

## Bamboo control of forest succession: *Guadua sarcocarpa* in Southeastern Peru

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### Abstract

Forest inventory data is presented as the basis for a conceptual model of bamboo-dominated forest successional dynamics in southwestern Amazonia. Forest succession is arrested in stands dominated by bamboo (*Guadua sarcocarpa*, Londoño and Peterson) as demonstrated by data on tree size class distributions and seedling mortality. Mean percent mortality of tree seedlings ( $\geq 1$  m height,  $< 1$  cm dbh) was over twice as high in forest plots dominated by bamboo (B+) versus forest plots without bamboo (B-). Soil texture data did not correlate with distribution of bamboo-dominated forest stands; however, bamboo-dominated stands do appear to be associated with perched water tables. Canopy light penetration, as calculated from hemispherical photographs, was significantly higher in B+ plots as compared with B- plots; thus competition for light does not appear to explain arrested succession.

Data on soil water content and stem damage to tree seedlings and saplings suggests that root competition and mechanical crushing by bamboo may cause arrested forest succession. Soil water content (0–10 cm) was significantly lower in B+ plots. On average, over four times as many seedlings and saplings were classified as having stem damage in B+ plots as compared with B- plots. Saplings of a given dbh were on average 29% taller in B- plots than those in B+ plots. We propose that the occurrence of bamboo-dominated forests can be explained by an interplay between mechanical properties of soils, wind disturbance, and elevated rates of tree mortality in the presence of bamboo.

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### 1. Introduction

In southwestern Amazonia, a region approximately the size of UK ( $\sim 180,000$  km<sup>2</sup>) has been classified as “bamboo-dominated forest” (Nelson, 1994). These terra firma forests are characterized by a mosaic of (1) forest stands without bamboo with heterogeneous forest structure, and (2) stands of trees scattered within

a canopy dominated by a single species of native arborescent bamboos (*Guadua* spp.). The mono-dominant species most commonly found in lowland terra firme forests of the Tambopata watershed, southeastern Peru, is *Guadua sarcocarpa* Londoño and Peterson, hereafter referred to as “bamboo”.

These bamboo-dominated forests, located in one of the most remote areas of the Amazon basin, were virtually unknown to Western science until the RADAM mapping project of the 1970s (Whitmore, 1998). These forests have since been noted as a

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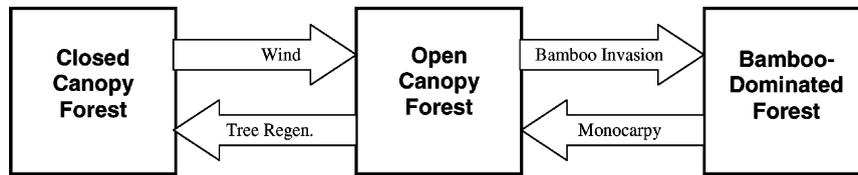


Fig. 1. Conceptual model of the successional relationship between forests with and without a bamboo-dominated canopy. Bamboo invasion is predicted to occur more frequently where soil horizons block tree taproot penetration.

remarkable anomaly in terms of physiognomy and bamboo abundance, but their ecology remains a mystery (Whitmore, 1998; Nelson, 1994; Conservation International, 1994). There appears to be a cycle of gradual increase in bamboo density, punctuated by a decrease of mature stem density following synchronized monocarpic flowering/die-off events. For *G. sarcoarpa*, monocarpic events occur at approximately 30-year intervals, synchronized at large (>10 km<sup>2</sup>) spatial scales. A similar vegetative growth form and synchronized 30-year monocarpic life cycle is exhibited by the other common mono-dominant arborescent bamboo of southwestern Amazonia, *Guadua weberbaueri* Pilger (Nelson et al., 2001). Nelson et al. (2001) have found that bamboo-dominated forests of Acre, Brazil have 29% less above-ground biomass than adjacent forests without bamboo due to the reduced density of trees.

