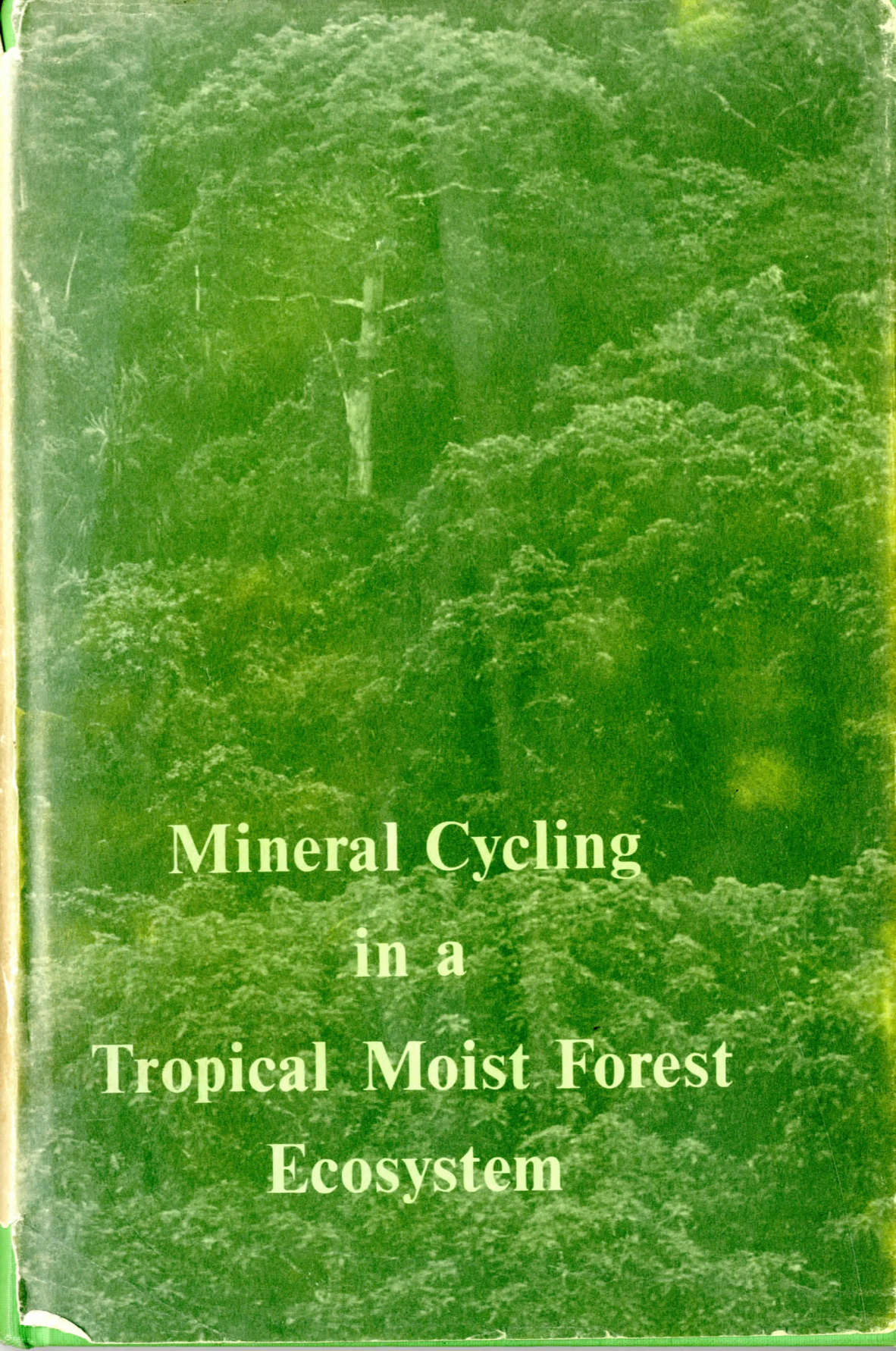

Mineral Cycling in a Tropical Moist Forest Ecosystem

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BIOMASS OF SECOND GROWTH TROPICAL MOIST FOREST*

Throughout the tropical world, forested lands are cultivated by a system of shifting agriculture in which clearings made in the forest are cropped for a shorter number of years than they are fallowed (Conklin, 1963). According to Guzman (1956), *cultivo de roza,* shifting, or slash-burn agriculture, is the basic farming practice in Panama. In the Darien and San Blas Provinces, all agriculture except that adjacent to the few permanent settlements is the shifting type. The major crops are maize, rice, plantains, and bananas. Since only about two percent of the land area is in agriculture or second-growth forest resulting from recent farming, second-growth forest is not very significant today in terms of land area. However, it will probably become increasingly important as more of the province is settled.

