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# Analysing the effects of local environment on the source-sink balance of *Cecropia sciadophylla*: a methodological approach based on model inversion

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## Abstract

• **Context** Functional–structural models (FSM) of tree growth have great potential in forestry, but their development, calibration and validation are hampered by the difficulty of collecting experimental data at organ scale for adult trees. Due to their simple architecture and morphological properties, “model plants” such as *Cecropia sciadophylla* are of great interest to validate new models and methodologies, since exhaustive descriptions of their plant structure and mass partitioning can be gathered.  
• **Aims** Our objective was to develop a model-based approach to analysing the influence of environmental

conditions on the dynamics of trophic competition within *C. sciadophylla* trees.

• **Methods** We defined an integrated environmental factor that includes meteorological medium-frequency variations and a relative index representing the local site conditions for each plant. This index is estimated based on model inversion of the GreenLab FSM using data from 11 trees for model calibration and 7 trees for model evaluation.

• **Results** The resulting model explained the dynamics of biomass allocation to different organs during the plant growth, according to the environmental pressure they experienced.

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**Contributions of the co-authors** P.H., P.C.Z. and E.N. designed the experimental protocol; V.L., P.H., E.N. and P.C.Z. collected the data; V.L. and P.H. designed the model; V.L. programmed the model and fitted the parameters; V.L., P.H. and P.C.Z. wrote the manuscript; P.H. and P.R. coordinated the research project.

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• **Perspectives** By linking the integrated environmental factor to a competition index, an extension of the model to the population level could be considered.

**Keywords** *Cecropia* · Functional-structural model · Model inversion · Morphology · Trophic competition

## 1 Introduction

Individual-based forestry models classically use simplified representations of the tree crown and characterise growth by variations in key indicators such as height or diameter at breast height (Pretzsch 2002). In recent decades, a new approach to plant growth modelling has emerged, representing trees at organ scale, integrating structural and functional processes and their interactions with the environment (Sievänen et al. 2000; Prusinkiewicz 2004). However, the potential application of such models to the field of forest management is not straightforward. A major obstacle is model calibration and validation against adequate data. For adult trees, their high stature, complex structure, and long life span drastically increase the fieldwork required to collect data at the organ scale. Thus, data used to develop and evaluate models consist mainly of global, aggregated or partial measurements (see, e.g. Perttunen et al. 2001; Lopez et al. 2008).

In this context, another promising approach is to consider “model trees” with reduced structural complexity and short lifespan to build and validate functional-structural tree models (FSTM).

The neotropical genus *Cecropia* Loefl. (Urticaceae) includes 61 species distributed from southern Mexico to northern Argentina, with two species occurring in the Antilles, and covering a wide range of climatic variation (Berg and Franco-Rosselli 2005). With some very widespread species (e.g. *C. sciadophylla*), *Cecropia* is one of the most emblematic pioneer genera in the Neotropics. These species are able to colonise cleared areas with high light levels, in particular after disturbances, and are thus essential contributors to the regeneration of mature forests. *Cecropia* species have several morphological traits that makes them good “model trees”: (1) *Cecropia* has a simple architecture following the Rauh model (Hallé et al. 1978). The number of phytomers constituting the whole tree remains relatively low even though the life span can reach several decades. Moreover, branch abscission occurs rather late, and stipules, leaves, and inflorescence scars remain visible along the growth axes over the entire tree lifespan. Therefore, it is possible to fully describe the tree structure and topology from morphological observations (Heuret et al. 2002; Zalamea et al. 2008), which is very uncommon for trees. (2) Previous studies (i.e. Heuret et al. 2002; Zalamea et al. 2008) have shown a high annual

periodicity in reproductive and branching processes, as well as an alternation of long and short nodes, for *C. obtusa* and *C. sciadophylla* respectively. Additionally, these latter studies provided a methodology based on morphological observations to estimate tree age in these species, which is especially interesting in tropical zones where tree age determination is a difficult task. (3) The large distribution of some species allows comparisons of the same species in contrasting environmental conditions, and evaluation of theoretical results on plasticity obtained through modelling against natural situations. (4) Its fast growth allows design of experimental protocols to include follow-up measurements to test some model hypotheses when necessary.

We therefore argue that *Cecropia sciadophylla* can be considered as a relevant “model tree” species for developing and evaluating a FSTM, with the biological objective of disentangling the complex interactions between the environment and tree trophic dynamics. More precisely, analysing the influence of fluctuating environmental conditions on the source–sink balance for *C. sciadophylla* should help answer the following question: might the annual periodicity in growth, branching and reproductive processes be linked, among others, to climatic fluctuations and/or dynamic trophic competition during plant development? To this end, we propose a FSTM for *C. sciadophylla* where environmental factors are reduced to a single variable for each plant, comparable to the competition index classically used in spatially explicit forest models. This single variable consists of two components: one representing seasonal variations, common to all plants and estimated from climatologic records, and the other representing local site conditions, specific to each plant and estimated using model inversion.

We present the application of this method, using the inversion of the FSTM GreenLab (Yan et al. 2004; Mathieu et al. 2009), to analysis of the influence of fluctuating environmental conditions on the source–sink balance for *Cecropia sciadophylla*. A preliminary test of this method was applied to two beech trees (*Fagus sylvatica* L.) with constant environmental factors (see Letort et al. 2008). Regarding fluctuating environmental conditions, no modelling analyses based on GreenLab have been performed on trees. Some results have been obtained with measured environmental variables on crops such as corn (Guo et al. 2006) or tomato (Dong et al. 2008; Kang et al. 2011), where daily potential evapotranspiration was computed from temperature, light intensity and air humidity. Furthermore, daily photosynthetically active radiation was used to compute biomass production in *Arabidopsis thaliana* (Christophe et al. 2008); and the effects of temperature, solar radiation and soil water content on organogenesis on grapevine, were modelled (Pallas et al. 2011). In a previous study by Letort et al. (2009), a model for *C. sciadophylla*

was constructed using GreenLab and data from 11 trees measured in French Guiana. However, because the environment was considered as a constant factor, the model did not allow analysis of the influence of the seasonal fluctuations in rainfall (alternation of dry and rainy seasons) on plant growth. Given that recent evidence suggests that internode lengths seem to be related to rainfall (Zalamea et al. 2008), the model and the methodology had to be adapted to take into account the intra-annual variations of this environmental pressure. Moreover, a new set of data from seven trees was collected and used as an independent dataset for validation of the method.

