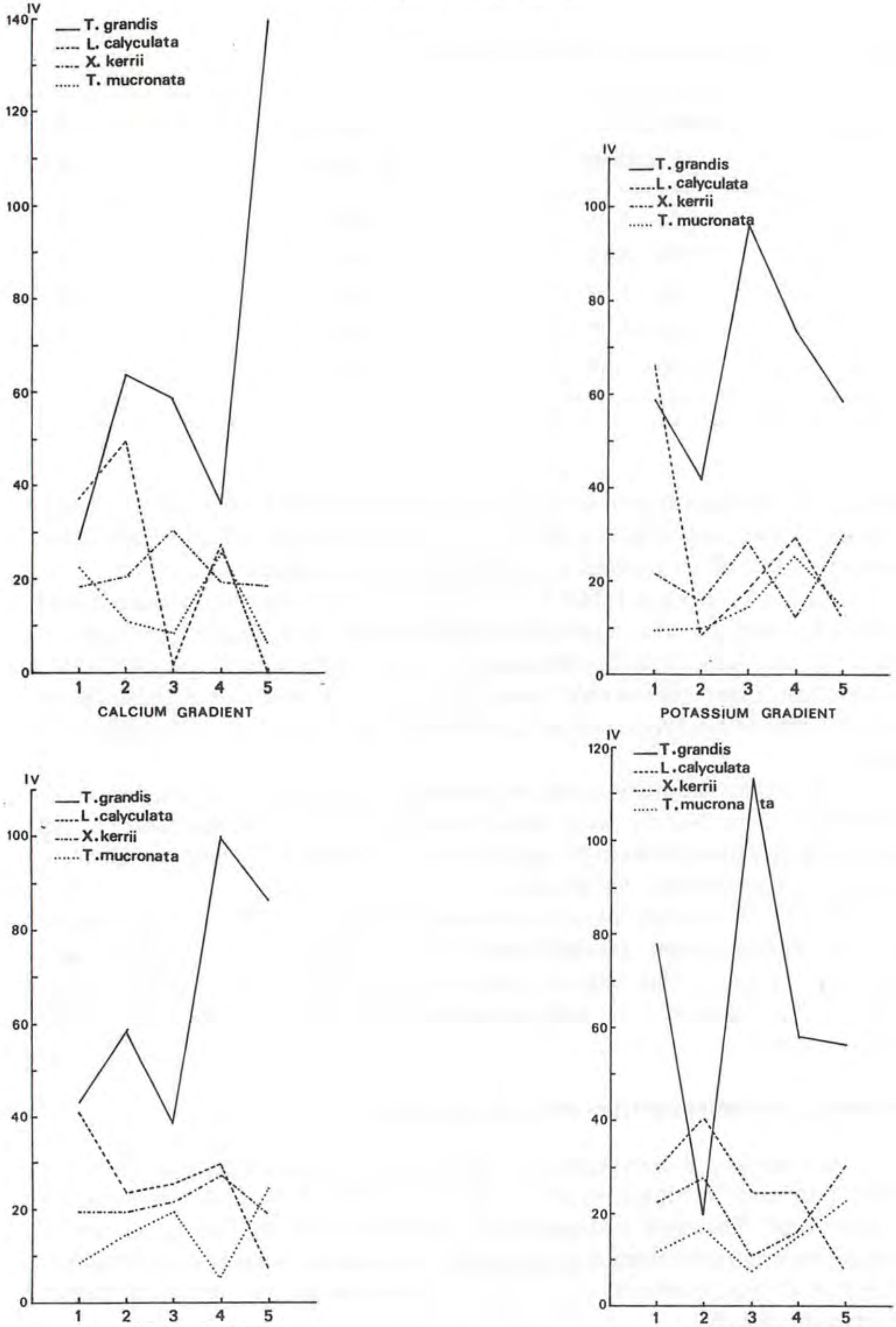

Figure 4. Distributions of four dominant species along the calcium, potassium, phosphorus and sodium gradients.

