

BIOMASS ACCUMULATION AFTER 10–200 YEARS OF SHIFTING CULTIVATION IN BORNEAN RAIN FOREST

DEBORAH LAWRENCE¹

Environmental Sciences Department, University of Virginia, P.O. Box 400123, Charlottesville, Virginia 22904-4123 USA, and Botany Department, Duke University, Durham, North Carolina 27708 USA

Abstract. I examined the effect of repeated long-fallow shifting cultivation on biomass accumulation in a rain-forest landscape occupied for over 200 years in West Kalimantan, Indonesia. The diameters of stems >5 cm dbh were measured in nine secondary forests using a stratified random design of nested plots (3000 m² per site). The stands were 9–12 years old and had experienced from 1 to 10 or more cycles of shifting cultivation. Accounting for differences in soil fertility, analysis of covariance (ANCOVA) demonstrated that aboveground live biomass increment (ABI, in megagrams per hectare per year) was significantly greater after four cycles than after six or more cycles. ABI was lowest after two cycles, highest after one or four cycles and intermediate after 6–10 cycles. Differences were driven by the density and biomass of trees >10 cm dbh, which followed a similar pattern. Although the diameter increment and contribution to total biomass of trees >10 cm dbh increased significantly with inherent soil fertility, variation in the rate of biomass accumulation depended primarily on the number of prior cultivation cycles. An ANCOVA with soil fertility as the main effect was not significant. One hypothesis to explain observed patterns of ABI associated with changes in tree density is a shift, over many cycles, in the dominance of seed-banking vs. resprouting species. Previous work has shown that total phosphorus did not decline after six or more cycles; however, a shift from available to occluded forms may be related to lower ABI in sites with the longest cultivation history. An 11% decline in ABI could substantially alter the carbon-sequestration value of secondary tropical forests as they enter their second century of persistent human disturbance.

Key words: biomass accumulation; carbon sequestration; cultivation history; deforestation; life-history turnover; phosphorus; shifting cultivation; tropical secondary rain forest; West Kalimantan, Indonesian Borneo.

INTRODUCTION

With over half of all aboveground biomass stored in the terrestrial biosphere, changes in the extent and structure of tropical forests will continue to have a major impact on the global carbon cycle (Saugier et al. 2001). In Asia, shifting cultivation was responsible for 50% of annual deforestation at the end of the 20th century; it accounted for 70% in Africa and 35% in South America (Whitmore 1997). Secondary-forest regeneration is an essential part of shifting cultivation, unlike industrial agriculture or cattle ranching. Accounting for regrowth during the fallow period, shifting cultivation was still responsible for 25% of estimated carbon emissions in Asia over the past 150 years (Houghton and Hackler 1999). Depending on the length of the fallow period, the potential for carbon storage under shifting cultivation is great relative to other agricultural land uses, but this depends on the long-term effects of shifting cultivation on biomass accumulation in secondary forests.

Biomass recovery following large-scale human disturbance in tropical forests has been well documented (e.g., Saldarriaga 1988, Zimmerman et al. 1995, Fearnside and Guimaraes 1996, Pascarella et al. 2000). More intensively cultivated sites (longer duration, or using heavy machinery) tend to have lower rates of biomass accumulation (Uhl et al. 1988, Hughes et al. 1999, 2002, Moran et al. 2000). However, very few studies have incorporated prior land-use history. To my knowledge, only Steininger (2000) and Hughes et al. (2000) have explicitly examined the effect of repeated disturbance such as the systematic clearing that occurs every 5–20 years under shifting cultivation. In short-fallow shifting cultivation in Brazil, Hughes et al. (2000) found no difference in successional biomass between sites regrowing after one or two cycles. Steininger (2000), working in medium-fallow systems of Bolivia, also found no difference in biomass accumulation rate between sites cultivated once and sites having experienced three cycles of shifting cultivation. Over several cycles, comprising two to three decades, shifting cultivation did not diminish the productive capacity of the land. Here, I investigate how biomass accumulation in secondary rain forest changes over the course of approximately 10 cycles, or two centuries, of long-fallow shifting cultivation in Indonesia.

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¹ E-mail: lawrence@virginia.edu

Local soil conditions should influence biomass recovery, and they may be affected either by human activity on the land or by intrinsic characteristics of the site, such as bedrock or soil type. At continental scales across a broad range of climate regimes, coarse soil texture significantly reduced the rate of biomass accumulation in secondary forests (Johnson et al. 2000, Zarin et al. 2001). However, differences in land-use history, management practices, or precipitation regime may influence constraints on biomass production at landscape or regional scales. Working in a Puerto Rican landscape, Chinae (2002) found that secondary-forest basal area (and, by inference, biomass) was higher on Entisols over alluvial deposits than on Inceptisols or Entisols over volcanic and plutonic deposits, presumed to have lower inherent fertility. I assess the effects of repeated shifting cultivation on biomass accumulation within the context of broader constraints imposed by soil fertility within a landscape.

