MODULE RESPONSES IN A TROPICAL FOREST TREE ANALYZED WITH A MATRIX MODEL

F. J. Sterck,[1,2,3,5] F. Bongers,[2] H. J. During,[1] M. Martínez-Ramos,[3] and H. De Kroon[4]

[1]Utrecht University, Plant Sciences, P.O. Box 80084, 3508 TB Utrecht, The Netherlands
[2]Wageningen University, Forest Ecology and Forest Management Group, P.O. Box 342,
6700 AH Wageningen, The Netherlands
[3]Centro de Investigaciones en ecosystemas, Universidad Nacional Autónoma de México, Morelia, Michoacán,
C.P. 58190, México
[4]Nijmegen University, Experimental Plant Ecology, Toernooiveld, 6525 ED Nijmegen, The Netherlands

Abstract. Module dynamics were studied for the shade-tolerant canopy tree species *Vouacapoua americana* in a French Guiana rain forest. A module life cycle graph was constructed, including all the possible transitions between four module states: apically growing (G), apically dormant (D), apically arrested (A), and branching (J). Transitions (module level) were translated to the module population growth rate λ (tree level) and related to the variance in λ among 18 different trees. This variance was also related to light availability (1–60% of ambient PAR) and tree height (5–30 m).

Three module life cycle pathways (or loops) were dominant in their contributions to λ: persistent apical dormancy (D→D), biannual apical growth (G→D→G), and biannual branching by dormant modules (J→D→J). This suggests that biannual or even slower module production rates predominate in the module life cycle. The positive covariance between biannual loops seems the result of synchronization in apical and axillary activity. Slow production rates and synchronization allow trees to accumulate carbon, flush massively, and escape from herbivore attacks, and at the same time allow the tree to replace its leaves.

The variance in λ (*V*(λ)) among trees was low. Apical trade-offs, which occur as one apical fate excludes other apical fates by definition, lead to negative covariances between apical growth and apical dormancy, and thus reduced the net contributions of the apical transitions to the variance in λ among trees. Branching (D→J) was independent of such trade-offs, was highly variable, increased with light availability, and almost fully accounted for *V*(λ). Module fates and *V*(λ) were unaffected by tree height.

The module mechanisms underlie the rather invariable module population growth rate λ in the shade, as well as the increasing λ during higher light episodes, enabling shade-tolerant canopy trees to grow up and survive in a heterogeneous forest light environment.

Key words: elasticity analysis; forest canopy; light response; loop analysis; modular growth; sympodial unit; tree architecture; tree development; up-scaling; variance decomposition analysis; Vouacapoua americana.

INTRODUCTION

Tropical rain forest trees grow up in a highly variable and dynamic light environment (Chazdon and Fetcher 1984, Sterck et al. 1999, Nicotra et al. 1999). Responses in physiological, morphological, and developmental plant traits determine their growth, survival, and reproduction in such an environment (Canham 1988). Many studies have shown how responses at the leaf (e.g., photosynthesis) and whole-plant level (e.g., biomass partitioning) contribute to growth and survival, particularly in seedlings and saplings (Veneklaas and

[5] Address for correspondence: Wageningen University, Forest Ecology and Forest Management Group, P.O. Box 342, 6700 AH Wageningen, The Netherlands.
E-mail: frank.sterck@wur.nl

Poorter 1998) and pioneer species (Ackerly 1996). However, responses at the module level (defined as the axis produced by an apex, Prévost 1967) have been neglected in a majority of such studies, as well as in studies scaling leaf to whole-crown processes (e.g., Horn 1971, de Pury and Farquhar 1997).

The fate of a module depends on its apex and lateral meristems. In trees, a module remains dormant when the apex is dormant, becomes arrested when the apex dies (or flowers) or the module breaks, grows in length when the apex produces new leaves, and branches when one or more lateral meristems produce new modules. The joint fate of all modules in a crown drives the demography of modules at whole-tree level, and determines the future module population size and the vegetative and reproductive growth capacity of the tree (Watson and Casper 1984, Tuomi and Vuorisalo 1989, Geber 1990). In this context, the performance of a tree

may be expressed by the growth rate of its module population. Module studies of trees, however, have largely neglected demographic module responses (White 1984). Instead, studies have presented architectural and developmental descriptions (Halle et al. 1978, Valladares 1999), morphological responses underlying crown photosynthesis (Honda and Fisher 1979, Sterck 1999), and morphological responses to light variation within crowns (Sorrensen-Cothern et al. 1993, Stoll and Schmid 1998). Matrix models have been used to investigate the consequences of bud demography for the growth rates of bud populations (Maillette 1982a, b, 1987, Jones 1985, Lehtilä et al. 1994), but have not explicitly addressed demographic module responses to environmental factors such as light. Here we apply the latest matrix modeling tools to investigate the consequences of demographic module responses to light for growth rates of module populations in juvenile trees of a shade-tolerant canopy tree species, *Vouacapoua americana* (Caesalpiniaceae, Fig. 1), in a French Guiana lowland rain forest. In line with the matrix model terminology (Caswell 2001), the growth rate of the module population in a tree is symbolized by λ, and the variance in such growth rates among different trees by $V(\lambda)$. We discuss module responses as the missing link between leaf responses and λ, allowing a tree to grow under and plastically respond to the highly variable light environment of the tropical forest.

