

# Pioneer species ecology: co-existence and ecological differences amongst contrasting species

A dissertation submitted in partial fulfilment of the requirements for the degree of *Master of Science* (MSc) in Environmental Forestry of the University of Wales

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## Abstract

Ecological differences were investigated for two co-existing pioneer species from the *Cecropia* family for variation of first branch height and canopy width across old field and old-growth forest habitats and within habitat variation between species. Forest enumeration data was collected, on all trees >5 cm DBH, from 4 study sites, each containing 9 old-growth forest and 4 old field plots, within the Los Cedros reserve, Ecuador. *Cecropia* species 1 was not locally more abundant but was found to be more spatially distributed at 32 of the 52 plots; *Cecropia* sp. 2 was only present at 7 of the 52 plots. Coefficients of variation and allometric relationships were investigated within species and between habitats. No significant variation was found for either species between habitats. For investigations of first branch height *Cecropia* species 1 was significantly lower than *Cecropia* sp. 2 in comparisons of actual first branch height (old-growth forest,  $p < 0.040$ ; all old field  $p < 0.0005$ ; all matched old field,  $p < 0.003$ ); the relationship between first branch height and tree height (all old-growth forest,  $p = 0.004$ ; all old field,  $p = 0.002$ ; matched old field  $p = 0.024$ ) and the relationship between first branch height and the ratio of DBH:tree height (all plot,  $p = 0.001$ ; all old field,  $p = 0.008$ ; all matched old field,  $p = 0.03$ ), across all habitats. The crown width investigations concluded that *Cecropia* species 1 was significantly wider than *Cecropia* sp. 2 in comparisons of actual crown width (all plots,  $p < 0.0005$ ; all matched plots,  $p = 0.021$ ); the relationship of crown width to DBH (all plot,  $p = 0.002$ ; all old field,  $p = 0.005$ ; all matched plots,  $p = 0.001$ , matched old field,  $p = 0.007$ ); relationship of crown width to tree height (all old field,  $p < 0.0005$ ; all matched plots,  $p = 0.010$ ); relationship of crown width to first branch height (all plots  $p < 0.0005$ ; all old-growth forest plots,  $p = 0.001$ ) and the relationship of crown height to DBH:tree height (all plots,  $p = 0.023$ ; all old fields,  $p = 0.034$ ). Plasticity (assessed as coefficient of variation) was apparent: highest in crown width (*Cecropia* sp. 1, 78.86% to 42.33%; *Cecropia* sp. 2, 92.24% to 41.84%); lowest in tree height (*Cecropia* sp. 1, 32.68% to 20.40%; *Cecropia* sp. 2, 14.97% to 18.02%); but not significantly different between species.

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# 1. Introduction

## 1.1 Pioneer species

Pioneer species are defined as light demanders that require full sunlight to enable their seedlings to germinate and establish (Swaine and Whitmore 1988). Once germination has taken place pioneers generally sacrifice stem stability for height gain, hence their ability to dominate after disturbance events. This definition has been challenged by Kyereh et al. (1999) with experimental studies showing pioneers germinating under differing light conditions. They suggest that the working definition for pioneer species should depend more upon their poor ability to survive in shade. Poorter et al. (2005) also state that the division between pioneer and shade tolerant species is far too simplistic and requires further study.

It is possible to further define pioneers in two ways: Firstly pioneers vary in the minimum size of gap they require before establishment can succeed (Ackerly 1996, Kwitt et al. 2000, Brokaw 1987). Brokaw (1987) suggests that this may be due to niche partitioning, with the gap area divided into different micro sites to which certain species are better adapted; as gap

size decreases niches are eliminated and species with them. Secondly, species can vary considerably in longevity and stature; at the smaller end species like *Carica papaya* grow to a maximum height of 5-6 m and complete a full lifecycle in less than 10 years (Sarukhán, Piñero & Martinez-Ramos 1985 in Ackerly 1996). Species such as *Cecropia* are intermediate in size, reaching canopy height with short (30-50 years) lifespans (Alvarez-Buylla and Martinez-Ramos 1992). Other pioneers attain canopy height and can dominate for many centuries, for example: *Ceiba pentandra* (Ackerly 1996).

Demographic traits that have previously been attributed to pioneer species include: (i) a spatial distribution that is strongly aggregated, (ii) a coincidence of size among individuals found in similar aged gaps, (iii) relatively high growth rates and (iv) early maturation; it is expected that height growth is selected for over strength and longevity in pioneers (Alvarez-Buylla and Martinez-Ramos 1992). Several studies have indicated that increased soil disturbance results in an increase in the concentration of pioneer species (Kwitt et al. 2000, Putz 1983), possibly attributed to a lack of litter or vegetation to inhibit growth. In this respect pioneer species can aid the recovery of forests after disturbance, retaining nutrients and

preventing erosion (Bazzaz 1991). The span of conditions and resources available within disturbed ground is also likely to be greater than on undisturbed ground so it is possible that early-successional species are able to succeed in a wider range of environments than late-successional species (Wilson, 1999).

## 1.2 Disturbance

Natural disturbance is stochastic by nature. This is part of what defines it as disturbance and is critical for the maintenance of natural biodiversity and processes (Healey 2006). Chesson (1985) suggests that an important factor in the dynamics of populations and communities is environmental variation. The persistence of a population is more likely to be affected by demographic factors linked to environmental events than by genetics (Lande 1988). Local abundance or population size is not addressed by demographic analyses as such but the differences among species in local abundance may still be reflected by demographic attributes; recruitment, individual growth rates over time, and mortality are synthesised in population size distributions (Kelly et al. 2001).

## 1.3 Light variation

Only approximately 1 to 2 % of above canopy radiation reaches the floor in tropical forests (Poorter, 1999). Solar radiation is measured as photon flux density (PFD) for the purposes of photobiology. That is the amount of quanta (Einsteins or moles of photons) reaching a unit surface ( $1 \text{ m}^2$ ) per unit of time (1 s or 1 day) (Percy 1989 in Chazdon et al. 1996). In clearings and gaps tropical plants frequently encounter high PFD levels. Leaves encounter PFD in excess of their photosynthetic requirements and the photosynthetic apparatus can become damaged; this is termed photoinhibition. Permanent damage is rare where factors such as water and nutrients are not limiting (Fernandez and Fetcher 1991b in Chazdon et al. 1996). It has been confirmed through comparative studies that less photoinhibition in forest gaps is exhibited by early successional species (Percy 1989 in Chazdon et al. 1996). Light demanding species have an inherently high photosynthetic capacity that affords a “built in” plastic ability (Chazdon 1992 in Chazdon et al. 1996). Light dependant variation tends to show with anatomical changes as well as in photosynthetic capacity per unit leaf



biomass (Chazdon & Kaufmann 1993 in Chazdon et al. 1996).

## 1.4 Plasticity

Sessile photosynthetic organisms have been shown to exhibit considerable plasticity (above and below ground) in response to changing environmental conditions (Valladares et al. 2005). Within a heterogeneous environment plant evolution follows one of two paths: specialisation to a niche environment or broader adaptation to a wider environment (Bazzaz 1996 in Valladares et al. 2000). So called gap-dependent species have been shown in previous studies to have greater photosynthetic plasticity than shade tolerant species (Bazzaz and Carlson 1982, Strauss-Debenedetti and Bazzaz 1991, 1996 in Valladares 2000). Valladares et al. (2000) state that this is the result of the gap dependant species' specialisation to this more favourable environment; natural selection may favour phenotypic plasticity in pioneer species due to a predictable decrease in light levels (as growing vegetation converges) within gaps. The mean difference in traits between environments can be used to estimate the heritability of plasticity (Stearns 1992). Schlichting (1986) argued that the degree of similarity of a taxon's phenotypic plasticity should demonstrate

whether or not that plasticity has arisen via drift.

The amount of light that an individual tree receives is influenced by its position in the environment (in the under-storey, in a clearing, whether that is a forest gap or old-field, or in the canopy). Tree limitations are such that they can only influence their position in the environment via vertical and horizontal growth. Vertical growth influences their position in the canopy, increasing available light with height. At any height the amount of photosynthesis that can take place is determined by the light available (over which the tree has no control except vertical or horizontal growth), by the amount of foliage it has, and its spatial distribution; these in turn are determined partially by the tree's crown depth and width (Poorter et al. 2003). Light exploitation is also assisted by an indeterminate pattern of leaf production and growth. (Bough and Ramakrishnan 1982). So in turn a tree's success can largely be determined by its architecture (Percy and Valladares 1999 in Poorter et al. 2003). Future growth in trees is influenced by the allocation of new biomass. Plants grown in contrasting nutrient or light regimes exhibit phenotypic plasticity in allocation and this can also vary with leaf life span, shade

tolerance and crown architecture (King 2003).

Pioneers are able to put high growth rates into extension due to their high light environment. Extension is necessary due to gap closure and competition from neighbouring plants. Initial rapid height growth is achieved by limiting increases in stem and crown diameter. (Poorter 1998 in Poorter et al. 2003). During gap colonisation one way to judge the success of a pioneer species is by comparison of height to other pioneers at the same site (Canham and Marks 1985, Fig 1, in Brokaw 1987). We would not expect a pioneer population to be at equilibrium. Alvarez-Buylla and Martinez-Ramos's (1992) study of *Cecropia obtusifolia* showed an increasing age population structure within forest gaps; no recruitment occurred to the 1cm stem diameter category after 4 years of gap formation and gaps older than 25 years only contained trees  $\geq 30$  cm in stem diameter. The study also found that stem diameter and height were allometrically related in all individuals of *C. obtusifolia*.

Nearly all of the approaches that exist to measure a taxon's plasticity in response to variation of environment have conceptual and operational difficulties. In consequence it is difficult to compare

differences, even between related taxa. To calculate variability across treatments the simplest methods include: variance, standard deviation, or the coefficient of variation (standard deviation/mean) of character means across treatments. Precision is increased with the control of within-treatment variation.

### 1.5 Allometry

A good deal of literature can be found focusing on inter-specific differences in architecture from the point of view that different light environments are utilised more efficiently with different architectures (Horn 1971, King 1990, Poorter and Werger 1999). Less time has been spent on the study of intra-specific architectures and adaptation to their environment (Poorter and Werger 1999). One important finding through the study of tree architecture is that allometric differences in coexisting understorey saplings can be caused by spatial and temporal variation in the light environment. (Yamada et al 2005)

There are two key ecological components to tree architectural responses: firstly they influence the levels of structural and physical stress that can be coped with; secondly they are responsible for the leaf display, light interception and the ability

to secure and utilise carbon. Therefore over long term it affects the ability of the tree to grow, survive and reproduce (Bongers and Sterck, 1996).

The architecture of trees varies greatly depending on their environmental pressure. These varying parameters such as crown shape, height and diameter can be correlated to other factors, for example: phylogenetic affinities, age and environmental conditions (Nascimento et al. 2005). Ecological investigations frequently use important allometric equations that relate diameter breast height (DBH) to attributes including, foliage area, carbon volume and biomass (Delgado et al. 2005). Standard regressions can be used to describe allometric patterns despite plant-form variables co-varying, enabling comparison with allometric relationships that have been previously published (Alvarez-Buylla and Martinez-Ramos 1992).

## 1.6 Tree crowns

The ability of early successional species to densely populate open areas rapidly may be related to their extension of foliage and height as there are individual strategies of niche occupancy caused by differences in allocation between crowns and trunks (Sposito and Santos, 2001).

A study by Sterck and Bongers (2001) found that crown development was influenced by canopy openness and tree height at all organisational levels. Trees have greater horizontal and lateral branch extension at higher light levels and relative crown depth increases with height (Poorter 2003). Branch extension increases as the canopy opens and height is increased. (Sterck and Bongers 2001). It is necessary for crown expansion to occur quickly for pioneers to survive, enabling them to shade their competitors and monopolise the higher light conditions. Pioneer species in gaps are able to maintain deeper crowns; with the possibility that several branches can overlap before the lowest layers light compensation point is reached (Poorter 2003, Horn 1978).

As height increases the tree moves into a richer light environment. It is likely then that crown development begins when the tree reaches PFD levels high enough to support lateral and vertical growth. In old fields these levels will be reached sooner than in forest gaps due to the lack of shading effects from surrounding trees. Rapid growth rates in pioneers result in thinner stems and reduced stability. There are well established correlations between crown diameter and DBH (Healey pers.

com), so we would expect stem diameter to increase as the crown develops.

The role of crown structure has mostly been studied from a morphological perspective and modelling tools such as Y-plant have been used to assess light environments heterogeneity. Valladares and Pearcy (1998) believe that future more dynamic models will need to include developmental plasticity along with the input of plant morphologists and ecophysiologists.

## 1.7 Phylogeny

Why do species differ from each other? Comparisons of plants that at some point shared a common ancestor can give indicators as to how evolution has led them to fill particular niches. It is natural to ask how similar character traits that evolve independently in similar environments benefit the bearers. Statistical events rely on independent events that phylogenies can help us to identify. Comparative studies can cautiously begin to make inferences about adaptation once probable causal variables and patterns have been identified (Harvey and Pagel 1991). By studying distantly related but ecologically similar species it

is possible to illustrate evolutionary *convergence*. Likewise by studying closely related but ecologically differentiated species it is possible to illustrate adaptive *divergence* (Ackerly 1998). When moving from observing species distributions to their interpretation for character traits ecologists encounter confounding variables (Harvey 1996).

By selecting for species within monophyletic taxonomic groups and limiting our study to congeneric comparisons, we seek to limit the confounding effects of phylogeny (Harvey and Pagel 1991, Harvey 1996, Kelly et al 2001). Comparing species collected from the same localities should also assist in limiting confounding effects (Buckley and Kelly 2003)

## 1.8 Pattern and process in forests

One aim of the research into stand dynamics is the explanation of patterns that, within different ecosystem types, may be tied to successional processes (Veblen 1985). Generally there are two patterns of forest stand development: autogenic and allogenic (Tansley, 1935 and, Spurr and Barnes, 1980 in Veblen, 1985). In traditional successional theory autogenics is attributed to reaction

(Clements 1916 in Veblen 1985); in subsequent successional theory community control is a reflection of the autogenic successional pattern (Odum 1975 and Whittaker, 1975 in Veblen 1985). Allogenics takes the view that the majority of trees reach a mature canopy status after disturbance of the previous canopy (by new establishment or release). Disturbance is important but allogenics and autogenics are not mutually exclusive; one may be more dominant in a certain environment but generally stand development is a combination of both (White 1979 in Veblen 1985).

Three general mechanisms were suggested by Connell and Slatyer (1977): facilitation, tolerance and inhibition. Facilitation requires an earlier species to change the environment in some beneficial manner that allows a later species to succeed. Tolerance relies on later species being able to tolerate reduced resources to earlier species and all species employing different strategies for exploitation of those resources. With inhibition earlier species will attempt to exclude or constrain competitors until they (the earlier species) die or are damaged.

A forest general development pattern was postulated by Oliver (1981 in Veblen 1985), which took place after large-scale

natural or human-created disturbances. This was divided into four stages: stand initiation, stem exclusion, understorey re-initiation and old growth.

Following a large scale disturbance loss of forest results in a sudden increase in the availability of certain resources. This may allow for the establishment of numerous seedlings over a short period of time. The span over tree ages would vary with the colonisation phase, determined by effects such as dispersal capabilities, size of area and habitat favourability (Veblen 1985).

Most natural “even aged” stands contain trees that have established over a range of years. In Veblen’s (1985) study of *N. alpina* new stems continued to arise for circa 10 years after disturbance. It is likely that colonisation continues for 20 to 30 years in areas where large scale disturbance (greater than 1 or 2 hectares) occurs. A ‘kinetic’ view of vegetation change has been put forward to replace equilibrium models by Drury and Nisbet (1971, in Veblen 1985); not requiring stable endpoints this view accepts the site is physically unstable and acknowledges that continuous change occurs.

Characteristic patterns of stand development may occur in narrowly even

aged populations due to competition (Veblen 1985). But it has been shown that diameter size class distributions used to examine the population structure of trees can give unreliable impressions of many species regeneration strategy (Hubbel and Foster, 1997 in Healey 2006).

### 1.9 Study species

*Cecropia* is a strongly mono-phyletic (Berg 1978) genus of pioneer species with a range that covers Mexico to Northern Argentina and the West Indies. It is well known as a genus that colonises high light environments such as cleared and open areas. It was selected due to its obvious importance to the regeneration of disturbed land on and around the Los Cedros reserve, the area selected for this study. An area fringed by old field sites that have been colonised by considerable numbers of *Cecropia*.

### 1.10 *Cecropia* Loebl.

The genus *Cecropia* belongs to the Urticaceae family and was previously considered to belong to the Moraceae family. In Ecuador *Cecropia* has twenty eight species, five of which are endemic (Jørgensen & León-Yáñez 1999.). There

are 70-80 species throughout the Americas (Berg 1978). Gentry (1993) described the genus as one of the predominants of early regeneration, with a few species components of mature forest canopy, particularly at elevation. *Cecropia* are intermediate in height (20-35 m) with branches and stems that have hollow internodes (Berg 1978). Leaves are simple and alternate, usually palmate. Its infructescence is digitate with thick spikes arising from the uppermost leaf axils. Fruits are numerous, light yellow, brown or dark brown, glossy and various shapes. Seeds are ovoid or oblong-ovoid, light yellow or light brown and glossy. (New York Botanical Gardens 2006). The bark is grey in colour. Some species are myrmecophytic and provide a glycogen rich food at the base of the petiole. Ants nest in the hollow stems and protect the trees from competitors and phytophagous insects (Lobova et al. 2003).

This study will focus on two species of *Cecropia* encountered on the reserve. *Cecropia* species 1 was located within more sites (4 of 4) and more plots (32 of 52) than *Cecropia* sp. 2; *Cecropia* sp. 2 was located at 2 of the 4 sites and within 7 of the 52 plots. Logically there must be some reason that *Cecropia* species 2 is less spatially distributed throughout the reserve than *Cecropia* sp. 1. Given the

importance architecture and morphology play in defining an individual's position and success in the environment we believe that *Cecropia* sp. 1 will be shown to be able to utilise the light environment more efficiently than *Cecropia* sp. 2. Pioneers are renowned for investing in height at the expense of stem diameter but we believe that crucial differences will be shown with species crown formation strategies; both between species and within species between habitats. To test this we will use the following hypotheses:

### 1.11 Hypotheses

The hypotheses to be tested are:

- I. that by making intra-species comparisons over different habitats the height of the first branch of trees in old fields will be lower than the height of the first branch of trees from the same species in old-growth forest;
- II. that by making inter-species comparisons over the same habitats the trees of the *Cecropia* species 1 will have a lower first branch than the trees of *Cecropia* species 2.
- III. that intra-species comparisons over different habitats will show the crown diameter of each species to be larger in old-field than in old-growth forest;
- IV. that inter-species comparisons over the same habitats will show that the trees of *Cecropia* species 1 will have larger diameter crowns than the trees of *Cecropia* species 2.

