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The object of this paper is to describe the biomass of three kinds of marsh and two ages of young second-growth vegetation in Chocó Province, Northwestern Colombia. Although the broad ecological life zones of Colombia have been described by Espinal and Montenegro (1963) there have been relatively few detailed studies of the vegetation in this section of the country. The study region is relatively remote and is poorly known. It lies just to the north of what is probably the wettest expanse of tropical lowlands in the Western Hemisphere: the upper Atrato Basin, where mean annual rainfall exceeds 10 m per year. Rainfall in the study area decreases from southwest to northeast. Along the Pacific coast near Cabo Marzo (Fig. 1) the annual rainfall is probably greater than 4 m per year, while Turbo, on the Gulf of Urabá in the northeast part of the study area, receives less than 2 m per year (Vann 1959, Espinal & Montenegro 1963). Espinal & Montenegro (1963) mapped the life zone change from Tropical Wet Forest to Tropical Moist Forest in the vicinity of the town of Riosucio, located about midway across the study area. The topography of the area is dominated by the Atrato River and its tributaries which debouch into the Caribbean Sea near Turbo, creating a large swamp on the eastern edge of the Province, which is a major feature of the physiography of the area. Transportation in this area is mainly by water.

The present study was made possible through support from the AEC and Battelle Memorial Institute for study of a sea-level canal carried out in 1966-67. The Universities of Georgia and Florida contracted to provide information on the terrestrial and agricultural ecology of the region (Golley *et al.* 1969, Gamble *et al.* 1969). Field trips were made into Chocó Province in May and August, 1967 by helicopter and canoe. The structural description of the vegetation is based on these reconnaissance trips and collections of vegetation by harvest sampling on a transect across the region.

DESCRIPTION OF THE AREA

The physiography of Northwestern Colombia consists of a vast swamp at the mouth of the Atrato River which flows northward and empties into the Caribbean Sea, a dissected upland region with considerable variation in elevation depending upon the drainage, a Pacific coastal cordillera with an elevation of about 700 m, and a narrow Pacific coastal plain (Fig. 1). The broad, periodically inundated Atrato River swamp in northwestern Colombia is a unique ecological situation compared to the forest ecosystems which cover the other portions of Chocó Province. There are numerous semi-aquatic communities in the swamp, four of which are: grass

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meadows, *Heliconia* thickets, an aroid (*Montrichardia arborescens*) community and palm (*Rafia taedigera*) thickets. These form a mosaic of vegetation depending upon the degree and depth of inundation (Vann 1969).