Two authors have proposed that bamboo-dominated forests of southwestern Amazonia result from catastrophic disturbance, although no field data has been published on the successional dynamics of these forests to support this hypothesis. Balée (1989) proposed that bamboo-dominated forests of the Amazon basin are a legacy of past anthropogenic horticultural activities. Nelson (1994) suggested that the bamboo-dominated forests of southwestern Amazonia may have resulted from forest fires occurring when a dry El Niño year coincides with a year of monocarpic bamboo mortality, as appears to occur in bamboo forests of India (Gadgil and Prasad, 1984). There is no published (nor, to our knowledge, unpublished) evidence of large scale natural or anthropogenic catastrophic disturbance (fire, flooding, hurricane, agricultural clearing) in the terra firme forests of this region prior to recent agricultural forest clearing of the last 30 years. There are, however, strong winds from the south that have been implicated in causing high rates of tree blow-down in the region of southeastern Peru (Forsyth and

Miyata, 1984). Researchers suggest in a recent article that bamboo itself inhibits tree recruitment (Nelson et al., 2001).

Evidence from this study supports this observation by Nelson et al. (2001), with evidence that bamboo inhibits tree recruitment into larger size classes. This inhibition, in association with wind disturbance causing tree blow-downs, may explain the occurrence of this forest type without catastrophic disturbance.

We propose the following conceptual model for invasion and dominance of forest stands by bamboo (Fig. 1): bamboo can invade mature forests with a partial open-canopy structure resulting from wind blow-down (intermediate disturbance rather than catastrophic disturbance). The presence of bamboo reduces the growth rate and survival of trees, causing arrested forest succession and persistent bamboo mono-dominance. The distribution of bamboo contracts following synchronized bamboo monocarpic flowering/die-off events. Following these events, bamboo may re-invade or trees may successfully regenerate to form a closed-canopy forest without bamboo.

## 2. Methods

### 2.1. Study site

The Tambopata watershed lies in a region of tropical moist forest with a mean temperature of 24 °C. We selected two study sites: (1) Bahuaja located along the lower section of the Tambopata river (below the Rio Malinowski confluence), and (2) Tambopata Research Center (TRC) located in the upper reaches of the Tambopata River 50 km southwest of Bahuaja. The dominant bamboo species at TRC was identified as *Guadua sarcoarpa* Londoño and Peterson from fertile specimens, while the dominant bamboo species at Bahuaja was identified as *Guadua* cf. *sarcoarpa*

Londoño and Peterson, from infertile specimens. Precipitation in the lower Tambopata watershed is approximately 2000 mm per annum (Johnson, 1976), increasing heading upriver towards the Andes reaching 3200 mm per annum at TRC (Pesce, 1997). The dry season in this region extends from June through September during which precipitation may fall below 100 mm per month (Johnson, 1976; Pesce, 1997). The terra firme forests studied at these two sites are located on high terraces. These flat-topped but dissected terraces are the westernmost extension of a band that stretches through the states of Madre de Dios, Peru and Pando, Bolivia into central Brazil along the southwestern margin of the Amazon Basin (Conservation International, 1994). These terra firme terraces are composed of both late Tertiary alluvium and younger alluvial formations (Räsänen and Salo, 1990).

## 2.2. Forest inventory

### 2.2.1. Transect inventories

Six transects were established within the Tambopata River watershed between June 1999 and September 2000. Three transects were located at each of the two sites separated by 50 km within the Tambopata River watershed in order to capture heterogeneity across the watershed landscape. These inventories were designed to provide comparative information on successional dynamics in forests with and without bamboo. Descriptive information was focused on gathering data on plant community structure of juvenile trees between 1 m height and 5 cm dbh (diameter at breast height), and the competitive and physical environment they experienced.

Each transect straddles the edge between a bamboo-dominated forest stand and a closed-canopy forest stand without bamboo. Each transect consists of eight  $10\text{ m} \times 10\text{ m}$  plots located along a 120 m transect (Fig. 2). Four of the plots were located in series along the final 40 m of each end of the transect. In this way, a set of four  $10\text{ m} \times 10\text{ m}$  plots was located within a bamboo-dominated stand (B+), and another set of four was located within the adjacent closed-canopy forest stand without bamboo (B–), separated by forty meters.