## 2. Materials and methodology

### 2.1 Study site

All areas used for data collection were located within the Reserva Los Cedros, Imbabura province, Ecuador (Figs. 1 and 2).



Fig. 1. Map of Ecuador showing Imbabura province (No. 2).

The reserve covers approximately 6400 hectares and altitudes range between 1000 m and 2710 m. The centre of the reserve is located at approximately 0°22'30N 78°48'00W.



Fig. 2. Map of Imbabura province showing location of Los Cedros reserve.

Climate data from the reserve is not available at present. The closest meteorological station is located at Otavalo, (TVL), 0°23'00N 78°27'00W, altitude 2856 m. Average annual precipitation data was unavailable. The climate diagram (Fig 3.) shows times of high humidity mid-January to May and mid September to late November; with dry periods late November to mid January and May to mid September. Maximum rainfall occurred during April and November.

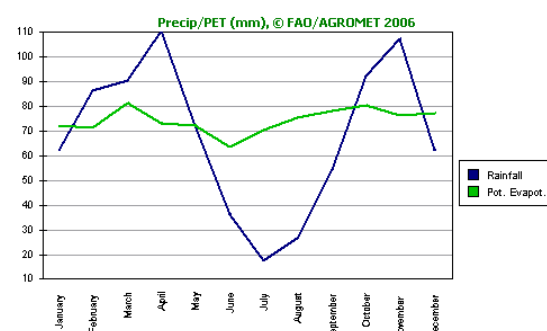


Fig 3. Otavalo precipitation map 2006 (FAO 2006)

Average temperature range is 13 - 15°C (Fig 4.)

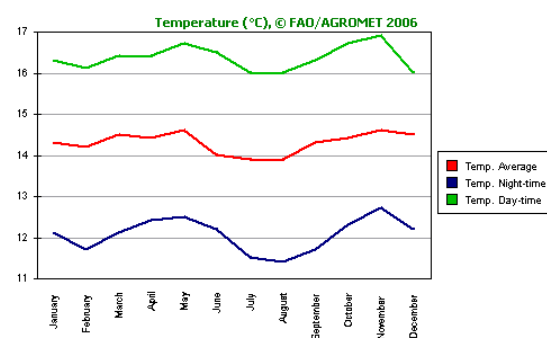


Fig 4. Otavalo temperature diagram. (FAO 2006)



The FAO-Unesco soil map of the world does not list a soil type for the area purely a lithological description; “Andean Montane formations; Jurassic-Cretaceous volcanics with some intrusives and Quaternary ashes west of the Andes” (FAO - Unesco 1971). No soil data was collected during the research.

Detailed information on past land use within the reserve was collected, through collaboration with local inhabitants, by Ana Mariscal and myself. The majority of these areas were cleared by colonists between 1978 and 1992. The information collected included: The name of the colonist, type of land use, type of grass on the pastures, the year the land was cleared and the year the land was abandoned to succession.

## 2.2. Data collection

From this information, and further investigation of the reserve, four separate study sites were identified by Ana Mariscal Chávez, the research team leader. These study sites were all situated at altitudes of between 1000 – 1500 m. Each was divided into:

- 3 sub-plots in un-cleared old-growth forest:

- each with 3 (15 m x 15 m) quadrants of:
  - closed canopy;
  - canopy gap, and
  - old canopy gap.
- 1 plot with 4 (15 m x 15 m) quadrants of old-field pasture that had previously had similar land use and grass type.

Each old field study site was divided into equal sectors and then four of these sectors were selected at random (using a series of electronically generated random numbers) for the location of the four 15 m x 15 m quadrants. The old field sites were all abandoned at similar times, circa 12 years from collection.

Each plot was given a unique three digit number to individually identify it in the format of: 2.6.5. The first number relating to the site (2), the second denoting the plot (6) and the third relating to the quadrant (5).

The following data was then collected by the research team on each individual tree with a DBH over 5 cm: estimated height of the first branch, two measurements of DBH, estimated total tree height and estimated crown width. Samples were taken from each new species encountered for identification at the National

Herbarium in Quito. My main role in this was collection of DBH measurements and samples.

It was discovered after the data collection that a slight, consistent, over-sampling of trees outside the square plots occurred. Further research was carried out by Ana and others to estimate the number.

### 2.3. Data

Two species from the family *Cecropia* were identified that were sufficiently well represented for comparison. Although not formally identified they have been separated to species. Within all the plots *Cecropia* species 1 had a total of 258 individuals present: Old-growth forest: 1 under closed canopy, 22 in regenerated canopy gaps and 4 in recent canopy gaps. Old fields: 4 in a regenerated sugar cane plantation and 227 in regenerated former grazing land. *Cecropia* species 2 had 23 individuals present in total: Within old-growth forest it had: 1 individual under closed canopy, 3 in regenerated canopy gaps and 2 in recent canopy gaps; within the old field habitat it had 17 in regenerated former grazing land.

### 2.4. Habitat division

For the all-plot comparisons all data available were used. For the purpose of better comparisons all data were grouped by distinction of old field plots or old-growth forest plots. Both species were sufficiently well represented in the old field habitat but it was necessary to investigate the old-growth forest DBH size class distributions before combining the plots

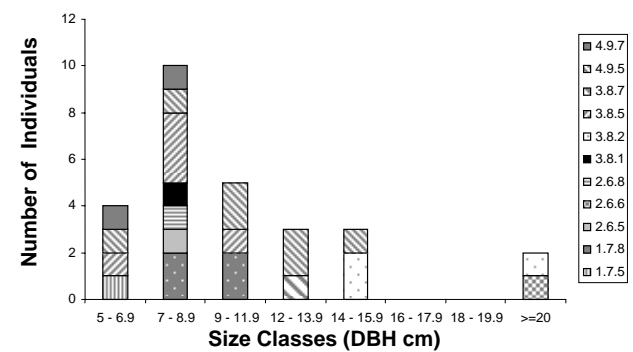


Fig. 5. Mean DBH size class distributions of *Cecropia* species 1 for all old-growth forest plots containing this species to assess distribution before combining plots.

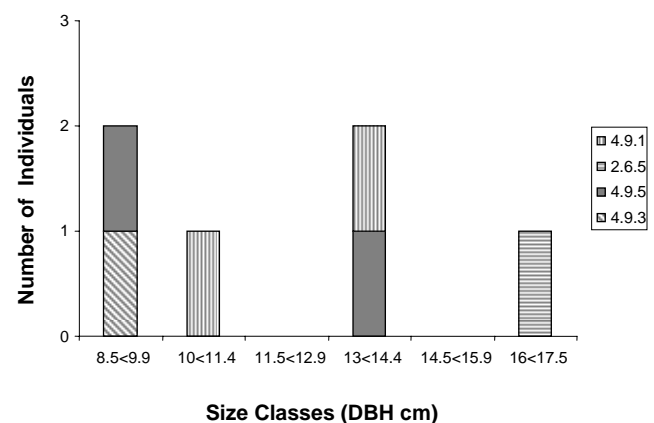


Fig. 6. Mean DBH size class distributions of *Cecropia* species 2 for all old-growth forest plots containing this species to assess distribution before combining plots.

When comparing plots for *Cecropia* sp. 1 (Fig 5.) all individuals were present with at least one other in each size class (up to 16 cm DBH).

*Cecropia* species 2 is only represented by six individuals in old-growth forest (Fig. 6). Plots 4.9.1 and 4.9.5 both contain two individuals with similar DBH's. Plot 4.9.3 matches one of 4.9.5's individuals. The individual from plot 2.6.5 in the largest size class is 3.7cm greater in diameter than the two individuals from 4.9.1 and 4.9.5.

## 2.5. Matched plots

The *Cecropia* sp. 1 population was much larger than sp. 2. To allow a more equal comparison between the two species it was necessary to only compare plots that both species were present in. *Cecropia* species 2 was present in seven plots:

- 2.5.1 OF 13 individuals;
- 2.5.2 OF 1 individuals;
- 2.5.3 OF 3 individuals;
- 2.6.5 OGF 1 individuals;
- 4.9.1 OGF 2 individuals;
- 4.9.3 OGF 1 individuals;
- 4.9.5 OGF 2 individuals.

*Cecropia* sp. 1 from these same 'matched' plots:

- 2.5.1 OF 8 individuals;
- 2.5.2 OF 22 individuals;
- 2.5.3 OF 9 individuals;
- 2.6.5 OGF 1 individuals;
- 4.9.1 OGF 0 individuals;
- 4.9.3 OGF 0 individuals;
- 4.9.5 OGF 7 individuals.

Plots 4.9.1 and 4.9.3 have zero individuals for *Cecropia* species 1. Exclusion of these plots would further reduce the *Cecropia* sp. 2 OGF data set by three individuals. It was therefore decided to keep these two plots in the matched set for sp. 2 and include plot 4.9.7, an adjacent plot which contained two individuals from sp. 1 and 0 individuals from sp. 2. Therefore, including plot 4.9.7 for *Cecropia* sp. 1, gave 39 individuals within OF and 10 individuals within OGF, 49 in total.

## 2.6. Preliminary investigations

Abundance was investigated using the two main indicators: density (number of stems per hectare) and dominance (basal area, m<sup>2</sup> per hectare). These were assessed for: all species combined, with all plots divided into old-growth forest and old-field; all species combined with the matched plots divided into old-growth forest and old-field; for *Cecropia* spp. 1 and 2 separately with all plots divided by

habitat and all matched plots divided by habitat.

Population size class distributions were investigated for DBH and tree height to gain information on the all-species data for all plots combined, and for the old-growth forest plots and the old-field plots separately. These investigations were then repeated for *Cecropia* spp. 1 and 2 for the matched plots in both habitats. Due to the sampling method (trees were selected by DBH >5 cm) trees in smaller height size classes interfered with comparison of the distributions between habitats. To remedy this only individuals > 6 m in height were included in the all species height population size class distributions.

## 2.7 Comparison of key attributes

Means for all key variables (crown width, first branch height, DBH and tree height) were compared first within species between habitats and second between species, within and between habitats: all plot data combined; all OF plot data combined; all OGF plot data combined and similarly for the matched data.

These means were then compared using individual t-tests to check for significant difference: firstly within species between

old-growth forest and old field habitats; then, between species for within habitat and between habitat variation

As an indicator of the variability within each population of the key variables their, coefficients of variation (CV) were then calculated for the same habitat conditions as means:

$$CV = \frac{\text{Standard deviation}}{\text{Mean}}$$

Further to this CV's for each variable were calculated by plot and compared using individual t-tests, as for the comparison of key attributes, to check for significant difference: firstly within species between old-growth forest and old field habitats; then, between species for within habitat and between habitat variation

In this instance we refer to allometry as changes in a specific attribute of an individual tree (or species) in relation to another attribute of that tree (or species). As a tree increases in height it needs a greater DBH to maintain stability. If, as shown by Alvarez-Buylla and Martinez-Ramos (1992) for *Cecropia obtusifolia*, these are allometrically related, then it should be possible to predict the dependent variables value by knowing the value of the independent variable; the

independent variable being that which is deemed to be the most fundamental or causal in the relationship (Healey, J.R. pers. com.).

When selecting which pairs of variables to compare it was necessary to identify that which we considered to be the dependent variable and which the independent variable. Increases in DBH are necessary to maintain the stability of trees under growth stress so the following were investigated with DBH as the independent variable: Crown height (tree height - first branch height); first branch height; crown width; tree height. Tree height was used as the independent variable with the following variables because it governed the vertical position in the light environment: crown height; crown width; first branch height. Crown height was also investigated with crown width as the independent variable. First branch height was also used as the independent variable for crown height to test the effect of a lower first branch on crown height. First branch was also used as the independent variable to test crown width as it was thought possible that the crown width may be wider with a lower first branch due to increased shade effects. Crown height, first branch height and crown width were also tested with the ratio of DBH:tree

height to assess the correlation explained above.

Initially to assess the differences between these ratios for species and habitat we followed convention (Healey, J.R. pers. com.) and divided the dependent variable by the independent variable. These resulting values were then compared in a similar manner to the key variables, using independent t-tests; comparisons were made to assess significant difference: firstly within species between old-growth forest and old field habitats; then, between species for within habitat and between habitat variation.

Linear regressions can be used to test the strength of a relationship between the dependent and independent variable by assessing whether the relationship can be described by a straight line (Hawkins, 2005). The allometric equation is normally described as:

$$Y = aX + b;$$

where  $Y$  is the dependent variable,  $X$  is the independent variable,  $a$  is the slope of the regression and  $b$  is the point where  $Y$  intercepts the vertical axis (ISCID, 2001). The regression coefficient ( $r^2$ ) can be gained from this type of analysis. This is "a measure of how much the dependent

variable varies with the independent variable" (Hawkins, 2005). The benefit of this is that it is readily understandable as a percentage: if  $r^2=0.75$ , then 75% "of the variation of the dependent variable is accounted for by the independent variable" (Hawkins, 2005).

Further to this we tested all paired variables used for linear regressions with a general linear model using species and habitat as factors to see if there were significant difference between them. This was to ensure an added robustness by comparison to the results of the regressions.

The CV of allometric relationships were further investigated using independent t-test and analysis of variance: Crown height/DBH, first branch height/DBH, crown height/tree height, crown height/crown width, crown width/DBH, crown width/tree height, tree height/DBH, first branch height/tree height, crown height/first branch height, crown width/first branch height.

It was necessary to exclude plot 2.6.5 from these comparisons as only one individual from each species was present therefore it was therefore not possible to calculate mean or standard error values. All other matched plots from this site were old fields. As 2.6.5 was regenerated

canopy gap it was not possible to add the data to another plot.

### 3. Results

#### 3.1. All species, all-plot data

The all species density and dominance was similar for both habitat types (Fig 7.).

The all-species population size class distribution for DBH in all plots shows an expected reverse J-shape curve with a steep decline in numbers as size classes increase (Fig 8a). The shape of the distribution was similar in both the old-growth forest and the old field plots (Fig 8c & e). *Cecropia* spp. 1 and 2 differ slightly between the habitat types. Within the old-growth forest both species are only present in the smallest size classes, whereas in the old-field they are spread more evenly across the DBH classes. The maximum DBH of any species within the old-growth forest was 79 cm whilst in the old fields it was 50 cm.

The pattern of height size-class distributions differs between old-growth forest and old fields habitat types (Fig. 8d & f). In both habitats the distributions for

all species show a decline in numbers with increasing size, this is much less steep than for the DBH distributions. The old fields distribution shows some evidence of bimodality between 6-12 cm and 14-16 cm.

Within the old-growth forest *Cecropia* is only present between 5 and 21 cm with one individual at 25 m. In the old field plots it is notable that *Cecropia* sp. 1 dominates the larger size classes, whereas the smaller size classes are very much dominated by the non-*Cecropia* species.

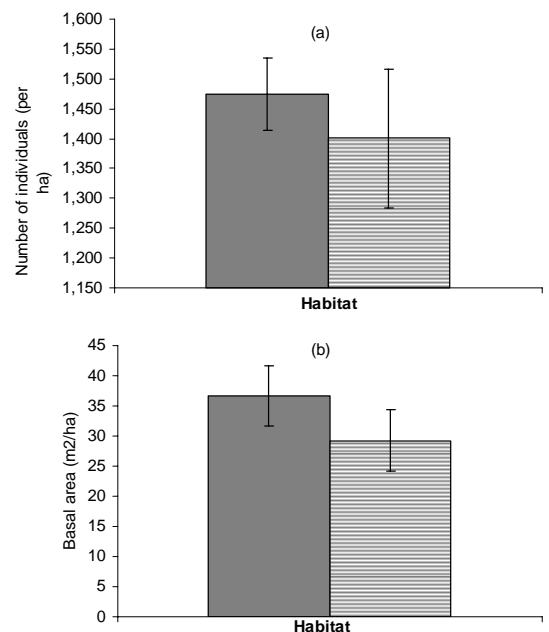


Fig 7. Stand mean density (trees per ha) (a) and mean dominance (m²/ha) (b) within both old-field (horizontal stripes) and old-growth forest plots.

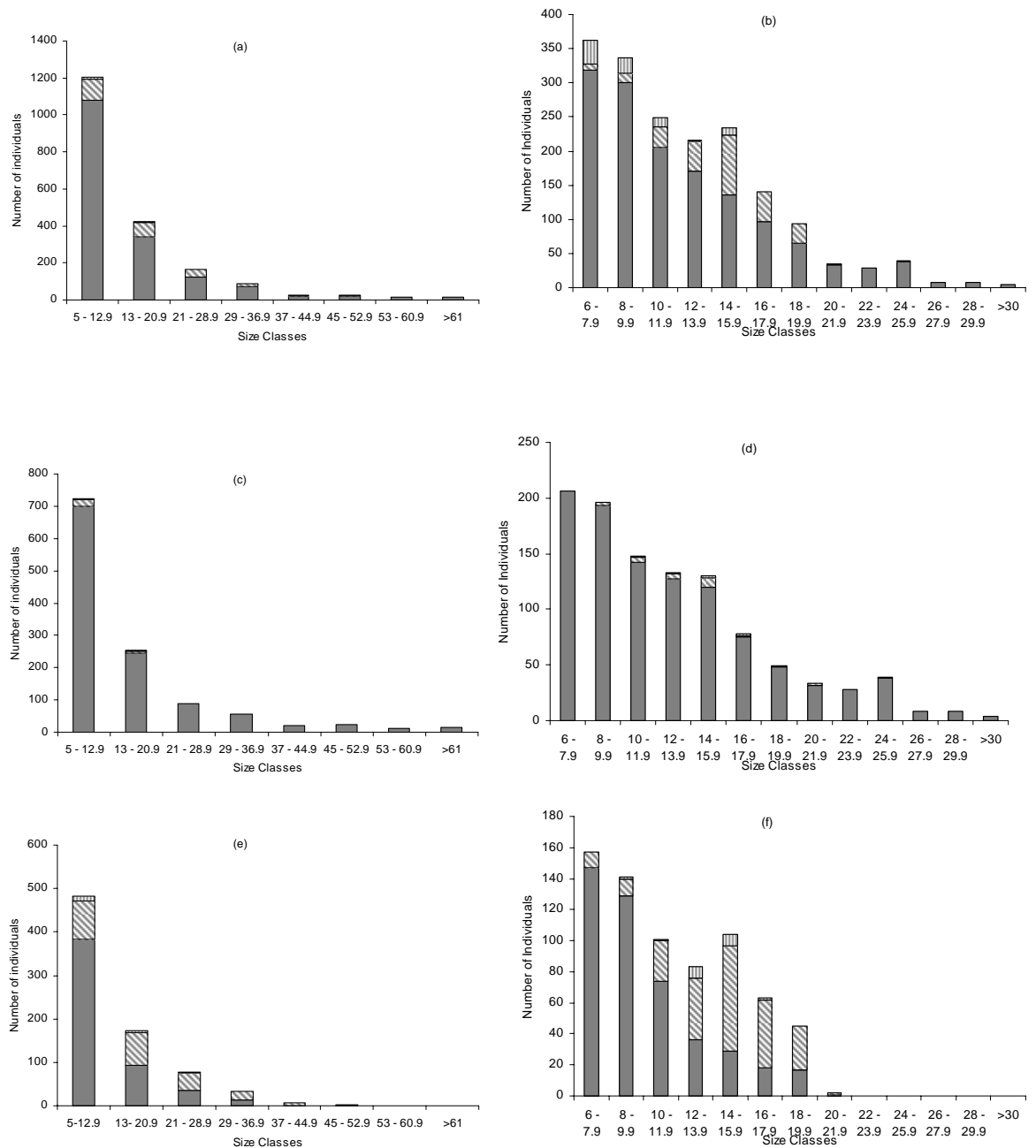


Fig 8. All plot stand size class distributions of DBH (cm) (left) and height (m) (right) for all species showing *Cecropia* spp. 1 (diagonal stripes) and 2 (vertical stripes); for all habitats (top), old-growth forest (middle) and old-fields (bottom).



