

NON-DESTRUCTIVE ANALYSIS OF ARCHITECTURAL EXPANSION AND ASSIMILATE ALLOCATION IN DIFFERENT TROPICAL TREE SAPLINGS: CONSEQUENCES OF USING STEADY-STATE AND DYNAMIC PHOTOSYNTHESIS MODELS

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Abstract. Six woody species from a successional series growing in their establishment phases in a premontane tropical Costa Rican rainforest were analysed in detail concerning whole canopy carbon gains – using two principally different photosynthesis models. Crown architectures of 65 individuals, 0.2 to 4.5 m high, were monitored over two years and precisely reconstructed in 3 dimensions. For each single leaf of 28 selected plants light absorption on daily bases was calculated using the reconstructed plant canopies and the light data as inputs. For identical daily light courses net photosynthesis was simulated using firstly, a steady-state and, secondly, a dynamic photosynthesis model which takes light-controlled photosynthetic induction states into account. Canopy carbon gain was determined by summing daily leaf net carbon gains for each individual leaf and integrating over a whole year. Observed biomass increments of all individuals showed only plausible agreement when the dynamic photosynthesis model was used. Comparing steady-state and dynamic model approaches resulted in strong, unrealistic overestimations by the steady-state model, showing at minimum 30% (in pioneers) and at maximum 650% overestimated annual canopy carbon gains in the mid- to late-successional plants. Lightflecks alternating with low light availability contributed to deficiencies in the photosynthetic induction state, which are only accounted for in the dynamic model. Pioneers invest about 33% of annual carbon in short-lived leaves and the remainder (ca. 42%) in supporting tissues. In contrast, late-successionals partition only 8–18% into leaves of much greater longevity and 57–67% to build “expensive” supporting structures of high wood density and high longevity – very likely forming the base for future growth into the forest canopy. We conclude that only dynamic photosynthesis models are appropriate to differentiate plant carbon economies of shade tolerant and intolerant species in tropical forest ecosystems. *Accepted 10 October 2004.*

Key words: Assimilate allocation, canopy carbon gain in dynamic light, dynamic photosynthesis model, growth strategies, shade tolerant/intolerant plants.

INTRODUCTION

Quantitatively correct annual carbon balances are an elementary prerequisite of many scaling calculations and simulations, whether based at the level of a leaf or an individual canopy (Ehleringer & Field 1993). Such valid calculations are needed to determine carbon allocation and plant inherent economy (e.g., Bloom *et al.* 1985, Chapin *et al.* 1990), whole plant water and nitrogen use in relation to available carbon (e.g., Schulze 1982, Roy & Garnier 1994) and assessment of plant competitive ability (Küppers 1987, 1994). In the context of C-sinks at the stand and landscape level (e.g., Running & Coughlan 1988, Aber *et al.* 1996, Wedler *et al.* 1996, Tenhunen *et al.* 1998) reliable assessments are also essential, especially when

politicians discuss trade with carbon sinks. Nearly all leaf, canopy, and stand carbon balance simulations are based on steady-state photosynthesis (Caldwell *et al.* 1986, Percy & Yang 1996, de Pury & Farquhar 1997, Niinemets & Tenhunen 1997, many others), despite increasing evidence (e.g., Chazdon & Percy 1986, Percy *et al.* 1997, Yanhong *et al.* 1997, Naumburg *et al.* 2001, Naramoto *et al.* 2001) that the time-scales of dynamic changes in light and steady-state simulations do not match (Jarvis 1995), causing strong discrepancies between steady-state simulations and true, measured net photosynthesis. One reason for these large discrepancies is the general neglect of dynamic, continuous alterations in the state of photosynthetic induction depending on the previous level of light (e.g., Percy *et al.* 1994, Schulte *et al.* 2003). A typical approach used to parameterize steady-state models is based on the determination of photosynthetic characters from “steady-state measurements”

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after having fully induced a leaf with light (light response curves or A/Ci curves). Therefore, since leaves rarely operate at full photosynthetic induction, systematic errors may result (see e.g., Pearcy *et al.* 1994, Stegmann *et al.* 1999, Timm *et al.* 2002).

It is unknown whether the phenomenon of induction changes carries over to the landscape. However, we address here whether up-scaling from the leaf to the canopy carries over such discrepancies. In addition to understanding canopy carbon inputs, we also address carbon economy of growth responses (e.g., Givnish 1986) of early-, mid- and late-successional woody saplings in their respective, gradually changing forest environment. Therefore we also focus on the successional replacement of species after gap formation, especially their use of the generally limited light for optimal carbon gain in the understory or in small gaps (Chazdon & Fetcher 1984, Givnish 1986). Even at optimal photosynthetic use, carbon gain is the main limitation for growth at limited light. Plant inherent mechanisms must be involved that support an economic, adequate use of assimilates (e.g., Farnsworth & Niklas 1995, Tremmel & Bazzaz 1995). We therefore study the investment of assimilates into different organs as affected by the different growth strategies of plants as shade-intolerant (pioneers) or tolerant (mid- to late-successional), all from the same successional series of a tropical forest in Costa Rica.

MATERIALS AND METHODS

Measurements were performed at the "Reserva Biológica Alberto Brenes" (RBAB) in the NW of Costa Rica (10°13'N, 84°37'W), an area between 800 and 1400 m above sea level (= a.s.l.), characterized by a hyperhumid tropical climate and covered by a premontane primary rainforest (Herrera 1985, Ortiz 1991, Breckle 1995). Annual precipitation exceeds 3000 mm at mean annual temperatures of ca. 20°C (Walter *et al.* 1975, Wattenberg & Breckle 1995). Between 1995 and 1997 an annual mean of 5320 mm was observed and in parallel an annual incident photosynthetic active radiation above the canopy of 5167 mol photons.

Plant Materials. All trees investigated grew within 2 km of the reserve research station at an altitude of between 850 m and 1000 m a.s.l.. All were in their establishment phases as juvenile trees with up to 250 leaves. In total, 65 individuals of 6 different species

were monitored regarding their architectural expansion, increment in biomass, leaf and canopy net photosynthesis, and annual carbon gain. Selected species are representative for (a) the late-successional forest understory (shade tolerant): *Salacia petenensis* Lundell (Hippocrateaceae) and *Calatola costaricensis* Standley (Icacinaceae), (b) the mid-successional situation during closure of gaps (partially shade tolerant): *Billia colombiana* Planchon & Lindley (Hippocastanaceae) and *Guarea glabra* Vahl (Meliaceae), and (c) the pioneer state of large gaps and clearings (shade-intolerant): *Heliocarpus appendiculatus* Turczaninow (Tiliaceae) and *Ochroma lagopus* Swartz (Bombacaceae). Successional classification is based on Oberbauer & Donnelly (1986), Coley (1988), Whitmore (1990), Wattenberg & Breckle (1995), and Gómez-Laurito & Ortiz (1996). Using several empirical criteria such as (1) dominance or co-dominance in the open (large gaps) and in recently closed gaps as well as in the understory, (2) rate of growth, height gain, and (3) photosynthetic characteristics (photosynthetic capacity, steady-state light compensation point; see e.g., Bazzaz & Pickett 1980, Oberbauer & Strain 1984, Swaine & Whitmore 1988, Küppers *et al.* 1996, Lüttge 1997), the species were ranked according to an arbitrary successional sequence from 1 (very early pioneer) to 10 (very late successional) (see Table 1). Of course, any ranking can be questioned regarding scales, resolution, etc, but despite certain problems it provides a useful framework (e.g.) to link forest succession with (relatively) characteristic species. Therefore, scaling is highly resolved. This is certainly not detrimental to the general ranking of species but it allows us to consider shades of differences. We are fully aware of the fact that not every worker might agree to such "shades" but, irrespective of this, applying a coarser resolution would have yielded fundamentally the same results.

Unfortunately, a certain loss of individuals occurred from sudden death, such as fungi diseases, ant and other animal attacks, or strong damage by falling debris (especially branches of canopy trees in several storm events; e.g., Chazdon 1988), so that only 28 out of the 65 plants could be used to calculate complete annual carbon budgets for healthy individuals and to perform statistical analyses.

Plant architecture and biomass increment. Leaf and axes orientations in space of all 65 individuals were monitored over a period of at least 2 years. According

TABLE 1: Ranking (from early to late) of the six species under investigation according to their estimated (optimal) position during succession. Criteria used are occurrence after gap formation, (co-) dominance at their sites, endurance in developing shade during closure of gaps, growth rates and photosynthetic characteristics, building on the long experience of Prof. R. Ortiz and V. Mora (Universidad de Costa Rica, San Ramón; personal communication as indicated by *) with the species in the Reserva, on own observations, and on information from the literature (for critical discussion see the Method section). Light regimes (canopy openness) at plant sites are indicated as DSF (= direct site factor) and ISF (= indirect site factor) (according to Anderson 1964), photosynthetic characteristics as light compensation point (I_{comp}), photosynthetic capacity at full induction (A_{max} , equivalent to $A_{max(P_{max})}$ in Timm *et al.* 2002), and dark respiration as R; m: number of individual plants or leaves, n: number of plant sites; all are means \pm SD.

