Elemental Status and Dynamics in Temperate (New Zealand) and Semi-arid Mangroves (New Caledonia)

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Abstract

Mangrove ecosystems demonstrate a high capacity to accumulate macronutrients and trace metals and play a significant role in global oceanic nutrient budget and water quality. With growing pressures from global change, this role is now at stake as mangroves experience increasing shifts in their biogeochemistry, distribution and productivity. In particular, the simultaneous influences of sea-level rise, increasing aridity and anthropogenic pressures worldwide are projected to have a significant impact on mangrove element cycles. The aim of this thesis was to improve our understanding of global change effects on macronutrient (C, N, P, K, Mg, Ca, S) and trace metal (Fe, Mn, Al, Ni, Cu, Zn, Cr, Co) dynamics and their transfers within the mangrove soil-plant continuum. In order to do so, this research focuses on the distribution of these elements and their interactions *in situ*, in contrasted climate conditions and in different physiographic contexts in temperate New Zealand and semi-arid New Caledonia.

Worldwide data showed that despite a decrease in mangrove biomass with increasing latitude, the various elemental sources and biogeochemical processes in mangrove ecosystems lead to a strong heterogeneity in elemental concentrations in plants and soils at every spatial scale. This point is further demonstrated in a case study in temperate *Avicennia marina* (Forsk.) Vierh subsp. *australasica* (Walp.) J. Everett estuarine mangroves in New Zealand, where soils were found to be a significant sink of C, macronutrients and trace metals. Although this research highlights the role of temperate mangroves as an efficient filter for terrigenous materials, findings also showed that this capacity significantly decreases with increasing length of immersion, tidal energy and reduction-oxidation potential (Eh). Thus, there is cause for concern over sea-level rise and erosion subsequent to mangrove stand removal.

As we move to a warmer and drier climate in New Caledonia, elevation measurements showed dramatic centimetre-scale variations of soil properties and elemental contents along a semi-arid toposequence. Strong evapotranspiration in landward areas results in a 200 and 400% increase in pore-water salinity and Eh compared to seaward areas. This difference in Eh was magnified during the dry season and coincided with a loss of trace metal content compared to mangrove soils at the lowest elevations. In addition, plant component analyses demonstrated the magnitude of the influence of soil Eh, salinity and total sodium variations on trace metal and macronutrient soil-plant transfers along semi-arid mangrove gradients.

The effect of a recent increase in tidal range on elemental distribution was also investigated at the two extremities of that same toposequence. Increase in soil elevation and a depletion of trace metals in fringe mangrove stands suggest that while mangroves may partly mitigate sea-level rise by vertical accretion or root accumulation, the effect of tidal pumping, perturbation and weathering on the pool of nutrients and trace metals in soils may remain significant. At the highest elevations, soil surface analyses in salt-flats recently colonized by *A. marina* give an insight into the ability of this pioneer species to transform hypersaline soils in a substrate favourable for plant growth. These results together with total Na contents analyses in *A. marina*'s tissues showed that the success of this species in colonizing arid mangrove soils is due as much to its capacity to modify soil structure, nutrient contents and water-holding capacity as to its ability to tolerate salinity stress.

Further research in different study sites adjacent to mining and aquaculture activities showed how variations of physico-chemical properties and OM cycling lead to polarized responses to labile OM and trace metal loads in mangrove plants and soils along semi-arid intertidal gradients. Results suggest that increased pollution, aridity and

sea-level rise are likely to increase P accumulation in mangrove soils and nutrient export from soil towards plant biomass and litterfall. This research also indicates a potential decline in mangrove ability to accumulate OM, N and K in soils in landward areas and trace metals in seaward areas.

The findings of this work contribute significantly to the understanding of macronutrient and trace metal dynamics in temperate and semi-arid mangroves. This work also provides insights into the implications of drought intensification on plant nutrition and their response to salinity and metal stresses.

Table of Contents

List of Figures

List of Tables

List of Appendices

Attestation of Authorship

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published by another person (except where explicitly defined), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.

Carine Bourgeois

Co-Authored Works

Chapter 2 - *Macronutrient and trace metal status in mangroves : literature review* In preparation			
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Andrea Alfaro	Review/edit	5	
Cyril Marchand	Review/edit	5	

Chapter 3 - *Stocks and soil-plant transfer of macronutrients and trace metals in temperate New Zealand estuarine mangroves* Published in Plant and Soil (2019), *436*(1-2), 565-586			
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Andrea Alfaro	Experimental design Data interpretation Writing Review/edit	5	
Cyril Marchand	Experimental design Data interpretation Writing Review/edit	5	
Amrit Dencer-Brown	Data collection Chemical analyses Review/edit	3	
Jean-Louis Duprey	Chemical analyses Review/edit	2.5	
Anne Desnues	Chemical analyses Review/edit	2.5	

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Rémi Andreoli	Data collection Statistical analyses	2.5	
Estelle Bisson	Data collection Chemical analyses	2	
Jean-Louis Duprey	Chemical analyses Review/edit	1.5	
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Chapter 6 - *Macroelement dynamics in Avicennia marina and Rhizophora stylosa mangrove stands developing in semi-arid climate with different anthropogenic influences (New Caledonia)*
Under review

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To my Mother, Michelle Ansay,
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Who did not get to say goodbye,
But whose love accompanied Her to the end

Chapter 1

Introduction and Research Questions

1.1 Background and general context

1.1.1 Mangroves, definition and adaptations

Mangroves are vegetated ecosystems that develop in the intertidal area along sheltered coastlines, estuaries and deltas of tropical and subtropical regions (Saenger 2002, Duke 2006a, FAO 2007). The term "mangroves" also refers to the vascular plants that develop exclusively in these ecosystems, sometimes called "true mangrove species". It may also refer to other "associate" plant species that are not restricted to mangrove ecosystems but often complete the mangrove plant assemblage (Tomlinson 2016). True mangrove species include 85 species, subspecies, hybrids and varieties of species of woody plants, ferns and palm trees distributed over 18 plant families globally (Duke and Kleine 2013, Duke and Schmitt 2015). These species have developed specific sets of adaptations that allow them to cope with the particular physico-chemical constraints of the intertidal environment and their variations during the tidal cycle. Such constraints may include waterlogged substrate, lack of oxygen, high salinity and strong tidal energy (Lugo and Snedaker 1974, Walsh 1974, Naidoo 1985, McKee 1993, Duke et al. 1998, Saenger 2002, Wang et al. 2011, Krauss and Ball 2013, Tomlinson 2016). Despite these harsh environmental conditions, mangroves prosper in these ecosystems and often form luxurious forests or dense shrubby stands. The diverse adaptations that lead to this success include the production of an aboveground root system (prop, plank, stilt or knee

roots, pneumatophores, buttresses) that fulfils the double function of anchorage in the substrate and oxygenation of the belowground root system. The diffusion of oxygen from the atmosphere to the plant tissues is also facilitated by a network of porous tissues, the lenticels and aerenchyma (see reviews of Hogarth 2015, Saenger 2002, Tomlinson 2016). Mangrove species also produce propagules with various degrees of floating capacity and embryonic development to ensure their dispersion and establishment in the aquatic environment (Rabinowitz 1978, Clarke et al. 2001). Finally, mangrove species are all halophytes and thus, show diverse adaptations to resist salinity stress, either through avoidance and/or through tolerance mechanisms (Popp 1995, Saenger 2002, Wang et al. 2011, Krauss and Ball 2013, Reef and Lovelock 2015).

As a result of these specific adaptations, mangrove species are often distributed in well-defined zonation patterns that follow those of the physico-chemical constraints along the intertidal gradient (Lugo and Snedaker 1975, Snedaker 1982, McKee 1993, Duke et al. 1998).

1.1.2 Mangroves : ecological filter and coastal reservoir of nutrients and trace metals

Over recent decades, there has been a surge of attention and value placed upon mangrove ecosystems, due to the numerous goods and services they provide. Mangroves shallow waters constitute for instance a nursery for numerous animal species and play an important role in the cycle of nutrients. Thus, mangroves contribute directly and indirectly to a high secondary productivity in tropical coastal ecosystems (Alongi 1996, Mumby et al. 2004, Dahlgren et al. 2006, Nagelkerken et al. 2008). Mangroves also protect shorelines from waves and wind and maintain coastal structure by preventing erosion (Danielsen et al. 2005, Dahdouh-Guebas et al. 2005, Alongi 2008,

Gedan et al. 2011). For these reasons, mangrove coastal areas harbour some of the largest human populations in the world, whose livelihoods depend greatly on fisheries and other resources provided by these ecosystems (Rönnbäck 1999, Barbier 2000, Lee et al. 2014, Das 2017). These ecosystems also constitute an important source of income in the ecotourism sector (Barbier 2017, Friess 2017), shelter an important number of endangered species (Duke et al. 2007, FAO 2007) and are regularly the centre of discovery of new biocompounds (e.g. Xu et al. 2014, Deshmukh et al. 2018, Kerry et al. 2018).

Above all, the interest in mangroves has been enhanced by the demonstration of their capacity to store carbon in their soil and biomass. Indeed, mangroves appear to be one of the most productive ecosystems in the world (Twilley et al. 1992, Bouillon et al. 2008, Kristensen et al. 2008, Donato et al. 2011). According to recent estimates (Alongi 2014), mangrove forests worldwide present a total gross primary production (GPP) of 699 Tg C y^{-1}, 91% of which is fixed from the atmosphere by mangrove trees through photosynthesis, and the remaining 9% by micro- and macro-algae communities. From this global production and after accounting for losses through the ecosystem respiration and various exports, Alongi (2014) estimates the global Net Ecosystem Production (NEP) at 90 Tg C y^{-1}. Although they may also constitute a substantial source of carbon for the adjacent marine ecosystems (Alongi 2014, Alongi and Mukhopadhyay 2015), mangroves store an average of 283 Mg of carbon per hectare in their soils and standing biomass (Atwood et al. 2017). In addition of that important pool of carbon, significant stocks of nutrients and trace metals are also found in mangrove biomass, in particular in the leaves and live roots of mangrove trees, whose subsequent burial progressively feeds the pool of nutrients and trace metals in mangrove soils (McKee 2001, Middleton and

McKee 2001, Alongi et al. 2003, Lewis et al. 2011, Alongi 2014, Ouyang et al. 2017, Tran et al. 2017).

Finally, the standing aboveground biomass that results from mangrove high productivity (in particular dense aerial root systems) significantly reduces tidal energy (Quartel et al. 2007, Hashim and Catherine 2013). This promotes sedimentation of autochthonous and allochthonous materials, including organic matter (OM), sediments, but also materials resulting from surface runoff and anthropogenic activities such as fertilizers, detritus and toxic elements (e.g. Tam and Wong 1993, Machado et al. 2002a, b, Li et al. 2018a). Once on the forest floor, a substantial part of these materials accumulates in mangrove substrates due to the specific biogeochemical characteristics of this ecosystem. These characteristics, further detailed in Chapter 2, include a high reactivity of the OM and microbial activity, combined with a slow decomposition of the OM in waterlogged conditions (Harbison 1986, Lacerda 1998, Furukawa et al. 1997, Marchand et al. 2011a, b, 2012). Thus, mangrove soils and plant biomass may contribute to the improvement of coastal water quality and may constitute a considerable reservoir of nutrients and trace metals.

1.1.3 Mangroves and global change

Due to their high storage capacity of nutrients and trace metals and the numerous other services they provide, conservation and development of mangrove ecosystems are of prime interest in the context of global change (Mcleod et al. 2011, Siikamäki et al. 2012). However, and despite the increasing recognition of mangrove ecological services, 35% of their global area has been lost over the last four decades and keeps disappearing at a rate of 1% every year (Duke et al. 2007, Alongi 2014, Thomas et al. 2017). The primary

causes of these past and ongoing losses include the deforestation of these ecosystems through land-use conversion in favour of rice, palm oil and aquaculture industries, development of urban and recreational areas, and also forestry, marine traffic, erosion and pollution (Valiela 2001, FAO 2007, Spadling 2010, Richard and Friess 2016, Feller et al. 2017).

In addition, mangrove ecosystems are experiencing further changes in their biogeochemistry, diversity, functioning and geographic distribution in the face of climate change. For instance, important mangrove areas have already been lost to sea-level rise in response to increasing coastal immersion and erosion (Ellison 1993, Gilman et al. 2007, Lovelock et al. 2015, Goldberg et al. 2020). Globally, an increase of seasonal climatic variation is also expected, and it is likely that an increasing number of regions will experience a contrasted climate with extreme drought and rainfall episodes. For instance, there has been significant expansion of semi-arid regions and drylands as a result of shorten monsoon season that have occurred in tropical areas over the last decades, particularly in East Asia (Huang et al. 2016). Where precipitation is low, increased temperature, salinity and radiation will divert from the optimal physiological threshold of mangrove plant species, and their net primary productivity (NPP) and coverage is expected to decrease (Waycott et al. 2011). Several authors report that this is already the case and numerous papers have described important structural changes and diebacks of mangroves as a consequence of sea level rise, prolonged episodes of droughts, increased salinity and nutrient limitation as rainfall decreases (Record et al. 2013, Lovelock et al. 2015, Duke et al. 2017, Meeder et al. 2017, reviewed in Feller et al. 2017, Sippo et al. 2018, 2020). However, other effects of climate change on mangroves are rather difficult to predict. Indeed, these effects depend strongly on the synergistic effects of rainfall, temperature and CO_2 variations, nutrient status, anthropogenic

pressures and the capacity of mangrove species to adapt to these variations (Lovelock et al. 2004, 2007a, McKee et al. 2007, Gilman et al. 2008, Waycott et al. 2011, Krauss et al. 2010, 2014). The effects of global change on mangroves are therefore expected to vary considerably at different spatial scales, and the anticipation of any adverse effects requires further research at both global and regional scales.

1.2 Thesis rationale

The combination of ongoing land-use conversion and climate change are projected to further alter elemental biogeochemical cycles in mangrove plants and soils and precipitate mangrove decline and coastal erosion worldwide (Ellison and Stoddart 1991, Chambers et al. 2013, Woodroffe et al. 2016, Feller et al. 2017, Alongi 2018). As a result, the important quantity of materials that mangroves have accumulated in soils over time could be increasingly exported toward the plant compartment, the water column and the atmosphere. Increasing erosion and modification of the biogeochemistry of these ecosystems under global changes could henceforth become a threat to coastal water quality, health security and a significant contributor to greenhouse gas emission (Lewis et al. 2011, Payo et al. 2016, Costa-Böddeker et al. 2017, Hamilton and Friess 2018). Hence, a deep understanding of the processes underlying elemental cycles in mangrove ecosystems and their response to global change is of far reaching importance in order to insure suitable monitoring and conservation of these pools of nutrients and trace metals. To that end, a growing number of studies are focusing on mangrove nutrient and toxic compound cycles. These studies are also increasingly resorting to powerful technologies to improve our understanding of elemental cycles in mangrove ecosystems. In particular, the development of sequential chemical extractions (e.g.

Jayachandran et al. 2018, Thành-Nho et al. 2019a), spectroscopy (e.g. Ferreira et al. 2007a, Noël et al. 2014, 2015, Lu et al. 2019a), stable isotope methods (e.g. Sadat-Noori and Glamore 2019, Harada et al. 2020), and gas flux measurements (e.g. Barr et al. 2010, Jha et al. 2014, Léopold et al. 2016, Rosentreter et al. 2018, Zheng et al. 2018) have contributed to important advances in the understanding of mangrove geochemistry and in the quantification of mangrove elemental fluxes and budget estimates. Similarly, the development of molecular and genetic techniques has led to an increasing amount of published information on the mechanisms underlying assimilation of trace metals and nutrients in mangrove tissues, and on their impact on plant metabolism under various environmental stresses (e.g. Jithesh et al. 2006, Mehta et al. 2005, Huang et al. 2010, Chanda et al. 2013, Ravi et al. 2020). While the means may be very different, all studies have the same ultimate goal: to decipher which processes, mechanisms or factors are more at risk under global change, and therefore, where and how to concentrate mangrove monitoring, management and restoration efforts. However, these publications often address specific mechanisms in controlled environments, in the field or in greenhouses during time- and space-limited experiments, or discuss a restricted number of factors or plant developmental stages (Hogarth 2015). In the face of these increasingly detailed information and given the numerous processes that can influence elemental cycles in mangrove plants and soils at regional and global scales, field studies are increasingly needed to reconcile experimental results with observations and data collected in the field.

1.3 Thesis main aim and significance

The overall aim of this thesis is to provide a comprehensive understanding of the factors and processes driving macronutrient (N, P, K, Mg, Ca, S) and trace metal (Fe, Mn, Ni, Al, Cu, Zn, Co, Cr) dynamics and status in mangrove plants and soils *in situ* over a large range of physiographic conditions, along intertidal gradients in temperate mangroves in New Zealand and semi-arid mangroves of New Caledonia.

By focusing on the elemental status in the mangrove soil-plant continuum of climatic regions with distinct seasons, the present study intends to contribute to our understanding of global change effects on mangrove capacity of elemental accumulation. The current elemental status of temperate and semi-arid mangrove stands *in situ* are indeed the reflection of long-term climatic processes on mangrove forests and adjacent watersheds. Thus, it provides valuable insights on the lasting effects of global change on mangrove capacity to accumulate elements. It also provides valuable information on the short term effects of strong climatic variations on mangrove biogeochemistry, tree adaptability and resilience. Finally, harsh conditions in temperate and semi-arid mangroves result in a low biodiversity and large monospecific stands. These conditions allow the study of interactions between environmental factors over a large range of conditions, in mangrove stands that still experience similar pedo-climatic conditions.

In a regional context, this research will be directly relevant to sustainable management and conservation strategies of mangrove ecosystems. In New Zealand for instance, mangroves have expanded at a rate of 4% over the last century (Morrisey et al. 2007, 2010). This expansion is mostly the result of sediment and OM loading in estuaries due to urbanisation, pastoral activities and climatic conditions (Swales et al. 2007, 2015,

Lovelock et al. 2010, Pérez et al. 2017). As a result, increasing numbers of mangrove stands have been removed to preserve coastal access, biodiversity and recreational areas since 1990 (De Luca 2015, Lundquist et al. 2017). However, the importance of mangrove ecological services in New Zealand is poorly understood. Specifically, there has been very little research into macronutrients and trace metal stocks and their fate after mangrove removal in these temperate ecosystems (Dencer-Brown et al. 2018). The findings of this work will therefore be directly relevant to local authorities and decision makers seeking to manage these ecosystems.

In New Caledonia, the study of semi-arid mangrove production is also of prime interest. Mangroves in New Caledonia are found at the edge of one of the richest coral reefs in the world and support a large biodiversity in their role as nurseries and erosion control (Duke 2007, Paillon et al. 2014, Dubuc et al. 2019). In addition, mangroves of New Caledonia often stand downstream ultramafic watersheds and aquaculture ponds, two important economic activities of the island (Thomas et al. 2010, Marchand et al. 2012, Molnar et al. 2013, Noël et al. 2014). A better understanding of the impact of transition metal and nutrient inputs on mangrove ecosystems is critical to evaluate mangrove resilience to these anthropogenic pressures.

1.4 Thesis specific objectives

This Thesis is composed of one literature review (Chapter 2) and four research chapters (Chapters 3 to 6). These research papers include several case studies of elemental dynamics along the soil-plant continuum at mangrove southernmost distribution limits, in semi-arid mangroves of New Caledonia (21° S) and temperate mangroves in New Zealand (36 °S). Together, these chapters aim to fulfil six specific objectives.

The first objective is to provide the reader with a review of the ranges of macronutrient and trace metal total concentrations measured in mangrove soils, sediments and vascular plant species worldwide, as well as to assess and explain their heterogeneity at different spatial scales, with an emphasis on the latitudinal gradient (Chapters 2 and 3).

The second objective is to characterize the status and dynamics of nutrients and trace metals in mangrove soils along a classic and undisturbed semi-arid toposequence as a function of elevation and seasonal changes in soil physico-chemical properties (Chapter 4)

With the third and fourth objectives, we then explore the effects of an increase in tidal range at the lowest and highest elevations of a toposequence, respectively, on the status of macronutrients and trace metals in soils of semi-arid mangrove stands (Chapter 4).

The fifth objective is to assess the effects of OM and trace metal inputs on the status and soil-plant transfer of nutrients and trace metals along semi-arid mangrove gradients, in an undisturbed site, in border of an aquaculture farm and downstream an ultramafic watershed (Chapter 5 and 6).

Finally, ***the sixth objective*** is to determine the drivers of nutrient and trace metal soil-plant transfers in temperate and semi-arid mangroves (Chapters 3, 5 and 6).

1.5 Thesis content

This Thesis follows a manuscript format, which, at the time of submission had three published manuscripts in international peer-reviewed journals (Chapters 3 to 5), one manuscript under review (Chapter 6) and one review in preparation (Chapter 2).

The first chapters of this thesis (Chapters 1 and 2) lay out the broad context of this research. Chapter 1 intends to provide the reader with all the information necessary to understand the general context of this study, as well as its relevance, significance, aim and objectives. Chapter 2 consists in a literature review on the concentrations and status of trace metals and macronutrients in mangrove soils and plant biomass worldwide. It also summarizes the natural sources of these elements in these ecosystems, as well as the main known biogeochemical processes that lead to their mobility and accumulation within mangrove substrates. In addition, Chapter 2 highlights the large heterogeneity of mangrove biomass and soil elemental concentrations recorded worldwide, from the luxurious humid equatorial mangrove forests to the shrubby mangrove stands in arid and temperate climates.

This last point is further explored in Chapter 3, in a case study in monospecific stands of *Avicennia marina* (Forsk.) Vierh subsp. *australasica* (Walp.) J. Everett, along an estuarine gradient in temperate mangroves in New Zealand. In this Chapter, the pools of organic carbon, macronutrients and trace metals measured in mangrove soils along an estuarine gradient are presented. These values were then compared with those found in tropical mangroves, and the ecological service of temperate mangroves to act as an ecological filter for macronutrients and trace metals is discussed. In addition, the variation of elemental mobility in soils along the upstream-downstream gradient of the estuary and their translocation toward mangrove biomass is also assessed as a function of the

concentrations of nutrients and trace metals in the soil and plant compartments, and of the different soil physico-chemical properties (pore-water salinity, total soil sodium concentrations, pH, reduction-oxidation potential Eh, bulk density BD).

The next chapters (Chapters 4 to 6) focus on several case studies in semi-arid mangroves of New Caledonia. These case studies further explore the long lasting consequences of a global decrease in rainfall and an increase in tidal frame, extreme drought episodes, temperature and anthropogenic pressures on elemental status and dynamics along mangrove intertidal gradients.

Chapter 4 highlights the effects of elevation and seasonal variation on soil elemental dynamics in undisturbed mangrove stands in the middle of a classic semi-arid toposequence. This chapter focuses on the soil component and allows the comparison of two mangrove species stands that belongs to two genera ubiquitous around the world. *Avicennia marina* subsp. *australasica* (Walp.) J. Everett dominates in hypersaline soils landward whereas *Rhizophora stylosa* Griff stands develop seaward and are exposed to longer duration of immersion. This chapter demonstrates how elevation influences the response of soil surface physico-chemical properties to this seasonal change, including Eh, pH, salinity, BD, water content and chlorophyll-a. These results are then compared with the two extremities of this toposequence: in mangrove stands at highest elevations that experience higher evapotranspiration and a recent increase in tidal frame, and in fringe mangrove stands that experience longer tidal frame and perturbations. This chapter also gives an insight into the changes of sediment properties mediated by the pioneer species *A. marina* within the early phase of succession in hypersaline soils landward.

Chapters 5 and 6 outline the effect of various physiographic conditions and ranges of OM and trace metal inputs on trace metal (Chapter 5) and macronutrient (Chapter 6)

distribution in semi-arid mangrove soils and their translocation and bioaccumulation in mangrove plants. This comparison was conducted in three study sites: a site located downstream a mined ultramafic watershed, another site influenced by both mining and aquaculture activities, and a site undisturbed by anthropogenic pressure, previously described in Chapter 4.

Finally, Chapter 7 consists in a discussion and conclusion and places each objective and chapter's core findings in a broad context. It also focuses on the method's limitations and provides recommendations for further research and monitoring on mangrove elemental status and their fate under global change.

1.6 General approach and experimental design

In order to fulfil the objectives of this thesis, extensive field-based works was conducted in temperate mangroves in New Zealand and in semi-arid mangroves in New Caledonia. The samples and data collected included in this study are the following:

- soil parameters: pH, salinity, Eh, BD, total organic carbon (TOC), total and exchangeable concentrations of macroelements (N, P, Ca, Mg, K), microelements (Fe, Mn, Ni, Co, Cr), other trace metals (Cr, Al) and total Na and chlorophyll-a.

- plant morphological and physiological parameters linked to tree productivity: height, basal area, canopy volume, chlorophyll-a,

- elemental concentrations in plant tissues, including roots, aerial roots, wood, green leaves and senesced leaves: macroelements (C, N, P, Ca, Mg, K), microelements (Fe, Mn, Ni, Co, Cr), other trace metals (Cr, Al) and total Na.

In order to capture the seasonal and spatial variations driving the accumulation of nutrients and trace metals in the soil-plant continuum, this fieldwork was conducted i)

during two contrasted seasons (wet and dry in semi-arid New Caledonia, summer and winter in temperate New Zealand) and ii) over a large range of environmental conditions. For temperate mangroves in New Zealand, solely the summer season is presented in the present manuscript.

1.6.1 Temporal component of the experimental design

For each season, the sampling window has been chosen to capture the favourable or detrimental impact of seasonal factors on the biological activity in the soil and plant compartments. Therefore, the sampling took place at a time well-advanced in the season rather than at its very beginning. Thus, data collection in New Zealand took place in the middle of the warm season in summer (average temperatures of 15 to 25 °C from December to March with precipitation ranging from 70 to 90 mm) and in the middle of the cold season in winter (8 to 15 °C with precipitation ranging from 100 to 120 mm from May to August).

In New Caledonia, the choice of the sampling window was not as straightforward. In this region, summer occurs from December to March (26 to 28 °C), and is characterized by high average monthly precipitation (80 to 140 mm), while the dry season presents colder temperatures (16 to 25 °C) and lower precipitation (40 to 70 mm). However, a period of transition with high precipitation is also observed from the end of May to June (90 to 130 mm, meteo France). Thus, the timing of the data collection was based instead on a previous thesis (Helen 2014) that reported the photosynthetic activity of mangrove trees in New Caledonia along the year using the Normalised Difference Vegetation Index (NDVI, Figure 1). In general, high photosynthetic activity coincides with high nutrient uptake by the root system to fulfil metabolic and reproductive functions. It determines

the distribution and concentration of nutrients within the soil and plant tissues at a given time (e.g. Clarke 1994, Sharma 2012, Sharma et al. 2012). Based on Helen's report, data collection during the dry season was set for mid-October, after the photosynthetic activity started to decline, likely as a result of water and salinity stress. For the wet season, sampling was set for the beginning of April, when photosynthetic activity was high, but before the decline of photosynthetic activity and surge in nutrient resorption that usually starts before the end of the season favourable for plant growth (Sharma 2012).
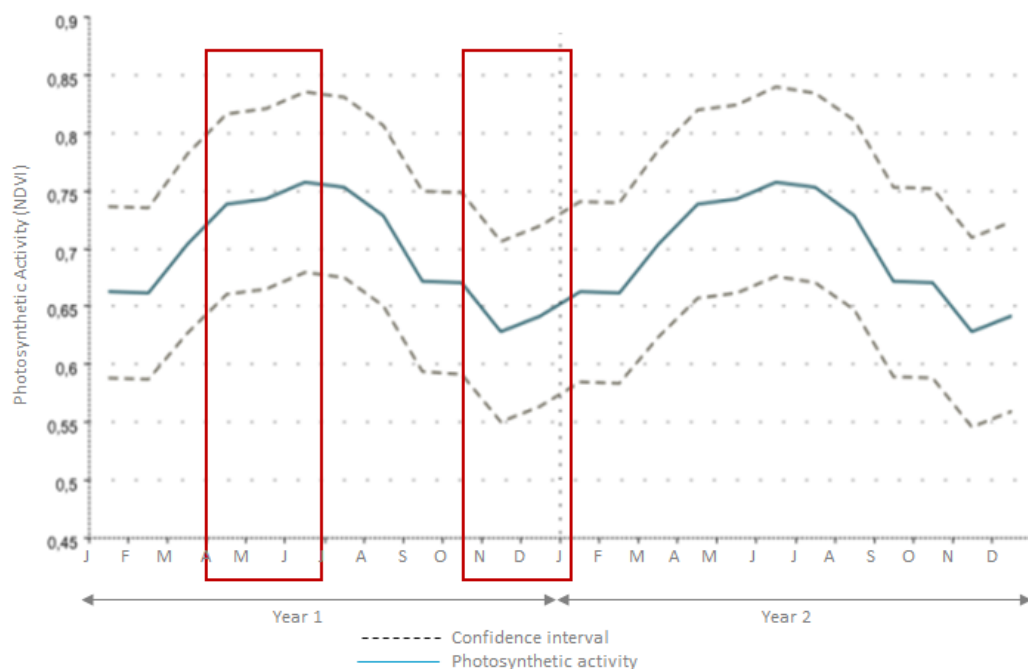
Figure 1. Mangrove tree seasonal photosynthetic activity in semi-arid mangrove New Caledonia and sampling window for data collection (modified from Helen 2014, courtesy of Bluecham SAS)

1.6.2 Spatial component of the experimental design

In each country, data collection occurred in different mangrove stands along the intertidal gradient and in different study sites that feature together a large range of

hydrographic conditions and are influenced by watersheds of various composition and different anthropogenic activities.

At each study site, data collection took place in a series of circular plots of 7 m radius, following the sampling layout given in Kauffman and Donato (2012). These plots were displayed according to a systematic sampling layout, along transects perpendicular to the water networks to analyse a potential zonation along the creeks, channels and the intertidal gradient (Figure 2). These transects were pre-established by satellite images and set out to maximize the area of exploration of the site.
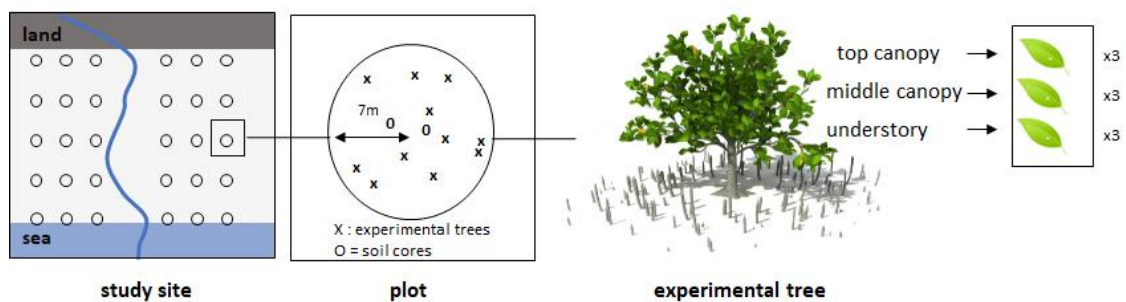
Figure 2. General experimental design and spatial aspects of the data collection

The soil parameters were measured from 0 to 50 cm depth. The plant parameters and samples were collected from a minimum of 10 trees within a plot. The physiology of leaves may vary according their exposition to light along the vertical gradient of the canopy. Thus, the functional traits of leaves were measured on three leaves in the understory, three in the middle tier and three in the top of the canopy (Figure 2). The leaves in the understory may bear characteristics of shade leaves, *i.e.* high concentration of Chl, lower Chla/b ratios, larger surface area and lower specific weights than leaves exposed to light (Ball and Critchley 1982). In addition, the leaves chosen were fully developed emergent leaves, positioned in the upper, middle and lower tiers of the canopy, respectively.

In total, these variables were sampled in 56 locations in mangrove in New Zealand and 127 in New Caledonia. The goal of this approach was to collect a dataset that covers a wide range of physico-chemical conditions that i) was representative of the environmental variations encountered in the same climate, 2) helped to identify the different responses of variables of interest to these environmental variations.

Chapter 2

Macronutrient and Trace Metal Status in Mangroves: Literature Review

2.1 Introduction

Mangroves are vegetated intertidal ecosystems that cover 138 000 km² of coastlines, estuaries and deltas of tropical and subtropical regions worldwide (Saenger 2002, Duke 2006a, FAO 2007, Giri et al. 2011). These ecosystems provide numerous ecological services whose values have been estimated at several tens of thousands of US dollars ha^{-1} y^{-1} (Das et al 2017). Among these services, mangroves act both as sinks and sources of macronutrients (e.g. C, N, P, K, S, Ca) and trace metals (e.g. Fe, Mn, Cu, Zn, Ni, Co, Cr) in marine ecosystems (Holloway et al. 2016, Alongi 2018). The position of mangrove stands in shallow coastal areas and their dense aerial root systems contribute to a low energy environment. This allows for the sedimentation of material, including sediments, organic matter (OM) and detritus and their subsequent sequestration in mangrove sediments, soils and plant biomass (Harbison 1986, Twilley et al. 1992, Furukawa et al. 1997, Lacerda 1998, Donato et al. 2011, Marchand et al. 2011a, b, 2012, Kristensen et al. 2008). Although a substantial amount of that material may end up exported from the ecosystem (e.g. Adame and Lovelock 2011, Holloway et al. 2016, Dutta et al. 2017, Alongi 2018, Taillardat et al. 2018, Thành-Nho et al. 2019a), a significant part also accumulates in biomass, soils and sediments (Rivera-Monroy et al. 1999, Trott & Alongi 2000, Bouillon et al. 2008, Maiti and Chowdhury 2013, Yan et al. 2017, Reis et al. 2017). Over time, mangroves act as a filter for autochthonous and allochthonous materials,

hence playing a key role in coastal water quality, as well as in primary and secondary production (Thomas et al. 2010).

With growing pressures from climate change and anthropogenic activities on mangrove ecosystems, the fate of the long-accumulated material and the risk it poses to adjacent coastal ecosystems are increasingly relevant for ecological safety and public health. Nutrient and trace metal pollution in coastal water directly and indirectly affects the survival, density and diversity of numerous marine species (Board 2000, Howarth et al. 2000, Johnston and Roberts 2009). In addition, assimilation of trace metals is particularly high in marine organisms. This high bioaccumulation undergoes biomagnification through the food chain and poses a serious risk to human health (e.g. Das et al. 2002, Baby et al. 2010, Bosh et al. 2016, Thành-Nho et al. 2019a,b). In addition, the potential CO_2 emission subsequent to the 0.29 to 1.67 % loss of mangrove area every year worldwide has recently been estimated at 7 Tg y^{-1} (Atwood et al. 2017, Feller et al. 2017, Thomas et al. 2017, Adame et al. 2021), a rather easily avoidable contributor to the 36 000 Tg of CO_2 y^{-1} emitted worldwide (Ritchie and Roser 2020). Conservation and monitoring of trace metal and macronutrient stocks are therefore of prime interest in the context of global change (Mcleod et al. 2011, Siikamäki et al. 2012, Sarkar 2018).

2.2 Aims

Numerous reviews have been written on the dynamics and biogeochemical cycles of nutrients or trace metals in mangrove ecosystems (e.g. Saenger 2002, Bouillon et al. 2008, Kristensen et al. 2008, Alongi 2009, 2014, Reef et al. 2010, Lewis 2011, Bayen 2012, Yan et al. 2017). The present review addresses both nutrient and trace metal distributions in mangrove ecosystems. In the first section of this chapter, median and ranges of published element concentration data are presented. This first section aims to provide the reader with a baseline of macronutrient (C, N, P, K, Mg, Ca, S), microelement (Fe, Mn, Ni, Zn, Cu), Na and other trace metal (Cr, Al) status found in mangrove ecosystems worldwide. It focuses on elemental concentration values measured *in situ* in mangrove soils, sediments and vascular plants (tree, shrub, palm and fern species). The next sections will then review the sources and main known biogeochemical processes and factors driving the status and variations of these elements in mangrove ecosystems reported in the first section. This will be followed by a brief conclusion reflecting on the ongoing actions and those that could be undertaken to preserve these pools of nutrients and trace metals at the frontier between land and sea.

2.3 Study selection, data extraction and further considerations

Data on elemental concentrations measured *in situ* were collected from 223 published field work-based studies and 2 462 data inputs from mangrove stands worldwide. For each study, concentration values (mean, SD, minimum and maximum, when available) of an element of interest in each of the soil, sediment and/or plant compartments (coarse and fine nutritive roots, aerial roots, wood, green leaves and senesced leaves) were reported from the literature. The location, geographic coordinates and tree

species composition of each studied stand were also recorded, when available. When relevant, concentrations in sediments, soils and plant tissues measured in different locations in a same study site were recorded separately (e.g. fringe versus landside, upstream versus downstream, different species, etc.). For elemental concentrations measured at several depths, mean concentrations along the entire soil or sediment profile were calculated, and the minimum, maximum and SD were recorded. Data published as illustration only were recovered with Plot Digitizer 2.6.8 software (Huwaldt and Steinhorst 2015). The global median, mean, SD and range of each element concentration in each of the substrate-plant continuum compartment were then compiled from these studies and summarised in a global table (Table 1 a-c).

Following Ferreira et al. (2007), the term sediment here-after refers to mangrove substrate that results from "deposits of solid material from any medium (air, water, ice)" and has not undergone any significant pedogenetic processes (Krumbein and Sloss 1963 in Ferreira et al. 2007). Conversely, soil is defined here as "a body comprised of solids, liquid and gases that occurs at the Earth's surface and has one or both of the following characteristics: (i) is organized into horizons or layers that are distinguishable from the initial material as a result of additions, losses, transfers and transformations of energy and matter and/or (ii) is capable of supporting rooted plants in a natural environment" (Soil Survey Staff 2003 in Ferreira et al. 2007).

In this review, unvegetated sediments and soils occupied by non-mangrove species (e.g. saltmarshes) are considered as part of the natural succession and zonation in mangrove ecosystems. Thus, elemental concentrations from sediments and non-mangrove vegetated soils were included in our database if they occurred within a mangrove study

site or within the zone of transition (ecotone) between mangroves and adjacent ecosystems (e.g. mud-flats, saltmarshes, salt-flats).

For soils and sediments, the so-called "total" and "semi-total" (acid extractable) elemental concentrations were recorded, i.e. the concentrations of all chemical species of an element (in its free, ionic forms and/or associated with other elements and materials), obtained via total or semi-total chemical extraction (typically via alkaline fusion or strong acid-based extraction, Van dijk and Houba 1999, Dijk 2002). Concentrations that refer to a more "loosened" fraction of the substrate (i.e. organic, carbonates or oxides-bound, exchangeable or "assimilable") were not included but discussed in the text.

Finally, it is worth noting that ideally, total elemental contents are expressed in terms of stocks held within the different pools of the ecosystem rather than in concentrations by dry weight of material sampled. However, when it comes to the calculation of elemental stocks in mangrove ecosystems, the task is very daunting and data extremely scarce. Although general and species-specific allometric equations are available in the literature to calculate mangrove plant biomass (e.g. Komiyama et al. 2008, Kauffman and Cole 2010, Kauffman and Donato 2012), site-specific allometric equations are relatively rare (but see Tran et al. 2017, Kangkuso et al. 2018, Van Vinh et al. 2019a, for instance).

As the density, morphology and thus biomass of each tree component of a particular species may vary significantly between and even within study sites,

Figure 3. Comparison of biomass values compiled for *Sonneratia alba* ("SOAL") in Micronesia by the means of different allometric equations ("eqn") that were developed using trees of different maximum diameters at beast height (given in parentheses) (Figure from Kauffman and Donato 2012 data from Kauffman and Cole 2010)

between individuals of different heights and diameters for instance, the use of a general allometric equation can therefore lead to dramatic differences in biomass for a given species (e.g. in Figure 3, Kauffman and Donato 2012). Similarly, soil bulk density (BD) varies among locations and depths. So does the depth of the substrate sampled in each study, which varies between the few first cm of the upper substrate layer up to 1 m deep, depending on the aims and objectives of the study (Kauffman and Donato 2012, Atwood et al. 2017). This high spatial variation coupled with differences in sampling methodology between studies adds to the difficulty in assessing elemental stocks in mangrove globally and in providing an average estimate that could be used to compare values measured within a particular mangrove stand with other study sites.

In addition, in order to compile such estimate for a given element, a high number of specific locations would therefore be required. This fact and the effect of sample size has been particularly well illustrated for the calculation of carbon stocks, the most documented element by far due to the importance of carbon dioxide and methane in

greenhouse effects (e.g. Whiting and Chanton 2001, Bouillon et al. 2008, Donato et al. 2011, Alongi 2014). In an extensive meta-analysis of 1 230 distinct sampling locations from 48 countries, Atwood et al. (2017) estimated total C mangrove soil stocks at 2 600 Tg globally, and the mean C mangrove soil stocks at 283 Mg ha^{-1}, with values ranging from 71.5 Mg C ha^{-1} (Saudi Arabia) to 935.67 Mg C ha^{-1} (Democratic Republic of Congo). This mean global C stock is significantly lower compared to previous estimates of 725 Mg C ha^{-1} based on data from Asia and the Indo-Pacific region (Alongi 2012) and of 1 023 Mg ha^{-1} from data in the Indo-Pacific region reported by Donato et al. (2011).

As indicated below, the number of studies on stocks, concentrations and spatial and temporal heterogeneity of elements other than C is far from being exhaustive. Therefore, this review does not aim to provide the complete inventory of nutrient and trace metal concentrations in mangrove ecosystems or their stocks. This review is rather an attempt to highlight what is known regarding elemental budgets in mangrove ecosystems and of the numerous determinants of their spatial and temporal variations as well as their co-variations. This review also indicates where the gaps in knowledge are so that future researchers can be guided to further investigate the effects of global changes on mangrove elemental budget.

2.4 Elemental contents in mangrove ecosystems: results

2.4.1 Overview

Overall, the ranges and SD of total elemental concentrations collected from the literature (Table 1 a-c) attest to the heterogeneous compositions of mangrove substrates and plants worldwide. Globally, most elemental concentrations range over several orders of magnitude in both plant and substrate compartments (Figure 4). Except for macronutrients C, N, K, P, and Mg essential in large quantities for plant growth (i.e. > 1 000 mg kg^{-1} of DW, Raven et al. 2005), the ranges of concentrations of other macronutrients (Ca, S), micronutrients (i.e. ≤ 100 mg kg^{-1} of DW: Fe, Mn, Cu, Zn, Ni, Co) and other trace metals (Cr, Al) in plant tissues were lower by one or two orders of magnitude than those measured in soils and sediments (Figure 4).
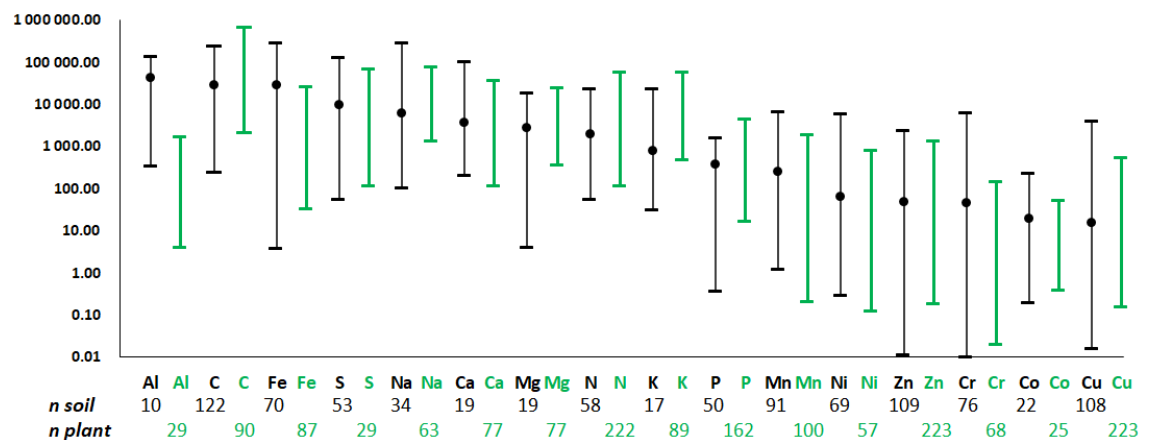
Figure 4. Median, minima and maxima of elemental concentrations found in mangrove soils and sediments worldwide (in black); ranges of elemental concentrations found in mangrove plants (all tissues) in mg kg^{-1} of DW (logarithmic scale, in green). "n" indicate the number of locations considered for each element in plant and soils. See Table 1 a-c for references

In contrast, when considering stock measurements only, most studies indicate that the vast majority of C stocks in mangrove ecosystems (up to 75%) are found in soils rather than in plant tissues (Donato et al. 2011, Alongi 2012, 2014, Figure 5). Data on total stocks of other elements among their different pools are extremely scarce in mangrove

literature. However, the few studies that have reported nutrient and trace metal stocks have demonstrated that, as for C, the pool of S and Ca is larger in mangrove substrate than in mangrove below and above ground biomass (Alongi et al. 2003). Conversely, N, P, K and Mg stocks may be similarly distributed among soils or plant biomass, depending on the location and the species considered (Alongi et al. 2003, Tran et al. 2017).
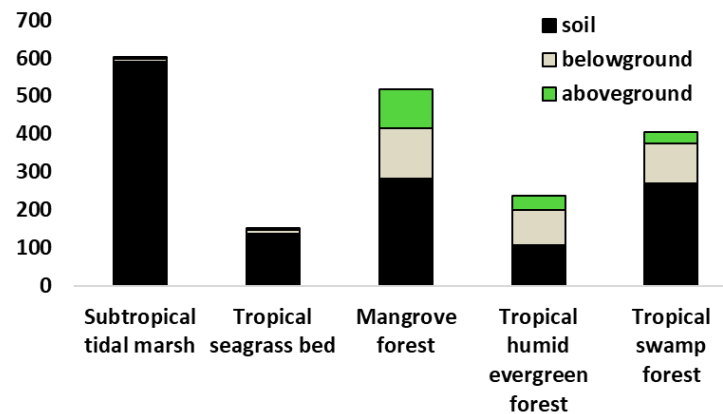
Figure 5. Comparison of mean global carbon stocks of different terrestrial and marine tropical and subtropical vegetated ecosystems. Figure re-drawn from Alongi (2014), with mangrove soil mean global C stock estimate of 725 Mg ha^{-1} compiled in 2012 replaced by recent estimate compiled by Atwood et al. (2017)

As for any ecosystems, the sources and biogeochemical processes driving elemental composition of mangrove soils and plant tissues vary at several spatial scales, which is reflected in the wide ranges of elemental concentrations illustrated in Figure 4. A deep understanding of these sources and processes is essential to assess elemental contents in ecosystems and their fate under global change. Chapin (1991) reported that nutrients available for plants enter the soils via three major sources : i) the atmosphere, ii) weathering (i.e. breaking down of rocks, soils, minerals and artificial materials by long exposure to the atmosphere, water and biological organisms) and iii) recycling of biological material. Ultimately, elemental composition and concentrations in mangrove plants and soils can therefore be traced to that of the atmosphere, terrestrial crust (Table 2), seawater (Table 3) and to the requirements of nutrients for mangrove plant growth (e.g. Feller 1996, Feller et al. 2002, 2003). Hence, the global rank of median trace

metal concentrations in soils and sediments illustrated in Figure 4 coincided with that of the major trace metal components of the upper terrestrial crust (Al > Fe > Mn, Table 2), followed by lower and similar median concentrations of its minor trace metal components Ni, Zn, Cr, Co, Cu. The abundance of macroelements (C > S > Ca > Mg > N > K > P) and that of Na in mangrove soils and sediments attests on the other hand to the combined influence of the atmosphere, weathering, seawater (Table 3) and OM recycling on the substrate.

Table 1a. Median, mean (+-SD) and ranges of C, N, P, K, Ca, Mg concentrations measured in soils and/or sediments, fine nutritive roots, coarse roots, aerial roots, wood, green and senesced leaves in mangroves worldwide. n = number of sample data used (references used to compiled this table are given in footnote*)

			median	mean	SD	min	max	n	references
C	(mg kg^{-1})	total soils & sediments	29 750	49 918	50 363	798	250 000	122	1-31
		fine/nutritive roots	351 400	351 400	23 052	330 000	390 000	3	1,5
		coarse roots	417 000	417 222	19 234	384 000	452 000	9	32
		aerial roots	440 000	437 757	9 573	418 000	449 600	7	1,32
		wood	440 000	429 055	34 430	344 900	492 000	41	5,17,18,32-35
		green leaves	431 000	426 145	43 740	320 000	509 000	58	1,17,18,32-46
		senesced leaves	421 214	418 867	63 195	289 000	539 000	14	5,41,42
N	(mg kg^{-1})	total soils & sediments	1 900	4 108	4 756	60	24 000	58	1,2,6,8,11-13,19,23,27,28, 41,43,47-65
		fine/nutritive roots	3 772	5 229	3 906	2 573	12 100	5	1,66,67
		coarse roots	8 000	7 444	3 841	1 300	12 800	6	40,55,60,66,68
		aerial roots	2 355	2 355	64	2 310	2 500	2	1,60
		wood	3 815	5 888	5 097	660	17 000	13	1,35,40,55,60,68
		green leaves	13 161	14 326	6 376	3 200	45 000	125	1,35-40,42,44,45,47,55,63, 65,69-101
		senesced leaves	5 100	6 027	3 600	400	20 300	76	35,37,41,42,45,55,60,65, 72,76,79,81,82,86,87,89- 91,94,97,100,101-109
P	(mg kg^{-1})	total soils & sediments	383	410	363	5	1 600	50	1,2,6,8,11,23,28,41,48,49, 53, 55-59,63-65,67,74,88, 110-114
		fine/nutritive roots	284	288	66	218	458	5	1,67
		coarse roots	1 110	1 141	406	100	1 660	6	40,55,60,68,114
		aerial roots	813	813	759	232	1 350	3	1,60,114
		wood	760	829	683	117	2 200	12	1,40,55,60,68,114
		green leaves	1 135	1 201	645	100	3 700	106	1,36-41,45,47,55,60,65,68, 70-83,85-89,92-101, 114- 118
		senesced leaves	566	621	427	90	2 326	34	2,45,55,60,65,76,79,81,82, 86,87,89,93,94,97,100, 101,117
K	(mg kg^{-1})	total soils & sediments	786	4 168	7 030	31	24 400	17	1,11,23,28,41,53,55,63- 65,74
		fine/nutritive roots	3 050	3 050	919	2 200	4 600	2	1
		coarse roots	10 250	10 250	6 435	5 700	14 800	3	40,55
		aerial roots	3 100	3 100	-	2 300	3 800	1	1
		wood	2 700	2 200	1 084	900	3 400	7	1,40,43,55
		green leaves	8 800	9 610	4 755	3 000	44 700	67	1,36,39,40,41,43,47,55,65, 70,71,74,76,77,84-86,92, 96,99,115,118-122
		senesced leaves	4 276	4 319	1 310	2 268	7 200	9	41,55,65,86,94
Ca	(mg kg^{-1})	total soils & sediments	3 731	12 635	18 305	210	106 400	19	1,11,23,28,41,53,64,65,74, 123,124
		fine/nutritive roots	11 500	11 500	4 384	5 200	29 300	2	1
		coarse roots	6 300	6 300	-	6 300	6 300	1	40
		aerial roots	9 000	9 000	-	2 000	12 900	1	1
		wood	7 100	5 820	4 327	1 100	14 300	5	1,40
		green leaves	2 711	5 065	5 461	130	19 708	60	1,36,39,40,47,65,70,71,74, 76,77,84,86,92,96,115,119- 122
		senesced leaves	22 516	21 664	4 880	12 384	26 334	8	41,65,86,94
Mg	(mg kg^{-1})	total soils & sediments	2 759	4 485	4 488	4	18 700	19	1,11,23,28,41,53,64,65,74, 123,124
		fine/nutritive roots	7 450	7 450	636	6 200	9 300	2	1
		coarse roots	3 000	3 000	-	3 000	3 000	1	40
		aerial roots	7 600	7 600	-	3 000	11 600	1	1
		wood	1 300	7 320	8 427	1 000	19 400	5	1,43
		green leaves	4 626	5 507	2 785	1 300	16 700	60	1,36,39,40,41,47,65,70,71, 74,76,77,84,86,92,96,115, 119-122
		senesced leaves	6 271	6 440	1 325	4 246	8 394	8	41,65,86,94

Table 1b. Median, mean (+-SD) and ranges of S, Na, Fe, Mn, Ni, Al concentrations measured in soils and/or sediments, fine nutritive roots, coarse roots, aerial roots, wood, green and senesced leaves in mangroves worldwide. n = number of sample data used (references used to compiled this table are given in footnote*)

			median	mean	SD	min	max	n	references
S	(mg kg⁻¹)	total soils & sediments	9 903	16 822	18 988	57	128 266	53	1,8,9,17-22,24,25-27,125
		fine/nutritive roots	34 700	34 700	11 172	18 500	54 000	2	1
		coarse roots	-	-	-	-	-	-	-
		aerial roots	700	700	-	700	800	1	1
		wood	450	450	58	300	600	4	1
		green leaves	2 360	3 893	3 020	1 700	12 084	19	1,41,70,74,77
		senesced leaves	7 274	12 055	9 669	5 708	23 182	3	41,94
Na	(mg kg⁻¹)	total soils & sediments	6 270	7 733	8 074	103	300 000	34	1,11,28,41,53,59,64,65,69, 123,124,126-128
		fine/nutritive roots	27 150	27 150	3 041	24 000	30 000	2	1
		coarse roots	38 500	38 500	-	38 500	38 500	1	43
		aerial roots	11 200	11 200	-	10 000	12 600	1	1
		wood	4 400	6 660	5 394	3 100	16 300	5	1,43
		green leaves	17 212	22 781	13 936	1 100	59 000	47	1,36,39,40,41,47,65,70,71, 76,84,86,92,96,115,119-122
		senesced leaves	19 526	24 370	13 659	16 185	51 954	7	41,65,86,94
Fe	(mg kg⁻¹)	total soils & sediments	28 974	43 936	43 751	4	300 000	70	1,2,9,10,17,18,20,21,23-26,29,74,123,129-139
		fine/nutritive roots	8 139	8 954	3 533	2 300	21 300	6	1,22,129
		coarse roots	7 433	7 248	6 301	15	19 897	9	22,40,140,141
		aerial roots	690	1 545	1 599	41	4 015	8	1,129,133,140
		wood	112	147	87	31	451	11	1,40,129,140
		green leaves	242	362	443	32	2 287	46	1,22,40,41,70,74,77,96, 117, 129,130,140-143
		senesced leaves	262	299	197	34	555	7	41,117,131
Mn	(mg kg⁻¹)	total soils & sediments	257	531	954	1	6 725	91	1,2,17,18,21-23,26,29,63, 74,118,123,129-133,138, 139,144-169
		fine/nutritive roots	63	60	27	14	154	6	1,22,129
		coarse roots	75	155	166	15	544	11	22,40,141,152,161
		aerial roots	52	334	446	4	1 045	8	1,129,133,148,161
		wood	7	20	37	2	118	12	1,40,129,148,161,163
		green leaves	113	248	293	5	1 552	57	1,22,40,41,63,70,74,77,99, 129,130,139,141,142,148, 152,155,157,159,161,165, 166,170,172
		senesced leaves	44	142	235	23	618	6	41,131
Ni	(mg kg⁻¹)	total soils & sediments	63	683	1 096	0	6 080	69	17,18,21,22,25,130-133, 136,139,141,144,145,147-153,155,156,158,160,162, 164,168,169,173-191
		fine/nutritive roots	33	212	284	1	666	5	22,129,177
		coarse roots	5	119	173	0	392	11	22,140,141,178,186,189
		aerial roots	4	4	1	2	9	7	129,133,140
		wood	3	3	2	0	14	8	129,140,150,178
		green leaves	5	15	24	0	108	22	22,129,130,139,140,141, 150,155,157,178,189
		senesced leaves	2	2	0	1	2	4	131
Al	(mg kg⁻¹)	total soils & sediments	44 255	37 745	34 697	348	136 400	10	18,23,123,131
		fine/nutritive roots	-	-	-	-	-	-	-
		coarse roots	74	74	79	4	130	2	40,140
		aerial roots	660	660	-	26	1 429	1	140
		wood	42	60	40	18	371	4	40,140
		green leaves	150	123	-	26	270	18	40,70,140
		senesced leaves	356	333	89	23	414	4	131

Table 1c. Median, mean (+-SD) and ranges of Cu, Zn, Co, Cr concentrations measured in soils and/or sediments, fine nutritive roots, coarse roots, aerial roots, wood, green and senesced leaves in mangroves worldwide. n = number of sample data used (references used to compiled this table are given in footnote*)

		median	mean	SD	min	max	n	references
Cu (mg kg^{-1})	total soils & sediments	15	37	72	0	4 050	108	1,17,18,22,29,63,74,123, 129-133,135,139,144, 145,147-158,160,161, 163-165,167,168,173-182,184-214
	fine/nutritive roots	18	39	52	6	447	7	1,22,129,177
	coarse roots	21	51	61	1	334	33	22,40,140,141,152,161, 165,168,178,186,189,192, 193, 201,202,213,215
	aerial roots	7	7	5	0	17	10	1,129,133,140,156,161
	wood	6	8	6	-	21	56	1,40,129,140,150,161,163, 178,192,216-218
	green leaves	8	13	36	0	412	112	1,22,40,63,70,74,77,96, 99,118,129,130,139-142,144,149,150,152,155, 157,159,161,165,168, 171,172,178,189,192,193, 201,202,205,213,216,217, 219-221
	senesced leaves	3	9	13	2	32	5	131,217
Zn (mg kg^{-1})	total soils & sediments	50	88	108	0	2 372	109	1,17,18,22,29,63,74,123, 129-133,135,139,144, 145,147-157,160,161, 163-165,167,168,173-182,184-214
	fine/nutritive roots	18	71	135	9	1 108	7	1,22,129,177
	coarse roots	37	68	85	0	640	34	22,40,140,144,152,161, 164,165,178,186,189,192, 193,201,202,213,215,222
	aerial roots	8	18	19	1	60	10	1,129,133,140,156,161
	wood	16	17	13	0	130	48	1,40,129,140,150,161,163, 178,192,217
	green leaves	15	19	16	0	120	112	1,22,40,63,70,74,77,96,99, 118,129,130,139-142,144,149,150,152,155, 157,159,161,164,165,169, 171,172,178,189,192,193, 201,202,205,213,216,217, 219-222
	senesced leaves	16	24	26	7	69	5	131,217
Co (mg kg^{-1})	total soils & sediments	20	57	78	0	229	22	17,18,22,29,123,133,156, 173,176,177,184,190,212
	fine/nutritive roots	19	23	21	0	47	3	22,177
	coarse roots	9	12	12	2	31	8	22,40,141
	aerial roots	3	3	0	3	4	4	133
	wood	7	7	-	7	7	1	40
	green leaves	1	3	4	0	9	9	22,40,70,141
	senesced leaves	-	-	-	-	-	-	-
Cr (mg kg^{-1})	total soils & sediments	46	190	440	0	6 240	76	17,18,21,29,123,129-133,139,144,148,150-153,155-158,160,161,164,165,168, 169,173,176,177,179,181-185,187-191,194,198,204,205,207, 208,211-213,223
	fine/nutritive roots	21	21	8	2	124	3	129,177
	coarse roots	13	14	7	0	26	15	140,141,152,161,165,189, 213
	aerial roots	7	7	3	0	12	9	129,133,140,156,161
	wood	0	1	1	0	18	8	129,140,150,161
	green leaves	2	6	11	0	53	29	70,129,130,139-141,144, 150, 152,155,157,161,165, 172, 189, 205,213
	senesced leaves	1	1	0	1	2	4	131

* [1]Alongi 2003; [2]Alongi et al. 2005a; [3]Ataullah et al. 2017; [4]Bouillon and Boschker 2006; [5]Bouillon et al. 2008; [6] Castañeda-Moya et al. 2006; [7]Das et al. 2019; [8]Deborde et al. 2015; [9,10]Ferreira et al. 2007a,b; [11]Hossain and Nuruddin 2016; [12]Kristensen et al. 1995; [13]Lacerda et al. 1995; [14-16]Leopold et al. 2013, 2015, 2016; [17-22]Marchand et al. 2011a,b, 2003, 2004, 2012, 2016; [23]Matsui et al. 2015; [24]Nobrega et al. 2013; [25]Noël et al. 2014; [26,27]Otero et al. 2006, 2017; [28]Sukardjo 1994; [29]Than-Nho et al. 2019a; [30]Upkong 2018; [31]Vaijayanthi and Vijayakumar 2014; [32]Rodrigues et al. 2014; [33,34]Marchand et al. 2005, 2008; [35]Sharma 2012; [36]Betoulle et al. 2001; [37]Bunt 1982; [38]Day et al. 1999; [39]Gong and Ong 1990; [40]Jayasekera 1991; [41]Medina et al. 2015; [42]Rao et al. 1994; [43]Saenger 2002; [44]Slim et al. 1996; [45]Wafar et al. 1997; [46]Weiper 1995 in Saenger 2002; [47]Balasubramaniam et al. 1992 in Saenger 2002; [48]Boto & Wellington 1984; [49]Cardona and Botero 1998; [50]Changprai 1984 in Saenger 2002; [51]Hong 1996; [52]Hossain et al. 2012; [53]Khan et al. 1993; [54]Kristensen et al. 1988; [55]Kumar et al. 2011; [56]Kuraishi et al. 1985; [57]McKee 2001; [58]Empi et al. 2010; [59]Sanchez-Andrés et al. 2010; [60]Silva et al. 2007; [61]Sukardjo et al. 1984 in Saenger 2002; [62]Sukardjo & Yamada 1992; [63]Tam and Wong 1995a; [64]Ukpong 1997; [65]Wang et al. 2003; [66]Bulmer et al. 2016; [67]Lovelock et al. 2006a; [68]Tran et al. 2017; [69]Macnae 1966; [70]Ahmed et al. 2010; [71]Aksornkoae and Khemnark 1984 in Saenger 2002; [72]Alongi et al. 2005b; [73]Barboza et al. 2006; [74]Berbini et al. 2006; [75]Chen et al. 1982 in Ahmed et al. 2010; [76]Clough and Attiwill 1975; [77]Cuzzuol & Campos 2001; [78]Feller 1995; [79-82]Feller et al. 1999,2002,2003,2007; [83]Gritcan et al. 2016; [84]Lacerda et al. 1986; [85]Lin and Lin 1985; [86]Lin & Wang 2001; [87]Lin et al. 2010; [88,89]Lovelock et al. 2004,2011; [90]McKee and Faulkner 2000; [92-94]Medina et al. 1995, 2001, 2010; [95]Medina and Fransisco 1997; [96]Naidoo 2006; [97]Ochieng and Erftemeijer 2002; [98]Saur et al. 1999; [99]Spain and Holt 1980; [100]Wei et al. 2015; [101]Zhou et al. 2010; [102]Fell et al. 1975; [103]Heald 1971; [104]McKee and Feller 1995; [105]Ong et al. 1982; [106]Poovachiranon et al. 1986; [107]Robertson 1988; [108]Steyer 1988; [109]Twilley et al. 1986; [110]Da Cruz et al. 2013; [111]Fabre et al. 1999; [112]Hesse 1961; [113]Lovelock et al. 2006b; [114]Silva et al. 1998; [115]Imbert and Portecop 1986; [116]Mendoza et al. 2012; [117]Nielsen and Andersen 2003; [118]Tam_et al. 1995a,b; [119]Golley et al. 1962; [120]Komiyama et al. 1988; [121]Lacerda et al. 1985; [122]Naidoo 2010; [123]Mejias et al. 2013; [124]Sah et al. 1989; [125]Molnar et al. 2014; [126]Hutchings and Saenger 1987; [127]Jiménez 1984; [128]Wells 1982; [129]Abohassan 2013; [130]Abou Seedo et al. 2017; [131]Almahasheer et al. 2018; [132]Awal et al. 2009; [133]D'Mello & Nayak 2016; [134]Ferreira et al. 2007a; [135]Hashem 1993; [136,137]Noël et al. 2015,2017; [138]Okbah and Shridah 2005; [139]Sadiq and Zaidi 1994; [140]e Silva 2006; [141]Thanh-Nho et al. 2019b; [142]Madi et al. 2015; [143]Saifullah et al. 2004; [144]Defew et al. 2005; [145]Farias et al. 2007; [146]Gueiros et al. 2003; [147]Jingchun et al. 2006; [148]Lewis et al. 2011; [149]Machado et al. 2002a; [150]Marchand et al. 2006; [151]Melville and Pulkownik 2007; [152]Nath et al. 2014a; [153]Perdomo et al. 1998; [154]Peters et al. 1997; [155]Peng et al. 1997; [156]Preda and Cox 2002; [157]Ragsdale and Thorhaug 1980; [158]Ray et al. 2006; [159]Sarangi et al. 2002; [160]Shridah 1999; [161]Silva et al. 1990; [162]Tam and Wong 2000; [163]Thomas and Fernandez 1997; [164]Weng-jiao et al. 1997; [165]Yadav et al. 2015; [166]Yan et al. 2017; [167,168]Zheng and Lin 1996a,b; [169]Zheng et al. 1996; [170]Agoramoorthy et al. 2008; [171]Bhosale 1979; [172]Lacerda 1998 in Lewis et al. 2011; [173]Alam et al. 2010; [174]Amin et al. 2009; [175]Bayen 2012; [176]Bodin et al. 2012; [177]Chaudhuri et al. 2014; [178]Chiu and Chou 1991; [179]Cuong et al. 2005; [180]Davari et al.2010; [181]Essien et al. 2009; [182]Fernandes et al. 2011; [183]Guzman and Jimenez 1992; [184]Kruitwagen et al. 2008; [185]Mackey and Hodgkinson 1995; [186]Ong Che 1999; [187]Shriadah 1999; [188]Silva et al. 1996; [189]Usman et al. 2013; [190]Vane et al. 2009; [191]Zöckler and Bunting 2006; [192]Analuddin et al. 2017; [193]Chen 2003; Kamau 2002; [194]Kehrig et al. 2003; [195]Guzman and Jimenez 1992; [196]Harris and Santos 2000; [197]Jara-Marini et al. 2008 ;[198]Kehrig et al. 2003; [199]Lacerda et al. 1993; [200-202]MacFarlane et al. 2000,2003,2007; [203]Machado et al. 2002b; [204]Mtanga and Machiwa 2007; [205]Negi 2017; [206]Praveena et al. 2007; [207]Qiu et al. 2011; [208]Ramanathan et al. 1999; [209]Sarkar et al. 2008; [210,211]Tam and Wong 1995b,2000 ; [212]Tue et al. 2012; [213]Wang et al. 2013; [214]Yap et al. 2009; [215]Ong 1999; [216]Chakrabarti et al. 1993; [217]Saenger

and McConchie 2004; [218]Yu et al. 2007; [219]Agoramoorthy et al. 2008; [220]MacFarlane et al. 2002; [221]Peterson et al. 1979; [222]Shete et al.2007; [223]Yang et al. 2019.

Table 2. Abundance of nutrients and trace metals in terrestrial crust from exposed regions of the continents (Rudnick and Gao 2003)

	elements (form)	concentrations in the upper crust
major components (in weight %)	Si (SiO$_2$)	66.6
	Al (Al$_2$O$_3$)	15.4
	Fe (FeO$_x$)	5.04
	Ca (CaO)	3.59
	Na (Na$_2$O)	3.27
	K (K$_2$O)	2.8
	Mg (MgO)	2.48
	Ti (TiO$_2$)	0.64
	P (P$_2$O$_5$)	0.15
	Mn (MnO)	0.1
minor components (in ppm)	F	557
	Cl	370
	Cr	92
	N	83
	Zn	67
	S	62
	Ni	47
	Cu	28
	Co	17.3
	B	17
	Pb	17
	Br	1.6
	Mo	1.1
	Cd	0.09

Table 3. Principal constituents of seawater (Allaby and Allaby 1999)

	Ionic form	mg g^{-1} of solution (‰)	% of dissolved material
Chloride	Cl$^-$	18.980	55.05
Sodium	Na$^+$	10.556	30.61
Sulphate	So$_4^{2-}$	2.649	7.68
Magnesium	Mg^{2+}	1.272	3.69
Calcium	Ca^{2+}	0.400	1.16
Potassium	K$^+$	0.380	1.10
Bicarbonate	HCO^{3-}	0.140	0.41
Bromide	Br$^-$	0.065	0.19
Borate	H$_3$BO^{3-}	0.026	0.07
Strontium	Sr^{2+}	0.008	0.03
Fluoride	F$^-$	0.001	0.00
total		34.477	99.99

The range of elemental concentrations found within mangrove plant tissues depends on the requirements of each species, elemental abundances and availability within the medium, but also on mangrove plant species ability to alter the chemistry at the soil-rhizosphere interface and to cope with eutrophication, metal stress as well as other constrains of the environment (Andersen and Kristensen 1988, Ball and Munns 1992, Saenger et al. 2002, Reef et al. 2010, Marchand et al. 2016). These influences result in differential elemental distribution in mangrove plant organs.

For instance, global median elemental concentrations in mangrove soils, roots and green leaves attest of higher bioaccumulation of nutrients essential for photosynthetic activities and osmotic balance within mangrove green leaves than within roots and soils (N and K, Figure 6). Conversely, median concentrations of trace metals – harmful for plant metabolism at high concentrations – remain higher in mangrove substrate than in plant tissues. Trace metals also accumulate in lower concentrations in aboveground tissues than in mangrove roots, where they tend to be bound and sequestrated within the root epidermis and cortex (Figure 6, Lacerda et al. 1988, Che 1999, Saenger 2002, MacFarlane et al. 2007, Marchand et al. 2016).
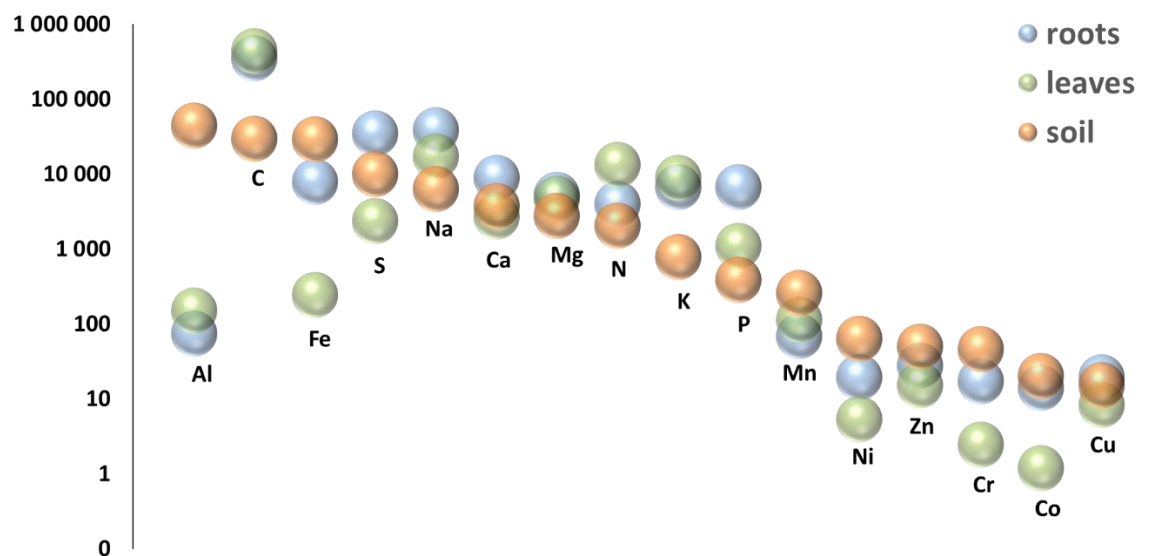
Figure 6. Median concentrations of macronutrients, trace metals and Na (mg kg^{-1} DW, logarithmic scale) in roots (blue bubbles), green leaves (green bubbles) ranked by median values measured in mangrove soils and sediments worldwide (orange bubbles). See Table 1 a-c for references

Regarding nutrient requirements, median elemental concentrations found in mangrove green leaves were very similar to leaf concentrations of essential macro (i.e. required in quantities ≥ 1 000 mg kg^{-1} for plant growth: C > N > K > Mg > Ca > S > P) and micronutrients (i.e. required in quantities ≤ 100 mg kg^{-1} of DW for plant growth: Fe >

Mn > Zn > Cu > Ni > Co) found across the plant kingdom, thus reflecting similar macro and micro nutrient needs for plant growth (see Figure 7 and Appendix 1 – Appendix 4). Although there is of course a great variation in elemental concentrations within and among plant tissues across the plant kingdom, several significant differences occur between mangrove species and other plant species (Figure 7). Markedly, the influence of seawater composition results in median concentrations in Mg and S in mangrove green leaves (4.6 and 2.4 g kg^{-1} DW, respectively) that are twice as high as those required for growth in the plant kingdom (2.0 and 1.0 g kg^{-1} DW, respectively, Figure 7). Most of all, sodium, non-essential element for plant metabolism in general, is the second most abundant element found in mangrove leaves after C (17 g kg^{-1} DW, Figure 7).
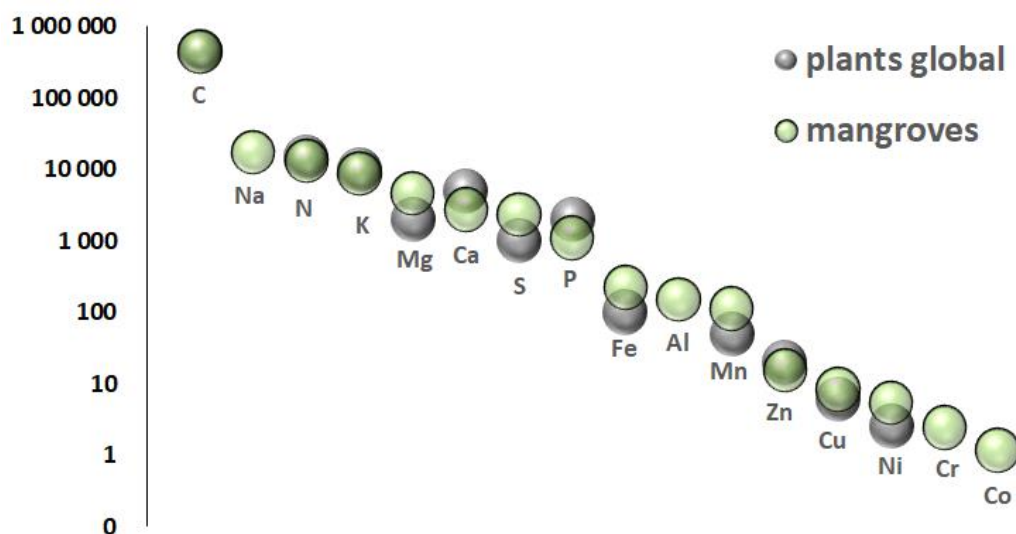
Figure 7. Differences between the recommended concentrations of essential macro (C > N > P > K > Ca > Mg > S) and microelements (Fe > Mn > Zn > Cu > Ni) for plant growth in general (grey bubbles, Raven et al. 2005), and the median elemental concentrations in mangrove leaves worldwide (green bubbles, see Table 1 a-c for references) in mg kg^{-1} of dry weight (logarithmic scale). Although Co is also required in small quantities for plant growth in general, no data exists on its adequate concentrations in plant tissues for the plant kingdom at large

This particularity is due to an overall high resistance (including both tolerance and avoidance mechanisms) of mangrove species to salinity stress (Popp 1995). For instance,

mangrove species resistance to salinity may include salt sequestration through storage within the root tissues and accumulation and/or translocation to senesced leaves (Wang and Lin 1999, Saenger et al. 2002, Wang et al. 2003, Medina et al. 2010). These last adaptations may reflect in the higher global median concentration values of Na found in fine and coarse roots (27.1 and 38.5 g kg^{-1} DW) and senesced leaves (19.5 g kg^{-1} DW) compared to the median values found in green leaves (17.2 g kg^{-1} DW) > aerial roots (11.2 g kg^{-1} DW) > wood (4.4 g kg^{-1} DW) (illustrated in Figure 6). Finally, mangrove leaf composition also differs from that of many species of the plant kingdom by lower concentration of P (Figure 7). Despite a high primary productivity and large variability between and within study sites, mangrove ecosystems are often oligotrophic, with particularly low levels of P and/or N, an inherent characteristic of heavily weathered soils observed in some tropical regions. In the case of N, this nutrient deficiency in mangrove soils is partially alleviated by atmospheric biological fixation (see section 2.5.1), whereas P availability for plant uptake depends mostly on nutrient recycling (Feller et al. 2007, Lovelock et al. 2007b, Reef et al. 2010).

2.4.2 Global elemental trends

The research of global trends and particularly that of gradients in ecological processes is a persistent theme for ecologists. The classification and ordering of ecological processes and services according to climatic regions and latitudes is of the utmost importance in terms of tackling, monitoring and anticipating global changes and their effects in specific regions. While 90% of mangrove specific diversity thrive between 5° S and 5° N in tropical humid areas, these ecosystems also develop in a large range of other climatic conditions, including semi-arid, arid, subtropical and temperate oceanic climates (*sensus*

Köppen classification, Blasco 1984, Clough 1992, Peel et al. 2007). The geographic limits of their distribution extend up to 32°20' N in Bermuda and to 38°45' S in Australia (Spalding 2010, Giri et al. 2011). Although the determinant of their distribution is still under debate, it is commonly accepted that mangrove expansion at upper latitudes is restricted by major oceanic currents and by the 20 °C winter isotherm of both atmosphere and seawater surface (Duke et al. 1998, Alongi 2009, Quisthoudt et al. 2012).

2.4.2.1 Latitudinal gradient in mangrove biomass and C stocks: discrepancy between plants and soils

Significant differences in vascular plant physiognomy, diversity, functionality and productivity are found along mangrove latitudinal spectrum (Clough 1992, Twilley et al. 1992, Saenger and Snedaker 1993, Lovelock et al. 2007b, Bouillon *et al.* 2008, Hutchison et al. 2014, Simard et al. 2019). Several studies have reported that, as within terrestrial ecosystems, mangrove daytime net canopy production shows an important decline from the equator to the tropics (Clough 1992, Alongi 2014), with a decrease in tree height (Kuchler 1972, Woodroffe and Grindrod 1991, Simard et al. 2019) and lower litterfall, stem growth and aboveground biomass values with increasing latitudes (Saenger and Snedaker 1993, Ye et al. 2003, Alongi 2014, Hutchinson et al. 2014, Xiong et al. 2019 Figure 8 and Figure 9).
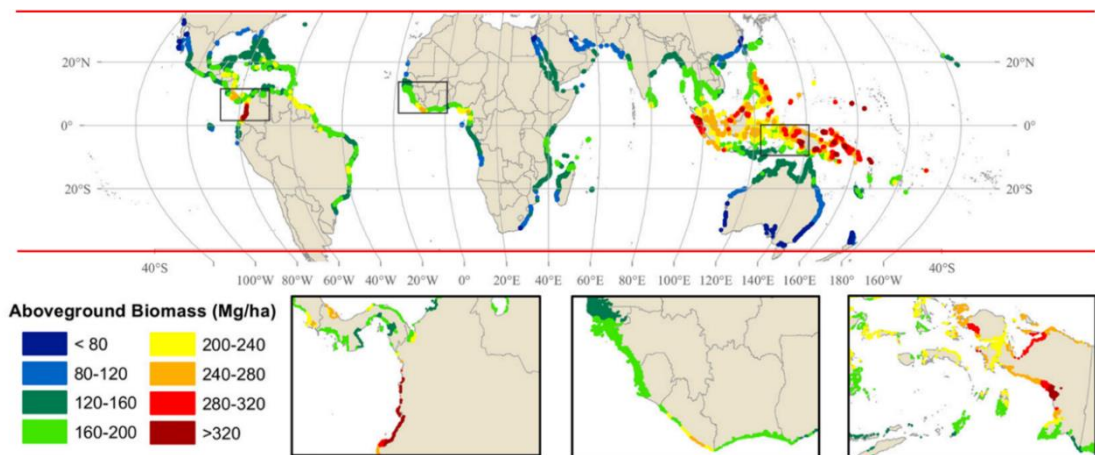
Figure 8. Upper latitudinal limits of mangrove global distribution (in red, from Giri et al. 2011) and aboveground biomass (Mg ha^{-1}) per unit areas (from Hutchinson et al. 2014)
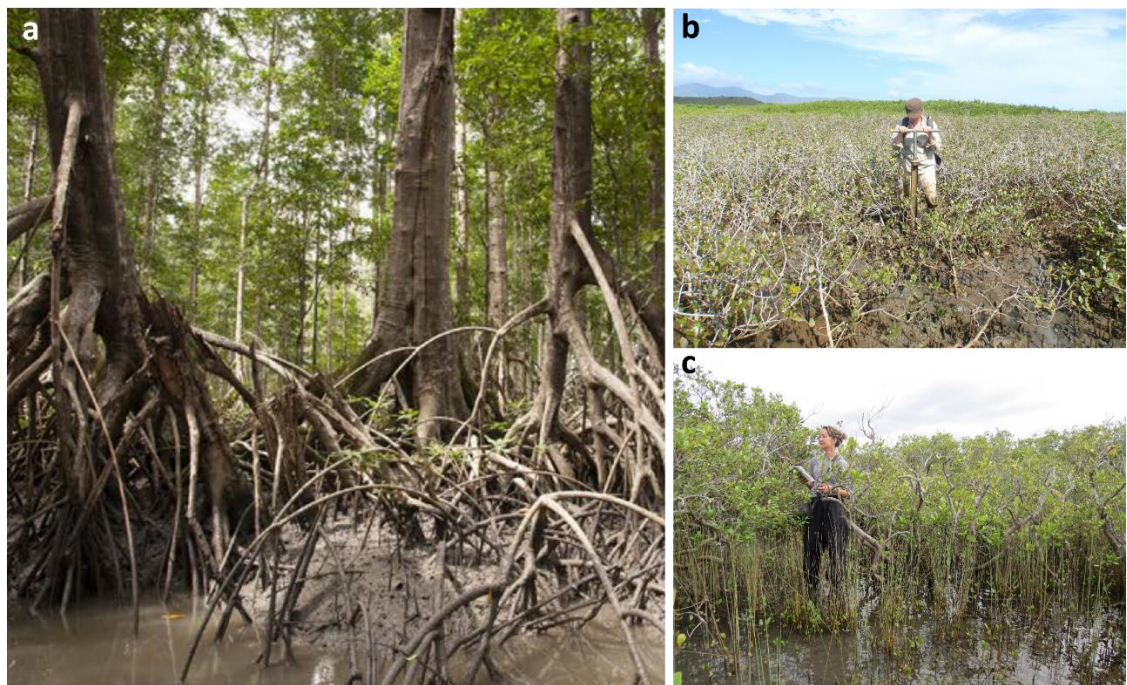
Figure 9. Contrast in mangrove tree heights and aboveground biomass across the latitudinal spectrum, from (a) the equatorial mangrove stands at 0.12° N in Gabon (the tallest mangrove trees in the world – up to 65 m tall – recorded so far, photo credit Simard et al. 2019) to (b) the semi-arid mangroves of New Caledonia (21° S) and (c) temperate mangrove stands in New Zealand (36° S, photo credits Carine Bourgeois)

A commonly accepted hypothesis to explain this decrease in tree productivity and structural characteristics with increasing latitude is a growth rate limitation induced by a briefer optimal season (Westoby et al. 2002, Zhang et al. 2009), particularly by lower mean annual precipitation and/or temperature away from the equator, as well as higher

cyclone relative frequency (Simard et al. 2019, Figure 10 a,b). Away from the humid tropics, extreme drought, winter temperatures, insulation, water deficit and lower amounts of solar radiation decrease stomatal conductance and electron transfer rate within the photosystems (Ball and Farquhar 1984a, b, Ball et al. 1988, Clough and Sim 1989, Kao et al. 2004, Lambers et al. 2008, Hutchinson et al. 2014). As a consequence, temperate, arid and semi-arid mangroves show lower photosynthetic CO_2 assimilation rates, lower global performances and growth than those in the humid tropics (Smith 1987, Clough 1992). In addition, other mechanisms involved in cold, drought and salinity stress resistance, are nutrient and energy-consuming and could contribute to reduce the amount of resources allocated to the production of aboveground biomass. This is the case for N, K, Ca, Fe, Mn, necessary for osmocompensation, production of osmoregulatory metabolites and/or enzymes to avoid chilling injury and oxidative stress (see Appendix 1 – Appendix 4, Ashihara et al. 1997, Sakamoto and Murata 2000, 2002, Saenger 2002, Li et al. 2009, Hayes et al. 2020, Liu et al. 2020).
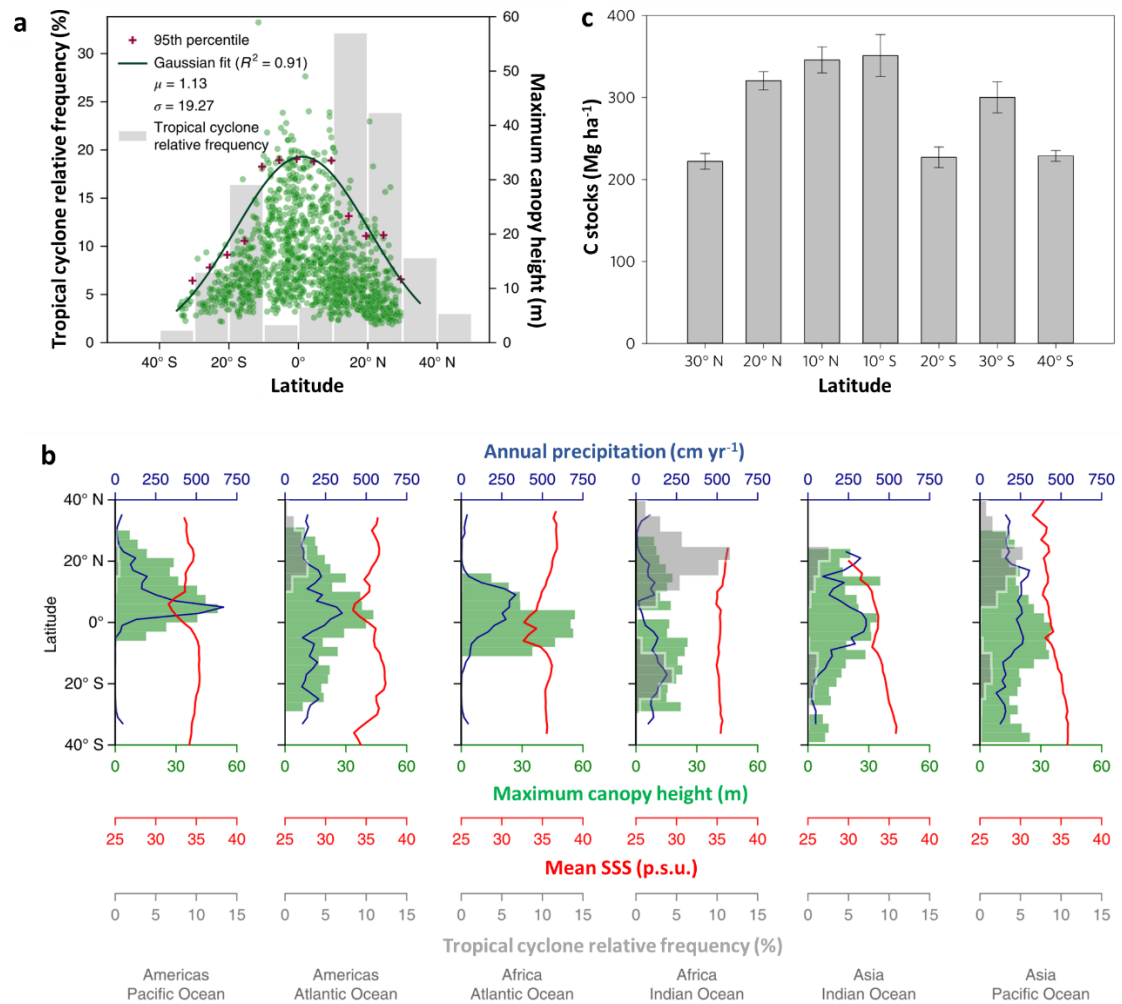
Figure 10. (a) Relationship between latitude and maximum canopy height, with tropical cyclone frequency showed as grey bars; (b) latitudinal trends in maximum canopy height (green bars), precipitation (blue line), sea surface salinity (SSS, red lines) and cyclone relative frequency (grey bars) along the major continental coastlines (figures from Simard et al. 2019) ; (c) mean (± SE) soil C stocks per unit area down to 1 m across southern and northern latitudes (figure from Atwood et al. 2017)

Contrastingly, and although hotspots for C stocks in mangrove soils are also found between 10° N and 10° S, Atwood et al. (2017) showed that there is no significant relationship between latitude and C stock in mangrove soils (Figure 10c). On the other hand, the authors did find important variations in mangrove soil C stocks among mangroves with different stand composition and genera (Figure 11), and increasing mangrove soil C stocks with increasing genus richness.
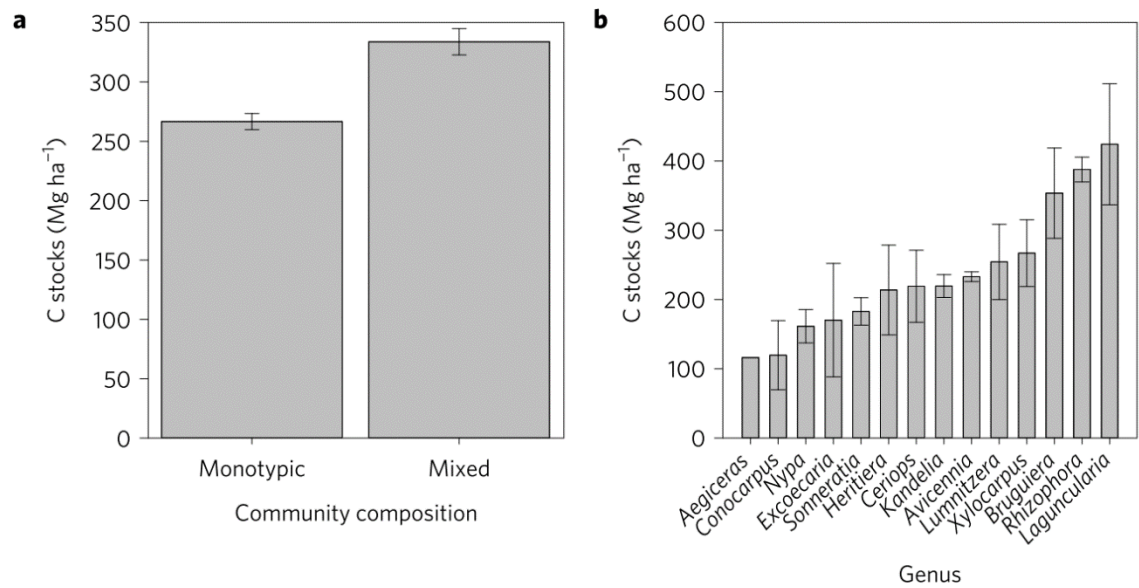
Figure 11. Mean (± SE) soil C stocks down to 1 m in (a) mixed versus monotypic mangrove stands and (b) in different monotypic genus stands (Atwood et al. 2017)

Atwood et al. (2017) conclude that the highest pools of C in mangrove soils do not necessarily overlap geographically with those of above-ground biomass. In terms of management and conservation, this is of great importance. Examples can be found in the literature in which ecological services of mangroves far from the equator are perceived as less valuable than those of their more diverse and luxurious tropical counterparts. As a result, large number of mangrove clearing occurs, either for land conversion (e.g. Saudi Arabia, Eid et al. 2019), to permit unimpeded coastal access, or to restore local biodiversity and recreational areas in sites that were previously free of mangroves (e.g. New Zealand, De Luca 2015, Lundquist et al. 2017). With their large database on soil C stocks, Atwood et al. (2017) show us that shrubby mangroves away from the humid tropics could still harbour important pools of blue carbon. Those could therefore significantly fuel atmospheric CO_2 concentrations if ever released with erosion subsequent to mangrove removal.