Previous work in the study area showed that farmers chose finer textured, richer soils at lower elevations when they originally settled the village over 200 years ago (Lawrence and Schlesinger 2001). Thus, the number of prior cultivation cycles is positively correlated with the inherent fertility of sites. This correlation informs specific expectations about the relationship between the number of prior cycles and biomass accumulation rate. If inherent fertility were the only constraint on productivity, biomass accumulation rate should increase with the number of prior cycles because sites with the longest cultivation history were the most fertile. This null hypothesis does not imply a positive effect of repeated cultivation. It depends on an assumption that biomass accumulation increases with inherent soil fertility and that fertility does not change over many cycles.

A positive response to repeated cultivation would increase the slope of a relationship between number of prior cycles and biomass accumulation rate. Alternatively, if repeated disturbance has a negative effect, biomass accumulation should be depressed in sites having experienced more cycles of shifting cultivation. Depending on the strength of the effect, it could counterbalance the positive effect of higher inherent fertility. With a weak negative effect, the relationship between biomass accumulation rate and number of prior cycles might be relatively flat, but a strong negative effect could result in a negative slope. To evaluate these alternative hypotheses, I first examined the accumulation rate of aboveground biomass as a function of the number of prior cycles. Then, to determine the independent effect of repeated cultivation, I used analysis of covariance to account for differences due to inherent soil fertility. Finally, I examined forest structure and biomass distribution to interpret differences in biomass accumulation rate.

METHODS

Study site and sampling design

The Dayak village of Kembera, West Kalimantan (0.4° S, 110.1° E), was chosen for study because long-fallow shifting cultivation has been continuous there for over 200 years, according to local inhabitants and early Dutch maps (ca. 1750). Techniques employed in Kembera were representative of the system of long-fallow shifting cultivation widespread on the island of Borneo, especially in areas more remote than Kembera (Dove 1985). The ~4000-ha secondary forest area was originally lowland mixed-dipterocarp rainforest on Ultisols and Oxisols (~100–600 m above sea level). Rainfall from January 1995 to January 1996 was 3608 mm (average >4000 mm/yr). Rainfall is rarely <200 mm/mo, and the driest months tend to be June through August.

In West Kalimantan, shifting cultivation of rice involves slashing and burning all vegetation in approximately one hectare of primary or secondary forest using axes or chainsaws (see Plate 1). No standing trees remain. Dry, upland agriculture of this type relies on no tillage, no terracing or mounding, no irrigation, and no inputs of green manure, fertilizer, herbicides, or pesticides. The field is usually abandoned to secondary-forest fallow after one rice crop (see Dove 1985). The mean fallow period of plots cleared from secondary forest in 1990–1995 was 19 years. For three communities within 20 km of Kembera, the mean fallow period was 13 years (Lawrence et al. 1998). Available data from East Kalimantan show a fallow range of 3–29 years (Inoue and Lahjie 1990). Anecdotal evidence suggests that the rotation period in Kembera is relatively high among communities of the outer islands of Indonesia where long-fallow shifting cultivation was once dominant. Fallows designated for future rice production are not planted or actively managed, but fuelwood and thatching material may be collected sporadically. This study focused on unmanaged, natural fallows.

In January–July of 1995 and January–March of 1996, vegetation and soils were sampled at nine sites, 9–12 yr old, concentrated in a 3 × 3 km area. I determined the number of prior swidden–fallow cycles through interviews, conducted after four years of working in the village, with the landowners and other knowledgeable informants. Further information was gleaned from colonial Dutch maps (ca. 1750). Only sites with histories corroborated by more than one reliable source were included in the analysis. One to four cycles seemed well within the capacity of a landowner's memory. Sites that had been cultivated for the known ~200-year history of the village were assigned a value of 10 cycles, assuming a 20-year mean fallow period, based on current patterns. This was deemed the most conservative assumption about cultivation history at the



PLATE 1. Two adjacent plots, recently cleared and burned in preparation for shifting cultivation of upland rice in West Kalimantan, Indonesia. Note huts for scale (approximate 8 m²). Photo credit: D. Lawrence.

oldest sites. Sites with an estimated five or six cycles represent an intermediate cultivation history.