Species	Successional state (early 1 \rightarrow late 10)	DSF	ISF	I_{comp} [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	A_{max} [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	R [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	Leaf-longevity [d]
<i>Heliocarpus appendiculatus</i>	2.0	0.69 \pm 0.121 n = 6	0.60 \pm 0.070 n = 6	23.6 \pm 4.2 m = 15 n = 5	21.9 \pm 5.1 m = 15 n = 5	-1.1 \pm 0.31 m = 13 n = 4	137 \pm 25.9 m = 12
<i>Ochroma lagopus</i>	2.5	0.74 \pm 0.081 n = 7	0.70 \pm 0.081 n = 7	18.9 \pm 3.85 m = 13 n = 4	22.2 \pm 3.91 m = 13 n = 4	-0.95 \pm 0.24 m = 13 n = 4	159 \pm 31.4 m = 12
<i>Guarea glabra</i>	6.5	0.20 \pm 0.099 n = 16	0.17 \pm 0.071 n = 16	10.1 \pm 2.13 m = 15 n = 5	6.5 \pm 1.91 m = 15 n = 5	-0.53 \pm 0.23 m = 13 n = 4	913 (Coley 1988)
<i>Billia colombiana</i>	7.0	0.22 \pm 0.038 n = 10	0.20 \pm 0.035 n = 10	6.8 \pm 2.45 m = 12 n = 5	6.1 \pm 1.15 m = 12 n = 5	-0.49 \pm 0.17 m = 13 n = 5	1088 \pm 192.8 m = 5
<i>Calatola costaricensis</i>	8,5	0.18 \pm 0.038 n = 15	0.17 \pm 0.030 n = 15	5.54 \pm 1.64 m = 16 n = 6	4.9 \pm 0.96 m = 16 n = 6	-0.4 \pm 0.21 m = 13 n = 5	ca. 1825*
<i>Salacia petenensis</i>	9.0	0.18 \pm 0.081 n = 13	0.16 \pm 0.082 n = 13	4.53 \pm 1.85 m = 15 n = 5	4.1 \pm 0.88 m = 15 n = 5	-0.31 \pm 0.12 m = 13 n = 5	ca. 1825*

to the routine in use (an improved version of “Y-Plant”, Percy & Yang 1996, see Stegemann 1999 and Timm 1999), an individual’s three-dimensional canopy is virtually split into segments (Fig. 1A) where the plant’s growth shape determines the number of modules or segments, beginning at the base of the main shoot, then proceeding to the top and to the outer canopy. Modules are indicated by nodes and leaves. For stem, twig and petiole segments, lengths and mean diameters are obtained to enable reconstruction as cylinders. Segment orientation in space is defined by neighboring module numbers (Fig. 1A) and its inclination and azimuth (Fig. 1B). Leaf size

is determined by the length of the mid-rib and a standardized, species-specific leaf shape. Loss of leaf area as caused by herbivores was estimated by eye (as percentage) and is corrected for in a plant’s virtual reconstruction. Figures 2B and D show the reconstruction of a *B. colombiana* and a *C. costaricensis* individual and their respective photographs (Figs. 2A and C). All 65 plants could be reconstructed with similarly high quality. This enables viewing the plants from all directions, e.g., from the side (Fig. 2E) or from above (Fig. 2F) to get an idea of crown architecture and the degree of overlapping by leaves within the canopy.

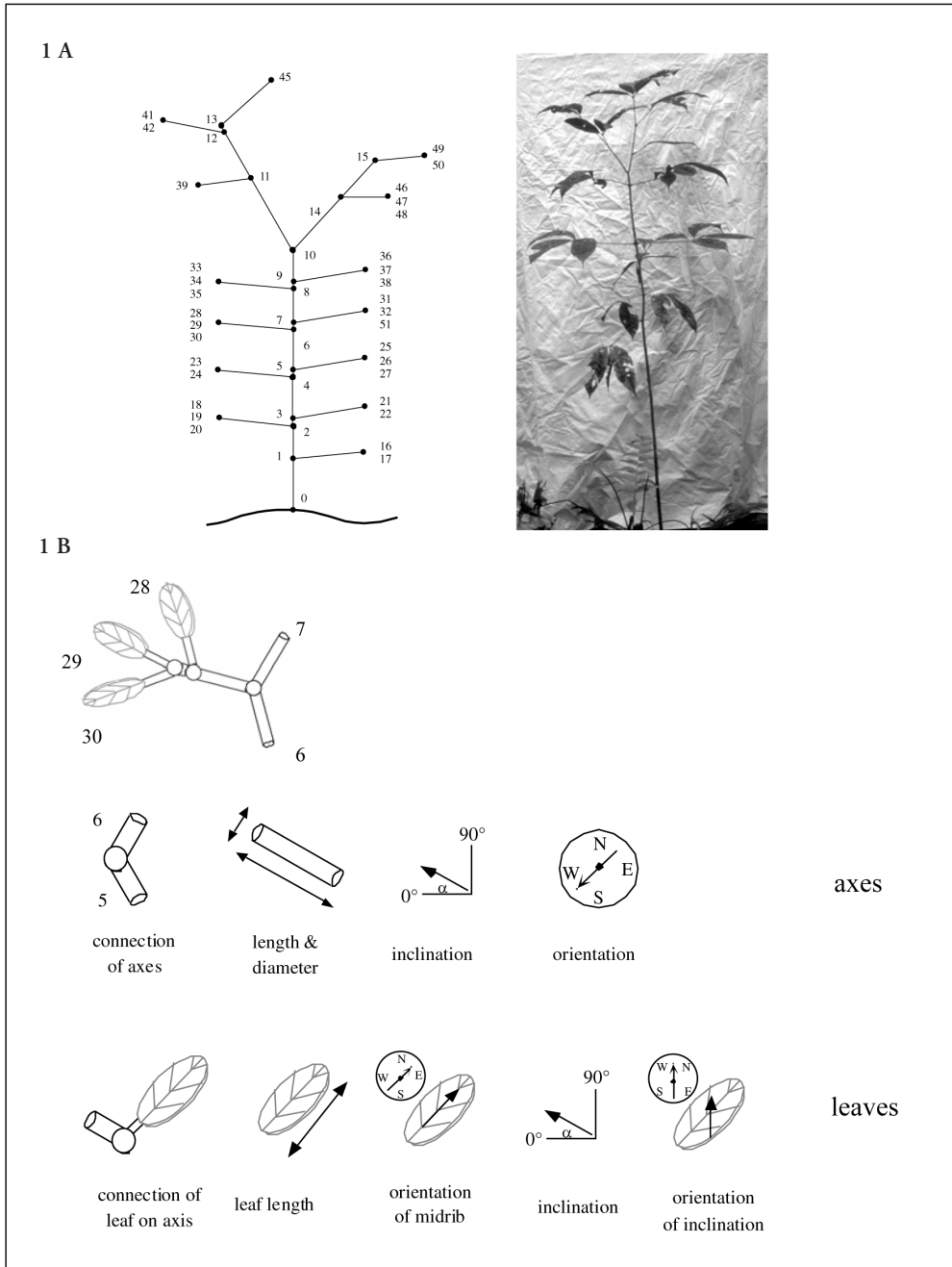


FIG. 1 A. Idealized scheme (left) of the figuratively segmented canopy of an individual *Billia colombiana* sapling (right) at its natural understory site. Numbers represent segments as determined by the plant's growth shape. FIG. 1 B: Connection of segments and additional information necessary for a plant's virtual reconstruction (for details see Pearcy & Yang 1996, Timm 1999).

We determined leaf life-span in species with short-lived leaves such as *H. appendiculatus*, *O. lagopus* and *B. colombiana* (e.g., Whitmore 1990). Leaf life-span can be determined from growth of new leaves and losses of marked ones, using equation 1 (after Ackerly 1993).

$L = (n_1 + n_2) * (b + d) * \Delta t / (4 * b * d)$ (equation 1)
 where L = life span (days), n_1 and n_2 are the number of marked leaves at time t_1 and t_2 respectively, b the

number of newly grown, and d of shed (marked) leaves in the time interval $\Delta t = t_2 - t_1$. When L was very long, as in *C. costaricensis* and *S. petenensis*, it was determined from loss of marked leaves.