With the aim of using the model as a tool to disentangle ontogenic (low-frequency trend) and environmental (medium-frequency trends) variations, the aims of this work were to (1) determine morphological allometries that will simplify future measurements, (2) evaluate the ability of the GreenLab model to trace back the dynamics of internal trophic competition within plants, (3) evaluate the possibility of driving morphological and architectural plasticity by a single control variable, and (4) define an index of competition that will pave the way to a forest model based on individual trees with explicit architectures to analyse emergent properties at the stand level.

## 2 Materials and methods

### 2.1 Measurements and experimental protocol

A detailed morphological and architectural description of *Cecropia sciadophylla* habit can be found in Zalamea et al. (2008) (see also Fig. 1). Each node bears three lateral buds that potentially give rise to a branch (central bud) and two inflorescences (Zalamea et al. 2008), as illustrated in Fig. 1b. Branching and flowering are immediate; growth is continuous (i.e. no period of cessation of growth). The enveloping stipule found on each node leaves a characteristic ring-shaped scar that can be used to locate the limits of each internode down to the base of the tree. After abscission, the two inflorescence stalks leave characteristic scars that can be identified retrospectively on all parts of the tree.

The individuals sampled for this study were taken from two sites in French Guiana: Saint-Elie Road (5°17'N, 53°04'W) and Counami Road (5°24'N, 53°11'W).

In September 2007, 11 individuals were felled and measured, 10 at Saint-Elie Road (from different stands) and 1 at Counami Road. All the trees from Saint-Elie population were sterile and only one had branches. The tree from Counami Road was pistillate and had branches. In addition, in December 2008, a new dataset was compiled with seven individuals measured at Counami Road. They

were all sterile and without branches. To estimate some of the allometric relationships, supplementary data on phytomers where leaves are present (i.e. at branch tips) were taken from one tree measured at Counami Road in September 2009.

Trees were described node by node following the protocol defined by Heuret et al. (2002) and Zalamea et al. (2008). Tree topology, i.e. the relative position of nodes and axes, was recorded following MTG formalism (Godin and Caraglio 1998) and analysed using AMAPmod software (Godin et al. 1997). Age determination of trees and annual growth delimitation were performed following the protocol proposed by Zalamea et al. (2008). For each phytomer, the following information was recorded: length of the underlying internode; diameter in the middle of the internode; and the presence of developed branches, inflorescences and/or leaves at each internode. For all the trees described in 2007, the foliar blades were weighed and pressed between two plates of Plexiglas and then photographed using a digital camera with a focal length of 50 mm. Foliar blade areas were estimated by analysing the photographs using ImageJ freeware v1.41o (<http://rsbweb.nih.gov/ij/>). The length, diameter in the middle and the fresh weight of the petioles were also recorded. Inflorescences or infructescences were weighed. The plant axes were then cut node-by-node, 1 cm above the stipule scar. The length of the cut segment (not exactly equal to the internode as there is a 1 cm shift) was recorded, as well as its fresh weight and two orthogonal diameters of the pith. Internodes, leaves, inflorescences, and petioles were dried at 103°C for 72 h and the dry mass was measured. For young individuals, the root system was extracted, washed, dried and weighed.

### 2.2 Model of biomass production in GreenLab for *Cecropia*

GreenLab is a dynamic model of plant growth that aims to simulate plant topological development, biomass production and allocation at the organ scale. For the sake of simplicity, we use here the discrete version of GreenLab (Mathieu et al. 2009), in which the simulation step is based on the rhythm of plant development in both the organogenesis part and the functional part of the model. This simulation step is set at the duration between emissions of two successive phytomers along the main axis and is called the growth cycle (GC). For *Cecropia* species, after some variability during the phase of growth establishment, the rate of emission of new phytomers is remarkably stable (Heuret et al. 2002), with increments of 2–3 nodes per month for each axis in *Cecropia sciadophylla* (Zalamea 2010).

At plant emergence, the initial biomass is provided by the seed,  $Q(0)$  (in g). Then, biomass production  $Q(t)$  at every GC  $t$  is set to be simply proportional to blade area

$S(t)$ , multiplied by a factor that represents the environmental pressure,  $E(t)$ :

$$Q(t) = \mu \cdot E(t) \cdot S(t) \tag{1}$$

where  $\mu$  can be seen as a coefficient of conversion of a given environmental input  $E$  into biomass (in  $\text{g cm}^{-2} \text{e}^{-1}$  where  $e$  is an arbitrary unit representing any environmental input; see next section). No self-shading is taken into account in this equation, given the particular arrangement of leaves, which are located at the tips of branches with phyllotaxy 5/13. Furthermore, low self-shading for *Cecropia longipes* was also reported by Kitajima et al. (2002).

### 2.3 Environmental factor

We divide the environmental factor into two parts: one with temporal variations that correspond to the climatic variations, common to every plant of the same zone; and the other a constant relative local site index. The index is defined, on an arbitrary scale, as a multiplicative factor that sets the relative level of local conditions on each site compared to other sites, thus accounting for local spatial variations. This integrated index might aggregate the levels of various local factors such as soil quality, nutrient and water availability, and local density.

Climate in French Guiana is seasonal, with a 3-month dry season from mid-August to mid-November and a rainy season during the remaining 9 months. Additionally, a short dry season may occur in February and March.

A new function was added to the model to represent these seasonal variations in precipitation over an average year. The absolute value of a sinusoidal function was chosen, truncated by a constant threshold  $B$  to set the duration of the dry season. The environmental factor integrated over the month  $i$  ( $0 \leq i < T$  with the origin  $i=0$  in October at the middle of the dry season) for an average year is then defined as follows:

$$e_i = m_i \cdot \text{Max} \left\{ B, \left| A \sin \left( \frac{i\pi}{T} \right) \right| \right\} \tag{2}$$

where  $T=12$  is the period (1 year),  $A$  is the amplitude of the variations in precipitation that will be fitted to the precipitation data,  $B$  the truncation threshold that corresponds to the average amount of precipitation during the dry season. The short dry season was included in the climate function using a multiplicative factor,  $m_i$  ( $0 \leq m_i \leq 1$ ), which is equal to  $1-a$  ( $0 \leq a \leq 1$ ) during the month  $m$  of the short summer season, and is equal to 1 otherwise. The parameters  $B$ ,  $A$ ,  $a$  and  $m$  were estimated using the precipitation data recorded in Saint-Elie Station from 1981 to 1991 during the Ecerex project (Sarrahil 1992).

