



Exploring Halophyte Hydrodynamics and The Role of Vegetation Traits on Shaping Salt-Tolerance in Coastal Ecosystems

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by

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Abstract

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Mangroves are among the most productive ecosystems worldwide against climate change. They act as carbon sinks due their high carbon burial rate, however, their future potential to store carbon is strictly connected to their capability to maintain high productivity in the face of several stress factors, like sea-level rise (SLR), increasing salinization and submersion, changes in climatic drivers and anthropogenic forcing.

Mangroves are halophytes, i.e., differently from most terrestrial forests, they can tolerate the presence of salt in the soil water. Nonetheless, their transpiration, productivity, and future response can be strongly limited by salinity. Analogously, their ability to exert a control on climate through the partitioning energy balance at the surface is modulated by salinity, and the strength of this control is proportional to their transpiration rate and productivity.

Despite this, Mangrove ecosystems are still unaccounted in Earth System Models (ESMs), i.e., the new generation of climate models incorporating the ‘biosphere-factor’ in their predictions. Similarly, ESMs are not considering a multitude of plant-specific traits, like salt and drought-resilience, which play a crucial role in energy partitioning at the vegetation-atmosphere interface.

Moreover, carbon dioxide concentration in the ambience is one of the major limiting factors for Mangrove growth. However, atmospheric concentrations of CO₂ have been steadily rising. Present projections for CO₂ concentrations are to continue to rise to as much as 500–1000 ppm by the year 2100, when it was approximately 315 ppm in 1959.

Photosynthetic assimilation of CO₂ is vital to the metabolism of plants. Therefore, its retrieving to understand how this will affect the plants and predict their responses to the future continuous CO₂ raise.

The goal of this thesis is to explore – through a set of Soil-Plant-Atmosphere Continuum (SPAC) models of increasing complexity – the effects of salinity on Mangroves’ energy partitioning and productivity. The main rationale behind the work is to produce an ‘easy to parametrize’ hydraulic model of Mangroves, incorporating their response to salinity. This model is parsimonious and general enough to allow for the inclusion in ESMs Land models parametrization schemes.

The Pre-existing model from Perri et al., (2019) provides the basic machinery to deal with the hydraulics of salt tolerance in Mangroves. This new model was implemented in Python to allow for enhanced accessibility for scientists in the field, and can account for different plant traits, Mangroves species, and regions. The model focuses on the hydraulic functional trait of Mangroves species in response to salinity at the root-soil

interface and simulates carbon, water, and energy fluxes at the terrestrial-aquatic interface.

The model is supported with additional database of parametrizations that covers 20 traits for most Mangrove species worldwide which are 60 species over 25 family. This parametrization enhances the understanding of the hydraulic behavior of different species and the responses of different traits to diverse environmental conditions.

Further, the available database is incorporated in the model to improve the simulation of Mangrove forest behavior and traits through the representation of stomatal control by water and salinity content in plant tissues. The effects of salinization and atmospheric carbon enrichment on Mangrove traits is analyzed to encapsulate productivity, transpiration, CO₂ assimilation and behavior of Mangroves with the different salinity and CO₂ concentration.

Also, the relation between traits and the different salt tolerant species is evaluated to understand the different behavior expected from each sub-tolerant species. The key pathways by which salinity and atmospheric CO₂ concentration impact Mangrove species productivity and behavior was captured for two different species that represent different characteristics in terms of salt tolerance (High Tolerant species is *Avicennia Marina* and the medium tolerant one *Rhizophora Stylosa*).

Results of study show that the capacity of plants generally to simulate carbon is declining with the increasing salinity. However, the high osmoregulation capacity for *Avicennia Marina* allow for a non-monotonic transpiration pattern with salinity, with the transpiration rate having its maximum at an intermediate salinity, where the low osmoregulation flux of *Rhizophora Stylosa* display strictly monotonic decaying transpiration patterns with salinity. On the other hand, carbon enrichment enhances plants productivity through its effects on assimilation and water use efficiency rates, thus, transpiration rates are lowering, and rates of carbon assimilation are increasing.

The study concluded that that interplay of salinization and carbon enrichment radically impact the dynamics of Mangrove ecosystems. Salinity affects different species in different ways depending on their salt tolerance and capacity to osmoregulate. CO₂ enrichment favors more tolerant species by drastically improving their water use efficiency. However, Salt tolerant species are less productive.

Indexing Terms: Costal wetlands, Halophytes, Mangroves, CO₂ enrichment, Salinity, Productivity, Transpiration.

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II. Declaration and Copyright

Declaration

I declare that the work in this thesis was carried out in accordance with the regulations of Khalifa University of Science and Technology. The work is entirely my own except where indicated by special reference in the text. Any views expressed in the thesis are those of the author and in no way represent those of Khalifa University of Science and Technology. No part of the thesis has been presented to any other university for any degree.

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VII. List of Symbols

Table 1: Terminology.

Symbol	Description	Unit
c	Soil salinity	mol m^{-1}
C_p	Salt concentration in the phloem	mol m^{-1}
C_s	Molar source concentration in the phloem	mol m^{-1}
C_a	Atmospheric CO ₂ concentration	ppm
C_c	Co ₂ concentration in the chloroplast	ppm
C_i	Intercellular co ₂ concentration	ppm
e_a	Atmospheric water vapor pressure	Mpa
e_i	Leaf water vapor pressure	Mpa
F_s	Sucrose transport rate	$\mu\text{mol s}^{-1}$
$f_{c,d}$	Co ₂ biochemical demand	$\mu\text{mol s}^{-1}$
$f_{c,s}$	Co ₂ atmospheric supply	$\mu\text{mol s}^{-1}$
$f_{e,d}$	Atmospheric water demand	$\mu\text{mol s}^{-1}$
$f_{e,s}$	Plant water uptake	$\mu\text{mol s}^{-1}$
f_w	Xylem-phloem water flux	$\mu\text{mol s}^{-1}$
G	Carbon gain	Dimensionless
g_m	Mesophyll conductance	mmol s^{-1}
g_p	Plant conductance per unit of water potential	$\text{mmol MPa}^{-1} \text{s}^{-1}$
g_s	Stomatal conductance	mmol s^{-1}
g_{s,CO_2}	Stomatal conductance to CO ₂	mmol s^{-1}
$g_{s,m}$	Stomatal-mesophyll conductance	mmol s^{-1}
g_{sr}	Soil-root conductance per unit of water potential	$\text{mmol MPa}^{-1} \text{s}^{-1}$
g_{srp}	Soil-root-plant conductance per unit of water potential	$\text{mmol MPa}^{-1} \text{s}^{-1}$
g_w	Xylem-phloem conductance per unit of water potential	$\text{mmol MPa}^{-1} \text{s}^{-1}$
\mathcal{L}	Phloem morphological parameter	μmol^{-1}
P_c	Sucrose production rate	$\mu\text{mol s}^{-1}$
\mathcal{R}	Hydraulic risk	Dimensionless
R_p	Resistance to sucrose transport	$\text{Mpa s } \mu\text{mol}^{-1}$
s	Relative soil moisture	Dimensionless
T_l	Leaf temperature	K
T_p	Phloem water temperature	K
T_r	Transpiration flux	mmol s^{-1}
U_c	Sucrose removal rate	mmol s^{-1}
V_p	Volume of loading cell	m ³
ε	Filtration efficiency	Dimensionless
η	Viscosity of the sap	$\text{Mpa s } \mu\text{mol}^{-1}$
θ	Leaf-level stress function	Dimensionless
λ	Marginal water use efficiency	$\mu\text{mol mol}^{-1}$
ψ_l	Leaf water potential	Mpa
ψ_p	Phloem water potential	Mpa
ψ_s	Matric water potential	Mpa
ψ_{tot}	Total soil water potential	Mpa
ψ_x	Xylem water potential	Mpa

ψ_{π}	Osmotic soil water potential	Mpa
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Chapter 1: Background and Motivation

1.1 Importance of Mangroves

Coastal ecosystems like Mangrove forests play a pivotal part in global carbon sequestration and climate change mitigation [Chmura et al.,2003; Duarte et al.,2005a; Bouillon et al.,2008; Nellemann et al.,2009; Duarte et al.,2010; Kennedy et al.,2010].

Over the last century, earth is warming in a way which cannot be explained by natural climate variability [Hamilton & Friess, 2018; Yilmaz et al., 2020]. Carbon dioxide (CO₂) is well known to be the main greenhouse gas [IPCC, 2007; Rehan & Nehdi, 2005] and the anthropogenic CO₂ emissions are largely liable to be the central factor causing the greenhouse effect, thus, the main driving factor of global warming [Florides & Christodoulides, 2009; Alongi et al., 2015]. This temperature increase on earth surface results in other huge impacts and changes in climate variables such as precipitation, sea level, humidity, wind speed, and cause extreme weather events, species extinctions, increased disease vectors and others [Florides & Christodoulides, 2009; Gilman et al., 2008; Yilmaz et al., 2020].

Forests can contributing directly to climate change mitigation and global warming by partially offsetting CO₂ emissions with their carbon storage [Rehan & Nehdi, 2005].

The Intergovernmental Panel on Climate Change(IPCC) estimates that, by the year 2050, global CO₂ emissions should be cut by 85% from the baseline of 2000 to avert a global mean temperature rise of 2°C (IPCC,2007). This can be achieved either by reducing the emissions of CO₂ or minimizing anthropogenic stressors, which may impair CO₂ uptake and storage in highly productive natural ecosystems [Canadell & Raupach 2008].

One of the most important environmental services Mangrove forest provide is carbon storage [Alongi et al.,2015; McLeod et al., 2011; Siteo et al., 2014], where they sequester CO₂ [Houghton et al., 1999; Ganguly et al., 2008; Alongi, 2014] by capturing it from the atmosphere, and convert it through photosynthesis and organic materials production, and store in plant biomass (e.g., trunks, stems, twigs, leaves, and roots) and in soil. Carbon is then reverted to the atmosphere through respiration. In costal -wet-environments such as Mangrove ecosystems, the submerged soil is typically anoxic, thus, decomposition and respiration rates are extremely low [McLeod et al., 2011; Kuwae & Hori,2019]. As a result, Mangroves store more carbon than they lose and act

as a net CO₂ sink and offset a percentage of society's greenhouse gas emissions [Kennedy et al., 2019; Chanda et al., 2013].

Mangrove forests are estimated to store 34.4 Tg C yr⁻¹ into sediments, aboveground (branches, leaves, and stems), belowground (roots), and nonliving biomass (e.g., litter and deadwood) [Alongi et al., 2015; Elizabeth et al., 2010; Mcleod et al., 2011]. These figures are comparable with the global carbon sequestration of the terrestrial ecosystems, which is approximated to be 181 Tg C yr⁻¹ [Mcleod et al., 2011]. However, global area occupied by terrestrial ecosystems is two orders of magnitude larger than the one of coastal ecosystems [of which Mangroves represent a huge fraction; Mcleod et al., 2011, Spalding et al., 2010].

Consequently, productivity and the impact of vegetated terrestrial habitats per unit area to long-term carbon sequestration are much smaller. The high carbon storage of coastal ecosystems is partially a result of their ability to trap particles and organic C during tidal inundation and store them in the soil – a process called carbon burial. In particular, Mangroves can trap around 80% of suspended sediment recirculated through the ecosystem. As a consequence, organic carbon's burial rates in coastal Mangrove ecosystems are exceptionally elevated, exceeding those in the soils in terrestrial forests by 30–50 fold [Chmura et al., 2003, Lovelock et al., 2010, Sanders et al., 2010; Mcleod, 2011; Duarte et al., 2013].

1.2 Coastal Wetlands Are Fragile Ecosystems

Climate variability, Environmental stress, changes in atmospheric composition (e.g., nutrient deposition, CO₂ fertilization, pollution) and anthropogenic forcing (e.g., agricultural practices, deforestation, afforestation; IPCC 2007) have the potential to trigger ecosystems shifts and reduce their capacity as an essential source of oceanic carbon and ultimately transform a net carbon sink – like Mangrove forests – into a carbon source.

In the case of Mangrove ecosystems, changes in land use, reclamation, coastal transformation, and coastal salinization are the most important stress factors that induce ecosystem's shift [Valiela et al., 2001; Adam, 2002]. Supremely, coastal salinization through sea-water intrusion and increased submersion, which are both predicted to

increase under future Sea Level Rise (SLR) scenarios [Craft et al.,2009; Farooqui,2010; Lovelock et al.,2015].

As a result, coastal habitats presently undergo a 10 times faster loss rate than terrestrial habitats [Pendleton et al.,2012; Duarte et al.,2013; Atwood et al., 2017].

This represents a chief loss of capacity of natural CO₂ sink and coastal protection and contributes to the increase of GHG emissions due to land-use changes. The short of vegetated coastal habitats is estimated to represent a loss of CO₂ sink capacity of approximately 7–20 Tg CO₂ yr⁻¹ [Valiela et al.,2001; Spalding et al., 2010; Duarte et al., 2013].

Moreover, the ability of coastal ecosystems to store soil carbon can be de-stabilized when Mangroves cover is eliminated, leaving soils exposed to the atmosphere, significantly reducing carbon burial rates, and act as sources of CO₂ and CH₄.

The world's Mangrove forests are now estimated to be less than half of what they once were [Spalding et al.,1997; Spiers,1999], with much of what remains is in poor condition [Giri1 et al., 2010; Siteo et al., 2014]. Namely, Mangrove cover is lost by a percentage of 1–8 yearly [FAO, 2007; Sriyanie,2008], and if the present trend continue, the whole Mangrove biome may be lost within the coming century [Duke et al.,2 007].

The erosion of a tertiary of the global cover of costal ecosystems involves a loss of CO₂ sinks and the emission of 1 Pg CO₂ yearly, presuming that all of the organic carbon in biomass and the topsoil is lost [Duarte et al., 2013]. This evaluation, which conveys substantial uncertainty, is equal to 3-to-19% of that from deforestation globally and could cause annual economic damages of 6- o 42 billion US\$ from loss of CO₂ sequestration alone, without considering the costs related to the loss of coastal protection capacity.

1.3 The Interest in Modeling Mangroves

Worldwide current estimates of Mangrove forests cover ranges from-110,000-to-240,000 km² [Wilkie & Fortune, 2003; FAO, 2007], approximately 137,760 km² in the year 2000 [Giri et al. ,2011; Siteo et al., 2014], and are more productive in terms of net primary production than most types of forests [Mcleod et al., 2011, Siteo et al.,2014].

However, numerous numbers of Mangrove species are categorized by the IUCN as threatened, near threatened or endangered [Daru et al.,2013], and they are progressively threatened and experiencing variety of contraction across the globe that requires urgent conservation action to help in prohibiting the elevation of carbon dioxide concentration at the atmosphere, loss of phylogenetic diversity as well as the other environmental consequence.

Considering all the favorable services Mangrove species can offer to the environment, discussed in section 1.1, its substantial to understand the dynamics and hydraulics of Mangroves to be able to protect, treat, and provide the best environment to support those species growth and productivity, hence, continue benefit from it.

The interest in this research is to see the revolution of Mangroves under series of stress factors. This helps enhance the understanding of the hydraulic behavior of different Mangrove species and the responses of different traits to diverse environmental conditions.

The focus here on the hydraulic functional trait of Mangroves species in response to salinity and carbon enrichment at the root-soil interface to simulates carbon, water, and energy fluxes at the terrestrial-aquatic interface will assist better projection on the interactive relation between Mangroves and climate.

Chapter 2: Mangroves and Climate

2.1 How Coastal Mangrove Ecosystems Interact with The Atmosphere

Mangroves as biosphere and the climatic atmosphere are two interacting subsystems of the Earth that have a bilateral relation [Kleidon et al.,2000; Jahn et al.,2005; Wilmers, 1990]. This interaction is accomplished through the well-known climate impact on biosphere and coastal ecosystems, on the one hand, and through the less-explored influence of biosphere on land surface exchange processes and climate on the other hand.

Climate can constrain the activity of the Mangroves, mainly through water availability, temperature, radiation, CO₂ concentrations and soil salinity [Valiela et al.,2001; Zhang et al.,2006]. These constraints lead to the general notion that the equilibrium distribution, growth and productivity of Mangroves can be understood by climate [Budyko , 1974; Holdridge,1947].

On the other hand, Mangroves can have a valuable role in the topo-climate and give a significant contribution to the climatic conditions [Wilmers, 1990]. The potential of Mangrove forests to act as carbon sinks is strictly related to their capability to exchange water and carbon with the atmosphere, thus influencing the surface energy budget, the soil water balance, and climate as a feedback [Mcleod, 2011; Barr et al., 2013; Duarte et al., 2013]. Besides affecting the composition of atmosphere through its important role for the exchange of atmospheric trace gases [Pielke et al., 1998], they can influence the physical appearance and functioning of the land surface in terms of its hydrological function, turbulent characteristics, and its radiative properties [Kleidon et al.,2000].

