Rev. Biol. Trop., 41 (1): 7-21, 1993

A quantitative model for relating species and tropical forest sites: A synecological study

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(Rec. 6-XII-1991. Acep. 15-VII-1992)

Abstract: A method is presented to assess forest site quality in tropical ecosystems. The method is based on the relation between site synecological scores (environmental quantifiers that are developed by using vegetation and botanical information) and site physiognomic characteristics. The relation can be used to identify species with good growth potential for particular sites and hopefully will be useful in estimating site productivity. A test of the methodology was done with data from Costa Rica collected from February to April 1991. The data set consisted of 190 plant species in 19 plots located in the premontane moist forest, and in 62 plots located in the tropical moist forest, premontane belt transition. Of these plant species, 81% were trees, 14% shrubs, 2% herbs, 4% lianas. Regression models were used to relate environmental quantifiers with site characteristics. The final equations showed good fits (R^2s > 0.6) with low mean squared errors. The results were used to develop forms to assess site quality that could be of practical use for foresters for these life zones.

Key words: site quality, assessment, synecology, synecological coordinates, tropical forest, Costa Rica.

An important component of forest management is assessing the potential productivity of a site. Although a number of techniques have been developed for assessing productivity of temperate forests (Davis 1966, Clutter *et al.* 1983), no technique has been developed that tropical foresters can easily use in their daily work.

A site quality assessment method is needed for natural regeneration projects, reforestation, for rehabilitating degraded sites to productive forests, and for decision making related to preserving tropical biodiversity. In general, an objective method is needed to evaluate forest site quality defined by Pritchett and Fisher (1987) as "the inherent capacity of the site to produce plant growth."

Tropical ecosystems are complex in nature, hence any method to evaluate site quality should be general and indicative. It also should be easily applied, reproducible, and inexpensive, and it should be quantitative to facilitate its use and applicability in further studies, such as land quality/growth relations and growth/yield studies.

Because tropical ecosystems are complex, site identification cannot be determined by putting together single facts about ecosystem components. Complex systems must be identified by the interactions among their components, and the interactions between the "parts" and the "whole" (Baku is 1959, Webb 1973).

This paper introduces a methodology to identify species suitable for various sites, which may be useful to foresters and ecologists involved with the management of tropical ecosystems. The methodology consists of using vegetation to quantify environmental factors (Baku is 1959), which are then related to physiognomic site characteristics. This relation can be used to identify species suitable for particular sites by predicting environmental factors from site characteristics. Gutiérrez-Espeleta (1991a) presents a theoretical discussion on part of the basis for the methodology.

MATERIAL AND METHODS

Model development: The Method of Synecological Coordinates (MSC) (Bakuzis 1959) is a powerful technique that can be used to quantify the environmental capital of a site. Synecological coordinates interpret the biotically effective part of the essential environmental factors, moisture, nutrients, heat, and light, on a species-presence basis (Pluth and Arneman 1963). The MSC uses botanical information and environmental conditions to quantify environmental factors. The graphical representation of two or more of these environmental factors (ecographs) helps identify the ecological distribution of plant species in an area in terms of the ecosystem space.

Synecological coordinate values for individual plant species found in an area are initially determined from descriptions in botanical literature or by taxonomists familiar with the plant's habitat. Values range from 1 for low requirement to 5 for high requirement or adaptation of plant species to essential environmental factors. Then, the initial estimates are adjusted by using data taken from plots covering a wide range of environmental conditions. These values are called species synecological coordinates. They are used to obtain site synecological scores by averaging the synecological coordinate values for the species found on a site.

We hypothesize that a site synecological score (S_i) is a function of the physiognomic characteristics of the site, *i.e.*:

$$\underset{}{S_i} = \underset{1xc}{X_i}\ \underset{cx1}{\beta_i} + \underset{cx2}{\delta_i} \qquad (I)$$

where

S_i = site synecological score for moisture, nutrient, heat and light coordinates

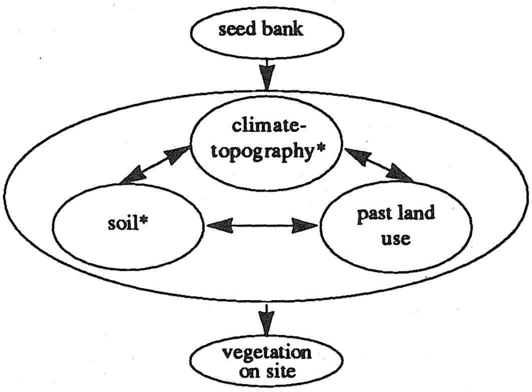
X_i = vector of c diagnostic variables

β_i = regression coefficients

δ_i = random error

Equation I constitutes the basic model under consideration. If this relationship can be established, site synecological scores (site environments) can be predicted by using physiognomic site characteristics.

The site physiognomic characteristics that need to be considered arise from the concept of forest site, as shown in Fig. 1.



* and associated organisms.

Fig. 1. Factors affecting current site characteristics.

For this study, site is defined as that piece of land capable of sustaining plant growth at time t. Although time is generally considered to be a soil forming factor, in this definition it refers to a much shorter span (1 to 25 years), pertaining to the land use history of that piece of land. If time is set equal to zero at the moment of site examination, then the current characteristics of that site depend upon the multiple interactions of climate/topography of the site, the soil substrate, and the past use of the site. These interactions act as an environmental filter for the seed bank.

We also hypothesize that the β_i in Equation I change as the environment changes. Thus, the β_i need to be developed for areas of fairly similar environments.

Soil and climate are perhaps the most influential factors of the environment (Kimmins 1987, Harper 1977, Webb 1968). To locate sites with similar environmental conditions, a climatic and soil classification is therefore needed.

To locate sites with similar environmental conditions, this study used the Holdridge Life Zones System (Holdridge 1978), as shown on the ecological map of Costa Rica (Tosi 1969), and the soil group classification of Costa Rica (Vásquez 1989).

Zones System (Holdridge 1978), as shown on the ecological map of Costa Rica (Tosi 1969), and the soil group classification of Costa Rica (Vásquez 1989).

Within a life zone, the soil map of Costa Rica (Vásquez, 1989) was used to identify areas of similar soil characteristics. The soil map classifies soils to the great group level according to the Soil Taxonomy of the United States Department of Agriculture.

All of the area within a life zone that has a particular soil group will be referred to as a Basic Study Unit (BSU).