To use this function as a control variable for the growth of *Cecropia* trees, a change of variable from calendar time to

GC was needed. A preliminary step is thus to input the number of phytomers,  $T_y^I$ , emitted every year for each plant, and then, for a given individual  $I$ , the environmental factor integrated over GC  $j$  of year  $y$  can be defined as:

$$E_{j,y}^I = E^I \cdot m_{j,y} \cdot \frac{T}{T_y^I} \cdot \text{Max} \left\{ B, \left| A \sin \left( \frac{j\pi}{T_y^I} + \phi_0^I \right) \right| \right\} \tag{3}$$

where the index  $I$  denotes the variables that are specific to each individual:  $E^I$  is the relative local index;  $\phi_0^I$  is the phase at origin, which it depends on the time when the plant  $I$  emerged from the seed;  $T_y^I$  is given for each plant  $I$  and each year  $y$ , based on the recorded annual growth delimitations. The ratio  $T/T_y$  comes from the change of variable and corresponds to a normalisation factor of the total amount of precipitation received by each plant over the year, regardless of its growth rate.

The short dry season is modelled by:

$$m_{j,y} = \begin{cases} 1 - a & \text{if } m \frac{T_y^I}{T} \leq j < (m + 1) \frac{T_y^I}{T} \\ 1 & \text{else.} \end{cases} \tag{4}$$

This equation is valid if  $\varphi_0=0$  and a simple translation of phase is performed otherwise.

### 2.4 Model of biomass allocation

The biomass allocation process was modelled in two steps. First, biomass is allocated to the four compartments of the plant: primary growth of phytomers, biomass for ring increment (i.e. secondary growth), expansion of inflorescences, and roots; followed by an intra-compartment partitioning to each organ. The root mass of young individuals allowed us to construct a simple allometric relationship for the biomass allocated to the root system at each GC that is proportional to biomass production. The remaining biomass,  $Q_r(t)$ , is then partitioned between the three other compartments in proportion to their respective demands,  $D_c(t)$ , where  $c$  stands for primary growth (pg), inflorescences (inflo) and ring increment (ring). So, if  $D(t)$  is the total plant demand at GC  $t$ , i.e. the sum of the demands of the three compartments, the amount of biomass that goes to compartment  $c$  is:

$$Q_c(t) = D_c(t) \cdot \frac{Q_r(t)}{D(t)} \tag{5}$$

$$\text{With } \begin{cases} c = pg : & D_{pg}(t) = \sum_{Buds(t)} P_b \cdot \left( 1 - e^{-K_b(o) \cdot k} \right) \\ c = inflo : & D_{inflo}(t) = \sum_{Inflos(t)} P_{fl} \cdot \varphi(n; a_{fl}, b_{fl}, T_{fl}) \\ c = ring : & D_{ring}(t) = P_{rg} \cdot L(t) + K_{rg} \cdot \frac{Q(t)}{D(t)} \end{cases}$$

where the demand for primary growth  $D_{pg}(t)$  is the sum of the demands of every active meristem (noted as “Buds” in the equations), designed by its rank  $k$  and branching order  $o$ . Letort et al. (2009) have shown the existence of a transitory phase when meristems are young (at axis emergence). The duration of that transitory phase is driven by the parameter  $K_b(o)$ , which depends on the branching order  $o$ . Afterwards, meristems reach a stable phase where they all have a similar sink strength,  $P_b$ , whatever their rank and branching order. This sink parameter  $P_b$  is taken as a reference for the other compartment demands so its value can be arbitrarily set.

The demand of inflorescences  $D_{inflo}(t)$  is defined as the sum of the sink strength of every growing inflorescence of the plant at GC  $t$ . The sink strength,  $P_{fi}$ , and its variations with inflorescence age  $n$  follow a beta law density function whose parameters are  $a_{fi}$ ,  $b_{fi}$ , and the expansion duration  $T_{fi}$  (for expression and use of beta law density function, see Yin et al. 2003 and Christophe et al. 2008).

The demand for ring increment is assumed to consist of two parts: the first is proportional to the total length of all axes of the plant,  $L(t)$ . The proportion coefficient, also called sink linear density, is  $P_{rg}$  (in  $\text{cm}^{-1}$ ). The second part is



**Fig. 1** a–d Habit of *Cecropia sciadophylla*. Sequence of internodes of an axis (a), inflorescence (b), youngest (c) and oldest (d) individuals—ID 4 and 10—that were measured in 2007 and are 35 cm and 12 m tall respectively

**Table 1** Characteristics of trees measured in September 2007 (ID 1–11) and December 2008 (ID 29–48). *ID* Identifier index, *Age* ontogenetical age (years), *Nphyts* total number of phytomers, *Loc* location (*E* Saint-

Elie, *C* Counami), *H* height, *DBH* diameter at breast height, *AerMass* total aerial fresh mass, *RootMa* fresh mass of the root system

ID	Age	NbPhyts	Loc	H (m)	DBH (cm)	AerMass (kg)	RootMa (kg)
1	2	55	E	3.61	3.9	5.481	0.960
2	2	55	E	2.97	2.3	1.092	0.216
3	2	45	E	2.2	1.2	0.341	0.054
4	1	18	E	0.35	-	0.038	0.009
5	1	29	E	0.08	-	0.002	0.00047
6	2	33	E	0.71	-	0.070	0.030
7	2	37	E	0.77	-	0.125	0.044
8	8	248	E	9.87	9.3	40.720	-
9	3	74	E	7.72	9.5	40.605	-
10	8	391	C	12.64	13.4	71.741	-
11	2	52	E	1.49	1.6	0.486	0.083
29	3	86	C	3.87	2.9	1.057	-
30	2	51	C	1.63	1.1	0.179	-
31	2	67	C	2.92	1.9	0.512	-
40	4	99	C	6.16	5.7	4.092	-
41	2	70	C	1.73	1.2	0.193	-
42	2	69	C	2.98	2.4	0.700	-
48	4	74	C	4.8	4.3	2.389	-

proportional to the ratio of biomass supply to demand,  $Q/D$ , and implies that vigorous plants invest relatively more in their ring compartments, compared to plants that are stressed and have thus a low  $Q/D$  value.

Intra-compartment partitioning is straightforward for the compartments of primary growth and inflorescence growth: each component receives an amount of biomass proportional to its demand. Then, inside each bud, biomass is partitioned between blade, petiole and internode following the allometric proportions  $p_b$ ,  $p_p$ , and  $p_i$  (see section on [Data analysis](#) in the [Results](#)). The partitioning of ring biomass to each phytomer follows principles similar to those of the Pipe model of Shinozaki et al. (1964): each internode receives an amount of biomass proportional to its length and to the total area of blades localised above it in the tree architecture (see Letort et al. 2008 for further details).