The changing radiative properties of Mangroves may cause variations in the balance between the radiant energy that reaches Earth from the sun and the energy that flows back out to space-which is termed as Energy budget [Trenberth et al.,2009].

The partitioning surface energy between sensible and latent heat fluxes is, in fact, largely impacted by plant transpiration and can be described through the relation between surface fluxes and the atmospheric state – i.e., the ensemble of processes which go under the name of *Soil–Plant–Atmosphere interactions/continuum* [Gu et al., 2006 ;Bonan, 2008; Santanello et al., 2011; Choi et al., 2012]. Sensible heat fluxes describe the transfer of heat from land-surface and/or biosphere to the atmosphere mainly by conduction and convection [Cayan,1992; Segal & Arritt,1992]. Sensible heating from

biosphere primarily warms the planetary boundary layer (PBL) of the atmosphere which constrain the elevation base of clouds [Desjardins,1976]. Whereas latent heat fluxes arising from vegetated surfaces take place in the form of plant transpiration, where transpiration is a significant component (about two-thirds) [Matheny et al., 2014; Wei et al., 2017] of evapotranspiration over land [Schlesinger and Jasechko, 2014; Lawrence et al., 2007] and is a fundamental path by which plants impact climate [Bonan, 2008; Seneviratne et al., 2010]. Therefore, the measurement of surface energy partitioning fluxes in the atmospheric boundary layer is of prime value to determine atmospheric stability conditions and land-surface temperatures.

Capillary force and water pressure gradients across the soil-root and leaf-air interfaces maintain uninterrupted water chains from roots to leaves, to then release water to the atmosphere through leaf stomata [Ball et al., 1987; Brown, 2013]. While water moves out through leaf stomata to the atmosphere, CO₂ diffuses through them ‘inside’ the leaf, to be used in photosynthesis [Ball et al.,1987; Sellers et al.,1996]. It is then clear that factors limiting the photosynthesis process can also restrict transpiration, since both carbon dioxide and water vapor are exchanged through stomata.

Growing consensus positions on stomatal behavior, the transport of water through the *Soil–Plant–Atmosphere Continuum (SPAC)* is built on the theory that plants reduce stomatal conductance as needed to regulate transpiration and avert hydraulic failure [Sperry et al.,1998,2002].

2.2 Soil-Plant-Atmosphere Continuum

Plant reactions to environment are affected by water loss regulations of from plants stomatal working, through effects on plant water-use, the development of plant water deficits, net photosynthesis, and temperature relations [Hall & Kaufmann, 1975; Hall et al., 1976; Passioura.1982].

In ecophysiology, exploring plant-environment relations [Daly et al., 2004; Fatichi et al., 2016; Gentine et al., 2015] and foreseeing responses of stomata to the environment and relating the physical state of plants to these responses to are important objectives [Asbjornsen et al., 2011; Molz, 1981]. These different features and responses between plant species and ecotypes strongly influence the plant performance and adaptation [Hall et al., 1976; Baird & Wilby, 1999].

SPAC express the transfer of water by plants from soil to the atmosphere in terms of the water potential, ψ , which is the difference in free energy per unit volume evaluated with respect to that of pure water at zero reference level and under standard temperature and pressure conditions [Slatyer, 1967; Oertli, 1976; Larcher, 1995]. See figure.1.

The continuum is a basic hydraulic model in which focus on water limitation that can be caused by the plant internal factors like: ability of roots to uptake water from the soil [Brooks et al., 2010], conductivity of the hydraulic system [Sperry et al., 1998], reliance on water storage within biomass [Matheny et al., 2017c], hormonal signaling [Deans et al., 2017], stomatal response to changes in leaf water potential [Martinez-Vilalta et al., 2014], and carbon demand [Paul and Foyer, 2001]. In addition, for the case of halophytes, as they grow in high salinity environments and must actively exclude salt from saline soils, and brackish intertidal zones, water flux is further restricted through the SPAC independently of water availability, making them a unique ecosystem from a hydrologic and energy flux perspective [Ball and Farquhar, 1984; Esteban et al., 2013; Krishnamurthy et al., 2014].

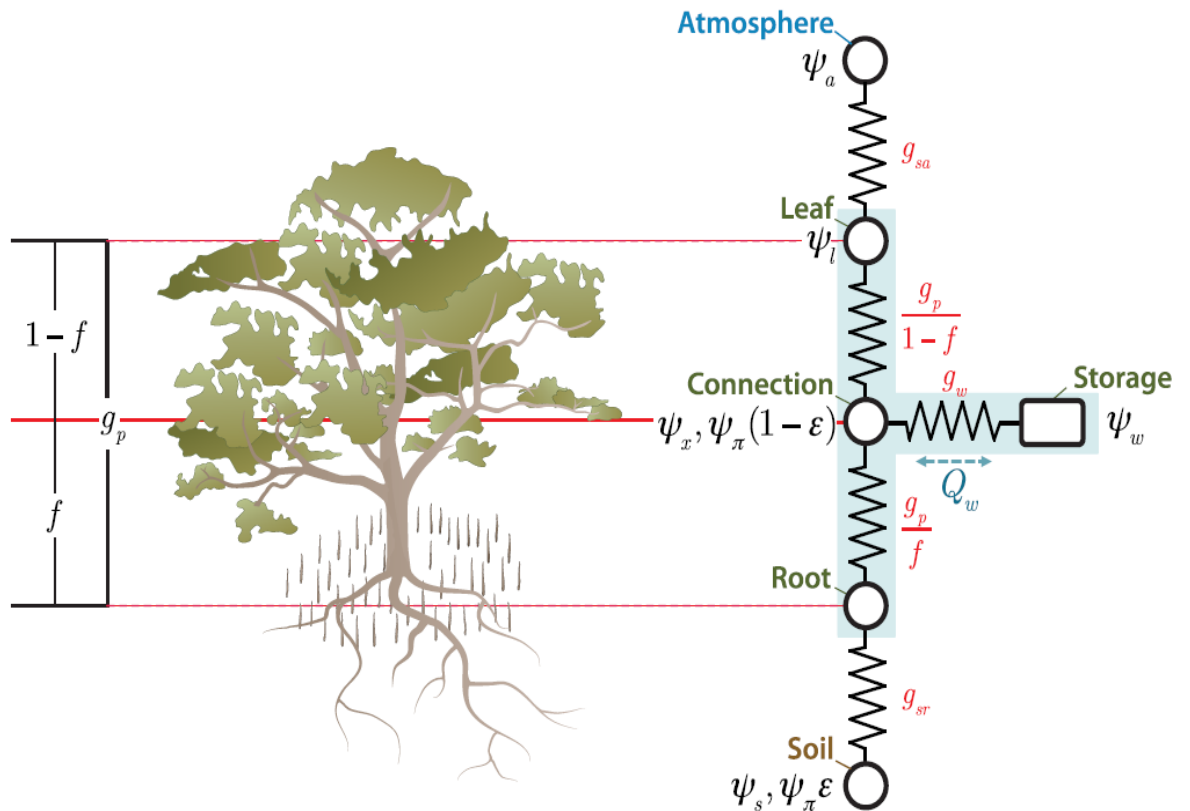


Figure 1: Representation of Soil-Plant-Atmosphere Continuum in Perri et al 2018.

As water flows through the xylem after it carried up by the roots, and exits through transpiration from the leaf stomata to the atmosphere, its water potential follows a declining path along the energy line from the soil at ψ_s , through the leaves at ψ_l , to the atmosphere at ψ_a [Rodríguez-Iturbe & Porporato,2007; Perri et al.,2019]. The rate of waterflow down potential gradients from the soil matrix to the leaf epidermis is in parallel relation to the conductance of the entire soil-to-leaf path, which depends on soil properties, plant hydraulic architecture, xylem construction, and leaf conductance [Bonan et al.,2014].

Overall, the soil–root conductance, g_{sr} , is a simplified cylindrical root model that have a proportional relation to the soil hydraulic conductivity divided by the average distance traveled by the water from the soil to the root surface [Rodríguez-Iturbe & Porporato,2007]. Knowing that water flux in xylem cavitation is a laminar driven by negative pressure gradients [Nobel, 1999], losses of energy gradually diminish the level of plant water potential, g_p , along the upward path, so that apoplastic water attains big negative pressure values, especially in the uppermost parts of the plant. We could say that the soil-root-plant conductance, g_{srp} , express the virtual significance of root and xylem conductance, defining which part adds more to the limitation of water flow [Sperry et al., 1998, 2002].

For water to be used efficiently, rates of water supply should always exceed the rate of water loss from leaves [Meinzer, 2003; Manzoni et al., 2013]. Thus, the concept of having a threshold to the rate of water transport within a given set of hydraulic conditions is generated.

Rate of transpiration is reduced by a series of complicated mechanisms and feedbacks, exerted at various stages in the SPAC [Rodríguez-Iturbe & Porporato,2007]. For instance, stomatal closure begins is not very sensitive to changes in vapor pressure deficit in the soil moisture, however, leaf conductance exerts the most important control on transpiration (transpiration rate is practically proportional to leaf conductance) [Jones, 1992; Nobel, 1999].

Relation between transpiration through stomatal cavity and vapor pressure gradient between the leaf and the air was broadly studied by scientist. Langley et al.,2009 proved the effect of vapor pressure gradient on the resistance of leaf where a direct negative response between transpiration and stomatal aperture would be capable of restricting

water loss so it would inhibit further development of water stress in the subepidermal tissues. Also, Schulze et al.,1972 showed, with xerophytic mesophytic species, that rises in leaf resistance come with rises in evaporative demand lower the level of water stress in leaves. Concluding that stomata may react to humidity independent of the traditional hydro active mechanism and illustrates the ability of the system to inhibit rises in leaf water stress. Thus, leaf conductance plays a vital role in regulating plants.

This behavior of stomatal conductance that cause alteration in the water flow rates and the capacity of Mangroves to respond to CO₂, are influenced by factors restricting growth such as nutrient and water availability, stress factors such as flooding and salinity [Langley et al.,2009; Cherry et al.,2009], and climate change (e.g., SLR, increased temperature, increased storminess, changing ocean currents, changes in precipitation and increased CO₂) [McKee et al. 2012].

2.3 Effect of Atmospheric Carbon Enrichment

Carbon dioxide is an important composite for life on this planet [Alongi et al., 2015; IPCC, 2007; Gifford,1992]. Slight change in the CO₂ concentrations could change the atmospheric composition and thus climate [Hamilton & Friess, 2018; IPCC, 2007; Norby & Luo, 2004].

These shifts in CO₂ concentration also behave directly and indirectly on biosphere through global climatic change [Woodward & McKee,1991]. On a global scale, it is well established that, patterns of vegetation and climate are closely correlated. Such relationships imply that climatic change will trigger the distribution and growth of vegetation to shift.

Therefore, understanding the direct effects of elevating atmospheric CO₂ concentration on vegetation is a concern independent of all other global CO₂ effects [Cifuentes et al.,1996; Dacey et al.,1994]. The amount of CO₂ in the atmosphere could be a limiting factor and a stressor of plants growth as they use it as food supply for photosynthesis and function [Bloom et al.,1985].

In particular, CO₂ enhancement of halophytes growth is one important direct effect of rising atmospheric CO₂ [Strain & Cure,1985; Sanders et al.,2014], where halophytes have increased photosynthesis rates that support the plants to survive and sustain its growth against the harsh saline environments [Dacey et al.,1994], in addition

to support the process of food and fiber production from carbon assimilated [Strain & Cure,1985; Sanders et al.,2014].

Global atmospheric CO₂ concentrations have grown from around 280ppm prior to the Industrial Revolution to around 353ppm in 1990 [Pearman 1988]. This rise, and the ongoing rise rate of about 1.5 ppm per annum is expected to trigger variation in major productivity of vegetation, and in the extent of net sequestration of atmospheric CO₂ into organic form [Amthor,1984; Strain & Cure,1985].

The quantitative role of the latter in mitigating the elevated amount of carbon dioxide in the atmosphere itself is an essential but uncertain component of the global carbon-cycle models that are required to forecast future increases of atmospheric CO₂ concentration [Gifford,1992]. Among the not well understood physiological processes directly affected by CO₂, are those involving net transpiration and whole-plant water use, where CO₂ reduces stomatal conductance but increases leaf size [Amthor,1984; Bloom et al.,1985; Gifford,1992].

As its crucial to understand how the world's vegetation will act as the CO₂ concentration of the global atmosphere continues to increase. The great diversity of plant types and environmental situations of the Earth 's vegetative cover requires that modeling be used to predict future responses to CO₂ enrichment.

2.4 The Role of Soil Water Salinity

The hydraulic stress determined by *low soil moisture, elevated air temperature, and soil water salinity* acts as limiting factors for photosynthesis and transpiration, thus inducing large variations in the uptake of CO₂ by vegetation and stomatal conductance of water vapor, which are key for vegetation controls on surface latent heat flux [Ball et al., 1987; Blaylock,1994; Katerji et al. 1986; Gu et al., 2006].

Under hydraulic stress, evapotranspiration rates are suppressed, resulting in latent heat flux equal to or lower than sensible heat flux [Barr et al., 2012]. Surplus salt concentration in soil or water, adversely affects the ratio of carbon dioxide assimilation to transpiration – termed as water-use-efficiency (WUE), thus impairing plant function [Blaylock,1994; Ball, 1988]. As Mangroves species, under such conditions, tend to decrease water loss by reducing transpiration, the less water use efficiency (i.e., carbon gain per unit of water lost) lower carbon assimilation rates, thus, photosynthesis and

plant growth rates are reduced [Bazzaz 1992; Taiz & Zeiger,2002; Lawrence et al., 2007].

Productivity for a certain level of soluble salts in the root medium is in general lower than the one under non-saline conditions (freshwater conditions), although many halophytes like Mangroves have evolved to have optimum transpiration and productivity at intermediate salinity values (optimal salinity; Perri et al., 2018; Perri et al., 2019). However, when soil salinity exceeds the plant's tolerance limits, growth reduction occurs, and plant water uptake becomes energetically disadvantageous [Ball, 1988; Blaylock,1994; Munns & Gilliam, 2015; Bazihizina et al., 2012].

Water has a critical role in the life of the plants and slight imbalances in the waterflow can trigger deficits and severe malfunctioning of many cellular processes as conferred. Thus, every plant faces the challenge of delicately balance its uptake and loss of water.

Mangroves are halophytes, i.e., they are able to exclude salt from saline soils and brackish intertidal zones, causing a further restriction in water flux through the soil-plant-atmosphere continuum independently of water availability, and again impacting energy partitioning at the surface [Passioura et al., 1992; Liang et al., 2008; Parida & Jha, 2010].

All biochemical processes imposed by plants are driven by an input of water free energy into the plant measured per unit volume- referred as Water potential, in which it majorly influenced by the solute concentration, pressure, and gravity [Taiz & Zeiger,2002; Hara -Nishimura & Hatsuga,2011].

The smaller productivity of Mangroves grown under saline soils is an obvious phenomenon, which is principally caused by the osmotic stress and excess ion toxicity [Katerji et al. 1998; Flexas & Medrano ,2002; Munns, 2002]. When active solute accumulates, osmotic driving force for water uptake is generated by the vacuole of plant cells, creating turgor pressure that provide the structural rigidity needed to keep the plants upright by regulating the movement of stomata [Nakamura & Matsuoka,1993; Taiz & Zeiger,2002]. However, the ability of vacuole to defense, the stomata to close, and the plant to tolerate this ionic salt stress varies, thus, the productivity reduction under different salinity levels greatly varies [Nakamura & Matsuoka,1993; Grattan, 2002; Perri et al., 2018]

Highly salt-tolerant species usually have a lower productivity as they use more energy to exclude salt and extract water from the soil solution. Thus, the effects of salinity on transpiration and productivity must be incorporated in Mangroves' SPAC models to predict the change in Mangrove traits in case of a shift in ecosystems from less tolerance to more tolerance species, and to understand their response (and feedback) on climate change and SLR.

Chapter 3: Earth System Models and Land System Models

3.1 What are Earth System Models (ESMs) and Land System Models (LSMs)

Earth system models (ESMs) study how biological processes and climate are related by integrating the interplay between the atmosphere, ocean, land, ice, and biosphere ‘physical climate system’ to assess the state of the regional and global climate under a range of circumstances [Dickinson, 1983; Pitman, 2003; Bonan,2008].

In ESMs, different biome types are commonly used to categorize world vegetation, and their parameters and responses to environmental changes are estimated. It includes, for instance, the CO₂ cycle and its interconnections to the terrestrial and coastal ecosystems [Pitman, 2003; Flato,2011].