2.4.2.2 Latitudinal trend in mangrove litter quality

Except for C stocks, research in elemental global trends in mangrove ecosystems have been mainly focused on leaf tissues and litter quality. Each mangrove species possesses a specific set of adaptations to the local constrains of the environment (salinity, water stress, insulation, trace metals, wave energy, etc.) and different strategies of nutrient use, which results in specific variations in tissue composition (e.g. Figure 12).
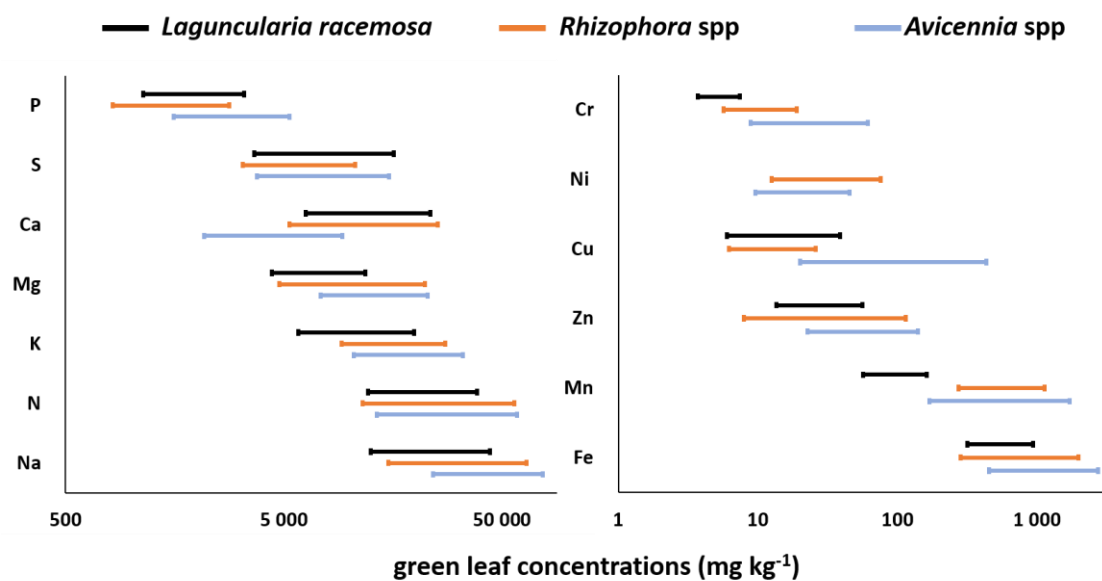
Figure 12. Examples of variations in ranges (minimum and maximum) of global elemental concentrations of P, S, Ca, Mg, K, N and N (left) and Cr, Ni, Cu, Zn, Mn and Fe (right) in the green leaf of the most studied mangrove genera : *Laguncularia*, *Rhizophora* and *Avicennia* (see Table 1 a-c for references)

In addition, a latitudinal trend in nutrient stoichiometry within mangrove leaf tissues has been highlighted by Lovelock et al. (2007b) through a fertilization experiment in mangrove stands in the Caribbean, New Zealand and Australia. The authors report a decrease in N:P ratios in leaf tissues with increasing latitudes as well as increasing growth rates and increasing concentrations in N and P in green leaves, a trend also observed in terrestrial plants (Reich and Oleksyn 2004). Although data from the literature (Table 1a) seem to confirm this last trend for P at a global scale, N

concentrations in green leaf tissues does not seem to vary significantly with latitudes (Figure 13). However, and as illustrated for C stocks previously, the detection of such global patterns necessitates perhaps a larger data set.
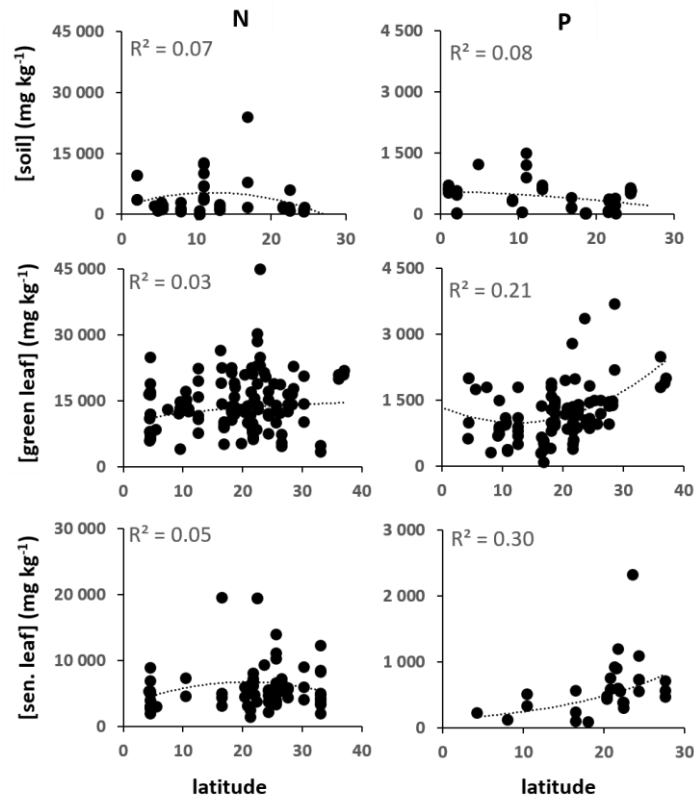
Figure 13. Relationships between latitude and mean N and P concentrations in mangrove soils (n_P = 53, n_N = 54), green leaves (n_P = 104, n_N = 123) and senesced leaves (n_P = 33, n_N = 75). References can be found in Table 1a

In terrestrial ecosystems, two hypotheses have been advanced to explain this trend. The first one is the "growth rate hypothesis'", which states that vascular plants that develop at high latitudes have to compensate their shorter growing period by having higher performances during favourable seasons, to grow and reproduce in a shorter period of time compared to their tropical counterparts (Sterner and Elser 2002, Kerkhoff et al. 2005). Thus, higher amounts of N and P are needed to sustain these higher growth rates. This would explain why many studies report that higher nutrient availability – particularly N, P and K – in temperate and arid mangroves increases mangrove

physiological performances, rates of photosynthesis and growth (e.g. Feller 1995, Koch and Snedaker 1997, Chen and Twilley 1998, Lovelock and Feller 2003, Lovelock et al. 2004, Lovelock et al. 2007b). The second hypothesis is the "geochemical hypothesis", which attributes these decreasing N:P ratios with increasing latitude to higher amounts of P in temperate soils than in older and more weathered tropical soils, which would mean that N:P ratios are driven by nutrient limitations (Vitousek 1984, Vitousek and Sandford 1986, Reich and Oleksyn 2004). In mangrove ecosystems, Lovelock et al. (2007b) tested both hypotheses and showed that nutrient use efficiency - i.e., the amount of nutrients by unit of weight produced - decreases with increasing latitude, particularly photosynthetic P use efficiency and P resorption efficiency before senescence. This last trend is the opposite of that observed in terrestrial taxa (Nordell and Karlsson 1995, Kerkhoff et al. 2005) and reflects perhaps higher limitation of P in tropical mangrove ecosystems compared to those that develop at higher latitudes, in accordance with the "geochemical hypothesis". Although global data on P concentrations in senesced leaves could confirm this, our small database of total P concentrations in mangrove soils does not show such a relationship with latitude (see Figure 13), and additional data would be needed to understand these particular patterns.

2.4.2.3 Global trends of other macronutrients and trace metals in mangrove plants and soils : a gap in knowledge

Except for the trends discussed above, very little is known about the variations of other mangrove elemental pools across the latitudinal gradient and climatic regions. The first reason for this lack of knowledge is that few elements have received as much attention as C, if only for Cu, Zn and N, which were extensively measured in green leaves for their

role in metal and salinity resistance and/or photosynthesis (see Table 1 a-c). There is also a vast disparity between the number of data available for the different compartments of the ecosystems, with for instance fewer data available for the total concentrations of N, K, P, Na, Ca and Mg measured in soils compared to those measured in plant tissues (see Table 1 a-c). According to their goals, studies also often focus on a particular chemical form of a given element, for instance on that available for plant uptake or export. Some elements are thus exclusively measured in their exchangeable and soluble forms within the pore water (e.g. Ca, Mg, NaCl) without their total concentrations and stocks being recorded.

The accumulation of materials in mangrove soils also depends on numerous processes, many of all independent from climatic factors and more related to local sources and physico-chemical properties of a given study site, resulting in strong variations in a same region and even in a same mangrove stand (e.g. Twilley and Day 1999, Otero et al. 2009, Adame et al. 2010, Naidoo 2016, Thành-Nho et al. 2019a). Finally, a recent study reported that mangroves are one of the ecosystems the most at risk from direct human activities and that this risk is rapidly increasing (Halpern et al. 2019). Direct anthropogenic pressures often result in direct nutrient and trace metal inputs, but also in the modification of the hydrological regime, sedimentation rates and/or chemical properties of the substrate. These changes strongly influence mangrove biogeochemistry and further increase the spatial heterogeneity in biomass and elemental distribution at the regional and local scales (e.g. Figure 14, e.g. Guong and Hoa 2012, Molnar et al. 2013, Nóbrega et al. 2013, Suárez-Abelenda et al. 2014, Barcellos et al. 2019).
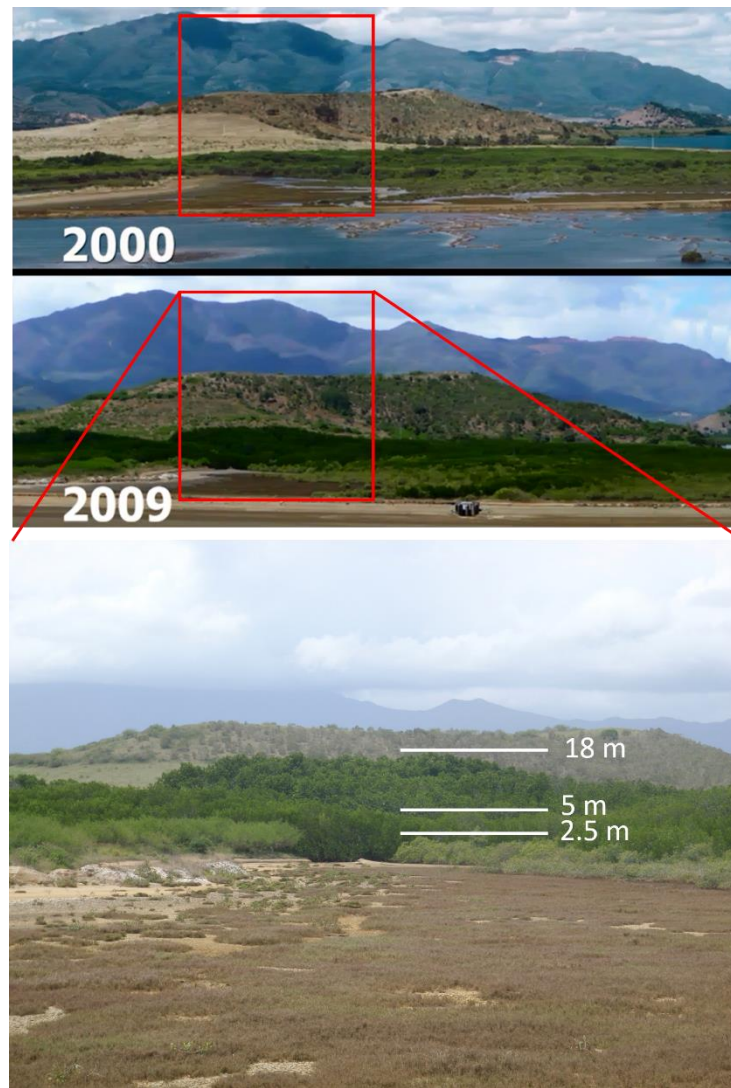
Figure 14. Illustration of the effect of 10-years of nutrient and water inputs on the structural characteristics of a semi-arid mangrove stand that developed downstream a shrimp farm, with mean tree height significantly increasing in the middle of the stand over the 10 years (modified from Molnar 2013, photo credits : C. Marchand, C. Bourgeois)

The next sections review the main sources of nutrients and trace metals in mangrove soils, sediments and plants, as well as the main biogeochemical processes driving elemental accumulation and mobility, and thus their high variations in mangrove soils and their transfers to mangrove standing plant biomass.

2.5 Allochthonous sources of macronutrients and trace metals in mangrove ecosystems

2.5.1 Atmospheric sources of nutrients and trace metals

Carbon, the common macro-element in both mangrove plants and soils, derives mainly from the assimilation of atmospheric CO_2 by photosynthetic organisms. According to recent estimates (Alongi 2014), mangrove vegetation worldwide exchanges a total of 699 Tg C y^{-1}, with the atmosphere, 91% of which is fixed from the atmosphere by
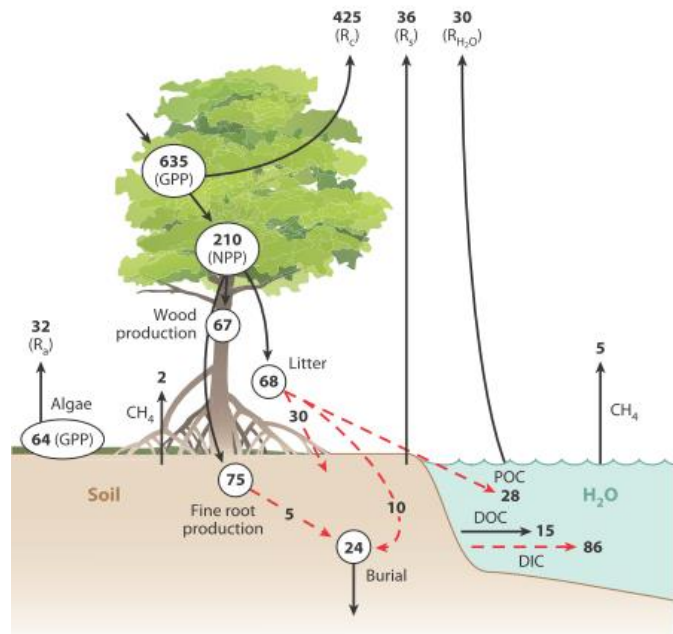
Figure 15. Stock and fate (fluxes) of mangrove global primary production (Tg C y^{-1}) based on the estimate of 138,000 km² of Giri et al. 2011, Alongi 2014)

mangrove trees through photosynthesis, and the remaining 9% by micro- and macro-algae communities (Figure 15). About 65% of this total gross primary production (GPP) is rapidly returned to the atmosphere as CO_2 through canopy and algal respiration. The remaining 35%, the Net Primary Production (NPP), enters the ecosystem as benthic (5%) and tree belowground (11%) and aboveground (19%) biomass production. Most of this NPP (242 Mg ha^{-1} globally) is then exported as litterfall and as dissolved and particulate organic C with the tide and through soil respiration and methanogenesis (Figure 15). After accounting for these losses and for the imports of OM-derived products from allochthonous sources and autochthonous material accumulation through burial, Alongi (2014) estimates mangrove global C net accumulation (Net Ecosystem Production NEP)

at 90 Tg y^{-1}. Over time, and as illustrated in Figure 5, most of this C assimilated from the atmosphere is therefore found in mangrove OM buried in soils.

It naturally follows that, in general, OM is a good predictor of total C contents in mangrove soils, a feature characteristic of peat soils (Kauffman and Donato 2012, Figure 16), i.e. soils formed from partially decomposed plant material under anaerobic water saturated conditions that present
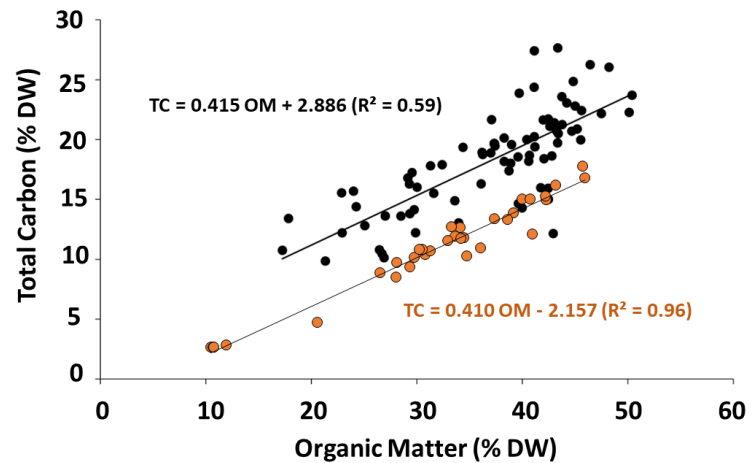
Figure 16. Relationship between total carbon and organic matter in mangrove soils (% of DW) measured in Republic of Palau (Kauffman and Donato 2012, black dots) and in New Caledonia (Osadnick 2015, Léopold 2015, orange dots)

high OM content. However, significant variations in this relationship may be observed between mangrove soils (e.g. Figure 16). Such variations may be due to the rate and nature of specific biogeochemical and physical processes taking place within the substrates (e.g. different oxidation rates, hydrodynamics) and to contrasting proportions of inorganic C, for instance (e.g. Ca and Mg carbonates). Those processes are further discussed in section 2.6.

As for C, most nitrogen naturally present in mangrove plants and soils is fixed from the atmosphere, and then recycled via mineralisation of the OM in soils. Besides C, N is also the only other element for which global stocks and fluxes have been extensively studied in mangrove ecosystems (Figure 17, Reis et al. 2017). Hence, global atmospheric N fixation in mangrove ecosystems ranges from 2 to 10 mg N m^{-2} d^{-1} (Reis et al. 2017) and

is exclusively performed by N_2-fixing bacteria and archaea that possess the nitrogenase enzyme complex that reduces N_2 into ammonium, following the general equation:

$$N_2 + 10 H^+ + 8e^- \rightarrow 2 NH_4^+ + H_2 \text{ (16 ATP)}$$
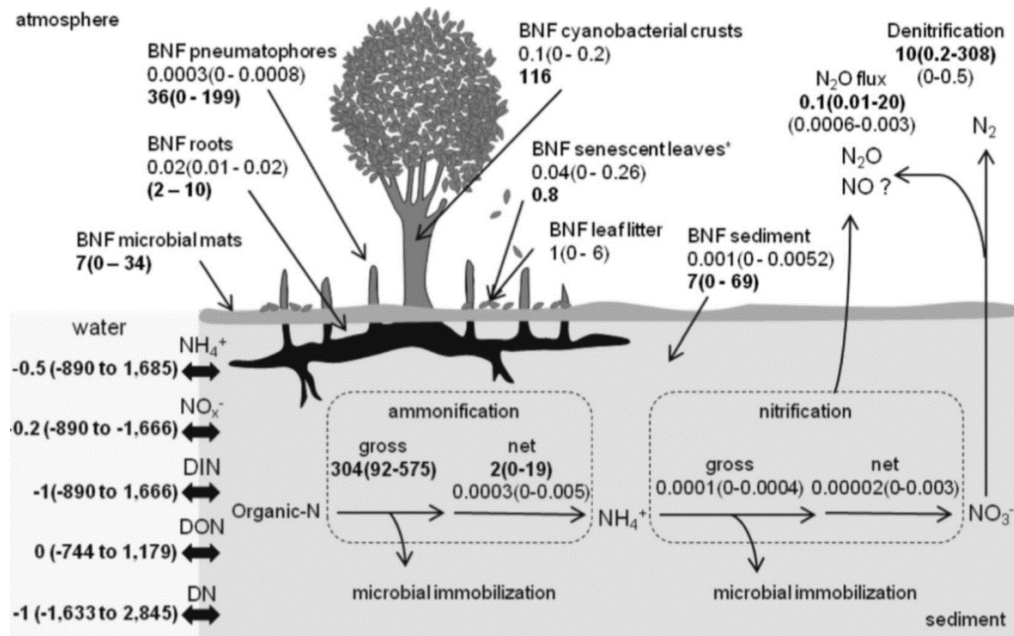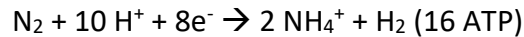
Figure 17. Assessment of N cycling in mangrove ecosystems : biological N fixation rates (BNF, bold : mg N m² d⁻¹, non-bold : mg N d⁻¹), fluxes, mineralisation rates and tidal imports and exports (negative values indicate net flux into the sediments) (Figure from Reis et al. 2017)

This fixation is operated by bacteria and archaea living in soils and sediments and microbial mats (e.g. *Azobacter* sp., *Pseudomonas* sp., *Bacillus* sp.), but also associated with mangrove roots, aerial roots, bark and leaf litter (e.g. *Enterobacter* sp., *Klebsiella* sp.) (Uchino et al. 1984, Bashan and Holguin 2002, Ray et al. 2014). In general, leaf litter shows a higher intrinsic capacity of N fixation than barks and roots, followed by sediments and pneumatophores (Pelegri et al. 1997, Pelegri and Twilley 1998). In comparison, the global rate of N fixation corresponds to 0.01 to 0.07% of that of CO_2 assimilation by photosynthetic organisms in mangrove ecosystems calculated by Alongi (2014). As for C, part of the N immobilised in microbial biomass then joins the pool of OM buried in mangrove soils or is exported with tidal flow as particulate and dissolved inorganic and organic N (Figure 17). The rest is rapidly mineralised in soils and lost to the

atmosphere as N_2O, N_2, or readily available for consumers, or mangrove trees as NH_4^+ and NO_3^-. In total, the entire stock of N in mangrove ecosystems is estimated at 20 Mg ha^{-1} (Reis et al. 2017).

In addition to C and N, the atmosphere can also be a source of macronutrients S, P, K, Ca, Mg and trace metals through wet deposition (i.e. transfer by inclusion or solution from the atmosphere in precipitation) or dry deposition (i.e. settling, impaction and interception of particles from the atmosphere by dry weather). For instance, S naturally occurs in the atmosphere, largely produced by outgassing during organic decomposition processes, and emitted from deep volcanic eruption, ocean, and deep sea vents (Berresheim et al. 1995). Although in decline, industrial activities that involve fossil fuel burning and mineral processing are also responsible for 99% of SO_2 emission in the atmosphere, with a global emission of ± 125 Tg y^{-1} in 2015 (Aas et al. 2019). Sulfur wet deposition has been recorded by Cerón-Bretón et al. (2015) at a rate of 9.22 kg SO_4^{2-} ha^{-1} y^{-1} in a mangrove in Mexico located next to a sour gas recompression plant, a rate that exceeds the maximum load advised in natural forests (Escoffie et al. 2014). In Ecuador, Quevedo et al. (2018) reported SO_2 deposition from shipping activities at a rate of 3.2 kg S ha y^{-1} in a *Rhizophora harrisonii* stand.

Ca, N, P, Mg, K along with Cl and Na, are also present in the atmosphere, transported from terrestrial or oceanic areas as aerosols, and then deposited in ecosystems via wet or dry deposition. In temperate forests, Chapin (1991) estimated that deposition from the atmosphere may account for respectively 7, 1, 2, 4% of the total source of N, P, K and Ca that enter the soil and for as much as 4% of the total P in the arctic tundra. In vegetated ecosystems, the return of nutrients to soil via rainwater may be augmented by the extraction of ions leached by the leaves, and by the washout of dry deposition

along branches and leaves during a rain event (Tan et al. 2018). This process results in higher nutrient concentrations in throughfall (i.e. water that reaches the soil by passing through the canopy) and stemflow (i.e. water that reaches the soil via branches and tree stems) than in bulk precipitations. Investigations on the amount of nutrients returned to soil through wet and dry deposition are scarce in mangrove ecosystems, but evidence shows that those can be significant and should therefore be accounted for in nutrient budgets (Biswas et al. 2005, Chatterjee et al. 2006). In a thorough investigation in a mangrove in Belize for instance, Wanek et al. (2007) measured significant concentrations of Cl^-, Na^+, SO_4^{2-}, Mg^{2+} Ca^{2+} and dissolved organic carbon and nitrogen (DOC, DON) returned to the soils after rainfall events. The authors demonstrated that these depositions were further enriched by dry deposition and canopy leaching (Ca^{2+} > Cl^- > SO_4^{2-} = K^+ > Mg^{2+} > Na^+), whereas NH_4^+ and inorganic P of terrestrial sources (industrial emissions, burning, soil dust) were retained by the canopy (Figure 18).
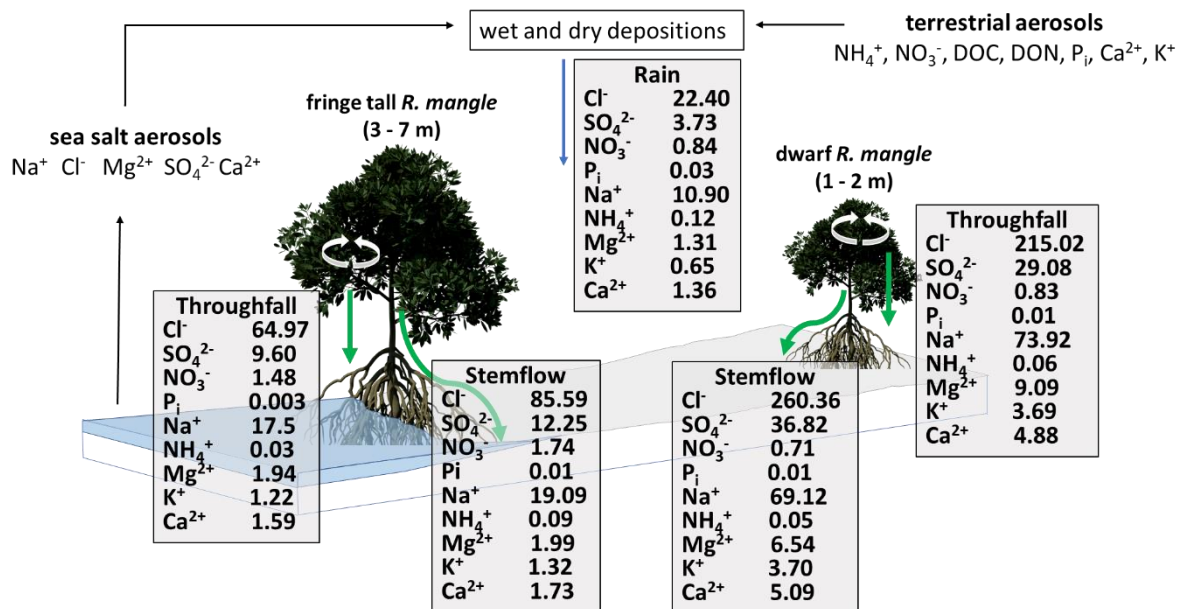
Figure 18. Mean concentrations of cations and inorganic P reaching the substrate in *Rhizophora mangle* mangrove stand in Belize, Florida, through wet and dry depositions from the atmosphere, via throughfall (accounting for products of canopy exchange, such as washing up of dry deposition > leaching > uptake by the canopy), stemflow and bulk precipitation. Data are given as mean concentrations in mg g^{-1} of water collected by rainfall event (after data from Wanek et al. 2007)

Finally, significant concentrations of trace metals Pb, Zn, Cd, As, Cr, Cu, In, Mn, Zn are also emitted to the atmosphere from natural sources (aeolian sands, fire debris, and volcanic, biogenic and oceanic emissions) and anthropogenic activities (electricity producing, vehicular traffic, metal manufacturing industries, cement production, waste disposal) (Pacyna and Pacyna 2001). Dry deposition and washout of these trace metals from the atmosphere through rainfall may therefore constitute a source of trace metals in the environment (Rivera-Rivera et al. 2020). Although direct quantification of trace metal deposition in mangrove ecosystems are extremely scarce, atmospheric sources of trace metals (notably Pb) have been inferred for several mangrove soils and sediments, either through direct atmospheric depositions or indirect deposition via road leaching and coastal transports (Conrad et al. 2017, Li et al. 2019).

2.5.2 Weathering

Except for C and N, weathering is the primary source of most macroelements and trace metals in mangrove soils and sediments. Elements derived from weathering processes in mangrove substrate may be i) allochthonous, i.e. transported in mangrove substrate by land or water or ii) autochthonous. The latter are directly derived from parent materials or from authigenic deposits, i.e. newly formed minerals generated within the substrate (authigenesis processes, see section 2.6.1). Prevalence of autochthonous or allochthonous weathering source in mangrove ecosystems largely depends on the geomorphic settings of a site of interest. While mangroves grow best on sheltered, regularly flooded, fine textured, organic and well-aerated substrates, they also develop on various types of coastal habitats more or less exposed to water and sediment inflow. Those may include sandflats or mudflats with various OM contents and textural

repartitions of sand, silt and clay, but also volcanic lava, carbonate sediments and rocky or coralline substrates (e.g. Figure 19, Woodroffe et al. 1992, Kathiresan 2001, Ferreira et al. 2007a).
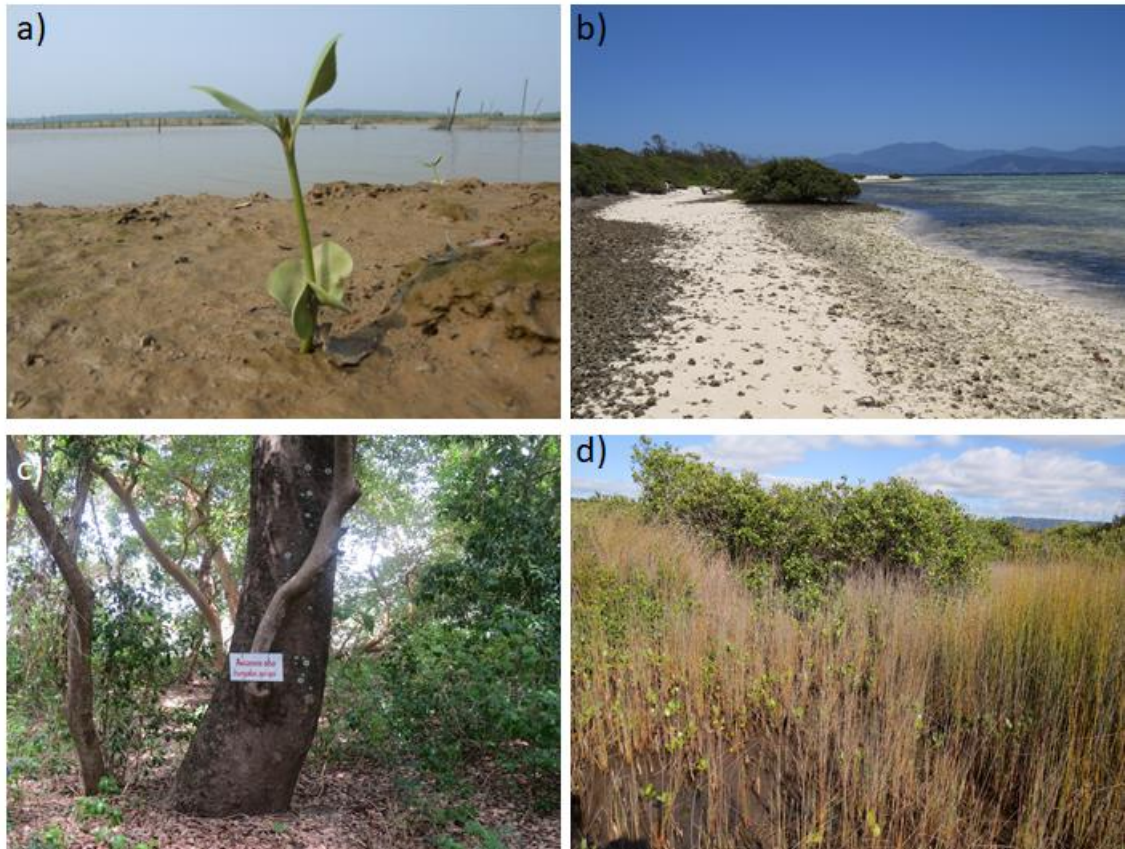
Figure 19. Various types of *Avicennia sp* habitats such as (a) mudflat in riverine mangrove (Guaqiao, China), (b) rocky sandy beach established on coral reef (Signal Island, New Caledonia), (c) landward litter-rich forest (Iloilo, Philippines), (d) saltmarshes peaty soils in an estuarine mangrove (Mangawhai, New Zealand, photo credits: Carine Bourgeois)

For mangroves less exposed to sedimentation and catchment runoff (i.e. low island and wave-dominated mangroves, Ellison 2015), some trends in elemental composition can be expected from the bedrock and parent material of a given location. For instance, elemental composition of coral reefs is dominated by various forms of calcium carbonate polymorphs, typically magnesium-enriched calcite, aragonite and amorphous calcium carbonate that may include significant concentrations of Na, Ba and Sr

(Weinbauer and Vellmirov 1995, Shoham et al. 2019). On the other hand, mangrove stands under the influence of rivers or deltas for instance mostly develop on allochthonous terrigenous clays inherited from catchment erosion (Ellison 2009, 2015). Allochthonous sources may also include material transported to mangroves from adjacent coastal ecosystems, via import of dissolved or particulate minerals from the open ocean or coastal erosion, for instance (Wolanski et al. 1998, Preda and Cox 2002, Adame et al. 2010).

In mangrove ecosystems, material input from allochthonous weathering sources have been mostly inferred from sediment accumulation (i.e. vertical growth of the substrate over a period of time, thus accounting for the accumulation of mineral and organic material and changes due to compaction and/or erosion) and sedimentation (volume of sediments deposited on the substrate, expressed as mass or volume by unit of time) rates. Few authors have directly measured the total sediment inflow and siltation in mangrove ecosystems over time. Of all elemental sources, input of materials through weathering is perhaps the most complex to measure and the most site-specific contributor to elemental contents in mangrove ecosystems. Their rate, accumulation and elemental composition depend indeed on numerous factors such as the composition of the parent materials upstream, watershed size, climate, seasonal variation in precipitation and temperature, and stochastic climatic events (storms, tsunamis, wave strength). Their rate of accumulation in mangrove ecosystems also depends on the inherent coastal morphology, current patterns, depth and duration of flooding, surface of deposition available, and types and density of mangrove aerial roots of a given mangrove stand (Young et al. 1994, Cahoon and Lynch 1997, Kitheka 2000,

Krauss et al. 2003, Lovelock et al. 2007a, Van Santen et al. 2007, Adame et al. 2010, Shearman et al. 2013).

Researchers who did measure siltation and accumulation rates of sediments in mangrove ecosystems reported a high spatial and temporal variations (e.g. Wolanski et al. 1998, Anthony 2004). Using oceanic moorings in the mouth of Fly River in Papua New Guinea, Wolanski et al. (1998) illustrate both the magnitude and heterogeneity of allochthonous weathering as a source of materials in mangrove ecosystems. These authors measured that the 874 km² of mangrove stand that borders the river mouth traps only 6% of the riverine inflow of sediment (107 tonnes year^{-1} of sediments), mostly as fine particles corresponding to almost 25% of the total clay riverine inflow. By comparison, other measurements of total suspended solid retention in mangroves worldwide reported various ranges of values, ranging from 30% in Palau to 80% in Australia (Furukuwa et al. 1997, Victor et al. 2004, Adame et al. 2010). However, Wolanski et al. (1998) also note that half of mangrove banks are subjected to erosion while the other half is more prone to siltation, reflecting the strong dynamic and natural fluctuations in mangrove capacity to trap sediments and clay (Shearman et al. 2013). Similarly, the dynamics of mud banks within and along the border of mangrove ecosystems complicate the task of weathering assessment. Wolanski et al. (1998) reported that a 2–3 m deep mud bank can be carried away in a single event, whereas other authors estimated a migration of mud banks from Brazil to Surinam at a rate of 1–3 km y^{-1} (Gratiot et al. 2008). Fluctuation of erosion-accretion rates have also been observed along the shorelines near the Amazon, where some areas retreated by 2 km in 20 years, while others propagated by 3 km in the same amount of time (Gratiot et al. 2008).

Despite these dynamics, short- and long-term vertical sedimentation rate measurements attest to net accretion rates in mangrove ecosystems over time (Table 4). For instance, Van Santen et al. (2007) measured short-term sedimentation rates of 2.94–3.46 g cm^{-2} y^{-1} in vegetated mangrove areas, whereas soil core isotopic dating revealed long-term sedimentation rates of 0.22–0.36 g cm^{-2} y^{-1} (1.8–2.4 mm y^{-1}).

Table 4. Vertical sediment accretion rates measured in different mangrove forests

short term accretion rates (mm y^{-1})	location	reference
1.0 to 4.4	Terminos Lagoon, Mexico	Lynch et al 1989
1.4−1.7	Rookery Bay, Florida, USA	Lynch et al 1989
2	Fly River, Papua New Guinea	Wolanski et al. 1998
6.4	Piako, New Zealand	Young et al. 1996
1.2−1.3	Enseada das Garças, Barra de Guaratiba, Brazil	Smoak and Patchineelam 1999
4.4−7.2	Rookery Bay, Florida, USA	Cahoon and Lynch 1997
2.9−20.8	Kosreae and Pohnpei, Federal States of Micronesia	Krauss et al. 2003
1.1− 3	Sherbro Bay, Sierra Leone	Anthony 2004
long-term accretion rates (cm y^{-1})		
0.42− 0.77	Guanabara bay, Brazil	Monteiro et al. 2012
2.44 ± 1.38	Vietnam	MacKenzie et al. 2016
0.47 ± 0.08	Republic of Palau	MacKenzie et al. 2016

As in other studies, Van Santen et al. (2007) also measured decreasing short-term sedimentation rates with increasing distance from the river bank (Adame et al. 2010, MacKenzie et al. 2016), but also a decrease in elevation in unvegetated areas next to the river banks during the wet season compared to the dry season. This indicates more dynamic in exposed areas compared to sheltered areas over time, whereas the inner density of mangrove trees and their aerial roots contribute significantly to the dissipation of turbulent kinetic energy within the water column, therefore allowing accretion over time (Quartel et al. 2007, Hashim and Catherine 2013, Norris et al. 2017). This gradient of hydrodynamics along the intertidal gradient in estuarine and tidal mangrove forests also results in a net textural sorting of deposited particles. Thus, low-

size particulate sedimentation rates are higher under vegetation cover where wave velocity is lowered by mangrove stem and root density, compared to areas exposed to high wave energy (Van Santen et al. 2007, Norris 2019, Figure 20). It naturally follows that, as showed by Wolanski et al. (1998), mangroves may retain large quantities of fine sediments over time.
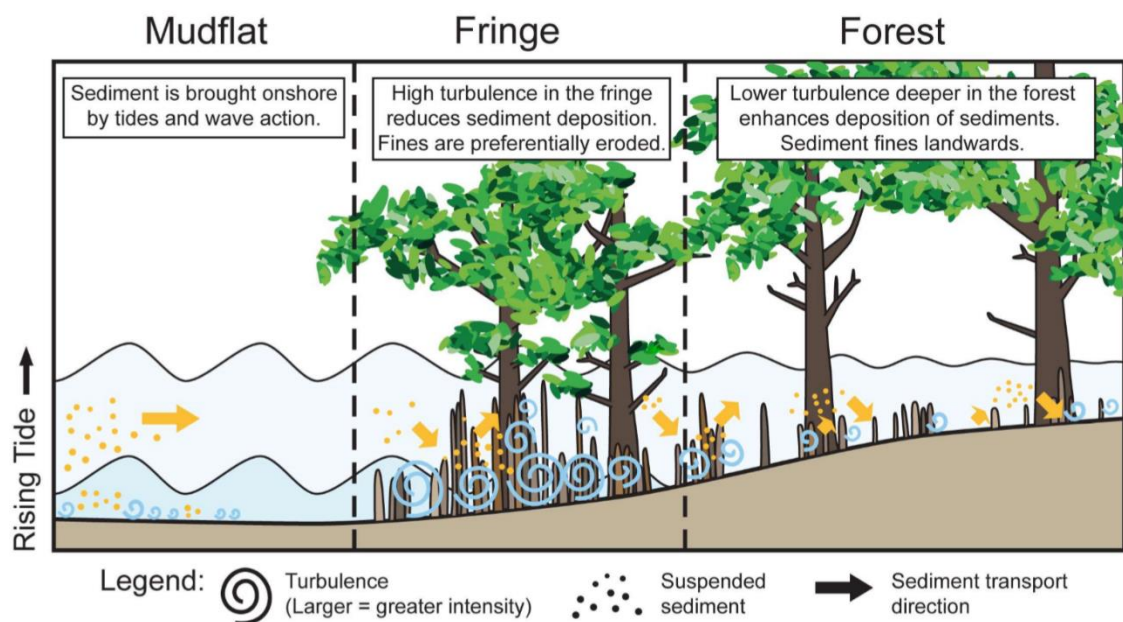
Figure 20. Conceptual diagram of turbulent kinetic energy dissipation by pneumatophores of *Sonneratia caseolaris* in Vietnam. Greater effects of turbulence and sediment transport are pictured by larger spirals and arrows, respectively (figure from Norris et al. 2017).

The material inherited from weathering that accumulate in mangroves are essential constituents of the substrate matrix and carry with them substantial traces of metals and nutrients (Preda and Cox 2002). For instance, net coastal and terrestrial inflow of trace metals and dissolved and particulate organic and inorganic nutrients have been observed in several studies (see Figure 15 and Figure 17 and the reviews of Bouillon et al. 2008, Monteiro et al. 2012, Reis et al. 2017). Sources of nutrients have been traced to algae, terrestrial plant debris and sewage imported from groundwater, tidal creeks or the ocean (Rivera-Monroy et al. 1995a Alongi 2002, 2004, Adame et al. 2010, Monteiro

et al. 2012). In addition, and although most nitrogen naturally present in soils are fixed from the atmosphere by prokaryotes and then recycled via mineralisation of the OM in soils, recent studies indicate that as much as 26% of N present in terrestrial ecosystems could actually come from rock weathering (Morford et al. 2011). Despite important differences found between the type of parent materials, Morford et al. (2016) calculated a global estimate of 15–35 Tg y^{-1} of N mobilised from rocks (Houlton et al. 2018). These recent findings open interesting research perspectives for N budget estimates in coastal areas, including mangrove ecosystems.

While mangrove ecosystems are undeniably exposed to numerous sources of minerals and organic materials that may accumulate in their substrate over time (Furukawa et al. 1997, Victor et al. 2004), this does not mean that mangroves necessarily act as a net sink for OM, nutrients and trace metals (Adame and Lovelock 2011, Reis et al. 2017). On the contrary, evidence shows that mangrove ecosystems are a significant source of carbon for adjacent coastal water (11% of the total terrestrial input) and sediments (15% of the total carbon accumulated) and thus, fuel oceanic secondary productivity (Twilley and Day 1999, Jennerjahn and Ittekott 2002). Ultimately, the net accumulation and export of materials of a given mangrove stand strongly depend on hydrodynamics, and on the types and rates of mineralisation and recycling to which those particles will be exposed after their deposition on the forest floor.

2.6 Main biogeochemical processes driving elemental concentrations in mangrove ecosystems : diagenesis, pedogenesis, and recycling

Within the substrate, elements imported via atmospheric deposition, water inflow, returned to the forest floor as OM, or already present within the substrate undergo a series of transformations and interactions with other elements and material that determine their distribution amongst defined chemical species. The specific distribution of a given element among its chemical species provides information on its solubility and thus mobility. The understanding of chemical speciation contributes to the assessment of trace metals and nutrients potential to accumulate in the ecosystem, or on the contrary to be exported from the substrate toward the water column, atmosphere, consumers and/or plant biomass (e.g. Rao et al. 2008, Borgese et al. 2013).

Elemental speciation and abundance in mangrove substrate are driven by diagenesis and pedogenesis, two groups of biogeochemical processes that occur simultaneously in mangrove substrates (Ferreira et al. 2007a). Diagenetic processes are defined as the "sum of all processes, chiefly chemical, by which changes in a sediment are brought about after its initial deposition but before its final conversion to rock" (i.e. solidification or metamorphism that result in lithification). Pedogenesis, on the other hand, refers to "all chemical and physical processes leading to the formation of soils" (Encyclopaedia Britannica).

Both diagenetic and pedogenetic processes are driven by interactions that are based on electron exchanges between the different chemical species present within the substrate. The nature and rate of the processes taking place in a given location depend therefore on the capacity of the existing ions present within the substrate to accept (oxidants) or give away electrons (reductants). Thus, the overall oxidising or reducing capacity of the main system is given by the proportion of reductants and oxidants, and

is measured by the oxidation-reduction potential (Eh) expressed as mV (Søndergaard 2009). As mangroves often develop along intertidal or riverine gradients, the Eh usually presents a gradient of its value that depends on the physiographic position of a given stand. Reducing conditions will occur typically in frequently flooded or waterlogged areas, at depth and close to the water ways, where water fills the interstitial pores of the matrix and progressively replace oxygen within the substrate. Conversely, oxidising conditions dominate close to the surface and in locations where evapotranspiration is higher and the duration of emersion longer (e.g. Baltzer 1982, Otero et al. 2006, Ferreira et al. 2007c). The presence of vegetation and that of macrobenthos also tends to promote oxic conditions within the substrate, the first via oxygen diffusion within the soil through the root system, the second via the ventilation of the substrate as a consequence of bioturbation (i.e. "the transport of solutes and solids by macrobenthos activities such as feeding and movement", Black et al. 2008) (Scholander et al. 1955, Curran et al. 1986, Allaway et al. 2001, Ferreira et al. 2007b). Both vegetation and macrobenthos may therefore extend oxic conditions at considerable depths and therefore mediate the direction of biogeochemical processes in mangrove soils and sediments (Ferreira et al. 2007c).

2.6.1 Diagenesis : transformation of clay minerals and effect on elemental composition

Clays inherited from authigenic or allogenic weathering in mangrove substrate may become very unstable when exposed to seawater or to a strong alternating oxidative and reducing conditions. During their crystal-chemical transformations, clays can trap or release substantial concentrations of metalloids (e.g. Si), metals (e.g. Fe, Al) and nutrients (e.g. K, Mg, NH_4), thus leading to their accumulation or depletion within the

substrate (Gouleau et al. 1982, Andrade et al. 2014, 2018, Cuadros et al. 2017). This is the case for kaolinite, a layered silicate mineral abundant in heavily weathered tropical soils. In marine sediments, kaolinite is highly susceptible to dissolution in seawater due to cation replacements between the mineral layers. This state is generally followed by a recrystallisation of these layers in other clay minerals, typically in illite or smectite (Taylor and Meredith 2012). In Brazilian mangroves, Cuadros (2017) and Cuadros et al. (2017) demonstrated that in reducing conditions and in presence of dissolved Fe^{2+} supplied by Fe-reducing bacteria, seawater ions K^+ and Mg^{2+} can be trapped in clay as Fe-illite through illitization of goethite and kaolinite imported in riverine sediments as follow:

$$Fe_{sol} + Kaolinite\ (Al_2O_2\ 2SiO_2 \cdot 2H_2O) + seawater \rightarrow Kaolinite\text{-}Smectite$$

$$Kaolinite\text{-}Smectite \rightarrow Smectite$$

$$Smectite + K^+ \rightarrow Illite\text{ - }Smectite \rightarrow Illite\ ((K,H_3O)(Al,Mg,Fe)_2\ (Si,Al)_4\ O_{10}[(OH)_2 \cdot (H_2O)])$$
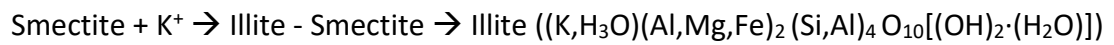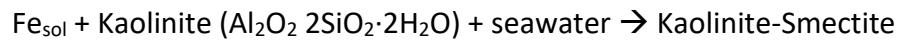
The authors reported that the reaction is quite significant in term of the global K budget, with $\pm$ 0.6–3 Tg km^{-2} y^{-1} of K trapped in mangrove worldwide, equivalent to 1–6% of the total K riverine input into the oceans every year. Similarly, Ferreira et al. (2007c) detected the presence of K, S and Ca associated with smectite of suspected authigenic origins at depth in mangrove substrates of Sao Paulo (Figure 21).
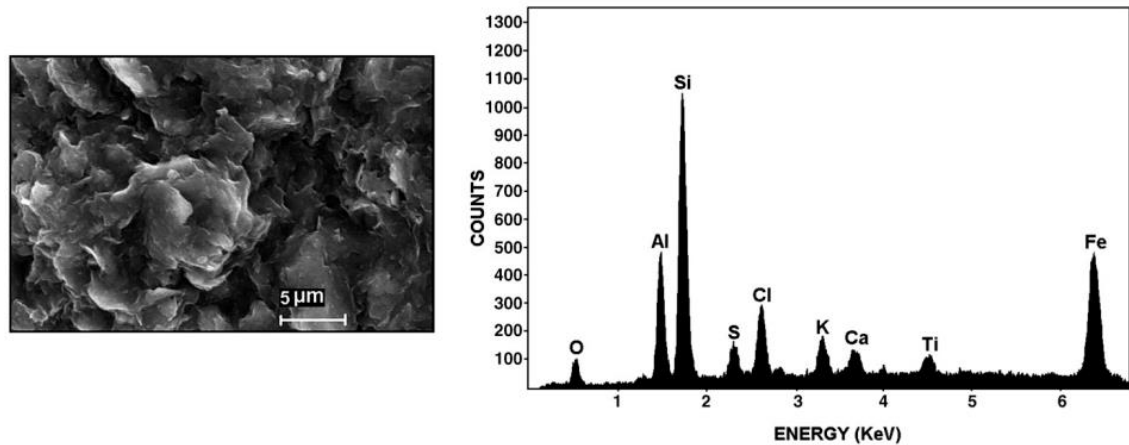
Figure 21. (left) Honeycomb morphology and (right) energy-dispersive X-ray spectroscopy spectrum of smectite minerals showing counts of macronutrients S, K and Ca (Figures from Ferreira et al. 2007c)

Other studies also demonstrated substantial adsorption of trace metals, such as Cu, Zn, Pb at the surface of clay minerals (e.g. smectite), whereas other trace metals (Ni, Co, Mn and Cr) do not show any relationship with clay mineral contents (Pandarinath and Narayana 1992).

Another example of clay transformation influencing elemental concentrations in mangrove substrate concerns the neoformation of Al hydroxides in acidic conditions. Acidic conditions with pH as low as 3 may be encountered in mangrove substrate rich in OM and subjected to strong variation of oxygenation over a given time frame (over the year or at a critical depth over a tidal cycle), which leads to a significant alternating oxidative and reducing conditions. Conditions such as these are found in tidal environments such as saltmarsh and mangrove stands exposed to the tidal cycle, or that develop in climates with contrasted seasons (Gouleau et al. 1982). When exposed to longer emersion and higher evapotranspiration, aerobic conditions prevail near the surface and the rate of OM decomposition and mineralisation by microorganisms

increases. As illustrated in Figure 22, such an increase in Eh induces an acidification of the substrate, mainly due to the rapid oxidation of the OM, and to the release of H^+

subsequent to the oxidation of solid sulphides (see section 2.6.3.4) (Lin and Melville 1993, Middelburg et al. 1996, Oxmann et al. 2009, Nóbrega et al. 2013). In several mangroves in Senegal, Vieillefon (1974) and Gouleau et al. (1982) observed an intense dissolution
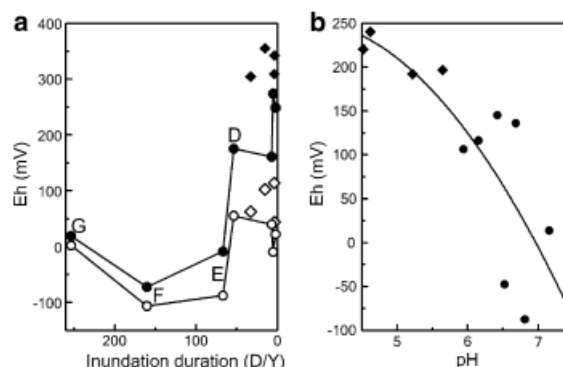
Figure 22. (left) Relationships between (left) Eh and inundation variations and (right) pH and Eh in mangrove substrates of Can Giao mangrove in Vietnam (Figures from Oxmann et al. 2009)

of clays – mainly composed of aluminium phyllosilicates – under these acidic conditions. The authors report that clay dissolution results in a depletion of Si in the soil profile, whereas Al oxidises and accumulates as small Al hydroxide crystals (0.8–10 µm) in the upper surface of the substrate. Those small crystals were found in abundance at the sediment and soil surface over the entire intertidal gradient, an observation that the authors related to aeolian dispersion. As for the recrystallisation of kaolinite into smectite and illite, the formation and propagation of Al hydroxides may have a significant impact on the budget of macro and micronutrients. In particular, Al hydroxides present a high affinity for Fe, P and Ca and contribute therefore to their accumulation within the substrate (Hesse et al. 1963, Naidoo and Raiman 1982, Silva and Sampaio 1998, Fabre et al. 1999, Mendoza 2007, Oxmann et al. 2009, 2015).

2.6.2 Fate of the organic matter and pedogenesis

Mangrove vascular plants (tree, shrub, palm and fern species) are the main contributors to the pool of OM found in mangrove soils. It is estimated that 58% of the organic C (used here as a proxy for OM) found in mangrove soils derived from mangrove plant, mostly from root and then litterfall, with leaves > fruits > woods > reproductive parts (i.e. flowers and buds) (Wafar et al. 1997, Sánchez-Andrés et al. 2010, Srisunont et al. 2017, Kamruzzaman et al. 2019). The remaining 42% derived from mangrove fauna, bacteria, archaebacteria, fungi and algal production and allochthonous organic sources (Kristensen et al. 2008, Alongi 2014).

The fate of the OM inherited from mangrove biomass or imported from adjacent ecosystems affects nutrient and trace metal accumulation within mangrove soils in two ways. Firstly, autochthonous and allochthonous OM may contain large amounts of macroelements and trace metals (see Table 1 a–c). Secondly, organic compounds and ions that result from OM decomposition also have a strong affinity for dissolved and particulate minerals already present within the substrate (e.g. Ferreira et al. 2007c, Nogueirol et al. 2015). The specific rate and pathways of OM decomposition may therefore contribute to their precipitation and accumulation within mangrove soils, or on the contrary to their export from the soil compartment (e.g. Araújo et al. 2012).

Once on the forest floor, OM and OM-derived products may undergo i) direct export toward adjacent ecosystems through physical processes (wave and tidal action), ii) consumption by herbivores, iii) decomposition and iv) burial. Decomposition refers to all physical, chemical and biological processes by which organic substances are converted into inorganic substances (Gregorich et al. 2001). This therefore includes physical processes such as the fragmentation and breaking down of the OM by wave,

tidal action and leaching, as well as biochemical processes, including humification, catabolism and OM mineralisation by the microbial community. The product of decomposition may then accumulate within the soil compartment through burial and precipitation, or can be exported from the soil compartment toward the water column, the atmosphere, and/or recycled within the microbial, plant and animal biomass (Figure 23).
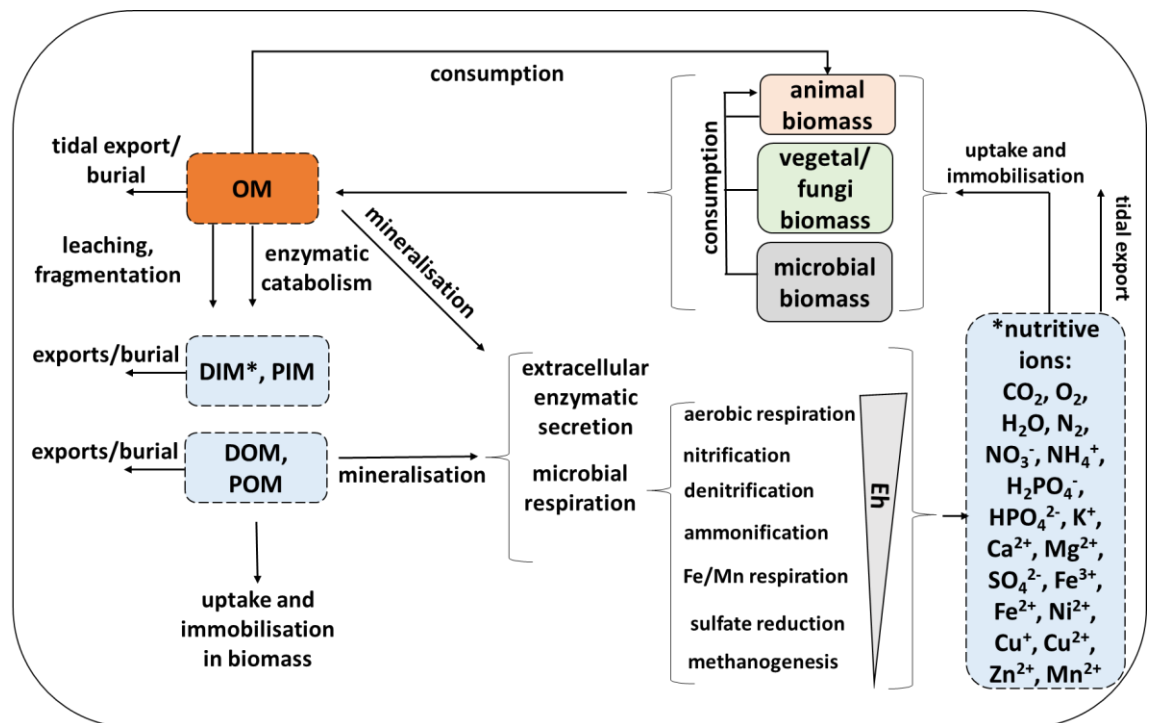
Figure 23. Fate of the OM in mangrove ecosystem, including : burial, tidal export, leaching, fragmentation and direct consumption by detritivores and herbivores ; OM mineralisation processes : enzymatic catabolism of the litterfall, OM mineralisation via extracellular enzymatic secretion and the different redox-dependent pathways of microbial respiration of the OM ; uptake and immobilisation of decomposition final products in mangrove biomass (DOM : dissolved OM; DIM: dissolved inorganic matter, PIM : particulate inorganic matter; POM: particulate OM)

2.6.3.1 Tidal export and elemental losses

Estimates of the global C and N balance export show that tidal export may account for as much as 50% of mangrove net primary production (Alongi 2013, 2014). The export of mangrove organic and inorganic matter that derives from OM decomposition through tidal inundation may therefore result in an important elemental loss from the system,

while having a strong impact on elemental biogeochemical cycles in adjacent coastal areas. For example, Jennerjahn and Ittekkot (2002) calculated that, although mangroves cover only 0.5% of coastal area, these highly productive ecosystems account for 15% of the total C accumulating in modern marine sediments. The authors assess that mangroves constitute a source of approximately 46 x 10^{12} g C per year for the ocean globally, for 23 x 10^{12} g C per year that accumulate in mangrove ecosystems. Similarly, Alongi (2013) gives a global estimate of 1 496 x 10^6 g N per year exported via tidal exchange out of the 2 787 x 10^6 g that constitute N total input in mangrove ecosystems globally.

However, these values are highly variable. In the section discussing weathering, we saw that mangrove OM export strongly depends on hydrology, including rainfall pattern, catchment area and tidal regime and frequency (Twilley et al. 1986, Sánchez-Carrillo et al. 2009). It varies also according to the geomorphology, climate and forest structure of a site of interest and naturally, according to the OM production rate of a given site (Sánchez-Carrillo et al. 2009, Norris et al. 2017). For instance, studies report that 20 to 71% of mangrove litterfall (i.e. leaves, wood, propagules, flowers and buds) is flushed by tidal action in Australia, but only 8% is exported in mangroves in Thailand (Robertson et al. 1992, Kristensen et al. 2008). Research has also shown that litterfall export is significantly higher during the spring tide and wet season than during neap tides and dry season (e.g. Schories et al. 2003, Sánchez-Carrillo et al. 2009). Thus, mangrove stands subject to strong tidal action are prone to sustain coastal water primary and secondary productivity, whereas OM in sheltered mangroves during the dry season and neap tides are more likely to accumulate within the system or to be recycled within mangrove biomass.

Although no exhaustive global budget has been published for other elemental export than C and N, data on elemental concentrations collected in Table 1 a–c suggest that the tidal export of mangrove litterfall could also be a significant conveyor of other macronutrients and trace metals in coastal ecosystems. For instance, senesced leaves – the major constituent of litterfall by far – are particularly rich in Ca, S, Mg, N, K (median global concentrations ≥ 1 000 mg kg^{-1}) and in P, Al and Fe (median global concentrations ≥ 100 mg kg^{-1}) (Figure 24). Even though the global median concentrations of other trace metals within senesced leaves are usually lower than 100 mg kg^{-1} (Figure 24), mangrove litterfall production can be relatively high. Based on 91 studies, Saenger and Snedaker (1993) calculated that mangrove litterfall production ranges from 1.3 t ha^{-1} to 18.7 t ha^{-1} globally. To get a better idea, if we extrapolate this range of litterfall production to the global mangrove area of 138 000 km² (Giri et al. 2011), using the median elemental concentrations in senesced leaves presented in Table 1 b-c, this could correspond to 8.4 to 120.6 Mt y^{-1} of macro elements and to 12 264.9 to 176 426.2 t y^{-1} of trace metals released to mangrove floor globally through senesced leaves only (Table 5), with more than half of it being potentially exported from the ecosystem (Jennerjahn and Ittekkot 2002, Alongi 2013, 2014).
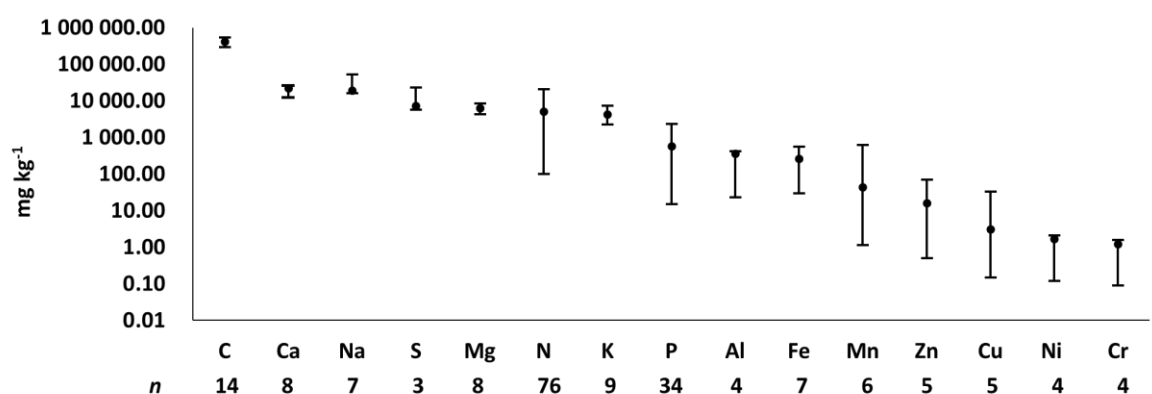
Figure 24. Median, minimum and maximum elemental concentrations (in mg kg $^{-1}$ DW) found in mangrove senesced leaves globally (references in Tables 1a - c)

Table 5. Range of annual elemental content in mangrove senesced leaves produced globally, estimated from total mangrove area of 138 00 km² (Giri et al. 2011), from the minimum and maximum global annual litterfall production (1.3 t ha^{-1} to 18.7 t ha^{-1} globally, Saenger and Snedaker 1993) and from the global median elemental concentrations in senesced leaves referenced in Tables 1a - c

	min (tonnes y^{-1})	max (tonnes y^{-1})
C	7 556 585	108 698 569
Ca	403 941	5 810 529
Na	350 288	5 038 763
S	130 489	1 877 039
Mg	111 901	1 609 658
N	91 494	1 316 106
K	81 806	1 176 753
P	10 159	146 130
Al	6 389	91 899
Fe	4 701	67 616
Mn	781	11 235
Zn	288	4 144
Cu	55	789
Ni	30	428
Cr	22	312

2.6.3.2 Direct OM consumption and other impacts of macrofauna on mangrove OM decomposition

Herbivores and detritivores that dominate mangrove detrital food chain have both a direct and indirect impact on mangrove nutrient cycling (Cannicci et al. 2008). Although negligible in some mangrove species stands (e.g. Macnae 1968, Schories et al. 2003), direct litter consumption and fragmentation by scraping, grazing and boring by tree-climbing and burrowing crustaceans (leaves, propagules, prop roots, wood e.g. Sesarmidae and Grapsidae crabs, Isopod borer *Sphoeroma*), molluscs (leaves, roots and trunks e.g. shipworm borer *Teredo*), and insects (leaves, wood, flowers, fruits, propagules, e.g. Chrysomelidae, Scolytinae, Bostrichindae) may strongly impact litter fluxes in mangrove forests (Feller and McKee 1999, Burrows 2003, Schaeffer-Novelli et al. 2000, Feller 2002, Kathiresan 2003, Emmerson et al. 2003, Fratini et al. 2005, Osorio

et al. 2017, see also review of Cannicci et al. 2008). In a mangrove in North Brazil for instance, Schories et al. (2003) report that decomposition and tidal export account only for 39% of the total annual leaf litter fall. The authors suggest that most of the unaccounted amount is removed by herbivores, predominantly by the leaf-removing crab *Ucides cordatus*. Similarly, Robertson (1986) measured that 28% of the annual mangrove leaf fall in a mangrove in Australia is removed by the leaf-removing crab *Sesarma messa* via direct consumption and burial, 78% of the buried leaves being consumed within the six first hours of burial. Severe insect outbreaks are also frequently observed in mangrove forests and may lead to the quasi complete defoliation of mangrove stands (e.g. Schaeffer-Novelli et al. 2000, Duke 2002, Fu et al. 2012). This is the case for the bud moth larvae, whose outbreak in a mangrove forest in China in 2010 damaged 90% of the foliage and reportedly decreased significantly the reproductive growth and net ecosystem productivity during the year following the outbreak (Lu et al. 2019b). These few examples show that direct consumption of OM could weight significantly in the elemental cycles and should therefore be incorporated in mangrove global elemental budgets.

2.6.3.3 Decomposition and mineralisation of the OM

Organic matter that are not directly exported from mangrove ecosystem or consumed by herbivorous and detritivores is then subjected to decomposition by physical and biological processes, with each of those processes being susceptible to have a positive feedback on litter consumption and decomposition. Hence, litterfall exposed to high humidity is more susceptible to be colonized by microorganisms, especially fungi, thus

speeding up decomposition processes. In turn, decomposition by microorganisms enhance OM leaching and breakdown, soften fibrous tissues, increase nutrient supply and palatability and thus favour OM consumption by herbivores and detritivores (Philips 1984, Ormeno et al. 2006, Raghukumar et al. 2008, Thatoi et al. 2013).

Rapid OM leaching and breakdown may lead to the enrichment of pore water in dissolved and particulate organic (DOM < 0.8–1 μm, POM > 0.8–1.0 μm) and inorganic matter (DIM, PIM) and to their mobilisation within the column water and out of mangrove ecosystems (Druffel et al. 1992). However, those may also promote nutrient conservation and burial. Indeed, leaching and breakdown products include recalcitrant molecules that have a strong affinity for OM and easily degradable molecules (e.g. proteins, sugars, lipids) (Alongi 2009). For instance, PIM and DIM include calcite and biogenic amorphous silica (opal) in their free or aggregate forms that originate from phytoplankton detrital frustules and from phytoliths (a polymer of $Si(OH)_4$ that derives from silica deposition within mangrove plant tissues, also called "plant opal") (Das et al. 2014, Zhang et al. 2017). Biogenic silica, together with other recalcitrant heavy weight molecules such as polyphenolics have a strong affinity for otherwise labile organic compounds and may thus promote significantly their long-term sequestration in mangrove soils (Parr and Sullivan 2005, Maie et al. 2008, Alongi 2009).

Simultaneously to these processes, microorganisms are the main driver of mangrove litterfall mineralisation, elemental speciation and solubility. This is especially the case of fungi and bacteria. Saprophytic fungi release a wide pool of hydrolytic enzymes able to aggressively break down high molecular weight molecules more recalcitrant to decomposition by other microorganisms (phenolics, cellulose). These organisms play a

key role in the first steps of mangrove OM breaking down and decomposition (Hyde 1996, Hyde et al. 1998, Thatoi et al. 2013). Studies report that once shed from the trees, mangrove leaves and wood are rapidly colonized (within the two first hours) by both marine and terrestrial saprophytic fungi that actively contribute to the degradation of lignocellulose into smaller compounds (Newell et al. 1987, Hyde et al 1998, Thatoi et al. 2013). In addition, several dozens of P-solubilizing fungi from at least seven genera have been found in mangrove rhizosphere and above ground biomass (Gupta and Das 2008, Thatoi et al. 2013). The most frequent, *Penicillium* and *Aspergillus*, rapidly release organic acids in the rhizosphere that solubilize phosphates bound to Ca, Fe and Al into forms available for plants (Turan et al. 2006, Bhattacharya et al. 2015).

Lignocellulolytic and P-solubilising bacteria and saprophytic protists that operate extracellular digestion (e.g. nanoflagellates, fungal-like Thraustochytrids) have also been frequently reported on mangrove litterfall and in the rhizosphere. However, bacteria and protists are less efficient degraders of high molecular weight molecules than saprophytic and P-solubilising fungi, particularly in acidic and anaerobic conditions (Thatoi et al. 2013). Nevertheless, these other microorganisms play a leading role in the secondary colonization and further mineralisation of fungi breakdown products (Matondkar et al. 1981).

2.6.3.4 The specific case of OM oxidation pathways by prokaryotes and elemental speciation

Organic matter mineralisation by prokaryotes (bacteria, archaebacteria) are considered as one of the main drivers of trace metal and macronutrient speciation and accumulation in mangrove soils. In presence of oxygen, prokaryotes produce energy for metabolic functions through aerobic cellular respiration. In that reaction that takes

place in the plasma membrane, chemical energy is released from dissolved and particulate organic carbon molecules and stored into molecules (ATP, adenosine triphosphate, ADP, adenosine diphosphate, NADH, nicotinamide adenine dinucleotide, etc) in presence of O_2, which acts as final electron acceptor in the electron transport chain of that reaction. As a result, O_2 combines with H^+ to form H_2O, whereas carbon compounds are slowly broken down in CO_2, a waste product then released into the atmosphere (Figure 25). Where O_2 decreases (typically at depth and in waterlogged conditions), numerous species of bacteria and archaebacteria are able to retrieve the energy necessary for their metabolism from OM by using other electron acceptors present in the substrate (Figure 25, Froelich et al. 1979). The main oxidants used by prokaryotes for cellular respiration in mangrove substrate are, ranked by their reduction potential, O_2 > nitrate (NO_3) > Mn^{4+} > Fe^{3+} > SO_4^{2-} > CO_2 (DeLaune and Reddy 2005, Kristensen et al. 2008). As for CO_2 in aerobic cellular respiration, the waste products of these associated OM oxidation pathways are then released into the atmosphere, or engaged in secondary reactions (illustrated in Figure 25) that lead to differential elemental solubility. This results in specific elemental composition of the substrate (summarized in Figure 26) that varies therefore importantly according to the Eh and availability of these electron acceptors.

Primary reactions

	Δ G° (Kj/mol)

(1) Aerobic respiration (Eh > 330 mV)

$138O_2 + OM + 18HCO_3^- \rightarrow 124CO_2 + 16NO_3^- + 122H_2O + H_3PO_4$ -479

(2) Denitrification (250 < Eh < 330 mV)

$94.4NO_3 + OM \rightarrow 52.2N_2 + 13.6CO_2 + 84.8H_2O + HPO_4^{2-} + 92.4HCO_3^-$ -453

(3) Oxidation by manganese oxides (130 < Eh < 230 mV)

$236MnO_2 + OM + 104H_2O + 364CO_2 \rightarrow 236Mn^{2+} + 470HCO_3^- + HPO_4^{2-} + 8N_2$ -349

(4) Oxidation by iron oxides (Eh < 130 mV)

$424FeO_3 + OM + 104H_2O + 740CO_2 \rightarrow 424Fe^{2+} + 846HCO_3^- + HPO_4^{2-} + 16NH_3$ -114

(5) Oxidation by sulfates (-150 < Eh < -75 mV)

$53SO_4^{2-} + OM \rightarrow 53HS^{2-} + 39CO_2 + 39H_2O + HPO_4^{2-} + 67HCO_3^- + 16NH_4^+$ -77

(6) Methanogenesis (Eh < -250 mV)

$OM \rightarrow 53CH_4 + 53CO_2 + HPO_4^{2-} + 16NH_4^+$ -30

Secondary reactions

Nitrification

$NH_4^+ + 3/2O_2 \rightarrow NO_2^- + 2H^+ + H_2O$
$NO_2^- + 1/2O_2 \rightarrow NO_3^-$
$NH_4^+ + 2O_2 \rightarrow NO_3^- + 2H^+ + H_2O$

Anammox

$NH_4^+ + NO_2^- \rightarrow N_2 + 2H_2O$

Mn²⁺ oxidation

$2Mn^{2+} + O_2 + 2H_2O \rightarrow 2MnO_2 + 4H^+$
$4Mn^{2+} + O_2 + 6H_2O \rightarrow 4MnOOH + 8H^+$
$5Mn^{2+} + 2NO_3^- + 2H_2O \rightarrow 5MnO_2 + N_2 + 8H^+$
$10Mn^{2+} + 2NO_3^- + 6H_2O \rightarrow 10MnOOH + N_2 + 18H^+$

Methane oxidation

$CH_4 + 2O_2 \rightarrow CO_2 + 2H_2O$
$CH_4 + SO_4^{2-} \rightarrow HCO_3^- + HS^- + 2H_2O$

Fe²⁺ oxidation

$4Fe^{2+} + O_2 + 10H_2O \rightarrow 4Fe(OH)_3 + 8H^+$
$5Fe^{2+} + NO_3^- + 12H_2O \rightarrow 5Fe(OH)_3 + 9H^+ + 1/2N_2$
$Fe^{2+} + MnOOH + H_2O \rightarrow Fe(OH)_3 + Mn^{2+}$
$2Fe^{2+} + MnO_2 + 4H_2O \rightarrow Fe(OH)_3 + Mn^{2+} + 2H^+$

Sulfure oxidation

$H_2S + 2O_2 + 2HCO_3^- \rightarrow SO_4^{2-} + 2CO_2 + 2H_2O$
$H_2S + 4CO_2 + 2Fe(OH)_3 \rightarrow S + Fe^{2+} + 4HCO_3^- + 2H_2O$
$H_2S + 4CO_2 + MnO_2 \rightarrow S + Mn^{2+} + 2HCO_3^-$

Fe²⁺ and sulfure precipitation

$Fe^{2+} + H_2S \rightarrow FeS + 2H^+$
$2FeS + 2H^+ \rightarrow FeS_2 + Fe^{2+} + H_2$

Figure 25. Primary and secondary reactions of OM oxidation/respiration by prokaryotes in marine sediments at different Eh established by Froelich et al. (1979). Stoichiometry of each equation is given for one mole of OM oxidised. Δ G° gives the Gibbs free energy for each mole of organic carbon oxidised (Deborde 2007). Figure from Molnar (2012). Eh data are from Reef et al. (2010) and Youssef (1995) in Saenger (2002), corrected to pH 7

- O_2 reduction is the dominant pathway for OM respiration
- nitrification ↑
- NO_3 most common form of N in the substrate
- abruscular mycorrhizae fungi and P solubilising bacteria may be present
- oxidation of Fe-S resuts in excess of SO_4^{2-} + dissolved Fe^{2+}
- Fe has a ↑ P sorption capacity, and thus, P absorbed to sediment
- adosprtion and co-precipitation of divalent metals (e.g. Cr^{2+}, Ni^{2+}) on Fe and Mn oxides and hydroxides

Oxic
Eh > 330 mV [1]

O_2 starts to disappear	< 330
denitrification ↑, NO_3^{2-} starts to disappear	250 < Eh < 330
ammonification ↑, NH^{4+} most common form of N	< 250
Mn^{4+} reduces in Mn^{2+} and releases to the pore-water solution	130 < Eh < 230
Fe^{3+} reduces in Fe^{2+} and releases to the pore-water solution. Fe reduction results in P released to the pore-water	~ 130

Suboxic
100 mV < Eh < 330 mV

sulfate reduction becomes the dominant pathway for OM respiration. SO_4^{2-} is reduced in S^{2-}, toxic for plants	- 75 < Eh < - 150
Fe^{2+} precipitates in Fe-S. Fe^{2+} disappears from the pore-water solution	
Sorption of Ni^{2+}, Cr^{2+}, K^+ on Fe-S minerals	
CO_2 becomes the dominant electron acceptor during OM respiration, with production of CH_4 gas (methanogenesis)	< - 250

Reduced
Eh < 100 mV

[1]Redox conditions defined as in Marchand et al. (2012)

Figure 26. Main chemical changes in mangrove substrate at different levels of oxidation-reduction potential (Eh). Figure adapted from Reef et al. 2010, with data from Reef et al. (2010), Youssef (1995) in Saenger (2002), corrected to pH 7

Oxidation of the OM by prokaryotes particularly influence the speciation and solubility of sulfurs, N, P, redox-sensitive elements such as Fe and Mn, and naturally, C. Typically, OM oxidation in well-oxygenated substrates (in the upper layers, in frequently emerged

substrates or in the vicinity of oxidizing root and burrows for instance) results in higher release of CO_2 toward the atmosphere compared to the other decomposition pathways (Figure 25), and in the precipitation and accumulation of Fe and Mn ions as oxides and hydroxides in the solid phase of the substrate (Kristensen et al. 1994, 2008). In oxic conditions, several studies have reported the adsorption and co-precipitation of divalent trace metals such as Ni^{2+}, Cr^{2+} and K^+ at the surface of Fe and Mn minerals, but also at the surface of OM particles or carbonates (Lacerda et al. 1988, Otero et al. 2009, Marchand et al. 2012, Noël et al. 2017). Phosphorous shows also a strong affinity for trace metal oxides/hydroxides (Fe, Al) and carbonates and thus, may accumulate in oxic conditions (e.g. Hesse 1962, 1963, Millero et al. 2001, Nóbrega et al. 2014, Queiroz et al. 2020).

With decreasing O_2 concentrations in soils, NO_3, and then Fe and Mn-(O)OH are used as final electron acceptors in suboxic conditions. This results in a loss of N from the soils toward the atmosphere, and in the dissolution of Fe and Mn oxyhydroxides, respectively (Figure 25). In suboxic conditions, mangrove pore-water are therefore enriched with $Fe^{2+/3+}$ and Mn^{2+}, P and associated trace metals that become therefore available for tidal export, plant uptake and/or re-precipitation within the solid phase of the substrate.

Conversely, anaerobic respiration pathways such as sulfato-reduction and methanogenesis occur in reduced substrates (waterlogged, frequently submerged and at depth) (Alongi 1998, Kreuzwieser et al. 2003, Kristensen et al. 2008, Jacotot et al. 2018). At these lower Eh, Fe and Mn oxides and hydroxides dissolve and $Fe^{2+/3+}$ and Mn^{2+} accumulate in pore water. Markedly, Mn oxides and hydroxides are particularly prone to dissolution and water export in mangrove substrates exposed to anoxic conditions and large tidal amplitude (Gueiros et al. 2003, Otero et al. 2009, Holloway et al. 2016). In a recent budget estimate, Holloway et al. (2016) actually designate mangroves as a

greater source of Mn for oceanic waters globally (~ 659 Gg y^{-1}) than riverine (~ 297 Gg y^{-1}) and atmospheric inputs (~ 604 Gg y^{-1}). On the other hand, ions Fe^{2+} also tend to co-precipitate with sulfides produced by prokaryotes during sulfate reduction (Figure 25) and accumulate in high concentrations within the solid phase of the substrate as iron sulfide minerals, such as pyrite and greigite (Figure 27, Ferreira et al. 2010). As in oxic conditions, divalent cations (Cr^{2+}, Ni^{2+}) may co-precipitate with these Fe-bearing minerals and thus accumulate in the solid phase of anoxic substrates (Figure 27, Ferreira et al. 2007a,b, Otero et al. 2009, Marchand et al. 2011b, Noël et al. 2014).
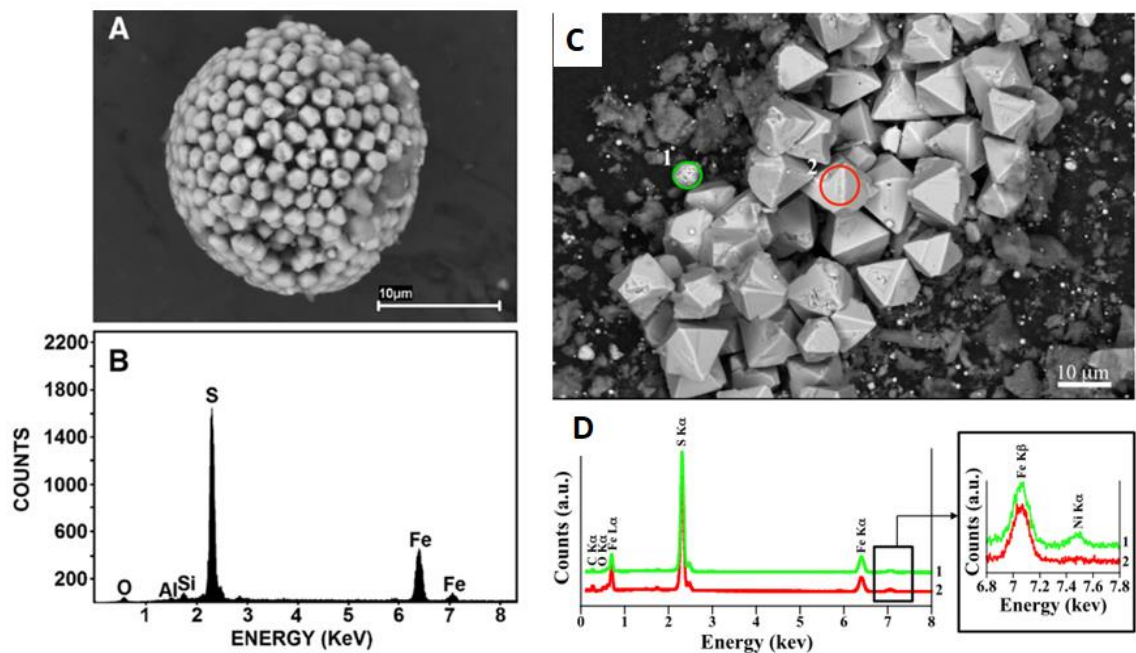
Figure 27. Examples of pyritic minerals (A and C) and corresponding energy-dispersive X-ray spectroscopy spectrum, showing intense peaks of Fe and S (C and D) and co-precipitation of Ni (D). A: framboidal pyrite ; C: small inclusion of spherulitic pyrite co-precipitated with Ni in green (1) and cuboctahedral pyrite in red (2). (A-B from Ferreira et al. 2007a, C-D from Noël et al. 2017)

Lastly, emission of CH_4 also occur in reducing conditions in mangrove soils (Eh < - 250 mV), aerial roots and water column through methanogenesis (Kreuzwieser et al. 2003, Jacotot et al. 2018), i.e. the use of organic C (low molecular C compounds or CO_2) as

electron-acceptor during anaerobic respiration by prokaryotes from the superkingdom Archaea (Canfield et al. 2005, Kristensen et al. 2008).

