

INVITED REVIEW: PART OF AN INVITED ISSUE ON TREE NUTRITION

## Nutrition of mangroves

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**Summary** Mangrove forests dominate the world's tropical and subtropical coastlines. Similar to other plant communities, nutrient availability is one of the major factors influencing mangrove forest structure and productivity. Many mangrove soils have extremely low nutrient availability, although nutrient availability can vary greatly among and within mangrove forests. Nutrient-conserving processes in mangroves are well developed and include evergreenness, resorption of nutrients prior to leaf fall, the immobilization of nutrients in leaf litter during decomposition, high root/shoot ratios and the repeated use of old root channels. Both nitrogen-use efficiency and nutrient resorption efficiencies in mangroves are amongst the highest recorded for angiosperms. A complex range of interacting abiotic and biotic factors controls the availability of nutrients to mangrove trees, and mangroves are characteristically plastic in their ability to opportunistically utilize nutrients when these become available. Nitrogen and phosphorus have been implicated as the nutrients most likely to limit growth in mangroves. Ammonium is the primary form of nitrogen in mangrove soils, in part as a result of anoxic soil conditions, and tree growth is supported mainly by ammonium uptake. Nutrient enrichment is a major threat to marine ecosystems. Although mangroves have been proposed to protect the marine environment from land-derived nutrient pollution, nutrient enrichment can have negative consequences for mangrove forests and their capacity for retention of nutrients may be limited.

**Keywords:** *Avicennia*, fertilization, nutrient resorption efficiency, *Rhizophora*, sewage treatment, soil redox potential.

### Mangroves—high productivity in low-nutrient environments

Mangroves dominate the majority of the world's tropical and subtropical coastline, forming 15 million hectares of forests worldwide that provide habitat for rich biodiversity, ranging from bacteria, fungi and algae through to invertebrates, birds and mammals (FAO 2004). Mangroves are highly productive,

fixing and storing significant amounts of carbon (Duarte and Cebrian 1996). Mean estimates of net primary productivity (NPP) for mangrove range from 2 to 50 Mg C ha<sup>-1</sup> year<sup>-1</sup> (Alongi 2009), rivalling some of the most productive old-growth tropical forests (Clark et al. 2001). Although mangrove ecosystems are rich in carbon, they are in a paradox often nutrient poor. How mangroves can sustain high levels of productivity in spite of nutrient limitation is the focus of many studies on mangrove nutrition. The emerging explanation is that high productivity of mangroves is achieved where nutrients limit growth through efficient nutrient cycling and nutrient conservation strategies.

Many mangrove soils have extremely low nutrient availability (e.g., Lovelock et al. 2005), but nutrient availability varies greatly between mangroves and also within a mangrove stand (Feller et al. 2003a). Using principal component analysis, Ukpong (1997) showed that nutrient availability is one of the three dominant components influencing mangrove vegetation performance in Africa. Additionally, nutrient availability has repeatedly been found to be an important factor limiting productivity in mangroves (e.g., Onuf et al. 1977, Boto and Wellington 1984, Feller et al. 2003b). The availability of nutrients to mangrove plant production is controlled by a variety of biotic and abiotic factors such as tidal inundation, elevation in the tidal frame, soil type, redox status and microbial activities of soils, plant species, litter production and decomposition. In this review, we explore the factors limiting nutrient availability in mangrove environments, particularly assessing the complexity of the feedbacks between abiotic and biotic factors that control nutrient availability and utilization by plants. We review the traits that give rise to nutrient conservation in mangroves and finally we discuss the consequences of eutrophication of mangrove environments and the implications for mangrove forests.

### Nutrient availability and the factors affecting nutrient availability in mangrove soils

The vast majority of the nutrient pool of mangrove forests is stored in the soil and not in the trees (Alongi et al. 2003).

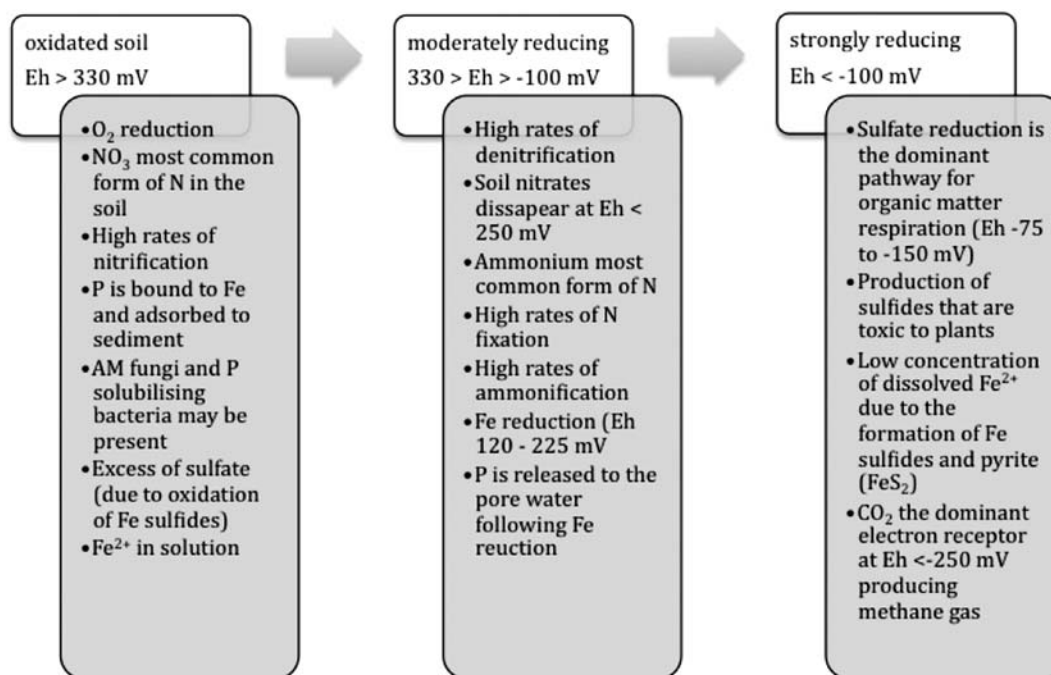


Figure 1. The sequence of reductive processes in flooded soils, as a function of the decrease in soil redox potential (Eh) (data from Patrick and Mahapatra 1968) and its control over the nutrients available for plant growth. Mangrove soils are generally moderately to strongly reducing (e.g., Thibodeau and Nickerson 1986, McKee et al. 1988).

