

SHORT COMMUNICATION

Leaf-area index change across river-beach successional transects in south-eastern Peru

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(Accepted 3 July 2002)

Key Words: ecotone, Leaf Area Index, Peru, plant succession, rain forest

As part of the programme *Écosystèmes et Paléoécosystèmes des Forêts Intertropicales (ECOFIT, France)*, we are engaged in multisite comparative studies of how forests regenerate across ecotones such as those between forests and savannas (Vincens *et al.* 2000). One such ecotone comprises the forest succession from bare soil that occurs naturally on beach successions along meandering rivers. To gauge the development of foliar layers during succession and quantify changes of efficiency of the vegetation in capturing the available solar energy, we are measuring the Leaf Area Index (LAI) of transects within forests and across their edges.

The strongly meandering silt-laden rivers of Amazonia construct a constantly resculpturing floodplain of newly created beaches of alluvial soil on the inside of curves, opposite eroding banks (Kalliola *et al.* 1993). New plant successional series continually form on new beaches, with a highly repetitive pattern of fixed floristic elements for a given river basin. Several studies have described the floristics and/or structure of increasing-age transects through river-bend successions within the Madre de Dios river basin of south-east Peru (Foster 1990, Foster *et al.* 1986, Losos 1993, Puhakka *et al.* 1993, Terborgh & Petren 1991). Terborgh & Petren (1991) recorded the increase in vertical complexity (occupancy by foliage of vertical strata) with age along river-beach successional transects on the río Manu. We here build on these studies with a description of patterns of change of LAI across successional transects on five bends of the río Los Amigos, a tributary of the río Madre de Dios.

As LAI is the area of leaves per unit area, it is a measure of light interception and therefore it is directly correl-

ated to photosynthetic activity. Our aim in the present study was to measure how the clear-cut floristic stages in river-beach succession evolve in light-capturing capacity from the open beach to a tall, mixed-species, transitional floodplain forest, a successional stage estimated by Foster *et al.* (1986) to be over 200 y old. Bamboo (*Guadua* spp.) has invaded many forests of the region, often occupying the entire understorey. We chose two transects including bamboo to compare the LAI of bamboo-invaded to uninvaded forests. We addressed the following questions: (1) Do sequential successional stages exhibit increasing LAI in an incremental manner from the beach through to tall, mixed-species, closed-canopy forest? (2) Does each stage have a distinctive LAI signature? Is Terborgh & Petren's (1991) model of increased foliage complexity mirrored by LAI measurements? (3) Does bamboo behave like other successional stages? Or if not, how does it influence succession?

LAI was measured from 8 to 13 May 2001 on transects from five beaches of the lower río Los Amigos, Dept. Madre de Dios, Peru; starting at the following coordinates on a beach (in decimal degrees, by GPS, map datum WGS 84): T1, -12.4517°S, -70.24366°W; T2, -12.50079°S, -70.1420°W; T3, -12.50554°S, -70.12239°W; T4, -12.5567°S, -70.09349°W; T5, -12.56221°S, -70.07872°W. Beaches were chosen visually for the presence of at least three clear successional stages broad enough to include a series of measurements. The river-beach successional vegetation on the study transects was similar or identical to that described on the adjacent Manu and Madre de Dios rivers (Foster 1990, Foster *et al.* 1986, Losos 1993, Puhakka *et al.* 1993, Terborgh & Petren 1991) with the exception that all but T4 lacked an initial band of *Tessaria integrifolia* Ruiz & Pavón. Instead, the

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first tall (> 2 m) band was of the cane-like grass *Gynerium sagittatum* (Aublet) P. Beauv.