Light availability. Since direct measurements of canopy carbon gain are difficult to perform over an extended period, and since this is almost impossible to do simultaneously in 28 individual plants, we

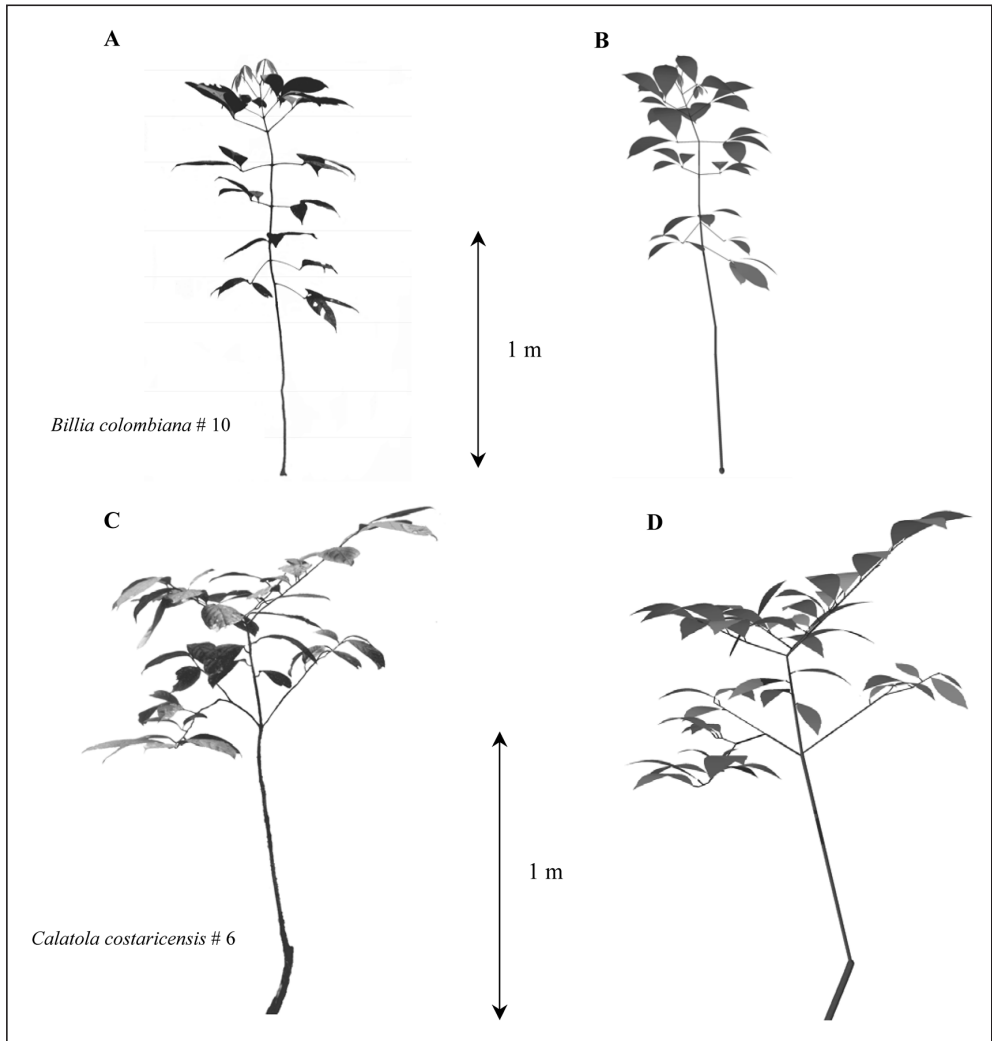


FIG. 2 A, C. Photographs of *Billia colombiana* and *Calatola costaricensis* individuals at their natural understorey sites (background removed) and their virtual reconstructions in B and D.

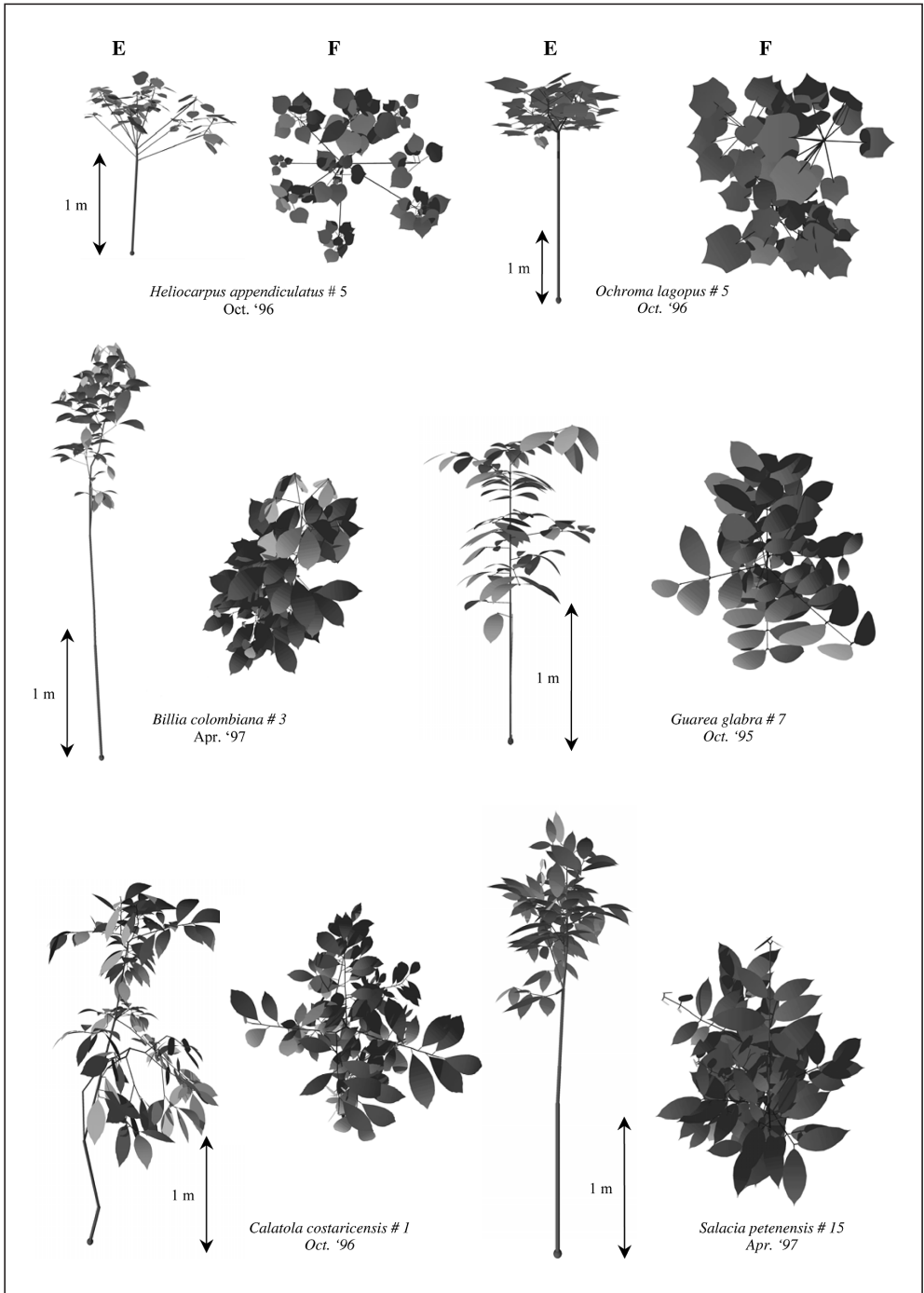


FIG. 2 E, F. Examples of virtual reconstructions of all species either viewed from the side (E) or from above (F). Overlapping of leaves within the canopies is clearly visible.

applied simulation models of net photosynthesis at the leaf level and successively integrated from daily leaf to canopy, and later on to annual carbon gains. Diurnal light courses were determined for each individual leaf of all 28 (remaining, undamaged, and healthy) plants. The following steps were performed: (1) diurnal courses of incident light had to be recorded above the forest canopy; (2) light below the forest canopy but just above an individual plant's uppermost leaves had to be determined; (3) light penetration and absorption with respect to temporal courses and daily amounts had to be deduced for all plant canopies. From the last step net photosynthesis could be calculated.

In the first step, photosynthetic active radiation (PAR), using a LiCor quantum sensor (Nebraska, USA), was recorded every minute above the forest canopy. We distinguished three classes of diurnal light courses: one for variable cloudy days (up to < 15 mol photons $m^{-2} d^{-1}$), a second for variable clouds (15 to < 30 mol photons $m^{-2} d^{-1}$), and a third for sunny days (> 30 mol photons $m^{-2} d^{-1}$). Most days of the observation period ($\sim 59\%$) were cloudy ranging from 5 to < 15 mol photons $m^{-2} d^{-1}$ and only 5.5% were sunny (Table 2).

