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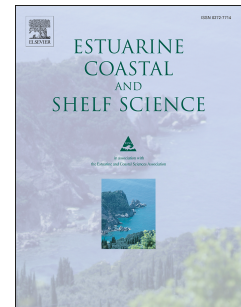
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Partial canopy loss of mangrove trees: mitigating water scarcity by physical adaptation and feedback on porewater salinity

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Abstract

Trees species in the mangrove genus *Avicennia* can shed canopy parts when exposed to adverse environmental conditions, such as increases in porewater salinity. The individual-based model BETTINA enables the quantification of the tree's water use depending on its allometric characteristics. It thus provides a tool to model the equilibrium between plant size and density in a mangrove stand and porewater salinity. When the model is coupled with a simple water balance approach, the water use of trees corresponds to water uptake from the soil and, in combination with water fluxes, an increase of salinity in the root zone. Annual variations of the sea level, the tidal regime, groundwater inflow, and precipitation have an impact on the equilibrium of the combined system. Higher salinities lead to lower potential gradients and reduced water uptake of the plant. With a combined modelling approach (single tree model BETTINA with a simple water balance approach), we examined the dampening effects of consecutive partial canopy loss for the survival of the tree. We found that (i) the tree is able to decrease water demand and uptake and thus may reduce the tree's effect on soil water salinity, (ii) the reduced branch length leads to a reduced xylem flow resistance, and (iii) the reduction in height has a small positive effect on the water potential gradient between leaves and soil. Individual-based models can enhance our understanding of the regulating impact of the partial canopy loss on water balance in the combined plant-soil system.

Introduction

Besides numerous episodes of local and regional extinctions, mangrove forests have survived a number of catastrophic climate events in the past and it is very likely that they will do so in the future. Their adaptability is due to several reasons, for example, they are able to cope with sea level rise, increases in CO₂ concentrations and global temperature as long as other factors like land use or frost events, which allow habitat shifts including expansions landwards and polewards (e.g., Duke et al. 2007, Alongi 2015).

The fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC), however, predicted regional differences in sea level rise (Church et al. 2013), sea water salinity, and precipitation (Collins et al. 2013). The interference of these three factors leads to complex effects including, among others, that arid coastal areas will become more arid. Considering these climatic predictions and the known and likely responses of mangroves, Alongi (2015) predicted, e.g., for NW Australia, Pakistan, Arabian Peninsula, and both Mexico coasts that "Mangrove forests along arid coasts will decline as salinities increase, freshwater becomes most scarce, and critical temperature thresholds are reached more frequently".

First signals that this prediction could become reality have been reported in terms of stand diebacks for Australia (Duke et al. 2017, Lovelock et al. 2017) and Belize (Servino et al. 2018), or in terms of physiological responses in wood characteristics in Mexico (Armitage et al. 2014) to name a few. Related to this, partial or total canopy loss in mangrove tree populations of *Avicennia* spp. are most impressive (Duke et al., 2017; Lovelock et al., 2017; Asbridge et al., 2018) and mostly interpreted as a response to greater soil porewater salinity associated with drought, evaporation or reduced inundation (Fig. 1). To our knowledge, there has been no systematic examination of the mechanisms of this response, yet it could be an essential adaptation to variation in environmental conditions in mangrove ecosystems. Decreased osmotic potential in mangrove soils (i.e., higher salinity) is similar to lower soil water potential due to drought in terrestrial forests. Therefore, studies of partial canopy loss in terrestrial forests provide insights which we use to develop a model exploring the mechanisms and effects of partial mangrove canopy loss on the soil-plant-atmosphere system.



Figure 1: Healthy (A) and impaired (B) *Avicennia germinans* trees with partial canopy loss in the Laguna de Tampamachoco (Veracruz, Mexico) as a response to increased salinity. Photos: Bartolo Mateos (2015).

The phenomenon of tree mortality due to decreasing water availability has been described and investigated for terrestrial tree species. The mechanisms responsible for tree mortality can be hydraulic failure due to xylem water conductivity loss, and transpiration, which ultimately leads to desiccation of plant tissues (Mcdowell et al., 2008; Nguyen et al., 2017), and carbon starvation (Lovelock et al., 2016; Savi et al., 2019). However, in many tree species, droughts induce temporary damage often observed as partial canopy loss, with the capability to recover. For example, Busotti et al. (1995) analysed canopy loss in Tuscany due to droughts between 1987 and 1991, and Bréda and Badeau (2008) investigated non-lethal declines in foliage cover following extreme climatic events, as well as the recovery of the trees.