The successional series forms clear bands associated with a series of levees and swales, in the following order, from the open beach inward, with gradually increasing age (excellent photos of the successional series can be found in Puhakka *et al.* 1993): (1) *Gynerium sagittatum* in pure stand; (2) *G. sagittatum* beneath a canopy of *Cecropia membranacea* Trécul; (3) mixed *Cecropia* and *Acacia lorentensis* J.F. Macbr. with an understorey first of *Piper* sp. treelets on levees or dense, 2–3-m-tall *Heliconia* spp. in wetter ground (swales), then 2–3-m *Costus scaber* Ruiz & Pavón and *Renealmia thyrsoides* (Ruiz & Pavón) Poepp. & Endl. in understorey; (4) this changing on the next levee to a canopy of trees of *Ficus insipida* Willd. mixed with a few other tree spp. including the first canopy-size *Socratea exorrhiza* (C. Martius) H. Wendl. palms; and (5) usually on a well-defined, high (about 1 m) levee above the usual waterline (but not above the highest floods) a mixed-species forest with *Ceiba pentandra* (L.) P. Gaertner, many palms such as *Euterpe precatoria* C. Martius, *Socratea exorrhiza*, *Iriartea deltoidea* Ruiz & Pavón, *Oenocarpus* spp. and *Geonoma* spp. and with, for the first time in the sequence, a sparse understorey (structural and floristic changes are described in Terborgh & Petren 1991). Each successional stage was associated with step-like levees (≤ 0.5 m) progressing upward in elevation; the swales or seasonally filled river backchannels were pronounced and mud- or water-filled, with open canopies or low vine mats of *Acacia* sp., (T4, T5), or barely defined, dry dips. One transect, T4, had a narrow band of *Tessaria integrifolia*, separated from the *Gynerium* by an open swale. Two transects (T1, T3) had been invaded by bamboo (*Guadua* cf. *weberbaueri* Pilger), in stage 3 only (T1), or from just inland of stage 1, to stage 4–5 at the transect end (T3).

The río Los Amigos is the first major tributary to enter the río Madre de Dios downstream of the río Manu and on the same (left) bank. The river arises entirely in the lowlands, from hilly terrain of dissected, eroded terraces. Tall terraces confine the river meanders and limit the river and floodplain width.

Light measurements were made with a simple and inexpensive apparatus (LAIL) described by Cournac *et al.* (2002) and compared with several other methods by Ferment *et al.* (2001). The principle of this method is to measure the attenuation of light by vegetation, following the Beer–Lambert law ($I = I_0 e^{-kL}$, where I = transmitted light, I_0 = incident light, k = extinction coefficient). As explained in detail in Cournac *et al.* (2002), I_0 is corrected for cloud-cover conditions. The transmitted light is measured with a light-dependent resistor (LDR) behind an economical off-the-shelf fish-eye lens (spy-hole optic). With this we directly derive a quantity which is not LAI, but rather $kLAI$ where k is a geometric factor of order unity

from ~ 0.3 in maize to typically 0.8 to 0.9 in broad-leaved forests (extreme values cited by Monsi & Saeki (1953) range from 0.2 (*Miscanthus sacchariflorus*) to 1.9 (*Hydrangea macrophylla*)). To understand the self-organization of forest architecture due to light availability, it is $kLAI$, not LAI which is the relevant parameter; nevertheless, to be consistent with the conventional use of this dimensionless parameter, we give values of LAI^* , defined as $kLAI/K$, where K is a constant. We use the value of $K = 0.88$ that was obtained in tall evergreen forests of French Guiana by comparison with Licor LAI 2000 measurements (Cournac *et al.* 2002). This value was corroborated in French Guiana by Walter & Torquebiau (2000) by analysis of hemispherical photographs. *In situ* measurements of leaf angle at various heights in Barro Colorado secondary forest (Wirth *et al.* 2001) led to the same value; thus the few published values show k to vary between 0.85 and 0.9 in South American tropical forests. In our transects, the value of k is likely to be lower under pure stands of bamboo and *G. sagittatum* than under a forest of dicot trees, with $k \sim 0.6$.

Light readings were taken between 11h00 and 13h00 at 1 m intervals on five transects (T1–T5) ranging in length from 145 m to 180 m, placed at right angles to the edge of the vegetation and the successional bands. The light sensor was held at 2 m height: only foliage above this level influenced readings. We corrected for cloud cover as described by Cournac *et al.* (2002), but we also took control readings on the open beach, away from any vegetation, at the end of each transect. We measured intervals with a lost thread distance measuring device. Each transect was unique in exact beach configuration and details of the plant succession, giving each a unique LAI^* signature (Figure 1). However, a number of generalizations emerge from our results.

(1) The pattern of levees and swales strongly influences the successional series. T5 (Figure 1a) shows this dramatically, but it is also clear in T2 and T4 (Figure 1b). Each swale is signalled by a sharp decrease in canopy foliage cover (LAI^*) compared with the previous levee. Sometimes open water or a low vine mat of *Acacia* sp. covers the first swale behind the beach and it lacks a canopy cover (T5). Each successively older levee shows a slightly increased LAI^* , suggesting increased foliage complexity. The dampening effect of swales can be seen far back into the successional series, after the closed canopy forest has developed (Figure 1a).

(2) The first successional band, with a canopy of pure *G. sagittatum*, has a high LAI^* value.

