# Chapter 6
# Latitudinal Variation in Brazilian Mangroves' Annual Litterfall as Evidence of Maximum Power and Geoecological Manifestation

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## 6.1 Introduction

One of the major paradigms in mangrove ecology is that mangroves are highly productive systems and are considered an azonal formation present over a wide latitudinal span from the tropics to well over the subtopics, reaching latitudes close to or slightly beyond 34° (Tomlinson 1986). Mangroves visibly do best between latitudes 25°N and S where they manifest their highest productivity in terms of biomass and litterfall (Cintrón and Schaeffer-Novelli 1983; Saenger and Holmes 1991). Although in the New World the species diversity of mangroves is lower than in Asia, mangrove productivity is similar and systems under similar conditions reach similar levels of development (Saenger and Snedaker 1993).

Mangrove aboveground biomass is correlated to litterfall production in the sense that larger trees can support a larger canopy and potential for producing higher litterfall levels. Observations show that productivity is linked to hydrology with riverine systems attaining the highest levels of structural development followed by

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fringes and, finally, basins (Lugo and Snedaker 1974). However, on an aerial basis, fringes are limited to edges whereas basins can dominate a landscape.

Twilley (1995) presented summaries of biomass and litterfall accumulation and productivity of mangroves with latitude worldwide. These data show a trend for biomass accumulation to/decline with latitude, as would be expected from climatic constraints, but, surprisingly, also show high litterfall production even near latitudinal extremes. In this context, the Brazilian coastline provides an attractive opportunity to examine latitudinal patterning and ecosystem functions as geoecological manifestations, since it extends from Equatorial to Subtropical latitudes (04°26′12″N to 33°45′07″S), an approximately 11 thousand km latitudinal span (IBGE 2016). Cintrón and Schaeffer-Novelli (1981) reported to Brazil that mangroves reach their latitudinal limit along this coast, occupying habitats below the Tropic of Capricorn (23°30′S to 28°30′S). Interestingly, solar energy decreases, and the planetary heat balance shifts from surplus incoming energy to energy deficits at about 35°S to 40°S where radiative deficits prevail (INMET: http://www.inmet.gov.br), which drive productivity patterns.

## 6.2 Brazilian Mangrove Forests' Annual Litterfall

This chapter shows assembled and analyzed data from published and unpublished studies on Brazilian mangrove forests' annual litterfall along the coast between latitudes 04°N and 27°S. The criteria for data inclusion took into consideration Proctor's (1984) considerations on data comparison issues. The requirements for inclusion were: (1) all litter components had to be included in the study, not merely the leaves; (2) all study sites should be georeferenced or ascertainably situated deriving from other sources; (3) all litterfall data had to represent at least a one-year collection, regardless of the season of commencement or termination of sampling; and (4) all collecting and weighing methods are well accepted in the literature as long as sufficient replicate traps were used to take variability into account.

Northern and southern litterfall values (all components of the litter expressed as g $m^2$ $day^{-1}$) were treated as equivalent for mixed and monospecific mangroves communities of the various species (Saenger and Snedaker 1993).

### *6.2.1 Annual Litterfall*

The obtained linear regression shows to be somewhat skewed (skewness = 0.1379), with several point accumulations of high tropical and subtropical values contributing to the skewing (Fig. 6.1). The assembled data ($N = 94$) are presented in Tables 6.1 and 6.2.