Studies of the physiological mechanisms by which droughts influence trees have concluded that changes in tree hydraulics are vital processes. For example, Tyree et al. (1993) related leaf shedding of canopies with xylem cavitation and the consequent loss of conductivity. Strong hydraulic links between roots and shoots have also been observed. For example, Larson et al. (1993) investigated the connection between the partial root and shoot mortality in *Thuja occidentalis* trees under extreme water deficits, providing evidence of high levels of connectivity, which supported the pipe theory for trees (Shinozaki et al., 1964). They found that dying roots and shoot sections were hydraulically connected, with mortality of root systems resulting in the nearly synchronous death of connected parts of the shoot. Rood et al. (2000) proposed the term 'branch sacrifice' to describe branch senescence and dieback of branches of poplar trees due to drought. They showed that branch sacrifice reduced transpiration demand on roots and soil water, enabling the remaining shoot to maintain a favourable water balance. They also observed that the phenomenon of branch sacrifice occurred mainly in the highest branches of the trees they examined. Finally, recovery from partial canopy loss in temperate and Mediterranean tree species was associated with new xylem production, rather than embolism repair (Bréda et al., 2006), suggesting that canopy recovery from extreme drought is a long-term process.

In this study, we used the BETTINA model to investigate the effects of partial canopy loss on mangrove trees and their soils. The BETTINA model (Peters et al., 2014, 2018) provides a single tree model that relates soil porewater salinity and species-specific hydraulic properties to the growth allocation and allometric relations of a tree. For the model setup, we assumed that an insufficient water supply due to high salinity or low soil water content would lead to a partial death of roots, stems, and leaves, applied equally to all tree compartments. With this model, we investigated the effects of partial canopy loss on the whole tree, soil water balance, and the hydraulic properties of the tree.

Methods

We employed the single-tree BETTINA model (Peters et al., 2014, 2018). The main characteristics of the model are that allometric relationships and physiological parameters control resource uptake. Trees use water and light in a constant proportion. Light interception of the canopy is proportional to the crown area (water uptake is described in detail below). Maintenance costs are also proportional to tree volume. Resources used for growth are the difference between uptake and supply for maintenance. In the model, tree growth is based on allometric relationships that maintain the proportional relationship between water and light. Below, we describe key components of the model concerned with allometry, water potential, and resistance to water flow.

Allometry

Four allometric variables characterise trees (all in meters): crown radius r_{crown} , stem radius r_{stem} , stem height h_{stem} , and root radius r_{root} (Fig. 2). The volume of leaves and fine roots are assumed to be 0.004 m^3 per m^2 of the projected crown area and root radius, respectively. Komiyama et al. (2008) described leaf biomass as the smallest portion of above-ground biomass and, based on the literature, specified a maximum value of 3 kg m^{-2} . Fine root biomass estimations vary over a wide range. In mixed-species mangrove stands in the Dominican Republic, Sherman et al. (2003) found dry

weights of fine-root biomass in the magnitude of 1 kg m^{-2} and fine-root biomass (2 mm or less) to leaf biomass ratios of 1 (0.5-1.5). In contrast to our single-tree approach in the model, this value refers to a whole stand and includes gaps in the canopy layer.

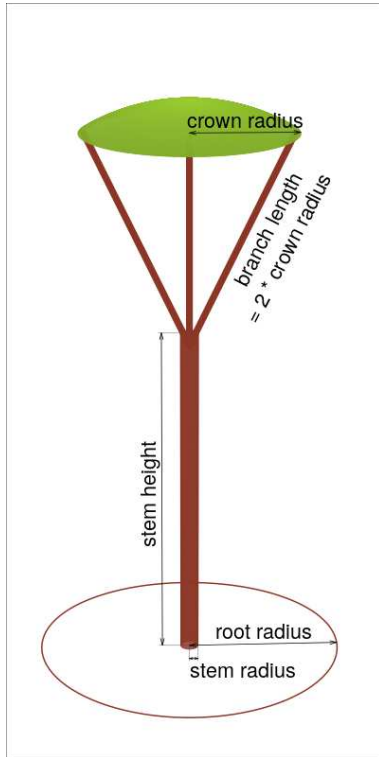


Figure 2. Allometric relationships of the model tree. Branch length equals the crown diameter, i.e., tree height is the sum of stem height and twice the crown radius.

Using the assumptions of the pipe theory (Shinozaki et al., 1964), the model describes the sum of the cross-sections of the branches as equal to the cross-section of the main stem. The crown of the tree is shaped as a spherical sector with a cone angle of 60° . The crown height (i.e., the branch length) is twice the crown radius. Analogously, we also apply this principle for the cable roots of *Avicennia* (horizontal roots that extend from the stem base which support the fine roots and pneumatophores), but as the root layer is flat and the cable roots connect to the equally distributed fine roots, the average length of the cable roots is $0.5^{0.5}$ times the root radius. With these assumptions, the tree volume was estimated as the sum of five cylinders: leaf layer, branches, stem, cable roots, and fine roots.