### 3.2. All species, matched-plot data

*Cecropia* species 1 was present in more plots than *Cecropia* sp. 2. Therefore to enable equal comparisons between the two species it was necessary to only compare plots that both species were present in. These 'matched' plots are used for the following comparisons.

Mean abundance values calculated with the all species matched plot data were similar for density and dominance between the two habitat types (Fig. 9). The mean values were comparable to the all plot data.

As with the all-plot data, the population DBH size class distributions for all habitats old-growth forest plots and old fields (Fig. 10c & e) follow a reverse J-shape. The maximum DBH within the old-growth forest was 79 cm. whilst in the old field plots it was 36 cm. The distributions for the *Cecropia* species are comparable to those from the all plot data.

The all matched plot size-class distribution for height showed an uneven decline in numbers with increasing size (Fig. 10b). In old-growth forest alone the decline was steeper (Fig 10d), but the

distribution was markedly even in the old field plots (Fig 10 f), which had a smaller maximum height. Bimodality is again evident between 6-12 cm and 14-16 cm within both habitats. *Cecropia* is only present in the size classes between 5 and 21 m in old-growth forest. Within the old field *Cecropia* spp. clearly dominate the height classes between 12 and 18 m.

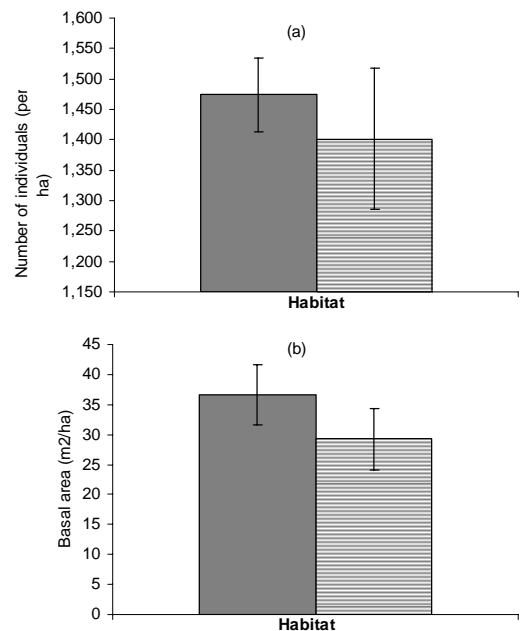


Fig 9. Stand mean density (trees per ha) (a) and mean dominance (m²/ha) (b) within both old-field (horizontal stripes) and old-growth forest matched plots.

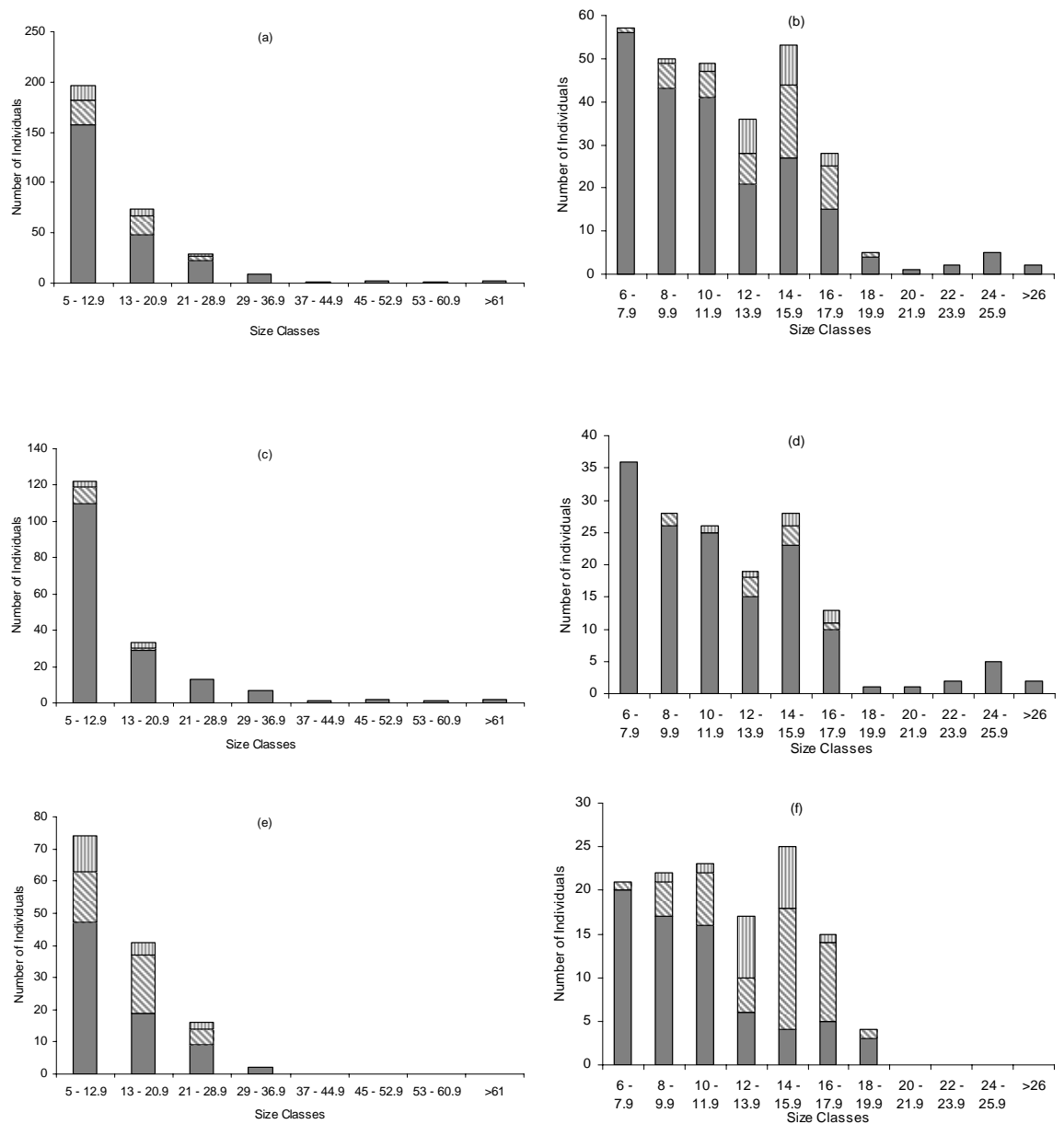


Fig. 10. Matched plot stand size class distributions of DBH (cm) (left) and Height (m) (right) for all species showing *Cecropia* spp. 1 (diagonal stripes) and 2 (vertical stripes); for all habitats (top), old-growth forest (middle) and old-fields (bottom).

### 3.3 *Cecropia* species 1 and 2

#### 3.3.1 Abundance

*Cecropia* sp. 1 had a higher density than sp. 2 in both old-growth forest and old fields (Fig. 11). The absolute density of both species was greater in the old fields than the old-growth forest.

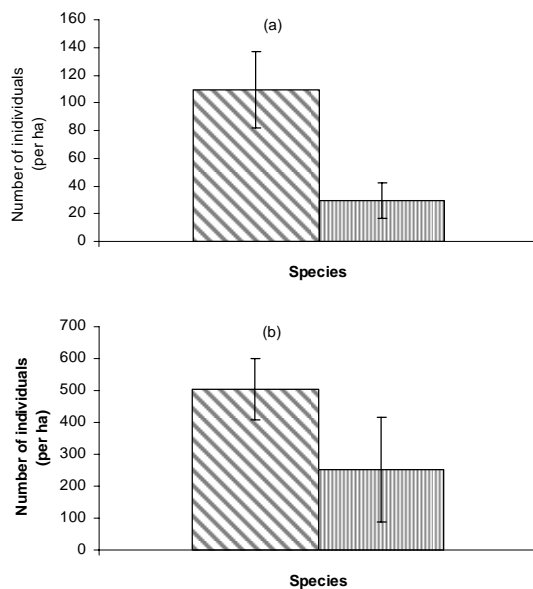


Fig. 11. Mean Density (number of individuals per ha) for *Cecropia* spp. 1 (diagonal stripes) and 2 within old-growth forest (a) and old fields (b).

Dominance within the old-growth-forest habitat was more similar between the species (Fig. 12), whereas in the old field habitat *Cecropia* sp. 1 was noticeably more dominant than *Cecropia* sp. 2.

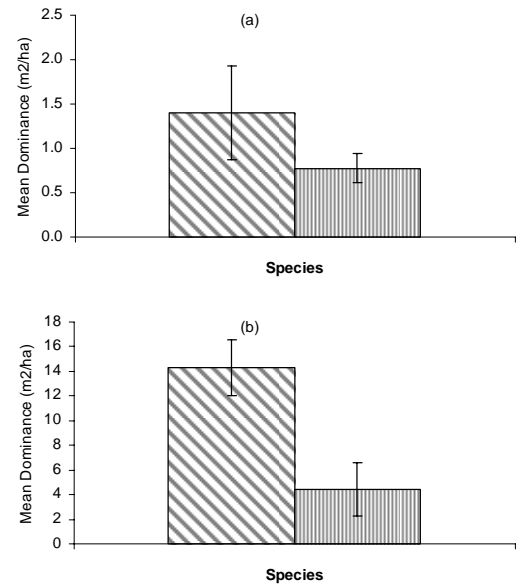


Fig.12. Mean Dominance (m²/ha) of *Cecropia* spp. 1 (diagonal stripes) and 2 within old-growth forest (a) and old field (b).

#### 3.3.2 DBH and tree height size class distributions

DBH and tree height size class diagrams were used to look at the population structure of *Cecropia* spp. 1 and 2 within the old-growth forest and old field habitats. Within the old-growth forest *Cecropia* sp. 1 was represented in all the size classes between 5 and >14 cm DBH whereas *Cecropia* sp. 2 was absent below 8 cm DBH. (Fig 13 a) The distinction was clear for height, for which *Cecropia* sp. 1 had a less even distribution. However its population did range between 4 m and >16 m, whereas *Cecropia* sp. 2 was only recorded > 10m in height (Fig. 13 b).

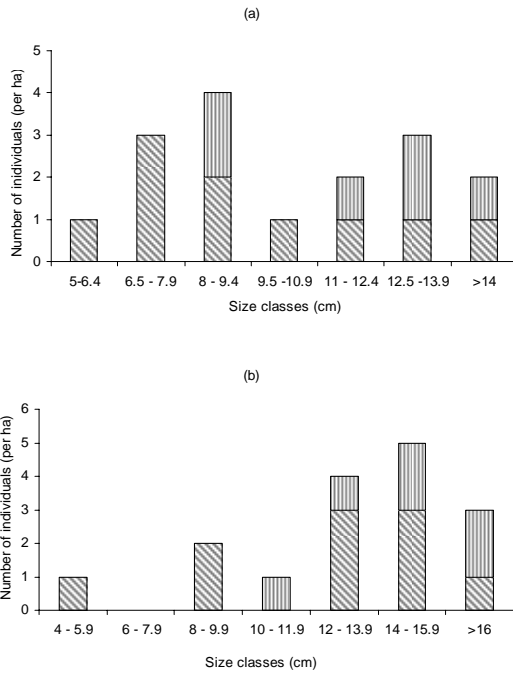


Fig 13. Population size class distributions for DBH (a) and height (b) within matched old-growth forest plots showing *Cecropia* spp. 1 (diagonal stripes) and 2 (vertical stripes).

Both species had uneven DBH distributions in the old fields with some evidence of bimodality (Fig. 14a & b) across the same range of size classes (6 - >23 cm DBH). The distributions for height showed evidence of unimodality in the old fields with a peak between 14-18 m for *Cecropia* species 1 and 12-16 m for *Cecropia* sp. 2 (Fig. 15 a & b).

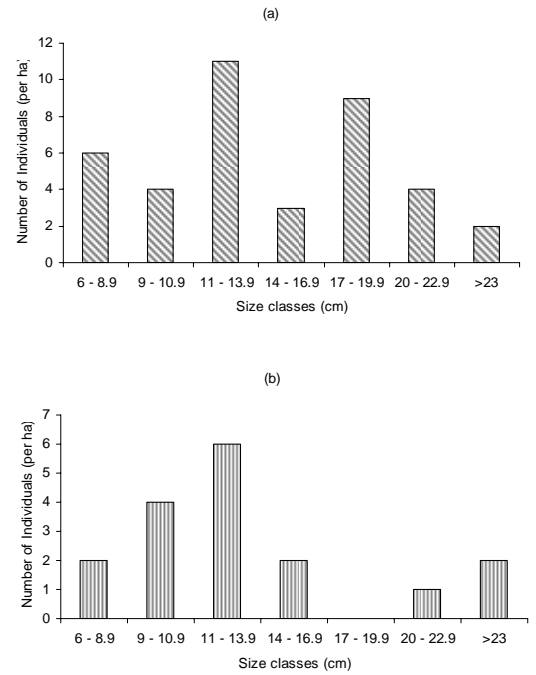


Fig 14. Population size class distributions for DBH, *Cecropia* sp. 1 (a) and *Cecropia* sp. 2 (b) within matched old-field sites

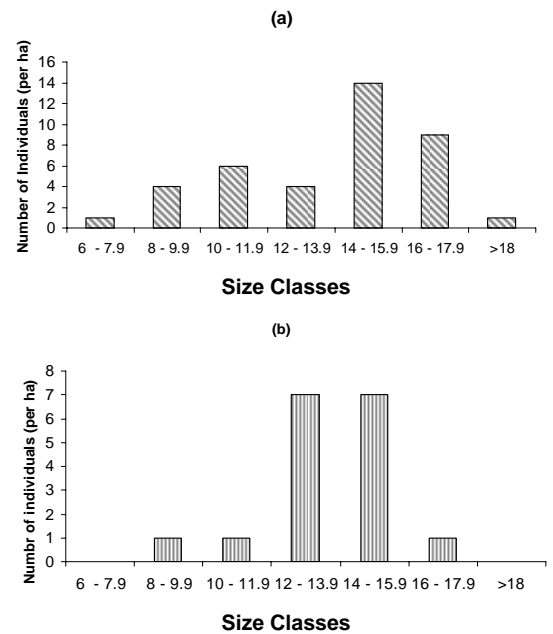


Fig 15. PSCD (Height) for *Cecropia* species 1 (a) and *Cecropia* sp. 2 (b) for matched old-field plots

### 3.4 Average dimensions

Average dimensions were compared using independent sample t-tests across all habitats and habitat combinations by species.

#### 3.4.1 DBH

For all plots DBH of species one ( $mean=16.518$ ,  $SE=0.53$ ) was greater than species two ( $mean=13.24$ ,  $SE=1.14$ );  $t(32.35)=2.60$ ,  $p=0.014$  (Fig. 16. The magnitude of the difference in the means was small to moderate (Eta squared=0.02). The same result was also found for *Cecropia* sp. 1 with the matched plots between old-growth forest ( $mean=9.23$ ,  $SE=3.05$ ) and old fields ( $mean=14.68$ ,  $SE=5.25$ );  $t(24.56)=-4.26$ ,  $p<0.0005$ . The magnitude of the difference in the means was a large effect (Eta squared = 0.3).

For *Cecropia* sp. 1 DBH was significantly less in all the old-growth forest plots ( $mean=10.9$ ,  $SE=1.31$ ) than in all the old field plots ( $mean=17.17$ ,  $SE=0.56$ );  $t(256)=-3.705$ ,  $p<0.0005$ . The magnitude of the difference in the means was small to moderate (Eta squared=0.051). This result was not confirmed with the matched data.

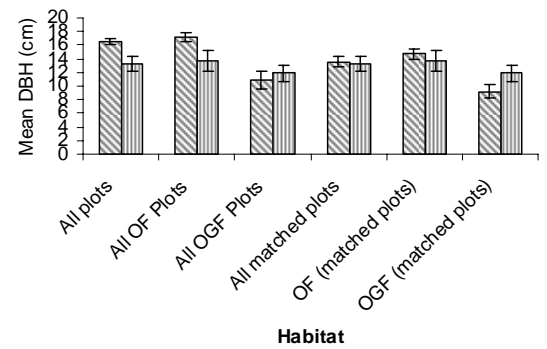


Fig. 16 Mean DBH (cm) of *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats

#### 3.4.2 First branch height

Height of the first branch in all plots was significantly less for *Cecropia* sp. 1 ( $mean=8.4$ ,  $SE=3.73$ ) than *Cecropia* sp. 2 ( $mean=11.35$ ,  $SE=3.07$ );  $t(28.13)=-4.34$ ,  $p < 0.0005$  (Fig. 17. The magnitude of the difference in the means was a moderate effect (Eta squared=0.06). The same result was found for all the matched plots between species one ( $mean=8.663$ ,  $SE=3.22$ ) and species 2 ( $mean=11.35$ ,  $SE=3.07$ );  $t(70)=-3.35$ ,  $p = 0.010$ ). The magnitude of the difference in the means was a large effect (Eta squared=0.14)

The same differences in first branch height between species were found in each habitat separately. For all old-growth forest plots, the height was lower for *Cecropia* sp. 1 ( $M=8.22$ ,  $SE=3.38$ ) than *Cecropia* sp. 2 ( $mean=11.75$ ,  $SE=4.81$ );  $t(31)=-0.336$ ,  $p=0.040$ . The magnitude of

the difference in the means was moderate to large (Eta squared=0.13) But no significant difference between the species was found for the old-growth forest matched plots.