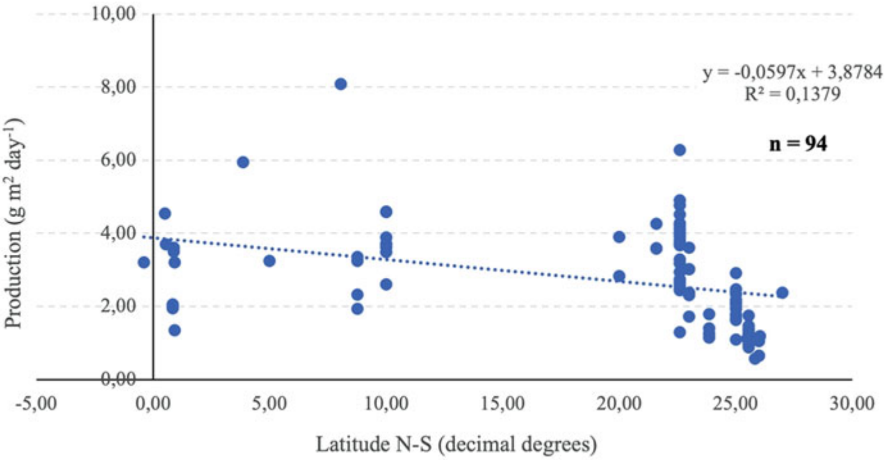

**Fig. 6.1** Scatter diagram of mangrove litterfall along the Brazilian coastline. Latitudinal degrees were transformed to latitudinal decimal degrees. Litterfall and latitudinal location fed a best-fit linear regression ($y = ax + b$)

The litterfall values ranged from the highest rate of 8.08 g $m^2$ $day^{-1}$ in a *Laguncularia racemosa* stand in Olinda (08°S) (Paiva and Coelho-Jr unpublished) to the lowest of 0.65 g $m^2$ $day^{-1}$ in Babitonga Bay (26°S) (Cunha 2001; Almeida 2004) (see Chap. 3, Maps 8 and 16, respectively). The latitudinal variation on its own was responsible for ca. 14% of the variation in productivity, with a lesser trend in higher latitudes.

## 6.3 On the Causes for Litterfall Productivity

When there are no site-specific growth constraints, litterfall production is proportional to solar insolation, which, in turn, reflects the generally increased structural complexity of mangrove communities under optimal growing conditions in the tropics.

Pool et al. (1977) presented data on tree height and latitude of mangroves in the western hemisphere. Their data, although not statistically significant, showed a similar trend for the relationship between biomass and latitude. Nevertheless, data on Brazilian litterfall show surprisingly high productivity even near the limits of distribution, as it has been observed in a few other studies, such as Twilley's (1995) and López-Medellín and Ezcurra's (2012) in Mexico.

Litterfall values strongly reflect latitude influences through insolation, temperature, and freshwater availability. Within equatorial latitudes, ample solar radiation in terms of day length duration and solar angle, combined with warm temperatures and suitable site factors, favors high productivity that prevails to about 10°S (Saenger

**Table 6.1** Ninety-four litterfall data (g $m^2$ $day^{-1}$) along the Brazilian coast latitudinal span with respective references

| Latitude | Production (g $m^2$ $day^{-1}$) | References |
|---|---|---|
| (04°N) | 3,20 | Fernandes (1997) |
| (00°) | 2,05 | Gonçalves et al. (2006) |
| (00°) | 1,95 | Gonçalves et al. (2006) |
| (00°) | 2,03 | Fernandes et al. (2007) |
| (00°) | 3,50 | Mehlig (2001) |
| (00°) | 3,60 | Mehlig (2001) |
| (00°) | 3,20 | Nascimento et al. (2006) |
| (00°) | 1,35 | Farias et al. (2006) |
| (00°) | 3,70 | Reise (2003) |
| (00°) | 4,55 | Nordhaus (2004) |
| (03°S) | 5,94 | Travassos et al. (2012) *unpublished* |
| (05°S) | 3,25 | Rêgo (1999) |
| (08°S) | 3,24 | Longo (2009) |
| (08°S) | 2,32 | Longo (2009) |
| (08°S) | 3,35 | Longo (2009) |
| (08°S) | 1,94 | Longo (2009) |
| (08°S) | 8,08 | Paiva and Coelho-Jr (unpublished) |
| (10°S) | 3,49 | Menezes (2010) |
| (10°S) | 3,89 | Menezes (2010) |
| (10°S) | 4,59 | Menezes (2010) |
| (10°S) | 4,58 | Menezes (2010) |
| (10°S) | 3,71 | Santos (2013) |
| (10°S) | 3,62 | Santos (2013) |
| (14°S) | 2,60 | Santos (2009) |
| (20°S) | 3,90 | Carmo et al. (1998) |
| (20°S) | 2,83 | Carmo et al. (1998) |
| (21°S) | 3,58 | Bernini and Rezende (2010) |
| (21°S) | 4,26 | Bernini and Rezende (2010) |
| (21°S) | 3,59 | Bernini and Rezende (2010) |
| (22°S) | 3,81 | Chaves (2007) |
| (22°S) | 3,67 | Chaves (2007) |
| (22°S) | 3,92 | Chaves (2007) |
| (22°S) | 2,93 | Chaves (2007) |
| (22°S) | 2,47 | Chaves (2007) |
| (22°S) | 4,90 | Chaves (2007) |
| (22°S) | 4,11 | Chaves (2007) |
| (22°S) | 4,52 | Chaves (2007) |
| (22°S) | 4,77 | Chaves (2007) |
| (22°S) | 4,22 | Chaves (2007) |
| (22°S) | 3,29 | Chaves (2007) |
| (22°S) | 4,00 | Chaves (2007) |
| (22°S) | 2,55 | Chaves (2007) |