Because the study was limited to one village, neither precipitation nor the historical context of land use varied systematically. However, inherent soil fertility varied with soil texture and cultivation history (Fig. 1a and b). Although sand content has been linked with diminished biomass accumulation rate among second-

ary forests worldwide (Johnson et al. 2000), I chose an indicator of the pre-cultivation phosphorus (P)-supplying capacity of the soil to indicate differences in original site fertility. Recent experimental studies in rainforests have found evidence for P limitation of ecosystem processes including productivity (Herbert and Fownes 1995, Vitousek and Farrington 1997, Hobbie and Vitousek 2000, Cleveland et al. 2002).

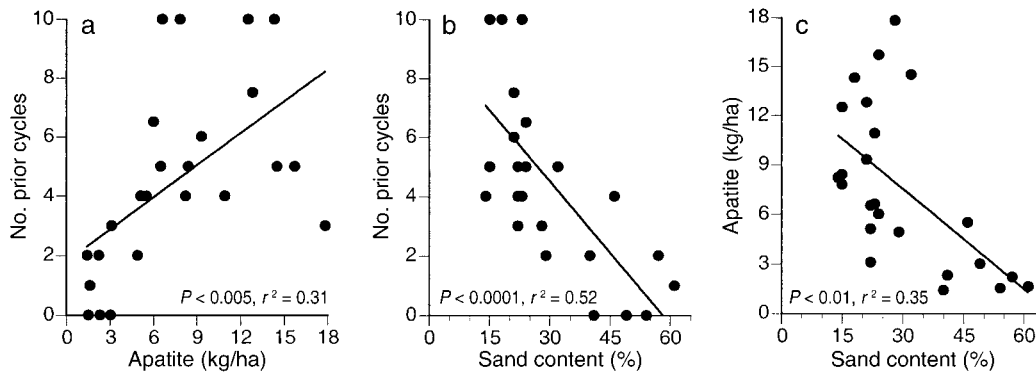


FIG. 1. Relationship between original soil fertility and the number of prior cultivation cycles at a site (modified from Lawrence and Schlesinger [2001]). (a) Apatite or primary mineral phosphorus, indicated by 1 mol/L HCl-extractable phosphorus, was higher in sites opened up to shifting cultivation long ago. (b) Sites having experienced the most cultivation cycles also had the lowest sand content. (c) Sand and apatite content were correlated over the entire range sampled, but within finer soils (<32% sand) and coarser soils (>40% sand), there was no relationship between them.

Primary mineral P (apatite) content of the top 30 cm of soil was determined by 1 mol/L HCl extraction in the sequential fractionation of Tiessen and Moir (1993). Across 30 sites including those in this study, apatite content was negatively correlated with sand content (Fig. 1c). However, among finer soils (<32% sand) and coarser soils (>40%), texture and apatite were not related. Apatite and total P were positively correlated ($r^2 = 0.71$, $P = 0.0001$, data not shown). Although total P could be used as an indicator of *current* soil fertility, it is less useful as an indicator of soil fertility prior to conversion. Because total P includes organic fractions, it is more likely to reflect the biological effects of cultivation, species composition, and forest age (see Tieszen et al. 1983, 1994, Garcia-Montiel et al. 2000). Apatite was considered to be the best indicator of *inherent* soil fertility because it is controlled primarily by geochemical rather than biological processes (Cross and Schlesinger 1995).

At each of seven fallows, I arrayed four plots (30 × 25 m) to capture the range of variation in biomass recovery. Along each edge of the roughly rectangular fallow, the location of the central axis of a plot was randomly chosen. Each plot was established 5 m into the fallow. “Large” trees (>10 cm in diameter at breast height (dbh), 1.5 cm above ground) were measured and identified in these four plots (total 3000 m² per site). “Small” trees 5–10 cm dbh were sampled in three 100-m² quadrats (5 × 20 m) within each of the large-tree plots (total 1200 m² per site). Two additional sites, aged 10 and 11 yr, were drawn from a concurrent study of succession. For these sites, a single 1000-m² plot (20 × 50 m) was established from a random point on one fallow edge. A transect angle was selected at random, and the central axis of the plot was placed randomly along it. All large trees were identified and measured for dbh. The plot was then divided into ten 10 × 10 m quadrats and two were randomly selected for measurement of small trees. Mean apatite stocks were determined from 12 measurements per site, each based on 10 systematically arrayed soil cores per 100-m² small-tree quadrat (see Lawrence and Schlesinger 2001).