It was not possible to simulate net photosynthesis for every day and every leaf in each of the plants under investigation, since this would have generated tremendous amounts of data. Therefore, in order to reduce the effort, we calculated mean daily amounts of PAR for each weather category (Table 2), which in turn were used to choose typical diurnal light courses from the light records above the forest canopy. Those were taken for pioneers on open sites and adapted to light conditions below the forest canopy (but just above the uppermost leaves of mid- and late-successional saplings) using hemispherical photography and the calculation routines of "HemiView" (Delta-T Devices

1998, Rich 1990, Fig. 3). We calculated the "Indirect" and "Direct" Site Factors (ISF and DSF; Anderson 1964) for all individual plant sites, updating the DSF for every sample day (see Fig. 3, there "calculation of quantum flux"). Plant architecture was subsequently entered into the program "Y-Plant" (Percy & Yang 1996) to calculate a typical diurnal light course for each individual leaf in the canopy. This information was then used to simulate net photosynthesis at the leaf level and to scale up to the canopy by summing the carbon gains over all leaves (Fig. 4).

Daily and annual canopy carbon gains. Detailed descriptions of gas exchange analyses in dynamic light have already been presented by Küppers *et al.* (1996), Stegemann *et al.* (1999) and Timm *et al.* (2002). All measurements shown here were performed using a LiCor 6400 photosynthesis system. Here determination of daily carbon gains occurred in two ways based on data of a representative number of leaves within the plant canopy (see Table 1). In the first approach, standard steady-state light response curves of leaf net photosynthesis were applied allowing for exactly one net photosynthesis rate at a given PAR (at otherwise identical microclimatic conditions, e.g., Farquhar & von Caemmerer 1982, Küppers & Schulze 1985, Percy & Yang 1996), in the other, allowing for changes in photosynthetic induction (e.g., Percy 1990, Stegemann *et al.* 1999) as a result of previous light conditions in a dynamic light environment.

In order to scale up to annual carbon gains, the typical diurnal simulations were run for every 21st day of every month (indicated as "Julian Day" in Fig. 3) taking half-annual changes in plant architecture into account (Figs. 3, 6, 7). Any changes in total canopy leaf area between two measurements were assumed to be linear over time. At every simulation day – as indicated in Fig. 3 – light and, consequently, net photo-

TABLE 2: Daily weather categories in the open used for the determination of annual carbon balances for all investigated plants. Data are from continuous measurements in 1-minute steps.

Range of PAR above canopy [mol $m^{-2} d^{-1}$]	Days observed in total	Days [%]	Mean daily PAR above canopy [mol $m^{-2} d^{-1}$]	SD
< 15	262	58.9	9.63	± 3.56
15–30	158	35.6	24.51	± 4.78
> 30	25	5.5	42.97	± 4.46
	445	100		

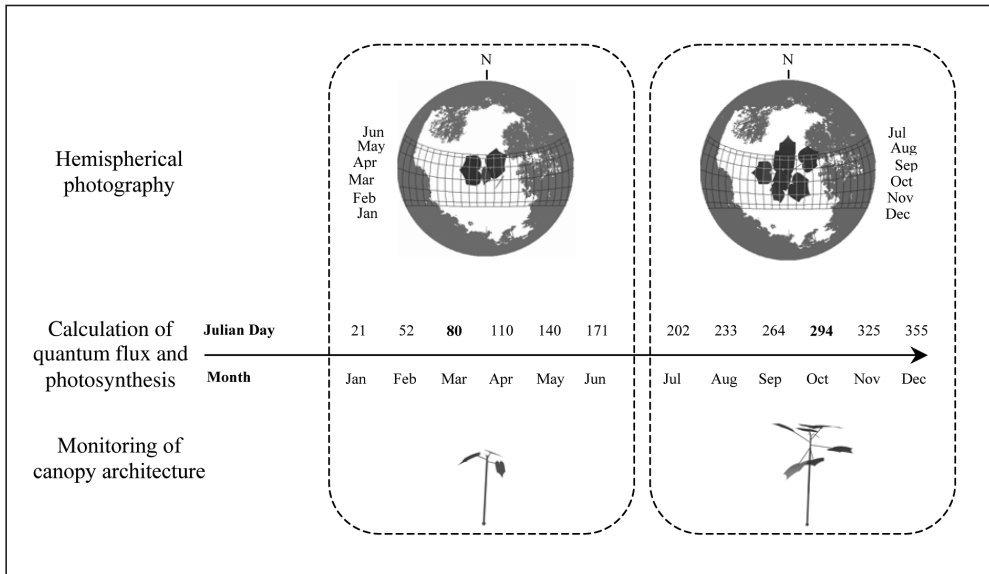


FIG. 3. Determination of daily and annual incident radiation at a particular plant site and in relation to an individual's architecture. For every indicated Julian day all three mean weather categories were calculated and applied for the respective month. On the bold-faced Julian days, plant architecture and hemispherical photographs were updated in the calculations for the period within the dotted frame. For further explanation see text.

synthesis were simulated for each of the three typical weather types. Total daily carbon gains were weighted with respect to frequency of weather conditions from Table 2. Canopy respiration at night was calculated via total leaf area in the canopy, a mean leaf respiration rate, and the length of the nights. The two different approaches are summarized in the flow chart of Fig. 5.

For comparison, a factor of deviation, F , is introduced as the quotient of annual canopy carbon gains from the "steady-state approach" and the "dynamic model approach" (for identical light conditions over the same plant individual). For example, an $F = 2$ means 100 %, an $F = 5$ means 400 % overestimation by the steady-state approach.

Carbon allocation. Aboveground dry matter increment in stem, twigs, and leaf material must be balanced by canopy carbon gain in order to allow for growth over extended periods (when no carbon is remobilized from storage organs). We calculated the amount of CO_2 that must be assimilated to match the respective dry matter increment of an organ or plant part

to determine the fraction of total annual carbon gain allocated to that organ. We summed all aboveground increments in dry matter to determine the amount of carbon gain available for root growth, root respiration, and exudation (Küppers 1982, Linder & Axelsson 1982). Net CO_2 -assimilation (in mol) was converted (after deduction of night respiration), via multiplication by 30, into dry matter (g), as carbohydrates based on glucose (Larcher 1980). Effects of isoprene emission (Hansen *et al.* 1997) were not important and were ignored.

RESULTS

In this section we present information of (1) a more technical nature when comparing the outcome of the two modeling approaches, and of (2) a biological nature concerning the carbon allocation of plants.

Plant architecture and biomass increment. As an example, the pioneer *O. lagopus* (Fig. 6) in an open gap site received high amounts of direct sun or cloud-affected light (mean DSF in March 1996: 0.76) with

a clear decline (to DSF = 0.60) a year later during gradual progression of gap closure (Fig. 6B). During the 380 days of observation the ca. one-year-old sapling grew continuously and its height nearly doubled (Fig. 6A, C), demonstrating substantial growth potential. The initially fast monopodial height growth was replaced by sympodial branching (March 1997, Fig. 6A). Note that the size of individual leaves after onset of sympodially branching is much reduced (from a mean of 2061.3 cm² in Oct. 1996 to 583.6 cm² in March 1997, Fig. 6A). Due to its short leaf longevity of 159 days, which is typical for many early tropical pioneers (e.g., Whitmore 1990), it lost all initial leaves and had grown a completely new cohort by Oct. 1996 and again by March 1997. At the same time above-ground standing crop increased four-fold from 560 g to 2327 g, whereas total gross biomass production (thus including losses) was 3561 g. Aboveground losses were as high as 50% of the total biomass gain.

For the mid- to late-successional *B. colombiana* (Fig. 7A) the situation was entirely different: it received much less light (DSF = 0.25 in March 1996, Fig. 7B) during a trend of further closure of the forest canopy (DSF = 0.18 a year later). Over the 380 days of observation it grew only 15 % in height, producing few new leaves but maintaining most of the initial ones (mean leaf-longevity: 1088 days). Therefore, *B. colombiana* increased its standing crop by a factor of just 1.67, from 86.3 g to 144.3 g (Fig. 7C). Total aboveground biomass gain averaged 64.9 g and aboveground losses only amounted to 6.9 g or 10 %.