Our first question is how module responses translate to the module population growth rate, λ. The question was investigated using the average of 18 matrix transition models, each for an individual. These trees differed in size (4–30 m) and light environment (1–60% of the open sky light). In the average matrix model, the transitions represent the average probabilities of switching between four alternative module states: apically growing, dormant or arrested, and branching (the average number of modules produced by each of the apical states). The module life cycle graph shows these transitions (Fig. 2), and the elasticities quantify the relative contributions of these transitions to λ (e.g., de Kroon et al. 2000). Modules follow alternative life cycle pathways (or loops, Fig. 2 B–D): the closed circuits of transitions that return to the same module state and do not encounter any module state more than once, and contain at least one unique transition (van Groenendael et al. 1994, Wardle 1998, Fig. 2). Only the transitions that are part of one or more of such loops contribute to λ. Loop analysis allows one to decompose the module life cycle graph into a limited number of ecologically relevant alternative module life cycle pathways, such as annual apical growth, persistent apical dormancy, or biannual apical growth (in which the dormant and growing state of the apex alternate), and to quantify the contributions of these pathways to λ.

Our second question is how module responses contribute to the variance in λ among trees in a rain forest.
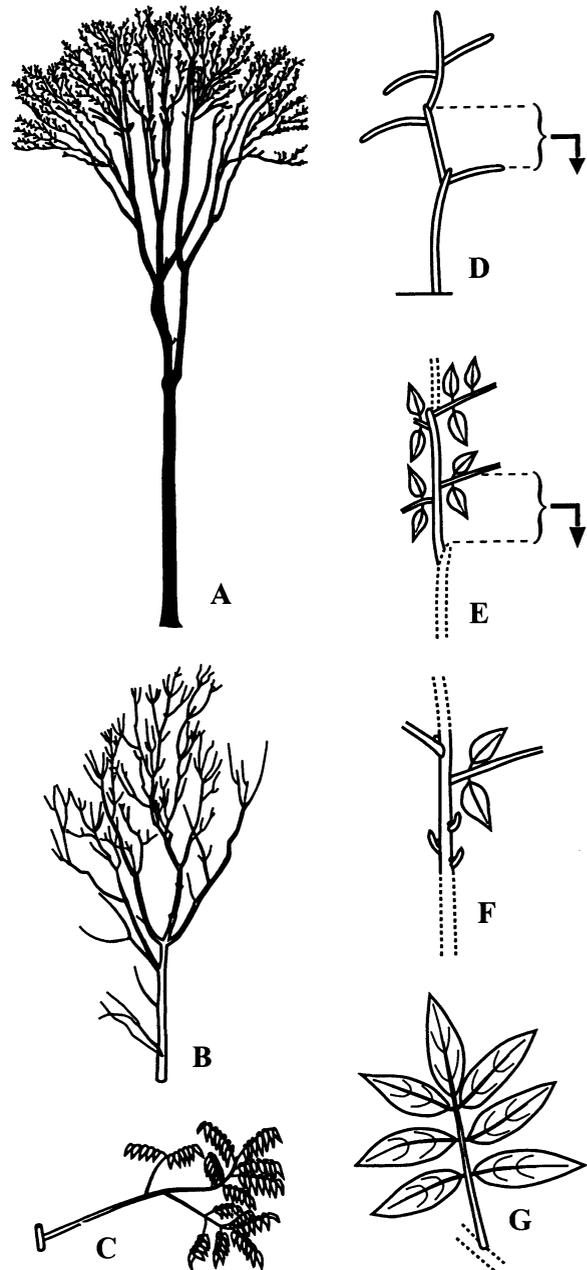
FIG. 1. *Vouacapoua americana* (the left panel has been adapted from Loubry [1994], our interpretation): (A) habitus of an adult tree (~35 m) and (B) habitus of a branch (~5 m). The thickest and straightest sympodium (sequence of modules) probably represents the future stem. (C) Habitus of a young branch (~1 m); the main module consists of two extension units, of which the proximal one supports side modules and the distal one leaves. The side modules consist of one extension unit. (Right panel, adapted from Sterck [1999], the plant component hierarchy): (D) the spatial organization of modules; (E) the module is the axis produced by one apical meristem; (F) the extension unit is produced during a flush and consists of proximal metamers with scale leaves and distal ones with (photosynthetic) leaves; (G) a photosynthetic compound leaf.

