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# Above-ground phytomass of a tropical deciduous forest on the coast of Jalisco, México

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**ABSTRACT.** Phytomass was determined for a tropical deciduous forest in Chamela, Jalisco, México. The mean canopy height was 6.9 m, and the total basal area was 25.6 m<sup>2</sup> ha<sup>-1</sup> (dbh > 3.0 cm). The estimated phytomass for this forest (85 Mg ha<sup>-1</sup>) is among the highest values for tropical dry forests with similar seasonal climates. A stepwise multiple regression analysis showed that phytomass can be predicted firstly by basal area ( $R^2 = 0.88$ ), then by wood specific gravity ( $R^2 = 0.91$ ), and finally by the inclusion of tree height in the regression ( $R^2 = 0.92$ ). Each new independent variable explained significant variance in the phytomass estimation.

**RESUMEN.** Se determinó la cantidad de fitomasa aérea viva de una selva baja caducifolia en Chamela, Jalisco, México. La altura promedio del dosel de vegetación fue de 6.9 m, y el área basal total de 25.6 m<sup>2</sup> ha<sup>-1</sup> (dbh > 3.0 cm). La fitomasa estimada para el sitio de estudio (85 Mg ha<sup>-1</sup>) es de las más altas en comparación con otras selvas tropicales secas con climas similares. Un análisis de regresión múltiple mostró que la fitomasa se puede predecir en primer lugar como una función del área basal ( $R^2 = 0.88$ ), luego como función de la gravedad específica de la madera ( $R^2 = 0.91$ ) y finalmente por la inclusión de la altura en la ecuación ( $R^2 = 0.92$ ). Cada nueva variable independiente explicó porciones significativas de la variancia en fitomasa.

**KEY WORDS:** above-ground, allometry, biomass, México, phytomass, seasonality, regression, tropical deciduous forest.

## INTRODUCTION

Tropical deciduous forests are found over large areas around the world. Despite the fact that they represent a potential natural resource, data regarding their structure and productivity are notably scarce (Murphy & Lugo 1986a). Also, attempts to balance the world's carbon budget suffer from the lack of good data on the carbon pool in tropical dry forests (Brown & Lugo 1984). In México, such forests cover about 8% of the country area (Rzedowski 1978) but they have been poorly studied. Since perturbation of these forests is increasing at an alarmingly high rate (Maass *et al.* 1988) studies at the ecosystem level are urgently needed.

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The present study is part of a long-term ecosystem research project started in 1975 in the tropical deciduous forest at Chamela, Jalisco, México. This research aims to analyse various aspects of the structure and function of the undisturbed forest, in an attempt to assess its productive capacity and ecosystem dynamics. The objectives of this study were: (1) to estimate the size of the above-ground phytomass of a Mexican tropical deciduous forest and to compare it with that of other tropical forests with similar climates, (2) to predict the above-ground phytomass of the forest using the dimensional analysis approach (Attiwil & Ovington 1968, Baskerville 1972, Whittaker & Marks 1975).

#### STUDY AREA

The study was conducted at the Estación de Biología Chamela, Universidad Nacional Autónoma de México, on the coast of Jalisco, México (19°30' N, 105°03' W). This is a 1600 ha reserve, occurring in a series of low hills (mostly below 150 m in elevation) with slopes typically 21–34° (Bullock 1988). The climate is warm and markedly seasonal, with a 6–8 month dry period extending from November to mid-June, with August and September being the wettest months. Mean rainfall for the years 1977–1988 is 707 mm. Monthly mean minimum and maximum temperatures are 15.9°C (February) and 32.2°C (August), respectively (Bullock 1988). The predominant vegetation in Chamela is the Tropical Deciduous Forest type of Rzedowski (1978) which dominates the slopes. This is a dense forest, 4–15 m tall, with a well-developed understorey of shrubs (Lott *et al.* 1987). The phenology of the forest is strongly seasonal. With few exceptions, the species bear no leaves for several months during the dry season each year (Bullock & Solís-Magallanes 1990, Martínez-Yrizar & Sarukhán 1990). Floristic diversity and structure of the vegetation have been reported by Lott *et al.* (1987) for woody plants > 2.5 cm dbh. The soils are young, weakly developed entisols on substrates of rhyolite and basalt (E. Solís pers. comm.).