Finally, mangrove substrates are also exposed to strong temporal variations of oxygenation over the tidal frame along its depth profile. At a critical depth, called "oxidation front", the alternance of submersion and emersion results in strong fluctuations of the Eh potential. These frequent alternance of oxidative and reducing conditions compromises the structural integrity of redox sensitive minerals and lead to acidic conditions (Noël et al. 2017). This results in general in an enrichment of pore-water in trace metals and sulfides and co-precipitated trace metals that are more easily mobilised and exported from the substrates toward the water column and plant compartment.

To conclude, the distribution and accumulation of macroelements and trace metals in mangrove substrate are largely a reflexion of its biological activity and chemical properties, particularly of the Eh, pH and OM contents. Although mangrove soils and sediments may contain important concentrations of macronutrients, those, when available, may be rapidly remobilised toward the water column and by living organisms (Rivera-Monroy et al. 1996, 1999, McKinnon et al. 2002, Costanzo et al. 2004, Alongi 2013, Molnar et al. 2013). On the other hand, most trace metals necessary for the metabolism are micronutrients, and thus required in relatively small quantities by the different biological communities, or sequestrated within mangrove root tissues and subsequently buried (e.g. Nath et al. 2014b, Chowdhury et al. 2015, 2017, Yan et al. 2017). This fact and the strong affinity divalent metals present for OM, Fe, Mn or Ca minerals over the entire Eh range explain why mangrove ecosystems are generally considered as such good ecological filter for trace metals. However, the important variations of oxidative and reducing conditions discussed above contribute to a vast

disparity of trace metal distribution among the chemical fractions of the substrate along the intertidal and depth gradient, and this even at a local scale (e.g. in Table 6). Trace metals bound to these chemical species present distinctive solubility. Different locations within a same mangrove stand will therefore show very different potential to lose or retain trace metals within their substrate over the tidal frame or over a specific disturbance. This may contribute to the large heterogeneity in trace metal concentrations within mangrove soil worldwide we presented at the beginning of this chapter, and probably to the absence of a clear latitudinal trend in trace metal concentrations.

Table 6. Examples of trace metal proportion ranges (% of DW) measured in different fractions of mangrove soils and sediments in the Red Sea, New Caledonia and India. The residual fraction corresponds to pre-existing, deposited or newly-formed minerals recalcitrant to chemical extractions (e.g. clays, Fe-S minerals)

	residual fraction	Fe/Mn oxides-bound	carbonate-bound	exchangeable	OM-bound	location	reference
Fe	36.6 - 90.8	0.8 - 2.3	1.8 - 3.4	0.1-0.7	3.0 - 24.5	Red Sea	Okbah et al. 2005
	40.2 - 98.3	1.2 - 38.9	0 - 12	0 - 22		New Caledonia	Marchand et al. 2016
Mn	46.1- 71.2	2.7 - 19.0	12.4 - 40.4	0.3 - 4.9	3.9 - 14.6	Red Sea	Okbah et al. 2005
	15.0 - 98.0	0.0 - 20.0	0.0 - 12.0	2.0 - 82.8		New Caledonia	Marchand et al. 2016
Ni	23.4 - 93.0	2.0 - 5.6	2.0 - 8.0	0.5 - 70.6		New Caledonia	Marchand et al. 2016
	86.7 - 91.3	3.2 - 7.2	2.1 - 2.9		3.4 - 10.3	India	Chakraborty et al. 2015
Zn	4.8 - 38.6	5.4 - 18.2	27.6 - 59.1	0.6 - 13.4	13.5 - 34.4	Red Sea	Okbah et al. 2005
	0.0 - 99.0	0.0 - 1.5	0.0 - 0.00	1.0 - 100.0		New Caledonia	Marchand et al. 2016
Cu	2.2 - 36.0	6.4 - 12.0	32.0 - 67.6	4.8 - 8.0	10.7 - 18.3	Red Sea	Okbah et al. 2005
	78.3 - 82.7	1.2 - 5.9	2.1 - 3.0		10.0 - 21.0	India	Chakraborty et al. 2015
	6.2 - 84.3	0.0 - 3.0	11.5 - 71.4	1.5 - 47.4		New Caledonia	Marchand et al. 2016
Co	10.2 - 88.0	7.0 - 44.35	0.0 - 0.0	4.0 - 69.7		New Caledonia	Marchand et al. 2016
Cd	1.3 - 23.8	22.9 - 31.9	29.1 - 46.8	8.6 - 22.9	8.6 - 16.0	Red Sea	Okbah et al. 2005
Pb	6.7 - 52.6	14.9 - 24.0	13.0 - 42.6	4.7 - 9.5	14.2 - 28.6	Red Sea	Okbah et al. 2005

2.6.3.5 Global trends in OM decomposition

The capacity of mangroves to act as a reservoir for nutrients and trace metals through burial largely depends on decomposition rates of the OM that are deposited and accumulate on mangrove forest floor. Indeed, rapid decomposition and mineralisation of litterfall that reach the forest floor in sheltered locations prevent burial and

contributes to nutrient and trace metal enrichment of pore water and their mobilisation toward the water column. Fast litter decomposition is also thought to sustain mangrove productivity where lower organic production occur within the ecosystem, in arid mangroves for instance (Sánchez-Andrés et al. 2010). The understanding of OM decomposition rates at a global scale is therefore essential to evaluate the efficiency of mangroves to act as a filter for materials, and the impact global changes could have on mangrove productivity and their long-buried stocks of OM.

The previous sections have demonstrated the complexity of mangrove pedogenesis processes and their influence in mangrove geochemistry and elemental speciation. The numerous factors that influence those processes and the becoming of OM contribute to a strong spatial and temporal heterogeneity in mangrove capacity to act as an elemental reservoir or source for adjacent coastal waters, and this both at a local and global scale. Nevertheless, data from OM decomposition experiments in the literature show that mangrove litterfall decomposition rates tend to decrease with increasing latitude and decreasing temperature (Figure 28). In Brazil for instance, litterfall of *Laguncularia racemosa* exhibits a half-time decomposition that may varies from 23 days in Bahia at 14.8° S (de Oliveira et al. 2013) to 216 days in Rio de Janeiro at 21.4° S (Barroso-Matos et al 2012). This corroborates with the fact that faunal and fungi diversity, bacterial activities and respiration rates tend to decrease with decreasing temperature (e.g. Alongi 1988, Gonzalez-Acosta et al. 2006, Chen et al. 2012, Li et al. 2018b, Van Vinh et al. 2019b).

However, these relationships are very weak (R^2 = 0.07, and 0.02, respectively, Figure 28), albeit they become more apparent when considering mangrove plant taxa separately. For the genus *Avicennia* for instance, differences in latitudes alone explain 24.0% of the total variation in half-time decomposition of the litterfall, whereas temperature explains

17.4% of the variation in the data (Figure 28). Decreasing decomposition rates with increasing latitudes could lead to higher OM burial at high latitudes. This could therefore partially explain the absence of a clear latitudinal trend in elemental concentrations in mangrove soils and sediments highlighted in the first section of this review, this despite lower primary productivity at high latitudes (Figure 10).
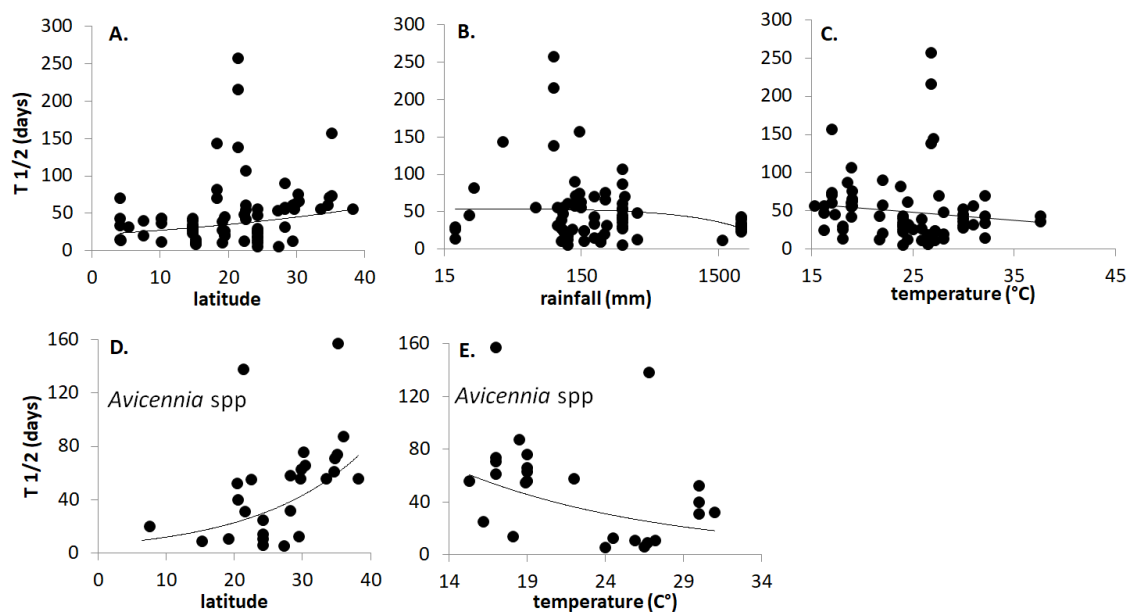
Figure 28. (A, B, C) Relationships between half-time litterfall decomposition rates (T ½ days), all species included, and latitude, rainfall and temperature in 85 locations worldwide; (D, E) relationships between half-time litterfall decomposition rates (days) of *Avicennia* spp and latitude and temperature. When non available, rainfall and temperature data where given as the average data from the region during the period equivalent to T1/2 (Heald 1971, Fell et al. 1975, Albright 1976, Boonruang 1978, Goulter & Allaway 1979, Van der Valk and Attiwill 1984, Robertson 1988, Steinke and Ward 1987, D'croz et al. 1989, Lee 1989, Lu and Lin 1988 in Lu and Lin 1990, Lu and Lin 1990, Steinke et al. 1990, Tam et al. 1990, 1998, Wafar et al. 1997, Ashton et al. 1999, Middleton and McKee 2001, Davis et al. 2003, Bosire et al. 2005, Aké-Castillo et al. 2006, Silva et al. 2007, Sánchez-Andrés et al. 2010, Barroso-Matos et al. 2012, de Oliveira et al. 2013, Li and Ye 2014, Ainley and Bishop 2015, Bourgeois et al. unpublished results, Van Vinh et al. 2020)

Comparatively, research worldwide has shown that inter-species differences are a greater contributor to the global variations in OM decomposition rates (Figure 29). Some authors explain this by important differences in mangrove litter quality between mangrove taxa,
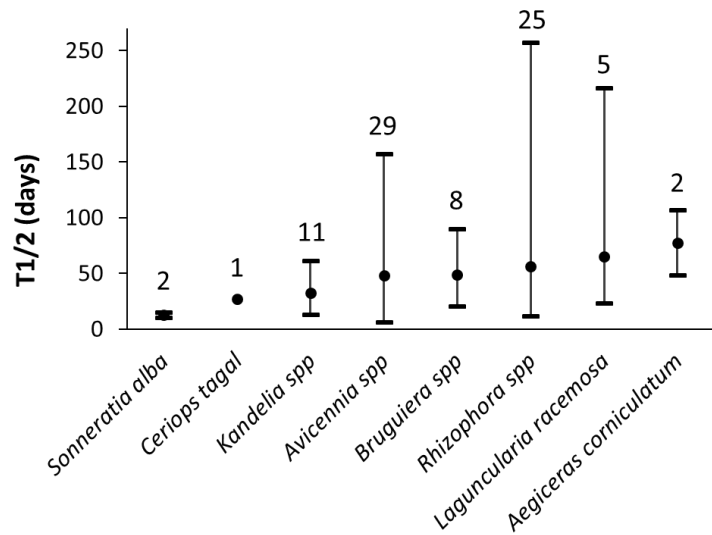
Figure 29. Mean, minimum and maximum half-time litterfall decomposition rates (T ½ days) in different taxa; number for each taxa corresponds to the number of locations recorded for each taxa (see Figure 28 for references)

which induces different rates of herbivory and susceptibility to mechanical breakdown. For instance, species with succulent and tannin-rich litter (e.g. *Rhizophora* spp) tend to decompose slower than N-rich litter (e.g. *Avicennia* spp, Figure 29) (Marchand et al. 2005, Lima and Colpo 2014, Ye et al. 2019). However, inter-species differences in decomposition rates are certainly also due to the fact that different mangrove species exhibit different resistance to salinity and water stress, and thus typically grow in specific locations along the intertidal gradient. As seen in the previous section, contrasting physico-chemical conditions along the intertidal and depth gradients may result in important differences in reducing-oxidation conditions and therefore in different OM oxidation rates by microbial communities. Typically, waterlogged and frequently submerged mangrove anoxic soils are therefore often enriched in OM and sometimes well-preserved plant roots at depth (Gonneea et al. 2004, Sanders et al. 2010, Breithaupt et al. 2012). However, the rate OM mineralisation and thus decomposition remains entirely co-dependent of humidity, herbivory, leaching and mechanical break-down processes (e.g. Aké-Castillo et al 2006). This intra-site variation in litterfall

decomposition is particularly well illustrated in a last example in Figure 30, which depicts a leaf decomposition experiment in temperate monospecific mangrove stands of *A. marina* in New Zealand (Bourgeois et al. unpublished results). The results after one month show that higher leaf decomposition rates occur on well-oxygenated but frequently submerged soils seaward than at higher elevations with longer duration of emersion and higher Eh values.
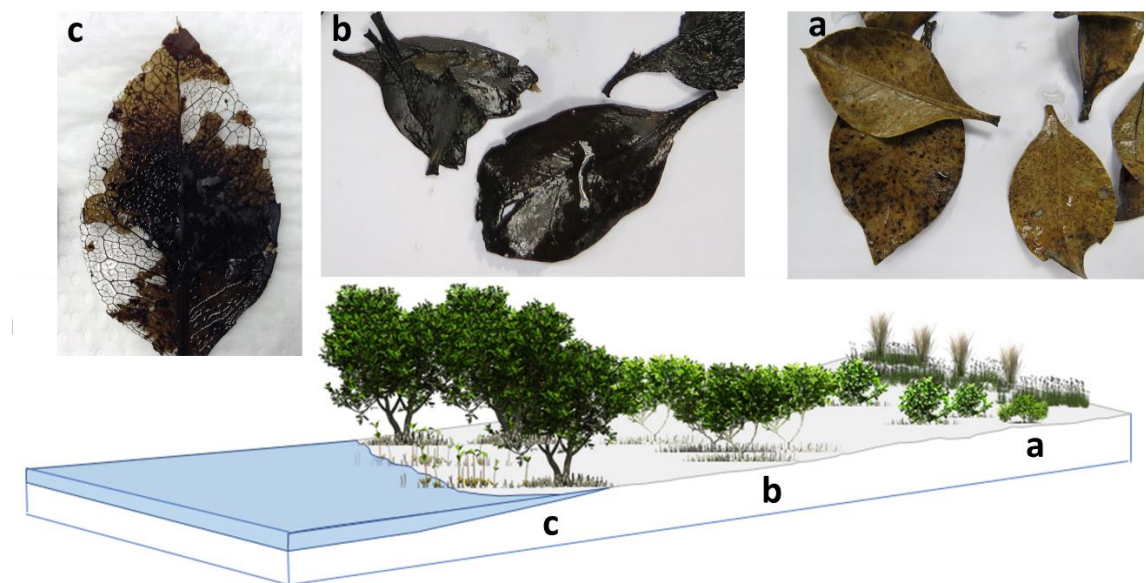
Figure 30. Leaf decomposition along a saltmarshes-river gradient after a one month mesh-bag leaf decomposition experiment in *A. marina* mangrove stands downstream Mangawhai Estuary, New Zealand in summer in (a) suboxic conditions and low immersion at the border of the saltmarshes at high elevations (+ 209 ± 50 mV), (b) reducing conditions and frequent immersion inside mangrove stands (- 33.02 ± 27.20 mV), (c) suboxic and frequently flooded conditions seaward (+ 167.72 ± 104.14 mV) (Bourgeois et al. unpublished results)

As we close this section on pedogenetic processes, this last example illustrates once more the strong spatial heterogeneity in mangrove biogeochemical processes. Much remains to be understood in terms of trace metal and nutrient cycles in mangrove ecosystems. However, the numerous examples cited in this review demonstrate that the assessment of the effects global changes could have on elemental pools should be specific to each study site.

2.7 Conclusions

The understanding and monitoring of nutrient and metal cycles in mangrove ecosystems is of utmost importance for the ecological safety of both terrestrial and marine ecosystems. Due to their high productivity and their position along shorelines, mangroves and the stocks of metals and nutrients they hold are particularly vulnerable to deforestation, sea-level rise, extreme climatic events and increase in aridity worldwide. Their degradation is likely to increase the transfer of material from the ecosystem toward the atmosphere and coastal areas, thus increasingly contributing to the greenhouse effect and to the eutrophication and metal pollution of the oceans.

Several actions could be undertaken by the different actors involved in mangrove monitoring and protection to predict and prevent elemental losses from mangrove ecosystems over time. For one, there is an urgent need to collect and forge a large database that could allow an easy and reliable comparison between elemental stocks and concentrations measured *in situ*. This was the aim of this review. The perspective of this review is now to complete, present and update the large dataset of nutrient and trace metal concentrations showed in Table 1 a-c in a meta-analysis and in a website accessible to researchers, managers and policy makers for further contributions, monitoring, analyses and modelling.

Secondly, the cycle of an element is rarely a solo affair, and most of the time, the complex chain of chemical reactions of an element biogeochemical cycle depends on the availability of several other elements. We saw that this is the case for the mineralisation and plant uptake of most macroelements present in high concentrations in the OM, whose cycle strongly depends on redox-sensitive elements that serves as electron acceptors during OM mineralisation, such as Al, Fe, Mn for instance. However,

as researchers increasingly call on advanced and often costly technologies for their fieldwork, analyses and experiments, we tend to focus more and more on one element and some environmental factors, thus disregarding the huge library of interactions between elements and molecules discovered over the last centuries. Furthermore, we know that the effects of climate change are inextricably linked with that of direct anthropogenic pressures (Gilman et al. 2006, 2007, 2008, Waycott et al. 2011, Quisthoudt et al. 2013, Lovelock et al. 2015). Therefore, in order to effectively monitor the effects of anthropogenic influences and climate change on nutrient cycles, now is the time more than ever before to reconciliate the valuable results obtained in controlled environments with multivariate elemental analyses *in situ*.

Thirdly, variability of experimental and sampling designs, measurement techniques and analyses has limited comparison between datasets and the understanding of global processes in mangrove biogeochemical cycles (e.g. Adame and Lovelock 2011). Sensible efforts have been made in publishing standardisation techniques to ease comparison between datasets and budget estimates in nutrient and metal cycles (see Kauffman et al. 2012 for example). However, differences in mangrove geomorphology, forest structure, soil composition and the lack of means in some areas still constitute a huge difficulty in unifying researchers under the same methodological banner, and much remains to do in this domain. The problem is easily solved in the case of elemental chemical analyses for which standards and reference samples can be used to test the accuracy and precision of a given method (e.g. Van Dijik and Houba 1999, Dijk 2002). For other aspects however, the solution is less obvious. This is the case for the sampling and measurements of elemental stock within plant biomass and the establishment of allometric equations for instance. The intricate structure of mangrove tree roots, trunks and aerial roots leave little chance for an easy comparison between or even within

mangrove stands without resorting to destructive and time-consuming methods (see Komiyama et al. 2008 and Figure 3 for instance). The development of new techniques – notably the combination of imagery and machine learning approaches – certainly constitutes a solution to many problems in the monitoring and conservation of mangrove elemental pools, including in the assessment and monitoring of mangrove biomass, density and biophysical parameters (see the review of Pham et al. 2019). However, some challenges remain to be solved, first in the technology development itself, but above all and as always, in the funding availability to access these technologies, particularly in remote areas where it is often the most urgently needed. Finally, and although we touch here upon considerations that go beyond the scientific aspect of this review, ultimately, the success of environmental research, conservation, restoration and management rests indeed on government policy, and on how good we are as ecologists "to convert our science into sound and environmental policy" (Lawton 2007). At the end of the day, only the dissemination of knowledge in communities through science communication for the public at large and education is able to change the public and politics' perception of mangroves, and lead to an adequate monitoring and protection of mangrove elemental stocks. However, scientific communications are slow to reach their target, and even slower at influencing it (Lawton 2007). People by nature are prone to made changes in their habits only when they can directly benefit from them. In addition, many players in policy-making have better and more attractive arguments to get their way than the long-term solutions proposed by ecologists to promote a sustainable restoration, conservation and management of ecosystems (Lawton 2007). In the history of mangrove ecology and its impact on politics and community thinking, catastrophic events and their sensationalism were often needed to attract media coverage and initiate the necessary changes (e.g. review of Marois and

Mitsch 2015). It took for instance the super cyclone that hit Orissa in India in 1999 (Das and Vincent 2009), the infamous Indian Ocean earthquake and tsunami of 2004 (e.g. Kathiresan and Rajendran 2005), the cyclone Larry that crossed the eastern Australian coast in 2006 (Williams et al. 2007) or the typhoon Haiyan that hit the Philippine in 2013 (Marois and Mitsch 2015) to convince the public, through some happy and less happier stories, that mangrove biomass can effectively protect communities and government from tragic human and economic losses. Apart from catastrophic events, rapid changes in mangrove restoration and conservation cannot happen without a direct benefit and investment from local communities at least equal to those brought by the industries at the origin of mangrove clearing. However, this would necessitate the following of scientific and technical guidance on environmental factors and mangrove tree species requirements, a global environmental consciousness, policy changes, a good socio-economic knowledge, and incentive funding to counter the slow benefits from mangrove elemental pools conservation and restoration (Kodikara et al. 2017, Lovelock and Brown 2019).

Chapter 3

Stocks and Soil-Plant Transfer of Macronutrients and Trace Metals in Temperate New Zealand Estuarine Mangroves

3.1 Abstract

Aims: Rapid expansion of temperate mangroves in New Zealand over the last decades has prompted an increase in resource consents for removal. However, little is known about the capacity of temperate mangroves to store elements, including pollutants. The main objective of this study was to assess the stocks and soil-plant transfer of macroelements (C, N, P, K, Mg, Ca, S) and trace metals (Fe, Mn, Al, Ni, Cu, Zn, Co, Cr) within temperate mangrove soils.

Methods: Soil samples and root, leaf and wood components were analysed for their total and available elemental concentrations over a wide range of environmental conditions along the head-mouth textural, salinity and nutrient gradients of the estuary. Physico-chemical characteristics of the soil of the different sites studied were also determined.

Results: Mangrove soils with lower Eh and currents upstream of the estuary trapped larger amount of macroelements and heavy metals in the soils than downstream. This results in higher translocation of macro elements from the soil toward the above-ground biomass and higher translocation of heavy metals from the soil toward the litterfall, likely as a mechanism to avoid long term metal toxicity in the root system.

Conclusions: This multi-elemental study provides a comprehensive understanding of soil-plant transfers in temperate mangroves and can be used to better evaluate the ecological services of these ecosystems.

3.2 Introduction

Mangroves are plant communities found in sheltered coastlines, estuaries and deltas of tropical and subtropical regions (Duke et al. 1998, FAO 2007, Tomlinson 2016). Although 35% of their global area has been lost over the last four decades (Valiela et al. 2001, Hamilton and Casey 2016), the increasing acknowledgment of the ecological services these ecosystems provide has led to a movement towards mangrove restoration in tropical areas (Feller et al. 2017). Conversely, temperate mangroves in New Zealand have expanded at a rate of 4% per year over the last century (Morrisey et al. 2007), mostly as a result of climatic factors and the loading of sediment and organic compounds in estuaries due to logging, urbanisation and pastoral activities (Swales et al. 2007, 2015, Lovelock et al. 2010). This expansion raises concerns for coastal access, local biodiversity and recreational areas (De Luca 2015). As a result, an increasing number of permits to remove mangroves have been granted by councils to communities or local estuary care groups throughout northern New Zealand since the 1990s (Lundquist et al. 2017). With the large number of removals taking place, there is a pressing need to understand the importance of mangrove ecological services in temperate climates (Dencer Brown et al. 2018). However, there has been little research into the stocks of macroelements and metals in these temperate mangrove stands and their transfer from the soils to plant communities. The studies carried out have been focused on the storage of carbon, nitrogen and phosphorus (Bulmer et al. 2016, Gritcan et al. 2016, Pérez et al. 2017, Tran et al. 2017).

In the tropics, the role of mangroves as a filter and reservoir for macroelements and metals is well recognized (e.g. Lacerda and Abrao 1984, Tam and Wong 1993, Marchand et al. 2011a, b, Usman et al. 2013). Numerous studies have shown that the specific chemical properties of mangrove soils (low Eh and oxygen content) allow for a slow decomposition of organic matter (OM) in the soils, which constitute an important pool of carbon and nutrients (Alongi et al. 2003, 2005a, Bouillon et al. 2008, Alongi 2014, Deborde et al. 2015). Similarly, the main OM decomposition pathways in these flooded environments (i.e. anaerobic sulfate reduction and aerobic and Fe respirations) may lead to the co-precipitation and subsequent accumulation of trace metals within pyrite or iron-oxides compounds (Ferreira et al. 2007a, Marchand et al. 2011a, 2012, Noël et al. 2014, 2015, 2017). This accumulation of nutrients and metals in the ecosystem is accentuated by the high tolerance of some mangrove species to metals, which tend to store a substantial pool of trace metals and macroelements within their biomass (e.g. Alongi et al. 2003, 2005a, Yan et al. 2017).

However, differences in ecological services with latitudinal gradients have already been observed in mangrove forests. Colder climates at high latitudes induce lower biodiversity in mangrove forests than in the tropics, and lower OM storage within biomass over time (Woodroffe and Grindrod 1991, Saenger and Snedaker 1993, Ellison 2002, Alfaro 2006, Morrisey et al. 2010). On the other hand, several studies conducted in New Zealand have shown that the total biomass and pool of nutrients in soils (C, N) and plant tissues (C, N, P) increase in mangrove stands subject to high sedimentation and nutrient inputs (e.g. Lovelock et al. 2007a, b, Gritcan et al. 2016, Tran et al. 2017). Despite the lower biomass and productivity at a global scale, these studies have shown

that expanding temperate mangroves in New Zealand could retain a significant amount of nutrients and heavy metals within their biomass over time.

In light of mangrove removals in New Zealand, the role of temperate mangroves in storing macroelements and metals needs to be better assessed and understood. This study aims to fulfil two specific objectives: i) evaluate the elemental pool in estuarine temperate mangrove soils over a wide range of texture, OM, nutrients and salinity and ii) characterize the elemental transfer in the soil-plant continuum along that gradient. In order to achieve these objectives, we analysed the storage, concentrations and soil-plant transfer of macro- (C, N, P, Ca, Mg, K, S), microelements (Fe, Cu, Zn, Ni, Cr) and other heavy metals (Co, Al) in soils and plant tissues through a spatial approach, in three mangrove stands that feature together a large range of textures, OM, nutrients and salinity.

3.3 Material and Methods

3.3.1 Site of study

The study was carried out during the growing season (summer), in February 2016 in Mangawhai Harbour (36° 7' 0'' S, 174° 34' 0'' E, 248 ha), about 80 km north of Auckland City, northern New Zealand (Figure 31). The study area consists of an estuarine area of 4.6 km² (McCabe et al. 1985) fed by two creeks that flow into the northern and southern arms of an 11 km long channel with a width ranging from 40 to 600 m (Figure 31). The surface geology surrounding both creeks is characterized by Neogene sedimentary rocks and by river, estuarine and swamp deposits from the Holocene and Late Pleistocene. In addition, the creek north of the estuary drains a volcanogenic formation located northwest of the estuary (Edbrooke and Brook 2001). In addition of the estuarine

gradient (head-mouth), a seaward-landward gradient also occurs along the main channel. This gradient consists of seaward sandflats and mudflats, followed by ~ 87 ha of monospecific mangroves composed of *Avicennia marina* (Forsk.) Vierh subsp. *australasica* (Walp.) J. Everett, and landward marsh grasses dominated by *Leptocarpus similis* and *Juncus kraussii* (Figure 32). For clarity purpose, only the estuarine gradient (from Upstream to Downstream of the estuary) has been analysed in the present chapter. A detailed analysis of the landward-seaward mangrove gradient along the estuary will be discussed separately (data not presented in this thesis).

Previous works carried out in the estuary have shown that since human settlements, changes in land use have generated a deposition of sediments onto the mudflats in Mangawhai Estuary, which contributed to mangrove spread at a rate of 1.5 ha y^{-1} since 1950 (Hulbert 2014, Lindsay 2014, Figure 33 and Figure 34). In addition, an Upstream-Downstream gradient in nutrient loading and soil texture, typical of New Zealand estuaries (Green 2006), has been observed in previous studies in the Mangawhai estuary (Hulbert 2014, Lindsay 2014, Tran et al. 2017). The upper creek is located near the city centre of Mangawhai, and is characterized by higher levels of turbidity, and higher mean concentrations in P and ammonium than the creek downstream of the estuary (Northland Regional Council State of the Environment Report 2002, MCWM 2015, Valois 2017). The different reports conclude that this is likely caused by pastoral and septic tank effluents. In addition to this higher nutrient loadings than downstream of the estuary, the lower tidal duration and energy flow at the head of the estuary likely led to higher sedimentation of fine particles and nutrients Upstream (Hulbert 2014, Lindsay 2014). As a result, the soils in the upper part of the estuary are characterized by higher percent of silt (20 to 54%) than downstream of the estuary (< 6%) (Hulbert 2014). The head of the estuary is also characterized by higher OM and N and P concentrations and

by the highest mangrove tree densities and total aboveground and belowground biomass (Table 7). All these characteristics decrease steadily from the head to the mouth of the estuary (Hulbert 2014, Tran et al. 2017).
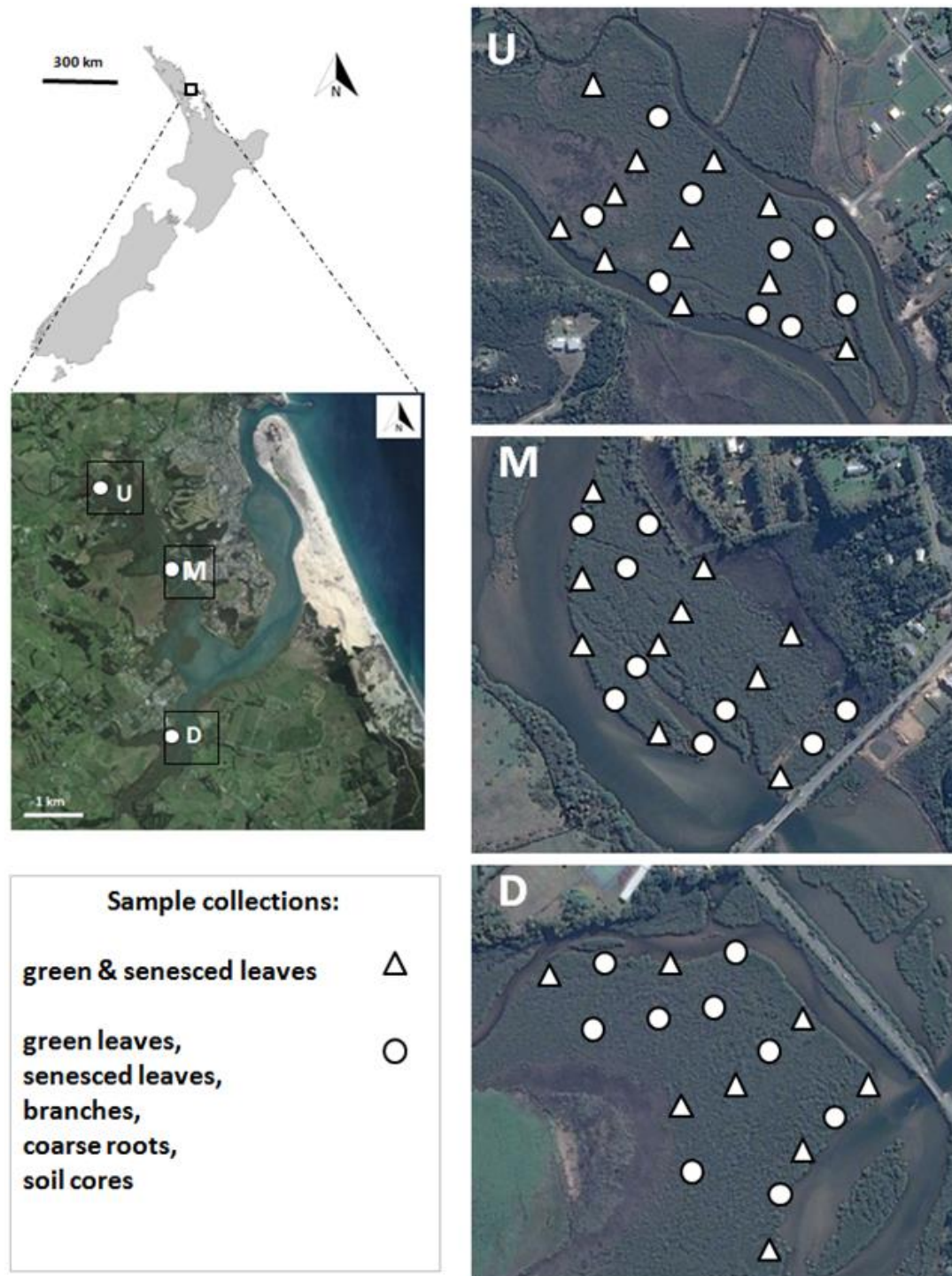
Figure 31. Mangawhai Estuary in northern New Zealand, showing the location of the three mangrove sites along the estuary (U = Upstream, M = Middle, D = Downstream) and sample layout in each site
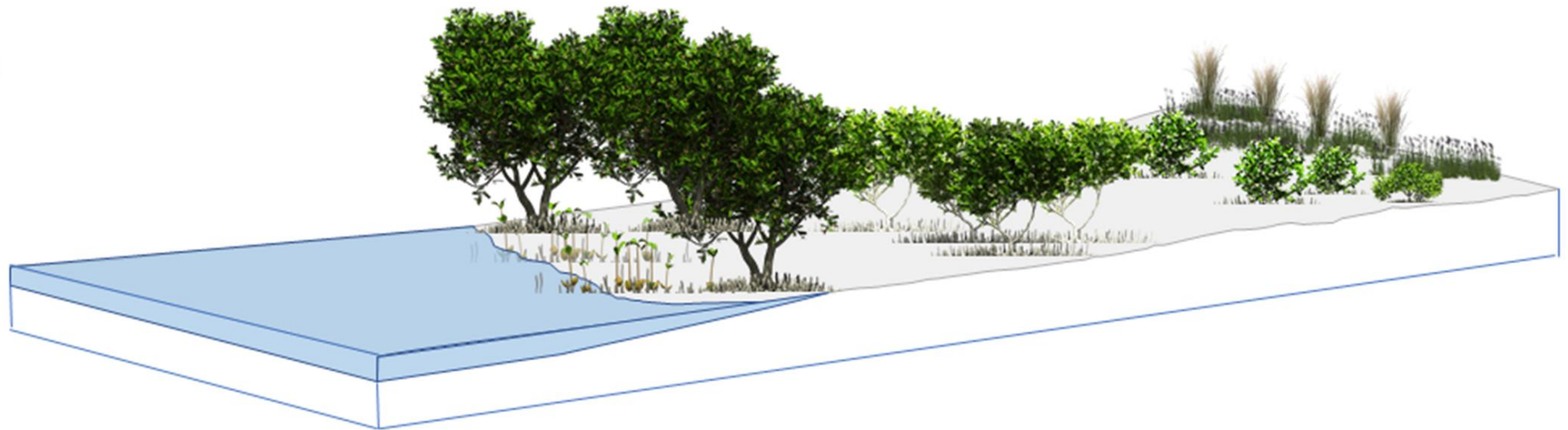
Figure 32. Seaward-landward gradient of mangroves and saltmarshes in each study site along the main channel in Mangawhai Estuary (New Zealand) with, from left to right, sandflats and mudflats seaward, with high abundance of seedlings on the mudflats, followed by tall and then small *Avicennia marina* tree stands and then landward marsh grasses dominated by *Leptocarpus similis* and/or *Juncus kraussii* (Photo credits: Carine Bourgeois)
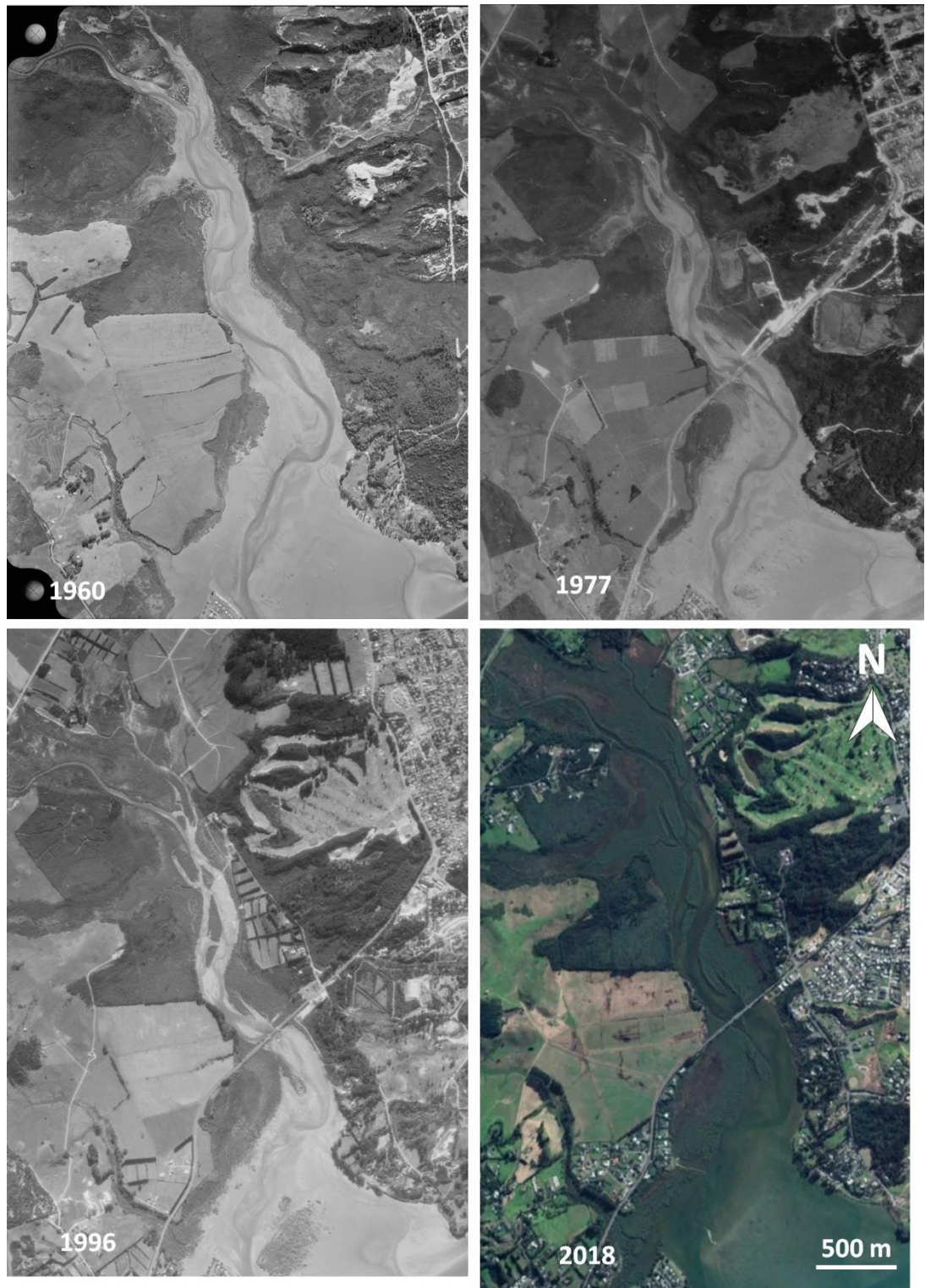
Figure 33. Mangrove expansion from 1960 to 2018 in the Upstream and Middle sites of Mangawhai Estuary, North Island, New Zealand (1960 - 1996 aerial photographs from http://retrolens.nz and licensed by LINZ CC-BY 3.0; 2018 satellite data from Maxar)
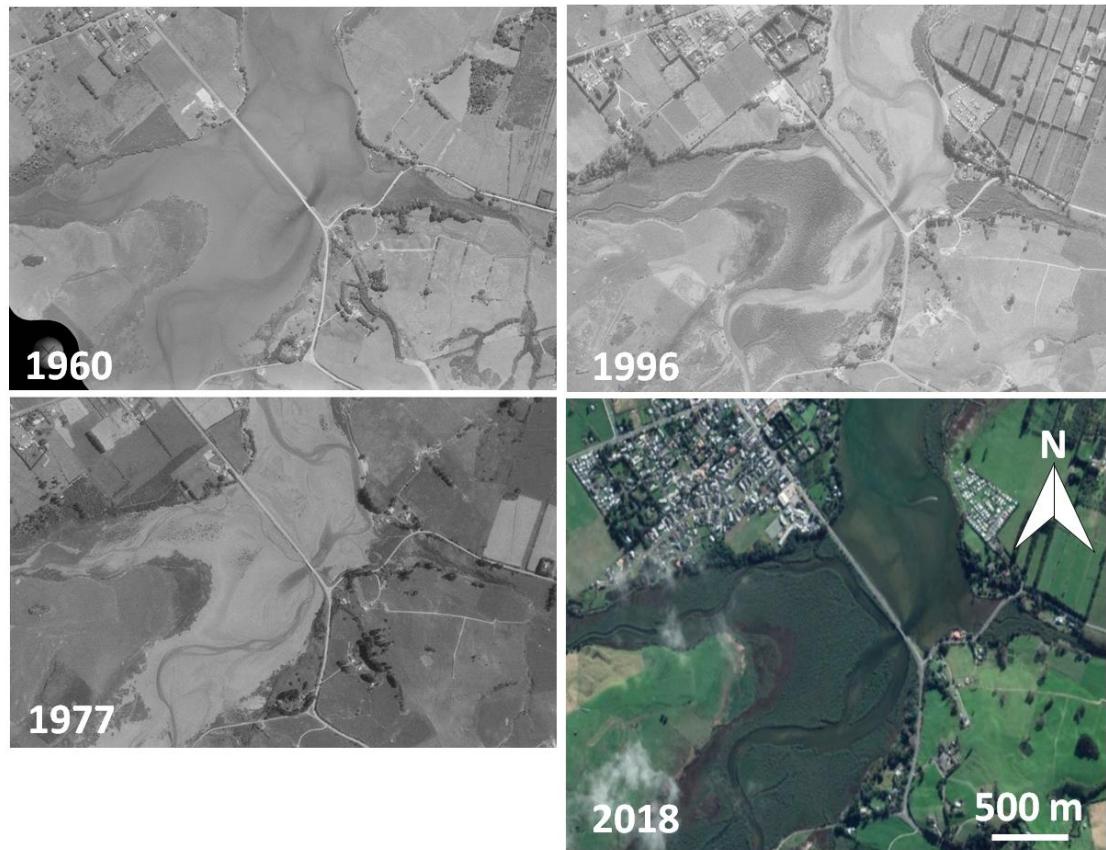
Figure 34. Mangrove expansion from 1960 to 2018 in Downstream of Mangawhai Estuary, North Island, New Zealand (1960–1996 aerial photographs from http://retrolens.nz and licensed by LINZ CC-BY 3.0; 2018 satellite data from Maxar)

Table 7. Mean (± SD) height, circumference at 30 cm height of the mature trees sampled and total density above ground biomass (AGB) and below ground biomass (BGB) in each mangrove site (U = Upstream, M = Middle, D = Downstream). The stem density, leaf and coarse root biomass data are from Tran et al. (2016) (NA = data not available)

Sites	Height (cm)	Girth at 30cm (cm)	no stems by 200 m²	AGB (kg m⁻²)	BGB (kg m⁻²)	Leaf biomass (kg m⁻²)	Wood biomass (kg m⁻²)	Coarse root Biomass (kg m⁻²)
U	130-454 (± 48)	27.9 (± 7.3)	300	8.9	14.7	0.6	8	5.46
M	160-430 (± 30)	35.9 (± 9.6)	146	5.5	11.6	0.4	5	5.63
D	162-380 (±11)	33.4 (± 5.6)	152	NA	NA	0.4	2.3	NA

3.3.2 Sampling layout

The study was conducted in three mangrove sites located along the head-mouth textural and nutrient gradient of the estuary (Figure 31). One mangrove site is located in the upper part of the estuary (8.9 km from the mouth of the estuary) and fed by the northern creek (Upstream site, U). A second site is located in the intermediate part of the estuary (7.6 km from the mouth of the estuary, Middle site, M) and a third one downstream, closer to the mouth of the estuary (6.6 km, Downstream site, D). The downstream site is fed by the southern creek. In each of the three sites, soils and plant samples were collected in a series of circular plots of 7 m radius along transects perpendicular to the main channel, following the sampling layout of Kauffman and Donato (2012). In each site, the sampling layout was designed to cover mangrove habitats from the salt marsh-mangrove ecotone to the channels. In total, 56 plots were set up along the estuary (Figure 31).

3.3.3 Soil collection

In 27 of the 56 locations along the estuary, 50-cm core samples were collected in duplicates during low tide with an 8 cm diameter stainless steel corer (Figure 31). In each site, three duplicates were collected in the salt-marsh-mangrove ecotone, three in the middle of the mangrove stand and three in mangroves located in border of the channels. The total sampling depth of 50 cm was chosen to include most *Avicennia* live roots, 70% of which are located between 0 and 40 cm depth in Mangawhai estuary (Tran et al. 2017). The soil in each core was divided into five sections (0–2.5, 7.5–10, 15–20, 25–30, and 40–50 cm) while in the field. These five sections were selected based on the main transitional depths in chemical and elemental soils properties observed by Marchand et al. (2004, 2006, 2008) in various mangroves of French Guyana and New Caledonia.

3.3.4 Soil physico-chemical parameters

Immediately after core collections, Eh, pH and temperature (T) of the pore water of each soil section were measured using a portable pH/mV/T meter (Multi 350i, Wissenschaftlich-Technische Werkstätten, Germany) with a Pt-Ag/AgCl electrode (SenTix ORP, WTW) and a pH electrode with temperature sensor (SenTix 81, WTW) directly inserted into the sediment. The Eh values were normalized with respect to a standard hydrogen electrode by adding the temperature-adjusted tension values of the Ag electrode (ranging from +210 mV for 20 °C to +200 mV for 35 °C) (SenTix, WTW).

In each soil section, a known volume of soil was collected using a graduated syringe (50 ml) with the tip cut off. Then, the samples were transported to the laboratory where fresh weights were recorded immediately. Pore-water samples were extracted from each of these small soil cores with a pressurised syringe connected to a soil moisture sampler (Rhizon SMS, Rhizosphere research products, Wageningen, The Netherlands). The pore-water samples were used to measure salinity with a hand-held refractometer (Atago MASTER -S/Millα, Japan). The small soil cores were then freeze-dried with a FreeZone 2.5 Liter Benchtop (Labconco, Kansas City, USA) at – 80 °C for three days until constant weight was achieved. Dry weights of each of these small soil cores were then recorded and used to calculate the pore water content (WC). The bulk density (BD) of each sample was calculated as the dry weight of the small soil core divided by its volume. The remaining soil samples from the initial large core were also freeze-dried at – 80 °C and kept in the dark until elemental analyses could be conducted.

3.3.5 Elemental analyses of soils

Total and EDTA elemental extractions were performed on each of the five sections of each soil core. Although the EDTA extracts (here after named "available") does not give speciation information, the use of this double extraction protocol is recognized as a reliable method to assess the mobility of elements in the soils and their bioavailability for plant uptake (Pansu and Gautheyrou 2007, Manouchehri and Bermond 2009). All elemental analyses were performed at the Institute of Research for Development (IRD) of Nouméa, New Caledonia (IMAGO, Certificate ISO 9001 : 2015), and three replicates were analysed for each sample. Each soil sample was divided into two sub-samples. One sub-sample was sieved through a 2 mm mesh and ground down to 250 μm grain size with a soil ball mill (PM100, Retsch, Germany), and total elemental measurements were taken for macro (C, N, K, Ca, Mg, P, S) and micro nutrients (Fe, Mn, Zn, Cu, Ni), sodium (Na), and other trace metals (Al, Cr, Co). The second sub-sample was sieved through a 2 mm mesh and used to measure available cations, including K, Ca, Mg, S, Fe, Mn, Al, Ni, Cu, Zn, Cr, Co.

Total organic carbon content (TOC) was determined by subtracting the measured inorganic carbon (IC) from the measured total carbon (TC), both measured using a solid sample module (SSM-5000A) combined with a total organic carbon (TOC-L) analyser (Shimadzu, Kyoto, Japan). Total nitrogen (ammonium, nitrate, nitrite- and organic N) contents were extracted by the Kjeldahl's wet oxidation method (ISO 11261 : 1995) and then quantified in a continuous flow analyser (Autoanalyser Technicon II, AxFlow, Milan, Italy). Total element concentrations were determined by inductively coupled plasma emission spectroscopy (ICP-OES, Varian, Australia) after extraction in a solution of 10% w/v solution of ammonium fluoride (FNH_4) and nitric acid (70%). The available elements in the soils were measured by ICP-OES in ammonium acetate and Ethyl Diamine

Tetraacetic Acid (EDTA)-Disodium extract at pH 7 (NF X 31-120, Pansu and Gautheyrou 2007).

3.3.6 Plant tissue collection

In each of the 56 locations, green and senesced yellow leaves were harvested directly from a minimum of 10 mature trees standing within the circular plot (Figure 31). Senesced leaves are here identified as yellow leaves easily detachable by a slight pull (Lovelock et al. 2007a, Silva et al. 2007) and therefore most likely to be in the next litterfall pool. In addition, coarse roots (≥ 2mm diameter) and branches were collected in 21 of the 56 locations. The coarse roots were thoroughly rinsed with demineralised water (Marchand et al. 2016). All samples were dried until constant weight at 55 °C.

3.3.7 Elemental analyses of plant samples

Each plant sample was divided into two sub-samples and ground down to 250 μm with a cutting mill (Fritsch, Pulverisette 15, Germany). Total C and N concentrations in plant tissues were analysed as in soils. Total element concentrations of Ca, Mg, K, S, Fe, Al, Ni, Cr, Co, Cu, Zn were determined by ICP-OES after extraction in a solution of 1% w/v solution of FNH_4 and nitric acid (70%). The accuracy of the methods was tested on reference samples of the International Soil-Analytical Exchange program (ISE, Wageningen Evaluating Programmes for Analytical Laboratories) following the validation method in van Dijk and Houba (1999) and in Dijk (2002). Our test results showed that the method allows for the total extraction of all targeted elements.

3.3.8 Bioassimilation and translocation of elements in plant material

For each element, bioconcentration factors (BCF) were calculated in each plant material by dividing the concentration of the element in the tissue by its mean total concentration in the soil. The translocation factor (TF) from the roots to the leaves was calculated by dividing the concentrations of elements within the green leaves by the concentrations in the coarse roots (Marchand et al. 2016).

3.3.9 Resorption efficiency, resorption proficiency

Resorption efficiency (RE) is defined as the mobilization and withdrawal of nutrients from senesced leaf tissues prior to abscission (Chapin 1980, Killingbeck 1986, 1996). The RE was measured as the percentage of the reduction of the element between green and senesced leaves:

$$X\ RE\ (\%) = \left(\frac{X\ green\ -\ X\ sen\ x\ MLCF}{Xgreen} \right) x\ 100$$

where, X stands for a given element and MLCF stands for Mass Loss Correction Factor, calculated as the ratio of dry mass of senesced leaves (sen) to that of green leaves (green) (Van Heerwaarden et al. 2003). The MLCF factor accounts for mass losses occurring during senescence due to resorption of soluble carbon compounds (Aerts 1996, Vergutz et al. 2012, Primicia et al. 2014). Negative values of RE indicate an accumulation of elements in senesced leaves compared to the green leaves, either through active transport by retranslocation of the elements from green leaf tissues toward senesced leaf tissues, either by higher uptake in green leaf tissues and accumulation over time. The resorption proficiency (RP) of an element is the level to which this element has been reduced in senesced leaves, and is therefore equivalent to the terminal element concentration in senesced leaves (Killingbeck 1996).

3.3.10 Elemental stocks in soils and plant material

At each site, the elemental stocks in soils were calculated using the total elemental concentrations and bulk density of each sample, and then integrated over the 50 cm depth. The elemental stocks in coarse roots, wood, and green leaves were calculated using the biomass partitioning compiled by Tran et al. (2017) in the same three sites. (Table 7). The nutritive roots were not considered in this study. Therefore, the elemental pools calculated here account for 77% of the standing biomass (Tran et al. 2017).

3.3.11 Data analyses

The spatial variations of all physico-chemical and elemental concentrations were analysed and tested by the mean of two-way ANOVAs (3 sites x 5 depths) and one-way ANOVAs (3 sites), for the soils and plant tissues, respectively, and Tukey's tests. Correlations between variables were analysed by Pearson's correlations. All analyses were performed with R software (R Core Team 2013).

3.4 Results

3.4.1 Soils physico-chemical properties

Most soil properties depicted high variations in their values along the estuary, and higher variations within the surface soils than at depth (Figure 35). Within the surface soil layer (0–2.5 cm), the pore water salinity increased significantly from 15.81 (± 0.52) in the upper site (Upstream) to 32.16 (± 0.68) in the downstream site (Downstream). In the Upstream and Middle sites, the salinity values increased significantly with increasing soil depth (Tukey tests, $p < 0.05$), while it remained constant with depth in the Downstream site (Tukey tests, $p > 0.05$). The mean pH values in the surface soils showed

an increasing gradient from the Upstream site (6.05 ± 0.27) to the Downstream site (6.36

± 0.16) of the estuary (Figure 35). Under the soil surface (i.e. under 0 to 2.5 cm depth),

the pH values did not vary significantly among sites and depths (Tukey tests, p > 0.05). The surface soils in the Upstream site were characterized by oxic conditions, with maximum Eh values of 355.1 mV. Underneath the surface, the Eh values dropped dramatically to anoxic conditions in the Upstream and Middle sites, with minimum of -

Figure 35. Mean values of physico-chemical parameters (salinity, total Na content, Eh, pH, water content WC, and bulk density BD) in the sedimentary column of each mangrove site

140.3 and - 160.3 mV, respectively. Conversely, positive Eh values along the entire depth

profile were found in the Downstream site. The maximum TOC values and lowest BD

values were found in the surface soils of the Upstream site (12%, 0.43 g cm^{-3},

respectively). In the Downstream site, the mean TOC and WC values were the lowest of

the estuary (2.2 ± 0.3%, 36.46 ± 9.9%), whereas the BD were the highest (1.04 ± 0.3 g

cm^{-3}) (Figure 35). In all sites, the TOC and WC values decreased steadily with increasing

depth, while the BD values depicted the reverse pattern (Figure 35).

3.4.2 Elemental concentrations and stocks in soils

The mean (± SD) total concentration of macro-nutrients (N, P, K and S) and trace metals (Fe, Cu, Zn, Co, Cr and Ni) decreased steadily and significantly (Tukey tests, $p < 0.05$) from the Upstream site, followed by the Middle site and were minimum in the Downstream site (Figure 36 and Figure 37). The concentration dataset can also be viewed in Appendix 5 and Appendix 6. Conversely to the other macro nutrients, significant higher mean total concentrations of Ca along with Mn were found in the Middle and Downstream sites compared to the Upstream site. The highest total concentrations of Al were also found in the Middle site of the estuary (43.0 g kg^{-1}), followed by the Upstream site of the estuary (36.6 g kg^{-1}) and the Downstream site (35.7 g kg^{-1}, Figure 37). Finally, the total concentrations of all elements were higher at the surface than at depth, except for Ca concentrations which were higher at depth (Figure 36 and Figure 37). The mean (± SD) available concentrations of all macro-nutrients and heavy metals showed a reverse pattern to that of the total concentrations, i.e. the available concentrations significantly increased from the head to the mouth of the estuary (Figure 36 and Figure 37).
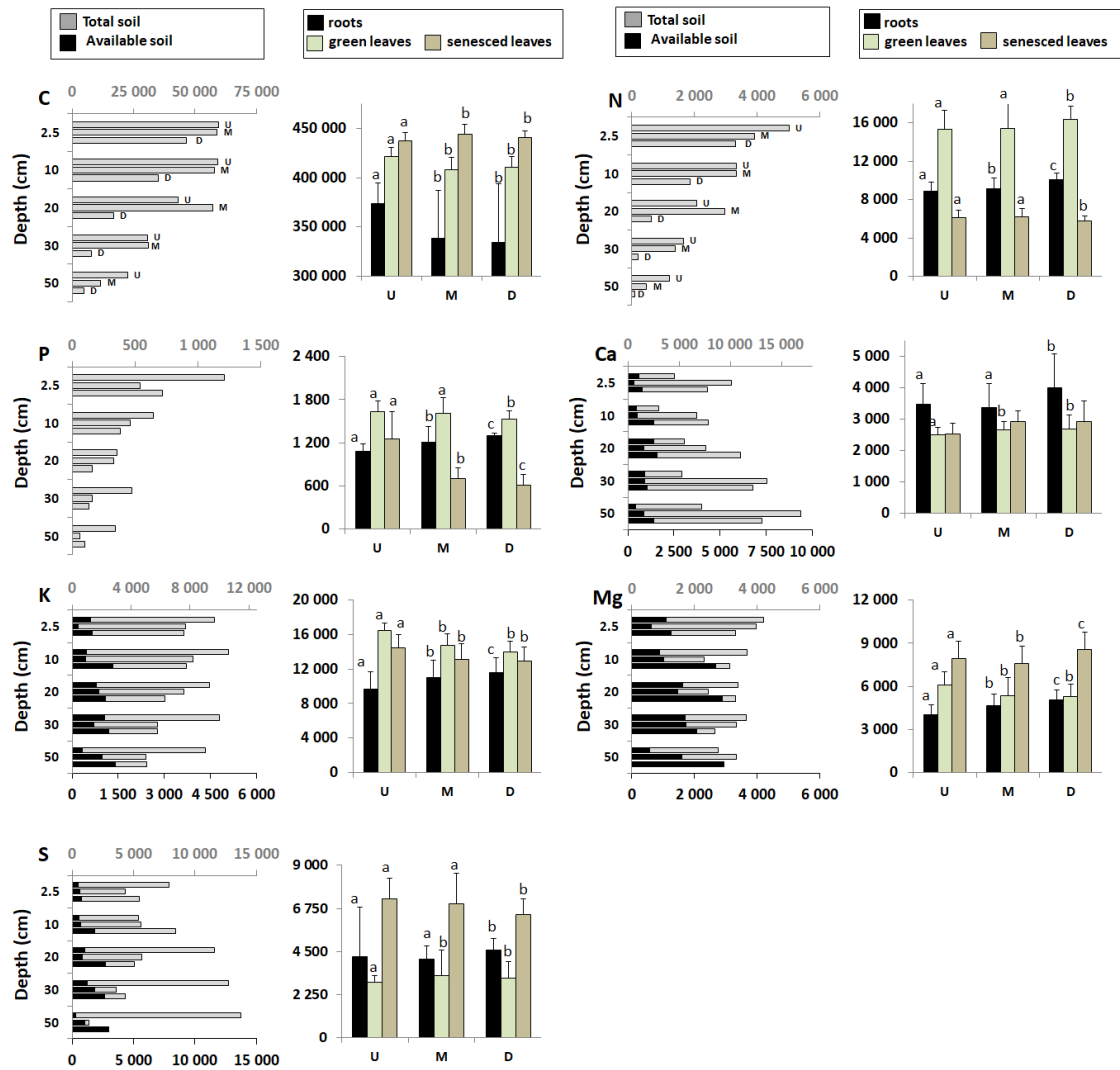
Figure 36. Variation in mean concentrations of total (grey scale) and available (black scale) concentrations of C, P, N, K and Mg in each mangrove site along the soil depth profile (U = Upstream, M = Middle, D = Downstream); mean concentrations (± SD) of total elements within the different plant tissues. All concentrations are given in mg kg^{-1}. For each type of plant tissue, same letters indicate concentrations that do not differ between sites at the 0.05 level of the Tukey test
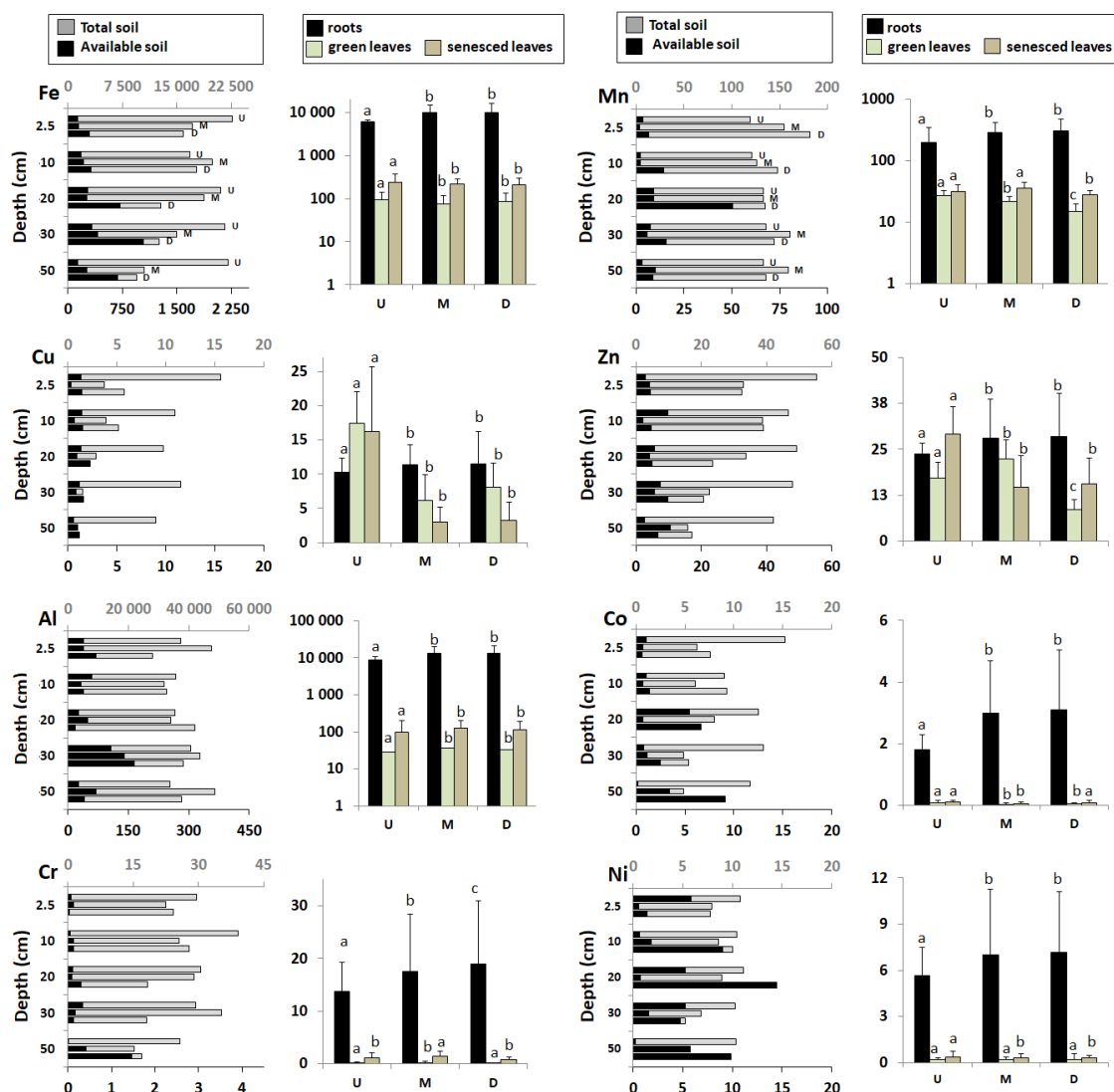
Figure 37. Variation in mean concentrations of total (grey scale) and available (black scale) S, Fe, Mn, Cu and Zn in each mangrove site along the soil depth profile (U = Upstream, M = Middle, D = Downstream); mean concentrations (± SD) of total elements within the different plant tissues. All concentrations are given in mg kg⁻¹. For each type of plant tissue, same letters indicate concentrations that do not differ between sites at the 0.05 level of the Tukey test

The correlations analyses between all edaphic variables (presented in Figure 38) showed that the Eh values were negatively and significantly correlated with the TOC contents ($r = - 0.42$, $p < 0.05$). The amount of TOC was negatively correlated with the BD ($r = - 0.77$, $p = 0.001$), whereas the BD values of the soil were negatively correlated with WC ($r = - 0.42$, $p = 0.01$). Higher total concentrations of macro nutrients (N, P, K and S) and trace metals (Fe, Cu, Zn, Co, Cr and Ni) were found within soils with high TOC and WC contents and with low EH and BD values (Pearson's correlation, $p < 0.05$, Figure 38).
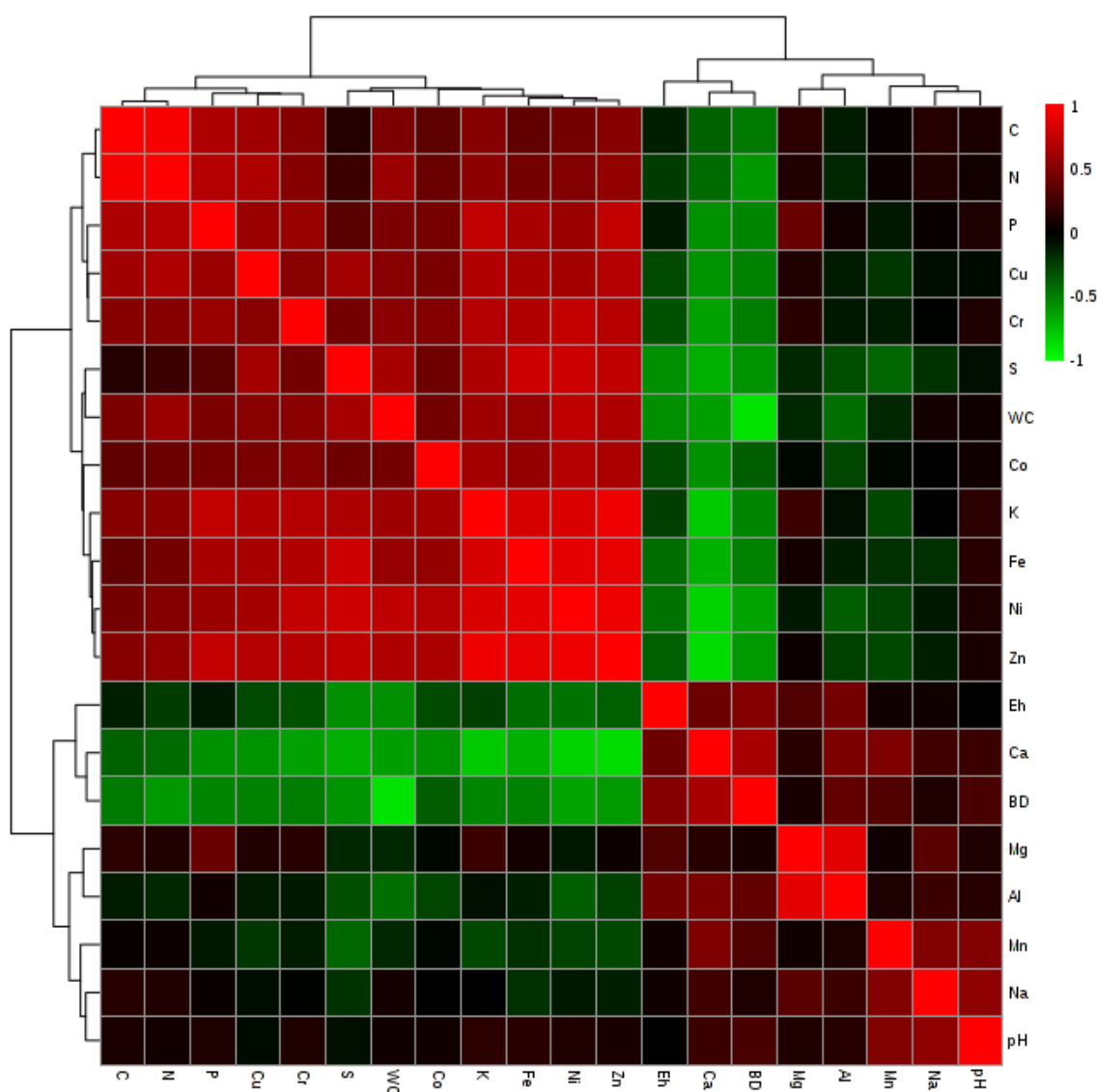
Figure 38. Heatmap of Pearson's correlation coefficients (r = -1 to +1) between the physico-chemical properties and the total elemental concentrations within the soils

In addition, positive and significant correlations were observed between the total concentrations of Fe and S (r = 0.89, p = 0.001), and between Fe and the other heavy metals (Pearson's correlation, p < 0.05). Total Ca concentrations were positively correlated with BD and Eh, and negatively correlated with the TOC, water contents and Mn (r = 0.81, p < 0.001). The total concentrations of Al were positively correlated with BD, Mg and Ca, and negatively correlated with TOC and water contents (p < 0.05, Figure 38).

Due to the higher soil BD measured in the Downstream site, the total soil stocks of all heavy metals combined for each site from the head to the mouth were 212.77 t ha^{-1}, 205.14 t ha^{-1} and 232.76 T ha^{-1} for 50 cm depth, respectively. The total stocks of all macro-nutrients combined within the soils were 234.47 t ha^{-1}, 229.50 t ha^{-1}, 190.37 t ha^{-1}, from the head to the mouth, respectively (Figure 39).
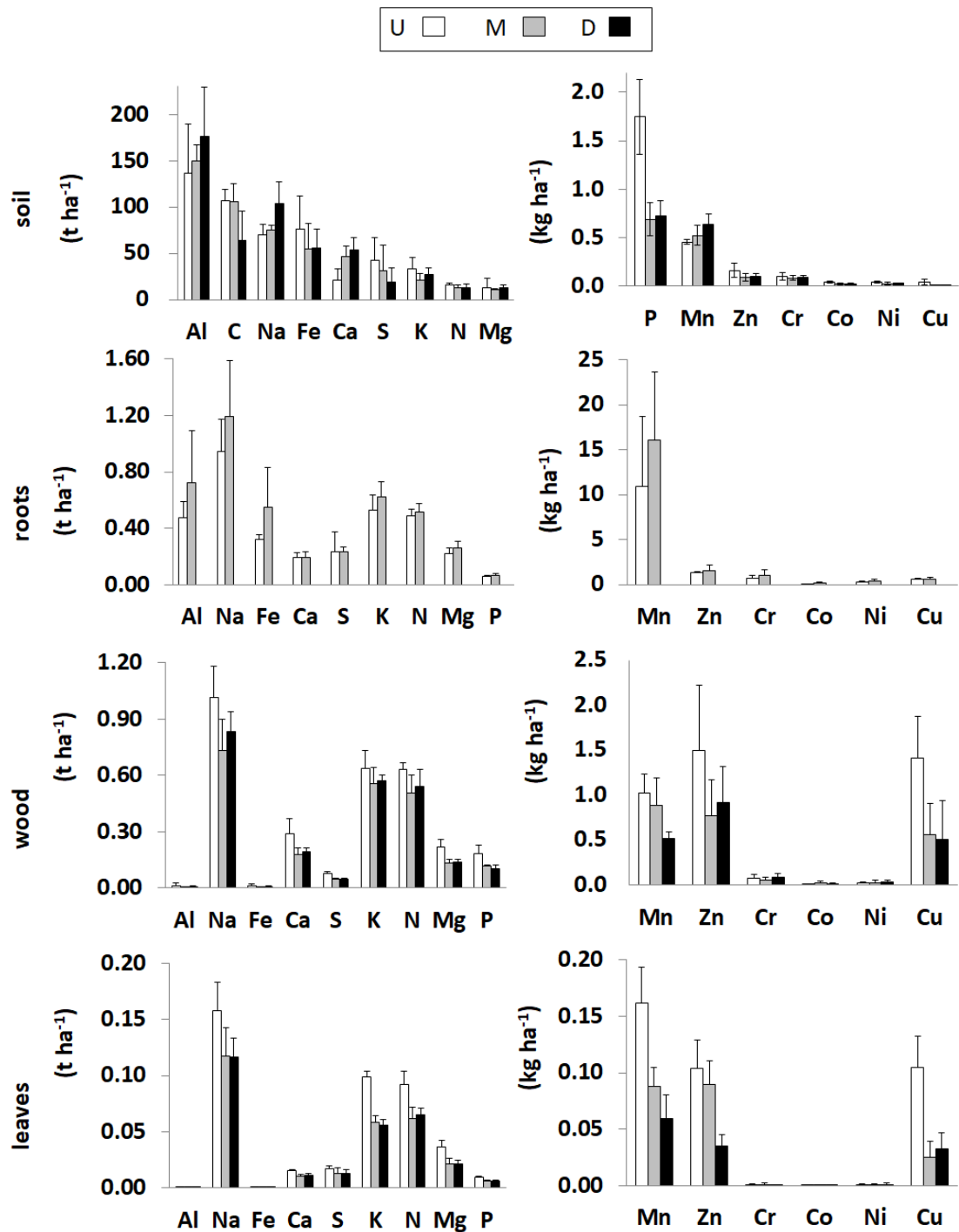
Figure 39. Mean (± SD) total elemental stocks in soils, coarse roots, wood and green leaves in each mangrove site (U = Upstream, M = Middle, D = Downstream)

3.4.3 Elemental concentrations, soil-plant transfers and stocks in standing vegetation

3.4.3.1 Elemental concentrations within mangrove tissues and BCF

Overall, the macro-nutrients N, P, Mg, K and Na were found in higher concentrations within plant tissues than in the soils, with BCF higher than 1 for all these elements and BCF ranging as high as 2.41 to 11.79 for N and 2.28 to 5.17 for P (Figure 36, Table 8). Conversely, the BCF of Ca and S within all plant tissues ranged from 0.25 to 0.79 and from 0.39 to 3.89 for Ca and S, respectively (Table 8). At all sites, the macro-nutrients (N, K, Na, Mg and P) were found in lowest concentrations within the root systems and showed TF toward the leaves higher than 1 for all samples (Table 8). Conversely, Ca and S accumulated mostly within the root system, with mean root BCF of 0.50 (± 0.25) and 2.15 (± 1.70) and mean TF of 0.74 (± 0.07) and 0.89 (± 0.09) for Ca and S, respectively.

Table 8. Mean (±SD) bioconcentration factors (BCF) in coarse roots and leaves, translocation factors (TF) and Resorption Efficiency (RE, %) for each macro-nutrient and Na in each site (Upper, Middle, and Downstream) at Mangawhai Estuary

		Upstream		Middle		Downstream	
N	BCF roots	3.55	(±0.20)	3.65	(±0.36)	7.60	(±1.51)
	BCF leaves	7.94	(±0.80)	5.71	(±0.79)	11.79	(±1.64)
	TF	2.22	(±0.13)	1.55	(±0.07)	1.54	(±0.11)
	RE (%)	58.06	(±12.19)	60.11	(±7.83)	68.36	(±6.43)
P	BCF roots	2.28	(±0.60)	3.82	(±0.39)	4.44	(±0.35)
	BCF leaves	3.42	(±0.72)	4.58	(±0.35)	5.17	(±0.49)
	TF	1.59	(±0.16)	1.22	(±0.11)	1.16	(±0.02)
	RE (%)	22.43	(±9.908)	55.90	(±11.84)	63.70	(±10.61)
Ca	BCF roots	0.79	(±0.15)	0.31	(±0.08)	0.39	(±0.05)
	BCF leaves	0.58	(±0.14)	0.25	(±0.04)	0.27	(±0.03)
	TF	0.72	(±0.06)	0.82	(±0.11)	0.68	(±0.03)
	RE (%)	0.78	(±5.82)	-5.86	(±6.46)	3.79	(±4.32)
Mg	BCF roots	1.57	(±0.43)	1.58	(±0.34)	1.77	(±0.25)
	BCF leaves	2.24	(±0.73)	2.01	(±0.40)	2.11	(±0.34)
	TF	1.34	(±0.11)	1.27	(±0.06)	1.19	(±0.07)
	RE (%)	-28.49	(±23.85)	-41.65	(±30.28)	-50.29	(±34.33)
Na	BCF roots	0.85	(±0.08)	0.99	(±0.16)	0.87	(±0.08)
	BCF leaves	1.36	(±0.19)	1.22	(±0.03)	1.12	(±0.11)
	TF	1.71	(±0.38)	1.36	(±0.27)	1.33	(±0.20)
	RE (%)	41.35	(±11.08)	43.81	(±15.16)	52.36	(±10.02)
K	BCF roots	1.05	(±0.20)	1.59	(±0.02)	1.80	(±0.11)
	BCF leaves	1.74	(±0.13)	2.03	(±0.19)	2.32	(±0.25)
	TF	1.77	(±0.21)	1.28	(±0.12)	1.29	(±0.08)
	RE (%)	13.06	(±18.02)	14.65	(±17.61)	16.07	(±12.97)
S	BCF roots	0.47	(±0.11)	3.89	(±0.14)	2.09	(±0.21)
	BCF leaves	0.39	(±0.07)	2.32	(±0.76)	1.73	(±0.06)
	TF	0.79	(±0.18)	0.93	(±0.20)	0.96	(±0.20)
	RE (%)	-150.06	(±52.85)	-121.31	(±60.30)	-96.73	(±51.47)

Table 9. Mean (±SD) bioconcentration factors (BCF) in coarse roots and leaves, translocation factors (TF) and Resorption Efficiency (RE, %) for each trace metal in each of three sites (Upper, Middle, and Downstream) at Mangawhai Estuary

		Upstream		Middle		Downstream	
Fe	BCF roots	0.31	(±0.06)	0.62	(±0.19)	0.75	(±0.25)
	BCF leaves	0.01	(±0.00)	0.01	(±0.00)	0.01	(±0.00)
	TF	0.02	(±0.01)	0.01	(±0.00)	0.01	(±0.00)
	RE (%)	-193.47	(±201.17)	-278.48	(±95.15)	-153.16	(±46.91)
Mn	BCF roots	1.62	(±0.33)	1.94	(±0.23)	2.04	(±0.25)
	BCF leaves	0.11	(±0.00)	0.10	(±0.01)	0.11	(±0.02)
	TF	0.14	(±0.03)	0.06	(±0.02)	0.07	(±0.02)
	RE (%)	-19.39	(±17.60)	-60.02	(±30.57)	-82.72	(±30.80)
Ni	BCF roots	0.55	(±0.11)	0.97	(±0.31)	1.14	(±0.35)
	BCF leaves	0.16	(±0.07)	0.11	(±0.05)	0.05	(±0.02)
	TF	0.20	(±0.09)	0.17	(±0.04)	0.03	(±0.01)
	RE (%)	-61.56	(±9.29)	-40.09	(±20.99)	-9.67	(±6.45)
Al	BCF roots	0.34	(±0.10)	0.33	(±0.12)	0.36	(±0.11)
	BCF leaves	0.00	(±0.00)	0.00	(±0.00)	0.00	(±0.00)
	TF	0.01	(±0.00)	0.00	(±0.00)	0.00	(±0.00)
	RE (%)	-453.42	(±56.47)	-388.87	(±53.66)	-308.89	(±68.58)
Cu	BCF roots	1.24	(±0.25)	4.51	(±0.28)	6.50	(±0.78)
	BCF leaves	1.83	(±0.08)	2.60	(±0.27)	4.73	(±0.54)
	TF	1.33	(±0.18)	0.51	(±0.11)	0.72	(±0.20)
	RE (%)	23.80	(±9.62)	50.14	(±8.29)	65.39	(±7.94)
Zn	BCF roots	0.53	(±0.10)	1.01	(±0.23)	1.12	(±0.27)
	BCF leaves	0.35	(±0.03)	0.66	(±0.11)	0.28	(±0.02)
	TF	0.70	(±0.07)	0.71	(±0.10)	0.30	(±0.08)
	RE (%)	-95.26	(±56.15)	33.40	(±19.11)	-70.93	(±5.66)
Co	BCF roots	0.15	(±0.01)	0.47	(±0.12)	0.54	(±0.20)
	BCF leaves	0.03	(±0.01)	0.00	(±0.00)	0.00	(±0.00)
	TF	0.17	(±0.07)	0.00	(±0.00)	0.00	(±0.00)
	RE (%)	3.31	(±4.78)	-3.29	(±3.301)	-3.84	(±3.53)
Cr	BCF roots	0.49	(±0.15)	0.64	(±0.18)	0.95	(±0.21)
	BCF leaves	0.00	(±0.00)	0.04	(±0.01)	0.02	(±0.01)
	TF	0.00	(±0.00)	0.09	(±0.02)	0.01	(±0.00)
	RE (%)	-364.84	(±60.65)	-436.74	(±51.44)	-470.65	(±40.92)

The concentrations and BCF of the heavy metals in the plant tissues depicted a trend different than that of the macroelements. The highest concentrations of all metals within plant tissues were found within mangrove coarse roots, in descending order: Al, Fe, Mn, Zn, Cu, Cr, Ni and Co (Figure 37). However, the root BCF values were very low for most metals, except for Cu and Mn for which the mean concentrations measured within roots were four and two times higher than the concentrations measured within the soils, respectively (Table 9). Except for Cu, Fe and Zn, for which the mean TF within leaves were higher than 0.5, the translocation from roots to aerial tissues were very low

for all metals (Table 9), with concentrations in green leaves lower or equal to 1 mg kg^{-1} for Co, Cr and Ni.

3.4.3.2 Elemental translocation from the roots to the canopy along the estuary

Important spatial variations of macro-nutrient concentrations were also observed within the root system along the estuary (Figure 36). The mean (± SD) concentrations of

C measured in the coarse roots were significantly higher in the Upstream site (42.14 ± 2.15%), and decreased significantly to 33.91% (± 59.47%) in the Downstream site. The concentrations of all other macro-nutrients within the root system were significantly lower Upstream and increased significantly from the head to the mouth of the estuary (Figure 36). The highest translocation of elements from the roots to the canopy were found Upstream for N, P, Ca, Mg, Na and K and decreased from the head to the mouth of the estuary (Table 8). Conversely, the TF of S increased from 0.79 at the head of the estuary to 0.96 at the mouth of the estuary (Table 8). The concentrations of N, Ca, and S within green leaves increased steadily and significantly from

Figure 40. Relationship and regression coefficient (R^2) between Na concentrations within green leaves and the concentrations of P, N and Mg (mg kg^{-1}) in green leaves for the entire estuary, (p < 0.01 for all)

the head to the mouth of the estuary. Conversely, the concentrations of C, P, K and Mg within the canopy decreased from the head to the mouth of the estuary. Finally, positive

and significant correlation coefficients were found between Na$^+$ and P (r = 0.74), C (r = 0.65) and Ca (r = 0.34) concentrations in green leaves, whereas Na+ was significantly and negatively correlated to S (- 0.44) and Mg (r = - 0.86) (all p-values < 0.05) (Figure 40). Conversely, higher green leaf concentrations and TF of Fe, Zn, Cu, Mn and were found in the Upstream and Middle sites compared to the Downstream site (Table 9, Figure 37). Only the concentrations of Ni measured within green leaves did not show any significant differences along the estuary. Among all the metals studied, Cu had the highest spatial variations, with maximum concentrations (17.40 mg kg^{-1}) and TF > 1 in the green leaves upstream and minimum values measured in the Middle and Downstream sites (6.07 and 8.06 mg kg^{-1}, respectively).