Aboveground, live biomass was calculated on a per stem basis following relationships developed by Hughes et al. (1999) and Brown et al. (1989) for tropical forests with rainfall similar to that of the study area. Liana biomass was estimated using the equation of Gerwing and Lopes Farias (2000). Since wood densities are not known for all identified species, and all trees have not yet been identified to species, I assigned a specific gravity of 0.60 for all stems. This number was derived from known values for Southeast Asian tree species with congeners in this study (Brown 1997, Ketterings et al. 2001). Bamboo (mostly <6–7 cm dbh) was present or abundant at four of nine sites. Because bamboo is hollow and has no woody canopy, I assumed its biomass was 35% of a woody stem with equal di-

ameter. Sensitivity analysis showed that reducing bamboo biomass to 20% of woody biomass did not alter the magnitude or significance of the results. Biomass accumulation rate was defined operationally as average annual biomass increment (ABI), or total live above-ground biomass (>5 cm dbh) divided by age. Another index of growth rate was average diameter increment, mean diameter of trees >10 cm dbh divided by age.

Analysis

The relationship between observed ABI and number of prior cultivation cycles was compared with relationships predicted by the four alternative hypotheses. Then, to distinguish the effects of repeated cultivation from effects of inherent fertility, analysis of covariance (ANCOVA) was performed on the same, site-level ABI data using SPSS version 10 (SPSS 2000). The complete model included number of prior cycles as a fixed effect with apatite content and age as covariates. Sites were assigned to five groups, depending on cultivation history (one, two, four, five and six, or ten cycles). Although age was restricted in this data set, inclusion of age as a covariate represented the most conservative statistical approach. For this and subsequent models, I present marginal means, indicated by an asterisk (e.g., “ABI*”), that account for the effects of inherent fertility and age. I tested an alternative model for predicting ABI with fertility group (apatite of 1.4–2.3 kg/ha, 5.0–6.7 kg/ha, 7.3–9.3 kg/ha, and 12.0–17.7 kg/ha) as the fixed effect and number of prior cycles and age as covariates.

Similar models were fit for stem density, actual biomass percentage biomass of large and small trees, and diameter increment of large trees. In models of the density, biomass, and percentage biomass of the two size classes, age did not contribute significantly to the model, and it was deleted. Where the remaining covariate, apatite, was the only significant factor explaining variance among sites, the model was rerun with fertility group as the fixed effect and number of prior cycles or age (where significant) as a covariate. Where no covariates were significant, the model was run as a linear regression.

RESULTS

In 9–12 yr old secondary forests, observed above-ground biomass increment of trees >5 cm dbh (annual biomass increment, ABI) was significantly lower in sites cultivated twice than in sites cultivated 1, 4, 6, or 10 times (Fig. 2a, Table 1a). Differences among the latter were not significant. Correcting for the effects of inherent soil fertility and age, this pattern of significant decline in ABI between one and two cycles followed by recovery to first-cycle levels by the fourth cycle persisted. However, corrected ABI (ABI*, marginal mean ABI, accounting for effects of age and inherent soil fertility) was significantly lower in the sixth cycle (5.4 Mg·ha⁻¹·yr⁻¹) than in the first and fourth cycles