For all the old-field plots the first branch height was lower for *Cecropia* sp. 1 ( $mean=8.42$ ,  $SE=3.77$ ) than *Cecropia* sp. 2 ( $mean=11.21$ ,  $SE=2.37$ );  $t(22.49)=-4.46$ ,  $p < 0.0005$ ). The magnitude of the difference in the means was moderate to large (Eta squared=0.07). The difference was also significant for the matched old field plots: with *Cecropia* sp. 1 ( $mean=8.5$ ,  $SE=3.17$ ) lower than *Cecropia* sp. 2 ( $mean=11.21$ ,  $SE=2.37$ );  $t(54)=-3.154$ ,  $p = 0.003$ . The magnitude of the difference in means was large (Eta squared=0.16).

Both species were markedly constant in mean first branch height between the habitats (Fig. 18) so no between habitat differences were significant.

This result was supported by analysis using a univariate general linear model (GLM) with species and habitat as factors. *Cecropia* sp. 1 ( $mean=8.66$ ,  $SE=0.46$ ) was significantly smaller than *Cecropia* sp. 2 ( $mean=11.35$ ,  $SE=0.64$ );  $F(1,65)=7.208$ ,  $p=0.009$ . The effect size was moderate to large (partial Eta squared=0.1). No

significant interaction effect was recorded between species and habitat.

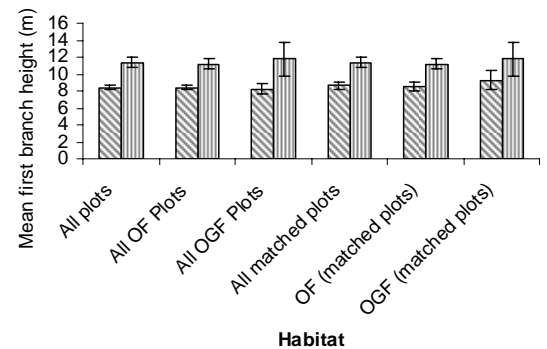


Fig. 17 Mean first branch height of *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats

### 3.4.3 Crown width

For all plots crown width was significantly greater for species one ( $mean = 3.72$ ,  $SE=2.94$ ) than for species two ( $mean=1.9$ ,  $SE=1.53$ );  $t(38.56)=4.96$ ,  $p<0.0005$ . The magnitude of the differences in the means was moderate to large (Eta squared=0.081) (Fig. 18). Similarly for all matched plots the crown width of *Cecropia* sp. 1 ( $M=2.92$ ,  $SE=2.03$ ) was significantly greater than for *Cecropia* sp. 2 ( $mean=1.9$ ,  $SE=1.53$ );  $t(55.96)=2.37$ ,  $p=0.021$ . The magnitude of the differences in the means was moderate to large (Eta squared=0.07).

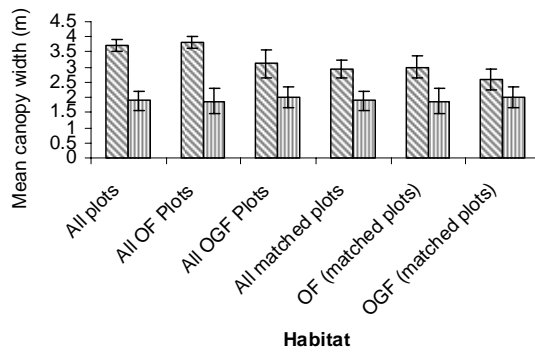


Fig. 18 Mean crown width of *Cecropia* spp. 1 (diagonal stripes) and 2 for all plots.

The crown widths of the species were then compared within habitats. There was no significant difference within old-growth forest. However within the old fields using all the plot data, *Cecropia* sp. 1 ( $mean=3.794$ ,  $SE=2.99$ ) was significantly greater than *Cecropia* sp. 2 ( $mean=1.87$ ,  $SE=1.73$ );  $t(23.77)=4.159$ ,  $p<0.0005$ . The magnitude of the differences in the means was moderate to large (Eta squared=0.07). Comparisons of the old field matched plot data showed a significant difference with *Cecropia* sp. 1 ( $mean=3.01$ ,  $SE=2.21$ ) greater than *Cecropia* sp. 2 ( $mean=1.87$ ,  $SE=1.73$ );  $t(38.67)=2.08$ ,  $p=0.045$ . The magnitude of the difference in the means was a moderate to large effect (Eta squared=0.07).

#### 3.4.4 Tree height

There were no significant differences in mean tree height between the species in

either habitat or between habitats for either species tested by independent t-tests.

Analysis with a univariate GLM contradicted these results. Tree height for *Cecropia* sp. 1 ( $mean=13.21$ ,  $SE=0.42$ ) was shown to be a significantly smaller than *Cecropia* sp. 2 ( $mean=13.478$ ,  $SE=0.441$ );  $F(1,65)=6.583$ ,  $p=0.013$  (Fig. 19). The effect size was moderate to large (partial Eta squared = 0.09). The GLM also recorded a significant interaction effect ( $F(2,65)=3.737$ ,  $p=0.029$ ) between species and habitat. The effect size was moderate to large (partial Eta squared=0.1).

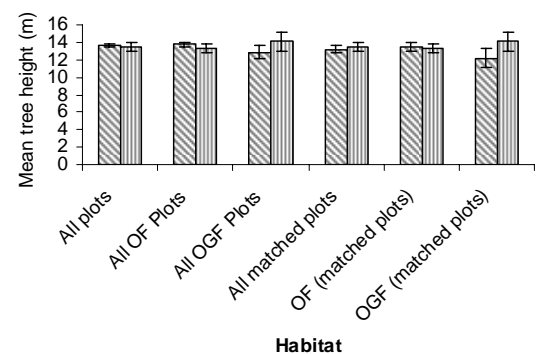


Fig. 19. Mean tree height of *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats

### 3.5 Ratios of average dimensions

#### 3.5.1 First branch height:DBH

Within the all plot data for *Cecropia* sp. 1, old-growth forest ( $mean=85.72$ ,  $SE=8.06$ ) was significantly lower than old fields

( $mean=62.02$ ,  $SE=2.59$ );  $t(256)=2.943$ ,  $p=0.004$  (Fig. 21). The magnitude of the difference in the means was small (Eta squared=0.03).

Upon investigating the all plot all data *Cecropia* sp. 1 ( $mean=85.72$ ,  $SE=8.06$ ) was significantly lower than *Cecropia* sp. 2 ( $mean=106.37$ ,  $SE=21.05$ );  $t(279)=-3.696$ ,  $p<0.0005$ . The magnitude of the difference in the means was small to moderate (Eta squared=0.05).

For the matched plots *Cecropia* sp. 1 ( $mean=73.68$ ,  $SE=5.61$ ) was significantly lower than *Cecropia* sp. 2 ( $mean=96.9$ ,  $SE=8.61$ );  $t(70)=-2.301$ ,  $p=0.024$ . The magnitude of the difference in the means was moderate to large (Eta squared=0.07).

With the all plot old fields, *Cecropia* sp. 1 ( $mean=62.02$ ,  $SE=2.59$ ) was significantly lower than *Cecropia* sp. 2 ( $mean=93.55$ ,  $SE=9.29$ );  $t(246)=-3.195$ ,  $p=0.002$ . The magnitude of the difference in the means was small to moderate (Eta squared=0.04).

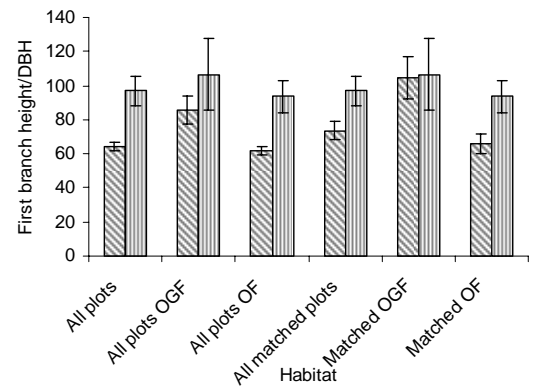


Fig. 20 Ratio of first branch height to DBH for *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats.

### 3.5.2 First branch height:tree height

For all plots the ratio of first branch height to tree height was significantly less for *Cecropia* sp. 1 ( $mean=0.63$ ,  $SD=0.01$ ) than for *Cecropia* sp. 2 ( $mean=0.83$ ,  $SD=0.03$ );  $t(31.178)=-5.550$ ,  $p<0.0005$  (Fig. 21). The magnitude of the difference in the means was moderate to large (Eta squared=0.78).

For all the matched plots *Cecropia* sp. 1 ( $mean=0.66$ ,  $SD=0.02$ ) was significantly smaller than *Cecropia* sp. 2 ( $mean=0.83$ ,  $SD=0.03$ );  $t(70)=-3.731$ ,  $p<0.0005$ . The magnitude of the difference in the means was large (Eta squared=0.17).

Within the old field plots there was significant difference with *Cecropia* sp. 1 ( $mean=0.62$ ,  $SD=0.02$ ) smaller than *Cecropia* sp. 2 ( $mean=0.84$ ,  $SD=0.03$ );



$t(28.602)=-6.993$ ,  $p<0.0005$ . The magnitude of the difference of the means was large (Eta squared= 0.17).

Between the matched old fields plots *Cecropia* sp. 1 ( $mean=0.63$ ,  $SD=0.03$ ) was significantly smaller than *Cecropia* sp. 2 ( $mean=0.84$ ,  $SE=0.03$ );  $t(3)=-5.027$ ,  $p=0.015$ . The magnitude of the difference was moderate to large (Eta squared=0.89).

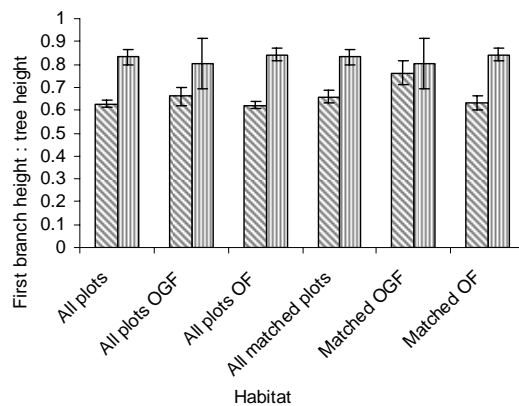


Fig. 21 Ratio of first branch height:tree height for *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats.

### 3.5.3 First branch/DBH:tree height

The all plot comparisons showed that *Cecropia* sp. 1 ( $mean=875.59$ ,  $SD=37.42$ ) was significantly less than *Cecropia* sp. 2 ( $mean=1336.20$ ,  $SD=139.34$ );  $t(279)=-3.490$ ,  $p=0.001$  (Fig 22). The magnitude of the difference in the means was small to moderate (Eta squared =0.04).

The all matched plot data showed *Cecropia* sp. 1 ( $mean=983.60$ ,  $SD=87.12$ ) to be significantly smaller than *Cecropia* sp. 2 ( $mean=1336.20$ ,  $SD=139.34$ );  $t(70)=-2.219$ ,  $p=0.030$ . The magnitude of the difference in the means was moderate to large (Eta squared=0.07).

Old field all plot investigation showed that *Cecropia* sp. 1 ( $mean=851.59$ ,  $SD=39.21$ ) was significantly less than *Cecropia* sp. 2 ( $mean=1250.28$ ,  $SD=144.79$ );  $t(246)=-2.662$ ,  $p=0.008$ . The magnitude of the difference of the means was small to moderate (Eta squared=0.03).

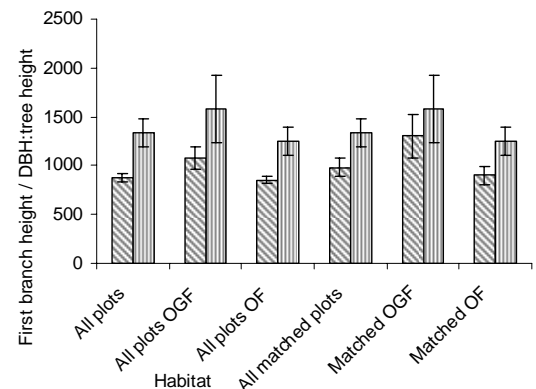


Fig. 22 Ratio of first branch height/DBH:tree height for *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats.

### 3.5.4 Crown width:DBH

Species one showed difference between habitat types for all plots, with old-growth forest ( $mean=27.62$ ,  $SD=2.33$ ) significantly larger than old fields

( $mean=20.49$ ,  $SD=0.92$ );  $t(256)=2.521$ ,  $p=0.012$  (Fig. 23). The magnitude of the difference in the means was small (Eta squared=0.02).

Species one showed significant difference between matched plot habitats with old-growth forest ( $mean=28.54$ ,  $SD=3.1$ ) larger than old-fields ( $mean=19.2$ ,  $SD=1.94$ );  $t(4)=2.848$ ,  $p=0.046$ . The magnitude of the difference in the means was moderate to large (Eta squared=0.67).

Comparing the ratio of crown width:DBH for all plots *Cecropia* sp. 1 ( $mean=21.24$ ,  $SD=0.87$ ) was significantly larger than *Cecropia* sp. 2 ( $mean=14.69$ ,  $SD=1.92$ );  $t(279)=2.192$ ,  $p=0.029$ . The magnitude of the difference in the means was small (Eta squared = 0.02).

The matched plots data echoed the all plot result with *Cecropia* sp. 1 ( $mean=21.1$ ,  $SD=1.74$ ) significantly larger than *Cecropia* sp. 2 ( $mean=14.7$ ,  $SD=1.9$ );  $t(70)=2.235$ ,  $p=0.029$ . The magnitude of the difference in the means was moderate to large (Eta squared=0.07).

For all plots old-growth forest *Cecropia* sp. 1 ( $mean=27.62$ ,  $SE=2.33$ ) was significantly larger than *Cecropia* sp. 2 ( $mean=16.82$ ,  $SE=2.4$ );  $t(31)=2.110$ ,  $p=0.043$ . The magnitude of the difference

of the means was moderate to large (Eta squared=0.13).

There was also difference within the old-growth forest matched plots with *Cecropia* sp. 1 ( $mean=28.5$ ,  $SD=3.09$ ) significantly larger than *Cecropia* sp. 2 ( $mean=16.82$ ,  $SD=2.41$ );  $t(4)=3.272$ ,  $p=0.031$ . The magnitude of the difference in the means was moderate to large (Eta squared=0.73).

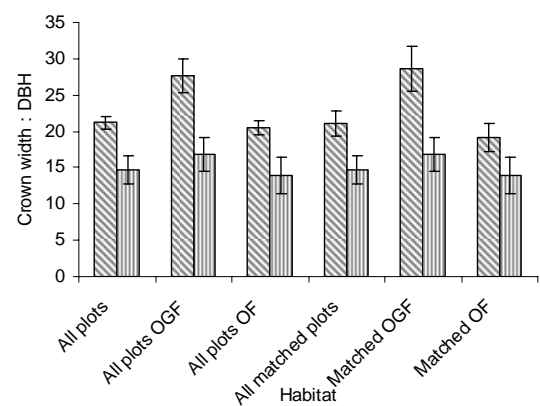


Fig. 23 Ratio of crown width to DBH for *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats.

### 3.5.5 Crown width:first branch height

*Cecropia* sp. 1 showed significant difference over all the plots with old-growth forest ( $mean=0.41$ ,  $SD=0.06$ ) larger than the old fields ( $mean=0.23$ ,  $SE=0.08$ ;  $t(245.617)=-3.418$ ,  $p=0.001$  (Fig. 24). The magnitude of the difference in the means was small to moderate (Eta squared=0.04).

Independent t-tests carried out for comparisons of crown width:first branch height for all plots showed *Cecropia* sp. 1

( $mean=0.83$ ,  $SD=0.11$ ) to be significantly greater than *Cecropia* sp. 2 ( $mean=0.19$ ,  $SD=0.03$ );  $t(278.926)=5.425$ ,  $p<0.0005$ . The magnitude of the difference in the means was low (Eta squared=0.1).

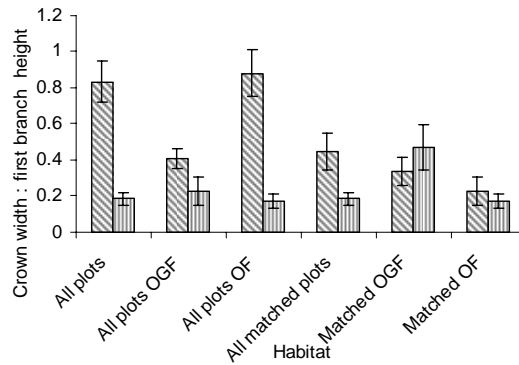


Fig. 24 Ratio of crown width: first branch height for *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats.

### 3.5.6 Crown width:tree height

The comparisons of crown width:height for all plots showed that within old fields *Cecropia* sp. 1 ( $mean=0.26$ ,  $SD=0.01$ ) was significantly larger than *Cecropia* sp. 2 ( $mean=0.14$ ,  $SD=0.02$ );  $t(23.454)=4.062$ ,  $p<0.0005$  (Fig. 25).

. The magnitude of the difference in the means was moderate (Eta squared=0.06).

Between all the matched plots *Cecropia* sp. 1 ( $mean=0.22$ ,  $SD=0.02$ ) was significantly larger than *Cecropia* sp. 2 ( $mean=0.14$ ,  $SD=0.02$ );  $t(56.539)=2.651$ ,  $p=0.010$ . The magnitude of the difference between the means was moderate to large (Eta squared=0.09).

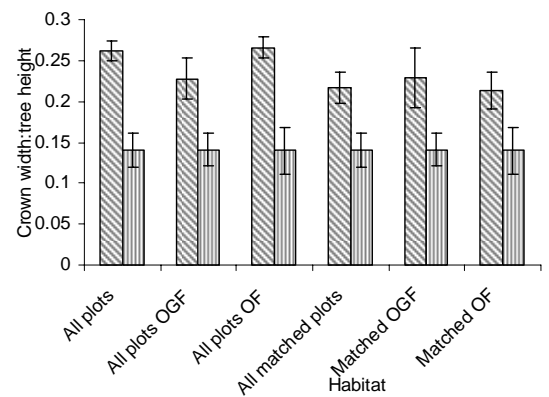


Fig. 25. Ratio of Crown width:tree height for *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats.

### 3.5.7 Crown width/DBH:tree height

The relationship between crown width/DBH:tree height was compared using individual t-tests.

The all plots all data showed *Cecropia* sp. 1 ( $mean=300.27$ ,  $SD=12.58$ ) to be larger than *Cecropia* sp. 2 ( $mean=201.94$ ,  $SD=30.72$ );  $t(279)=2.279$ ,  $p=0.023$ . The magnitude of the difference in the means was small to moderate (Eta squared = 0.02) (Fig. 26).