Potential locations of transects were limited to the terra-firme forests within 3 km of each base camp at Bahuaja and TRC. A 1996 Landsat TM image was used to randomly select potential transect locations perpendicular to the transition zone between bamboo-dominated forest stands (B+) and forest stands without bamboo (B–). Potential locations of transects were limited to transition zones of 30 m or less between B+ and B– stands as seen on the Landsat TM image (transition zones have spectral signatures intermediate between those of B+ and B– stands in Landsat TM images). Bamboo-dominated stands were a-priori defined as having ten or more bamboo stems per  $100\text{ m}^2$ , and potential transect locations where this criterion was not met were discarded. Inventory plots thus established had an average of 33 mature bamboo stems per  $100\text{ m}^2$  for B+ plots, with a range from 11 to 50 stems per plot. B– plots had an average of 0.7 bamboo stems per plot with a range from 0 to 4 (none of which attained canopy occupancy). The total number of B+ plots was 24, and the total number of B– plots was 23 (one “B–” plot was eliminated from analysis retroactively from a Bahuaja site transect due to the presence of canopy-occupying bamboo stems).

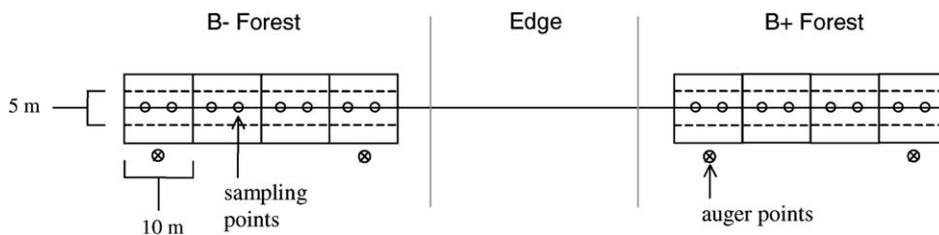


Fig. 2. Transect sampling design. Four  $10 \times 10\text{ m}$  plots were arranged at either end of a 120 m transect centerline (solid line) crossing from bamboo-dominated forest (B+) to forest without bamboo (B–). Transects were located where transition zone edges were no greater than 30 m in width. Dotted lines identify the boundaries of nested plots for juvenile tree measurements. Circles identify the location of sampling points for hemispherical photographs and soil moisture.

### 2.2.2. Plant community structure

Within each 10 m × 10 m plot, structural data were collected on trees and bamboo during August and September of 2000. All trees ≥ 10 cm dbh (diameter at breast height) were measured for dbh, and the number of mature bamboo stems (those with ramified branches and leaves) per plot was tallied. Within each 10 m × 10 m plot, a nested plot of 5 m × 10 m was established with its long axis along the centerline of the transect. Within these nested plots, all trees within three size classes were tallied: (1) seedlings (≥1 m height, <1 cm dbh), (2) saplings (≥1 cm dbh, <5 cm dbh), and (3) poles (≥5 cm dbh, <10 cm dbh). All seedlings and saplings within these nested plots were also measured for diameter at 10 cm above the ground, and height. These diameter and height data were used for calculation of height/diameter ratios of each stem.

Within three of the six transects (one at TRC Site, two at Bahuaja Site), mortality and stem damage data were taken in 1999. Mortality data was taken by tagging all seedlings in August of 1999 and re-inventorying the plots in August of 2000. Any seedling or sapling with “stem damage” was noted as such. Two categories were defined for stem damage: (1) any stem bent past the horizontal, (2) any stem that had been snapped off and the re-sprouting primary stem was less than one-fourth the diameter of the original stem at point of breakage.

### 2.2.3. Soil

Soil samples for texture analysis were collected during initial visits to Bahuaja site before transect inventories were established. Two samples were collected from within each bamboo patch where transects were established and two from adjacent forest without bamboo for a total of 12 samples collected. Each sample was composited from two sub-samples of 0–10 cm depth separated by approximately 5 m. Soil texture analysis was conducted on site with a LaMotte “Soil Texture Unit” kit no. 1067, separating sand and silt through sedimentation using Stokes’ Law (Brady and Weil, 1996). Clay content was calculated from sand and silt measurements.

