



Review and analysis of mangrove litter production in Mexico: A contrasting regions approach

Revisión y análisis de la producción de hojarasca de manglar en México: Un enfoque de regiones contrastantes

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ABSTRACT

The mangrove ecosystem is recognized as one of the most productive worldwide; in most cases, this productivity has been quantified through the amount of leaf litter produced per unit area and time. However, there is a large variability in the values recorded for each latitudinal interval, which has been attributed to the diversity of local environmental characteristics. Managing leaf litter production data is the first consideration for the technical management of mangrove resources as an ecosystem. The present review (scientific articles, theses, reports, etc.) shows an analysis of the productivity of mangroves in Mexico, with the objective of synthesizing the knowledge of leaf litter production generated by different structural types of forests, described and explained according to environmental conditions. We consulted 68 publications, where the highest value of litterfall contribution (19.30 Mg/ha/year) was recorded in Atasta, Campeche, a semi-humid tropical region, and the lowest (1.75 Mg/ha/year) in Las Guásimas, Sonora, a semi-arid subtropical region. The causal factors of leaf litter fall correspond mainly to precipitation, salinity, nutrients, structure, and physicochemical parameters of the interstitial water. It is important to increase and unify efforts between governmental agencies and research centers to generate and organize existing data on the mangrove's primary productivity for a better understanding of the patterns and controls of the productivity and health of these coastal ecosystems.

KEYWORDS: coastal zone, halophytes, precipitation, primary productivity, salinity, wetland.

RESUMEN

El ecosistema de manglar es reconocido como uno de los más productivos a escala mundial. En la mayoría de los casos esta productividad ha sido cuantificada a través de la cantidad de hojarasca producida por unidad de área y tiempo. Sin embargo, existe una variabilidad muy grande en los valores registrados para cada intervalo latitudinal, lo que se ha atribuido a la diversidad de características ambientales locales. El manejo de datos de producción de hojarasca es la primera consideración para el manejo técnico de los recursos manglares como ecosistema. El presente trabajo de revisión (artículos científicos, tesis, informes, etc.) muestra un análisis de la productividad de los manglares de México, con el objetivo de sintetizar el conocimiento de la producción de hojarasca generada por diferentes tipos estructurales de bosques, descrita y explicada según las condiciones ambientales. Se consultaron 68 publicaciones, donde el mayor valor de aporte de hojarasca (19.30 Mg/ha/año) se registró en Atasta, Campeche, región tropical semihúmeda y el más bajo (1.75 Mg/ha/año) en Las Guásimas, Sonora, una región subtropical semiárida. Los factores causales de la caída de hojarasca corresponden principalmente a precipitación, salinidad, nutrientes, estructura y físico químicos del agua intersticial. Es importante aumentar y unificar esfuerzos entre agencias gubernamentales y centros de investigación para la generación y organización de los datos existentes relacionados con la productividad primaria del manglar, que permita una mejor comprensión de los patrones y controles de la productividad y salud de estos ecosistemas costeros.

PALABRAS CLAVE: zona costera, halófitas, precipitación, productividad primaria, salinidad, humedal.

INTRODUCTION

Mangrove ecosystems are located at the land-sea border with areas that have been reduced, mainly due to changes in the land use of anthropogenic activities (Diop, 1993; Lacerda, 1993; Tovilla-Hernández et al., 2007). Mangroves provide society with several environmental services, among the main ones: protection of the coastline against storms and hurricanes, stabilization of sediments, primary productivity (litterfall), and biological filtering; they also constitute areas of high landscape value as they harbor great biodiversity, and they are a habitat for fish, mollusks and crustaceans, for breeding and spawning, many of them of high commercial value (Pannier & Pannier, 1989; Twilley et al., 1996; Lacerda et al., 2002). Mangroves are among the most productive ecosystems on earth, exceeding the productivity of continental platform regions by an average factor of 4 and that of open ocean by a factor of 40 (Ong, 1982; Berger et al., 1989; Bunt, 1992).

The mangrove ecosystem works on the basis of matter subsidies (nutrients, sediments, organic matter, fresh and brackish water) and energy (light, temperature, waves, tides, and hurricanes). These elements allow the photosynthetic apparatus to produce a certain biomass quantity that is expressed in terms of organic matter (primary productivity), which is variable depending upon different factors such as latitude, seasonality, type of soil, microtopography, geomorphology, and precipitation (Orihuela-Belmonte et al., 2004; Torres et al., 2018). This primary productivity, in most cases, has been quantified in mangroves through the leaf fall (Rico-Gray & Lot-Helgueras, 1983; Steinkey & Charles, 1984), which can be expressed by the amount of litterfall produced by area-time (Kristensen et al., 2008). Furthermore, it is one of the most important services provided by these ecosystems (López-Medellín & Ezcurra, 2012). The vital cycles of the species that make up the mangrove vary as a result of a very complex combination of abiotic environmental factors, the physiology of trees, and other ecologic aspects like pollination and dispersion of propagules (Leach & Burgin, 1985).

In a world-scale review, Bouillon et al. (2008) found that the amount of litterfall produced annually by area units varies according to latitude and is higher at the equatorial latitudes. A similar review was proved for the northwest region of Mexico by López-Medellín and Ezcurra (2012). This altitudinal variation has been attributed to diverse local environmental characteristics (Saenger & Snedaker, 1993). These include factors like salinity (Bunt, 1995; Utrera-López & Moreno-Casasola, 2008; Coronado-Molina et al., 2012), the nutrients content (Adame et al., 2012), the tides (Lugo & Snedaker, 1974), the flooding levels (Day et al., 1987; Agraz-Hernández et al., 2011), physicochemical characteristics of soil, extreme weather effects (Adame et al., 2012, 2015), temperature and evapotranspiration (Sánchez-Andrés et al., 2010).

The most recent esteemed global figure of mangrove surface from Global Mangrove Watch for 2016 was 135 881.65 km², distributed throughout about 120 countries and territories, covering around 12% of the world's coastline (Global Mangrove Watch [GMW], 2020; Velázquez-Salazar et al., 2021). In Mexico, mangrove cover is 905 086 ha; the largest part is located at the Yucatan Peninsula with 544 169 ha (60%) and the north Pacific with 181 036 ha (20%), the central Pacific is the less covered with 7275 ha (0.8%; Fig. 1) (Velázquez-Salazar et al., 2021). Nevertheless, at a regional level, there are differences in the mangrove structure that are along from Chiapas (14°32'1.47"N) to Baja California (29° 3'13.57"N) (the latter is the northern limit of the Mexican Pacific mangroves), as well as the Gulf of Mexico and Caribbean mangroves that comprise from Quintana Roo (18°10'N) to Tamaulipas (25°55'N) (Rodríguez-Zúñiga et al., 2013).