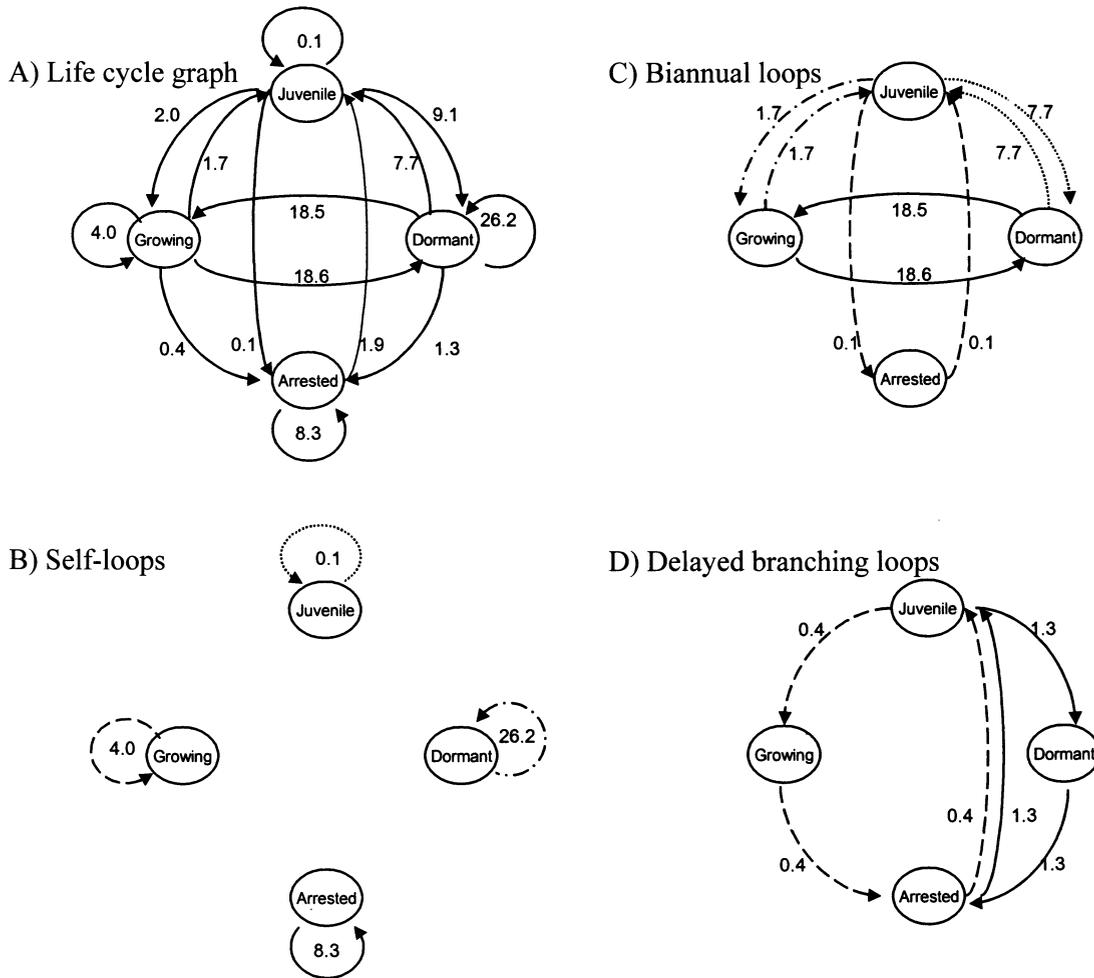FIG. 2. Description of the module life cycle graph and the alternative life cycle pathways (or loops), following loop analysis. Four different model states are given in the four boxes: an apically *growing* module (**G**), producing new leaves by producing a new extension unit at the apex; an apically *dormant* module (**D**); an apically *arrested* module (**A**), the apex being aborted or the module being broken; a *juvenile* module (**J**), produced by an axillary meristem. Values along arrows are elasticities of the mean matrix and are presented as percentages. (A) The full life cycle graph is subdivided into 10 loops belonging to three categories: (B) self-loops, (C) biannual loops, and (D) delayed branching loops. (Note that the two central arrows refer to the same transition: arrested–juvenile.) Elasticities belonging to loops are given in parts B–D: these are the characteristic elasticities of the pathway and are identical for all transitions of the same loop (see Table 3 for terminology). Different loops are represented by different line styles.

This question is addressed by investigating the projection matrices of the 18 individual trees in more detail. A variance decomposition analysis (Brault and Caswell 1993, Caswell 2000) quantified (1) the variances and covariances among transitions and life cycle loops and (2) the contributions of these (co-) variances to the variance in λ. These contributions depend on the absolute contributions of transitions and loops to λ (sensitivities), and on the variances and covariances among the transitions and loops (see *Methods* for details). The results of this analysis are interpreted as responses of an individual tree to its light environment and its height, and, in turn, as responses underlying the variation in the module population growth rate λ during the life of a tree in a heterogeneous rain forest.

METHODS

Site and species

Field work was carried out in a pristine lowland rain forest at the Nouragues biological field station (4°05' N; 52°40' W), French Guiana (Bongers et al. 2001). Annual rainfall is ~3000 mm, with dry seasons (<100 mm) in September and October, and sometimes in March. The forest is covered with well-drained, clay to sand–clay soils on weathered granite (Grimaldi and Riera 2001), and dominated by species of the Lecythidaceae, Leguminosae, Sapotaceae, Chrysobalanaceae, and Burseraceae (Sabatier and Prévost 1989).

Vouacapoua americana Aubl. (Caesalpiniceae) is abundant in the canopy of the Nouragues forest. Gen-

erally, Caesalpiniaceae and other Legume species are (co-) dominant in many neotropical forests and, similar to our study species, most are characterized as shade tolerant (e.g., Schulz 1960) and conforming either to Troll's model of canopy architecture, or to other mixed plagiotropic models (Oldeman 1989).

In *Vouacapoua*, a module consists of one or more extension units, i.e., the structures produced by the apex during one flush. Each extension unit consists of 5–10 proximal scale-leaf-metamers and 1–10 distal photosynthetic-leaf-metamers (Fig. 1 F, see also Loubry 1994). Initially, one lateral meristem is found in each of the axils of photosynthetic leaves and scale leaves. A module branches when one or more lateral meristems produce modules, thus turning into the apices of new juvenile modules. A module is dormant when the apex is dormant, grows in extension when the apex produces a new extension unit, and becomes arrested when the apex dies or the module breaks. Note that a module that is considered dormant or arrested may still branch and produce juvenile modules. In the long run, the modules may individually die and fall off the tree, die as part of a dying ramified branch, or become part of the basic woody structure. In the latter case, the modules usually stay in the arrested state.

