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Integrated Analysis of Tropical Trees Growth: A Multivariate Approach

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•*Background and Aims* One of the problems analysing cause–effect relationships of growth and environmental factors is that a single factor could be correlated with other ones directly influencing growth. One attempt to understand tropical trees' growth cause–effect relationships is integrating research about anatomical, physiological and environmental factors that influence growth in order to develop mathematical models. The relevance is to understand the nature of the process of growth and to model this as a function of the environment.
•*Methods* The relationships of *Aphananthe monoica*, *Pleuranthodendron lindenii* and *Psychotria costivenia* radial growth and phenology with environmental factors (local climate, vertical strata microclimate and physical and chemical soil variables) were evaluated from April 2000 to September 2001. The association among these groups of variables was determined by generalized canonical correlation analysis (GCCA), which considers the probable associations of three or more data groups and the selection of the most important variables for each data group.
•*Key Results* The GCCA allowed determination of a general model of relationships among tree phenology and radial growth with climate, microclimate and soil factors. A strong influence of climate in phenology and radial growth existed. Leaf initiation and cambial activity periods were associated with maximum temperature and day length, and vascular tissue differentiation with soil moisture and rainfall. The analyses of individual species detected different relationships for the three species.
•*Conclusions* The analyses of the individual species suggest that each one takes advantage in a different way of the environment in which they are growing, allowing them to coexist.

Key words: Phenology, radial growth, climatic periodicity, microclimate, tropical trees, multivariate analysis, *Aphananthe monoica*, *Pleuranthodendron lindenii*, *Psychotria costivenia*.

INTRODUCTION

More than 50 years ago, tropical trees were thought of as plants with continuous growth throughout their life cycle, lacking growth boundaries due to the imperceptible climatic variability and seasonality (Mariaux, 1981; Détienne, 1989). However, inter-tropical climate regimes are extremely diverse, i.e. rainfall seasonality is only absent in a narrow zone of one unit of latitude north and south from the equator, and seasonality increases when annual rainfall diminishes and a dry period increases through the year (Mariaux, 1995; Lüttge, 1997). It has now been recognized that most trees growing in seasonal climatic regions have dormant periods in response to vascular cambium inactivity. Moreover, there is evidence of seasonal growth in trees distributed in non-seasonal environments (Killmann and Hong, 1995).

Studies inferring causal relationships among trees' radial growth or phenology and local environmental factors in tropical forests have been carried out in recent years (Fahn *et al.*, 1981; Mariaux, 1981; Breitsprecher and Bethel, 1990; Borchert, 1994, 1999; Rao and Rajput, 1999; Ogata *et al.*, 2001). However, studies revealing significant correlations among them are very scarce (Bullock, 1997; Schöngart *et al.*, 2002; Dünisch *et al.*, 2003). Kozlowski (1971) stated that researchers must be careful when cause–effect relationships in the analyses of growth and individual environmental factors are recognized, because changes in a particular environmental component could be correlated with other factors and have a direct influence on growth. Another problem is the evaluation of local climatic influence on species growing in the same area, because growth could be correlated with different climatic variables.

One attempt to understand tropical trees' growth cause–effect relationships is integrating research about dendrometric, anatomical, physiological and environmental factors that influence growth, and further to develop empirical mathematical models. These models predict the performance of a system, such as a forest stand, based on a set of functional components and their interactions with each other and the physical environment (Bossel, 1994). This is relevant to understanding the nature of the process of growth, and to the modelling of this process as a function of the physical environment, to facilitate the understanding of cause–effect relationships and genotype–environment interactions, modelling the result of growth not only in terms of dimensional change (Tharakan *et al.*, 2000).

In Mexico, particularly in the north-central region of the coastal plain of the Gulf of Mexico, the subtropical rainforest is floristically and ecologically well defined (Rzedowski, 1963; Gómez-Pompa, 1973). In this forest, three evergreen species were selected to study the nature of the process of growth in subtropical trees and to explain

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its process as a function of the physical environment. *Psychotria costivenia* (Rubiaceae) is an understorey shade-tolerant species, while *Aphananthe monoica* (Ulmaceae) and *Pleuranthodendron lindenii* (Tiliaceae) are intermediate shade-tolerant species characteristically dominant in late-succession and distributed in the middle and upper canopy strata, respectively (Yáñez-Espinosa *et al.*, 2003).