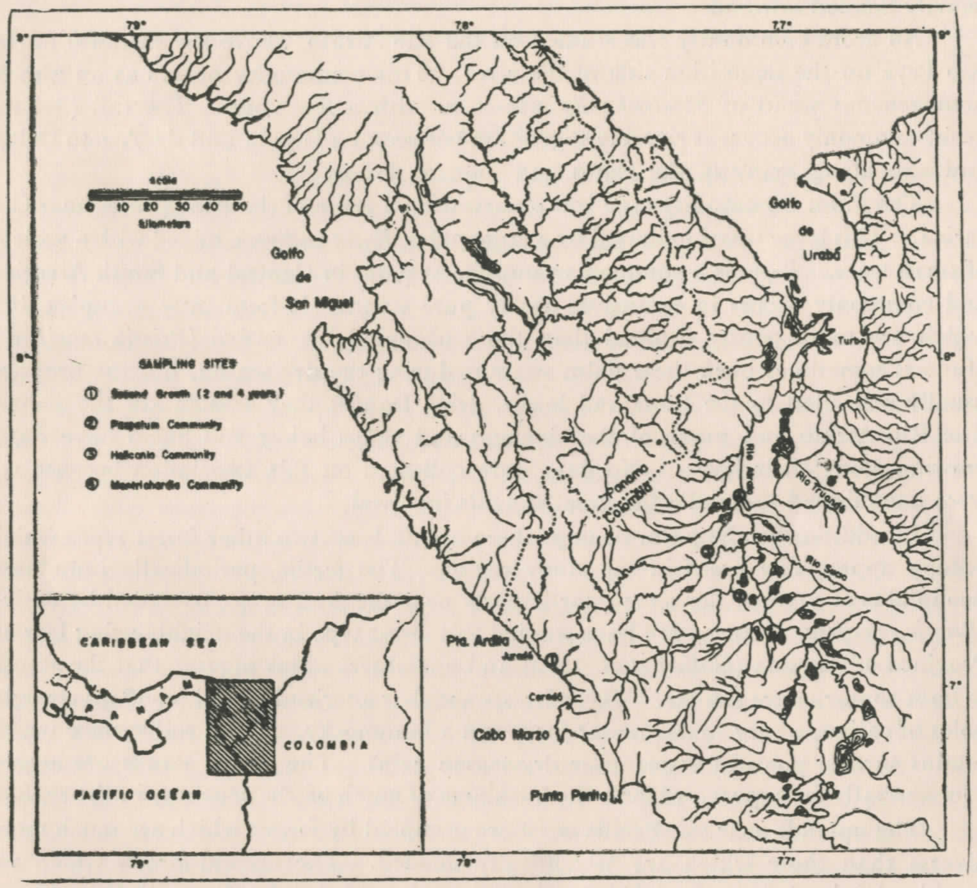

Fig. 1. Location of the sampling sites.

The grass community was studied on the Caño Ramón, 1 km from its confluence with the Rio Truandó. This grass (*Paspalum repens*), which grows in pure stands about 1 m above the water surface, is common and widespread along the caños and rivers between La Nueva and the Rio Salaquí. *Paspalum repens* forms extensive meadows along the margins of many tropical American rivers, including the Orinco and the Amazon, where it is frequently the dominant species in the varzea lakes. The floating grass meadows sometimes support one of the most diverse animal communities to be found in Amazonian waters (Sioli 1968). At the time of our sampling there was about 1-2 m of slow flowing water in the *Paspalum* community. This water carried considerable amounts of minute organic particles, many of which had been trapped on the culms and sheaths of the plants. The rank smell of the underwater vegetation suggested a reduced condition. Residents reported that these areas dry up during the dry season and are occasionally used for cattle pasture.

The study location of the *Heliconia* community was on the Caño La Honda near its confluence with the Rio Salaquí. Monospecific stands of *Heliconia latispatha* are common along the river and stream banks and as small hummocks throughout the heavily floaded lowlands.

An aroid community was studied on the Rio Atrato, above the entrance of the Rio Peye on the deposition side of the river. This community occurs as an almost homogeneous stand of *Montrichardia arborescens* with a few vines. The tall (3-4 m) aroid commonly occurs as riverine vegetation between La Honda and the Atrato Delta, and also along many of the caños and cienaga levees.

The Palm Community type was observed on a levee of the Rio Atrato near Cacarica. This levee was dominated by a large palm, *Rafia taedigera*, mixed with a variety of small trees. *Rafia* is a common swamp-forest palm in Central and South America and commonly occurs in extensive, nearly pure stands. It frequently occupies sites which are more poorly drained than those occupied by cativo (*Prioria copaifera*). Hunters sometimes burn these palm swamps during the dry season, but the fires are usually restricted to the litter and lower, dried fronds; they seldom kill the palms. The Rio Atrato and many of the cienagas and caños below Rio Sucio have *Rafia* growing along their levees. No data were collected on this association because we were unequipped to handle the great weights involved.

In addition to the palm swamps there are at least two other forest types which occupy appreciable areas in the study region. The fertile, periodically inundated floodplains of some of the rivers, particularly near the Atrato, are occupied by cativo (*Prioria copaifera*) forests. We have studied this forest type in the neighbouring Darien Province of Panama (Golley *et al.* 1975) and our observations suggest that the stands in both countries are similar. These forests are characterized by tall (c. 45 m) straight boles of cativo, a very sparse understory, and a hummocky, uneven soil surface which retains surface pools of water after dry-season rains. The cativo stands are logged commercially for export and form the backbone of much of the economy in the region.

The uplands near the Pacific coast are occupied by forests which are much more diverse than those which are periodically flooded. The upland forests which we examined inland from Curiche Beach and upslope from the Truandò Base Camp occupied deep, well-weathered latosols. The height of the tallest trees in this forest exceeded 50 m and the forest was rich in palms, epiphytes, and tree species.