3.4.3.3 Elemental concentrations in the litterfall and RE along the estuary

In general, the concentrations of N, P and K within the litterfall were lower than within the green leaf tissues, with RE coefficient ranging from 56.0 to 73.5% for N, 31.4 to 68.3% for P and 3.8 to 20.6% for K, whereas the RE was close to 0 for Ca and negative for S and Mg in all samples (Table 8, Figure 36). The RE of N, P, K and S increased strongly from the Upstream site to the mouth of the estuary (Table 8). Accordingly, the content of macro-nutrients (N, P, K and S) within the litterfall (RP) were higher in mangroves Upstream and decreased steadily in the Middle and then Downstream sites of the estuary (Figure 36). Notably, a net accumulation of P was also observed in four samples collected in the Upstream site (Appendix 7). These samples coincided with sampling locations where P concentrations in soils were maximum (1.84 g. kg^{-1}) and were N:P ratios in leaves were the lowest measured in the estuary (7.79 < 10, Güsewell 2004). Conversely, Mg RE and RP, respectively, decreased and increased significantly with increasing salinity Downstream (r = - 60 and r = 0.45, respectively, with p < 0.01). The

concentrations of Na^+ within the senesced leaves were lower than within the green leaves and showed positive RE in all sites (Table 8). Although all macro-nutrients had a positive and linear relationship between their concentrations within green leaves and their concentrations in senesced leaves, these relationships were very weak and not significant for N (r = 0.28), C (r = 0.24) and P (r = 0.03) (all p > 0.05) (Figure 41).
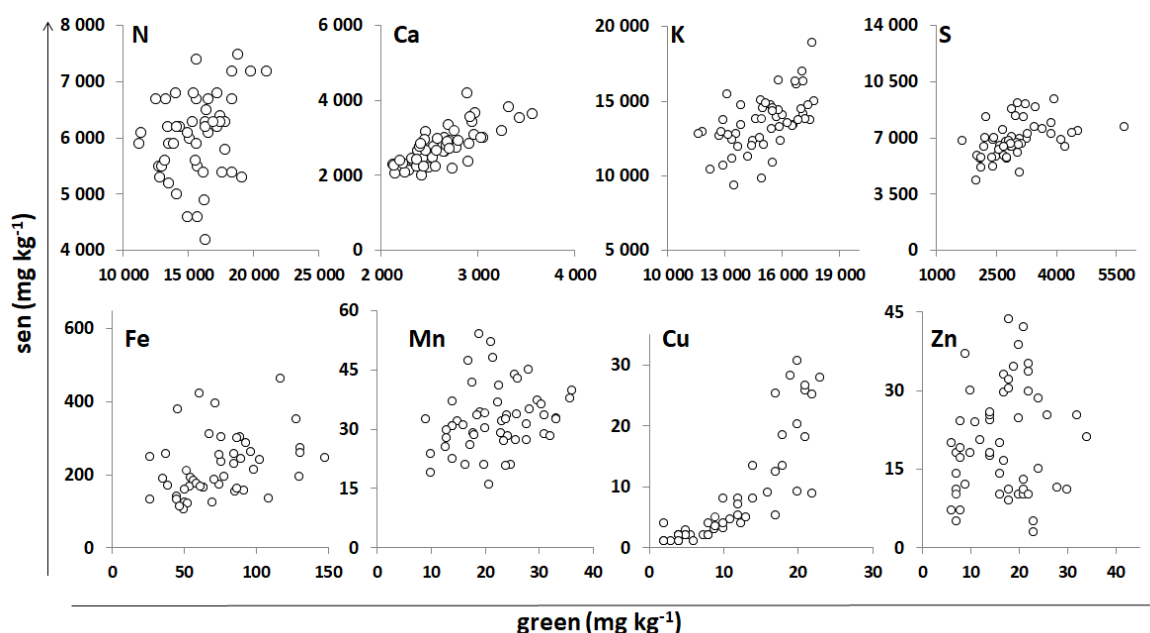
Figure 41. Relationship between the elemental concentrations in green and senesced leaves (sen) for N, Ca, K, S, Fe, Mn, Cu and Zn for the entire estuary

Finally, the litterfall collected in the Upstream and Middle sites had higher metal concentrations than the litterfall collected Downstream (Figure 37). Most metals showed negative values of RE in every sample, and thus showed a net retranslocation from green to senesced leaves, except for Cu and Zn (Table 9). While negative values of RE were also observed Upstream for Cu and Upstream and Downstream for Zn, positive RE of Cu and Zn were observed in most other samples. Markedly, Cu was the only element that showed an exponential and significant relationship between its concentrations within green leaves and senesced leaves: Cu tended to be less

concentrated in senesced leaves under a threshold of 20 mg kg^{-1} in green leaves, and accumulated more above this threshold (Figure 41 and Appendix 8).

3.4.3.4 Elemental stocks within mangrove tissues

The total elemental stocks of macroelements were highest in the Upstream site (64.72 t ha^{-1}, Figure 39), followed by the Middle site (46.50 t ha^{-1}) and the Downstream site (32.90 t ha^{-1}). Conversely, the stocks of heavy metals in the standing biomass were highest in the Downstream site (1.34 t ha^{-1}), followed by the Middle site (1.32 t ha^{-1}), and lowest in the Upstream site (0.88 t ha^{-1}). However, the stocks of macro-nutrients and heavy metals in green leaves increased with increasing elemental total concentrations in soils and were thus higher Upstream (Figure 39). Furthermore, the allocation of C, K, N, Mg, P, Ca, Zn and Cu to wood biomass increased in the Upstream site, whereas Al, Fe, Co, Ni and Cr did not significantly accumulate within the wood biomass (Figure 39). Interestingly, while the highest pool of Cu was found within the root biomass in the Middle and Downstream sites (0.64 and 0.65 kg ha^{-1}), it accumulated more in wood (1.41 kg ha^{-1}) than in the coarse roots (0.59 kg ha^{-1}) in the Upstream site.

3.5 Discussion

3.5.1 Soil elemental concentrations and stocks in soils similar to tropical mangroves

As for many mangrove stands in New Zealand, mangrove expansion in the three mangrove sites sampled in this study is a relatively recent trend (less than 100 years, Hulbert 2014). As a result, the concentrations of TOC and most elements found within the soils along the estuary were relatively low at depth and higher at the surface. Those concentrations of TOC contrast with those found in older soils of tropical mangrove

stands in which generally OM accumulates over time, which leads to high TOC at depth and higher TOC and total C stocks in soils (e.g. Marchand et al. 2005). However, the TOC concentrations and stocks measured in this study are within the range of values measured in other New Zealand mangroves (e.g. 51.7–111.6 t C ha^{-1} for 1 m depth, Bulmer et al. 2016).

Despite these low C contents, the maximum TOC contents measured within the top layers of the soil in the Upstream and Middle sites of the estuary (6–12%) are in the upper ranges of the concentrations found in mangrove forests worldwide (0.5–19%) (Bouillon et al. 2003, 2008, Kristensen et al. 2008) and higher than in other New Zealand mangrove stands (e.g. 2.20–4.78%) (Yang et al. 2013). These soils rich in OM were also characterized by concentrations of N, P, K, S and Fe, Cu, Cr, Zn, Co and Ni significantly higher than those recorded in the site Downstream. Fe and Al are naturally present in volcanogenic deposits north of the estuary (Edbrook and Brook 2001, Christie and Barker 2007), but were in the lower ranges of concentrations found in mangroves worldwide (1.26–300 and 0–136.4 g kg^{-1}, for Fe and Al, respectively) (Lewis et al. 2011, Bayen 2012, Matsui et al. 2015, Table 1b,c). Conversely, the concentrations of N, P, K, Zn, Cu and Cr recorded at the surface of the soil in the Upstream and Middle sites were higher or comparable to values found in tropical mangrove worldwide (Saenger 2002, Lewis et al. 2011, Bayen 2012, Matsui et al. 2015, Table 1a–c). The maximum concentrations of P were particularly high (0.15% of DW) compared to global data, (0.02–0.16 % of DW) (Saenger 2002), probably as a result of pastoral activities and septic tank effluents (Northland Regional Council State of the Environment Report 2002, MCWM 2015). However, Gritcan et al. (2016) reported that the input of anthropogenic N in this estuary was moderate compared to other harbours in New Zealand. This may explain the unusually low N:P ratios measured in this study (ranging from 4.19 to 8.16),

which suggests a limitation of N over P in the entire estuary. This also confirms previous assumptions that temperate mangroves are N limited (Lovelock et al. 2007a, Morrisey et al. 2010, Tran et al. 2017). No significant mineral deposits with high Cu, Cr and Zn contents have been recorded in the catchment around Mangawhai (Christie and Baker 2007). This suggests that the high concentrations of Cu, Cr and Zn found in the soils Upstream could also have an anthropogenic origin. Several studies have reported such high concentrations of Cu, Cr and Zn in harbours of the North Island as a result of industrial activities (Dickinson et al. 1996, Abrahim and Parker 2008). Notably, the maximum concentrations of Cu recorded within the surface soils Upstream (20.86 mg kg^{-1}) and of Cr at depth in the Middle site (56.39 mg kg^{-1}) exceeded their respective threshold effect levels for benthic life (TEL) of 18.7 μg g^{-1} and 52.3 μg g^{-1} (CCME 2001). Finally, the comparison between the total and available concentrations of the elements studied here showed that the redox potential is the main factor correlated to elemental accumulation in the soil. We hypothesise that lower Eh in deep soil layers in the Upstream site contributes to stock larger amounts of macro-nutrients and of most heavy metals (Cr, Co, Ni, Cu) within the soil organic matter and/or in the solid phase. The increasing total concentrations of S and Cu, Cr, Co, Ni and Cu with increasing OM and decreasing available concentrations and decreasing Eh and BD suggest that these metals could also precipitate within the solid phase. Those results are consistent with previous studies that have shown that these elements are possibly associated to S-Fe compounds as a result of the sulfato-reduction processes that dominate anaerobic mangrove soils with high OM contents (Otero et al. 2009, Marchand et al. 2011a, Noël et al. 2014). Similarly, PO$_4^{3-}$ can be adsorbed onto Fe-oxides, such as goethite, resulting in an increase of total P under oxic conditions (Lambers et al. 2008, Deborde et al. 2015), which may explain its accumulation within the oxygenated surface soils in the Upstream site.

Conversely, the lower total concentrations of Fe, Cr, Cu, Ni, Zn and K observed in the oxic soils in the Downstream site are likely to be the result of a larger mobilization and export of these elements (Saenger 2002, Marchand et al. 2016), which would also explain the higher available concentrations of these elements in this Downstream site. With regard to our first objective, our data showed that temperate mangrove soils with reducing conditions have total concentrations of C, macro-nutrients and trace metals comparable or higher than those reported in highly productive tropical mangrove forests. Although partitioning analyses and experiments on filtering functions should be realized to confirm this, this suggests that expanding temperate mangroves in New Zealand could fulfil similar ecological services in storing macroelements and trace metals as tropical mangroves, thus protecting adjacent coastal waters from eutrophication and metal pollution.

3.5.2 Elemental transfer to living plant tissues and litterfall

Tran et al. (2017) reported that the standing biomass in Mangawhai is in the upper ranges of biomass measured in mangroves in New Zealand and Australia. Moreover, the authors found that the below and above ground biomass in the Upstream site were larger than in the Middle site of the estuary. Our results showed that the accumulation and/or translocation of all macro-nutrients and heavy metals toward the canopy increases with increasing elemental concentrations in the soils. Conversely, no significant amounts of Al, Fe, Co, Ni and Cr accumulated in the wood biomass. We hypothesise that the higher accumulation of these heavy metals in senesced leaves and/or their translocation from the canopy towards the litterfall in the Upstream site is rather the result of a mechanism to avoid long-term metal toxicity than an allocation to biomass and growth. Similar examples of heavy metal accumulations in plant leaves and

litterfall have already been identified as a mechanism of tolerance in various metal (hyper)accumulators (Krämer 2010). Conversely, the allocation of C, N, P, K, Mg, Ca, Cu and Zn in the wood biomass increases with increasing nutrient concentrations in the soils Upstream, particularly for P and K, which concentrations in green leaves increase dramatically in the Middle and Upstream sites. Thus, it is likely that these two nutrients particularly contribute to the increased total AGB and height of the trees observed in the OM-enriched site Upstream (Tran et al. 2017). Previous fertilization experiments in mangrove ecosystems have previously shown that N and P are the most limiting nutrients for mangrove growth (Feller 1995, Feller et al. 2003, 2007, Naidoo 2009, Gritcan et al. 2016). In addition, it has been suggested that higher concentrations of K^+ in association with N and P increase mangrove branch production and leaf standing biomass (Feller 1995, Osman and AboHassan 2010).

3.5.2.1 Soil-plant transfer of macroelements driven by nutrient availability and salinity

The high bioaccumulation and translocation factors of all macroelements in mangrove tissues reflect the requirements of these elements in high concentrations for plant metabolism (Raven et al. 2005). The positive values of RE calculated for N, P and K indicate a decreasing conservation of these three nutrients, and thus a decreasing limitation of these nutrients in the ecosystem for plant growth and metabolic processes (Feller et al. 1999, 2003, 2007). Conversely, Mg, Ca and S accumulated in senesced tissues during leaf shedding in every sample (negative RE values). Although these nutrients are also required in high concentrations to fulfil metabolic functions in plant tissues (Raven et al. 2005), these are found in high concentrations in seawater (Millero 1996) and unlikely to be limiting in mangrove ecosystems (Boto 1992 *in* Alongi 2009). The accumulation of these elements in senesced tissues may also be explained by their

low mobility within the phloem (Ca, von Fircks et al. 2001, Medina et al 2015), their accumulation as structural constituents in tissues (Ca, Lambers et al. 2008) and higher regulation of their transfer to avoid competition with other cations and toxicity (Mg, S, Fry et al. 1982).

Among the macroelements studied, Ca was the only element for which the values of assimilation in roots, transfer to aerial tissues, RE and RP do fit the hypothesis of an increasing uptake and a lower conservation strategy of nutrients with increasing concentrations within the soils in the Downstream site (Chapin 1980, Feller et al. 1999). Conversely, the spatial variations of BCF, RP and RE of S, K, N, P and Mg along the estuary indicate that the uptake, BCF and TF of these elements in plant tissues are driven by other factors than nutrient bioavailability within the soils. For instance, S accumulates in senesced leaves Upstream in higher proportion than trees Downstream, despite the lower availability in the soils and lower concentrations in roots and green leaves. Several studies have shown that $S-SO_4^{2-}$ can be reduced to sulphides and precipitate as pyrite in the presence of Fe at lower Eh (Marchand et al. 2004, Deborde et al. 2015). Sulfides are highly toxic for plants and have been found to damage the root cell membranes and to inhibit photosynthesis in *Avicennia marina* (Youssef and Saenger 1998). Although a partitioning of S should be analysed to confirm this, we hypothesise that the higher accumulation of S in senesced leaves in the Upstream and Middle sites could be a regulation mechanism to sulfide toxicity in response to lower Eh conditions prevailing at these sites.

On the other hand, the bio-accumulation, transfer and conservation of N, K and Mg seem strongly regulated by salinity, while the uptake and conservation of P appears to be affected by both its nutrient supply within the soils, as well as by salinity. We hypothesise that the higher N and P uptake and translocation observed in the

Downstream site compared to the other sites is a response to the higher salinity stress rather than in response to higher bioavailability within the soils in the Downstream site. One the one hand, the water stress induced by high pore-water salinity reduces the stomatal conductance in *Avicennia* (Ball and Farquhar 1984, Naidoo et al. 2002). In order to sustain sufficient metabolic performances in such conditions, an adaptation of mangroves is to maintain high photosynthesis efficiency. This requires a sufficient uptake and use efficiency of P and N as the macro-nutrients required for growth (Martin et al. 2010, Reef et al. 2010). Moreover, N-rich compounds also accumulate in the cytoplasm with increasing salinity to counterbalance the compartmentalisation of Na^+ within the vacuole and to avoid Na^+ toxicity (Popp et al. 1985, Cha-um et al. 2007).

Conversely, the translocation of K and Mg from the roots to the green leaves declined downstream, despite the higher concentrations found in the available phase of the soils, and the higher accumulation in roots compared to those upstream. While there was no correlation between the concentrations of Na and K in green and senesced leaves, competition between K^+ and Na^+ has been reported in many studies (e.g. Ball and Farquhar 1984, Popp et al. 1985, Ball et al. 1987, Naidoo 2006, 2010). We hypothesise that the decreasing translocation of K from roots to green leaves with increasing salinity could be the result of a mechanism aiming to increase the exclusion of Na by saturating the transporter channels K^+/Na^+ in roots, while maintaining an osmotic balance at the root-soil interface. Whereas KRE increases in such conditions, the Mg RE and concentrations in green leaves decreased significantly with increasing salinity downstream ($r = -0.84$, $p < 0.001$). Magnesium toxicity has already been described in terrestrial ecosystems, mainly because this element competes with K^+ and Ca^{2+} and can induce a deficiency in these elements (Guo et al. 2016). We hypothesise that the lower TF and BCF of Mg in the leaves and the lower RE could be the result of a mechanism

aiming to optimize K accumulation in green leaves over Mg under high salinity regimes. Since Mg is abundant in the mangrove soils studied here and quite mobile in the phloem (Medina et al. 2015), it is also possible that the higher translocation levels of Mg^{2+} under high salinity is an adaptation to reduce the negative soil-plant gradient of osmotic pressure generated by large Na^+, K^+ and Ca^{2+} uptakes.

3.5.2.2 Metal translocation in aerial tissues and litter as a mechanism to avoid toxicity in roots

Overall, the BCF of all metals in roots and leaves were very low across the entire estuary. Similar results have been observed in mangroves worldwide and for *Avicennia* in particular (Tam and Wong 1997, MacFarlane and Burchett 2000, Machado et al. 2002a, Marchand et al. 2016). This species has many mechanisms that limit the uptake of metals and/or restrict their transfer to the aerial tissues. At the root system level, a first barrier to metal assimilation is induced by the diffusion of oxygen in the rhizosphere of *Avicennia* (Scholander et al. 1955, Curran et al. 1986, Allaway et al. 2001). The oxygen induces the formation of solid iron plaques at the surface of the root system, in which other metals, such as Mn and Zn precipitate (Machado et al. 2005). The metals that are assimilated by the roots tend to have a restricted mobility due to the different tissues of the root system that act as barriers to metal transfer to the stele and the phloem (Saenger 2002, Machado et al. 2005).

Despite these low BCF, significant contents of Al, Fe, Mn, Zn and Cu were measured within the root and leaf tissues, and increasing concentrations were found in roots with increasing available concentrations of metals within the soils. Except for Al, all other metals assimilated in significant concentrations are essential microelements required in small concentrations in many physiological processes (e.g. Fe, Alongi 2010). Despite the lower concentrations in the available phase of the soils in the site Upstream, we

observed a higher transfer of metals from the roots to the aerial biomass in the Upstream compared to the Downstream site. A similar increase of metal translocation from roots to leaves in *Avicennia* has been observed for Cu and Al above a certain total concentration threshold within the soils in previous studies (Rout et al. 2001, MacFarlane et al. 2003, Oxmann et al. 2010). We hypothesise that this increasing bioaccumulation of metals in aerial biomass could be the result of a regulation mechanism aiming to avoid long term metal toxicity in roots. Indeed, several studies have shown that the alternation of oxidation-reduction conditions during the tidal range combined with high metal concentrations lead to the production of dissolved metallic cations in soils (Marchand et al. 2006, 2016, Noël et al. 2014, Deborde et al. 2015). While this is also the case Downstream of Mangawhai Estuary, the small soil particles and lower tidal range in the site Upstream of the estuary could further limit the export of these metals by the tide in this site. As hypothesised by Marchand et al. (2016), this situation could lead to a saturation of the binding sites at the surface of clay particles, OM and Fe-precipitates. As a result, the pool of dissolved metals in pore water and mangrove roots could build up over time and reach toxic levels. The higher concentrations of these metals within senesced leaves in the Middle and Upstream site compared to the Downstream site seem to confirm this hypothesis. In particular, Fe, Al, and Ni showed a net accumulation in every senesced leaf sample (negative RE) up to - 300% and - 400% for Fe and Al, respectively. Al is produced in high concentrations in flooded ecosystems and is highly toxic for plants (Lambers et al. 2008). Although no data are available in the literature for comparison, these results show that Al excretion in shedding tissues must play an important role in the regulation of this element. The higher accumulation of Cu and Zn in senesced leaves in the Upstream and Middle sites compared to the Downstream site suggests a similar saturation of these elements within

the soils and plant tissues. The relationship between green and senesced concentrations of Cu illustrates clearly this pattern. Indeed, Cu is the only element for which this relationship is exponential, with Cu being resorbed under a total concentration of 20 mg kg^{-1} in green leaves, and increasingly accumulated in senesced leaves and/or translocated from green to senesced leaves passed that threshold.

Surprisingly, the relationship between the concentrations of all other metals in green and senesced leaves tended to be much less significant. These results departed from those observed in previous studies, where a clear linear correlation has been observed between the content of metals in green and senesced leaves (e.g. Naidoo et al. 2014, Martuti et al. 2017). This could either suggest a lower time of residence for these elements in green leaves and thus a rapid metal transfer to shedding leaves, or that an additional mechanism intervenes in metals regulation in *Avicennia* leaf tissues. For example, research has shown that *Avicennia* secretes metals and Na as combined alkaline salts at the surface of the glandular trichomes of the leaves (MacFarlane and Burchett 2000, MacFarlane et al. 2007). However, no correlations were found between the concentrations of metals and Na in senesced leaves in the present study. In addition, the positive NaRE factors and lower Na concentrations within senesced leaves compared to green leaves indicate that Na was leashed from the senesced leaves before sample collection. This result contrasts with many previous findings that have reported an accumulation of Na in mangrove litter as a mechanism of salt excretion (e.g. Wang and Lin 1999, 2003, Medina et al. 2010). As there was no significant rainfall at the time of our fieldwork, we suspect that Na, together with these metal secretions, could have been leached out from the leaf surface by the abundant morning dew. However, this hypothesis would need further measurements to be confirmed.

Based on our data and the biomass partitioning presented by Tran et al. (2017) for the entire estuary, we hypothesise that i) the coarse roots of mangroves trap a significant pool of metals along the estuary, ii) that high concentrations in metals within low Eh and hydrodynamics in soils may restrict dissolved metal exports, which could accumulate in the root system over time, and iii) as a result, the metal translocation from the roots toward the canopy and then to the litterfall increases, probably as a mechanism to avoid long term metal toxicity in the root system.

3.6 Conclusions

While mangrove expansion has certainly changed the landscape of New Zealand estuaries, the present study shows that, as in the tropics, significant concentrations and stocks of macro-nutrients and trace metals are found in these temperate mangroves. Thus, the particular geochemical and physiological processes of these mangrove ecosystems may lead to the build-up of an important sink for metals and macro-nutrients in estuaries over time. The comparison among sites along the estuarine gradient has also shown that the remobilisation and export of elements in the dissolved phase of soils increases with increasing oxidation and hydrodynamics. In addition, the approach chosen in this study to understand the elemental soil-plant transfer has highlighted similar patterns between different groups of elements in the soil and plant tissues. Although further work is required to understand these interactions and the cycle of elements in mangrove ecosystems, the present study has highlighted the importance of using a multi-elemental approach over a wide range of environmental conditions. In particular, a partitioning of the different elements in the soils and a multi-elemental isotopic tracing analysis over a wide range of environmental conditions would be needed to confirm the different hypotheses proposed in this work.

In the context of increasing mangrove removals in New Zealand, the disturbance and subsequent exposition and erosion of the soils and the buried biomass could result in a significant export of macroelements and trace metals to the water column. This could impact significantly the quality of coastal water and could impact the communities living in the coastal ecosystems. The results of the present study highlight the role of temperate mangroves as a buffer for terrigenous pollutants. In addition, it emphasizes the need for further studies on the elemental distribution and transport in the water column and the need for short and long term seasonal monitoring of water quality after mangrove removal.

Chapter 4

Sedimentary and Elemental Dynamics as a Function of the Elevation Profile in a Semi-Arid Mangrove Toposequence

4.1 Abstract
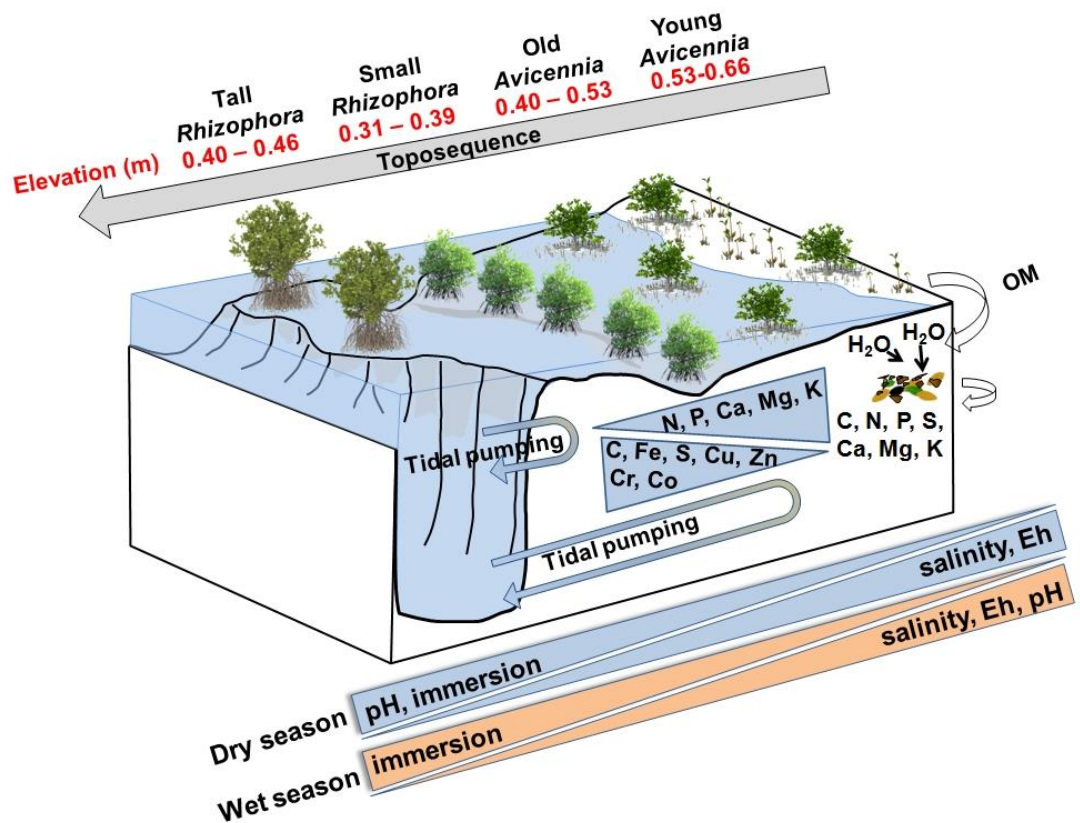
Figure 42. Graphical abstract of the elemental distribution and seasonal variation of chemical properties along the semi-arid mangrove toposequence studied

The effect of elevation and seasonal variations on the elemental status of soils was investigated along a semi-arid mangrove profile in the Heart of Voh, New Caledonia. Similar to other mangroves in the world, this mangrove site experienced an increase of tidal range that led to the recent colonisation of salt flats at the highest elevations landward by *Avicennia marina* (Forsk.) Vierh subsp *australasica* (Walp.) J. Everett. This young *Avicennia* stand was compared with an old *Avicennia* stand at lower elevations on its edge. Down the elevation profile, the soil properties of a short *Rhizophora stylosa* Griff stand were compared with a taller *Rhizophora* stand seaward that experienced longer immersion periods. Our results show that centimetre-scale variation in elevation significantly affects all soil properties along the semi-arid profile and induces a strong seasonal variation in reduction potential and pH at high elevations over the year. We suggest that during the dry season, the oxygenated soils enhanced the oxidation of organic matter (OM), which led to the dissolution of Fe-S compounds and the subsequent acidification of the soils. This in turn induced a loss of metal content (Fe, Cu Ni, Mn) compared to the soils at lower elevation. Moreover, our results show that the accumulation of OM during the colonisation phase by *Avicennia* coincided with higher water content and higher total and exchangeable concentrations of N, P, Mg and K within the surface soils than in the old *Avicennia* stand. The tall *Rhizophora* stand at the borders of the channel was characterized by an increase in elevation, denser soils and a depletion of elements in several horizons of the depth profile compared to the short *Rhizophora* landward. These results provide a better understanding of i) the impact of elevation differences on macroelements and trace metals in a semi-arid mangrove ecosystem, and ii) the changes of soil properties mediated by a pioneer species within the early phase of succession in hypersaline mangroves.

4.2 Introduction

Mangrove ecosystems include over 70 species of woody plants, ferns and palm trees that grow along the intertidal gradient within tropical, subtropical and temperate coastlines, deltas and estuaries (Duke et al. 1998, Duke 2006a, FAO 2007, Saenger 2002). These species have unique and diverse physiological adaptations that allow them to cope with specific physico-chemical constraints, such as high variability in salinity, oxygen concentration, sediment and soil stability, inundation time and others (Lugo & Snedaker 1974, Walsh et al. 1974, Naidoo 1985, McKee 1993, Duke et al. 1998, Ball et al. 1999, Saenger 2002, Tomlinson 2016). These specific adaptations often result in well-defined zonation patterns along the intertidal zone.

Among the numerous variables that affect mangrove zonation patterns, inundation time and salinity are thought to be dominant factors (Watson 1928, Ball 1996, Duke et al. 1998, Krauss et al. 2006, Crase et al. 2013) and are directly related to topographical characteristics that determine the geochemical properties of a given site (Baltzer et al. 1982, Otero et al. 2006). Accordingly, within humid tropical climates, mangroves in landward areas are exposed to significant freshwater inputs, whereas highly salt-resistant species dominate in seaward areas. Conversely, the opposite zonation pattern is observed in semi-arid climates, where only saltmarsh plants and mangrove species resistant to high salinity develop in hypersaline landward environments (e.g. Cintrón et al. 1978, Feller et al. 2003, Marchand et al. 2011b). Although less productive than their humid tropical counterparts (Leopold et al. 2016, Saenger and Snedaker 1993), several studies have demonstrated that semi-arid mangroves show an important capacity to store organic matter (OM) and heavy metals in their soils (Alongi et al. 2003, Alongi 2005, Marchand et al. 2011b, Noël et al. 2014, Usman et al. 2013).

Previous studies conducted in semi-arid mangroves of New Caledonia have provided a comprehensive understanding of OM, key nutrient and trace metal cycling under varying hydrological conditions (Marchand et al. 2011b, 2012, 2016, Noël et al. 2015, 2017, Deborde et al. 2015, Leopold et al. 2016). These studies have shown that soils with low water and organic contents and high oxido-reduction potential (Eh) induce specific OM decomposition pathways, elemental mobility and patterns that are characteristic of drought and hypersaline environments. For example, Deborde et al. (2015) and Marchand et al. (2011b) found that suboxic sediments and soils in landward areas are associated with high concentrations of dissolved iron and sulphates, whereas sulphides, particulate iron and sulphur precipitated as pyrite are usually favoured in reduced anoxic mangrove soils in seaward areas. As a consequence, the aerobic oxidation of OM pathway prevails in oxic and suboxic conditions, while the sulphate reduction pathway dominates in regularly flushed soils. In addition, previous studies have suggested that oxygenation of landward soils modulates the availability of key nutrients (Deborde et al. 2015, Marchand et al. 2016, Noël et al. 2017). For example, Marchand et al. (2016) and Noël et al. (2015, 2017) described how some trace metals (e.g., Cu, Ni) are found in the exchangeable phase and thus are more available for plant uptake and exports, while other micronutrients (e.g. Zn) tend to be bound in the refractory phase in suboxic conditions. Similarly, the availability of macronutrients is modulated by oxygen and iron in dry landward habitats. For example, phosphorus is trapped in landward soils when bound to oxygen and iron (Deborde et al. 2015) and the nitrogen source changes from ammonification to nitrification in anaerobic conditions (Boto and Wellington 1984). In other hypersaline and dry mangrove substrates, researchers have found that high evapotranspiration leads to high K^+, Mg^+, Ca^+ concentrations (Böer 1996, Alongi et al. 2003, Naidoo 2006). Finally, several authors have documented that the actual uptake of

nutrients by plants depends on the physiological requirements of each species, their capacity to alternate nutrient mobility within the substrate and their adaptations to cope with salinity (Andersen and Kristensen 1988, Ball and Munns 1992, Reef et al. 2010, Marchand et al. 2012, 2016).

In light of climate change conditions, semi-arid mangroves may be particularly susceptible to OM mineralisation and mobility of elements within their soils and sediments. This may be especially true for mangrove soils and sediments located at extreme elevations and thus more susceptible to undergo strong changes of hydrodynamics. However, no study has measured the influence of elevation on mangrove soil properties and their elemental status at the extremities of a semi-arid mangrove toposequence. Thus, the present study aims to investigate the physico-chemical properties along a topographic gradient in semi-arid New Caledonia. Specifically, we characterized the spatial and seasonal variations of soil properties (Eh, pH, bulk density, salinity, water content, chlorophyll-a (chl-a), total and weakly-bound elemental concentrations) as a function of the elevation and depth profile along a classical *Avicennia-Rhizophora* gradient landward. Then, we compared the soil properties of this gradient with i) a young *Avicennia* stand that recently developed into salt flats at higher elevations landward and ii) a *Rhizophora* stand that experienced longer immersion times and periodic hydrodynamic disturbances seaward.

4.3. Material and methods

4.3.1 Site of study

The study site is located in the "Heart of Voh", New Caledonia ("Coeur de Voh", 20° 56.0'
S, 164° 39.2' E), which constitutes a heart-shaped mangrove stand of about 5.1 ha
(Figure 43). The site is undisturbed by direct human activity and is composed of two
mangrove species, *Avicennia marina* (Forsk.) Vierh subsp. *australasica* (Walp.) J. Everett,
and *Rhizophora stylosa* Griff. Historically, the Heart of Voh has undergone several
changes in vegetation cover in its centre since 1943 (Figure 43). Twenty-five years ago,
it was characterized by bare soils in the centre of the heart (highest elevation), followed
by a concentric band of shrubby *Avicennia* and a subsequent band of short and then tall
Rhizophora stands next to channels and rivers (Figure 43). However, in more recent
years, the centre of the mound has been filled in by a younger population of *Avicennia*.
In addition, a small tidal creek runs between the two lobes of the Heart.
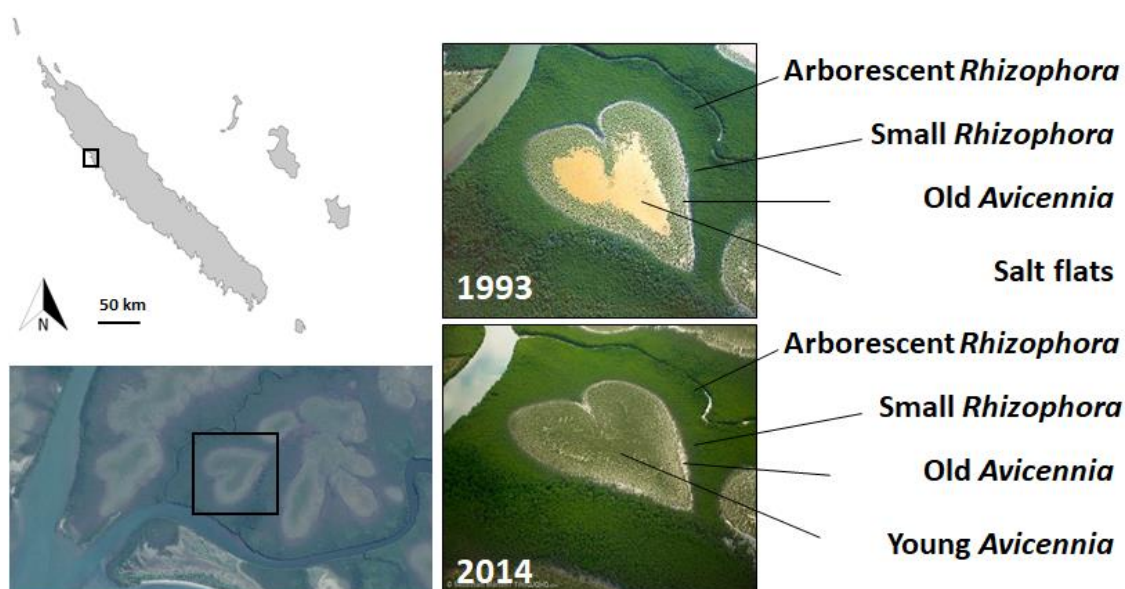
Figure 43. (left) Location of the study site in New Caledonia ; (right) evolution of the vegetation from 1993
to 2014, illustrating the filling of the centre of the Heart by *Avicennia*

The precipitation at the study site is relatively high (monthly average of 80 to 140 mm)
in summer (26 to 28 °C) and low (monthly average of 40 to 70 mm) in winter (16 to 25

°C). The annual average precipitation is less than 800 mm (Leopold et al. 2016), and the evaporation rate may be twice as high as the amount of rainfall, resulting in a negative water balance for at least four months of the year (Météo France 2017). The tidal regime is semi-diurnal with diurnal inequality. The maximum water level in the area is of 30 cm at lowest elevations during the wet season. In addition, the soil in the centre of the study site was submerged more than 20% of the time during the wet season, and less than 10% of the time during the dry season (Leopold et al. 2016).

4.3.2 Elevation measurements

Elevation data were acquired over two days in April 2017, using a differential global positioning system (DGPS, Trimble, USA). A reference station was set up on a permanent platform within the Heart of Voh. The elevation of the reference station and two control
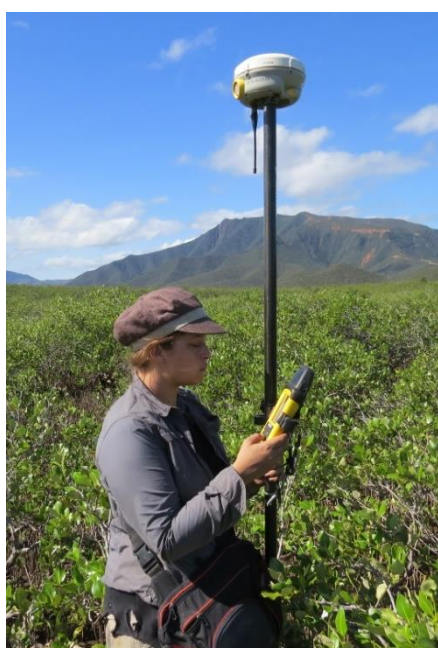
Figure 44. Use of the GNSS receptor Trimble R4 and record of an elevation point in the mangroves of the Heart of Voh, New Caledonia (photo credit : Rémi Andreoli)

points were measured in Real Time Kinetic (RTK), using the New Caledonian RTK Banian GPS/GNSS network (Direction of the Infrastructure, Topography and Terrestrial Transports, DITTT, centimetric resolution) with a GNSS receptor (Trimble R4, USA, Figure 44). The Banian network is a geodesic Caledonian network that sends GPS differential corrections computed from the Lambert neocaledonian projection (RGNC91-93) and the ellipsoid IAG GRS 1980 (a = 6378137.00 m ; 1/f = 298.257222101). Once measurements were taken, a GPS base (Trimble 4000, USA) and an ultra-high frequency (UHF) radio were installed at the reference points, and control points were measured again in order to detect any

deviation in the x, y, z planes. This deviation (± 3 cm) provided the absolute or global accuracy and was used to correct the entire elevation data set for the study site. Relative or local accuracy (i.e., the relative accurate of any given point to the other points in the data set) was ± 1 cm. Measurements were taken in a total of 5 204 points within the Heart of Voh and in its periphery. An additional transect was measured from the centre of the Heart of Voh to the channel, difficult to access. The main creeks were measured by taking sets of paired points on the banks and creek bed.

4.3.3 Sample collection

Surface soil samples were collected at ± 35 locations with three replicates per location during low tide in the wet season (productive season; March 2015 and March 2016) and the dry season (October 2015 and October 2016). In addition, 50-cm core samples were collected in triplicates at 16 locations with a stainless steel corer (8 cm diameter) during the wet season only. The soil in each core was divided into five sections (0–2.5, 7.5–10, 15–20, 25–30, and 40–50 cm) while in the field. The total sampling depth of 50 cm was chosen to include most mangrove live roots, which in New Caledonia are found down to 20–30 cm for *Avicennia* sp. and down to 50 cm for *Rhizophora* spp. (Marchand et al. 2016). Five of the sampling locations were in the middle of the Heart of Voh (within the young *Avicennia* sp. stand), five locations were in the old *Avicennia* stand, and three locations were in the short and tall *Rhizophora* stands, respectively.

4.3.4 Measurements of physico-chemical parameters

The reduction-oxidation potential (Eh), pH and temperature (T) were measured within each soil section using a portable pH/mV/T meter (Multi 350i, Wissenschaftlich-

Technische Werkstätten, Germany) with a Pt-Ag/AgCl electrode (SenTix ORP, WTW) and a pH electrode with temperature sensor (SenTix 81, WTW) immediately after core collection. The Eh values were reported relative to a standard hydrogen electrode by adding the temperature-adjusted tension values of the Ag electrode (ranging from +210 mV for 20 °C to +200 mV for 35 °C) (SenTix, WTW). The deepest sections (in general more anoxic) were measured first to avoid potential biases due to prolonged contact with air in these sections. A small core of a known volume of soil was collected from each section using a graduated syringe (50 ml) with the tip cut off. Then, the samples were transported in a cooler to the laboratory where fresh weights were recorded immediately upon arrival.

Pore-water samples were extracted from each small core with a pressurised syringe connected to a soil moisture sampler (Rhizon SMS, Rhizosphere research products, Wageningen, The Netherlands). These samples were used to measure salinity with a hand held refractometer (Atago MASTER -S/Millα, Japan). The small cores were then freeze-dried with a FreeZone 2.5 Liter Benchtop (Labconco, Kansas City, USA) at − 80 °C for three days until constant weight was achieved. Dry weights of the samples were recorded and used to calculate the sample bulk density (BD) and pore-water content (WC). Chlorophyll-a pigments were analysed as in Leopold et al. (2013). The remaining soil from the initial large cores were also freeze-dried at − 50 °C and kept in the dark until elemental analyses could be conducted.

4.3.5 Elemental analyses

Total and exchangeable (bioavailable) elements were measured from each of the five depth sections from each soil core. All elemental analyses were performed at the

Institute of Research for Development (IRD) of Nouméa, New Caledonia (Certificate ISO 9001 : 2015), and three technical replicates were measured for each sample.

At the laboratory, each soil sample was divided into two sub-samples. One sub-sample was sieved through a 2 mm mesh and ground down to 250 μm grain size with a soil ball mill (PM100, Retsch, Germany), and total elemental measurements were taken for macro (C, N, K, Ca, Mg, P, S) and microelements (Fe, Mn, Zn, Cu, Ni), sodium (Na), and other trace metals (Cr, Co). The second sub-sample was sieved through a 2 mm mesh and used to measure weakly bound and exchangeable cations, including K, Ca, Mg, S, Fe, Mn, Ni, Cu, Zn, Cr, Co.

Total organic carbon content (TOC) was determined by the 900 °C combustion catalytic oxidation method using a solid sample module (SSM-5000A) combined with a total organic carbon (TOC) analyzer (Shimadzu, Kyoto, Japan). Total nitrogen (ammonium-N, nitrate-N, nitrite-N and organic N) contents were determined by the Kjeldahl's method (ISO 11261: 1995). The exchangeable elements in the soils (Ca, Mg, K, S, Fe, Ni, Cr, Co, Cu, Zn) were measured by inductively coupled plasma emission spectroscopy (ICP-OES, Varian, Australia) in ammonium acetate and Ethyl Diamine Tetraacetic Acid (EDTA)-Disodium extract at pH 7 (NF X 31-120, Pansu and Gautheyrou 2007). Total elemental concentrations were determined by inductively coupled plasma emission spectroscopy (ICP-OES, Varian, Australia) after extraction in a solution of 10% w/v solution of ammonium fluoride (FNH_4) and nitric acid (70%). Briefly, 1 ml of this acid solution was added to 100 mg of soil sample weighted in a 15 ml polypropylene tube, vortexed and left over night. Then, the samples were vortexed again and left to mineralize during 6 hours in a dry bath at 100 °C (IsoTemp, Fisher Scientific, USA). After cooling, each tube was brought to a volume of 10 ml with ultra-pure demineralised water, vortexed again, centrifuged for 5 minutes at 3000 rpm, and stored in a refrigerator until ICP-OES analysis.

The accuracy of the method was tested on reference samples of the International Soil-Analytical Exchange program (ISE, Wageningen Evaluating Programmes for Analytical Laboratories, van Dijk and Houba 1999, Dijk 2002). After extraction and measurements, each elemental value was compared with the total (alkaline fusion) and the so-called semi-total (aqua regia and acid extractable) values found in the ISE reports following the validation method in van Dijk and Houba (1999) and in Dijk (2002). Our test results on these reference samples showed that the method allows for the extraction of the total concentrations of Ca, Na, K, P, Co, Fe, Mn, Ni, Cu, Zn, S (- 2 < z-scores < + 2) and the acid extractable concentrations (semi total) of Mg (z-scores total = - 2.3; z-scores acid extractable = 1.2) and Cr (z-scores total = - 3.4; z-scores acid extractable = 1.8), where the z-scores of a given element is calculated as follow :

$$z - score \ = \ \frac{A-B}{C}$$

, where *A* stands for the concentrations of a given element extracted with the 10% *w/v* FNH_4 HNO_3 10% method selected in this study ; *B* stands for the total concentration values of the same element published in the ISE reports, compiled as the mean of all the concentration values provided by the different laboratories that participated to the ISE report ; *C* stands for the standard deviation of the values published by the ISE. Figure 45 illustrates the z-score results compiled with different concentrations of $FNH_{4 \ /} \ HNO_3$ tested (1%, 5%, 10%), with the selected 10% acid method showing the lowest deviation from the ISE values.
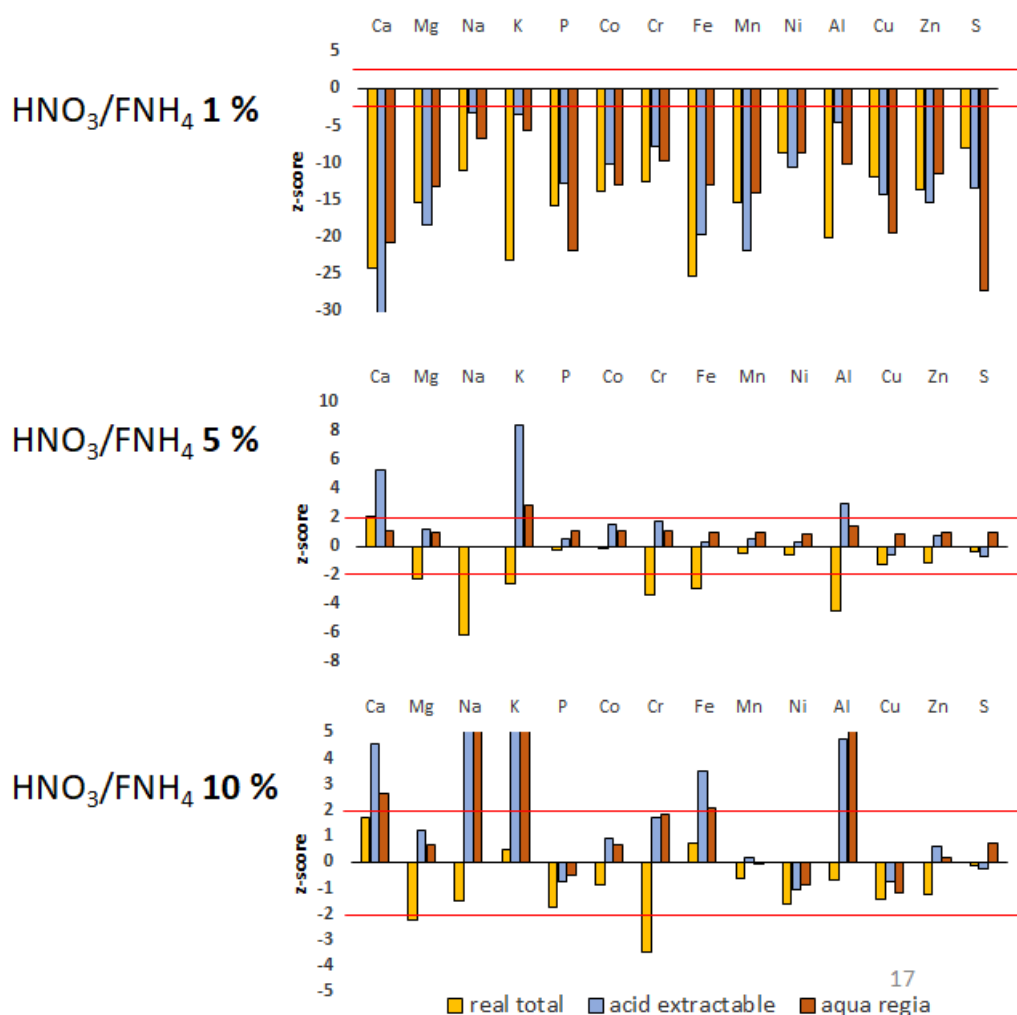
Figure 45. (from top to bottom) Comparison between the z - score values obtained with different concentrations of HNO_3/FNH_4 tested (1%, 5%, 10%). In each graph, the z-score of an elemental concentration is given relative to the ISE values obtained with a total extraction method (yellow bars) and two so-called semi-total extraction method (aqua regia, red bars, and acid extractable, blue bars). The red lines indicate the z-score interval of - 2 to + 2 considered as an acceptable deviation from the mean concentration values published in the ISE report for a given target fraction (i.e. total vs semi-total)

4.3.6 Data analyses

All physico-chemical and elemental data were analysed with two-ways ANOVAs (4 stands x 5 depths and 4 stands x 2 seasons) and Tukey's post-hoc tests. The Pearson coefficient was used to measure correlations between variables. All analyses were performed and tested with R software.

4.4. Results

4.4.1 Topography and tree measurements

The elevation of the study site ranged from 0.31 to 0.66 m with a mean (± SD) of 0.45 ± 0.07 m above the topographic zero (= 1.12 m above the hydrographic chart datum corresponding to the lowest astronomical tide, chart datum conversion coefficient, Maritime Altimetry Reference RAM, SHOM 2016, ISO 9001). The highest areas were found in the middle of each lobe of the Heart of Voh and the lowest areas were beyond the margins (Figure 46). A 290 m long cross sectional view of the topographic profile from the channel bank (point A) to the other side of the Heart of Voh (point B) is presented in Figure 46.
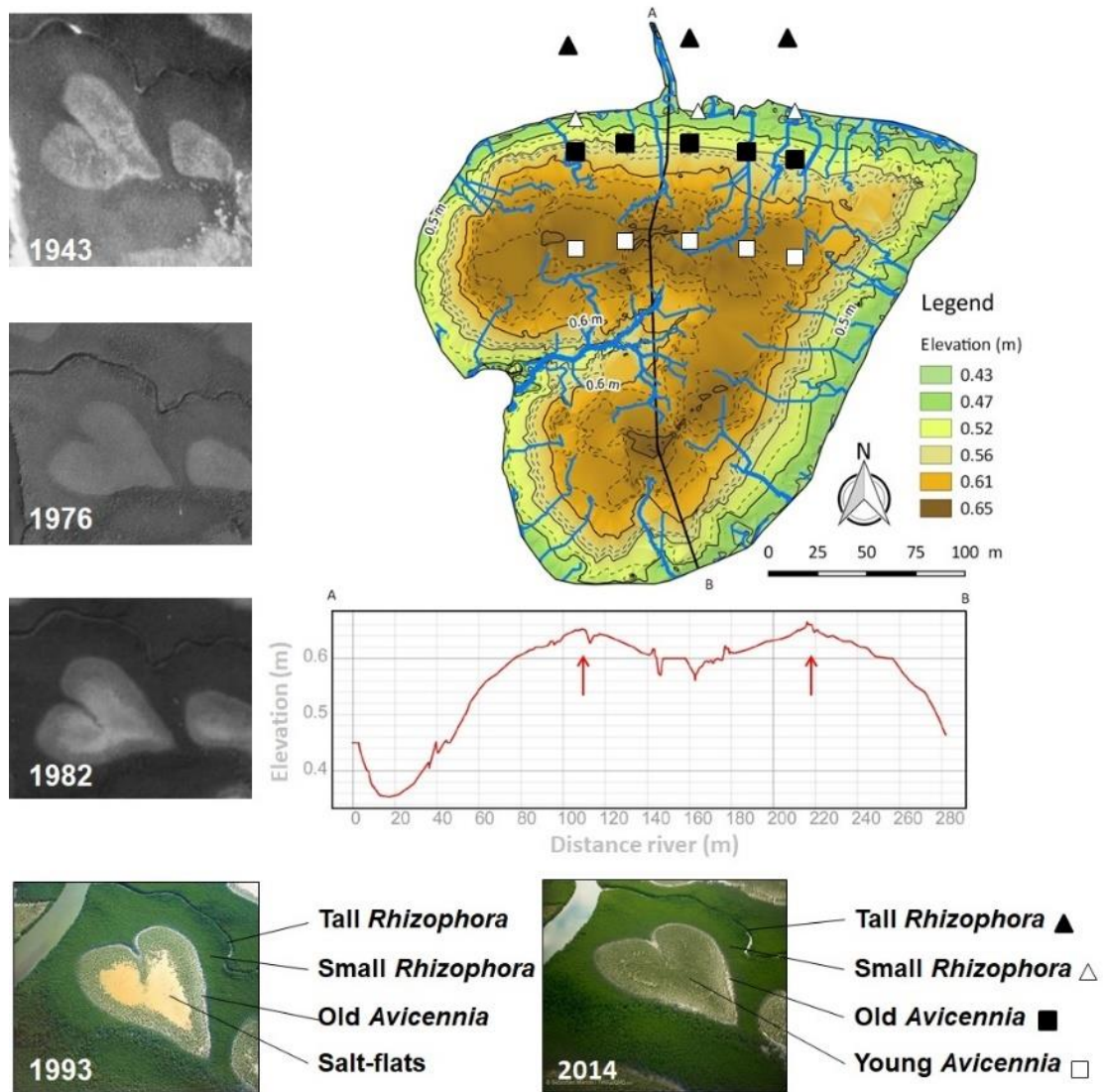
Figure 46. Temporal evolution of the Heart of Voh, from 1943 to 2014 (aerial photographs 1943 to 1982 from the Direction of the Infrastructure, Topography and Terrestrial Transports, DITTT, 1993 photograph Y. Arthus-Bertrand, 2014 S. Mérion). Elevation map of the Heart of Voh; cross sectional view of the topographic profile of the site of study passing by the highest points of the site from (A) the main channel in the arborescent *Rhizophora* to the other side of the Heart of Voh (B). The arrows on the figure indicate the highest point of each lobe. The black and white triangles indicate the locations of the 3 triplicate cores sampled in the tall and small *Rhizophora*, respectively. The black and white squares indicate the locations of the 5 triplicate cores sampled in the old and young *Avicennia*, respectively
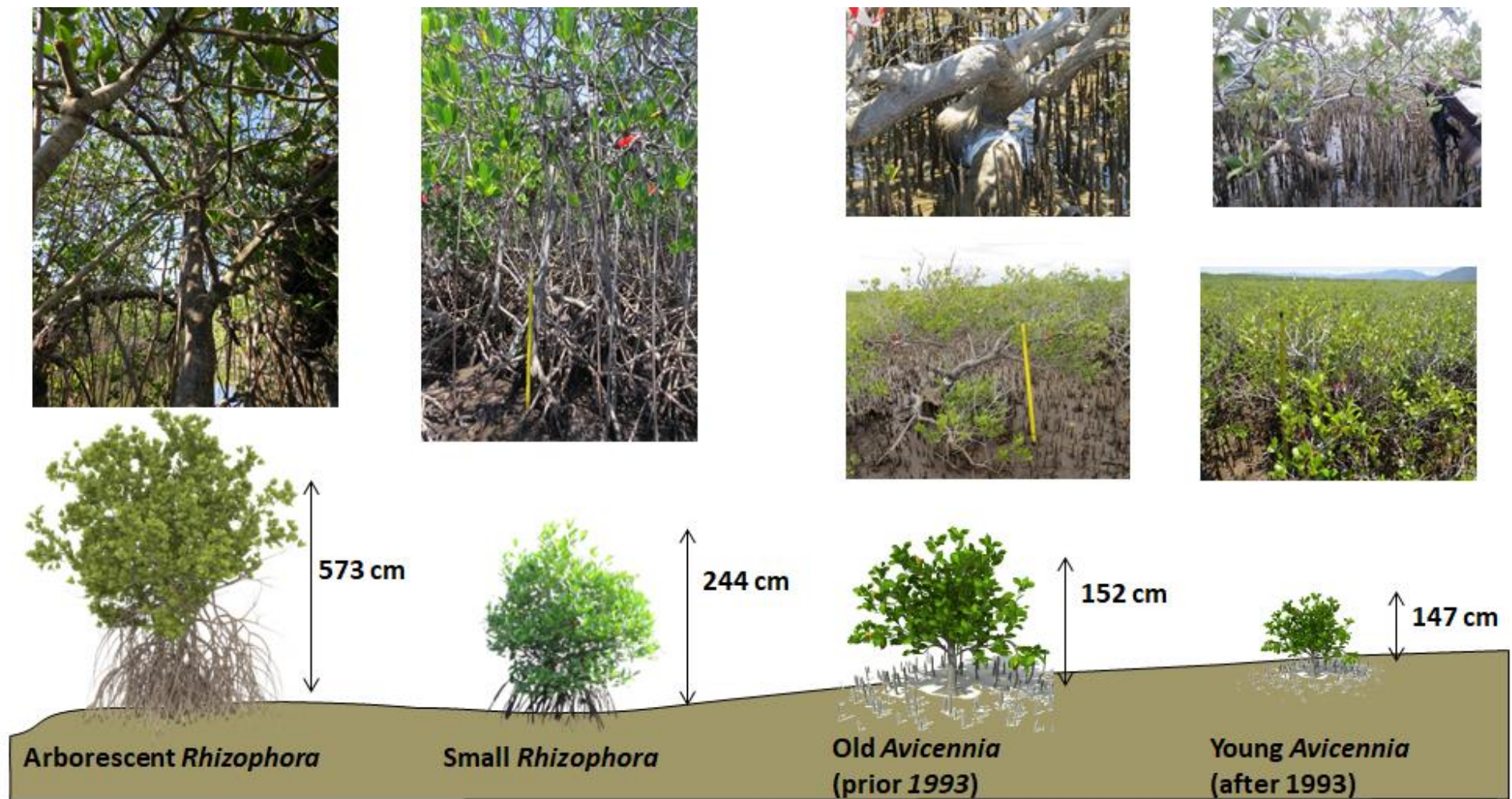
Figure 47. Distribution and height (cm) of *Avicennia* and *Rhizophora* along the elevation gradient (photo credit : C. Bourgeois)

Along the elevation profile, *Avicennia* and *Rhizophora* species were differentially distributed without any transition areas containing both species (Figure 46, Table 10). The recently established *Avicennia* stand (young *Avicennia*) occurred at the highest areas in the middle of the site (0.53 to 0.66 m), while the old *Avicennia* stand was found on the margins within a band ranging from 0.40 to 0.53 m. The *Rhizophora* distribution had a clear gradient from small trees at the lowest elevation beyond the margins of the site (0.31 m) to the tallest trees along the channel banks (0.46 m) (Table 10).

Table 10. Elevation ranges and means (±SD) of four mangrove stands within the study site. Mean (±SD) adult tree heights, total basal area and volume of canopy in each mangrove stand

	Elevation range (m)	Elevation means (m)	Tree height (m)	∑ basal area (cm²)	Crown volume (m³)
Young *A.marina*	0.53-0.66	0.59	1.47 (± 0.16)	57.8 (± 21.9)	3.7 (±1.9)
Old *A.marina*	0.40-0.53	0.50	1.52 (± 0.22)	196.6 (± 35.1)	6.5 (±5.2)
Small *R.stylosa*	0.31-0.39	0.35	2.44 (± 0.54)	71.3 (± 47.3)	9.0 (±7.9)
Tall *R.stylosa*	0.40-0.46	0.42	5.73 (± 0.65)	190.4 (±43.5)	79.3 (±9.1)

4.4.2 Surface soil physico-chemical properties

All physico-chemical properties of surface soil varied significantly between stands (*$p_{ANOVA\ stand}$ < 0.05). Markedly, all soil properties were significantly correlated with the elevation, with the best-fitted models between each of the soil properties and the elevation corresponding to a quadratic function (Figure 48). Additionally, all physico-chemical properties varied significantly between seasons (*$p_{ANOVA\ season}$ < 0.05) except for the WC, BD and TOC (Table 11, Figure 48). During the wet season, the surface soils were characterised by a significant increase in salinity and Eh from the channel banks in the tall *Rhizophora* to the highest elevations in the young *Avicennia* stand (Table 11, Figure 48). During the wet season, the surface soils were anoxic in every stand (mean Eh < 100 mV, Marchand et al. 2012) and ranged between -123.0 ± 148.8 mV in the old

Rhizophora and +23.3 ±70.3 mV in the young *Avicennia*. The highest values of pH were observed in the tall *Rhizophora* soils (6.76 ± 0.37) and decrease steadily up to 6.59 ± 0.10 in the young *Avicennia* stand (Table 11). In addition, the TOC and BD were strongly correlated (r = 0.72, **p < 0.01). Surface soils in the young *Avicennia* and small *Rhizophora* stands had higher water and TOC contents and significantly lower BD than the corresponding values in the tall *Rhizophora* and old *Avicennia* stands (Table 11). The highest concentrations of chl-a were measured in the young *Avicennia* stand (235.2 ± 51.7 µg g^{-1}), and decreased steadily in the old *Avicennia* (109.4 ± 61.2 µg g^{-1}) and small *Rhizophora* stands (54.1 ± 30.3 µg g^{-1}).

Table 11. Mean (±SD) values for various surface soils parameters in four mangrove stands at the study site over two seasons (WS = Wet Season, DS = Dry Season). Different letters indicate significant differences between stands and/or seasons (Tuckey, p< 0.05). NA indicates missing values

	Young *A. marina*	Old *A. marina*	Small *R. stylosa*	Tall *R. stylosa*
Temperature (°C) WS	34.3 (±1.6)^a	31.7 (±2.7)^b	29.9 (±2.1)^b	27.6 (±0.7)^c
Temperature (°C) DS	23.7 (±2.4)^d	25.2 (±3.2)^d	29.0 (±2.5)^c	28.3 (±0.4)^c
Salinity WS	46.2 (±5.1)^c	40.4 (±6.7)^{cd}	31.3 (±4.0)^d	23.5 (±3.5)^{bd}
Salinity DS	62.2 (±7.3)^a	58.9 (±11.9)^a	41.2 (±11.4)^b	33.5 (±2.1)^b
Redox Potential (mV) WS	+23.3 (±70.3)^a	+24.3 (±76.4)^{ab}	-91.4 (±89.2)^b	-123.0 (±148.8)^b
Redox Potential (mV) DS	+202.1 (±74.9)^c	+147.7 (±89.1)^d	-124.0 (±25.5)^b	-197.0 (±27.7)^b
pH WS	6.59 (±0.10)^a	6.51 (±0.15)^a	5.89 (±1.08)^b	6.76 (±0.37)^{ab}
pH DS	5.23 (±0.14)^c	5.49 (±0.49)^c	6.00 (±0.24)^b	6.16 (±0.21)^b
Water content (%) WS	76.5(±3.8)^a	72.8 (±4.7)^{ab}	75.8 (±4.5)^a	62.2 (±0.2)^b
Water content (%) DS	72.4 (±3.8)^{ab}	68.9 (±4.8)^b	72.7 (±3.6)^{ab}	62.2 (±0.2)^b
Chl-a (µg g^{-1}) WS	235.2 (±51.7)^a	109.4 (±61.2)^b	54.08 (±30.3)^c	NA
Chl-a (µg g^{-1}) DS	138.0 (±44.5)^b	78.8 (±36.1)^c	NA	NA
TOC (%) WS	13.5 (±1.4)^{ac}	10.3 (±2.0)^b	13.0 (±2.7)^{ac}	9.9 (±0.2)^{ab}
TOC (%) DS	15.2 (±1.9)^c	11.4 (±1.6)^{ab}	13.3 (±1.3)^{abc}	12.0 (±1.0)^{ab}
Bulk density (mg cm^{-3}) WS	0.40 (±0.08)^b	0.48 (±0.11)^a	0.40 (±0.12)^b	0.53 (±0.03)^a
Bulk density (mg cm^{-3}) DS	0.48 (±0.16)^{ab}	0.61 (±0.21)^a	0.31 (±0.08)^b	0.51 (±0.01)^{ab}
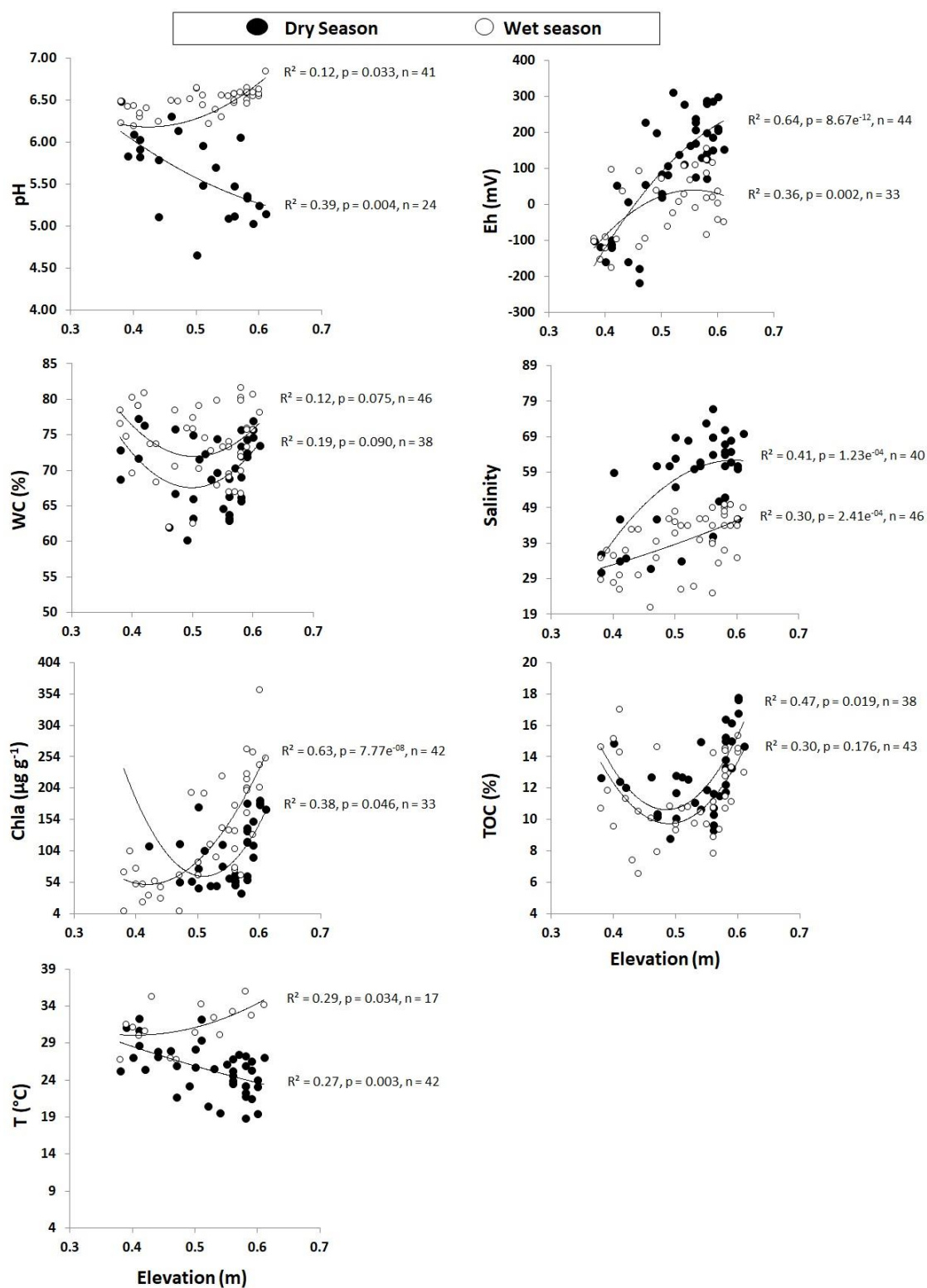
Figure 48. Best-fitted models, regression coefficient R², p-values and number of triplicates (n) of the physico-chemical parameters (pH, Eh, WC, Salinity, Chl-a, TOC, T) in the surface soils according to the elevation during the dry (black circles) and wet (white circles) seasons

During the dry season, there were no significant differences in any of the surface soil properties in the tall *Rhizophora* when compared to the wet season. Within the other stands, salinity and Eh had similar trends as during the wet season, but their mean values increased significantly (Table 11, Figure 48). Salinity increased by about 20% in both *Avicennia* stands and about 10% in the short *Rhizophora* stand. The surface soils were suboxic within both *Avicennia* stands (100 < Eh < 400 mV, Marchand et al. 2012) and remained anoxic in both *Rhizophora* stands. In addition, the mean values for temperature, pH, water content and chl-a decreased significantly in all mangrove stands compared to the wet season, except for the tall *Rhizophora*. Contrary to the wet season, the pH decreased significantly with increasing elevation (from 6.16 ± 0.21 in the tall *Rhizophora* to 5.23 ± 0.14 in the young *Avicennia* stand) during the dry season. In addition, chl-a decreased by 98 µg g^{-1} in the young *Avicennia* stand and by 31 µg g^{-1} in the old *Avicennia*, compared to the wet season.

4.4.3 Soil physico-chemical properties

The physico-chemical properties within the soil column during the summer season are presented in Figure 49. Mean (±SD) salinity values increased consistently with increasing depth and elevation from the tall *Rhizophora* (28.7 ± 4.8) to the young *Avicennia* stand (63.3 ± 9.9). Conversely, the Eh values decreased significantly with increasing soil depth within all stands (***$p_{ANOVA-depth} < 0.001$) until 20 cm depth, at which point the Eh values remained constant until the deepest horizon. The pH values varied greatly within the depth profile across all mangrove stands (*$p_{ANOVA-depth} < 0.05$), but there was a general decrease in pH with increasing depth.
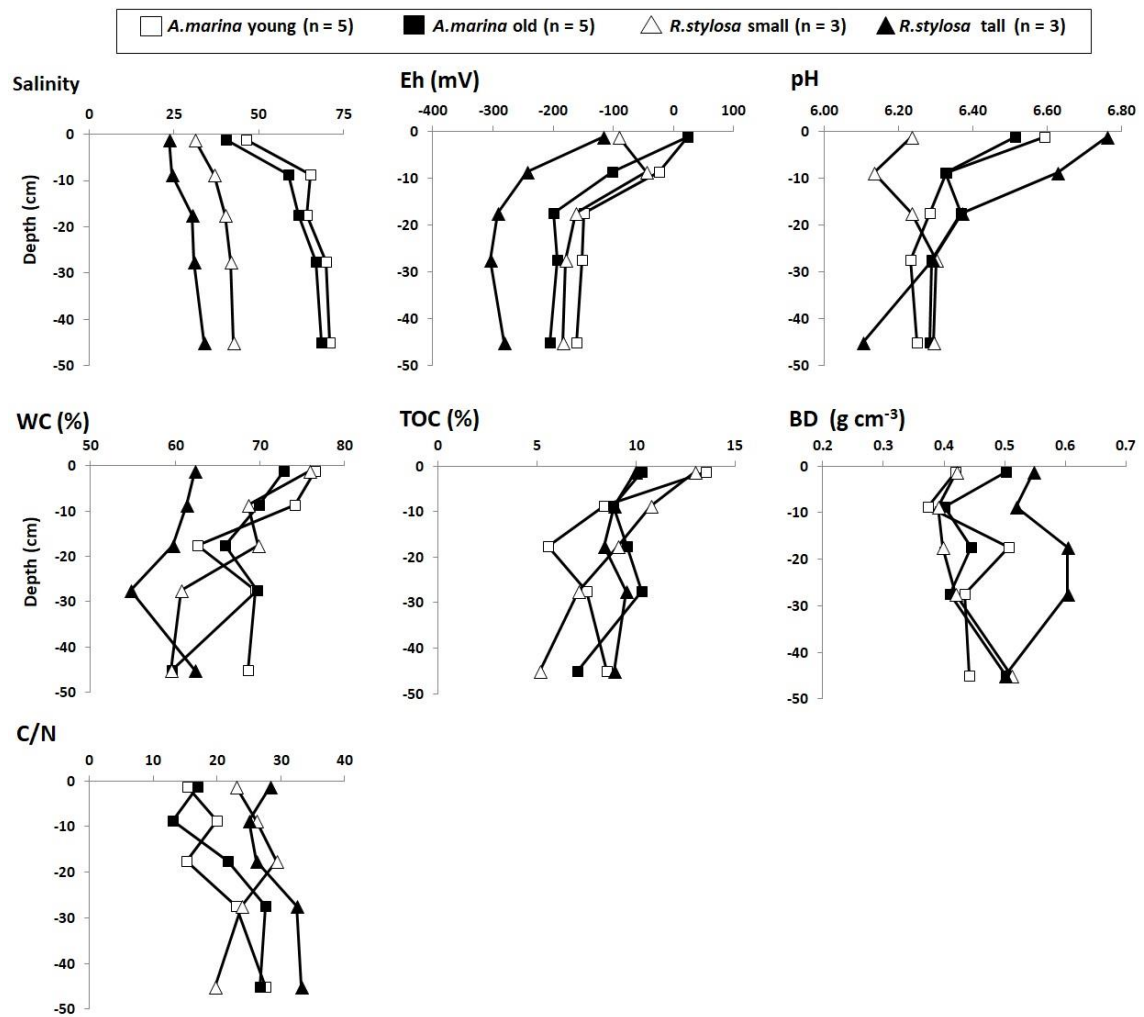
Figure 49. Mean salinity, Eh, pH, water content (WC), organic carbon contents (TOC), bulk density (BD) and C/N ratios in soils within each of four mangrove stands. n indicates the number of triplicate cores sampled in each mangrove stand

A particularly strong increased acidification with increasing depth was observed in the tall *Rhizophora* stand, where pH values changed from 6.76 ± 0.17 at the surface to 6.09 ± 0.09 at the deepest horizon. Great variability was also observed in WC, TOC and BD values with increasing depth and across all mangrove stands. Mean (±SD) WC values tended to decrease with increasing depth and with decreasing elevation, from 70.3 ± 5.4% in the young *Avicennia* stand to 60.0 ± 3.2% in the tall *Rhizophora* stand. The TOC values across the depth profile were lowest in the young *Avicennia* and small *Rhizophora* stands (8.7 ± 2.4 and 9.0 ± 2.3%, respectively), and highest in the old *Avicennia* and the

tall *Rhizophora* stands (9.2 ± 3.9 and 9.1 ± 2.6%, respectively). Noticeably, the 15–20 cm depth section of the young *Avicennia* stand was marked by a sharp decrease in TOC and WC (5.6 ± 2.9 and 62.7 ± 7.8%, respectively) and by an increase in BD (0.49 ± 0.17 g.cm^{-3}). A clear pattern of greater BD values, compared to the other mangrove stands, was recorded in the tall *Rhizophora* stand across soil depths, with mean (±SD) values of 0.58 ± 0.09 g.cm^{-3}.

4.4.4 Elemental concentrations during the summer season

Mean (±SD) concentrations of total and exchangeable elements under each mangrove stand are given in Table 12 and illustrated in Figure 50 and Figure 51.

Within the study site, the mean total concentrations of total elements within the soils in descending order were (g.kg^{-1}): Na (39.2), Fe (38.2), S (26.5), Mg (13.0), K (9.6), Ca (6.3), N (3.9) and (mg kg^{-1}) Mn (264.7), P (263.2), Ni (213.0), Cr (157.5), Zn (39.1), Co (24.4), Cu (20.3).

4.4.4.1 Redox sensitive elements (Fe and Mn)

The highest total mean (±SD) values of total Fe and Mn were measured in the soils of the short *Rhizophora* stand (46,157.5 ± 2,356.2 and 363.5 ± 75.0 mg kg^{-1}, respectively), and the lowest values were found within the soils of the young *Avicennia* stand (26,950.2 ± 5,032.4 and 165.4 ± 35.9 mg kg^{-1}, respectively) (Table 12, Figure 50). In general, exchangeable concentrations of Fe and Mn within the soils accounted for 1 and 5% of their total concentrations of these elements, respectively. The exchangeable concentrations of Fe and Mn followed a similar pattern among mangrove stands (r = 0.51, **p < 0.01), with the highest values found in the short *Rhizophora* (1148.3 ± 98.0

and 21.6 ± 4.1 mg kg^{-1}, respectively) and the lowest values found in the old *Avicennia*

(188.3 ± 33.3 and 8.2 ± 3.5 mg kg^{-1}, respectively) and young *Avicennia* stands (223.6 ±

21.3 and 2.0 ± 0.6 mg kg^{-1}, respectively) (Table 12, Figure 50). In general, exchangeable

Fe and Mn concentrations were highly variable in the *Rhizophora* stand with dramatic

decreases at 10 and 30 cm depth and quite uniform along the depth profile for the

Avicennia stands.

Table 12. Total mean (±SD) concentrations (mg kg^{-1}) of total and exchangeable elements in the soil column in four mangrove stands. For each type of extraction (total vs. exchangeable), different letters indicate significant differences of total mean elemental composition in the soil column between stands (Tuckey, p< 0.05). *n* indicates the number of triplicate cores analysed in each stand

		Total elements				Exchangeable elements			
		Young *A.marina* *n* = 5	Old *Avicennia* *n* = 5	Small *R.stylosa* *n* = 3	Tall *R.stylosa* *n* = 3	Young *A.marina* *n* = 5	Old *Avicennia* *n* = 5	Small *R.stylosa* *n* = 3	Tall *R.stylosa* *n* = 3
N	mean	4,511.6[a]	4,492.2[a]	3,922.7[a]	3,183.1[b]	-	-	-	-
	± SD	700.8	959.1	733.4	824.6	-	-	-	-
P	mean	233.5 [a]	334.8 [b]	233.2 [a]	323.1 [b]	-	-	-	-
	± SD	35.6	54.1	24.0	26.5	-	-	-	-
Ca	mean	5,248.1 [a]	6,010.2 [b]	7,332.8 [c]	6,179.0 [b]	2,462.0 [a]	2,404.3 [a]	2,978.0 [a]	1,151.0 [b]
	± SD	656.3	324.1	425.2	402.1	201.7	534.2	433.1	43.8
Mg	mean	12,652.1 [a]	17,115.4 [b]	14,674.6 [b]	11,744.9 [a]	5,944.4 [a]	5,227.0 [a]	4,686.0 [a]	1,883.0 [b]
	± SD	1,025.3	895.5	759.6	1,001.2	307.7	423.9	228.3	502.0
Na	mean	52,436.2 [a]	55,688.8 [a]	36,538.7 [b]	28,629.5 [c]	-	-	-	-
	± SD	5,234. 6	7,045.2	1,025.4	4,987.2	-	-	-	-
K	mean	11,317.3 [a]	9,478.2 [b]	8,884.7 [b]	8,607.3 [b]	2,214.4 [a]	1,862.7 [a]	1,396.3 [b]	798.0 [c]
	± SD	513.5	798.6	421.0	870.0	413.7	470.8	281.4	50.9
S	mean	19,372.9 [a]	41,801.3 [b]	38,717.0 [b]	21,499.9 [a]	4,288.0 [a]	3,528.3 [a]	5,111.3 [a]	1,688.0 [b]
	± SD	623.1	4,050.6	2,405.6	5,971.5	683.2	308.7	650.9	613.8
Fe	mean	26,950.2[a]	41,656.5 [b]	46,157.5 [c]	41,476.0 [b]	223.6 [a]	188.3 [a]	1,148.3 [b]	476.0 [a]
	± SD	5,032.4	1,489.0	2,356.2	2,678.1	21.3	33.3	98.0	31.7
Mn	mean	165.4 [a]	202.1 [b]	363.5 [c]	265.3 [d]	2.0 [a]	8.2 [b]	21.6 [b]	15.0 [b]
	± SD	35.9	16.2	75.0	42.6	0.6	3.5	4.1	2.9
Ni	mean	130.0 [a]	230.0 [b]	269.9 [b]	239.0 [b]	30.2 [a]	47.4 [b]	64.2 [b]	39.5 [a]
	± SD	12.4	9.8	35.1	46.2	3.0	11.6	6.2	9.7
Cu	mean	17.9 [a]	29.7 [b]	28.1 [b]	14.9 [a]	1.3 [a]	1.8 [a]	3.0 [b]	1.0 [a]
	± SD	1.9	2.2	4.6	3.2	0.2	0.2	0.3	0.2
Zn	mean	33.2 [a]	35.4 [a]	38.7 [b]	45.2 [b]	2.7 [a]	3.7 [a]	5.9 [b]	3.7 [a]
	± SD	4.5	3.6	5.1	4.3	0.7	0.9	1.0	1.0
Co	mean	16.1 [a]	16.6 [a]	30.6 [b]	26.4 [b]	1.8 [a]	2.0 [a]	5.3 [b]	3.4 [a]
	± SD	2.8	3.6	7.1	9.2	0.5	1.2	1.6	1.3
Cr	mean	119.1 [a]	198.9 [b]	201.6 [b]	151.6 [a]	0.5 [a]	0.5 [a]	5.6 [b]	0.3 [a]
	± SD	10.2	15.1	8.1	7.1	0.1	0.1	0.1	0.1
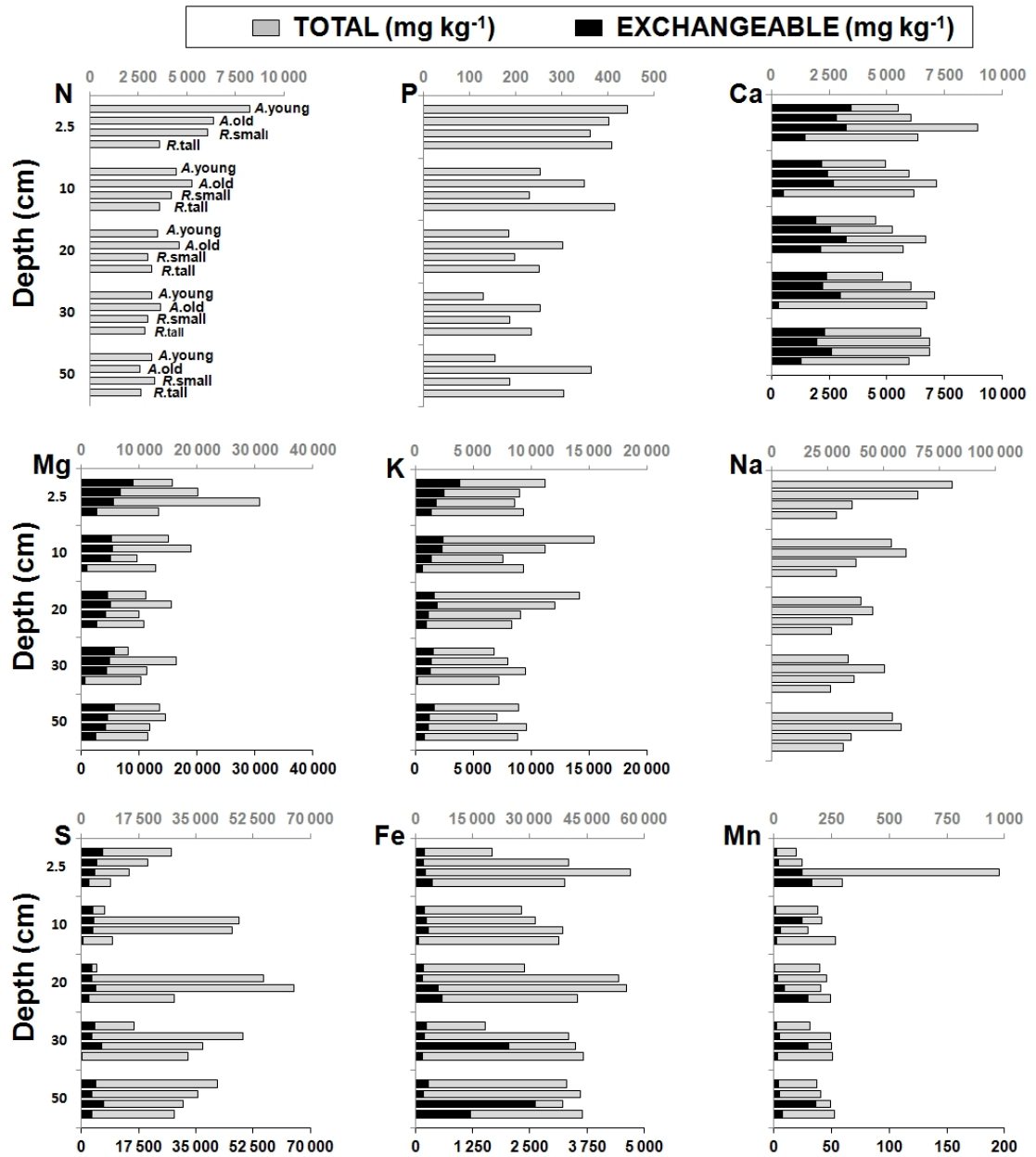
Figure 50. Mean concentrations (mg kg^{-1}) of total (grey scale, grey bars) and exchangeable (black scale, black bars) N, P, Ca, Mg, K, Na, S, Fe, Mn along the depth profile in each mangrove stand (*A.*young = Young *Avicennia* stand, *A.*old = old *Avicennia* stand, *R.*small = small *Rhizophora* stand, *R.*tall = tall *Rhizophora* stand)

3.4.4.2 Transitional metals (Ni, Zn, Co, Cr, Cu)

The main patterns observed with all transitional metals were that of a decrease in total and exchangeable concentrations from the short *Rhizophora* toward the young *Avicennia* stand in the middle of the Heart of Voh, and generally lower total and exchangeable concentrations in the tall *Rhizophora* compared to the short *Rhizophora* stand (Table 12, Figure 51). With regards to the depth profile, there was high variability in total concentrations of all transitional metals at the surface (above 10 cm) and less variation was observed with increasing depth. The highest mean (±SD) total concentrations were found at the surface in the short *Rhizophora* stand for Ni (269.9 ± 35.1 mg kg^{-1}), Zn (38.7 ± 5.1 mg kg^{-1}), Co (30.6 ± 7.1 mg kg^{-1}), and Cr (201.6 ± 08.1 mg kg^{-1}), whereas the highest total concentrations of Cu was found at the surface of the old *Avicennia* stand (29.7 ± 2.2 mg kg^{-1}).