Mangrove soils are typically saline, anoxic, acidic and frequently waterlogged. The delivery of nutrients in sediments and water during tidal inundation and sporadically in floodwaters associated with cyclones and hurricanes provides significant sources of nutrients for mangroves (Lugo and Snedaker 1974, Davis et al. 2003). The high level of carbon allocation to roots in many forests (Komiya et al. 2008) in conjunction with mangrove litter fall and the low rates of decomposition imposed by anoxic soils results in mangrove ecosystems being rich in organic matter (Nedwell et al. 1994). Despite low rates of decomposition in anoxic soils, decomposition of mangrove vegetative material is also a major source of nutrients in the mangrove ecosystem, as well as for adjacent coastal ecosystems via tidal flushing (Lee 1995). Topographic factors such as elevation determine the frequency and duration of tidal inundation, which subsequently affects the salinity, oxidation state and nutrient availability of the soil, resulting in complex patterns of nutrient demand and supply that contribute to the variable structure of mangrove forests.

The redox state of the soil surrounding the mangrove roots is important for determining the nutrients available for plant uptake (Figure 1). In conjunction with the frequency and intensity of inundation, the redox state of soils is also influenced by the biota, particularly by bioturbation (e.g., crab burrows; Smith et al. 1991) and the occurrence and abundance of mangrove roots. Radial oxygen loss from the roots creates an aerobic zone in the area immediately adjacent to the roots, which may vary in extent among mangrove tree species due to differences in the rate of oxygen loss from

the roots to the rhizosphere among species (McKee 1996, Pi et al. 2009). Thus, the redox state of the soil can be highly heterogeneous, facilitating a plethora of biogeochemical processes, which influence nutrient availability.

Denitrifying bacteria are abundant in mangrove soils. Denitrification rates can be high due to the anaerobic conditions in combination with high organic matter content (Alongi 1994, Corredor and Morell 1994). High rates of denitrification deplete the nitrate and nitrite pools and produce ammonia, making ammonium the most common form of nitrogen (N) observed in mangrove soils (e.g., Twilley et al. 1986, Alongi 1994, Kristensen et al. 2008). Furthermore, ammonium adsorption to mangrove soil particles is lower than in terrestrial environments due to the high concentration of cations from the seawater that compete for binding sites, making the ammonium available for plant uptake (Holmboe and Kristensen 2002). High rates of ammonification (Alongi et al. 2002) and N fixation also contribute to the production of ammonium.

The anaerobic, organic matter-rich soils of the mangroves are favourable for N fixation (Figure 1). As in other tropical forests (e.g., Cusack et al. 2009), N fixation in mangroves can be a significant source of N (Holguin et al. 2001). High levels of both light-dependent and light-independent N fixation have been recorded in microbial communities living on the trees (Uchino et al. 1984), in association with roots, in decaying leaves and on pneumatophores, as well as in the soil (Boto and Robertson 1990). Benthic microbial mats are found in many intertidal mangrove habitats and can also contribute significantly to the N cycle of the mangrove particularly when the mat is dominated by N-fixing cyanobacteria

(Lee and Joye 2006). Foliar uptake of N in the form of ammonia from the atmosphere or from rainwater has also recently been suggested to be a potentially important source of N for mangroves, particularly under conditions that favour ammonia volatilization (i.e., acidic, warm, flooded soils rich in organic matter) (Fogel et al. 2008).

The top layer of the soil and the thin layer of aerobic soil around the mangrove roots support populations of nitrifying bacteria that in turn can convert ammonium into nitrate for the plant, although nitrification rates are generally low (Shaiful et al. 1986, Alongi et al. 1992, Kristensen et al. 1998). In a study on mangrove soils in the Dominican Republic, nitrate concentrations in the soil were found to be negligible, with the vast majority of inorganic N being in the form of ammonium (Sherman et al. 1998). However, recent evidence suggests that nitrification can occur in anaerobic environments, including mangroves (Krishnan et al. 2007, Krishnan and Loka Bharathi 2009) via a heterotrophic reaction that relies on redox metals such as iron and manganese, and thus the role of nitrate in mangrove nutrition remains unclear and open to future research. Mangroves grown in pots appear to readily use nitrate over ammonium and showed a major reduction in plant N uptake when a nitrification inhibitor (N-Serve) was added to the soil (Boto et al. 1985). However, in a field experiment in a mangrove forest, nitrate did not seem to be taken up by the trees (Whigham et al. 2009). Nitrate reductase activity in mangrove trees in the field was also determined to be very low (Smirnov et al. 1984), further supporting the claim that nitrate is not an important source of N for mangrove trees under field conditions. It is likely that the discrepancy between pot and field studies is due to competition for available nitrate. Soil bacteria have been shown to significantly respond to nitrate additions (Whigham et al. 2009) and, in addition to the microbial demand for nitrate, algae attached to the pneumatophores of the mangroves and to the soil surface have also been shown to compete for nitrate with both the trees and the denitrifying bacterial community (Rodriguez and Stoner 1990). These results might imply that the microbial community in the mangroves, with its high rates of denitrification (Alongi et al. 1992), outcompetes the trees for nitrate and, consequently, nitrate does not play a major role in N nutrition of mangrove trees in the field despite a possible preference for nitrate in pot experiments.