#### METHODS

An area of 50 m × 20 m (subdivided into 40 plots, each 5 m × 5 m) was located during the dry season within the tropical deciduous forest in the station. The area, on a 20–25° slope, was chosen because it was considered homogeneous and structurally representative of the forest.

In each sample plot, all individual plants of at least 3.0 cm in diameter at 1.3 m above-ground were identified and their diameter measured (dbh). All the plants in each plot were harvested, and their height and total fresh mass measured in the field. Subsamples of boles, stems and branches of each individual plant were taken to the laboratory for drying to constant mass at 105°C.

The herbaceous vegetation was sampled in 24 subplots (3 m × 2 m) randomly selected before the arboreal vegetation was cut down. All herbs, saplings and

stems < 3.0 cm dbh were identified, harvested at ground level and weighed in the field. Subsamples were dried to constant mass at 80°C.

Because most leaves had fallen at the season of measurement, leaves remaining on the plants at harvest time were discarded. Standing dead trees and dead branches on living individuals were separated and are considered in another study (J. M. Maass & C. Patiño unpubl.). An estimate of below-ground phytomass of the forest has been obtained by Castellanos *et al.* (1991).

A stepwise multiple regression analysis was performed on the log<sub>10</sub>-transformed data. Basal area (cm<sup>2</sup>), tree height (m) and wood specific gravity (WSG) were used as independent variables in the regression analysis. Most of the WSG values were taken from Barajas-Morales (1985, 1987). For those species not included in her lists, WSG values were determined (Table 1) as the ratio of the oven-dry mass of the wood sample, divided by the mass of the water displaced when the sample was completely submerged. Cacti were not included in the regression analysis.

## RESULTS

### *Forest structure*

A total of 214 individual trees, shrubs, lianas and cacti, representing 48 species and 23 families, were present in the 1000 m<sup>2</sup> sample area. Eleven standing trees were dead. The understorey layer (herbs, saplings and small stems less than 3.0 cm dbh) was represented by 93 species. The number of individual stems > 3.0 cm dbh in each of the 40 plots ranged from 2 to 10. Species-area curve for stems > 3.0 cm dbh is shown in Figure 1. The regression coefficient of the log-linear relationship of cumulative species on cumulative area was 0.538 (Pearson-*r* = 0.99).

Total basal area was 25.6 m<sup>2</sup> ha<sup>-1</sup> for stems > 3.0 cm dbh. Of the total living individuals 70% had less than 100 cm<sup>2</sup> basal area. Only three stems were more than 1000 cm<sup>2</sup> and 1582 cm<sup>2</sup> was the largest basal area measured (Figure 2a).

Table 1. Wood specific gravity (WSG) of the species at Chamela tropical deciduous forest not reported by Barajas-Morales (1985, 1987).

Species	Family	WSG
<i>Esenbeckia berlandieri</i> Baill.		
subsp. <i>acapulcensis</i> (Rose) Kaastra	Rutaceae	0.93
<i>Croton alamosanus</i> Rose	Euphorbiaceae	0.92
<i>Samyda mexicana</i> Rose	Flacourtiaceae	0.89
<i>Lagrezia monosperma</i> (Rose) Standl.	Amaranthaceae	0.87
<i>Zanthoxylum fagara</i> (L.) Sarg.	Rutaceae	0.85
<i>Croton pseudoniveus</i> Lundell	Euphorbiaceae	0.82
<i>Achatocarpus gracilis</i> H. Walt	Achatocarpaceae	0.80
<i>Dyospyros aequoris</i> Standl.	Ebenaceae	0.73
<i>Phyllanthus mocinianus</i> Baill.	Euphorbiaceae	0.73