The initial study region was the Tropical Premontane Moist Forest (bh-P) (the basal belt transition was not considered). It is located roughly within longitudes 83°45' and 85°00' and latitudes 9°45' and 10°40'. It covers an area of approximately 80,000 hectares in Costa Rica.

There are six distinguishable soil groups within the bh-P (Vásquez 1989). They constitute the BSUs in the bh-P. The distribution of plots among BSU's in the premontane moist forest is as follows: five plots were classified as Haplustalf (Ah), four plots as Andisol (Ix), four as Humitropept (Im), four as Ustropept (Iw), and two plots as Ustorthent (Eu).

The field work was conducted from February to April 1991. Only nineteen 250-m² plots could be located in the bh-P. Because 19 plots did not provide enough data to test the model under consideration, approximately 7,000 hectares of Tropical Moist Forest, premontane belt transition (bh-TΔ) were added. The area, including a reserve forest that belongs to the University for Peace in Costa Rica, is located at 84°15'- 84°30', and 9°'40' - 9°50'.

Sixty two 150-m² plots were located in this region and classified into four soil groups. In the bh-T Δ, we classified 23 plots as Haplustalf (Ah), 24 plots as Ustropept (Iw), 11 plots as Ustorthent (Eu), and four plots as Tropohumult (Ut).

In all BSUs, plots were chosen to assure a wide representation of the different environments encountered within the BSU.

On each plot, species were recorded for all plants over 1.3 m in height. In the bh-P, three 1-m² quadrats were taken along the center line of the plot, and in the bh-TΔ, four 1-m² quadrants were taken in each corner of the plot for lower vegetation sampling.

Table 1 shows the scales and definitions used for each variable.

TABLE 1

Definition of site diagnostic characteristics

Climate/topography

Heat: normal annual temperature trend in the site. It is determined by asking people who live in the area (at least 2 persons).

cool	the site is continually cool
cool-warm	warm for less than six months
warm-cool	cool for less than six months
warm	continually warm

Slope position: refers to geomorphic segment of the topography in which the plot is located (Sandor 1989). It is the slope between major topographic irregularities (Klinka et al. 1984). Determined by observation.

Summit	highest level of an upland landform with a relatively gentle slope.
Shoulder	rounded (convex-up) hillslope component below the summit.
Backslope	steepest slope position.
Footslope	at the base of a hillslope, commonly concave-up in cross section.
Gradient < 2%	Slope at the site is less than 2%, and not classified in one of the classes above.
Floodplain	Evident flooding due to the proximity of the site to the stream.

Slope shape: refers to the shape of the main slope or gradient at the site. Determined by observation.

Convex	gradient decreases upslope per unit of length (dry).
Straight	gradient is constant per unit of length.
Concave	gradient increases upslope per unit of length (wet).
Undulating	

Slope aspect: refers to the direction of exposure of the main slope to solar radiation (Sandor 1989). Determined by using a compass.

North	from 315° to less than 45° azimuth
East	from 45° to less than 135° azimuth
South	from 135° to less than 225° azimuth
West	from 225° to less than 315° azimuth

Soil

Texture: refers to the variation in the relative abundance of different sized particles in the < 2 mm diameter mineral material. Textural classes and the key for field assessment were taken from Kimmis (1987).

Depth: refers to the effective soil depth, i.e., the depth of soil that can be easily penetrated by plant roots. Determined by a scaled probe.

deep	depth to restricted layer greater than or equal to 90 cm.
moderately deep	more than or equal to 45 cm but less than 90 cm
shallow	less than 45 cm but greater than 20 cm.
very shallow	less than or equal to 20 cm.

Cont...

Cont.Table 1

Three probe samples are taken, starting from the center plot, and following with one 5 m N and one 5 m S from the center. If they vary more than ±20 cm, two more samples are taken at 5 m E and 5 m W of the center. The median is used.

Past land use

Organic matter (OM): refers to the amount of organic compounds in the soil, particularly in the form of humus. The initial classes were established according to results of Holdridge *et al.* (1977).

low	less than 3% of OM
medium	between 3 and 10%
high	more than 10%

Compaction: refers to the soil pore space. It is measured by a penetrometer devised by the senior author. The following two classes were used:

1	if reading is £ 15 cm
0	otherwise

Moisture: refers to soil moisture at the moment of inspection. It is determine by hand squeezing a sample of soil. Soil moisture is classified as:

wet	if some material is left on the palm, and the clod breaks easily.
moist	if the clod breaks easily but leaves almost no material on the palm of the hand
dry	if clod is hard to break and leaves just dust on the palm of the hand.

Development of synecological scores: SYCOOR (Gutiérrez-Espeleta 1991b), a computer program that can be used to make the calculations needed to do MSC, was used to adjust species synecological coordinates to local conditions for all the plots in the study (step 1). Because a difference in environments was observed between the two life zones ($p<0.05$), a second adjustment was done to the conditions of each of them, separately (step 2). Due to differences found between some BSU's environments (using scores from step 2 as initial scores), a third adjustment was performed for BSU environmental conditions. At each level, species synecological coordinates were adjusted if the species was found on five or more plots; otherwise, the initial estimates were used. Finally, SYCOOR was used to calculate plot synecological scores and to provide information needed to draw the species ecographs by BSUs.

Fitting the model: Field information was converted to binary data (0,1) so the coefficients in the regression equation could be used to develop forms that can be used to easily calculate site scores.

Equations were fit to predict each of the four synecological scores for the plots, so the scores were the dependent variables. Then, a series of multiple linear regressions were done. To determine which descriptor variables were useful in the model, a "fit-all" model was applied to give insight into potential problems among descriptor variables. Later, stepwise regression, backward elimination, was performed to obtain a set of variables that, from a statistical point of view, represented a good fit. And finally, a "best" subset of descriptor variables was sought through maximizing R^2, the squared multiple correlation coefficient. This was done because more than one set of variables gave a good fit.

These results were used to construct models that contained descriptor variables that estimate the effect of each factor considered in the initial model (Fig. 1).

A limitation of the data set was its size. As a result of having relatively few observations, some diagnostic variables had very few, if any, observations in some classes. The data were collected to test the methodology, not to develop equations precise enough for actual use. Thus, fitting Equation I has to be considered as exploratory and as a methodological procedure. Large data sets in future studies will allow development of precise results.