Organic forms of N such as freely extractable amino acids present in the soil are currently emerging as critical components of the N cycle in many forests. While traditionally believed to take up only inorganic forms of N, numerous studies are now showing that some trees have the physiological capacity to and readily take up amino acids (Schmidt and Stewart 1999, Schimel and Bennett 2004, Finzi and Berthrong 2005) and even proteins (Paungfoo-Lonhienne et al. 2008), especially in low-N environments. Amino acid availability in mangrove soils can be high (Stanley et al. 1987) but amino acid uptake by mangrove trees has not been investigated directly. A recent study on mangrove nitrogen isotope compo-

sition in Belize suggested that amino acid uptake was unlikely given the isotopic signature of the soil, roots and leaves (Fogel et al. 2008), but further investigation could clarify the role of organic N in mangrove nutrition.

Phosphate (P) in mangrove soils can be immobile and unavailable for plant use (Figure 1), thus organisms that solubilize P can have important implications for plant growth, especially in nutrient-limited environments. Symbiotic associations between roots and arbuscular mycorrhizal (AM) fungi are widespread in nearly all soils (Treseder and Cross 2006) and are important for the uptake of immobile nutrients, especially for the solubilization of phosphorus (P) (Smith et al. 2003). While very common and important in terrestrial ecosystems, AM fungi have been found only in low-salinity mangrove soils (Sengupta and Chaudhuri 2002). The absence of AM fungi in high-salinity soils can have a negative influence on the uptake of some nutrients such as zinc, copper, Fe and P and could potentially increase the susceptibility to toxic metals (Bradley et al. 1982). Very few studies thus far have studied the occurrence of AM fungi in mangrove soils. Sengupta and Chaudhuri (2002) and Kothamasi et al. (2006) observed AM associations in the low-salinity soils (<11 PSU) of the Ganges River estuary in India and that all of the 31 mangrove species in that study were receptive to mycorrhizal colonization. However, an analysis we have drawn from the Sengupta and Chaudhuri (2002) data indicates that such associations might be strongly inhibited by higher salinities. The effect of soil salinity on AM fungi has been under much debate (Evelin et al. 2009), but there does appear to be a threshold of 20 PSU to AM fungi salinity tolerance, above which it is unable to colonize soils (Johnson-Green et al. 2001). For example, increased soil salinity leads to reduced colonization by AM fungi in citrus (Levy et al. 1983) and in the saltmarsh halophyte *Aster tripolium* (Carvalho et al. 2003). AM fungi might also be inhibited by anaerobic conditions (LeTacon et al. 1983), although it is possible that the thin oxygenated layer surrounding the roots can provide enough oxygen for their survival (Brown and Bledsoe 1996). However, if their occurrence were limited to the area immediately surrounding the roots, their ability to mobilize nutrients that are beyond the reach of the mangrove roots would be restricted. It is clear that further investigation into the colonization and abundance of AM fungi in mangrove roots and soils is needed.

The possible absence of AM fungi from many mangrove ecosystems is countered by the occurrence of phosphate-solubilizing bacteria in association with mangrove roots (Vazquez et al. 2000, Kothamasi et al. 2006). Bacteria solubilize phosphate in areas where the soil is oxygenated (e.g., near the mangrove roots) and may, therefore, serve an important role in P uptake by the plant.

In addition to altering the availability of nutrients in soils, the anoxic conditions in mangrove soils can have adverse effects on growth as they facilitate the microbial conversion of sulphate, which is abundant in seawater, to sulphides, which are toxic to plants (Nickerson and Thibodeau 1985). Most of



the degradation of organic matter occurs via sulphate reduction (Kristensen et al. 1991). Oxidation of the soil around the roots can reverse the conversion of sulphate to sulphides, thus reducing the toxicity of the soil. However, this process also releases  $H^+$  protons, which results in acidification of the soil. The high concentration of sulphate in seawater makes sulphide toxicity more probable in mangrove forests compared with terrestrial ecosystems (Raven and Scrimgeour 1997). On the other hand, sulphate-reducing bacteria also play a pivotal role in increasing P availability in the soil (Sherman et al. 1998). In sediments that are Fe rich (such as some mangrove soils; Holmboe and Kristensen 2002), P binds to Fe in the presence of oxygen. Under anoxic conditions, sulphate-reducing bacteria reduce Fe to forms that are unfavourable for P binding (Holmer et al. 1994), thereby releasing P to the pore-water potentially for plant uptake (Figure 1). Additional benefits of sulphate reduction may be concurrent N fixation as many populations of sulphate-reducing bacteria can also fix N (Nedwell and Azni bin Abdul Aziz 1980).

### Nutrients limiting mangrove growth

Mangroves have evolved in the oligotrophic tidal environment of the tropics (Plaziat et al. 2001) where the total N and P content of the soils was likely to have been very low due to strong weathering of the old highly leached soils of the tropics (Romine and Metzger 1939). Accordingly, we expect many mangrove environments to be nutrient limited and that, in general, tropical soils will be less fertile, particularly in P, which in contrast to N cannot be replaced through biological fixation (Vitousek 1984, Reich and Oleksyn 2004, Lovelock et al. 2007a). We also expect that mangroves will have evolved traits for the acquisition and conservation of nutrients in low-fertility environments (see 'Mangrove nutrient conservation strategies', below). Although there are broad-scale latitudinal patterns in N and P concentration in leaves of mangroves and other plants that indicate differing nutritional requirements over latitude, there is also a high level of variability in nutrient limitations to growth observed within regions (Lovelock et al. 2007a, Feller et al. 2009b), indicating that nutrient limitation is determined by multiple factors, including sediment and nutrient fluxes, tidal range and substrate type.