The land surface, as one of the principal constituents at the atmosphere-lithosphere border, has a significant impact on energy and mass exchanges with the lower border of atmosphere. Land surface has a complex series of exchanges that begins with the radiative energy provided by the Sun, going through the change/imbalance of energy flow and fluxes that is associated with the conversion of natural land surface [Schaldach, 2008; Flato,2011], resulting in all the varying attributes we live in (e.g., temperature, rainfall, release and uptake of carbon dioxide, biological diversity, and ocean currents) [Rockström et al.,1999; Sala et al.,2000; Key et al., 2004].

Land surface model (LSM), one of the core submodules of ESMs, offers the lower boundary condition for the atmosphere in climate forecast models [Pitman, 2003]. LSM simulations mainly focus on closing surface energy balance, surface water balance, and surface carbon balance by considering surface air temperature, humidity, wind, air pressure, and precipitation [Pitman, 2003 ; Zhao and Li, 2015]. For instance, agriculture is affected by weather and climate and in reply influences climate by energy and water fluxes and the release of greenhouse gases [Flato,2011].

To study climate–biosphere interactions, the measurements at leaf, plant and canopy scales are applied to develop, test, and parameterize process-based LSM [Dickinson,1983; Sellers et al.,1996]. For that, and to describe how plants are transporting water and energy to and from the atmosphere, different models could be included in LSMs depending on the selected parameterization of vegetation in LSM [Dickinson, 1983].

Coupled models are widely used to have more comprehensive study of land-atmosphere interactions and feedbacks by coupling strength of all models and evaluate sensitivity to perturbations. In another words, coupled models view potentially enforces the integration of the different climate system components to have higher complex models [Grassl, 2000; Flato,2011].

An important aspect of the coastal ecosystems is the varying quantity and spatial extent of different vegetation types associated with climate change. This could be exemplified, in some measure, in models with specified vegetation distributions, in which productivity and vegetation biomass can vary as the physical climate vary [Claussen et al.,2000; Grassl, 2000]. For instance, coupling LSM with a plant hydrodynamics model such as FETCH2 (the finite difference ecosystem-scale tree crown hydrodynamics model version 2) [Munns, 2002; Bohrer et al., 2005; Mirfenderesgi et al., 2016], can mechanistically calculate stomatal conductance depending on water potential and salinity content in plant tissue, while accounting for the effect of water potential on root and xylem conductance and capacitance [Williams and Torn, 2015; Mirfenderesgi et al., 2016].

Mangrove forests have a unique seasonality of energy flux partitioning that can be caused by transpiration limits from hydraulic stressors [Barr et al., 2014; Hubeau et al., 2014]. Hydraulic stressors apply variation on the water fluxes, and it develop when water is lost through transpiration more quickly than it can be replenished [Zhang et al., 2013; Zweifel et al., 2002]. As hydraulic stressors affect water and energy fluxes, the ability of Mangroves to sequester CO₂ is also affected.

3.2 The Need for Including Coastal Ecosystems and Salt-Tolerance in Earth System Models

Regardless of the significance of salinity controls on vegetation in salt-affected soils, (likely to cover above 83,109 ha worldwide; Hasanuzzaman et al., 2014; Wicke et al., 2011) and in intertidal and coastal environments, ecohydrologists have infrequently studied on the effects of salt stress on plant-water interactions [Eberbach,2003; Perri et al.,2017; Vermue et al.,2013], assuming that the concentration of soluble salts in the soil can be negligible in most terrestrial biomes [Rodríguez -Iturbe and Porporato, 007; Sumner,1999].

Different plant species can implement diverse strategies to protect themselves from hydraulic failure due to abiotic stress. *Halophyte, in particular, are extremely efficient in using water under both water- and salt-stress conditions, but remain understudied due to their low percentage respect to the total number of flowering plants.*

Existing earth system models (ESMs) and land surface models (LSMs) inadequately represent Mangroves and halophytes, and this is because those models do not account for the effect of salinity on water/soil and energy fluxes as the influence of salinity on root-water uptake and the dynamics of stomata (connections between changes in stomatal conductance and soil moisture availability) is not considered. Therefore, having an inadequate representation of transpiration and carbon fluxes, and thus incorrect partitioning of the surface energy balances of these ecosystems [Christoffersen et al., 2016; Mirfenderesgi et al., 2016; Xu et al., 2016].

Moreover, halophytes strategies for salt exclusion in saline soils and brackish intertidal zones, and the change in water fluxes are not accounted for in ESMs. Consequently, variation in traits like growth, productivity, and mortality of these species remain elusive and not accounted for in EMSs. For example, there are no distinct plant functional types (PFT, i.e., a band of species that share same traits impacts) for salt-tolerant species in the dynamic vegetation models used by LSMs. These inaccurate/missing PFT parameterizations, in turn, impact the projection of CO₂ fluxes and plsnts distribution in coastal ecosystems [Verheijen et al., 2013].

Plant hydrodynamics models (PHMs) have been newly and broadly developed and been incorporated into ESMs and LSMs as substitutes for the conventional empirical approaches to calculate stomatal conductance [Bartlett et al., 2019; Christoffersen et al., 2016; Xu et al., 2016], thus, modeling of water transport through the SPAC has improved drastically in the last years. These models simulate the transport of water in the SPAC as flow through a porous media, using the Darcy or Richards equations for saturated or unsaturated flow, respectively, and restrict stomatal conductance on the basis of leaf and branch water potentials [Mirfenderesgi et al., 2016; Lawrence et al., 2018].

A first effort was made by Perri et al.,2018 to introduce salinity effects and salt-tolerance mechanisms in a parsimonious SPAC model. They adopted a minimalistic water fluxes description, from the soil to the atmosphere through the plant under various proposed salinity environments. Their model is considering processes (a) during the

osmotic phase of salt stress (having the greatest impacts on plant-transpiration) processes and (b) for salt exclusion at the root level, that describes the major exclusion mechanism in highly tolerant halophytes [Glenn et al., 1999; Reef & Lovelock, 2014].

On the other hand, *FETCH2* is a tree-scale hydrodynamic model of transpiration that solves Richard's equation waterflow launched by Sperry et al., 1998. It's assuming a croustillant approach for non-saturated porous media flow to simulate sap flow and water pressure through xylem, allowing it to capture the influence of dynamic changes to hydraulic capacitance and conductance on water movement and storage within the plant system [Chuang et al., 2006], which standard PHMs using Darcy's Law do not. Additionally, not many models that undertake stem water potential using a mechanistic description of porous medium flow through the stem have been presented [Bohrer et al., 2005; Janottet al., 2011; Nikinmaa et al., 2014] to support the added electric-equivalence capacitor models to compensate for the complexity of the hydrodynamics of waterflow through xylem.

FETCH2, as discussed in 3.1, clearly resolves for within-tree spatial and temporal dynamics of xylem water pressure, water potential on root and xylem conductance and capacitance and stomatal conductance depending on water potential within leaves and branches. Besides, transpiration, sap flux and aboveground water storage are also computed [Bohrer et al., 2005; Mirfenderesgi et al., 2016].

The necessity for a mechanistic approach that can account for salinity and render its control on plants and vice versa, triggered the focuses -in this thesis work- on the osmoregulation scale in SPAC that is characterized by passive dehydration and active osmotic adjustment phases that the direct water flux adjustment operated by salt-tolerant species. In addition to that, the thesis investigates the importance of introducing salinity and salt stress in ESMs to assess the contribution of coastal ecosystems to climate variability and carbon storage.

Chapter 4: Model

4.1 Model Optimizations and Schemes

Earth system models could be reliably used to project Mangrove forest responses to regional and global environmental and climatic change if salinity effects, salt-tolerance, and halophyte's traits are included in their parametrizations. It is possible to include salinity in a such a simplified plant-scale like SPAC model and allow it construct internal salinity relations, for instance, the effect of salinity on plants' transpiration.

Our model here that is originally generated by Perri et al., (2019), is a new physically-based model of terrestrial-aquatic plant ecosystems that represents the impacts of short-term salinity on plant–water relations and xylem–leaf–phloem hydraulic coupling (schematically represented in Figure 1).

The initial model was expanded and formulated in Python language to guarantee easy-to-use and parsimonious tool to be used for halophyte modeling in climate applications. Model is now able to represent the behavior of Mangroves under the different limitations caused by salinity which are (1) movement of water from sink to storage, (2) CO₂ uptake, and (3) carbohydrate synthesis and transport through phloem. Thus, the main premise in the different schemes is assuming that plants grown to immediately maximize either (1) water uptake, (2) CO₂ assimilation, (3) sucrose production and loading, or (4) profit function – i.e., the difference between CO₂ gain and hydraulic cost.

Each theory can be seen as an individual mathematical closure allowing to solve the combined cohesion–tension theory, Munch osmoregulation theory for carbohydrate movement in the phloem, and balance between biochemical need and atmospheric uptake of CO₂.

The first hypothesis is a typical description of postulates plants optimizing water transport to maintain leaf turgor and elevated stomatal conductance [Begg & Turner, 1976; Morgan, 1984; Meinzer & Grantz, 1990; Comstock & Sperry, 2000].

Secondly, a hypothesis assumes CO₂ uptake optimization for a stable amount of preliminary soil water available in the root zone per unit of leaf area [Cowan &

Farquhar,1977; Hari et al.,1986; Katul et al.,2010; Manzoni et al.,2011, 2013a; Medlyn et al.,2011; Novick et al., 2016; Buckley et al., 2017; Paschalis et al., 2017].

Third one presumes that plants adjust plant leaf potential to optimize sucrose transport from leaf (source) to root and other plants tissues (sinks) [Huang et al.,2018; Konrad et al.,2018].

Last hypothesis assumes that stomatal opening is regulating instantly to optimize the difference among CO₂ gain and hydraulic cost (profit-maximization theory; Sperry et al.,2016,2017; Wolf et al.,2016; Anderegg et al.,2017,2018; Love et al.,2019).

Such optimality schemes have been meant to replenish the empirical estimation of stomatal conductance used earlier in studies investigating the hydraulic characteristics of salt tolerance [Perri et al.,2017,2018].

4.2 SPAC Model

The model, as discussed, integrates salinity and salt-tolerance in parametrizations that aims to describe the impacts of rising soil salinity on vegetation. Where the effects of salt are confined in the soil water potential that is presumed under the osmotic component of salt stress control for well-watered or irrigated conditions.

A ‘chemical-equilibrium’ is reached amongst leaf and soil salt concentration when salinity raises in vegetation due to the saltwater absorption from soil (Scholander et al.,1966; Glenn et al.,1999; Khan et al.,2000).

The four different numerical optimization hypotheses are differentiated at the initial point when chemical equilibrium is reached to reduce the huge manifold of feasible scenarios and parameters.

First focus is on the Plant water flux:

The transpiration flux per unit of ground surface area T_r , is the difference between plant water uptake $f_{e,s}$ and water flux to the phloem f_w , presuming a continuous water potential (Nobel, 1983).

$$T_r = f_{e,s} - f_w \quad \text{Eqn 1}$$

The ability of plants to uptake water is determined by their hydraulic properties, and it is a function of the soil–root–plant conductance g_{srp} and the gradient of water potential between soil ψ_{tot} and ψ_l :

$$f_{e,s} = g_{srp}(\psi_{tot} - \psi_l) \quad \text{Eqn 2}$$

Knowing that the net soil water potential ψ_{tot} is the sum of osmotic potential ψ_p in addition to matric potential ψ_s . Soil matric potential becomes further negative as the relative soil moisture s is decreased; s is marked by the ratio of actual root-zone soil moisture content and soil porosity. Conventional soil water retention curves can describe the functional relation between ψ_s and s (Buckingham, 1907; Clapp & Hornberger, 1978) by $\psi_s = \psi_{ss}^{-m}$, where ψ_{ss} is water potential of soil near field saturation and m is a parameter accounting for the curvature of the retention curve.

Van't Hoff equation illustrates the dependency of the definite osmotic water potential on the molar salt concentration in the soil water C by: $\psi_p = \varepsilon C R \ln T_w$, where ε is the efficiency of root filtration, R is the universal gas constant, \ln is the van't Hoff coefficient for NaCl, and T_w is the soil water temperature. Efficiency of root filtration, ε , is assumed to be a linearly growing function of C given by $\varepsilon = a + b C$, where a is the filtration efficiency in clean water. Salt filtration is powered by the gradient in water potential between the soil and the xylem as filtration at the root level is thought to work in a similar way to membrane filtration. However, because salt is not completely eliminated at the root level, some ions can enter the plant due to filtration efficiency [Parida & Jha, 2010].

Soil–root–plant conductance, g_{srp} , is defined by the sequence of the soil–root, g_{sr} , and plant, g_p , conductances: $g_{srp} = \frac{LAI g_{sr} g_p}{LAI g_{sr} + g_p}$, where the conductance g_{srp} is re-scaled to LAI (leaf area index; leaf area per unit ground area) to convey the water supply per unit of ground area.

The xylem cavitation caused by lower leaf water potential is represented by an effective vulnerability curve, which is given by (Sperry et al., 1998):

$$g_p = g_{pmax} \exp\left(\frac{\psi_l}{d}\right)^c \quad \text{Eqn 3}$$

where $g_{p,max}$ is ultimate plant conductance, d and c are factors approximated such that g_p reaches 0 for the most negative values of ψ_l and is equivalent to $g_{p,max}$ for $\psi_l = 0$.

Water flux from the xylem to the phloem, f_w , could be calculated as a function of water potential gradient at the xylem-phloem interaction surface. This water flux accounts on water permeability and area of the xylem–phloem interaction surface, and by considering the hydraulic conductance at the interface g_w , the attributes, which alters as a function of water potential with a relation parallel to Eqn 3, of this membrane are modeled. The flux f_w is hence given by (Bartlett et al., 2014; Perri et al., 2018a):

$$f_w = g_w LAI (\psi_l - \psi_p) \quad \text{Eqn 4}$$

where ψ_p here is indicating the total of osmotic pressure owing to molar sucrose C_s and salt C_p (i.e. $\psi_p = R T_p (i_v,s C_s + i_v C_p)$, with i_v,s presenting the van't Hoff coefficient for sucrose and T_p the phloem temperature assumed to be equal to leaf temperature T_1).

As per observations, the amplitude of turgor terms (positive) of phloem water potential is lesser than the osmotic component (negative), hence, the turgor term is neglected here. This can be undertaken for nonsucculent plants considering that they have relatively small volume of water in the phloem compared to the xylem, whereas they have extremely high phloem ion concentration [Jensen et al., 2016].

Water uptake by plant in Eqn 2 must be balanced by water cost to the atmosphere, $f_{e,d}$, at steady-state. Presuming that cuticular transpiration is very low and negligible compared to the water flux through the stomata, the water loss must be proportionate to the stomatal conductance g_s and the vapor pressure gradient between the leaf e_l and the atmosphere e_a , and could be conveyed as (Nobel, 1983; Daly et al., 2004):

$$f_{e,d} = g_s \frac{MWratio}{p_0} (e_l - e_a) \quad \text{Eqn 5}$$

where p_0 represents the pressure of atmosphere and $MWratio$ is the water to dry-air molecular weight ratio.

Stomatal conductance can be found by formulating the equations 2 and 5:

$$g_s = gsrp \frac{p_0 (\psi_{tot} - \psi_l)}{MWratio (e_l - e_a)} \quad \text{Eqn 6}$$

The system of Eqns 1–6 requires ψ_l to be concluded which hang on the sucrose concentration in the phloem (Eqn 4). It can be calculated by linking and coupling plant hydraulics to CO₂ assimilation and sucrose transport, as shown in the next section.

Regarding CO₂ assimilation rate:

The CO₂ biochemical demand ($=f_{c,d}$) for C₃ metabolic pathway plants is determined from the model of Farquhar photosynthesis (Farquhar et al., 1980):

$$f_{c,d} = \frac{k_1(c_c - \Gamma^*)}{k_2 + c_c} - R_d \quad \text{Eqn 7}$$

where C_c is the concentration of CO₂ in chloroplast, Γ^* is the CO₂ compensation point with no mitochondrial respiration, and R_d is the respiration rate in daytime. The photosynthetic parameters, k_1 and k_2 , differ with photosynthetically active radiation (PAR) and leaf temperature, and they are characterized based on whether photosynthesis is Rubisco or Ribulose biphosphate (RuBP) limited [Collatz et al., 1991; Medlyn et al., 2002; Vico et al., 2013].

The stomatal conductance toward carbon, g_{s,CO_2} regulates the rate of CO₂ supply, ($f_{c,s}$), from the atmosphere into the intercellular space within the leaf; $f_{c,s}$ is processed by the CO₂ concentration difference between them:

$$f_{c,s} = g_{s,CO_2} (c_a - c_i) = gm(c_i - c_c) \quad \text{Eqn 8}$$

atmospheric and intercellular CO₂ concentrations are represented by c_a and c_i , respectively, and gm is the mesophyll conductance. g_{s,CO_2} could be determined from value of g_s : $g_{s,CO_2} = g_s/r$, where r is the relative molecular diffusivity of water vapor with respect to CO₂ (≈ 1.6).