Allometric relationships link organ volume and geometrical dimensions. Internode length  $l$  is calculated from internode volume  $V$  by assuming a cylinder shape:

$$l = Be \cdot V^\beta \tag{6}$$

where  $\beta$  is a unitless parameter. Foliar blade area  $S$  is calculated from blade mass  $M$  by:

$$S = \frac{M}{SBM} \tag{7}$$

where  $SBM$  is the specific blade mass ( $\text{g cm}^{-2}$ ). The parameters  $Be$  and  $SBM$  are of special interest for *Cecropia*

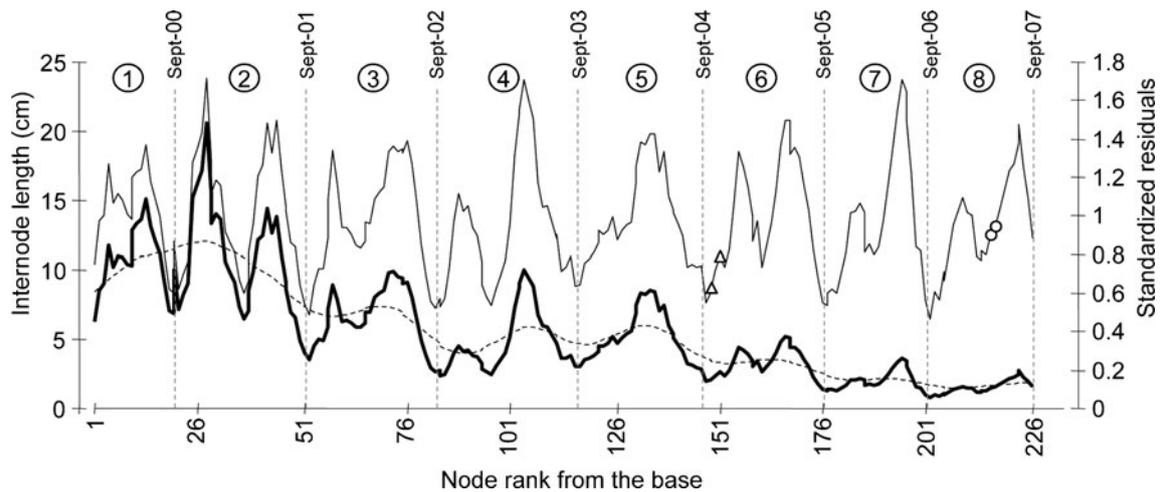
since they have a strong influence on the source–sink balance: internode length determines ring demand and blade area determines plant biomass production. It was also observed that these parameters vary with time and among individuals. Therefore, a mechanistic modelling was the objective: these allometries were set dependent on the source–sink balance of each plant. Classically, the ratio of biomass supply to demand,  $Q/D$ , is taken as a key variable of the GreenLab model and is considered as an index of the level of internal trophic competition (Mathieu et al. 2009). Here, the variations of  $Q/D$  are from two sources: the medium-frequency variations represent the response of the plant to seasonal environmental stress while the low-frequency variations represent the global trend of trophic competition. Since it seems unrealistic to have such rapid variations of these allometries, we extracted this low-frequency trend as follows: we defined the variable  $A_T[Q/D(t)]$ , which is the moving average of the  $Q/D$  values over the previous year. For the sake of simplicity,  $[Q/D(t)]$  is used hereafter instead of  $[Q(t)/D(t)]$ .

Thus, the following equations were chosen:

$$(1) Be(t, k) = Be_{\min} + Be_{\text{var}} \cdot e^{-K_{Be} \cdot k \cdot A_T(Q/D(t))} \tag{8}$$

at GC  $t$  and rank  $k$ , where  $Be_{\min}$ ,  $Be_{\text{var}}$  and  $K_{Be}$  are the parameters to be estimated.

$$(2) SBM(t) = \text{Min}\{SBM_{\max}, SBM_{\min} + K_{SBM} \cdot A_T(Q/D(t))\} \tag{9}$$



**Fig. 2** Age determination for tree 10. Internode length along the main stem (*bold line*) and standardized residuals (*thin line*) obtained after extraction of the trend by a moving average filter, together with

localization of branches (*triangles*) and inflorescences (*small circles*) used to delineate the different annual growth segments

where  $SBM_{max}$  is the SBM at measurement date, input for each tree,  $SBM_{min}$  is the minimal observed value and  $K_{SBM}$  is the parameter to estimate.

Additionally, leaf functioning duration was also set as an affine function of  $A_T(Q/D)$ . It was indeed observed that the number of active leaves varied with tree development and environmental conditions. A leaf appearing at GC  $t$  will stay photosynthetically active during  $T_a$  GC:

$$T_a(t) = T_{a,min} + K_a \cdot A_T(Q/D(t)) \quad (10)$$

where  $T_{a,min}$  is the minimal value observed and  $K_a$  is a parameter to be estimated.

## 2.5 Parameter identification of the model

Some allometric relationships were first estimated directly from the data, using the linear regression method `lm` from the stats package of the R software (R Development Core Team 2008, v2.8.1). In particular, we used the 2007 data to derive a model of faithful prediction of blade area using petiole fresh sectional area. Indeed, biomass production is exported to the rest of the plant through the petiole so large blades are associated to petioles with large sectional area. The allometry was then applied to estimate blade areas for the 2008 data.

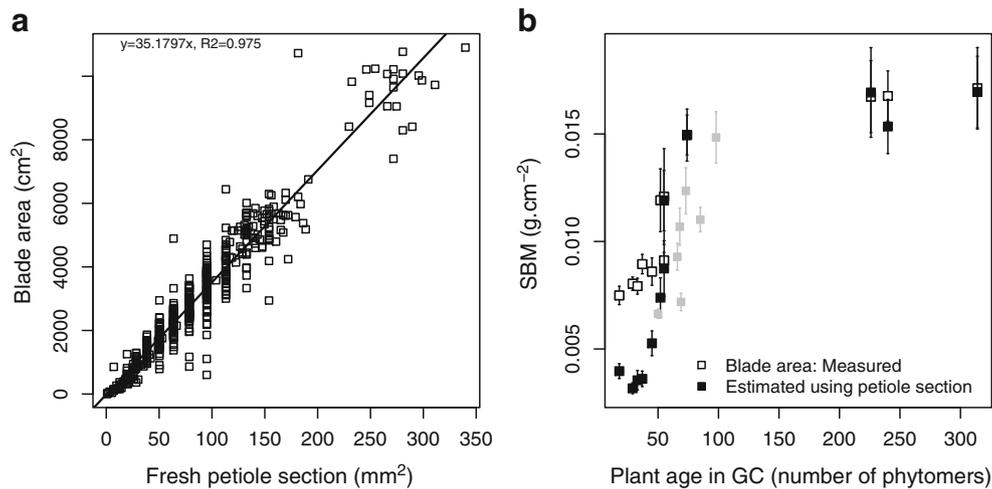
Target files were filled with the data of tree topology (position of branches and inflorescences), and data of organ mass and dimensions for the 11 trees from the 2007 sampling: dry mass, length and diameter of internodes; blade dry mass and area of blades; petiole dry mass; and inflorescence dry mass, for each phytomer. The topological position of branches and inflorescences were assigned for each tree. Additionally, a file giving the number of phytomers emitted per year was used as an input for each plant, based on the annual growth

