

Mangroves are unique ecosystems found in estuarine and coastal areas between 30° N and 30°S in tropical, subtropical and a few temperate latitudes. Mangrove forests consist of about 80 species worldwide of halophilic, convergently evolved, 16 diverse families of shrubs and trees, with more than 174 faunal associates. Mangroves, uniquely positioned between terrestrial and marine ecosystems, exchange gases and materials with both land and sea. Fine sediment particles of rich organic content protected from strong wave action accumulates in mangroves. Mangroves ecosystems are highly efficient in capturing and storing carbon and nutrients, including nitrogen, phosphorus, iron, and copper.

Carbon cycle and sequestration

Mangrove forests are highly productive ecosystems, capturing a significant amount of carbon dioxide from the atmosphere. Atmospheric CO₂ is captured through photosynthesis by coastal plants, which then sequester it as organic matter in the soil for centuries. This process can reduce atmospheric CO₂ concentrations, and the stored carbon is often referred to as "blue carbon. Being major sinks of blue carbon, mangroves contribute very significantly to mitigating climate. This carbon is either stored within the mangrove forest as living biomass or organic matter in the sediment, or is exported to nearby coastal areas as organic and inorganic carbon. Net primary productivity (NPP) of mangrove forests is estimated to be around 208 Tg C yr⁻¹. Mangrove forests attain a steady state around 20-30 years, when maximum biomass is reached. This equilibrium is maintained through a continuous cycle of growth and decay. Assuming no increase in carbon density of living biomass, the carbon fixed as Net Primary Productivity (NPP) must be balanced by an equivalent loss. This carbon is retained within the mangrove forest sequestered in sediments (77%), standing biomass (15% in shoots, leaves, trunks and roots), and 8% as below ground root systems. Carbon is exported to adjacent ecosystems as litter, particulate organic carbon (POC), dissolved organic carbon (DOC), and dissolved inorganic carbon (DIC), or released into the atmosphere. The outwelling hypothesis posits that the export of locally-derived Particulate Organic Carbon (POC) and Dissolved Organic Carbon (DOC) is a critical ecosystem service provided by mangroves. This exported organic matter fuels detritus-based food webs in neighboring coastal habitats. Estimates suggest that mangrove carbon export significantly contributes to the trophic structure of these adjacent ecosystems. Mass balance assessments corroborate the outwelling theory, demonstrating that the carbon fixed by mangroves often surpasses the amount stored within the forest itself. However, the magnitude of this export varies substantially among different mangrove forests, influenced by factors such as coastal geomorphology, tidal regimes, freshwater input, and productivity. Sedimentation rates are rapid in mangrove environments, leading to significant carbon sequestration. Over time, mangrove forests build up substantial soil profiles, creating a habitat for diverse microbial and faunal communities. Over decades, following initial colonization of a mudflat, mangrove forests undergo development and vertical accretion, adapting to sea-level fluctuations, subsidence, and uplift. This process results in the accumulation of several meters of soil. In time, these deposits are further penetrated by mangrove roots, various flora (e.g., microalgae), fauna (especially burrowing crabs), and diverse microbial communities. The forest floor becomes a complex matrix of mounds, burrows, tubes, cracks, fissures, and a variety of root structures, layered with decaying organic matter, epifauna, and diverse micro- and macroalgae. Complex biogeochemical processes govern the exchange of dissolved and particulate matter between mangroves and adjacent tidal waters, influenced by factors like tidal

currents, water flow, and sediment dynamics with dissolved organic and inorganic solutes and particulates imported and exported by both tides, porewater pumping, and subsurface groundwater advection. 30% of carbon storage in coastal margins in tropics and subtropics come from mangrove deposits.