One soil sample was collected for soil moisture analysis from each 10 m × 10 m plot of each of the six transect inventories. Each sample was composited from two 0–10 cm depth samples taken at a distance of 2.5 and 7.5 m along the mid-line of each plot. Soil

samples were weighed in “field moist” condition, dried for 8 h at 80 °C, and weighed again for calculations of percent soil water content. Samples were collected from the three TRC transect inventories on 18 August 2000 after 7 days without rain. Samples were collected from the three Bahuaja transect inventories on 20 September 2000 after 5 days without rain.

Soil auger holes were made at four points along each transect (0, 40, 80, 120 m) during August 2000. The occurrence of mottling, indicating a seasonal water table, was noted to a depth of 160 cm.

### 2.2.4. Light

Hemispherical photographs of the forest canopy were taken along all transects in August and September of 2000. Photographs were taken with a system designed by Delta-T Devices Ltd. (Cambridge, UK). Hemispherical photography involves using a camera fitted with an approximately 180° field of view. Once classified, these images provide a detailed map of canopy openings relative to the location from which the photograph was taken (Rich and Wood, 1999). A Nikon Coolpix 950 digital camera was fitted with a Nikon FC-E8 fisheye converter lens. A Delta-T devices mount was used for horizontal leveling and north–south orientation of the camera and lens. All photographs were taken on uniformly overcast days to provide even sky lighting. Photographs were taken at a height of 1 m, at 5 m intervals along the mid-line of each transect, arranged as two photos per 10×10 m plot (at a distance of 2.5 and 7.5 m along the mid-line of each plot). Locations of the photographs were adjusted to within 1 m radius of these points to ensure that no light-intercepting surfaces were within 50 cm of the lens (in some cases branches were bent aside to ensure this criterion was met). At no site did slope steepness effect the image. The resulting images were classified using HemiView software (Delta-T Devices Ltd.) into (a) exposed sky, or (b) sky obscured by plant tissue. Classified images were inspected for errors in classification. In a small number of images (>10) tree trunks and plant leaves were misclassified as sky due to sun reflection. These pixels were darkened in photoshop in order to insure correct classification. From these classified images, HemiView software calculated global site factor (GSF, proportion of direct and diffuse solar radiation reaching a given location over the course of the year, relative to that in a location

with no sky obstructions). GSF ranges in value from 0 to 1, with 0 being no radiation and 1 being the radiation for an open location. Calculation of GSF involves overlaying the image with a “sunmap” of the annual track of the sun, generated from a knowledge of the UTM coordinates of the study area, and the north–south orientation of the image. The classification threshold for differentiating between “sky” and “vegetation” pixels in each image was determined independently by three different individuals trained in the classification procedure. An average of the three threshold values thus generated was calculated for each image. This average threshold was used to classify each image. Percent error in classification was calculated from the S.D. of GSF values generated from each of the independently generated thresholds as a percent of the GSF value generated from the average threshold value. All percent errors in classification were <7%.

#### 2.2.5. Data analysis

The mean values of the measurements within the four plots of each transect within each forest type (B+, B–) were used as sample means for statistical analysis of light, soil moisture, tree basal area, stem height/diameter ratios, and stem densities of each size-class. Therefore, for each of these variables, the B+ and B– grand means of the six sample means were statistically tested to determine whether the null hypothesis of no difference between means could be rejected (two-tailed). Normal distribution of the sample means was assumed based on the central limit theorem. This assumption was supported by verifying that approximately 70% or more of the sample means of each variable listed above fell within the interval: grand mean  $\pm$  S.D. (Fowler et al., 1998). Variances were assumed to be equal if the larger variance of the two means compared for each variable was less than three times the smaller variance. Accordingly, the variances for light and pole density were assumed to be equal, and these two variables were analyzed with a paired *t*-test (sample means paired for a given transect). The variances for soil moisture, height/diameter ratios, tree density, and tree basal area, were not assumed to be equal, and these variables were analyzed with Welch’s modified two-sample *t*-test.