delimitation. The shape of environmental variations was set using the parameters estimated on the precipitation data. The estimation of the relative local index for each site and of the remaining hidden parameters was performed using Digiplant software (Cournède et al. 2006). An adaptation of the two-stage Aitken estimator was used, where the observations are classified into groups with respect to the type of organs (which have potentially very different size orders); the error term of each group has common unknown variance and errors are mutually independent (Zhan et al. 2003; Cournède et al. 2011). Only the data from the 2007 protocol were used for estimating the model parameters. The data from 2008 protocol were then used for validation, using the same file formats, and estimating only their relative local index of environment.

## 3 Results

### 3.1 Data analysis

Figure 1c,d shows two of the measured individuals (ID 4 and 10). Table 1 presents some characteristics of the measured trees. Tree age was assessed from the procedure of year delimitation based on the sequence analysis of organ dimensions along the main stem, and based on the position of branches and inflorescences when they were present (Fig. 2). The oldest measured trees are 8 years old and had approximately 230 phytomers on the main stem. There is large inter-tree variability: for instance, tree 9 is 5 years younger than tree 8 but is nearly as large (ca. 40 kg). For trees 1, 2, and 30, which all have between 50 and 55 phytomers, aerial mass varies from 0.2 to 5.5 kg.



**Fig. 3** **a** Foliar blade area with respect to fresh petiole section, and **b** dry specific blade mass (SBM) calculated using measured blade area (filled symbols) or blade area estimated using the petiole fresh

sectional area (open symbols). Gray symbols represent plants from the 2008 measurements for which blade area was not measured

Root dry mass was measured for the eight youngest individuals of 2007 measurements. The ratio between root mass and total mass was found of 0.19 in average (SD=0.06). There is some evidence in the literature (McConnaughay and Coleman 1999; Weiner 2004) that this ratio varies with plant age. However, no data were available so it was taken as a constant.

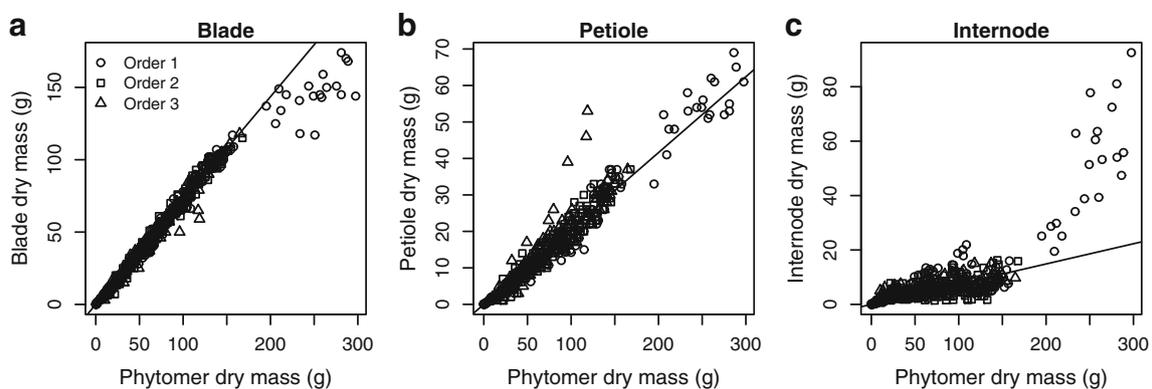
The allometry relationship between blade area (cm<sup>2</sup>) and petiole sectional area (mm<sup>2</sup>) was obtained using  $n=523$  data points, giving a coefficient of 35.18 ( $R^2=0.975$ ; Fig. 3a). More precisely, a key variable of our model is the SBM (blade dry mass/ blade area); Fig. 3b shows the comparison between SBM calculated from measured or estimated blade areas. The results are satisfactory except for low values in the petiole section.

For intra-phytomer partitioning of biomass, observations of young phytomers ( $n=540$  phytomers where leaves are present) suggested a linear model of organ dry mass with respect to phytomer dry mass. To be biologi-

cally realistic, organ mass was forced to zero when phytomer mass is zero. Figure 4 and Table 2 present the results for blades ( $y=0.7177 x$ ,  $R^2=0.99$ ), petioles ( $y=0.2080 x$ ,  $R^2=0.97$ ) and internodes ( $y=0.07423 x$ ,  $R^2=0.81$ ). Note that individual 9 was not included (although represented on the graphs) since its high values of internode mass led to the suspicion that secondary growth might not be negligible for this individual even on young phytomers.

### 3.2 Environmental factor representing precipitations at St Elie station

Analysis of our precipitation data showed that the so-called “short summer of March” was more likely found in February ( $m=4$  in Eq. 4). The parameters estimated for environmental fluctuations over an average year are given in Table 2. The comparison between recorded and fitted data is presented in Fig. 5.



**Fig. 4a–c** Biomass allocation for primary growth with respect to phytomer dry mass, for each branching order. **a** Blade dry mass, **b** petiole dry mass, **c** internode dry mass

### 3.3 Fitting results

Table 2 groups the values of all parameters used in the simulations. The values of the model-hidden parameters and individual local environment indices were estimated using the 11 individuals of the 2007 sampling. Fitting the data of organ dimensions and mass data in parallel led to more than 4,600 data points, while the number of degrees of freedom (number of parameters to identify in parallel) was 24. Some parameters were fixed, based on observations and biological knowledge: the initial biomass, coming from the seed, was set to 0.1 g; the parameter  $\beta$  defining internode shape was set to 0.9 since internode length was highly variable; duration of inflorescence expansion was

observed to last approximately 7 GC; the initial value of leaf functioning duration was set to 7 according to the minimal number of active leaves observed on young plants; primary growth compartment (buds) was chosen as the reference for the model of proportional sinks and could be set arbitrarily: the value 10 was chosen. It is interesting to note that the ratio between the sink bud parameters  $K_b(1)$  and  $K_b(2)$  is 1.04, which means that the demands of the apical meristem on branches follows nearly the same trajectory as that of the main stem. The parameters  $P_{rg}$  and  $K_{rg}$  are close but the resulting ring demand consists in fact of approximately 90% of the demand, which in turn depends on the total axis length (linear density of sink strength for rings).