Mexico's mangroves have been a subject of research for more than 30 years, with studies made by Mexican institutions and by specialists of several disciplines about the coastal wetlands, where in some cases long haul projects have been conducted, providing continuity on the study along the coastline of the Pacific Ocean, Gulf of Mexico, and Caribbean Sea (Rodríguez-Zúñiga et al., 2013; Valderrama-Landeros et al., 2017). Most of these studies have aimed at assessing litterfall production of



Mexico's four most representative mangrove species: *Rhizophora mangle* L. (Rm, red mangrove), *Laguncularia racemosa* (L.) Gaertn (Lr, white mangrove), *Avicennia germinans* (L.) Stearn (Ag, black mangrove), and *Conocarpus erectus* L. (Ce, "botoncillo" mangrove) (Flores-Verdugo et al., 1990; Day et al., 1996; Barreiro-Güemes, 1999). In the Yucatan peninsula and the Isthmus of Tehuantepec, there is a variety of Ce named *Conocarpus erectus* var. *sericeus* D.C. (Valderrama-Landeros et al., 2017), while at the Chiapas coastline, the *Rhizophora harrisonii* Leech species spread. (Rhizophoraceae, yellow mangrove) and *Avicennia bicolor* Standl. (Acanthaceae, black mangrove); (López-Portillo & Ezcurra, 2002; Tovilla-Hernández et al., 2010, 2018; Nettel et al., 2008).

The ecosystem services that mangroves provide differ in importance according to the structure types; for instance, riverside woods tend to be more important as sedi-

ment traps, sources of detritus towards the coastal waters, they provide food and habitat for fauna, while basin mangroves tend to be more relevant as nitrogen and carbon sinks, they even improve water quality and provide diverse products; finally those on the fringe tend to be more important as a protection for the coastal line (Ewel et al., 1998). A remarkable aspect is that mangroves provide a constant income of organic matter into the coastal bodies of water through the leaf fall; this implies that an important part of the net primary production ($\approx 45\%$) is destined for decomposition (Duarte & Cebrian, 1996; Tovilla-Hernández, 1998; Orihuela-Belmonte, 2001; Orihuela-Belmonte et al., 2004) and together with it, the maintenance of coastal ecological processes, for example, supporting trophic frames by way of detritus, apart from the internal recycling of nutrients through remineralization (Sánchez-Andrés et al., 2010).

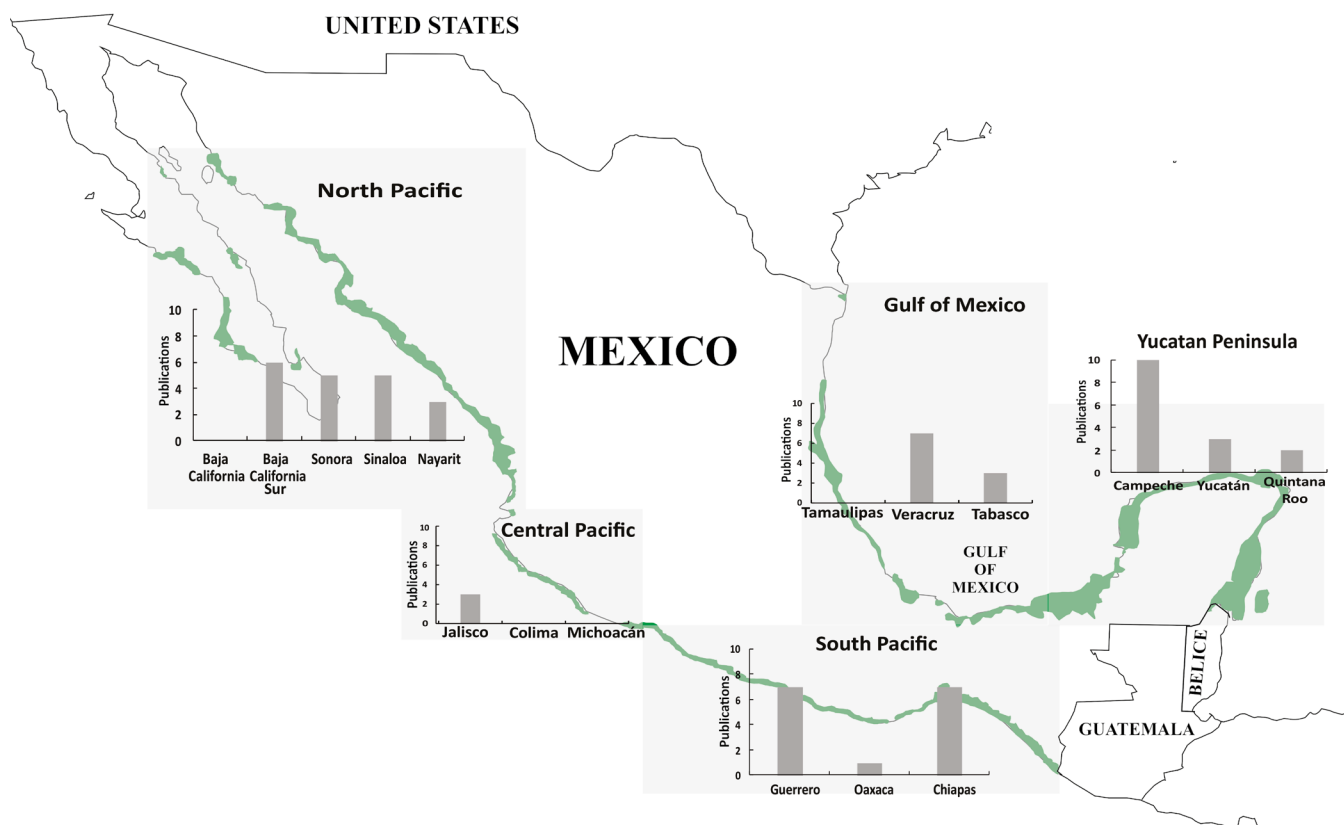


FIGURE 1. Map representing the number of publications regarding litterfall (own elaboration) on different regions of mangrove distribution in Mexico, as proposed by Conabio (Velázquez-Salazar et al., 2021).

The data management resulting from these studies is the first consideration for the technical management of the resources of the mangrove as an ecosystem. It is, therefore, valuable to recognize the ecological role and the need to compile data about productivity at different scales and, on the other hand, to standardize their registration, to share them on databases (Rodríguez-Zúñiga, 2018). This usage of techniques and methods, apart from the different ways of reporting the results, like the use of measurement units, will be reflected in different ways of interpreting the observations and the status of the ecosystem. On Mexican mangroves, it is essential to identify the differences in structure and litterfall production associated with different coastline regions of the country, as they exhibit variations in the weather and other environmental conditions that control the structure and productivity of these forests. This knowledge provides elements to guide the specific strategies for managing mangroves at a regional and local level. Furthermore, a review and analysis of the mangrove productivity are presented nationwide to synthesize the knowledge about litterfall productivity generated by the different structures of the forest in different coastal regions according to environmental conditions.

OBJECTIVES

The present review (scientific articles, theses, reports, etc.) analyzes the productivity of mangroves in Mexico. The objective was to synthesize the knowledge of leaf litter production generated by different structural types of forests, described and explained according to environmental conditions.