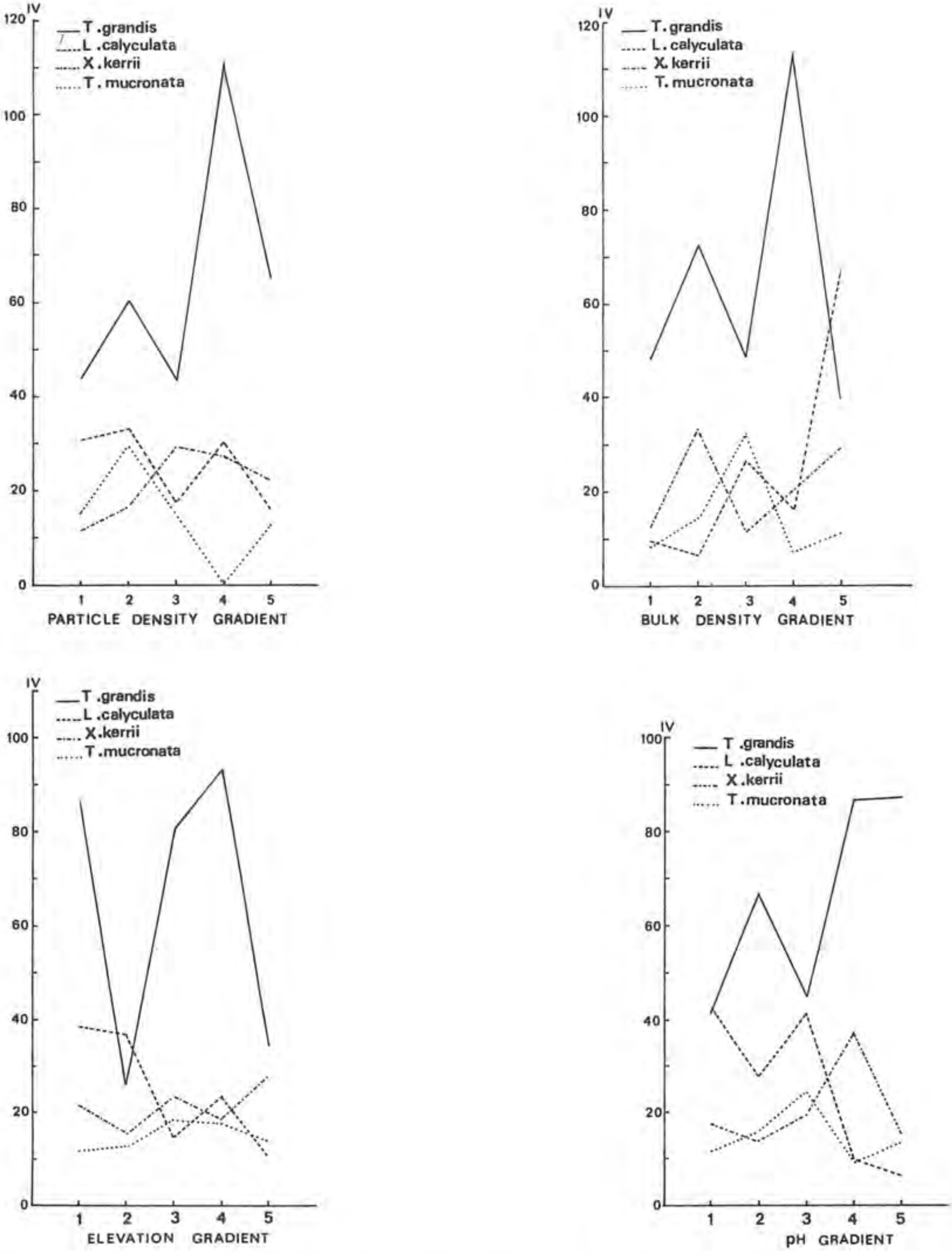

Figure 5. Distributions of four dominant species along the particle density, bulk density, elevation and pH gradients.

