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## Review article

# Pantropical trends in mangrove above-ground biomass and annual litterfall

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**Abstract.** A major paradigm in biosphere ecology is that organic production, carbon turnover and, perhaps, species diversity are highest at tropical latitudes, and decrease toward higher latitudes. To examine these trends in the pantropical mangrove forest vegetation type, we collated and analysed data on above-ground biomass and annual litterfall for these communities. Regressions of biomass and litterfall data show significant relationships with height of the vegetation and latitude. It is suggested that height and latitude are causally related to biomass, while the relationship with litterfall reflects the specific growing conditions at the respective study sites. Comparison of mangrove and upland forest litterfall data shows similar trends with latitude but indicates that mangrove litterfall is higher than upland forest litterfall. The regression equations allow the litterfall/biomass ratio to be simulated, and this suggests that the patterns of organic matter partitioning differ according to latitude.

**Key words:** Mangroves – Litterfall – Biomass – Latitude

A major paradigm in biosphere ecology is that organic production, carbon turnover and, perhaps, species diversity are highest at tropical latitudes, and decrease toward the higher latitudes. Although the pantropical mangrove forest vegetation type has a remarkably low and uniform species diversity (Tomlinson 1986), we hypothesized that this halophytic plant community would nevertheless exhibit similar latitudinal trends in both organic production and carbon turnover. To test this hypothesis, we have assembled and analyzed data from published and unpublished sources pertaining to mangrove forest biomass and forest height (indices of organic production), and annual litterfall (an index of carbon turnover).

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## Materials and methods

### Above-ground biomass

Our analysis is limited to above-ground biomass because there are relatively few reported estimates of below-ground biomass for mangroves (Lugo and Snedaker 1974; Golley et al. 1975; Clough and Attiwill 1975; Komiyama et al. 1987, 1988). Whereas most of the data were derived from published sources, unpublished reports were included for those sites and studies with which we were familiar.

Criteria for inclusion of published and unpublished data for the biomass analyses included the following requirements: (1) biomass data sets had to include all above-ground components including root structures, e.g., pneumatophores and prop roots; (2) forest height and latitude data had to have been reported or otherwise readily ascertainable; and (3) all harvest and weighing methods had to have been adequately explained to ensure that appropriate techniques had been used; allometric methods were accepted when an account of the statistical variance was provided. When upper and lower canopy heights were given, median values were used in the analysis.

### Annual litterfall

In view of the problems of data comparison identified by Proctor (1983), criteria for inclusion of the data for the litterfall analyses included the following requirements: (1) all components of the litter had to be included in the study, not merely the leaf component; (2) height of the study-site vegetation and the latitude of the study area had to have been given, or be ascertainable from other sources; (3) only litterfall data collected over at least 1 calendar year were accepted, regardless of season of commencement or termination; and (4) all collecting and weighing methods were accepted as long as sufficient replicate traps were used to take variability into account.

### Statistical analyses

For all analyses, northern and southern hemisphere latitudes were treated as equivalent. Since there were no consistent differences in biomass or litterfall between mixed mangroves and monospecific communities of the various species, data from all mangrove community types were pooled for detailed analyses.

Linear regressions ( $y = ax + b$ ) were used without transformations. However, as height and latitude were highly negatively correlated in both data sets (see below), the ratio of latitude to height was used as a combined variable with logarithmic transformation. More complex transformations (e.g., exponential, quadratic, and curvilinear) or regression models [e.g., joint function regressions such as  $y = ax_1 + (b + cx_2)x_3 + d$ ] were investigated but were not used further because, in general, they did not explain the variance in the data to any markedly greater extent than did the simpler linear models. Also, the linear models were deemed to be sufficient in illustrating the major trends.

Analyses of variance were calculated for all regressions because not all data were normally distributed, specifically latitude and biomass. All statistical analyses were carried out on standard software packages for the Macintosh computer, including Statview 512+.