Annual canopy carbon gains and allocation determined using both a steady-state and a dynamic photosynthesis model. Steady-state and dynamic photosynthesis models gave entirely different results in assimilated carbon amounts and therefore allocation percentages. The evident and consistent overestimation of real CO₂ uptake by the steady-state model is first shown at the leaf level by a section from a diurnal course of measured and modeled net photosynthesis of the late-successional species *S. petenensis* (Fig. 8). Secondly, for the pioneer *O. lagopus* (Fig. 6) and the mid- to late-successional species *B. colombiana* (Fig. 7) we observed large discrepancies in total annual canopy carbon gains as calculated for identical light conditions. Even in case of the pioneer *O. lagopus* in a wide gap the difference amounted to 41 % (Fig. 6D; F = 1.41), whereas in the mid- to late-successional

growth stages (Fig. 7) it rose to 237 % (F = 3.37). The smaller deviation in the pioneer is simply a consequence of the generally higher light level at the gap site, resulting in a generally higher photosynthetic induction level. Table 3 summarizes model comparisons (Factor F) for all plants studied. In the mid- to late-successional situation, just after gap closure, the highest variations in light dynamics were observed (e.g., number of lightflecks per unit of time) resulting in the strongest deviations of up to 640 % (F = 7.4). Indeed, the correlation between maximum F observed in a species and the percentage of lightflecks, taken as a measure of light dynamics, is highly significant (p = 0.027; Wilcoxon ranking).

Without exception, the allocation percentages obtained via the steady-state approach gave much higher

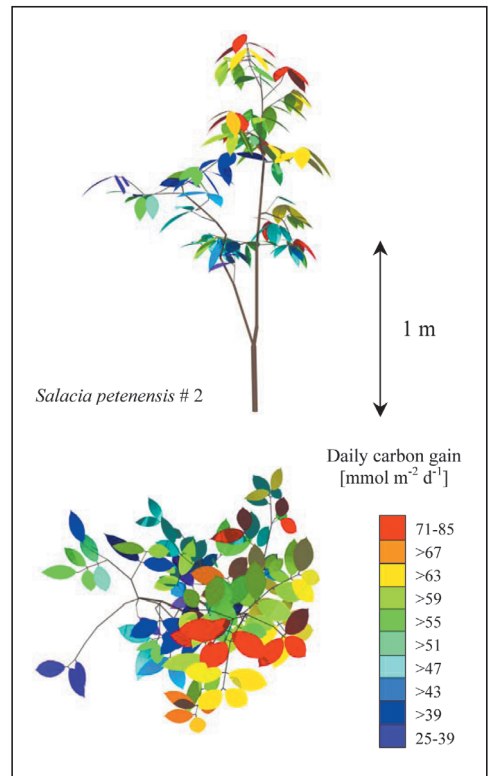


FIG. 4. An example from the sunny day of February 12, 1997 for daily carbon gain by every individual leaf of a *Salacia petenensis* sapling growing in the understory (dynamic model approach).

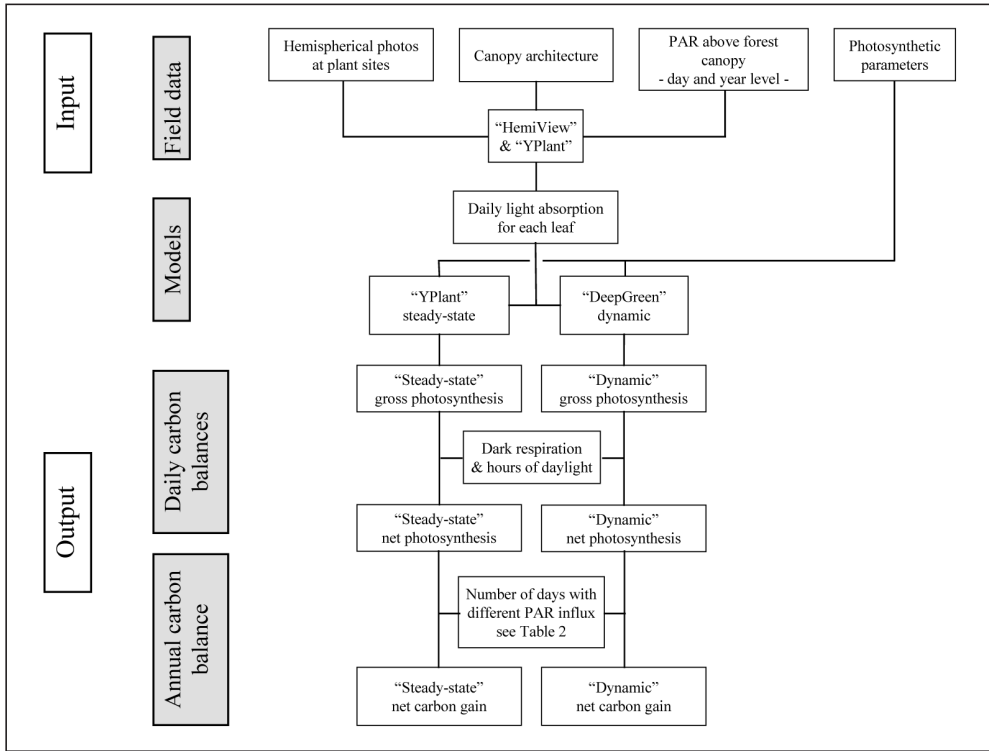


FIG. 5. Flow chart for the determination of annual canopy carbon gain of every individual plant, either via a steady-state or a dynamic photosynthesis model (“Y-Plant” after Percy & Yang 1996, “HemiView” after Rich 1990, Delta-T Devices 1998, “DeepGreen” from Stegemann *et al.* 1999).

TABLE 3: Comparison of modeled annual carbon balances, via the steady-state on the one hand and the dynamic model on the other, results in a factor of deviation, F (for definition see the Methods section; range is given). Especially for the late- and mid-to-late-successional trees the deviation (always an overestimation by the steady-state approach) is enormous. Obviously, dynamics of light, here indicated as percentage of light in lightflecks (the day chosen is for the plant of maximum observed F; see, e.g., Küppers *et al.* 1996 for detailed analysis of the site) rather than absolute amounts of radiation, are related to F, whereas other photosynthetic characteristics (I_{comp} , A_{max}) clearly depend on the amount of light available as indicated by DSF and ISF in Table 1. n: number of plants studied.

	gap		mid-successional		late-successional	
	<i>H. appendiculatus</i>	<i>O. lagopus</i>	<i>G. glabra</i>	<i>B. colombiana</i>	<i>C. costaricensis</i>	<i>S. petenensis</i>
factor of deviation F	1.6–2.0 (n=5)	1.3–1.4 (n=5)	4.0–7.4 (n=3)	2.4–2.7 (n=5)	2.6–2.8 (n=5)	2.0–3.6 (n=5)
PAR in lightflecks (< 5min) on a sunny day in April 1997 ([%] of time in daylight)	19	15	78	73	62	67