(continued)

**Table 6.1** (continued)

| Latitude | Production (g m$^2$ day$^{-1}$) | References |
|---|---|---|
| (22°S) | 3,70 | Chaves (2007) |
| (22°S) | 6,27 | Chaves (2007) |
| (22°S) | 2,68 | Chaves (2007) |
| (22°S) | 2,44 | Chaves (2007) |
| (22°S) | 4,27 | Chaves (2007) |
| (22°S) | 3,73 | Chaves (2007) |
| (22°S) | 1,29 | Chaves (2007) |
| (22°S) | 2,63 | Chaves (2007) |
| (22°S) | 3,95 | Chaves (2007) |
| (22°S) | 2,74 | Chaves (2007) |
| (22°S) | 3,18 | Chaves (2007) |
| (23°S) | 2,31 | Machado (2014) |
| (23°S) | 3,02 | Machado (2014) |
| (23°S) | 3,60 | Machado (2014) |
| (23°S) | 3,02 | Machado (2014) |
| (23°S) | 2,33 | Machado (2014) |
| (23°S) | 1,72 | Machado (2014) |
| (23°S) | 2,38 | Silva et al. (1998) |
| (23°S) | 1,79 | Lamparelli (1995) |
| (23°S) | 1,40 | Lamparelli (1995) |
| (23°S) | 1,25 | Lamparelli (1995) |
| (23°S) | 1,14 | Lamparelli (1995) |
| (25°S) | 2,34 | Valadares (2015) |
| (25°S) | 1,09 | Ponte et al. (1990) |
| (25°S) | 2,08 | Adaime (1985) |
| (25°S) | 1,67 | Adaime (1985) |
| (25°S) | 2,47 | Menezes (1994) |
| (25°S) | 1,77 | Menezes (1994) |
| (25°S) | 2,11 | Menezes (1994) |
| (25°S) | 2,91 | Almeida (2004) |
| (25°S) | 2,17 | Almeida (2004) |
| (25°S) | 2,05 | Almeida (2004) |
| (25°S) | 1,93 | Almeida (2004) |
| (25°S) | 1,62 | Almeida (2004) |
| (25°S) | 1,12 | Larcher (2014) |
| (25°S) | 0,57 | Larcher (2014) |
| (25°S) | 0,97 | Sessegolo (1997) |
| (25°S) | 1,75 | Sessegolo (1997) |
| (25°S) | 1,39 | Sessegolo (1997) |
| (25°S) | 1,26 | Sessegolo (1997) |
| (25°S) | 0,97 | Sessegolo (1997) |
| (25°S) | 0,87 | Sessegolo (1997) |

(continued)