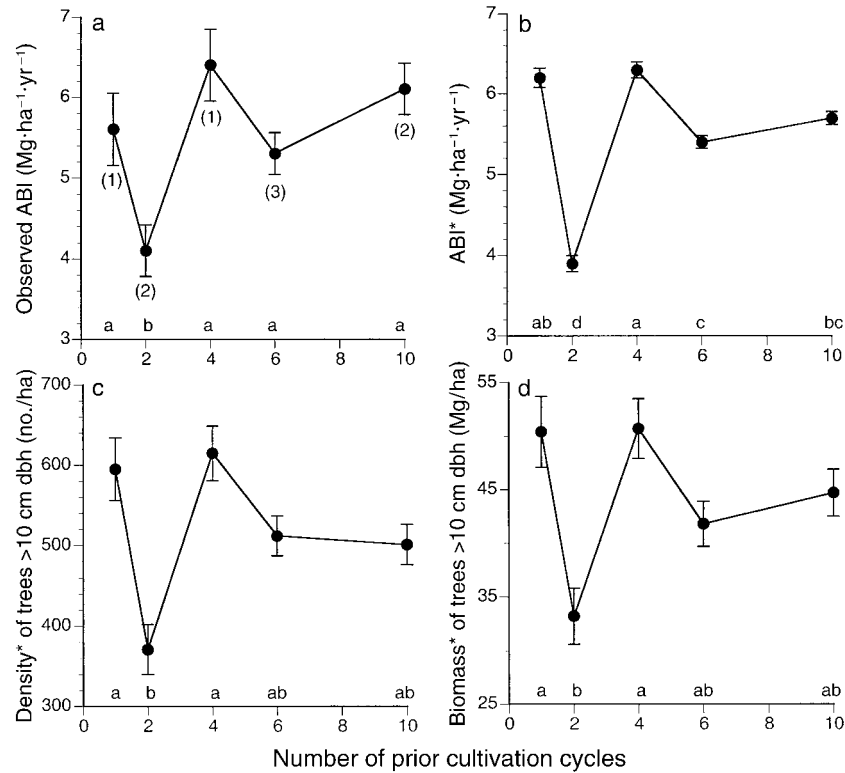


FIG. 2. (a) Aboveground live biomass increment (ABI) as a function of the number of prior cultivation cycles, (b) ABI*, corrected for age and inherent soil fertility, (c) density*, and (d) biomass* of trees >10 cm dbh, corrected for inherent soil fertility; all varied significantly with cultivation history. Data are means \pm 1 SE. Marginal means assume an age of 10.3 years [in panel (b)] and an apatite content of 7.5 kg/ha [in panels (b), (c), and (d)] to account for the effect of significant covariates. In panel (a) the numbers in parentheses indicate the number of sites sampled. The number of cycles with the same lowercase letters above the x-axes are not significantly different at $P = 0.05$.

(>6.3 Mg·ha⁻¹·yr⁻¹) (Fig. 2b, Table 1b). Sites cultivated 10 times also had lower ABI* (5.7 Mg·ha⁻¹·yr⁻¹) than those cultivated once (marginally significant, $P = 0.10$) or four times ($P < 0.05$). ANCOVA with fertility as the main effect and number of prior cycles and age as covariates did not explain variation in ABI (Table 1c).

Variation in biomass and forest structure was substantial among these young forests (Appendix). The range of aboveground live biomass >5 cm dbh was 38–64 Mg/ha (26–51 Mg/ha >10 cm dbh). Biomass and contribution to total biomass varied two- to three-fold for stems 5–10 cm dbh. Their density varied three- to four-fold. The structural characteristics of large trees varied less than two-fold.

The density and biomass of large trees (>10 cm dbh), corrected for inherent fertility, followed a pattern similar to that of ABI* (Fig. 2c and d). Marginal means were significantly lower in the second cycle than in the first or fourth. Levels in the sixth and tenth cycles were intermediate. Variation in density and biomass of small trees was not related to the number of prior cycles or inherent fertility. The diameter increment of large trees was not significantly related to cultivation history, but rather to inherent fertility (with age as a significant

covariate). Mean diameter increment increased by 19% from the lowest to the highest fertility group (marginal mean of 1.18 cm/yr to 1.40 cm/yr) (Fig. 3a). The distribution of biomass between large and small trees did not vary significantly with the number of prior cycles. On average, for 9–12 yr old secondary forests, 76% of the biomass >5 cm dbh was comprised of trees >10 cm dbh and 24% consisted of stems 5–10 cm dbh. The percentage of biomass in trees >10 cm dbh increased significantly with inherent fertility (Fig. 3b).

DISCUSSION

The pattern in the observed aboveground annual biomass increment (ABI) of trees >5 cm dbh is consistent with a weak negative effect of repeated cultivation on biomass accumulation. Where an increase in ABI with number of cultivation–fallow cycles was expected due to the greater inherent soil fertility of longer cultivated sites, the (uncorrected) ABI of inherently poorer sites cultivated 1 or 4 times was not significantly different from that of inherently richer sites cultivated 6 or 10 times. Accounting for higher original fertility in sites with the longest cultivation history suggests that beyond four cycles, biomass accumulation rate is diminished. Although the difference in corrected ABI (ABI*,

TABLE 1. Models of biomass accumulation, structure, and distribution in nine secondary forests of West Kalimantan (Borneo), aged 9–12 years old and with 1–10 prior cycles of shifting cultivation.

Dependent variable	Fixed factor		Covariate(s)		Full model		
	Factor	F	Factor	F	P	F	Adjusted r ²
a) ABI >5 cm dbh	no. prior cycles	6.8*	none	...	0.045	6.8	0.75
b) ABI >5 cm dbh	no. prior cycles	137.7**	age	70.2*	0.008	117.8	0.99
c) ABI >5 cm dbh	fertility group	0.64	apatite	18.6*	0.61	0.8	-0.14
			age	0.93			
d) Density >10 cm dbh	no. prior cycles	12.5*	no. prior cycles	0.018	0.035	11.6	0.87
e) Biomass >10 cm dbh	no. prior cycles	10.0*	apatite	6.1†			
f) Diameter increment >10 cm dbh	fertility group	13.7*	age	54.5**	0.006	20.7	0.91
g) Percentage biomass >10 cm dbh	apatite	18.7**	none	...	0.003	18.7	0.69

Note: ABI = annual aboveground live biomass increment.
* $P < 0.05$; ** $P < 0.01$; † $P < 0.10$.

marginal mean ABI, accounting for effects of age and inherent soil fertility) between the first and the tenth cycle was only marginally significant, the trend is compelling, especially given the failure of models based on soil fertility to explain variation in ABI. However, the pattern of change in ABI* was more complex.