In general, the exchangeable concentrations of Ni, Zn, Co, and Cu were one order of magnitude lower than their total concentrations, and the exchangeable concentration of Cr was two orders of magnitude lower than its total concentration (Table 12, Figure 51). As with the exchangeable concentrations of Fe, the exchangeable concentrations of Ni, Zn, Co and Cu in the tall *Rhizophora* stand were lower at the 10 and 30 cm depths. In addition, the highest exchangeable concentrations of Ni, Zn, Co, Cr and Cu were measured in the short *Rhizophora* (64.2 ± 6.2, 5.9 ± 1.0, 5.3 ± 1.6, 5.6 ± 0.2 and 3.0 ± 0.3 mg kg^{-1}, respectively), where a general increase in metal concentration was observed with increasing soil depth. Conversely, Ni, Zn, Co and Cr had relatively lower and constant values along the depth profiles of both *Avicennia* stands.
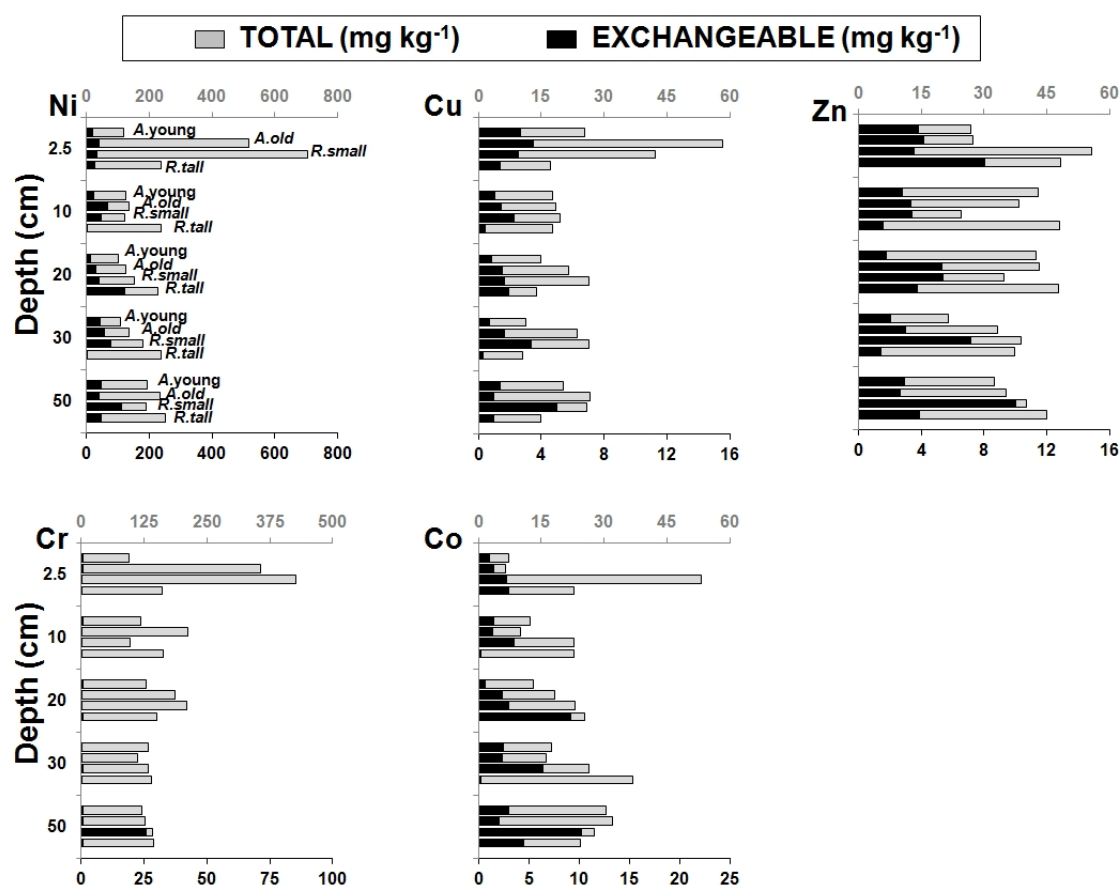
Figure 51. Mean concentrations (mg kg^{-1}) of total (grey scale, grey bars) and exchangeable (black scale, black bars) Ni, Cu, Zn, Cr and Co along the depth profile in each mangrove stand (*A*.young = Young *Avicennia* stand, *A*.old = old *Avicennia* stand, *R*.small = small *Rhizophora* stand, *R*.tall = tall *Rhizophora* stand)

4.4.4.3 Macroelements (N, P, S, K, Mg, Ca) and Na

The total concentrations of all macroelements and Na were highly variable among mangrove stands, whereas the exchangeable concentration of all the macroelements, except for Ca and S, decreased from the young *Avicennia* at the centre of the study site toward the tall *Rhizophora* at the edge of the site (Figure 50). The most striking result for the macroelements was found in the depth profiles of the young *Avicennia* stand, where surface soils had the highest total and exchangeable N, P, K, Na and S values and decreased rapidly with increasing depth (Table 12, Figure 50).

A generally uniform total concentration pattern was observed for N along the depth profile, with the highest mean (± SD) concentrations in the young *Avicennia* (4 511.6 ±

700.8 mg kg^{-1}) and the lower concentration in the tall *Rhizophora* (3 183.1 ± 824.6 mg kg^{-1}). The highest mean C/N ratios in the study site were found in the soils of the tall *Rhizophora* (26), followed by the tall *Avicennia* (23), the short *Rhizophora* (21) and lowest in the soils of the young *Avicennia* (16) (Figure 49). In every mangrove stand, those ratios increased with increasing depth, with the highest ratios of 33 found in the lowest sections of the tall *Rhizophora* soils. The general total P concentrations decreased with increasing depth down to 30 cm with a slight increase thereafter. The highest concentrations of total P were found in the old *Avicennia* (334.8 ± 54.1 mg kg^{-1}), and the lowest concentrations were recorded in the young *Avicennia* stand (233.5 ± 35.6 mg kg^{-1}).

The highest mean (±SD) total concentrations of S were found in the old *Avicennia* (41,801.0 ± 4,050.6 mg kg^{-1}), and were twice as low in the tall *Rhizophora* (21,499.9 ± 5,971.5 mg.kg^{-1}) and young *Avicennia* stands (19,372.9 ± 623.1 mg kg^{-1}). In general, the exchangeable S concentrations accounted for 12% of the total S concentrations. The exchangeable S concentrations were higher in the short *Rhizophora* (5,111.3 ± 650.9 mg kg^{-1}) and lowest in the tall *Rhizophora* (1,688.0 ± 613.8 mg kg^{-1}). As with most elements, the exchangeable S concentration decreased at 10 and 30 cm depth in the tall *Rhizophora* stand. While the exchangeable S concentrations were relatively constant along the depth profile in both *Avicennia*, an increase in S concentration was observed with increasing depth in the short *Rhizophora* stand (Figure 50).

The total concentrations of K and Na were higher in both *Avicennia* stands compared to the *Rhizophora* stands. However, there was a marked increase in total K concentration from the surface down to 20 cm, while total Na concentrations decreased in the same soil layers within both *Avicennia* stands. Conversely, the total K and Na concentrations were relatively constant along the depth profile in both *Rhizophora* stands. In general,

the exchangeable concentration of K accounted for about 16 % of its total concentration. Exchangeable K concentrations decreased from the young *Avicennia* stand (2 214.4 ± 413.7 mg kg^{-1}) to the tall *Rhizophora* (798.0 ± 50.9 mg kg^{-1}), as well as with increasing depth.

The total Ca concentrations were highest in the short *Rhizophora* (7 332.8 ± 425.2 mg kg^{-1}) and decreased rapidly with increasing depth, and the lowest total Ca concentrations were found in the young *Avicennia* stand (5 248.1 ± 656.3 mg kg^{-1}). In general, the exchangeable Ca concentrations accounted for 36% of the total Ca concentrations. The highest exchangeable Ca concentrations were found in the short *Rhizophora* (2 978.1 ± 433.1 mg kg^{-1}), and the lowest values were measured in the tall *Rhizophora* (1 151.1 ± 43.8 mg kg^{-1}), where the same low concentrations were also found at 10 and 30 cm, as previously described. The patterns for total and exchangeable Mg concentration profiles were similar to those of Ca ($r = 0.45$, $**p < 0.01$), except that total Mg concentrations were generally higher in the *Avicennia* stands compared to the *Rhizophora* stands.

4.5 Discussion

4.5.1 Soil properties along a classical semi-arid gradient (old *Avicennia* and short *Rhizophora* stands)

4.5.1.1 Influence of zonation and topography on OM and soil properties

The variations of soil properties observed in the old *Avicennia* and short *Rhizophora* stands are characteristic of other undisturbed semi-arid intertidal gradients previously reported in New Caledonia (Deborde et al. 2015, Leopold et al. 2013, Léopold 2015, Marchand et al. 2011b, 2016). Our results in these two stands have confirmed that the topography exercises a strong control on soil properties and zonation in mangrove

ecosystems. Although this has been a well-known fact, to our knowledge, no numerical model has previously demonstrated the magnitude of this influence along a semi-arid mangrove gradient. In addition, our seasonal measurements have shown that the variations in salinity and Eh along the elevation profile is twice as high during the dry season, and that the spatial gradient of pH and temperature is reversed compared to the wet season. Thus, these results emphasise the importance of elevation as a driver of spatial and seasonal variations of soil properties in contrasted climates. Accordingly, *Avicennia* persists in a hypersaline soil environment at the highest elevation of the study site where tidal inundation is rare and evapotranspiration important. The observed accumulation of Na^+ in the solid phase at the surface soils of the old *Avicennia* stand may have precipitated due to higher evaporation and/or plant transpiration at these higher elevations. These salts may have the potential to be remobilized by dilution in the pore water after tidal flushing or freshwater input and then transported downward by percolation and density-driven convection process, as suggested by Marchand et al. (2004, 2006) and Noël et al. (2017). The sharp increase in total Na and pore-water salinity observed at the rhizosphere level (10–20 cm depth) may also be partly due to the high capacity of *Avicennia marina* to exclude Na^+ at the root level (Popp et al. 1993, Saenger 2002, Reef and Lovelock 2015). This mangrove species is clearly well adapted to these extreme salinity conditions and can mitigate water losses successfully to ensure survival (Saenger 2002, Reef and Lovelock 2015).

Conversely, *Rhizophora* can dominate areas where there is low precipitation and high vapour pressure deficits only due to the frequent tidal inundation that maintains a constantly lower pore-water salinity and total Na^+ concentration within the depth profile. Due to the shorter immersion time in the old *Avicennia* stand, these soils also experience higher Eh over the year compared to the short *Rhizophora* stand, a

phenomenon likely enhanced by the oxygen diffusion of the cable root system of *Avicennia* (Scholander et al. 1955, Curran et al. 1986, Allaway et al. 2001). During the dry season, high evapotranspiration and emersion time in the *Avicennia* stand have been shown to also induce a change in Eh from anoxic to suboxic along the depth profile, as well as an acidification of the substrate (Leopold et al. 2016) as observed here in the old *Avicennia*. Such acidification of soils and sediments under oxic or suboxic conditions in mangroves has been observed by several authors, who related this to an enhanced OM oxidation, nitrification and solid sulphides oxidation (Lin and Melville 1993, Middelburg et al. 1996, Marchand et al. 2004, Nóbrega et al. 2013). Within the soils of the short *Rhizophora* stand, the longer immersion time maintains higher pH, lower Eh and smaller variations of these properties throughout the year, with all these parameters decreasing along the depth profile.

The surface soils of the short *Rhizophora* stand showed higher C/N ratios (23 ratio) and lower chl-a concentrations than in the old *Avicennia* stand over the year, which most probably indicates mangrove litterfall and root detritus as a primary source of OM in the *Rhizophora* stand. Conversely, the high concentrations of chl-a and low C/N values (15 ratio) found in the upper 20 cm of the old *Avicennia* stand indicate an OM enrichment which results from decomposition of algal mats (8 ratio) and *Avicennia* litterfall (23 ratio) (Meyers 1994, Marchand et al. 2005). Leopold et al. (2013) suggested that this development of microphytobenthos under the sparse canopy of *Avicennia* is likely due to better conditions of solar radiation compared to the dense canopy of *Rhizophora*, but also to specific soil water contents being too high beneath *Rhizophora* due to frequent flooding. However, low C/N values may also indicate an active OM mineralization process within the soils (Meyers 1994, Lallier-Vergès 1998, Marchand et al. 2011b).

Down the depth profile of the old *Avicennia* stand, the horizons remained enriched in TOC, with C/N ratios of 22 and more similar to those derived from the OM decomposition of higher plant debris. These results may also indicate a buried accumulation of OM from a previous population on which this stand now grows, as observed in several other mangrove forests of the west coast of New Caledonia (Marchand et al. 2011b, 2012, Deborde et al. 2015). The presence of this buried layer is less clear beneath the short *Rhizophora.* This is possibly due to the fact that the *Rhizophora* root system extends deeper than that of *Avicennia* trees and deeper than our 50 cm depth core in New Caledonia. However, it is also possible that this former forest was less productive or that part of the primary productivity was exported by the tides, including the buried OM through porewater seepage, as previously reported by Maher et al. (2013).

4.5.1.2 Redox-sensitive elements

It is well known that soil properties influence the total and exchangeable elemental concentrations of redox sensitive compounds and the elements susceptible to react with them (e.g. Harbison 1986, Clark 1998). Accordingly, surface soils at the study site were characterized by an increase in total S and total metal concentrations (Fe, Mn, Ni, Zn, Cr, Co), and a decrease of exchangeable S from the old *Avicennia* stand to the short *Rhizophora* stand. In anaerobic soils of the short *Rhizophora* stand, the main pathway of OM mineralization is dominated by sulphate reduction processes (Marchand et al. 2011b). As a result, most of the Fe in these anoxic soils would have been trapped in the solid phase, and accumulated as pyrite or greygite (Marchand et al. 2011b, Noël et al. 2014). High total concentrations in other trace metals (Mn, Ni, Zn, Cr, Co) were also observed, likely as a result of their co-precipitation with pyrite, and from their high

affinity for the numerous anionic sites at the surface of mineral and organic particles (Marchand et al. 2011b, 2012, 2016, Noël et al. 2014, 2017).

However, this increase in total metals and S concentrations was not observed in the deepest anoxic sections of the short *Rhizophora* stand. Instead, their exchangeable concentrations increased downward in the depth profile, which contrasts with previous observations in mangroves of New Caledonia (e.g. Deborde et al. 2015, Marchand et al. 2011b). We suggest that possible lateral groundwater exchange through permeable soils (either sandier or enriched in organic fibres, such as a buried root system of a former mangrove forest) may have induced a renewal of electron acceptors at these lowest elevations. This would have limited the anoxic conditions and would have resulted in this enrichment of exchangeable metals and S, which for the most part exceeded by one fold the concentrations measured in other areas at the study site.

Within the suboxic surface soils of the old *Avicennia* stand, aerobic respiration is likely the main pathway of the OM decomposition and S is thus present as SO_4^{2-} and Fe as exchangeable Fe^{3+} or bound with oxides (Marchand et al. 2011b, Noël et al. 2014, 2017). Under suboxic conditions, dissolved Fe^{3+} is more susceptible to be exported by the tides, which might explain the loss of Fe (Nóbrega et al. 2013) and other metals usually bound with pyrite or Fe-oxides (Clark et al. 1998) in the surface soils of this old *Avicennia* stand. Underneath the surface (10–20 cm depth) of the old *Avicennia* stand, suboxic and anoxic conditions change throughout the year (Leopold et al. 2016) and probably with the daily tides. As a result, the total and exchangeable concentrations of Fe, S and other trace metals were more variable within the depth profile of this stand. With fluctuations of Eh, Fe and S can accumulate as precipitated Fe-S compounds in anoxic conditions and re-oxidize as ferric oxyhydroxides and SO_4^{2-} or as poorly ordered Fe in suboxic conditions

(Noël et al. 2017). The later form is more susceptible to being re-dissolved and exported (Noël et al. 2014), which could explain the fluctuations of total Fe concentrations and associated trace metals (Ni, Co, Cr) observed within the depth profile of this old *Avicennia* stand.

4.5.1.3 Macroelements

At the study site, the total concentration of macroelements (P, N, Mg, K) and exchangeable concentration of Ca^{2+}, Mg^{2+} and K^+ decreased from inland to seaward sites. In addition, P concentrations decreased with increasing depth in every stand. P cycling in mangrove soils is tightly linked to that of Fe, iron hydroxides and oxyhydroxides, that acting as a trap for inorganic P. Their dissolution in suboxic conditions results in a release of dissolved inorganic P in porewater, which is subsequently subjected to an uptake by the root systems or to a tidal export to adjacent habitats for the small *Rhizophora* stand that is the more frequently inundated (Holmer et al. 1994, Deborde et al. 2015). These processes may explain the decrease in total P with increasing depth or towards the seaside of the mangrove. The total N content did not vary at the surface of the soils between the *Avicennia* and *Rhizophora* stands. However, total N concentrations decreased faster at lower depths in the *Rhizophora* stand. This may possibly be the result of i) more intense denitrification processes due to more anoxic conditions beneath this stand, ii) a higher uptake of NH_4^+ by the root system of *Rhizophora* trees at depth, and iii) due to tidal exports, as suggested for dissolved inorganic phosphorus.

We also suggest that the decrease in N, Ca, Mg and K seaward of the mangroves resulted from an increased tidal export or from an increased uptake by the *Rhizophora* root system. Higher concentrations of ions (Ca^{2+}, Mg^{2+} and K^+) inland have also been

observed in other semi-arid mangrove stands landward (Naidoo 2006). These ions are the most abundant ions found with SO_4^{-2} in seawater (Millero 1996), and thus may have been imported with the tide and accumulated at higher elevations as a result of low tidal immersion and high evapotranspiration in these areas.

4.5.2 Soil properties in a younger *Avicennia* stand

4.5.2.1 Impact of Avicennia colonisation

The soils at the highest elevations of the topographic profile have undergone three changes of vegetation cover since 1943 (Figure 46). The last change observed on the aerial photographs showed that these higher elevations were previously dominated by salt flats (Figure 46) and were colonized ~20 years ago by *Avicennia marina*. Several hypotheses could explain these changes in vegetation covers over time. A recent study (Aucan et al. 2017) showed that the sea level in New Caledonia rose by 0.86 mm.y^{-1} between 1957 and 2016. This sea level rise may have increased the tidal range and decreased the salinity in the centre of the Heart of Voh, thus promoting conditions more favourable for the establishment of *Avicennia*. The change in vegetation cover observed over time could also be the result of inter-annual climatic events like El Ninõ or the result of a change in elevation due to an alternation of accretion (mediated by mangrove roots) and erosion (mediated by tidal cycles) of the substrate. Thus, once past an elevation threshold above which salinity becomes incompatible with tree growth and surviving, the vegetation progressively disappears, and natural erosion by tide progressively decreases the elevation until a non-critical salinity is reached for plants to colonize it again.

This stand is 10 cm higher than the old *Avicennia* stand, which follows down the height profile. Although the young *Avicennia* stand canopy reaches heights similar to those in the old *Avicennia* stand (Table 10), Leopold et al. (2016) reported that 70% of individuals were smaller than 60 cm. This suggests that this stand may still be in the early phase in the succession process. Indeed, TOC values in the intermediate horizons (10–20 cm) corresponding to the rhizosphere were quite low, indicating that a significant decomposition of the root system has not occurred yet in these soils, and that arid salt flat characteristics (i.e. dense and poor in TOC and WC) remain (Leopold et al. 2013, Deborde et al. 2015). Additionally, the high TOC and low BD measured in the deepest anoxic horizons at this stand may also indicate a buried accumulation of OM from a previous population on which this stand now grows. The colonisation by *Avicennia* changed significantly the soil properties. Indeed, the soil characteristics and elemental status at the surface of this newly established mangrove stand differed considerably from those observed in the other stands of the study site and from other high elevated stands (i.e. *Avicennia* stands and salt flats) studied in New Caledonia. These parameters included a lower BD and lower total concentrations of trace metals, and higher concentrations of TOC, WC, chl-a and total and extractable macroelements than in the previous studies (Leopold et al. 2013, Deborde et al. 2015). We hypothesize that the high number of saplings established once the salinity level decreased due to sea-level rise lead to a significant accumulation of OM at the surface of these soils. *Avicennia* is a fast growing species that can produce a high number of propagules (2 000 000 propagules ha^{-1} y^{-1}, Hogarth 2007). Lacerda et al. (1995) demonstrated that the nature of this OM can sustain a higher rate of microbial activity in *Avicennia* stands, and is mineralised faster than *Rhizophora*'s. This would result in an increase in nutrient cycling in this younger *Avicennia* stand, particularly under suboxic conditions (Twilley and

Rivera-Monroy 2009, Nóbrega et al. 2013). Additionally, dense bacterial community and the important network of thin nutritive roots produced by saplings are known to promote water holding capacity in soils (Tisdall and Oades 1982, Chenu 1993, Saxton and Rawls 2006). This would explain the unusual high WC observed in this younger stand during both seasons, despite the higher evapotranspiration that occurs at these highest elevations.

4.5.2.2 Elemental status in a younger Avicennia stand

The increase in WC and OM driven by the colonisation in salt flat soils induced different elemental distribution compared to the surface soils of the old *Avicennia* stand. Elevated total concentrations of macroelements N, P and K likely resulted from i) the mineralisation of the mangrove derived organic debris and of the biofilm, and from ii) the low tidal export due to the highest position in the intertidal zone. Furthermore, the exchangeable concentrations of the macroelements Ca, Mg and K were the highest measured in the study site. We suggest that the important amount of water in these relatively well-oxygenated surface soils increased the solubility of these elements, whereas the shorter duration of tidal immersion compared to the old *Avicennia* stand would limit their export, thus increasing their availability for plants uptake.

Conversely, the total and exchangeable concentrations of most metals (Fe, Cu, Ni, Mn) were lower within the depth profile of this young *Avicennia* stand than in the old *Avicennia* and short *Rhizophora* stands. This was particularly striking for the total concentrations of Fe, which were twice lower than in the surface soils of the old *Avicennia* stand. We do not know the soil composition of the salt flat before being colonized by the *Avicennia* trees. However, it is possible that this colonization induced a dissolution of some bearing phases of these metals due to increased organic and water

content, and led to their tidal export that was not compensated by inputs from the litter fall decomposition like for the macroelements. Some of them are also micronutrients, which may have been requisitioned by the young *Avicennia* trees and saplings in development (e.g. for Fe in Alongi 2010).

4.5.3 Impact of longer immersion on *Rhizophora's* soils properties

When moving closer to the channel, the height of the *Rhizophora* trees increased again and the elevation profile increased steadily from 31 cm to 46 cm. Krauss et al. (2003) have detected such increase of elevation of the soils in mature mangrove forests of Micronesia over time (1.3 mm year^{-1}). The authors attributed this to a vertical accretion process facilitated by mangrove aerial roots and reported that the sedimentation is more effective with prop roots than pneumatophores and bare soil. Additionally, increase of elevation has also been reported in mangrove stands following root accumulation (McKee et al. 2007). We hypothesise that similar processes occur close to the channel in the mature *Rhizophora* stand. Thus, the well-developed network of prop roots reduces the velocity of the flowing tides and induces a sedimentation process in this stand and an increase of elevation over time. We suggest that in New Caledonia, this process is enhanced during the rainy season in summer, when materials are drained from the watershed by rainfalls.

However, when compared to the small *Rhizophora* stand, these soils were particularly dense and poor in water, TOC and total N. A depletion of extractable macro (Ca^{2+}, Mg^{2+}, K^+, SO_4^{2-}) and microelements (Mn^{2+}, Ni^{2+}, Cu^{2+}, Zn^{2+}, Co^{2+}) was also observed at 10 and 30 cm depths. These decreases of extractable elements in these horizons do not seem to be linked with a particular change of Eh, pH, TOC or WC, nor with the total

concentrations of these elements. This could suggest that one or several disturbance events took place in these soils in alternation with the sedimentation process described above, such as cyclones or heavy rainfall events for instance, New Caledonia being frequently subject to cyclonic events. During a cyclone, in addition to strong wind and heavy rainfall, the low pressure induces an increase in sea-level, whose consequences may be more important for the stands close to the sea that are already frequently submerged. Such events could have induced erosion or sedimentation but also may have influenced diagenetic processes within the soils (Krauss et al. 2003, Spenceley 1977). These events may have induced the winnowing of light particles and of OM. Additionally, high flow rates of water at the surface of the soils at that time could have modified the redox potential and pH of these soils (Eggleton and Thomas 2004). This could have increased the mobility of these elements and their export under their dissolved, exchangeable and/or poorly crystallized forms. In the contrary, the elements precipitated within the solid phase of these anaerobic soils would not have been flushed away, explaining the high BD observed along the depth profile.

4.6 Conclusion

Increased tidal frame due to sea level rise and/or the increase of extreme climate events are likely to induce important changes in mangrove soils and their capacity to store macro, microelements and other trace metals.

In semi-arid mangroves, our results have emphasised the influence of small variations of topography on soil properties and elemental cycling in contrasted climates. The present study shows that changes in elevation as low as 5 cm along the intertidal profile can lead to drastic change in reduction-oxidation potential, which affects in turn significantly the cycling of the OM and subsequently the pH and fate of trace metals such

as Fe, Cu, Ni and Mn within the soils. Additionally, and although the exact causes of the recent re-colonization of the Heart of Voh are not fully understood, the present study also shows the drastic changes semi-arid littoral could undergo with small changes in elevation under a change of tidal frame. Our observations showed that this rising tidal regime results in decreased salinity with mangrove expansion landward, and increased sedimentation, bulk density, elevation and elemental mobility seaward. Our results in a newly established *Avicennia* stand landward corroborates the pioneer properties of a fast growing species such as *Avicennia*. The results also indicate that a longer length of immersion in stands previously dominated by salt flats has a significant impact on the fate of trace metal accumulated in these stands, particularly on Fe. Longer immersions and increased acidity appear to increase the mobility of elements and their vertical migration downward in the depth profile as well as a horizontal migration toward other stands and coastal water.

These results contribute to the understanding that under sea level rise and increased extreme climatic events, semi-arid mangroves could be a conveyor of trace metals, macroelements and potentially other pollutants toward adjacent marine ecosystems. While this research focused essentially on the soil compartment, the uptake and translocation of these elements in mangrove tissues and the role of standing vegetation as a sink for these elements should be investigated. Further studies on elemental exports should also be conducted in order to predict the impact of sea level rise and perturbations on the cycling of these elements along semi-arid tropical coastlines.

Chapter 5

Trace Metal Dynamics in Soils and Plants along Intertidal Gradients in Semi-arid Mangroves (New Caledonia)

5.1 Abstract
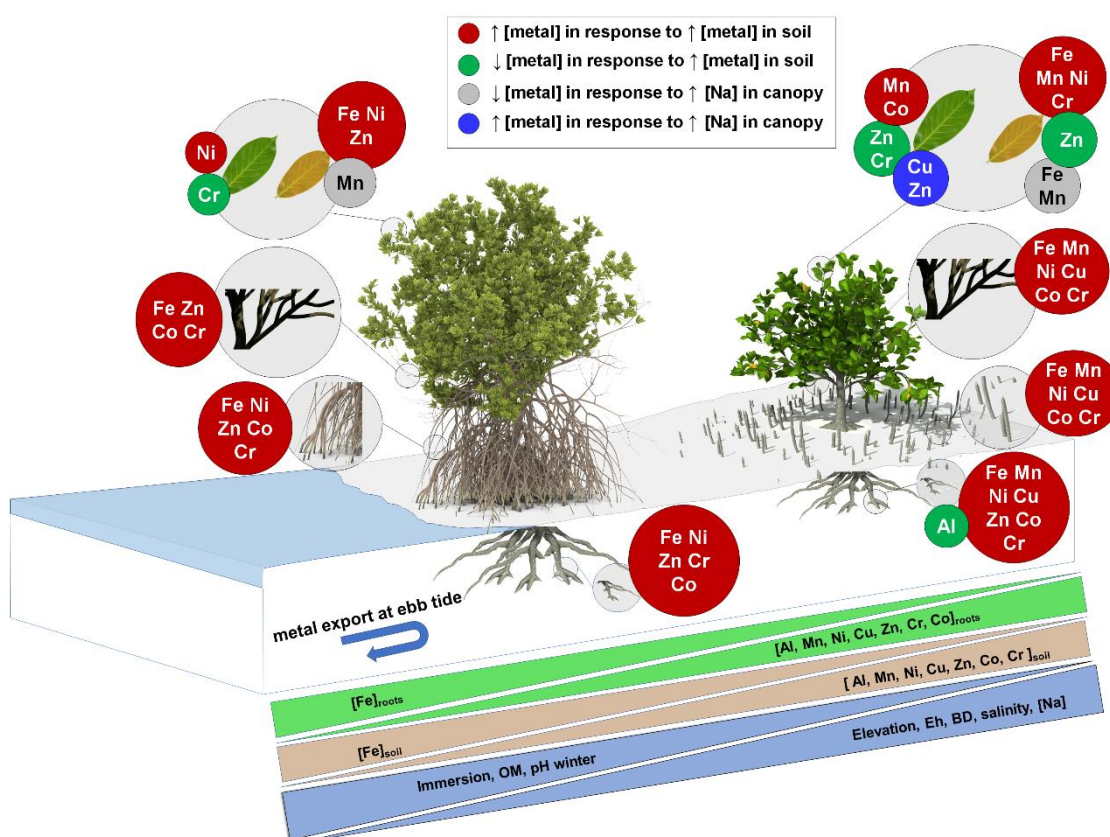
Figure 52. Graphical abstract of trace metal soil-plant transfers and spatial variation in soils along semi-arid mangrove intertidal gradient (New Caledonia)

Trace metal dynamics were investigated in mangroves developing in semi-arid New Caledonia, where *Avicennia* and *Rhizophora* stands grow in the upper and lower intertidal zone, respectively. We collected soil samples and mangrove tissues in an undisturbed site, a mining-influenced site and in a mining and aquaculture-influenced

site. Differences in duration of immersion and organic matter (OM) cycling resulted in a sharp decrease of metal concentrations in soils and plants from landside to seaside. Both species were tolerant to metals mainly via exclusion, (i.e. metal bioaccumulation restricted to roots and leaf litter). Strong correlations ($p < 0.05$) were found between Na and Fe, Mn, Cu and Zn in green and senesced leaves of *Avicennia marina*, indicating a possible role of those metals in mechanisms to cope with hypersaline conditions.

 Increasing metal pollution, aridity and sea-level rise are likely to result in a decrease in mangrove efficiency in filtering trace metals seaward.

5.2 Introduction

Mangroves are intertidal vegetated ecosystems that develop along the coastlines of tropical and subtropical shallow areas (Duke et al. 1998, FAO 2007). Over these last decades, numerous studies have reported that these ecosystems have the ability to effectively retain trace metals in their soils, thereby reducing their transport to adjacent marine habitats (see reviews Bayen 2012, Lee et al. 2014). Once on the forest floor, the fate of these trace metals varied significantly along the intertidal gradient, often characterised by an elevation gradient that controls immersion rates and hydrodynamics which influenced soil oxygenation, pH and temperature (Baltzer 1982, Duke et al. 1998, Otero et al. 2006, Chapter 4). For instance, in anoxic conditions that usually prevail in waterlogged locations and at depth, sulfate-reduction mediated by prokaryotes is the main pathway of organic matter (OM) decomposition (Kristensen et al. 2008). It leads to the precipitation of H_2S with dissolved iron in Fe-S compounds that accumulate in the solid phase of the soils (Ferreira et al. 2007a, Otero et al. 2009, Marchand et al. 2011b, Noël et al. 2014). Conversely, aerobic and Fe and Mn oxidations of the OM may dominate in oxic and suboxic conditions and result in an increase of

dissolved trace metals in soil pore-water (Reef et al. 2010, Thành-Nho et al. 2019a). In both anoxic and (sub)oxic conditions, several studies have reported the adsorption and re-precipitation of those dissolved metals at the surface of OM particles, carbonates, and Fe- and Mn-bearing minerals within those solid phases (Otero et al. 2009, Marchand et al. 2012, 2016, Deborde et al. 2015, Noël et al. 2017).

On the other hand, dissolved metals are available for export toward the water column or for plant uptake. Several metals, including Cu, Zn, Fe, Ni, Mn and Co are essential micronutrients, required by plants in small quantities to fulfil numerous metabolic functions (Raven et al. 2005, Seregin and Kozhevnikova 2006). However, dissolved trace metals are often found in concentrations that are toxic to mangroves due to their high reactivity with OM (Harbison 1986, Marchand et al. 2012, 2016). Although mangroves do not hyperaccumulate heavy metals in their biomass, each species has developed different mechanisms to tolerate metal stress (Sruthi et al. 2017, Yan et al. 2017). Some of those mechanisms are associated with coping with salinity stress, such as the secretion of metals through salt glands of some mangrove species (MacFarlane and Burchett 2000, 2002, Naidoo et al. 2014). These adaptations may result in substantial differences in accumulation of trace metals in dead and live mangrove biomass over time, depending on the species considered, the properties of the substrate and their ability to cope with salinity (Lacerda et al. 1995, Alongi et al. 2003, Mejias et al. 2013, Analuddin et al. 2017, Chapter 3).

Given global climate change effects on numerous processes in the soil and bioaccumulation of trace metals in mangrove ecosystems, a better understanding of metal accumulation in mangrove ecosystems is needed. Specifically, pollution, drought and sea-level rise may influence OM and metal cycles and rise serious concerns regarding the fate of metal stocks in mangroves. In this study, we address this issue and

aim to assess the capacity of mangroves to accumulate metals along the soil-plant continuum over a wide range of OM content, oxidation-reduction potential (Eh), frequency of inundation, salinity and trace metal supplies in New Caledonia. This location features a contrasted semi-arid climate that generates a clear zonation of oxygenation and salinity along the intertidal gradient (Chapter 4). As a result, these mangroves are dominated by two species that have well-contrasted strategies to cope with salinity: *Avicennia marina* subsp. *Australasica* (Walp.) J. Everett dominates in hypersaline soils landward whereas *Rhizophora stylosa* Griff. Stands develops seaward and are exposed to longer duration of immersion. In addition, mangroves of New Caledonia often develop downstream ultramafic watersheds whose lateritic soils are currently exploited for their large Ni ores and whose effluents are often enriched in Fe, Ni, Mn, Co and Cr (Becquer et al. 2003, Noël et al. 2017).

In this context, the first specific objective of this study was to investigate the range of metal soil concentrations (Fe, Ni, Mn, Al, Cu, Zn, Co, Cr) in these two species stands and in different physiographic conditions: undisturbed by direct anthropogenic influence, and influenced by different anthropogenic pressures (aquaculture and mining). The second objective was to analyse and compare the capacity of each species to accumulate and translocate metals to their aboveground components as a function of the soil conditions and their ability to cope with salinity.

5.3 Material and Methods

5.3.1 Sites of study

Data and sample collections were conducted on the West Coast of New Caledonia at the end of the growing season (wet season), in March and April 2016, at three study sites

(Figure 53). The first study site was a site undisturbed by direct anthropogenic activities (here after named "natural"), a second site was influenced by mining outcrop (here after named "mining site"), and a third site was under the influence of both mining and aquaculture activities ("aquaculture site"). The "natural" site was the "Heart of Voh" (20° 56.0' S, 164° 39.2' E), a mangrove stand of 5.1 ha within a 1 370 ha mangrove area upstream of Chasseloup Bay. This bay is under the influence of watersheds dominated by laterite and serpentinite formations upstream, by some areas of dolerites and basalts, as well as alluvial and littoral fields downstream (Georep 2019). A more complete description of this site, its physico-chemical properties and the trace metal status along the soil profile can be found in Chapter 4. The mining site is located downstream the lateritized ultramafic massif of Koniambo, in the Vavouto Bay (20°59'57S, 164°42'19E). The Koniambo massif is currently exploited for its nickel deposits that outcrop at the land surface by the Koniambo Nickel SAS company (Georep 2019). The western side of the Koniambo is drained by two rivers richly loaded with Fe, Ni, Mn, Zn and Al (Falconbridge SAS 2001, Noël et al. 2014), one of which flows directly into the northern side of the study site (Figure 53). The aquaculture site is situated in ~ 24 ha mangrove area located in the St Vincent Bay (21° 56' S, 166° 4' E). The mangrove stands border the "Ferme Aquacole de la Ouenghi" (F.A.O.), a shrimp farm growing the blue shrimp *Penaeus stylirostris* Stimpson, 1871. This farm was built on the salt-flats at the edge of the mangroves, following local regulations that prevent construction of aquaculture farms within the mangroves.
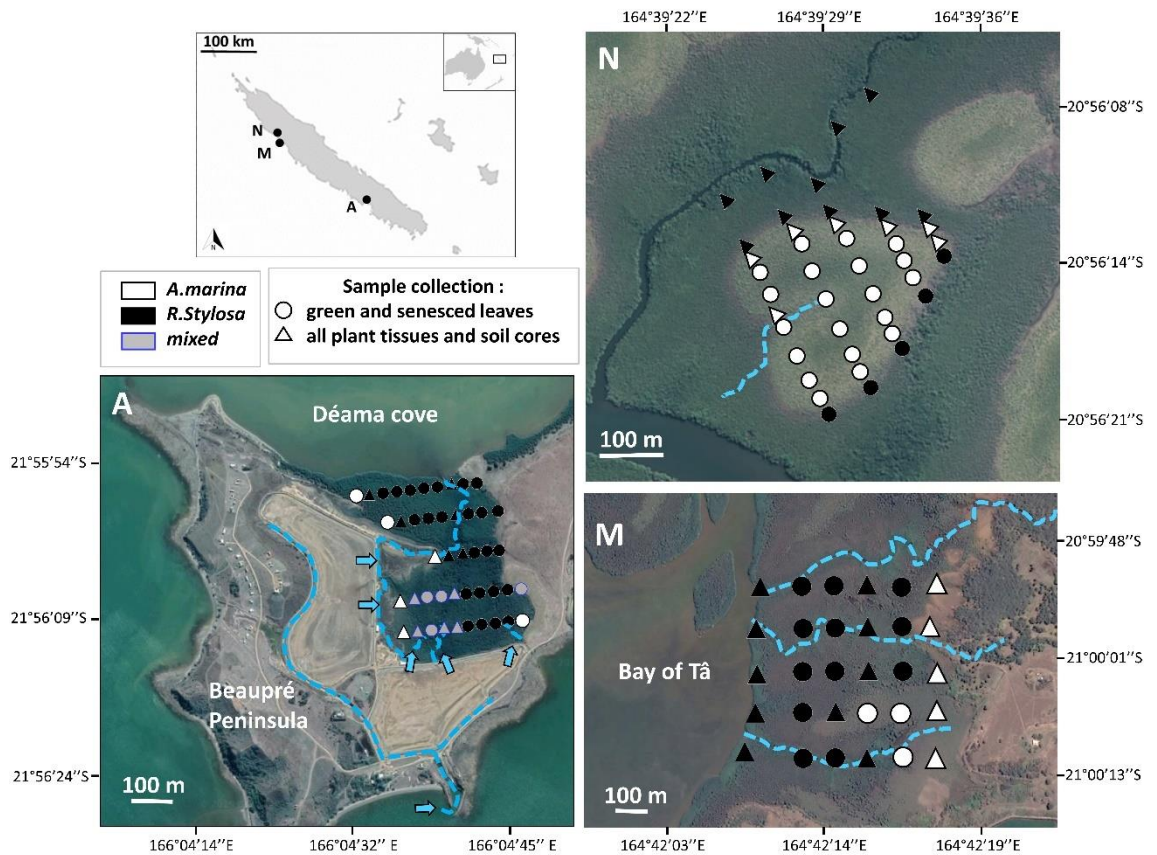
Figure 53. Location of New Caledonia in Australasia and location of each plot and sampling layout in each study site (N = Natural, M = Mining influenced, A = Aquaculture influenced. Satellite data from Digital Globe, 2018). Blue dotted lines indicate permanent creeks in the natural and mining-influenced sites and effluents in the aquaculture-influenced site. Blue arrows indicate pond effluent outlets in the aquaculture-influenced site. Soil cores and root, aerial root and wood tissues of both species have been sampled in a total of 51 locations (17 in the N site, 19 in the A site and 15 in the M site). Green and senesced leaves have been sampled in 121 locations (37 in the N site, 54 in the A site and 30 in the M site)

From December to July, the farm operates two 1-m deep semi-intensive rearing ponds of 10.5 and 7.5 ha, respectively, whose water is partially renewed daily. The water is pumped from the south of the peninsula through intake canals of the ponds, whereas waste water is discharged in the mangroves through the outlets (Figure 53). Over the rearing period, approximately 100 kg ha^{-1} of particulate and dissolved organic matter is discharged in this mangrove site (Molnar et al. 2014). The southern peninsula is under the influence of the Ouenghi Delta. Upstream, the Ouenghi drains laterites and peridotites massifs, including the entire active mining outcrop of Thio Camp des Sapins.

In the coastal piedmont, the Ouenghi river drains formations of volcanic rocks, siliceous arenites and globigerina limestones (Georep 2019). Organic matter, Fe and Mn speciation in the soils and effluents of this mangrove area have been detailed by Molnar et al. (2013, 2014), Deborde et al. (2015) and Aschenbroich et al. (2015).

The vegetation in mangrove ecosystems in New Caledonia feature a zonation of mangrove species, driven by a gradient of salinity, which is in turn controlled by the frequency of inundation and thus by an elevation gradient (Chapter 4). Bare soils and salt marshes occur at the highest elevation landward, followed by a band of shrubby *A. marina* (1.69 ± 0.83 m high), and then by small (2.93 ± 0.82 m high) and then tall (6.46 ± 2.17 m high) *R. stylosa* trees next to the channel banks and coastline.

5.3.2 Sampling Layout

At each study site, soil and plant samples were collected in circular plots of 7-m radius established along transects perpendicular to the main water body, following the sampling layout of Kauffman and Donato (2012, Figure 53). In each site, the sampling layout was designed to cover mangrove habitats along the intertidal gradient between the salt marshes to the main channel or the sea. A minimum of 30 plots were set up in each of the three sites (Figure 53).

5.3.3 Soil collection

In a total of 51 plots, 50-cm core samples were collected in duplicate at low tide with a 8 cm inner diameter stainless steel corer. At each study site, a minimum of five duplicates were collected in the *A. marina* stands on the border of the salt marshes

(seven in the natural site, eight in the aquaculture site and five in the mining site), a minimum of five duplicates were collected in the small *R. stylosa* stands (five in the natural site, six in the aquaculture site and five in the mining site) and five duplicates were collected in the tall *R. stylosa* stands located on the channel borders (Figure 53). The total sampling depth of 50 cm was chosen to include most *A. marina* and *R. stylosa* live roots. The soil in each core was divided into ten sections (0–2.5, 2.5–5, 5–7.5, 7.5–10, 10–15, 15–20, 20–25, 25–30, 30–40 and 40–50 cm) while in the field. For logistic reasons, only five of the ten fractions were analysed (0–2.5, 7.5–10, 15–20, 25–30, and 40–50 cm). Those particular fractions were selected based on the main transitional depths in chemical and elemental mangrove soil properties observed in New Caledonia. Mangrove soil profiles in the region are typically characterised by an oxic surface horizons loaded with fresh OM, followed by subsurface horizons under the influence of the root system and characterised by a gradient in oxidation-reduction potential, and an anoxic horizons enriched in buried OM at depth (40–50 cm), typically inherited from previous *Rhizophora* sp. stands (e.g. Marchand et al. 2011, Molnar et al. 2014, Leopold et al. 2016).

5.3.4 Soil physico-chemical parameters

The Eh, pH and temperature (T) of the pore water of each soil section were measured immediately after core collections, using a portable pH/mV/T meter (Multi 350i, Wissenschaftlich-Technische Werkstätten, WTW, Weilheim, Germany) with a Pt-Ag/AgCl electrode (SenTix ORP, WTW) and a pH electrode with temperature sensor (SenTix 81, WTW) directly inserted into the soil. The Eh values were reported relative to a standard hydrogen electrode by adding the temperature-adjusted tension values of

the Ag electrode (ranging from +210 mV for 20 °C to +200 mV for 35 °C) (SenTix, WTW). Each core section was then transferred separately in a cooler to the laboratory, where they were kept in the dark at − 80 °C until elemental analyses. In addition, a known volume of soil was collected in each soil section while in the field using a graduated syringe (50 ml) with the tip cut off. Those samples were also transported individually to the laboratory for direct measurement of salinity, water content (WC) and bulk density (BD). Pore-water salinity was measured with a hand held refractometer (Atago MASTER -S/Millα, Tokyo, Japan) after extraction with a pressurised syringe connected to a soil moisture sampler (Rhizon SMS, Rhizosphere research products, Wageningen, The Netherlands). The small cores were then freeze-dried with a FreeZone 2.5 Liter Benchtop (Labconco, Kansas City, USA) at − 80 °C for three days until constant weight was achieved. Dry weights of the samples were recorded and used to calculate the sample bulk density (BD) and pore-water content (WC). The full details of each equipment and measurements are presented in Chapters 3 and 4

5.3.5 Plant tissue collection

In each plot, green and senesced leaves were hand-picked directly from a minimum of ten mature trees standing within the circular plot (Figure 53). Senesced leaves most likely to be in the next litterfall pool were identified as yellow leaves easily detachable by a slight pull (Lovelock et al. 2007b, e Silva et al. 2007). As leaf chemical composition and structural characteristics are likely to vary along the vertical gradient of the canopy, an equal number of leaves were hand-picked from the bottom, middle and top layers of the canopy of each tree. The leaves of each tree layers were transferred separately in sterile paper bags to the laboratory. The leaves of each tree were then pooled together,

and two sets of leaves (from five trees each) were pooled together by plots for further elemental analyses as duplicate. In addition, coarse roots (≥ 2mm diameter), aerial roots (pneumatophores of *A. marina* and stilt roots of *R. stylosa*) and branches from the previously sampled trees were collected in the same plots as those where the soil cores were sampled (Figure 53). The coarse roots and pneumatophores of *A. marina* were thoroughly hand-washed and rinsed with demineralised water (Marchand et al. 2016). All plant material samples were dried at 55 °C until they reached constant weight.

5.3.6 Plant and soil elemental analyses

Total chemical extractions and analyses of organic carbon (TOC), essential microelements (Fe, Mn, Ni, Cu, Zn, Co), other trace metals (Al, Cr) and sodium (Na) were performed in duplicates on each of the five sections of each soil core and on each plant material type. All elemental analyses were conducted at the Institute of Research for Development (IRD) of Nouméa, New Caledonia (IMAGO, Certificate ISO 9001: 2015). Reference samples of the International Soil-Analytical Exchange program (ISE, Wageningen Evaluating Programmes for Analytical Laboratories) were used to validate the accuracy of the method (van Dijk and Houba 1999, Dijk 2002). Details of sample preparation, chemical extractions, elemental analyses and validation of the method are fully described in Chapters 3 and 4. Briefly, total trace metals and Na concentrations were determined by inductively coupled plasma emission spectroscopy (ICP-OES, Varian, Australia). Those elements were extracted in a 10% (soil samples) and 1% (plant samples) w/v solution of ammonium fluoride (FNH_4) and nitric acid (70%), left over night, and then mineralised during 6 hours in a dry bath at 100 °C (IsoTemp, Fisher Scientific, New Hampshire, USA). TOC was determined by the 900 °C combustion catalytic

oxidation method using a solid sample module (SSM-5000A) combined with a total organic carbon (TOC) analyzer (Shimadzu, Kyoto, Japan).

5.3.7 Metal bioconcentration and translocation in plant material

For each plant component (coarse roots, aerial roots, wood, green and senesced leaves), the bioconcentration factor (BCF) of each metal was calculated by dividing the concentration of this metal within each of the plant components by its mean total concentration in the soil. For each of the aboveground plant components (aerial roots, wood, green and senesced leaves), the translocation factor (TF) of each metal was calculated by dividing its concentration within each of those aboveground components by its concentration in the coarse roots (Baker and Brooks 1989, Ali et al. 2013, Marchand et al. 2016).

5.3.8 Data analyses

In each of the soil-plant continuum compartments, the elemental and physico-chemical variables were transformed by the Box-Cox power transformation (Osborne 2010). In each of the soil-plant continuum compartments, the means of each variable in the six different stands (3 sites x 2 species) were compared and tested by the means of unbalanced two-way ANOVAs followed by Tukey's tests. When the assumptions of the ANOVA (normality and homoscedasticity) were violated, an aligned ranks transformation ANOVA was substituted to the two-way ANOVA (Mangiafico 2016). In each compartment, the relationships between the variables were analysed by Pearson's correlation analyses for normally distributed variables, and by Spearman rank correlation method when the assumptions of normality has not been met. Soil

parameters (14 variables for 51 locations) were also analysed by principal component analyses (PCA). All analyses were performed with R software (3.5.3).

5.4 Results

5.4.1 Geochemical conditions and elemental availability along a semi-arid intertidal gradient

The results of the ANOVA and PCA showed important variations of all trace metal soil concentrations between the study sites (Figure 54a,b, Figure 55, Figure 56. All data are detailed in Appendix 9 to Appendix 11). Specifically, the maximum total concentrations of Fe (118.20 g kg^{-1}), Ni (4.00 g kg^{-1}), Cr (1.74 g kg^{-1}), Mn (1.03 g kg^{-1}), Co (216.75 mg kg^{-1}) and Zn (86.76 mg kg^{-1}) at the mining site were generally twice as high as at the aquaculture site, and up to two fold higher than at the natural site (Figure 55 and Figure 56). At the natural site, lower concentrations of Mn, Fe, Zn, Ni, Co, and Cr were measured in the *A. marina* stands landside than in the *R. stylosa* stands seaside (Figure 55 and Figure 56), whereas the opposite pattern was observed at the other study sites (Figure 54b, Figure 55, Figure 56). The natural site also stood out by higher mean (± SD) WC and concentrations of Al (72.5 ± 6.2%, 42.2 ± 4.6 g kg^{-1}, respectively) than the other study sites (mining : 63.6 ± 9.11%, 25.2 ± 7.4 g kg^{-1}, respectively; aquaculture : 67.9 ± 7.5%, 35.8 ± 8.0 g kg^{-1}, respectively), whereas the highest mean (± SD) soil concentrations of Cu were measured at the aquaculture site (31.1 ± 8.6 mg kg^{-1}). The BD values (0.43 ± 0.13 g cm^{-3}) did not vary significantly between study sites (Table 13).
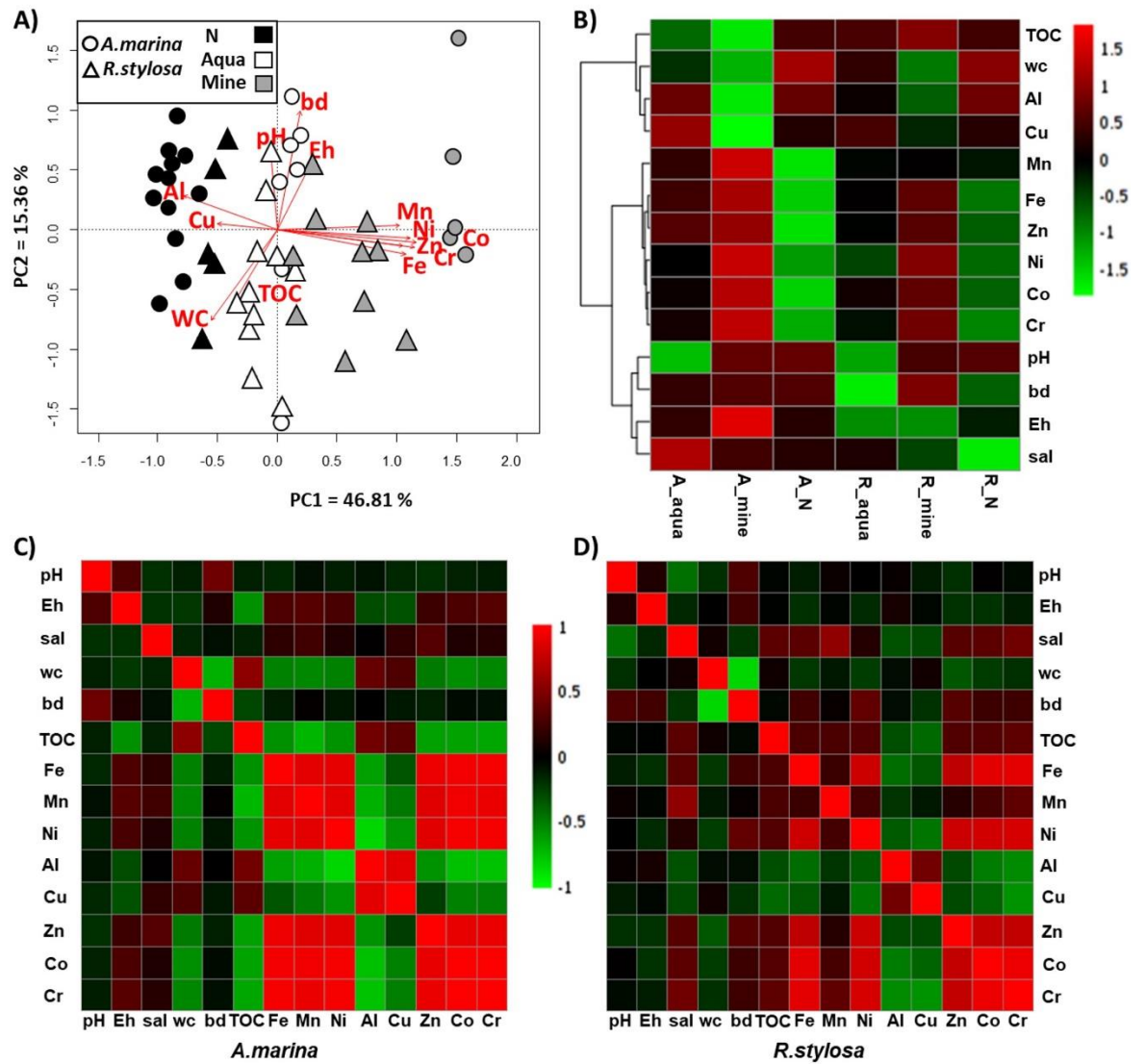
Figure 54. A) Principal Component Analysis of the soil properties, all study sites and species stands combined (14 parameters and 51 samples) ; B) heatmap and ward-euclidian transformed clustering of the soil properties in each mangrove stand ("A" = *A. marina*, "R" = *R. stylosa* ; "aqua" = aquaculture site, "mine" = mining site, "N" = natural site). Green and red coded colours indicate low and high values for a variable in a particular stand, respectively; C & D) heatmaps of the simple Pearson correlation coefficients (r from -1 to +1) between all soil properties in the *A. marina* (C) and in the *R. stylosa* stands (D). Green and red colours indicate low and high values of the Pearson correlation coefficients between two variables, respectively
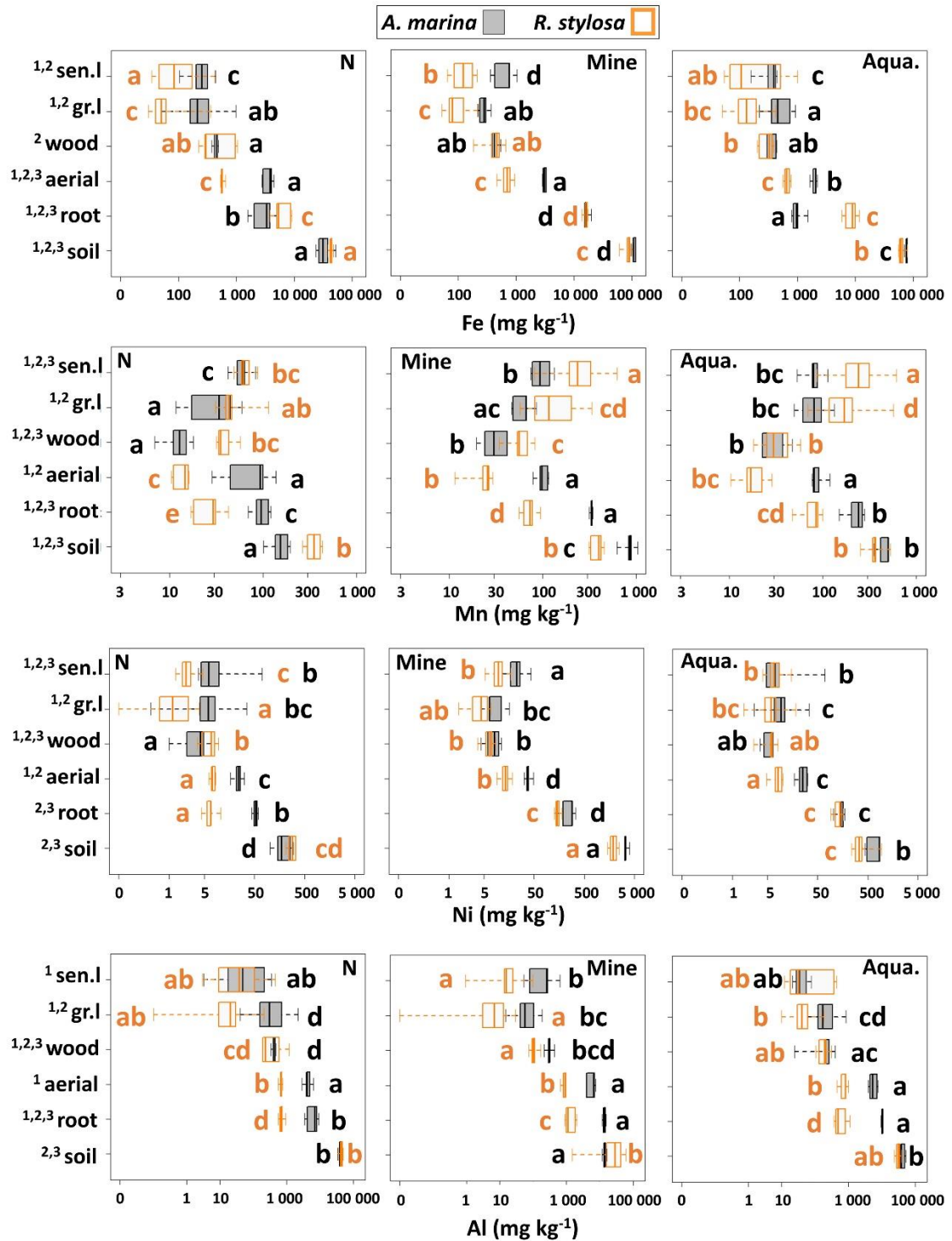
Figure 55. Box plots (mean, upper and lower quartiles, minimum and maximum) of Fe, Mn, Ni and Al concentrations of (in g kg^{-1} of dry weight) in the different soil and plant compartments of the *R. stylosa* (orange boxes) and *A. marina* (grey boxes) stands in each study site ("N" = Natural site, "Mine" = mining site, "Aqua." = Aquaculture site). Fe, Mn, Ni, Al concentrations are given in logarithm scale. For each variable, "[1]", "[2]" and/or "[3]" indicate inter-species, inter-site variations and/or species-site interactions of their values, respectively (two-ways ANOVA). Same lowercase letters indicate stands that did not differ significantly by their values (post-hoc comparison tests, $p < 0.05$)
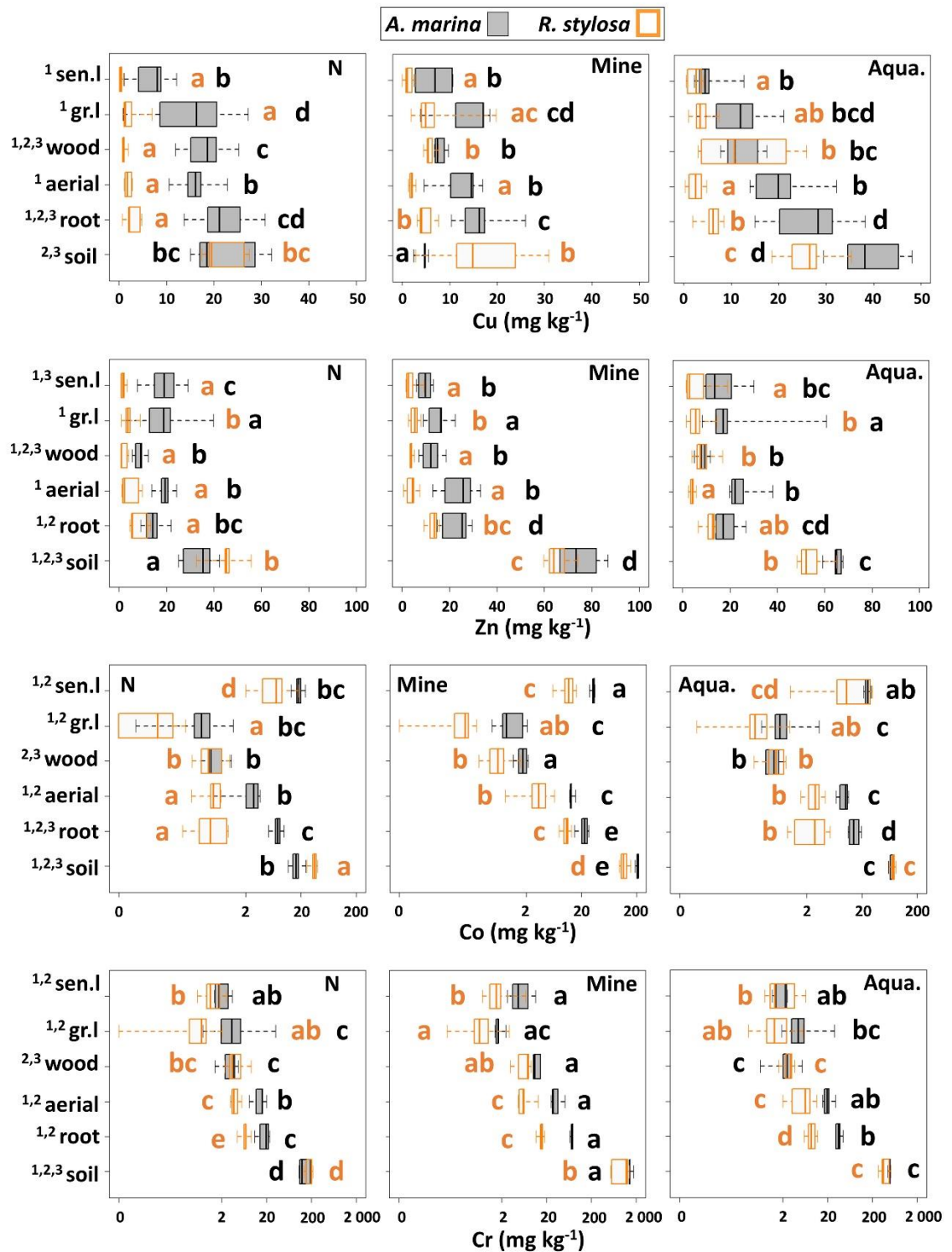
Figure 56. Box plots (mean, upper and lower quartiles, minimum and maximum) of Cu, Zn, Co and Cr concentrations (in g kg^{-1} of dry weight) in the different soil and plant compartments of the *R. stylosa* (orange boxes) and *A. marina* stands (grey boxes) in each study site ("N" = Natural site, "Mine" = mining site, "Aqua." = Aquaculture site). Co and Cr concentrations are given in logarithm scale. For each variable, "[1]", "[2]" and/or "[3]" indicate inter-species, inter-site variations and/or species-site interactions of their values, respectively (two-ways ANOVA). Same lowercase letters indicate stands that did not differ significantly by their values (post-hoc comparison tests, p < 0.05)

Table 13. Mean values (±SD, minimum - maximum) of the physico-chemical properties in *A. marina* and *R. stylosa* stands in each of the three study sites (Natural, Mining and Aquaculture influenced). For each variable, "[1]", "[2]" and/or "[3]" indicate inter-species, inter-site variations and/or species-site interactions of their values, respectively (two-ways ANOVA). Same lowercase letters indicate stands that did not differ significantly by their values (post-hoc comparison tests, p < 0.05)

variable	unit	*A. marina*		*R. stylosa*	
		Natural site			
Salinity [1,2]	-	41.09 [bc]	(±8.85, 25.00 - 50.00)	27.45 [a]	(±5.30,21.00 - 35.5)
total Na [1,2,3]	g kg^{-1}	54.51 [c]	(± 3.70 , 50.28 - 63.32)	33.33 [ab]	(± 4.46, 27.89 - 37.92)
TOC [1,3]	%	8.63 [bc]	(±2.22, 6.32 - 13.97)	8.47 [bc]	(±1.89, 6.23 -10.87)
Eh [1]	mV	6.26 [ab]	(±67.33,-95.00 - +106.67)	-30.30 [ab]	(±115.09, -122.5 - +98)
pH[-]	-	6.53	(±0.11, 6.3 - 6.65)	6.46	(±0.33, 6.20 - 7.02)
wc[2]	%	72.93 [a]	(±5.34,62.56 - 81.65)	72.12 [a]	(±9.11, 62.07 - 80.31)
BD [-]	g cm^{-3}	0.46	(±0.12, 0.30 - 0.70)	0.40	(±0.13, 0.22 - 0.55)
		Mining-influenced			
salinity	-	42.03 [bc]	(±8.07,35.00 -55.50)	36.35 [ab]	(±10.33,25.00 -55.00)
total Na	g kg^{-1}	35.80 [b]	(± 1.63, 33.58 - 37.68)	30.11 [a]	(± 3.35, 24.92 - 36.37)
TOC	%	3.8 [a]	(±1.43, 2.26 - 5.17)	10.93 [c]	(±3.94, 5.04 -15.44)
Eh	mV	227.1 [b]	(±137.65, 40.30 - +373.90)	-80.17 [a]	(± 77.93, -198.00 - +82.50)
pH	-	6.53	(±0.01, 6.51 - 6.55)	6.34	(± 0.56, 2.53 - 7.10)
wc	%	62.24 [b]	(±8.70, 49.18 - 73.47)	63.31 [b]	(± 9.72, 55.28 -77.21)
BD	g cm^{-3}	0.47	(±0.14, 0.33 - 0.70)	0.51	(± 0.17, 0.33 - 0.87)
		Aquaculture-influenced			
salinity	-	48.71 [c]	(±3.45, 45.00 -54.00)	42.11 [bc]	(±7.19, 30.00-50.00)
total Na	g kg^{-1}	32.48 [ab]	(± 3.55, 28.97 - 38.97)	30.07 [a]	(± 3.74, 23.06 - 34.44)
TOC	%	5.8 [ab]	(±2.82, 1.84 - 9.71)	8.74 [bc]	(±1.84, 5.25 - 12.03)
Eh	mV	44.66 [ab]	(± 107.46, -89.00 - +159.80)	-115.89 [a]	(± 50.09, -176.00 - -27.5)
pH	-	5.63	(± 1.84, 2.47 - 6.53)	5.34	(± 1.50, 2.47 - 6.46)
wc	%	66.08 [ab]	(± 7.45, 55.28 -74.60)	71.57 [ab]	(± 6.97, 55.28 - 76.89)
BD	g cm^{-3}	0.45	(± 0.12, 0.26 - 0.66)	0.30	(± 0.05, 0.26 - 0.36)

Significant variations in Eh, TOC and concentrations of all trace metals but Cu and Al were also observed between the soils of the *A. marina* and *R. stylosa* stands. Overall, the soils of the *A. marina* stands were characterised by lower TOC and higher Eh and pH values (6.80 ± 2.97%, + 65.95 ± 128.39 mV, 6.26 ± 1.05, respectively, Table 13) than in the *R. stylosa* stands (9.58 ± 3.02%, - 81.96 ± 81.96 mV, and 6.02 ± 1.22, respectively). The lowest TOC found in this entire study were measured in the *A. marina* stands at the aquaculture site (1.84%, Table 13). The BD and WC did not vary significantly between the *A. marina* (0.46 ± 0.12 g cm^{-3} and 68.56 ± 7.74%, respectively) and *R. stylosa* stands (0.41 ± 0.15 g cm^{-3} and 67.64 ± 8.99%, respectively) (Table 13).

Lastly, simple correlation analyses showed that soils with high TOC were also characterised by high WC and low pH, Eh and BD values (p_{adj}-values < 0.05, Figure 54 a). The soil concentrations of Fe, Mn, Ni, Zn, Co and Cr were positively correlated with each other and negatively correlated with Cu and Al concentrations in both species stands (Figure 54 c,d). However, those correlations were much stronger and significant in the *A. marina* stands compared to the *R. stylosa* stands. The pattern of the Mn concentrations departed particularly from that of the other trace metals Fe, Ni, Zn, Co and Cr in the *R. stylosa stands* (all r ≤ 0.37, p_{adj}-values ≥ 0.06, Figure 54 c,d) when compared to the *A. marina stands* (all r > 0.87, p_{adj}-values < 0.02, Figure 54 c,d). In addition, the direction of the correlations between soil properties and the trace metals showed remarkable differences between both species stands. Specifically, the soil TOC and WC in the *A. marina* stands were significantly and negatively correlated with the concentrations in Fe, Mn, Ni, Zn, Co and Cr (all r ≤ - 0.48, p_{adj}-values ≤ 0.02, Figure 54 c). Conversely, no significant correlations were observed between the WC and other metals in the *R. stylosa* stands (all p_{adj}-values ≥ 0.08), whereas the TOC in these stands tended to be positively correlated with all trace metals (all r ≥ 0.31, p_{adj}-values ≤ 0.05) but Cu and Al (r = - 0.49, r = - 0.31, respectively, p_{adj}-values ≤ 0.03, Figure 54 d).

5.4.2 Trace metal bioconcentrations in the coarse roots

Within the plant materials, the highest concentrations of trace metals were found in the coarse roots of both species. The most striking pattern observed was a significant higher concentration and BCF of all metals but Fe in the coarse roots of *A. marina* than in that of *R. stylosa* (Figure 55, Figure 56). In particular, mean concentrations of Mn, Cu, Co and Cr were twice to four times higher in the coarse roots of *A. marina* (184.22 ± 99.80, 21.66 ± 6.94, 12.74 ± 6.51 and 34.57 ± 21.85 mg kg^{-1}, respectively) than in those of *R. stylosa* (66.08 ± 23.03, 5.07 ± 1.95, 5.44 ± 4.47, 11.02 ± 3.92 mg kg^{-1} respectively) and up to one-fold higher in the case of Al (9.08 ± 3.33 and 0.96 ± 0.50 g kg^{-1}, respectively). Conversely, mean concentrations of Fe were twice as high in the coarse roots of *R. stylosa* (11.26 ± 4.50 g kg^{-1}) than in that of *A. marina* (5.28 ± 6.04 mg kg^{-1}, Figure 55, Figure 56). The concentrations of most metals in the coarse roots of both species tended to increase with increasing concentrations of these metals in the soil (Figure 57). The opposite pattern was observed for
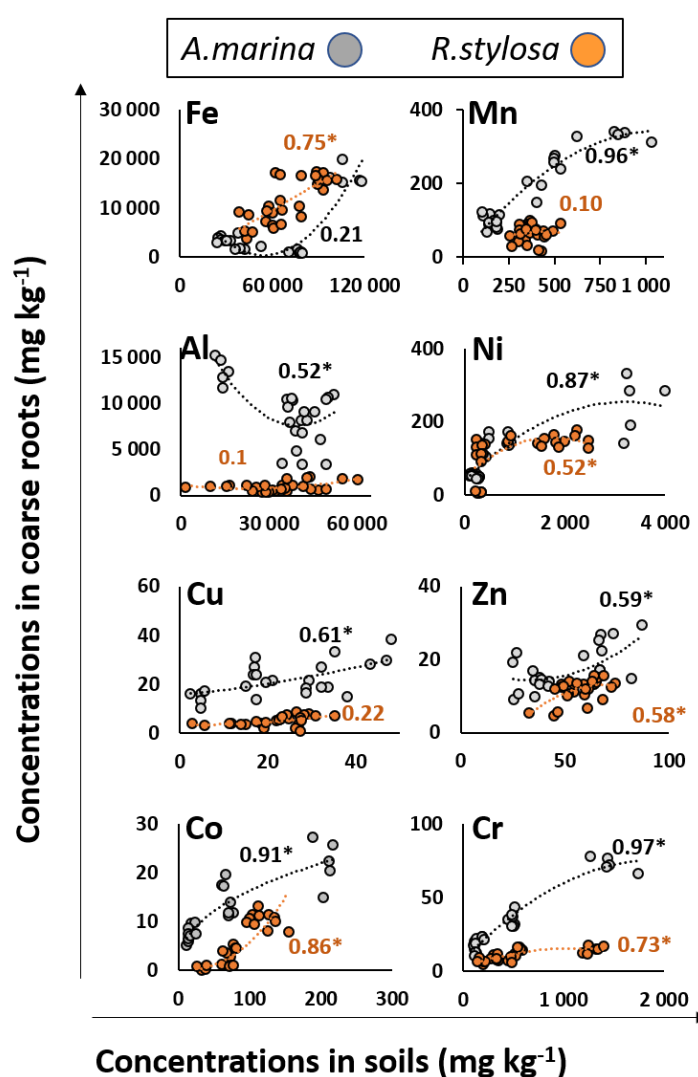
Figure 57. Relationships and Pearson correlation coefficients between metal concentrations in soils and plant materials of the *A. marina* stands (grey dots) and *R. stylosa* stands (orange dots), all study sites combined. All concentrations are given in mg kg^{-1}. Significant Pearson correlation coefficients (p$_{adj}$-values < 0.05) are marked by a " * "

Al in the coarse roots of *A. marina*. Conversely, the BCF_{roots} of all metals decreased with increasing concentrations of these elements in the soil (detailed in Appendix 12, Appendix 13). For both species, the maximum metals BCF_{roots} values were observed for Cu, with median values of 0.98 and 0.29 for *A. marina* and *R. stylosa*, respectively. At their lowest soil concentrations, Mn and Al also reached high maximum BCF values in the coarse roots of *A. marina* compared to the other metals (Mn-BCF_{roots} = 1.20 at the natural site, Al-BCF_{roots} = 1.29 at the mining site) (Figure 58).
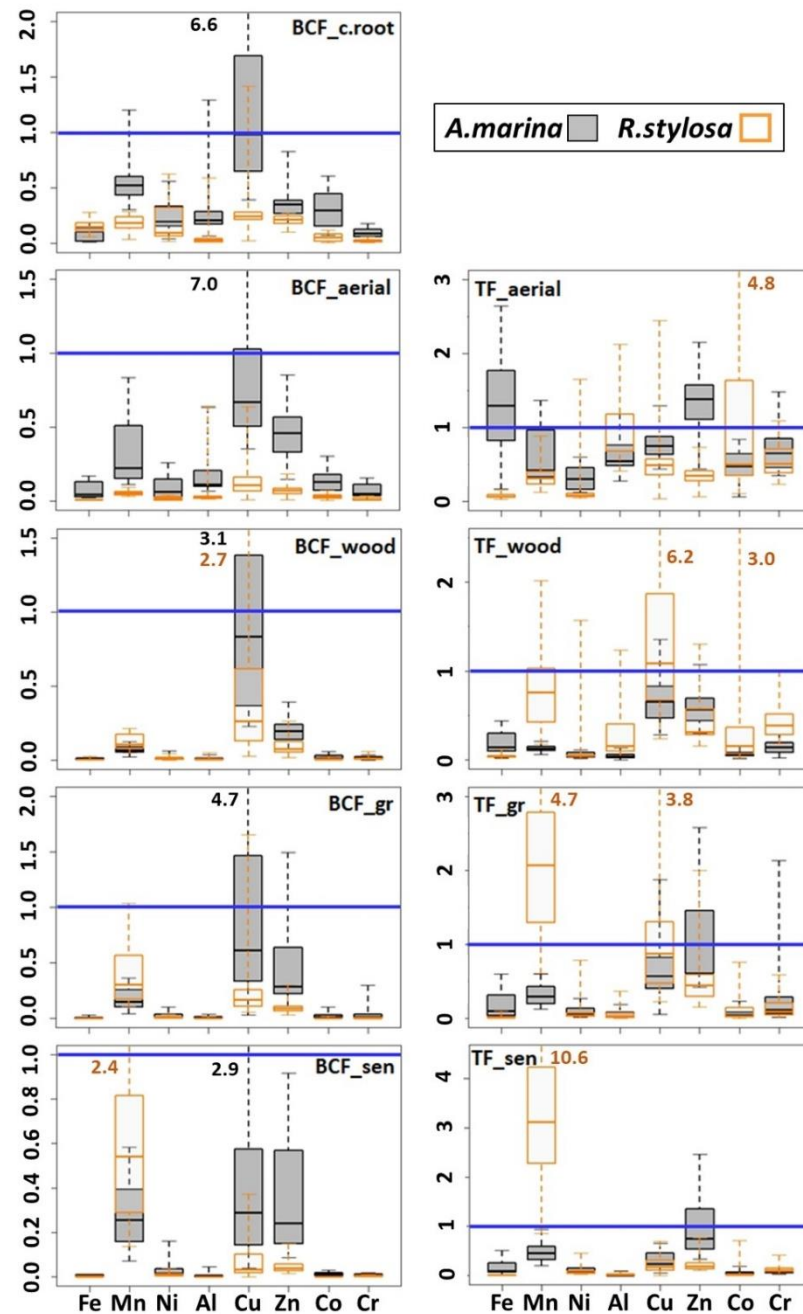
Figure 58. Boxplots (median, upper and lower quartiles, minimum and maximum) of the Bioconcentration (BCF) and Translocation (TF) factors of all trace metals in the plant materials of *A. marina* (grey boxes) and *R. stylosa* (orange boxes), all study sites combined. The blue lines indicate the threshold of 1. Numbers indicate maximum values left out of the plots for better visibility

5.4.3 Transfer to the aboveground plant materials

Overall, Fe, Al and Mn were the most abundant metals found in the aboveground tissues of both species, with concentrations higher by one to two orders of magnitude than Ni, Cu, Zn, Cr and Co.

As observed in the root system, metal concentrations were higher in the aboveground components of *A. marina* than in those of *R. stylosa*, except for the concentrations of Mn that were twice to three times higher in the wood, green leaves and senesced leaves of *R. stylosa* than in those of *A. marina* (Figure 55, Figure 56).

Comparatively, higher metal concentrations were found in the pneumatophores of *A. marina* than in any of the other aboveground components of both species (Figure 55, Figure 56), with similar patterns as those found in the coarse roots of *A. marina* for each metal, but slightly lower BCF (Figure 58, detailed in Appendix 12, Appendix 13). Relative to soil and root composition, the bioaccumulation of most metals in the other aboveground components of both species were strongly restricted (BCF and TF < 0.5, Figure 58, Appendix 12, Appendix 13). However, exceptions to these trends were observed for Mn, Cu and Zn, for which maximum BCF and TF values close or higher than 1 were measured in the wood (Cu) and canopy (Cu and Zn) of *A. marina* and in the canopy (Cu and Mn) of *R. stylosa*.

Although metal concentrations in the aboveground components were low compared to those measured in soils and coarse roots, the concentrations of all metals but Al increased in most aboveground components of both species with increasing concentrations in the soil and root system (Figure 55, Figure 56). These increases in metal concentrations were particularly high in the canopy of both species. On the other hand, Zn concentrations in the green and senesced leaves of *A. marina* were found to decrease with increasing concentrations of Zn in the soils, as illustrated in Figure 59 (r = - 0.48 and - 0.60 respectively, both p_{adj}-values ≤ 0.03). The same pattern was observed for Cr in the green leaves of *A. marina* and *R. stylosa* (r = - 0.56 and - 0.43, respectively, both p_{adj}-values ≤ 0.03). Lastly, increasing Al in the coarse roots of both species also coincided with an increase contents of Al in their aerial roots (r = 0.54 in *A. marina*, 0.53 in *R. stylosa*, both

p_{adj}-values ≤ 0.004), and with a decrease of Al in the wood (r = - 0.48, p_{adj}-value = 0.01) and green leaves (r = - 0.56, p_{adj}-value = 0.002) of *R. stylosa*.
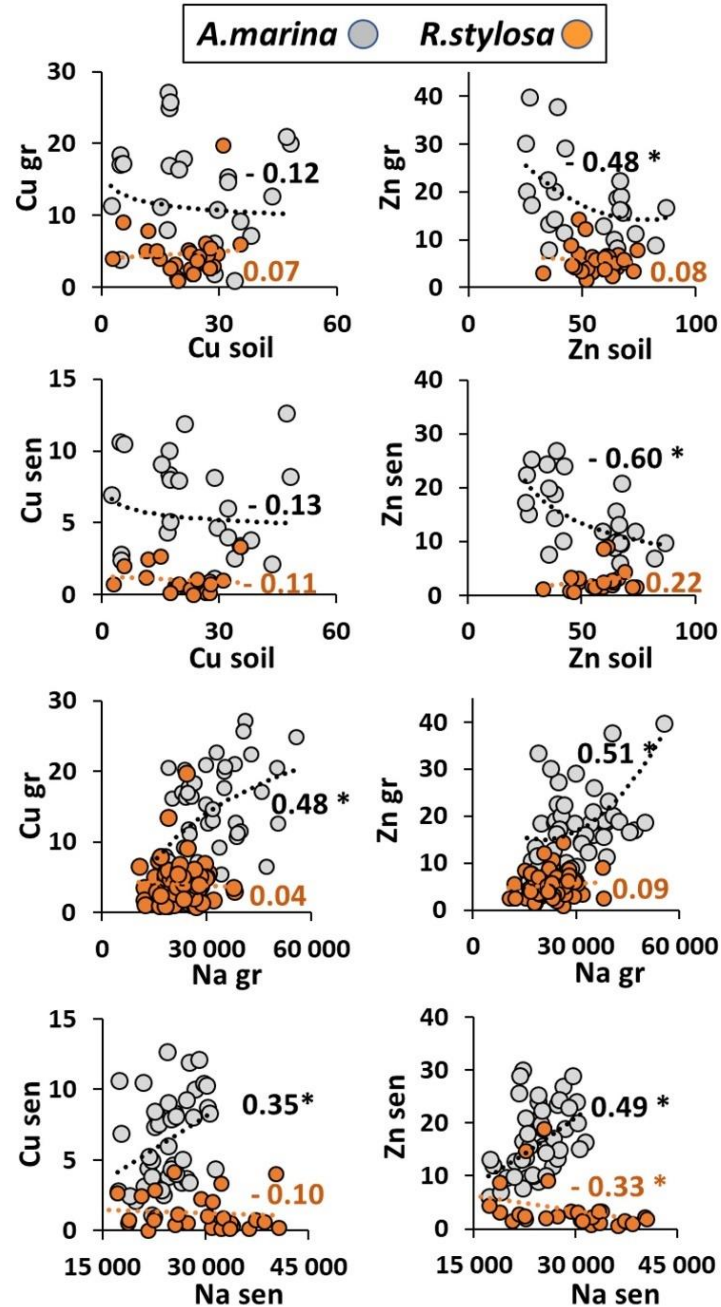
Figure 59. Relationships between the concentrations of Cu and Zn within the soils and their concentrations within the green (gr) and senesced (sen) leaves of the *A. marina* (grey dots) and *R. stylosa* stands (orange dots), all study sites combined (top); relationships between the concentrations of Na and Cu and Zn within the green and senesced leaves of *A. marina* and *R. stylosa* (bottom), all study sites combined. Significant Pearson correlation coefficients (p_{adj}-values < 0.05) are marked by a " * "

5.4.4 Correlations between trace metals and Na in the green and senesced leaves

All sites combined, the mean (± SD) concentrations of Na measured in the coarse roots

(54.95 ± 4.09 g kg^{-1}), pneumatophores (28.50 ± 4.30 g kg^{-1}) and green leaves (30.38 ± 9.99

g kg^{-1}) of *A. marina* were higher than those found in that of *R. stylosa* (28.47 ± 3.85, 18.25

± 2.00 and 22.47 ± 4.12 g kg^{-1}, respectively). Conversely, higher mean (± SD) Na

concentrations were measured in the senesced leaves of *R. stylosa* (26.70 ± 3.011 g kg^{-1})

compared to that of *A. marina* (23.66 ± 3.36 g kg^{-1}). In addition, while Na concentrations

increase in the senesced leaves of *R. stylosa* with increasing Na concentrations in the

green leaves of this species ($r = 0.43$, p_{adj}-value = 0.02), no such correlations were found

in the foliage of *A. marina* ($r = 0.04$, p_{adj}-value = 0.15).

In *A. marina* only, the concentrations of Cu and Zn were both correlated with the

concentrations of Na, and both in the green and senesced leaves (all $r \geq 0.35$, p_{adj}-values

< 0.05), whereas those were not correlated – if only negatively for Zn – with their soil

concentrations (Figure 59). In addition, Mn concentration decreased with increasing Na

concentrations in the senesced leaves of both species ($r \leq -0.53$, p_{adj}-values ≤ 0.03, Figure

60). The same negative correlation was found for Fe in *A. marina* ($r = -0.69$, p_{adj}-value =

0.01, Figure 60). However, the soil concentrations of Mn and Fe also covaried negatively

with the soil concentrations of Na in the *A. marina* stands (Figure 60).
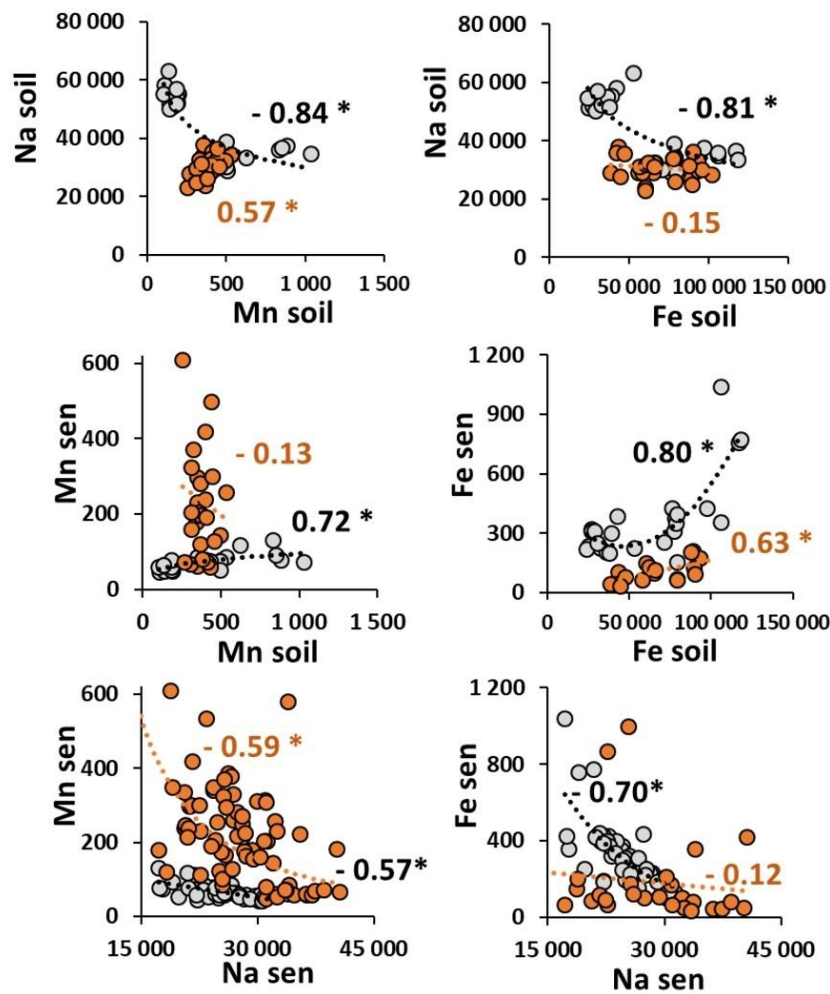
Figure 60. Relationships and Pearson correlation coefficients between the concentrations of Na and Fe and Mn within the soils and the senesced (sen) leaves in the *A. marina* stand*s* (grey dots) and in *R. stylosa* stands (orange dots), all study sites combined. Significant Pearson correlation coefficients (p_{adj}-values < 0.05) are marked by a " * "

5.5 Discussion

5.5.1 Trace metal accumulation in mangrove soils along a semi-arid gradient

Mangroves in New Caledonia present a large diversity of soil characteristics as a result of the different watershed compositions and the particularity of open-cast mines. Mangrove soils downstream ultramafic watersheds in New Caledonia were substantially more concentrated in Fe, Mn, Co, Cr and Ni than the undisturbed site and mangroves worldwide, carried in oxyhydroxide and phyllosilicate minerals eroded from the mining

outcrops upstream those two sites (Noël et al. 2014 Marchand et al. 2016). Those concentrations were also above the thresholds suggested in the sediment quality guidelines for the protection of Aquatic Life and Environmental and Human Health (> 52.3 and 18.0 mg kg^{-1} for Cr and Ni respectively, CCME 2001). On the other hand, the soil concentrations of Cu and Zn were within the range of concentrations found in the literature in every study site (Bayen 2012, Lewis et al.2011, Matsui et al. 2015).