In the crown, the stem usually leans over to support a horizontal spray of distichously arranged leaves and the process is repeated at different positions in the crown as a result of modules sprouting from the bends. Stem and branches are inseparable from one another in young crown parts, until the stage in which one branch straightens vertically and continues secondary growth to become the stem, while the other branches fall or develop in a more horizontal direction (Fig. 1, left panel).

Field methods

A population of trees was monitored from October/November 1992 until October/November 1997 as part of a long-term study of tree growth (Sterck et al. 2001). In a 12-ha plot, trees with stem diameters ≥10 cm at 1.30 cm (dbh) were mapped. In a central 1.5-ha plot, trees with stem diameters <10 cm, but with heights >0.5 m, were mapped. From this inventory 18 4–30 m tall trees were selected for this study, i.e., those individuals that had sufficient modules to obtain reliable estimates of the various module fates.

At the start of the census period (November 1992) every crown was drawn to scale and a sample of modules in the crown periphery was marked, while all the modules in the crown periphery were marked in smaller crowns. Module fates (branching, growth, dormancy, arrested, module death) were determined annually over a period of five years (1992–1997) for selected and new juvenile modules (result of branching), by climbing taller neighboring trees with alpinist ropes or spikes, or by constructing rope bridges.

In 1992 and 1997, tree height was measured with 50-m tapes (marked in centimeters) providing height measurements with an error <0.1 m. In 1993, light intensity was measured continuously above each crown center during 1–2 days, using LI-COR SA-190 sensors (LI-COR, Lincoln, Nebraska, USA) measuring photosynthetic active radiation (PAR, with light spectrum ~400–700 nm). PAR sensors were leveled horizontally and fixed just above the crown center. At the same time, one PAR sensor was leveled above a 52 m tall emergent canopy tree, towering above its tree neighbors and thus providing open-sky PAR values. Using LI-COR L-1000 dataloggers, PAR values were integrated and logged every five minutes between 0600 and 1800 hours. From these measurements we calculated light availability as the crown-PAR to reference-PAR ratio.

Construction of matrices

The various module pathways are summarized in the module life cycle graph (Fig. 2). We distinguished four different module states: growing (G) modules as the ones that recently (<1 year) formed new leaves and grew in extension; dormant (D) modules with a dormant apex during the last year; arrested (A) modules with a dead or aborted apex, or broken below the apex; juveniles (J) as newly formed modules due to branching events (<1 year ago). The data set provided a number of initial module states and their transitions for five consecutive years (1992–1993 to 1996–1997). These data were for most trees too limited to construct five annual transition matrices per tree. They were, however, sufficient to construct a single matrix per tree by dividing the number of transitions for a given module by the number of modules in this state, summed over the five transition periods. The transition probabilities were based on the observations of 4–74 modules per tree over the period of five years. Subsequently, the matrices were averaged over all 18 trees so as to obtain a mean matrix.

Analysis of the mean matrix

The module population growth rate λ of the mean matrix was calculated using a stage-based matrix model (Lefkovitch 1965):

$$\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t) \qquad (1)$$

where $\mathbf{n}(t)$ and $\mathbf{n}(t + 1)$ are population structures at time t and $t + 1$, respectively, and $\mathbf{A}$ is a square matrix containing transitions among module states (see also Fig. 2). The asymptotic growth rate of the module population is the dominant eigenvalue λ of matrix $\mathbf{A}$ and was calculated analytically (Caswell 2001).

Elasticities e_{ij} quantify the proportional changes in module population growth rate λ due to proportional changes in matrix elements a_{ij} (Caswell 2001). The subscripts stand for the modular transitions of row i and column j in the matrix. Elasticities of the mean matrix were calculated as follows:

TABLE 1. The mean matrix: mean transition values among the 18 trees studied (with variances given in parentheses).

Matrix values	Juvenile (J)	Growing (G)	Dormant (D)	Arrested (A)
Juvenile (J)	· 0.01 (0.001)	0.09 (0.026)	0.20 (0.056)	0.11 (0.032)
Growing (G)	0.16 (0.055)	0.18 (0.048)	0.40 (0.042)	...
Dormant (D)	0.76 (0.127)	0.76 (0.058)	0.52 (0.062)	...
Arrested (A)	0.02 (0.002)	0.04 (0.003)	0.06 (0.005)	0.98 (0.097)

Note: Module population growth rate, $\lambda = 1.127$; variance in λ, $V(\lambda) = 0.0142$.

$$e_{ij} = \frac{\partial \log(\lambda)}{\partial \log(a_{ij})}. \qquad (2)$$

Elasticities sum to 1 and may be interpreted as relative contributions of the modular transitions to λ (de Kroon et al. 1986).

Module life cycles are composed of life cycle pathways (or loops). Loops are defined as closed circuits of transitions that return to the same module state and do not encounter any module state more than once, and contain at least one unique transition (van Groenendael et al. 1994, Wardle 1998) (Fig. 2). Henceforward, loops and transitions will be represented by sequences of module state symbols that have to be read from the left to the right. Two examples illustrate this. (1) Transition DG starts with a module in apical dormancy in year t, which grows in extension in year $t + 1$. (2) Loop JDJ starts as a juvenile produced in year t, the juvenile becomes dormant in year $t + 1$ (JD) and then produces new juvenile(s) in year $t + 2$ (DJ). Note that loops are cyclic and a JDJ loop is synonymous with a DJD loop (see Fig. 2C), and that stasis in one of the four states (e.g., DD) is considered both a transition and a (self-) loop.