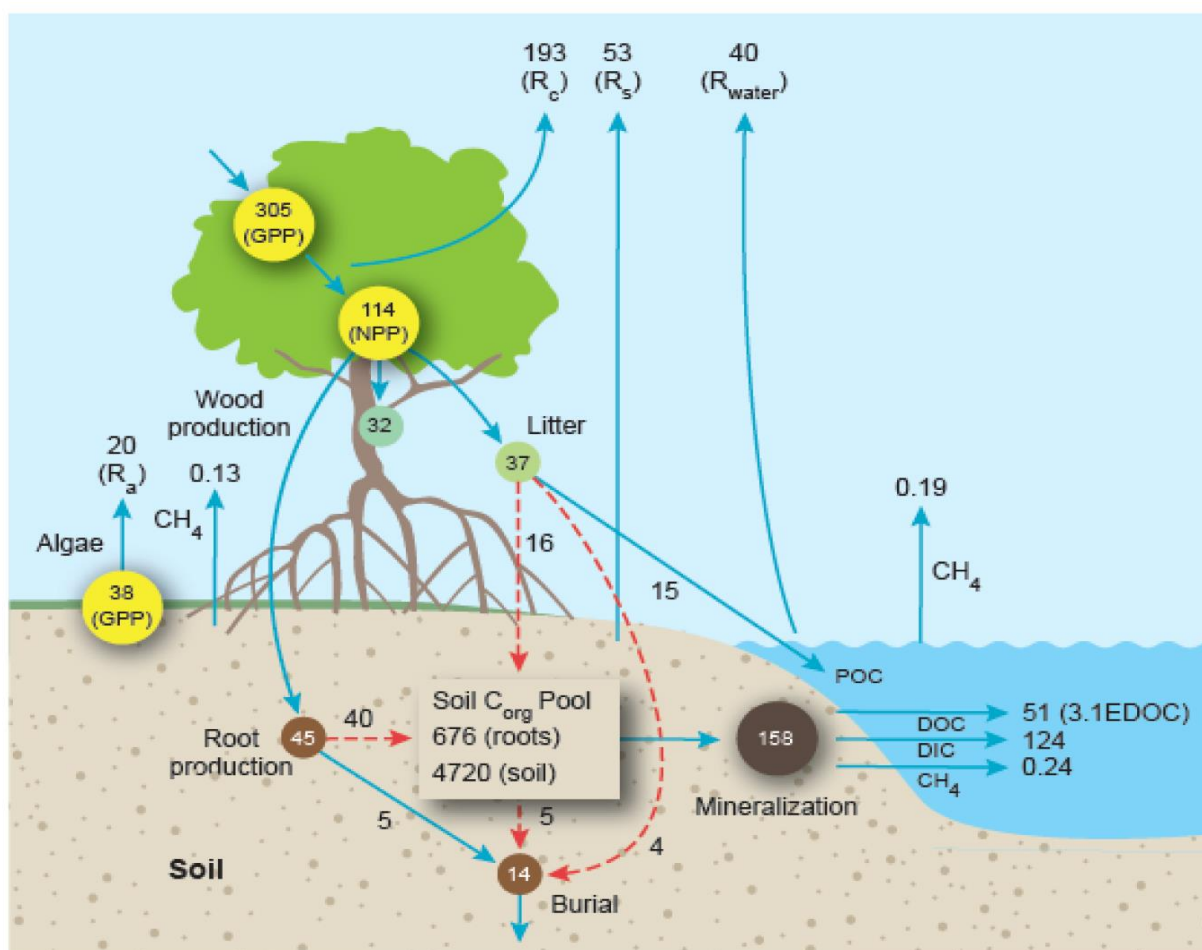


Fig. 1: Carbon cycle in mangroves (Source: Modified from Alongi, 2020)

Nitrogen cycle in mangrove forests

Mangrove forests and coastal marshes are typically nitrogen-limited ecosystems, despite their high primary productivity. Mangrove plants are highly efficient at utilizing soil nitrogen, making them important sinks for excess nitrogen from upstream sources. However, environmental factors, such as soil salinity, can negatively impact nitrogen assimilation rates. Nitrogen fixation by soil microbes can be a significant external nitrogen source for mangrove ecosystems, in addition to nitrogen inputs from upland drainage. This process is influenced by the availability of soil carbon and nitrogen. Studies have shown that sulfate-reducing bacteria are important nitrogen-fixing organisms in coastal ecosystems, contributing up to 50% of total nitrogen fixation in mangrove ecosystems. Additionally, molecular studies indicate that members of the genus *Vibrio* may play a crucial role in nitrogen fixation. In environments with sufficient sunlight, diatoms and cyanobacteria can also contribute significantly to nitrogen fixation in coastal ecosystems.