METHODS

The review includes the analysis of diverse publications such as science articles, government reports (i.e., from the National Commission for the Knowledge and Use of Biodiversity, Conabio, by its Spanish acronym), thesis, conference proceedings, as well as non-published data. The databases used were Google Scholar, SpringerLink, and Scopus, with the search for the following keywords in English and Spanish: mangrove litter production, primary

productivity, and mangrove leaf litter. In addition, researchers specializing in mangroves in Mexico, listed in the directory of CONABIO, were consulted directly by e-mail. All the consulted publications use the baskets under the canopy method to collect all the fallen matter; the results are expressed on dry weight grams by square meters per year. Based on the consulted sources, a database was organized with the litterfall production values, and the species and mangrove type variables were considered, as well as the region, state, and study site.

RESULTS

To locate the litterfall data from mangroves in the coasts of Mexico spatially, we used the regions proposed by the Conabio (Velázquez-Salazar et al., 2021): North Pacific (Baja California, Southern Baja California, Sonora, Sinaloa, and Nayarit), Central Pacific (Jalisco, Colima, and Michoacan), South Pacific (Guerrero, Oaxaca, and Chiapas), Gulf of Mexico (Tamaulipas, Veracruz, and Tabasco), and the Yucatan Peninsula (Campeche, Yucatán, and Quintana Roo) (Fig. 1).

We consulted 68 publications: 19 belonging to the North Pacific Region, 15 to the Yucatan Peninsula, 10 to the Gulf of Mexico, three to the Central Pacific, and 21 to the South Pacific (Table 1). The average figure by region was: North Pacific (615.2 g/m²/year), Central Pacific (611 g/m²/year), South Pacific (1289.1 g/m²/year), Gulf of Mexico (823.6 g/m²/year), Yucatan Peninsula (1240.5 g/m²/year). The highest litterfall (1930 g/m²/year) was registered at Atasta, Campeche on a border forest made up of Ag-Lr-Rm (1930 g/m²/year) (Agraz-Hernández et al., 2012), a humid tropical region; on the contrary, the lowest figure (175 g/m²/year) at Las Guasimas, Sonora, a subtropical semi-arid region (Arreola-Lizárraga et al., 2004).

This contribution of litter by regions indicated carbon production of 8.23 Mg/ha/year or 3.7 Mg/ha/year for the North Pacific (Kauffman & Donato, 2012); the Central Pacific would produce 6.11 Mg/ha/year or 3.7 Mg/ha/year; while most of the production belongs to the South Pacific with 12.9 Mg/ha/year or 5.8 Mg/ha/year; on the Gulf of Mexico it was 9.1 Mg/ha/year or 4.1 Mg/ha/year);



finally, at the Yucatan Peninsula was 8.46 Mg/ha/year or 3.8 Mg/ha/year. This litterfall production becomes very significant if we consider the extent of the mangroves at a national level (905 086 ha) (Velázquez-Salazar et al., 2021) and in each of the country's coastal regions. By the above, the contribution of mangroves to carbon storage by region was for the North Pacific, with 181 036 ha of mangroves multiplied by the amount of carbon per hectare, 501 469.72 Mg/year; the Central Pacific, with 7275 ha, 23 800.16 Mg/year; the South Pacific, with 77 021 ha, 443 640.98 Mg/year; the Gulf of Mexico, with 95 581 ha of mangroves, around 387 103.04 Mg/year; and finally,

the Yucatan Peninsula region, with 544 169 ha, 3 036 463.02 Mg/year. A big part of this production would be stored on the mangroves' soil, while the other part is exported towards the adjacent marine zone, where it will contribute to the food chains of the continental platform (Tovilla-Hernández, 1998; Orihuela-Belmonte et al., 2004). The total of the captured carbon in other reservoirs such as the tree structure, root pneumatophores, forest regeneration, dead wood, and carbon stored in the ground (Adame, 2013, 2015; Velázquez-Pérez, 2018; Dharmawan et al., 2019; Gutiérrez-Hernández, 2019; Salas-Roblero, 2021).

TABLE 1. Research regarding litterfall production in Mexico by region, state, and site (Part 1/4).

State	Site	Type of mangrove	Productivity (g/m ² /year)	Species	Author	Year
North Pacific						
Baja California Sur	Bahía Magdalena	Fringe	1 094.14	Ag, Lr, Rm	Chávez-Rosales	2006
Baja California Sur	El Conchalito	Basin	805	Lr	Félix-Pico et al.	2006
Baja California Sur	Balandra	Fringe	697.15	Ag, Lr, Rm	Ochoa-Gómez	2014
Baja California Sur	El Mogote	Fringe	740.2	Ag, Lr, Rm	Jiménez-Quiroz	1991
Sonora	Las Guásimas	Fringe-Dwarf	175	Ag	Arreola-Lizárraga et al.	2004
Sonora	Yaqui	Fringe	712	Ag	Sánchez-Andrés et al.	2010
Sonora	Tóbari	Fringe	556	Ag	Robles-Zazueta	2016
Sonora	Agiabampo	-	740	Rm	López-Medellín and Ezcurra	2012
	El Soldado		320			
Sonora	Tóbari	Fringe-Dwarf	350	Ag, Lr, Rm	Torres et al.	2021
	Moroncarit		497			
Sinaloa	El Verde	Fringe	1 100	Lr	Flores-Verdugo et al.	1987
Sinaloa	Teacapán-Agua Brava	River	1 015	Ag, Lr, Rm	Flores-Verdugo et al.	1990
Sinaloa	Estero de Urías	Fringe	1 010	Rm	Flores-Verdugo et al.	1992
Sinaloa	Estero de Urías	Fringe	651.7	Ag	Agraz-Hernández	1999
Nayarit	Agua Brava	Fringe	1 417	Lr	Ramírez	1987
Nayarit	Punta Raquel Agua Brava	Basin	1 015	Rm, Lr	Flores-Verdugo et al.	1987

Ag: *Avicennia germinans*; Lr: *Laguncularia racemosa*; Rm: *Rhizophora mangle*; Ce: *Conocarpus erectus*. *Non-published data

TABLE 1. Research regarding litterfall production in Mexico by region, state, and site (Part 2/4).

State	Site	Type of mangrove	Productivity (g/m ² /year)	Species	Author	Year
Central Pacific						
Jalisco	Barra de Navidad	-	290	Ag, Lr, Rm, Ce	Mendoza-Morales et al.	2015
Jalisco	Estero El Salado	-	256	Ag, Lr, Rm	Estrada-Durán et al.	2001
Jalisco	Barra de Navidad	River-Fringe	1 287	Ag, Lr, Rm	Flores-Verdugo et al.	1992
South Pacific						
Guerrero						
16°30'52.55"N	Barra de Tecoaapa	Fringe	876	Ce, Ag	González-Angelito	1993
98°43'59.53"O						
Guerrero						
16°30'52.55"N	Barra de Tecoaapa	River	1 771.2	Rm, Lr	Tovilla-Hernández	1998
98°43'59.53"O						
Guerrero						
16°30'0.72"N	Barra de Tecoaapa	Basin	1 360.8	Ag, Lr	Tovilla-Hernández	1998
98°43'18.96"O						
Guerrero						
16°29'50.81"N	Barra de Tecoaapa	Fringe	805.2	Ag, Ce	Tovilla-Hernández	1998
98°43'27.59"O						
Guerrero						
98°43'31.64"O	Barra de Tecoaapa	Basin	949	Ce	Tovilla-Hernández and De-La-Lanza-Espino	1999
98°43'21.37"O						
Chiapas						
15°15'28.52"N	Laguna Chantuto	Fringe-River	897.9	Rm, Ag, Lr, Ce	Escobar-Colmenares	2005
92°54'26.42"O						
Oaxaca						
15°58'26.24"N	Laguna La Pastoría	Fringe-Basin	946	Ag, Lr, Rm, Ce	Tovilla-Hernández et al.	2012
97°32'26.64"O						
Chiapas						
14°38'58.03"N	Sistema Laguna de Pampa Murillo	Fringe-Basin	1 423.5	Ag, Lr, Rm, Ce	Orihuela-Belmonte et al.	2004
92°20'53.15"O						
Chiapas						
15°11'1.88"N	Barra San Juan Cerritos-Panzacola	River	1 649.1	Rm, Ag, Lr	Tovilla-Hernández and Romero-Berny	2015
92°49'13.92"O						