Most mangrove species that have been studied have been found to be highly sensitive to variation in nutrient availability both in the laboratory (e.g., Boto et al. 1985, Naidoo 1987, McKee 1996, Yates et al. 2002, Naidoo 2006) and in the field (e.g., Onuf et al. 1977, Boto and Wellington 1983, Feller 1995, Koch 1997, Feller et al. 2003b, Lovelock et al. 2005, Feller et al. 2007, Lovelock et al. 2007b, Naidoo 2009). In the Atlantic East Pacific biogeographic province, the response of the three dominant species, *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*, to nutrient availability have been investigated in multiple studies, but in the Indo-West Pacific region, few studies documenting the effects of

nutrient availability on mangrove species performances have been published, and those studies only considered a few of the comparatively greater species diversity that comprises the mangrove forest communities of this region.

Most investigations of nutrient limitations to mangroves have focused on the macronutrients N and P, which have both been implicated as the nutrients most likely limiting primary productivity of mangrove ecosystems (reviewed in Krauss et al. 2008). Limitations to growth imposed by iron are also likely (Alongi 2010), but have yet to be assessed in the field. In many marine ecosystems, N was considered the primary nutrient that limits growth, although more recent analysis found that N and P limit growth in approximately equal proportions (Elser and Hamilton 2007). An early theoretical analysis suggests that P limitation should be expected in areas with low exchange rates with the oceans and N limitation in more 'open' systems (Smith 1984). Mangroves can be either open, having regular tidal or riverine exchange, or with more restricted exchange, e.g., high intertidal and microtidal settings. Thus, we expect and find both N and P limitation in mangroves. Additionally, variation in soil anoxia (flooding) and salinity may also affect the nutrient demand imposed by tree growth and, thus, the extent to which growth is nutrient limited (Krauss et al. 2006), in addition to directly affecting nutrient availability (see above).

Here, we summarize the range of studies and the evidence for nutrient limitations to growth in mangrove ecosystems. In the southern USA, mangroves have been experimentally shown to be both N limited (Feller et al. 2003b) and P limited (Lin and Sternberg 1992, Koch 1997). In Belize, both N and P limitation were observed, depending on location within the forest (Feller et al. 2003a). Forests fringing the ocean were N limited while those internal to the islands and permanently flooded were P limited. Forests internal to the island in Puerto Rico were also found to be P limited (Medina et al. 2010). In Bocas del Toro, Panama, growth of trees was found to be both N and P limited (Lovelock et al. 2004). There are also differences between species in the magnitude of response to nutrient enrichment. For example, in a fertilization experiment of *A. germinans* vs. *L. racemosa*, the increase in photosynthetic performance in N-fertilized *A. germinans* was much greater than that of N-fertilized *L. racemosa* (Lovelock and Feller 2003).

Studies in the Indo-Pacific and the African continent have also shown variation in whether N or P limits growth, although in these mostly mesotidal settings, N is the nutrient most frequently observed to limit growth (Lovelock et al. 2007a). N was found to limit growth of *A. marina* in South Africa (Naidoo 2009) and New Zealand (Lovelock et al. 2007b). In more tropical latitudes, P was found to limit growth in high intertidal scrub forests (Boto and Wellington 1983, Lovelock et al. 2007a).

The ratio N:P in plant tissue has also been used to infer N or P limitations to growth (Güsewell 2004). Variation in leaf N:P, particularly where N:P is >32 (which is a global average for mangroves; Lovelock et al. 2007a), indicates that P may

limit growth in many mangrove habitats (e.g., Malaysia, Kenya, China, Puerto Rico, Venezuela, Victoria, Australia, Florida and Honduras; reviewed in Lovelock et al. 2007a).

Although experimental additions of P have yielded increases in growth in mangroves, it has long been recognized that it is possible that some of the beneficial effect of applied phosphate in acid soils is due to fixation of aluminium and not just due to phosphate uptake by the plant (Pierre and Stuart 1933). The presence of phosphate can precipitate aluminium, thus suppressing aluminium uptake (Hesse 1963). Aluminium can be relatively abundant in mangrove soils (Naidoo and Raiman 1982) and the acidic conditions of mangrove soils may result in aluminium being mobilized to toxic levels. Based on the few studies that have addressed the effects of aluminium on mangrove growth, it has been concluded that mangroves are relatively tolerant to aluminium, having a large storage capacity in the canopy (Rout et al. 2001, Oxmann et al. 2009). However, more studies are required for understanding the tolerance of mangrove to aluminium and other potentially toxic metals.

All plants require potassium (K) for maintaining intracellular electric neutrality, osmotic regulation, enzyme activation, protein synthesis and photosynthetic metabolism (Leigh and Wyn Jones 1984). In high-salinity environments, K is also vitally important for osmotic regulation (Downton 1982) and helps form the electrical potential required to facilitate water uptake against the strong external salt (mostly Na) gradient.  $K^+$  deficiencies in mangroves as in other plants have been shown to result in loss of chlorophyll and photosynthetic function (Ball et al. 1987). The availability of K in mangrove soils is variable, and there is some evidence for K limitation in some mangroves (Ukpong 1997). Furthermore, due to the saline conditions,  $Na^+$  cations can interfere with  $K^+$  uptake (Mäser et al. 2002), thereby reducing the efficiency of  $K^+$  uptake from the soil. In some neotropical mangrove forests, K concentrations in green leaves were weakly but positively correlated with growth rates (Feller et al. 2009b). In a Belizean mangrove where P was a limiting factor for growth, the addition of K did not result in greater growth rates even when P limitation was lifted (Feller 1995), but K-use efficiency increased with growth rates, indicating that, when N or P limitation is relieved, K limitation to growth may develop. In other areas, such as Nigerian mangrove forests, percent cover was not strongly correlated with K availability in the soil (Ukpong 2000), but rather with other macronutrients and micronutrients such as P, calcium (Ca) and magnesium (Mg). This was also suggested in a pot study where interacting effects between N, P and K availability and mangrove seedling growth were detected (Yates et al. 2002).