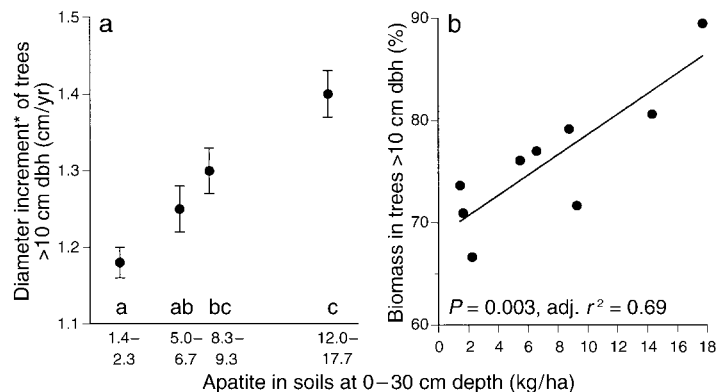
The initial decline in ABI*, by one third from the first to the second cycle, was greater than predicted, and the subsequent rebounding was not predicted. Changes in large-tree density seem to be driving the pattern (Fig. 2c). Sites cultivated once or twice had relatively low inherent fertility, with correspondingly low tree-growth rates (Fig. 3a). Yet, the high density of trees in the first cycle allowed a significantly higher biomass accumulation rate. Why then, does large-tree density decline precipitously during the second cycle of shifting cultivation? What allows it to recover by the fourth cycle? And what causes a subsequent decline?

One hypothesis is that depletion of the seedbank causes the decline in tree density following the first cycle. Most seeds in the surface soil would germinate following fire associated with primary forest conversion. Replenishment of the seedbank during the first cycle would be limited by the number of trees that reach

reproductive age within the 20-year fallow period. Because Dayaks do not till the soil, but use dibble sticks, few of the seeds stored deeper in the soil are brought up during the second cycle of cultivation. With a diminished seedbank, resprouting or well-dispersed species would assume increasing importance in subsequent cycles. Such species may require one or more cycles to effectively colonize sites. Once present, a resprouting habit should confer a competitive advantage under a regime of repeated agricultural disturbance. Rapid resprouting, often with multiple stems, would also lead to rapid biomass increment, potentially explaining recovery of ABI* by the fourth cycle.

Lower density from the sixth to the tenth cycles could be due to a decline in the resprouting species that were once dominant. If root stocks of the original resprouting colonizers begin to die after a century of repeated disturbance, stem density would decline and recruitment opportunities would increase. The tree community would shift back to individuals that regenerate from seed, including well-dispersed and/or seed-banking species. Resprouters may also be among this group, but, coming from seed, they would not initially have multiple stems.

FIG. 3. Distribution of tree biomass as a function of inherent soil fertility. (a) Large-tree diameter increment* (adjusted for the effects of age, assuming all forests were 10.3 years old); data are marginal means \pm 1 SE. Data with the same lowercase letter above the x-axis are not significantly different at $P = 0.05$. (b) Percentage of biomass in trees >10 cm dbh. The number of prior cycles was not a significant covariate.



Data appropriate for testing this hypothesis are not readily available, but there is a significant, directional shift in the species composition of fallows through 10 cycles (Lawrence 2004). The most common resprouting species (*Peronema canescens*) peaked in abundance after 6 cycles (40% of all basal area), but was still very abundant after 10 cycles (16–31% of basal area) (D. Lawrence, V. Suma, and J. P. Moge, unpublished manuscript). As predicted, the most common seed-banking species (*Macaranga gigantea*), was abundant in the first cycle, declined 50% by the fourth cycle, and then exceeded its original abundance by the tenth cycle. Further assessment of this hypothesis requires better understanding of post-fire dominance by resprouting species (e.g., Uhl et al. 1988, Kauffman 1991, Kammescheidt 1998) and of seedbank dynamics through many cycles.