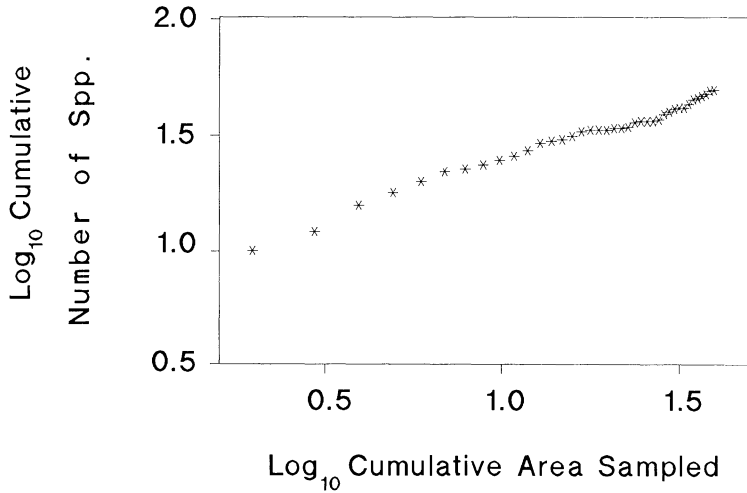


Figure 1. Species-area curve for woody species (dbh > 3.0 cm) on a 1000 m<sup>2</sup> area of tropical deciduous forest at Chamela, Jalisco, México. Equation is of the form  $\log_{10} Y = a + b \log_{10} X$ , where  $a = 0.811$ ,  $b = 0.538$ ,  $r = 0.99$ ,  $P < 0.001$ .

Average canopy height was  $6.9 \pm 0.2$  (SE) m. Only seven individuals were more than 10.5 m tall; the tallest tree recorded was 14.6 m high (Figure 2b).

#### *Forest above-ground phytomass*

Phytomass values ranged from 0.25 to 23 kg m<sup>-2</sup>. Most of the plots (70%) had above-ground phytomass values lower than 10 kg m<sup>-2</sup>. The distribution of the above-ground phytomass in the 40 sample plots is shown in Figure 3.

Total above-ground phytomass for trees, shrub, lianas and cacti > 3.0 dbh amounted 77.7 Mg ha<sup>-1</sup>. Since data for six individual trees were missing, we estimated their phytomass contribution as 2.3 Mg ha<sup>-1</sup>, based on the average dry mass value per tree. An additional 1.0 Mg ha<sup>-1</sup> was contributed by the understorey layer, yielding a total above-ground phytomass of 81 Mg ha<sup>-1</sup>. The mean annual litterfall value of 4.0 Mg ha<sup>-1</sup> obtained from a long-term study in an adjacent forest site (Martínez-Yrizar & Sarukhán 1990), increased our phytomass estimate to a final value of 85 Mg ha<sup>-1</sup>. Litterfall data were used to correct our phytomass estimate assuming that most of the leaves in the canopy are annual and that retranslocation before shedding is insignificant.

The relative contribution of the most abundant species to the total above-ground phytomass is shown in Table 2. *Caesalpinia eriostachys* Benth., the dominant species, contributed 33.4%, followed by *Thouinia paucidentata* Randlk. and *Apoplanesia paniculata* Presl. with 8.7 and 7.9%, respectively. Nine species accounted for 75% of the total standing crop mass.

Juveniles of trees and shrubs were the most abundant component of the understorey layer. Saplings of *Apoplanesia paniculata* (a tree) and *Justicia candicans*