In this study, the following questions were asked. (*a*) Are the growth patterns of the three species similar and associated with the same set of environmental factors and by microclimate on each stratum? (*b*) Would a unique model integrate the three species, or must there be developed one model for each species? To answer these questions the relationships between radial growth and phenology processes and environmental factors (local climate, microclimate of vertical strata, and soil physical and chemical variables) were integrated into mathematical relations that then were used to develop a new model. Multivariate statistics were used to obtain a set of environmental factors that most strongly correlated both within and with radial growth and phenology, as well as to show the most relevant 'dependent' and 'independent' variables for each variate.

MATERIALS AND METHODS

Study site and sampling methods

The study was carried out on a 1-ha long-term research plot in a subtropical rainforest located in central Veracruz, Mexico (19°49′37" to 19°51′50"N, 96°32′37" to 96°37′39"W, 420 m a.s.l.). The mean annual temperature measured over 2 years of continuous recording was 22·4 °C. Data from Misantla, the nearest weather station, 15 km away and at 410 m a.s.l., indicated total annual rainfall was 2217·2 mm. The rainy season lasts 4 months (June–September), and 15 % of total precipitation falls in winter. There is a short dry season (March and April) with 82–84 mm mean monthly rainfall, during which humidity is its lowest annual level. In this study plot, the soil is rich in organic matter and calcium.

A sample of 83 trees was selected, based on a census previously made of all trees with a diameter at breast height (DBH) ⩾1 cm (Godínez-Ibarra and López-Mata, 2002), and arranged by diametric classes (Table 1). From April 2000 to September 2001, including two complete growth periods, measurements in diameter increment were recorded bimonthly. Increment rates were calculated for each tree by difference of two consecutive measurements; and for each diameter class, increments were calculated as the trees' average bimonthly increment. Phenological observations were conducted either directly or by use of binoculars.

TABLE 1. *Species characteristics, tree sample and diameter categories*

Species	DBH (cm)	Height (m)	Trees (no.)	Diameter classes	Class range (cm)
Aphananthe monoica	1·9–116·2	3–30	30	10	12
Pleuranthodendron lindenii	2·9–23·3	2·8–20	33	6	4
Psychotria costivenia	2·9–10·1	3–6	20	4	2

Laboratory methods

Cambium activity and vascular tissue growth were observed by collecting branches from five trees per species, which were sectioned in 1–2 cm long segments and fixed in gluteraldehyde (Ruzin, 1999). The fixed segments were cut to half their size and rinsed with phosphate buffer solution (pH 7·4), infiltrated with 2-hydroxyethyl methacrylate (Aldrich Chemical Co.), and polymerized at 45 °C for 24 h. Transverse sections 2 μm thick were cut with a rotary microtome and stained with toluidine blue (Ruzin, 1999). Stem vascular cambium of the same trees was wounded bimonthly with a 5-mm-diameter wooden skewer. At the end of the first growing season, a section of stem with the wounds or the complete stem was removed from five trees per species. The samples were fixed in formalin–ethanol–glacial acetic acid and stored in 1:1:1 glycerine/ethanol/water. The wounded samples were then washed in running water and 30- to 40-μm-thick transverse sections cut with a sliding microtome. Sections were stained with safranin-fast green (Ruzin, 1999) and mounted with synthetic resin. Sections were analysed in an image analyser (Media Cybernetics, Image-Pro Plus v.3.1) connected to an Olympus BX50 light microscope.

Environmental data

Three thermohygrometer data loggers (HOBO H8 Pro; Onset Computer Corp., Pocasset, MA, USA) were positioned on tree branches at 5, 15 and 25 m high in April 2000 to obtain air temperature and humidity data on the canopy strata in the study plot. Data were unloaded using the Boxcar version 3·6 (Onset Computer Corp.). Vapour pressure deficit was calculated using mean monthly temperatures and relative humidity. Light availability on trees was estimated using hemispherical canopy photographs taken over individual *Psychotria* tree crowns with a 180° diagonal angle of view fisheye lens (Canon Inc.). From these photographs total photosynthetic photon flux density (PPFD) was calculated for June–August with the HEMIPHOT program by ter Steege (1994). Soil samples ($n = 24$) were analysed for pH, organic matter content, electrical conductivity, cation-exchange capacity and chemical composition (N, P, K, Ca, Mg, Na). Gravimetric soil moisture was taken in bimonthly samples from each 20 × 20 m (400 m^2) quadrat in the plot.

Statistical methods

The goal of canonical correlation is to analyse the relationships between two sets of variables, and to elucidate the relationship between the two sets of variables of high dimension by generating two sets of low dimension. One set of variables may be response variables and the other set explanatory variables, like in a multiple regression, except that there are several variables in both sides of the equation. Sets of variables on each side are combined to produce, for each side, a predicted value that has the highest correlation with the predicted value on the other side. Regarding terminology, first there are variables (variables measured in research), then there are canonical variates. These canonical variates are linear combinations of variables, one combination on the 'response' variable side and a second combination on the 'explanatory' variable side, and finally there are pairs of canonical variates (the combination of the canonical variates) (Tabachnick and Fidell, 1989).