Our results also showed a sharp loss of Mn, Ni, Zn, Co and Cr from the *A. marina* landward to the *R. stylosa* stands seaward at the two influenced sites. Previous authors have shown that this loss along the land-sea gradient in New Caledonia likely results from a differential structural preservation of metal-bearing minerals that depends i) on the rates of immersion and ii) on the OM decomposition pathways that dominate the soils (Marchand et al. 2012, 2016, Deborde et al. 2015). The *A. marina* stands are dominated by oxic to suboxic conditions and low immersion rates that result in a relatively good preservation and accumulation of those minerals in the upper soil horizons (Noël et al. 2014). In these stands, aerobic respiration and oxidation of the OM by Fe, Mn are expected to be the main pathways of OM decomposition (Kristensen et al. 2008, Marchand et al. 2012). During Fe and Mn oxidation of the OM, Fe and Mn oxides are used as electron acceptors by microorganisms. This results in a loss of OM, and in substantial concentrations of dissolved Fe^{2+} and Mn^{2+} in these soils (Marchand et al. 2012, 2016, Noël et al. 2014, Deborde et al. 2015). Part of these dissolved cations are then susceptible to be exported from the soil to the water column and plant compartment (see next section). However, important fractions also re-precipitate and accumulate as Fe and Mn oxides and oxyhydroxides in presence of oxygen, as demonstrated by Noël et al. (2014, 2017) at the site influenced by mining effluent. We hypothesise that, in the *A. marina* stands downstream ultramafic watersheds and shrimp ponds, these OM oxidation pathways

may be significant, stimulated by the large availability of OM and metallic electron acceptors in these soils. Thus, an increase of OM mineralisation would result in a lesser fraction of metals bound to the OM (Feller et al. 1999, 2002, Nóbrega et al. 2013, Molnar et al. 2014, Aschenbroich et al. 2015). This is likely reflected in the negative correlations found between Fe and Mn and the TOC in the *A. marina* stands. Furthermore, Aschenbroich et al. (2015) report that fresh OM inputs from the shrimp ponds are highly labile, which likely contributes to increased microbial activity and OM mineralisation rates. This could explain the lowest TOC (1.84 %) measured at the aquaculture site, which receives tons of organic particles every year from the shrimp pond effluents (Molnar et al. 2014). Finally, the strong correlations between the different trace metals studied in the *A. marina* stands may be explained by substantial adsorption of trace metals at the surface of Fe-oxyhydroxides in (sub)oxic conditions. Adsorption of Ni^{2+} and Cr^{2+} at the surface of Fe-oxyhydroxides has already been observed by Noël et al. (2015, 2017) in similar conditions in New Caledonia. The similar patterns we observed between the concentrations of Fe and other divalent trace metals in the *A. marina* stands suggest that similar interactions might also occur with Co and Zn.

Conversely, the soils in the *R. stylosa* stands experience lower oxygen supply (supported by lower Eh values), as well as longer immersion rates. In these soils, anoxic conditions prevail, and aerobic respiration is then supplanted by sulfate-reduction as the main pathway of OM decomposition by the microbial community (Kristensen et al. 2008). Hence, sulfate-reducing prokaryotes use sulfates (SO_4^{2-}), abundantly supplied by seawater (Millero 1996, Allaby and Allaby 1999), as terminal electron acceptors during anaerobic respiration. As observed in other mangroves worldwide, sulfates are then reduced to hydrogen sulfides (H_2S), which precipitate in turn with dissolved Fe^{2+}/Fe^{3+} and accumulate in the solid phase – here as pyrite or greigite – thus becoming the dominant

forms of Fe-bearing minerals (Otero et al. 2009, Otero and Macias Vazquez 2010, Noël et al. 2014, 2017, Deborde et al. 2015). As in the *A. marina* stands, divalent cations Ni^{2+} and Cr^{2+} have been found to co-precipitate and accumulate within these Fe-bearing minerals (Noël et al. 2014, 2015, 2017). This is not the case of Mn^{2+}, which tends to easily dissolve in anoxic conditions and ends up exported from the soil compartment (Gueiros et al. 2003, Otero et al. 2009, Holloway et al. 2016, Marchand et al. 2012, 2016). This reflects in the decrease of Mn landward to seaward, as well as the antagonistic relationships observed between Mn and the other metals in both species' stands. In all study sites, important amounts of intact *R. stylosa* live and dead roots and wood were observed in every horizon of the *R. stylosa* stands. These buried forests preserved from decomposition by the anaerobic environment likely serve as a large reservoir of OM, true catalysts of sulfate-reduction by the anaerobic bacteria. Furthermore, the OM provides numerous anionic sites at the surface of the organic particles for which metallic ions have an important affinity (Clark et al. 1998, Okbah et al. 2005, 2020, Otero and Macias Vazquez 2010, Marchand et al. 2011b, 2012, 2016, Noel et al. 2014, 2017). These interactions are likely to emphasize the fixation of metals in the soil of the *R. stylosa* stands, and may be reflected in the similar patterns observed between the TOC and the total concentrations of Fe, Ni, Cr, Co, Zn in the *R. stylosa* stands of the present study.

Despite the occurrence of processes favourable to metal accumulations in both species stands, longer immersion and the frequent alternance of oxidation-reduction processes may compromise the structural integrity of pyrite minerals in the *R. stylosa* stands. Thus, those minerals may dissolve and a substantial concentration of Fe^{2+} and associate divalent cations (e.g. Cr^{2+}, Ni^{2+}) may be freed in the dissolved phase. Those would then be available for export at ebb tide and plant uptake, adsorption on the OM particles, or re-precipitation in carbonates, oxyhydroxides or pyrite compounds (Sanders et al. 2015,

Noël et al. 2014, 2017, Marchand et al. 2006, 2012). Thus, in the long term, redissolution-oxidation cycles and longer duration of immersion under sea-level rise could enhance significantly metal mobility and losses in semi-arid mangroves.

5.5.2 Mangrove tree metal uptake partly influenced by soil properties

As observed in several studies worldwide, most metals increased in the root of both species with increasing metal concentrations in the soils (MacFarlane et al. 2003, Chaudhuri et al. 2014, Marchand et al. 2016, Chowdhury et al. 2017, see also field-studies reviewed in MacFarlane et al. 2007 and Yan et al. 2017). The highest concentrations of the essential micronutrients Fe, Mn and Ni measured in the roots of both species exceeded by two folds the adequate concentrations for terrestrial plant growth worldwide (100, 50 and 5 mg kg^{-1} of DW, respectively), by 250% in the case of Cu (6 mg kg^{-1} of DW, respectively) and up to 50% in the case of Zn (20 mg kg^{-1} of DW) (Seregin and Kozhevnikova 2006, Raven et al. 2005). While higher mean concentrations of metals were measured in the soils of the *A. marina* stands compared to those of the *R. stylosa* stands, we also illustrated that, at equal soil concentrations, higher metal concentrations were measured in the root system of *A. marina* than in that of *R. stylosa*. At the belowground level, the causes of this inter-species differences in metal accumulation in the root system must be found in: i) the total concentration and mobility of metals within the bulk soil and their transport toward the root surface and ii) the aptitude of each species to avoid and/or tolerate metal stress.

Regarding the first point, and as discussed in the previous section, we hypothesise that as OM mineralisation rates are higher in oxic and suboxic conditions in the *A. marina* stands than in the anoxic conditions of the *R. stylosa stands*. This may result in a lower

amount of binding sites for metallic cations in the *A. marina* stands. Thus, the metals bound to these organic particles and oxyhydroxides would be released in the dissolved phase after the mineralisation of OM. As the immersion rates are lower in the *A. marina* stands, those dissolved metals could accumulate in these stands, thus resulting in higher availability for uptake by the roots of *A. marina*. Similarly, the high concentrations of dissolved Fe^{2+} in the *R. stylosa* stands that result from the oxidation-reduction cycles could explain the higher uptake of this metal by *R. stylosa* compared to *A. marina*. As discussed above, the other metals in the soils of the *R. stylosa* stands would remain less mobile and thus less available for plant uptake, being bound to organic particles or re-precipitated within newly formed pyrite compounds, where they substitute to Fe^{2+} (Noël et al. 2015, 2017).

Furthermore, the soils of the *A. marina* stands also feature several other properties that could explain the higher bioaccumulation of other trace metals in the root system compared to that of *R. stylosa*. For instance, salinity may facilitate metal mobility in soils and uptake by plants due to the competition with Na^+ for binding sites and/or to the complexation with Cl^- (Lutts and Lefèvre 2015, Yan et al. 2017). In addition, high evapotranspiration in this semi-arid climate results in higher soil temperature landward than in the longer-immersed stands seaward (see Chapter 4). Higher temperatures facilitate metal uptake by immersed plants by altering the structure of their plasma membrane, thus increasing fluidity and the transport of metals within the roots (Lynch and Steponkus 1987, Fritioff et al. 2005). In addition, the soils of the *A. marina* stands in New Caledonia acidify significantly during the dry season in winter as result of OM oxidation, whereas the pH remains unchanged in the *R. stylosa* stands (see Chapter 4, Lin and Melville 1993, Middelburg et al. 1996, Marchand et al. 2004, Nóbrega et al. 2013). The subsequent supply of H^+ is known to increase the solubility of Al and of Fe by

reduction and to increase the availability of Mn^{2+} and Zn^{2+} by competing for the same cation-binding sites in soils. This results in their desorption and accumulation in the dissolved phase of the soils (Lambers et al. 2008, Greger 2004), hence resulting in higher availability for plant uptake.

Thus, different soil properties may explain the higher metal uptake in *A. marina* landward than in *R. stylosa*, likely as a result of higher metal availability in suboxic conditions, higher temperature along the year and possibly lower pH during the dry season.

5.5.3 Metal stress avoidance in the rhizosphere and the roots

At the root surface, a primary mechanism of heavy metal stress avoidance is for mangrove species to alter the mobilisation of trace metals by changing the chemistry of their rhizosphere (Yan et al. 2017). In the *Avicennia* and *Rhizophora* genera, the diffusion of oxygen in the root system for belowground respiration through the aerenchyma constitutes an effective barrier to metals (Souza et al. 2015). Part of this oxygen – the radial oxygen loss, ROL – reaches the rhizosphere, resulting in the precipitation of $Fe^{2+/3+}$ in Fe plaques around the roots (Scholander et al. 1955, Curran et al. 1986, Allaway et al. 2001). This mechanism can also constitute a barrier to other metals, such as Mn, Zn, Cu, Ni, Cr (Machado et al. 2005, Liu et al. 2009, Pi et al. 2011). However, in *R. stylosa*, Cheng et al. (2012, 2014) reported lower metal uptake and ROL due to lower root permeability through thickening and lignification of the exodermis cells in response to metal stress. Liu et al. (2009) have also demonstrated that the ROL in *A. marina* seedlings decreased with increasing metal concentrations in soils, whereas metal uptake into the roots increased. On that basis, further research hypotheses could be that higher metal uptake in the root system of *A. marina* compared to that of *R. stylosa* could be the result of i)

lower lignification in the exodermis of *A. marina* than in that of *R. stylosa*, and/or of ii) decreasing ROL with increasing metal concentrations in the soil of the *A. marina* stands. Once passed this first barrier, another mechanism of metal stress avoidance involves the restriction of metal uptake and/or its detoxification into the rhizosphere. For instance, *A. marina* secretes at its root surface exudates rich in fulvic acids that showed a high complexation ability with Cu^{2+} > Mn^{2+} > Cd^{2+} (Zhu et al. 2019). In the present study, this mechanism possibly applies to Al, the only metal in this study whose content tends to decrease in the roots of *A. marina* and in the wood and green leaves of *R. stylosa* with increasing concentrations in the soil or coarse roots. Although little is known about Al avoidance and tolerance mechanisms in mangroves, Ma (2007) reports that some terrestrial species detoxify Al^{3+} externally or within the root cells by binding them to organic acid anions. This allows to neutralise Al^{3+} in the rhizosphere and restrict its uptake, or to neutralise it within the cells before releasing it into the rhizosphere (Ma et al. 2001, Ma 2007). We suggest that similar mechanisms may occur at high Al concentrations in the soil.

5.5.4 Accumulation in the root system and transfer to the aboveground components

Both *A. marina* and *R. stylosa* present a good ability to confine metal accumulation to their root systems and restrict metal accumulation in their aboveground components (Saenger 2002, Lacerda et al. 1988, Che 1999, MacFarlane et al. 2007, Marchand et al. 2016). Therefore, both species can be considered good candidates for phytostabilisation in the present semi-arid context, especially *A. marina* (Peer et al. 2005). Previous studies reported that mangrove species prevent the translocation of metals by binding and sequestrating them within the root epidermis and cortex (MacFarlane and Burchett

2000, 2002, MacFarlane et al. 2007, Arrivabene et al. 2016). However, *A. marina* also shows a high capacity to concentrate and translocate metals in its pneumatophores. This may be because those are also immersed at high tide and may be subjected to similar conditions than the belowground roots. Those may also contain, as with roots, residual soil particles notoriously difficult to wash off in belowground tissues (Azcue 1996, Cuske 2014). High metal translocation to the pneumatophores may also be a good mechanism to avoid metal stress in the belowground root system.

Within the range of metal concentrations studied here, neither species fulfil all the criterions necessary to fit the definition of trace metal hyperaccumulor (i.e. TF > 1 and nominal threshold in plant materials ≥ 1 000 mg kg^{-1} for Co, Cu, Cr and Ni and ≥ 10 000 mg kg^{-1} for Mn and Zn, Baker and Brooks 1989, Peer et al. 2005). Yet, most of the metals studied accumulate in the aboveground components with their increased concentrations in soil. As reported in other mangrove studies, metals may be relatively mobile and accumulate in substantial concentrations in the aboveground tissues of mangrove trees (Chowdhury et al. 2017, Yan et al. 2017, Analuddin et al. 2017). This was particularly the case for Mn in the aboveground components of *R. stylosa*, but also for non-essential metals such as Cr and Al in the present study (Chowdhury et al. 2017, Alzahrani et al. 2018). Despite metal toxicity, these transfers allow for metal storage and sequestration in the wood tissues, or for transfer to the litterfall when present in excess (e.g., Arrivabene et al. 2016, Naidoo et al. 2014, Chowdhury et al. 2017, Martuti et al. 2017, Almahasheer et al. 2018, see also Chapter 3). Our results illustrate that such removal through the litterfall may be a significant mechanism of metal exclusion for Mn, Fe, Ni and Zn in *R. stylosa* and for Fe, Mn, Ni and Cr in *A. marina*.

5.5.5 Influence of salinity on metal concentrations in the canopy

While metal contents in the canopy and litterfall may be partly controlled by their soil concentrations, our results also suggest that increasing Na may influence the transfer and accumulation of these elements in the litterfall of *R. stylosa* (Mn only) and *A. marina* (Fe, Mn, Cu, Zn). Several studies on terrestrial plants report that Fe and Mn addition to plant medium may increase salt tolerance and prevent damage in plants growing at high salinity (e.g. Cramer and Nowak 1992, Heidari and Sarani 2012, Pandya et al. 2005). After exposure of the mangrove *Bruguiera parviflora* to salt treatment, Parida et al. (2004) also recorded an increase expression of the Mn and Fe-superoxide dismutases, SOD, an antioxidant enzyme known to play a primary role in the defence against reactive oxidative species, including in hypersaline conditions (Rahman et al. 2016). Thus, salinity stress could increase the requirement of Mn and Fe in the foliage of mangrove species, which could be reflected in the decrease transfer of those metals towards the litterfall. On the other hand, Arrivabene et al. (2016) also recorded the presence of Fe in the salt exudates of the glandular trichomes of the leaves of *Avicennia schaueriana*. In *A. marina*, salt may bind with metals (e.g. Cu, Zn) as alkaline compounds and secreted through the glandular trichomes of the leaves, likely as a way to remove metals and salt from the leaves (MacFarlane and Burchett 2000, 2002, MacFarlane et al. 2007, Naidoo et al. 2014). In the present study, the loss of Na in the senesced leaves compared to the green leaves and the absence of correlation between Na in the green and senesced leaves showed that salt excretion from the green leaves likely occurs in the *A. marina* stands. However, further studies would be needed to confirm these hypotheses and understand the interaction between salinity and Mn and Fe nutrition in mangrove plants.

On the other hand, the accumulation of Cu and Zn in the green and senesced leaves of *A. marina* does not appear to be associated to their soil concentrations within the ranges studied here – if only negatively for Zn – but rather by the concentrations of Na into the leaves. We hypothesise that within the present hypersaline context, Cu and Zn are increasingly translocated and accumulated into the canopy, not as a response to metal stress, but as a mechanism that facilitates salt excretion from the leaves as alkaline compounds.

5.6 Conclusion

In semi-arid New Caledonia, mangrove soils receive and filter important quantities of Fe, Ni, Cr, Co and Mn eroded from exploited lateritic soils in ultramafic watersheds over time. This study has highlighted the determinant role of soil properties and OM cycling in the accumulation of metals in the soils and in the tissues of mangrove species, and the increasing loss of metals in soils with increasing duration of inundation along the intertidal gradient. Although accumulation of trace metals was mostly limited to the root system, bioaccumulation factors close or higher than 1 were also found in the aerial roots (Cu, Zn, Mn, Al), wood (Cu) and green and senesced leaves (Mn, Cu, Zn). *A. marina* and *R. stylosa* are therefore good indicators of trace metals and suitable candidates for metal phytoremediation. In these hypersaline soils, the need for further research on the control of Na on the accumulation of Fe, Mn, Cu and Zn in the foliage of mangrove trees has also been highlighted.

In a context of increasing aridity, pollution and sea-level rise worldwide, this study stresses the likelihood of an increasing loss and export of those metals from the soil compartment toward less durable pools in the ecosystem and the water column. Further

studies and management strategies should therefore be directed toward the assessment of global change effects on trace metal cycles and budgets and on the monitoring of adjacent coastal water quality.

Chapter 6

Macroelement Dynamics in *Avicennia marina* and *Rhizophora stylosa* mangrove stands developing in a semi-arid climate with different anthropogenic influences (New Caledonia)

6.1 Abstract
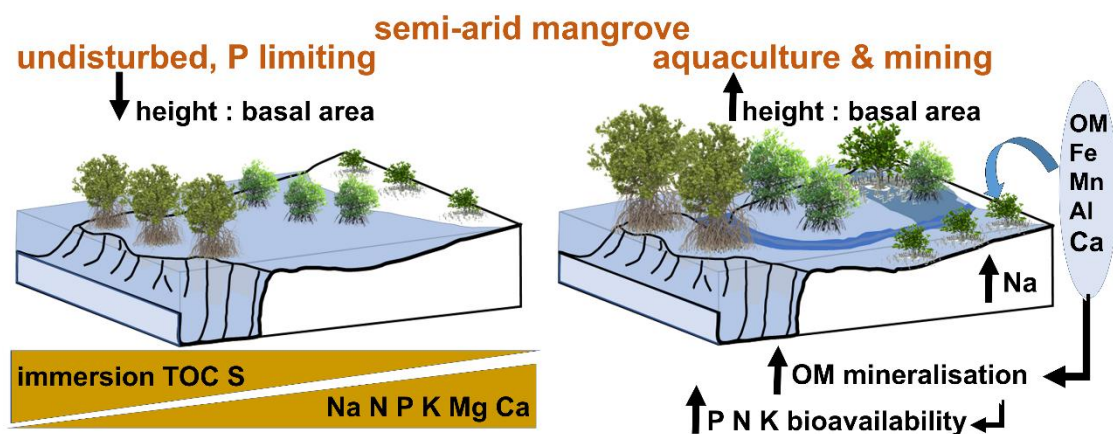
Figure 61. Graphical abstract of macronutrient spatial variation in soils along an undisturbed semi-arid mangrove intertidal gradient (left) and effects of trace metal and labile OM inputs on mangrove tree height and basal ratios in mangrove in border of aquaculture and mining activities in New Caledonia (right)

Aim: the ability of two ubiquitous mangrove species stands to accumulate macroelements under different anthropogenic influences was investigated in semi-arid New Caledonia. The salt hyperaccumulator species *Avicennia marina* dominates in landward areas, whereas *Rhizophora stylosa* dominates in seaward areas.

Methods: N, P, K, Ca, Mg and S concentrations along the soil-plant continuum of these two species stands were compared at three study sites - undisturbed, mining and aquaculture.

Results: our results suggest that loads of OM and Fe and Mn electron acceptors in mangrove stands characterised by (sub)oxic conditions stimulates organic matter mineralisation. This reflects in sharp losses of soil organic carbon, N and K in *A. marina* stands landward compared to *R. stylosa* stands seaward. Conversely, P soil contents increased in the *R. stylosa* stands with increasing Fe in soils. We suggest that while Fe-oxides tend to dissolve in these reducing conditions, their renewal with mining activities contributes to P adsorption and accumulation in these soils. In addition, higher macroelement concentrations were found in the tissues of *A. marina* than in those of *R. stylosa* at every site. Strong interactions found between Na and K, N, P and Mg in the foliage of *A. marina* and K in the foliage of *R. stylosa* suggest a significant allocation of these nutrients in mechanisms to cope with salinity. At the influenced sites, lower salinity with high nutrient availability decrease nutrient remobilisation from senesced leaves of both species. This may contribute to soil enrichment through litterfall and allocation of nutrients to growth rather than coping with salinity, therefore resulting in increased tree heights and canopy volumes.

Conclusions: simultaneous increases of aridity, nutrient and metal pollution worldwide are likely to i) increase P accumulation in mangrove soils, ii) lessen mangrove ability to accumulate OM, N and K in soils in landward areas and iii) increase nutrient exports from soil towards the plant biomass and litterfall.

6.2 Introduction

Dwelling between land and sea in shallow tropical and subtropical coastal areas, mangrove ecosystems may form an effective barrier against nutrient pollution of marine habitats (Ewel et al. 1998, Saenger 2002, Reef et al. 2010). Previous studies in mangrove ecosystems reported a potential for macroelement removal from anthropogenic effluents, with sometimes apparent benefits for mangrove tree productivity (Ewel et al. 1998, Rivera-Monroy et al. 1999, Reef et al. 2010, Molnar et al. 2013). However, this ability to retain nutrients largely depends on the geochemical conditions found along the intertidal gradient, which vary especially with strong elevation gradient and contrasted climates (Otero et al. 2006, Deborde et al. 2015). More specifically, mangrove soils in seaward areas in arid and semi-arid mangroves are often characterised by longer inundation time and low oxygen content and reduction-oxidation potential (Eh) than in landward areas where high evapotranspiration occurs (Chapter 4). These characteristics favour P export, N benthic fixation in seaward areas and allow for a slow decomposition of organic matter (OM) in soils, which constitute an important sink of carbon and nutrients (Alongi 2005a, Bouillon et al. 2008, Alongi 2014, Deborde et al. 2015). On the other hand, oxygen, nitrates, sulfates, iron and/or manganese oxides can all act as electron acceptors during the oxidation of OM in oxic and suboxic conditions that usually prevail at the soil surface and in landward areas. These isolated or combined reactions coupled with the action of microbial communities lead to the production of mineralized forms of N (N_2, N_2O, NH_4^+, NH_3) or P (H_3PO_4, HPO_4^-) (Corredor and Morell 1994, Rivera-Monroy and Twilley 1996, Kristensen et al. 2000, Vasquez et al. 2000, Allen et al. 2007). Those mineralized forms are then available for plant uptake, export to the atmosphere and outflowing effluents, or re-precipitation

within metal complexes, depending on the physico-chemical context within each mangrove substrate (Saenger 2002, Ferreira et al. 2007a, c, Reef et al. 2010, Marchand et al.2011a, 2012, Naidoo et al. 2014).

In addition, macroelement uptake, translocation and bioaccumulation in the plant compartment of semi-arid mangrove ecosystems also depend on numerous factors. Those include i) the requirement of each species found along the intertidal gradient, ii) their ability to alter the chemistry at the soil-rhizosphere interface, iii) their strategy of nutrient retention/restitution to the forest floor and iv) their adaptations to cope with salinity (Andersen and Kristensen 1988, Ball and Munns 1992, Saenger et al. 2002, Reef et al. 2010, Marchand et al. 2012, 2016, see also Chapter 3). These factors determine in turn the quality of mangrove litter, which constitutes a major source of macroelements in mangrove soils (e Silva et al. 2007).

Given the numerous factors that can influence nutrient accumulation in mangrove soils and plants, it is difficult to assess the primary factors that actually influence nutrient mobilisation and their impact on tree nutrition and productivity. As increasing aridity and anthropogenic activities are projected to influence the biogeochemical cycles of nutrients worldwide (Hu and Schmidhalter 2005, Delgado-Baquerizo et al. 2013, 2016), further research is urgently needed to improve our understanding of nutrient accumulation in mangrove ecosystems. In this study, we investigate macroelement distribution and soil-plant transfer along the intertidal gradient of semi-arid mangrove ecosystems. The first specific objective was to understand the determinants of macroelement distribution in soils as a function of the zonation and nutrient inputs. The second objective was to understand soil-plants nutrient transfer as a function of soil geochemistry and of plant species requirement and their capacity of adaptation to physico-chemical conditions. In order to do so, we compared the spatial patterns of

macroelements N, P, K, Mg, S and Ca along the soil plant-continuum (from soils to senesced leaves) of two species that belong to two genera ubiquitous around the world and that feature different strategies to cope with salinity. *Avicennia marina* (Forsk.) Vierh subsp. *australasica*, (Walp.) J. Everett is a pioneer species and a salt hyperaccumulator that dominates saline soils in landward areas, whereas *Rhizophora stylosa* Griff is less tolerant to salinity and dominates in seaward areas (Duke 1992, 2006b). This inter-species comparison was carried out in the semi-arid context of New Caledonia, at three study sites subject to different anthropogenic pressures (undisturbed, mining and aquaculture) and already studied for their trace metal concentrations and soil-plant transfers in Chapter 5. The characteristics of these study sites allow an inter-species comparison over a wide range of salinity, nutrient and metal inputs, the status and fractionation have been well described in previous studies (see next section).

6.3 Material and Methods

6.3.1 Sites of study

The sampling and data collection were conducted at three sites located on the semi-arid west coast of New Caledonia during the growing season (wet season), in March and April 2016 (Figure 62), in the same sampling locations as described in Chapter 5.

Briefly, the first study site was the "Heart of Voh", here-after named "natural". The natural site was composed of a 5.1 ha mangrove stand upstream the Chasseloup Bay (20° 56.0′ S, 164° 39.2′ E). This site was unaffected by direct anthropogenic pressures and experienced an increase of tidal range that led to the recent colonisation of salt flats by *A. marina* at the highest elevations landward. This mangrove stand is under the

influence of two large watersheds, the Voh and Temala, dominated by laterite (iron and aluminium oxide clays) and serpentinite (iron-magnesium silicate rock) formations upstream, as well as alluvial and littoral deposits downstream (Georep 2019). A more complete description of the site and the elemental status in its soils can also be found in Chapters 4 and 5.

The second site was located downstream of a mining outcrop in the Bay of Tâ (Vavouto Bay) (21° 0'4.48"S, 164°42'17.52"E), here after named "mining site". This second site is located downstream of the lateritized ultramafic massif of Koniambo, currently exploited for its nickel deposits that outcrop at the land surface (Georep 2019). The western side of the Koniambo is drained by two rivers, one that flows directly into the northern side of the study site (Figure 62). Due to the important concentrations of Mg in the ultramafic rocks upstream, the Coco River waters are particularly alkaline and richly loaded with iron, manganese, zinc and nickel (see Chapter 5 and Falconbridge SAS 2001, Noël et al. 2014).

The third site was located at the border of an aquaculture facility, the "Ferme Aquacole de la Ouenghi" (F.A.O.), farming the blue shrimp *Penaeus stylirostris* Stimpson, 1871 (21°56'6.71"S, 166° 4'38.15"E), here after named "aquaculture site". From December to July, the farm operates two 1 m deep semi-intensive rearing ponds of 10.5 and 7.5 ha, respectively. During this period each year, the water in the ponds is partially renewed daily. The water is pumped from the south of the peninsula and dispatched to the ponds through intake canals. Over the entire rearing period, approximately 79 kg N ha^{-1} and 19 kg P ha^{-1} are discharged into the mangrove through the pond outlets (Molnar et al. 2014, Figure 62). Up to two years prior the present research, important quantities of Ca mineral-rich extract were also frequently added to the ponds to regulate pond water pH (Farm Manager, personal communication). The southern peninsula is under the

influence of the Ouenghi Delta, that drains massifs of laterites and peridotites (dark, Fe-
and Mg-rich igneous rock composed mainly of olivine and pyroxene minerals), including
the active mining center of Thio Camp des Sapins (Georep 2019). The elemental (S, Fe,
Mn, N, P, S) speciation in the mangrove effluents and soils of this bay can be found in
Deborde et al. (2015) and Molnar et al. (2013, 2014).
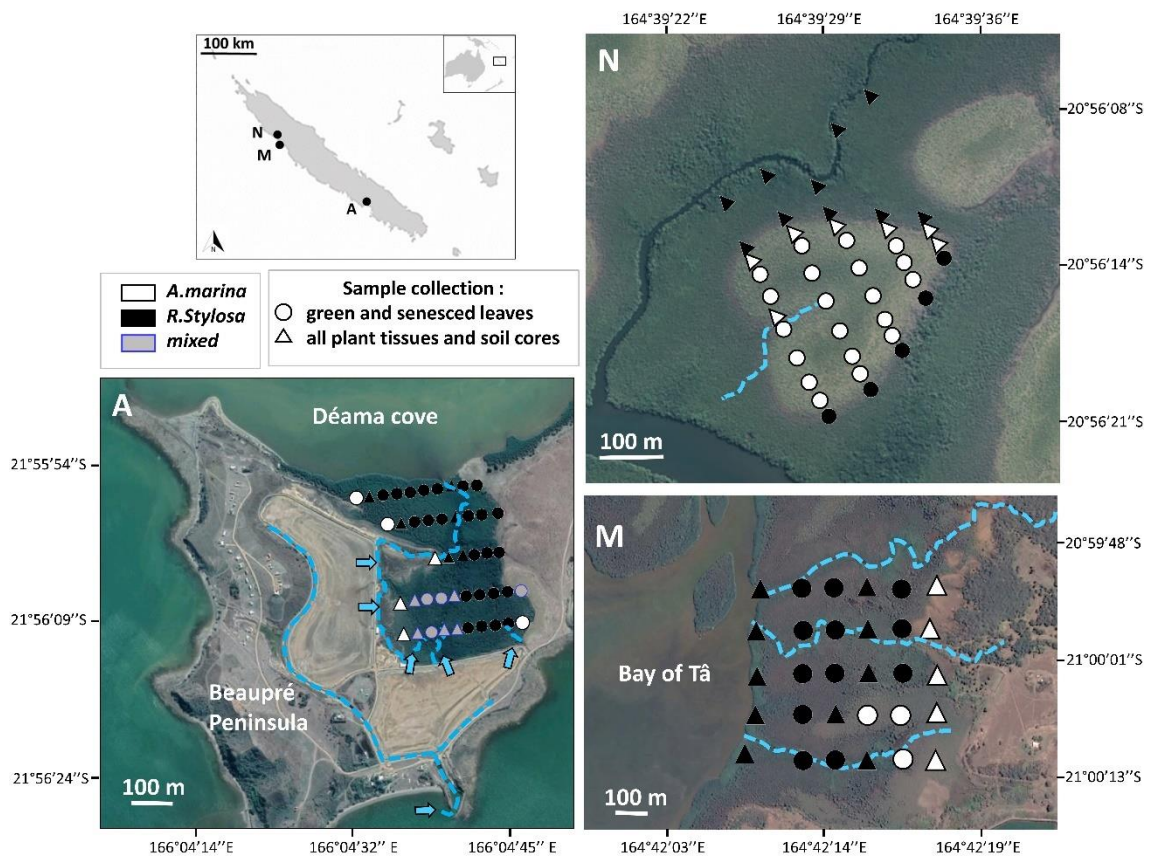
Figure 62. Location of New Caledonia in Australasia and location of each plot and sampling layout in each
study site (N = Natural, M = Mining influenced, A = Aquaculture influenced. Satellite data from Digital
Globe, 2018). Blue dotted lines indicate permanent creeks in the natural and mining-influenced sites and
effluents in the aquaculture-influenced site. Blue arrows indicate pond effluent outlets in the aquaculture-
influenced site. Soil cores and root, aerial root and wood tissues of both species have been sampled in a
total of 51 locations (17 in the N site, 19 in the A site and 15 in the M site). Green and senesced leaves
have been sampled in 121 locations (37 in the N site, 54 in the A site and 30 in the M site). The sampling
locations and samples were identical to those studied in Chapter 5

As described in Chapter 5, the vegetation in the three studied mangrove sites featured
the typical zonation of the semi-arid mangroves of New Caledonia. This zonation is

driven by a gradient of salinity, which is in turn controlled by the frequency of inundation and thus by an elevation gradient (Chapter 4). Landside, the summit of this gradient is dominated by salt-flats of bare soils and/or herbaceous species resistant to hypersaline conditions (i.e. pore-water salinity > 40 psu, Brinson 1993). The salt-flats are followed by a short band of shrubby *Avicennia marina* and a subsequent and predominant band of short, and then tall *Rhizophora stylosa* stands next to the channels and coastlines. While both the natural and mining sites featured a clear vegetation zonation, the aquaculture site also included a mixed zone of arborescent *A. marina* and *R. stylosa* after a band of shrubby *A. marina* (Figure 62).

6.3.2 Sampling layout

Soil and plant samples were identical as those studied in Chapter 5. Samples were collected at each site in a minimum of 30 circular plots of 7 m radius along transects perpendicular to the main channel, following the sampling design of Kauffman and Donato (2012). This sampling protocol was designed to cover mangrove habitats along the intertidal gradient, from the shrubby *A. marina* at the border of the salt marsh to the arborescent *R. stylosa* at the border of the river or coastlines (Figure 62).

6.3.3 Soil collection

Soil samples were collected with a stainless steel corer (8 cm in diameter and 50 cm length) in duplicates during low tide. Within each site, duplicate samples were collected in a minimum of 15 plots, at five sampling locations in the *A. marina* stands at the border of the salt-marsh, five sampling locations in the small *R. stylosa* stands, and five in the

big *R. stylosa* stands at the border of the channels or coastlines. At the aquaculture site, an additional five locations were selected in the mixed zone of the arborescent *A. marina* and *R. stylosa* (Figure 62). The total sampling depth of 50 cm was chosen to include most *A. marina* and *R. stylosa* live roots. Each soil core was divided into five sections (0–2.5, 7.5–10, 15–20, 25–30, and 40–50 cm) while in the field. These five sections and the core depth were selected based on the main transitional depths in chemical and elemental soil properties observed by Marchand et al. (2004, 2011a, 2011b, 2012, 2016) in various mangroves of French Guiana and New Caledonia.

6.3.4 Soil physico-chemical parameters

Soil sample Eh, pH and temperature (T) of the pore water of each soil section were measured using a portable pH/mV/T meter (Multi 350i, Wissenschaftlich-Technische Werkstätten, Germany) with a Pt-Ag/AgCl electrode (SenTix ORP, WTW) and a pH electrode with temperature sensor (SenTix 81, WTW) directly inserted into the soil sample immediately after collection. In addition, a known volume of soil was collected using a graduated syringe (50 ml) with the tip cut off to measure the pore-water salinity, pore-water content (WC) and bulk density, i.e. the ratio of dry mass of solids to bulk volume of the sample (BD). Full details of these measurements are presented in Chapter 3. The remaining soil samples from the initial large core were freeze-dried at − 80 °C (FreeZone 2.5 Liter Bench-top, Labconco, Kansas City, USA) and kept in the dark until elemental analyses could be conducted.

6.3.5 Plant material collection and tree measurements

At each circular plot, green and senesced leaves were harvested directly from a minimum of 10 mature trees (Figure 62). Senesced leaves were identified as yellow leaves easily detachable by a slight pull (Lovelock et al. 2007, e Silva et al. 2007) and therefore most likely to be in the next litterfall pool. As leaf chemical composition and structural characteristics are likely to vary along the vertical gradient of the canopy, an equal number of leaves were handpicked from the bottom, middle and top layers of the canopy of each tree. In each plot, three leaves of each layer of the canopy were kept at − 80 °C until further chlorophyll-a analyses could be conducted in the laboratory. The remaining leaves of each tree were then pooled together, and two sets of leaves per plot (from five trees each) were used as replicates for elemental analyses. In addition, coarse roots (≥ 2mm diameter), aerial roots (pneumatophores of *A. marina* and stilt roots of *R. stylosa*) and branches from the same trees were collected (Figure 62). The coarse roots and pneumatophores of *A. marina* were thoroughly rinsed with demineralised water (Marchand et al. 2016). All plant samples were dried at 55 °C until they reached constant weight.

Total basal area, canopy volume and tree height were measured for each sampled tree. The tree height was measured with a 16 m length telescopic stick, from the ground level to the upper boundary of the canopy, discounting inflorescences and any exceptional branches projecting above the foliage (Cornelissen *et al.* 2003). Canopy volume was calculated using the length, width and height of the canopy measured with a telescopic stick (Ross et al. 2001). Girths of *R. stylosa* were measured above the highest stilt root, where a true main stem existed (Clough and Scott 1989, Komiyama *et al.* 2005, Kauffman

and Donato 2012). Girth of *A. marina* stems were measured at 30 cm above the soil surface, following Tran et al. (2017).

6.3.6 Elemental analyses

Total elemental extractions of C, N, K, Ca, Mg, P, S, Na, Fe, Mn and Al were conducted in duplicate at each of the five sections of soil cores and on each plant material type. All elemental analyses were performed at the Institute of Research for Development (IRD) of Nouméa, New Caledonia (IMAGO, Certificate ISO 9001: 2015). Total Organic Carbon content (TOC) in soil and total C in plants were measured using a solid sample module (SSM-5000A) combined with a total organic carbon (TOC-L) analyser (Shimadzu, Kyoto, Japan). Total nitrogen (ammonium, nitrate, nitrite- and organic N) content in plant and soil samples was extracted by the Kjeldahl's wet oxidation method (ISO 11261 : 1995, Pétard 1993) and then quantified in a continuous flow analyser (Autoanalyser Technicon II, AxFlow, Milan, Italy). Total element concentrations were determined by inductively coupled plasma emission spectroscopy (ICP-OES, Varian, Australia) after extraction in a solution of 10% w/v solution of ammonium fluoride (FNH_4) and nitric acid (70%) for soil samples, and in a solution of 1% w/v solution of ammonium fluoride (FNH_4) and nitric acid (70%) for plant samples. The elemental analyses and sample preparation are fully described in sections 3.3.5 and 3.3.7 of this work.

6.3.7 Bioconcentration and translocation of elements in plant material

For each plant component (coarse root, aerial root, wood, green and senesced leaves), the bioconcentration factor (BCF) of each element was calculated by dividing the concentration of the element within each of the plant components by its mean total

concentration in the entire soil core. For each of the aboveground plant components, the translocation factor (TF) of each element was calculated by dividing the concentration of the element within each of the aboveground components by its concentration in the coarse roots (Marchand et al. 2016).

6.3.8 Resorption Efficiency

Resorption efficiency (RE) is defined as the mobilization and withdrawal of nutrients from senesced leaf tissues prior to abscission (Chapin 1980, Killingbeck 1996). The RE of an element was measured as the percentage of its reduction between green and senesced leaves as follow:

$$X\ RE\ (\%) = \left(\frac{X\ green - X\ sen\ x\ MLCF}{X green} \right) x\ 100$$

where, X stands for a given element and MLCF stands for Mass Loss Correction Factor, calculated as the ratio of dry mass of senesced leaves (sen) to that of green leaves (green) (Van Heerwaarden et al. 2003). The MLCF factor accounts for mass losses occurring during senescence due to resorption of soluble carbon compounds (Aerts 1996, Vergutz et al. 2012). Negative value of RE indicates a retranslocation of the element toward senesced leaves. This results in an accumulation of elements in senesced leaves compared to the green leaves. Thus, RE gives information on nutrient conservation strategy in plants. It is complementary to the terminal elemental concentrations in senesced leaves (resorption proficiency), which gives the concentration of an element before leaf abscission (Killingbeck 1996).

6.3.9 Chlorophyll-a analyses

Chlorophyll-a (chl-a) contents in green leaves were measured by a Konica Minolta SPAD-502 meter (Osaka, Japan), a non-destructive method that measures the difference of spectral absorbance in the red and near-infrared regions (650 and 950 nm). The SPAD values obtained (unitless) were then converted in chlorophyll-a (μg cm^{-2}) by empirical calibrations between SPAD units and extracted chl-a values (Coste et al. 2010). This calibration curve was developed for each species after extracting the chlorophyll from a minimum of 30 leaves kept at − 80 °C. Briefly, a total of 0.78 cm² of leaf tissue was sampled (area cover by the SPAD meter disk), weighted, and grounded in 10 ml of acetone 80% in a tissue grinder Potter-Elvehjem until complete discolouration of the leaf disks. The extracts were then centrifuged, and their absorbance measured at 663.2 and 646.8 nm in a spectrophotometer (Evolution 201, Thermo Scientific, resolution range 1 - 4 nm) calibrated using a commercial solution of spinach. The concentration in chl-a was then determined using the equations developed by Wellburn (1994):

$$\text{Chl-a } (\mu g\ ml^{-1}) = 12.21\ A_{663.2} - 2.81\ A_{646.8}$$

The coefficient of determination of the relationship SPAD - Chl-a was 0.89 for *R. stylosa* and 0.91 for *A. marina* (p-values < 0.05).

6.3.10 Data analyses

For each soil parameter, we compiled the mean total values within the entire soil depth profile. Variables whose distribution did not meet the assumption of normality were transformed with the Box-Cox power transformation (Osborne 2010). In each of the soil-plant continuum compartments, the means of each variable in the six different stands

(3 sites x 2 species) were compared and tested by the means of unbalanced two-way ANOVAs followed by Tukey's tests. When the assumptions of the ANOVA (normality and homoscedasticity) were violated, an aligned ranks transformation ANOVA was substituted to the two-way ANOVA (Mangiafico 2016). In each of the soil-plant continuum compartments, the spatial patterns and relationships between variables were analysed with principal component analyses (PCA) and Pearson's correlation analyses. The relationship between the tree parameters of each species (height, volume of canopy, basal area) and the elemental concentrations in the different plant material were tested in variation partitioning, by the means of multiple regression analyses (Borcard et al. 2018). All analyses were performed with R software.

6.4. Results

6.4.1 Interspecies differences of tree traits along a semi-arid intertidal gradient

The mean heights and canopy volumes of *R. stylosa* trees were approximately twice to three times as high as those of *A. marina* at all study sites (Table 14, illustrated in Figure 63). A dramatic increase in tree heights and canopy volumes was also observed in *R. stylosa* stands from landside to seaside at every site. In general, *A. marina* had more stems per individual and lower basal area than *R. stylosa*. The total tree basal area per individual of *A. marina* was 20% higher at the natural site compared to the mining and aquaculture sites (Table 14), whereas it reached the greatest values in the aquaculture site for *R. stylosa*, followed by the natural and then mining sites. For both species, the lowest values of tree height and canopy volume were measured in the natural site; they were greater at the mining site and reached a maximum at the aquaculture site (Table 14). The heights

of *R. stylosa* trees in the aquaculture site reached a maximum of 12.5 m along the

outflowing creek and a minimum of 2.2 m height next to the pond outlets (Table 14).

Conversely, the height of *A. marina* trees reached maximum value of 4.3 m next to the

pond outlets in the mixed species stands and decreased progressively down to ~ 1.1 m

high away from the pond outlets (Table 14). Lastly, the mean (± SD) leaf chl-a

concentrations were about six times higher in the canopy of *R. stylosa* (6.21 ± 0.78 mg g^{-1}) compared to that of *A. marina* (1.21 ± 0.22 mg g^{-}1, Table 14). While chl-a contents did

not vary significantly among study sites for *R. stylosa*, chl-a content in the foliage of *A.*

marina was significantly higher in the undisturbed site than in the aquaculture site (Table

14).

Table 14. Mean values (±SD, minimum - maximum) of the physico-chemical properties and tree characteristics in *A. marina* and *R. stylosa* stands in each of the three study sites (Natural, Mining, Aquaculture). Variables featuring significant inter-species, inter-site variations and/or species-site interactions of their values are indicated by "[1]", "[2]" and/or "[3]", respectively (two-ways ANOVA). For each variable, same lowercase letters indicate stands that did not differ significantly by their values (post-hoc comparison tests, p < 0.05)

variable	unit	*A. marina*		*R. stylosa*	
		Natural			
Salinity [1,2]	-	41.09[bc]	(± 8.85, 25.00 - 50.00)	27.45[a]	(± 5.30,21.00 - 35.5)
TOC[1,3]	%	8.63[bc]	(± 2.22, 6.32 – 13.97)	8.47[bc]	(± 1.89, 6.23 -10.87)
Eh [1]	mV	6.26[ab]	(± 67.33, -95.00 - +106.67)	-30.30[ab]	(± 115.09, -122.5 - +98)
pH [-]	-	6.53	(± 0.11, 6.3 - 6.65)	6.46	(± 0.33, 6.20 - 7.02)
wc [2]	%	72.93[a]	(± 5.34, 62.56 - 81.65)	72.12[a]	(± 9.11, 62.07 - 80.31)
BD [-]	g cm^{-3}	0.46	(± 0.12, 0.30 - 0.70)	0.40	(± 0.13, 0.22 - 0.55)
Fe [1,2,3]	g kg^{-1}	33.44[a]	(± 8.51, 24.01 - 52.73)	43.13[b]	(± 3.25, 38.42 - 47.25)
Mn [1,2,3]	g kg^{-1}	0.15[b]	(± 0.03, 0.10 - 0.20)	0.35[b]	(± 0.07, 0.26 - 0.43)
Al [2]	g kg^{-1}	41.76[c]	(± 4.23, 34.57 - 49.65)	43.27[bc]	(± 5.87, 34.16 - 49.50)
Tree height [1,2]	cm	143[a]	(± 33, 58 - 198)	279[b]	(± 119, 175 - 573)
Basal area [1,2]	cm²	98.79[ab]	(± 128.47, 6.69 - 663.57)	92.97[ab]	(± 82.25, 23.00 - 254.45)
Nb of stems [1]		2.3[a]	(± 1.3, 1 - 6)	1.5[b]	(± 0.8, 1 - 4)
Canopy volume [1,2]	m³	5.32[a]	(± 4.71, 0.53 - 21.37)	15.24[ab]	(± 28.60, 1.55 - 100.60)
Chl [1,2,3]	mg g^{-1}	1.33[b]	(± 0.11, 1.01 - 1.42)	6.24[c]	(± 0.72, 4.83 - 7.17)
		Mine			
sal	-	42.03[bc]	(± 8.07,35.00 -55.50)	36.35[ab]	(± 10.33,25.00 -55.00)
TOC	%	3.80[a]	(± 1.43, 2.26 – 5.17)	10.93[c]	(± 3.94, 5.04 -15.44)
Eh	mV	227.1[b]	(± 137.65, 40.30 - +373.90)	-80.17[a]	(± 77.93, -198.00 - +82.50)
pH	-	6.53	(± 0.01, 6.51 - 6.55)	6.34	(± 0.56, 2.53 - 7.10)
wc	%	62.24[b]	(± 8.70, 49.18 - 73.47)	63.31[b]	(± 9.72, 55.28 -77.21)
BD	g cm^{-3}	0.47	(± 0.14, 0.33 - 0.70)	0.51	(± 0.17, 0.33 - 0.87)
Fe	g kg^{-1}	108.75[e]	(± 8.75, 97.19 - 118.20)	86.01[de]	(± 12.45, 61.76 - 101.74)
Mn	g kg^{-1}	0.84[c]	(± 0.15, 0.62 - 1.03)	0.38[b]	(±0.05, 0.31 - 0.45)
Al	g kg^{-1}	14.01[a]	(± 1.64, 11.72 - 16.28)	30.25[ab]	(± 19.01, 1.51 - 60.42)
Tree height	cm	161[a]	(± 26, 134 - 196)	382[bc]	(± 145, 213 - 685)
Basal area	cm²	72.89[ab]	(±41.47, 36.48 - 121.41)	80.72[ab]	(± 69.20, 11.55 - 327.15)
Nb of stems		2.5[a]	(± 2.5, 1 - 9)	2.2[a]	(± 1.9, 1 - 9)
Canopy volume	m³	33.95[ab]	(± 49.15, 6.32 - 107.42)	45.19[b]	(± 48.38, 2.11 - 154.03)
Chl	mg g^{-1}	1.18[ab]	(± 0.05, 1.13 - 1.24)	5.85[c]	(± 0.84, 4.34 - 7.61)
		Aquaculture			
sal	-	48.71[c]	(± 3.45, 45.00 -54.00)	42.11[bc]	(± 7.19, 30.00-50.00)
TOC	%	5.79[ab]	(± 2.82, 1.84 – 9.7)	8.74[bc]	(± 1.84, 5.25 – 12.03)
Eh	mV	44.66[ab]	(± 107.46, -89.00 - +159.80)	-115.89[a]	(± 50.09, -176.00 - -27.5)
pH	-	5.63	(± 1.84, 2.47 - 6.53)	5.34	(± 1.50, 2.47 - 6.46)
wc	%	66.08[ab]	(± 7.45, 55.28 -74.60)	71.57[ab]	(± 6.97, 55.28 - 76.89)
BD	g cm^{-3}	0.45	(± 0.12, 0.26 - 0.66)	0.30	(± 0.05, 0.26 - 0.36)
Fe	g kg^{-1}	76.93[cd]	(± 2.82, 70.90 - 79.15)	64.06[c]	(± 7.83, 55.66 - 78.79)
Mn	g kg^{-1}	0.46[b]	(± 0.06, 0.35 - 0.53)	0.37[b]	(± 0.08, 0.25 - 0.53)
Al	g kg^{-1}	42.89[bc]	(± 7.25, 36.18 - 52.16)	31.30[ac]	(± 4.48, 24.26 - 38.17)
Tree height	cm	267[ab]	(± 117, 116 - 433)	476[c]	(± 220, 224 - 1250)
Basal area	cm²	75.16[a]	(± 116.88, 5.35 - 448.82)	185.79[b]	(± 181.09, 15.60 - 881.78)
Nb of stems		2.3[a]	(± 1.2, 1 - 4)	2.1[ab]	(± 0.8, 1 - 4)
Canopy volume	m³	15[a]	(± 23.54, 0.83 - 75.90)	26.63[ab]	(± 20.25, 4.11 - 65.52)
Chl	mg g^{-1}	0.99[a]	(± 0.23, 0.70 - 1.40)	6.36[c]	(± 0.74, 4.99 - 7.72)
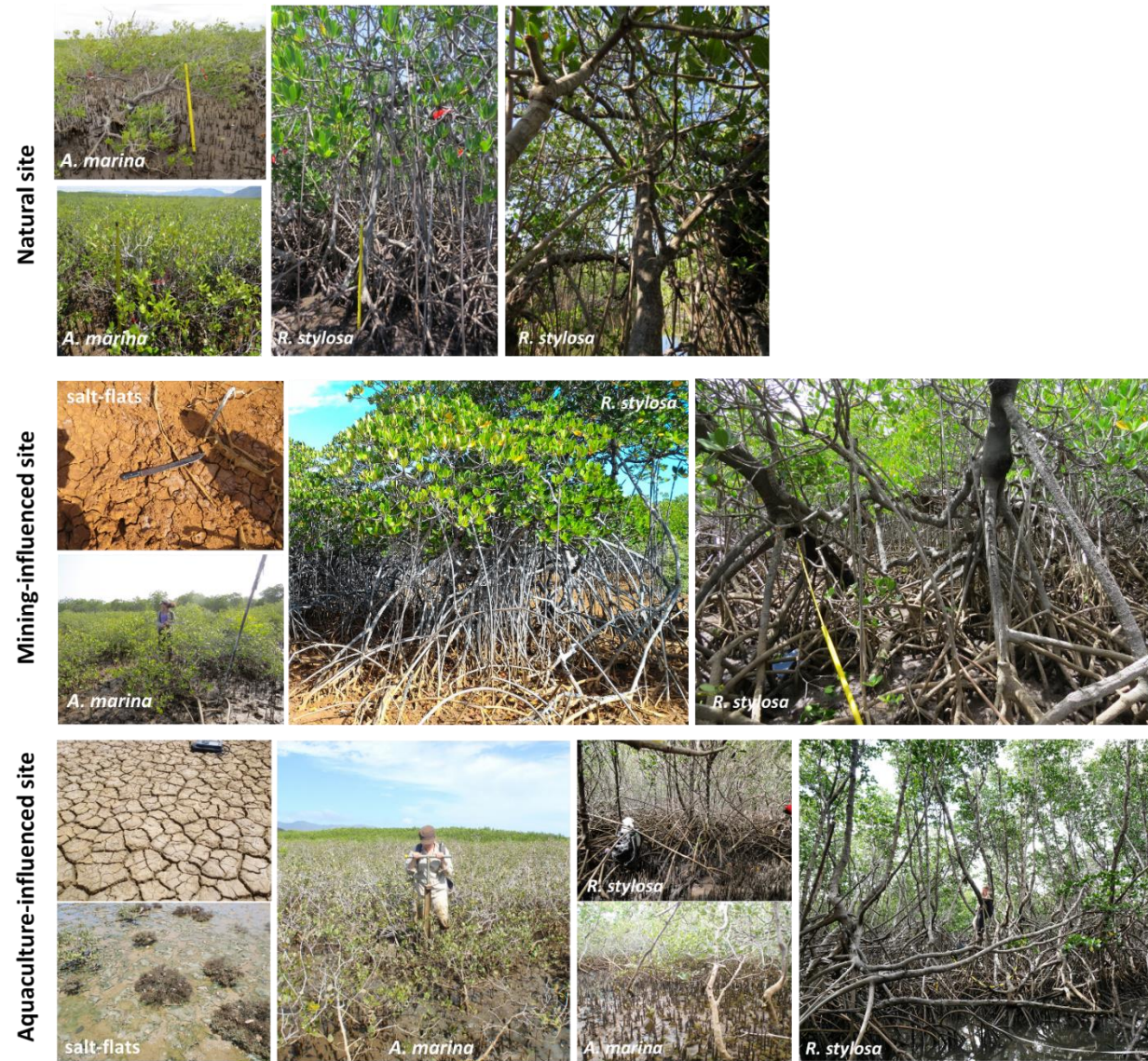
Figure 63. Mangrove zonation and vegetation physiognomy along the intertidal gradient in the three study sites. In each site, salt-flats at the summit of the elevation gradient in landward areas are followed by shrubby *A. marina* stands and subsequent short then tall *R. stylosa* stands next to the channels and coastlines, illustrated from left to right on the figure. In the aquaculture site, tall *A. marina* and *R. stylosa* stands also develop in landward areas next to the pond outlets

6.4.2 Soil properties and macroelement status along a semi-arid intertidal gradient

The mean (± SD) and range of each macroelemental concentration in the soil and plant compartments are illustrated in Figure 64 and Figure 65 and fully detailed in Appendix 14 to Appendix 16 of this work. The ANOVA and PCA showed that high soil variations occurred between study sites (Figure 66).
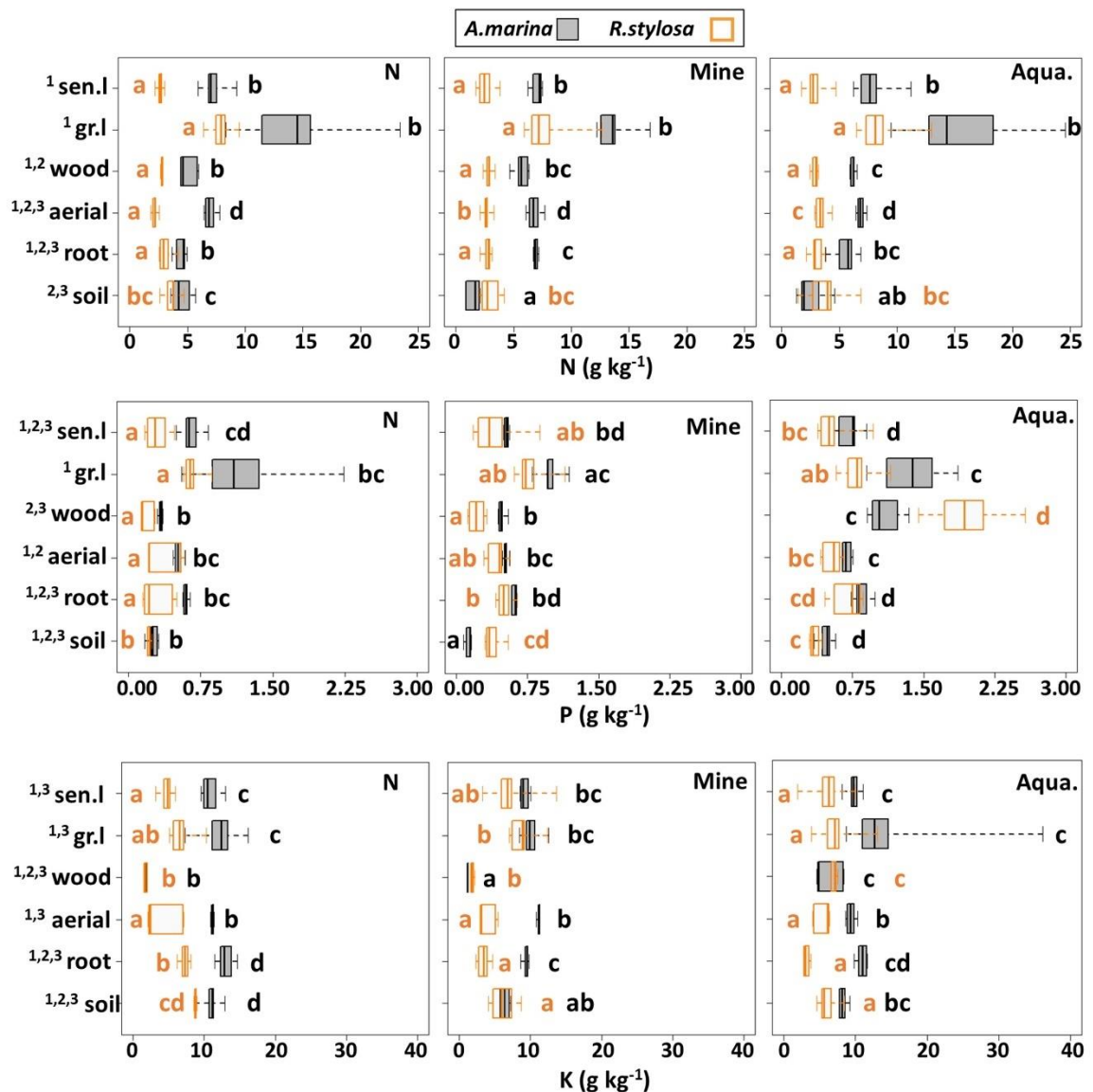
Figure 64. Box plots (mean, upper and lower quartiles, minimum and maximum) of the elemental concentrations of N, P and K (in g kg^{-1} of dry weight) in the different soil and plant compartments of the *R. stylosa* (orange box plots) and *A. marina* (grey box plots) stands in each site of study ("sen.l" = senesced leaves, "gr.l" = green leaves, "aerial" = aerial roots). Variables featuring significant inter-species, inter-site variations and/or species-site interactions of their values are indicated by "[1]", "[2]" and/or "[3]", respectively (two-ways ANOVA). Same lowercase letters indicate stands that did not differ significantly by their values (post-hoc comparison tests, $p < 0.05$)
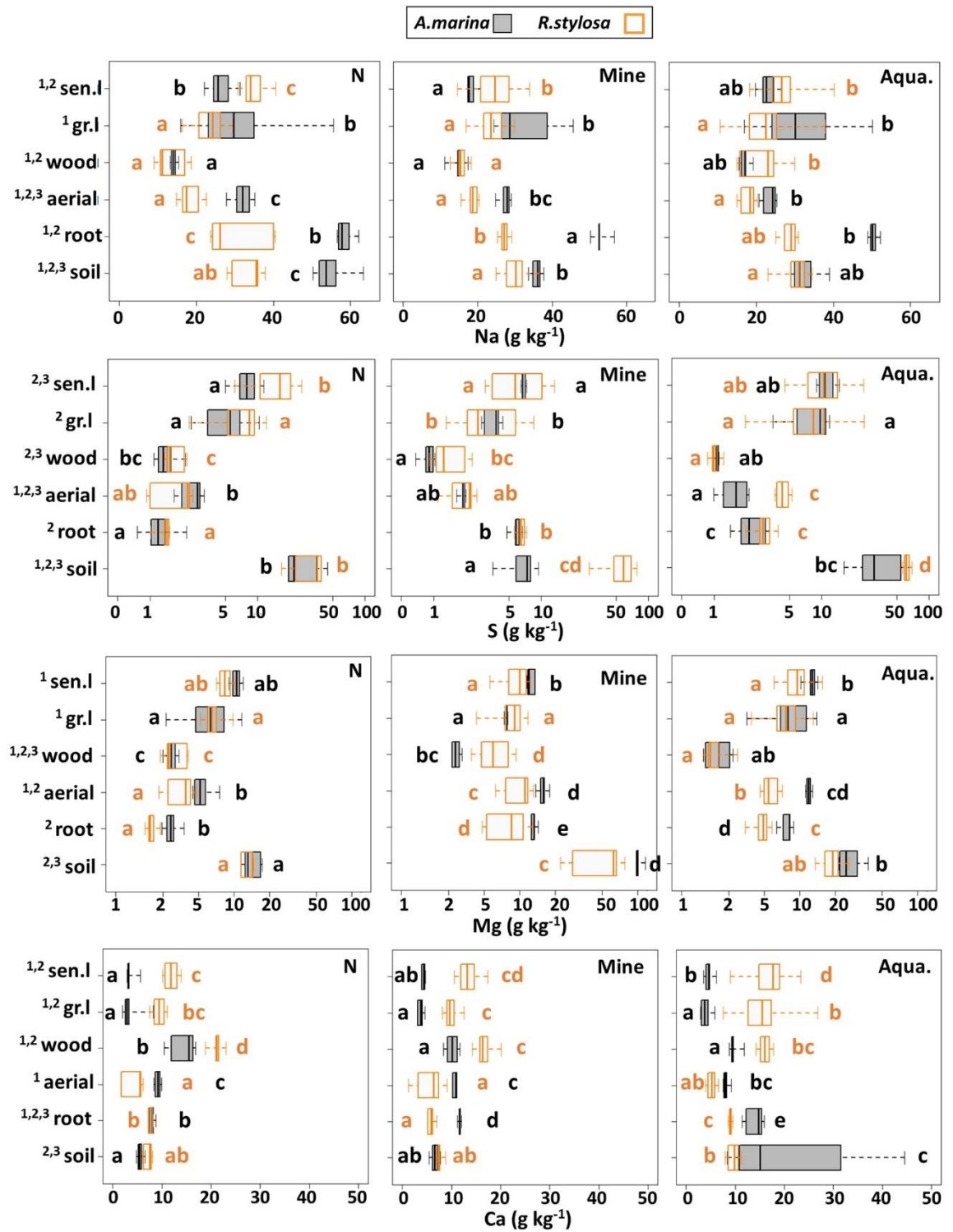
Figure 65. Box plots (mean, upper and lower quartiles, minimum and maximum) of the elemental concentrations of Na, S, Mg and Ca (in g kg^{-1} of dry weight) in the different soil and plant compartments of the *R. stylosa* (orange box plots) and *A. marina* (grey box plots) stands in each site of study ("sen.l" = senesced leaves, "gr.l" = green leaves, "aerial" = aerial roots). Variables featuring significant inter-species, inter-site variations and/or species-site interactions of their values are indicated by "[1]", "[2]" and/or "[3]", respectively (two-ways ANOVA). Same lowercase letters indicate stands that did not differ significantly by their values (post-hoc comparison tests, $p < 0.05$)
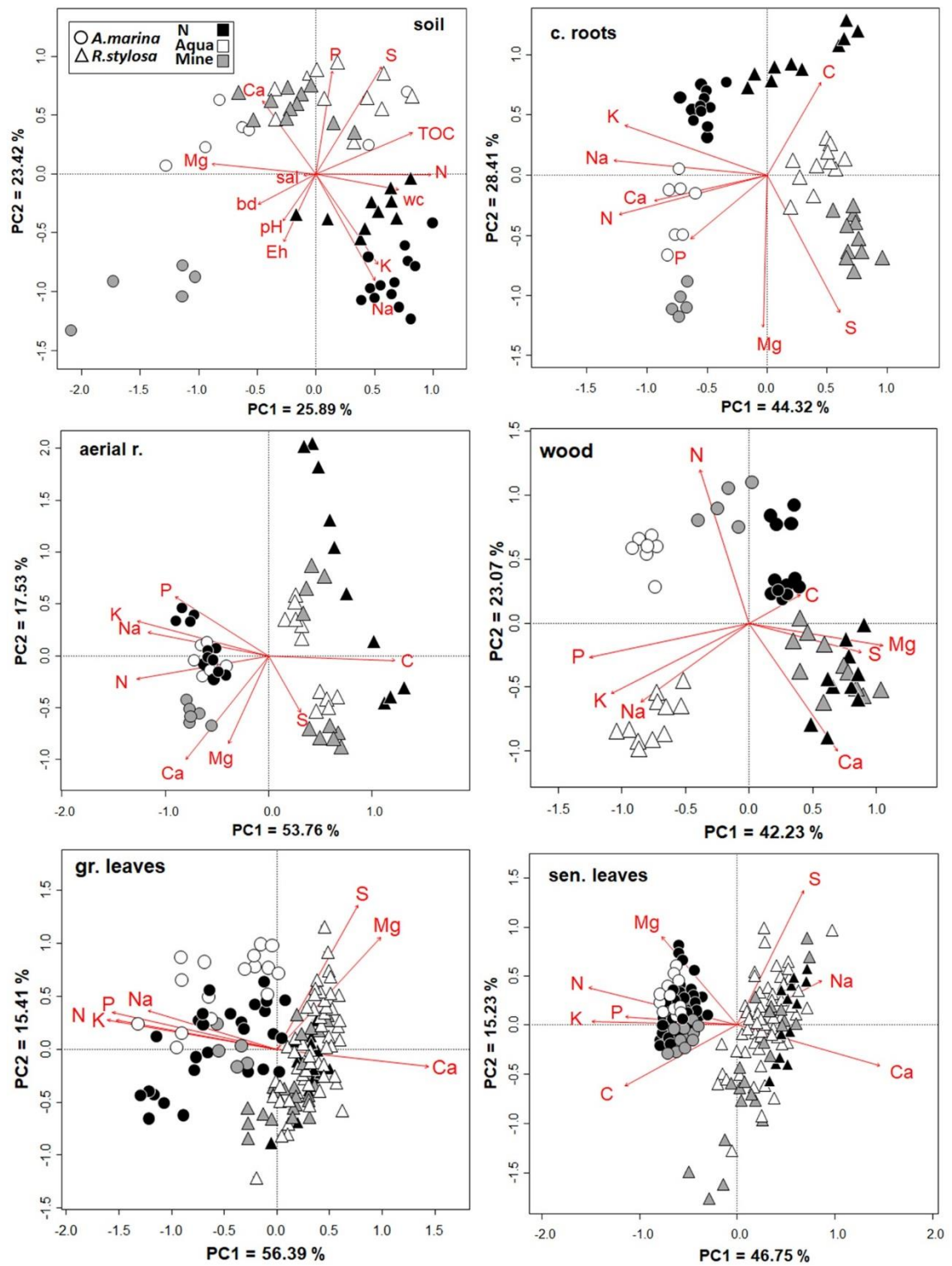
Figure 66. Principal Component Analyses of the macroelements in each compartment of the plant-soil continuum in the *A. marina* and *R. stylosa* stands (c.root = coarse root, aerial r. = aerial root, gr. leaf = green leaf, sen. leaf = senesced leaf), all study sites combined (N = Natural, M = Mining-influenced, A = aquaculture-influenced). The contribution of each principal component (PC1 and PC2) to the total variation of the data set are indicated on each axes in %

The soils of the natural site were characterized by higher mean concentrations of TOC, N, Na and K compared to the other study sites (Table 14, Figure 64, Figure 65). However, the maximum N concentrations recorded in this study were found in the small *R. stylosa* stands next to the pond outlets (6.8 g kg^{-1}). The soils of the aquaculture site also stood out with the highest mean concentrations of Ca and P measured in this study (maximum values of 44.52 and 0.52 g kg^{-1}, respectively), and with the lowest minimum values of the TOC recorded in this study (1.84%, Table 14). The mining site was characterized by lower mean TOC and concentrations of Na, K, N and Al (Table 14, Figure 64 and Figure 65), while showing total concentrations of Mg up to twofold greater than those found in the other study sites (Table 14, Figure 65). Maximum Fe and Mn concentrations were also found in the mining site, followed by the aquaculture and the natural site (Table 14).

All sites considered, the soils of the *A. marina* stands had mean values of salinity, Na, Eh, pH, K, Mg, Fe, Mn higher than those recorded in *R. stylosa* stands by 16, 30, 224, 4, 29, 17, 20 and 25 %, respectively. Conversely, the mean concentrations of TOC and S recorded in the *A. marina* stands were 23 and 51% lower, respectively, than those measured in *R. stylosa* stands (Table 14, Figure 65). Although N did not vary significantly between species stands, N concentrations in soils at the natural site were higher in the *A. marina* stands than in the *R. stylosa* stands, whereas the opposite trend was observed in the other sites. Higher P concentrations were found in *A. marina* stands than in that of *R. stylosa* at the natural and aquaculture sites, whereas the opposite trend was observed in the mining site (Figure 64). No significant differences in Ca and Al concentrations were observed between *A. marina* and *R. stylosa* soils (Table 14, Figure 65). Finally, the soils of the mixed stands located just next to the pond outlets had the lowest BD, pH and Eh values, and the highest N and S concentrations recorded in this study (Table 14, Figure 64 and Figure 65).

Results from correlation analyses between soil variables varied considerably between the two species stands (Figure 67). In the soils of *A. marina* stands, the TOC, WC, N, K, S and Al patterns were similar and negatively correlated with those of Eh, BD, Ca, Mg, Fe and Mn (Figure 68, all p_{adj}-values < 0.05). In these stands, P was also positively correlated with Ca, S and Al. Conversely, the pattern of TOC in the *R. stylosa* stands tended to be positively correlated to that of Fe, Mn and Mg, although none of those relationships were statistically significant (all p_{adj}-values > 0.05). In these species stands, P concentrations were positively correlated with Fe, S and Mg (Figure 68, all p_{adj}-values < 0.05).
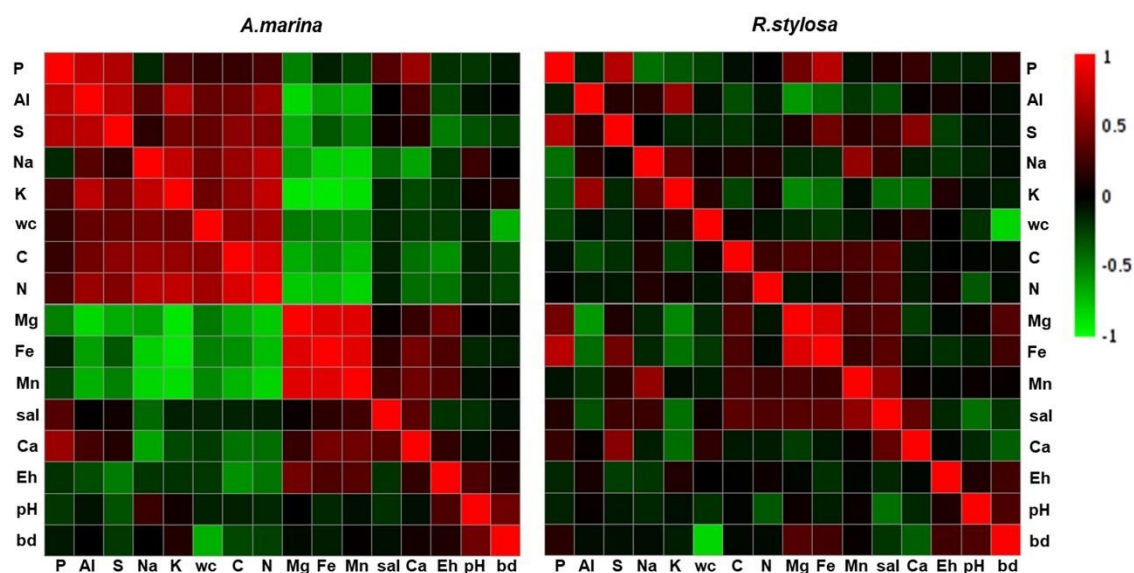
Figure 67. Heatmap of the Pearson's correlation coefficients (r from -1 to +1) between the physico-chemical properties and the total elemental concentrations within the soils of the *A. marina* stands (left) and the *R. stylosa* stands (right), all study sites combined. Green and red colours indicate low and high values of the Pearson correlation coefficients between two variables, respectively
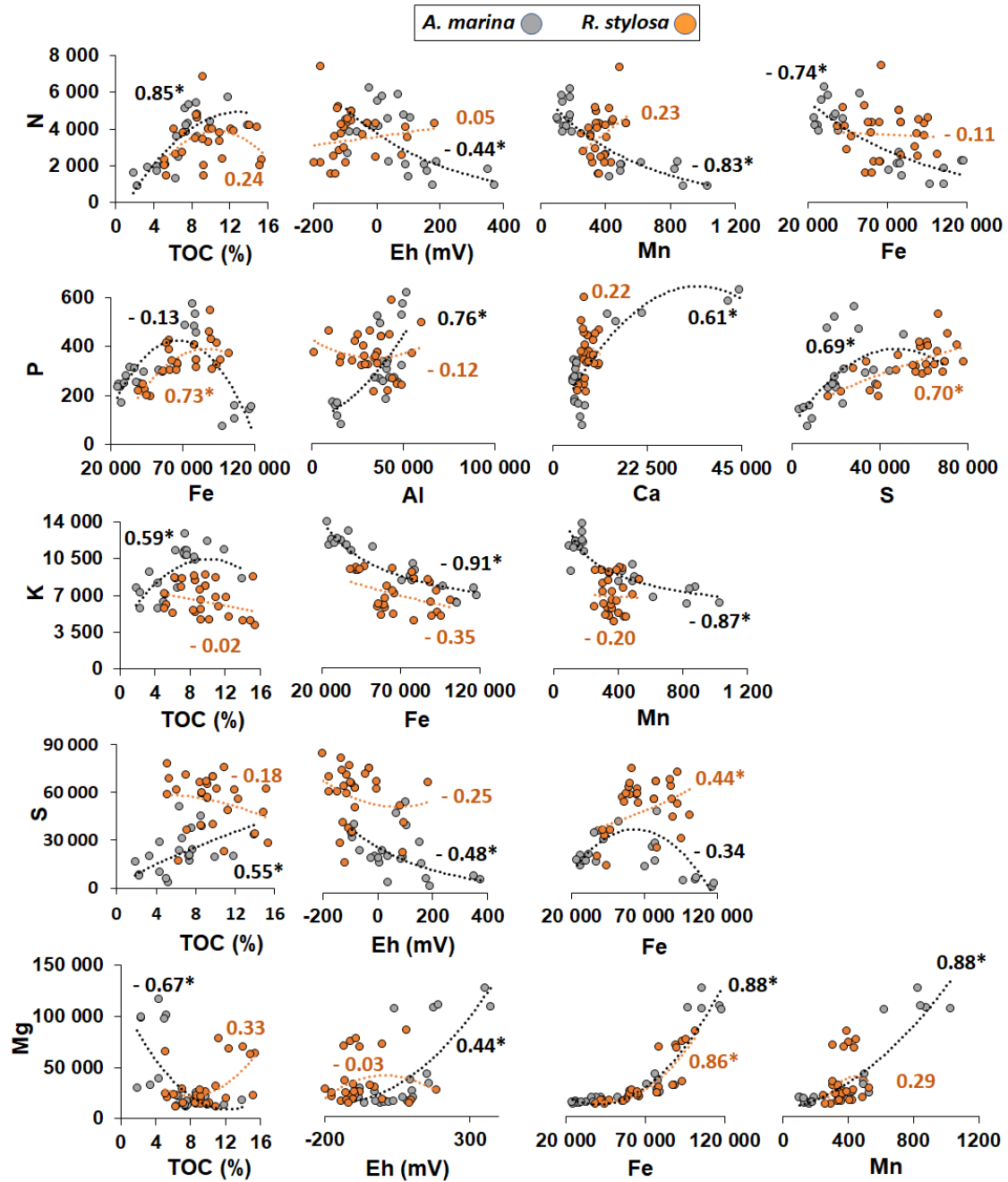
Figure 68. Details of the significant relationships between each macroelement concentration in soils and the other soil parameters in the *A. marina* stand*s* (grey dots) and *R. stylosa* stands (orange dots), all study sites combined. All concentrations are given in mg kg $^{-1}$. Significant Pearson correlation coefficients are marked by a " * "

6.4.3 Interspecies differences in elements concentrations and soil-plant transfers

The elemental distribution of the different plant materials along the components of each

PCA also showed a clear variation between the two mangrove species (Figure 66). This

interspecies variation was greatest in the green leaves (PC1 = 56.39%) > aerial roots (PC1

= 53.76%) > senesced leaves (PC1 = 46.75%) > coarse roots (PC1 = 44.32%), and lowest in the wood (PC2 = 23.07%).

The most striking result was that the concentrations of all macronutrients were higher in the green leaves and in the coarse and aerial roots of *A. marina* than in those of *R. stylosa* (Figure 64, Figure 65). The BCF of N, P, K and Ca (fully detailed in Appendix 17, Appendix 18) were also higher than 1 in each of those components. Overall, the RE of N, P and K of both species were positive and in general 10% higher for *R. stylosa* than *A. marina* (Figure 69, Appendix 17, Appendix 18).

Conversely, Mg and S were the only elements for which the BCF were lower than 0.5 in every plant material type of both species. For both species, the highest concentrations and TF of these elements were found in the aerial roots, green leaves and senesced leaves (Figure 65 and Figure 69). Both species also had a net negative RE for Mg and S (Appendix 17, Appendix 18). On the other hand, Ca was the only macronutrient that had BCF values higher or close to 1, with negative RE in all study sites. Maximum concentrations of this element were found in the wood, coarse and aerial root systems of *A. marina*, whereas the highest Ca concentrations were found in the wood and green and senesced leaves of *R. stylosa* (Figure 65). Finally, N, P, S, Mg and Ca concentrations in senesced leaves of *R. stylosa* and S, Ca and P concentrations in senesced leaves of *A. marina* increased significantly with increasing concentrations of these elements in the green leaves of each species (all $r > 0.65$ and p_{adj}-values < 0.05; details of these relationships can be found in Figure 70). There were no significant correlations between the concentrations of K in green and senesced leaves of both species, nor for N and Mg in *A. marina*.
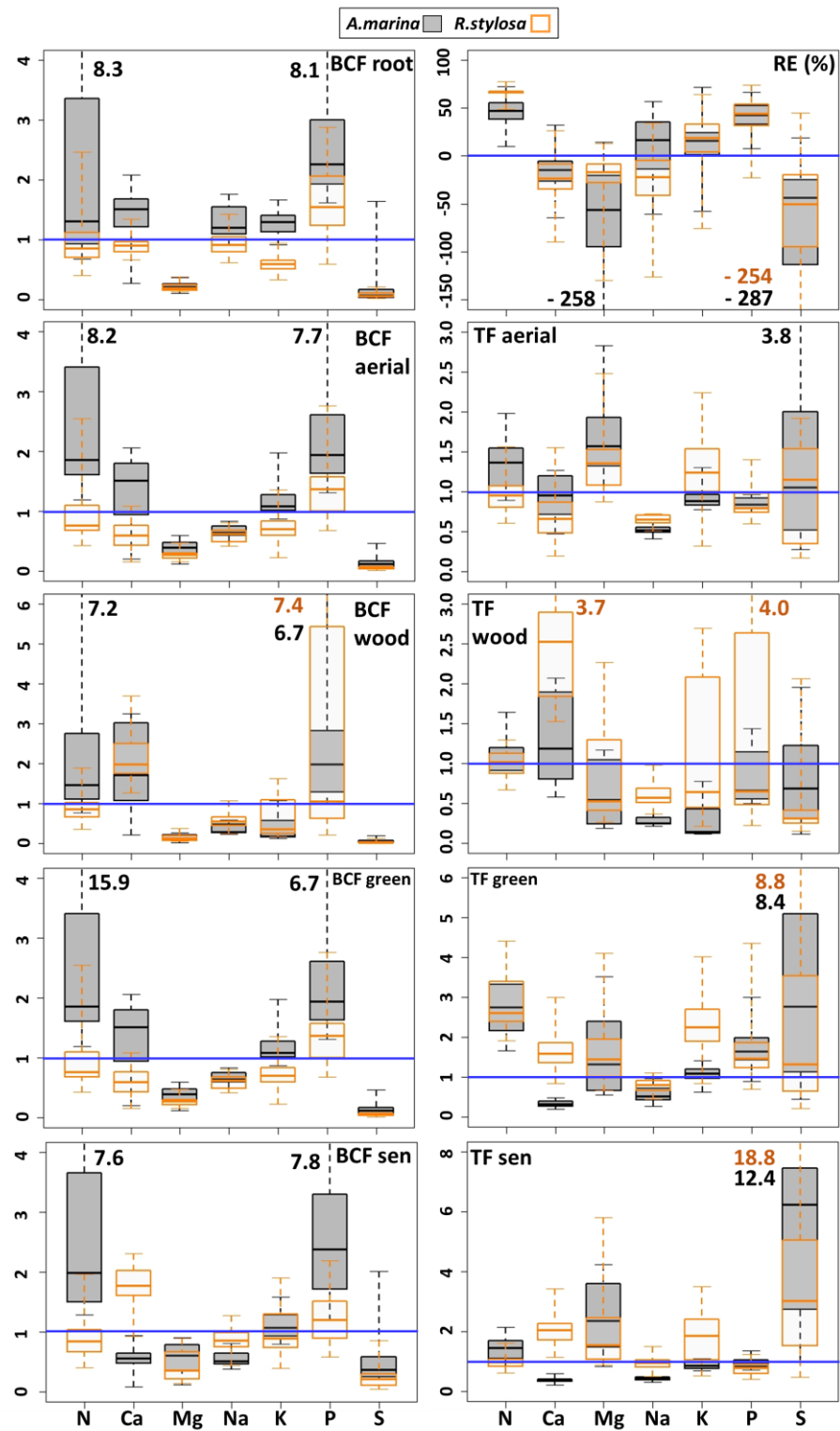
Figure 69. Boxplots (median, upper and lower quartiles, minimum and maximum) of the Resorption Efficiency (RE, %) and the Bioconcentration and Translocation Factors (unitless) of all macroelements and Na in the plant materials of *A. marina* (grey boxes) and *R. stylosa* (orange boxes), all study sites combined. The blue lines indicate the threshold of 1 for the BCF and TF and of 0 for the RE. Numbers indicate missing maximum values left out of the plots for better visibility
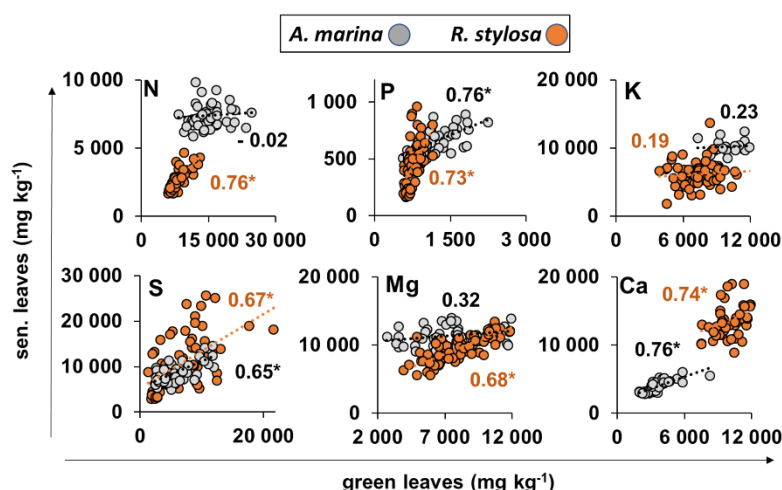
Figure 70. Relationship and regression coefficient (R^2) between the elemental concentrations in green and senesced leaves (sen) of *A. marina* and *R. stylosa* for N, P, K, Mg, S and Ca, all study sites combined. All concentrations are given in mg kg $^{-1}$. Significant regression coefficients are marked by a " * "

6.4.4 Correlation between macroelement concentrations in plant material and soils

All study sites combined, we observed a strong and positive relationship between macroelement concentrations in soils and those measured in the coarse roots of both species (Figure 71). The opposite pattern was only observed for N and S in the coarse roots of *A. marina* (Figure 71). Consequently, macroelement concentrations in the coarse roots of both species also co-varied with the soil variables correlated with the concentrations of these macroelements in soils (see second section of these results).