Old fields comparisons for all plots showed *Cecropia* sp. 1 ( $mean=292.35$ ,  $SD=13.22$ ) to be significantly greater than *Cecropia* sp. 2 ( $mean=186.14$ ,  $SD=37.63$ );  $t(246)=2.132$ ,  $p=0.034$ . The magnitude of the difference in the means was small (Eta squared=0.02).

These results were not supported by the matched data.

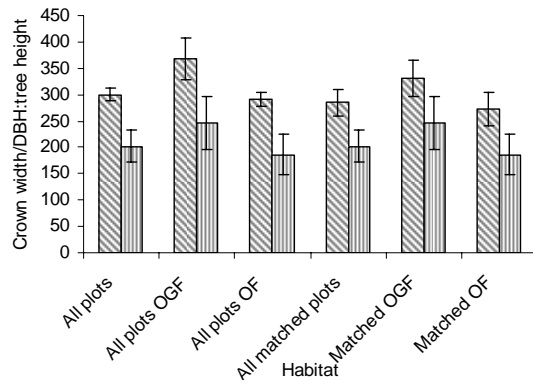


Fig. 26 Ratio of crown width / to DBH:tree height for *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats.

### 3.5.8 Crown height:DBH

Independent t-tests were again used to compare species and habitat.

For all plot comparisons of species: *Cecropia* sp. 1 ( $mean=32.61$ ,  $SE=1.42$ ) was considerably larger than *Cecropia* sp. 2 ( $mean=17.33$ ,  $SE=3.27$ );  $t(279)=3.152$ ,  $p=0.002$  but the magnitude of the difference in the means was small to moderate (Eta squared =0.03) (Fig. 27). This was supported when comparing all the matched plots *Cecropia* sp. 1 ( $mean=34.88$ ,  $SE=3.17$ ) was significantly larger than *Cecropia* sp. 2 ( $mean=17.33$ ,  $SE=3.27$ );  $t(70)=3.410$ ,  $p=0.001$ . The magnitude of the difference in the means was a large effect (Eta squared=0.14).

Within the old-field plots the ratio of crown height:DBH *Cecropia* sp. 1 ( $mean=31.28$ ,  $SD=1.38$ ) was significantly larger than *Cecropia* sp. 2 ( $mean=16.65$ ,  $SE=3.54$ );  $t(246)=2.825$ ,  $p=0.005$ . The magnitude of the difference in the means was small to moderate (Eta squared=0.03). Again for the old field matched plots *Cecropia* sp. 1 ( $mean=35.82$ ,  $SE=3.41$ ) was significantly larger than *Cecropia* sp. 2 ( $mean=16.65$ ,  $SE=3.54$ );  $t(3)=6.663$ ,  $p=0.007$ . The magnitude of the difference in the means was moderate to large (Eta squared=0.94) (Fig 20).

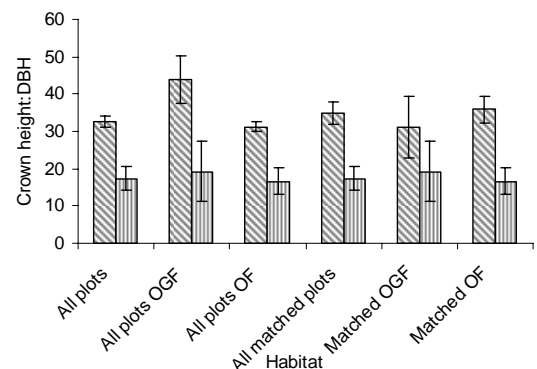


Fig. 27 Ratio of crown height to DBH for *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats.

### 3.5.9 Crown height:first branch height

For crown height:first branch height all plots showed a significant difference, with *Cecropia* sp. 1 ( $mean=1.48$ ,  $SD=0.22$ ) larger than *Cecropia* sp. 2 ( $mean=0.31$ ,  $SD=0.13$ );  $t(200.645)=4.558$ ,  $p<0.0005$

(Fig. 28). The magnitude of the difference in the means was moderate to large (Eta squared= 0.07).

The all plot old field comparisons showed *Cecropia* sp. 1 ( $mean=1.57$ ,  $SD=0.25$ ) to be significantly larger than *Cecropia* sp. 2 ( $mean=0.22$ ,  $SD=0.05$ );  $t(243.179)=5.348$ ,  $p<0.0005$ . The magnitude of the difference in the means was moderate to large (Eta squared=0.10).

These were not echoed by matched plot analyses.

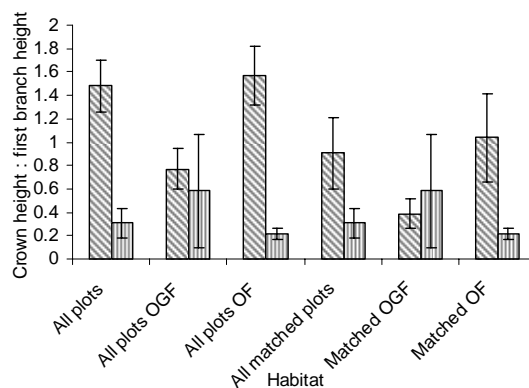


Fig. 28 Ratio of crown height: first branch height for *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats.

### 3.5.10 Crown height: tree height

For all plots combined *Cecropia* sp. 1 ( $mean=0.37$ ,  $SE=0.01$ ) was significantly larger than *Cecropia* sp. 2 ( $mean=0.17$ ,  $SE=0.03$ );  $t(31.178)=5.550$ ,  $p<0.0005$  (Fig. 29). The magnitude of the difference

in the means was small (Eta squared=0.1). The all plots result was confirmed by the matched plot data: *Cecropia* sp. 1 ( $mean=0.34$ ,  $SE=0.03$ ) was significantly larger than *Cecropia* sp. 2 ( $mean=0.17$ ,  $SE=0.03$ );  $t(70)=3.731$ ,  $p<0.0005$ . The magnitude of the difference in the means was large (Eta squared=0.17).

The all plot old fields comparisons showed *Cecropia* sp. 1 ( $mean=0.38$ ,  $SE=0.02$ ) to be significantly greater than *Cecropia* sp. 2 ( $mean=0.16$ ,  $SE=0.03$ );  $t(28.602)=6.993$ ,  $p<0.0005$ . The magnitude of the difference in the means was large (Eta squared=0.16). Old fields matched plots also showed that *Cecropia* sp. 1 ( $mean=0.37$ ,  $SE=0.03$ ) was significantly larger than *Cecropia* sp. 2 ( $mean=0.16$ ,  $SE=0.03$ );  $t(3)=5.027$ ,  $p=0.015$ . The magnitude of the difference in the means was moderate to large (Eta squared=0.89).

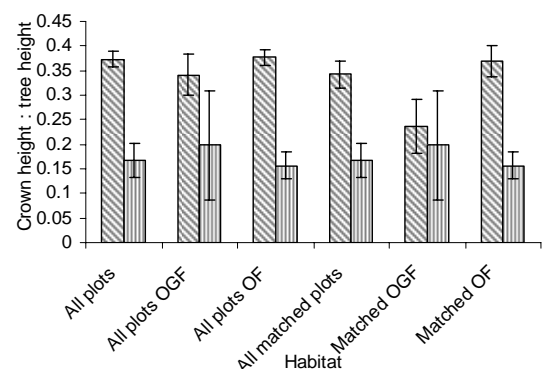


Fig. 29 Ratio of crown height to tree height for *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats.

### 3.5.11 Crown height/DBH:tree height

Comparisons of all plots showed *Cecropia* sp. 1 ( $mean=456.06$ ,  $SD=21.93$ ) was higher than *Cecropia* sp. 2 ( $mean=224.15$ ,  $SD=38.90$ );  $t(37.877)=5.193$ ,  $p<0.0005$ . The magnitude of the difference in the means was moderate to large (Eta squared = 0.09) (Fig. 30). The all matched plot comparisons agreed that *Cecropia* sp. 1 ( $mean=464.53$ ,  $SD=45.27$ ) was greater than *Cecropia* sp. 2 ( $mean=224.15$ ,  $SD=38.9$ );  $t(66.246)=4.027$ ,  $p<0.0005$ . Magnitude of the difference in the means was large (Eta squared=0.19).

Within the all plot old fields *Cecropia* sp. 1 ( $mean=591.52$ ,  $SD=94.68$ ) was larger than *Cecropia* sp. 2 ( $mean=240.77$ ,  $SD=77.8$ );  $t(246)=2.737$ ,  $p=0.007$ . The magnitude of the difference in the means was small (Eta squared=0.03). Between the matched old fields *Cecropia* sp. 1 ( $mean=485.26$ ,  $SD=50.03$ ) was also larger than *Cecropia* sp. 2 ( $mean=218.28$ ,  $SD=46.25$ );  $t(3)=7.216$ ,  $p=0.005$ . The magnitude of the difference was moderate to large (Eta squared=0.95).

There were no significant results for the old-growth forest habitats.

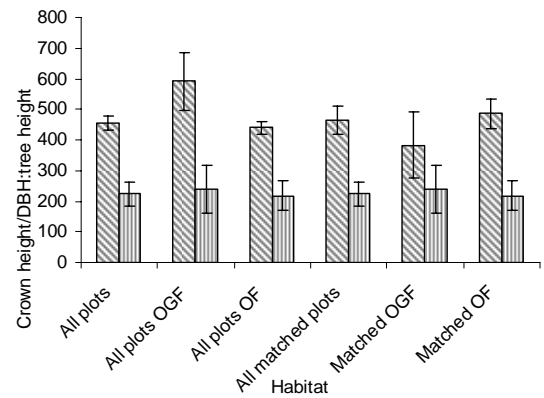


Fig. 30 Ratio of crown height/DBH:tree height for *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats.

### 3.5.12 Tree height:DBH

All plots *Cecropia* sp. 1 showed the ratio in old-growth forest ( $mean=129.7$ ,  $SD=7.03$ ) to be significantly larger than old fields ( $mean=93.3$ ,  $SD=2.43$ );  $t(256)=4.855$ ,  $p<0.0005$ . The magnitude of the difference of the means was moderate to large (Eta squared=0.08).

Comparisons between all plots for height:DBH showed *Cecropia* sp. 1 ( $mean=97.11$ ,  $SD=2.39$ ) to be significantly smaller than *Cecropia* sp. 2 ( $mean=114.22$ ,  $SD=8.1$ );  $t(279)=-2.044$ ,  $p=0.042$ . The magnitude of the difference between the means was only a small effect (Eta squared = 0.01) (Fig. 31).

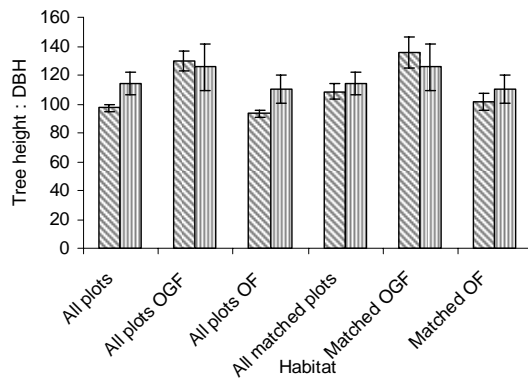


Fig. 31 Ratio of tree height:DBH for *Cecropia* spp. 1 (diagonal stripes) and 2 for all habitats.

### 3.6 Linear Regressions

#### 3.6.1 First branch height/DBH

There was no significant correlation between tree first branch height and DBH for either species in either habitats (Fig. 32).

This was partially supported by analysis with a univariate GLM as there was found to be significant difference between habitats: Old-growth forest ( $mean=105.19$ ,  $SE=10.736$ ) was greater than old fields ( $mean=74.21$ ,  $SE=5.11$ );  $F(1,68)=5.202$ ,  $p=0.03$ . The effect size was moderate to large (partial Eta squared=0.071). There were no significant interaction effects between species and habitat.

#### 3.6.2 First branch height/tree height

For the height of first branch by height all results were significantly positively correlated. *Cecropia* sp. 1 within old-growth forest ( $r^2=68.9\%$ ,  $p=0.003$ ) and old fields ( $r^2=28.4\%$ ,  $p<0.0005$ ). *Cecropia* sp. 2 within old-growth forest ( $r^2=87.4\%$ ,  $p=0.006$ ) and old fields ( $r^2=61.8\%$ ,  $p<0.0005$ ) (fig. 33).

Again analysis using species and habitat as factors for a univariate GLM found significant difference between *Cecropia* sp. 1 ( $mean=0.66$ ,  $SE=0.03$ ) and *Cecropia* sp. 2 ( $mean=0.83$ ,  $SE=0.03$ );  $F(1,68)=5.424$ ,  $p=0.023$ ). The effect size was moderate to large (partial Eta squared=0.074). There were no significant interaction effects between species and habitat.

#### 3.6.3 First branch/DBH:tree height

For first branch by DBH:tree height *Cecropia* sp. 1 showed significant correlation within old-growth forest ( $r^2=70.1\%$ ,  $p=0.015$ ) and old fields ( $r^2=37.8\%$ ,  $p<0.0005$ ). *Cecropia* sp. 2 also showed significant correlation over both habitats: old-growth forest ( $r^2=88.4\%$ ,  $p=0.039$ ) and old fields ( $r^2=62.6\%$ ,  $p=0.001$ )

The use of a univariate GLM with habitat and species as factors found that old-

growth forest ( $mean=1406.66$ ,  $SE=185.37$ ) was significantly different than the old fields habitat ( $mean=1007.55$ ,  $SE=79.34$ );  $F(1,68)=3.988$ ,  $p=0.05$ . The effect size was small to moderate (partial Eta squared=0.06). There were no significant interaction effects between species and habitat.

### 3.6.4 Crown width/DBH

The populations of *Cecropia* sp. 1 showed a significant positive correlation between crown width and DBH in the old fields ( $r^2=47.4\%$ ,  $p=0.028$ ) and old-growth forest ( $r^2=47\%$ ,  $p<0.0005$ ). The population of *Cecropia* sp. 2 showed no significant correlation in either habitat (Fig. 34).

Investigations using a univariate GLM with species and habitat and factors showed *Cecropia* sp. 1 ( $mean=21.1$ ,  $SE=1.74$ ) to be significantly different to *Cecropia* sp. 2 ( $mean=14.69$ ,  $SE=1.92$ );  $F(1,68)=6.738$ ,  $p=0.012$ ) in the ratio of crown width: DBH. The effect size was moderate to large (partial Eta squared=0.09). There was no significant interaction effect between species and habitat.

### 3.6.5 Crown width/first branch height

There were no significant correlation results for crown width and first branch height for either species or habitat.

### 3.6.6 Crown width/tree height

*Cecropia* sp. 1 within the old fields had a significantly positive correlation between crown width and tree height ( $r^2=27.6\%$ ,  $p=0.001$ ). The correlations for old-growth forest were insignificant as was *Cecropia* sp. 2 old fields (Fig. 35).

### 3.6.7 Crown width/DBH:tree height

For crown width by DBH:tree height *Cecropia* sp. 1 showed significant correlation over both habitats: old-growth forest ( $r^2=62.2\%$ ,  $p=0.033$ ) and old fields ( $r^2=52.6\%$ ,  $p<0.0005$ ). The correlation was not significant for *Cecropia* sp. 2 in either habitat.

### 3.6.8 Crown height/DBH

*Cecropia* sp. 1 showed a significant positive correlation between tree crown height and DBH in its old-field population ( $r^2=22\%$  with  $p=0.003$ ). The correlation between crown height and DBH was not significant for *Cecropia* sp. 2 in either habitat (Fig. 36).



### 3.6.9 Crown height/First branch height

There was significant negative correlation between crown height and first branch height for all species and habitats except *Cecropia* sp. 1 within old-growth forest; *Cecropia* sp. 1 within old fields ( $r^2=34.8\%$ ,  $p<0.0005$ ) and *Cecropia* sp. 2 old-growth forest ( $r^2=88\%$ ,  $p=0.006$ ) and old fields ( $r^2=30.1\%$ ,  $p=0.023$ ) (Fig. 37).

### 3.6.10 Crown height/tree height

The population of *Cecropia* sp. 1 in the old fields had a significantly positive correlation between crown height and tree height ( $r^2=13.6\%$ ,  $p=0.021$ ). The regression was not significant in the old-growth forest or for *Cecropia* sp. 2 in the old fields (fig. 38).

Significant difference was shown between species with a univariate GLM using species and habitat as factors: *Cecropia* sp. 1 ( $mean=34.22$ ,  $SE=0.03$ ) was shown to be greater than *Cecropia* sp. 2 ( $mean=0.17$ ,  $SE=0.03$ ); ( $F= (1,68)=5.424$ ,  $p=0.023$ ). The effect size was moderate to large (partial Eta squared=0.07). There were no significant interaction effects between species and habitat.

### 3.6.11 Crown height/crown width

The old fields population of *Cecropia* sp. 1 showed a significant positive correlation between crown height and crown width ( $r^2=13.5\%$ ,  $p=0.021$ ). The correlation was not significant in the old-growth forest or for *Cecropia* sp. 2 in the old fields (Fig. 39).

### 3.6.12 Crown height/DBH:tree height

Only *Cecropia* sp. 1 in old fields showed a significant correlation for crown height with DBH:tree height ( $r^2=25\%$ ,  $p=0.006$ ).

Analysis using species and habitat as independent factors in a univariate GLM *Cecropia* sp. 1 ( $mean=464.53$ ,  $SE=45.27$ ) was shown to be a significantly different from *Cecropia* sp. 2 ( $mean=224.15$ ,  $SE=38.90$ );  $F(1,68)=0.018$ ,  $p=0.018$ . The effect size was moderate to large (partial Eta Squared=0.08). Again there were no significant interaction effects between species and habitat.

### 3.6.13 Tree height/DBH

The regressions showed significant positive correlation for *Cecropia* sp. 1 old-growth forest ( $r^2=51.9\%$ ,  $p=0.019$ ) and old fields ( $r^2=21.1\%$ ,  $p=0.003$ ).

There were no significant correlations for *Cecropia* sp. 2 in either habitat (Fig. 40).

### 3.7 Within-population variability of dimensions

#### 3.7.1 Coefficient of variation comparisons.

Comparisons of each variables coefficient of variation between the two species for each habitat and between the two habitats for each species gave no significant differences with t-tests

To further explore the within-population variability of the measured tree dimensions, one-way between groups analysis of variances were conducted.