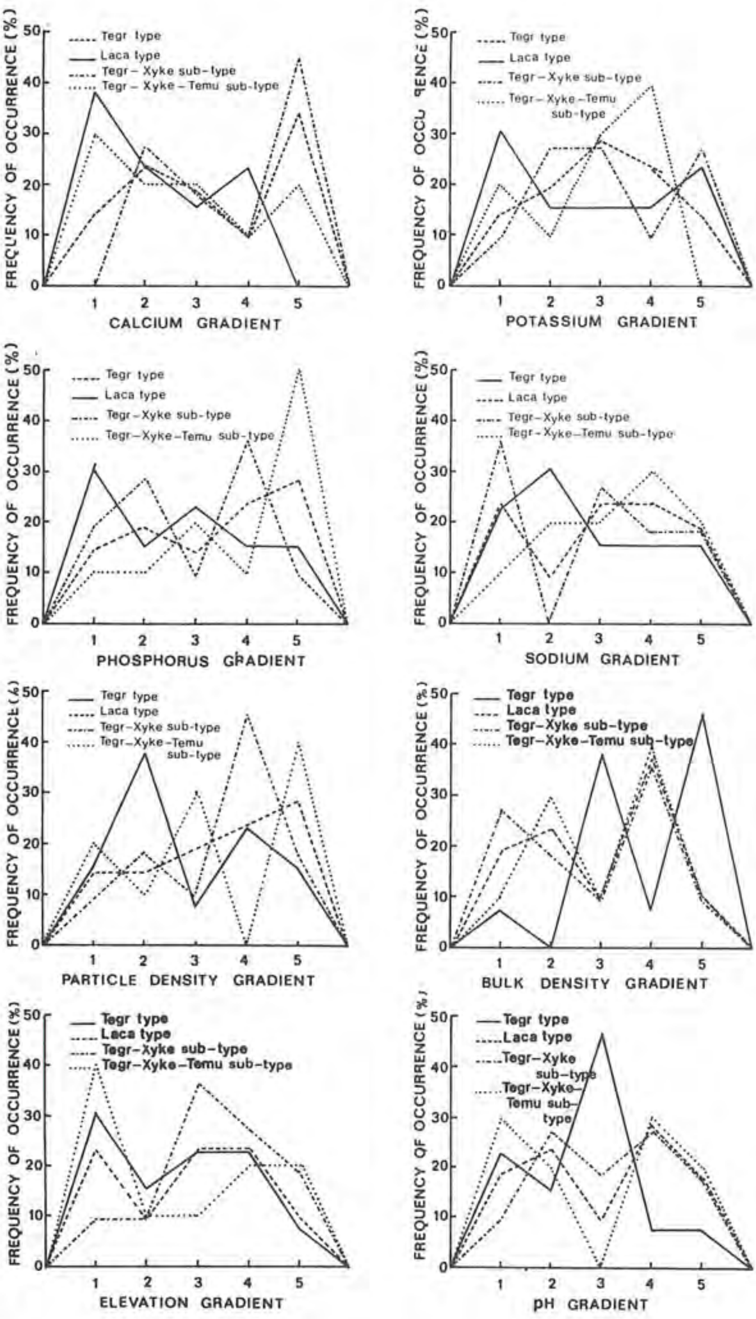

Figure 6. Frequency of occurrence of dominance-types along the calcium, potassium, phosphorus, sodium, particle density, bulk density, elevation and pH gradients. Tegr type = *Tectona grandis* type; Laca type = *Lagerstroemia calyculata* type; Tegr-Xyke sub-type = *Tectona grandis - Xylia kerrii* sub-type; and Tegr-Xyke-Temu sub-type = *Tectona grandis - Xylia kerrii - Terminalia mucronata* sub-type.

The surface soil of this type is low in available P, and exchangeable K and Ca. The *Tectona grandis* type dominates low and middle elevation sites. Surface soil under this type is high in exchangeable Ca and available P. Both the *Tectona grandis - Xylia kerrii* sub-type and *Tectona grandis - Xylia kerrii - Terminalia mucronata* sub-type cover sites within the same environmental gradients as the *Tectona grandis* type except in calcium gradient.

The distributions of the *Tectona grandis* type and the *Lagerstroemia calyculata* type clearly separate, particularly along the exchangeable Ca, available P, and particle density gradients. This reflects a distinct contrast in some environmental characteristics and some of the species composition between these dominance-types. Although the two sub-types of the *Tectona grandis* type do not show a peak at the same points, they tend to parallel each other along several gradients. This is consistent with the fact that the vegetation is similar in these two sub-types. However, their patterns are separate from each other on some gradients.

CONCLUSIONS

This study was designed to determine the canopy structure of the tropical dry deciduous forest and to obtain the relationships between the dominant tree species, dominance-types, and selected environmental factors.

Ordination technique was used to analyze canopy structure of this forest type. The canopy structure is best described as a pattern of continuous variation in different parts of which individual species achieve peak performance.

The distribution of the dominant tree species was evaluated by stepwise multiple regression. Environmental factors appearing most highly correlated to dominant species distributions are exchange-able K, Ca and Na, available P, pH, particle density, bulk density, and elevation.

The distributions of the dominant tree species along environmental gradients are continuous. The distribution patterns of the *Tectona grandis* type and *Lagerstroemia calyculata* type separate from each other on some environmental gradients. The distributions of both the dominant tree species and the dominance-types of the tropical dry deciduous forest are continuous, overlapping and nondiscrete.

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