### Mangrove nutrient conservation strategies

Mangroves are a diverse group of plants and are an ecological entity with little phylogenetic association. This may lead to many intrinsic differences among coexisting species in nu-

trient uptake and nutrient-use efficiency, with significant differences observed between species in their response to nutrient availability (McKee 1993, Lovelock and Feller 2003), which may be partially responsible for differential distribution of species (zonation) observed in mangrove landscapes (Feller et al. 2003b). However, convergent evolution has led to similar adaptations among mangrove species in traits such as water relations (Ball 1988a, Macinnis-Ng et al. 2004) and architecture (Tomlinson 1986). Thus, convergence in some strategies for nutrient conservation among species might also be expected.

Mangrove trees are highly productive and this is due in part to the evolution of many adaptations for nutrient conservation (Figure 2). Most mangrove trees are evergreen with sclerophyllous leaves and high root/shoot biomass ratios (Komiya et al. 2008). The evergreen habit implies a smaller nutrient investment in new leaves and lower nutrient loss rates due to the long lifespan of the tissue (Aerts 1995). Mangroves have an average leaf life span of 16 months (1.33 years), although this can vary between species and over latitude (Saenger 2002, Suárez and Medina 2005). The leaf life spans of mangroves are typical for broadleaved tropical and subtropical evergreens (Reich et al. 1992).

Sclerophylly is a trait related to low soil nutrient availability, especially low P (Loveless 1961, Wright et al. 2001). In mangroves, sclerophylly declined with increases in P in P-limited environments (Feller 1995). Sclerophylly is also linked to low water availability and, in mangroves, to high-salinity habitats (e.g., Naidoo 1987), as sclerophyllous leaves can lose a great deal of their water content before wilting and can exhibit extremely low leaf water potentials (Salleo et al. 1997 and references therein). Sclerophylly has also been linked to leaf longevity and evergreen traits and to ecosystem nutrient retention through slowed decomposition (Schlesinger and Hasey 1981) and through reductions in herbivory by primary consumers (Coley 1983).

The capacity to sustain low growth rates and consequently reduced nutrient requirements over periods of time are an adaptation to low-nutrient environments (Chapin 1980). Mangroves are capable of very slow growth rates (and lower rates of NPP), often forming dwarf forests, which are mature forests in which tree growth is stunted and trees are <1.5–2 m in height (Lugo and Snedaker 1974). These dwarf (or scrub) trees can experience periods of rapid growth when nutrient limitation is lifted (e.g., Feller et al. 2003b, Lovelock et al. 2005, Feller et al. 2007, Lovelock et al. 2007a).

Root biomass in mangroves can be high, partially because of the contribution of aboveground roots, which have both supportive functions and roles for aerating roots in anoxic soils and also due to high belowground root biomass (Golley et al. 1962, Snedaker 1995 and references therein). Root/shoot ratios have been observed that are sometimes an order of magnitude higher than those for tropical terrestrial forests and similar or higher than those found in desert plants (Mokany et al. 2006). Root/shoot ratios can vary considerably as a function of environmental factors and are in part an adap-