The goal of the generalized canonical correlation is to analyse the relationships among more than two sets of variables, to measure the intensity of the relationships and to delineate strategies of simple canonical correlation by pairs of canonical variates, i.e. both procedures must be complementary. Furthermore, there are variables and canonical variates as before, but the first canonical variates of each set of variables generate a canonical vector of canonical variates; in contrast to simple canonical correlation where there are pairs of canonical variates, and the correlation matrix of the canonical variates is designated the first canonical correlation. The first vector of canonical variates is composed of canonical variates of each set of variables, optimizing a function of their correlation matrix. In the method of maximum variance, the first vector of canonical variates presents the maximum variance of the first eigenvector, corresponding to maximization of the first eigenvalue of the vector of the canonical variates' correlation matrix. In other words, the optimum vector of canonical variates for this method is the one whose first eigenvector maximizes their variance (Ortega-Alcalá *et al*., 1992).

The three species studied exhibited differences in reproductive phenology, mainly at the size when trees reach maturity. Then, flowering and fruiting were not included in the analysis, neither was leaf senescence which is present all year round. The relationship among the five sets of variables, phenology (leaf initiation and expansion), radial growth (cambial activity, vascular tissue differentiation and diameter increment), climate (rainfall, maximum temperature and day length), microclimate (mean temperature, relative humidity, photosynthetic photon flux density and soil moisture) and soil (electrical conductivity and Ca), was determined by the generalized canonical correlation analysis (GCCA). From the GCCA results, a simple canonical correlation analysis (CCA) was applied to the original variables more related to their canonical variates (phenology, radial growth, climate and microclimate), arranged in two sets, one for tree growth and the other for environmental variables (Table 5). A redundancy analysis was also used to calculate the variance in a set of original variables explained by a canonical variate of another set (McGarigal *et al*., 2000). All statistical analyses were performed with SAS software (SAS Institute Inc.).

TABLE 2. *Single values partition from the first correlation matrix*

Eigenvalue	λ_1	λ_2	λ_3	λ_4	λ_5
Three species	3·669	0·608	0·354	0·317	0·050
A. monoica	4·019	0·465	0·344	0·214	0·049
P. lindenii	4·246	0·944	0·469	0·239	0·074
P. costivenia	3·492	1·050	0·766	0·473	0·178
Eigenvector	e_1	e_2	e_3	e_4	e_5
Three species	0·422	–0·490	0·749	0·058	0·131
	0·444	–0·309	–0·543	0·587	0·256
	0·509	−0·007	−0·133	−0·146	−0·837
	0·467	0·079	−0·233	−0·722	0·446
	0·383	0·810	0·266	0·329	0·125
A. monoica	0·422	0·002	0·799	0·230	0·125
	0·451	0·089	−0·189	−0·755	0·324
	0·487	−0·040	−0·147	−0·018	−0·856
	0·439	−0·208	−0·524	0·580	0·351
	0·371	−0·360	0·164	−0·105	0·133
P. lindenii	0·431	0·161	0·347	0·623	−0·062
	0·472	−0·025	0·297	−0·496	0·658
	0·476	0·004	−0·004	−0·489	−0·722
	0·433	−0·156	−0·847	0·171	0·185
	0·340	−0·555	0·265	0·293	−0·074
P. costivenia	0·426	0·266	0·565	−0·558	0·089
	0·441	0·007	−0·368	0·124	0·056
	0·517	−0·126	0·090	0·190	−0·809
	0·485	−0·150	−0·036	0·606	0·522
	0·123	0·921	0·321	0·176	0·004

RESULTS

In the method of maximum variance applied to the GCCA, the number of generated canonical variates is equal to the number of variables of the smallest set, so in this case there were only two canonical variates. Vectors defining canonical variates to produce the vector of the first canonical variates are shown in Table 3 and the results of the correlation matrix among canonical variates in Fig. 1. Eigenvalues and eigenvectors of the correlation matrix are presented in Table 2. The first eigenvalue accounts for most of the variance of the first canonical variate, indicating that the first canonical variate is generated by only one common factor. However, the eigenvalue indicated that only three sets of variables are highly correlated and not all the sets had the same weight in the determination of the first canonical variate. The first eigenvector elements showed that the soil characteristics set had the lowest value among the sets for each species and jointly, and also revealed that phenology, radial growth, climate and microclimate presented similar values (Table 2). Higher correlations among canonical variates were different for each species and jointly (Fig. 1). For the species jointly, the highest correlation was between climate and microclimate, followed by climate–radial growth and climate–phenology, with similar values. For *A. monoica* and *P. lindenii*, the highest correlation was between radial growth and climate, followed in *A. monoica* by climate–microclimate and phenology–climate. In *P. costivenia* the highest correlation was between climate and microclimate, followed by radial growth–climate and phenology–climate.