The loop elasticity is the product of the "characteristic elasticity," i.e., the elasticity of the unique transition in a loop, and the number of paths in the loop (van Groenendael et al. 1994, Wardle 1998). The elasticities of matrix elements that are part of more than one loop equal the sum of the characteristic elasticities of the loops involved (see Fig. 2, e.g., the JD transition). Loop elasticities sum to 1 and may be interpreted as the relative contributions of the loops to λ.

Light and tree height

Backward linear multiple regression analyses were used to relate the variance in the 14 module transitions to light availability and tree height. Each regression thus started from the full model, with light availability and tree height as independent variables and one transition as the dependent variable. The multiple use (14 times) of the regression was corrected for, using Bonferroni corrections ($P < 0.05/14$, or $P < 0.00357$, Sokal and Rohlf 1995).

Variance decomposition analysis

The variance decomposition analysis consisted of three steps. First, we calculated the variances and co-variances among matrix elements in our sample of 18 transition matrices (one for each individual tree). Second, we calculated the contributions of these variances and covariances to the variance in λ among different trees, $V(\lambda)$. These contributions were calculated as follows (Brault and Caswell 1993, Horvitz et al. 1997):

$$V(\lambda) \approx \sum_{k,l} X_{ij} = \sum_{k,l} \text{cov}(a_{ij}, a_{kl}) \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial \lambda}{\partial a_{kl}}. \qquad (3)$$

This index sums the contributions to the variance in λ of the variance in a_{ij} and all the covariances involving a_{ij}; half of the contribution of $\text{cov}(a_{ij}, a_{kl})$ is allocated to the contributions of a_{ij} and a_{kl} (Caswell 2000). The partial derivatives are the sensitivities of each of the two transitions. The sum of all contributions approximates $V(\lambda)$. Note that contributions of variances are positive because variances and sensitivities are positive by definition. Negative contributions to λ can only be due to negative covariances with other matrix transitions, particularly when negatively covarying transitions have strong sensitivities. A negative contribution of a_{ij} thus indicates that the variability involving a_{ij} reduced λ, while a positive contribution indicates that its variability increased λ (cf. Caswell 2000).

Third, we calculated net variance contributions of the loops to $V(\lambda)$. For each transition, covariance contributions were equally allocated to the contributions of the loops in which the transition appeared. Net contributions to $V(\lambda)$ were calculated by summing the variance and covariance contributions per loop.

RESULTS

Module life cycle

The module population growth rate, λ, of the mean matrix was 1.127 (Table 1). Of the modules, 94–98% survived annually. Juvenile modules tended to die more frequently (6%) than other modules (2%). Juvenile and growing modules became frequently apically dormant (52–76%). Dormant modules grew and branched more frequently than did other modules. Arrested modules were usually in apical stasis, but with an ability to branch. How these transitions contributed to alternative module life cycle pathways was analyzed by a loop analysis.

The module life cycle graph was decomposed into 10 loops: four self-loops, one for each module state (JJ, GG, DD, AA); four biannual loops, with alternate

TABLE 2. Covariances among transitions are shown in the upper right triangle, each value reflecting the covariance between the corresponding top row transition and the right column transition. The contributions of covariances to variance in the module population growth among different trees, $V(\lambda)$, are presented in the bottom left triangle, each value corresponding with the top row and left column transitions.

Contributions to $V(\lambda)$	Covariances						
	JJ	GJ	DJ	AJ	JG	GG	DG
	0.06	0.18	0.14	0.05	0.01	−0.03	0.14
		2.57	0.89	0.17	2.62	0.91	0.25
			5.62	0.42	0.21	−1.65	1.95
JJ	**0.00**			**3.15**	0.62	0.22	−0.21
GJ	0.01	**0.11**			**5.49**	1.99	−0.49
DJ	0.01	0.15	**0.99**			**4.77**	−1.01
AJ	0.00	0.01	0.06	**0.11**			**4.20**
JG	0.00	0.15	0.02	0.03	**0.10**		
GG	0.00	0.09	−0.34	0.02	0.13	**0.29**	
DG	0.02	0.05	0.83	−0.04	−0.07	−0.25	**1.07**
JD	0.00	−0.13	0.11	0.06	−0.18	0.01	0.22
GD	0.00	−0.12	0.17	−0.06	−0.16	−0.65	0.12
DD	−0.03	−0.09	−1.37	−0.04	0.04	0.42	−2.63
JA	0.00	0.01	0.00	0.00	0.01	0.01	0.00
GA	0.00	0.00	0.00	0.02	0.01	0.02	0.04
DA	0.00	0.00	0.17	0.03	0.02	−0.06	0.14
AA	0.00	0.05	0.14	0.05	0.05	0.10	0.09
Sums	0.01	0.20	0.98	0.18	0.13	0.03	0.33

Notes: Sequences of capital letters refer to annual module transitions (Fig. 1), to be read from the left (year t) to the right (year $t + 1$), see *Methods*. Bold diagonal values refer to variances. Note that sum calculations (Horvitz et al. 1997, see *Methods*) take the sum of the variance contribution and *half* of the covariance contributions ($= 0.0167$); total variance contribution $= 0.0526$; total covariance contribution $= -0.0359$ (see also Table 3). All values should be multiplied by 10^{-2} to get the actual values.

switching between the growing and dormant apical state (GDG), or between the juvenile state and one of the apical states (JDJ, JGJ, JAJ); two delayed branching loops, with a juvenile module produced on an arrested module, and the juvenile becoming arrested after a year of either dormancy or apical growth (AJGA or AJDA, Fig. 2, Tables 2 and 3). The elasticities strongly differed among loops (Fig. 2). Mean λ depended for >75% on 3 out of 10 loops: biannual apical growth (GDG, 37%), biannual branching (JDJ, 15%), and persistent apical dormancy (DD, 26%). An intermediate elasticity was found for the apical arrested loop (AA, 8%). Apparently, the rather slow module production frequencies strongly contributed to λ, while the lowest elasticities (0–4%) were found for transitions involving continuous apical growth and continuous branching (Table 3), as well as delayed branching.