**Table 2** Parameters used in the simulations, parameters for the climate function fitted on Saint Elie precipitation data, allometries estimated directly from the data, relative local environmental index for

each tree (from 1 to 11 for trees of 2007, and from 1 to 7 for trees of 2008) and model hidden parameters estimated against the data of 2007

Climate function (temporal variation of the environment)		
$A$	Amplitude	430.8 mm
$B$	Threshold	74.8 mm
$m$	Month of short dry season	4 (February)
$a$	Coefficient short dry season	0.45
Allometries estimated directly from data		
$r$	Biomass proportion to roots	19.00%
$Q_0$	Initial biomass	0.1 g
$p_b$	Blade sink coefficient	0.718
$p_p$	Petiole sink coefficient	0.208
$p_i$	Internode sink coefficient	0.074
$E^i$ : Relative local index for each tree		
2007 trees	1.03; 0.81; 0.62; 0.52; 0.33; 0.37; 0.30; 0.98; 1.12; 1; 0.67	
2008 trees	0.50; 0.37; 0.70; 0.70; 0.36; 0.67; 0.83	
Parameters common to all trees		
$\mu$	Production efficiency	$6.4 \times 10^{-5}$
$P_b$	Bud sink strength	10 (fixed)
$K_b(1)$	Bud sink parameter order 1	0.0062
$K_b(2)$	Bud sink parameter order 2	0.0064
$P_{fl}$	Inflorescence sink strength	4.89
$T_{fl}$	Inflorescence expansion duration	7 GC (fixed)
$a_{fl}, b_{fl}$	Inflorescence parameter expansion	1.82, 22.8
$P_{rg}$	Linear sink strength of rings	$0.024 \text{ cm}^{-1}$
$K_{rg}$	Q/D-coefficient sink of rings	$0.024 \text{ g}^{-1}$
$SBM_{min}$	Initial SBM	$0.00749 \text{ g cm}^{-2}$ (fixed)
$K_{SBM}$	Q/D-coefficient for SBM	$0.0012 \text{ cm}^{-2}$
$\beta$	Internode shape coefficient	0.9 (fixed)
$Be_{min}$	Initial Be (internode shape coefficient)	75.1
$Be_{var}$	Variation amplitude of Be	2.66
$K_{var}$	Q/D-coefficient for Be	0.0069
$Ta_{min}$	Initial leaf functioning duration	7 GC (fixed)
$K_a$	Q/D-coefficient for Ta	1.0

Figure 6 presents some of the fitting graphs: measured and simulated values of internode mass, foliar blade mass, petiole mass, and inflorescence mass for the main stems of the 11 individuals. The sinusoidal variations of internode mass are generated by the environmental fluctuations. Although the fitting accuracy seems to be correct upon visual inspection, the coefficients of determination are relatively low (0.43, 0.79, 0.43, 0.45, 0.50 for internode mass, diameter, blade mass, foliar blade area, and petiole mass, respectively) because of the sinusoidal shape of these curves. The coefficients of determination for the cumulated values (internode, foliar blade and petiole compartments) are all above 0.98.

Validation with the 2008 data was as follows: coefficients of determination were 0.43, 0.75, 0.07, and 0.18 for the same variables—except blade foliar area, which was not measured for these trees. The inaccuracy regarding foliar blade and petiole mass is due to variability in the number of active leaves present. For cumulated values, the coefficients of determination are also all above 0.98.

The above fit proves that it is possible to reproduce the large variability that was observed for our target trees with a common model where the environmental pressure is integrated into a single factor.

The variations in the biomass supply to demand ratio  $Q/D$  are presented in Fig. 7. The strong fluctuations are related to seasonal variations of the environment. The inset graph shows the global trend of  $Q/D$ : its values were averaged over 1 year. A strong increase was observed after the appearance of the first tier of branches for trees 8 and 10. In contrast, the growth inflorescences decreased the  $Q/D$  ratio. As expected, trees with the largest local environmental index  $E^I$  (trees 1 and 9, for instance) had dominant  $Q/D$  trajectories. The influence of  $E^I$  on  $Q/D$  is nevertheless not linear since many other variables come into play, among which the organogenesis dynamics, especially the time of emergence within

the seasonal fluctuations, or the feedback effects of the  $Q/D$  ratio on allometries defining organ dimensions and on ring demand.

#### 4 Discussion

The relative simplicity of *Cecropia* architecture makes it possible to analyse the growth of this tree with the GreenLab model, using a complete description at the same scale as the simulation scale. A total of 18 plants (11 for model calibration and 7 for model evaluation) were included in the analysis. The advantage of multi-fitting (i.e. fitting several plants in parallel) with GreenLab has been demonstrated for crops (Guo et al. 2006) and is even more crucial for trees given their high variability. By fitting several plants in parallel, we expect to extract a set of stable parameters that would be representative of the species, and to avoid overfitting, i.e. the possibility that fitting would be significantly perturbed by individual random particularities of single plants (Guo et al. 2006). Additionally, it allows the robustness of the model and its ability to simulate several plants with the same parameter values to be tested, with only one site-specific factor explaining the observed variability.