## Results

### Above-ground biomass

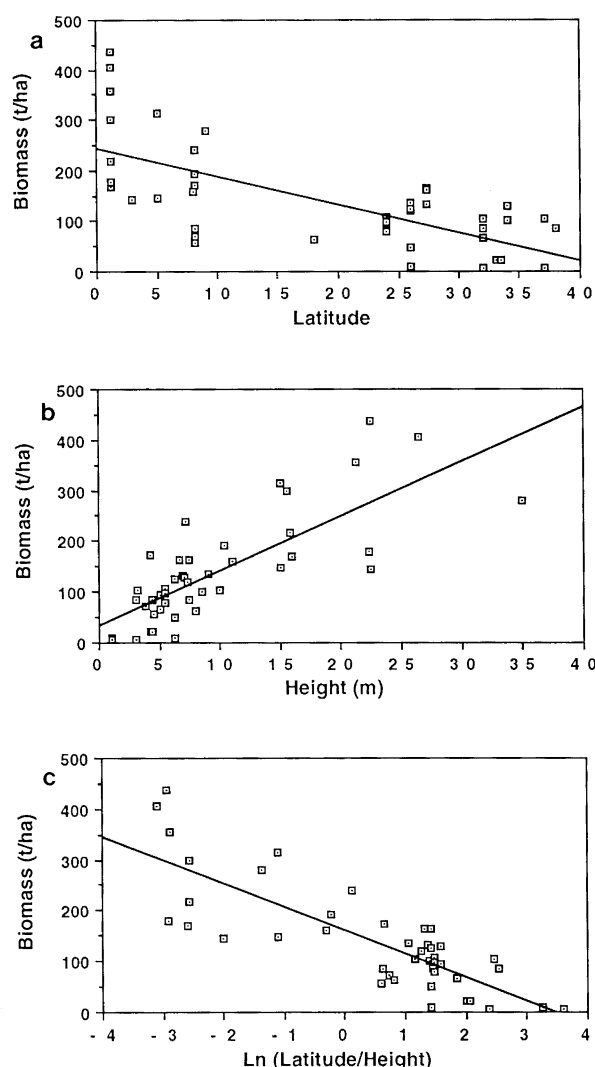
The assembled data ( $n = 43$ ) are presented in Table 1. The biomass ranged from  $436.4 \text{ t.ha}^{-1}$  in tall *Rhizophora apiculata* forests in Indonesia (Komiyama et al. 1988) to  $6.8 \text{ t.ha}^{-1}$  in low *Avicennia marina* communities (Woodroffe 1985). Other biomass data, not included in these analyses because of failure to meet the stated criteria, showed values up to  $281.0 \text{ t.ha}^{-1}$  for mixed mangroves in Thailand (Tamai et al. 1983).

The frequency distribution of the biomass data shows it to be somewhat skewed (skewness = 1.13), with several high values contributing to the skewing. Plots of biomass against latitude and height of the vegetation are shown