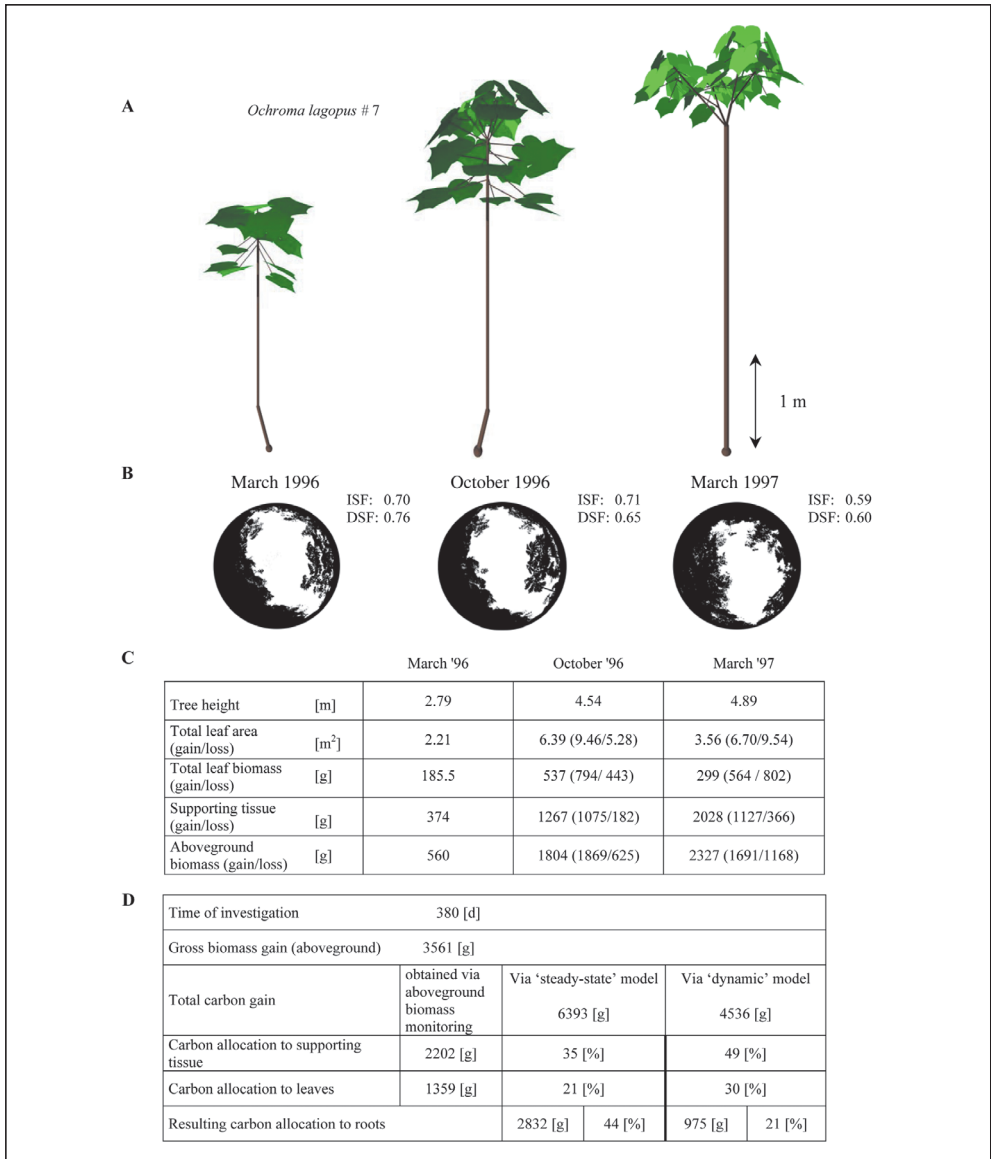


FIG. 6. Development of an individual of the pioneer *Ochroma lagopus* and deduction of its annual carbon allocation. A: Aboveground architectural development as reconstructed via the method described above. Note that in October 1996 and in March 1997 a completely new leaf cohort was grown while the previous was shed. Mean leaf size declined from March and October 1996 ($1187.3 \text{ cm}^2 \pm 87.28 \text{ SE}$, $n = 17$ and $2061.3 \text{ cm}^2 \pm 100.43 \text{ SE}$, $n = 31$) to March 1997 ($583.6 \text{ cm}^2 \pm 34.50 \text{ SE}$, $n = 61$). B: Change in the individual's light environment as indicated by hemispherical photography immediately above its uppermost leaves. Note the loss of (*Cecropia* sp.) trees at position "3 p.m." from October 1996 to March 1997 as a consequence of a storm event. C: Growth and biomass parameters of the respective individual. D: Deduction of annual assimilate flux balances (carbon allocation) as percentage of total annual canopy carbon gain, either via the steady-state or the dynamic photosynthesis model. Carbon gain and allocation are given in equivalents of dry matter $(\text{CH}_2\text{O})_n$ (= biomass).

values for carbon investment into roots (Figs. 6D and 7D) and, consequently, much lower values for investment into aboveground structures. This difference between the two approaches is the more pronounced the lower a mean induction state of photosynthesis. This is shown in detail for the two plants in Figs. 6D and 7D. A complete list of all studied individuals is given in the Appendix (Table A1). We conclude that the steady-state approach – by yielding a strong overestimation of annual plant carbon gain – results in a strong overestimation of carbon investment into belowground functions, both in relative and absolute terms, and underestimates relative investments into aboveground components. Therefore the results in Fig. 9 are based only on the annual carbon balances obtained via the dynamic model.

Irrespective of successional position and site of species, all of them invested very similar percentages (means of 23 to 30%) of carbon in their root biomass and root functions (Fig. 9). Obviously, in all species a strong physiological control of root functions is evident in order to support the shoot. Although total aboveground allocation was also similar in all species (70–77%), allocation to aboveground supporting tissues like stem, twigs and petioles differed strongly with successional position. Pioneers and mid-successional species invested large amounts of carbon in leaf material and relatively little into long-lasting supporting tissue, while this was the opposite in late-successional plants (Fig. 9). Obviously, there is a general trade-off in aboveground carbon allocation being related to species requirements in their typical environments.

DISCUSSION

Model comparison. There are undoubtedly many scientific problems where accurate quantitative estimates of canopy photosynthesis and total (annual) net carbon input of a plant are needed. From the ecophysiological point of view, these concern (e.g.) carbon allocation and plant inherent economy (e.g., Bloom *et al.* 1985, Chapin *et al.* 1990, Küppers 1994, Bazzaz 1997, Poorter & Villar 1997), or whole plant water and nitrogen use in relation to available carbon (e.g., Schulze 1982, Schulze *et al.* 1983, Dewar 1993, Roy & Garnier 1994, Heilmeyer *et al.* 1997), the assessment of plant competitive ability (Küppers 1987), costs of defense (Lerdau & Gershenson 1997) and reproduction (Reekie 1997), and the understanding

of advantages and disadvantages of certain morphologies and physiologies in given or changing environments (e.g., Givnish 1986, Küppers 1989, Ackerly 1996). Giving the many functions where carbon is involved this list could be considerably extended.

Almost all models used in scaling from leaf to canopy are based on the assumption of steady-state photosynthesis. But most leaves worldwide are likely not to experience steady-state-enabling light conditions, for clouds as well as a few outermost leaves of a canopy generate lightflecks; this has been shown for two widespread vegetation physiognomies – grass steppe and forest canopy (e.g., Küppers *et al.* 1996, Fig. 3; 1997, Fig. 1). Consequently, constant states of photosynthetic induction forming the basis of steady-state photosynthesis models cannot generally be assumed. When tests of such models are successful (e.g., Tenhunen *et al.* 1980, Küppers & Schulze 1985, Wang & Jarvis 1990, Aber *et al.* 1996) we should ask why this is so rather than accept it for every situation, especially not in dynamic light. There is sufficient direct and indirect evidence that steady-state models overestimate true carbon gains by leaves (e.g., Chazdon & Pearcy 1986, Küppers & Schneider 1993, Pfitsch & Pearcy 1989, Naumburg *et al.* 2001, Naramoto *et al.* 2001, Poorter & Oberbauer 1993, Schulte *et al.* 2003, Yanhong *et al.* 1997).

We wanted to know if this discrepancy carries over from the leaf to the canopy level. Even though simulations of light in the canopies of the studied trees are difficult, especially concerning penumbral effects (Ross 1981), it is plausible to test a steady-state model against a dynamic one using exactly the same time courses of light and the same plant morphology in both cases. Detailed monitoring of aboveground plant structures and components yielded in highly exact increments of aboveground plant biomass, against which the results of the two photosynthesis-modeling approaches are compared (Figs. 6, 7 and Appendix). Both models gave clearly higher carbon gains than necessary to cover aboveground increments, therefore the remaining carbon should equal the fraction that is required to support all belowground functions. For the dynamic model this root function yielded plausible numbers around 25.7% of annual carbon gain (with a few exceptions: minimum 7.1%, maximum 43.5%; see Appendix), while for the steady-state approach it amounted to 66.6% (minimum 44.4%, maximum 89.8%). These latter numbers are, looking at what is known from the literature, much too high, especially since none of the species is a kind of a