Light availability and tree height

The λ was positively correlated with light availability, but not with tree height (Fig. 3). Of the module transitions, the branching of previously dormant modules (DJ) increased significantly with an increase in light availability ($R^2 = 0.45$, $P = 0.0030$), but was unaffected by tree height. None of the other transitions was significantly related to light availability and tree height.

Variance decomposition

The contributions to $V(\lambda)$ of the variances and covariances of the 18 transition matrices summed to 0.0167, which can be considered a good approximation to the observed $V(\lambda)$ (0.0142). Covariances were more often positive (59 cases) than negative (31) (Table 2). In absolute terms, however, some contributions of the negative covariances (absolute values) were an order of magnitude larger than the positive ones (in summary: Σ variance $= 0.0527$, Σ positive covariance $= 0.0386$, Σ negative covariance $= -0.0739$). Hence, negative covariance markedly damped $V(\lambda)$.

Apical fates excluding one another had negative covariance contributions, in particular dormant modules that persist in dormant state or turn into growing state (DD and DG, −0.0263) and growing modules that persist growing or turn into dormant state (GG and GD, −0.0065, Table 2). Additionally, persistent dormant state and branching from dormant state had a negative contribution (DD and DJ, −0.0137). The covariance between apical growth from dormant state and branching from dormant state (DG and DJ) had the largest positive contribution (0.0083).

The three life cycle pathways (or loops) with particularly high variance contributions to $V(\lambda)$ were also those that determined the λ of the mean matrix, i.e., persistent apical dormancy (DD), biannual apical growth (GDG), and biannual branching (JDJ, Table 3, Fig. 2). However, the variance contributions to $V(\lambda)$ of the two former loops were reduced by large negative covariances. The variance contribution of biannual apical growth was reduced (from 0.0147 to 0.0018, Table 3) by the strong negative covariances between growing modules that persist in growing and those that turn into

TABLE 2. Extended.

			Covariances				
JD	GD	DD	JA	GA	DA	AA	
0.01	−0.02	−0.26	0.03	0.00	0.07	0.11	JJ
−2.10	−1.1	−0.43	0.36	0.09	0.05	1.09	GJ
0.92	0.77	−3.02	0.09	−0.02	0.88	1.63	DJ
1.12	−0.59	0.22	−0.11	0.41	0.37	1.22	AJ
−4.43	−2.29	0.26	0.68	0.34	0.26	1.70	JG
−0.13	−4.98	1.59	0.20	0.43	−0.49	1.94	GG
1.49	0.54	−4.85	0.01	0.30	0.57	0.92	DG
12.68	−0.03	−1.69	−0.63	0.10	0.06	1.97	JD
	5.75	−0.84	−0.19	−0.73	0.33	−2.57	GD
		6.21	−0.12	−0.32	−1.15	−1.69	DD
0.27			0.15	−0.04	0.09	0.25	JA
0.00	**0.40**		**0.30**	0.02	0.38		GA
−0.26	−0.24	**1.79**			**0.52**	0.65	DA
−0.01	0.01	−0.01	**0.00**			**9.68**	AA
0.00	−0.04	−0.04	0.00	**0.00**			
0.00	0.04	−0.29	0.00	0.00	**0.03**		
0.06	−0.14	−0.14	0.00	0.01	0.03	**0.10**	
0.20	−0.14	−0.57	0.01	0.01	0.08	0.23	

dormant state (GG and GD), and between dormant modules that persist in dormant state and those that turn into growing state (DD and DG). The net contribution of persistent apical dormancy was even negative (from 0.0179 to −0.0057) mainly due to large negative covariances with growth (DD and DG) and branching of dormant modules (DD and DJ). The variance contribution of only the third main life cycle loop, biannual branching, was hardly reduced (from 0.0113 to 0.0108) by covariance contributions. For this loop, the negative covariance contributions were almost fully compensated for by the positive covariance contribution between growth and branching of dormant modules (DG

and DJ). Consequently, the net contribution of biannual branching largely accounted for the total $V(\lambda)$ (0.0142).

Variation and elasticities

The mean matrix elasticities were negatively related with the coefficients of variation of the transitions of the 18 individual matrices (Fig. 4). The transitions with the highest mean elasticity and the lowest coefficients of variation were those in the persistent apical dormancy loop (DD), the apical arrested loop (AA), the biannual apical growth loop (GDG), and the biannual branching loop (JDJ). These transitions had coefficients of variation <53. The production of juvenile modules

TABLE 3. Description of 10 life cycle pathways (loops) for *Vouacapoua americana* in French Guiana; loop elasticities of the mean matrix and contributions to variance in λ, $V(\lambda)$.