**Table 1.** Above-ground biomass data for mangroves

Lat. (°)	Ht. (m)	Type	Biomass ( $\text{t.ha}^{-1}$ )	Locality	Reference
1.2	21.2	So	356.8	Indonesia	Komiyama et al. 1988
1.2	22.3	Rh	178.2	Indonesia	Komiyama et al. 1988
1.2	22.4	Rh	436.4	Indonesia	Komiyama et al. 1988
1.2	15.5	Rh	299.1	Indonesia	Komiyama et al. 1988
1.2	15.8	Rh	216.8	Indonesia	Komiyama et al. 1988
1.2	15.9	Br	169.1	Indonesia	Komiyama et al. 1988
1.2	26.4	Br	406.6	Indonesia	Komiyama et al. 1988
3	22.5	M	143.5	Colombia	Mullen & Hernandez 1978
5	15	Rh	147.0	Malaysia	Ong et al. 1981
5	15	Rh	314.0	Malaysia	Ong et al. 1981
8	11	Rh	159.0	Thailand	Christensen 1978
8.2	10.3	Av	193.0	Sri Lanka	Amarasinghe & Balasubramaniam 1992a
8.2	4.3	M	172.0	Sri Lanka	Amarasinghe & Balasubramaniam 1992a
8.2	3.9	Rh	71.0	Sri Lanka	Amarasinghe & Balasubramaniam 1992a
8.2	4.4	M	85.0	Sri Lanka	Amarasinghe & Balasubramaniam 1992a
8.2	4.5	M	57.0	Sri Lanka	Amarasinghe & Balasubramaniam 1992a
8.2	7.2	Rh	240.0	Sri Lanka	Amarasinghe & Balasubramaniam 1992a
9	35	Rh	279.2	Panama	Golley et al. 1975
18	8	Rh	62.9	Puerto Rico	Golley et al. 1962
24	5.5	Rh	108.1	Japan	Suzuki & Tagawa 1983
24	5.5	Rh	97.6	Japan	Suzuki & Tagawa 1983
24	5.5	M	78.6	Japan	Suzuki & Tagawa 1983
24	5	Ka	93.4	China	Peng & Lu 1990
26	7.3	Rh	118.9	USA	Lugo & Snedaker 1974
26	6.3	M	49.0	USA	Lugo & Snedaker 1974
26	6.3	Rh	124.6	USA	Lugo & Snedaker 1974
26	9	Rh	136.0	USA	Lugo & Snedaker 1974
26	6.3	La	8.1	USA	Lugo & Snedaker 1974
26	1	Rh	7.9	USA	Lugo & Snedaker 1974
27.3	6.6	Rh	162.1	USA	Lahmann 1988
27.3	7.4	Rh	164.0	USA	Lahmann 1988
27.3	6.9	Rh	131.9	USA	Lahmann 1988
32	5	Av	66.0	Australia	Burchett & Pulkownik 1983
32	10	Av	104.0	Australia	Burchett & Pulkownik 1983
32	3	Av	7.1	Australia	Burchett & Pulkownik 1983
32	7.5	Av	86.0	Australia	Burchett & Pulkownik 1983
33	4.4	Av	21.8	Australia	Murray 1985
33.5	4.3	Av	21.7	Australia	Murray 1985
34	8.5	Av	99.7	Australia	Goulter & Allaway 1979
34	7	Av	128.4	Australia	Briggs 1977
37	3.3	Av	104.1	New Zealand	Woodroffe 1985
37	1	Av	6.8	New Zealand	Woodroffe 1985
38	3	Av	86.0	Australia	Clough & Attiwill 1975

So: *Sonneratia* spp.; Av: *Avicennia* spp.; Rh: *Rhizophora* spp.; M: Mixed mangroves; Ka: *Kandelia candel*; La: *Laguncularia racemosa*



**Fig. 1.** **a** Linear regression of biomass data with latitude ( $r^2=0.48$ ). **b** Linear regression of biomass data with height ( $r^2=0.59$ ). **c** Linear regression of biomass data with log-transformed ratio of latitude/height ( $r^2=0.66$ )

in Fig. 1a and b, together with their respective linear regression lines. The highly significant regression equations found were:

$$\text{Biomass (t.ha}^{-1}\text{)} = 10.800 \times \text{Height (m)} + 34.994 \quad (1)$$

( $r=0.774$ ,  $F_{1, 41}=61.93$ ,  $P<0.0001$ )

$$\text{Biomass (t.ha}^{-1}\text{)} = 244.994 - 5.570 \times \text{Latitude (}^\circ\text{)} \quad (2)$$

( $r=-0.686$ ,  $F_{1, 41}=36.47$ ,  $P<0.0001$ )