The proportional variables of stem damage and seedling mortality were analyzed with the Mantel–Haenszel test (two-way). For each transect, a single

value was calculated for each of the four plots of each forest type (B+, B–). The data were arranged for analysis as three  $2 \times 2$  contingency tables, one for each of the three transects where data was collected. S-plus 2000 software was used for all statistical calculations.

### 3. Results

#### 3.1. Forest inventory

Results from the six transects found over eight times lower average tree basal area (for trees  $\geq 10$  cm dbh) in bamboo-dominated forest plots (B+) as compared with adjacent forest plots without bamboo (B–) (Table 1). Mature trees ( $\geq 10$  cm dbh) occurred at an average density over four times lower in bamboo-dominated forest plots (B+). Pole-sized trees ( $\geq 5$  cm dbh,  $< 10$  cm dbh) occurred at an average density over two times lower in bamboo-dominated forest plots (B+). Seedlings ( $\geq 1$  m height,  $< 1$  cm dbh) and saplings ( $\geq 1$  cm dbh,  $< 5$  cm dbh) occurred at an average density in B+ plots not significantly different from that found in plots without bamboo (B–) (Fig. 3). The average sapling height/diameter ratio was significantly lower in B+ plots versus B– plots. Saplings of a given dbh were on average 29% taller in forest plots

Table 1  
Plant inventory data for two forest types

Measurement	B–	B+	<i>P</i> -value
Tree basal area (m <sup>2</sup> /ha)	38.7 (11.3)	4.6 (3.1)	>0.001
Percent damaged juvenile tree stems	5.2 (4.8)	22.6 (12.7)	>0.001
Percent seedling mortality	13.0 (4.7)	26.5 (7.0)	0.052

Values for measurements are given for each of two forest types: forest plots without bamboo (B–) as compared with bamboo-dominated forest plots (B+). Tree basal area data (all trees  $\geq 10$  cm dbh) are grand means of sample means from the six transect inventories. Basal area data was analyzed with Welch’s modified two-sample *t*-test. Data on stem damage and mortality are means of values from three of the six transect inventories. “Damaged” juvenile tree stems (1 m height–5 cm dbh) are those individuals with primary stems snapped off or bent past the horizontal (Section 2). Mortality data are for seedlings (1 m height–1 cm dbh) over a 1 year period (1999–2000). Mortality and stem damage data were analyzed with Mantel–Haenszel  $\chi^2$ -test. Each mean value is followed by a value in parentheses giving S.D. from the mean.

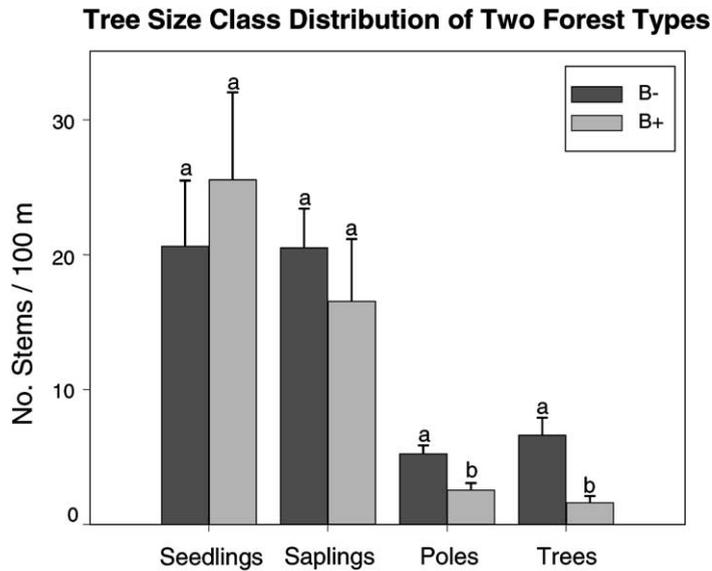


Fig. 3. Size class distribution of seedlings (1 m height–1 cm dbh), saplings (1–4.9 cm dbh), poles (5–9.9 cm dbh) and mature trees ( $\geq 10$  cm dbh) in plots without bamboo (B–), and in bamboo-dominated plots (B+). Bars indicate S.D. from the mean. Letters quantitatively indicate significant differences ( $a > b$ , at  $P = 0.01$ ) between stem densities for each size class.

without bamboo (B–) than those in bamboo-dominated forest plots (B+). The average seedling height/diameter ratio was not significantly different in B+ plots versus B– plots (Fig. 4).