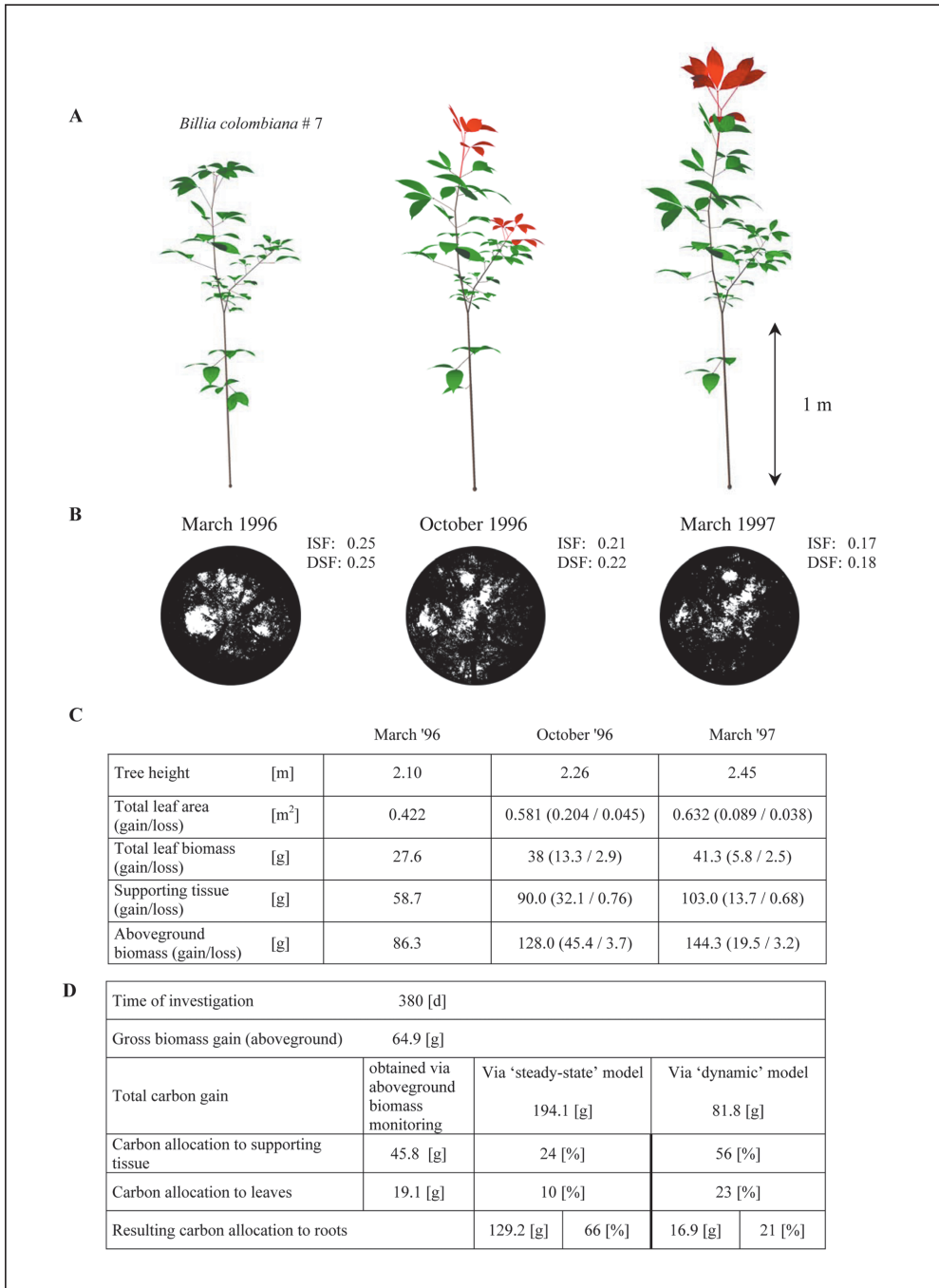


FIG. 7. Same as Fig. 6 but for an individual of the mid- to late-successional *Billia colombiana*. Note that most leaves remained in the canopy over the time span of investigation while only a few new ones (in red) were grown.

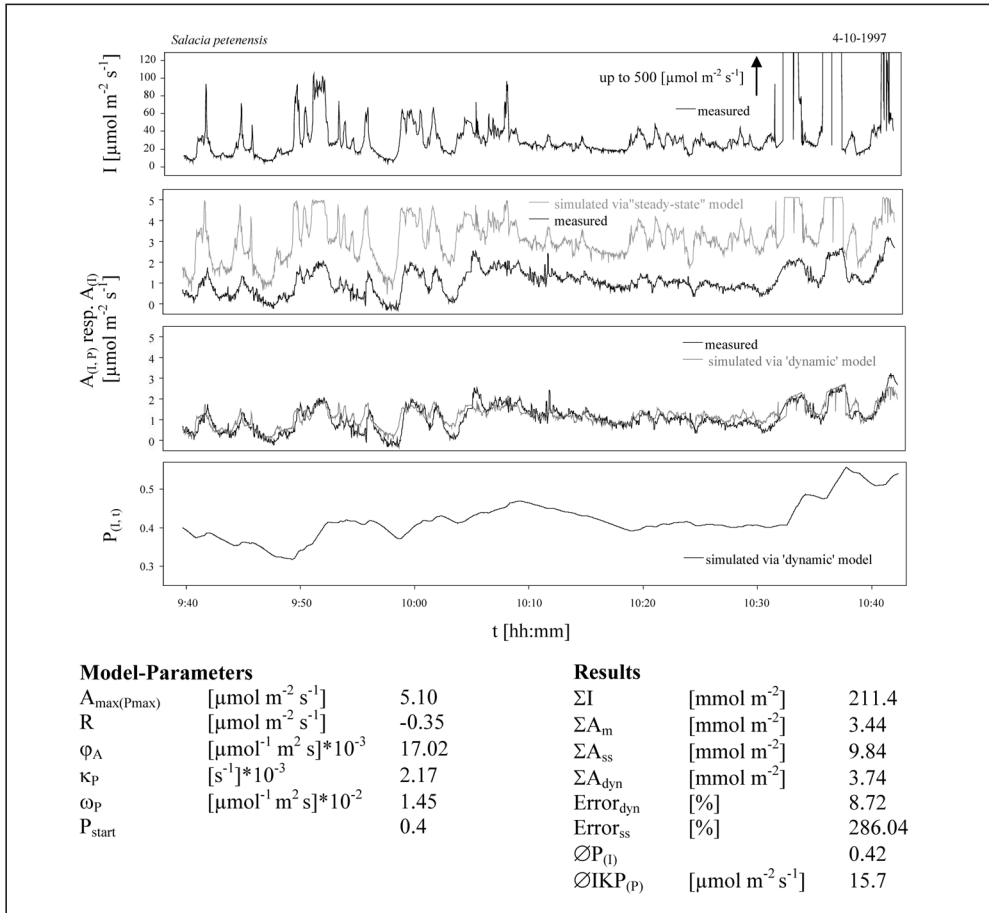


FIG. 8. Section from a daily light course (I) and leaf net photosynthesis (A) of a *S. petenensis* individual in the understory. Measured A is compared to the modeled net photosynthesis using either the steady-state approach ($A_{(I)}$) or the dynamic model ($A_{(I, P)}$). In the latter, the large variation in photosynthetic induction ($P_{(I, t)}$) is evident. The following equation was used for the steady-state model:

$$A_{(I)} = R + (A_{\max(P_{\max})} - R) * (1 - e^{-(\varphi_A * I)}) \quad \text{equation 2}$$

Parameters for the dynamic and steady-state models are (for details see Stegemann *et al.* 1999):

$A_{\max(P_{\max})}$ = light-saturated net photosynthesis rate at maximum induction

R = dark respiration rate

φ_A = photosynthesis-determining curvature factor

κ_P = induction-determining curvature factor

ω_P = induction-determining curvature factor

P_{start} = initial photosynthetic induction

ΣI = sum of light over the section interval

ΣA_m = measured CO_2 -gain

ΣA_{ss} = steady-state simulated CO_2 -gain

ΣA_{dyn} = dynamic model CO_2 -gain

Error_{dyn} = discrepancy between ΣA_m and ΣA_{dyn}

Error_{ss} = discrepancy between ΣA_m and ΣA_{ss}

$\overline{\varnothing} P_{(I)}$ = mean induction state over the time interval

belowground storer (see e.g., Chalmers & van den Ende 1975, with root/shoot dry matter ratios of 3/7 and declining when more and more carbon accumulates in stem biomass; e.g., Givnish 1988). Even for the pioneers *O. lagopus* and *H. appendiculatus*, growing exclusively in open sites, the root fraction by the steady-state approach yielded ca. 45–65% (Appendix), unrealistically high, although for these sites best fits at high photosynthetic induction could be expected. From direct measurements of leaf gas exchange (Stegemann *et al.* 1999, Timm *et al.* 2002), as well as comparison with biomass increments, we conclude that only dynamic models give plausible results. Table 3 summarizes the substantial discrepancies between steady-state and dynamic modelling approaches.

Most likely photosynthetic induction varies not only in whole canopies but also in stands and even over landscapes, e.g., when clouds suddenly cause a deep light step and shade the canopy long enough to allow induction losses. Although this phenomenon still has to be shown, it is more likely to occur than steady-state-like photosynthesis at constant “landscape photosynthetic induction”.

Comparing carbon use in pioneer, mid- and late-successional tropical saplings. Astonishingly, all species studied here exhibited a very similar root-to-shoot allocation of carbohydrates (flux balances as percentage of annual carbon gain, Fig. 9), clearly demonstrating the strong physiological balance between above- and belowground functions as a whole, irrespective of plant age (late successional were all much older than the pioneers though their exact age could not be detected), of the degree of shade tolerance, of successional position or growth rate. In this respect the findings fully agree with other observations on woody species from a successional series (Küppers 1994).