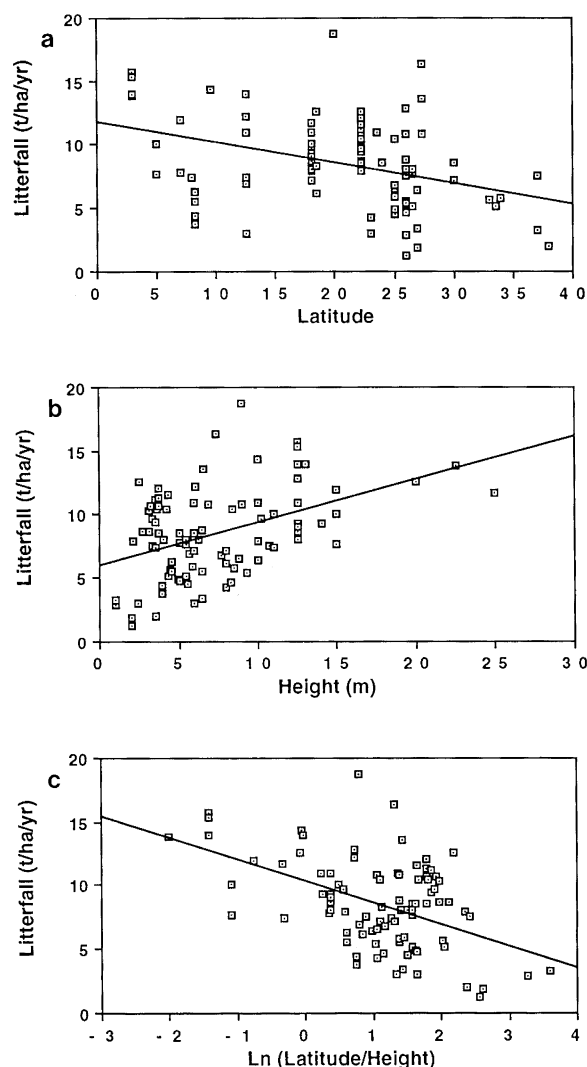
The linear regression of biomass against the ratio of latitude and height is shown in Fig. 1c with the following equation:

$$\text{Biomass (t.ha}^{-1}\text{)} = 161.405 - 46.393 \times \log_e (\text{Latitude/Height}) \quad (3)$$

( $r=-0.814$ ,  $F_{1, 41}=80.68$ ,  $P<0.0001$ )

#### Annual litterfall

The assembled data ( $n=91$ ) are presented in Table 2. The litterfall values ranged from 18.7 t.ha $^{-1}$  in *Bruguiera*



**Fig. 2.** **a** Linear regression of litterfall data with latitude ( $r^2=0.13$ ). **b** Linear regression of litterfall data with height ( $r^2=0.19$ ). **c** Linear regression of litterfall data with log-transformed ratio of latitude/height ( $r^2=0.24$ )

*sexangula* forests in China (Peng and Lu 1990) to 1.3 t.ha $^{-1}$  for low *Rhizophora mangle* communities in southern Florida (Teas 1979). The frequency distribution of the litterfall data shows it to be normally distributed (skewness=0.27).

Plots of litterfall against latitude and height of the vegetation are shown in Fig. 2a and b together with their respective linear regression lines. The regression equations found were:

$$\text{Litterfall (t.ha}^{-1}\text{)} = 0.342 \times \text{Height (m)} + 5.976 \quad (4)$$

( $r=0.444$ ,  $F_{1, 89}=21.86$ ,  $P<0.0001$ )

$$\text{Litterfall (t.ha}^{-1}\text{)} = 11.786 - 0.160 \times \text{Latitude (}^\circ\text{)} \quad (5)$$

( $r=-0.364$ ,  $F_{1, 89}=13.61$ ,  $P<0.0004$ )

The linear regression of litterfall against the ratio of latitude and height is shown in Fig. 2c with the following equation:

$$\text{Litterfall (t.ha}^{-1}\text{)} = 10.366 - 1.669 \times \log_e (\text{Latitude/Height}) \quad (6)$$

( $r=-0.495$ ,  $F_{1, 89}=28.84$ ,  $P<0.0001$ )