The CO₂ supply rate represented in equation 8 can be expressed as $f_{c,s} = g_{sm} (c_a - c_c)$, where g_{sm} can be obtained from the series of stomatal and mesophyll conductances $g_{sm} = g_{s,CO_2} / (g_{s,CO_2} + g_{s,mCO_2})$. Dewar et al., 2018 introduced an expression that defines the ratio between the intercellular CO₂ concentration and chloroplast as it is managed by a stress function at the leaf level, $\theta(\psi_l)$, which embodies a reduction parameter depending on ψ_l and the critical leaf water potential, ψ_c . Using the mentioned formulation, a reasonable model for θ is estimated: $\theta(\psi_l) = 1 - \frac{\psi_l}{\psi_c}$. The parameter ψ_c describes the value of c_l at which stomatal and mesophyll conductance are fully diminished.

$$\frac{c_c}{c_i} = \frac{\Gamma^* + c_i \theta(\psi_l) - \Gamma^* \theta(\psi_l)}{c_i} \quad \text{Eqn 9}$$

Eqn 9 reflects a few facts regarding the relation between C_c and C_i at low ψ_l : The chloroplast has a lower CO₂ content than the intercellular space, therefore, $C_c < C_i$, mesophyll conductance witnesses a reduction with salt stress and thus a consequent decline in photosynthetic capability, and the C_c is constrained by the value of C_i at the CO₂ compensation point Γ^* regardless of the ψ_l value.

If the biochemical need balances the atmospheric carbon supply, f_c can be obtained by resolving the Eqns 7–9 and leads to:

$$f_c = \frac{1}{2\theta} [g_{s,co_2}(k_2 + \theta^*) + \theta(k_1 - R_d) - \Theta], \quad \text{Eqn 10}$$

where Θ is given by:

$$\Theta = \sqrt{4g_{s,co_2} [k_2g_{s,co_2}\theta^* + \theta(k_2R_d + \Gamma^*k_1)] + [g_{s,co_2}(k_2 - \theta^*) + \theta(k_1 + R_d)]^2},$$

Eqn 11

The f_c is independent of C_c or C_i but depends on ψ_l for specific soil vegetation features and environmental circumstances. The photosynthetic capacity depends on T_1 , which typically represent the ambient air temperature T_a . However, due to the events of heat elevation and scant evaporative cooling in salt-affected ecosystems, T_1 feasibly greater than T_a . To consider this effect, an energy balance at the leaf level is calculated using the ‘big leaf approximation’ $T_l = T_a + (\Phi - T_r \Delta H_{vap} \rho_w) / (\rho g_a c_p)$, where Φ is the net radiation, ΔH_{vap} is the latent heat of vaporization of water, ρ_w is the density of water, ρ is the mean air density, c_p is the air isobaric specific heat capacity, and g_a is the aerodynamic conductance calculated utilizing conventional flow over flat-plate theory [Dingman, 2015; Perri et al., 2017].

The concern of Sucrose transport:

Sucrose ($C_{12}H_{22}O_{11}$) is thought to be the final and most important carbohydrate produced by photosynthesis, and it transferred into the loading zone for actual functioning.

Because environmental elements like atmospheric forcing and soil water conditions are relatively constant over short periods (sub-hourly), the sucrose production rate (P_C) in the loading zone can be described as $P_C \approx \alpha(\beta f_c LAI) - U_c$. P_C is proportional to α ,

a loading efficiency factor that depends on species, and β that represents reflects how many sucrose molecules created for each molecule of CO_2 assimilated (Huang et al.,2018).

$$\frac{d(V_p C_s)}{dt} = P_C - U_C = \alpha(\beta f_c LAI) - U_C \quad \text{Eqn 12}$$

C_s is the sucrose concentration, U_C is the sucrose removal rate from the loading cell, and V_p is the constant volume of loading cell. Using the first-order kinetics, a maximum simplicity model can be obtained for U_C so that $U_C = C_s/S$, where s is a characteristic timescale related to the production-to-transport phase (usually minutes to hours) per unit of phloem volume (Huang et al., 2018).

At steady-state, $C_s = P_C s$ is the concentration of sucrose in the phloem loading zone (leaf), and $d(V_p C_s)/dt = 0$ could be related to the production rate. Sucrose transport rate inside the phloem, taking both advective and diffusive transport into account, is then:

$$F_s = C_s f_w + \frac{(\psi_p + \Delta p)}{R_p} \quad \text{Eqn 13}$$

Δp denotes the difference in xylem pressure between leaf, and soil and root, $\psi_l - \psi_{tot}$. R_p is the total plant resistance to sucrose transport (Konrad et al.,2018), and is determined by the phloem's geometry and sap viscosity (Jensen et al.,2016):

$$R_p(C_s) = \eta(C_s) \mathcal{L} \quad \text{Eqn 14}$$

\mathcal{L} represents a geometric factor that depends on phloem morphology. By using the approximate expression $\eta(C_s) = \eta_w \exp(b_1 C_s - b_2 C_s^2 + b_3 C_s^3)$, the viscosity of sap rises non-linearly with sucrose concentration. In the above equation η_w shows the dynamic viscosity of pure water, and are b_1 , b_2 and b_3 are parameters provide the best fit to observed functional relations between η and C_s .

Optimality hypotheses and mathematical closure assumptions:

All the discussed equations above are governing the relationship between water transport, photosynthesis, and sucrose production is expressed as a function of ψ_l . To move forward and reach the mathematical closure that enable determining ψ_l , one additional equation is needed. The four differing maximization hypotheses are expressed as:

$$\left. \begin{aligned}
 & \frac{\partial f_{e,s}}{\partial \psi_l} = 0 & (a) \\
 & \frac{\partial f_c}{\partial \psi_l} = 0 & (b) \\
 & \frac{\partial F_s}{\partial \psi_l} = 0 & (c) \\
 & \frac{\partial}{\partial \psi_l} (\mathcal{G} - \mathcal{R}) = 0 & (d)
 \end{aligned} \right\} \text{Eqn 15}$$

where $\mathcal{G} = (f_c/f_{c,max})$ represents the relative gain of carbon and $\mathcal{R} = (1 - g_p/g_{pmax})$ is hydraulic risk. The system of Eqn 15 is solved to determine ψ_l depending on soil salinity by maximizing water uptake (Eqn 15a), carbon assimilation rate (Eqn 15b), sucrose transport (Eqn 15c), or carbon profit (Eqn 15d). The solution is obtained under steady-state and well-watered conditions, with constant plant morphological traits assumed (short-term salinity exposure; Perri et al.,2018a). Table 1 reports the list of variables and units used throughout the text.

4.3 Parametrizations and Data Collection

Different salt-tolerance species behave in different ways, and to be able to better understand their distinct dynamics, hydraulics, and responses of different traits to different environmental conditions, parametrization of their traits is essential.

Therefore, the model was further expanded to incorporate and construct robust parametrizations for different Mangrove species, their salt-tolerance and hydraulic traits.

This parametrization could as well inform Mangroves' carbon budget models and support our understanding of the interaction between vegetation, the soil water budget, and atmosphere, and see whether the hydraulics of halophytes is accurately represented and reproduced at regional scales knowing the sensitivity of Mangroves toward the different climatic forces.

Moreover, it helped improve the simulation of Mangrove forest function, growth, and mortality through the representation of stomatal control by water and salinity content in plant tissues, in addition to identifying the key pathways by which salinity and CO₂ concentration in the atmosphere influence plant productivity.

The primary step to parametrize species is to have their traits data available. Hence, collection of data is one of the major stages in this thesis work.

Traits of about 60 Mangrove species were assembled in one enormous database. The species' names are spelled according to The Plant List (201). However, some of the species listed are presently considered synonyms in the list (e.g. *Avicennia alba* is now a synonym of *Avicennia marina*). But in this database, they were separately chosen to be included under the names given by the authors in order to allow the original information to be tracked.

Species studied include:

Table 2: List of the species covered in the database.

Family	Scientific Name	Family	Scientific Name
Acanthus	<i>Acanthus ebracteatus</i>	Heritiera	<i>Heritiera fomes</i>
	<i>Acanthus ilicifolius</i>		<i>Heritiera globosa</i>
Aegialitis	<i>Aegialitis annulata</i>		<i>Heritiera littoralis</i>
	<i>Aegialitis rotundifolia</i>	Kandelia	<i>Kandelia candel</i>
Aegiceras	<i>Aegiceras corniculatum</i>	Lumnitzera	<i>Lumnitzera littorea</i>
	<i>Aegiceras floridum</i>		<i>Lumnitzera racemosa</i>
Aglaia	<i>Aglaia cucullata</i>	Nypa	<i>Nypa fruticans</i>
Avicennia	<i>Avicennia alba</i>	Osbornia	<i>Osbornia octodonta</i>
	<i>Avicennia integra</i>	Pemphis	<i>Pemphis acidula</i>
	<i>Avicennia marina</i>	Rhizophora	<i>Rhizophora apiculata</i>
	<i>Avicennia officinalis</i>		<i>Rhizophora mucronata</i>
	<i>Avicennia rumphiana</i>		<i>Rhizophora samoensis</i>
	<i>Avicennia schaueriana</i>		<i>Rhizophora stylosa</i>
	<i>Avicennia bicolor</i>		<i>Rhizophora mangle</i>
	<i>Avicennia germinans</i>		<i>Rhizophora racemose</i>

Bruguiera	Bruguiera cylindrica	Scyphiphora	Scyphiphora hydrophylacea
	Bruguiera exaristata	Sonneratia	Sonneratia alba
	Bruguiera gymnorrhiza		Sonneratia apetala
	Bruguiera hainesii		Sonneratia caseolaris
	Bruguiera parviflora		Sonneratia griffithii
	Bruguiera sexangula		Sonneratia lanceolata
Camptostemon	Camptostemon philippinense		Sonneratia ovata
	Camptostemon schultzi	Xylocarpus	Xylocarpus granatum
Ceriops	Ceriops australis		Xylocarpus moluccensis
	Ceriops decandra		
	Ceriops tagal		Tabebuia palustris
Cynometra	Cynometra iripa	Conocarpus	Conocarpus erectus
Diospyros	Diospyros littorea	Laguncularia	Laguncularia racemosa
Dolichandrone	Dolichandrone spathacea	Excoecaria	Excoecaria agallocha
Mora	Mora oleifera		Excoecaria indica

The collected data included general information of species like: dominant photosynthetic parameters & pathway, salt-adaptation mechanism, position within the intertidal range, and salt-tolerance level. In addition to that, physical parameters (e.g. maximum observed canopy height, mean canopy height, displacement height, momentum roughness height and water vapor roughness height), Morphology parameters (e.g. The maximum observed assimilation rate, maximum carboxylation rate, and CO₂ compensation point), species' leaf water potentials (at which stomatal conductance is maximum, minimum, and critical), and vulnerability curve parameters of plants' conductance were also collected for each species.

Part of the collected traits were easy to find from literature. However, there is a huge research shortage in this field and Mangrove data are actually lacking. Hence, other part of traits was particularly impossible to find. Some, if not few, of those unattainable data could be extrapolated, in this context, Farquhar et al., 1980 and Perri et al., 2019 models were expanded and used to integrate and calibrate those parameter's inclusion of different Mangrove hydraulic traits.

Table 3 show the traits that were found and collected from literature and their respective references list.

Table 3: List of traits in literature and their respective references.

Trait name	Symbol	Possible values	References
Maximum carboxylation rate	Vc,max0	Float	Chen.L, 2008
CO2 compensation point	Γ	Float	Venkatesalu,2008
Maximum canopy height	Hmax	Float	Atlas of living Australia; Bashir,2014; Cooper,2015; Desai and Chavan, 2010; Duke, N.C. 1991; Farnsworth & Moore, 2010; FloraBase florabase.dpaw.wa.gov.ae; Gunawan,2013; Hasan, 2018; Kostermans,1959; Little & Wadsworth, 1964; Mahmud,2014; Nparks 2017; Pandey et al.,2019; Pannell1992taxonomic; Protabase - Plant Resources of Tropical Africa; Sahoo,2018; Soepadmo2004; Spalding2010world; Tomlinson, P.B. 1986; Uddin,2007
Average canopy height	hc	Float	Aksornkoae,1993; Allen & Duke,2006; Bashir,2014; Clough,1982 ; Cole et al.,2007; Cooper et al.,2016; Deshar,2012; Duke & Jack, 1987; Duke,1991; Estrada,2008; Estrada,2014; Farnsworth & Moore, 2010; Fuchs,1970; Ghosh et al.,2019; Gilman et al.,1993; Green et al.,1998; Gross et al.,2014; Guiesen et al. 2007; Handra et al.,2011; Hossain,2011; Ill,E ,1996; Jiao et al.,1997; Jones, 2014; Joshi,2003; Kangkuso, A.2016; Khan,2005; Komiyama et al.,1988; Kostermans,1959; Kusmana et al.,1992; Li.F et al.,2020; Lin et al.,2010; Lin,2006; Lu.W et al.2014; Matsui& Takahashi,2016; Meepol et al.,2020; Middeljans, 2014; Mojiol et al.,2019; Nakasuga,1979; Pandaet al.,2017; Pandey et al.,2019; Peñaranda et al.,2019; Perera et al.,2013; Pototan et al.,2021; Pulver,1976; Ragavan et al.,2015 ; Reef 2010; Simlai, A.,2014; Sirajudin et al.,2019; Soepadmo,2004; Suwa,2009; Suzuki and Saenger,1996; Suzuki and Tagawa,1983; Tamai et al.,1986; Thatoi et al.,2016; The Useful Tropical Plants Database; Tolangara and Aloysius, 2014; Tropical Plants Database; Ukpong,1997; USDA database; Woodroffe et al.,1988
Displacement height	d	Float	Arya, 1998; Stull, 1988; Verhoef, 1997
Momentum roughness height	zo	Float	Arya, 1998; Stull, 1988; Verhoef, 1997
Water vapor roughness height	zoq	Float	Arya, 1998; Stull, 1988; Verhoef, 1997

Leaf area index	LAI	Float	Athiresan,2013; Chen.L.,2012; Clough et al.1997; Clough et al.2000; Ill,E ,1996; Ishii,2004; Kathiresan,2013; Komiyama et al.,1988; Kusmana et al.,1992; Nakasuga,1979; Odum et 1982; Sherman et al.2003; Sobrado,2006; Steinke,1995; Suzuki and Tagawa,1983; Tamai et al.,1986; Zhu et al.,2017
Critical leaf water potential	psi_lc	Float	Deshar,2009
Leaf water potential at which the stomatal conductance is null	psi_l0	Float	Naidoo,1986
Maximum Salinity		Float	Banerjee,2010; Desai and Chavan, 2010; Djamaluddin, 2018; Meepol et al.,2020; Mishra,2002; Paliyavuth et al.,2004; Palliyath &Puthur,2018; Smith 1992
Optimum growth salinity	Cmax	Float	Allen,2003; Arachchilage 2017; Ball & Pidsle, 1995; Ball,C. 1997; Burchet 1989; Chen,2014; Clough,B.K., 1984; El-Mahrouk,2010; Hasegawa2014; Hoppe & Speer,2011; Khan & Aziz, 2001; Mulik & Bhosale, 1987; Naseer et al.,2017; Neha, T. 2010; Palliyath 2018; Parida, A., 2004; Reef 2014; Robertson and D.M. Alongi,1992; Sedas 2019; Smith 1992 ; Suarez, 2005; Takemura, 2010; Theerawitaya 2014; Wong 2007; Ye,200
Leaf area		Float	Arrivabene et al. 2014; Ball 1988; Lin and Wang 2001; Medina 1997; Medina et al. 2001 ; Nasrin et al.,2017; Parida, A., 2004; Reise 2003; Saenger and West 2016; Suarez, 2005; Yuanyue et al. 2009;
Sucrose const.		Float	Guangqiu,2007; Parida,2004; Popp,1984; Tamunaidu,2013 Theerawitaya.C, 2014
Maximum photosynthesis CO2 assimilation	Amax	Float	Balun, 2011; Clough, 1989; Garcia, 2017; Jiang, 2017; Kraussa and Allen,2003; Leng, 2020; Nandy et al. 2005; Rocha, 2009; Shang-Qing et al.,2016; Sobrado, 2000
Photosynthetic pathway	PP	C3; C4; CAM	Andrew,1985; Ball,1984; Cheeseman,1997; Joshi, 1980
Salt-adaptation mechanism	SAM	SE; SS; SA	Bibi,2019; ehalophytes database; Hogarth,1999; Krishnamurthy,2014; Kumar.A, 2010; Nguyen and Ho, 2006; Parida.a &jha, 2010; Reef and Lovelock 2015; Shan.L, 2008; Ye 2005
Intertidal range		LI= Low intertidal; MI= Middle intertidal; HI= High intertidal	Clough 1992; Duke, 1998; Saenger 2002

Salt-tolerance		LT= Low tolerance; MT= Medium tolerance; HT= High tolerance	Ahmed,2011; Allen,2003; Bot. Bull. Acad. Sin.,2001; Chen,2014; Clough,B.K., 1984; Cunha,2006; Larcher,2016; Djamaluddin, 2018; Hasegawa2014; Hoppe & Speer,2011; Jimenez,1992; List2010iucnIUCN Red List ; Palliyath 2018; Parida, A., 2004; Perera,2013; Reef 201,4; Reef and Lovelock 2015; Riascos,2018; Robertson and D.M. Alongi,1992; Thomas,1988; Tomlinson, P.B. 1986; Wijayasinghe,2019; Wong,2007
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4.4 Traits and Characteristics

This section contains description of all the 20 directly found and/or integrated characteristics (e.g., physical, morphological etc.) included in the database to help simulate Mangroves traits and behavior.