Results from 1 year of seedling mortality data found average percent mortality of seedlings ( $\geq 1$  m height,  $< 1$  cm dbh) over twice as high in B+ plots versus B– plots (Table 1). In the same transects, on average, over

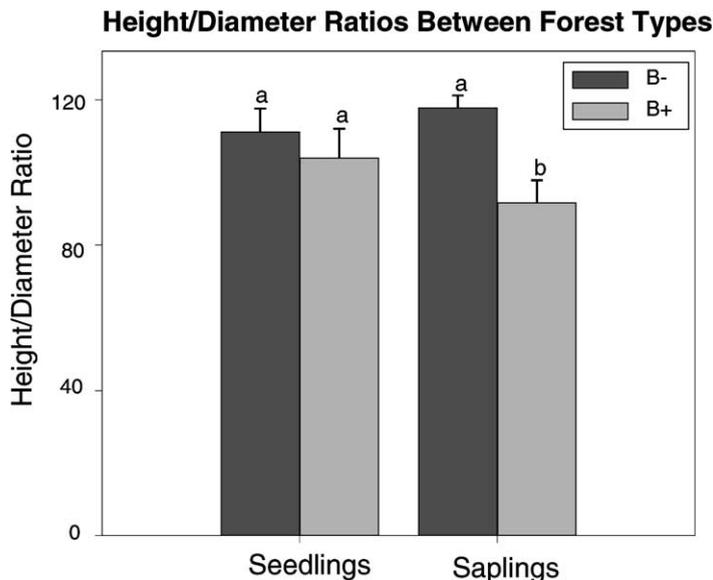


Fig. 4. Height/diameter ratios of seedlings (1 m height–1 cm dbh) and saplings (1–4.9 cm dbh) in forest plots without bamboo (B–) and bamboo-dominated forest plots (B+). Bars indicate S.D. from the mean. Letters quantitatively indicate significant differences ( $a > b$ , at  $P = 0.01$ ) between stem densities for each size class.

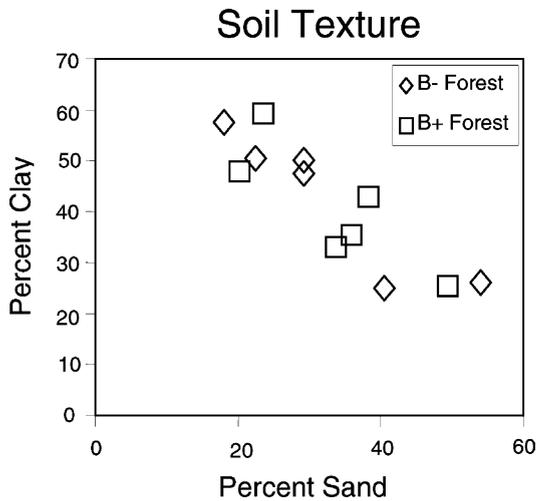


Fig. 5. Soil texture analysis of bamboo-dominated forest stands (B+) as compared with adjacent mature forests without bamboo (B-). These samples range from “clay” (upper left portion of graph) to “clay loam” to “sandy clay loam” (lower far right two points) (USDA classification scheme).

four times as many juvenile trees ( $\geq 1$  m height,  $< 1$  cm dbh) were classified as having stem damage in B+ plots as compared with B- plots (Table 1).