**Table 2.** Annual litterfall data for mangroves

Lat. (°)	Ht. (m)	Type	Litterfall (t.ha <sup>-1</sup> yr <sup>-1</sup> )	Locality	Reference
3	12.5	Av	14.01	Malaysia	Sasekumar & Loi 1983
3	12.5	Rh	15.40	Malaysia	Sasekumar & Loi 1983
3	12.5	So	15.77	Malaysia	Sasekumar & Loi 1983
3	22.5	M	13.82	Colombia	Mullen & Hernandez 1978
5	15	M	7.63	Malaysia	Gong et al. 1984
5	15	M	10.07	Malaysia	Ong et al. 1981
7	15	M	11.96	Malaysia	Ong et al. 1980
7	5	Rh	7.77	Tuvalu	Woodroffe & Moss 1984
8	11	Rh	7.40	Thailand	Christensen 1978
8.2	4.5	M	5.53	Sri Lanka	Amarasinghe & Balasubramaniam 1992b
8.2	4.5	Rh	6.24	Sri Lanka	Amarasinghe & Balasubramaniam 1992b
8.2	3.9	Rh	4.41	Sri Lanka	Amarasinghe & Balasubramaniam 1992b
8.2	3.9	Av	3.74	Sri Lanka	Amarasinghe & Balasubramaniam 1992b
9.5	10	Rh	14.30	PNG	Leach & Burgin 1985
12.5	6.1	Rh	12.21	Australia	Woodroffe et al. 1988
12.5	3.5	M	7.46	Australia	Woodroffe et al. 1988
12.5	5.7	Ce	6.86	Australia	Woodroffe et al. 1988
12.5	2.4	Ce	3.00	Australia	Woodroffe et al. 1988
12.5	13.0	Av	14.02	Australia	Woodroffe et al. 1988
12.5	10.0	Rh	10.96	Australia	Woodroffe et al. 1988
18	10.2	M	9.74	Puerto Rico	Pool et al. 1975
18	4	Av	8.01	Australia	Duke et al. 1981
18	10	So	7.90	Australia	Duke et al. 1981
18	6	Ce	7.18	Australia	Duke et al. 1981
18	12.5	Rh	10.91	Australia	Duke et al. 1981
18	12.5	Rh	9.34	Australia	Duke et al. 1981
18	12.5	Rh	8.69	Australia	Duke et al. 1981
18	11	Br	10.00	Australia	Duke et al. 1981
18	12.5	Br	7.99	Australia	Duke et al. 1981
18	14.0	So	9.34	Australia	Duke 1988
18	25	So	11.68	Australia	Duke 1988
18	12.5	So	9.05	Australia	Duke 1988
18.5	8	Av	6.14	Mexico	Lopez-Portillo & Ezcurra 1985
18.5	6	M	8.34	Mexico	Day et al. 1987
18.5	20	M	12.52	Mexico	Day et al. 1987
20	9	Br	18.70	China	Peng & Lu 1990
22.2	3.1	Ka	8.71	Hong Kong	Lee 1989
22.2	3.5	Ka	9.42	Hong Kong	Lee 1989
22.2	3.1	Ka	10.29	Hong Kong	Lee 1989
22.2	3.7	Ka	12.08	Hong Kong	Lee 1989
22.2	3.7	Ka	11.26	Hong Kong	Lee 1989
22.2	3.2	Ka	10.72	Hong Kong	Lee 1989
22.2	2.7	Ka	8.67	Hong Kong	Lee 1989
22.2	3.5	Ka	11.24	Hong Kong	Lee 1989
22.2	3.7	Ka	8.53	Hong Kong	Lee 1989
22.2	3.6	Ka	10.5	Hong Kong	Lee 1989
22.2	3.7	Ka	10.69	Hong Kong	Lee 1989
22.2	2.1	Ka	7.96	Hong Kong	Lee 1989
22.2	4.2	Ka	10.5	Hong Kong	Lee 1989
22.2	2.5	Ka	12.59	Hong Kong	Lee 1989
22.2	4.3	Ka	11.63	Hong Kong	Lee 1989
22.2	3.3	Ka	9.69	Hong Kong	Lee 1989
23	6	Rh	3.04	Australia	Saenger unpubl.
23	8	Ce	4.32	Australia	Saenger unpubl.
23.6	6	La	11.00	Mexico	Flores-Verdugo et al. 1987
24	5	Ka	8.52	China	Peng & Wenjiao nd
25	4.9	La	4.89	Brazil	Adaime 1985
25	5.6	La	4.58	Brazil	Adaime 1985
25	5.9	La	5.94	Brazil	Adaime 1985
25	7.7	M	6.74	Brazil	Adaime 1985
25	8.4	M	10.42	Brazil	Adaime 1985
25	8.8	M	6.50	Brazil	Adaime 1985
26	9	M	10.76	USA	Pool et al. 1975
26	12.5	Rh	12.80	USA	Pool et al. 1975
26	10.7	M	7.51	USA	Twilley 1982
26	9.3	Av	5.38	USA	Twilley 1982