Ag: *Avicennia germinans*; Lr: *Laguncularia racemosa*; Rm: *Rhizophora mangle*; Ce: *Conocarpus erectus*. *Non-published data



TABLE 1. Research regarding litterfall production in Mexico by region, state, and site (Part 3/4).

State	Site	Type of man-grove	Productivity (g/m ² /year)	Species	Author	Year
Guerrero						
17°54'41.76"N 101°51'55.23"O	Río La Unión	Basin-Fringe	273.4	Lr, Ag, Rm, Ce	Carbajal-Evaristo and López-Santos	2018
Chiapas						
15°11'20.47"N 92°49'59.99"O	La Palma, La Encrucijada Reserve	River	1 100.6	Rm, Lr, Ag	Salas-Roblero	2021
Chiapas						
15°15'31.63"N 92°56'51.40"O	El Salitral, La Encrucijada Reserve	River	1 281.6	Rm, Lr, Ag	Montoya-Robalino	2021
Chiapas						
14°37'24.06"N 92°19'10.82"O 14°37'21.04"N 92°18'55.24"O	Barra de Cahocacán: La Cigüeña Brisas del Mar	Fringe	734.2	Ce	Tovilla-Hernández and Torres*	2022
Oaxaca						
15°58'23.45"N 97°32'14.78"O	Laguna Pastoria-Chacahua	River	1 017.8	Rm, Lr	Tovilla-Hernández and Romero-Bermy*	2022
Oaxaca						
15°58'43.81"N 97°42'57.76"O	Laguna Chacahua-Pastoria	Fringe	1 054.3	Ag, Lr	Tovilla-Hernández and Romero-Bermy*	2022
Oaxaca						
15°59'40.14"N 97°39'11.65"O	Laguna Chacahua-Pastoria	Fringe	885.1	Lr, Rm	Tovilla-Hernández and Romero-Bermy*	2022
Oaxaca						
16° 0'51.58"N 97°35'43.93"O	Laguna Pastoria-Chacahua	Fringe	730.4	Ce, Ag	Tovilla-Hernández and Romero-Bermy*	2022
Chiapas						
15°11'20.47"N 92°49'59.99"O	La Palma, La Encrucijada Reserve	River	1 098.9	Rm, Lr, Ag	Tovilla-Hernández and Salas-Roblero*	2022
Gulf of Mexico						
Veracruz						
	La Mancha	River	1 224.9	Ag, Lr, Rm	Agraz-Hernández et al.	2011
Veracruz						
	Sotecomapan	Border-Basin	1 116	Rm	Aké-Castillo et al.	2006

Ag: *Avicennia germinans*; Lr: *Laguncularia racemosa*; Rm: *Rhizophora mangle*; Ce: *Conocarpus erectus*. *Non-published data

TABLE 1. Research regarding litterfall production in Mexico by region, state, and site (Part 4/4).

<i>State</i>	<i>Site</i>	<i>Type of mangrove</i>	<i>Productivity (g/m²/year)</i>	<i>Species</i>	<i>Author</i>	<i>Year</i>
Veracruz	La Mancha	Basin	1 025	Mixed	Rico	1979
Veracruz	Tampamachoco	-	338	Ag	López-Portillo	2012
Veracruz	La Mancha	River	1 263	Ag, Lr, Rm	Rico-Gray and Lot-Helgueras	1983
Veracruz	La Mancha	Basin	1 069.45	Ag, Lr, Rm	Utrera-López and Moreno-Casasola	2008
Tabasco	Laguna Mecoacán	Muddy Plateau	614	Ag	López-Portillo and Ezcurra	1985
Tabasco	Laguna Mecoacán	Fringe-Basin	515	Ag, Lr, Rm	Torres et al.	2017
Tabasco	Pantanos de Centla	River-Basin	1 045	Ag, Lr, Rm	Torres et al.	2018
Yucatan Peninsula						
Campeche	Laguna de Términos	River	1 160	Rm	Agraz-Hernández et al.	2015
Campeche	Pom-Atasta	Fringe-River	1 642	Ag, Lr, Rm	Barreiro-Güemes	1999
Campeche	Los Petenes	Fringe-Basin	1 658.8	Ag, Lr, Rm	Conde	2014
Campeche	Laguna de Términos	Fringe	330	Ag, Rm	Coronado-Molina et al.	2012
Campeche	Laguna de Términos	Fringe	793	Ag, Rm	Day et al.	1996
Campeche	Laguna de Términos	River	1 452.5	Ag	Day et al.	1987
Campeche	Atasta	Fringe	1 930	Ag, Lr, Rm	Agraz-Hernández et al.	2012
Campeche	Río Champotón	Fringe-Internal	1 620	Ag, Lr, Rm	Agraz-Hernández et al.	2012
Campeche	Río Verde	Fringe-Internal	1 720	Ag, Lr, Rm	Agraz-Hernández et al.	2012
Campeche	Arena	Fringe	981.8	Ag, Lr, Rm	Espinosa-Garduño	2012
Yucatan	Ría Celestún	Basin	1 492.8	Ag, Lr, Rm	Zaldívar-Jiménez et al.	2004
Yucatan	Yucatan Peninsula - 2009	Fringe	868.7	Ag, Lr, Rm	Adame et al.	2012
Yucatan	Yucatan Peninsula - 2010	Fringe	959.9	Ag, Lr, Rm	Adame et al.	
Yucatan	Celestún	Fringe	974.5	Ag, Lr, Rm	Herrera-Silveira	2012
Quintana Roo	Bacalar Chico	Dwarf	261	Ag, Lr, Rm, Ce	De-Jesús-Navarrete and Oliva-Rivera	2002
Quintana Roo	Laguna Bojórquez	Fringe	995.4	Lr, Rm, Ce	Agraz-Hernández	2006

Ag: *Avicennia germinans*; Lr: *Laguncularia racemosa*; Rm: *Rhizophora mangle*; Ce: *Conocarpus erectus*. *Non-published data



STRUCTURE AND PRODUCTION OF LITTERFALL

In 1974, Lugo and Snedaker developed a mangrove classification scheme based on characteristics of tide and hydroperiod; this classification system is used to identify some common response patterns of mangroves to environmental variables. They recognized four general types of forests: river, fringe, overwashed, and basin; besides, dwarf mangroves and scrub are known as particular subtypes that respond to edaphic conditions (Kathiresan & Bingam, 2001). Mangroves increase their productivity and structural complexity as the size progresses, from dwarf to river type (Pool et al., 1977; Brown & Lugo, 1982), and the primary production of the mangrove is related to the physiographic structure of the forest (Lugo & Snedaker, 1974), such as the hydric regime to which it is subject, the influence of tide, winds and climate, and edaphic characteristics in general (Uncles et al., 1992; Rivera-Monroy et al., 1995). Thereon, Mitsch and Gosselink (2000) mentioned that a minimal change in the hydrological pattern may produce changes in the biota in terms of composition and diversity of species, including the litterfall production.