TABLE 3. *Results from the first canonical variates vector*

Sets	Original variables	Canonical variates Three species	 *A. monoica*	 *P. lindenii*	 *P. costivenia*
Phenology	Leaf initiation	0·974	0·959	1·186	0·799
	Leaf expansion	0·047	0·075	−0·323	0·430
Growth	Cambial activity	0·514	0·428	0·612	2·259
	Vascular tissue differentiation	−0·631	−0·735	−0·525	1·553
	DBH increment (mm month^{-1})	0·028	0·146	0·030	0·090
Climate	Rainfall (mm)	−0·665	−0·668	−0·684	−0·714
	Maximum temperature (°C)	0·328	0·335	0·130	0·064
	Day length (h)	0·542	0·533	0·658	0·827
Microclimate	Canopy mean temperature (°C)	0·603	0·594	0·629	−0·044
	Canopy relative humidity (%)	0·369	0·278	0·565	0·936
	PPFD (mol m^{-2} d^{-1})	0·002	−0·088	0·024	0·242
	Soil moisture (%)	−1·037	−0·996	−1·086	−0·784
Soil	Electrical conductivity (dS m^{-1})	−0·984	−0·988	−0·970	−0·949
	Ca (cmol kg^{-1})	−0·112	−0·084	−0·272	0·637