(3) The second successional band is a mixture of *Cecropia* and *G. sagittatum*, but eventually the *G. sagittatum* dies back, leaving a band of even-aged *Cecropia*. The mixed *G. sagittatum/Cecropia* stand regularly shows a decrease in LAI^* compared with the pure *G. sagittatum*

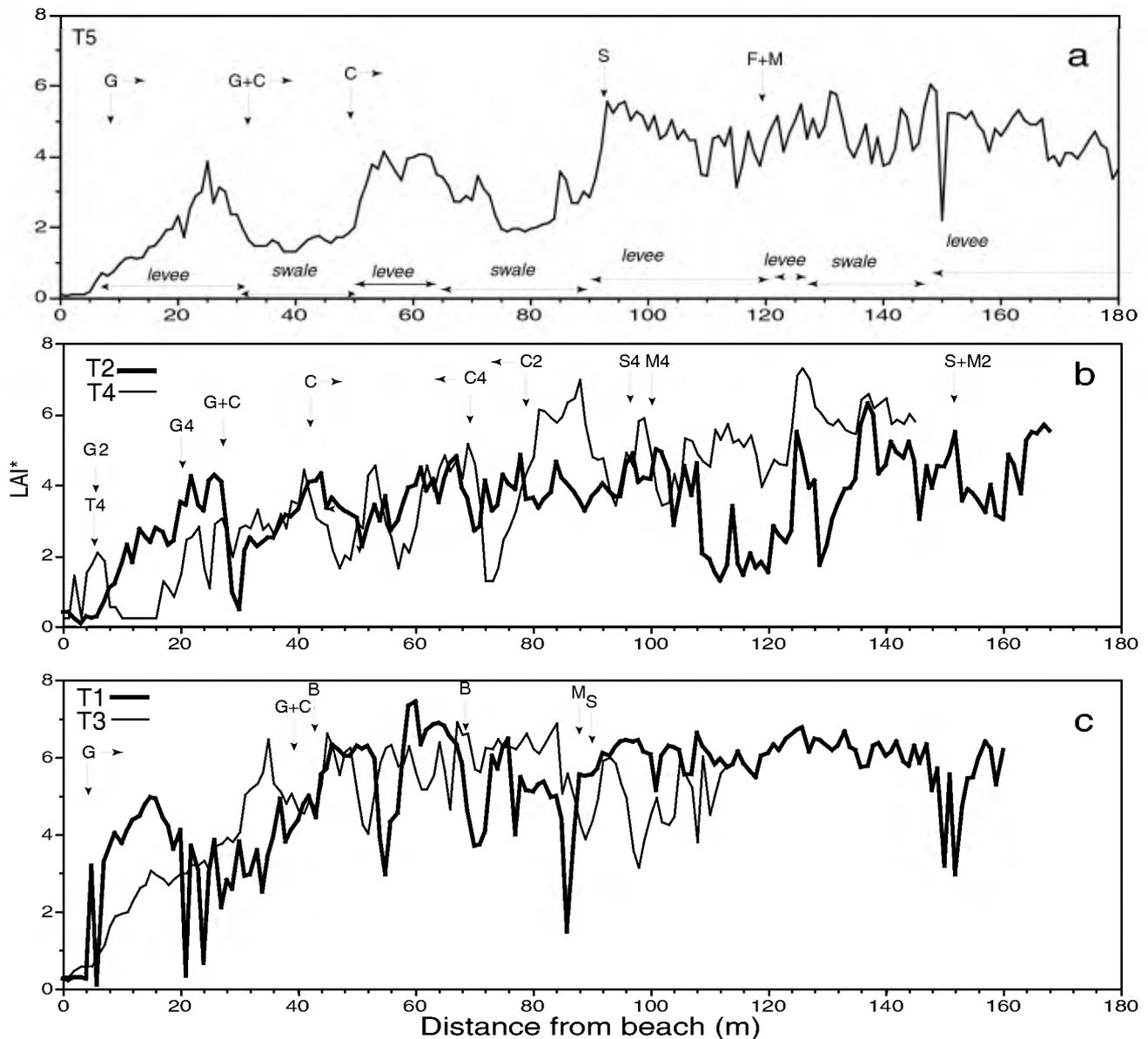


Figure 1. LAI* profiles of the five transects (LAI* = $k \cdot \text{LAI} / 0.88$). (a), T5; (b), transects T2 and T4; (c), T1 and T3, both with bamboo invasions. T = *Tessaria integrifolia*; G = *Gynerium sagittatum*; C = *Cecropia* spp.; S = first canopy-sized *Socratea exorrhiza* palm; F = *Ficus insipida*; M = mixed transition forest; B = bamboo. Numbers following letters in (b) refer to the transect number. In (c), letters all refer only to T1, T3 had bamboo invasion from 20 m to the end of transect. Vertical arrows = point of initiation or end of vegetation type, as indicated by horizontal arrows.

of younger age (Table 1), but it is also superimposed on a swale.