Most second-growth vegetation in eastern Panama and northwestern Colombia occurs below an elevation of 100 meters, since cultivated fields are normally located on level terrain adjacent to the coasts and navigable rivers. In more populated areas, farmlands extend from the water's edge onto moderately to steeply sloping hillsides. The vegetation on a site to be planted is cut near the onset of the dry season in January, allowed to dry, and is burned during March or April. One or two crops are grown the first year and sometimes another the second year. Regrowth of natural vegetation often begins with the first crop. Fields may be allowed to remain fallow for six or more years.

Although there are numerous reports on shifting agriculture (see bibliographies of Conklin, 1963; Bartlett, 1955-61; Edwards and Rasmussen, 1942; and MacLeish et al., 1940), there are fewer studies on the natural fallow, or second-growth vegetation following agriculture (Bartholomew et al., 1953; Nye and Greenland, 1960; Tergas, 1965; Ewel, 1971). It is important in the comparison of tropical forests, to understand the dynamics of the succession stages leading to the stable Tropical Moist forest type.

Four second-growth sites were harvested in Panama during 1967. They included two sites where vegetation regrowth had occurred over two years, and two sites where regrowth had occurred over four and six years. The first two-year site and the four-year and six-year sites were harvested in July; the second two-year site was harvested in October. The sites were located in Tropical Moist forest within three kilometers of Santa Fe, Darien Province (latitude 8°39′, longitude

* Prepared with John Ewel, University of Florida.

Table 4.14. Vegetation biomass and percent of the biomass in green parts in major vegetation regions. Based on data from Rodin and Bazilevich (1967).

Vegetation	Biomass wt/ha	% Biomass in green parts
Tundra	28	11
Northern coniferous forest	137	6
Temperate deciduous forest	224	2
Tropical wet forest	564	5

78°09′). This study was a cooperative venture between the University of Florida and the University of Georgia and some of the data has been reported by Ewel (1971).

The general aspect of young (10 years old) second-growth vegetation in eastern Panama was a low, dense growth of small trees, vines, and herbaceous plants. The canopy at each site was dominated by *Cecropia spp.*, but contained other common genera including *Ochroma, Trema, Spondias*, and *Persea*. Palms such as *Bactris* were present but not common. *Heliconia* and *Calathea* were abundant at all sites, as were herbaceous and woody vines. Scattered large trees are often left standing after the initial clearing of the mature forest. Nonvascular stem epiphytes were common, but epiphyllae were almost nonexistent. All sites were on slightly undulating terrain which appeared to result from disintegration of large roots, stumps, and logs left after the original clearing, and from fallen trees when the area was in mature forest.

The first two-year site, harvested in July, was originally cleared of forest at least eight years prior to this study and had gone through several plantings. Charred stumps and large boles from the original forest were still present (fig. 4.10), as were maize stalks from the last planting. At the time of harvest a dense growth of vegetation with a low canopy reaching a height of five meters existed. The aspect of the vegetation was markedly uneven and dense stands of grass or low-growing herbs, under one meter in height, were common. At about seven meters, the taller trees formed an open canopy of scattered emergent crowns.

Figure 4.10. Two-year-old site after the understory harvest in July. Note the charred boles and stumps still remaining from the original clearing from forest. A large tree that was not cut during the original clearing may be seen in the background. (Photograph by Peter McGrath.)

The second two-year site, harvested in October, had been planted only once since it was cleared. Stumps and fallen boles of forest trees were still much in evidence. The general aspect of the vegetation on this site was that of a better developed forest than the first two-year site. The ground flora was relatively open, with the bulk of the leaves and vines located in the canopy, approximately eight meters (range 3-10 meters) in height.

The four-year site, cropped once since clearing, was generally similar to the second two-year site, except that it was structurally more uniform. Canopy height averaged about ten meters (range 5-12 meters), or almost the same as Ross (1954) reported for five-year-old second-growth in Nigeria.