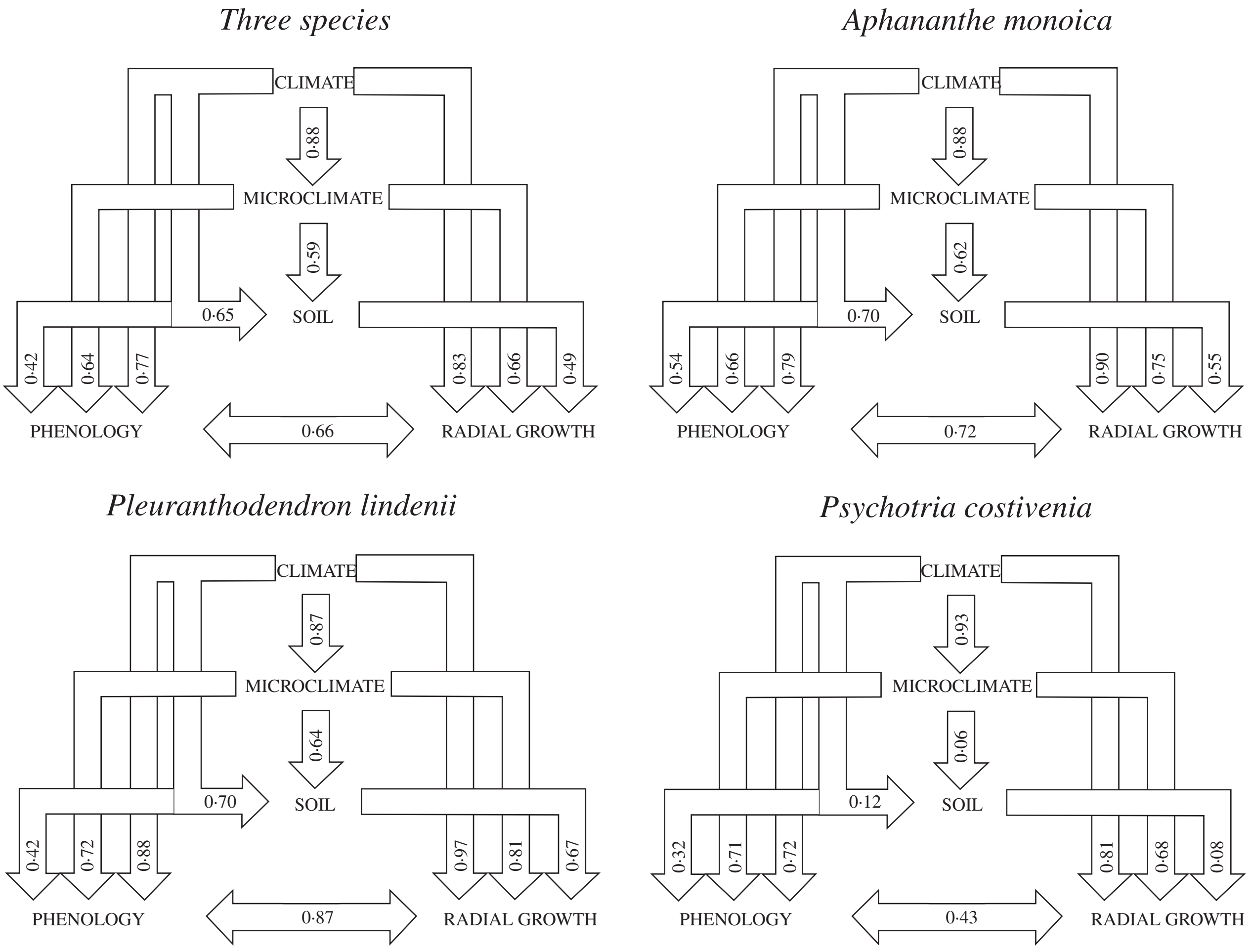

FIG. 1. Canonical variates correlations for the three species, jointly and individually.

Table 4 shows correlations between original variables and canonical variates within sets for each species and jointly. When the correlation of those original variables with their first canonical variate is low, they generally have higher correlation with the second canonical variate, showing the minute relevance within their corresponding set, and then the analysis of the information about the second eigenvector is less important and consequently not shown. These correlations corroborated that leaf initiation had high correlation with phenology (their first canonical

TABLE 4. *Correlation between original and canonical variables within groups for the three species, jointly and individually*

		Canonical variates			
Sets	Original variables	Three species	*A. monoica*	*P. lindenii*	*P. costivenia*
Phenology	Leaf initiation	0·999	0·997	0·970	0·909
	Leaf expansion	0·510	0·563	0·467	0·635
Growth	Cambial activity	0·837	0·711	0·894	0·810
	Vascular tissue differentiation	−0·895	−0·903	−0·852	−0·551
	DBH increment (mm month^{-1})	0·183	0·213	0·157	0·294
Climate	Rainfall (mm)	−0·634	−0·580	−0·652	−0·504
	Maximum temperature (°C)	0·498	0·588	0·455	0·642
	Day length (h)	0·755	0·778	0·750	0·724
Microclimate	Canopy mean temperature (°C)	0·255	0·292	0·255	0·531
	Canopy relative humidity (%)	−0·098	−0·103	−0·055	0·609
	PPFD (mol m^{-2} d^{-1})	0·009	0·033	0·085	0·517
	Soil moisture (%)	−0·848	−0·861	−0·799	−0·417
Soil	Electrical conductivity (dS m^{-1})	−0·995	−0·996	−0·962	−0·787
	Ca (cmol kg^{-1})	−0·173	−0·177	−0·244	0·397

TABLE 5. *Canonical cross-loadings of the first pair of canonical variables for the three species, jointly and individually*

	First pair of canonical variates							
	Three species		*A. monoica*		*P. lindenii*		*P. costivenia*	
	Correlation	Coefficient	Correlation	Coefficient	Correlation	Coefficient	Correlation	Coefficient
Tree growth set								
Leaf initiation (% trees)	0·796	0·407	0·798	−0·066	0·855	0·162	0·656	0·495
Cambial activity (% trees)	0·758	0·229	0·834	0·547	0·910	0·674	0·838	0·734
Vascular tissue differentiation	−0·823	−0·516	−0·889	−0·653	−0·804	−0·447		
Environment set								
Rainfall (mm)	−0·703	−0·412	−0·675	−0·503	−0·635	−0·499	−0·724	−0·181
PPFD (mol m^{-2} d^{-1})	0·287	−0·045	0·458	0·160	0·329	−0·087	0·089	−0·009
Maximum temp. (°C)	0·575	1·033	0·684	0·816	0·739	1·106	0·399	1·476
Day length (h)			0·141	−0·324	0·216	−0·341	−0·122	−1·251
Canopy mean temp. (°C)							−0·163	−0·043
Canopy relative humidity (%)							0·264	−0·117
Soil moisture (%)	−0·691	−0·102	−0·779	−0·075	−0·585	0·077	−0·601	−0·006
% of variance	89		84		84		82	
Redundancy	0·627		0·702		0·735		0·525	
Canonical correlation	0·852		0·969		0·973		0·815	

variate), which means that this variable is the most important in the resolution of the canonical variate. The highly associated variables with radial growth were cambial activity and vascular tissue differentiation. Regarding environmental variables, day length, rainfall and maximum temperature, correlation with climate was high, indicating that those three variables have equal weight in the determination of the variate, as well as soil moisture with microclimate and electrical conductivity with soil. In *P. costivenia*, correlations of variables within microclimate in the understorey had a similar pattern (Table 4). Based on these results, the two sets of variables selected by the GCCA were tree growth with the most important of the phenology and radial growth sets, and environment with the climate and microclimate sets.