With DBH as the dependent variable there was a statistically significant difference for species and habitat ( $F(3,5)=8.2$ ,  $p=0.022$ ) (Fig. 41). The effect size calculated using Eta squared was moderate to large, 0.8. Post-hoc comparisons using the Tukey HSD showed that the population of *Cecropia* sp. 2 in old-growth forest ( $CV=25.62\%$ ) had a significantly lower coefficient of variation for its DBH than the populations of both *Cecropia* sp. 1 ( $CV=33.03\%$ ,  $p=0.033$ )

and *Cecropia* sp. 2 ( $CV=44.68\%$ ,  $p=0.022$ ) in the old fields.

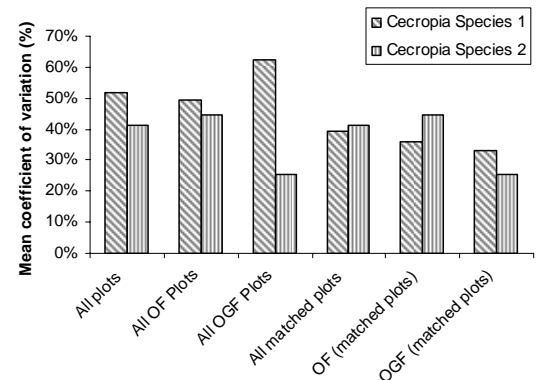


Fig. 41. Coefficient of variation of DBH for both *Cecropia* spp. within all habitat types.

Although there was no significant difference in the coefficient of variation for crown width the level was still considerable for most species and habitats (Fig. 42). *Cecropia* species 1 had a maximum CV of 78.86% within all plots and a minimum of 42.33% within the old-growth forest matched plots. *Cecropia* species 2 had a maximum CV of 92.24% within the old field plots and a minimum of 41.84% within the old-growth forest plots.

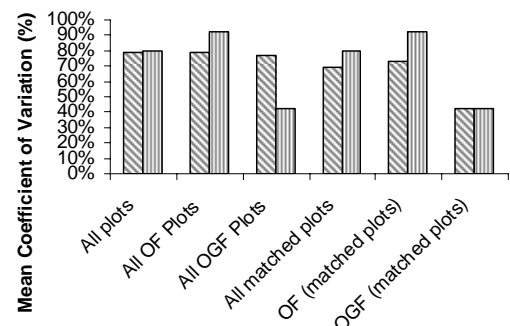


Fig. 42. Coefficient of variation of crown width for *Cecropia* spp. 1 (diagonal stripes) and 2 within all habitat types.

Again there was no significant difference between the CV's for first branch height (Fig. 43) *Cecropia* species 1 had a maximum CV of 44.78% within all plots and a minimum of 37.11% within all matched plots. *Cecropia* species 2 had a maximum CV of 40.97% within the old-growth forest plots and a minimum of 21.11% within the old field plots.

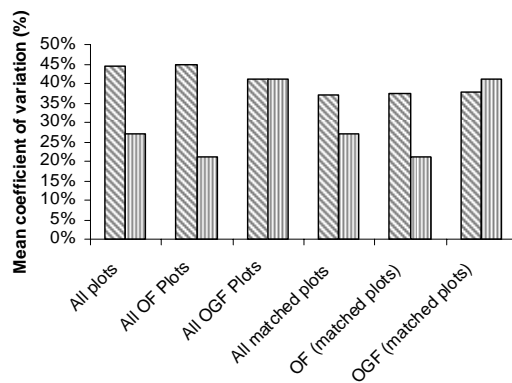


Fig 43. Coefficient of variation of first branch height for *Cecropia* spp.1 (diagonal stripes) and 2 within all habitat types.

### 3.7.2 Variability of attribute ratios

Due to variation in age and size of trees straight comparisons of measurements are not ideal. The results will be biased towards those trees with larger attributes i.e. older trees or faster growing species. Analysing ratios of variables (e.g. tree height/DBH) allow for comparisons that are independent of age and size.

Coefficients of variation of the ratios between measured dimensions were compared using the matched plots between populations with independent t-tests for species and habitat.

In the old fields matched plots the coefficient of variation for crown height:tree height was significantly less for *Cecropia* sp. 1 ( $CV=0.51$  (51%)) than for *Cecropia* sp. 2 ( $CV=0.70$  (70%));  $t(3)=-3.481$ ,  $p = 0.04$  (Fig. 44). The magnitude of the differences in the means was moderate to large (Eta squared=0.8).

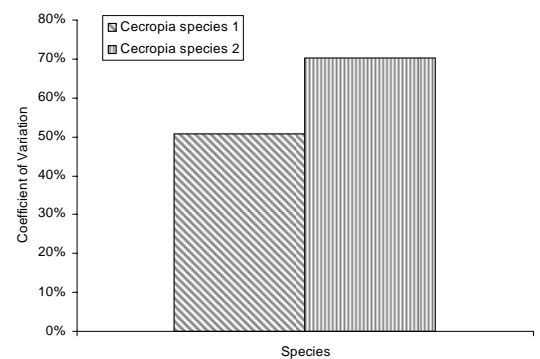


Fig. 44. Coefficient of variation of crown height:tree height for *Cecropia* spp. 1 and 2 old fields.

Also in the old fields the coefficient of variation for first branch height:tree height was significantly greater for *Cecropia* sp. 1 ( $CV=0.31$  (31%)) than for *Cecropia* sp. 2 ( $CV=0.14$  (14%));  $t(3)=4$ ,  $p=0.028$  (Fig 45). The magnitude of the difference in the means was again moderate to large (Eta squared=0.8).

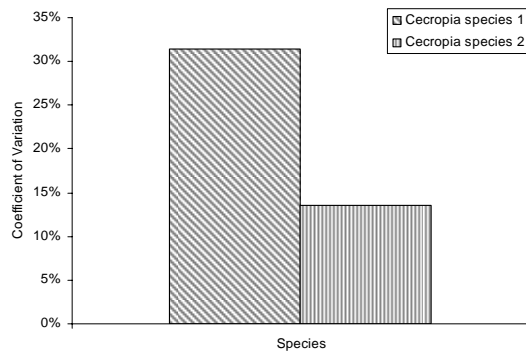


Fig. 45. Coefficient of variation of first branch height:tree height for *Cecropia* spp. 1 and 2 old fields.

For *Cecropia* sp. 2 the coefficient of variation for crown width:tree height was significantly greater in the old field ( $CV=0.47$  (47%)) than the old-growth

forest ( $CV=0.17$  (17%)) populations:  $t(1.67)=-5.219$ ,  $p=0.05$  (Fig. 46). The magnitude of the difference in the means was moderate to large (Eta squared=0.9).

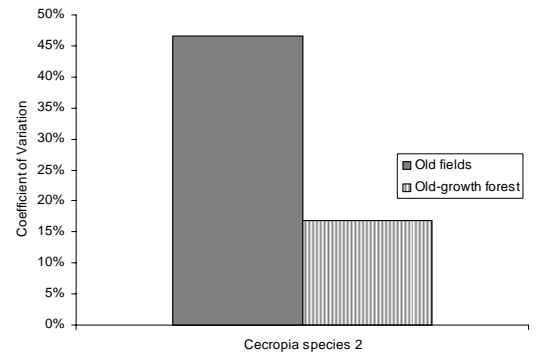


Fig. 46. Coefficient of variation for crown width:tree height for *Cecropia* sp. 2 old fields and old-growth forest.

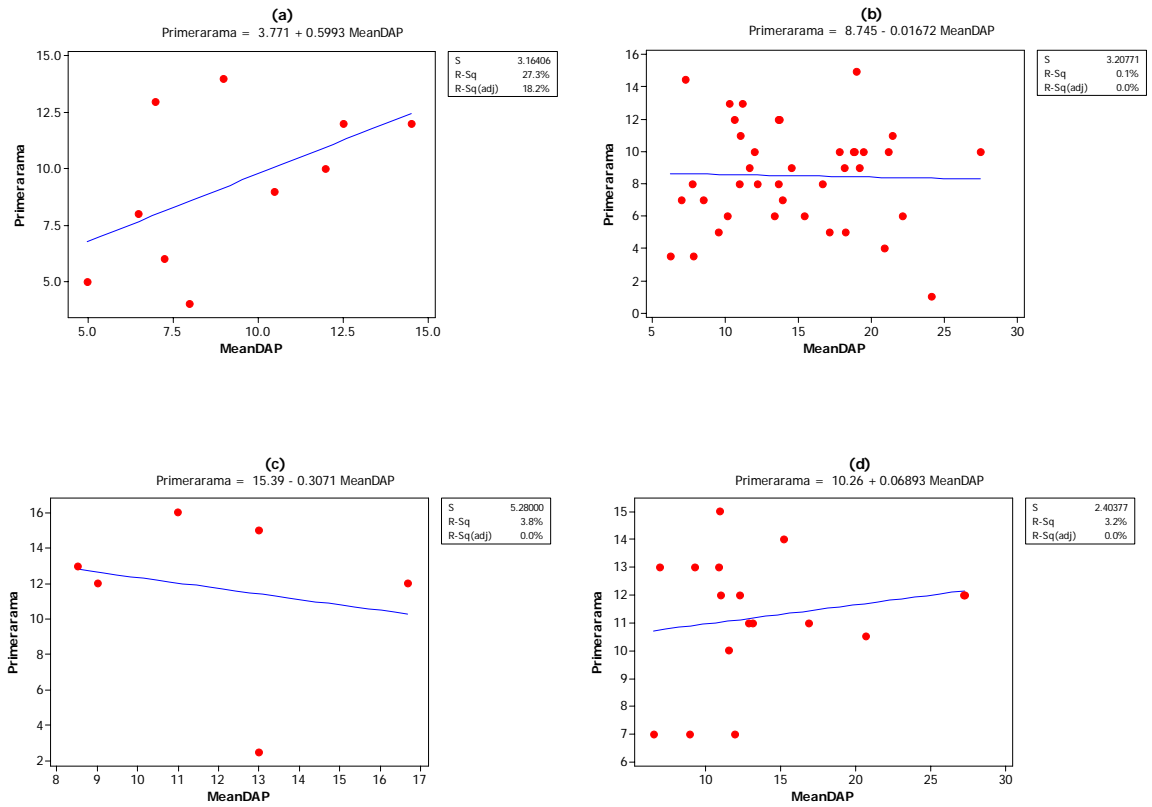


Fig. 32. Linear regressions of first branch height/DBH for *Cecropia* species 1 old-growth forest (a), old fields (b), *Cecropia* species 2 old-growth forest (c) and old-fields (d)

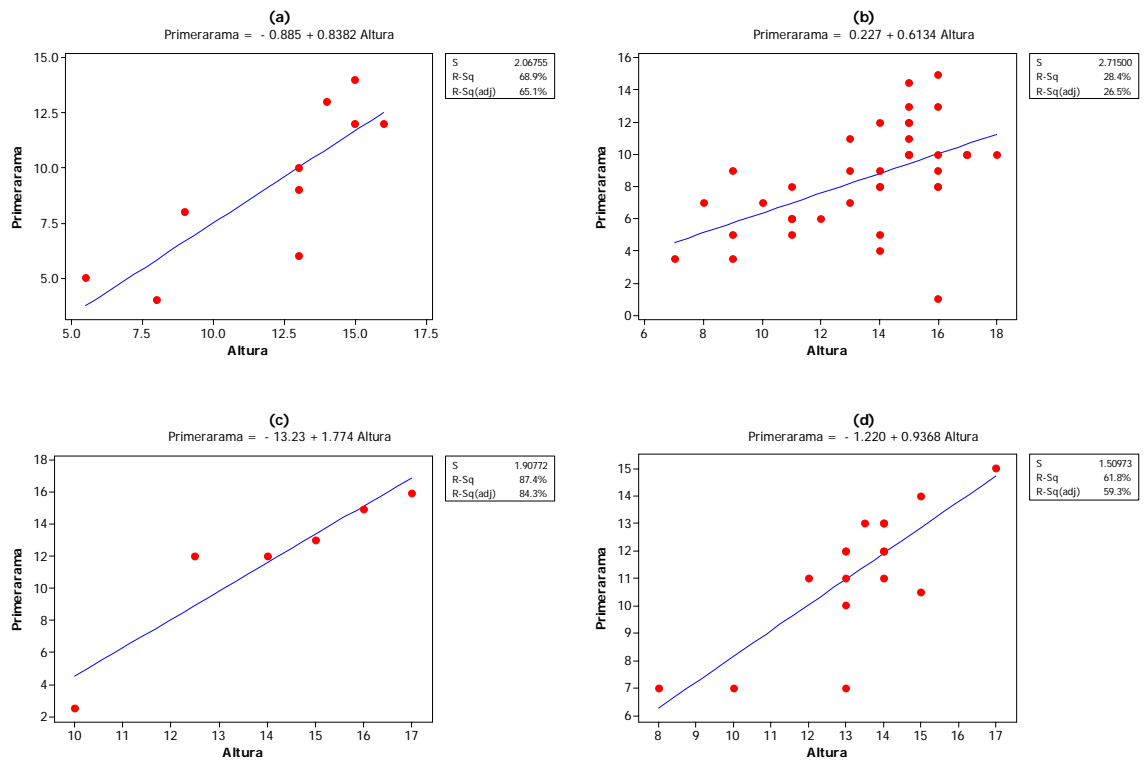


Fig. 33 Linear regressions of first branch height/tree height for *Cecropia* species 1 old-growth forest (a), old fields (b), *Cecropia* species 2 old-growth forest (c) and old-fields (d)

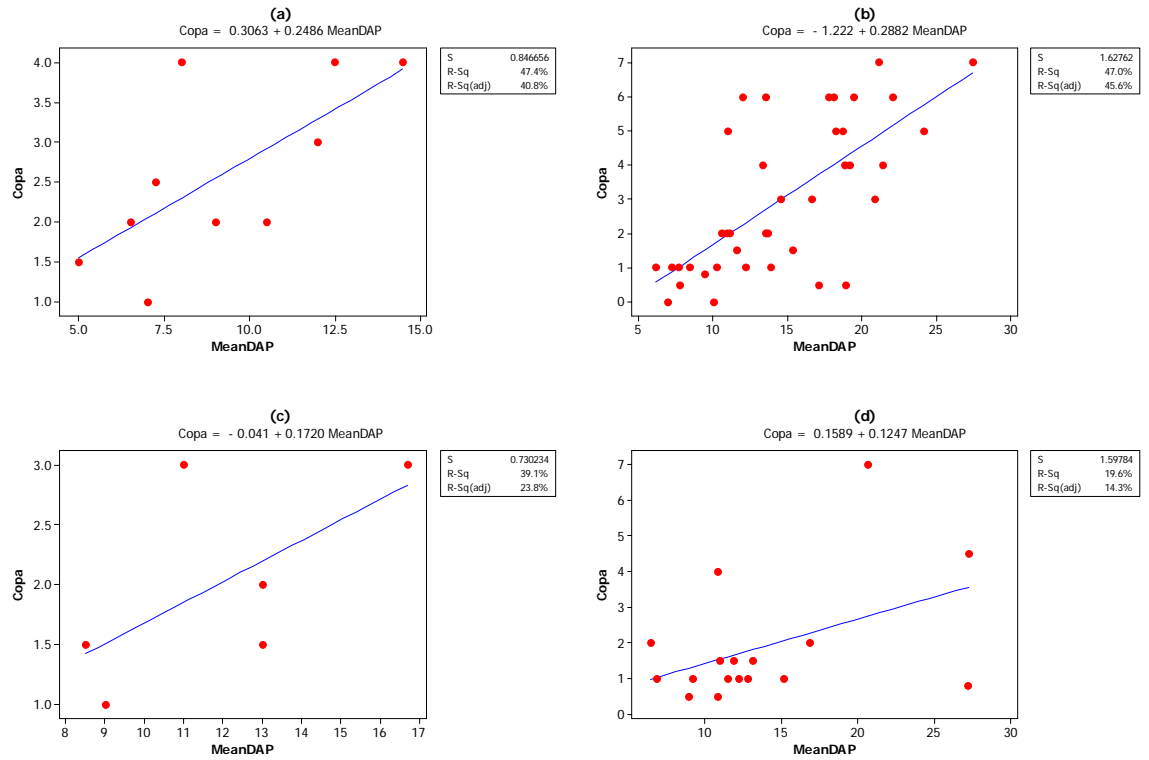


Fig. 34 Linear regressions of crown width/DBH for *Cecropia* species 1 old-growth forest (a), old fields (b), *Cecropia* species 2 old-growth forest (c) and old-fields (d)

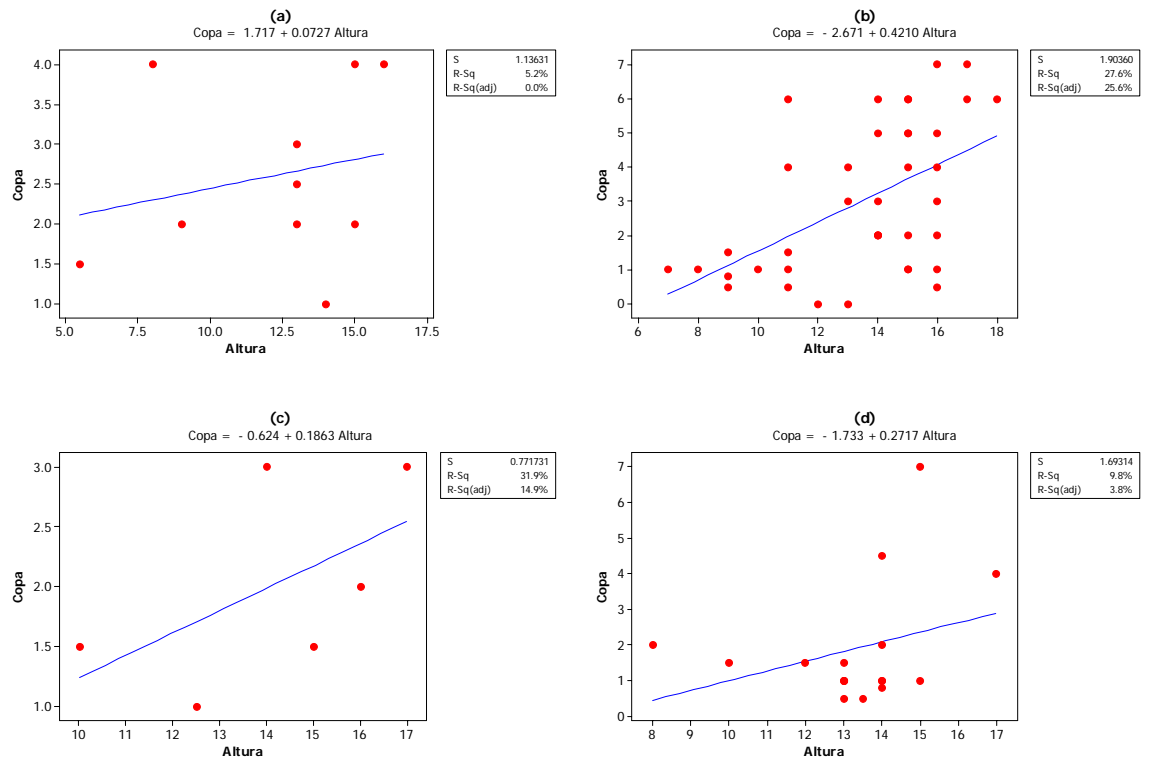


Fig. 35 Linear regressions of crown width/tree height for *Cecropia* species 1 old-growth forest (a), old fields (b), *Cecropia* species 2 old-growth forest (c) and old-fields (d)