(4) The mixed *Ficus insipida* zone was poorly defined on some transects, but where it was clearest, it initiated on a high levee. The first, large canopy-level *Socratea exorrhiza* palm likewise appeared on an abrupt levee, and usually was a marker for the beginning of mixed forest (Figure 1), where the understorey markedly thinned under a closed multilayer canopy of 30–40 m trees (see description in Terborgh & Petren 1991). From this point inward,

there was no net increase in mean or median LAI* within the length of our transects.

In another study, we are monitoring LAI* changes on a 500-m transect of floodplain forest near the mouth of the río Los Amigos, at least 1 km from the river edge and behind three levels of old oxbow lakes. Its median LAI* was 5.07 (mean 4.8; maximum 7.1) measured during the same week as the present study. This is indistinguishable from the values we see on the mixed-forest ends of our transects, which generally begin about 90 m from the

Table 1. Median LAI measurements and (variance) for five successional vegetation bands on transects T1–T5. Columns arranged with increasing distance from beach, from left to right. Parts of T1 and T3 are dominated by bamboo (*Guadua* cf. *weberbaueri*).

Vegetation band	T1	T2	T3	T4	T5
<i>Tessaria integrifolia</i>				1.55 (0.48)	
<i>Gynerium sagittatum</i>	3.73 (1.8)	2.77 (0.8)	2.64 (0.24)	absent	2.71 (0.36)
<i>Gynerium</i> + <i>Cecropia</i> sp.	3.62 (1.5)	2.13 (0.49)		2.87 (0.53)	1.57 (0.02)
<i>Cecropia</i> sp.			3.68 (0.38)	4.51 (0.34)	3.44 (0.40)
<i>Guadua</i> + <i>Gynerium</i> + <i>Cecropia</i>	6.02 (1.17)		3.92 (1.14)		
<i>Guadua</i>	6.30 (1.17)		5.80 (0.54)		
<i>Ficus insipida</i> + first other trees		4.04 (0.32)	4.95 (0.17)*	4.91 (0.13)	4.96 (0.25)
Mixed forest	6.12 (0.40)	4.53 (0.84)		5.85 (0.13)	4.57 (0.50)

**Guadua* and *Triplaris*

beach. We therefore believe that our transects captured the succession to full structural development. Mixed floodplain forest is characterized by large variations in LAI* from the heterogeneity caused by many palms punching holes in the canopy, treefalls of giants such as *Ceiba pentandra*, *Ceiba* itself when deciduous (the dip in LAI* at T1, 150 m is due to its being under a leafless *C. pentandra*, Figure 1) and variations in soil wetness (old swales or other watercourses).

(5) Bamboo radically altered the succession. On the two bamboo-invaded transects, T1 and T3 (Figure 1c; Table 1), bamboo stems occurred mixed with the *G. sagittatum* 21 m from the beach on T3, but at 40 m, after the *Cecropia* zone, on T1. LAI* on both transects reached deep-forest values at about 50 m from the beach, but the signal is smoother, because of the more continuous occupation of space by bamboos than by big trees. If we were to take for k the expected value for plants with more vertical leaves such as bamboo and *G. sagittatum*, $k \sim 0.5$ to 0.7, this conclusion would be reinforced as the derived LAI (in contrast to LAI*) would be even higher. Once a dense canopy of bamboo was present, it could become a pure stand (T3), to the exclusion of other successional species. An interesting phenomenon on T3 was that at about 90 m, near where mixed forest usually began, many *Triplaris* sp. trees (inhabited by fierce, stinging ants) overtopped the bamboo canopy, at which point LAI* decreased slightly.

(6) In the model proposed by Terborgh & Petren (1991), 'Total cover increases monotonically through succession . . . Simple arithmetic integration of the profile diagrams indicates a sixfold increase in the space occupied by crowns between the *Tessaria* stage and mature forest' (1991:37). Because on our transect the T4 *Tessaria* band was so narrow that edge effects were strong, the maximum LAI* value, 2.09, rather than the median, 1.54, may best represent this stage. Likewise, because Terborgh & Petren probably picked plots free from gaps and with well-developed canopies, the maximum LAI* in the mixed forest (5.07–6.06, depending on the transect) and not the median (Table 1), should be used to compare with their results. On our transects the LAI* maxima from canopies above 2 m therefore increased a total of threefold through the successional series (about LAI* 2 to 6).