Increasing macroelement concentrations in soils also coincided with a significant increase of the corresponding elements in some of the different aboveground plant materials of both species. Thus, P concentrations increased in wood and green leaves of both species with increasing soil concentrations of P at the mining and aquaculture sites (*A. marina*: r = 0.78 and 0.62, respectively; *R. stylosa*: r = 0.44, and 0.45, respectively, all p_{adj}-values < 0.03). K concentrations in green and senesced leaves of *A. marina* also increased with increasing concentrations of K in the soils (r = 0.42 and 0.62, respectively, p_{adj}-values < 0.05). Mg concentrations increased in the aerial roots and senesced leaves of both species and in the wood and green leaves of *R. stylosa* with increasing Mg concentrations in the

soils (*A. marina*: r = 0.80, 0.47, respectively; *R. stylosa*: r = 0.93, 0.40, 0.34, 0.64 respectively, p_{adj}-values < 0.05). Increasing concentrations of Ca in the soils of the aquaculture site were accompanied by increasing concentrations of the same element in the green and senesced leaves of *R. stylosa* (r = 0.52, 0.62, respectively, p_{adj}-values < 0.04). Conversely, Ca concentrations in other plant materials of *A. marina* remained constant along the entire Ca spectrum in the soils of this species stands. A strong bell curve of soil-coarse root relationship was caused by extreme Ca concentrations in soils of the *A. marina* stand at the border of salt-flats in the aquaculture site (21 – 45 g kg^{-1}, r = 66, p_{adj}-value = 0.02). However, and as illustrated in this curve, the Ca translocation from the soil to the coarse roots of *A. marina* in those plots was restricted at those high concentrations in the soil (Figure 71). Contrastingly, N and S concentrations in the coarse roots of *A. marina* decreased sharply with increasing concentrations of these elements in soils. N also increased in the wood of *A. marina* with decreasing N concentrations in the soils at the aquaculture and mining sites (r = - 0.54, p_{adj}-value = 0.006, Figure 64). In addition, S concentrations increased in the green and senesced leaves of *A. marina* with increasing S concentrations in soils (r = 0.72, 0.76, respectively, p_{adj}-values < 0.01). Conversely, N remained constant in all plant materials of *R. stylosa* with increasing concentrations of these elements in the soils (all r < 0.1 and p_{adj}-values > 0.05, Figure 64 and Figure 71).
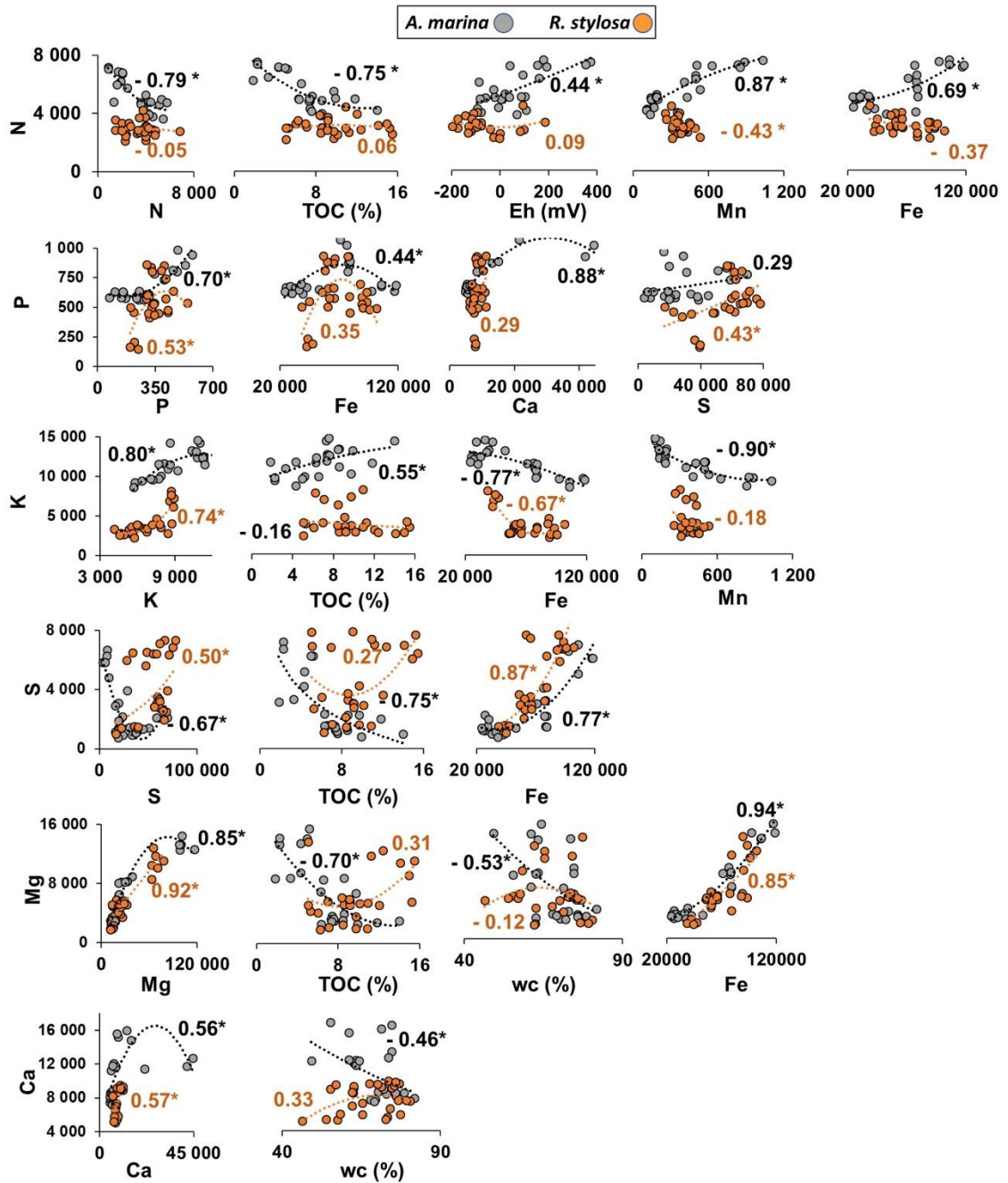
Figure 71. Details of the significant relationships between each macroelement concentration in soils and the other soil parameters in the *A. marina* stand*s* (grey dots) and *R. stylosa* stands (orange dots), all study sites combined. All concentrations are given in mg kg $^{-1}$. Significant Pearson correlation coefficients are marked by a " * "

6.4.5 Interspecies differences in Na concentrations in plant material

Overall, higher concentration and BCF of Na were found in every plant component of *A. marina* than in those of *R. stylosa*, with the exception of senesced leaves (Figure 65). As

Na concentrations increased in soils at the natural site, the concentrations of Na decreased in the wood material of both species and in the root system of *R. stylosa* (Figure 72). Conversely, Na concentrations in the coarse roots, aerial roots and in the senesced leaves of *A. marina* increased steadily with increasing Na concentrations in soils, with Na-BCF of the coarse roots > 1 in every study site (Appendix 18).

In the *A. marina* stands, leaf chl-a content increased with increasing Na concentrations in soils (r = 0.65, p_{adj}-value = 0.02, Figure 73). In the
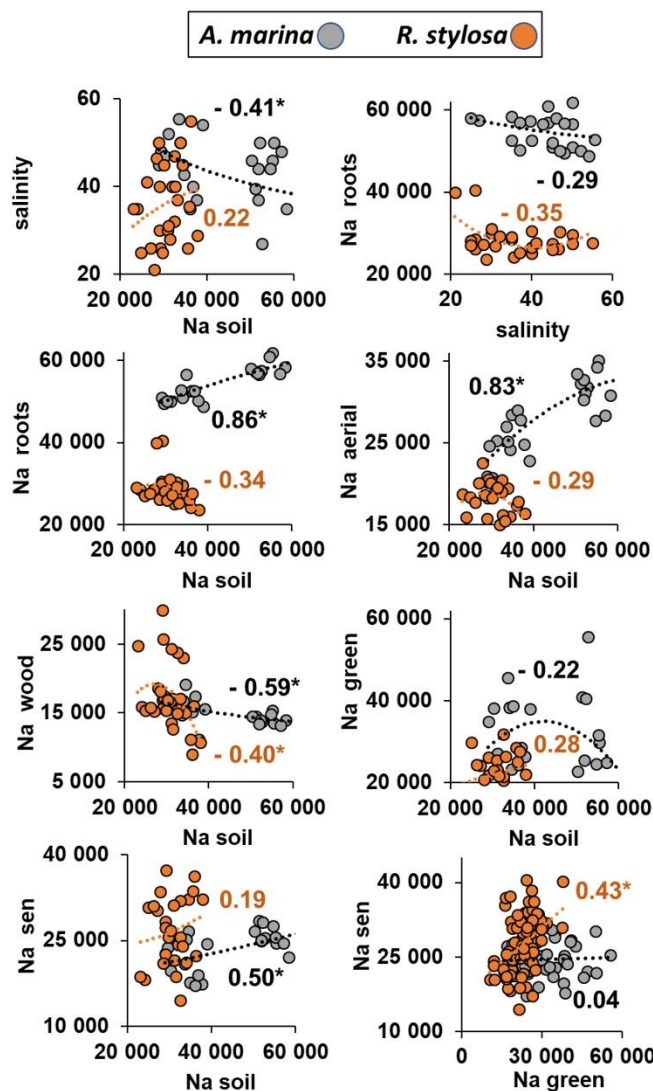
Figure 72. Relationship between salinity and total Na in soils of the *A. marina* and *R. stylosa* stands and total Na in the different plant materials of the *A. marina* and *R. stylosa* stands, all study sites combined. Pore-water salinity is unitless, all total Na concentrations are given in mg kg $^{-1}$. Significant Pearson correlation coefficients are marked by a " * "

green leaves of *A. marina*, Na concentrations were also positively correlated with the concentrations of N, K, P and negatively correlated with that of Mg (Figure 73). No significant correlations were found between Na and those macroelements in the green leaves of *R. stylosa* (Figure 73). However, K concentrations in senesced leaves of *R. stylosa*

decreased significantly with increasing concentrations of both Na in green and senesced leaves of this species (p_{adj}-value = 0.001, Figure 73). In contrast, K concentrations in senesced leaves of *A. marina* increased with increasing concentrations of Na in senesced leaves (p_{adj}-value = 0.001).
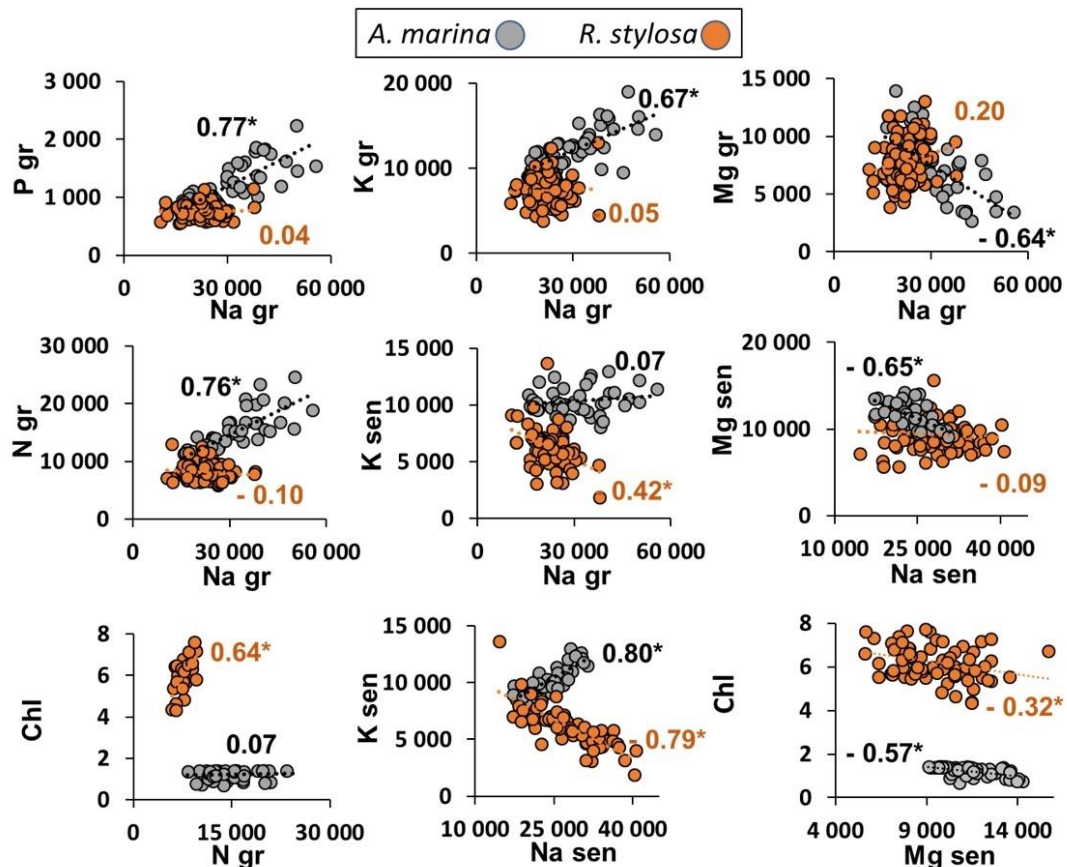
Figure 73. Details of the significant relationships between macronutrient concentrations and Na and chl-a in the foliage of *A.marina* stands (grey dots) and *R.stylosa* stands (orange dots), all study sites combined. Nutrient concentrations are given in mg kg $^{-1}$, chl-a concentrations are given in mg g $^{-1}$. Significant Pearson correlation coefficients are marked by a " * "

6.4.6 Relationship between macroelements and plant traits

Total Na and P were the only soil parameters significantly correlated with tree heights of both mangrove species and together explained 46% of the tree height variation of *A. marina*, and 31.6% of that of *R. stylosa* (R^2_{adj}, p_{adj}-values = 0.001 and 0.04, respectively, Figure 74).
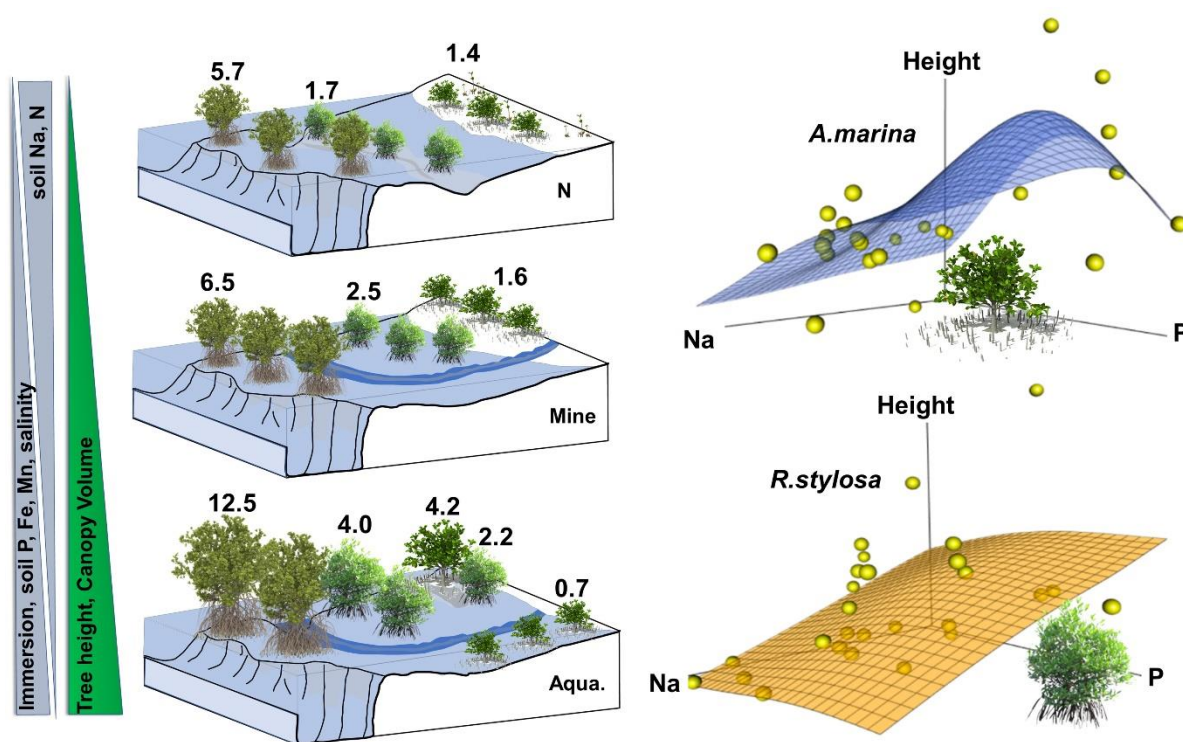
Figure 74. Diagram of the soil parameters and tree heights (given in m) in the sites of study (left); three-dimensional scatterplots of the relationship between tree height and Na and P concentrations in the soils in *A. marina* (top right) and *R. stylosa* stands (bottom right), all study sites combined

In addition, results of the variation partitioning of each tree morphological trait as a function of nutrient concentrations showed that nutrient patterns in coarse roots, aerial roots, wood and green leaves of *A. marina* coincided with 70, 37 and 59% of the total variations (R_{adj}^2 total) of tree height, basal area and canopy volume of this species, respectively (Figure 75). In *R. stylosa*, nutrients patterns coincided with 67, 58 and 56% of the total variations (R_{adj}^2 total) of tree height, basal area and canopy volume of this species, respectively (Figure 75).

The canopy volume of *A. marina* also increased with increasing Ca in its senesced leaves (r = 0.59, p_{adj}-value = 0.002). In *R. stylosa*, tree height, basal area and canopy volume increased with increasing P in the senesced leaves (r = 0.67, 0.52, 0.64, respectively, p_{adj}-values < 0.05). Tree heights of this species also increased with increasing N in the senesced

leaves (r = 0.55, p_{adj}-value = 0.002). Lastly, leaf chl-a contents were positively correlated with the concentrations of N in the green leaves of *R. stylosa* (p_{adj}-value = 0.01, Figure 73) and negatively correlated with Mg concentrations in the senesced leaves of both species (*A. marina* : p_{adj}-value = 0.02, *R. stylosa* : p_{adj}-value = 0.05, Figure 73).
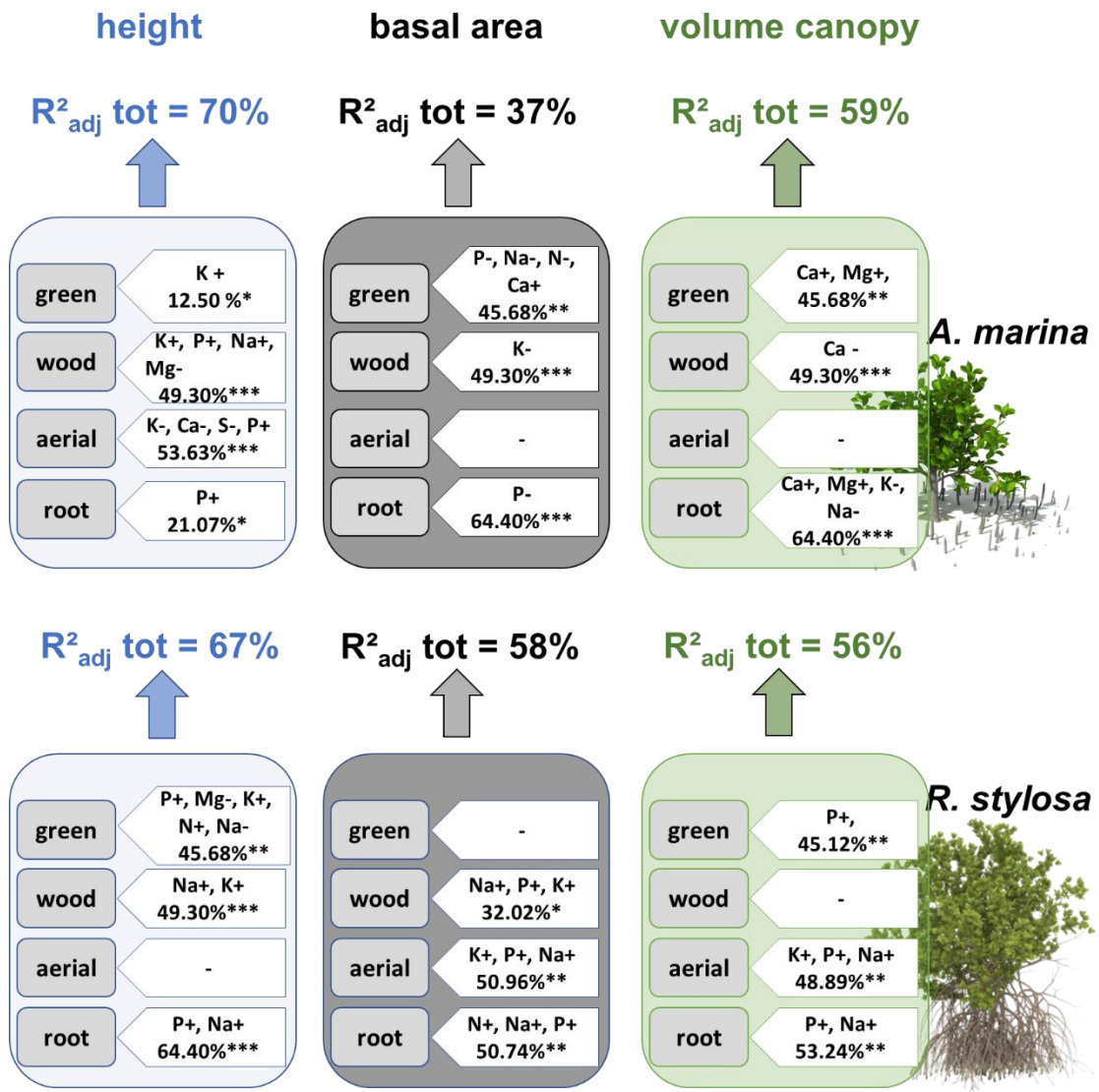
Figure 75. Variation partitioning of each tree morphological trait (tree height, basal area, canopy volume) as a function of nutrient concentrations in the different plant compartments of each species (coarse root, aerial root, wood and green leaves) by the means of regression analyses. In each plant compartment, nutrients that significantly contribute to the coefficient of determination (R^2_{adj}) are indicated. "R^2_{adj} tot" indicates the total variation of each tree morphological traits correlated to all selected nutrient concentrations in all compartments measured by variation partitioning once inter-correlations taken into account (« + » and « - » indicate the direction of the relationship between each nutrient and the tree morphological trait. « * » indicates significant coefficient of determination with p_{adj}-value ≤ 0.05, « ** » indicates p_{adj}-value ≤ 0.01 and « *** » indicates p_{adj}-value ≤ 0.001)

6.5 Discussion

6.5.1 Contrasting accumulation of macroelements along mangrove intertidal gradients in response to aridity and anthropogenic influences

In semi-arid New Caledonia, differences in watershed compositions and the development of anthropogenic activities significantly influence macroelement status in mangrove soils. Mangroves exposed to open-cast mines downstream of watersheds with ultramafic bedrock were characterised by higher concentrations of Mg, imported from mining outcrops as Fe-oxides and oxyhydroxides, than in the undisturbed site, (Falconbridge SAS 2001, Noël et al. 2014, see section 6.3.1). The site influenced by both mining and aquaculture activities is also characterised by high concentrations of P and Ca loaded by pond effluents in mangrove soils.

Regarding our first objective, the results of this study show that any observed effect of anthropogenic activities on the status of macroelements in soils along the semi-arid intertidal gradient was largely related to physico-chemical conditions, OM and trace metals contents and thus, varies between both species stands. Furthermore, our results indicate that anthropogenic activities influence the soil physico-chemical conditions. As a result, macroelement distribution observed along the intertidal gradient at these influenced sites, particularly that of N and P, departs from the classical distribution reported in the literature.

For instance, previous mangrove studies report that longer immersion and reducing conditions that prevail seaward result in higher N accumulation compared to landward areas due to the lower OM decomposition in these stands and higher N benthic fixation (Reef et al. 2010). Therefore, higher N concentrations were measured in the *R. stylosa* stands seaward compared to the *A. marina* stands, as observed at the influenced sites.

However, N also accumulates in higher concentrations in some of the *A. marina* stands than in the *R. stylosa* stands, in waterlogged soils with high OM input in the undisturbed and aquaculture sites. We suggest that the recent recolonization event in the undisturbed site and the poor drainage next to the shrimp pond outlets in these stands have led to a decrease in the mineralisation of N-rich organic particles and to an increase in N benthic fixation in the uppermost soil layer (see Chapter 4, Gier et al. 2017, Molnar et al. 2014, Reef et al. 2010). As a result, N accumulates in these landward areas and its concentrations in these stands (3.56 - 6.83 g kg^{-1}) fall above the median of values found in mangrove soils worldwide ($\sim$ 2.40 g kg^{-1}, based on the review of Saenger, 2002). Conversely, well drained soils in the *A. marina* stands under the influence of aquaculture and mining activities showed low N contents compared to mangrove soils worldwide and at the undisturbed site, as well as a loss of TOC and N contents compared to the *R. stylosa* stands at these sites. As observed in other nutrient-enriched mangroves worldwide, Molnar et al. (2013, 2014) and Aschenbroich et al. (2015) have reported that the mineralisation and turnover of OM and N loaded by pond effluents increases in response to increasing OM decomposition rates stimulated by increasing input of labile OM in relatively well oxygenated conditions (e.g. Alongi 2009, Feller et al. 1999, Keuskamp et al. 2015, Nóbrega et al. 2013). At the aquaculture site, Molnar et al. (2013) also observed high concentrations of N in the water column on the other side of the bay. Thus, we hypothesised that some mineralised N are likely exported by outflowing effluents and/or assimilated by mangrove trees in these influenced sites (see below). In the *A. marina* stands of the mining and aquaculture-influenced sites, the decline of N and K in soil with increasing total concentrations of Mn and Fe indicates that these metals could also play a key role in the mineralisation and export of TOC, N and K from mangrove soils landward. Numerous studies in marine, wetland and terrestrial

ecosystems have shown that Fe and Mn act as electron acceptors or donors during several steps of the biotic and abiotic mineralisation and transformation processes of the OM and N (e.g. Fe and Mn oxidation of OM, Feammox) (Froelich et al. 1979, Kostka et al. 1999, Kristensen et al. 2000, 2008, Tobias and Neubauer 2019). The authors conclude that Fe and Mn can significantly increase OM decomposition and N mineralisation rates and exports from the soils (Thamdrup and Dalsgaard 2000, Clément et al. 2005, Huang et al. 2016b). This fact has been demonstrated in mangrove ecosystems by Kristensen et al. (2000), who reported that Fe suboxic respiration of the OM may account for as much as 80% of carbon oxidation in some mangrove stands. In the present study, additional Fe and Mn oxides imported from mining outcrops could therefore contribute to the observed loss of N from the soils of these *A. marina* stands, compared to the *R. stylosa* stands. However, further measurements are needed to assess the extent of these processes in the field, especially in tropical soils rich in Fe.

Although OM oxidation also leads to the production of mineralized forms of K, Mg and P (Froelich et al. 1979, Deborde et al. 2015), K has a high affinity for adsorption sites on the surfaces of OM particles (Böer 1996, Wang and Huang 2001, Alongi et al. 2003, Naidoo 2006), whereas P and Mg tends to be trapped in Fe oxides in (sub)oxic conditions landward (Tam and Wong 1993, Wang and Huang 2001, Nóbrega et al. 2014, Deborde et al. 2015). Thus, and contrary to N, K, Mg and P soil contents tend to remain higher in *A. marina* stands compared to the *R. stylosa* stands. Over time, these nutrients are lost in the soils of the *R. stylosa* stands with the washout of K^+ adsorption sites at the surface of OM and with the dissolution of iron oxides under longer immersion seaward. However, the distribution of P observed at the mining site departed from that trend, and we suggest that the renewal of Fe oxides from the open-cast mines contributes to a greater accumulation of P in the *R. stylosa* stands than in the *A. marina* stands at this

site. In addition, the strong correlations between P and Ca and between P and Al found in the soil and plant compartments of the *A. marina* stands echo the suggestion of previous mangrove studies that Ca and Al phosphate minerals could also act as reservoirs of P in mangrove ecosystems (Hesse et al. 1963, Naidoo and Raiman 1982, Fabre et al. 1999, Oxmann et al 2009). This could further explain the higher P retention in *A. marina* soils receiving P-rich aquaculture effluent compared to the *R. stylosa* soils in that site.

6.5.2 Nutrient bioconcentrations as a function of availability and plant requirement

At every site studied in the present semi-arid context, the concentration of primary macronutrients N, P and K was higher for every type of plant material of *A. marina* compared to that of *R. stylosa*; whereas, their conservation through resorption was higher in *R. stylosa*. While *R. stylosa* is a slow-growing species, *A. marina* is a pioneer species, and thus may have adaptations that enable fast uptake and accumulation of nutrients for rapid growth. For instance, the root system of *A. marina* has a widespread aerenchyma that facilitates the transfer of oxygen from pneumatophores to the extensive belowground root system that spreads radially just underneath the soil surface (Scholander et al. 1955, Allaway et al. 2001). This oxygen input into the rhizosphere facilitates OM oxidation and the settlement of bacterial communities, including in waterlogged substrate as those next to the aquaculture pond outlets. This increases in turn OM mineralisation rates and nutrient availability over a large surface (Thibodeau and Nickerson 1986, Gomes et al. 2014, Alzubaidy et al. 2016), including nutrients that would have been otherwise unavailable for plant uptake in reducing conditions. High nutrient uptake and low nutrient RE result in lower C/N ratios and lignin

contents in the litter of *A. marina* than in that of *R. stylosa* (Marchand et al. 2005). As observed in other pioneer species, these litter characteristics are likely to contribute to higher OM decomposition rates and thus, to a higher bioavailability of N and P than in the *R. stylosa* stands (Lima and Colpo 2014, Ye et al. 2019).

As discussed in the previous section, our results also suggest that (sub)oxic conditions in the *A. marina* stands may facilitate the mineralisation and availability of macronutrients for root uptake, hence explaining the clear increase of nutrient concentrations in the root systems of *A. marina* with increasing concentrations of these nutrients into the soils. In particular, the depletion of OM and N with the simultaneous N and P accumulation in the root system of the *A. marina* stands in the influenced sites also support the hypothesis discussed above on the stimulation of OM and nutrient mineralisation under high OM and/or Fe and Mn input.

Comparatively, the bioaccumulation of primary nutrients in the plant materials of *R. stylosa* appears to be limited, probably as the combined results of nutrient losses under significant tidal flow, and of lower OM mineralisation rates that lead to nutrient immobilisation into the soil. In *R. stylosa*, these lower bioconcentrations may be partially compensated by higher RE before senescence, reflecting the high nutrient use efficiency of this slow-growing species compared to that of *A. marina* (Alongi et al. 2005a, Feller et al. 1999). However, in *R. stylosa*, bioconcentrations of N, P and K in the wood and canopy also increase in geochemical conditions favourable to nutrient availability in the well-drained soils of the aquaculture-influenced site (i.e. high nutrient concentrations and Eh), whereas RE depicted a sharp decrease in these same conditions. This shows that the lower bioconcentrations of P and K in *R. stylosa* compared to *A. marina* may partially be the result of limited availability of these elements in suboxic conditions rather than a lesser requirement for plant functions.

Finally, the secondary nutrients Ca, Mg and S are required by plants in lower quantities than primary nutrients and as they are significant components of seawater (Millero 1996, Raven et al. 2005, Lambers et al. 2008), they are unlikely to be limiting in mangrove ecosystems. This reflects in the lower inter-species and inter-sites variations of these nutrient bioconcentrations when compared to the primary nutrients, but also in their negative RE and high immobilisation in the root system of both species. In addition, the bioconcentrations of Ca and Mg were substantially higher in the wood (Ca and Mg) and green and senesced leaf (Ca) tissues of *R. stylosa* than in those of *A. marina*. This could be the result of a longer immersion in the *R. stylosa* stands, leading to the dissolution of carbonates and Mg-Fe oxides seaward, hence increasing the availability of Ca and Mg for plant uptake. Furthermore, Ca is a key component of lignin (Lambers et al. 2008). This metabolite is present in higher concentrations in *R. stylosa* tissues than in those of *A. marina* (Marchand et al. 2005) and could therefore be required in higher quantities in the aboveground tissues of *R. stylosa*. However, the roles of Ca, Mg and S in plants and their interactions with other ions are numerous and complex and the understanding of their distributions in the present context would require further research.

6.5.3 Influence of salinity on nutrient bioconcentrations along a semi-arid intertidal gradient

High evapotranspiration in the semi-arid west coast of New Caledonia leads to strong water deficits that results in high pore-water salinity and important precipitation of NaCl within mangrove soils, even during the wet season (Chapter 4). Our results confirmed that, with increasing Na contents in the soils, *R. stylosa* increasingly excludes Na^+ at the root level (Saenger 2002). Thus, this species dominates seaward, where regular flooding

prevents salt accumulation in the rhizosphere. Conversely, and as suggested in other studies, the leaching of Na through the green leaf adaxial glandular trichomes could be the main mechanism of salt regulation in hyperaccumulator *A. marina* (Chapter 3, Drennan and Pammenter 1982, MacFarlane and Burchett 2000, Saenger 2002), at least during the rainy season. This reflects in Na hyperaccumulation in the root system and in the recorded loss of Na between the green and senesced leaves of this species with increasing salinity.

Our results also show that the contrasted strategies of *A. marina* and *R. stylosa* to cope with salinity stress were strongly related to the differences of nutrient distribution in the tissues and litter observed between both species. For instance, both species increasingly accumulate K in their canopy in response to increasing Na contents in soils and leaves. The accumulation of K in the cell cytosol contributes to osmocompensation under salinity stress and allows for the maintenance of high K:Na ratios. This may limit any detrimental effects resulting from the competition between Na^+ and K^+ (Saenger 2002, Reef et al. 2010). However, our results suggest that while *R. stylosa* achieves the accumulation of K in its canopy through increasing K resorption from its senesced leaves with increasing Na, *A. marina* rather increases K uptake from the soils and returns an increasing amount of K in its litterfall with increasing salinity. We hypothesise that this low nutrient use efficiency allows the restitution of K to the forest floor through litterfall. This could then facilitate further K uptake by the root system of *A. marina* as well as the maintenance of an osmotic balance in these hypersaline soils (Downton 1982, Reef et al. 2010).

Conversely to *R. stylosa*, N and P also accumulate in the green and senesced leaves of *A. marina* with increasing Na leaf contents. Cha-um et al. (2007) and Popp et al. (1985) have suggested that N may accumulate in the canopy of *A. marina* as N-rich secondary

metabolites in response to salinity stress. This could contribute to maintain a normal cytosolic osmolarity to counterbalance the compartmentalisation of Na^+ within the vacuole. An increase in P uptake in water stress conditions has also been reported to improve stomatal conductance, water use efficiency and cell-membrane stability (Hu and Schmidhalter 2005, Martin et al. 2010). In addition, several studies have suggested that an adaptation to climates with short periods of time favourable for growth could underpin maximum metabolic efficiency during the growing season (Reef et al. 2010). We suggest that the increase of chl-a contents in the canopy of *A. marina* with increasing Na soil contents could be an indication of such adaptation to salinity stress (Abou Seedo et al. 2018).

Finally, and as observed in Chapter 3 in temperate mangroves, our results suggest that the uptake, translocation and resorption of Mg could be hampered by Na^+, possibly as a result of competition between Mg^{2+} and Na^+ (Lambers et al. 2008, Guo et al. 2016). As Mg is often abundant in mangrove ecosystems (Ukpong 2018), any damage that could result from the exclusion of this essential element (e.g. decrease in chl-a content, reduced growth) may have been overlooked. On the other hand, the understanding of Mg deficiency mechanisms as a response to unbalanced fertilization, acidity, salinity and drought is an urgent problem in crops worldwide (Guo et al. 2016). Therefore, further experiments in plants well adapted to salinity such as mangrove species could provide valuable understanding of the complex environmental and physiological drivers of this nutrient.

6.5.4 Influence of anthropogenic activities on tree traits linked with productivity in semi-arid mangroves

In the site undisturbed by direct anthropogenic effluents, salt hyperaccumulator species *A. marina* is restricted to short bands of multi-stemmed shrubs characterised by high basal area and low canopy volume. This shrub and multi-stemmed life-form may enable fast recovery and re-sprouting in case of injury due to water stress and salinity (Götmark et al. 2016). Conversely, *R. stylosa* is not exposed to salinity and water stress as much as *A. marina* stands, and forms therefore taller stands, with larger tree basal areas and canopy volume.

With regular effluent releases in the aquaculture and mining influenced sites, salinity stress and nutrient limitation (particularly P) decrease. As observed in other mangroves, this coincides with an increase in tree height, canopy volume and with an increase of other primary macroelements in the root systems, wood and canopy of both species (Lovelock and Feller 2003, Lovelock et al. 2004, 2006a, b, Naidoo 2009). However, our results also show that without further studies and analyses, the effect of these variations in nutrient concentrations on tree morphology with decreasing salinity cannot be disentangled from nutrient availability in the soils, nor from growth strategies specific to each species.

Regarding our second objective, the results discussed in the previous sections supported various authors' hypotheses regarding which frequent effluent releases coupled with higher nutrient supply (and possibly Fe and Mn) in well drained soils leads to i) lower salinity stress and ii) to higher OM mineralisation rates and nutrient availability in both species stands. Based on our results and on the various hypotheses presented in the previous sections, we suggest that lower salinity stress in both species stands lessen the competition between Na and other nutrients (Mg, K, Ca) in the plant-soil continuum of

semi-arid mangroves. This may, in turn, enable the reallocation of nutrients to metabolic activities linked to growth rather than to mechanisms to cope with salinity. Finally, we hypothesise that under high nutrient regimes and lower salinity stress, both species also lessen the allocation of energy on nutrient conservation (P, K, N). This then leads to increasing nutrient concentrations in the litterfall, which could contribute to higher nutrient mineralisation and availability in soils for further plant uptake, but also to higher nutrient exports from these ecosystems.

6.6 Conclusions

The present research reports on the influence of salinity, watershed composition and anthropogenic activities on macroelement status and soil-plant transfers along a semi-arid mangrove gradient. This study shows that the clear zonation that results from the salinity gradient induces differences in N, P, K and Mg concentrations in the different plant materials along the intertidal gradient. Our results suggest that macroelement nutrition of salt-hyperaccumulator and multi-stemmed shrub *A. marina* that dominates hypersaline stands landward is closely connected to mechanisms to cope with salinity stress. Conversely, salinity stress is lower seaward in the stands of the salt-excluder *R. stylosa* and hence, this enables this species to allocate more nutrients to metabolic processes linked to growth and productivity. This leads to higher tree height and canopy volume seaward. Strong similarities between spatial patterns of macroelements in soils and those of OM and trace metals Fe and Mn during the season favourable to growth also suggest that mining and aquaculture effluents may stimulate OM mineralisation and N mobilisation in landward areas and P retention in mangrove soils in seaward areas. This results in P accumulation and TOC and N losses in soils, and in higher nutrient

transfers from the soils to mangrove trees and to the litterfall. Thus, regular effluent release and/or lower elevation lessen salinity stress and increase nutrient availability for plant uptake but also for nutrient export from the ecosystem. In the context of global change, this research emphasises the importance of mangrove stands as buffers for eutrophication, but also illustrates important differences in nutrient accumulation along mangrove intertidal gradient in response to aridity and anthropogenic influences. With increasing aridity, nutrient and metal pollution worldwide, this study suggests that mangrove structure and role as a filter for macronutrients will be increasingly affected by global change.

Chapter 7

General Discussion and Conclusion

7.1 Introduction: thesis background

With ongoing global change, one of the major challenges facing humanity is to ensure food and environmental security for a growing global population. In order to do so, a deep understanding of ecology and plant nutrition under environmental stresses is critical to achieve suitable monitoring and sustainable practices in natural and agricultural ecosystems. To this end, the conservation and knowledge we have to gain from mangrove ecosystems is of the utmost importance. In tropical and subtropical coastal areas, mangroves demonstrate a high capacity to accumulate nutrients and trace metals in their soils and plant biomass. These vegetated ecosystems are located in coastal areas where tidal energy is significantly reduced, thus promoting sedimentation of autochthonous and allochthonous material. Once on the substrate, the specific edaphic properties of these ecosystems allow for a substantial accumulation of nutrients and trace metals in soils, sediments, and in highly productive mangrove vegetation. This last point is of far reaching importance. Of all ecosystems, mangroves and saltmarshes alone endure tidal and seasonal fluctuations in water stress simultaneously with salinity, anoxia, metal stress, nutrient limitation and even short frost episodes. And yet mangrove species do not just survive these constraints but also manage to thrive in these extreme environments. The understanding of nutrient and trace metal accumulation in soils and plant biomass under these simultaneous constraints can

therefore be of direct use to comprehend and anticipate the impact of global change on plant nutrition in other ecosystems.

However, with growing pressure from land-use conversion and climate change, the fate of mangrove capacity to filter nutrients and trace metals is at increasing risk. These changes lead to important structural changes in vegetation and diebacks of mangrove trees and shrubs. The ensuing soil erosion could henceforth fuel greenhouse gas emission and become an increasing source of nutrients and trace metals to adjacent coastal waters.

Over the last decades, the emergence of powerful tools in molecular biology, crystallography and chemistry has improved our understanding of the influence of these changes on elemental dynamics. However, these studies often address a few number of variables, or are realized in early plant developmental stages in controlled environments and space and time limited experiments. Therefore, reconciling the results obtained with the myriad of historical, climatic, edaphic and physiological factors that influence the mangrove soil-plant continuum *in situ* remains a necessary and essential challenge. In this context, this Thesis aims to improve our understanding of nutrient and trace metal dynamics in the mangrove soil-plant continuum, by focusing on their distribution and interactions *in situ* in contrasted climates and in different physiographic contexts, in temperate New Zealand and semi-arid New Caledonia.

7.2 Chapter findings and practical implications

Objective 1: status and dynamics of nutrients and trace metals in mangroves worldwide and their latitudinal variations (Chapters 2 and 3)

When it comes to the ecological services of mangrove, ecosystems that develop at the highest latitudes tend to receive less credit than their tropical counterparts do. As latitude increases, the intensity of solar energy, rainfall and temperature progressively depart from the optimum for mangrove growth (see review in Chapter 2). This results in a steady decline in aboveground standing biomass and primary production of mangrove vegetation away from the equator, and there is certainly no comparison between the shrubby physiognomy of arid, semi-arid and temperate mangroves and that of the cathedral mangrove forests that prevail in tropical humid climates. Although maximum canopy height, biomass, productivity and carbon concentrations in soils have been recorded between 10° S and 10° N of latitude (Clough 1992, Alongi 2014, Saenger and Snedaker 1993, Simard et al. 2019), data collected from the literature reviewed in Chapter 2 also shows that there is no clear latitudinal trend in carbon, nutrient and trace metal contents in mangrove soils (Atwood et al. 2017). Even though elemental dynamics are intimately linked to the cycle of OM, nutrient and trace metal contents in mangrove soils vary with a combination of latitude-dependent and regional and local factors. These include specific richness and vegetation structure, duration of immersion, anthropogenic activities, allochthonous inputs, decomposition rates, mangrove age and frequency of disturbances, among others (Chapter 2). Thus, the conservation of mangrove soils and the pool of nutrients and trace metals they contain are of prime concern regardless of latitude.

Chapter 3 illustrates this very fact through a case study in temperate mangroves, in Mangawhai Estuary, North Island of New Zealand, where the frost and hypersaline tolerant *Avicennia marina* subsp. *australasica* develops at these high latitudes. As for many areas in New Zealand, mangrove habitats in this estuary have started to expand seaward from the 1960s as a result of climatic factors and urban, pastoral and coastal development (Morrisey et al. 2007, Lovelock et al. 2010, Swales et al. 2007, 2015). Amid this rapid expansion, an increasing number of mangrove removal permits have been granted since the 1990s (De Luca 2015, Lundquist et al. 2017), prompting the need for further research on the ecological services these ecosystems provide (Dencer-Brown et al. 2018). In Chapter 3, measurements over a 50 cm depth profile in monospecific *A. marina* stands of Mangawhai Estuary showed that over the last 80 years, mangrove soils have trapped up to 120 tons of organic C (OC) per ha. In addition, median organic C concentrations measured in mangrove soils along the estuary (3.64 g kg^{-1}) were close to the median C concentration values found in tropical mangrove soils worldwide (see Table 1, reviewed in Chapter 2). However, dramatic variations in nutrient and trace metal contents were also found along the estuary (Chapter 3). The upstream-downstream gradient is characterised by an increase in reduction-oxidation potential (Eh) and bulk density (BD) in soils as a result of increasing immersion and tidal energy downstream of the estuary. In these conditions, total concentrations of OC, N, P, K, S, Fe, Zn, Cu, Cr, Co and Ni decrease along the upstream-downstream gradient of the estuary whereas elemental exchangeable concentrations increased, reflecting an increasing mobilization and export of these elements closer to the estuary mouth. Conversely, shorter immersion duration upstream of the estuary may have facilitated the sedimentation of terrigenous material over time. These conditions result in total

concentrations of organic Carbon (OC), P, N, K, Zn, Cr, Cu and Co close or above median values found in mangroves worldwide.

These findings have direct implications for coastal management in New Zealand. They outline the role of temperate mangroves as a filter for terrigenous material and raise the question of their fate and impact on coastal water quality with soil exposure after mangrove removal.

Objective 2: elemental status and dynamics in soils along a classic semi-arid gradient (Chapter 4, part I)

As global change leads to a decrease in rainfall and to an increase in extreme drought episodes and temperatures in tropical and temperate regions, mangrove stands close to land are projected to experience increasing evapotranspiration (Huang et al. 2016). Conversely, fringe stands directly exposed to the tide are being washed away due to sea-level rise and waves and storms of high energy. Chapter 4 sets the stage and illustrates the potential lasting consequences of such a Charybdis and Scylla scenario on nutrient and trace metal distribution in soils of a semi-arid mangrove. In this second case study, elevation, soil elemental concentrations and physico-chemical properties were investigated in a site undisturbed by direct anthropogenic pressure, but that recently experienced an increase in tidal frame in New Caledonia. As seawater and air temperatures increase compared to temperate mangroves, frost-intolerant mangrove species *Rhizophora stylosa* develops and dominates mangrove ecosystems alongside *A. marina*. In this context, elevation measurements carried out with a differential global positioning system (DGPS) demonstrated that strong evapotranspiration that occurred at the highest elevations resulted in a 200 and 400% increase in pore-water salinity and Eh, respectively, when compared to the lowest elevations. Thus, shrubby stands of the

hypersaline tolerant and pioneer species *A. marina* developed between 0.40 and 0.66 m above sea-level, whereas *R. stylosa* (less tolerant to salinity) formed higher stands at lower elevations and in borders of the main channels and along the coastlines.

This contrasts strongly with the classic gradient of soil physico-chemical properties and species composition usually observed in humid temperate and tropical mangrove regions, where higher rainfall all year long maintain lower salinity an reduction-oxidation potential in landward areas. Chapter 4 also shows that these differences in species zonation and reduction-oxidation potential induce fundamental changes in soil nutrient and trace metal distributions along semi-arid intertidal gradient compared to temperate and tropical mangrove soils. Investigations conducted in two adjacent *A. marina* and *R. stylosa* stands in the middle of semi-arid toposequence (away from the channel and from any disturbance) demonstrate that anaerobic conditions prevailed in the *R. stylosa* stands in seaward areas. This is likely due to frequent immersion and increased sedimentation mediated by the dense aerial root system of *R. stylosa*. In these soils, sulfate-reduction was the main pathway of OM decomposition and thus, sulphates were reduced and precipitated with Fe ions in the solid phase of the soil. Results in these *R. stylosa* stands also suggest a co-precipitation and subsequent accumulation of Cu, Ni, Cr, Co and Zn in the soil solid phase. Comparatively, longer duration of emersion and higher evapotranspiration in the *A. marina* stands at higher elevations contribute to an increase in soil reduction-oxidation potential. In addition, our elevation measurements indicate that this influence of topography at higher elevations in *A. marina* stands was magnified during the dry season compared to the wet season, whereas frequent tidal inundation contributed to low seasonal variations in soil properties in the *R. stylosa* stands. Thus, surface soils sampled at the summit of the intertidal gradient were significantly oxidised during the dry season compared to the wet season, leading to an

enhanced mineralisation and loss of OM. This results in turn in a strong soil acidification during the dry season compared to the wet season, possibly enhanced by oxidation of solid sulphides in these stands. Compared to the reduced soils in the short *R. stylosa* stand at lower elevations, the dissolution of these minerals resulted, over time, in the observed scarcity of Mn, Fe and that of transitional metals (Cu, Ni, Cr, Co, Zn) accumulated in these Fe-bearing minerals in soils. Despite this enhanced OM mineralisation at higher elevations, N contents did not vary significantly along the elevation profile. This was attributed to i) a rapid assimilation of N by *R. stylosa* trees, ii) lower immersion and subsequent mineral export in the old *A. marina* stands compared to the short *R. stylosa* stands, iii) high C/N ratios in the litterfall of *A. marina* compared to those of *R. stylosa*, and iv) enhanced development of microphytobenthos with increasing solar radiation at these higher elevations. Finally, total concentrations of P, K, Mg and Ca decreased with decreasing elevation as a result of mineral dissolution and export with longer immersion and lower reduction-oxidation potential.

In conclusion, elevation measurements taken in this first part of Chapter 4 showed that cm-scale variations in soil reduction-oxidation potential strongly influence pH, OM cycling and elemental accumulation within the substrate. Given the increase scarcity in rainfall events and increase aridity in tropical mangroves worldwide, the question arises for coastal management as to the future ability of mangroves to filter and accumulate OM and trace metals in their soils in landward areas, and the need to monitor the existing pools at these highest elevations in these ecosystems.

Objective 3: effect of increased tidal frame on soil properties and elemental status at lowest elevations in semi-arid mangroves (Chapter 4, Part II)

The third objective of this thesis was to assess the effect of an increase in tidal frame on nutrient and trace metal status in soils directly exposed to tidal energy, along the borders of the channels in the same semi-arid toposequence as discussed in the previous section (Chapter 4, Part I). To fulfil this objective, soil properties along the soil profile of the tall *R. stylosa* stands that experience longer immersion times and periodic hydrodynamic disturbances seaward were compared with those of the short *R. stylosa* stand landward.

The results of this chapter showed that when moving closer to the channel, soil elevation steadily increases by 15 cm from the short *R. stylosa* stand landward to the tall *R. stylosa* stand next to the channel. However, a depletion in total and exchangeable nutrients and metal contents was also measured along the soil profile of this tall *R. stylosa* stand when compared to that of the short *R. stylosa*. Other authors have observed similar increase in soil elevation as a result of root accumulation and vertical accretion (Young and Harvey 1996, Krauss et al. 2003, McKee et al. 2007). However, these authors also reported that the rate of vertical accretion is site- and species-specific and that in the long term, disturbance due to high tidal energy may induce perturbation and erosion in the prop roots of *Rhizophora* spp. The findings in this study suggest that similar perturbations may occur in this fringe stand, possibly during disturbance and sea-level rise that occur during the frequent cyclones in New Caledonia, which are reflected in the observed loss of nutrient and trace metals in this stand. These findings suggest that while mangroves may partly mitigate sea-level rise by vertical accretion or root accumulation, the effect of tidal pumping, perturbation and weathering on the pool of nutrients and trace metals in soils may remain significant.

Objective 4: effects of increased tidal frame and recent colonization event on soil properties and elemental status at highest elevations in semi-arid mangroves (Chapter 4, Part III)

At the other extremity of the toposequence, the analysis of the soil profile at the highest elevations in a recently developed *A. marina* stand gives an interesting insight into the processes underlying the colonization of hypersaline soils subsequent to an increase in tidal frame and its effect on soil composition (Chapter 4, Part III). In the plant compartment of these stands, 40-year-old satellite images and the characteristics of the soil horizons underneath the surface attest to the existence of a time when emersion duration and evapotranspiration was likely longer, and when maximum salinity was probably in the upper range of the 62–100 range currently observed at the peak of the dry season in these stands (Chapter 4, Part III and Leopold et al. 2016). In these soil horizons, the low total OC content and concentrations of macroelements N, P, K, and S reflect the lack of vegetation and intense OM mineralisation that likely prevailed at the time and that are characteristics of other salt-flats in semi-arid climate of New Caledonia (Deborde et al. 2015). As the tidal frame started to increase in this area a few decades ago, salinity progressively decreased, and the *A. marina* stand that developed 9 cm lower than these elevation started to expand and colonize these desertic and nutrient deprived elevations. That a new population survives salinity twice that of the seawater with few nutrients at their disposal is a feat of nature at odds with controlled experiments on propagule resistance to salinity, even for this hypersaline tolerant species. Several studies have indeed shown that *A. marina*'s propagules and seedlings grown in controlled experiments at salinity equal or higher to that of the seawater experience a dramatic decrease of their growth and survival rate (e.g. Saenger 2002, Morrisey et al. 2010, Kodikara et al. 2018, Gritcan 2019). In the present study, the

analysis of the surface soils at this highest elevation suggests that *A. marina*'s successful colonization of hypersaline soils is due more to its ability to modify the characteristics of the substrate rather than to its ability to resist salinity at its earliest developmental stage. Quite remarkably, pore-water and total OC, N, P and K contents in the top 2.5 cm of the soil profile of this stand were higher and bulk density was lower than any other horizons down the elevation profile all year around. These favourable characteristics for plant growth indicate an OM enrichment that could result from the decomposition of a large number of propagules in the early phase of this colonisation. *A. marina*'s propagules are cryptoviviparous, i.e. the hypocotyl does not undergo secondary growth before abscission from the mother tree, in contrast to other true viviparous mangrove species, such as *R. stylosa*. As a result, the energy allocated in their production is lower than in *R. stylosa*, which allows for the production of a very large number of propagules (Hogarth 2015). In this chapter, I hypothesize that the accumulation of OM and thin nutritive roots produced by the numerous aborted propagules and saplings at an early stage of the succession modified the soil structure. Over time, this would have likely promoted the development of a thin particle soil matrix with a high number of binding-sites. This would have then contributed to an increased i) water-holding capacity, ii) total and exchangeable nutrient contents, and iii) salt adsorption and immobilization in the solid phase of the soil. This hypothesis is consistent with previous investigations that reported higher recruitment density for *A. marina* than for other mangrove species in various conditions (Das et al. 2019). Similarly, this explains why *A. marina* seedlings grown in hypersaline conditions have higher survival rates in clay-rich soils compared to sandy soils or sediments (McMillan 1975 in Saenger 2002). In arid and semi-arid climates, *A. marina* could therefore owe its status of pioneer species to its ability to transform hypersaline soils into a fertile and hospitable land. Further investigations of

the physico-chemical properties of surface soils in the early stage of mangrove succession might be of direct use to mangrove reforestation in dry lands around the world. In terrestrial ecosystems, Mori et al. (2014) tested this very same hypothesis and successfully promoted drainage, OM retention, while preventing surface runoff and soil loss with the use of artificial macropores (i.e. soil pores larger than 75 μm). Similar techniques, adapted for mangrove soils, could significantly contribute to the preservation and restoration of their pools of C, nutrients and trace metals.

Objective 5: effect of OM and trace metal inputs on the status and soil-plant transfers of nutrients and trace metals along semi-arid mangrove gradient (Chapters 5 And 6)

Chapters 5 and 6 outline the effect of large ranges of OM and trace metal inputs on trace metal (Chapter 5) and nutrient (Chapter 6) distribution in semi-arid mangrove soils along the *A. marina - R. stylosa* gradient. This comparison was conducted in three study sites: a site located downstream a mined ultramafic watershed, another site influenced by both mining and aquaculture activities, and a site undisturbed by anthropogenic pressure, previously described in Chapter 4. These investigations highlight a very different trend in elemental accumulation between the two species stands, mainly driven by the significant variation in reduction-oxidation potential along the intertidal gradient (Chapter 5 and Chapter 6). In contrast to the undisturbed site that does not receive direct metal inputs in the *A. marina* stands, decreasing concentrations of Fe, Mn, Ni, Zn, Co and Cr were measured along the land-sea gradient in both influenced sites. This metal loss in seaward areas suggests an enhanced dissolution and export of metal-bearing minerals loaded in these stands under tidal action, likely caused by the alternation of reductive and oxidative conditions throughout tidal cycles. Conversely, (sub)oxic conditions and the lower duration of immersion in *A. marina* landward stands

contributed to the structural preservation and accumulation of Fe and Mn oxides and hydroxides imported from the mining watersheds, as well as Ni, Zn, Co and Cr co-precipitated in these Fe and Mn-bearing minerals (Chapter 5).

The differential reductive conditions and trace metal contents in soils lead in turn to contrasted OM cycles and nutrient contents along the intertidal gradient of each site (Chapter 6). In (sub)oxic conditions in the *A. marina* stands, increasing Eh and total Fe and Mn concentrations in soils coincide with a sharp decrease in OM, total N and total K in soils, and with a sharp increase of N, P, K in the root system of *A. marina*. These findings suggest a stimulation of OM mineralisation and nutrient bioavailability with increasing oxygen and Fe and Mn electron acceptors in these oxic and suboxic soils. In addition, the lowest OC and N concentrations of this entire work were measured in the oxidated soils of the *A. marina* stands that receive aquaculture effluents, despite an annual discharge close to 100 kg ha^{-1} of particulate organic P and N measured in this site (Molnar et al. 2013). This result emphasises the enhanced turnover of macronutrients such as N and K in mangrove ecosystems with the input of labile OM (Aschenbroich et al. 2015). Conversely to N and K, the effects of P loads were visible in aerobic mangrove soils. Results in Chapter 6 indicate that in these conditions, Fe, Ca and Al-minerals may act as significant reservoirs of P. Similarly, P loss that usually occurs in reducing conditions (Reef et al. 2010) appeared to be prevented in the soils of the *R. stylosa* stands, probably due to the renewal of Fe oxides downstream of these mining watersheds.

In summary, simultaneous increase in drought, sea-level rise and trace metals and organic matter in mangroves worldwide are likely to result in i) a decrease in mangrove efficiency in filtering heavy metals in soils seaward, ii) an enhanced OM mineralisation

and export of C, N and K from the soil compartment in landward areas and iii) an increase in P accumulation in mangrove soils.

Objective 6: drivers of elemental soil-plant transfers in temperate and semi-arid mangroves (Chapters 3, 5 And 6)

The investigations carried out in the different physiographic contexts studied in this thesis give a good understanding of elemental soil-plant transfers in two mangrove species belonging to two genera ubiquitous around the world with contrasted strategies to resist salinity (Chapters 3, 5 and 6). These results also outline the important pools of nutrients and trace metals held by mangrove roots, aerial roots, wood, green leaves and senesced leaves, as well as their role in trace metal phytostabilisation at these high latitudes. Based on the distribution of nutrients and trace metals measured over a large range of environmental conditions, three general drivers were found to determine the distribution of macroelements and trace metals in the tissues of these two mangrove species.

Firstly, trace metal and nutrient concentrations in the root system of both species were found to increase with increasing total concentrations of these elements in soils and with increasing Eh (Chapters 3, 5, 6). Higher elemental uptake by the root system with increasing soil oxygenation may reflect higher nutrient availability and trace metal concentrations in the dissolved phase of the soils, likely as a result of higher OM mineralisation in these conditions.

Secondly, the observed higher accumulation of trace metals and nutrients found in the root system of *A. marina* than in that of *R. stylosa* at equal soil concentrations in semi-arid New Caledonia has been attributed to contrasted strategies of nutrient acquisition and resistance to salinity and metal stress (Chapters 5, 6). This set of adaptations leads

to higher Na, nutrient and metal uptake in the root system of *A. marina*, and to high nutrient and trace metal translocation to its litterfall. This is one of *A. marina*'s key to success in colonizing substrates exposed to high evapotranspiration. High metal and salt uptake by the root system and translocation to the litterfall would avoid the build-up of metals and salt in the rhizosphere less frequently washed out by the tide than in the *R. stylosa* stands. Low nutrient resorption efficiency would also ensure nutrient restitution to the forest floor, therefore stimulating OM mineralisation and nutrient acquisition by the extended radial cable roots of this species within the narrow time window favourable for plant growth.

Lastly, evidence was found that salinity may have a strong influence on the concentrations of N, P, K, Mg, Cu, Zn, Fe and Mn in the tissues of *A. marina* and on that of K and Mn in the foliage of *R. stylosa* (Chapters 3, 5 and 6). As illustrated in Chapter 5 and 6, these variations in nutrient and trace metal bioconcentrations recorded in the tissues of both mangrove species with increasing salinity may be consequential. For instance, the observed variations of N, K and Mg in the foliage of *A. marina* in New Caledonia is as high as 10 g kg^{-1} over the total range of Na leaf contents analysed in this study. These findings show that salinity and associated water stress have important implications in terms of soil-plant transfers, bioaccumulation and exports of trace metals and nutrients via the litterfall. It is therefore likely that intensification of drought worldwide is going to play an increasingly large role on plant nutrition and fluxes of nutrients and metals in mangrove ecosystems (Hu et al. 2005). These interactions and the physico-chemical context in which they took place could also be of direct use to understanding plant response to stress in natural and agricultural ecosystems. Convergent adaptations to environmental stresses are common in the plant Kingdom, and similar adaptations have often evolved in very different genetic lineages

independently, through different genetic and molecular mechanisms (e.g. Bartels and Sunkar 2007, Pichersky and Lewinsohn 2011, Lee et al. 2018). It is hoped that the relationships between the different parameters studied in this thesis will contribute to the library of information on plant biochemical responses to stresses, and assist ecophysiologists in the construction and testing of further hypotheses in their research. Finally, it is also worth noting that in the semi-arid mangroves studied in this work, total Na contents in soils and plants depict stronger interactions with nutrient and trace metal concentrations in plant tissues than soil pore-water salinity. In Chapter 4, it has been hypothesised that significant amounts of salt precipitate in the soil solid phase as a result of evapotranspiration, and that this salt may be rapidly remobilized and available for plant uptake after tidal flushing or fresh-water input. It is therefore possible that with increasing drought, total Na and Cl contents may be a better indicator of the effect of salt stress on plant nutrition than pore-water salinity.

7.3 Research limitations and suggestions for future studies

As with any scientific research, the chosen experimental design and methods of this study are the result of several compromises that present some major trade-offs that need to be addressed. This research highlights relationships between a large number of physico-chemical variables, macronutrients and trace metals, in all the soil horizons containing mangrove roots, and in different plant tissues, from the roots to the senesced leaves. Although the results found with this approach have echoed the findings of many research obtained in controlled environments and opened new perspectives regarding nutrient and metal biogeochemical cycles in mangroves, one must distinguish correlation from causality. The next natural and necessary step would therefore be to

analyse and quantify the fluxes of these elements by the mean of tracer methods such as isotopic labelling experiments, for instance. These complementary analyses will contribute to a better understanding of the effects of global changes on nutrients and trace metal dynamics in mangroves. Furthermore, the dynamics of some nutrients, nitrogen notoriously, are difficult to assess based solely on their concentrations in soils, particularly in an intertidal ecosystem regularly flushed by the tides. This has been stressed in Chapter 3 and Chapter 6, in the mangrove stands developing in suboxic conditions. In this context, N mineralisation by the microbial activity is likely enhanced by labile OM input and/or O_2, Mn and Fe oxyhydroxides electron acceptors and results in a fast export from the soil compartment. While the effect of these inputs may remain identifiable in mangrove roots, the chosen approach did not allow the detection of such processes based solely on N concentrations in soils.

In addition, these last decades have seen the emergence of powerful statistical tools, designed to discriminate correlation from causality, and build large spatial and causal models that include a large number of variables. Asymmetric eigenvector map analysis, path analysis or causal modelling are a few examples (Blanchet et al. 2008, Shipley 2016). Such models will nicely complete the analyses presented in this study and could highlight causal mechanisms that take into account both direct and indirect effects of different variables on the different nutrients and trace metals studied (Mitchell 1992, Wootton 1994).

Another limitation of this research that calls for further study is the lack of information on metal and nutrient partition in soils of temperate mangroves in New Zealand. In the semi-arid component of this research, the different hypotheses and conclusions regarding the processes driving nutrient and trace metal dynamics were strongly

supported by the detailed work of previous authors, often realised in the same study sites, on crystallography and speciation of trace metals and nutrients in soils and sediments. However, the environmental context is quite different in New Zealand, and it is likely that the lowest temperature and higher precipitation characteristic of this temperate climate would result in very different biogeochemical processes compared to a semi-arid context.

Consideration of the seasonal variation is essential to have a thorough understanding of plant nutrition and their resistance to salinity and metal stresses. In this study, elemental status in mangrove plants and soils were investigated during the season favourable for tree growth, when the nutrients and metals are expected to be assimilated by trees in higher quantities, and before the significant resorption of nutrients that usually precede winter and the dry season. However, it is well known that the lower temperature, pH and higher pore-water salinity, total NaCl contents and Eh observed during the dry season in New Caledonia may also influence OM cycling and elemental soil-plant transfer (e.g. Fritioff et al. 2005, Chen et al. 2012, Marchand et al. 2016, Yan et al. 2017). During the dry season, the accumulation of NaCl and that of H^+ subsequent to OM mineralisation describes in Chapter 4, could contribute to higher solubility of Al, Fe, Mn and Zn by competition for the same binding sites and/or by complexation with Cl^- by reduction (Lutts and Lefèvre 2015). Similarly, microbial activity fluctuates with seasonal variations of the seawater temperature and may therefore significantly impact processes associated with OM mineralisation (Alongi 1988, Gonzalez-Acosta et al. 2006, Li et al. 2018b), and thus the accumulation of nutrients and metals in soils. Further studies should therefore include a seasonal monitoring of element status in order to

better understand the impact of these seasonal variations on element accumulation and mobility over the year.

Finally, it would be interesting to investigate the status and soil-plant transfer of the studied elements in the early developmental stage of mangrove trees in these contrasted climates. The extended root system found in the adult trees of *Avicennia marina* species deeply changes the chemistry of the rhizosphere and by consequent, the availability of nutrients and trace metals. Further investigation of the root system development from saplings to mature trees under various environmental stresses and the effect of the root system effect on nutrient and trace metal availability could provide valuable information for phytoremediation, restoration and management of mangrove ecosystems.

7.4 Final conclusions

This work reports on significant seasonal and spatial variations of physico-chemical properties along the intertidal gradient of mangrove ecosystems that develop in contrasted climates. The findings of this study outline the numerous processes underlying species zonation and nutrient and trace metal distribution along the mangrove soil-plant continuum. These investigations in different physiographic contexts showed that as human activity increases worldwide, the capacity of mangroves to act as filter for nutrients and trace metals will strongly depends on species composition, elevation and exposure to tidal energy of each mangrove stand. This thesis also demonstrates that increasing drought and sea-level rise worldwide are likely to emphasis differences in physico-chemical properties along mangrove intertidal gradient. Furthermore, the pool of nutrients and trace metals in mangrove soils

experiencing simultaneous sea-level rise and drought stress could be increasingly exported from the soil compartment, and mangrove plants and soils could therefore become an important conveyor of trace metals and nutrients for adjacent coastal ecosystems. A major challenge of our times will undoubtedly be to preserve mangrove ecological services in these conditions and to advocate for further efforts and resources for mangrove monitoring, conservation and restoration.

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Appendices

Appendix 1. Functions and adequate concentrations of macronutrients C, O, H, N in dry tissues of plants in general, and specific functions in mangrove plants documented in the literature

	Element	Forms available for plant uptake	Adequate concentrations in dry tissues for plants in general		Functions in plants in general	Examples of additional functions in mangrove plants	References for mangrove plants
			mg kg^{-1}	%			
macronutrients	Carbon (C)	CO_2	450 000	45	backbone of most biomolecules, including proteins, lipids, carbohydrates; involved in most physiological processes, driver of photosynthesis	accumulation of carbon-rich compounds in the xylem vessels to regulate water transport and transpiration; secretion of fulvic acids associated to Cu, Mn and Cd complexation at the root surface; accumulation of stress-protective phenolic compounds and soluble carbohydrates under salinity and drought stress (e.g. *Avicennia marina*)	Zimmermann et al. 1994, Zhu et al. 2019, Ravi et al. 2020
	Oxygen (O)	O_2, H_2O, CO_2, NO_3^-, $H_2PO_4^-$, HPO_4^{2-}, SO_4^{2-}	450 000	45	backbone of most biomolecules, including proteins, lipids, carbohydrates; involved in most physiological processes, including electron transport chains	diffusion of oxygen in the root system for belowground respiration through the aerenchyma constitutes a barrier to metals	Allaway et al. 2001, Curran et al. 1986, Scholander et al. 1955, Souza et al. 2015
	Hydrogen (H)	H_2O	60 000	6	backbone of most biomolecules, including proteins, lipids, carbohydrates; involved in most physiological processes, including cellular respiration	-	-
	Nitrogen (N)	NO_3^-, NH_4^+	15 000	1.5	components of amino acids, proteins, nucleotides	accumulation of specific amino acid under salnity to counterbalance the compartmentalisation of Na^+ within the vacuole; essential component of osmolytes and antioxidative enzymes involved in resistance to salinity and drought stress (e.g. *A. marina*)	Popp et al. 1985, Mishra and Das 2003, Cha-um et al. 2007, Ravi et al. 2020, Ashihara et al. 1997

Appendix 2. Functions and adequate concentrations of macronutrients P, K, Ca, Mg and S in dry tissues of plants in general, and specific functions in mangrove plants documented in the literature

	Element	Forms available for plant uptake	Adequate concentrations in dry tissues for plants in general		Functions in plants in general	Examples of additional functions in mangrove plants	References for mangrove plants
			mg kg^{-1}	%			
macronutrients	Phosphorus (P)	$H_2PO_4^-$, HPO_4^{2-}	2 000	0.2	component of energy-transporting molecules (ATP, ADP), nucleic acids, several coenzymes, phospholipids, component of the cell wall	component of enzymes involved in metal detoxification (e.g. *Kandelia obovata*, *A. marina*) and salinity stress (e.g. fructose-1,6-biphosphate aldolase in *A. marina*)	Ashihara et al. 1997, Dai et al. 2017 a,b
macronutrients	Potassium (K)	K^+	10 000	1	intervenes in osmosis and ionic balance, in the opening and closing of stomata, activator of many enzymes	accumulation in the cell cytosol contributes to osmocompensation under salinity and drought stress	Saenger 2002, Reef et al. 2010, Ashihara et al. 1997
macronutrients	Calcium (Ca)	Ca^{2+}	5 000	0.5	cell wall component, enzyme cofactor, intervenes in the permeability of cell membranes, regulator of membrane and enzymatic activities	component of calmodulin involved in salt tolerance (e.g. *Bruguiera gymnorrhiza*), Ca-dependent protein kinase involved in resistance to heat, cold, light stresses, among others (e.g. *A. marina*)	Li et al. 2009, Liu et al. 2020
macronutrients	Magnesium (Mg)	Mg^{2+}	2 000	0.2	component of chlorophyll; activator of many enzymes	-	-
macronutrients	Sulfur (S)	SO_4^{-2}	1 000	0.1	component of some amino acids, coenzyme A, involved in the tertiary structure of proteins	-	-

Appendix 3. Functions and adequate concentrations of micronutrients Fe, Ni, Cu, Zn in dry tissues of plants in general, and specific functions in mangrove plants documented in the literature

	Element	Forms available for plant uptake	Adequate concentrations in dry tissues for plants in general		Functions in plants in general	Examples of additional functions in mangrove plants	References for mangrove plants
			mg kg^{-1}	%			
micronutrients	Iron (Fe)	Fe^{3+}, Fe^{2+}	100	0.01	role essential in chlorophyll synthesis; components of cytochroms and nitrogenase	cofacteur of Superoxide Dismutase SOD - a pivoting enzyme to resist oxidative stress caused by ROS in saline conditions - in *Bruguiera parviflora* ; essential component of the antioxidative ascorbate peroxidase, and guaiacol peroxidase and catalase involved in resistance to salinity and water stress ; associated to salt excretion via glandular trichome in *Avicennia schaueriana*	Takemura et al. 2000, Mishra and Das 2003, Parida et al. 2004, Arrivabene et al. 2016
	Nickel (Ni)	Ni^{2+}	0.01 - 5	0.000001 - 0.0005	essential component of urease, involved among other things in N assimilation and seed germination	-	-
	Copper (Cu)	Cu^{+}, Cu^{2+}	0.6 - 10	0.0006 - 0.001	activator and component of several enzymes involved in cellular oxidation and reduction processes	associated to salt excretion via glandular trichome in *Avicennia* spp	MacFarlane and Burchett 2000, 2002, MacFarlane et al. 2007, Naidoo et al. 2014
	Zinc (Zn)	Zn^{2+}	20 - 100	0.002 - 0.01	activators or components of many enzymes	associated to salt excretion via the glandular trichome of *Avicennia* spp	MacFarlane and Burchett 2000, 2002, MacFarlane et al. 2007, Naidoo et al. 2014

Appendix 4. Functions and adequate concentrations of micronutrients Mn, B, Mo, Co and Cr and Al in dry tissues of plants in general, and specific functions in mangrove plants documented in the literature

	Element	Forms available for plant uptake	Adequate concentrations in dry tissues for plants in general		Functions in plants in general	Examples of additional functions in mangrove plants	References for mangrove plants
			mg kg^{-1}	%			
micronutrients	Manganese (Mn)	Mn^{2+}	50 - 80	0.005 - 0.008	activates certain enzymes; necessary for the integrity of the chloroplastic membrane and for the release of O_2 in photosynthesis	cofacteur of Superoxide Dismutase SOD - a pivoting enzyme to resist oxidative stress caused by ROS in saline conditions - in *Bruguiera parviflora*	Parida et al. 2004
	Bore (B)	H_3BO_3	20	0.002	involved in Ca^{2+} metabolism and amino acid synthesis; intervene in cell wall integrity	-	-
	Molybdenium (Mo)	MoO_4^{2-}	0.1	0.00001	intervene in N fixation and nitrates reduction	-	-
	Cobalt (Co)	Co^{2+}	1	0.0001	increase crop plant yield by increasing chlorophyll content, net assimilation rate and growth rate, possibly because of their essential role in N_2 fixation in microorganisms, but also on ethylene production regulation in plants (Shkolnik 1984 and Raj 1987); constituant of vitamin B12; reduce transpiration rate and regulate plant water utilization (Arif et al. 2016)	-	-
non-essentials	Chromium (Cr)	Cr^{2+}, Cr^{3+}	1	0.0001	not considered as essential micronutrient in plants	-	-
	Aluminium (Al)	Al^{3+} ($Al(OH)^{2+}$, $Al(OH)_2^+$, $Al(OH)_4^-$)	-	-	not considered as essential micronutrient but stimulates root growth of some species at very low concentrations in specific conditions (Bojórquez-Quintal et al. 2017)	-	-

Appendix 5. Mean values (±SD) concentrations (by dry weight, in g.kg^{-1}) of total (*tot s*) and exchangeable (*exch s*) macro-elements in the soils, and total concentrations of the elements within coarse roots (*root*), green leaf tissues (*gr*) and senesced leaf tissues (*sen*) in each mangrove site, Mangawhai Estuary, New Zealand

		Upstream		Middle		Downstream	
C	*tot s*	43.81	(±4.49)	43.38	(±5.69)	22.15	(±3.36)
	root	373.26	(±21.45)	338.14	(±49.33)	333.91	(±59.47)
	gr	421.37	(±8.93)	409.59	(±12.21)	410.51	(±10.39)
	sen	436.98	(±8.41)	444.16	(±9.35)	441.05	(±6.48)
N	*tot s*	2.55	(±0.20)	2.61	(±0.27)	1.56	(±0.21)
	root	8.89	(±0.90)	9.13	(±1.10)	10.07	(±0.66)
	gr	15.33	(±1.98)	15.42	(±2.58)	16.38	(±1.33)
	sen	6.14	(±0.73)	6.17	(±0.85)	5.76	(±0.52)
Ca	*tot s*	5.12	(±0.93)	12.26	(±2.00)	10.38	(±0.78)
	exch s	0.75	(±0.01)	0.73	(±0.05)	1.20	(±0.05)
	root	3.48	(±0.66)	3.38	(±0.77)	4.01	(±1.07)
	gr	2.51	(±0.24)	2.67	(±0.25)	2.69	(±0.45)
	sen	2.53	(±0.33)	2.92	(±0.34)	2.92	(±0.68)
Mg	*tot s*	3.53	(±0.93)	3.23	(±0.35)	2.98	(±0.18)
	exch s	1.07	(±0.06)	1.33	(±0.11)	2.20	(±0.15)
	root	4.01	(±0.72)	4.67	(±0.76)	5.08	(±0.68)
	gr	6.11	(±0.92)	5.36	(±1.25)	5.26	(±0.89)
	sen	7.95	(±1.16)	7.57	(±1.22)	8.58	(±1.19)
Na	*tot s*	20.36	(±0.33)	21.68	(±0.82)	24.30	(±1.00)
	root	17.30	(±4.16)	21.18	(±6.98)	20.99	(±2.81)
	gr	26.35	(±4.16)	29.28	(±6.31)	29.26	(±4.07)
	sen	15.62	(±2.75)	16.10	(±2.57)	15.38	(±1.67)
K	*tot s*	9.73	(±0.71)	6.96	(±0.40)	6.49	(±0.33)
	exch s	0.58	(±0.04)	0.67	(±0.05)	1.03	(±0.07)
	root	9.69	(±1.99)	11.04	(±1.92)	11.60	(±1.69)
	gr	16.49	(±0.86)	14.69	(±1.38)	13.94	(±1.30)
	sen	14.44	(±1.56)	13.09	(±1.81)	12.87	(±1.69)
P	*tot s*	0.61	(±0.13)	0.32	(±0.01)	0.30	(±0.02)
	root	1.08	(±0.10)	1.21	(±0.22)	1.30	(±0.03)
	gr	1.64	(±0.15)	1.60	(±0.22)	1.53	(±0.11)
	sen	1.25	(±0.38)	0.70	(±0.15)	0.61	(±0.15)
S	*tot s*	10.28	(±1.82)	10.09	(±2.86)	5.09	(±1.43)
	exch s	0.72	(±0.07)	1.11	(±0.17)	1.98	(±0.17)
	root	4.25	(±2.55)	4.09	(±0.71)	4.59	(±0.59)
	gr	2.88	(±0.36)	3.26	(±1.30)	3.13	(±0.86)
	sen	7.25	(±1.08)	6.98	(±1.58)	6.41	(±0.82)

Appendix 6. Mean values (±SD) concentrations (by dry weight, in g.kg^{-1}) of total (*tot s*) and exchangeable (*exch s*) heavy metals in the soils, and total concentrations of the elements within coarse roots (*root*), green leaf tissues (*gr*) and senesced leaf tissues (*sen*) in each mangrove site, Mangawhai Estuary, New Zealand

		Upstream		Middle		Downstream	
Fe	*tot s*	20 900.00	(±2 180.00)	17 400.00	(±2 030.00)	13 720.00	(±740.00)
	exch s	230.00	(±50.00)	350.00	(±70.00)	530.00	(±60.00)
	root	5 920.00	(±290.00)	9 690.00	(±2 540.00)	9 880.00	(±3 150.00)
	gr	93.20	(±45.46)	75.32	(±43.95)	85.13	(±50.52)
	sen	240.00	(±60.00)	220.00	(±33.62)	220.00	(±40.00)
Mn	*tot s*	128.48	(±3.57)	149.21	(±6.00)	148.67	(±3.98)
	exch s	6.22	(±1.15)	7.67	(±0.91)	17.29	(±3.23)
	root	199.44	(±71.38)	284.59	(±67.90)	304.26	(±81.88)
	gr	26.92	(±5.29)	21.94	(±4.23)	14.83	(±5.26)
	sen	32.11	(±8.62)	35.98	(±8.05)	27.76	(±4.88)
Ni	*tot s*	10.58	(±0.61)	7.99	(±0.31)	6.77	(±0.41)
	exch s	13.53	(±3.94)	9.26	(±2.81)	40.59	(±8.16)
	root	5.65	(±0.93)	7.01	(±2.13)	7.18	(±1.98)
	gr	0.19	(±0.06)	0.21	(±0.08)	0.20	(±0.09)
	sen	0.37	(±0.18)	0.31	(±0.13)	0.29	(±0.08)
Al	*tot s*	36 603.55	(±8 983.93)	43 004.22	(±4 703.06)	35 721.00	(±401.45)
	exch s	47.00	(±3.49)	76.26	(±14.46)	58.16	(±6.94)
	root	8 732.77	(±1 024.03)	12 903.65	(±3 247.60)	12 963.29	(±3 912.14)
	gr	28.50	(±11.14)	36.95	(±16.59)	32.88	(±11.31)
	sen	96.20	(±54.61)	128.42	(±36.61)	113.07	(±40.18)
Cu	*tot s*	11.38	(±2.26)	2.76	(±0.44)	2.65	(±0.58)
	exch s	1.07	(±0.13)	0.87	(±0.09)	1.54	(±0.07)
	root	10.34	(±0.99)	11.42	(±1.41)	11.50	(±2.37)
	gr	17.40	(±4.68)	6.17	(±3.72)	8.06	(±3.58)
	sen	16.20	(±4.74)	2.96	(±1.08)	3.29	(±1.30)
Zn	*tot s*	48.30	(±4.35)	30.84	(±3.81)	26.61	(±1.78)
	exch s	5.15	(±1.04)	6.34	(±0.96)	5.46	(±0.33)
	root	23.74	(±1.50)	28.11	(±5.30)	28.38	(±5.87)
	gr	17.25	(±4.27)	22.47	(±5.16)	8.69	(±2.70)
	sen	29.13	(±3.69)	14.64	(±4.28)	15.71	(±3.40)
Co	*tot s*	12.29	(±0.66)	6.43	(±0.50)	6.39	(±0.49)
	exch s	2.09	(±0.62)	2.51	(±0.95)	3.48	(±0.60)
	root	1.80	(±0.25)	2.99	(±0.85)	3.09	(±0.98)
	gr	0.08	(±0.03)	0.03	(±0.01)	0.04	(±0.02)
	sen	0.10	(±0.03)	0.05	(±0.03)	0.08	(±0.03)
Cr	*tot s*	30.84	(±2.54)	26.45	(±0.77)	21.08	(±0.91)
	exch s	0.18	(±0.08)	1.67	(±0.92)	0.36	(±0.06)
	root	13.78	(±2.72)	17.51	(±5.48)	19.02	(±5.97)
	gr	0.18	(±0.05)	0.24	(±0.17)	0.14	(±0.05)
	sen	1.13	(±0.46)	1.39	(±0.50)	0.84	(±0.26)

P green leaves

P senesced leaves

mg kg⁻¹ ○ 500   ○ 1000   ○ 1 500   ○ 2 000
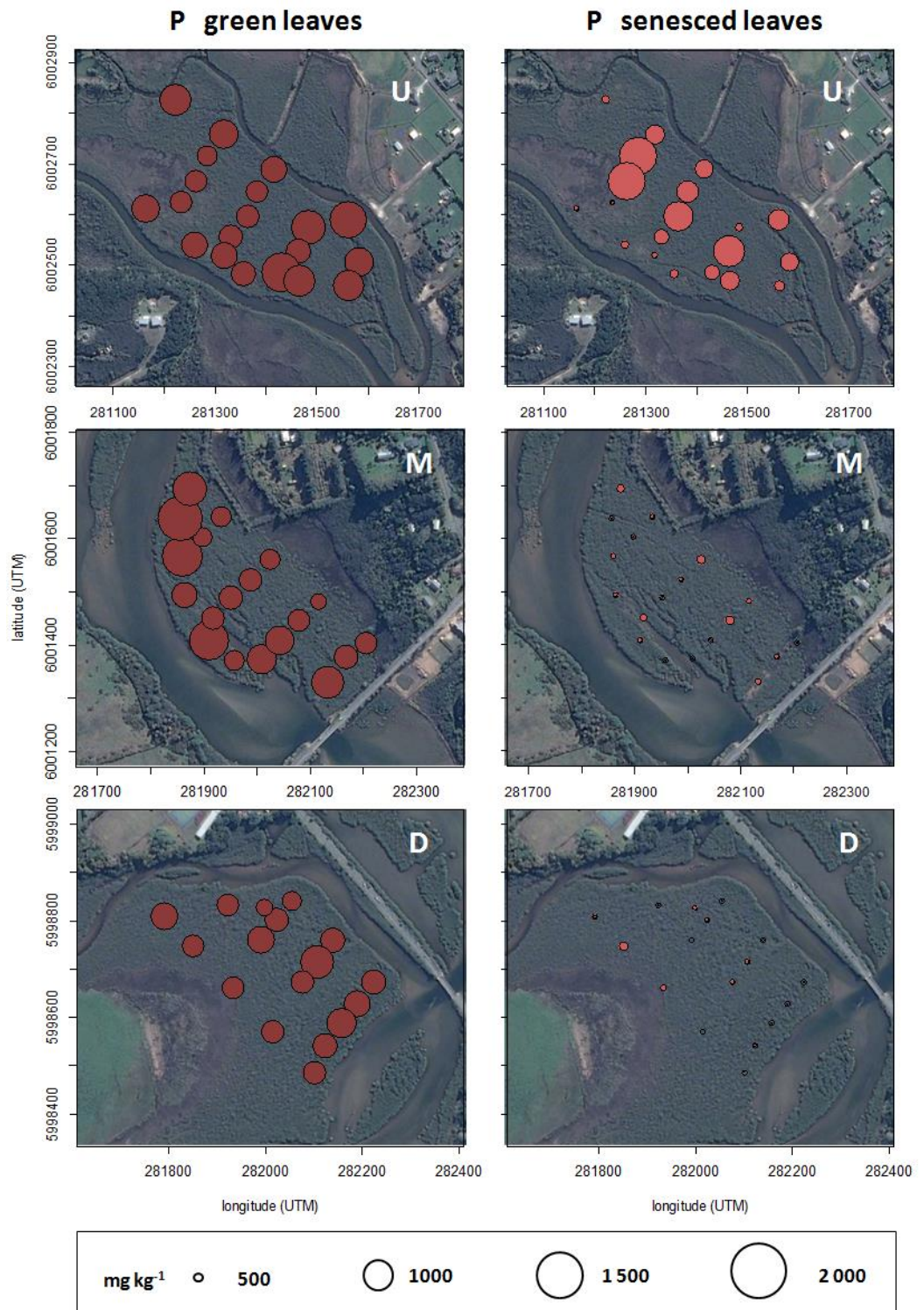
Appendix 7. Maps of the mean values concentrations of total phosphorus in green leaf tissues (*gr*) and senesced leaf tissues (*sen*) in each mangrove site, Mangawhai Estuary, New Zealand
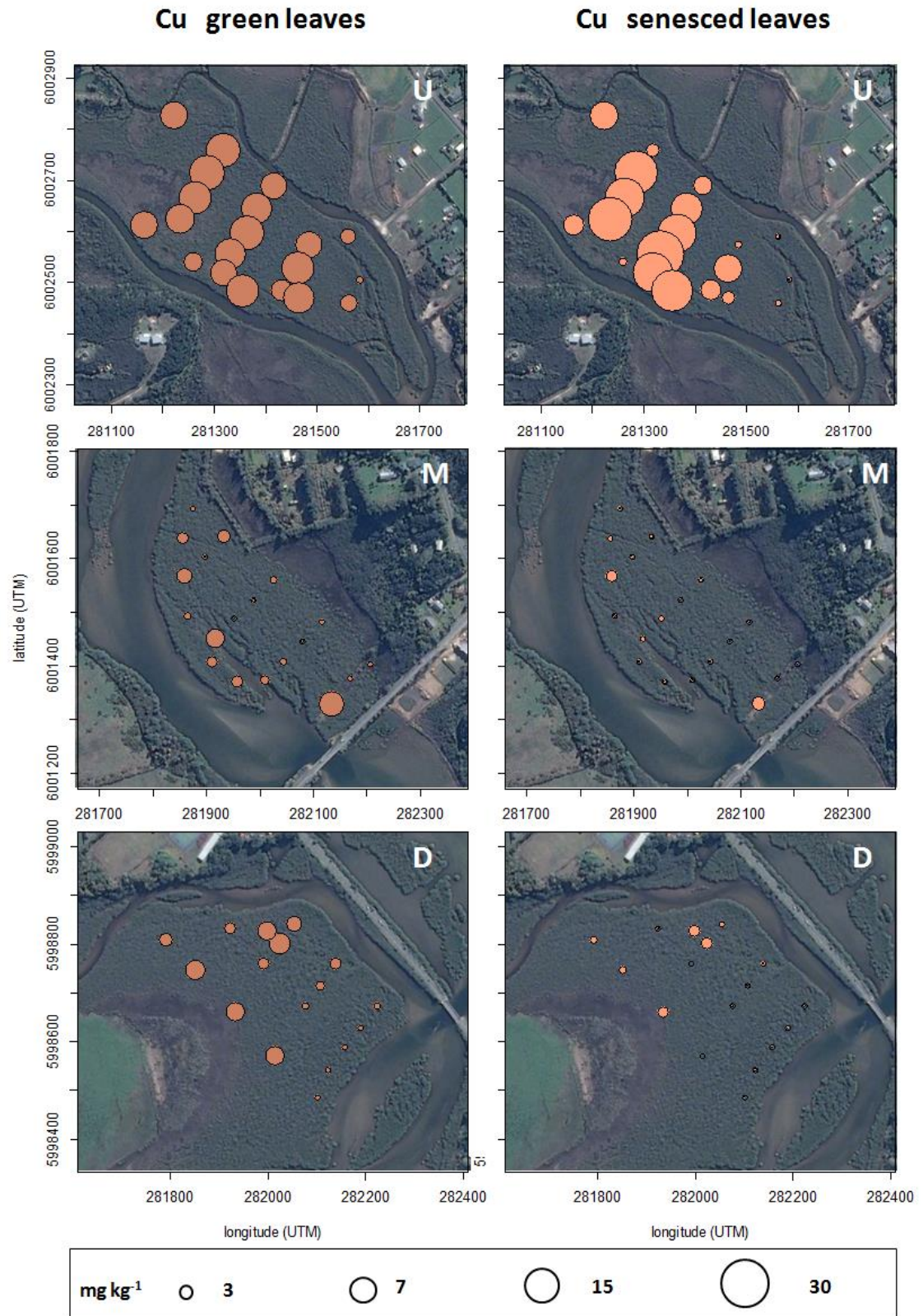
Appendix 8. Maps of the mean values concentrations of total copper in green leaf tissues (gr) and senesced leaf tissues (sen) in each mangrove site, Mangawhai Estuary, New Zealand