**Table 6.1** (continued)

| Latitude | Production (g $m^2$ $day^{-1}$) | References |
|---|---|---|
| (25°S) | 1,36 | Sessegolo (1997) |
| (25°S) | 1,19 | Sessegolo (1997) |
| (25°S) | 1,35 | Sessegolo (1997) |
| (25°S) | 1,47 | Sessegolo (1997) |
| (25°S) | 1,05 | Cunha (2001) |
| (25°S) | 0,65 | Cunha (2001) |
| (26°S) | 1,19 | Silva (2001) |
| (27°S) | 2,37 | Panitz (1986) |

and Snedaker 1993; Simrad et al. 2019). However, what is interesting in these data is the peak extending south of about 23°30′S in a region where sun radiative deficits become more pronounced and evident. It seems that this reflects the propensity of mangroves to persist by maximizing the use of available subsidiary energies through autocatalytic growth that reinvests high-quality energy into compartments that reinforce further production, thus generating maximum power. Following Boltzmann (1886), Lotka (1922) proposed the Principle of Maximum Power, which has wide application in all thermodynamic systems. In Ecology, Odum and Pinkerton (1955) associated this phenomenon with autocatalysis. This Principle suggests that evolutionary selection favors systems that can maximize energy flow by using all available site energies and reinvesting captured energy into ways favorable to persistence close to the edge of species' or system's tolerances.

At the ecosystem level, Lotka's Maximum Power Principle (MPP) means selection for increasingly tolerant species or beyond into higher-level designs that combine other systems such as salt marshes. We suggest that the MPP is manifested in mangroves as Maximum Ascendency (sensu Ulanowicz 1980). The Brazilian litterfall data provides empirical evidence for the MPP and associated maximization functions, for example, Goal Functions (i.e., ascendency) described in the literature by Odum (1969) and Jørgesen (1992), among others. The MPP is increasingly recognized as an ecological law of thermodynamics (Odum and Pinkerton 1955; Jørgensen 1992).

In the case of Brazil, the assertiveness of mangroves is combined with coastal geomorphology, tidal regime, and local climate (see Chap. 3) to create extremely favorable conditions that allow mangroves to persist poised at the edge of chaos where environmental conditions preclude further occupation of coastal habitats.

In Southeast Brazil, the coastal escarpment reaches about latitude 23°S; beyond that point, the coastline becomes more indented (or higher fractal dimension) within a region increasingly influenced by the South Atlantic Convergence Zone convective activity (SACZ); at 20°–25°S. The SACZ conveys enhanced precipitation and increasing moisture that, combined with a favorable microtidal (less than 2 m) regime and geomorphology, creates favorable habitats very close to the latitudinal limit. Notably, a microtidal to mesotidal pulsing regime is considered optimal for salt marsh development (Odum et al. 1995) as is for barrier island formation (Davies 1973; Hayes 1975). Thus, the 20°–28°S structural setting of the Brazilian coast

**Table 6.2** Ninety-four litterfall data (g $m^2$ $day^{-1}$) along the Brazilian coast latitudinal span with respective references

| Latitude | Production (g $m^2$ $day^{-1}$) | References | Latitude | Production (g $m^2$ $day^{-1}$) | Reference | Latitude | Production (g $m^2$ $day^{-1}$) | References |
|---|---|---|---|---|---|---|---|---|
| (04°N) | 3,20 | Fernandes (1997) | (22°S) | 3,92 | Chaves (2007) | (23°S) | 1,25 | Lamparelli (1995) |
| (00°) | 2,05 | Gonçalves et al. (2006) | (22°S) | 2,93 | Chaves (2007) | (23°S) | 1,14 | Lamparelli (1995) |
| (00°) | 1,95 | Gonçalves et al. (2006) | (22°S) | 2,47 | Chaves (2007) | (25°S) | 2,34 | Valadares (2015) |
| (00°) | 2,03 | Fernandes et al. (2007) | (22°S) | 4,90 | Chaves (2007) | (25°S) | 1,09 | Ponte et al. (1990) |
| (00°) | 3,50 | Mehlig (2001) | (22°S) | 4,11 | Chaves (2007) | (25°S) | 2,08 | Adaime (1985) |
| (00°) | 3,60 | Mehlig (2001) | (22°S) | 4,52 | Chaves (2007) | (25°S) | 1,67 | Adaime (1985) |
| (00°) | 3,20 | Nascimento et al. (2006) | (22°S) | 4,77 | Chaves (2007) | (25°S) | 2,47 | Menezes (1994) |
| (00°) | 1,35 | Farias et al. (2006) | (22°S) | 4,22 | Chaves (2007) | (25°S) | 1,77 | Menezes (1994) |
| (00°) | 3,70 | Reise (2003) | (22°S) | 3,29 | Chaves (2007) | (25°S) | 2,11 | Menezes (1994) |
| (00°) | 4,55 | Nordhaus (2004) | (22°S) | 4,00 | Chaves (2007) | (25°S) | 2,91 | Almeida (2004) |
| (03°S) | 5,94 | Travassos et al. (2012)[a] | (22°S) | 2,55 | Chaves (2007) | (25°S) | 2,17 | Almeida (2004) |
| (05°S) | 3,25 | Rêgo (1999) | (22°S) | 3,70 | Chaves (2007) | (25°S) | 2,05 | Almeida (2004) |
| (08°S) | 3,24 | Longo (2009) | (22°S) | 6,27 | Chaves (2007) | (25°S) | 1,93 | Almeida (2004) |