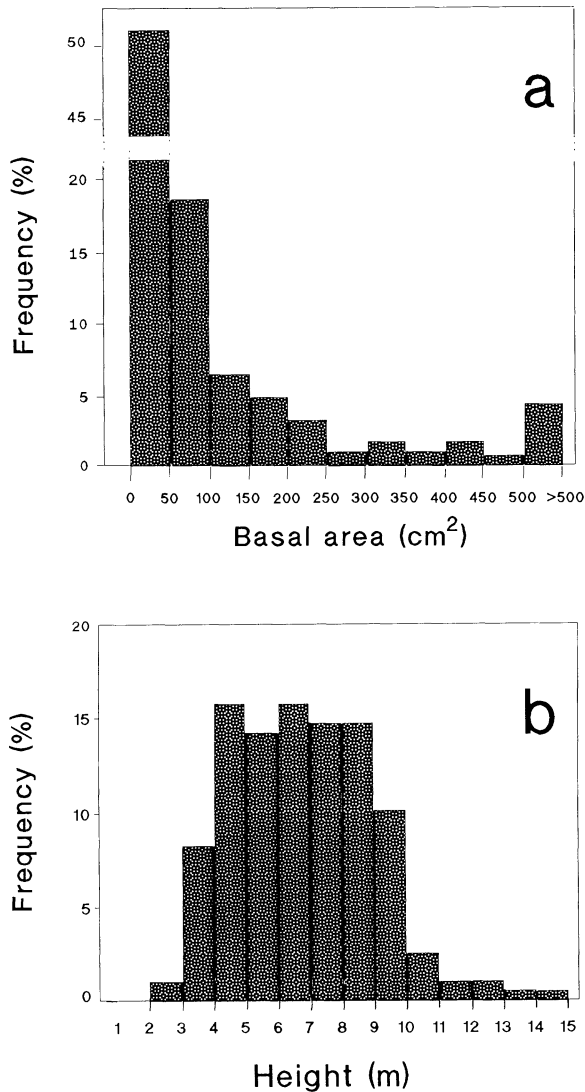


Figure 2. Forest structure of a 1000 m<sup>2</sup> area of tropical deciduous forest at Chamela, Jalisco, México. (a) Basal area class distribution (cm<sup>2</sup>), mean =  $130.7 \pm 15.4$  SE. (b) Height class distribution (m), mean  $6.9 \pm 0.2$  SE. Data for woody species (dbh > 3.0 cm).

(Nees) *L. Benson* (a shrub) made up the highest contribution of the total understorey phytomass (18 and 11%, respectively).

#### *Regression analysis*

Multiple regression equations of dry mass on basal area, wood specific gravity and height are given in Table 3. A very high proportion (88%) of the phytomass variance was explained by basal area only. Wood specific gravity and tree height significantly increased the accuracy of the prediction by increasing the multiple

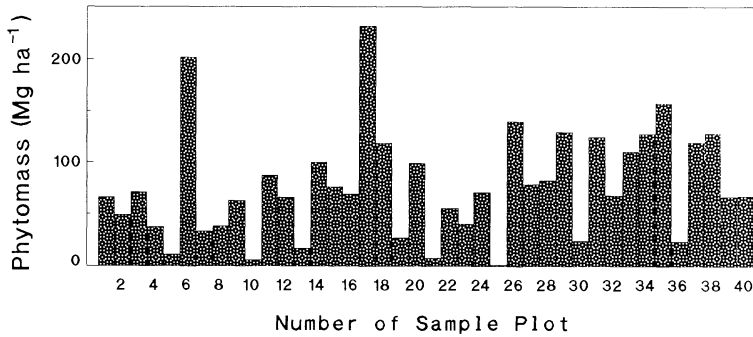


Figure 3. Distribution of above-ground phytomass ( $\text{Mg ha}^{-1}$ ) on 40 sample plots of  $5 \text{ m} \times 5 \text{ m}$ . Data for woody species ( $\text{dbh} > 3.0 \text{ cm}$ ) harvested during the dry season from a  $1000 \text{ m}^2$  area of tropical deciduous forest at Chamela, Jalisco, México.

Table 2. Relative and cumulative contribution (%) to total above-ground phytomass of the most important species on a tropical deciduous forest at Chamela, Jalisco, México. Nomenclature follows Lott (1985).

Rank	Species	Family	Phytomass	
			Relative contribution (%)	Cumulative contribution (%)
1	<i>Caesalpinia eriostachys</i> Benth.	Leguminosae	33.43	33.43
2	<i>Thouinia paucidentata</i> Radlk.	Sapindaceae	8.70	42.13
3	<i>Apoplansia paniculata</i> Presl.	Leguminosae	7.94	50.07
4	<i>Lonchocarpus constrictus</i> Pitt.	Leguminosae	6.56	56.63
5	<i>Caesalpinia coriaria</i> (Jacq.) Willd.	Leguminosae	5.08	61.71
6	<i>Ipomea wolcottiana</i> Rose	Convolvulaceae	3.67	65.38
7	<i>Lonchocarpus lanceolatus</i> Benth.	Leguminosae	3.37	68.75
8	<i>Opuntia excelsa</i> Sanchez-Mejorada	Cactaceae	3.32	72.07
9	<i>Lysiloma microphylla</i> Benth.	Leguminosae	3.01	75.08
10	<i>Heliocarpus pallidus</i> Rose	Tiliaceae	1.83	76.91
11	<i>Bursera excelsa</i> (HBK.) Engl.	Burseraceae	1.77	78.68
12	<i>Caesalpinia sclerocarpa</i> Standl.	Leguminosae	1.74	80.42
13	<i>Cordia allagroparva</i> DC.	Boraginaceae	1.66	82.08
14	<i>Jatropha malacophylla</i> Standl.	Burseraceae	1.56	83.64
15	<i>Guetarda elliptica</i> Sw.	Rubiaceae	1.50	85.14

r coefficient and lowering the standard error of the estimated  $\log_{10}$  phytomass. However, although significant, their contribution to explained variance in phytomass is small once basal area is considered.