Most agricultural activity in the region is confined to the coast and consists of shifting agriculture coupled with grazing on cutover lands. The interior had previously been somewhat more densely populated but the population declined under the influence of rural violence which spread through much of Colombia during the early 1960's. Most second-growth vegetation in both eastern Panama and northwestern Colombia occurs below an elevation of 100 m, since farmlands are normally located on level terrain adjacent to the coasts and navigable rivers. The vegetation on a site to be planted is usually cut near the onset of the dry season in January, allowed to dry, and is burned during March or April. In the wet climate of the Atrato Basin it is sometimes impossible to attain a burn, in which case the farmers sow directly into the mulch. One or two crops are grown the first year and sometimes another the second year. Generally, maize and rice are the initial crops, followed by plantain, banana, yuca, or other perennial crops which grow among the second-growth vegetation. Regrowth of natural vegetation often begins with the first crop. Sites are commonly farmed on a four to eight year cycle. They are planted for one or two years and allowed to remain fallow for three to six years. The length of the rotation cycle can vary considerably, depending on soil conditions and population density.

METHODS

Representative areas for study were selected subjectively using the following criteria: (1) average topographic situation within the geographic area of interest, (2) similarity of vegetation strata to the average condition, (3) average species composition, and (4) stand maturity. Plots were selected arbitrarily in what we felt were typical portions of the study area. The vegetation was harvested, weighed, and triplicate subsamples (c. 1 kg each) were transported to the laboratory in the Panama Canal Zone and dried at 80°C for 24 hours.

Second-growth stands of two and four years of age were studied on the Pacific coast near Curiche. The two-year-old stand was located on a poorly drained, hydromorphic soil, while the four-year-old stand was located on a moderately well-drained latosol. The four-year-old vegetation showed evidence of disturbance by wood cutters. In the second-growth vegetation was collected from 3×3 m plots. Roots were not sampled. Litter was collected from 3 square-meter plots in each stand.

The three marsh vegetation types were sampled by driving a motor-powered dugout canoe well into the community to be harvested. The *Montrichardia*, growing in c. 0.3 m of water, occupies a relatively narrow band along the fringe of the levee. This community was harvested by cutting the above substrate parts on a meter-square plot. The *Paspalum* and *Heliconia* were harvested by marking four meters off on the gunwale of the canoe and extending two one-meter-long outriggers into the vegetation. All vegetation within the resulting 1×4 m plot was brought aboard by pulling the plants free from the bottom (in the case of *Paspalum*) or by cutting free the above-water portions (in the case of *Heliconia*). The *Heliconia* was growing on the levee in about 0.5 m of water, while the *Paspalum* was growing partially submerged and partially emergent in 1-2 m of water. *Montrichardia* and *Heliconia* were separated into leaves, stems, and reproductive organs before weighing, while the *Paspalum* was weighed entire, including leaves, culms, and roots. Two replicates were harvested in the *Paspalum* community.

RESULTS AND DISCUSSION

The biomass data for the two-year-old second-growth were relatively uniform, while those from the four-year-old stand exhibited an unusually high amount of sample-to-sample variability (Table 1). This was due, in part, to the heterogeniety of the four-year-old stand (partially because of fence post and firewood cutting) and, in part, to the small size of the sample plots. Small sample plots in heterogeneous stands lead to the chance inclusion (or exclusion) of the scattered large trees, and this is reflected in the variation in stem biomass observed, ranging from about 0.4 to almost 12 kg m^{-2}. The mean values for total above-ground biomass are somewhat higher than those we obtained from much larger plots (two samples, each 25×25 m) in Darien Province, Panamá (Ewel 1971, Golley *et al.* 1975). The two-year-old stand we measured in Panamá had 1300 g m^{-2} above-ground-biomass (18 per cent lower than the Colombian site) and the four-year old Panamanian site had 3800 g m^{-2} (23 per cent lower than the Colombian site). The differences may be due to sampling errors or they may reflect important differences between the two sites. The Panamanian sites receive only about 2 m of rain per year, and fall in the Tropical Moist Forest life zone (FAO 1971), whereas the Colombian site probably receives close to 4 m of rain per year and falls in the Tropical Wet Forest life zone (Espinal & Montenegro (1963). The greater rainfall and longer wet season may account for the 20 per cent higher biomass on the Colombian sites.

TABLE 1. *Biomass of second-growth stands in Northwest Colombia (g m^{-2} dry weight)*

Age (years)	*Sample	Leaves	Stems	Fruits & Flowers	Total Above-Ground Living	Litter
2 ..	1	197	976	9	1182	524
	2	222	1415	9	1646	615
	3	322	1580	24	1926	748
	Mean	247	1324	14	1585	629
4 ..	1	1194	11941	5	13140	535
	2	172	1020	0	1192	908
	3	109	373	5	487	918
	Mean	492	4445	3	4940	787

*Above-ground biomass harvested from 3×3 m plots. Litter harvested from 1×1m plots.