RESULTS AND DISCUSSION

There were 306 plants in the 81 plots. One hundred ninety plants (62%) were identified to species, 49 plants (16%) were identified to genus, and 67 plants (22%) were not identified. Of the plants identified to species (Table 2), most were classified as trees (153 or 81%), 27 (14%) as shrubs, three (2%) as herbs, and seven (4%) as lianas. Of those that were identified to genus, 22 plants (45%) were considered trees, 16 (33%) shrubs, four (8%) herbs, five (10%) lianas, and two (4%) as "others" (one *Bactris* sp. and one *Chamaedorea* sp.). Of the plants that were not identified, 20 (30%) were trees, 19 (28%)

were shrubs, 14 (21%) were herbs, and 14 (21%) were lianas.

We tested to determine if site synecological scores varied among BSUs (Table 3). Analysis of variance procedures indicated that site synecological scores varied considerably between life zones and soil groups within a life zone ($p < 0.01$). Given such differences, it seems likely that the diagnostic variables and coefficients in Equation I would differ among life zones and BSUs.

Final models for each synecological coordinate in each life zone were obtained. As previously mentioned, the regression equations developed to predict site synecological coordinates scores were developed in such a way so as to allow the development of forms that can be easily used to estimate the site scores for an area (see Appendix).

TABLE 2

Species list with species synecological coordinate values, initial and adjusted

Type = 1 tree 2 shrub 3 herb 4 liana
5 other (*) introduced species

						Synecological bh-P†				Coordiantes bh-TD†			
		Initial				Adjusted				Adjusted			
Family/Species	Type	M	N	H	L	M	N	H	L	M	N	H	L
Acanthaceae													
Aphelandra scabra (Vahl.) Smith	2	1	1	5	5	1	1	5	5	2	2	5	4
Ruellia paniculata L.	2	1	1	4	5	1	1	4	5				
Anacardiaceae													
Anacardium excelsum (Bert. & Balb.) Skeels	1	5	4	4	5	5	4	4	5				
Mangifera indica L. (*)	1	4	3	3	5					4	3	3	5
Mauria birringo Tulasne	1	3	3	3	3	3	3	3	3	3	2	3	4
Mauria heterophylla H.B.K.	1	3	2	3	3	3	2	3	3	3	2	3	3
Rhus striata Ruiz & Pavon	1	3	3	3	4					3	3	3	4
Spondias mombin L.	1	3	3	4	5	3	3	4	5				
Spondias radlkoferi J. Donn. Sm.	1	3	3	4	5					3	3	4	5
Tapirira brenesii Standl.	1	3	3	3	4					3	3	2	3
Annonaceae													
Annona cherimolia Mill.	1	3	2	3	4	3	2	3	4				
Annona pittieri Donn. Sm.	1	3	3	2	3	3	3	2	3				
Annona purpurea Moc. & Ses.	1	2	3	4	3					2	2	4	4
Desmopsis bibracteata (Rob.) Saff.	1	2	2	2	2	2	2	2	2	3	3	3	3
Guatteria diospyroides Baillon	1	3	3	2	3	3	3	2	3				
Apocynaceae													
Stemmadenia alfari Donn. Sm.	1	4	3	3	3	4	3	3	3				
Stemmadenia donnell-smithii (Rose) Woodson	1	2	3	4	4	2	3	4	4	3	3	3	4
Stemmadenia glabra Benth.	1	2	3	3	4	2	3	3	4				
Araliaceae													
Oreopanax xalapensis (H.B.K.)Done.&Planch.	1	3	3	2	4	3	3	2	4				
Sciadodendron excelsum Griseb.	1	2	3	4	5	2	3	4	5				
Asclepiadaceae													
Asclepias curassavica L.	3	2	1	4	5	2	1	4	5				
Asteraceae													
Eupatorium glaberrimum D.C.	1	2	2	3	4	2	2	3	4				
Eupatorium morifolium Miller	1	3	3	3	3	3	3	3	3				
Onoseris onoseroides (H.B.K.) B.L.Rob.	2	2	2	4	5	2	2	4	5	2	2	4	5
Vernonia patens H.B.K.	2	3	1	3	5	3	1	3	5				
Bignoniaceae													
Pithecoctenium crucigerum (L.) A. Gentry	4	2	3	3	4	2	3	3	4				
Tabebuia rosea (Vertol.) D.C.	1	3	3	4	5	3	3	4	5	2	2	4	4
Tecoma stans (L.) H.B.K.	1	2	2	4	5	2	2	4	5				
Bombacaceae													
Ceiba pentandra (L.) Gaert.	1	3	3	3	4					3	3	3	4
Pochota quinata (Jacq.) W.D. Stevens	1	2	3	4	5					2	3	4	5
Pseudobombax septenatum (Jacq.) Dugand	1	3	3	3	4	3	3	3	4				

Cont.