Different species of mangrove and physiognomic types produce different vegetal biomass (Agraz-Hernández et al., 2012; Tovilla-Hernández et al., 2007; Tovilla-Hernández et al., 2018; Efriyeldi et al., 2021). Trees' growing conditions have been considered mainly to be one of the factors affecting litterfall production. For instance, Woodroffe et al. (1988) categorized the production rate and the relationship between the tree's height; furthermore, the density affects the amount of litter a mangrove produces. Flores-Verdugo et al. (1987) mentioned that there is no correlation between litterfall production and the mangrove forest structure; there are other factors involved, such as precipitation, freshwater refill, and the nutrient load (Estrada-Durán et al., 2001), which is ultimately an answer to complex environmental factors that operate at a local scale like type of substrate (texture), humidity, hydroperiod, organic matter content, and

microtopography (Bunt, 1995; Day et al., 1996; Torres et al., 2017).

In addition, productivity and biomass of mangroves diminish as the latitude increases (Saenger & Snedaker, 1993; Morrissey et al., 2007), due mainly to freezing that produces embolism in the xylem during the freezing-thawing cycle, but also by other factors such as cold currents, air temperature, and insolation (Stuart, 1985). The significant variation in the litterfall and the carbon exportation rates can be attributed to regional differences in coastal geomorphology and oceanography (Jennerjahn & Ittekkot, 2002), i.e., variations in the Gulf of California, Pacific Ocean, Gulf of Mexico, and the Caribbean Sea.

Subtropical arid semi-arid region (Northeast of México)

Mangrove forests present as isolated fringe stands, scrub type, and with scarce cover (Rollet, 1974); because of the lack of permanent rivers and the hypersalinity of many estuaries, mangroves grow in suboptimal conditions, made evident by their limited heights and their structures and extensions less developed (Flores-Verdugo et al., 1992; Whitmore et al., 2005). Nevertheless, despite the conditions of the arid, semi-arid coasts of the northeast of Mexico, some mangroves in this region keep high rates of leave fall, similar to those of the humid tropical zones, with significant ecological and economic implications (Félix-Pico et al., 2006; Aburto-Oropeza et al., 2007; López-Medellín & Ezcurra, 2012; Adame et al., 2015). Alongi et al. (2005) suggest that mangroves show fast rates of leaf rotation and high leaf fall in environments with scarce nutrients. This litterfall is a valuable source of nutrients that sustain marine and terrestrial food webs, and its importance can be especially high in lagoons and estuaries on arid coastal zones (Holguín et al., 2001).

Humid tropical region (Southeast and Gulf of México)

The leave fall, a complex phenomenon, exhibits variability among sites. This variability has been found to be

correlated with the latitude and the height of the tree. Interestingly, the highest litterfall is observed in tropical latitudes, where forests showcase their most distinct structural shapes (Saenger & Snedaker, 1993; Aké-Castillo et al., 2006). A remarkable structural development is recorded in zones closer to the tropics with high precipitation (Lot-Helgueras et al., 1975), particularly in mangroves situated in estuarine zones with high river discharges. This is attributed to the abundant nutrient-rich sediments of exogenous origin (Lugo & Cintrón, 1975; Corella et al., 2001), highlighting the intricate interplay of environmental factors in shaping forest ecosystems.

Karstic Region (Yucatan Peninsula)

The karstic characteristics do not allow the presence of rivers, caused by low rainfall and dry climate; the presence of springs becomes more important as a source of nutrients and water flow that keeps salinity diluted (Her-

era-Silveira et al., 1998). The surrounding land vegetation conditions (structure and function) belong to arid zone mangroves with poor development of structure and litterfall production as a consequence of the high salinity and low concentration of inorganic nutrients, mainly phosphorus in the soil (Twilley, 1998; Zaldívar-Jiménez et al., 2004).

PHENOLOGY

A pattern of mangrove flower production has been identified at the end of the dry season and the propagule production during the maximum rain period, with the highest levels of flooding (Rico-Gray & Lot-Helgueras, 1983; Tovilla-Hernández, 1998; Escobar-Colmenares, 2005; Torres et al., 2017). These conditions favor the propagules dispersion through the surface hydrodynamics, including the buoyancy patterns and the soil rooting (Fig. 2; Rabinowitz, 1978; Jiménez, 1990; Tovilla-Hernández, 1998).