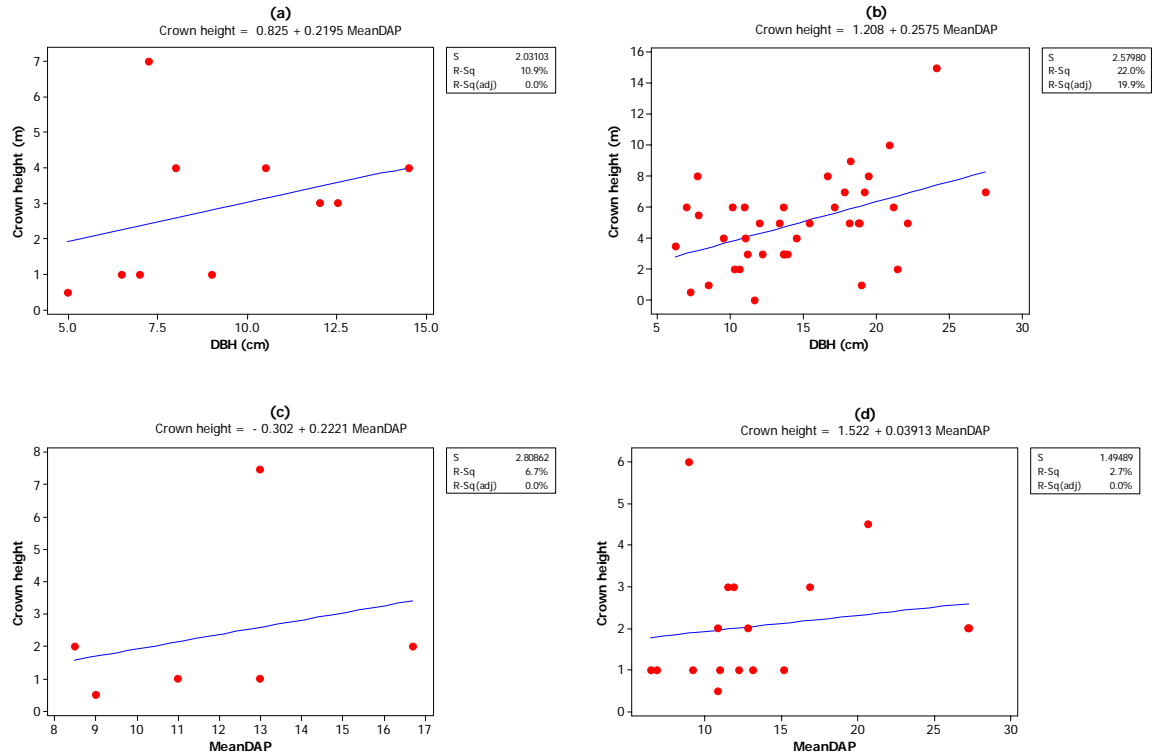


Fig 36. Relationship of crown height to DBH for *Cecropia* species 1 old-growth forest (a), old fields (b), *Cecropia* species 2 old-growth forest (c) and old-fields (d)

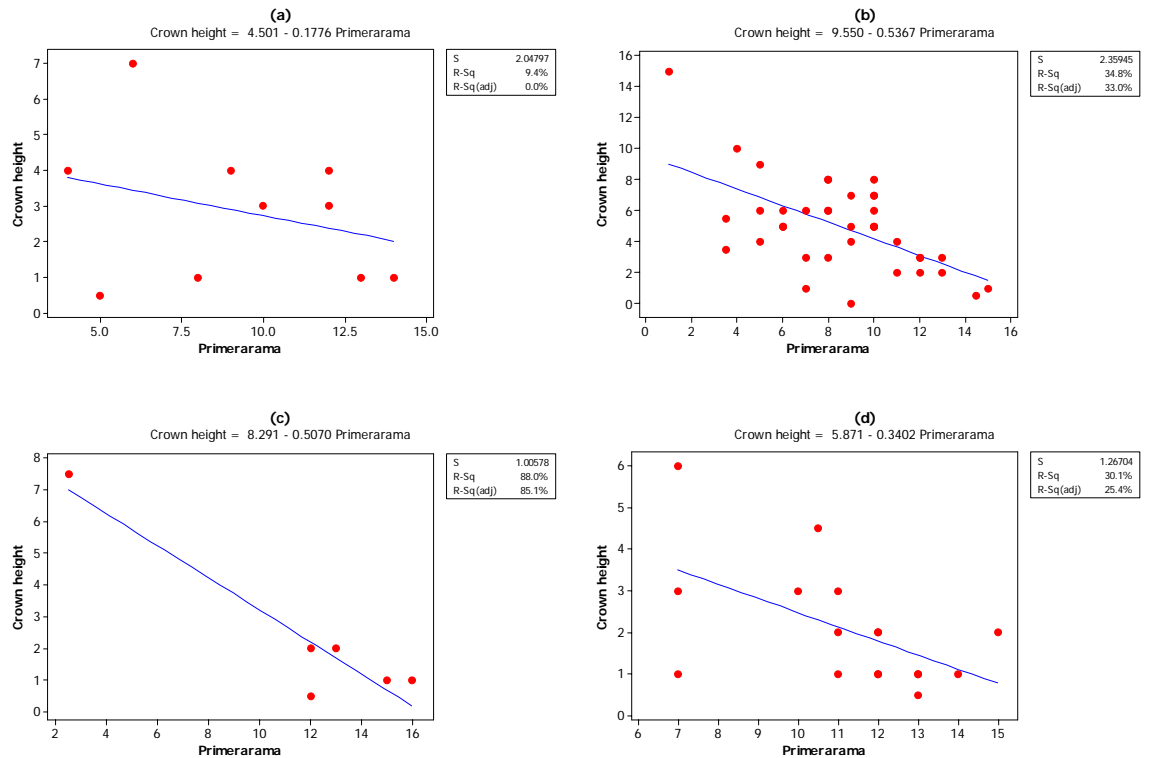


Fig. 37 Linear regressions of crown height/first branch height for *Cecropia* species 1 old-growth forest (a), old fields (b), *Cecropia* species 2 old-growth forest (c) and old-fields (d)

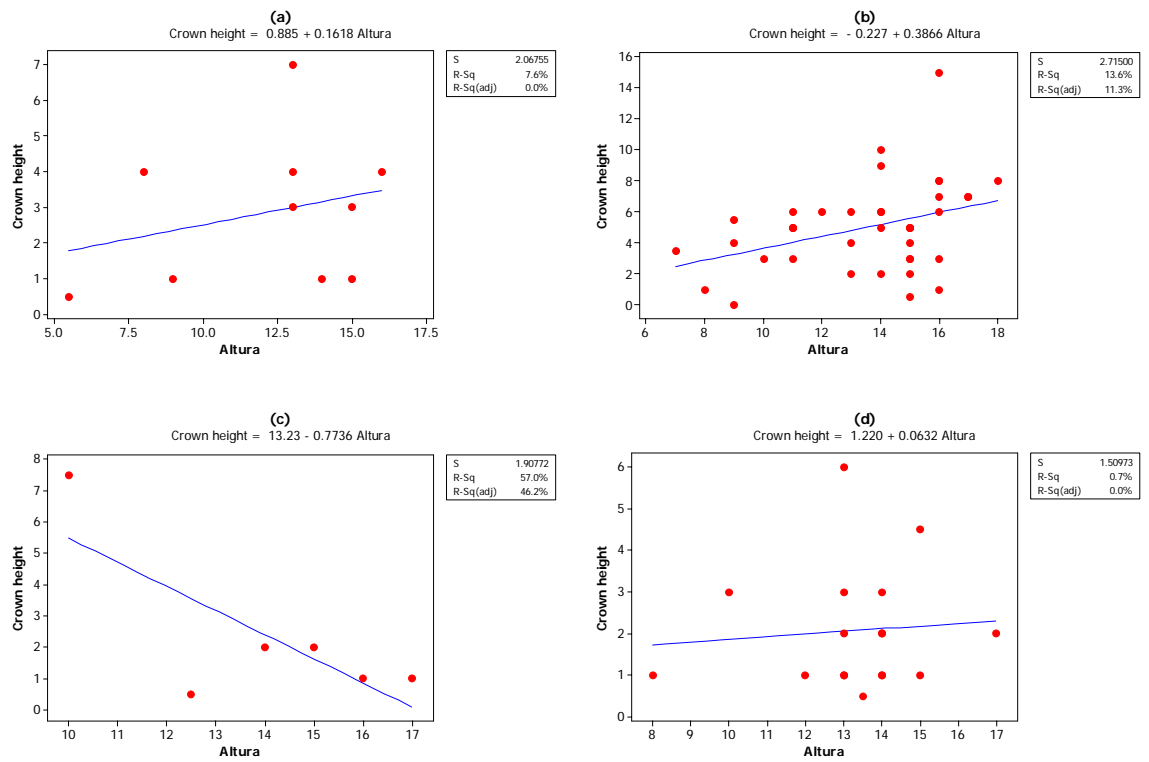


Fig. 38. Linear regressions of crown height/tree height for *Cecropia* species 1 old-growth forest (a), old fields (b), *Cecropia* species 2 old-growth forest (c) and old-fields (d)

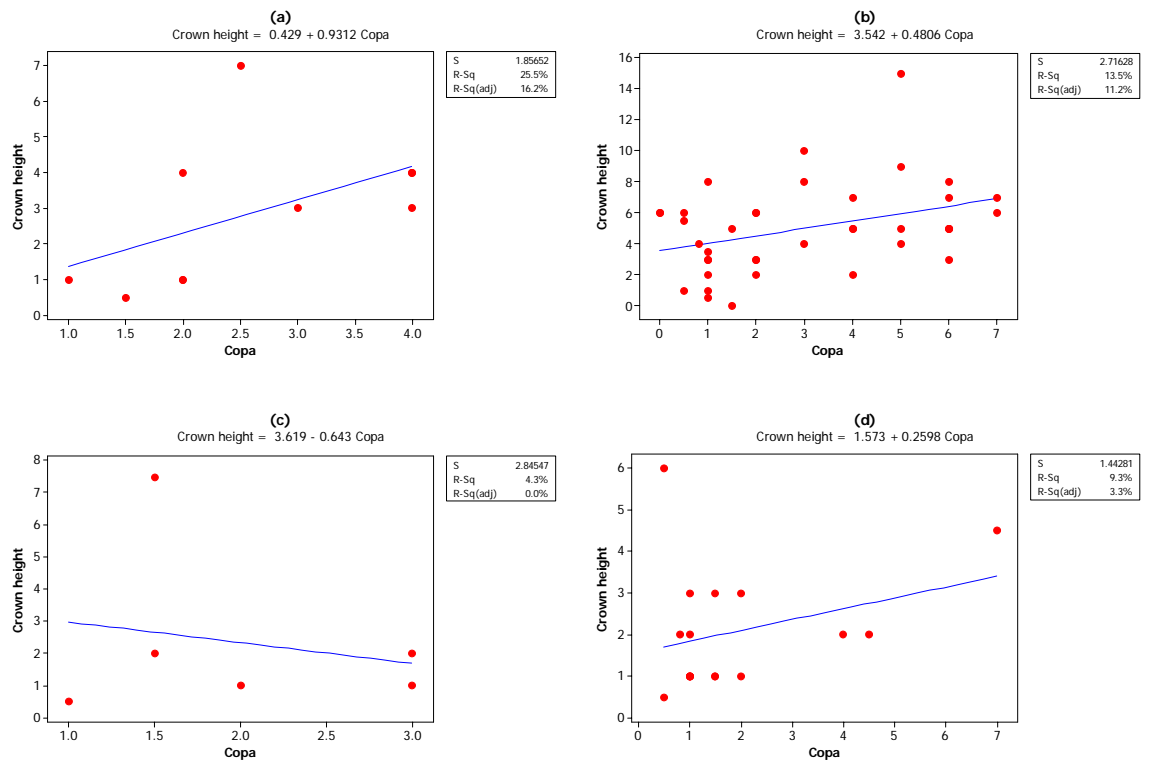


Fig. 39 Linear regressions of crown height/crown width for *Cecropia* species 1 old-growth forest (a), old fields (b), *Cecropia* species 2 old-growth forest (c) and old-fields (d)



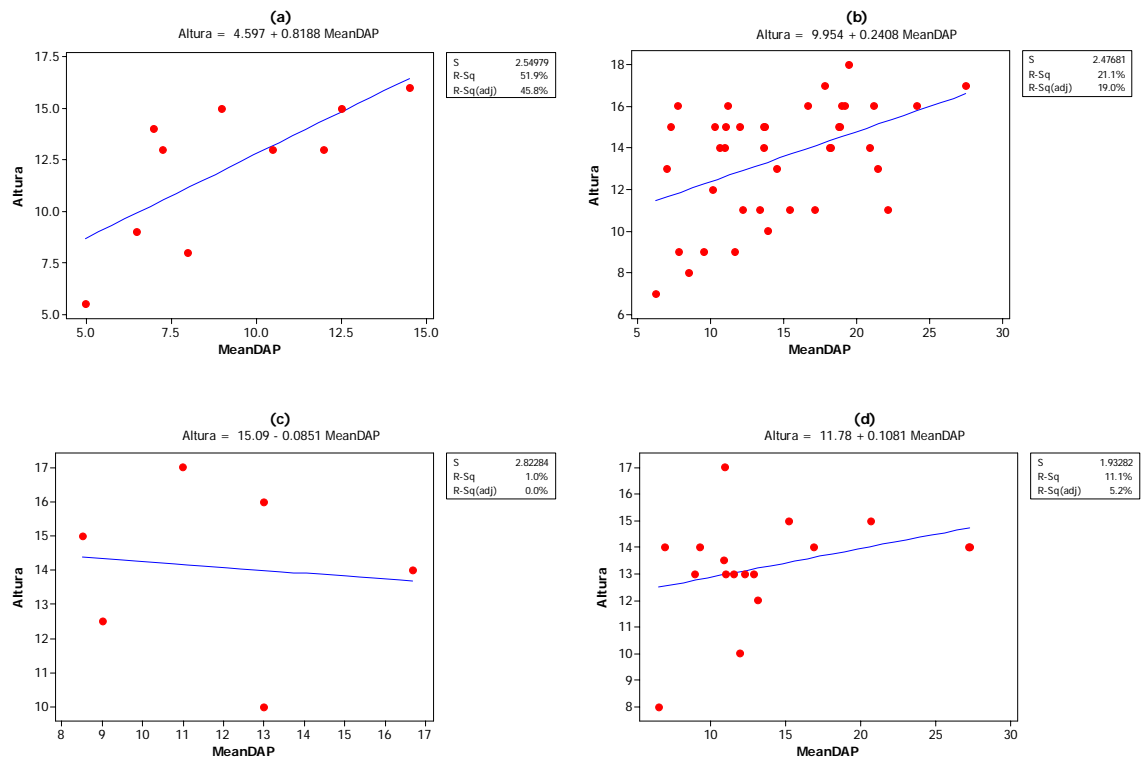


Fig. 40 Linear regressions of tree height/DBH for *Cecropia* species 1 old-growth forest (a), old fields (b), *Cecropia* species 2 old-growth forest (c) and old-fields (d)

## 4. Discussion

### 4.1 Stand Composition

#### 4.1.1 All species all plot data

From analysis of the all plots (Fig 8) and old-growth forest (Fig 8) DBH population size class distributions it is possible to infer that the population is in equilibrium. The reverse J-shaped distribution is expected where a large amount of individuals are continuously being recruited into the smaller size classes. A decreasing percentage of these are then recruited over time upwards through the size classes leaving only a few individuals in the largest classes. Few trees (comparatively) reach "large" tree status due to the dynamic nature of tropical forests (mortality due to age, epiphyte growth etc.).

If we ignore the accentuation of the *Cecropia* in the old fields distributions (Fig 8) it would be possible to infer that this population is in equilibrium also. Highlighting the *Cecropia* spp. changes this. With no large individuals we have an indication that the land has been cleared at some stage. In the size classes between 13 cm and 37 cm circa 50% of each class is *Cecropia*. The smallest size class has the greatest number of other

species, showing that regeneration is occurring.

The height population size class distribution for all plots (Fig 8a) and old-growth forest (Fig 8c) show the approximate straight line decline to be expected with populations in equilibrium.

The picture of both *Cecropia* spp. painted by the DBH and tree height distributions together is as expected for a pioneer. Both species occur in the smallest DBH size classes. Height wise the bulk of both species are towards the middle range indicating species that invest strongly in height at the expense of DBH.

The all plots old field height distribution (Fig 8f) shows evidence of disturbance. The trend is similar to the all-plot and all old-growth forest distributions in the early size classes up to 20 m in height, after which there are few individuals. This lack of older, larger individuals indicates that the site has at some time suffered a disturbance event; through our knowledge of the site we know that this was slash and burn for conversion to pasture. The few largest individuals in this distribution are potentially forest remnants from conversion. We can also see from this graph (Fig. 8f) how *Cecropia* species 1 dominates the largest

size classes. As a pioneer species it will have been one of the initial colonisers of the old fields and once allocation switched to crown development it would begin to affect the light environment, affecting the growth of all other plants under its crown. *Cecropia* sp. 2 is present in similar classes to *Cecropia* sp. 1 but in lesser numbers. *Cecropia* are present in all old field size classes, evidence that a number of cohorts have been recruited over continuous years up until some point i.e. when the light environment changed sufficiently to hinder new seeds from establishing after germination. As the number of *Cecropia* in each size class decreases the number of other species increases, this could be evidence of facilitation. Late successional and mature forest trees do not generally colonise old field sites until after they have been well established and dominated by fast growing pioneer species (Finegan 1984). One explanation for this is leaf litter replenishing nutrients in the soil, combined with the closed canopy initially smothering whatever ground vegetation remains and also root mass reducing compaction and aerating the soil. There are no *Cecropia* individuals over the 20 m mark but still growing, the sites are only approximately 12 years old. Pioneers such as *Cecropia* continue to grow for their lifespan. The later

successional trees do not grow as rapidly as pioneers, some will wait sub-canopy for a new gap to form before attempting to gain height. Others may continue to grow to canopy status and eventually compete with the *Cecropia*. Species richness is almost always quicker to recover than species composition (Finegan 1996 in Kennard, D.K. 2002).