Cont. TABLE 2

Type = 1 tree 2 shrub 3 herb 4 liana
5 other (*) introduced species

		Initial				Synecological bh-P† Adjusted				Coordiantes bh-TD† Adjusted			
Family/Species	Type	M	N	H	L	M	N	H	L	M	N	H	L
Boraginaceae													
Cordia alliodora (Ruiz & Pavon) Oken	1	3	4	4	5	3	4	4	5	1	1	5	5
Cordia panamensis Riley	1	2	3	4	5	2	3	4	5				
Tournefortia glabra L.	2	2	2	3	4	2	2	3	4				
Burseraceae													
Bursera simaruba (L.) Sarg.	1	1	2	4	5	1	2	4	5	1	2	4	5
Capparidaceae													
Capparis cynophallophora (Eichl.) Iltis	1	4	3	4	2					4	3	4	2
Celastraceae													
Crossopetalum tonduzii (Loes.) Lundell	1	3	3	3	4	3	3	3	4				
Chrysobalanaceae													
Hirtella racemosa Lam.	2	3	3	3	3					3	3	3	3
Clethraceae													
Clethra mexicana A.D.C.	1	1	1	3	5	1	1	3	5	1	1	5	5
Clusiaceae													
Calophyllum brasiliense Cambess.	1	3	4	4	4					4	4	2	2
Garcinia intermedia (Pitt.) Hammel	1	3	3	3	3					3	3	3	3
Symphonia globulifera L.f.	1	3	3	2	3	3	3	2	3				
Vismia guianensis (Aubl.) Pers.	1	3	2	4	5	3	2	4	5	3	2	4	5
Cochlospermaceae													
Cochlospermum vitifolium Willd.	1	1	2	4	5	1	2	4	5				
Combretaceae													
Terminalia oblonga (R. L. & P.) Stendal.	1	3	3	3	4					3	3	3	4
Elaeocarpaceae													
Sloanea brenesii Standl.	1	3	3	2	3	3	3	2	3				
Sloanea terniflora (Moc.& Sesse) Standl.	1	2	3	4	5					4	4	2	2
Euphorbiaceae													
Alchornea costaricensis Pax & Hoff.	1	3	3	2	3					3	3	2	3
Alchornea latifolia Sw.	1	3	3	2	3					3	3	2	3
Croton decalobus Muell.-Arg.	2	3	3	3	4					3	3	3	4
Croton glabellus L.	1	3	2	3	3	3	2	3	3	4	4	2	2
Croton gossypiifolius Vahl.	1	2	2	3	5	2	2	3	5	2	2	3	5
Croton niveus Jacq.	1	3	2	3	4	3	2	3	4				
Croton panamensis Muell.	1	2	2	4	5	2	2	4	5				
Phyllanthus lathyroides H.B.K.	3	3	2	3	5	3	2	3	5				
Sapium thelocarpum Schum. & Pitt.	1	3	3	3	3	3	3	3	3	3	3	3	3
Fabaceae/Caesalpinioidea													
Cassia maxonii (Britt. & Rose) Schery	1	2	2	4	4	2	2	4	4	2	2	4	4
Schizolobium parahybum (Vell.) Blake	1	3	3	4	5	3	3	4	5				
Swartzia picramnoides Standl.& Wms.	1	2	3	3	4					4	4	2	2
Swartzia simplex (Sw.) Spreng.	1	2	3	3	3					2	3	3	3
Fabaceae/Mimosoideae													
Acacia costaricensis Schenck	2	2	2	4	5	2	2	4	5	1	1	5	5
Acacia tenuifolia (L.) Willd.	4	3	2	4	3					2	2	5	4
Albizzia adinocephala (Donn.Sm)Britt.&Rose	1	2	2	4	5					1	1	5	5
Calliandra costaricensis (Britt.&Rose)Sta.	1	2	2	4	4					2	2	4	4
Enterolobium cyclocarpum (Jacq.)Griseb.	1	2	3	4	5	2	3	4	5	2	3	4	5
Inga punctata Willd.	1	2	2	3	5	2	2	3	5	2	2	3	5
Pithecelobium saman (Jacq.) Benth.	1	2	3	4	5					2	3	4	5
Fabaceae/Papilionoideae													
Acosmium panamense (Benth.) Yakov.	1	2	3	4	4					2	3	4	4
Andira inermis (Sw.) H.B.K	1	2	3	4	5	2	3	4	5				
Diphysa americana (Mill.) M. Sousa	1	2	2	4	5	1	1	4	5	1	1	5	5
Hymenaea courbaril L.	1	3	3	4	5	3	3	4	5	3	3	4	5
Lonchocarpus atropurpureus Benth.	1	2	3	3	5	2	2	5	5				
Lonchocarpus costaricensis (Donn.Sm.)Pitt.	1	2	3	3	4	1	1	4	5	2	2	5	4

Cont.

Cont. TABLE 2

Type = 1 tree 2 shrub 3 herb 4 liana
5 other (*) introduced species

Family/Species	Type	Synecological Coordiantes											
						bh-P†				bh-TD†			
		Initial				Adjusted				Adjusted			
		M	N	H	L	M	N	H	L	M	N	H	L
Lonchocarpus sericeus Benth.	1	2	3	3	4	2	3	3	4	1	1	4	5
Machaerium arboreum (Jacq.) Vogel	2	3	2	3	3					4	4	2	2
Machaerium biovulatum Micheli	1	2	2	4	5	2	2	4	5	1	2	5	5
Machaerium marginatum Standl.	4	2	2	4	5					3	3	3	3
Pterocarpus hayesii Hemsl.	1	3	3	3	3					3	3	3	3
Fagaceae													
Quercus oocarpa Liebm.	1	3	3	2	5	3	3	2	5				
Quercus seemannii Liebm.	1	3	3	2	4	3	3	2	4				
Flacourtiaceae													
Banara guianensis Aubl.	1	2	3	4	3					2	3	4	3
Casearia aculeata (Jacq.)	1	2	2	4	5					3	3	2	3
Casearia arguta H.B.K.	1	2	2	4	5	2	2	4	5	2	2	4	5
Casearia commersoniana	1	2	2	4	4					2	2	4	4
Casearia nitida (L.) Jacq.	1	2	2	4	4	2	2	4	4				
Casearia sylvestris Swartz	1	2	2	4	4	2	2	4	4	2	2	4	5
Lozania mutisiana Roem. & Schult.	1	4	4	3	3					4	4	3	3
Xylosma velutinum Triana & Planch.	2	2	2	3	4					2	2	3	4
Hemandiaceae													
Gyrocarpus jatrophifolius Domin	1	2	3	3	4					2	3	3	4
Lacistemaceae													
Lacistema aggregatum (Berg.) Rusby	1	3	3	3	4					3	3	3	3
Lauraceae													
Nectandra cufodontisii (Schm.)C.K.Allen	1	3	3	3	5	3	3	3	5				
Nectandra sinuata Mez.	1	3	3	3	3	3	3	3	3				
Ocotea helicterifolia (Meiss.) Hemsley	1	3	3	3	2					3	3	3	2
Ocotea nicaraguensis Mez	1	3	2	3	3					3	2	3	3
Ocotea veraguensis (Meissn.) Mez	1	2	3	4	4	1	2	4	5	2	2	5	5
Persea caerulea (R.& P.) Mez	1	2	3	3	4	2	3	3	4	2	2	3	4
Phoebe brenesii Standl.	1	2	3	3	5	1	1	4	5	2	2	4	4
Phoebe cinnamomifolia (Kunth) Nees	1	2	2	3	5					2	2	4	5
Malpighiaceae													
Banisteriopsis muricata (Cav.) Cuatrec.	4	2	1	4	4					3	2	4	3
Bunchosia pilosa H. B. K.	1	2	3	4	4	2	3	4	4	2	3	4	4
Byrsonima crassifolia (L.) D.C.	1	1	1	4	5	1	1	4	5	1	1	4	5
Heteropteris laurifolia (L.) A. Juss.	4	3	1	4	5					2	2	5	4
Malpighia glabra L.	2	3	3	3	3	3	3	3	3				
Malvaceae													
Malvaviscus arboreus Cav.	1	3	3	3	4	5	4	2	2	3	2	4	3
Melastomaceae													
Miconia argentea (Sw.) D.C.	1	2	3	3	5	2	3	3	5	2	2	4	5
Meliaceae													
Cedrela odorata L.	1	2	3	4	5	2	3	4	5	2	3	4	5
Guarea rhopalocarpa Radlk.	1	3	3	3	3	3	3	3	3	3	3	3	3
Trichilia havanensis Jacq.	1	3	3	4	5	3	2	3	4	3	3	3	3
Trichilia martiana C.D.C.	1	2	3	4	4	2	2	5	4	2	2	4	5
Menispermaceae													
Cissampelos pareira L.	4	2	1	4	5	2	1	4	5				
Monimiaceae													
Mollinedia costaricensis Donn. Sm.	2	3	3	2	2	3	3	2	2				
Siparuna griseo-flavescens Perkins	2	2	2	3	2	2	2	3	2	2	2	3	2
Moraceae													
Brosimum alicastrum Sw.	1	2	3	4	2					3	3	2	3
Brosimum costaricanum Liebm.	1	3	3	4	2	3	3	4	2	4	4	2	2
Cecropia peltata L.	1	1	2	4	5	1	2	4	5	1	2	4	5
Clarisia biflora Ruiz Lopez & Pavon	1	3	3	3	4	3	3	3	4	4	4	2	3