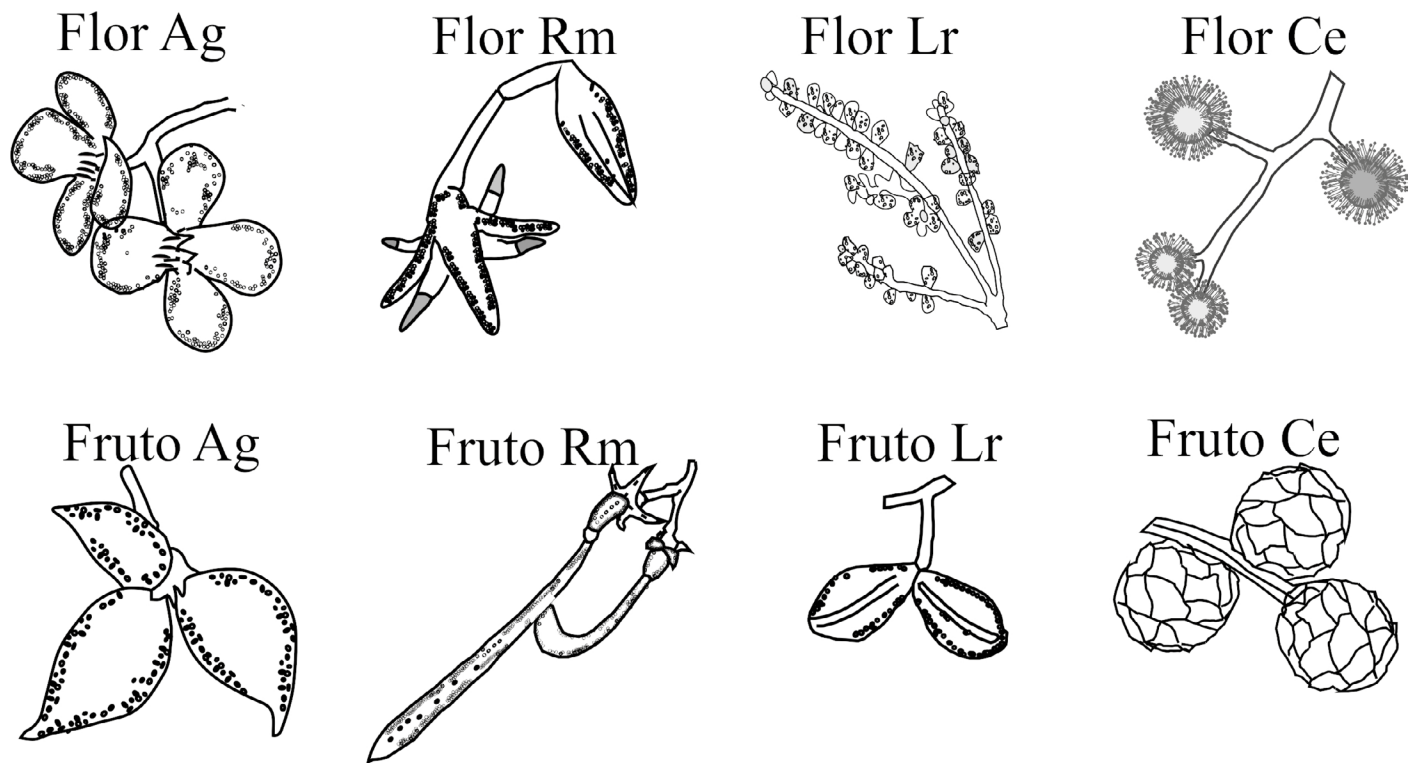


FIGURE 2. Fruits and flowers of the different mangrove species. Ag: *Avicennia germinans*; Rm: *Rhizophora mangle*; Lr: *Laguncularia racemosa*; Ce: *Conocarpus erectus*.



Avicennia germinans

Regarding reproduction, *A. germinans* generally has flowers from April to August and produces fruits between August and October, as reported by Tovilla-Hernández (1998) and Agraz-Hernández et al. (2012).

Rhizophora mangle

R. mangle produces flowers and propagules the whole year. Nevertheless, the highest contributions of the flowers occur from May to October, while the propagules appear from June to November (Agraz-Hernández et al., 2012; Tovilla-Hernández, 1998).

Laguncularia racemosa

Flowering starts at the end of the dry season, and the propagule production is at its highest peak in the rainy season as a survival strategy to guarantee the successful settling of the seedling (Rico-Gray & Lot-Helgueras, 1983; Tovilla-Hernández, 1998).

Conocarpus erectus

It produces flowers all year long. In addition, they occur when plants reach 3.5 m in height and are more than two years old. This is a continuous process throughout the tree's life, present even in old individuals (Tovilla-Hernández, 1998; Tovilla-Hernández & De-la-Lanza, 1999; Tovilla-Hernández, 2021).

SALINITY

Salinity conditions are regulated by the climate, hydrology, topography, and the tide flooding, and ultimately, they affect the productivity and development of the mangrove forests (Kathiresan & Bingham, 2001). Several studies have reported an inverse correlation between salinity concentration and litterfall productivity (Espinosa-Garduño, 2012; Conde, 2014; Torres et al., 2017). Salinity affects the growth of plants in several ways: 1) limiting the availability of water against the osmotic gradient, 2) reducing nutrient availability, 3) causing the Na⁺ and Cl⁻ buildup towards a toxic concentration causing hydric stress

conditions, with increased closure of stomata and reduced photosynthesis (Benerjee et al., 2013).

Although most mangroves are halophytic and can tolerate salinity, some species need salt to grow and complete their life cycle (Ball, 2002). Nevertheless, high salinity negatively affects physiological processes and growth rates (Ball, 1988); it limits the height and productivity of trees (Cintrón et al., 1978). In the Nichupté-Bojorquez lagoon system, Quintana Roo, Agraz-Hernández (2006) identified an increase in litterfall production attributed to the salinity decrease, organic matter removal, oxygenation and nutrients' entry through the groundwater layer.

PRECIPITATION

There is a general trend that a litterfall peak occurs during the rainy season in all the world's mangroves (Pool et al., 1975; Williams et al., 1981; Bunt, 1982). On the moment when fresh water is abundant and flows through the area, the maximum litterfall might help explain the high production of photosynthetic material (Day et al., 1987); as this hydrodynamics reduces salinity in the soil, washes the exceeding salts and leaves and decreases the temperature of the air (Orihuela-Belmonte et al., 2004; Félix-Pico, 2006).

For the southeast and the Mexican Caribbean, Yañez-Arancibia and Day (1982) proposed three climatic seasons: 1) rainy season from June up to the end of September, 2) "nortes" (literally norths) or storms from October to March, and 3) dry season from February to May. Nevertheless, seasons could be classified as rainy starting in June for the northwest of Mexico, with arid-semiarid conditions. In typical years, the highest contributions to litterfall occur in the rainy season from July to October (Agraz-Hernández, 1999), declining in winter (November to February; "nortes") and further diminishing during the dry season from March to June (Torres et al., 2017). It is worth mentioning that in Mexico, most studies on mangrove litterfall have found a positive correlation with rainfall (Espinosa-Garduño, 2012; Mendoza-Morales et al., 2015). However, it is crucial to consider that the maximum monthly precipitations exhibit different pat-

terns based on latitude. They may occur at the end of the rainy months and/or the onset of the “nortes” (Guerra-Santos & Kahl, 2017).

On the Mexican Pacific coasts, the phenomenon “El Niño” reverses the standard weather pattern and produces a warm water mass on the surface of the Pacific Ocean. This water mass travels from near Central America northbound to the California coast, significantly reducing the amount of rainfall (Agraz-Hernández, 1999). The decrease limits the availability of fresh water in the mangroves, with changes in their reproductive cycles (phenological phases), primary productivity, and litterfall degradation (Jiménez, 1994; Torres et al., 2018).

Extreme weather events have a significant influence on the production of mangrove litterfall. In a few hours, hurricanes may cause rapid defoliation of up to 60% of the mangroves, which creates an immediate but temporary rise in litterfall (Doyle & Robblee, 1995); this occurs when strong winds cause wood breakage and rapid temporary defoliation (Doyle & Robblee, 1995). However, hurricanes cause extraordinary fertilization in the estuarine lagoon system waters, undoubtedly resulting in a rise in secondary production in these systems (Adame, 2015).

NUTRIENTS

It has been shown that a higher nutrient contribution is related to a higher productivity of mangroves (Boto & Wellington, 1984; Lugo & Brinson, 1988;). Therefore, best-drained soils, lower salinity, and nutrient contribution are associated with higher productivity (Day et al., 1987). One part of the litterfall production enters the soil detritus system, the primary energy source within the mangrove ecosystem (Odum & Heald, 1972; Morrisey et al., 2007). Bosire et al. (2005) mentioned that high productivity is often attributed to high litterfall decomposition rates through efficient nutrient recycling, in which organic matter is supplied by native and nonnative, natural, and anthropogenic sources.

The nutrient cycle starts when leaves fall from mangroves and are subjected to a combination of leaching and microbial degradation (Chale, 1993). Mangrove litter,

decomposed by microorganisms, provides a basic food resource in mangrove forests and associated ecosystems (Kawaida et al., 2018). Leaching alone can remove a significant part of organic substances and produce high levels of dissolved organic matter (Benner et al., 1990). Nevertheless, the nutrient cycle depends on both leaf decomposition and production. The decomposition rate is determined by the quality of litterfall and the physical environment (Swift et al., 1979; Tovilla-Hernández, 1998; Torres et al., 2018).