Appendix 9. Mean (±SD, minimum - maximum) concentrations (by dry weight) of trace metals in the soils, coarse roots (c. root), aerial roots (aerial), wood, green leaves (green) and senesced leaves (sen) in the *A. marina* and *R. stylosa* stands at the natural site (New Caledonia)

|		Natural site			
		A. marina		*R. stylosa*	
Fe	soil	33.44	(± 8.51, 24.01 - 52.73)	43.13	(± 3.25, 38.42 - 47.25)
(g kg⁻¹)	c.root	3.10	(± 1.08, 1.57 - 4.88)	6.40	(± 2.37, 3.78 - 9.10)
	aerial	3.62	(± 0.63, 2.76 - 4.49)	0.57	(± 0.04, 0.53 - 0.64)
	wood	0.45	(± 0.03, 0.38 - 0.49)	0.56	(± 0.40, 0.22 - 1.04)
	green	0.27	(± 0.19, 0.05 - 0.98)	0.08	(± 0.08, 0.03 - 0.36)
	sen	0.26	(± 0.08, 0.10 - 0.44)	0.14	(± 0.14, 0.03 - 0.42)
Mn	soil	154.41	(± 31.56, 101.26 - 195.05)	350.65	(± 70.29, 263.85 - 429.44)
(mg kg⁻¹)	c.root	97.27	(± 16.69, 69.26 - 121.94)	27.50	(± 10.46, 16.83 - 42.40)
	aerial	81.10	(± 33.83, 28.42 - 136.47)	13.58	(± 2.67, 10.45 - 16.04)
	wood	12.90	(± 3.15, 6.94 - 17.88)	40.15	(± 10.26, 31.81 - 56.76)
	green	32.71	(± 15.43, 11.76 - 59.47)	46.89	(± 19.58, 30.94 - 114.00)
	sen	59.26	(± 9.60, 42.09 - 83.11)	64.17	(± 9.74, 48.79 - 87.18)
Ni	soil	195.75	(± 68.76, 103.67 - 298.24)	283.55	(± 55.52, 212.20 - 338.81)
(mg kg⁻¹)	c.root	52.86	(± 5.29, 44.36 - 59.31)	6.86	(± 2.27, 4.43 - 10.54)
	aerial	24.23	(± 4.36, 16.82 - 31.65)	7.47	(± 0.94, 6.18 - 8.50)
	wood	3.70	(± 1.83, 1.01 - 6.77)	6.62	(± 2.51, 3.67 - 9.78)
	green	7.57	(± 6.99, 0.43 - 35.11)	1.57	(± 1.29, 0.10 - 4.00)
	sen	11.27	(± 14.31, 3.83 - 72.34)	2.36	(± 0.83, 1.34 - 4.75)
Al	soil	41 760.37	(± 4 230.45, 34 572.55 - 49 647.69)	43 273.86	(± 5 866.53, 34 159.40 - 49 504.11)
(mg kg⁻¹)	c.root	6 446.03	(± 2 169.92, 3 399.32 - 9 056.44)	708.54	(± 143.94, 565.94 - 944.64)
	aerial	4 407.33	(± 991.00, 2 857.81 - 6 290.54)	678.42	(± 74.90, 566.65 - 769.93)
	wood	417.53	(± 45.01, 335.28 - 474.01)	475.51	(± 422.77, 190.65 - 1 164.84)
	green	487.89	(± 495.25, 40.00 - 2 180.00)	34.44	(± 51.90, 0.10 - 210.00)
	sen	133.19	(± 139.83, 3.21 - 350.31)	109.21	(± 176.54, 2.99 - 461.44)
Cu	soil	21.92	(± 6.53, 15.10 - 32.20)	21.99	(± 4.61, 17.47 - 27.48)
(mg kg⁻¹)	c.root	21.85	(± 4.89, 13.74 - 30.78)	2.85	(± 1.74, 0.70 - 4.78)
	aerial	15.83	(± 3.26, 10.55 - 22.82)	1.92	(± 0.77, 1.07 - 2.80)
	wood	18.18	(± 3.80, 11.88 - 25.28)	1.09	(± 0.53, 0.73 - 1.99)
	green	14.91	(± 7.38, 0.90 - 27.20)	2.22	(± 1.90, 0.78 - 7.00)
	sen	6.99	(± 3.01, 1.12 - 12.13)	0.41	(± 0.28, 0.13 - 0.89)
Zn	soil	34.08	(± 6.28, 25.10 - 42.38)	45.04	(± 8.21, 32.73 - 55.77)
(mg kg⁻¹)	c.root	14.30	(± 3.74, 9.11 - 21.95)	8.21	(± 4.15, 4.50 - 13.44)
	aerial	19.45	(± 2.63, 13.86 - 24.17)	4.67	(± 4.06, 1.24 - 9.82)
	wood	8.70	(± 1.89, 5.66 - 12.24)	2.13	(± 1.62, 0.87 - 4.22)
	green	18.54	(± 8.75, 3.10 - 39.81)	4.14	(± 1.90, 1.00 - 8.99)
	sen	18.64	(± 5.45, 7.69 - 29.01)	1.80	(± 0.97, 0.71 - 3.44)
Co	soil	16.78	(± 3.83, 11.63 - 24.68)	34.17	(± 5.53, 25.37 - 39.55)
(mg kg⁻¹)	c.root	7.62	(± 1.39, 5.15 - 9.86)	0.55	(± 0.37, 0.14 - 0.96)
	aerial	2.55	(± 1.07, 0.51 - 3.66)	0.51	(± 0.20, 0.20 - 0.70)
	wood	0.56	(± 0.23, 0.31 - 1.09)	0.54	(± 0.33, 0.21 - 1.02)
	green	0.38	(± 0.27, 0.02 - 1.19)	0.08	(± 0.06, 0.01 - 0.16)
	sen	0.27	(± 0.08, 0.16 - 0.43)	0.08	(± 0.08, 0.01 - 0.27)
Cr	soil	141.97	(± 39.97, 105.40 - 205.28)	179.89	(± 32.74, 136.26 - 212.41)
(mg kg⁻¹)	c.root	18.27	(± 4.47, 10.63 - 23.38)	6.64	(± 1.64, 4.36 - 8.97)
	aerial	14.28	(± 3.75, 8.08 - 19.98)	4.04	(± 0.99, 3.10 - 5.55)
	wood	3.19	(± 1.07, 1.39 - 4.61)	4.59	(± 2.65, 2.33 - 8.92)
	green	4.76	(± 5.83, 0.76 - 31.80)	0.89	(± 0.65, 0.00 - 2.00)
	sen	2.06	(± 0.81, 1.35 - 3.41)	1.37	(± 0.69, 0.56 - 2.46)

Appendix 10. Mean (±SD, minimum - maximum) concentrations (by dry weight) of trace metals in the soils, coarse roots (c. root), aerial roots (aerial), wood, green leaves (green) and senesced leaves (sen) in the *A. marina* and *R. stylosa* stands at the mining-influenced site (New Caledonia)

		Mining-influenced site			
		A. marina		*R. stylosa*	
Fe	soil	108.75	(± 8.75, 97.19 - 118.20)	86.01	(± 12.45, 61.76 - 101.74)
(g kg⁻¹)	c.root	16.47	(± 1.94, 15.25 - 19.87)	16.13	(± 1.15, 13.59 - 17.37)
	aerial	3.10	(± 0.22, 2.85 - 3.33)	0.70	(± 0.14, 0.46 - 0.93)
	wood	0.43	(± 0.07, 0.38 - 0.54)	0.44	(± 0.15, 0.18 - 0.65)
	green	0.28	(± 0.06, 0.22 - 0.36)	0.10	(± 0.05, 0.05 - 0.21)
	sen	0.67	(± 0.28, 0.36 - 1.04)	0.13	(± 0.05, 0.06 - 0.21)
Mn	soil	843.13	(± 146.32, 622.73 - 1 030.94)	379.98	(±54.41, 309.22 - 452.70)
(mg kg⁻¹)	c.root	331.45	(± 11.08, 314.05 - 342.36)	72.09	(± 11.84, 55.59 - 94.22)
	aerial	99.74	(± 15.06, 78.48 - 115.95)	23.58	(± 5.75, 11.45 - 29.22)
	wood	31.35	(± 10.13, 19.61 - 41.75)	59.43	(± 15.11, 33.99 - 81.86)
	green	62.41	(± 15.92, 46.14 - 84.80)	157.39	(± 89.54, 57.10 - 335.47)
	sen	98.95	(± 25.29, 74.38 - 131.95)	275.52	(± 142.92, 80.93 - 620.29)
Ni	soil	3400.35	(± 338.36, 3 166.59 - 3 996.55)	1947.06	(± 359.81, 1 455.55 - 2 470.04)
(mg kg⁻¹)	c.root	245.65	(± 78.44, 139.82 - 331.37)	148.06	(± 15.20, 127.44 - 176.40)
	aerial	38.35	(± 6.50, 31.43 - 48.88)	13.48	(± 2.61, 9.16 - 18.44)
	wood	7.93	(± 2.77, 4.39 - 11.16)	6.43	(± 1.40, 3.71 - 8.43)
	green	8.88	(± 4.72, 4.34 - 16.04)	4.41	(± 1.66, 1.60 - 6.89)
	sen	24.13	(± 11.94, 11.58 - 42.99)	10.12	(± 3.10, 5.29 - 17.02)
Al	soil	14 011.40	(± 1 637.87, 11 724.57 - 16 282.43)	30 250.38	(± 19 009.28, 1 513.10 - 60 415.55)
(mg kg⁻¹)	c.root	13 537.05	(± 1 412.12, 11 655.58 - 15 144.10)	1 397.07	(± 456.40, 890.06 - 2 019.20)
	aerial	5 781.61	(± 1 706.91, 3 859.20 - 7 432.44)	881.14	(± 100.52, 670.89 - 979.58)
	wood	312.82	(± 79.73, 215.86 - 437.18)	106.59	(± 25.47, 73.47 - 170.43)
	green	80.35	(± 67.00, 14.89 - 184.99)	9.81	(± 9.80, 0.01 - 29.31)
	sen	259.24	(± 235.20, 53.44 - 641.98)	28.09	(± 31.61, 0.92 - 97.59)
Cu	soil	4.46	(± 1.18, 2.42 - 5.53)	17.20	(± 9.18, 2.77 - 30.93)
(mg kg⁻¹)	c.root	14.64	(± 2.85, 10.30 - 17.36)	4.99	(± 1.55, 3.11 - 7.65)
	aerial	12.23	(± 4.95, 4.55 - 16.98)	1.94	(± 0.47, 1.35 - 2.87)
	wood	7.96	(± 1.28, 6.77 - 9.68)	5.86	(± 0.98, 4.49 - 7.60)
	green	13.57	(± 6.11, 3.83 - 18.45)	6.04	(± 3.96, 1.87 - 19.78)
	sen	6.66	(± 3.98, 2.44 - 10.62)	1.25	(± 0.88, 0.02 - 2.66)
Zn	soil	75.01	(± 9.14, 66.45 - 86.77)	65.46	(± 4.83, 59.64 - 74.01)
(mg kg⁻¹)	c.root	22.74	(± 6.40, 14.82 - 29.46)	13.03	(± 2.10, 9.16 - 15.62)
	aerial	23.74	(± 8.13, 12.93 - 33.10)	3.92	(± 2.25, 0.56 - 7.49)
	wood	12.35	(± 4.65, 7.05 - 18.62)	3.82	(± 0.57, 3.29 - 5.21)
	green	15.13	(± 5.24, 8.87 - 22.35)	5.36	(± 1.57, 2.58 - 7.90)
	sen	9.62	(± 3.08, 6.04 - 13.18)	3.85	(± 2.82, 1.55 - 9.15)
Co	soil	206.23	(± 11.04, 188.55 - 216.75)	119.00	(± 18.19, 95.54 - 154.22)
(mg kg⁻¹)	c.root	22.20	(± 4.87, 14.98 - 27.36)	10.37	(± 1.54, 7.89 - 13.13)
	aerial	13.15	(± 1.32, 12.11 - 15.41)	3.46	(± 1.55, 0.84 - 6.52)
	wood	1.71	(±0.42, 1.15 - 2.17)	0.71	(± 0.43, 0.28 - 1.59)
	green	1.17	(± 0.68, 0.47 - 2.06)	0.15	(± 0.06, 0.06 - 0.25)
	sen	2.02	(± 1.38, 0.78 - 4.34)	0.14	(± 0.05, 0.06 - 0.21)
Cr	soil	1 465.87	(± 170.32, 1 270.30 - 1 739.94)	959.09	(± 384.60, 538.32 - 1 398.94)
(mg kg⁻¹)	c.root	72.89	(± 4.62, 66.44 - 77.97)	15.02	(± 1.80, 11.69 - 17.84)
	aerial	33.29	(± 11.03, 24.75 - 51.52)	6.24	(± 2.29, 4.62 - 12.80)
	wood	12.04	(± 2.50, 9.86 - 14.76)	6.57	(± 1.99, 3.07 - 8.88)
	green	1.72	(± 0.40, 1.39 - 2.41)	0.88	(± 0.76, 0.12 - 2.90)
	sen	5.99	(± 3.57, 2.65 - 11.33)	2.14	(± 1.92, 0.73 - 6.83)

Appendix 11. Mean (±SD, minimum - maximum) concentrations (by dry weight) of trace metals in the soils, coarse roots (c. root), aerial roots (aerial), wood, green leaves (green) and senesced leaves (sen) in the *A. marina* and *R. stylosa* stands at the aquaculture-influenced site (New Caledonia)

		Aquaculture-influenced site			
		A. marina		*R. stylosa*	
Fe	soil	76.93	(± 2.82, 70.90 - 79.15)	64.06	(± 7.83, 55.66 - 78.79)
(g kg⁻¹)	c.root	1.00	(± 0.24, 0.79 - 1.52)	8.60	(± 1.87, 5.91 - 11.60)
	aerial	1.97	(± 0.21, 1.62 - 2.19)	0.66	(± 0.07, 0.56 - 0.77)
	wood	0.36	(± 0.07, 0.30 - 0.44)	0.30	(± 0.08, 0.20 - 0.39)
	green	0.54	(± 0.24, 0.22 - 0.93)	0.16	(± 0.08, 0.05 - 0.42)
	sen	0.35	(± 0.09, 0.16 - 0.44)	0.30	(± 0.39, 0.05 - 1.00)
Mn	soil	458.14	(± 66.00, 348.45 - 531.67)	371.98	(± 76.73, 253.38 - 531.67)
(mg kg⁻¹)	c.root	228.11	(± 46.41, 149.13 - 277.57)	77.61	(± 16.27, 46.71 - 100.36)
	aerial	87.69	(± 15.28, 76.55 - 117.83)	18.56	(± 5.60, 10.41 - 28.48)
	wood	31.15	(± 9.45, 22.38 - 46.71)	34.12	(± 13.31, 18.25 - 57.37)
	green	83.74	(± 28.00, 49.05 - 132.82)	182.66	(± 86.52, 69.19 - 568.98)
	sen	81.32	(± 14.59, 52.86 - 112.96)	255.05	(± 110.91, 86.66 - 610.97)
Ni	soil	701.61	(± 220.44, 435.28 - 924.37)	420.85	(± 240.17, 237.37 - 924.37)
(mg kg⁻¹)	c.root	146.26	(± 23.70, 103.45 - 172.63)	130.02	(± 20.90, 92.56 - 161.53)
	aerial	25.59	(± 5.88, 16.96 - 31.94)	8.27	(± 1.71, 4.79 - 10.26)
	wood	5.57	(± 1.62, 3.59 - 8.16)	5.90	(± 1.46, 2.64 - 8.13)
	green	11.64	(± 8.29, 2.71 - 33.57)	6.35	(± 3.08, 1.69 - 18.51)
	sen	14.06	(± 19.86, 3.98 - 70.08)	7.62	(± 2.93, 3.97 - 15.08)
Al	soil	42 891.60	(± 7 248.09, 36 179.69 - 52 156.62)	31 299.65	(± 4 483.28, 24 262.40 - 38 167.90)
(mg kg⁻¹)	c.root	10 399.07	(± 404.02, 9 617.28 - 10 939.15)	629.10	(± 278.43, 367.31 - 1 120.80)
	aerial	5 811.55	(± 1 588.11, 3 966.86 - 7 747.34)	757.79	(± 160.09, 450.35 - 1 002.10)
	wood	220.41	(± 113.18, 24.13 - 391.59)	189.32	(± 65.13, 105.83 - 312.84)
	green	273.33	(± 231.17, 60.00 - 840.00)	51.92	(± 35.71, 10.00 - 180.00)
	sen	43.74	(± 29.02, 20.74 - 76.35)	151.13	(± 199.09, 12.14 - 444.05)
Cu	soil	39.31	(± 7.08, 29.44 - 48.14)	25.93	(± 4.47, 18.58 - 35.28)
(mg kg⁻¹)	c.root	26.36	(± 8.28, 14.92 - 38.27)	6.16	(± 1.58, 3.64 - 8.51)
	aerial	20.22	(± 6.38, 13.94 - 32.12)	2.47	(± 1.66, 0.25 - 4.80)
	wood	12.24	(± 3.86, 7.72 - 17.43)	12.67	(± 9.55, 2.98 - 25.83)
	green	11.62	(± 5.96, 0.99 - 21.06)	3.67	(± 1.45, 1.06 - 7.38)
	sen	5.08	(± 2.88, 2.15 - 12.67)	2.35	(± 1.51, 0.53 - 4.16)
Zn	soil	64.99	(± 2.87, 59.18 - 67.58)	54.08	(± 5.42, 48.35 - 65.02)
(mg kg⁻¹)	c.root	18.45	(± 5.06, 13.33 - 26.70)	11.92	(± 2.17, 6.73 - 13.94)
	aerial	24.77	(± 6.53, 19.93 - 38.05)	4.10	(± 0.95, 2.47 - 5.90)
	wood	8.71	(± 2.06, 5.01 - 11.61)	8.80	(± 3.97, 3.93 - 17.03)
	green	20.19	(± 12.97, 8.24 - 60.78)	5.73	(± 2.79, 1.59 - 14.43)
	sen	16.50	(± 7.52, 8.95 - 30.04)	6.06	(± 6.82, 1.59 - 19.06)
Co	soil	68.67	(± 5.65, 60.40 - 76.53)	72.39	(± 6.59, 60.61 - 80.99)
(mg kg⁻¹)	c.root	14.77	(± 3.35, 11.22 - 19.57)	2.74	(± 1.67, 0.88 - 5.27)
	aerial	9.39	(± 1.77, 6.83 - 11.34)	2.79	(± 0.85, 1.54 - 4.28)
	wood	0.49	(± 0.20, 0.22 - 0.74)	0.55	(± 0.22, 0.22 - 0.83)
	green	0.99	(± 0.93, 0.30 - 3.32)	0.28	(± 0.18, 0.00 - 0.97)
	sen	0.59	(± 0.22, 0.32 - 0.87)	0.41	(± 0.48, 0.00 - 1.13)
Cr	soil	489.37	(± 23.05, 444.03 - 514.20)	396.48	(± 91.31, 273.69 - 519.65)
(mg kg⁻¹)	c.root	35.15	(± 4.87, 30.25 - 43.69)	9.02	(± 2.00, 5.98 - 11.87)
	aerial	20.19	(± 4.96, 15.34 - 29.70)	6.10	(± 3.35, 2.01 - 11.46)
	wood	2.67	(± 1.47, 0.63 - 5.42)	2.73	(± 0.61, 1.60 - 3.67)
	green	6.42	(± 6.76, 1.89 - 28.45)	1.98	(± 1.51, 0.34 - 5.61)
	sen	1.96	(± 0.62, 1.17 - 2.53)	2.42	(± 2.25, 0.79 - 6.46)

Appendix 12. Mean (±SD, minimum - maximum) Bioconcentration Factors (BCF, unitless), Translocation Factors (TF, unitless) and Resorption Efficiency (RE, %) of Fe, Mn, Ni, Al in the different plant materials (green = green leaves, sen = senesced leaves) in the *A. marina* and *R. stylosa* stands at the natural site, the mining influenced site, and the aquaculture influenced site (New Caledonia)

		Natural site		Mining-influenced site		Aquaculture-influenced site	
		A. marina	*R. stylosa*	*A. marina*	*R. stylosa*	*A. marina*	*R. stylosa*
Fe	BCF root	0.10 (± 0.05, 0.04 - 0.17)	0.15 (± 0.06, 0.09 - 0.24)	0.15 (± 0.02, 0.13 - 0.19)	0.17 (± 0.07, 0.06 - 0.28)	0.01 (± 0.00, 0.01 - 0.02)	0.14 (± 0.03, 0.10 - 0.18)
	BCF aerial	0.12 (± 0.04, 0.05 - 0.17)	0.01 (± 0.00, 0.01 - 0.01)	0.03 (± 0.00, 0.02 - 0.03)	0.01 (± 0.00, 0.01 - 0.01)	0.03 (± 0.00, 0.02 - 0.03)	0.01 (± 0.00, 0.01- 0.01)
	BCF wood	0.01 (± 0.00, 0.01 - 0.02)	0.01 (± 0.01, 0.00 - 0.03)	0.00 (± 0.00, 0.00 - 0.01)	0.01 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.01)
	BCF green	0.01 (± 0.01, 0.00 - 0.03)	0.00 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.00)	0.00 (± 0.00, 0.00 - 0.00)	0.01 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.01)
	BCF sen	0.01 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.00)	0.01 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.00)	0.00 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.00)
	TF aerial	1.26 (± 0.31, 0.78 - 1.81)	0.10 (± 0.04, 0.06 - 0.15)	0.19 (± 0.01, 0.17 - 0.20)	0.06 (± 0.03, 0.03 - 0.12)	2.05 (± 0.46, 1.29 - 2.64)	0.08 (± 0.01, 0.06 - 0.10)
	TF wood	0.17 (± 0.07, 0.09 - 0.30)	0.08 (± 0.03, 0.04 - 0.11)	0.03 (± 0.00, 0.02 - 0.03)	0.03 (± 0.02, 0.01 - 0.07)	0.37 (± 0.06, 0.29 - 0.44)	0.03 (± 0.00, 0.03 - 0.04)
	TF green	0.11 (± 0.08, 0.04 - 0.28)	0.03 (± 0.04, 0.01 - 0.10)	0.02 (± 0.00, 0.01 - 0.02)	0.01 (± 0.01, 0.00 - 0.02)	0.45 (± 0.13, 0.25 - 0.60)	0.02 (± 0.01, 0.01 - 0.05)
	TF sen	0.10 (± 0.05, 0.04 - 0.23)	0.01 (± 0.01, 0.00 - 0.03)	0.04 (± 0.02, 0.02 - 0.07)	0.01 (± 0.00, 0.00 - 0.02)	0.34 (±0.12 , 0.15 - 0.50)	0.01 (± 0.00, 0.01 - 0.02)
Mn	BCF root	0.67 (± 0.24, 0.42 - 1.20)	0.08 (± 0.04, 0.04 - 0.14)	0.40 (± 0.08, 0.30 - 0.53)	0.20 (± 0.05, 0.13 - 0.28)	0.5 (± 0.08, 0.37 - 0.59)	0.21 (± 0.05, 0.14 - 0.27)
	BCF aerial	0.53 (± 0.20, 0.20 - 0.83)	0.04 (± 0.00, 0.03 - 0.05)	0.12 (± 0.01, 0.11 - 0.13)	0.06 (± 0.02, 0.03 - 0.09)	0.19 (± 0.03, 0.15 - 0.23)	0.05 (± 0.02, 0.03 - 0.08)
	BCF wood	0.09 (± 0.03, 0.05 - 0.13)	0.12 (± 0.06, 0.08 - 0.22)	0.04 (± 0.02, 0.02 - 0.07)	0.16 (± 0.04, 0.08 - 0.21)	0.07 (± 0.02, 0.04 - 0.09)	0.09 (± 0.03, 0.05 - 0.16)
	BCF green	0.22 (± 0.09, 0.08 - 0.36)	0.18 (± 0.11, 0.11 - 0.38)	0.08 (± 0.03, 0.04 - 0.11)	0.38 (± 0.25, 0.15 - 0.88)	0.17 (± 0.06, 0.11 - 0.26)	0.50 (± 0.27, 0.14 - 1.03)
	BCF sen	0.40 (± 0.09, 0.26 - 0.58)	0.20 (± 0.05, 0.14 − 0.28)	0.12 (± 0.05, 0.07 - 0.19)	0.77 (± 0.46, 0.21 - 1.81)	0.17 (± 0.04, 0.11 - 0.25)	0.78 (± 0.59, 0.30 - 2.41)
	TF aerial	0.86 (± 0.39, 0.32 - 1.37)	0.58 (± 0.29, 0.25 - 0.88)	0.30 (± 0.05, 0.24 - 0.37)	0.34 (± 0.10, 0.12 - 0.46)	0.39 (± 0.07, 0.31 - 0.51)	0.24 (± 0.08, 0.14 - 0.41)
	TF wood	0.13 (± 0.03, 0.10 - 0.21)	1.59 (± 0.52, 1.02 - 2.01)	0.10 (± 0.03, 0.06 - 0.13)	0.86 (± 0.31, 0.43 - 1.47)	0.14 (± 0.03, 0.09 - 0.18)	0.47 (± 0.26, 0.18 - 1.15)
	TF green	0.35 (± 0.17, 0.13 - 0.60)	2.22 (± 0.73, 1.45 - 3.10)	0.19 (± 0.04, 0.14 - 0.25)	2.03 (± 1.29, 0.61 - 4.67)	0.34 (± 0.10, 0.22 - 0.47)	2.31 (± 1.10, 0.97 - 4.56)
	TF sen	0.63 (± 0.15, 0.41 - 0.94)	2.74 (± 1.01, 1.63 - 4.03)	0.30 (± 0.07, 0.23 - 0.39)	4.09 (± 2.24, 0.86 - 8.03)	0.35 (± 0.11, 0.21 - 0.53)	3.60 (± 2.46, 1.64 - 10.64)
Ni	BCF root	0.31 (± 0.13, 0.16 - 0.56)	0.03 (± 0.01, 0.02 - 0.05)	0.07 (± 0.02, 0.04 - 0.10)	0.08 (± 0.01, 0.05 - 0.10)	0.23 (± 0.08, 0.16 - 0.35)	0.37 (± 0.14, 0.17 - 0.62)
	BCF aerial	0.14 (± 0.07, 0.06 - 0.26)	0.03 (± 0.01, 0.02 - 0.04)	0.01 (± 0.00, 0.01 - 0.02)	0.01 (± 0.00, 0.01 - 0.01)	0.04 (± 0.02, 0.02 - 0.07)	0.02 (± 0.01, 0.01 - 0.04)
	BCF wood	0.02 (± 0.02, 0.01 - 0.07)	0.02 (± 0.01, 0.01 - 0.05)	0.00 (± 0.00, 0.00 - 0.00)	0.00 (± 0.00, 0.00 - 0.01)	0.01 (± 0.01, 0.00 - 0.02)	0.02 (± 0.01, 0.01 - 0.03)
	BCF green	0.04 (± 0.04, 0.01 - 0.10)	0.01 (± 0.00, 0.01 - 0.01)	0.00 (± 0.00, 0.00 - 0.00)	0.00 (± 0.00, 0.00 - 0.00)	0.02 (± 0.02, 0.01 - 0.05)	0.02 (± 0.01, 0.01 - 0.04)
	BCF sen	0.05 (± 0.05, 0.01 - 0.16)	0.01 (± 0.00, 0.01 - 0.01)	0.01 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.01)	0.03 (± 0.05, 0.00 - 0.14)	0.02 (± 0.01, 0.01 - 0.04)
	TF aerial	0.46 (± 0.06, 0.34 - 0.60)	1.17 (± 0.34, 0.78 - 1.65)	0.17 (± 0.05, 0.13 - 0.26)	0.09 (± 0.01, 0.07 - 0.11)	0.18 (± 0.04, 0.12 - 0.24)	0.06 (± 0.01, 0.04 - 0.08)
	TF wood	0.07 (± 0.03, 0.02 - 0.12)	1.00 (± 0.39, 0.63 - 1.57)	0.03 (± 0.00, 0.03 - 0.04)	0.04 (± 0.01, 0.03 - 0.06)	0.04 (± 0.02, 0.02 - 0.08)	0.04 (± 0.01, 0.03 - 0.06)
	TF green	0.13 (± 0.07, 0.02 - 0.27)	0.42 (± 0.26, 0.10 - 0.78)	0.04 (± 0.01, 0.02 - 0.06)	0.03 (± 0.01, 0.01 - 0.05)	0.06 (± 0.04, 0.04 - 0.15)	0.05 (± 0.02, 0.02 - 0.09)
	TF sen	0.16 (± 0.12, 0.08 - 0.46)	0.33 (± 0.11, 0.18 - 0.46)	0.10 (± 0.04, 0.05 - 0.15)	0.06 (± 0.01, 0.04 - 0.09)	0.1 (± 0.14, 0.02 - 0.41)	0.06 (± 0.03, 0.03 - 0.12)
Al	BCF root	0.16 (± 0.05, 0.07 - 0.22)	0.02 (± 0.00, 0.01 - 0.02)	0.98 (± 0.20, 0.82 - 1.29)	0.10 (± 0.16, 0.03 - 0.59)	0.25 (± 0.04, 0.21 - 0.29)	0.02 (± 0.01, 0.01 - 0.03)
	BCF aerial	0.11 (± 0.02, 0.07 - 0.15)	0.02 (± 0.00, 0.01 - 0.02)	0.42 (± 0.15, 0.27 - 0.63)	0.09 (± 0.18, 0.02 - 0.64)	0.14 (± 0.06, 0.08 - 0.21)	0.02 (± 0.01, 0.02 - 0.03)
	BCF wood	0.01 (± 0.00, 0.01 - 0.01)	0.01 (± 0.01, 0.00 - 0.03)	0.02 (± 0.01, 0.02 - 0.04)	0.01 (± 0.01, 0.00 - 0.05)	0.01 (± 0.00, 0.00 - 0.01)	0.01 (± 0.00, 0.00 - 0.01)
	BCF green	0.01 (± 0.01, 0.00 - 0.04)	0.00 (± 0.00, 0.00 - 0.00)	0.01 (± 0.00, 0.00 - 0.01)	0.00 (± 0.01, 0.00 - 0.02)	0.01 (± 0.00, 0.00 - 0.02)	0.00 (± 0.00, 0.00 - 0.01)
	BCF sen	0.00 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.00)	0.02 (± 0.02, 0.00 - 0.05)	0.00 (± 0.00, 0.00 - 0.00)	0.00 (± 0.00, 0.00 - 0.05)	0.00 (± 0.00, 0.00 - 0.00)
	TF aerial	0.75 (± 0.24, 0.45 - 1.19)	1.00 (± 0.24, 0.60 - 1.18)	0.43 (± 0.13, 0.27 - 0.56)	0.70 (± 0.25, 0.41 - 1.09)	0.56 (± 0.15, 0.38 - 0.75)	1.35 (± 0.45, 0.77 - 2.12)
	TF wood	0.07 (± 0.03, 0.04 - 0.14)	0.61 (± 0.41, 0.29 - 1.23)	0.02 (± 0.01, 0.01 - 0.03)	0.08 (± 0.04, 0.05 - 0.16)	0.02 (± 0.01, 0.00 - 0.04)	0.38 (± 0.24, 0.12 - 0.85)
	TF green	0.08 (± 0.05, 0.02 - 0.19)	0.10 (± 0.15, 0.01 - 0.37)	0.01 (± 0.00, 0.00 - 0.01)	0.01 (± 0.01, 0.00 - 0.03)	0.03 (± 0.02, 0.01 - 0.08)	0.09 (± 0.10, 0.03 - 0.36)
	TF sen	0.02 (± 0.04, 0.00 - 0.10)	0.08 (± 0.01, 0.07 - 0.08)	0.02 (± 0.02, 0.00 - 0.05)	0.02 (± 0.02, 0.00 - 0.05)	0.00 (± 0.00, 0.00 - 0.01)	0.04 (± 0.03, 0.01 - 0.08)

Appendix 13. Mean (±SD, minimum - maximum) Bioconcentration Factors (BCF, unitless), Translocation Factors (TF, unitless) and Resorption Efficiency (RE, %) of Cu, Zn, Co, Cr in the different plant materials (green = green leaves, sen = senesced leaves) in the *A. marina* and *R. stylosa* stands at the natural site, the mining influenced site, and the aquaculture influenced site (New Caledonia)

		Natural site		Mining-influenced site		Aquaculture-influenced site	
		A. marina	*R. stylosa*	*A. marina*	*R. stylosa*	*A. marina*	*R. stylosa*
Cu	BCF root	1.08 (± 0.41, 0.58 - 1.79)	0.14 (± 0.10, 0.03 - 0.27)	3.62 (± 1.74, 2.15 - 6.60)	0.41 (± 0.35, 0.19 - 1.42)	0.67 (± 0.17, 0.39 - 0.94)	0.24 (± 0.05, 0.13 - 0.32)
	BCF aerial	0.78 (± 0.29, 0.44 - 1.33)	0.09 (± 0.05, 0.04 - 0.16)	3.17 (± 2.29, 0.95 - 7.01)	0.17 (± 0.16, 0.06 - 0.64)	0.52 (± 0.13, 0.35 - 0.68)	0.10 (± 0.06, 0.01 - 0.18)
	BCF wood	0.92 (± 0.38, 0.41 - 1.47)	0.05 (± 0.03, 0.03 - 0.10)	1.93 (± 0.72, 1.26 - 3.08)	0.59 (± 0.74, 0.17 - 2.75)	0.31 (± 0.06, 0.23 - 0.40)	0.51 (± 0.42, 0.10 - 1.29)
	BCF green	0.80 (± 0.50, 0.07 - 1.60)	0.12 (± 0.07, 0.05 - 0.23)	3.20 (± 1.46, 0.80 - 4.66)	0.55 (± 0.54, 0.08 - 1.65)	0.29 (± 0.14, 0.03 - 0.45)	0.15 (± 0.05, 0.08 - 0.24)
	BCF sen	0.36 (± 0.19, 0.04 - 0.60)	0.02 (± 0.02, 0.01 - 0.04)	1.62 (± 1.04, 0.51 - 2.86)	0.13 (± 0.13, 0.00 - 0.37)	0.13 (± 0.07, 0.05 - 0.27)	0.05 (± 0.03, 0.02 - 0.10)
	TF aerial	0.76 (± 0.24, 0.44 - 1.29)	0.95 (± 0.84, 0.49 - 2.45)	0.80 (± 0.23, 0.44 - 1.06)	0.41 (± 0.10, 0.20 - 0.53)	0.79 (± 0.16, 0.54 - 1.02)	0.39 (± 0.23, 0.04 - 0.72)
	TF wood	0.86 (± 0.23, 0.55 - 1.35)	0.50 (± 0.34, 0.24 - 1.09)	0.56 (± 0.12, 0.40 - 0.67)	1.26 (± 0.38, 0.76 - 1.94)	0.48 (± 0.12, 0.32 - 0.65)	2.21 (±1.84, 0.40 - 6.24)
	TF green	0.73 (± 0.44, 0.10 - 1.88)	1.61 (± 1.59, 0.22 - 3.81)	0.90 (± 0.36, 0.37 - 1.28)	1.33 (± 0.89, 0.28 - 2.94)	0.43 (± 0.21, 0.05 - 0.71)	0.69 (± 0.30, 0.30 - 1.25)
	TF sen	0.33 (± 0.17, 0.06 - 0.59)	0.15 (± 0.10, 0.03 - 0.28)	0.43 (± 0.20, 0.21 - 0.65)	0.30 (± 0.26, 0.00 - 0.70)	0.20 (± 0.12, 0.08 - 0.43)	0.21 (± 0.18, 0.06 - 0.47)
Zn	BCF root	0.44 (± 0.18, 0.28 - 0.82)	0.18 (± 0.07, 0.10 - 0.26)	0.31 (± 0.08, 0.18 - 0.38)	0.20 (± 0.03, 0.13 - 0.24)	0.28 (± 0.08, 0.21 - 0.40)	0.22 (± 0.05, 0.11 - 0.27)
	BCF aerial	0.59 (± 0.15, 0.40 - 0.85)	0.10 (± 0.08, 0.04 - 0.18)	0.32 (± 0.12, 0.15 - 0.45)	0.06 (± 0.04, 0.01 - 0.11)	0.38 (± 0.10, 0.31 - 0.57)	0.08 (± 0.02, 0.05 - 0.11)
	BCF wood	0.26 (± 0.08, 0.18 - 0.39)	0.05 (± 0.03, 0.02 - 0.08)	0.17 (± 0.07, 0.09 - 0.25)	0.06 (± 0.01, 0.05 - 0.08)	0.13 (± 0.03, 0.08 - 0.17)	0.16 (± 0.06, 0.08 - 0.27)
	BCF green	0.68 (± 0.38, 0.23 - 1.50)	0.12 (± 0.05, 0.09 - 0.20)	0.21 (± 0.09, 0.11 - 0.34)	0.08 (± 0.02, 0.04 - 0.11)	0.22 (± 0.06, 0.13 - 0.29)	0.12 (± 0.08, 0.03 - 0.30)
	BCF sen	0.58 (± 0.22, 0.22 - 0.92)	0.03 (± 0.02, 0.02 - 0.08)	0.13 (± 0.05, 0.09 - 0.20)	0.06 (± 0.05, 0.02 - 0.15)	0.19 (± 0.06, 0.14 - 0.31)	0.04 (± 0.02, 0.03 - 0.07)
	TF aerial	1.45 (± 0.42, 0.82 - 2.15)	0.49 (± 0.22, 0.23 - 0.73)	1.12 (± 0.46, 0.44 - 1.73)	0.29 (± 0.16, 0.06 - 0.53)	1.36 (± 0.20, 1.01 - 1.58)	0.35 (± 0.07, 0.24 - 0.49)
	TF wood	0.65 (± 0.24, 0.29 - 1.07)	0.23 (± 0.07, 0.15 - 0.31)	0.55 (± 0.17, 0.30 - 0.70)	0.30 (± 0.04, 0.23 - 0.37)	0.49 (± 0.12, 0.35 - 0.68)	0.74 (± 0.31, 0.31 - 1.30)
	TF green	1.54 (± 0.57, 0.56 - 2.58)	0.83 (± 0.66, 0.40 - 2.00)	0.68 (± 0.22, 0.42 - 0.95)	0.42 (± 0.15, 0.18 - 0.64)	0.81 (± 0.28, 0.59 - 1.29)	0.54 (± 0.38, 0.16 - 1.22)
	TF sen	1.43 (± 0.66, 0.54 - 2.47)	0.19 (± 0.07, 0.11 - 0.29)	0.43 (± 0.08, 0.33 - 0.52)	0.30 (± 0.24, 0.12 - 0.77)	0.70 (± 0.24, 0.36 - 1.08)	0.18 (± 0.06, 0.12 - 0.26)
Co	BCF root	0.46 (± 0.08, 0.30 - 0.61)	0.02 (± 0.01, 0.00 - 0.04)	0.11 (± 0.03, 0.07 - 0.15)	0.09 (± 0.02, 0.05 - 0.12)	0.22 (± 0.06, 0.16 - 0.30)	0.04 (± 0.02, 0.01 - 0.07)
	BCF aerial	0.16 (± 0.08, 0.03 - 0.30)	0.02 (± 0.01, 0.01 - 0.02)	0.06 (± 0.01, 0.06 - 0.07)	0.03 (± 0.01, 0.01 - 0.06)	0.14 (± 0.03, 0.10 - 0.18)	0.04 (± 0.01, 0.02 - 0.07)
	BCF wood	0.03 (± 0.01, 0.02 - 0.06)	0.02 (± 0.01, 0.01 - 0.03)	0.01 (± 0.00, 0.01 - 0.01)	0.01 (± 0.00, 0.00 - 0.01)	0.01 (± 0.00, 0.00 - 0.01)	0.01 (± 0.00, 0.00 - 0.01)
	BCF green	0.03 (± 0.03, 0.00 - 0.10)	0.00 (± 0.00, 0.00 - 0.00)	0.01 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.00)	0.01 (± 0.01, 0.01 - 0.05)	0.00 (± 0.00, 0.00 - 0.02)
	BCF sen	0.02 (± 0.01, 0.01 - 0.03)	0.00 (± 0.00, 0.00 - 0.00)	0.01 (± 0.01, 0.00 - 0.02)	0.00 (± 0.00, 0.00 - 0.00)	0.01 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.00)
	TF aerial	0.35 (± 0.17, 0.07 - 0.69)	1.82 (± 1.89, 0.21 - 4.84)	0.62 (± 0.15, 0.46 - 0.83)	0.32 (± 0.11, 0.11 - 0.50)	0.65 (± 0.14, 0.46 - 0.84)	1.65 (± 1.26, 0.39 - 3.36)
	TF wood	0.08 (± 0.03, 0.04 - 0.15)	1.28 (± 0.98, 0.46 - 2.97)	0.08 (± 0.03, 0.04 - 0.11)	0.07 (± 0.04, 0.02 - 0.16)	0.03 (± 0.01, 0.02 - 0.05)	0.24 (± 0.10, 0.15 - 0.42)
	TF green	0.07 (± 0.06, 0.00 - 0.23)	0.31 (± 0.29, 0.01 - 0.64)	0.05 (± 0.03, 0.03 - 0.08)	0.02 (± 0.01, 0.00 - 0.03)	0.06 (± 0.05, 0.02 - 0.16)	0.18 (± 0.22, 0.02 - 0.76)
	TF sen	0.04 (± 0.02, 0.02 - 0.07)	0.18 (± 0.29, 0.02 - 0.71)	0.09 (± 0.06, 0.03 - 0.19)	0.01 (± 0.00, 0.01 - 0.02)	0.03 (± 0.01, 0.02 - 0.04)	0.04 (± 0.03, 0.02 - 0.09)
Cr	BCF root	0.13 (± 0.03, 0.10 - 0.18)	0.04 (± 0.01, 0.02 - 0.06)	0.05 (± 0.01, 0.04 - 0.06)	0.02 (± 0.01, 0.01 - 0.03)	0.07 (± 0.01, 0.06 - 0.09)	0.02 (± 0.01, 0.01- 0.04)
	BCF aerial	0.11 (± 0.04, 0.04 - 0.16)	0.02 (± 0.01, 0.02 - 0.04)	0.02 (± 0.01, 0.02 - 0.04)	0.01 (± 0.01, 0.00 - 0.02)	0.04 (± 0.01, 0.03 - 0.07)	0.02 (± 0.01, 0.01 - 0.03)
	BCF wood	0.02 (± 0.01, 0.01 - 0.04)	0.03 (± 0.02, 0.01 - 0.06)	0.01 (± 0.00, 0.01 - 0.01)	0.01 (± 0.00, 0.00 - 0.02)	0.01 (± 0.00, 0.00 - 0.01)	0.01 (± 0.00, 0.00 - 0.01)
	BCF green	0.05 (± 0.08, 0.01 - 0.30)	0.01 (± 0.01, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.00)	0.00 (± 0.00, 0.00 - 0.00)	0.01 (± 0.01, 0.00 - 0.03)	0.01 (± 0.00, 0.00 - 0.01)
	BCF sen	0.01 (± 0.00, 0.01 - 0.02)	0.01 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.01)	0.00 (± 0.00, 0.00 - 0.00)	0.00 (± 0.00, 0.00 - 0.01)
	TF aerial	0.84 (± 0.33, 0.35 - 1.48)	0.62 (± 0.08, 0.50 - 0.71)	0.45 (± 0.12, 0.35 - 0.66)	0.42 (± 0.14, 0.28 - 0.80)	0.58 (± 0.16, 0.41 - 0.85)	0.65 (± 0.26, 0.24 - 1.09)
	TF wood	0.18 (± 0.06, 0.06 - 0.29)	0.67 (± 0.24, 0.37 - 0.99)	0.17 (± 0.04, 0.14 - 0.22)	0.44 (± 0.14, 0.20 - 0.72)	0.07 (± 0.04, 0.02 - 0.14)	0.32 (± 0.10, 0.19 - 0.53)
	TF green	0.40 (± 0.56, 0.07 - 2.13)	0.22 (± 0.12, 0.10 - 0.39)	0.02 (± 0.01, 0.02 - 0.03)	0.05 (± 0.04, 0.01 - 0.16)	0.14 (± 0.09, 0.06 - 0.33)	0.25 (± 0.21, 0.03 - 0.59)
	TF sen	0.10 (± 0.03, 0.06 - 0.14)	0.16 (± 0.09, 0.09 - 0.27)	0.08 (± 0.05, 0.03 - 0.16)	0.14 (± 0.12, 0.05 - 0.42)	0.05 (± 0.01, 0.03 - 0.06)	0.12 (± 0.04, 0.08 - 0.16)

Appendix 14. Mean (±SD, minimum - maximum) concentrations (by dry weight) of the macroelements and Na in the soils and the plant materials (c.root = coarse root, a.root = aerial root, g.leaf = green leaf, sen = senesced leaf) in the *A. marina* and *R. stylosa* stands in the Natural study site (New Caledonia)

			A. marina		*R. stylosa*	
				Natural		
N	(g kg-1)	tot soil	4.45	(±0.75, 3.56 - 5.73)	3.63	(±0.78, 2.60-4.72)
		c.root	4.47	(± 0.42, 3.64 -4.96)	3.13	(± 0.68, 2.53 - 4.22)
		a.root	6.94	(± 0.44, 6.45 - 7.79)	2.16	(± 0.28, 1.81 - 2.55)
		wood	4.99	(± 0.69, 4.37 - 5.98)	2.78	(± 0.07, 2.67 - 2.85)
		g.leaf	14.33	(± 3.52, 8.30 - 23.40)	7.89	(± 0.76, 6.40 - 9.50)
		sen	7.22	(± 0.74, 5.90 - 9.25)	2.65	(± 0.20, 2.20 - 3.01)
P	(g kg-1)	tot soil	0.26	(±0.04, 0.17 - 0.31)	0.22	(±0.02,0.2 - 0.24)
		c.root	0.60	(± 0.02, 0.56- 0.64)	0.30	(± 0.17, 0.15 - 0.50)
		a.root	0.52	(± 0.04, 0.46 - 0.59)	0.35	(± 0.19, 0.21 - 0.58)
		wood	0.33	(± 0.02, 0.30 - 0.36)	0.19	(± 0.07, 0.13 - 0.28)
		g.leaf	1.16	(± 0.42, 0.55 - 2.24)	0.66	(± 0.08, 0.57 - 0.86)
		sen	0.64	(± 0.09, 0.49 - 0.83)	0.29	(± 0.11, 0.17 - 0.48)
K	(g kg-1)	tot soil	11.03	(± 1.02, 8.61 - 12.88)	8.75	(± 0.14, 8.56 - 8.91)
		c.root	12.97	(± 1.02, 11.50 - 14.62)	7.24	(± 0.75, 6.18 - 8.15)
		a.root	11.15	(± 0.16, 10.90 - 11.37)	4.17	(± 2.67, 2.07 - 7.14)
		wood	1.76	(± 0.13, 1.56 - 1.96)	1.74	(± 0.25, 1.51 - 2.00)
		g.leaf	12.16	(± 2.25, 7.28 - 16.16)	6.81	(± 1.53, 5.09 - 10.30)
		sen	10.86	(± 1.06, 9.53 - 12.99)	4.76	(± 0.74, 3.18 - 5.96)
Na	(g kg-1)	tot soil	54.51	(± 3.70 , 50.28 - 63.32)	33.33	(± 4.46, 27.89 - 37.92)
		c.root	58.44	(± 2.01, 56.58 - 62.12)	30.87	(± 8.56, 23.66 - 40.39)
		a.root	31.91	(± 2.41, 27.72 - 35.18)	18.34	(± 3.16, 14.80 - 22.58)
		wood	14.12	(± 0.62, 13.18 - 15.35)	13.28	(± 4.25, 8.95 - 18.57)
		g.leaf	29.78	(± 10.31, 15.86 - 55.58)	23.44	(± 3.89, 16.35 - 29.41)
		sen	26.35	(± 2.74 , 22.11 - 31.36)	34.78	(± 2.79, 30.76 - 40.55)
S	(g kg-1)	tot soil	26.39	(± 9.45, 16.62 - 44.67)	30.71	(± 10.46, 16.67 - 39.38)
		c.root	1.28	(± 0.40, 0.76 - 2.18)	1.36	(± 0.20, 1.02 - 1.51)
		a.root	2.54	(± 0.52, 1.67 - 3.18)	1.80	(± 0.77, 0.93 - 2.49)
		wood	1.42	(± 0.32, 1.08 - 2.13)	1.73	(± 0.39, 1.35 - 2.21)
		g.leaf	5.43	(± 2.19, 2.41 - 10.30)	7.69	(± 2.77, 2.31 - 12.11)
		sen	8.11	(± 1.83, 5.01 - 11.39)	15.84	(± 6.83, 6.16 - 25.65)
Mg	(g kg-1)	tot soil	14.14	(±2.20, 11.49 -17.41)	13.27	(±1.65, 11.40 - 14.63)
		c.root	2.97	(± 0.38, 2.47 - 3.78)	2.02	(± 0.23, 1.78 - 2.38)
		a.root	5.47	(± 0.99, 4.51 - 7.55)	3.64	(± 1.06, 2.32 - 4.86)
		wood	2.97	(± 0.27, 2.51 - 3.42)	3.21	(± 0.78, 2.40 - 4.09)
		g.leaf	6.58	(± 2.43, 2.68 - 11.67)	6.67	(± 1.16, 5.22 - 9.86)
		sen	10.47	(± 0.80, 9.10 - 11.98)	8.52	(± 1.05, 7.10 - 10.28)
Ca	(g kg-1)	tot soil	5.49	(±0.51,4.80 - 6.57)	7.15	(±0.91, 6.09-8.01)
		c.root	7.95	(± 0.48, 7.20 - 8.73)	7.67	(± 0.47, 7.27 - 8.20)
		a.root	9.17	(± 0.55, 8.34 - 9.88)	4.17	(± 2.25, 1.64 - 6.14)
		wood	14.44	(± 2.48, 10.49 - 16.90)	21.14	(± 1.49, 18.89 - 23.05)
		g.leaf	3.09	(± 1.18, 1.96 - 8.25)	9.45	(± 1.20, 7.51 - 11.14)
		sen	3.43	(± 0.71, 2.86 - 5.59)	12.16	(± 1.35, 10.15 - 14.06)

Appendix 15. Mean (±SD, minimum - maximum) concentrations (by dry weight) of the macro-elements and Na in the soils and the plant materials (c.root = coarse root, a.root = aerial root, g.leaf = green leaf, sen = senesced leaf) in the *A. marina* and *R. stylosa* stands in the study site under mining influence (New Caledonia)

			A. marina		*R. stylosa*	
				Mine		
N	**(g kg-1)**	tot soil	1.50	(±0.60, 0.87-2.06)	2.97	(±0.84, 2.01 -4.18)
		c.root	6.92	(± 0.19, 6.71 - 7.17)	2.75	(± 0.30, 2.10 - 3.11)
		a.root	6.80	(± 0.63, 6.08 - 7.70)	2.63	(± 0.31, 2.09 - 3.28)
		wood	5.66	(± 0.69, 4.63 - 6.34)	2.86	(± 0.31, 2.36 - 3.38)
		g.leaf	13.79	(± 1.81, 12.20 - 16.80)	7.95	(± 1.91, 5.90 - 12.60)
		sen	7.00	(± 0.54, 6.20 - 7.50)	2.66	(± 0.73, 1.70 - 4.24)
P	**(g kg-1)**	tot soil	0.13	(±0.04, 0.07 - 0.16)	0.38	(±0.08, 0.30 - 0.54)
		c.root	0.61	(± 0.03, 0.58 - 0.63)	0.51	(± 0.07, 0.41 - 0.64)
		a.root	0.52	(± 0.03, 0.49 - 0.56)	0.42	(± 0.10, 0.29 - 0.56)
		wood	0.48	(± 0.04, 0.44 - 0.54)	0.21	(± 0.08, 0.12 - 0.32)
		g.leaf	0.99	(± 0.14, 0.80 - 1.19)	0.77	(± 0.13, 0.61 - 1.14)
		sen	0.53	(± 0.03, 0.50 - 0.56)	0.37	(±0.18, 0.17 - 0.88)
K	**(g kg-1)**	tot soil	6.41	(± 0.71, 5.69 - 7.22)	6.17	(± 1.53, 4.12 - 8.73)
		c.root	9.36	(± 0.45, 8.61 - 9.75)	3.42	(± 0.76, 2.28 - 4.66)
		a.root	11.16	(± 0.21, 10.80 - 11.30)	3.98	(± 1.13, 2.91 - 5.40)
		wood	1.20	(± 0.05, 1.14 - 1.25)	1.84	(± 0.19, 1.60 - 2.14)
		g.leaf	10.19	(± 1.53, 8.41 - 12.53)	8.74	(± 1.31, 7.03 - 12.38)
		sen	9.20	(± 0.64, 8.55 - 10.01)	6.87	(± 1.84, 3.22 - 13.68)
Na	**(g kg-1)**	tot soil	35.80	(± 1.63, 33.58 - 37.68)	30.11	(± 3.35, 24.92 - 36.37)
		c.root	52.98	(± 2.28, 50.31 - 56.63)	27.21	(± 1.15, 25.28 - 29.14)
		a.root	27.44	(± 1.66, 24.80 - 29.04)	18.73	(± 1.42, 15.49 - 20.44)
		wood	14.72	(± 2.24, 11.17 - 17.38)	15.56	(± 1.56, 12.68 - 18.23)
		g.leaf	32.71	(± 9.08, 24.31 - 45.60)	23.60	(± 3.88, 16.80 - 29.76)
		sen	18.44	(± 1.53, 17.21 - 20.88)	24.52	(± 5.16, 14.53 - 33.87)
S	**(g kg-1)**	tot soil	6.87	(± 2.27, 3.54 - 9.49)	56.78	(± 16.20, 28.02 - 77.95)
		c.root	5.90	(± 0.70, 4.83 - 6.70)	6.60	(± 0.54, 5.64 - 7.35)
		a.root	1.86	(± 0.14, 1.63 - 1.99)	1.87	(± 0.49, 1.10 - 2.53)
		wood	0.89	(± 0.14, 0.68 - 1.02)	1.49	(± 0.51, 0.91 - 2.27)
		g.leaf	3.60	(± 0.69, 2.79 - 4.39)	3.84	(± 2.60, 1.31 - 8.56)
		sen	6.87	(± 0.36, 6.46 - 7.35)	6.97	(± 3.73, 3.01 - 13.33)
Mg	**(g kg-1)**	tot soil	102.32	(±7.94, 97.39 -116.33)	49.17	(±21.85, 22.08 - 77.92)
		c.root	13.23	(± 0.78, 12.52 - 14.47)	8.27	(± 3.09, 4.84 - 12.83)
		a.root	15.81	(± 1.57, 13.65 - 17.95)	9.81	(± 2.50, 6.24 - 13.12)
		wood	2.92	(± 0.26, 2.68 - 3.27)	6.31	(± 1.85, 3.91 - 9.35)
		g.leaf	7.78	(± 0.21, 7.42 - 7.94)	8.72	(± 2.04, 4.31 - 11.82)
		sen	12.48	(± 1.00, 11.53 - 13.59)	9.70	(± 2.08, 5.62 - 12.36)
Ca	**(g kg-1)**	tot soil	6.61	(±0.91, 5.38 -7.75)	7.57	(±0.55, 6.79-8.74)
		c.root	11.70	(± 0.30, 11.23 - 12.05)	5.80	(± 0.67, 5.07 - 7.02)
		a.root	10.67	(± 0.45, 10.18 - 11.09)	5.45	(± 2.54, 1.21 - 9.05)
		wood	10.12	(± 1.36, 8.39 - 11.69)	16.67	(± 1.68, 14.22 - 20.07)
		g.leaf	3.73	(± 0.62, 3.10 - 4.56)	10.24	(± 1.16, 8.59 - 12.56)
		sen	4.26	(± 0.37, 3.85 - 4.66)	13.78	(± 1.82, 10.93 - 17.37)

Appendix 16. Mean (±SD, minimum - maximum) concentrations (by dry weight) of the macro-elements and Na in the soils and the plant materials (c.root = coarse root, a.root = aerial root, g.leaf = green leaf, sen = senesced leaf) in the *A. marina* and *R. stylosa* stands in the study site receiving both mining and aquaculture effluents (New Caledonia)

			A. marina		*R. stylosa*	
				Aquaculture		
N	**(g kg-1)**	tot soil	2.53	(±1.26,1.31 - 4.58)	3.68	(±1.58, 1.45 - 6.83)
		c.root	5.51	(± 1.10, 3.79 - 6.83)	3.04	(± 0.52, 2.16 - 3.76)
		a.root	6.86	(± 0.34, 6.46 - 7.37)	3.39	(± 0.45, 2.87 - 4.40)
		wood	6.17	(± 0.22, 5.89 - 6.54)	2.91	(± 0.25, 2.43 - 3.20)
		g.leaf	15.69	(± 4.24, 9.50 - 24.60)	8.27	(± 1.24, 6.50 - 13.00)
		sen	7.87	(± 1.34, 6.21 - 11.20)	2.83	(± 0.55, 1.70 - 4.70)
P	**(g kg-1)**	tot soil	0.47	(±0.08, 0.34 - 0.57)	0.35	(±0.05,0.29 - 0.43)
		c.root	0.85	(± 0.09, 0.74- 0.99)	0.69	(± 0.15, 0.46 - 0.86)
		a.root	0.69	(± 0.05, 0.62 - 0.76)	0.53	(± 0.10, 0.41 - 0.66)
		wood	1.09	(± 0.17, 0.90 - 1.35)	1.94	(± 0.32, 1.45 - 2.57)
		g.leaf	1.35	(± 0.31, 0.90 - 1.86)	0.79	(± 0.11, 0.58 - 1.15)
		sen	0.72	(± 0.11, 0.55 - 0.90)	0.52	(± 0.13, 0.38 - 0.97)
K	**(g kg-1)**	tot soil	8.23	(± 0.56, 7.67 - 9.21)	6.07	(± 1.23, 4.62 - 8.42)
		c.root	10.91	(± 0.75, 9.77 - 11.65)	3.16	(± 0.39, 2.78 - 3.78)
		a.root	9.37	(± 0.63, 8.64 - 10.29)	5.30	(± 1.09, 4.00 - 6.38)
		wood	6.28	(± 1.89, 4.63 - 8.39)	6.97	(± 0.38, 6.48 - 7.50)
		g.leaf	14.22	(±6.64, 8.73 - 36.14)	6.95	(± 1.51, 3.86 - 13.08)
		sen	9.75	(±0.77, 8.09 - 11.04)	6.31	(± 1.54, 1.90 - 9.85)
Na	**(g kg-1)**	tot soil	32.48	(± 3.55, 28.97 - 38.97)	30.07	(± 3.74, 23.06 - 34.44)
		c.root	50.38	(± 1.10, 48.86 - 52.14)	28.63	(± 1.83, 25.09 - 30.94)
		a.root	23.40	(± 1.93, 20.72 - 25.26)	17.73	(± 1.96, 15.01 - 20.22)
		wood	16.91	(±1.23, 15.51 - 19.13)	20.93	(± 5.28, 15.01 - 29.95)
		g.leaf	31.09	(± 10.08, 16.90 - 50.17)	21.91	(± 5.72, 10.58 - 37.87)
		sen	22.96	(± 1.87, 19.74 - 26.56)	26.62	(± 4.44, 18.20 - 40.19)
S	**(g kg-1)**	tot soil	39.18	(± 20.54, 16.14 - 69.48)	62.32	(± 4.52, 56.36 - 69.48)
		c.root	2.43	(± 0.92, 1.42 - 3.92)	2.96	(± 0.54, 1.97 - 3.95)
		a.root	1.60	(± 0.48, 0.99 - 2.12)	4.42	(± 0.60, 3.70 - 5.33)
		wood	1.06	(± 0.04, 0.99 - 1.11)	1.03	(± 0.11, 0.87 - 1.23)
		g.leaf	8.56	(± 3.03, 3.53 - 11.88)	9.29	(± 5.47, 1.96 - 24.87)
		sen	11.48	(± 2.03, 9.00 - 14.60)	11.71	(± 5.41, 4.53 - 26.61)
Mg	**(g kg-1)**	tot soil	27.22	(±6.42, 21.55 - 38.26)	19.20	(±3.90, 13.61 - 26.14)
		c.root	7.81	(± 0.96, 6.39 - 8.94)	4.84	(± 0.74, 3.45 - 5.84)
		a.root	12.00	(± 0.63, 11.16 - 12.92)	5.74	(± 0.87, 4.63 - 7.16)
		wood	9.71	(± 0.53, 1.54 - 2.71)	16.01	(± 0.45, 1.52 - 2.97)
		g.leaf	8.80	(± 3.01, 3.56 - 13.93)	7.94	(± 1.99, 3.91 - 13.03)
		sen	12.71	(± 1.14, 10.25 - 14.23)	9.58	(± 2.01, 6.10 - 15.67)
Ca	**(g kg-1)**	tot soil	21.84	(±15.21, 8.37 - 44.52)	9.70	(±1.17, 7.98 - 11.20)
		c.root	13.92	(± 1.91, 11.43 - 15.95)	9.02	(± 0.27, 8.58 - 9.49)
		a.root	8.08	(± 0.56, 7.52 - 9.17)	5.16	(± 0.90, 3.91 - 6.59)
		wood	9.71	(± 0.96, 8.82 - 11.79)	16.01	(± 1.25, 14.25 - 17.80)
		g.leaf	3.99	(± 1.02, 2.87 - 5.83)	15.33	(± 3.93, 7.51 - 26.81)
		sen	4.53	(± 0.68, 3.50 - 6.13)	17.42	(± 3.20, 8.94 - 23.37)

Appendix 17. Mean (±SD, minimum - maximum) Bioconcentration Factors (BCF, unitless), Translocation Factors (TF, unitless) and Resorption Efficiency of N, P, Ca, Mg in the different plant materials (g.leaf = green leaf, sen = senesced) in the *A. marina* and *R. stylosa* stands of the non-influenced site (Natural), the mining influenced site (Mine) and the aquaculture influenced site (Aquaculture) (New Caledonia)

		Natural				Mine				Aquaculture			
		A. marina		*R. stylosa*		*A. marina*		*R. stylosa*		*A. marina*		*R. stylosa*	
N	BCF roots	1.03	(± 0.20, 0.67 - 1.33)	0.90	(± 0.30, 0.54 - 1.29)	4.73	(± 2.37, 3.25 - 8.25)	0.95	(± 0.25, 0.70 - 1.42)	2.68	(± 1.20, 0.83 - 3.78)	1.04	(± 0.70, 0.40 - 2.46)
	BCF aerial	1.59	(± 0.31, 1.19 - 2.08)	0.62	(± 0.16, 0.43 - 0.85)	4.55	(± 2.43, 3.00 - 8.17)	0.90	(± 0.24, 0.66 - 1.27)	3.21	(± 1.24, 1.61 - 4.94)	1.09	(± 0.67, 0.43 - 2.54)
	BCF wood	1.15	(± 0.27, 0.77 - 1.63)	0.79	(± 0.16, 0.60 - 1.03)	3.83	(± 2.23, 2.68 - 7.18)	1.00	(± 0.28, 0.56 - 1.45)	2.95	(± 1.25, 1.29 - 4.63)	0.91	(± 0.52, 0.36 - 1.89)
	BCF g.leaf	3.16	(± 1.00, 1.45 - 4.93)	2.21	(± 0.21, 1.97 - 2.46)	9.54	(± 4.28, 6.58 - 15.88)	3.03	(± 1.59, 1.58 - 6.28)	7.43	(± 3.87, 3.01 - 12.61)	2.71	(± 1.48, 1.21 - 5.79)
	TF aerial	1.57	(± 0.21, 1.34 - 1.98)	0.70	(± 0.08, 0.60 - 0.80)	0.98	(± 0.07, 0.89 - 1.09)	0.97	(± 0.15, 0.67 - 1.24)	1.29	(± 0.32, 1.03 - 1.95)	1.15	(± 0.25, 0.80 - 1.56)
	TF wood	1.14	(± 0.26, 0.92 - 1.64)	0.92	(± 0.19, 0.67 - 1.12)	0.82	(± 0.09, 0.67 - 0.90)	1.05	(± 0.17, 0.79 - 1.28)	1.15	(± 0.21, 0.91 - 1.55)	0.98	(± 0.17, 0.77 - 1.29)
	TF g.leaf	3.13	(± 0.76, 1.74 - 4.18)	2.62	(± 0.75, 1.92 - 3.75)	2.00	(± 0.29, 1.73 - 2.47)	2.98	(± 0.72, 2.06 - 4.41)	2.85	(± 0.87, 1.65 - 4.41)	2.84	(± 0.66, 2.05 - 4.08)
	TF sen	1.59	(± 0.18, 1.31 - 1.91)	0.84	(± 0.19, 0.62 - 0.99)	1.01	(± 0.10, 0.86 - 1.12)	1.03	(± 0.25, 0.68 - 1.37)	1.46	(± 0.48, 1.08 - 2.14)	0.99	(± 0.25, 0.73 - 1.61)
	RE (%)	47.00	(± 12.41, 9.64 - 72.22)	66.24	(± 2.72, 62.16 - 73.68)	48.69	(± 6.56, 40.98 - 55.95)	66.68	(± 4.23, 54.60 - 72.31)	46.21	(± 17.13, 18.39 - 69.11)	65.79	(± 4.45, 48.21 - 77.78)
P	BCF roots	2.35	(± 0.43, 1.91 - 3.45)	1.40	(± 0.85, 0.60 - 2.53)	5.26	(± 1.80, 3.94 - 8.06)	1.38	(± 0.27, 0.98 - 2.01)	1.84	(± 0.24, 1.61 - 2.28)	2.01	(± 0.51, 1.08 - 2.88)
	BCF aerial	2.03	(± 0.35, 1.58 - 3.01)	1.66	(± 0.96, 0.84 - 2.76)	4.54	(± 1.88, 3.23 - 7.74)	1.13	(± 0.29, 0.68 - 1.59)	1.5	(± 0.23, 1.31 - 1.93)	1.54	(± 0.34, 0.97 - 2.19)
	BCF wood	1.32	(± 0.29, 1.00 - 2.11)	0.89	(± 0.38, 0.58 - 1.36)	4.13	(± 1.52, 2.86 - 6.66)	0.59	(± 0.27, 0.22 - 1.05)	2.37	(± 0.39, 1.88 - 2.99)	5.64	(± 1.18, 3.58 - 7.35)
	BCF g.leaf	4.50	(± 1.69, 1.87 - 7.47)	3.26	(± 0.66, 2.61 - 3.97)	8.49	(± 3.03, 5.57 - 13.31)	2.22	(± 0.65, 1.44 - 3.78)	2.94	(± 0.73, 1.87 - 3.83)	2.34	(± 0.45, 1.79 - 3.25)
	TF aerial	0.87	(± 0.07, 0.76 - 0.96)	1.21	(± 0.15, 1.02 - 1.40)	0.85	(± 0.08, 0.77 - 0.96)	0.82	(± 0.14, 0.60 - 1.05)	0.82	(± 0.07, 0.74 - 0.92)	0.77	(± 0.07, 0.68 - 0.90)
	TF wood	0.56	(± 0.04, 0.50 - 0.62)	0.70	(± 0.17, 0.54 - 0.97)	0.79	(± 0.10, 0.69 - 0.93)	0.41	(± 0.14, 0.23 - 0.63)	1.29	(± 0.11, 1.12 - 1.43)	2.92	(± 0.72, 1.70 - 3.98)
	TF g.leaf	1.92	(± 0.70, 0.90 - 3.00)	2.86	(± 1.15, 1.57 - 4.35)	1.61	(± 0.19, 1.37 - 1.89)	1.59	(± 0.24, 1.23 - 1.94)	1.61	(± 0.38, 1.12 - 2.09)	1.21	(± 0.30, 0.69 - 1.85)
	TF sen	1.05	(± 0.15, 0.82 - 1.35)	0.99	(± 0.20, 0.78 - 1.25)	0.87	(± 0.07, 0.78 - 0.96)	0.76	(± 0.22, 0.41 - 1.05)	0.88	(± 0.14, 0.71 - 1.05)	0.73	(± 0.17, 0.53 - 1.09)
	RE (%)	39.22	(± 16.10, 7.63 - 66.12)	56.47	(± 12.55, 30.14 - 72.58)	45.80	(± 7.91, 34.07 - 54.15)	52.61	(± 20.58, -20.90 - 74.05)	45.25	(± 10.38, 24.95 - 63.29)	33.00	(± 15.64, -23.06 - 53.84)
Ca	BCF roots	1.46	(± 0.17, 1.16 - 1.71)	1.09	(± 0.21, 0.92 - 1.35)	1.79	(± 0.23, 1.51 - 2.09)	0.77	(± 0.10, 0.66 - 0.92)	0.99	(± 0.66, 0.28 - 1.86)	0.94	(± 0.10, 0.80 - 1.10)
	BCF aerial	1.69	(± 0.22, 1.38 - 2.06)	0.56	(± 0.26, 0.26 - 0.77)	1.64	(± 0.20, 1.43 - 1.89)	0.72	(± 0.33, 0.16 - 1.09)	0.53	(± 0.31, 0.20 - 0.95)	0.54	(± 0.10, 0.35 - 0.66)
	BCF wood	2.68	(± 0.63, 1.60 - 3.25)	2.99	(± 0.43, 2.69 - 3.69)	1.55	(± 0.27, 1.27 - 1.89)	2.21	(± 0.27, 1.77 - 2.60)	0.64	(± 0.35, 0.22 - 1.13)	1.67	(± 0.22, 1.27 - 2.00)
	BCF g.leaf	0.53	(± 0.12, 0.39 - 0.76)	1.42	(± 0.22, 1.21 - 1.79)	0.57	(± 0.10, 0.48 - 0.74)	1.37	(± 0.18, 1.07 - 1.69)	0.24	(± 0.15, 0.07 - 0.49)	1.50	(± 0.50, 0.68 - 2.45)
	TF aerial	1.16	(± 0.09, 0.96 - 1.27)	0.56	(± 0.32, 0.20 - 0.84)	0.91	(± 0.03, 0.88 - 0.95)	0.92	(± 0.40, 0.24 - 1.55)	0.59	(± 0.11, 0.48 - 0.72)	0.57	(± 0.10, 0.42 - 0.74)
	TF wood	1.81	(± 0.26, 1.38 - 2.07)	2.77	(± 0.26, 2.30 - 2.93)	0.87	(± 0.12, 0.70 - 0.99)	2.91	(± 0.45, 2.11 - 3.67)	0.71	(± 0.14, 0.58 - 0.93)	1.78	(± 0.15, 1.53 - 2.00)
	TF g.leaf	0.37	(± 0.07, 0.25 - 0.48)	1.32	(± 0.20, 0.99 - 1.51)	0.32	(± 0.05, 0.26 - 0.39)	1.79	(± 0.24, 1.35 - 2.09)	0.26	(± 0.07, 0.19 - 0.41)	1.61	(± 0.58, 0.84 - 3.00)
	TF sen	0.42	(± 0.06, 0.37 - 0.60)	1.64	(± 0.24, 1.29 - 1.89)	0.36	(± 0.03, 0.33 - 0.39)	2.41	(± 0.46, 1.70 - 3.42)	0.31	(± 0.06, 0.22 - 0.41)	1.90	(± 0.41, 1.15 - 2.62)
	RE (%)	-16.12	(± 21.14, -64.29 - 32.24)	-30.35	(± 19.88, -73.25 - 5.41)	-15.98	(± 15.18, -37.21 - -2.08)	-35.82	(± 21.49, -87.91 - 0.80)	-17.29	(± 18.70, -47.47 - 21.56)	-16.76	(± 23.90, -89.43 - 26.27)
Mg	BCF roots	0.21	(± 0.03, 0.17 - 0.26)	0.15	(± 0.01, 0.14 - 0.17)	0.13	(± 0.01, 0.11 - 0.14)	0.18	(± 0.03, 0.14 - 0.24)	0.29	(± 0.05, 0.23 - 0.37)	0.27	(± 0.08, 0.13 - 0.38)
	BCF aerial	0.40	(± 0.11, 0.27 - 0.59)	0.27	(± 0.05, 0.20 - 0.34)	0.16	(± 0.02, 0.12 - 0.18)	0.22	(± 0.07, 0.16 - 0.37)	0.46	(± 0.12, 0.30 - 0.60)	0.31	(± 0.07, 0.22 - 0.47)
	BCF wood	0.21	(± 0.04, 0.15 - 0.27)	0.25	(± 0.09, 0.16 - 0.36)	0.03	(± 0.00, 0.02 - 0.03)	0.18	(± 0.13, 0.06 - 0.38)	0.08	(± 0.01, 0.06 - 0.09)	0.11	(± 0.04, 0.07 - 0.20)
	BCF g.leaf	0.46	(± 0.16, 0.26 - 0.72)	0.50	(± 0.05, 0.45 - 0.56)	0.08	(± 0.01, 0.06 - 0.08)	0.19	(± 0.05, 0.13 - 0.29)	0.35	(± 0.18, 0.14 - 0.55)	0.40	(± 0.16, 0.21 - 0.75)
	TF aerial	1.87	(± 0.44, 1.19 - 2.83)	1.79	(± 0.48, 1.31 - 2.48)	1.20	(± 0.14, 1.08 - 1.43)	1.25	(± 0.21, 0.88 - 1.56)	1.56	(± 0.25, 1.29 - 1.98)	1.23	(± 0.34, 0.87 - 1.73)
	TF wood	1.01	(± 0.15, 0.77 - 1.17)	1.63	(± 0.54, 1.15 - 2.27)	0.22	(± 0.02, 0.20 - 0.25)	0.95	(± 0.58, 0.31 - 1.66)	0.27	(± 0.06, 0.19 - 0.33)	0.41	(± 0.09, 0.27 - 0.58)
	TF g.leaf	2.22	(± 0.85, 1.00 - 3.52)	3.32	(± 0.57, 2.75 - 4.11)	0.59	(± 0.03, 0.55 - 0.62)	1.05	(± 0.23, 0.78 - 1.51)	1.16	(± 0.50, 0.60 - 1.79)	1.54	(± 0.53, 0.67 - 2.54)
	TF sen	3.54	(± 0.42, 2.74 4.25-)	4.74	(± 0.73, 4.00 - 5.80)	0.95	(± 0.12, 0.83 - 1.09)	1.15	(± 0.23, 0.88 - 1.54)	1.65	(± 0.18, 1.48 - 2.00)	1.93	(± 0.52, 1.09 - 2.70)
	RE (%)	-75.74	(± 65.79, -215.99 - 14.14)	-30.05	(± 19.70, -63.83 - 12.73)	-60.81	(± 16.34, -82.51 - -45.28)	-12.80	(± 14.98, -65.52 - 5.62)	-65.36	(± 72.35, -258.15 - 11.41)	-23.58	(± 23.46, -130.11 - 6.09)

Appendix 18. Mean (±SD, minimum - maximum) Bioconcentration Factors (BCF, unitless), Translocation Factors (TF, unitless) and Resorption Efficiency of Na, K and S in the different plant materials (g. leaf = green leaf, sen = senesced) in the *A. marina* and *R. stylosa* stands of the non-influenced site (Natural), the mining influenced site (Mine) and the aquaculture influenced site (Aquaculture) (New Caledonia)

		Natural				Mine				Aquaculture			
		A. marina		*R. stylosa*		*A. marina*		*R. stylosa*		*A. marina*		*R. stylosa*	
Na	BCF roots	1.08	(± 0.07, 0.92 - 1.15)	0.97	(± 0.40, 0.62 - 1.43)	1.48	(± 0.12, 1.34 - 1.63)	0.91	(± 0.11, 0.76 - 1.09)	1.57	(± 0.16, 1.25 - 1.76)	0.97	(± 0.16, 0.78 - 1.26)
	BCF aerial	0.59	(± 0.05, 0.50 - 0.66)	0.57	(± 0.18, 0.42 - 0.81)	0.77	(± 0.07, 0.66 - 0.82)	0.63	(± 0.09, 0.47 - 0.74)	0.73	(± 0.08, 0.59 - 0.83)	0.60	(± 0.11, 0.46 - 0.81)
	BCF wood	0.26	(± 0.02, 0.23 - 0.29)	0.42	(± 0.19, 0.25 - 0.67)	0.41	(± 0.07, 0.30 - 0.47)	0.52	(± 0.08, 0.40 - 0.64)	0.53	(± 0.07, 0.40 - 0.59)	0.71	(± 0.22, 0.44 - 1.07)
	BCF g.leaf	0.54	(± 0.23, 0.27 - 1.05)	0.69	(± 0.09, 0.58 - 0.80)	0.92	(± 0.30, 0.67 - 1.36)	0.78	(± 0.18, 0.56 - 1.19)	0.96	(± 0.26, 0.57 - 1.26)	0.72	(± 0.14, 0.53 - 0.98)
	TF aerial	0.55	(± 0.04, 0.46 - 0.61)	0.61	(± 0.09, 0.51 - 0.72)	0.52	(± 0.02, 0.49 - 0.55)	0.69	(± 0.04, 0.61 - 0.72)	0.46	(± 0.04, 0.41 - 0.50)	0.62	(± 0.04, 0.56 - 0.66)
	TF wood	0.24	(± 0.01, 0.22 - 0.25)	0.43	(± 0.04, 0.37 - 0.46)	0.28	(± 0.04, 0.22 - 0.33)	0.57	(± 0.07, 0.47 - 0.70)	0.34	(± 0.02, 0.31 - 0.37)	0.72	(± 0.15, 0.55 - 0.98)
	TF g.leaf	0.50	(± 0.20, 0.27 - 0.97)	0.81	(± 0.30, 0.45 - 1.09)	0.62	(± 0.16, 0.46 - 0.86)	0.85	(± 0.16, 0.60 - 1.10)	0.62	(± 0.17, 0.34 - 0.78)	0.75	(± 0.13, 0.59 - 1.05)
	TF sen	0.44	(± 0.04, 0.38 - 0.50)	1.18	(± 0.29, 0.84 - 1.50)	0.35	(± 0.03, 0.31 - 0.40)	0.89	(± 0.20, 0.50 - 1.13)	0.47	(± 0.04, 0.39 - 0.51)	0.90	(± 0.18, 0.64 - 1.18)
	RE (%)	2.11	(± 31.01, -60.44 - 54.16)	-52.54	(± 30.39, -126.12 - -10.37)	41.05	(± 12.15, 29.20 - 54.21)	-5.37	(± 22.15, -52.10 - 34.72)	19.87	(± 30.15, -40.89 - 56.57)	-28.66	(± 31.10, -118.92 - 17.56)
K	BCF roots	1.19	(± 0.19, 0.92 - 1.66)	0.83	(± 0.09, 0.70 - 0.94)	1.47	(± 0.11, 1.33 - 1.61)	0.57	(± 0.11, 0.40 - 0.82)	1.33	(± 0.11, 1.17 - 1.51)	0.54	(± 0.10, 0.34 - 0.65)
	BCF aerial	1.02	(± 0.10, 0.87 - 1.29)	0.48	(± 0.31, 0.23 - 0.82)	1.76	(± 0.18, 1.55 - 1.98)	0.65	(± 0.08, 0.51 - 0.78)	1.14	(± 0.08, 1.04 - 1.26)	0.90	(± 0.24, 0.51 - 1.35)
	BCF wood	0.16	(± 0.02, 0.13 - 0.21)	0.20	(± 0.03, 0.17 - 0.23)	0.19	(± 0.01, 0.17 - 0.21)	0.31	(± 0.06, 0.23 - 0.40)	0.76	(± 0.23, 0.56 - 1.07)	1.19	(± 0.24, 0.82 - 1.62)
	BCF g.leaf	1.15	(± 0.22, 0.79 - 1.47)	0.86	(± 0.22, 0.66 - 1.18)	1.59	(± 0.15, 1.47 - 1.78)	1.51	(± 0.26, 1.17 - 1.99)	1.58	(± 0.33, 1.14 - 2.14)	1.20	(± 0.32, 0.75 - 1.81)
	TF aerial	0.86	(± 0.07, 0.77 - 0.97)	0.56	(± 0.31, 0.32 - 0.93)	1.19	(± 0.06, 1.16 - 1.31)	1.17	(± 0.21, 0.78 - 1.54)	0.86	(± 0.06, 0.77 - 0.95)	1.70	(± 0.44, 1.07 - 2.24)
	TF wood	0.14	(± 0.01, 0.12 - 0.16)	0.24	(± 0.02, 0.22 - 0.26)	0.13	(± 0.01, 0.12 - 0.14)	0.56	(± 0.12, 0.40 - 0.78)	0.57	(± 0.15, 0.42 - 0.78)	2.24	(± 0.32, 1.71 - 2.69)
	TF g.leaf	0.98	(± 0.21, 0.63 - 1.30)	1.03	(± 0.17, 0.84 - 1.26)	1.09	(± 0.12, 0.98 - 1.29)	2.73	(± 0.62, 1.92 - 4.01)	1.18	(± 0.19, 0.85 - 1.41)	2.25	(± 0.44, 1.39 - 3.00)
	TF sen	0.82	(± 0.10, 0.68 - 1.04)	0.69	(± 0.16, 0.53 - 0.95)	0.98	(± 0.07, 0.89 - 1.05)	2.19	(± 0.77, 0.95 - 3.49)	0.88	(± 0.14, 0.70 - 1.09)	1.95	(± 0.52, 0.86 - 2.73)
	RE (%)	7.74	(± 20.17, -57.82 - 30.48)	26.94	(± 19.43, -10.35 - 58.01)	8.01	(± 15.30, -6.70 - 30.49)	20.28	(± 23.36, -63.67 - 56.94)	23.93	(± 24.03, -9.98 - 71.49)	3.92	(± 36.05, -75.72 - 64.07)
S	BCF roots	0.05	(± 0.03, 0.03 - 0.10)	0.05	(± 0.01, 0.04 - 0.06)	0.97	(± 0.42, 0.51 - 1.65)	0.13	(± 0.04, 0.09 - 0.21)	0.09	(± 0.07, 0.03 - 0.18)	0.05	(± 0.01, 0.03 - 0.06)
	BCF aerial	0.11	(± 0.05, 0.04 - 0.17)	0.06	(± 0.01, 0.04 - 0.07)	0.30	(± 0.10, 0.20 - 0.46)	0.04	(± 0.02, 0.02 - 0.08)	0.06	(± 0.04, 0.02 - 0.12)	0.07	(± 0.01, 0.06 - 0.08)
	BCF wood	0.06	(± 0.01, 0.04 - 0.08)	0.07	(± 0.04, 0.04 - 0.13)	0.14	(± 0.03, 0.10 - 0.19)	0.03	(± 0.01, 0.02 - 0.04)	0.04	(± 0.02, 0.02 - 0.07)	0.02	(± 0.00, 0.01 - 0.02)
	BCF g.leaf	0.21	(± 0.11, 0.08 - 0.45)	0.30	(± 0.15, 0.10 - 0.53)	0.57	(± 0.18, 0.37 - 0.79)	0.08	(± 0.07, 0.03 - 0.25)	0.22	(± 0.08, 0.12 - 0.35)	0.13	(± 0.11, 0.03 - 0.42)
	TF aerial	2.13	(± 0.76, 1.13 - 3.79)	1.30	(± 0.45, 0.65 - 1.64)	0.32	(± 0.04, 0.28 - 0.39)	0.29	(± 0.09, 0.17 - 0.40)	0.69	(± 0.16, 0.49 - 0.98)	1.53	(± 0.26, 1.15 - 1.92)
	TF wood	1.19	(± 0.40, 0.62 - 1.95)	1.32	(± 0.48, 0.89 - 2.06)	0.15	(± 0.03, 0.12 - 0.19)	0.22	(± 0.07, 0.15 - 0.33)	0.49	(± 0.18, 0.27 - 0.76)	0.36	(± 0.07, 0.26 - 0.50)
	TF g.leaf	4.23	(± 2.04, 2.14 - 8.41)	6.56	(± 2.88, 1.62 - 8.78)	0.62	(± 0.15, 0.45 - 0.79)	0.62	(± 0.42, 0.22 - 1.31)	4.09	(± 2.70, 0.90 - 7.77)	2.66	(± 1.85, 0.92 - 7.14)
	TF sen	6.95	(± 2.55, 3.11 - 12.37)	13.93	(± 5.57, 4.47 - 18.73)	1.18	(± 0.16, 1.00 - 1.38)	1.24	(± 0.64, 0.48 - 2.28)	5.45	(± 2.47, 2.39 - 8.50)	4.11	(± 1.60, 1.61 - 7.00)
	RE (%)	-73.87	(± 80.97, -287.45 - 18.46)	-107.22	(± 59.27, -254.50 - -9.15)	-97.09	(± 43.18, -155.83 - -47.13)	-55.65	(± 34.56, -115.31 - -11.78)	-50.48	(± 54.01, -165.69 - 16.07)	-50.98	(± 71.24, -243.53 - 44.65)