The vast majority of the biomass is accounted for by stems, which was also the compartment which increased most from two to four years. The stem-leaf ratio of the four-year-old stand was about twice as high as that of the two-year-old stand.

The amount of litter which was accumulated on the forest floor was about 25 per cent higher in the four-year-old stand than in the two-year-old stand, indicating that litter accumulated more rapidly during the first two years of regrowth than during the second two years. This was nearly identical to our observations of comparable two- and four-year-old stands in Darien, Panamá, where we found the amount of accumulated litter to be about 10 per cent lower than under equal-aged second growth in Colombia (Golley *et al.* 1975).

The biomass of the marsh vegetation was remarkably similar in the three communities sampled (Table 2). In all cases the per cent moisture of the marsh vegetation was greater than 70 per cent and in some cases was above 85 per cent. The dry weights of the *Paspalum* community can be compared with those reported by Junk (1970), who studied this same community-type near Manaus in the Amazon Basin. He reported values for ten samples, which ranged in weight from 281 to 1139 g m^{-2}.

These are much lower than our value of 4150 g m^{-2} and there may be several possible explanations for the large difference in biomass. First, the Amazonian *Paspalum* communities may simply be less dense than those we observed in the Atrato Basin. A photograph accompanying Junk's paper shows an open stand of *Paspalum repens*, in which water was clearly visible. In the stands we sampled in the Atrato region, however, the *Paspalum* formed a deep, dense mat which entirely covered the water. Second, Junk (1970) weighed the sediments trapped among the roots and found that they sometimes weighed ten times as much as the roots in which they were trapped. We weighed the roots together with their trapped organic sediments. Roots account for about 25 per cent of the total weight of *Paspalum* (including attached dead plant tissues), so a ten-fold increase in "root" biomass due to trapped organic sediments would result in a two-to-three fold increase in the total weight. Finally, we may have over-estimated the biomass per unit area because we harvested by grasping all surface *Paspalum* within our sample plot and hauling it into the dugout. Although we attempted to cut free any *Paspalum* which extended beyond the plot boundaries, any errors which did occur were likely to have resulted in over-estimates of *Paspalum* biomass because of the invisible subsurface extensions of the *Paspalum*, many of which may have extended beyond the plot borders.

TABLE 2. *Biomass of swamp vegetation in the Atrato Basin (g m^{-2} dry weight)*

Community	Leaves	Stems	Fruits & Flowers	Total
Paspalum ..	..	..	..	4150
Heliconia ..	650	1230	1970	3850
Montrichardia ..	610	2080	750	3440

The *Heliconia* and *Montrichardia* communities, which occupy much shallower water than the *Paspalum*, were much less subject to sampling errors. The biomasses of 3.4 and 3.8 kg m^{-2} reported for these types (Table 2) are not unusual when compared with other swamp vegetation described by Westlake (1963). Rich marshes have annual productivities nearthe standing crops of the Atrato communities, but production may reach 6 kg m^{-2} yr^{-1} in some cases (Westlake 1963). In a tropical swamp of *Cyperus papyrus* Pearsall (1959) reported a standing crop of shoots of 7 kg m^{-2}, which is higher than any of the three values we observed in the Atrato swamps. The Atrato marsh communities seem, therefore, to have the high biomasses that might be expected from a tropical lowland area where growing conditions are favourable for much of the year.

SUMMARY

Biomass was measured in two- and four-year old second-growth vegetation plus three kinds of marsh communities in Chocó Province, Northwestern Colombia. Biomass in the second-growth was separated into leaves, stems, fruits & flowers, and litter. Values ranged from 1.7 to 2.7 ($\bar{x}$=2.2) kg m^{-2} in the two-year-old stand and

from 1.4 to 13.7 ($\bar{x}=5.7$) kg m^{-2} in the four-year-old stand. The three marsh communities were almost-monospecific stands of: *Paspalum repens*, *Heliconia latispatha* and *Montrichardia arborescens*. Dry weights of each of these communities were 4.2, 3.9, and 3.4 kg m^{-2} respectively. Approximately half of the biomass in the *Heliconia* community consisted of inflorescences. The biomasses of the second-growth stands are about ten per cent higher than those reported for equal-aged stands in the somewhat drier Darien Province nearby in Panamá. The three marsh communities have biomasses which are high compared to temperate marshes, but in line with values reported from other tropical marshes.

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