(continued)

**Table 6.2** (continued)

| Latitude | Production (g m$^2$ day$^{-1}$) | References | Latitude | Production (g m$^2$ day$^{-1}$) | Reference | Latitude | Production (g m$^2$ day$^{-1}$) | References |
|---|---|---|---|---|---|---|---|---|
| (08°S) | 2,32 | Longo (2009) | (22°S) | 2,68 | Chaves (2007) | (25°S) | 1,62 | Almeida (2004) |
| (08°S) | 3,35 | Longo (2009) | (22°S) | 2,44 | Chaves (2007) | (25°S) | 1,12 | Larcher (2014) |
| (08°S) | 1,94 | Longo (2009) | (22°S) | 4,27 | Chaves (2007) | (25°S) | 0,57 | Larcher (2014) |
| (08°S) | 8,08 | Paiva and Coelho-Jr (unpublished)[a] | (22°S) | 3,73 | Chaves (2007) | (25°S) | 0,97 | Sessegolo (1997) |
| (10°S) | 3,49 | Menezes (2010) | (22°S) | 1,29 | Chaves (2007) | (25°S) | 1,75 | Sessegolo (1997) |
| (10°S) | 3,89 | Menezes (2010) | (22°S) | 2,63 | Chaves (2007) | (25°S) | 1,39 | Sessegolo (1997) |
| (10°S) | 4,59 | Menezes (2010) | (22°S) | 3,95 | Chaves (2007) | (25°S) | 1,26 | Sessegolo (1997) |
| (10°S) | 4,58 | Menezes (2010) | (22°S) | 2,74 | Chaves (2007) | (25°S) | 0,97 | Sessegolo (1997) |
| (10°S) | 3,71 | Santos (2013) | (22°S) | 3,18 | Chaves (2007) | (25°S) | 0,87 | Sessegolo (1997) |
| (10°S) | 3,62 | Santos (2013) | (23°S) | 2,31 | Machado (2014) | (25°S) | 1,36 | Sessegolo (1997) |
| (14°S) | 2,60 | Santos (2009) | (23°S) | 3,02 | Machado (2014) | (25°S) | 1,19 | Sessegolo (1997) |
| (20°S) | 3,90 | Carmo et al. (1998) | (23°S) | 3,60 | Machado (2014) | (25°S) | 1,35 | Sessegolo (1997) |
| (20°S) | 2,83 | Carmo et al. (1998) | (23°S) | 3,02 | Machado (2014) | (25°S) | 1,47 | Sessegolo (1997) |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| (21°S) | 3,58 | Bernini and Rezende (2010) | (23°S) | 2,33 | Machado (2014) | (25°S) | 1,05 | Cunha (2001) |
| (21°S) | 4,26 | Bernini and Rezende (2010) | (23°S) | 1,72 | Machado (2014) | (25°S) | 0,65 | Cunha (2001) |
| (21°S) | 3,59 | Bernini and Rezende (2010) | (23°S) | 2,38 | Silva et al. (1998) | (26°S) | 1,19 | Silva (2001) |
| (22°S) | 3,81 | Chaves (2007) | (23°S) | 1,79 | Lamparelli (1995) | (27°S) | 2,37 | Panitz (1986) |
| (22°S) | 3,67 | Chaves (2007) | (23°S) | 1,40 | Lamparelli (1995) | | | |