In addition to microbial nitrogen fixation, dissimilatory nitrate reduction to ammonium (DNRA) is a significant process in mangrove forest soils, aiding in nitrogen retention. The dominant pathway for nitrate reduction, whether denitrification or DNRA, is largely determined by the availability and

composition of soil carbon and nitrogen. In typical carbon-rich, nitrogen-limited mangrove ecosystems, DNRA is the primary nitrate reduction pathway, enabling efficient nitrogen recycling and mitigating nutrient limitations. However, in human-impacted, nitrogen-rich estuarine mangrove soils, denitrification may become the dominant pathway. This shift is likely due to the need to conserve nitrogen in nutrient-limited environments. Microbial denitrification in mangrove forests can be significantly impacted by increased nitrate loading from upstream sources and potential saltwater intrusion due to climate change. These conditions can lead to higher nitrous oxide (N_2O) emissions, a potent greenhouse gas. N_2O emissions from mangrove forests can vary seasonally, with higher rates observed during warmer months. Anaerobic soil conditions can transform mangrove forests into sources of greenhouse gases like methane (CH_4) and nitrous oxide (N_2O), particularly as temperatures rise. Additionally, climate change-induced environmental alterations may influence nitrogen cycles, impacting processes like nitrogen fixation, dissimilatory nitrate reduction to ammonium, and denitrification.