The six-year fallow, which has been planted twice, was the oldest second-growth stand harvested. The understory was more open than that of younger stands (fig. 4.11) and the average height of the relatively even canopy was about 12 meters (range 10-13.5 meters) (fig. 4.12). Several palms *(Scheelea sp.),* which had not been killed during the original clearing, had grown to a considerable size. Species of plants observed in these second growth stands are listed in appendix table 5.

Table 4.15. Structural features of second-growth vegetation in eastern Panama.

Age of stand in years	2	2	4	6
Month of harvest	July	October	July	July
Leaf area index (m^2/m^2)	7.5	6.9	11.6	16.5
Percent cover	66	80	80	84
Crown diameter of largest trees (m)	2	4	4	6
Height of largest trees (m)	7.2	10.1	12.3	13.6
DBH of largest trees (cm)	6	12	13.5	17.5

The structural characteristics measured in the Panama second-growth (table 4.15) changed rapidly with age of the vegetation. The leaf area index of four- and six-year-old stands (11.5 and 16.5

Figure 4.11. Second-growth stand being harvested near Santa Fe, Darien, Panama. (Photograph by the authors.)

Fig. 4.12 Six year old second growth stand after harvest of the plot. The large trees in the background were not cut when the original agricultural field was established.

m^2/m^2) were nearly the same as the leaf areas observed in mature forests. In contrast, height, and DBH were three to four times lower than that observed in Tropical Moist forests. These data suggest that the production capacity of the forest is quickly reestablished while the supporting structure of stems and branches is more slowly developed.

Table 4.16. Dry-weight biomass (kg/ha) by compartment and age of second-growth in eastern Panama.

Age of stand	2	2	4	6
Month of harvest	July	October	July	July
Overstory				
Leaves	1200	2200	3300	4800
Stems	4300	18000	22700	27100
Fruits and flowers	10	40	30	140
Understory				
Leaves	2400	800	2600	1700
Stems	5100	3300	9300	8800
Fruits and flowers	10	20	110	10
Roots	2600	4100	4500	14200
Total live biomass	15620	28460	42540	56750
Litter	4600	4400	5700	6100

The results of the standing crop determinations are shown in table 4.16. Biomasses of compartments and sites were significantly different. With two exceptions, all compartments and stand totals increased with age. The six-year field, although highest in total biomass, was lower than the four-year stand in all understory compartments. The second deviation from the general trend was the low weight (800 kg/ha) of understory leaves in the two-year stand harvested in October. Both replications at this site had low biomass of understory leaves: 750 and 850 kg. Although some of the variation between the two-year-old stands may have resulted from growth from July to October, it also probably reflects the variation in site quality. The October site was located in a large area of two-year fallow, portions

of which appeared similar to the July two-year harvest site, while other parts of the same field resembled the four-year stand.

Much of the increase in total biomass from four to six years is accounted for by the high biomass of roots in the six-year fallow field. Above ground biomass increased only 4,500 kg/ha from four to six years, as opposed to an increase of 14,200 kg/ha for total biomass.

The biomass values for fruits and flowers (20 to 150 kg/ha) were considerably greater than observed for most of the mature forests. However, Tropical Moist forest harvested at about the same time during the wet season had a fruit and flower biomass of 139 kg/ha. Fruit and flowers in second growth were mainly from *Heliconia*, and in the six-year stand, from the palm *Scheelea*. Other genera probably accounted for less than five percent by weight of the inflorescences.

Table 4.17. Dry weight standing crop of second-growth vegetation in Panama and the Congo (Bartholomew et al., 1953).

Age	Location	Standing crop (kg/ha)			
		Leaves	Stems	Roots	Litter
2	Panama-July	3600	9400	2600	4600
2	Panama-October	3000	21300	4100	4400
2	Congo	5560	12299*		—
4	Panama	5900	32000	4500	5700
5	Congo	5627	71067	25753	7320
6	Panama	6500	35900	14200	6100
8	Congo	5379	116313	22682	7983

* Representing both stems and roots.

The standing crops of second-growth Tropical Moist forest vegetation can be compared with similar data from the Congo (Bartholomew et al., 1953) (table 4.17). In general, the values for successional stands in the Congo basin do not differ greatly from those we obtained in Panama. However, the standing crop of stems of five and eight-year Congo vegetation was two to four times that of six-year vegetation in Panama. This was also true for six- and seven-year-old stands studied by Kellman (1970) in Mindanao.