Additionally, it has been found that the low availability of nutrients is a relevant factor that limits the productivity of mangroves (Onuf et al., 1977; Boto & Wellington, 1984; Feller et al., 2003). The high plasticity of mangroves allows them to withstand low nutrition conditions and to exploit high levels of nutrients when available (Fromard et al., 2004). Adame et al. (2012) registered that the drop of leaves at the Yucatan Peninsula appears to be driven mainly by the total phosphorus content in the soil, which variability might be explained by the proportion of fresh underground water mixed with flood water and phosphorus concentrations of seawater entering the system. Agraz-Hernández (2006) attributes high productivity in Cancun, Quintana Roo, to the significant amount of total dissolved Nitrogen (NO_2 , NO_3 , and NO_4) and phosphates (PO_4) of anthropogenic origin (Tovilla-Hernández, 1998).

FISHERIES

Relatively fresh litter, such as fallen leaves, twigs, flowers, fruits, or seeds, continuously produced by the mangrove forests, often float or drift in coastal surface water layers, thereby likely playing important roles for aquatic animals (Twilley & Day, 1999; Onrizal et al., 2020). The role of mangrove litterfall is fundamental in sustaining benthic communities (Odum & Heald, 1972; Félix-Pico et al., 2006); it is also reduced when systems are more open regarding the exchange of material with adjacent systems (Bouillon et al., 2002).

Crabs have a fundamental ecological role as they are considered the ecologic engineers of the ecosystem; it is known that of all the litterfall produced in a year, bet-



ween 30% to 90% will be consumed by these organisms, and even after digestion, their feces become key to sustain the trophic networks as they reduce the litter into small particles (Kristensen et al., 2008), which could later be used by soil microorganisms (Lovelock, 2008). Mangrove litterfall becomes the main energy source for consumers on the trophic network via detrital, provided that algae and plankton biomass is low (Wafar et al., 1997). This export depends on debris removal mechanisms, forest cover, flood level, tide height, litterfall production, and degradation rates (Orihuela-Belmonte et al., 2004). Tovilla-Hernández et al. (1994, 1998) reported that 40% of organic matter produced by Mexican coastal ecosystems is transported to the sea and nearby areas through its leaves litter.

Likewise, efforts have been made to estimate the monetary values of mangrove areas in relation to fisheries in different parts of the world, thereby achieving fisheries management from a socio-economic perspective (Table 2).

A large number of marine species depend on mangroves as a rearing and feeding area for fingerlings and larvae of mollusks and crustaceans (Flores-Verdugo et al., 2007). In this sense, it is important to recognize that the high productivity of coastal lagoons frequently depends not only on the contributions of mangroves but also on the

freshwater wetlands of the lowlands surrounding them, which constitute the transition to non-floodable land (Flores-Verdugo et al., 2007).

REGULATIONS FOR THE PROTECTION OF MANGROVES IN MEXICO

The ecosystemic approach to the management of coastal resources integrates ecological processes of environmental systems together with human socio-economic systems characteristics (Fig. 3). Many ecosystemic models of coastal systems, like mangroves, currently lack a quantitative analysis, therefore, in many cases, specific management plans for the site should be applied to a variety of systems and problems (Twilley & Day, 1999).

Fast and unplanned coastal population growth is causing significant degradation of natural environments, which endangers providing services to the mangrove ecosystem (Berlanga-Robles et al., 2011). In this context, Mexico has been working on implementing policies that promote the preservation and restoration of mangroves and has also signed international conventions and protocols, such as Kyoto (United Nations Framework Convention on Climate Change [UNFCCC], 2014) and the Convention on Wetlands Secretariat (1971), that include direct or indirect benefits for mangrove ecosystems.

TABLE 2. Relationship between mangrove cover and fisheries.

<i>Author and year</i>	<i>Information</i>
Turner (1991)	The author estimated an annual loss of around 800 kg of fish and shrimp per each destroyed mangrove hectare.
Mumby et al. (2004)	The biomass of the parrot fish populations, a species characteristic of coral reefs of fishing importance, doubles with the presence of mangroves.
Moreno-Casasola et al. (2002)	They observe a strong positive and significant correlation between the fishing catch and catchment area in Veracruz state.
Aburto-Oropeza et al. (2007)	The average annual economic value of fisheries on the California Gulf was USD 37 500 (MXN 436 789) per mangrove hectare, which is within the upper limit of previously calculated values worldwide for all mangrove services.

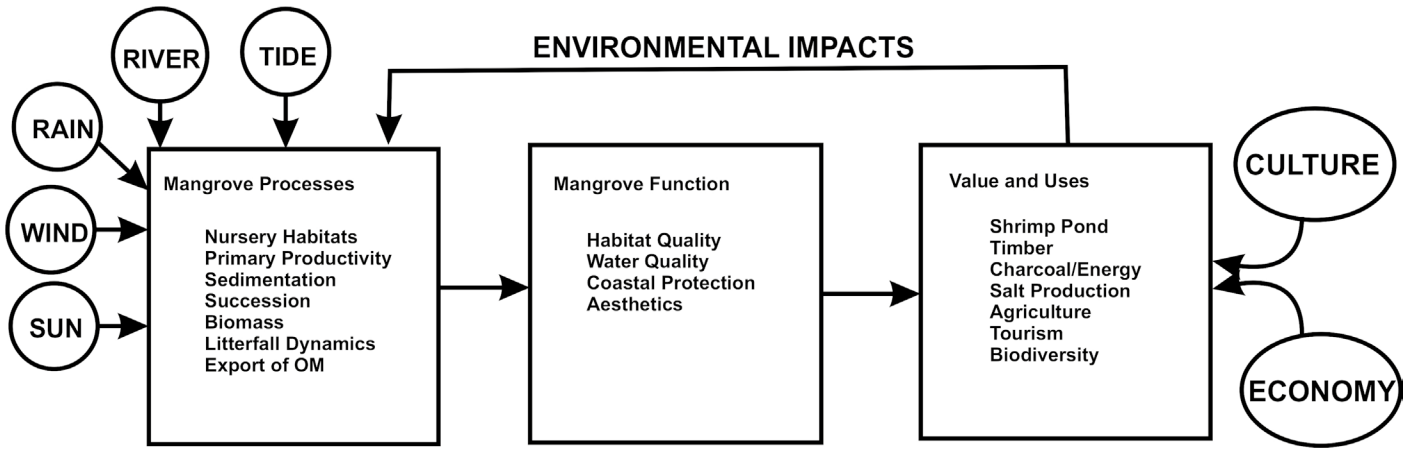


FIGURE 3. Diagram of links between the energetic signature and the ecological function, as well as the attributes and uses of mangrove ecosystems.

Source: Twilley and Day, 1999. OM: Organic matter.