### 3.2. Soil and light environments

No significant difference was found between the mean percent clay, sand, or silt of B+ versus B- soil

Table 2  
Light and soil moisture environment for juvenile trees in two forest types

Measurement	B-	B+	P-value
Understory Light (GSF)	0.140 (0.010)	0.158 (0.011)	0.009
Soil water content (Gravimetric)	0.257 (0.014)	0.214 (0.044)	0.065

Values for measurements are given for each of two forest types: forest plots without bamboo (B-) as compared with bamboo-dominated forest plots (B+). Light and soil moisture data are grand means of sample means from each of the six transect inventories. Each mean value is followed by values in parentheses giving one S.D. from the mean. Light values were generated from computer analysis of hemispherical photographs taken at 1 m height. Soil water content data were measured from soil core samples of 0–10 cm depth. Light data were analyzed with a paired *t*-test. Sample means of the two forest types were paired for each transect. Soil moisture data were analyzed with Welch’s modified two-sample *t*-test.

samples (Fig. 5). Within each of the six transects, consistently lower mean soil water content values were found in the B+ plots, resulting in a significant difference between grand means (Table 2). Within each of the six transects, consistently higher mean light penetration values (GSF) were found for B+ plots, resulting in a significant difference between grand means (Table 2).

Mottling, was found at between 50 and 100 cm on the B+ side of three of the six transects. These shallow mottled horizons were all immediately underlain by barriers to water percolation (clay matrix gravel beds or lateritic duricrusts). No mottling was found within 160 cm of the soil surface for the remaining three B+ transects or any of the B- transects.

## 4. Discussion

The size-class distribution we report (Fig. 3) suggests that succession is arrested in bamboo plots not due to inability of juvenile trees (seedlings and saplings) to germinate and establish, but because seedlings and saplings are failing to recruit into larger size classes. However, size class does not necessarily accurately represent age class (Oliver and Larson, 1996). Thereby, one year of mortality data from three of the transects confirm that reduced density of poles and mature trees in bamboo-dominated (B+) plots is associated with higher mortality of seedlings in B+ plots.

The results from surficial soil texture analysis found a nearly complete overlap in the range of soil texture encountered in the two forest types (B+ and B-). It seems unlikely that the dramatic differences in stand structure found between B+ and B- plots are driven by surficial soil characteristics that inhibit tree growth.

Data collected on deeper soil horizons (50–160 cm) suggest that mechanical characteristics of soil may play a role in the successional dynamics of bamboo-dominated forests. Mottled soil horizons indicate the presence of seasonal water tables which block the development of roots due to anoxic conditions. In the three B+ transects with perched water tables as indicated by shallow mottled horizons ( $< 1$  m depth), trees are expected to have an elevated susceptibility to windthrow due to poor taproot development and seasonally unstable saturated soil. The landscape scale

pattern of such soils with raised water tables due to barriers to water percolation has been generated in southwestern Amazonia during multiple fluvial soil formation events since the Tertiary (Räsänen and Salo, 1990; Räsänen and Linna, 1995).

Various authors suggest that competition for light is the key limiting resource organizing successional “gap dynamics” in tropical rainforest ecosystems (Denslow and Hartshorn, 1994; Brokaw, 1982, 1989; Hubbell and Foster, 1999). Studies of the influence of understory bamboo on forest succession in China (Taylor and Zisheng, 1988) and Japan (Tanaka, 1988) have attributed reduced density of both tree seedlings and saplings to reduced light levels beneath bamboo. Both studies actually found higher light levels in the presence of bamboo at heights of 1.5 and 0.5 m (Tanaka, 1988) and 1.8 m (Taylor and Zisheng, 1988), but both discounted these results and attributed a scarcity of tree seedlings and saplings in the presence of bamboo to reduced light levels at ground level. Light values were not taken at ground level in this study because, unlike the above two studies, reduced tree density was found only above the sapling size-class. The results from this study suggest that competition for light is not a sufficient hypothesis to explain arrested succession in bamboo-dominated forests of southeastern Peru, since light values are slightly higher in the understory of bamboo-dominated plots (B+) (Table 2).