A CCA was performed between the set of tree growth variables and the set of environmental variables for the three species jointly and for each species. Regarding the three species jointly, the first canoncial correlation was 0·852 (82 % of variance, $P < 0{\cdot}0001$), the second was 0·553 (18 % of variance, $P < 0{\cdot}001$), and the remaining correlations were zero. The first pair of canonical variates, therefore, accounted for the significant relationships between the two sets of variables. However, remaining pairs were less related, and their interpretation was trivial. For *A. monoica* the first canonical correlation was 0·969 (87 % of variance, $P < 0{\cdot}0001$), the second was 0·814 (13 % of variance, $P < 0{\cdot}001$). For *P. lindenii* the first canonical correlation was 0·973 (87 % of variance, $P < 0{\cdot}0001$), the second was 0·840 (13 % of variance, $P < 0{\cdot}001$). For *P. costivenia* the first canonical correlation was 0·815 (90 % of variance, $P < 0{\cdot}0001$), the second was 0·320 (10 % of variance, $P < 0{\cdot}073$). For each species the remaining correlations were zero.

Data on the first pair of canonical variates (cross-loadings) appear in Table 5 showing the correlations between the variables and the canonical variates, standarized canonical variate coefficients, with opposite-set variance

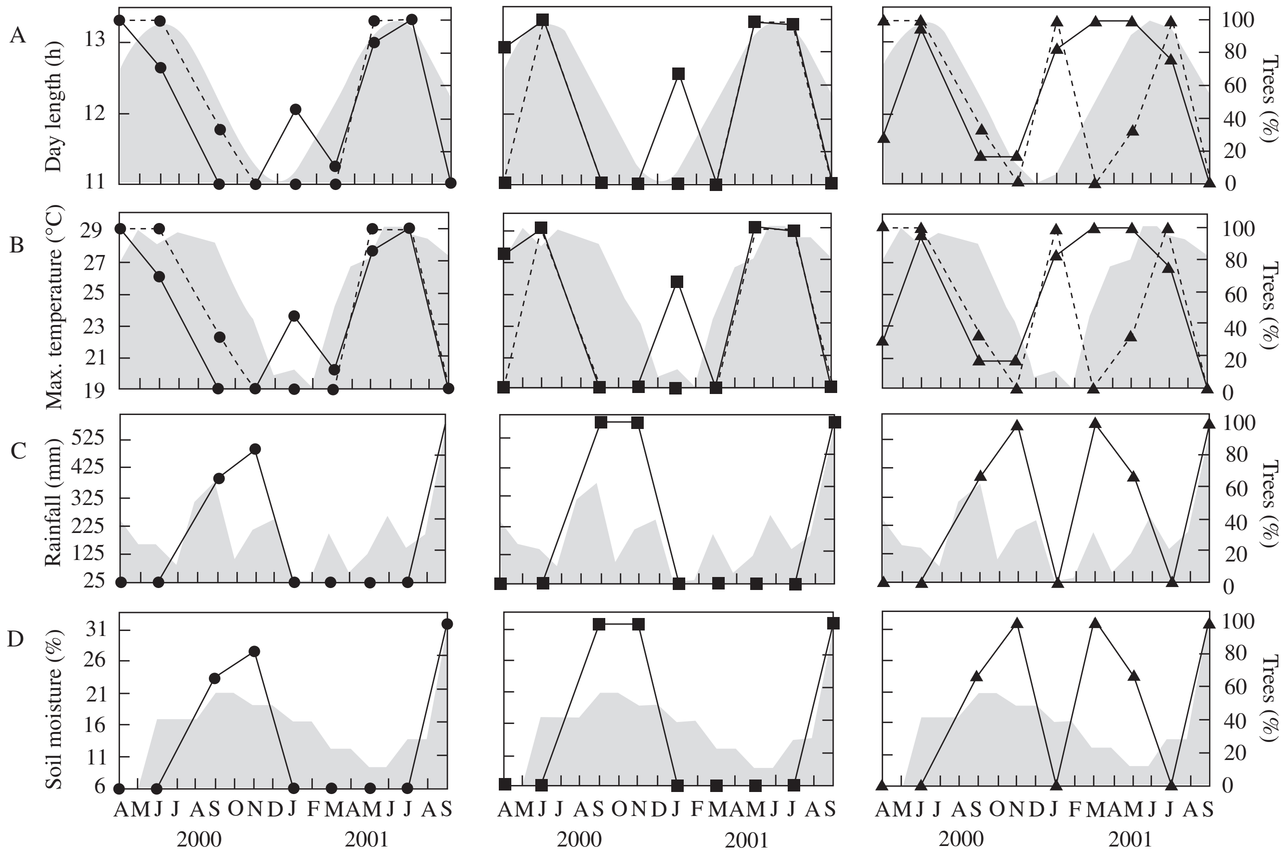

FIG. 2. Radial growth and environmental original variables performance. *A. monoica*, circles; *P. lindenii*, squares; *P. costivenia*, triangle. (A) Day length, grey; leaf initiation, continuous line; vascular cambium activity, dotted line. (B) Maximum temperature, grey, leaf initiation; continuous line; vascular cambium activity, dotted line. (C) Rainfall, grey; vascular tissue differentiation, continuous line. (D) Soil moisture, grey; vascular tissue differentiation, continuous line.

accounted for by the canonical variate (% of variance), redundancies and canonical correlations. Percentage of variance and redundancy indicate that the first pair of canonical variates was highly related. The cross-loadings for the three species jointly showed that periods of leaf initiation and cambial activity were strongly associated with maximum temperature and day length, and vascular tissue differentiation with soil moisture and rainfall (Table 5 and Fig. 2). For the three species the cross-loadings showed that periods of leaf initiation and cambial activity were positively associated with day length and maximum temperature, and negatively with rainfall and soil moisture (Table 5 and Fig. 2). In addition to these variables, canopy mean temperature was positively associated in *A. monoica* and negatively associated in *P. costivenia* to canopy mean temperature and canopy relative humidity (Table 5 and Fig. 2).

DISCUSSION

In general, the analysis showed that the strongest influence was between climate and microclimate, because the last one was determined by the vertical structure, tree density and vertical gradients of specific variables like light intensity, temperature, air humidity and CO_2 contents (Kira and Yoda, 1989; Lüttge, 1997). In the present results, influence of climate on soil is more robust than microclimate on soil, except in the understorey where microclimate influence is greater because the forest cover effect near the soil surface is stronger, as suggested by Richards (1952).