The late-successional tree saplings generally operate at much lower plant carbon gains (see the Appendix) than pioneers, which is not *a priori* a consequence of different canopy leaf areas, for the pioneers are much younger (maximally three years old) and have at least initially smaller total canopy leaf areas. These lower carbon gains are largely a consequence of the shade in the late successional environment. So it is surprising that the shade-tolerant species invest significantly more carbon into non-green, aboveground supporting biomass (Fig. 9). This investment of a higher carbon fraction into valuable, stable supporting tissue can be interpreted as a “conservative strategy”

to build a stem strong enough to gradually place the crown into the overgrowing forest canopy and to maintain this position. In the long term it is counterbalanced by high longevities of the components (Whitmore 1990). Pioneers, on the other hand, grow cheap supporting material to quickly gain height and occupy available gap space, thus initially avoiding becoming overtopped by competitors. However, their strategy does not allow for enduring height gain: both studied pioneers grow very light wood (one species is balsa) that would not withstand (e.g.) a strong storm event. Their leaves are of a “throw-away” type, as their longevity is short. It can be explained as a way to avoid

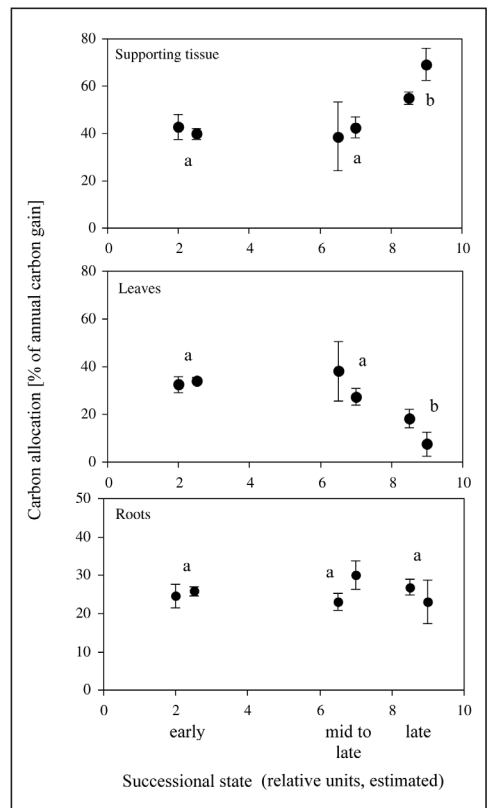


FIG. 9. Annual assimilate flux balances of the species in Table 1, here as a function of the species' successional positions. Different letters indicate significantly different ($p < 0.002$) allocation percentages for the respective plant part. Error bars: SE; factorial ANOVA. Original data are given in the Appendix.

self-shading by quickly growing new leaves overtopping older ones (compare Fig. 6A).

No doubt the allocation patterns are decisive for a species' success in its given environment. This can be interpreted even as an analogy to human economy (Chapin *et al.* 1990): with limited resources, fast growth and throw-away strategies could be fatal, whereas slow growth of high endurance quality, despite the limitation in resources (!), is appropriate. However, if resources (and money) are not limiting, the throw-away type may help to quickly produce new products and to ensure being the first in competition for new developments – thus enabling the occupation of market (= gap) space...

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APPENDIX. Aboveground gross biomass (dry matter) increment, total canopy net carbon gain (carbohydrate equivalents) and deduced carbon allocation for the individual plants studied. “Supporting tissue” refers to aboveground non-green components, “roots” to all belowground functions and structures receiving carbon (including a small fraction of aboveground maintenance respiration of non-green tissues). Species-specific mean values for allocation percentages are given in Fig. 9.

Individual	Time of investigation [d]	Gross biomass gain (above-ground) [g]	Total carbon gain via ‘steady-state’ model [g]	Total carbon gain via ‘dynamic’ model [g]	Carbon allocation to	via ‘steady-state’ model [%]	via ‘dynamic’ model [%]
<i>Salacia petenensis</i> # 2	380	93.6	357.8	161.9	supporting tissue	19.9	44.0
					leaves	6.3	13.8
					roots	73.8	42.2
<i>Salacia petenensis</i> # 3	531	27.8	122.9	34.3	supporting tissue	22.6	81.0
					leaves	0	0
					roots	77.4	19.0
<i>Salacia petenensis</i> # 9	531	5.3	22.1	7.2	supporting tissue	22.1	73.4
					leaves	0	0
					roots	77.9	26.6
<i>Salacia petenensis</i> # 13	380	32.8	127.8	41.2	supporting tissue	25.7	79.5
					leaves	0	0
					roots	74.3	20.5
<i>Salacia petenensis</i> # 15	380	246.2	537.1	265.0	supporting tissue	33.9	68.7
					leaves	11.9	24.2
					roots	54.2	7.1
<i>Calatola costaricensis</i> # 2	531	30.3	105.6	38.4	supporting tissue	19.3	53.1
					leaves	9.4	25.8
					roots	71.3	21.1
<i>Calatola costaricensis</i> # 7	531	41.9	166.6	63.4	supporting tissue	21.2	55.8
					leaves	3.9	10.3
					roots	74.9	33.9
<i>Calatola costaricensis</i> # 9	531	22.6	81.5	30.5	supporting tissue	23.2	62.1
					leaves	4.5	12.1
					roots	72.3	25.8
<i>Calatola costaricensis</i> # 12	531	57.0	206.9	76.5	supporting tissue	16.9	45.7
					leaves	10.7	28.8
					roots	72.4	25.5
<i>Calatola costaricensis</i> # 13	531	44.9	164.3	62.1	supporting tissue	22.0	58.1
					leaves	5.3	14.2
					roots	72.7	27.7
<i>Billia colombiana</i> # 2	531	42.0	156.1	57.3	supporting tissue	17.6	48.0
					leaves	9.3	25.4
					roots	73.1	26.6

Appendix continued

Individual	Time of investigation [d]	Gross biomass gain (above-ground) [g]	Total carbon gain via 'steady-state' model [g]	Total carbon gain via 'dynamic' model [g]	Carbon allocation to	via 'steady-state' model [%]	via 'dynamic' model [%]
<i>Billia colombiana</i> # 3	531	113.3	395.1	163.4	supporting tissue	17.4	42.0
					leaves	11.3	27.3
					roots	71.3	30.7
<i>Billia colombiana</i> # 4	531	32.4	110.2	45.4	supporting tissue	12.6	30.6
					leaves	16.8	40.7
					roots	70.6	28.7
<i>Billia colombiana</i> # 6	531	52.5	222.3	92.8	supporting tissue	15.2	36.5
					leaves	8.4	20.0
					roots	76.4	43.5
<i>Billia colombiana</i> # 7	380	64.9	194.1	81.8	supporting tissue	23.6	55.9
					leaves	9.9	23.4
					roots	66.5	20.7
<i>Guarea glabra</i> # 6	380	4.9	48.2	6.4	supporting tissue	5.4	40.1
					leaves	4.8	35.9
					roots	89.8	24.0
<i>Guarea glabra</i> # 11	531	48.4	235.1	59.5	supporting tissue	16.1	63.5
					leaves	4.5	17.8
					roots	79.4	18.7
<i>Guarea glabra</i> # 12	531	9.2	83.5	12.5	supporting tissue	1.9	12.8
					leaves	9.1	60.8
					roots	89.0	26.4
<i>Ochroma lagopus</i> # 3	531	73.2	134.5	97.7	supporting tissue	29.6	40.7
					leaves	24.8	34.2
					roots	45.6	25.1
<i>Ochroma lagopus</i> # 4	531	42.9	79.4	58.1	supporting tissue	26.2	35.8
					leaves	27.8	38.0
					roots	46.0	26.2
<i>Ochroma lagopus</i> # 5	380	2036.9	4058.0	2822.9	supporting tissue	26.9	38.7
					leaves	23.3	33.5
					roots	49.8	27.8
<i>Ochroma lagopus</i> # 6	380	1275.6	2495.1	1787.0	supporting tissue	25.8	36.0
					leaves	25.3	35.4
					roots	48.9	28.6
<i>Ochroma lagopus</i> # 7	380	3560.6	6393.2	4536.1	supporting tissue	34.4	48.6
					leaves	21.2	29.9
					roots	44.4	21.5

Appendix continued

Individual	Time of investigation [d]	Gross biomass gain (above-ground) [g]	Total carbon gain via 'steady-state' model [g]	Total carbon gain via 'dynamic' model [g]	Carbon allocation to	via 'steady-state' model [%]	via 'dynamic' model [%]
<i>Heliocarpus appendiculatus</i> # 1	531	59.9	156.8	86.5	supporting tissue	17.0	30.9
					leaves	21.2	38.4
					roots	61.8	30.7
<i>Heliocarpus appendiculatus</i> # 3	380	147.5	336.8	173.4	supporting tissue	31.3	60.7
					leaves	12.5	24.3
					roots	56.2	15.0
<i>Heliocarpus appendiculatus</i> # 4	380	117.5	337.7	170.4	supporting tissue	17.9	35.4
					leaves	16.9	33.6
					roots	65.2	31.0
<i>Heliocarpus appendiculatus</i> # 5	380	276.0	656.5	366.7	supporting tissue	27.6	49.4
					leaves	14.4	25.8
					roots	58.0	24.8
<i>Heliocarpus appendiculatus</i> # 6	380	75.1	154.3	95.5	supporting tissue	23.5	37.9
					leaves	25.2	40.7
					roots	51.3	21.4