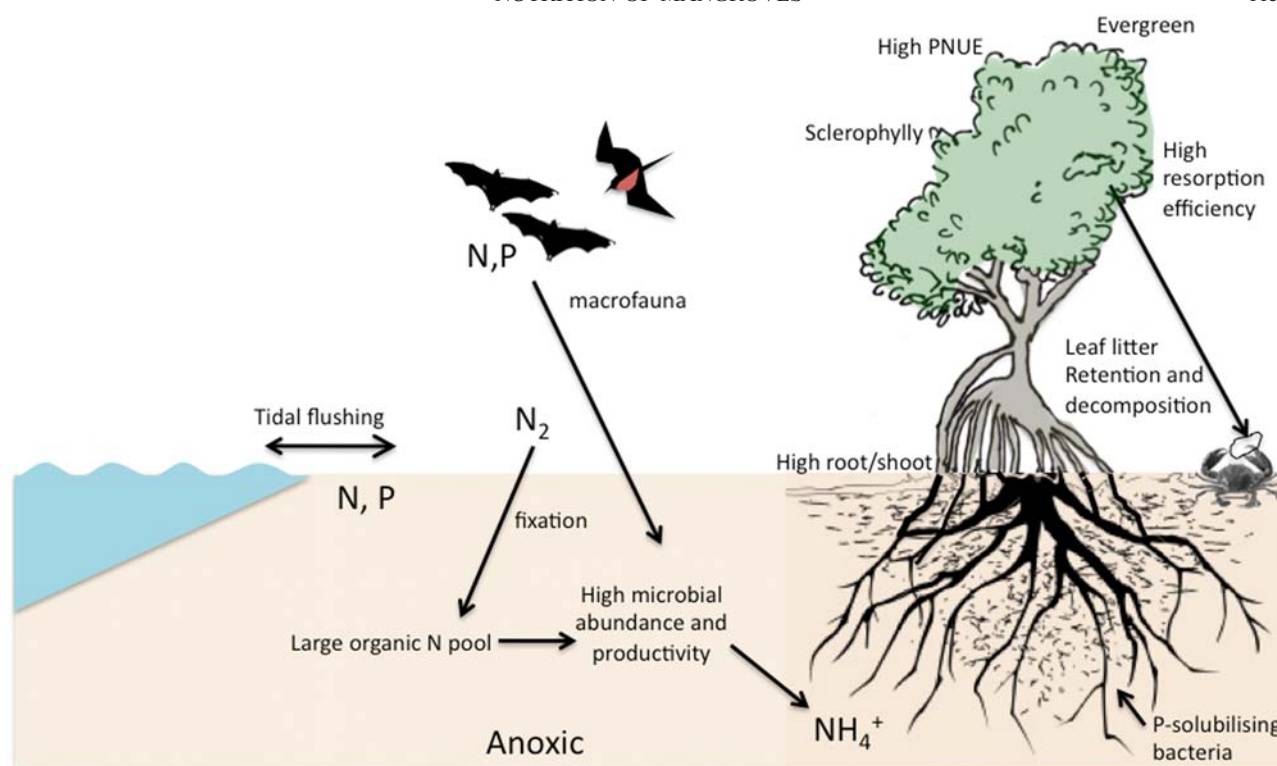


Figure 2. A schematic summarizing the major nutrient inputs (tidal flushing, nitrogen fixation, microbial activity, leaf litter and abundant macrofauna) as well as the nutrient conservation mechanisms characteristic of mangrove forests (evergreen, high nutrient RE, high root/shoot ratios, high PNUE and sclerophylly). This figure appears in color in the online version of *Tree Physiology*.

tation to saline environments (Ball 1988b, Saintilan 1997). Root/shoot ratios in many trees are sensitive to soil moisture, usually decreasing with increased waterlogging (Kozłowski 1984), but this is not necessarily the case for all mangrove species (Ye et al. 2003, Krauss et al. 2006). Root/shoot ratios also vary between mangrove species, over time and with forest structure (Tamoooh et al. 2008), resulting in non-linear relationships between soil conditions and root/shoot ratios. However, the overall high root biomass in mangroves, especially the abundance of fine roots (Komiyama et al. 2000), is conducive to nutrient capture and uptake from soils low in nutrients, particularly as fine roots proliferate in response to high nutrient microsites, such as inside decaying roots (McKee 2001).

Processes that alter biomass-partitioning patterns in mangroves, such as salinity or anoxia, can affect their potential to acquire nutrients. Low oxygen levels in the soil due to flooding can have an opposite effect to salinity, reducing root extension rates and even cause root tip dieback in some species (McKee 1996). Nutrient availability is another factor that plays a role determining the allocation to root biomass. Similar to other plants (Chapin 1980), studies on mangrove seedlings have demonstrated that, when nutrient availability is high, mangrove seedlings invest more in aboveground biomass (which maximizes carbon acquisition) than in roots, while when nutrient availability is low, seedlings redirect resources to enhance their root biomass (McKee 1995, Naidoo 2009).

Increasing the efficiency of metabolic processes is also an effective nutrient conservation strategy (Chapin 1980). In most plants, a large proportion of root respiration goes towards the uptake and assimilation of N (Bloom et al. 1992). Trees that occur in habitats where the soil is ammonium rich generally exhibit a preference for ammonium uptake and do not appear to suffer from ammonium toxicity, which can have a significant metabolic cost in ammonium-sensitive plants (Kronzucker et al. 1997 and references therein). The assimilation and uptake of ammonium requires the least energy investment compared with uptake and assimilation of any other form of N (Gutschick 1981). Thus, the use of ammonium may in part be responsible for the low respiration rates observed in mangrove roots (McKee 1996, Lovelock et al. 2006). Furthermore, the large root biomass in mangroves may overcome the relative immobility of ammonium in the soil by covering large soil volumes. The poor nitrate assimilation potential in mangroves, demonstrated by low activity levels of nitrate reductase under field conditions (Smirnov et al. 1984), suggests that the mangroves are well suited for utilizing ammonium as their primary N source.

Photosynthetic nitrogen-use efficiency (PNUE) is an index of resource-use efficiency and can be estimated as the ratio of photosynthetic capacity to leaf N content. PNUE measured for mangroves (e.g., Alongi et al. 2005) is amongst the highest recorded for trees, reflecting a high level of adaptation to growth under nutrient-limited conditions (reviewed in Feller



et al. 2009a). Interspecific differences in nutrient-use efficiency have been observed between mangrove species (Love-lock and Feller 2003) and are also modified by plant interactions with environmental variables (Martin et al. 2010). For example, PNUE differed among mangrove species and decreased with increased nutrient availability and salinity (Martin et al. 2010). PNUE decreases with increasing salinity because, under highly saline conditions, mangroves achieve higher photosynthetic water-use efficiency by increasing N leaf content in order to maximize photosynthetic carbon gain when stomatal conductance is low.

Nutrient recycling processes in trees include resorption of nutrients prior to leaf fall (Chapin 1980), a process where nutrients resorbed from senescent leaves are directly available for continued plant growth (Hortensteiner and Feller 2002). The effect of nutrient availability on nutrient resorption efficiency (RE) for plants is variable. In an analysis of 60 published nutrient-enrichment experiments, only 32% of the cases exhibited reduced nutrient RE as a result of nutrient enrichment (Aerts 1996). However, for mangrove trees, resorption of nutrients has been mostly observed to become less efficient when nutrients become more available in the soil (Feller et al. 1999, 2003b, 2007, Lovelock et al. 2007a). In some cases, RE of an initially non-limiting nutrient has been shown to increase as a result of the alleviation of a limiting nutrient (e.g., N enrichment in N-limited trees results in higher RE of P; Feller et al. 2003b), indicating the complexity of internal nutrient conservation and the interacting effects of growth rates (and the demand for nutrients) and their supply.