Kozlowski (1971) mentioned light, water, temperature, mineral elements, atmospheric composition above and below ground, soil chemical and physical properties, insects, other plants and diverse animals, as the most remarkable physical and biological factors contributing to cambial activity. Additionally, cambial growth is considerably modified by shoot and reproductive growth in the same tree. Species analysis corroborated that radial growth is associated with phenology, and both are as well related to climate, microclimate and soil. Although the species are associated with the same variables, it is evident that these relationships are different, depending on the species and its position in the forest vertical strata. For this reason, when the species are analysed jointly, several relationships are not characterized and could be underestimated, as is the relationship between phenology and radial growth in *A. monoica* and *P. lindenii*.

The association of climate with radial growth and phenology was the most important for each species and jointly. Radial and apical growth in most woody species is periodic and periodicity is clearly correlated with seasonal changes (Iqbal, 1994). Fluctuations in environmental stress greatly influence radial growth when the flux of photosynthates towards the branches and stem become altered. Environmental factors eventually affect cambial activity and consequently bud development and their expansion, as well as fully expanded leaf physiological activity. The association between phenology and radial growth is important, but less than with climate and microclimate. In the case of *P. costivenia*, which is exclusively distributed in the understorey, the relationship between phenology and radial growth is more relevant than the association with microclimate. In other tropical species, vascular cambium activity is mainly determined by the activity of the apical buds (Wilson, 1970; Tomlinson and Longman, 1981; Creber and Chaloner, 1990; Borchert, 1999). For the species in the study site, it was found that the phenology influence on radial growth is more relevant than vice versa. This could be explained because the period of leaf initiation produces growth regulators directly involved in the cambial activity period, but radial growth only facilitates the incorporation of photosynthetic products necessary for leaf expansion.

The cambial activity and consequently the increment in xylem cells, number and size, results in long-term diameter increment (Kozlowski *et al.*, 1991; Catesson, 1994). In the species studied the association between diameter increment and vascular cambium activity was low. Division and expansion were scant in cambial cells, as revealed by the annual increment average rate of *A. monoica* (5 mm), *P. lindenii* (3 mm) and *P. costivenia* (2 mm). The reversible contraction and dilatation of cells, mainly in secondary phloem and cambial cells, associated with changes in stem water and temperature results in short-term diameter increment (Kozlowski *et al.*, 1991). Such a variation was confirmed in the species studied, because stem diameter decrement occurred in the March–June period and in January.