In this regard, laws, territorial systems, official norms, and regulations to protect mangroves have been developed. The Federal Environmental Liability Act (Congreso General de los Estados Unidos Mexicanos, 2013), General Wildlife Act (Congreso General de los Estados Unidos Mexicanos, 2013), the Regulations of the General Law on Balance and Protection of the Environment (Congreso General de los Estados Unidos Mexicanos, 2014), and the General Law on Climatic Change (Congreso General de los Estados Unidos Mexicanos, 2015) to name some of the more relevant. The latter provides in article 26 that “*in the formulation of the national climate change policy, principles of preservation of ecosystems and their biodiversity will be observed, giving priority to mangroves [...]*”.

One of the strategies for preserving different ecosystems considered for Mexico is the creation of Natural Protected Areas. Still, it was not until the last decade of the 20th century that the Mexican State capacity truly began to address and manage them, so they provided staff, social participation schemes, and instruments for planning that indicated the paths to follow towards their protection (Bezaury-Creel & Gutiérrez-Carbonell, 2009). A special case is the Areas Voluntarily Intended for Conservation (*Áreas Destinadas Voluntariamente a la Conservación*, ADVC, by its acronym in Spanish) that could be private or

social, and since 2008 are of federal competence (Congreso de los Estados Unidos Mexicanos, 1988).

On the other hand, Mexico signed the Ramsar Convention in 1986, where all the commitments accepted by the contracting parties are to designate wetlands of international relevance, promote the rational use of the wetlands on their territory, establish reserves on wetlands, promote the training on studies matters, manage and custody of wetlands, and promote international cooperation (Convention on Wetlands Secretariat, 1971; Velázquez-Salazar et al., 2021).

In Mexico, the main actions in favor of mangroves have been the inclusion of the four more abundant mangrove species (*R. mangle*, *L. racemosa*, *A. germinans*, and *C. erectus*) in the Mexican Official Norm (Secretaría de Medio Ambiente y Recursos Naturales [Semarnat, by its acronym in Spanish], 2002) that set them on the special protection category. These species are currently included in the NOM-059-SEMARNAT (Semarnat, 2002), cataloged under the threatened category. Besides, article 60 TER of the General Wildlife Act of 2007 (Semarnat, 2007) forbids any change that may affect the integrity of mangrove ecosystems. The Semarnat (2003) establishes specifications for the preservation, conservation, sustainable use, and restoration of the coastal wetlands in man-



grove areas, which includes the rest of the mangrove species not specified on the NOM-059-SEMARNAT (Semarnat, 2002) (i. e., *Conocarpus erectus* var. *sericeus*, *Rhizophora harrisonii*, and *Avicennia bicolor*).

BLUE CARBON

Mangrove forests are among the most productive tropical coastal ecosystems compared to continental forests. Globally, mangroves have produced $11.1 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ as net primary productivity (NPP) and stored 956 Mg C ha^{-1} of carbon stock (Velázquez-Pérez, 2018; Dharmawan et al., 2019; Gutiérrez-Hernández, 2019). Blue carbon is about preserving carbon within coastal water systems such as mangroves, marshes, and seagrass, especially in soils and sediments. The term is increasingly used to describe projects aimed at improving carbon storage by expanding the mangrove cover (Alongi, 2014). Hence, it is necessary to determine the stocks of carbon and the emission baseline to take part in mitigation strategies for climate change, such as the “Reducing emissions from deforestation and forest degradation in developing countries” (REDD+) framework (Aceituno-Caal et al., 2016; Gómez-Xutuc, 2017; Rodríguez-Hernández, 2016).

The most reliable forest estimates come from measuring the litterfall (foliage production), the increase of the stem circumference (wood production) (Alongi, 2014; Velázquez-Pérez, 2018), and the underground biomass (roots) (Adame et al., 2014; Torres et al., 2021). Net mangroves primary productivity is higher than on the marshes (8.34 Mg/ha/year), seagrass (1.04 Mg/ha/year), macroalgae (3.8 Mg/ha/year), and coastal phytoplankton (1.7 Mg/ha/year) but approximately equivalent to the coral reefs (10 Mg/ha/year) (Duarte & Cebrián, 1996; Duarte et al., 2010). The soils of many mangroves and marshes are rich in organic matter, containing exceptionally large amounts of carbon (Donato et al., 2011) that could be two or three times higher than those measured in most terrestrial forests (Adame et al., 2013, 2015). Mangroves stock more carbon over a specific area base than other ecosystems, especially in soils; their total ecosystem average carbon stock is 956 t/ha , as compared to 241 t/ha in tropical

forests, 408 t/ha in turf swamps, 593 t/ha in marshes, and 142.2 t/ha in seagrass (Alongi, 2014).

Mangroves in the dry tropics are smaller in height than those in the humid tropics. Independently of the trees' height, soils are the largest reservoir of carbon, with a percentage of the total set of soils varying from 44% for tropical forests to 70% for swampy peat lands, 75% for mangroves, and 90% for marshes and seagrass (Adame et al., 2013, 2015). For the Yucatan peninsula, Adame et al. (2013) found the most significant stocks of C in the tallest mangroves associated with a freshwater spring, followed by other high, medium, and dwarf mangroves, respectively. They also concluded that the mangrove forests, including those below 1 m high (dwarfs), contain exceptionally large C reserves.

CONCLUSIONS

Increasing and unifying efforts between government institutions and research centers to produce and organize existing data related to mangroves' primary productivity is important. The results presented in this work could represent a starting point for integrating a database with the main variables influencing litter production in different regions of Mexico. In a short-term scenario, it would be valuable to count with a comparative analysis of the litterfall production of mangroves on a multi-annual scale, considering a spectrum of structural types of mangrove forests in different countries and regions, including key environmental variables, as well as the conditions and trends of the forest. This kind of analysis would provide a better understanding of patterns and controls of litterfall production, aiming to improve these coastal ecosystems' health.

This type of data regarding litterfall production often works for local analysis. From a future perspective, a broader overview of this productivity distribution is required to offer interpretations of carbon storage content, which is becoming increasingly important. Thus, accurate georeferenced data will help integrate and synthesize regional analysis, providing a good sampling point distribution. Besides, the results of this kind of research could be incor-

porated into ecological models to establish future scenarios, a significant resource for applying knowledge and strengthening the management and conservation actions of these valuable Mexican ecosystems.

Unpublished studies likely exist but were not available for review. Nevertheless, the studies shown in this analysis are representative of the mangrove litterfall production in Mexico. The region with the most studies was the North Pacific. The regions with fewer studies were Central Pacific and South Pacific. Notably, studies are lacking in Baja California, Colima, Michoacan, and Tamaulipas, highlighting the need to carry out new research to update information and expand the knowledge about production in mangrove litterfall, standing biomass (basal area) and in the underground (roots). All studies estimating litterfall production in Mexico have been made based on leaf fell traps and report their results on grams of leaves per square meter or in tons per hectare. These allow us to make comparisons at a latitudinal level, between different regions of the country, and even between sites. The highest litterfall contribution value per mangrove (2575.1 g/m²/year) was recorded in a semi-dry tropical Pacific region, and the smallest (175 g/m²/year) was in a semi-arid subtropical region. The main recognized variables as causal factors of the number of leaves falling to the ground were precipitation, salinity, nutrients, environmental conditions (arid, karstic, humid), the structure, and physico-chemical properties of sediments and water (salinity, pH, oxidation-reduction potential).

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