Traits collected are the following:

Photosynthetic pathway (PP)

There are three different ways for plants to convert atmospheric CO₂ into organic compounds (photosynthetic CO₂ assimilation) by using the energy from sunlight [Ehleringer, & Monson ,1993; Smith, 1997; Hartzell et al.,2018]. Thus, there are three categories of plants (i) C₃ plants, in which it produces a three-carbon compound and it's the majority of terrestrial and costal plants; (ii) C₄ plants; and (iii) CAM plants [Raines, 2011; Ruan et al., 2012]. Generally, Mangroves species display characteristics that are common to C₄ and CAM plants, but C₃ is the dominant pathway [Andrews et al.,1984; Ball et al.,1997; Perri et al.,2019].

Identifying the photosynthetic metabolism is critical to understand plants' morphology and invert behavior [Brugnoli & Lauteri, 1991; Dasgupta and Nanddy,2011], and the conditions under which each species could have an advantage over the other [Hnatiuk,1980; Dasgupta & Nanddy,2011]. The different PP also indicates the Mangrove's sustained productivity, transpiration, and performance throughout the year and under harsh seasons and ecosystems [Leuning, 1995; Cheeseman et al.,1997].

Knowledge of photosynthetic pathways is also essential for estimating the gross carbon and energy fluxes between the land surface and the atmosphere [Beer et al., 2010; Boden et al., 2013; Rogers et al.,2017] in earth system models. Therefore,

PP, in this database, was collected from the literature to distinct the species to be used in Farquhar's model that is valid for C₃ plants only.

Salt-adaptation mechanism (SAM)

SAM is the way Mangroves can imply a change to cope and well suit the present environment of excess salt [Downton 1982; Clough,1982; Liang et al.,2008]. These salt regulation mechanisms are held by the aerial roots -that have morphological and anatomical features- and it can be divided into exclusion, extrusion and accumulation [Mizrachi et al., 1980; Tomlinson, P.B. 2016].

Salt-adaptation mechanisms were collected from the literature to help understand the role that Mangroves can take under salinity (e.g. productivity, transpiration, relative growth, and mortality rates) [Parida & Jha, 2010; Krauss and Ball, 2013], and indicate how salt tolerant are the Mangrove species based on the mechanism they adapt [Zheng et al. 1999; Parida & Jha, 2010]. Also, to help locating the occupancies of species with the same salt-adaptation mechanism [Scholander 1968; Ball and Pidsley, 1995], thus the salinity and tidal zones to which it is best suited and is best adapted physiologically.

In this database, salt-adaptation mechanism is a qualitative parameter. It was not used in earth system model as we are not modelling the salt balance inside the plant.

Maximum canopy height (H_{max})

The maximum canopy height is an important parameter to allocate biomass stocks [Kaufman et al.,2014; Rovai et al.,2016] and the different species in special scales by using remotely sensed measurements and field data that can distinguish the structural attributes of forests (such as type of species) [Hutchison et al.,2014; Simard,2019].

Furthermore, because Mangrove canopy height is highly correlated with carbon turnover via leaf or litterfall production, H_{max} is used to quantify contemporary global aboveground productivity and carbon sequestration rates [Saenger & Snedaker,1993; Alongi & Dixon,2000; Sherman et al.,2003].

In earth system models, H_{max} is crucial for parameterization and initialization of plants, and in some cases, models improvements can be directly linked to better simulation of biodiversity [Levine et al. 2016].

All H_{\max} data was collected from the literature. However, it was not used in our SPAC model, but a characteristic (average) canopy height, h_c , was used.

Intertidal range

Mangrove intertidal ranges limited chiefly by physiological intolerance to the changes in environmental conditions due to tides [Duke, 1998; Kelleway et al.,2016], thus, intertidal ranges can be defined as the ranges of intertidal zones species can tolerate.

Tidal inundation, floods, and the increased salinity gradient caused by tides, all have a direct impact on vegetation distribution along the land-sea hydrologic gradient, in addition to soil and sediment biogeochemistry and geomorphology [Kelleway et al.,2016; Ward et al.,2020]. The hydrological and hydrodynamic process of tidal interchange influence coastal species at different levels according to their intertidal ranges [Duke, 1998; Waycott et al.,2011].

The value of such a parameter is noted where Mangrove species group in diverse forest community associations [Duke et al.,1998; Reis-Filho et al.,2016], and in distinct distributional ranges at different geographic scales [Duke et al., 1992]. Further, the intertidal range of species is a crucial concerning factor for any model and/or database as it effects water energy with consequences for carbon and nutrient exchanges in tidally affected wetland and species to be used in earth and vegetation system models [Tzortziou ,2008; Jay et al.,2016]. In another words, it influences the critical functions of dynamic exchange of energy and matter in coastline stabilization, species, nutrient and carbon [Bridgewater, 1989; Ward et al.,2020].

Intertidal data available in the database, collected from the literature, is considered as a qualitative parameter, and was not used in our SPAC model.

Leaf area index (LAI)

Leaf area index is the total area of one-sided leaf per unit horizontal ground surface area [Breda, 2003; Yan et al., 2019]. It is a vital vegetation factor for ecophysiology and biogeochemical cycles in ecosystems; determines and controls mass (water and carbon) and energy (radiation and heat) exchange between the biosphere canopy and the atmosphere [Asner et al.,2003; Tian et al., 2015].

LAI ground measurement is essential in plants observing because it provides the actual value for remote sensing validation[Breda ,200; Yan et al., 2016b]. Our model,

like many ESMs, calculates CO₂ and water fluxes at the level of leaf, which are then rescaled on regional and global basis based on LAI. The surface energy budget, in addition to plant-based emissions and deposition of aerosols and chemically and radiatively key gases, are also sensitive to expected LAI [Osborne et al., 2004; Mahowald et al., 2015]. Consequently, minor inaccuracies in simulated LAI can become significant errors in ESMs' biophysical and biogeochemical processes, and changes in LAI alone can change the surrounding climate [Bounoua et al., 2000; Ganzeveld et al., 1998; Lawrence and Slingo, 2004a].

LAI data were found in the literature for different sites and countries. For the model, either a characteristic (average) value was used or a site-specific value for a certain country/region.

Maximum photosynthesis CO₂ assimilation (A_{max})

It is the maximum rate at which leaves can uptake and fix carbon during photosynthesis, and is typically calculated as the amount of carbon dioxide that is fixed per meter squared per second [Chen et al.,2008; Hartzell et al.,2018; Perri et al., 2019].

Maximum CO₂ assimilation is an important factor to represent the stomatal conductance; where vegetation with a elevated photosynthetic capacity have a high stomatal conductance, in the absence of environmental stress [Rogers et al.,2017; Osnas et al.,2018]. The change in photosynthesis CO₂ assimilation is therefore an indication to the stress degree the Mangroves are facing [Ball and Farquhar,1984; Perri et al., 2018]. When A_{max} is given in leaf-level versus c_i , curves may provide a simple method for quantifying the limitation stomata enforce on CO₂ assimilation [Farquhar et al.,1980; Rogers et al.,2017].

Moreover, photosynthetic CO₂ assimilation by biosphere is the largest of the global carbon fluxes that most ESMs need for the aim of global change projection [Woodrow & Berry,1988; Rogers,2014]. It is a core parameter for models tend to project plants' photosynthetic capacity, and others that aim to improve land-atmosphere carbon and energy exchange under changing climatic conditions by incorporating other environmental factors to parameterize large-scale stomatal conductance and photosynthesis [Long & Bernacchi, 2003; Ali et al.,2015].

However, A_{max} is not a parameter of our SPAC model. It was collected from literature to verify that the model is in agreement with observations in absence of stress.

Maximum carboxylation rate ($V_{c,max0}$)

The maximum rate of carboxylation of the enzyme Rubisco- the major enzyme assimilating CO_2 into the biosphere- is a fundamental parameter of the SPAC [Kucharik et al. 2000; Andersson and Backlund,2008] and a key parameter for estimating photosynthesis as it defines the maximum number of CO_2 molecules that can be assimilated per unit of area and time [Rogers ,2014; Eckert et al.,2020]. Also, it can potentially influence the percentage of respiration [Knorr 2000; Sitch et al. 2003]. $V_{c,max0}$, is from the most vital parameters to have successful projection of future global change [Long & Bernacchi, 2003; Rogers,2014].

In practice, it has been found that $V_{c,max0}$ can be estimated through the relation between net assimilation rate (A_n) as a function of intercellular CO_2 (c_i) and the initial slope of the A_n / C_i response representing photosynthesis is limited by $V_{c,max0}$ [Long & Bernacchi, 2003; Rogers et al.,2017]. Thus, other than the directly collected values of $V_{c,max0}$ from literature, it was inferred as the best-fit of the A_n vs c_i curve that returns the $V_{c,max0}$ that results in the best agreement between observations and model. Based Linear regression on Equation 40 of Farquhar's model:

$$A = V_{c,max0} \cdot \frac{c - \Gamma^*}{c + KC \left(1 + \frac{o}{KO}\right)} - Rd \quad \text{Eqn 16}$$

where the Michaelis-Menten constants KC and KO for CO_2 and O_2 at $T_o(25C)$ are 420, 330. Partial pressures of O_2 is 210mbar. Dark respiration rate Rd , of 1.1 $gmol\ m^{-2}\ S^{-1}$ at 25 C is assumed (Farquhar et al.,1980).

and

$$\Gamma^* = \frac{KC \cdot o \cdot ko}{2 KO \cdot kc} \quad \text{Eqn 17}$$

where $kc=2.5$ and $ko=0.21 \cdot kc$.

In many cases, parameterization was based on limited data sets.

CO_2 compensation point (Γ)

It is the minimum atmospheric CO_2 level required to sustain growth of the plant [Krenzer et al., 1975; Campbell et al.,2005], at this point photosynthesis is

reserved to such a notch that respiratory and photorespiratory processes consume all the assimilated CO₂ and thus plant growth is reduced to zero [Sage & Reid, 1992; Campbell et al.,2005]. In another words, it is the concentration of CO₂ at which no net assimilation occurs [Frquhar et al.,1980].

Therefore, it's an essential parameter to understanding biosphere feedbacks (e.g. respiration and photosynthesis etc..) on the carbon cycle during low CO₂ episodes [Raggi, 1980; Campbell et al.,2005]. It's also critical for climate models that tend to predict and potentially optimize CO₂ assimilation [Sage and Kubien 2007; Zhu et al. 2008], where the photorespiratory CO₂ compensation point can quantify the Rubisco's specificity - cornerstone of these models - for reaction with CO₂ as opposed to O₂ and the carbon lost through photorespiration [Farquhar et al. 1980; Walker et al.,2016].

Nevertheless, true values of Γ stay hard to estimate [Walker & Cousins, 2013]. In the absence of "dark respiration" in this database, if Γ was not found in the literature, it was measured the gas-exchange method by using the known $V_{c,max0}$ as the following:

$$\Gamma = \frac{\Gamma^* + KC \left(1 + \frac{O}{KO}\right) \cdot \left(\frac{Rd}{V_{c,max0}}\right)}{1 - \left(\frac{Rd}{V_{c,max0}}\right)} \quad \text{Eqn 18}$$

Michaelis constants and partial pressure of O₂ were for 25C as Farquhar's model, maximum carboxylation rate was measured from photosynthetic CO₂ response ($A_n - C_i$) curves at the same temperature. Similar to any mechanistic model, accuracy depends on precise assumptions of plant physiology.

Salt-tolerance (Optimum growth salinity)

As salinity fluctuate from lower to/from higher concentrations seasonally through pulses of seawater [Wang et al.,2011; Krauss & Ball, 2013], its important to know the degree or level in which coastal species such as Mangroves can tolerance salinity.

To some extent, exposure of plants to salt can affirmatively effect plant growth and crop productivity but a turnover of adversely affect can happen when exceeding limits. Osmotic stress is one of the most important,if not the most, causes of salt stress, especially in arid and semi-arid regions [Munns & Tester,2008]. Understanding the range of salt-tolerance of each species is crucial to understand the most dramatic

response of plants after highly exposing to salinity owing to the osmotic effect of salt outside the roots; the decrease in stomatal aperture [Brugnoli & Lauteri, 1991; Munns & Tester, 2008]. Consequently, rates of transpiration and photosynthesis are reduced leading to extremely low relative growth rate of plants [Clough; 1989; Greiner La Peyre et al., 2001].

The salinity level in which species have the maximum transpiration and photosynthesis and reach the best relative growth rate due to the high stomatal conductance is the Optimum growth salinity (C_{max}) [Khan & Aziz, 2001; Zelm et al., 2020]. Rise in growth with rise in salinity may reflect rising availability of nutrients or higher osmotic potentials required to support photosynthesis and growth [Flowers & Colmer 2008].

Salt-tolerance levels were found in the literature whereas optimum growth salinity values were either obtained directly from literature or interpolated from graphs of relative growth rate and/or transpiration as function of salinity. C_{max} is the value of salinity where optimum value of relative growth rate and/or transpiration was found. Salt-tolerance levels and C_{max} were not used directly in the model, but studied and expanded to incorporate parametrizations of different Mangrove species, allowing a better understanding of their dynamics, hydraulics, and responses to salinity.

Maximum Salinity

Salt stress is one of the paramount abiotic stressor leading to reduction in plant growth, development and productivity worldwide [Yadav et al., 2019], and can be generally viewed as the toxicity to the plants due to development of salinity [Taiz & Zeiger, 2002]. The higher level of salt concentration species can endure with their environment, function as autotrophs, and survive within is called the maximum salinity [Ball 2002; Suárez & Medina, 2005]. Species' functions weaken at high salt concentrations, but eventually die at/after the maximum salinity [Khan & Aziz, 2001; Suárez & Medina, 2005; Lawrence et al., 2007] and this is due the fact that salt-adaptation mechanisms are not enough for Mangrove when reaching the maximum salinity [Parida & Jha, 2010; Tomlinson, P.B. 2016].

Maximum salinity is as important as salt-tolerance ranges, if not more, where saline soils are reported to bring about changes in morphological, physiological and biochemical responses of plants [Locy et al., 1996; Amirjani, 2010; Siringam et al., 2011].

In this database, maximum salinity is a quantitative value, and was collected from the literature to shape the morphology of Mangroves and track the changes in the plant metabolism and alteration in the ability of a plant to harvest water considering its stomatal conductance and water potential, plant growth, biomass and survival.

Vulnerability curve parameters (d_1 , c , d_{1w} , c_w)

Vulnerability is the change in Mangrove species over time, caused by both human impacts and natural influences including climate change such as SLR [Ellison & Zouh,20 12]. Vulnerability curve is usually employed to model xylem cavitation due to low leaf water potential and describe the decline of conductance due to cavitation and embolism [Perri et al.,2018]. The parameters of the vulnerability curve can be rarely found in the literature, even more scarcely for Mangroves. It can be estimated from observation of plant conductance as a function of $g_{p,max}$ or $g_{s,max}$ as a function of leaf water potential. The following classic theoretical vulnerability curve equation was used to model xylem cavitation by returning d_1 and c [Sperry et al., 1998]:

$$gp = gp, max. exp\left(\frac{\Psi_l}{d}\right)^c \quad \text{Eqn 19}$$

Approximations were also made as $d_1=d_{1w}$ and $c=c_w$.

Concentration of salt in the phloem (M_w)

Concentration of salt in the phloem is an important key of the osmoregulation mechanisms of plants under saline conditions [Blaylock,1994; Munns & Gilliam, 2015]. Because the reaction to salt stress is focused on preserving an adequate internal salt content, less conservative water techniques may be used [Konrad et al.,2019; Perri et al., 2019].

The presence of inorganic ions within the plant could be advantageous for osmotic stress tolerance as its also evident for sucrose transport [Jensen et al., 2013; Perri et al., 2019]. The greater the NaCl concentration in the phloem, the bigger the driving force for diffusive transport [Jensen et al.,2016; Konrad et al.,2019].