In addition to the equations presented in Table 3, forest phytomass was also estimated by using the allometric equation of  $\log_{10}$  dry mass on  $\log_{10}$  (basal area  $\times$  height  $\times$  wood specific gravity), which proved to have a very tight fit. This equation has the general form:  $\log_{10} Y = \log_{10} a + b X$ , in which, for our case,  $Y =$  phytomass (kg);  $a$ , the regression constant =  $-0.8092 (\pm 0.0473 \text{ SE})$ ;  $b$ , the regression coefficient =  $0.8247 (\pm 0.0187)$  and  $X$  the independent variable. The standard error of the estimate = 0.17. Multiple correlation coefficient = 0.95 ( $F = 1940$ ,  $df 191, 1$ ,  $P < 0.0001$ ).

Table 3. Multiple regression equations of  $\log_{10}$  dry mass (kg) on  $\log_{10}$  basal area (BA,  $\text{cm}^2$ ),  $\log_{10}$  wood specific gravity (WSG) and  $\log_{10}$  height (h, m). Sample set includes: living boles, stems and branches of trees, shrubs and lianas with dbh > 3.0 cm in the Chamela forest. Regressions are in the form  $Y = A + B_{Y_1}X_1 + B_{Y_2}X_2 + \dots + B_{Y_i}X_i$ , where Y is the  $\log_{10}$  phytomass (kg);  $X_1, X_2 \dots$  refer to the separate, independent variables,  $B_{Y_i}$  is the regression coefficient of Y on variable  $X_i$ , and A is the regression constant or Y-intercept. Mult-r = multiple correlation coefficient. The standard error of regression statistics are in parentheses.

Step	Constant (A)	Regression coefficient of Y on variable X (B)			Standard error of estimate	Mult-r	F	P
		$\log_{10}$ BA	$\log_{10}$ WSG	$\log_{10}$ h				
1	-0.5352 (0.0483)	0.9996 (0.0264)	—	—	0.20	0.94	1437	***
2	-0.4492 (0.0431)	0.9972 (0.0228)	0.7127 (0.0885)	—	0.17	0.95	991	***
3	-0.7590 (0.0808)	0.9011 (0.0306)	0.5715 (0.0902)	0.5654 (0.1268)	0.16	0.96	733	***

\*\*\*P < 0.0001; N = 191.

#### DISCUSSION

The species-area curve for our study site was a log-linear relationship. This result agrees with Lott *et al.* (1987) who found that the correlations of cumulative species on cumulative area, for transects of deciduous forest at Chamela, were linear with correlation coefficients exceeding 0.99. Regression coefficients were also very close between the two studies (0.54 v. 0.55–0.64) suggesting that in terms of the number of species present, the sites are very similar.

The total basal area of  $25.6 \text{ m}^2 \text{ ha}^{-1}$ , estimated for the shrub and tree strata (stems > 3 cm dbh) at the study site lies within the upper end of the range of values reported for other similar forest sites at Chamela reserve ( $14.0\text{--}26.1 \text{ m}^2 \text{ ha}^{-1}$ ; mean =  $20.3 \pm 1.3$  (SE)  $\text{m}^2 \text{ ha}^{-1}$ ,  $n = 11$ ) (Castellanos *et al.* 1991, Lott *et al.* 1987, A. Pérez-Jiménez & A. Solís-Magallanes, unpubl.).

Multiple regression equations predicted the above-ground phytomass (for stems > 3 cm dbh) of the tropical deciduous forest at Chamela better than allometric relationships. The error in the estimate using multiple regressions was lower. Also, the advantage of using these equations over the allometric regressions is that they can be applied even if WSG and tree height were not determined in a particular forest site.

Our equation of dry mass on basal area was used by Castellanos *et al.* (1991) to predict the above-ground phytomass of a site in Chamela forest. They found a value of  $174 \text{ Mg ha}^{-1}$ . This estimate is lower than our results. The difference probably lies in the larger amount of relatively small stems (< 5 cm dbh) found by Castellanos *et al.* (46% v. 23% at our site).

The paucity of data on above-ground phytomass of tropical deciduous forests allowed only limited comparisons; there are only five other deciduous forest sites, in different parts of the world, for which direct measurements on total above-ground phytomass have, so far, been published (Table 4). Of this, Chamela is



Table 4. Above-ground phytomass (ABG, dry mass Mg ha<sup>-1</sup>) of tropical deciduous forests. Data arranged according to increasing phytomass value.