RE can vary greatly between species but, on average, plants resorb ~50% of the nutrients (N and P) from their senescent tissue (Aerts and Chapin 2000). Maximum resorption efficiencies appear to be rather uniform amongst different co-occurring mangrove species; a comparison between eight mangrove species in Gazi Bay, Kenya revealed similar RE values of around 65% (Rao et al. 1994). The high RE found in Kenya is consistent with other studies that indicate that RE in mangroves is high compared with other angiosperms (Feller et al. 2003b, Lin et al. 2009), often resulting in almost complete resorption of limiting nutrients. Nitrogen resorption efficiency (NRE) in the Kenyan mangroves was as high as 69% for *Avicennia marina* (Rao et al. 1994, Ochieng and Erfemeijer 2002). Similar and even higher values were found for *A. marina* and *R. stylosa* in Western Australia (Alongi et al. 2005), for *R. mangle* in Belize (Feller et al. 2003a) and for *Kandelia candel* in China (Wang et al. 2003). The lowest levels of NRE were recorded for *A. germinans* at Twin Cays (<5%; Feller et al. 2007), *A. marina* trees in New Zealand (as low as 20%; Lovelock et al. 2007b) and *R. mangle* trees in Florida (<50%; Lin and Sternberg 2007) and in northern Australia (~50%; Woodroffe et al. 1988), but in those areas, low NRE was usually accompanied by high P RE (Feller et al. 1999, 2007, Lovelock et al. 2007b). These high N and P resorption values indicate that internal cycling of N and P can supply a significant fraction of the required nutrients for plant growth in mangroves. For example, in an

*A. marina* stand in Kenya, the resorption from senescent tissue was more than two-thirds of the N and P requirements of that stand (Ochieng and Erfemeijer 2002).

Because of the importance of nutrient resorption prior to tissue senescence to tree nutrient budgets, processes that remove leaves prior to complete senescence have the potential to influence the nutrient resorption recycling efficiency. Such processes include biotic and abiotic stressors such as herbivory (Feller and Chamberlain 2007) and destructive weather (wind, hail, etc.). Freezing temperatures led to substantial non-senescent leaf loss from mangroves in Tampa Bay, Florida and prevented nutrient resorption (Ellis et al. 2006). Cyclones and hurricanes can also result in dramatic loss of foliage (Smith et al. 1994, Baldwin et al. 2001). The result of a loss of RE is elevated nutrient levels in the litter available for export and for decomposers if leaf litter remains within the forest. Decomposition of fallen leaves through microbial processes is another component of efficient nutrient cycling in mangroves (reviewed by Holguin et al. 2001). As in other tropical marine ecosystems, microbial abundance and productivity in mangrove soils are very high (Alongi 1994), albeit patchy (Alongi 1988), and there is tight nutrient cycling within the microbial population in the soil (e.g., of dissolved free amino acids; Stanley et al. 1987).

Macrofaunal assemblages are emerging as important biotic factors for nutrient cycling in mangroves. Birds nesting in mangroves can contribute a significant source of nutrients for mangrove growth (Onuf et al. 1977). However, despite the widespread occurrence of bird and bat roosts in mangroves, this is the only study to document the influence of vertebrates (such as birds or bats) on tree growth. By transplanting epibiotic invertebrate fauna onto roots of the mangrove *R. mangle*, Ellison et al. (1996) demonstrate that root-fouling sponges growing on the roots of the mangrove can significantly increase root elongation rates. Isotopic analysis of the N in sponges and along the mangrove root indicated that the sponges provided a source of inorganic N for the tree. Epibiotic fauna can colonize a substantial area on the roots; however, the factors affecting successful colonization, such as invertebrate larval supply, sedimentation rates and environmental conditions, vary on a spatial and temporal level. This makes the contribution of epibiotic fauna to the nutrient pool available for tree growth highly variable between sites and seasons, but evidence suggests that animal-plant interactions can significantly enhance nutrient supply for plant growth and should be included in the analysis of mangrove forest nutrient fluxes. For example, crabs play a significant role in many mangrove forests, especially in the Indo-Pacific (reviewed in Lee 1998). At some sites, crabs can consume more than a quarter of the leaf litter fall, producing faecal material that has higher nutritional content and significantly lower tannin concentrations than the leaves themselves, promoting recycling of the detrital matter (Robertson 1986). Other fauna, such as gastropods and worms, promote nutrient recycling by consuming plant litter and microorganisms from the sediment (Kristensen et al. 2008) as do insects, such as termites, that

feed on dead wood or decaying organic matter (Nagelkerken et al. 2008).

### The threat of eutrophication and climate change to mangroves

Eutrophication is one of the major changes coastal ecosystems are facing worldwide (Cloern 2001, Verhoeven et al. 2006). In addition to anthropogenic nutrient loading in coastal waters, mangroves are also being suggested as potential treatment systems for effluent purification. The interest in mangroves as treatment systems for sewage and aquaculture effluent has increased greatly over the past few years. Nedwell (1975) was one of the first to suggest that the high potential denitrification in mangrove soil might be manipulated to remove N discharge of secondary sewage effluent, serving as low-cost alternatives to sewage treatment plants in the developing world. The high biomass and productivity of mangrove forests and their extensive root systems make them potential candidates for uptake of discharged nutrients and heavy metals. The microbial communities in the soil are also capable of depurating large amounts of wastewater inorganic N (Corredor and Morell 1994). As summarized above, nutrient additions can stimulate mangrove growth. Weak sewage discharge on a short time scale did not result in a detectable effect on nutrient concentration in mangrove soils or leaves or affect the plant community structure compared with a site without wastewater effluent applied (Wong et al. 1995). Similar results were found for the effects of shrimp pond effluent on a mangrove estuary (Trott and Alongi 2000). These and other studies have all led to the conclusion that nutrient enrichment can be beneficial for mangrove growth and ecosystem health. However, evidence is mounting that eutrophication can also have negative consequences for mangrove growth.