The influence of soil in radial growth and phenology was less significant. In *P. costivenia* the association between soil and radial growth was lower. In tropical forests, physical soil factors, e.g. water content, which is mostly controlled by climate (Richards, 1952), are more involved than chemical ones in plant growth. Richards (1952) suggested that vegetation can affect soil conditions, modifying the microclimate or adding humus which has originated from litter at the soil surface, as was observed at the study site. However, humus accumulation and nutrient release are complex processes which are poorly understood (FitzPatrick, 1984).

The GCCA recognized that the environment explained 84–89 % of phenology and radial growth variance, suggesting that radial growth and phenology variables are seasonal. This seasonality is clearly related to climate and microclimate fluctuations, considering soil moisture as a continuum with air humidity through the year. The remaining 11–19 % of variance must be determined by physiological factors like transpiration, photosynthesis, growth regulators and stored substances that were not studied in this research but must be included in the future.

CCA allowed recognition of consecutive environmental factors affecting radial growth (Fig. 2). Initially, during spring and summer, increase in day length, maximum temperature, canopy mean temperature (*A. monoica* and *P. lindenii*) and light intensity (PPFD) in the understorey (*P. costivenia*) have influence on leaf initiation and cambial activity periods. Afterwards, increases in rainfall during summer and autumn, soil moisture, relative humidity, and mean temperature in the understorey (*P. costivenia*) influence xylem differentiation.

Rao and Rajput (1999) recognize a similar relationship in *Tectona grandis*, where high temperature is necessary for leaf initiation during spring and summer, favouring simultaneously cambial activity. Subsequently, vascular tissue differentiation, involving cell expansion, corresponds with rainfall during the summer. The study area in India (20°52′N) is similar in latitude to the study site in Mexico; maybe this could explain their coincident events. Studies in tropical dry forests of Mexico (Bullock, 1997; Makocki, 2000) and Brazil (Dünisch *et al.*, 2003), found a positive correlation between rainfall period and radial growth, corroborating that vascular tissue differentiation and expansion is highly related to rainfall. Water availability affects cambial activity, because positive hydrostatic pressure in cells favours expansion (Philipson *et al.*, 1971). Drew (1998) and Makocki (2000) also observed that the rainfall period influences the structural arrangement of anatomical elements within each growth ring.

Schöngart *et al.* (2002) showed that the activity of vegetative buds is not controlled by the photoperiod in the Amazons (3°S, with 20-min difference between the longest and shortest day) contrary to the findings of Borchert and Rivera (2001) in Cost Rica and Drew (1998) in Puerto Rico (18° N). At the site in Mexico (19°49′–19°51′N) used in the present study, the association between leaf initiation, cambial activity and photoperiod could be attributed to the 2·3 h difference between the longest and the shortest day. In some species the photoperiod effect influences indirectly the length of the cambial active period, because internal hormonal control balance is greatly involved (Kozlowski, 1971).

Various studies had analysed the relationship between tropical trees species phenology and/or radial growth with individual environmental factors, generalizing their associations (Fahn *et al.*, 1981; Mariaux, 1981; Breitsprecher and Bethel, 1990; Borchert, 1999; Rao and Rajput, 1999; Ogata *et al.*, 2001). Nonetheless in a few studies, simple correlation analyses have been carried out (Bullock, 1997; Makocki, 2000; Schöngart *et al.*, 2002; Dünisch *et al.*, 2003). Recently, Borchert (1999) proposed integrating phenology and radial growth of tropical trees with environmental factors involved in their control, adding physiological process like water relations. However, growth models are deductive in most occasions, and simultaneous analysis of the components involved as well as the hierarchy of their associations have not been considered or generalized for different species coexisting in a community (Alder, 1995).

The GCCA applied here allowed a general model to be developed to understand tree phenology and radial growth as a function of the climate, microclimate and soil factors. In addition, the GCCA recognized the magnitude of their relationships and the most relevant dependent and independent variables of each variate. Tharakan *et al.* (2000) mentioned that these kinds of models have been criticized as being too abstract, difficult to understand, use and apply, as well as requiring too many data. However, they are useful for synthesizing research where the number of variables is complex and for integrating, from a reductionism approach, the study of growth. The same climate and soil variables explain radial growth pattern and phenology in trees; however, each species association magnitude is quite different. This means that each species takes advantage differentially of the environment where is growing, even more when relevant microclimatic variables are different for each one, mainly for *P. costivenia* which is exclusively distributed in the understorey. Such differential responses to varying local physical factors allow the species studied to exploit its particular vertical strata and coexist in this subtropical rainforest.

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