Locality	Altitude (m)	ABG (Mgha <sup>-1</sup> )	Rainfall (mm)	Dry period (months)	Author
Udaipur, India 24°35' N, 75°49' E	587	28.2	603	10	Vyas <i>et al.</i> (1977)
Guanica, Puerto Rico 17°57' N, 65°52' W	175	44.17	860	10	Murphy & Lugo (1986b)
Indian Church, Belize 17°45' N, 88°40' W	—	56.7	1480	5	Lambert <i>et al.</i> (1980)
Ping Kong, Thailand 19°50' N, 99°00' E	—	78.1	1500	5	Ogawa <i>et al.</i> (1965)
Chamela, México 19°30' N, 105°03' W	90	85.0	707	6–8	This study
Chandraprabha, India 25°52' N, 83°9' E	—	95.0	1050	6–8	Singh (1989)

among the highest. The phytomass value reported for a site in Guanica, Puerto Rico (Murphy & Lugo 1986b), which is most similar in total rainfall to Chamela, is about half the value found by us (Table 4). Structural differences between the two forests may again explain the phytomass difference. Both forests are characterized by a large number of small stems. However, a much higher proportion of trees in Guanica forest (about 80%) fall below the 5 cm dbh size class category (Murphy & Lugo 1986b).

The very low phytomass for the dry deciduous forest reported from Udaipur, India seems to be strongly influenced by both the semi-arid climate and the human activity in the forest of the hilly region (Vyas *et al.* 1977).

Lambert *et al.* (1980) estimated the phytomass of a seasonally dry tropical hardwood forest in Belize at 56.7 Mg ha<sup>-1</sup>. This intermediate value (Table 4) is probably associated with the secondary character of this 40–50-year-old forest. A forest in Ping Kong, Thailand (Ogawa *et al.* 1965) showed a similar value of phytomass to that of Chamela. However, as in Belize, rainfall is about twice the rainfall in Chamela. Differences in forest phytomass between sites might lie in successional status as in Belize, or other factors associated with structure and growth such as soil type, and both ancestral and recent human perturbation.

Although our estimate of phytomass at Chamela is high compared with other values reported for tropical deciduous forests, we suspect that, at best, we have a minimum estimate. Attention should be paid in future work to the contribution to phytomass by the cacti. These are difficult to measure in the same units as other trees because of their particular growth form: large phytomass and low basal area. In Chamela two cacti species are very important, *Opuntia excelsa* Sánchez-Mejorada and *Pachycereus pecten-aboriginum* (Engel.) Britt. & Rose. These two species are large arborescent plants which, in our site, attain heights of 6–10 m. Also, epiphytes, a distinctive element of the forest structure (Lott 1985, Lott *et al.* 1987), might contribute a proportion of phytomass that is obscured by its fragmentation in the tree canopies. Finally, since our phytomass measure-

ments were made during the dry period, it is likely that the phytomass of the understorey layer has been underestimated.

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- HOLMBERG, J., BASS, S. & TIMBERLAKE, L. 1992. *Defending the future: a guide to sustainable development*. Earthscan, London. 40 pages. ISBN 1-85383-099-2. Price: £3.95 (paperback).

This slim, large-format volume has been written as 'the essential crib' in the lead-up to the United Nations Conference on Environment and Development to be held in Brazil in June 1992. It is thoroughly readable, excellently produced with many attractive photographs and well divided text, and provides a fine introduction to exactly what is meant by that much used – and misused – phrase, 'sustainable development'.

- SPITZER, K., LEPŠ, J. & ZACHARDA, M. 1991. *Nam Cat Thien: Czechoslovak/Vietnamese Expedition Research Report, November 1989*. Institute of Entomology, Czechoslovak Academy of Sciences, České Budějovice, Czechoslovakia. 45 pages. ISBN 80-900045-5-5. Price: US \$8.00 (from the publisher, including postage).

This report on the results of a joint Czechoslovak/Vietnamese three-week expedition to the Nam Cat Thien Forest Reserve (National Park), contains 12 papers of which half are on insect groups and three on plants. It provides a preliminary insight into the richness of one of the few areas of good lowland forest remaining in the country, an area proposed for a Biosphere Reserve under the MAB-UNESCO programme.

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