Cntinuación Tabla 2

Cont.

Cont. TABLE 2

Type = 1 tree 2 shrub 3 herb 4 l ana
5 other (*) introduced species

Fam ly/Species	Type	Initial				Synecological bh-P† Adjusted				Coordiantes bh-TD† Adjusted			
		M	N	H	L	M	N	H	L	M	N	H	L
Clarisia mexicana (Liebm.) Lanj.	1	3	3	4	3					4	4	2	2
Clarisia racemosa Ruiz & Pavon	1	3	3	4	3					4	4	2	2
Ficus costaricana (Liebm.) Miq.	1	2	2	3	5	2	2	3	5	2	2	3	5
Ficus jimenezii Standl.	1	2	3	3	5	2	3	3	5				
Ficus morazaniana W. Burger	1	2	3	3	4					2	3	3	4
Pseudolmedia oxyphyllaria Donn. Sm.	1	3	3	3	3	3	3	3	3				
Sorocea trophoides W. Burger	1	3	3	3	3	3	3	3	3				
Trophis racemosa (L.) Urban	1	3	3	3	2	3	3	3	2	3	3	3	2
Myrsinaceae													
Ardisia compressa H.B.K	1	3	3	2	3	4	4	2	3	3	3	2	3
Ardisia revoluta H. B. K	1	1	2	4	5	2	2	5	5	3	3	3	4
Rapanea ferruginea (R. & P.) Mez	1	3	2	3	4	3	2	3	4				
Rapanea pellucido-punctata (Oerst.) Mez	1	2	3	3	4	1	1	4	5	2	3	3	4
Myrtaceae													
Eugenia cartagensis Berg.	1	2	3	3	4	2	3	3	4	3	3	3	3
Eugenia salamensis Donn. Smith	1	2	3	4	4					2	3	4	4
Eugenia truncata Berg.	1	2	3	3	3	2	3	3	3				
Myrcia oerstediana Berg.	1	2	3	3	4	2	2	4	4				
Psidium guajava L.	1	2	3	3	5	2	3	3	5	2	3	3	5
Syzygium jambos (L.) Alston (*)	1	2	3	2	4	2	3	2	4	3	3	2	3
Nyctaginaceae													
Neea psychotrioides Donn. Sm.	2	3	3	3	2	3	3	3	2	4	4	2	2
Pisonia aculeata L.	1	2	2	4	4	2	2	4	4	2	2	4	4
Olacaceae													
Heisteria macrophylla Oerst.	1	2	3	3	3					4	4	2	2
Onagraceae													
Hauya lucida Donn.Sm.	1	3	3	3	3	3	3	3	3	3	3	3	3
Phytolaccaceae													
Rivina humilis L.	2	2	2	2	3	2	2	2	3				
Piperaceae													
Piper marginatum Jacq.	2	3	2	3	4	3	2	3	4	3	2	3	4
Polygonaceae													
Coccoloba porphyrostachys Gomez-Laurito	1	4	3	3	3	4	3	3	3				
Proteaceae													
Roupala montana Aubl.	1	3	3	3	4	3	3	3	4	2	2	4	4
Rosaceae													
Eriobotrya japonica Lindl. (*)	1	3	4	3	4	3	4	3	4				
Rubiaceae													
Calycophyllum candidissimum (Vahl.) D.C.	1	1	3	4	5					1	2	4	5
Coffea arabica L. (*)	2	3	4	3	5	5	4	2	2	2	2	4	4
Faramea quercetorum Standl.	2	3	3	2	3	3	3	2	3	3	3	2	3
Genipa americana L.	1	2	2	4	4					2	2	4	4
Hamelia patens Jacq.	2	2	3	3	5	2	3	3	5	2	3	3	5
Psychotria carthaginensis Jacq.	1	2	3	3	3	2	3	3	3				
Psychotria pubescens Sw.	2	3	2	3	4					3	2	3	4
Randia armata (Sw.) D.C.	2	2	2	2	3	2	2	2	3	2	2	2	3
Randia karstenii Polak.	2	2	2	2	3	3	3	3	2	1	1	5	5
Randia subcordata Standl.	1	2	2	3	3	2	2	3	3	4	4	2	2
Rutaceae													
Amyris pinnata Kunth.	1	2	3	3	3					3	3	3	3
Amyris sylvatica Jacq.	2	3	3	2	2	3	3	2	2				
Casimiroa edulis Llave & Lex.	1	2	3	3	4	2	3	3	4	2	2	4	5
Citrus sinensis (L.) Osbeck (*)	1	3	2	3	5	3	2	3	5				
Zanthoxylum elephantiasis Macfad.	1	3	3	3	4	2	2	5	4	3	3	3	4
Zanthoxylum limoncello Planch. & Oerst.	1	3	3	3	2	3	3	3	2				
Zanthoxylum microcarpum Griseb.	1	3	3	3	4	1	1	4	5	1	1	5	5

Cont.