[a] Unpublished

shapes a mesoscale physiographic/climatic complex that harbors the largest estuarine systems of Southeast Brazil (Angulo et al. 2009). This geomorphic template subsidizes mangrove occupation, where they can act as an endogenous living force capable of modifying geomorphic processes and buffering exogenic (climate-driven limitations). As a result, mangrove productivity instead of decreasing gradually ends abruptly at Laguna, Santa Catarina State, near 28°30′S (see Chap. 3, Map 16), contradicting/contrasting with what is assumed as a pattern for Australia, New Zealand, and Japan (Tomlinson 1986; Friess 2018). We suggest that mangroves here can be considered as "surfing at the edge of chaos," and this is manifested in fractal dynamics on the ground, such as persistent change (or pulsing) at local scales, rather than a steady state.

An appearance of steady state may be induced by constant recruitment. Pulsing at a local scale can induce persistent changes in vegetation patterns consistent with pulsing driven by slight external changes in climate and internal (local scale) changes. A steady state at the landscape level is an emergent function of local scale pulsing. The prevalence of pulsing in nature led Odum et al. (1995) to propose it as a paradigm of nature's organization and suggest that pulsing can be interpreted as oscillations at the edge of chaos.

Mangroves frequently express a high within-region diversity of structural patterns, and an equally high diversity of functional roles (Lugo and Snedaker 1974; Pool et al. 1977). Based on knowledge of the dataset here analyzed, structural characteristics (i.e., high values for height, biomass, and litterfall) indicate optimum habitats, particularly concerning reduced salinity regimes, optimal climatic conditions, site-specific fertility, as also observed where human input of domestic sewage nutrients influences the high values of productivity at Olinda (PE) and Guanabara Bay (RJ) (see Chap. 3, Maps 8 and 13, respectively). The slope of the present regression (0.138) is not significantly different from the slope in Saenger and Snedaker's (1993) regression (0.201, Eq. 5). The high value at Fernando de Noronha (see Chap. 1) (see Chap. 3, 18) can be explained by rich volcanic soil and low salinity values. In contrast, the low-value sites are mainly characterized by natural stress situations, for example, aridity and poor fertility (Cintrón et al. 1978). Although the correspondence is not precise, these general regional trends are consistent with the more specific conclusions drawn by Pool et al. (1977) and Saenger and Snedaker (1993).

Finally, south of 28°30′S, sediment transport by wave action, the microtidal tidal regime (mean range only 0.5 m) and freshwater runoff from a humid climate become too adverse for mangrove establishment. Particularly, a barrier system of Rio Grande do Sul State acts as a dam to freshwater input, which combined with restricted tidal influence favors freshening of the choked lagoon and the emergence of a "cut-off" filter or "brick wall" that impedes mangrove and salt marsh development further south. This barrier system is one of the longest in South America and one of the longest in the world. Salt marshes do reappear at the southern end near Cassino Beach (see Chap. 1) where the inlet allows seawater intrusion into the lower lagoon. The reduction in tidal influence reflects the influence of an amphidromic point off the coast of Rio Grande do Sul that reduces the main lunar component of the tide (Schwiderski 1980) (see Chap. 3, 17).

## 6.4 Final Remarks

The assembled data on Brazilian litterfall and corresponding analyses fully support Saenger and Snedaker's (1993) results that within the global mangrove community, the indices of organic production are highest at the lower latitudes. Nevertheless, mangrove communities below the Tropic of Capricorn latitudes are capable of larger litterfall rates relative to their biomass than more tropical ones. We suggest that this reflects the propensity of mangroves to persist by maximizing the use of available subsidiary energies combined by a combination of unusually favorable biotic and abiotic factors south of 23°30′S.

The Brazilian coast provides an attractive opportunity to examine latitudinal patterning and ecosystem functions as geoecological manifestations due to its extension. Also, its range makes it possible to study mangroves at the edge of chaos near their latitudinal limit. There is a great potential of addressing important questions about mangrove species' evolution and adaptation, especially in a country with such extensive coastal length. We hope that this chapter will bring more visibility and interest to combined studies on mangrove structure and genetics.

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