An alternative hypothesis, to explain lower ABI* at sites cultivated ≥ 6 times, is that differences in phosphorus availability develop with repeated cultivation. Lawrence and Schlesinger (2001) showed that total P in the top 30 cm increased over the first four cycles at poorer sites, including some from this study. Half of the increase was in potentially available, organic forms, but half of the “new” P was in occluded forms that must be physically or chemically transformed before becoming available. At richer sites (including some of these sites), total P did not change with repeated cultivation. Considering rich and poor sites together, as in this study, the proportion of non-occluded (potentially available), inorganic P declined $\sim 20\%$ over the first five or six cycles. Sixty percent of this decline went into organic fractions, but 40% became occluded (Lawrence and Schlesinger 2001). Despite the enhanced P-supplying capacity suggested by a relative increase in organic P (Tiessen et al. 1983, 1994), lower biomass accumulation observed after five or six cycles might be related to shifts from readily available to occluded P. Since soil P dynamics do not correspond with the pattern of ABI* over the first several cycles, I suggest that changes in life-history structure are a more likely driver early in the history of shifting cultivation.

In the shorter fallow systems of Brazil and Bolivia, three cycles of cultivation did not slow biomass accumulation (Hughes et al. 2000, Steininger 2000). Results from this study are consistent, suggesting that up to four cycles may occur without loss of regenerative capacity in secondary forests. In tropical frontier areas colonized over the past 20–50 years, secondary forests have now been through two to four cycles of shifting cultivation. A continuation of current fallow and crop management practices may result in a slow decline in secondary forest productivity.

With an 11% decline in the rate of biomass accumulation over 10 cycles, the carbon-sequestration value of secondary forests would diminish at sites with a relatively long history of shifting cultivation. In 2000, approximately 60% of tropical forests worldwide were

considered secondary or degraded forest (ITTO 2002); many of these forests are subject to shifting cultivation. Continued expansion of secondary forests in the tropics, combined with lower rates of biomass accumulation, could significantly alter regional and global carbon budgets.

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LITERATURE CITED

- Brown, S. 1997. Estimating biomass and biomass change of tropical forests: a primer. FAO Forestry Paper. Food and Agriculture Organization, Rome, Italy.
- Brown, S., J. R. Gillespie, and A. E. Lugo. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Science* **35**:881–902.
- Chinea, J. D. 2002. Tropical forest succession on abandoned farms in the Humacao municipality of eastern Puerto Rico. *Forest Ecology and Management* **167**:195–207.
- Cleveland, C., A. R. Townsend, and S. K. Schmidt. 2002. Phosphorus limitation of microbial processes in moist tropical forests: evidence from short-term laboratory incubations and field studies. *Ecosystems* **5**:680–691.
- Cross, A. F., and W. H. Schlesinger. 1995. A literature review and evaluation of the Hedley fractionation: applications to the biogeochemical cycle of soil phosphorus in natural ecosystems. *Geoderma* **64**:197–214.
- Dove, M. R. 1985. Swidden agriculture in Indonesia. Mouton, Berlin, Germany.
- Fearnside, P. M., and W. M. Guimaraes. 1996. Carbon uptake by secondary forests in Brazilian Amazonia. *Forest Ecology and Management* **80**:35–46.
- Garcia-Montiel, D. C., C. Neill, J. Melillo, S. Thomas, P. A. Steudler, and C. C. Cerri. 2000. Soil phosphorus transformation following forest clearing for pasture in the Brazilian Amazon. *Soil Science Society of America Journal* **64**:399–405.
- Gerwing, J. H., and D. Lopes Farias. 2000. Integrating liana abundance and forest stature into an estimate of total above-ground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology* **16**:237–335.
- Herbert, D. A., and J. H. Fownes. 1995. Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil. *Biogeochemistry* **29**:223–35.
- Hobbie, S. E., and P. M. Vitousek. 2000. Nutrient limitation of decomposition in Hawaiian forests. *Ecology* **81**:1867–77.
- Houghton, R. A., and J. L. Hackler. 1999. Emissions of carbon from forestry and land-use change in tropical Asia. *Global Change Biology* **5**:481–492.
- Hughes, R. F., J. B. Kauffman, and D. L. Cummings. 2000. Fire in the Brazilian Amazon. III. Dynamics of biomass, C, and nutrient pools in regenerating forests. *Oecologia* **124**:574–588.
- Hughes, R. F., J. B. Kauffman, and D. L. Cummings. 2002. Dynamics of aboveground and soil carbon and nitrogen stocks and cycling of available nitrogen along a land-use gradient in Rondonia, Brazil. *Ecosystems* **5**:244–259.
- Hughes, R. F., J. B. Kauffman, and V. J. Jaramillo. 1999. Biomass, carbon, and nutrient dynamics of secondary for-