Cont. TABLE 2

Type = 1 tree 2 shrub 3 herb 4 liana
5 other (*) introduced species

Family/Species	Type	Initial				Synecological bh-P† Adjusted				Coordiantes bh-TD† Adjusted			
		M	N	H	L	M	N	H	L	M	N	H	L
Zanthoxylum monophyllum (Lam.) P.Wilson	1	3	3	3	4	3	3	3	4	3	3	3	4
Zanthoxylum setulosum P. Wilson	1	3	3	3	4					3	3	3	4
Sapindaceae													
Allophylus occidentalis (Sw.) Radlk.	1	2	2	4	5	2	2	4	5	2	2	4	5
Cupania glabra Swartz	1	2	3	3	5	5	4	2	3				
Cupania guatemalensis Radlk.	1	2	2	4	4	1	1	4	5	3	3	3	3
Dilodendron costaricense Radlk.	1	2	3	3	5					2	2	4	5
Paullinia costaricensis Radlk.	4	2	3	3	4	2	3	3	4	2	2	5	4
Thouinidium decandrum (H.& B.) Radlk.	1	2	3	4	4	2	3	4	4	4	4	2	2
Sapotaceae													
Chrysophyllum brenesii Cronq.	1	2	3	3	3					2	3	3	3
Chrysophyllum cainito L.	1	2	3	4	5	2	3	4	5				
Manilkara chicle (Pittier) Gilly	1	3	3	4	4					3	3	2	3
Sideroxylon persimile (Hemsl.) Penn.	1	3	3	3	4	3	3	3	4				
Scrophulariaceae													
Russelia verticillata H.B.K.	3	2	2	3	4	2	2	3	4				
Simaroubaceae													
Picramnia antidesma (D.C.) W. Thomas	1	3	2	3	3	2	2	5	4	2	2	4	4
Picramnia latifolia Tulasne	1	2	2	3	3					4	4	2	2
Picramnia teapensis Tulasne	1	2	2	3	3	2	2	3	3	2	2	3	3
Solanaceae													
Cestrum baenitzii Lingel.	2	2	1	3	4					2	1	3	4
Cestrum lanatum Mart. & Gal.	2	2	2	3	4	2	2	3	4	2	2	3	4
Solanum brenesii Morton & Standl.	2	3	3	3	4	1	1	4	4	2	2	4	5
Staphyleaceae													
Turpinia occidentalis (Sw.) G. Don.	1	3	3	3	3	3	3	3	3				
Sterculiaceae													
Guazuma tomentosa H.B.K.	1	2	2	4	5	1	1	4	5	1	1	5	5
Tiliaceae													
Apeiba tibourbou Aubl.	1	2	2	4	5	2	2	4	5	3	3	3	3
Heliocarpus appendiculatus Turcz.	1	3	3	3	5	3	3	3	5	3	3	3	5
Luehea speciosa Willd.	1	2	2	4	5	1	1	4	5	2	2	4	5
Ulmaceae													
Ulmus mexicana (Lieb.) Planchon	1	3	3	2	4	3	3	2	4				
Urticaceae													
Myriocarpa longipes Liebm.	2	3	3	3	3	3	3	3	3				
Urera baccifera (L.) Gauld.	1	3	3	3	3					1	2	4	5
Verbenaceae													
Aegiphila costaricensis Moldenke	1	2	3	3	3	2	3	3	3	2	3	3	3
Citharexylum donnell-smithii Green.	1	3	3	3	4	3	3	3	4				
Cornutia grandifolia (Schl.&Cham.) Schauer	1	2	3	3	5					2	3	3	5

† Plants not showing adjusted synecological coordinate values were not present in that life zone or found in fewer than six plots

Table 4 summarizes the results of the final equations for both life zones. The Appendix shows them in forms developed for easy calculation of site scores.

Because bh-P did not yield enough data for analysis by BSUs, the edaphic (nutrient against moisture coordinates) and climatic (light against heat coordinates) fields became those corresponding to the life zone as a whole. The edaphic and climatic fields for bh-TD, were obtained by appending its BSU's fields. Ecographs for ten species in the BSU bh-TDIw are presented as an example in Fig. 2.

The data set has two problems. First, changing the sampling scheme from bh-P to bh-TD was necessary because of time constraints. And secondly, the data set is fairly small, which presented limitations to testing whether the coefficients for Equation I were BSU dependent or not. This test should be performed to indicate which BSUs need separate sets of coefficients. Despite these shortcomings, we believe that strong evidence exists to encourage further investigations in this direction.

As an example, assume a deforested site in bh-TD with the following diagnostic observations: the site is classified as belonging to the Iw soil group, warm (continuously warm), in a backslope position with a straight slope shape, and SE aspect (108∞Azimuth). Soil texture is silty sand, and soil depth is more than 90 cm. The organic matter content is 8%, and the soil at the moment of inspection was dry. We want to know what plant species have some growth potential at this site.

TABLE 3

Summary statistics for BSUs by synecological coordinates.
(mean ± standard error)

BSU	Moisture	Nutrient	Heat	Light
bh-P Ah	1.8±0.2	1.9±0.2	3.9±0.1	4.5±0.1
bh-P Ix	3.0±0.1	2.9±0.1	2.8±0.1	3.4±0.3
bh-P Im	2.7±0.1	2.6±0.1	3.2±0.1	3.7±0.2
bh-P Iw	2.1±0.2	2.3±0.2	3.6±0.1	4.2±0.1
bh-P Eu	1.8±0.0	1.8±0.0	3.8±0.0	4.6±0.1
bh-TDAh	2.4±0.1	2.4±0.1	3.3±0.1	3.7±0.1
bh-TDIw	3.0±0.1	3.0±0.1	3.0±0.1	3.0±0.1
bh-TDEu	3.1±0.2	3.1±0.2	2.8±0.2	3.1±0.2
bh-TDUt	3.0±0.1	2.9±0.1	2.9±0.2	3.2±0.1

TABLE 4

Statistics summary for the fitting of Equation I by life zone

Life Zone	Synecological Coordinate	MSE[a]	p-value	R^2
bh-P	Moisture	0.024	<0.01	0.955
	Nutrient	0.019	<0.01	0.950
	Heat	0.015	<0.01	0.958
	Light	0.018	<0.01	0.967
bh-TD	Moisture	0.087	<0.01	0.708
	Nutrient	0.090	<0.01	0.704
	Heat	0.086	<0.01	0.613
	Light	0.121	<0.01	0.645

[a]MSE=Mean Square Error

By using the information above in Tables 5 to 8 in the Appendix, plot synecological scores for moisture, nutrient, heat and light, are obtained as follows:

moisture 2.74 round to 2.5
nutrient 2.78 round to 3.0
heat 3.25 round to 3.0
light 3.32 round to 3.5

These values mean that if the plot were vegetated under natural conditions, it would be composed, in average, of species with low to medium moisture and nutrient requirements and medium light requirement. Because the heat coordinate is more closely related to species geographic distribution, it is of little use in this example because only one life zone is being analyzed.