A Red Sea study demonstrated that *A. marina* grown under sewage pollution stress showed stunted morphology and that mortality rates within the effected mangrove strand were high, probably due to the loss of pneumatophores and soil anoxia (Mandura 1997). Nutrient enrichment can also increase sensitivity to drought and hypersalinity because nutrient-induced increases in allocation to canopy rather than roots can indirectly increase mortality rates due to enhanced susceptibility to water deficits (Lovelock et al. 2009). Eutrophication results in higher activities of marine wood-borers (Kohlmeyer et al. 1995) and increased herbivory rates of some bark-mining moths (Feller and Chamberlain 2007). In addition to inorganic N, wastewater contains heavy metals, pesticides and organic matter, which can be damaging to mangrove health (Clough et al. 1983, Yim and Tam 1999). Heavy metal concentrations in some mangrove soils are high (Ong Che 1999, Defew et al. 2005), and this can result in reduced leaf numbers and stem diameter (Yim and Tam 1999). Conversely, in anoxic environments where sulphate reduction occurs, the solubility and toxicity of low levels of zinc, cadmium and other chalcophilic heavy metals can be reduced by metal sulphide formation

(Klerks and Bartholomew 1991). However, above certain thresholds, these heavy metals become toxic to the sulphate-reducing bacteria due to their ability to compete with essential cations for cellular activity, denaturize proteins and deactivate enzymes (Utgikar et al. 2003).

Mangroves are a significant source of nitrous oxide ( $N_2O$ ; Allen et al. 2007) and eutrophication of mangrove soils can cause an increase in the rate of release of  $N_2O$  to the atmosphere.  $N_2O$  is a highly potent greenhouse gas produced as an intermediate product of both nitrification and denitrification by microbial organisms. In mangrove soils, both reactions can contribute to the production of  $N_2O$  (Meyer et al. 2008). The  $N_2O$  produced in mangrove soils is rapidly released to the atmosphere because pneumatophores facilitate the transport of  $N_2O$  from the soil to the atmosphere (Krithika et al. 2008).  $N_2O$  production increases exponentially with external input of inorganic N to the soil (Corredor et al. 1999), demonstrating yet another negative impact for eutrophication in mangroves.

Climate change can affect both plant and soil biochemical processes by means of increased  $CO_2$  levels, elevated temperatures, rising sea levels and higher storm frequency. These are all likely to have a significant impact on mangrove physiology and ecosystem function and impact nutrient availability and cycling. Elevated  $CO_2$  conditions (twice ambient) enhance stem elongation, leaf production, photosynthesis rates and root production in *R. mangle* (Farnsworth et al. 1995) as well as increase water-use efficiency (Ball and Munns 1992), responses similar to those observed for other trees (Ainsworth and Long 2005). Another common plant adaptation to elevated  $CO_2$  concentrations is decreased nitrogen invested in leaves and a concomitant increase in the carbon:nitrogen ratio of plant tissues, which have flow-on effects to consumers (Stiling et al. 1999) and on decomposition processes (Bosire et al. 2005).

Although increases in atmospheric  $CO_2$  result in elevated growth rates, these are smaller than the reductions in growth rates observed when mangroves are increasingly inundated (Farnsworth et al. 1995), e.g., as a consequence of sea level rise and with low humidity and high salinity (Ball and Munns 1992, Ball et al. 1997). Mangroves are within the intertidal zone and are thus highly sensitive to rising sea level, but the community may adapt to rising sea level if the rate of vertical accretion of the soil surface of the forest equals or exceeds the rate of sea level rise (Cahoon et al. 1999, Morris et al. 2002). This can be achieved, for example, if the higher photosynthesis rates observed under increased  $CO_2$  conditions result in increased carbon allocation to roots, increasing the soil root volume and thus soil elevation (Langley et al. 2009). While nutrient availability strongly influences short-term root accumulation, the long-term effects of nutrient enrichment on mangrove peat are unclear and can be negative (McKee et al. 2007). Added to anthropogenic eutrophication, increased nutrient delivery to the mangroves could result from coastal erosion following sea level rise or due to changing rainfall patterns.



Photosynthesis and respiration are both highly sensitive to temperature. Mangrove photosynthesis is usually limited by high midday leaf temperatures (Cheeseman 1994); thus, increases in temperature with declines in humidity and rainfall could reduce productivity in some mangrove forests by accentuating midday depressions in photosynthesis. Microbial soil respiration rates are also strongly temperature dependent, doubling every 10 °C (Kirschbaum 1995, Lovelock 2008); thus, soil nutrient availability for tree growth could be strongly temperature dependent, as bacteria and trees compete for the limited nutrient supply. The picture emerging is that climate change will influence mangroves ecosystems in the form of a suite of many interacting factors, the result of which will probably be specific to the conditions at each site.

## Conclusions

Mangroves inhabit environments that have a wide range of nutrient availability, even over small spatial scales (e.g., high compared with low intertidal zone). Correspondingly, many mangrove tree species have traits that are consistent with adaptation to growth under low-nutrient conditions, for example, slow growth rates, high root/short ratios, sclerophylly and high levels of nutrient resorption from senescent tissue. The evidence suggests that nutrient availability to the plants is strongly controlled by the demands of the soil microbial community, in addition to other abiotic factors. However, mangroves also appear to be highly plastic in their responses to changes in nutrient availability, achieving high growth rates when nutrient limitations are relieved that are accompanied by associated reductions in nutrient-use efficiency and other nutrient conservation mechanisms. Thus, perhaps what characterizes mangrove forest nutrition in comparison to other forested ecosystems is that the component tree species have a comparatively high level of plasticity in traits for growth, nutrient acquisition and conservation. High plasticity confers the capacity to withstand low-nutrient conditions while still permitting the ability to exploit high levels of nutrients when they are available (e.g., Fromard et al. 2004). Such a flexible strategy permits rapid colonization of newly available marine sediments but can also accommodate persistence under unfavourable conditions in environments where replacement by competing plant communities (succession) is prevented by tidal inundation.

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