- ests in a humid tropical region of Mexico. *Ecology* **80**:1892–1907.
- Inoue, M., and A. M. Lahjie. 1990. Dynamics of swidden agriculture in East Kalimantan. *Agroforestry Systems* **12**:269–284.
- ITTO [International Tropical Timber Organization]. 2002. ITTO guidelines for the restoration, management and rehabilitation of degraded and secondary tropical forests. ITTO Policy Development Series Number 13. International Tropical Timber Organization, Yokohama, Japan.
- Johnson, C. M., D. J. Zarin, and A. H. Johnson. 2000. Post-disturbance aboveground biomass accumulation in global secondary forests. *Ecology* **81**:1395–1401.
- Kammescheidt, L. 1998. The role of tree sprouts in the restorations of stand structure and species diversity in tropical moist forest after slash-and-burn agriculture in Eastern Paraguay. *Plant Ecology* **139**:155–165.
- Kauffman, J. B. 1991. Survival by sprouting following fire in tropical forests of the eastern Amazon. *Biotropica* **23**:219–224.
- Ketterings, Q. M., R. Coe, M. van Noordwijk, Y. Ambagau, and C. A. Palm. 2001. Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. *Forest Ecology and Management* **146**:199–209.
- Lawrence, D. 2004. Land-use change, biodiversity and ecosystem functioning in West Kalimantan. Pages 253–268 in G. Gerold, M. Fremery, and E. Guhardja, editors. *Land use, nature conservation and the stability of rainforest margins in Southeast Asia*. Springer-Verlag, Berlin, Germany.
- Lawrence, D., D. R. Peart, and M. Leighton. 1998. The impact of shifting cultivation on a rainforest landscape in West Kalimantan: spatial and temporal dynamics. *Landscape Ecology* **13**:135–148.
- Lawrence, D., and W. H. Schlesinger. 2001. Changes in the distribution of soil phosphorus during 200 years of shifting cultivation. *Ecology* **82**:2769–2780.
- Moran, E. F., E. S. Brondizio, J. M. Tucker, M. C. de Silva-Forsberg, S. McCracken, and I. Falesi. 2000. Effects of soil fertility and land-use on forest succession in Amazonia. *Forest Ecology and Management* **139**:93–108.
- Pascarella, J. B., T. M. Aide, M. I. Serrano, and J. K. Zimmerman. 2000. Land-use history and forest regeneration in the Cayey Mountains, Puerto Rico. *Ecosystems* **3**:217–228.
- Saldariagga, J. G., D. C. West, M. L. Tharp, and C. Uhl. 1988. Succession in the upper Rio Negro of Columbia and Venezuela. *Journal of Ecology* **76**:938–958.
- Saugier, B., J. Roy, and H. A. Mooney. 2001. Estimations of global terrestrial productivity: converging toward a single number? Pages 543–557 in J. Roy, B. Saugier, and H. A. Mooney, editors. *Terrestrial global productivity*. Academic Press, San Diego, California, USA.
- SPSS. 2000. SPSS version 10. SPSS, Chicago, Illinois, USA.
- Steininger, M. K. 2000. Secondary forest structure and biomass following short and extended land-use in central and southern Amazonia. *Journal of Tropical Ecology* **16**:689–708.
- Tiessen, H., E. Cuevas, and P. Chacon. 1994. The role of soil organic matter in sustaining soil fertility. *Nature* **371**:783–785.
- Tiessen, H., and J. O. Moir. 1993. Characterization of available P by sequential extraction. Pages 75–86 in M. R. Carter, editor. *Soil sampling and methods of analysis*. Lewis Publishers, Boca Raton, Florida, USA.
- Tiessen, H. J., W. B. Stewart, and J. O. Moir. 1983. Changes in organic and inorganic phosphorus composition of two grassland soils and their particle size fractions during 60–90 years of cultivation. *Journal of Soil Science* **34**:815–823.
- Uhl, C., R. Buschbacher, and E. A. S. Serrao. 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. *Journal of Ecology* **76**:663–681.
- Vitousek, P. M., and H. Farrington. 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Biogeochemistry* **37**:63–75.
- Whitmore, T. C. 1997. *Tropical rain forests of the Far East*. Clarendon Press, Oxford, UK.
- Zarin, D. J., M. J. Ducey, J. M. Tucker, and W. A. Salas. 2001. Potential biomass accumulation in Amazonian re-growth forests. *Ecosystems* **4**:658–668.
- Zimmerman, J. K., T. M. Aide, M. Rosario, M. Serrano, and L. Herrera. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management* **77**:65–76.

APPENDIX

A table of site characteristics, biomass, and structural parameters for nine plots in 9–12 year old forests in West Kalimantan, Indonesian Borneo, following long-fallow (20-yr) shifting cultivation of upland, dry rice is available in ESA's Electronic Data Archive: *Ecological Archives* E086-001-A1.