The LAI instrument is highly sensitive to small canopy changes, and gives a detailed record from which it may be possible to see the effects not only of large inhomogeneities such as light gaps, but also the signatures of individual trees. The pattern of levees and swales (described by Foster 1990 as a compact and well-defined set of rolling levees) creates precisely corresponding alternating waves of LAI* from bands of denser and lighter foliage. The levee vegetation has better development of foliar layers throughout all stages of the successional series, under canopies of different species sets, than does that of neighbouring swales. Swales are evidently relatively non-productive: perhaps the periodically saturated soil may have poor gas exchange or limited availability of mycorrhizal symbionts or increased fungal rot. It is remarkable that our instrument detects distinct decreases in LAI* across old swales far inland under tall mixed forest (marked by surface depressions and levees), where our eyes did not detect any differences in light conditions (Figure 1a, at 140 m).

Our data show that monospecific stands of *G. sagittatum*, with its densely packed stems topped by geometrically arrayed foliage fans, are highly effective in intercepting light, with maximum LAI* of 3.1–4.3. However, *Guadua* bamboo thickets are even more efficient, and their complex, many-branched architecture expands to fill all spaces and levels, shading out all below. Because bamboo sequesters as much sunlight as a mature forest canopy, and can do so rapidly and in an early successional stage, it completely inhibits the development of the normal successional vegetation. It is curious that trees of *Triplaris* spp. were apparently almost alone able to invade the bamboo thicket, and it would be interesting to know if its ant associates can prune bamboo. We have noted *Triplaris* seedlings growing in low-light conditions (despite its small, winged seed), so it may simply be one of the few species able to grow in wet soil under deep bamboo shade.

In contrast to Terborgh & Petren's (1991) model of monotonically increasing foliage cover, we found on every beach succession a wave-like pattern of gradually increasing LAI* regularly interrupted by sharp decreases over swales. The increase in foliage as measured by LAI*

from the first canopy above 2 m on the beach to the fully developed LAI* level of tall, mixed floodplain forest was only threefold, half as much as the sixfold suggested by Terborgh & Petren (1991). The discrepancies appear easily explained.

Terborgh & Petren (1991) estimated foliage cover with a model, based on field measurements, that calculated the amount of space occupied by all tree crowns at different heights within a series of sample plots. We suppose that their model records presence or absence of foliage in a given layer, but does not take into account that the size of leaves and the space between them changes according to the species and where it is in the foliage column. As layers increase, the number of leaves or their sizes and the spaces between them in overtopped, shaded lower layers decreases, such that LAI* increases at half the rate expected if all layers were of equivalent density. Because k is smaller in the erect vegetation types of earlier successional stages (bamboo, *G. sagittatum*) than in tall mixed forest, the true value of LAI in these vegetation stages should be higher than that given by LAI*, and the difference between the beginnings and ends of the transects consequently somewhat smaller.

These results show that starting from bare soil in a tropical rain forest, the successional vegetation quickly fills in with leaves and attains high LAI* values. It can do so when few species are present, or even only one, such as bamboo. The continued maturation of the forest results in increased height and complexity of layering, a process that may take centuries and involve the turnover of many species. But even at maximum development of tall, terra firme rain forest the added mean LAI* increment is small compared with that achieved by quite young successional forest. Increased forest maturation and tree species diversity on floodplain therefore does not entail greatly higher LAI* values and capture of more of the sunlight. Instead, trees appear to accommodate by increased light efficiency: getting along with less.

ACKNOWLEDGEMENTS

This research results from a joint collaboration between the Amazon Conservation Association (ACA) and ECOFIT (France). We thank ACA for their funding of this project, especially Adrian Forsyth and Enrique Ortiz for supporting our research. Travel for MAD was partially funded by the ECOFIT programme. For help in expediting the logistics we are grateful to Renán Valega R. The Peruvian authorities kindly allowed us to conduct research at Los Amigos. Robin Foster and Adrian Forsyth reviewed the manuscript, and we thank anonymous reviewers for good comments that helped us improve the manuscript. LHE thanks the Smithsonian Institution, Division of Mammals for providing office facilities. She owes special

thanks to Ellen Wessel of Moving Comfort® for keeping her comfortable and dry while moving.

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