#### 4.1.2 All species matched plot data

The DBH distributions for all matched plots (Fig. 10a) and matched old-growth forest plots (Fig. 10) follow similar distributions to the all plot data (Fig. 8, a & c). The reverse J shape curve is much shallower in the matched old-growth forest habitat than the all-plot old-growth forest and the upper size classes are less well populated. Abundance is comparable for both data sets. The distribution for the matched old field plots is a very steep straight line decline indicating that individuals are progressing through the size classes. The lack of any individuals larger than 37 cm DBH again indicates the previous disturbance. Both *Cecropia* spp. are well represented in all the size classes contributing to the straight line effect. Again the number of *Cecropia* in each class reduces as DBH increases.

The tree height distributions are all more uneven than the all plots distributions. All distributions show some evidence of bimodality with a peak between 14 and 16 m. This is slightly evident in the all-plots old fields distribution (Fig. 8) but more evident with the matched plots. There is no evidence of this in the DBH distribution though. The mean heights within old-growth forest for *Cecropia* species 1 (Mean=12.15 m) and *Cecropia* sp. 2 (Mean=14.08) and within old fields forest: *Cecropia* sp. 1 (Mean=13.49) and *Cecropia* sp. 2 (Mean=13.27) are close to the height of this peak in the size classes. No standard error is included in the tree height population size class distributions. This mean height may be an approximation of the canopy level which may explain the high number of individuals in that range. It may be unnecessary for individuals to grow much beyond this point as they have canopy status.

Apart from this the old-growth forest shows a gradual decline in numbers up until the 18 m point where numbers decrease considerably. The old field distribution is almost completely flat, showing a distinct shortage of regeneration. With the removal of the *Cecropia* spp. from this distribution the decline is more straight line indicating

that regeneration by late successional species is taking place (Fig 10f). This flat size class distribution does indicate potential for deterioration in population size due to a shortage of regeneration. Possible reasons are "(1) rapid growth in small size classes (2) high survival rate over all" (Condit et al. 1988 in McLaren, K.P. et al 2005). In this example the rapid growth of late successional species in the lower size classes and a high survival rate of *Cecropia* in the upper size classes.

#### 4.2 *Cecropia* spp. 1 and 2

The results can show that the species are similarly abundant depending on which measure is used. Both dominance and density are a measure of per hectare. This may influence the results as *Cecropia* sp. 2 was only encountered in 7 plots at 2 of the 4 sites, whilst *Cecropia* sp. 1 was encountered in 32 plots at all 4 sites.

Investigation of the DBH and tree height size classes for old-growth forest (Fig 7) show that DBH has been sacrificed for height as mentioned previously. *Cecropia* sp. 1 has a greater range of DBH's whilst *Cecropia* sp. 2 is mostly present in the upper size classes. When looking at the tree height size classes *Cecropia* sp. 2 is

only present in the upper size classes. Greater height requires greater stability (greater DBH) accounting for its bias towards the larger DBH classes. Comparisons of height and DBH showed that *Cecropia* species 1 was significantly smaller than *Cecropia* sp. 2 although the effect size was small. This could be one factor in *Cecropia* sp. 1's abundance. *Cecropia* sp. 1 may be putting less energy into height and DBH growth, needing less energy to reach maturity and reproduce.

The DBH distributions for both species within old field (Fig. 14 a & b) and to a lesser extent in old-growth forest (Fig. 13 a) appear to be bimodal; although size class distributions can be inadequately sensitive to detect this properly. This formation of two distinct subpopulations occurs through interaction effects. Four primary factors, that can be influenced by a number of determinants, can cause changes to population structure: (1) initial size; (2) random environmental and/or genetic factors causing differences in the growth rate; (3) the life history pattern interacting with the environment and affecting each individuals growth rate; (4) differences in size class mortality. (Huston and DeAngelis, 1987).

Holthuijzen and Boerboom (1982) studied the *Cecropia* seedbank in Surinam and found that seeds of the two species studied (*C. iciadophyllia* and *C. obtusia*) germinated strongly with normal daylight and also germinated moderately in darkness. One explanation for the bimodality could be that the first cohort is populated by *Cecropia* that had already germinated before the gap formed or the field was abandoned; the second cohort being those of the species that germinated from seed after the gap had formed or the field had been abandoned. Further study would be needed to test this hypothesis.

In contrast to this both species tree height distributions appear unimodal in the old fields and old-growth forest. Again this peak appears in the 12 - 16 m range with *Cecropia* species 1 pushing 18 m.

### 4.3 First branch height

#### 4.3.1 Intra-specific differences

No significant difference was found for first branch height when compared directly, each species was similar across both habitats.

When compared as a ratio of DBH, first branch was considerably lower within the old-growth forest than the old fields for

*Cecropia* species 1. DBH and first branch were not significantly correlated by linear regression. There was no significant difference for *Cecropia* species 2. DBH was found to be considerably smaller in the old-growth forest plots than in the old fields for *Cecropia* species 1; this may have influenced the ratio results.

Height of first branch was also significantly correlated with the ratio of DBH:tree height for all species over all habitats. Both species had high  $r^2$  values *Cecropia* species 1 ( $r^2=70.1\%$ ) and *Cecropia* sp. 2 ( $r^2=88.4\%$ ) for old-growth forest. The allometric relationship between DBH:tree height has been shown in the *Cecropia* species (Alvarez-Buylla and Martinez-Ramos, 1992) and is expected in others.

Heuret et al (2002) state that a given species of *Cecropia* will always have a highly stable first branch height. By this it is presumed they meant within a certain environment as they continue to say that environmental conditions may modify the trees development. Barthélémy (1988 in Heuret et al 2002) observed *Cecropia obtusa* growing on bare soils that were eroded and free of humus; these trees only grew to a few metres in height and remained single stemmed. This indicates

that the stage where the first tier of branches is produced may be more developmentally influenced rather than concerned with chronological age. It was expected that after establishment each individual would gain height until they sensed a change in the light environment sufficient to warrant leaf production. At this point the tree would commence allocation to its first lateral branch, gaining energy for continuing height growth. Due to differing light regimes in old fields and old-growth forest we expected that each species would branch earlier in old fields as full sunlight would be more readily available.

There was no significant difference between the habitats in terms of plasticity. Therefore it can be concluded that the species have a similar range over both habitats supporting Heuret et al's (2002) statement of each species stability of first branch height.

The hypothesis that by making intra-species comparisons over different habitats the height of the first branch of trees in old-fields would be lower than the height of the first branch of trees from the same species in forest gaps was rejected. The results did not indicate significant intra-specific variation in first branch height between habitats.

#### 4.3.2 Inter-specific differences

The results indicate significant inter-specific variation in first branch height, the relationship between first branch height and tree height and the relationship between first branch height and the ratio of DBH:tree height. Across all habitats, except for the matched old-growth forest plots, the first branch of *Cecropia* species 1 was significantly lower than *Cecropia* species 2. The results were most significant within the old fields.

There was significant differences between the species DBH: for all plots *Cecropia* sp. 1 one ( $mean=16.518$ ,  $SE=0.53$ ) was significantly larger than *Cecropia* sp. 2 ( $mean=13.24$ ,  $SE=1.14$ );  $t(32.35)=2.60$ ,  $p=0.014$ . The effect size was small (Eta squared=0.02). In all other tests there were no significant differences between the species. With the matched plot data tree height was shown to be significantly smaller for *Cecropia* sp. 1 than for *Cecropia* sp. 2 using a GLM with species and habitat as factors. There was also significant interaction effect between species and habitat.

Therefore it is possible to conclude that there is genuine difference in first branch

height between the species and from this that crown depth is deeper for *Cecropia* sp. 1.

Pioneers typically put maximum energy into height growth. A species that can reach a suitable light environment and begin allocation to branches more rapidly than its competitors will out compete them. There must be a balance between lateral branch growth and height gain whilst still enabling an individual to compete for canopy space. There must then be a trade-off in *Cecropia* spp. between production of first branch and the reduction of allocation/energy to height growth. This short term trade-off will, upon production of leaf area and providing the light environment is sufficient, improve each individual's ability to out compete un-branched rivals. Branch production also enables fruit growth therefore it is possible that earlier branch growth reduces the time from germination to fecundity.

## 4.4 Crown diameter

### 4.4.1 Intra-specific

Straight comparisons of crown width across habitats yielded no significant results for either species.

No evidence was found to support the hypothesis that intra-species comparisons over different habitats would show the crown diameter of each species to be larger in old-field than in forest gaps. In fact for ratio comparisons of crown width:DBH, *Cecropia* species 1 was significantly larger in all the old-growth forest plots than in all the old field plots and all the matched old-growth forest plots.

Crown width and DBH were significantly positively correlated with linear regression for *Cecropia* species 1 in old-growth forest ( $r^2=47\%$ ) and old fields ( $r^2=47.4\%$ ). Crown width and height were also significantly ( $r^2=27.6\%$ ) positively correlated by linear regression for *Cecropia* species 1 old fields.

Crown width increases place greater stresses on individual trees. As with height growth, it is necessary for greater DBH to maintain stability as crown width

increases. Primarily, accelerated height growth is gained by reducing increases in crown and stem diameter. (Poorter et al 2003). Once sufficient height has been gained more energy can be allocated to crown production. Therefore it is to be expected that crown width and height would be positively correlated. Alvarez-Buylla and Martinez-Ramos (1992) found in their study of *C. obtusifolia* that stem diameter explained a greater proportion of the variation in crown size than height. These relationships are reflected in the findings that crown width was significantly correlated with the ratio of DBH:tree height for *Cecropia* species 1 in the old-growth forest ( $r^2=62.2\%$ ) and the old fields ( $r^2=52.6\%$ ). There was no significant correlation for *Cecropia* sp. 2. There may be no correlation or it may be due to the limitations of the sample size.

The co-efficient of variation for DBH of *Cecropia* sp. 2 within old-growth forest (25.62%) was significantly smaller than in old fields (44.68%). This implies that the potential for crown width expansion is reduced in old-growth forest or that the tree will be under more stress. Both are limiting factors

The coefficient of variation for crown width:tree height of *Cecropia* species 2 was significantly ( $p=0.05$ ) smaller in the



old-growth forest ( $CV=17\%$ ) than in the old fields ( $CV=47\%$ ). Sample size may have affected this result: the old-growth forest sample contained 6 individuals whilst the old fields contained 17 individuals. However if spatial and temporal variations in the light environment encourage allometric differences in co-existing saplings (Yamada et al 2005) it is possible that this also induces greater plastic responses in the same and related species.

#### 4.4.2 Inter-specific

Crown width was shown to be significantly greater for *Cecropia* species 1 in all habitats except old-growth forest with straight comparisons. These results were confirmed when contrasting species over habitat with ratios of crown width by DBH, tree height, first branch height and DBH:tree height. As expected crown width was also significantly correlated with DBH:tree height for *Cecropia* species 1 within both habitats: old-growth forest ( $r^2=62.2\%$ ,  $p=0.033$ ) and old fields ( $r^2=52.6\%$ ,  $p<0.0005$ ).

Alvarez-Buylla and Martinez-Ramos (1992) state that the number of branches produced by *Cecropia obtusifolia* is determined by the space free for crown

growth. In this gap size limits a trees potential fecundity because number of branches is positively allometrically related to number of floral buds. Therefore it is also possible that crown size limits a species ability to reproduce. Developmental differences are present between the species. Both exist within the same habitat and so gap size cannot solely determine crown size. As *Cecropia* sp. 1 has a greater crown size it potentially has greater reproductive capability.

In contrast to *Cecropia* species 1 within the old-growth forest plots, *Cecropia* sp. 2 had negative correlations for: Crown height/tree height; crown height/crown width and tree height/DBH. These could be artefacts of the reduced sample size. However this negative relationship must be limiting for *Cecropia* species 2 and alternatively the reduced numbers in old-growth forest could be a consequence of this negative relationship. Although these results were not statistically significant they do indicate that *Cecropia* sp. 2's crown height may reduce with increases in tree height and with increases in crown diameter.

Tapering in stem diameter is expected with height gain, but this could indicate a limiting difference in this species as

compared to *Cecropia* sp. 1. *Cecropia* Species 1 was shown to have larger crown height to *Cecropia* sp. 2 in all plots, matched plots and old fields, through comparisons as a ratio of tree height and DBH..

We can accept the hypothesis that inter-species comparisons over the same habitats showed that the trees of the *Cecropia* species 1 had larger diameter crowns than the trees of *Cecropia* species 2.

## 5. Conclusion

The difference between the *Cecropia* species populations in the less disturbed old-growth forest and the old fields is apparent in the population size class diagrams. The old-growth forest shows the distribution of a population in equilibrium with *Cecropia* sparsely populated throughout. The old fields distribution, in contrast, shows an aging population of *Cecropia*. No *Cecropia* regeneration is occurring, but later successional species are regenerating. The old fields distributions are clearly dominated by the *Cecropia* spp with both having similar distributions.

*Cecropia*, as pioneers, typically select for early height gain at the expense of stem stability and longevity (Alvarez-Buylla and Martinez-Ramos 1992). This genus is renowned for dominating after larger (than forest gap) disturbance events; perhaps due to the more diverse conditions and realisable nutrients at these sites (Wilson, 1999).

Sessile organisms, such as trees have three main mechanisms for affecting their access to the light environment: height extension, crown extension and plasticity of above ground biomass; the transport of

energy intercepted by leaf matter is governed by woody matter (i.e. stem and branches). Photosynthetic plasticity allows an individual greater range to adapt to its environment. Therefore, leaf production aside, the trees ability to harness its environment and out compete its competitors is partially determined by crown depth and width (Poorter et al. 2003).

For these reasons we hypothesised that there would be variation within each species that would make each a better coloniser of old fields than old-growth forest. In short that the first branch of each species would be lower and the crown width wider in old fields. No evidence was found to support these hypotheses. In line with Heuret et al (2002) first branch height was relatively stable for each species over the different habitats. Both species showed evidence of plasticity, particularly for crown width. CV comparisons for DBH and for crown width:tree height showed *Cecropia* species 2 to be less plastic within old-growth forest than within old fields.

First branch height was significantly correlated with the ratio of DBH:tree height for all species within all habitats.

We also hypothesised that within these two environments the first branch of *Cecropia* species 1 would be lower, and the crown width wider, than *Cecropia* species 2. *Cecropia* sp. 1, whilst not more locally abundant, was more spatially distributed throughout the reserve. We therefore believed that these comparisons would indicate reasons for this greater distribution.

Our results supported the hypotheses for first branch height in all habitats except the matched old-growth forest. The first branch of *Cecropia* species 1 was significantly lower than *Cecropia* species 2. The results were most significant within the old fields. The hypothesis for crown width was also supported over all habitats.

We believe that early production of first branch and wider crown growth assist *Cecropia* sp. 1 in outcompeting its rivals by greater utilisation of light energy and earlier fecundity. Fecundity is affected by crown size (Alvarez-Buylla and Martinez-Ramos 1992) and crown size by height of first branch. It is therefore possible that these partially contribute to *Cecropia* sp. 1's greater spatial distribution. But because allometric relationships between stem diameter, tree height and crown diameter alter as

overall size and canopy position change (Montgomery and Chadzon, 2001) it is difficult to theorise without more temporal investigation.

## 6. Further research

The old fields plots in this study were all believed to be of a similar age, circa 12 years since abandonment. Poorter and Werger (1999) argued that the ontogenetic trajectory studied and the choice of species, to a great extent determine the outcome of inter-specific comparisons so it is preferable to study the entire route of development from seedling to maturity.

Sapling size at gap formation can greatly influence colonisation. We suggested that the bimodality of height distributions could be explained by two different developmental cohorts. Comparisons of this data set with more recently abandoned old field sites could test this. Allometric relationships are known to change within species throughout the lifecycle. A more involved understanding of the ecological development of this species over time would allow greater insight into the two species interactions; particularly in terms of tree height:DBH trade off and triggers for branch production. Understanding which stage of development these species produce branches and the variability in that would aid assessment of regeneration age,

simply by counting the number of branch tiers (Heuret et al, 2002).

Sposito and Santos (2001) believe that *Cecropia* species' life spans "increase in a gradient from open to forest habitats, and taller species with larger leaf area would be the longer lived". Therefore further research is required to establish the relationship of tree allometry and habitat, with the species life span.

The reverse J-shaped DBH distributions indicate that late successional shade tolerant species are regenerating. Future investigation of stand development as *Cecropia* numbers decline would allow a greater understanding of this species effect on stand regeneration.

Gathering a larger data set, with more individuals from *Cecropia* species 2, would enable more robust comparisons to be carried out. This would enable us to gain a clearer picture of this species. The negative correlations for crown height/tree height; crown height/crown width and tree height/DBH contrast with the findings for *Cecropia* sp. 1 and may be an important difference. As mentioned though this may be an artefact of the sampling size and so requires further investigation.

Investigation of both species seed production, seed bank and germination rates would allow for a more accurate assessment of differences in spatial distribution.

It was assumed throughout the study that the two species of *Cecropia* started on an equal footing. Perhaps *Cecropia* species 2 is a later species than *Cecropia* sp. 1. A genetic study to determine the relationship between these *Cecropia* species would allow for more informed discussion.

## 7. Critical appraisal

Temporally the data set was limited. Population size class distributions give a wealth of information about current stand situation and regeneration trajectory. Though there are certain limitations to this ability and some discussion of their accuracy. The ability to collect data from the same sites over successive years would have enabled a deeper comparative study. Widening the collection to include plots of differing age ranges would also have assisted in assessing stand development.

Whilst *Cecropia* species 1 was collected in sufficient quantities, *Cecropia* sp. 2 was sparsely represented. After realisation of this and the desire to focus on these two species it would have been beneficial to be able to collect from a wider area on the reserve.

The data was initially collected in a system of circular quadrants. Due to a problem with the sampling technique it was later realised that there was slight over-sampling and some trees outside the circular plots were included. This was consistent and subsequent analysis found that the plots were actually better defined as square

quadrats. In each section (a,b,c,d) it was found that the average error was: Section a (2), Section b (3), Section c (2), section d (1).

Data was also collected from 5 distinct habitats: Within old-growth forest: closed canopy, old-gap and new gap plots; within old fields: regenerating pasture and regenerating sugar cane. The lack of individuals from *Cecropia* species 2 it was necessary to pool the data set as "Old-growth forest" and "Old fields". It would have been preferable to assess differences between all 5 habitat types rather than the two. Regenerating sugar cane was ignored for the matched comparisons as *Cecropia* sp. 2 was not present so the old fields data was not weakened. It is possible the combination of the 3 habitats (closed canopy, old-gap and new gap) for old-growth forest may have introduced a greater diversity than would have been apparent when comparing between them.

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