Mangroves can regulate internal water potential thorough ions movement across plant compartments [Liang et al., 2008; Parida & Jha, 2010; Perri et al., 2018] and the ions flux from the xylem to the phloem (and inversely) supports optimal turgor and osmotic pressure maintenance in saline conditions [Katerji et al. 1986; Taiz &

Zeiger,2002; Perri et al., 2019]. Nevertheless, at minimal salinity and elevated soil moisture, strongly negative internal water potential sustains a substantial osmoregulatory flux that limits transpiration [Flexas & Medrano ,2002; Hara-Nishimura & Hatsuga,2011].

In the database, M_w was assumed to be constant for short-term salinity exposure and to be equivalent to C_{max} which was found in the literature.

Phloem morphology (V_p , Δt)

Volume of loading cell, V_p , and loading time constant, Δt , are allied to the production-to-transport process (typically ~ minutes to hours) per unit of phloem volume [Huang et al., 2018; Perri et al.,2019].

The network of minor vein phloem is quite extensive and represents an efficient collecting system for photosynthate. Sucrose primarily follows a symplastic path from its site of synthesis in the mesophyll cells [Lunn & Furbank, 1999; Slewinski et al.,2009], diffusing through different plant-specific ways [Russin et al., 1996; Gottwald et al.,2000], and finally imported into the phloem cells [Giaquinta, 1983; Fritz et al., 1983; Huang et al., 2018]. At steady-state, the amount of sucrose in the phloem loading zone (leaf) can be related to the production rate [Giaquinta, 1983; Perri et al.,2019].

ESMs, including ours, uses each CO₂ molecule enters through stomata for sucrose production [Perri et al.,2019]. Hence, sucrose production is proportional with stomatal conductance and photosynthesis assimilation rate. Consequently, sucrose production in ESMs can indicates the species productivity and photosynthetic capacity, help in projecting the surrounding environmental stress, and model leaf-level gas and energy exchange under different climatic conditions [Long & Bernacchi, 2003; Nikinmaa et al., 2013; Jensen et al., 2016; Perri et al.,2018].

Phloem morphology parameters were fitted in our model to obtain a realistic value of sucrose production rate. These parameters cannot be found directly in literature. However, it can be modeled using the sucrose concentration data. The expanded model was used to tune the morphological parameters until the modeled sucrose concentration is in good agreement with the observed one from literature. Phloem morphology for *Avicennia marina* and *Rhizophora mangle* were estimated from Perri et al.,2018 and Perri et al.,2019, and were used as first guess to tune the other species.

Physical traits (hc , d , Zo , Zoq)

Physical traits are the main characteristics to feature any plant and species. The main Physical traits concerning the database and model are: (i) The average canopy height, hc , as the name implies is the average height of all simulated trees along a particular species and/or community or the characteristic height a species often reaches [Nelson,1997]. (ii) The displacement height, d , is an empirical parameter instituted to uphold the ‘log-law’ above tall vegetation [Dong et al.,2001]. In another words, it is the depth of still air trapped among the roughness elements [Abtew et al., 1989]. (iii) The momentum roughness height, Zo , represents the point at which the wind speed approximately becomes zero at distance above the surface [Verhoef, 1997]. (iiii) The water vapor roughness height, Zoq , is the height where the specific humidity assumes its surface value when the logarithmic profile, which humidity obey within the dynamic layer, is extrapolated downward outside its range of validity [Brutsaert,1975].

Boundary-layer meteorology is the challenge associated with turbulent flow [Stull, 1988], and in view of analogy which often exist between the turbulent transfer of momentum and that of any other passive/inert admixture of flow [Verhoef, 1997]. Thus, it’s very tempting to characterize the surface as regards to its surrounding fluids (air and water vapor) to draw a rough estimate of the boundary-layer around the plants surface.

Those physical traits are significant factors in climate models where they play a vital role in calculating the radiation partitioning and the within-canopy radiation regime by simulating the reflected, intercepted, and transmitted fluxes into the ground of diffuse radiation through the canopy [Fisher et al.,2018]. They can be utilized to assess the disturbance of vegetation to the near-surface airflow [Abtew et al., 1989] and are -especially hc measurements- a huge benefit for the evaluation of forest biomass and carbon stock [Lisein et al.,2013; Steinmann et al.,2013].

Further, they are important in any ESM and LSM as they represent fundamental concepts of the dynamical meteorology and physical morphology [Zilitinkevich et al.,2008] that depend on the height and spacing of the canopy elements acting to retard the surface air flow, and necessary to fully identify the state of wind and the protective role of standing vegetation in wind erosion [Dong et al.,

2001]. Thus, they have regularly been assessed for local sites from vertical wind profiles and micrometeorological theory.

Such traits are hard to be estimated, therefore, climate modelers have uses landcover characterization with a roughness length associated with each land-cover type [Schaudta and Dickinson,2000]. This association was used by collecting the mean height of the canopy of each land-cover type/species to be used in prescribed ratios of d , Z_o , Z_oq to hc of the given canopy:

$$d = hc \times 0.7 ,$$

$$Z_o = d/10 , \tag{Eqn 20}$$

$$Z_oq = Z_o \times 0.2$$

It's important to note that the estimated ratios are not constant but vary in small ranges according to the different experimental studies on the aerodynamic parameters. However, the ratios used in this database are the commonly used values for the estimation of water and CO₂ fluxes.

Sucrose loading efficiency (Alpha)

Photosynthetically produced sugar, principally sucrose, the major carbohydrate product of photosynthesis in higher plants, transported rapidly long distances into the loading zone to sustain growth and metabolism [Baker et al., 2012; Braun, 2012], this uptake capacity is what is called the sucrose loading efficiency [Wang, et al.,2005; Kühn & Grof, 2010].

Sucrose transport could enforce a serious restriction on leaf-level gas exchange [Nikinmaa et al., 2013; Jensen et al., 2016], thus, appropriate control of sucrose partitioning is essential to plant functioning, productivity, crop yield ...ect [Braun, 2012]. Therefore, increasing sink grain by regulating leaf water potential [Huang et al.,2018; Konrad et al., 2018] and strengthen sucrose loading efficiency characterizes a strategy to enhance yields, respiration, carbon storage and productivity of plants [Wang, et al.,2005; Kühn & Grof, 2010].

As it extremely difficult to estimate Alpha and studies looking into such a detailed parameter are very rare, Alpha in this model was assumed to be equal to 1.

Depth of water storage (D_w) & Maximum depth of water ($D_{w,max}$) in phloem

As known phloem transports carbohydrates and load it into phloem for the growth, storage and respiration [Rennie & Turgeon 2009], which is a procedure that increases the solute concentration. This augmented solute concentration then increases turgor pressure in the transport river by escorting water from the xylem through osmosis [Ryan & Asao, 2013]. At the growth or storage sinks, carbohydrates are vigorously drop or inactively leak out of phloem, letting down the solute concentration and water then transfers back into the xylem from the phloem, dropping the turgor pressure [Münch 1930]. This turgor driven transport mechanism is what defines the depth of water storage in phloem [Coussement, 2018; Ryan & Asao, 2013].

D_w is considered to be an important physiological trait for drought tolerance in water deficit environments [Plain et al. 2009]. As its essential to understand how stress (e.g. water deficit, salinity increase, temperature stress) is going to affect water content in phloem and what are the rates of turgor loss which point out the decreased metabolic processes, photosynthesis and eventual productivity [Dannoura et al. 2011; Mahajan and Tuteja, 2006].

In ESMS and LSMs that concern plant's water uptake, values of D_w and $D_{w,max}$ are critical to track cells turgor and maximize the water uptake, by maintain optimal turgor, especially in stress conditions [Morgan,1984; Meinzer & Grantz,1990; Sperry,2000]. Further, in phloem–xylem transport models, such traits can predict phloem transport rate, water/ions flux from the xylem to the phloem (and contrariwise) under the different environmental conditions [Perri et al., 2019; Plain et al. 2009], as well as tracking the osmoregulatory flux that limits transpiration and respiration streams [Högberg et al. 2008; Epron et al. 2012].

These data are rare and cannot be found easily in literature due to the sensitivity of phloem and attempts to measure these traits often induces wound reactions in plants [Ehlers et al. 2000; van Bel 2003]. Therefore, in this database and model, most if not all values were assumed to be similar to the ones of *A. marina* and *R. mangle*. In any case, the osmotic pressure is usually negligible in Mangroves compared to the osmotic pressure as they are able to store a significant amount of organic and inorganic ions in their tissues [Perri et al.,2019].

Leaf water potential at which the stomatal conductance is null (ψ_{l0})

Stomatal conductance and leaf water potential are generally interconnected as they are simultaneously affected by a number of environmental variables [P. G. Jarvis, 1976]. Leaf water potential indicates the whole plant water status, and the stomatal conductance indicates the intensity of plant stress status by measuring the degree of stomatal opening [Yan et al., 2012; Gamage et al., 2018]. In another words, maintenance of high ψ_l is found to be associated with avoiding dehydration stress with the different regulating mechanisms [Kadioglu & Terzi,2007; Rosenow et al., 1983]. However, when stress is stronger than the plant's capacity to cope (e.g. increasing salt concentration), water potential reduces and harden water uptake for the plant [Parida & Das, 2005], resulting in a progressive decrease of leaf stomatal conductance and eventually stomata plant closure and null stomatal conductance [Chaves et al.,2003]. Null stomatal conductance force leaves to roll over and avoid unnecessary transpirations [Kadioglu 2007].

The decline of g_s with decreasing ψ_l is crucial between the complex of internal and external factors that define general stomatal responses [Aasamaa & Sober,2011] and influences the photosynthesis capacity, dynamics of gas exchange, CO₂ storage capacity, productivity, and drought tolerance across plant species [McElwain et al.,2016]. Also, ψ_l is an important physiological trait for drought tolerance under water deficit conditions and incorporating its value, especially when stomatal conductance is null, in ESMs and LSMs is essential for the models to function. It's a core parameter to simulate biotic regulation of evapotranspiration, photosynthesis, CO₂ and water fluxes and general hydraulics of plants [Bonan et al.,2014].

In this DB, ψ_{l0} was collected from literature for the available species and assumed to be equal to the critical leaf water potential ranging from -3.5 to -4.5 MPa.

Leaf water potential at which the stomatal conductance is maximum (ψ_{l1})

When leaf water potential is pleasing (i.e., well-watered plants) and atmospheric evaporative demand is down, the stomata are completely open all through daylight periods which exploits assimilation of CO₂ and thus safeguarding optimal rates of photosynthesis [Gimenez 2005; Janes & Gee,1973]. Osmosis regulation is the key mechanism allowing plants to uphold water absorption and cell turgor pressure,

therefore contributing to continuous higher photosynthetic rate, cell expansion, and growth [Nayyar & Gupta,2006; Jongdee et al., 2002].

Water potentials generally and ψ_{l1} specifically are necessary to maintain life in plants [O'Toole & Cruz, 1980], and is a very high factor in understanding the favorable atmospheric and soil conditions of each species [Mott & Parkhurs,1991]. In ESMs, ψ_{l1} is a core parameter in resolving profiles of gas exchange [Bonan et al., 2014], and is very helpful in models concerning stomatal conductance that links leaf gas exchange, plant hydraulic constraints, and the soil-plant-atmosphere continuum [Farquhar et al., 1980]. In addition to its role in investigating water flow along the soil-to leaf pathway in SPAC [Egea et al., 2011; De Kauwe et al., 2013].

In the database, when ψ_{l1} is not found in literature, its assumed to be the same as other Mangrove species as ψ_{l1} is usually near zero (from -0.5 to -0.05 MPa) and is not expected to significantly vary among species.

Critical leaf water potential (ψ_{lc})

Under the different climatic stressors, when leaf water shortfalls develop and ψ_l decreases, partial stomatal closure arises and continue to decrease to a threshold value prior to stomatal closure originates [Gimenez 2005]. This threshold is where critical leaf water potential is measured. Threshold values for stomatal closure vary with species, leaf age, previous exposure to radiation, the stress history of the plant, and environmental conditions [Gimenez 2005; O'Toole & Cruz, 1980].

Using ESMs and/or LSMs with decoupled surface (vegetation physiology) and atmospheric (radiative) CO₂ responses, ψ_{lc} show that the CO₂ physiological response has a leading role in evapotranspiration fraction variations [Woodruff et al., 2008; Yan et al.,2017]. The value of ψ_{lc} embodied in SPAC models imposes that plants consider both water-use efficiency and hydraulic safety in adjusting stomatal conductance, it also implies a notion of optimum plant approaches and provide testable model theories rather than empirical representations of plant behavior [Sperry et al., 1998,2002]. Moreover, it constrains stomatal opening to avert leaf water potential from falling below a critical minimum by vegetation in regulating potential terrestrial hydrologic responses, as well as the close relationship between the carbon and water cycles [Huang & Xu, 2015; Flowers 1986].

Mostly, ψ_{lc} was either found directly in the literature or assumed to be equal to the osmotic potential when turgor is zero. However, when none is found, it was rationally assumed to be the same value for other species.

Chapter 5: Results & Discussion

The focus in this last part of work is to evaluate the behavior of different halophytes under different environmental conditions for the inclusion of halophytes hydraulic traits in ESMs' parametrizations. As discussed earlier in the document, atmospheric carbon concentrations beside salinization through sea-water intrusion represent the major stress factors and are expected to further exacerbate under future scenarios [Craft et al.,2009; Farooqui,2010]. Therefore, to understand the future dynamics and structure of these ecosystems, as well as future vegetation–climate interactions [Kumar et al.,2017; Volpe et al.,2011], it is paramount to realistically assess how salinity and carbon affects plant-water relations and productivity in Mangroves, depending on their salt tolerance level.

5.1 Calibration and Validation

Mangroves can be, in general, considered as facultative halophytes where the level of salt-tolerance across different species is widely variable, and the reaction of the different species to salt introduction is related to their capability to regulate the concentration of salt in the xylem–leaf–phloem system. It is essential to ensure the realisticity of model and have a good understanding of its reliability.

Model calibration is taking a place by validating our results with other observed results from literature. For instance, observed data of transpiration and relative transpiration versus salinity from different studies were used to validate the model's results of the highly salt-tolerant species, *Avicenia Marina*, and medium salt-tolerant species, *Rhizophora Stylosa*.

Avicenia Marina was validated by comparing the model results and observations from Ball & Farquhar, 1984 in term of relative transpiration Tr/Tr_{max} . Authors collected Propagules of *Avicennia marina* from trees growing along Cullendulla Creek, Australia. Propagules were developed in sand beds, and subirrigated with 10% and 50% seawater, respectively. The beds were kept in a growth cabinet adjusted to provide the appreciate environment to optimally grow the species for 6 weeks. Selected seedlings from the population were then placed in plastic containers with salinities adjusted at a rate of around 10% seawater (50 mM NaCl/d) to provide the 3 final concentrations of 50, 250, and 500 mm NaCl. Seedlings

were then spread among three chambers adjusted for different humidity regimes. The light period was 12h and the average quantum flux density close to the leaves was $400\mu\text{mol}/\text{m}^2 \cdot \text{s}$. Day/night air temperatures were adjusted to give average leaf temperatures of $25/20^\circ\text{C}$. The plants were grown for 3 months before gas exchange characteristics were studied on leaves which had developed fully under the different salinity and humidity regimes.

Environmental conditions of the running model were adjusted accordingly. Solar radiation set is $800\mu\text{mol}/\text{m}^2 \cdot \text{s}$, relative humidity is 80%, atmospheric CO_2 concentration fixed at 400 ppm and g_p, max was set at $0.00033\mu\text{mol}/\text{MPa} \cdot \text{s}$. Other parameters were used from the DB. Figure 2 illustrates the differences between the observed and the modeled relative transpiration.

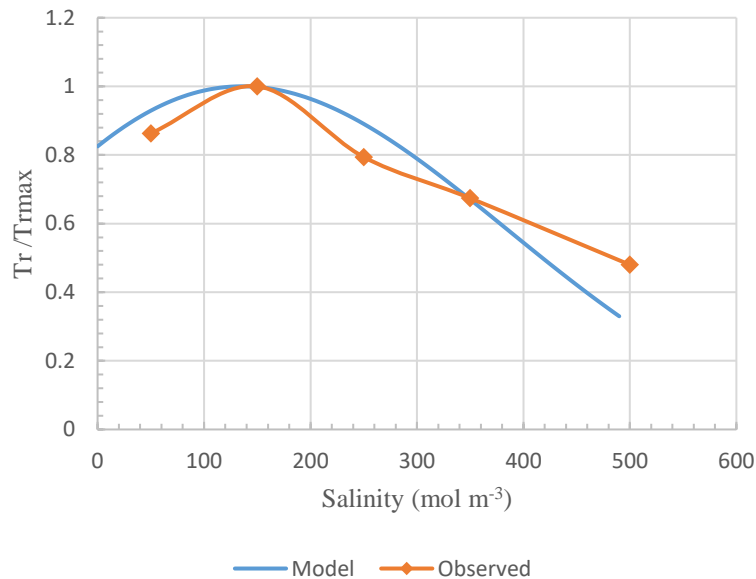


Figure 2: Modeled relative transpiration as a function of salinity compared with observed measurements from Ball & Farquhar, 1984 for *A. marina*.