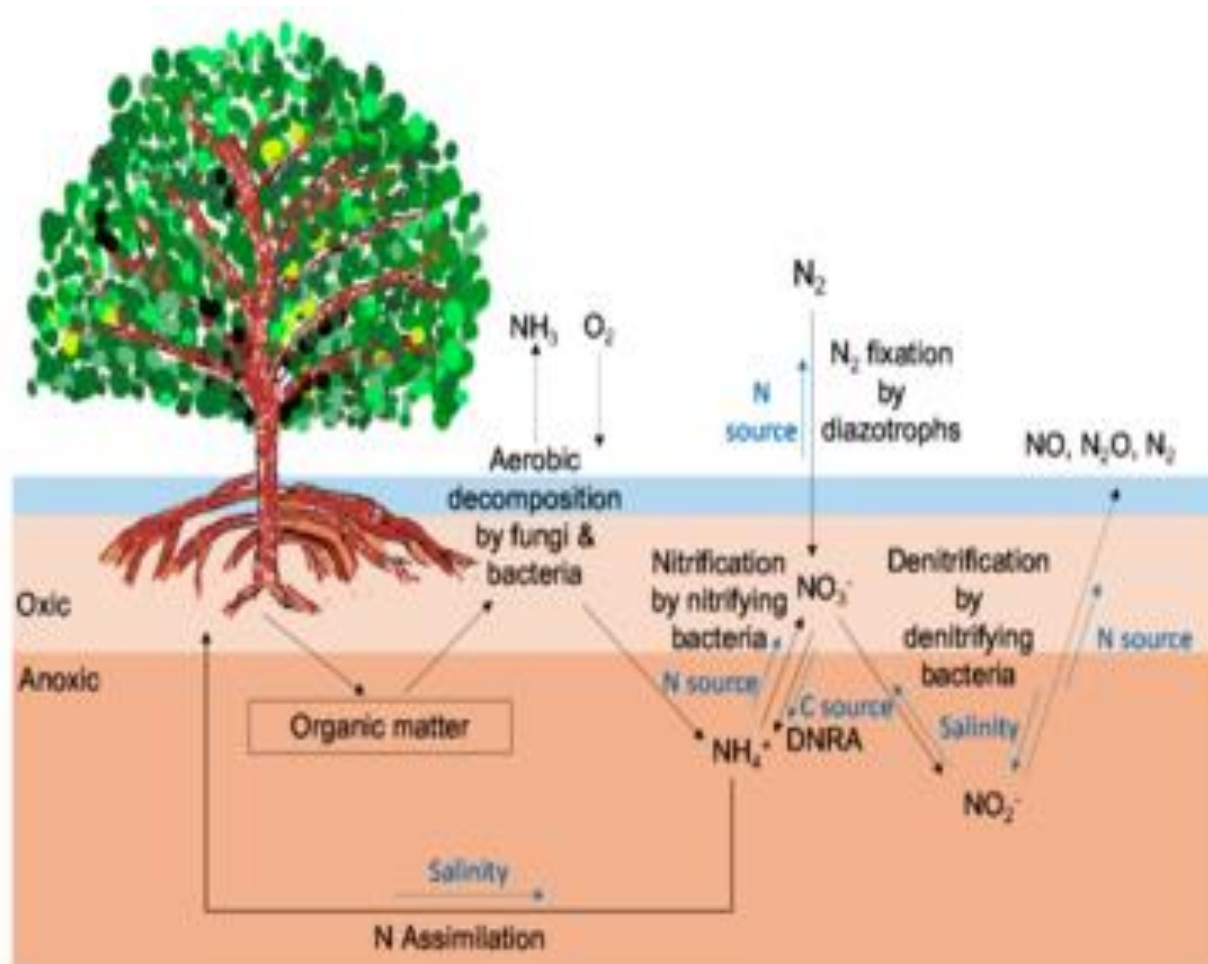


Fig. 2: Nitrogen cycle in mangroves (Source: Modified from Vepraskas and Craft, 2015)

Black arrows - nitrogen pathways, Blue arrows- environmental factors (salinity, carbon source, nitrogen source) affecting nitrogen pathways.

Heavy metal sequestration

Mangrove forests trap heavy metals in their fine, oxygen-deprived sediments. These metals, bound to colloidal particles, are removed from the water. When mangroves are removed, these sediments are disturbed, potentially releasing these metals into the surrounding water and harming marine organisms.

Biological adaptations

A number of unique ecological and physiological adaptations help mangroves to survive in low-oxygenated environs with a wide range of salinities, soil water retention and dessication, submergence. Many mangrove forests are characterized by their distinctive prop roots, which elevate the trees above the waterline. This intricate root system enables mangroves to withstand the daily tidal fluctuations, as most are inundated at least twice daily. The roots slow water flow, facilitating sediment deposition and coastal accretion.

Adaptations to low oxygen availability

The red mangrove, *Rhizophora mangle*, thrives in the most inundated areas, utilizing stilt or prop roots to elevate itself above the waterline and absorb oxygen through lenticels in its bark. The black mangrove, *Avicennia germinans*, inhabits higher ground and develops specialized aerial roots known as pneumatophores. These "breathing tubes" extend upwards from the soil, facilitating oxygen exchange. Both root types possess aerenchyma tissue, which enhances internal gas transport. The waterlogged, anaerobic soil limits oxygen availability, leading to the release of nitrogen gas, soluble iron, inorganic phosphates, sulfides, and methane by anaerobic bacteria. Pneumatophores enable mangroves to directly acquire oxygen from the atmosphere and extract nutrients like iron from the nutrient-poor soil. These roots can store and process gases internally, even during periods of submergence.

Salt reduction and filtration

Red mangroves possess highly suberized roots that act as a filtration system, excluding sodium ions and other salts from entering the plant. This mechanism, particularly evident in species like *Avicennia officinalis*, allows the plant to maintain low salt levels within its tissues. The production of suberin and the activity of specific genes are upregulated in response to increased salinity. A 2016 study on *Rhizophora stylosa* revealed a hierarchical, triple-layered pore structure in the root epidermis, which efficiently filters sodium ions. The high surface zeta potential of the outermost layer contributes to this filtration process. Halophytes, including mangroves, must balance sodium ion uptake for osmotic regulation and survival with the potential toxicity of excess sodium. Mangroves, especially species like *Bruguiera*, exhibit remarkable salt exclusion capabilities, filtering up to 90% of sodium ions from seawater through their roots. This efficient filtration mechanism has garnered significant scientific interest and could inspire the development of bio-inspired desalination technologies. Salt may be concentrated in older leaves of mangrove plants which fall off, ridding the plant of salt.

Shoreline protection

Mangrove forests stabilize shorelines, mitigating erosion caused by storm surges, currents, waves, and tides. Mangrove conservation and restoration promotes these resilient species as bioshields against coastal erosion and storm surges which are consistently on the rise due to climate change by limiting high energy wave action. The complex root system also provides essential habitat for a diverse array of marine organisms, offering shelter and food sources. These ecological functions, including coastal protection, nutrient cycling, and carbon sequestration, have made mangrove ecosystems a significant focus of scientific research.



SUGGESTED READINGS

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