Simulations using the parameter values estimated in this multi-fitting process provide the dynamics of the different biomass compartments and of the biomass supply-to-demand ratio ( $Q/D$ ) for each plant. No obvious conclusion can be drawn concerning the link between this ratio and the appearance of the first tiers of branches and inflorescences. Nevertheless, it shows that tree 8 has a  $Q/D$  value a bit lower than that of tree 10, which might explain its later emission of branches. But given that tree 9 had a very high  $Q/D$  ratio but no branches, it is likely that factors other than trophic competition are involved in the appearance of

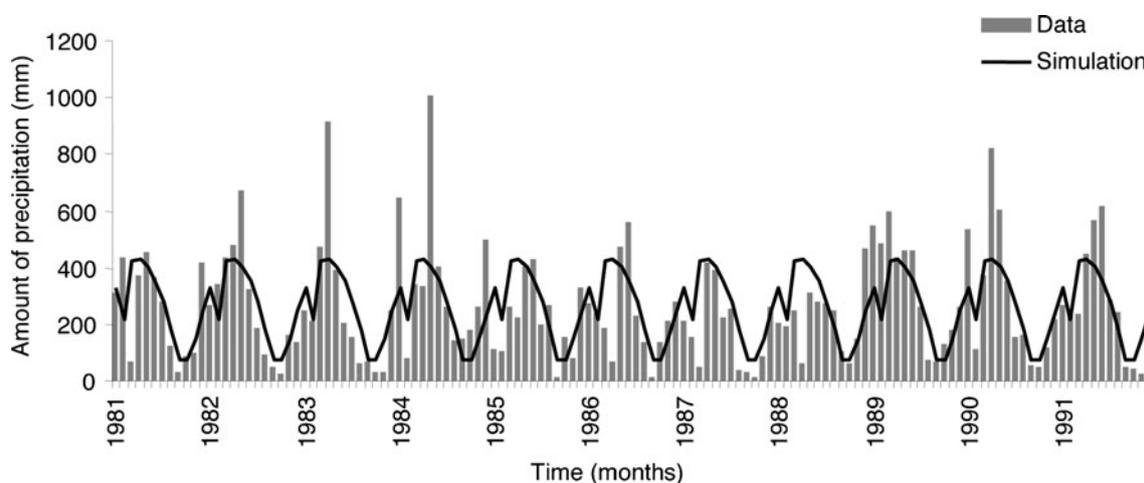


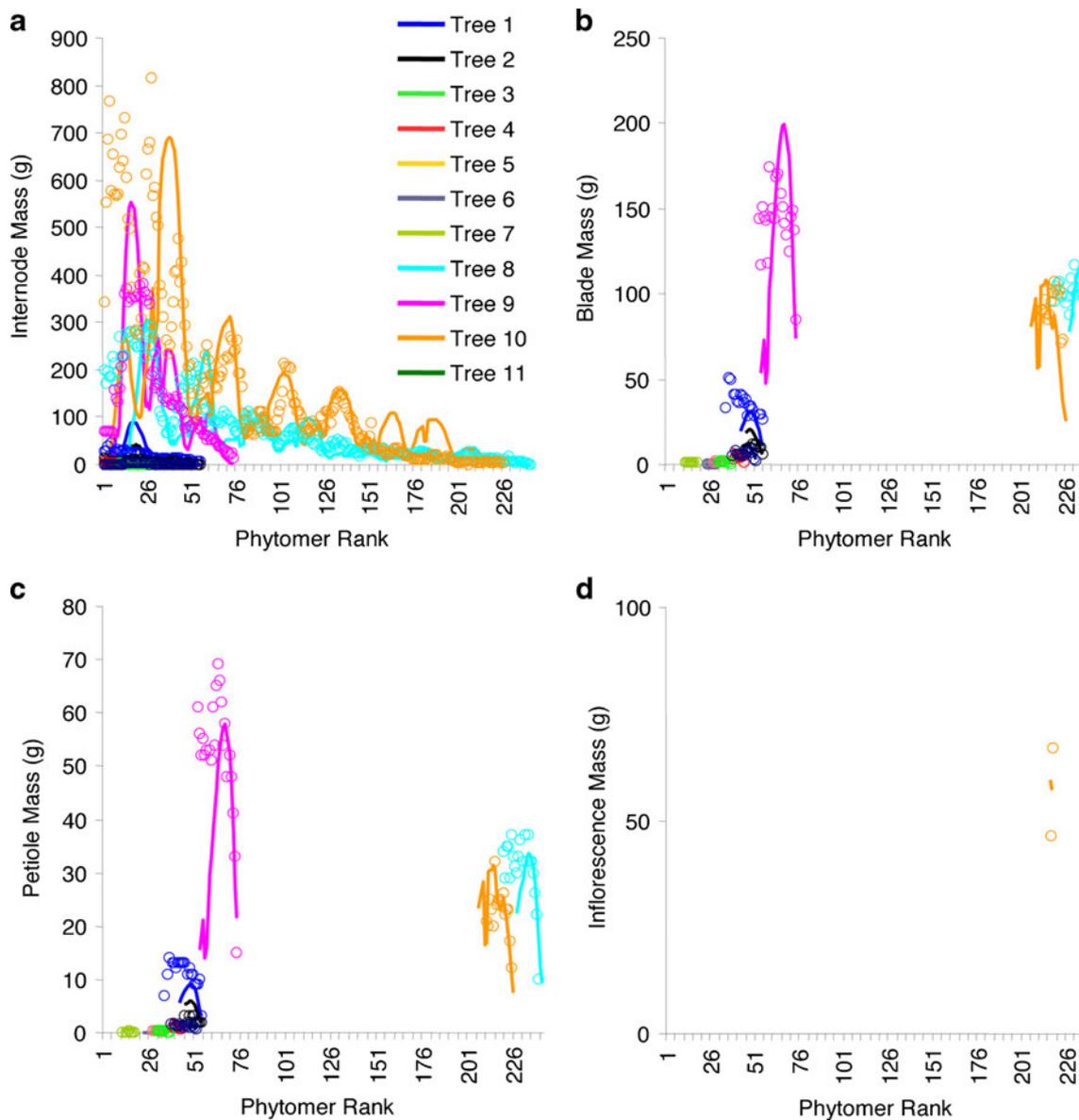
Fig. 5 Fitting of precipitation data from Saint Elie station, obtained from Sarrailh (1992)

branches. From Fig. 7, it seems that branches contribute greatly to plant production and are more sources than sinks. The interpretation of Fig. 7 suggests new hypotheses for the senescence of *Cecropia*: when an axis grows in height, its production tends to reach a saturation level, while its demand increases steadily because of the increasing load of rings. If no branches appear, this would end with the death of the plant.