Pathway	Description	Elasticity	Contributions to $V(\lambda)$		Net
			Σ variance	Σ covariance	
Self-loops					
JJ	persistent branching	0.001	0.00	0.01	0.01
GG	persistent apical growth	0.040	0.29	−0.26	0.03
DD	**persistent apical dormancy**	**0.262**	**1.79**	**−2.37**	**−0.57**
AA	apical arrest	0.083	0.10	0.13	0.23
Biannual growth					
GDG	**biannual apical growth**	**0.371**	**1.47**	**−1.29**	**0.18**
JDJ	**biannual branching by dormant module**	**0.154**	**1.13**	**−0.05**	**1.08**
JGJ	biannual branching by growing module	0.034	0.16	0.11	0.27
JAJ	biannual branching by arrested module	0.002	0.04	0.03	0.06
Delayed branching					
AJGA	growing after branching by arrested module	0.012	0.09	0.05	0.14
AJDA	dormant after branching by arrested module	0.039	0.20	0.04	0.24
Sums		1.000	5.27	−3.59	1.67

Notes: For calculations, see *Methods*. The three dominant loops (see *Results* and *Discussion*) are shown in boldface. All values should be multiplied by 10^{-2} to get the actual values.
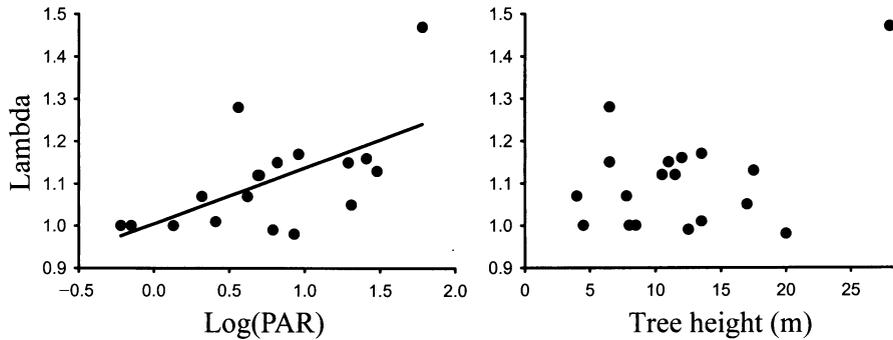
FIG. 3. Relationships of λ with tree height and light availability as $\log_{10}$ values of percentage PAR compared to open sky. Light availability affected λ significantly (backward regression, $P < 0.01$, $R^2 = 0.36$); tree height did not.

by previously dormant modules (DJ) is the exception. It had both a relatively high mean elasticity (7.7%) and a high coefficient of variation (>110%). All other transitions also had a coefficient of variation >110%, but a much lower mean elasticity.

DISCUSSION

In studies of forest trees, module responses have been the missing link between highly plastic light responses at the leaf level, and growth and survival at the whole-plant level. For 18 trees of a shade-tolerant canopy species of the rain forest of French Guiana, we translated fates of individual modules into module transition probabilities, constructed a module life cycle graph, and calculated the module population growth rate λ (tree level). Our results show that λ was mainly determined by three different module life cycle pathways (or loops): persistent apical dormancy (DD), biannual apical growth (GDG), and biannual branching by dormant modules (JDJ). We first discuss how the variances in module transitions, loops, and λ among trees relate to a developmental trade-off at the module and at the tree level. Second, the variances are discussed in the light of physiological and ecological mechanisms (from leaf to tree level), permitting a

shade-tolerant tree to grow to adulthood in a heterogeneous forest light environment.

Variances in development among trees

Trees varied in λ because they differed in module dynamics. Using a variance decomposition analysis, actual contributions of variations in transitions and loops to the variance in λ among trees, $V(\lambda)$, were analyzed. Strikingly, the variance decomposition analysis indicated that contributions to $V(\lambda)$ of variances in module transitions (0.0527) were strongly reduced (to 0.0142) by the negative covariances with other transitions. While negative covariances appear in other published variance decomposition analyses (e.g., Horvitz et al. 1997, Picó et al. 2002), the magnitude of negative covariances in our analysis is surprisingly high.

These negative covariances may be traced back to apical developmental trade-offs at the module level, as one apical fate excludes any other apical fate by definition. These trade-offs are also manifested at the tree level. A higher probability of the persistent dormant module (DD) is accompanied by a lower probability of the dormant module that turns into growing state (DG), and vice versa. Similarly, a higher probability of a
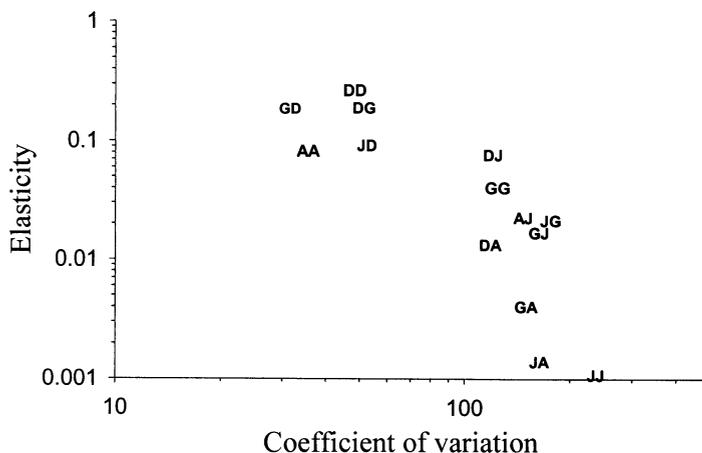

FIG. 4. A negative relationship was found for elasticities of the mean matrix vs. coefficients of variation of the 18 matrixes ($P < 0.001$, $r = -0.85$, Spearman rank correlation test).

growing module turning into a dormant state (GD) was accompanied by a lower probability of the continuously growing module (GG). These results suggest that "competing" apical loops were expressed in different ways in different trees, leading to strong negative covariance contributions that reduced the net contributions of competing apical loops to the variance in λ among trees. Thus, while module fates vary considerably, λ was stabilized by developmental apical trade-offs. Additionally, λ was stabilized by a high module survivorship (>98% for nonjuvenile modules) and the relative invariability in the two dominant apical loops, i.e., persistent dormancy and biannual apical growth.