On the other hand, *Rhizophora stylosa*, the desired curve was obtained from Yan&Guizhu,2007, where authors collected one-year old seedlings of *Rhizophora stylosa* from the Mangrove nature reserve, Dongzhai Gulf, Hainan, China. The seedlings were planted in under natural light in plastic pots and were moistened daily for three months with 6L of brine (0 to 50 salinity). The mature, stable leaves were chosen as research objects and measured, with temperature controlled between $(20 \pm 2)^\circ\text{C}$, light quantum flux between $600\text{--}800\mu\text{mol}/\text{m}^2 \cdot \text{s}$, relative humidity between $60\% \pm 5\%$, and CO_2 density 3.6×10^4 .

For the sake of comparison and validation, the above parameters were calibrated in the model where solar radiation was set to be $700 \mu\text{mol}/\text{m}^2 \cdot \text{s}$, relative humidity to be 60% and atmospheric CO_2 concentration fixed at 400 ppm. Other parameters used from the DB collected. To obtain the most realistic values by the model to observations, $g_{p,\text{max}}$ was tuned to shift up the T_r values from the model and best fit the observed T_r values. Using the mean standard error, minimum distance of modeled curves with different $g_{p,\text{max}}$ were found from the observed. Accordingly, $g_{p,\text{max}}$ was set to $0.00063 \mu\text{mol}/\text{MPa} \cdot \text{s}$. The figure below show the corresponding modeled and observed transpiration of *Rhizophora stylosa*.

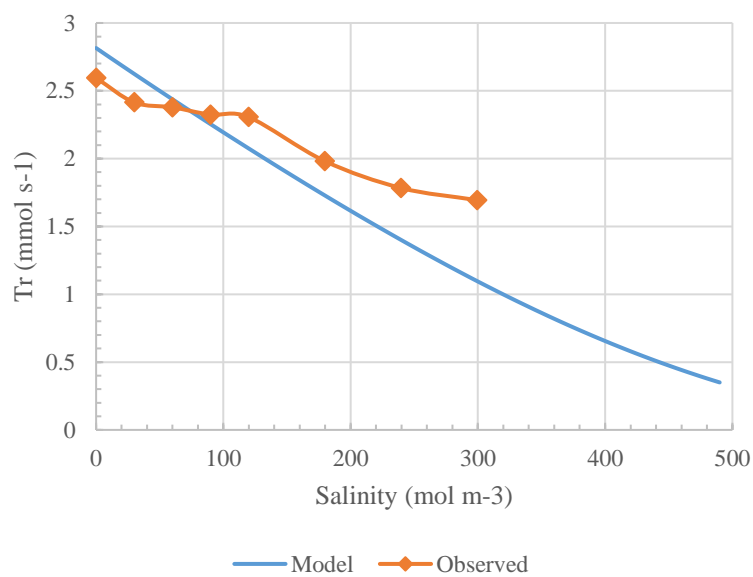


Figure 3: Comparison between modeled and observed transpiration rates (from Yan&Guizhu,2007) for *Rhizophora stylosa*.

Overall, the SPAC results for both species are in good agreement with experimental data. There are slight variation and differences, mainly represent appear due the variability of a maximum plant conductance and maximum xylem-phloem conductance used in the model and the studies. Model results are sensitive to uncertainty in $g_{p,\text{max}}$, and $g_{w,\text{max}}$ although the characteristic and behavior of transpiration along different level of salinities are maintained.

5.2 Transpiration and Assimilation as Function of salinity

Succeeding the satisfactory validation results, the model was parametrized with different salt-tolerance traits to reproduce the hydraulic behavior of the two

Mangrove species, *Avicennia Marina* and *Rhizophora Stylosa*, under the different salinity levels (C).

Fig. 4 shows transpiration and CO₂ assimilation rate as a function of soil water salinity as obtained from SPAC model for high and medium salt-tolerant species. The Tr -C configurations occurring from model computations are different across salt-tolerant and salt-sensitive species (Fig. 4), even though the effect of salinity on xylem conductance is assumed similar [Perri et al.,2019].

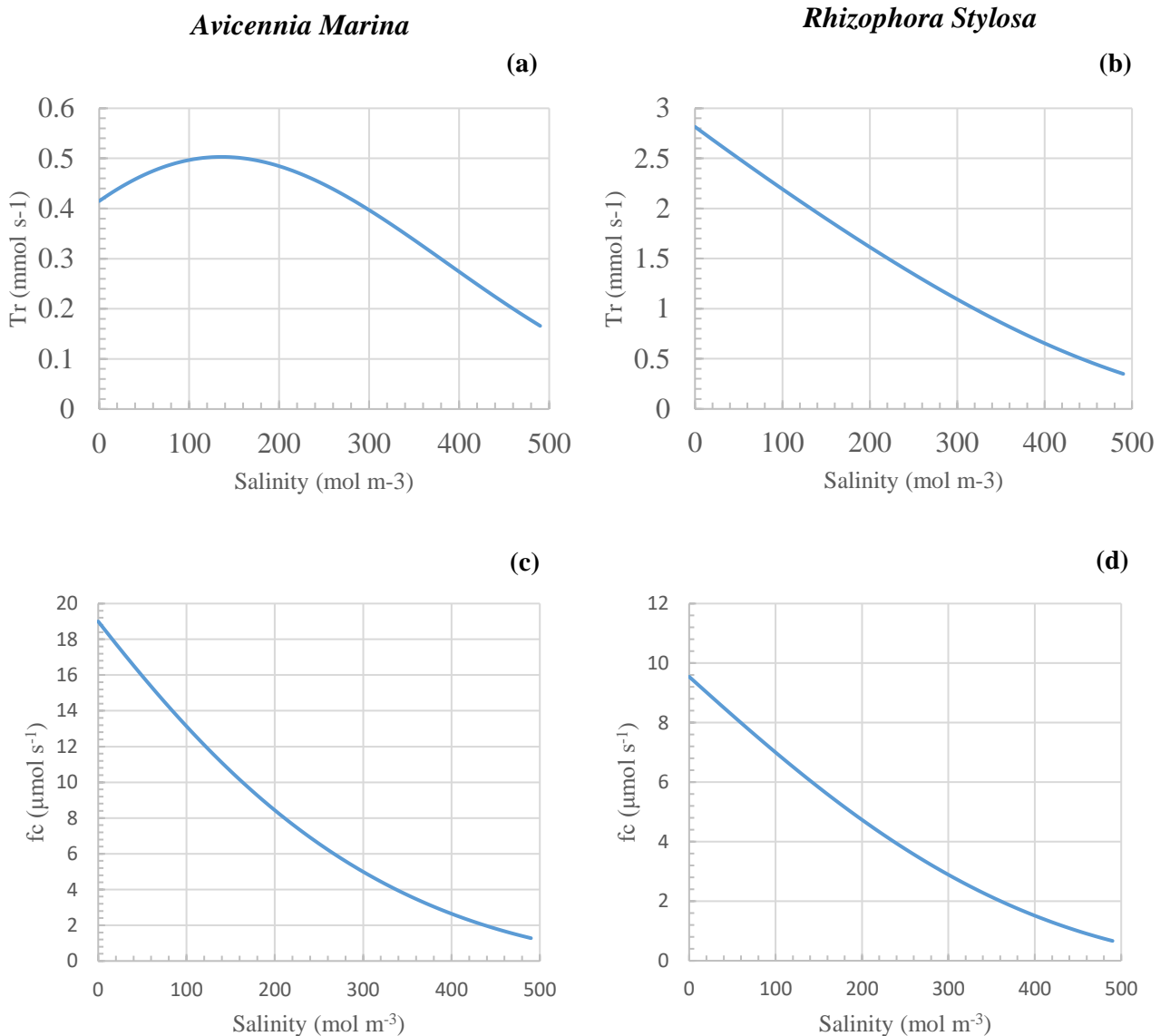


Figure 4: (a,b) Transpiration rate Tr as function of salinity C. (c,d) CO₂ assimilation rate as function of salinity C.

Avicennia Marina possesses a non-monotonic transpiration pattern, with the transpiration rate showing a maximum at an (optimal) intermediate salt concentration, C_{max} . This behavior can be supported by the higher osmoregulation capacity of this species, with the peak transpiration at C_{max} , representing here the trade-off between the enhancement of salt-tolerance and optimal carbon assimilation. On the other hand, less-tolerant species like *Rhizophora Stylosa*, display strictly monotonic decreasing transpiration patterns. This can be physically explained by the relatively low osmoregulation flux of these species, which allows for salt accumulation in the plant's tissue before it can adapt, causing a reduction in the water using efficiency and significant limitation to gas exchanges – from which the fast transpiration decline.

Furthermore, CO_2 assimilation rate is relatively declining with salinization for both species as expected. This behavior may be explained through the association between leaf water potential and elevated salt concentration in the leaf. The increase in salt uptake along with water absorption leads to salt stress and reduced mesophyll conductance which cause a partial or complete deficiency of the carbon assimilation capability. On another note, f_c is approximately the double for *A.mariana* at fresh water and low salinity concentrations when compared to *R.stylosa*, and it's reduction rate get sharper after C_{max} . This is possibly due the larger CO_2 storage capacity and higher salinity resistance in *A.mariana*.

5.3 Transpiration and Assimilation as Function of CO_2 Enrichment

Analyzing the contribution of atmospheric fertilization is another way to determine Mangroves productivity under extreme climatic conditions such as the one we have at arid regions. Fig.5 shows transpiration and carbon assimilation rate at a fixed salinity concentration and changing ca .

Overall results show that with increasing ca , rates of transpiration are lowering, and rates of carbon assimilation are increasing. This indicates that the concurrent increase of the atmospheric CO_2 concentrations (atmospheric carbon enrichment) is predicted to enhance plant productivity through its effects on assimilation and water use efficiency [Wendelberger et al.,2017; Perri et al.,2018]. Simply explained as the increased CO_2 supply to the plant to process photosynthesis and produce organic matter as food, in addition to the closing stomata behavior that

control the water through the plants to avoid water stress through lowering the transpiration loss [Housman et al.,2006; Nowak et al.,2001].

Moreover, comparing the different salt tolerant species, *R.Stylosa* is less affected by carbon enrichment than *A.Mariana*. The conservation of water through transpiration is limited in *R.Stylosa* as the increase in the assimilation rate and carbon concentration in the plant is relatively not huge.

Generally and in agreement with other studies of plant responses to elevated CO₂ (Drake et al., 1996; Koch & Mooney 1996; Nowak et al., 2001), it could be said that carbon enrichment is favorable by halophytes and Mangroves as they could grow and develop better under future carbon fertilization.

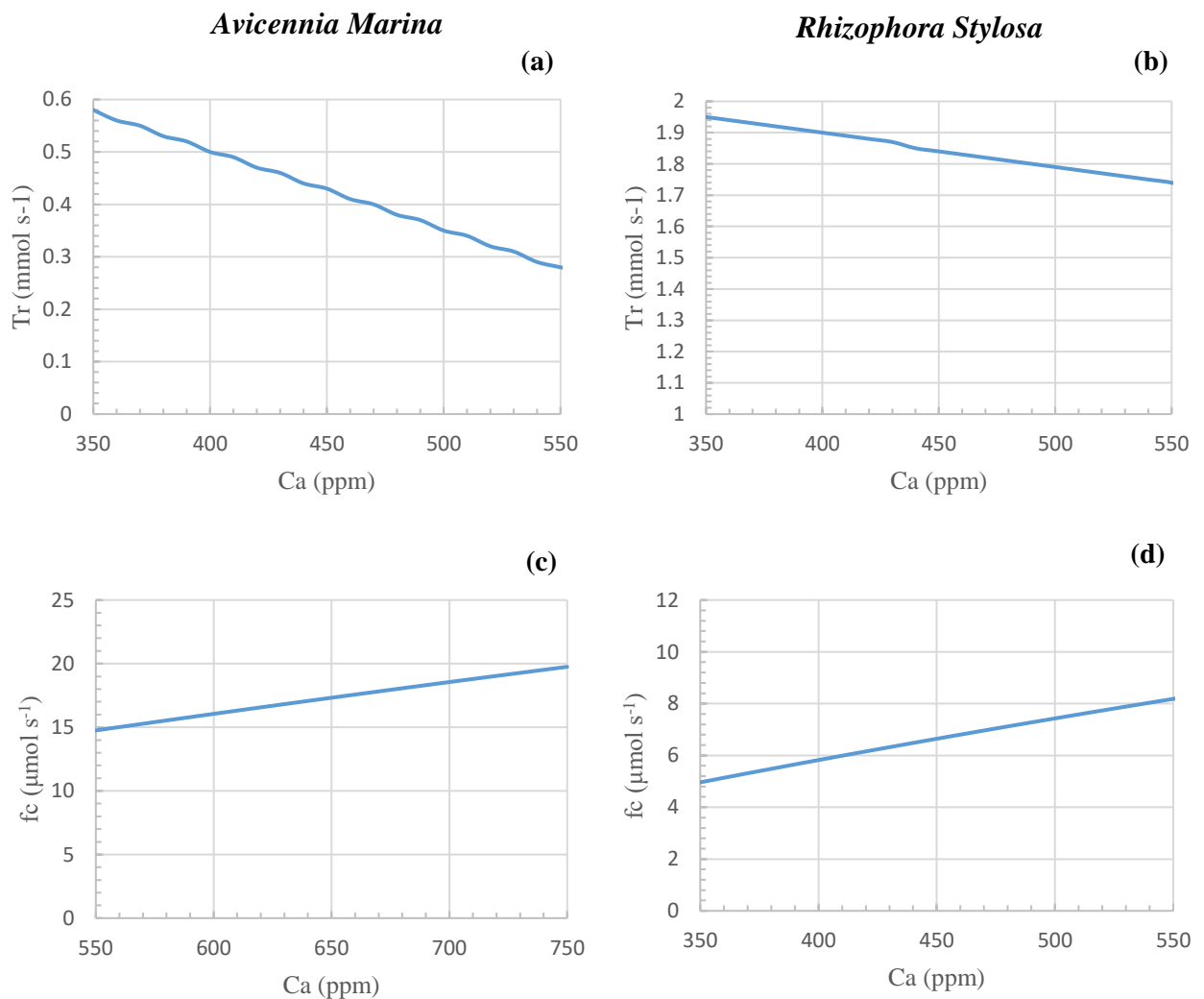


Figure 5: (a,b) Transpiration rate Tr as function of CO₂ enrichment Ca . (c,d) CO₂ assimilation rate as function of CO₂ enrichment Ca

5.4 Tradeoff Between Salinization and CO₂ Enrichment

As stated earlier, projecting future responses of Mangrove forests to different sources of environmental stress and climatic change is essential to understand the interaction between vegetation, particularly halophyte, the soil water budget, and atmosphere.

Using the data collected and the developed SPAC model, tradeoff between salinization and CO₂ enrichment was examined for the different salt tolerant halophytes. Fig.6 shows that the increase of c_a cause in higher assimilation rate and lower transpiration losses for the different salt-tolerant species. This diminish in Tr is effective up to moderate salinity and becomes negligible when approaching very high salinity.

Further, results from fig. 6 suggest that high salt-tolerance halophytes could be preferred by future atmospheric fertilization through a water-use-efficiency enhancement within their optimal range of salinity. Clearly, *Rhizophora Stylosa* is less sensitive to c_a variation than *Avicennia Marina*. This outcome is in agreement with a number of experiments performed in controlled environments [Geissler et al.,2015; Melgar et al.,2008].

The discussed behaviorism is dominant by the strength of osmoregulatory fluxes. Increasing atmospheric CO₂ concentration, enhances the CO₂ biochemical supply to the plant and fosters water uptake and water use efficiency. Namely, to reach higher productivity requires to store “more molecules of CO₂ than the water ones transpired”. Conversely, lowering c_a strengthen the osmotic potential in the phloem and weaken the water flux, causing, eventually, a monotonically decreasing transpiration pattern.

Moreover, in the case of *Avivennia Mariana*, the salinity at which optimum growth and maximum Tr occurs, C_{max} , moves to higher C values with increasing c_a . From an ecological perspective, this finding suggests that less sensitive C₃ halophytes could be favored by elevated CO₂ conditions when competing with more sensitive C₃ species [McKee et al., 2012].