Drought stress has been found to be an important factor in seedling mortality in a seasonally dry Costa Rican forest (Gerhardt, 1993, 1996). A Panamanian bamboo (*Rhipidocladum racemiflorum*) was found to be extremely resistant to xylem vessel cavitation and able to tolerate severe drought stress (Cochard et al., 1994; Ewers et al., 1997). It is possible that bamboo (*G. sarcocarpa*) reduces tree seedling survival by increasing soil moisture stress during the dry season. The data presented on soil water content (Table 2) suggest that below-ground competition for soil moisture in the presence of bamboo may reduce tree growth and/or survival. However, it seems unlikely that reduced soil water content alone would fully arrest forest succession, as a number of canopy tree species found in this neotropical moist forest (e.g. *Hymenaea courbaril*, *Cedrela odorata*, *Swietenia macrophylla*) also occur in neotropical dry forests where lower soil water content values have been measured (Gerhardt, 1996).

Physical damage to juvenile trees due to litterfall has been shown to be an important cause of seedling mortality in neotropical forests (Clark and Clark, 1989, 1991). Uhl (1982) found that mechanical damage was the largest cause of mortality for trees 1–10 cm dbh in an Amazonian terra firme forest. The capacity of seedlings to survive mechanical damage has also been shown to differ by tree species (Guariguata, 1998). However, mechanical damage has not previously been demonstrated to be associated with arrested forest succession.

The branches of bamboo (*G. sarcocarpa*) culms are equipped with re-curved barbs that function as grappling hooks that tenaciously attach themselves to available tree branches. Bamboo culms have poor structural properties, tending to buckle under their own weight. The hollow internodes of bamboo culms fill with water, adding significantly to their mass. Bamboo culms are constantly growing, collapsing, and dying, creating an environment where tree saplings within a bamboo stand have a high probability of being physically crushed. This physical damage effect may increase with juvenile tree size since bamboo tends to bear its load on taller trees within its height growth range (maximum culm length measured by the authors, 30 m). The two measures of mechanical damage to juvenile trees reported here (height/diameter ratios, and data on stem damage) suggest that mechanical damage is an important phenomenon causing arrested succession in bamboo-dominated forest stands.

Enough evidence has been gathered to develop a model for the successional dynamics of the bamboo-dominated forests of southwestern Amazonia. The emerging picture for this system contradicts assumptions of successful tree regeneration found in existing models of tropical forest dynamics (Whitmore, 1984, 1998; Denslow and Hartshorn, 1994). We propose that the lower biomass of bamboo-dominated forests may result not from catastrophic disturbance, but from a combination of intermediate disturbance and the capacity of an aggressive bamboo to invade tree canopies with multiple gaps, and competitively exclude juvenile trees. A positive feedback loop of forest collapse and reduced biomass will ensue after bamboo invasion if (1) the remaining trees bearing the load of bamboo culms have an enhanced likelihood of blow-down, and (2) bamboo maintains a heterogeneous, wind-exposed forest canopy by suppressing regeneration of juvenile

trees. At the edges of bamboo-dominated stands this positive feedback loop may result in bamboo invasion of adjacent areas. This process of bamboo-invasion may be re-set to a tree-dominated canopy following bamboo monocarpic events, regionally synchronized at approximately 30-year intervals (Fig. 1).

Sites with perched water tables may be zones of initiation where bamboo establishes after monocarpic events. Established bamboo-dominated stands may expand outward into sites without perched water tables, until the next monocarpic event. More extensive data on the association between perched water tables in terra-firme soils and bamboo distribution is necessary. Human disturbance may also cause expansion of bamboo-dominated forests by de-coupling the relationship between tree canopy disturbance and site characteristics that influence tree wind-firmness.

In a region with so little prior research, lack of evidence for catastrophic disturbance does not preclude the existence of catastrophic disturbance phenomenon such as fire occurring at long time intervals (Turcq et al., 1998). While catastrophic disturbance may be expected to facilitate bamboo invasion, it does not explain long-term persistence of bamboo dominance. The evidence presented here suggests that whether or not catastrophic disturbance does occur, it is not necessary to explain the maintenance of bamboo mono-dominance because the presence of bamboo arrests tree recruitment into larger size classes. Experimental research is necessary to further confirm a causal link between bamboo presence and tree growth and survival in order to test the model proposed here.

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