Using this information and knowing the ecological distribution of plant species, it is possible to match the estimated plot synecological scores with those species values shown in the ecographs (Fig. 2). The species meeting those requirements, and therefore, with some growth potential in that site, are *Casearia commersoniana, Clarisia biflora* and *Trichilia havanensis*. Not enough data has been collected on all the species for them to have ecographs; therefore, it might be that more of them meet the requirements.

For site species identification, the moisture, nutrient, and light synecological coordinates summarize the interactions among the factors considered in Fig. 1. The edaphic and climatic fields are useful for site identification

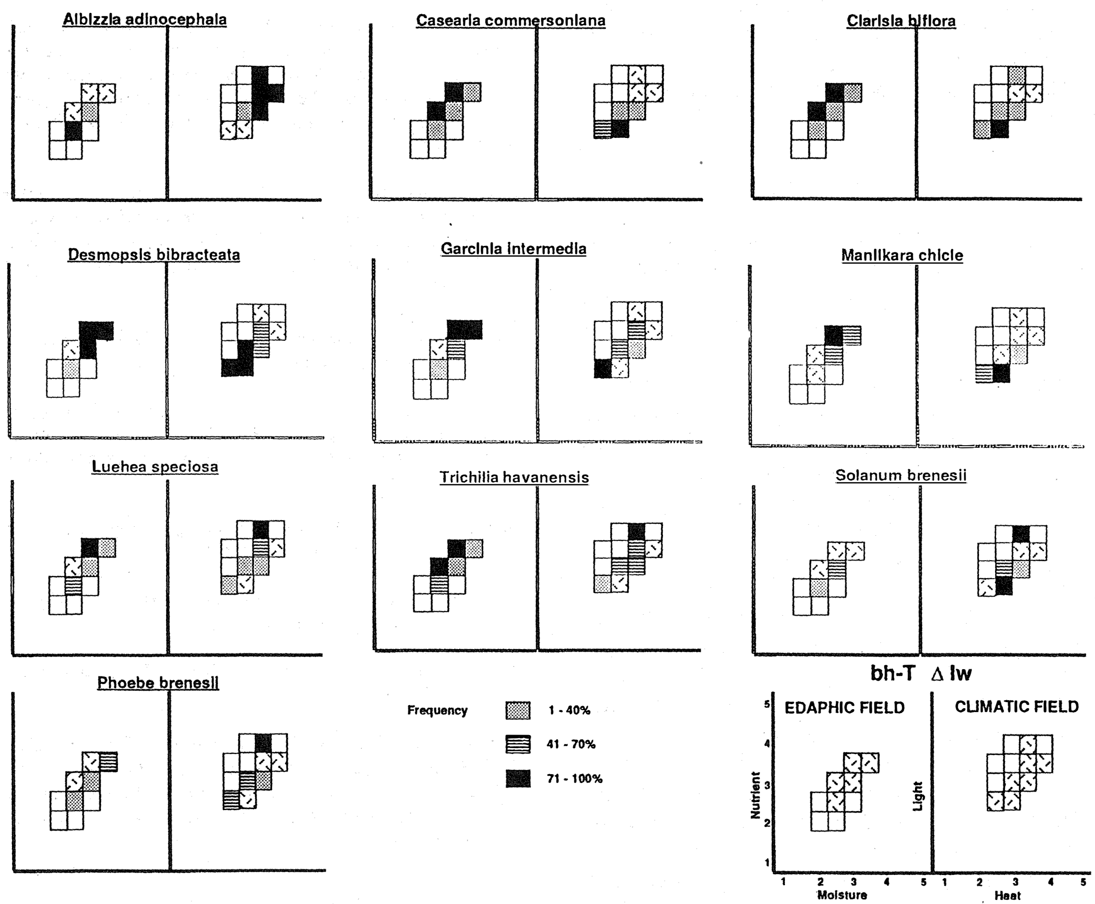


Fig. 2. Ecographs for 10 plant species in bh-TD Iw. The area within the squares represents the portion of the edaphic and climatic fields occupied by bh-TD. The dashed area represents the portion within bh-TD that is occupied by the BSU Iw.

for classification purposes within the ecosystem space.

ACKNOWLEDGMENTS

Carlos Morales, and Lizeth Días identified plants in the field and at the University of Costa Rica Herbarium; Quírico Jiménez, and Carlos Morales assigned initial synecological coordinate values to species; Rafael Mata provided assistance in soil identification, and Rafael Bolaños provided an update of life zone limits. José DiStefano and Luis Fournier gave, very timely, ecological and field advice. The Centro de Investigaciones

Agrónomicas - Universidad de Costa Rica- provided useful assistance. R. Hall, D. Glenn-Lewin, J. Sandor, and R. Schultz from Iowa State University commented constructively on the proposal for this project. The Editor of Revista de Biología Tropical, and two anonymous reviewers made constructive comments.

The Vicerrectoría de Investigación of the Universidad de Costa Rica and the Department of Forestry of Iowa State University provided financial support.

The senior author thanks them all for their help.

RESUMEN

Se presenta un método para evaluar la calidad de sitios forestales en ecosistemas tropicales. El método está basado en la relación entre calificaciones sinecológicas de los sitios (cuantificadores ambientales desarrollados a partir de información botánica de las especies) y características fisionómicas de los sitios. La relación puede ser usada para identificar especies con crecimiento potencial para sitios específicos y se espera que pueda ser usada también para estimar productividad. Este método fue sometido a prueba con datos obtenidos en Costa Rica de febrero a abril de 1991. Fueron identificadas 190 especies de plantas en 19 parcelas localizadas en el bosque premontano húmedo, y en 62 parcelas localizadas en el bosque tropical húmedo, transicional a premontano. Se encontró que un 81% fueron árboles, un 14% arbustos, un 2% hierbas y un 4% bejucos. Se utilizaron modelos de regresión para relacionar los cuantificadores ambientales con las características de los sitios. Las ecuaciones finales mostraron buenos ajustes (R^2s > 0,6) con bajos cuadrados medios de errores. Los resultados fueron utilizados para desarrollar guías (fórmulas) para calificar calidad de sitio en estas zonas de vida utilizables por ingenieros forestales.

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APPENDIX A

Forms to calculate site synecological scores

Equations used to developed each form can be found at the bottom of the form.Variable definitions are found in the text.