Branching is represented by the third important life cycle pathway, biannual branching (JDJ). This pathway shared the high contribution to λ (see elasticities) with the two apical loops, discussed in the previous paragraph. The branching transition (DJ), however, differed from the transitions in the two former apical loops in its variability due to responsiveness to light (see also Sterck and Bongers 2001). Furthermore, the DJ transition was independent of other apical fates, i.e., not subject to the developmental trade-offs discussed above. As a result, the variance contribution of this pathway was not dampened by negative covariance contributions with other transitions. Our analysis thus showed that the light response of branching by dormant modules (the DJ transition in the biannual branching loop) almost fully accounted for the observed variance in λ among trees.

Ecophysiological implications at the tree level

Of the 18 trees, only two individuals faced a slightly shrinking module population size ($\lambda = 0.98$ and 0.99), while the other 16 individuals had positive module population growth rates ($\lambda = 1.00–1.47$). Apparently, none of the trees faced large carbon deficits, as deficits would have increased module mortality, leading to a much lower λ. As *Vouacapoua* trees spend ~30 to 70 years growing from 5 to 20 m in height (Sterck 1997), the data imply that *Vouacapoua* trees may pass these and later life phases with little death risk due to low light levels alone. In contrast, seedlings and saplings of smaller size and younger age usually have higher mortality rates due to low light levels (Veneklaas and Poorter 1998).

None of the life cycle pathways was affected by tree height. Similarly, most of the morphological traits of the extension units, the "building blocks" of modules, were unaffected by tree height either (Sterck and Bongers 2001). The differential modular responses of trees to light were consistent with the notion that apical dominance is released at high light availability (Thimann 1977, Sachs 1991). The birth of juvenile modules by dormant modules increased at high light availability and lead to a higher λ. Apical dormancy and apical growth transitions were not significantly affected by light. The dominance of the apical dormancy and bi-

annual apical growth loops (DD and GDG) suggests that modules grow slowly, producing new extension units biannually, or even less frequently, both at low and high resource level. Given the high levels of flush synchronization in this species (e.g., Loubry 1994), the positive covariances between the biannual branching loop and the biannual apical growth loop suggest synchronization among apical and axillary activity, probably driven by hormones controlling apical dominance (Thimann 1977, Sachs 1991).

The low flush frequency and the synchronization in module production result in massive leaf production, even among different trees (Loubry 1994), and may thus enable young, still palatable leaves to escape from herbivory (Coley and Barone 1996). Conversely, variable flush frequencies and lack of synchronization in small 1–2 m tall *Vouacapoua* saplings (F. J. Sterck, *unpublished data*) may reflect an inability to escape herbivory by massive flushing. A flush frequency of 2–4 yr seems sufficient to replace older leaves, given leaf ages of 1.6–2.7 and 2.2–4.1 yr in sunny and shaded conditions, respectively (Sterck 1999). In the shade, the leaf replacement costs were kept low by producing short extension units with few, thin leaves (Sterck and Bongers 2001), and total growth costs of modules were reduced by lack of branching. Such a growth pattern may be beneficial to the tree in various ways: (1) trees may keep sufficient live lateral meristems, enabling them to branch in response to abrupt increases in light level (see also Aarssen 1995); (2) leaves are more widely spaced in the shade (Sterck and Bongers 2001), thus reducing levels of leaf self-shading; (3) closer spacing of leaves at high light results in the occupation of high-resource sites and is at the cost of available space and high light recourse levels to competing neighbors.

At both high and low resource levels, dormancy leads to slow growth rates that enabled trees to escape herbivore attacks while they were still able to replace their leaves. In the temperate tree species *Betula pubescens*, dormancy permitted trees to survive unfavorable periods (winter) and to recover from herbivore outbreaks (Lehtilä et al. 1994, Ruohomäki et al. 1997). The invariable apical growth and the increased branching in response to high light have been observed between sun and shade modules within conifers (Stoll and Schmid 1998), broad-leaved trees (Jones 1985), and clonal plants (de Kroon and Schieving 1990). It thus appears that the same controls may drive the same variety of apical growth and branching in contrasting plant life forms, while different factors seem to control dormancy.

Conclusions

Despite huge variation in light availability (~1–60% of open sky PAR), tree height (5–30 m), module dynamics, and light responses of leaves (Rijkers et al. 2000), the module population growth rates (λ's) varied little and may thus permit trees to survive, particularly

during long, persistent periods of shade. Only in high-light episodes, did λ increase due to accelerated branching, thus permitting the tree to occupy the new high-resource site and to expand to greater height at the same time. Our analysis shows how a shade-tolerant tree may accomplish this.

The module biannual branching pathway was the most variable, responded to light, and strongly contributed to variance in λ among trees. The apical dormancy and apical growth loops varied less and were not responsive to light. These latter apical loops hardly contributed to variance in λ, mainly due to the high survivorship of modules and the developmental apical trade-offs discussed above. We showed how these properties enable trees to survive low-light episodes and herbivory attacks, and to expand during high-light episodes. Given the basic underlying developmental and physiological mechanisms, these modular growth patterns of *Vouacapoua americana* may apply to other shade-tolerant trees growing and surviving in a heterogeneous and dynamic forest light environment.

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