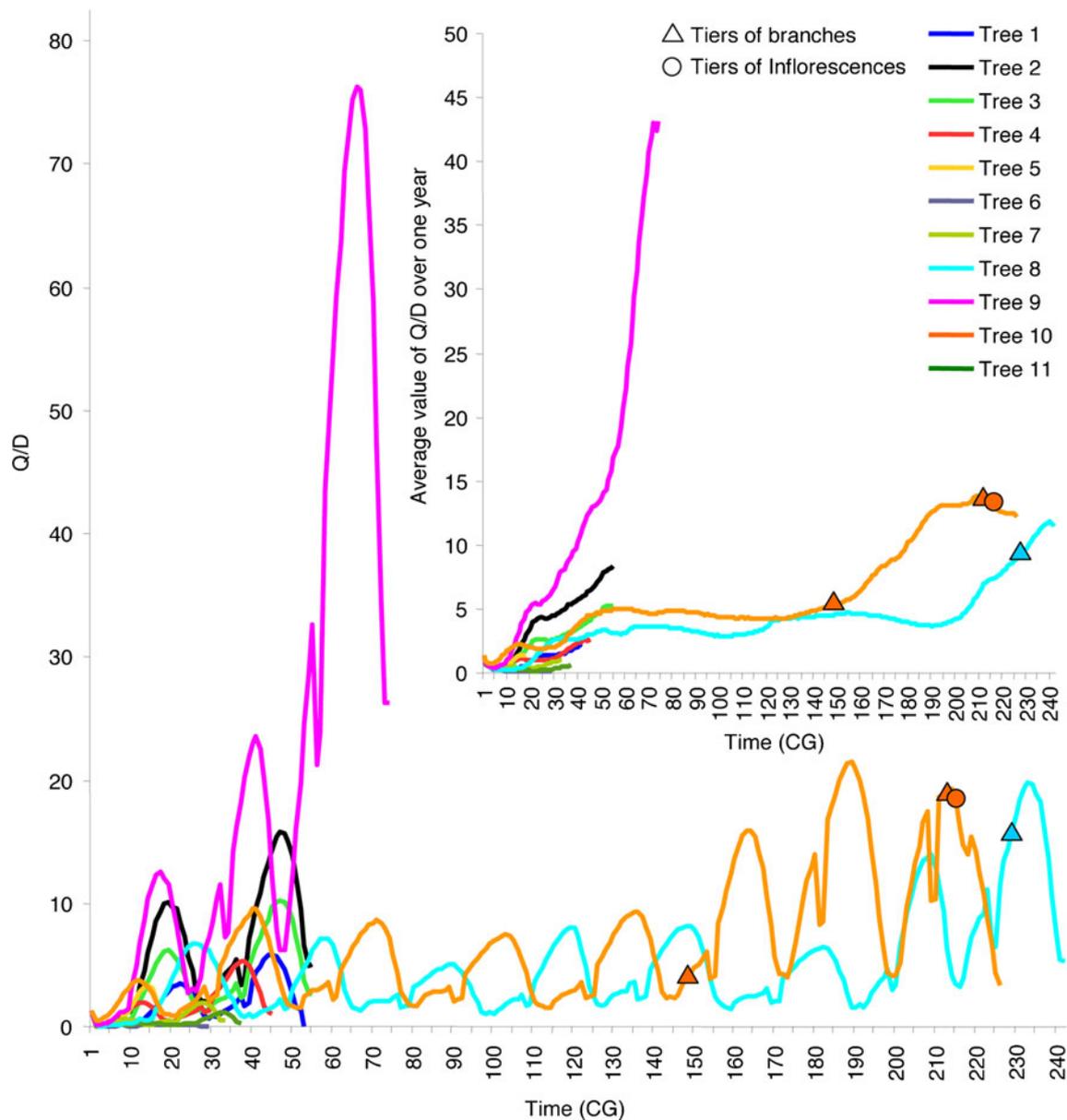
However, this behaviour is linked strongly to the modelling choice, as illustrated by the comparison with the curves found in Letort et al. (2009), which were obtained in a constant environment and with a less mechanistic model. In particular, several weaknesses of the current model can be highlighted. Two variables are still input directly into the simulation

instead of being modelled: the maximal value for the specific blade mass and the number of phytomers emitted per year. The latter is the more important when considering the annual environmental variations, since a difference in phase would perturb the fitting results. But questions remain on which factors affect organogenesis rhythm more, and it is likely that strong random effects induce the variability observed during the first years after plant emergence.

A second question that arises from this work is the possible existence of interactions between plant structure and its strategy for biomass allocation. First, the presence of stilt roots has been observed on some individuals, but these were considered as part of the root system in this study. However, given the particular candelabrum-like architecture



**Fig. 6** Measured (*dots*) and simulated (*lines*) values of **a** internode mass, **b** blade mass, **c** petiole mass and **d** inflorescence mass for the main stems of the 11 individuals from the data of 2007



**Fig. 7** Variations in the biomass supply to demand ratio ( $Q/D$ ): values at each growth cycle and average values over one year (*inset*) to extract the global trend. *Triangles* and *circles* represent the date of appearance of branches and inflorescences, respectively

of *Cecropia* and the great heights that they can reach rapidly, one hypothesis could be that the appearance of stilt roots, as well as the demand of the ring compartment, could be influenced by requirements to ensure the mechanical stability of the tree. This hypothesis could be investigated in parallel by both experimental and model-based approaches: indeed, since the calibrated model faithfully reproduces internode masses and dimensions along the main stem, it would be possible to calculate the biomechanical stresses in the trunk at each growth step, as done by Qi et al. (2009) with the GreenLab model for a virtual tree. Thus, virtual experiments could be performed to help understand the potential relationship between ring

increment or stilt root growth and the mechanical stability of the tree.

One contribution of our study was the introduction of an environmental factor that consisted of two parts: one corresponding to medium-frequency variations and the other to low-frequency variations. The first is related to the amount of precipitation over an average year; and the other, which is constant through time and set for each individual, represents the global level of environmental pressure on the plant and corresponds to the integration of many different factors. This might look like an oversimplification in contrast with most FSTM, which integrate the effects of many environmental factors (for example PAR,

water, nitrogen content) on the plant growth at fine scale (e.g. Lopez et al. 2008). But, under natural conditions, it is difficult to characterise the environment of each plant in detail, or to unravel the respective influences of the different factors, because of the numerous local heterogeneities. The choice of a single, integrative factor might then be considered and, in our study, the large inter-plant variability of the data was successfully reproduced. The interest of a model where tree growth and, potentially, architecture (see Mathieu et al. 2009) are driven by a single environmental factor, is that it paves the way to extension from individual-based models to population level models (Cournède et al. 2008). Indeed, scaling to the stand level requires simplifications and the use of an integrative competition index. The low-frequency part of the environmental factor, which was set as constant in our study, could be linked to the competition status of the tree. Since tree architecture is modelled explicitly, it could also help define the foliage density indices that are used in models representing the tree crown by its envelope shape (e.g. Pretzsch 2002) or by a stratified module shape (e.g. Sorresen-Cothorn et al. 1993). This model would thus be an extension of the classical distance-dependent individual-based models of stand growth.

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