Table 2. (continued)

Lat. (°)	Ht. (m)	Type	Litter fall (t.ha <sup>-1</sup> yr <sup>-1</sup> )	Locality	Reference
26	8.3	Av	4.69	USA	Twilley 1982
26	5	Av	4.80	USA	Lugo et al. 1980
26	2	Rh	1.30	USA	Teas 1979
26	6.5	Rh	8.76	USA	Heald 1971
26	1	Av	2.90	USA	Pool et al. 1975
26	6.3	Av	8.00	USA	Courtney 1980
26	6.5	Rh	5.50	USA	Lugo & Snedaker 1974
26	1	Av	2.90	USA	Teas 1979
26.5	5.5	Br	7.63	Japan	Nishira pers. comm. 1978
26.5	5.5	M	5.11	Japan	Nishira pers. comm. 1978
26.5	5.5	Ka	8.04	Japan	Nishira pers. comm. 1978
27	10	Av	6.42	Australia	Davie 1984
27	2	Av	1.94	Australia	Davie 1984
27	6.5	Av	3.42	Australia	Davie 1984
27.3	6.9	Rh	10.76	USA	Lahmann 1988
27.3	7.4	Rh	16.31	USA	Lahmann 1988
27.3	6.6	Rh	13.54	USA	Lahmann 1988
30	6	Br	8.61	South Africa	Steinke & Charles 1984
30	8	Av	7.15	South Africa	Steinke & Charles 1984
33	4.4	Av	5.62	Australia	Murray 1985
33.5	4.3	Av	5.14	Australia	Murray 1985
34	8.5	Av	5.80	Australia	Goulter & Allaway 1979
37	1	Av	3.28	New Zealand	Woodroffe 1985
37	3.3	Av	7.61	New Zealand	Woodroffe 1985
38	3.5	Av	2.00	Australia	Clough & Attiwill 1982

Av: *Avicennia* spp.; Rh: *Rhizophora* spp.; M: Mixed mangroves; Ka: *Kandelia candel*; La: *Laguncularia racemosa*; So: *Sonneratia* spp.; Br: *Bruguiera* spp.; Ce: *Ceriops tagal*

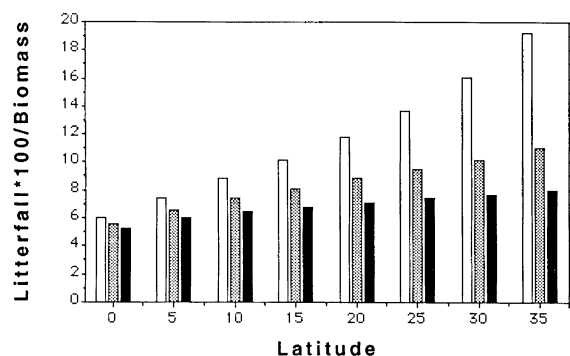


Fig. 3. Simulation of litterfall-to-biomass ratios for low (2 m, white), medium (4 m, stippled) and tall (10 m, black) mangrove communities over 35° of latitude using Eqs. 3 and 6

## Discussion

The assembled data and analyses fully support the principal hypothesis that, within the global mangrove community, the indices of organic production and carbon turnover are highest at the lower latitudes (Eqs. 2 and 5). The analyses of height, latitude, and biomass (Eqs. 1 and 2) suggest that there is a strong relationship between biomass and both height (structural development) and latitude (solar insolation). In other words, when there are no site-specific growth constraints, the accumulation of biomass is proportional to the ambient solar insolation. In turn, this finding reflects the generally increased struc-

tural complexity of mangrove communities under the optimal growing conditions of the tropics.