APPENDIX TABLE 1

Calculation of site moisture synecological score. Tropical premontane moist forest (bh-P)

Factor	Class	Add
Soil	Ah, Iw, Eu	-69
	Ix, Im	0
Heat	Warm-cool	-34
	Anything else	0
Slope position	Shoulder	48
	Otherwise	0
Soil texture	Fine silty	-22
	Loam	-115
	Otherwise	0
Soil O.M.	£ 10%	-34
	> 10%	0
Soil moisture	Moist	59
	Otherwise	0
		+ 254 =
		____/ 100 =____

Equation: M = 2.544 - 0.688 (Ah,Iw,Eu) - 0.340 (Warm-cool) + 0.478 (Shoulder) - 0.222 (Fine silty) --1.149 (Loam) - 0.342 (O.M.) + 0.593 (Moist)
n=18, R^2=0.96, MSE=0.024

APPENDIX TABLE 2

Calculation of site nutrient synecological score. Tropical premontane moist forest (bh-P)

Factor	Class	Add
Soil	Ah, Iw, Eu	-61
	Ix, Im	0
Heat	Warm-cool	-57
	Anything else	0
Slope position	Shoulder	40
	Otherwise	0
Site aspect	NE - SE	-27
	SE -SW	30
	Otherwise	0
Soil texture	Loam	-96
	Otherwise	0
Soil moisture	Moist	65
	Otherwise	0
		+ 232 =
		____/ 100 =____

Equation: N = 2.321 - 0.612 (Ah,Iw,Eu) - 0.567 (Warm-cool) + 0.394 (Shoulder) - 0.267 (NE-SE) + 0.296 (SE-SW) - 0.957 (Loam) + 0.648 (Moist)
n = 18 R^2 = 0.95 MSE = 0.019

APPENDIX TABLE 3

Calculation of site heat synecological score Tropical premontane moist forest (bh-P)

Factor	Class	Add
Soil	Ah, Iw, Eu	-69
	Ix, Im	0
Heat	Cool-warm	-36
	Anything else	0
Slope position	Concave	23
	Otherwise	0
Site aspect	NE - SE	16
	Otherwise	0
Soil texture	Loam	36
	Otherwise	0
Soil depth	Moderate	17
	Otherwise	0
		+ 294 =
		____/ 100 =____

Equation: H = 2.944 + 0.691 (Ah,Iw,Eu) - 0.358 (Cool-warm) + 0.226 (Concave) + 0.162 (NE-SE) + 0.364 (Loam) + 0.166 (Moderately deep)
n = 18 R^2 = 0.96 MSE = 0.015

APPENDIX TABLE 4

Calculation of site light synecological score.
Tropical premontane mosit forest (bh-P)

Factor	Class	Add
Soil	Ah, Iw, Eu	106
	Ix, Im	0
Heat	Warm - cool	72
	Anything else	0
Slope position	Footslope	-45
	Otherwise	0
Slope shape	Concave	53
	Otherwise	0
Site aspect	NE - SE	48
	Otherwise	0
Soil texture	Fine silty	-40
	Otherwise	0
Soil compaction	£ 15 cm	25
	Otherwise	0
		+ 302 =
		____/ 100 =____

Equation: L = 3.025 + 1.058 (Ah,Iw,Eu) + 0.717 (Warm-cool) -0.449 (Footslope) + 0.528 (Concave) + 0.478 (NE-SE) - 0.401 (Fine silty) + 0.252 (Compaction £ 15 cm)
n = 18 R^2 = 0.97 MSE = 0.018

APPENDIX TABLE 5

Calculation of site moisture synecological score.
Tropical moist forest (bh-TD)

Factor	Class	Add
Soil	Iw, Eu, Ut	59
	Ah	0
Heat	Warm-cool	-41
	Anything else	0
Slope position	Footslope	49
	Otherwise	0
Soil texture	Fine clay	33
	Fine silty	36
	Otherwise	0
Soil O.M.	£ 10%	18
	> 10%	0
Soil moisture	Moist	30
	Otherwise	0
		+ 197 =
		____/ 100 =____

Equation: M = 1.966 + 0.589 (Iw,Eu,Ut) - 0.408 (Wann-cool) + 0.491 (Footslope) + 0.332 (Fine clay) + 0.362 (Fine silty) + 0.176 (O.M. £ 10%) + 0.297 (Moist)
n = 62 R^2 = 0.71 MSE = 0.087

APPENDIX TABLE 6

Calculation of site nutrient synecological score
Tropical moist forest (bh-TD)

Factor	Class	Add
Soil	Iw, Eu, Ut	62
	Ah	0
Heat	Warm-cool	-42
	Anything else	0
Slope position	Footslope	49
	Otherwise	0
Soil texture	Fine clay	31
	Fine silty	34
	Otherwise	0
Soil O.M.	£ 10%	19
	> 10%	0
Soil moisture	Moist	27
	Otherwise	0
		+ 197 =
		____/ 100 =____

Equation: N = 1.974 + 0.621 (Iw,Eu,Ut) - 0.425 (Warm-cool) + 0.487 (Footslope) + 0.309 (Fine clay) + 0.339 (Fine silty) + 0.188 (O.M. £ 10%) + 0.274 (Moist)
n = 62 R^2 = 0.70 MSE = 0.089

APPENDIX TABLE 7

Calculation of site heat synecological score
Tropical moist forest (bh-TD)

Factor	Class	Add
Soil	Iw, Eu, Ut	-36
	Ah	0
Heat	Warm-cool	36
	Anything else	0
Slope position	Footslope	-47
	Otherwise	0
Site aspect	NE - SE	19
	Otherwise	0
Soil texture	Fine silty	-21
	Otherwise	0
Soil O.M.	£ 10%	-24
	> 10%	0
Soil moisture	Moist	-31
	Otherwise	0
		+ 366 =
		____/ 100 =____

Equation: H = 3.664 - 0.363 (Iw,Eu,Ut) + 0.358 (Warm-cool) -0.471 (Footslope) + 0.192 (NE-SE) - 0.207 (Fine silty) - 0.237 (O.M. £ 10%) - 0.308 (Moist)
n = 62 R^2 = 0.61 MSE = 0.086

APPENDIX TABLE 8

Calculation of site light synecological score
Tropical moist forest (bh-TΔ)

Factor	Class	Add
Soil	Iw, Eu, Ut	-79
	Ah	0
Heat	Warm-cool	69
	Anything else	0
Soil depth	Shallow	-35
	Otherwise	0
Soil moisture	Moist	-38
	Otherwise	0
		+ 411 =
		____ / 100 = ____

Equation: L = 4.115 - 0.789 (Iw,Eu,Ut) + 0.687 (Warm-cool) -0.346 (Shallow) - 0.385 (Moist)
n = 62 R^2 = 0.64 MSE = 0.121.