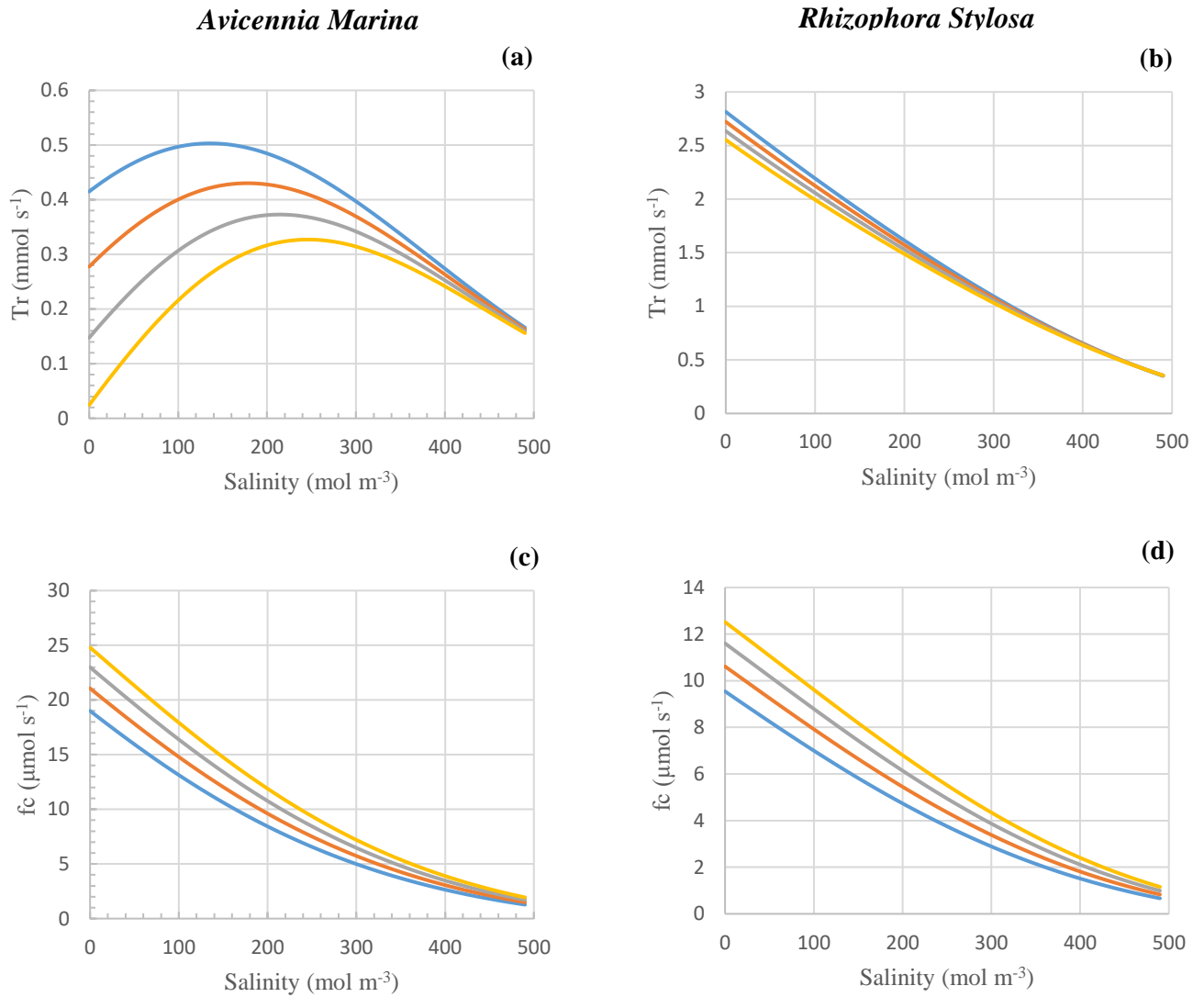


Figure 6 (a,b) Tr as a function of salinity C for different levels of atmospheric CO_2 concentration. (c,d) CO_2 assimilation rate as function of salinity C for different levels of atmospheric CO_2 concentration.

5.5 Model Capabilities

It was availed from section 5.1 that the model is working decently with the validated data of halophyte species. Therefore, this section will exhibit the flexibility of model in simulating the behavior of other unvalidated sub-tolerant species. In addition to that, it will highlight the adequacy of model in producing the halophytes behavior under the four closer assumptions.

5.5 .1Unvalidated Species

For the aim of giving qualitative idea of whats happening across different sub-tolerant species, three more species (Ceriops Tagal, Bruguiera Gymnorrhiza, and Sonneratia Apetala which are high tolerant, midium tolerant, and low tolerant species, respectively) where modeled. Those species where not validated in any way, thus,

correct scale of their behavior cannot be insured. However, it can be manifested if the model is producing the correct pattern of species transpiration and assimilation rates.

Fig. 7 show transpiration rates and CO₂ assimilation rates for the three unvalidated species under saltanization. The high tolerant species, C.Tagal, is following a non-monotonic transpiration pattern whereas the less salt tolerant species have monotonic behavior where they transpire best at fresh water. fc is declining with salinity in all species as salt stress force the plants to photosynthesis less to save energy and regulate water and carbon fluxes.

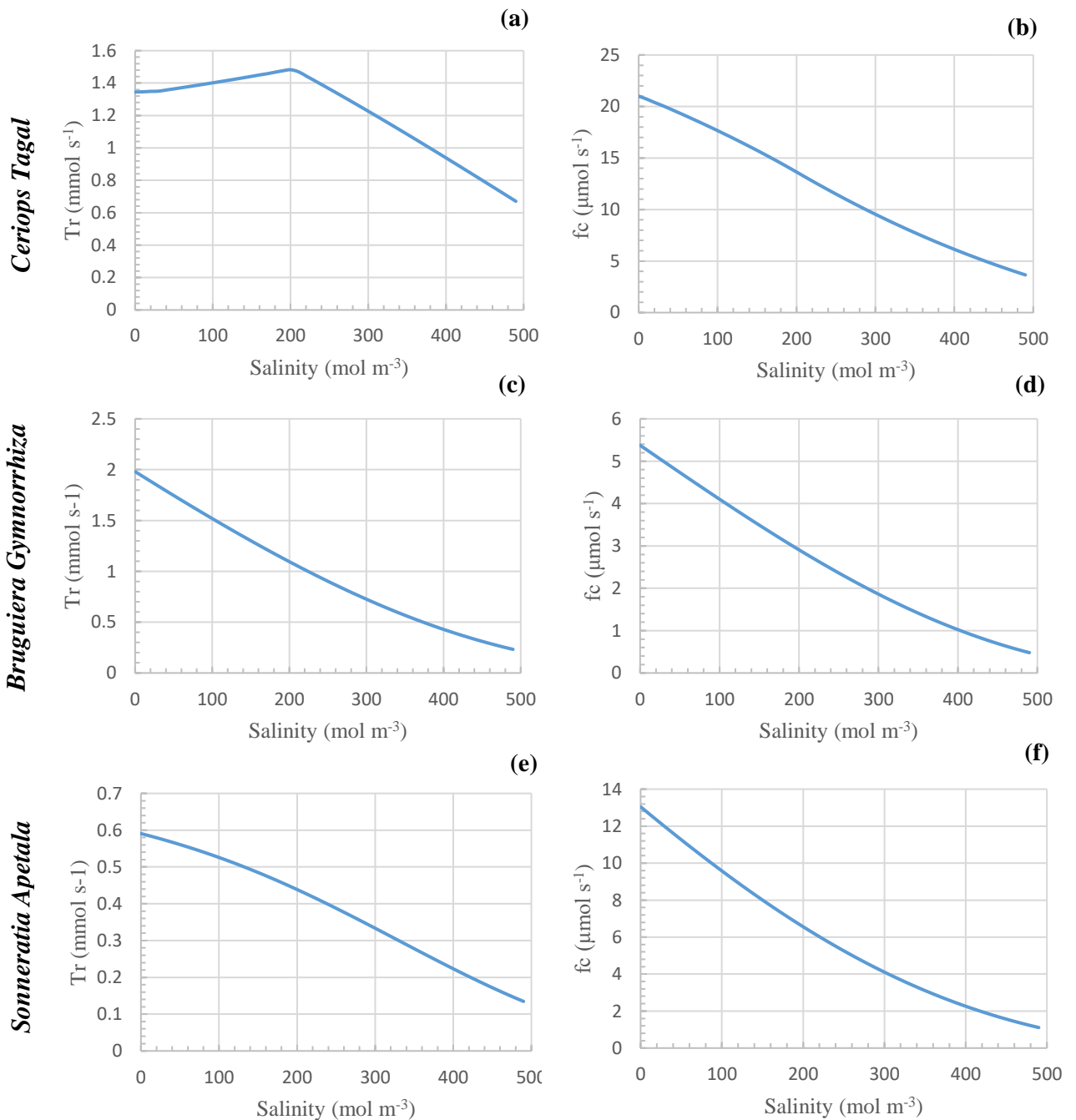


Figure 7: Tr and fc as function of salinity for (a,b) *Ceriops Tagal*, (c,d) *Bruguiera Gymnorhiza*, and (e,f) *Sonneratia Apetala*.

From the extensive literature search done for parametrization of species, It could be said that the shape of behavior and pattern of the corresponding different sub-tolerant species from the model is realistic, even if the scale of traits produced is not completely accurate and confirmed. Model is therefore decent and reliable, and can be used for similar applications where data are available.

5.5 .2 Different Closures

It is important to note that all the above results were conducted under the second hypothesis which maximize CO₂ uptake to for a stable quantity of available initial soil water in the root per leaf area unit. However, the model is capable of producing the behavior of halophytes under all the four maximization assumption closures: water absorption, CO₂ assimilation, sucrose transport, and profit.

Plant responses to soil salinity (change in water uptake, CO₂ uptake, and/or sucrose production) are well-known and have been investigated for more than half a century [Yeo et al.,1985; Barr, 2005; Yarami & Sepaskhah, 2015]. However, improvements in linking xylem–leaf–phloem transport mechanisms in response to salt stress is in early state (Munns and Termaat, 1986; Bui, 2013; Perri et al., 2018a) and it is not yet clear which maximization scheme best represent the behavior of halophytes where soil salinization is widespread. Therefore, this model is built to help address the future role of salt-tolerant plants in managed and natural ecosystems and recognizing the interactions between vegetation and salinity.

Fig. 8 represents Tr and fc for *A.mariana* through the four optimality rules. It can be clearly seen from fig. 8 that transpiration rate shifts with the different schemes. Tr is significantly higher when plants adjust leaf water potential to maximize water uptake, as expected. It could be noted that the other three maximization assumptions are the ones better reproducing the Tr–C relation up to the optimum transpiration value for *A.mariana*, but not necessarily for all species. fc does not substantially change in *A.maiana* for the various maximization schemes.

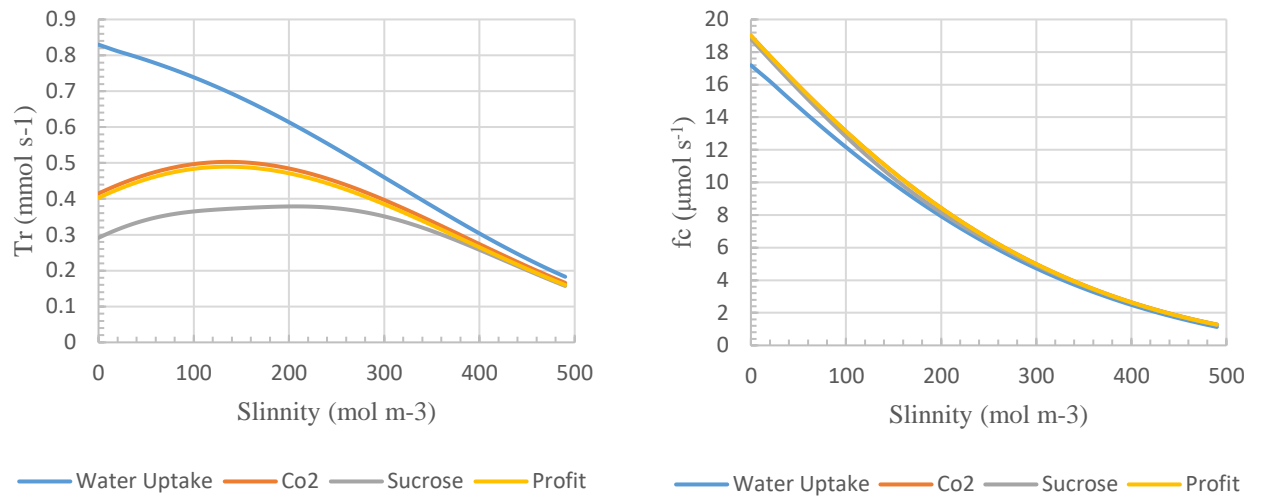


Figure 8: Tr and fc as function of salinity C obtained from the four optimality rules for *A.mariana*.

Chapter 6: Challenges & Limitations

As all studies and projects, there were various challenges I faced while conducting this study but overcame.

To begin with, the implementation of SPAC model in Python programming language was effortful since I had no background or knowledge about this specific program and used Python language for the first time in this thesis, however, I dedicated my time to learn and initiate several experimental codes until I successfully developed the SPAC model code in a short period of time.

Further, after having the model, the big challenge was finding data of Mangroves' traits in literature to build the database. Traits of Mangrove are very difficult to attain due to the shortage in research in this field. In the few available studies, experiments provide limited pool of the data that are based on single point experiments, due to the very specific and difficult environmental conditions needed for the experiments, which limits the certainty of the collected data point and introduce bias to the observation processes. In addition, the attainable traits data were found in different forms in the different studies, where researchers and scientist were collecting and expressing their data in very different contexts and experimental conditions. Thus, a big effort was spent on homogenizing the data to be interpreted and integrated for the database.

Moreover, some traits were completely lacking in literature, and to overcome this challenge, I read plethora of studies in very detailed way be able to interpret data from in an accurate way. Along with the extrapolated data from literature, the model was used in few cases to integrate parameter's inclusion of different Mangrove hydraulic traits.

More limitations of this study were consisting in the model development stage. The SPAC model was developed to account for salinity impacts on different salt-tolerant plants productivity in the osmotic-stress phase where plants osmoregulation (main factor determining the different response to short-term salinity exposure exhibited by halophytes) could be processed. At longer time scales, plants apply morphological modification and start to balance salt mass and soil moisture,

result in changing the dynamics of the water storage flux which significantly affect the plant response to salinity.

These limitations could be used to open routes for future enhancements. To better develop the model, salinity fluctuations could be encapsulated and accountancy for changes in the ionic long-term phase of salinity exposure along with the osmotic phase should be considered. Also, the effects of transient dynamics on plant-water interactions can be evaluated through solving the model for plants at non steady state.

Chapter 7: Conclusion

The remarkable ability of Mangrove ecosystems to store and bury carbon is subjected to reduction due future salinization and other limiting factors. Thus, the importance of including salinity in ESMs is nothing less than the need to precisely understand the whole biosphere-atmosphere interaction.

The wide research done for halophyte species, parametrization of different salt tolerant species, in addition to expanding Perri et al.,2019's hydraulic model were to be compelled measures for this purpose.

The model developed was proven to run in a modest way that fit nicely the observed and available data from literature. It can be used for variety of applications, one of which projecting plant's productivity through transpiration and CO₂ assimilation under different environmental factors, as was done in this thesis. However, the model's capabilities are not restricted to that.

It can be concluded from this work, that the exposure of halophytes to carbon enrichment and short-term salinity could significantly affect their behavior in different ways where it can radically impact the plant's core dynamics, represented in the four closures, to grow and produce.

Change in halophyte's patterns vary and range differently according to their tolerant levels. The general reaction of salt-tolerant species to salinization and carbon enrichment in terms of transpiration and CO₂ assimilation is the answer of optimal turgor pressure maintenance in such environments, where osmotic and water use adjustments contribute to reducing the stress. As a result of this, the carbon-intense ecosystems like Mangrove forests could undergo significant ecological shifts, impacting their carbon storage capacity.

The maximum transpiration for highly tolerant plants occurs at the optimum salinity C_{max} , whose value grows with the storage osmotic potential. They can adjust osmotic pressure over a species-specific limited range that is likely to move toward high salinities. This would justify why obligate halophytes (especially, less sensitive species) do not complete their life cycle in freshwater. In despite the low tolerant species, they have their maximum Tr at less saline water and then decline as they adjust to better save water with salinity rise.

Fertilization is also another measure which strong influence on Mangroves hydraulics and dynamics. Halophytes generally favor enriched environments of CO₂ where it increases its CO₂ sequestering rates, typically assimilation rates, and in photosynthesis process. Stomatal closer take a place under carbon enrichment, reducing transpiration for all sub-tolerant species. However, high tolerant species have sharper Tr reduction as its able to faster adjust for the changing environmental conditions.

The outcomes of this study are in good accord with the available literature in the field. Future extensions of this line of study could be useful to further enhance the understanding of atmospheric-biosphere interaction and better represent the relation in ESMs for future assessment of plants contribution in global warming and climate change.

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