The fact that there is also a strong correlation between latitude and height ( $r = -0.678$ ,  $P < 0.0001$ ) suggests that latitude influences height of the vegetation through insolation, temperature, and, perhaps, water availability, which in turn influence the biomass. This strong correlation between height and latitude is reflected in the ratio that combines latitude and height into a single variable and accounts for 66% of the variance in the biomass data. Pool et al. (1977) presented data on height and latitude of mangroves from 25 western-hemisphere study sites. Their data, although not statistically significant, showed a similar relationship between height and latitude.

Similar considerations apply to the litterfall data. As Eqs. 5 and 6 show, latitude and height individually account for 13% and 20% of the variance respectively, while the ratio of latitude to height explains 25%. In this regard, however, we do not suggest a causative relationship between height and litterfall for two principal reasons: (1) the use of the height parameter across the latitudinal gradient is merely a general index of structural development; and (2) the correlation between the litterfall and height may simply reflect other variables indicative of more suitable growing conditions that result in increased organic production and carbon turnover via leaf or litterfall.

Mangroves frequently show a high within-region diversity of structural patterns, and an equally high diversity of functional roles (Lugo and Snedaker 1974; Pool

et al. 1977). As shown in Figs. 1a and 2a, there is considerable variation in all reported parameters for any given latitude. Based on a knowledge of the study sites, high values for height, biomass, and litterfall indicate optimum habitats, particularly with respect to reduced salinity regimes, more optimal climatic conditions, and better site fertility. In contrast, the low-value sites are mainly characterized by natural stress factors, e.g., aridity and poor fertility (Cintron et al. 1978). Although the correspondence is not precise, these general trends are consistent with the more specific conclusions drawn by Pool et al. (1977).

Caution should be exercised in using any of the equations not only beyond the range of the data, but also at the extremes of their range. However, Eqs. 3 and 6 allow the ratio of litter production to biomass to be calculated. This ratio is similar to the production/biomass ratio proposed by Margalef (1963) with the caveat that litterfall is a variable fraction of total production. Nevertheless, our simulated litterfall/biomass ratios (Fig. 3) show that, particularly at higher latitudes, short communities produce more litter per unit of biomass than taller communities. For example, low communities have a reported biomass around  $7 \text{ t.ha}^{-1}$  (Table 1) and a litterfall of  $2 \text{ t.ha}^{-1}$  (Table 2), which represents a litterfall/biomass ratio of  $286 \text{ kg litter t}^{-1} \text{ biomass}$ . In contrast, taller communities, with a biomass around  $200 \text{ t.ha}^{-1}$  and a litterfall around  $13 \text{ t.ha}^{-1}$  have a litterfall/biomass ratio of  $65 \text{ kg litter t}^{-1} \text{ biomass}$ .

Proctor (1984) collated global data on litterfall for tropical and subtropical forest communities together with latitudes of the study sites. These data, exclusive of the mangrove data, give the following regression:

$$\text{Litterfall (t.ha}^{-1}\text{)} = 9.949 - 0.201 \times \text{Latitude (}^{\circ}\text{)} \quad (7)$$

$$(r = -0.404, F_{1, 153} = 29.88, P < 0.0001)$$

The slope of this regression (0.201) is not significantly different ( $t = 0.475$ ,  $df = 242$ ,  $P > 0.7$ ) from the slope of the mangrove regression (0.160 in Eq. 5), suggesting that similar latitudinal factors influence both upland forest and mangrove communities. The intercepts, however, suggest that mangrove communities have a higher litterfall ( $11.8 \text{ t.ha}^{-1}$  on the equator) than do upland forests ( $9.9 \text{ t.ha}^{-1}$  on the equator).

Analyses of the assembled data on mangrove biomass and litterfall fully support the principal hypothesis that, within the global mangrove community, the indices of organic production are highest at the lower latitudes, and decrease linearly with increasing latitudes, as in upland forests. Positive relationships between height and biomass or litterfall can also be recognised, reflecting the reduced constraints on structural and functional development in the generally more benign growing conditions in the tropics (Saenger and Holmes 1991). Nevertheless, the shorter mangrove communities at the higher latitudes apparently produce larger litterfalls relative to their biomass than do more tropical ones, suggesting that patterns of organic matter partitioning change with latitudinal gradients and that at higher latitudes carbon turnover is higher relative to biomass.

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