Water potential

The physical laws behind the water uptake of a mangrove tree are described by Peters et al. (2014, 2018). Darcy's law describes the water flow:

$$Q = \frac{-k_f \cdot A_{flow} \cdot \Delta\Psi}{l_{flow}} = \frac{\Delta\Psi}{R} \quad (1)$$

With flow (water uptake) Q [$\text{m}^3 \text{s}^{-1}$], hydraulic conductivity k_f [$\text{m}^2 \text{s}^{-1} \text{Pa}^{-1}$], flow cross-section A_{flow} [m^2], potential gradient $\Delta\Psi$ [Pa], and flow path length l_{flow} [m]. Analogously to electricity, the measures and material constants of the conducting medium can be represented by the resistance R (for further explanations see below). The potential gradient for a tree is

$$\Delta\Psi = \Psi_{leaf} - \Psi_{matric} - \Psi_{osmo} - \Psi_{height} \quad (2)$$

The water potential at the upper end of the flow path is the leaf water potential Ψ_{leaf} . The value is highly negative and must be lower than the sum of the other potentials to ensure that flow is directed upwards (see below for further explanations). Empirical studies estimated species-specific minimal values. E.g., Epron and Dreyer (1993) specified values down to -3.0 MPa for several oak species and Sturm et al. (1998) estimated -1.5 MPa for Scots pine (*Pinus sylvestris*). (In the model we used only S.I. units. For a better understanding, values here are indicated in MPa.) Such values have been used to model the water balance of a site (BROOK90, e.g., Federer, 1995) or tree (BETTINA, Peters et al., 2014). Tomlinson (1994) stated an upper salinity limit where mangroves can grow at 90 ppt which corresponds to a water potential of -7.65 MPa. Further, the leaf water potential must be lower than this value to guarantee a water flow

towards the leaves (Tyree and Ewers, 1991). Hence, we will use a constant minimum value of -7.86 MPa for our model species *Avicennia germinans*.

The matric potential Ψ_{matric} describes the soil matric suction and depends on soil properties and soil moisture. We assume saturated conditions, i.e.

$$\Psi_{matric} = 0 \quad (3)$$

The osmotic potential Ψ_{osmo} depends on the concentration of ions in the soil water, which is directly proportional to salinity (S) in ppt:

$$\Psi_{osmo} = -85,000 Pa \cdot S \quad (4)$$

The height water potential Ψ_{height} is the water potential of the water column due to gravity. With h_{leaf} as the height of the water column up to the leaf and our definitions of the allometry of the model we get:

$$\Psi_{height} = -\rho_{water} \cdot g \cdot h_{leaf} \approx -1000 \frac{kg}{m^3} \cdot 9.81 \frac{m}{s^2} \cdot (h_{stem} + 2 \cdot r_{crown}) \quad (5)$$

With water density ρ_{water} and gravitational acceleration g .

In a similar way as voltage in electricity, the potential gradient is the driving force behind water flow. To provide an impression of the magnitudes of the water potentials, we give a few typical values. For crops in European temperate climates, the permanent wilting point (i.e. the minimum soil water potential below which the plant cannot access soil water) is assumed at a matric potential of -1.5 MPa. In eq. 4, the osmotic potential is proportional to the salinity. For instance, sea water with 35 ppt has the osmotic potential of -3.0 MPa, which implies many mangroves grow under what may be considered as conditions indicative of very low water availability.

Equation 5 describes the water potential gradients to tree height. For example, a tree of a size of 20 m has to overcome a height potential of -0.2 MPa. Simard et al. (2019) report the highest values for tree heights in mangrove forests of up to 60 meters in areas characterised by low soil salinity values, higher nutrient levels, and protection from damage from intense storms. These tree heights would correspond to height potentials of approximately -0.6 MPa. Thus, the height potential in mangroves has a higher magnitude than the osmotic potential.

Hydraulic Resistance

The term

$$R = \frac{l_{flow}}{k_f \cdot A_{flow}} \quad (6)$$

describes resistance to flow [s Pa m³]. As described in Peters et al. (2014), we assume two resistors in series: the root surface resistance R_1 and the xylem resistance to the axial flow R_2 :

$$R_1 = \frac{1}{L_P \cdot A_{root.surface}} = \frac{1}{L_P \cdot \pi \cdot r_{root}^2 \cdot RAI_{fine.root}} \quad (7)$$

$$R_2 = \frac{l_{flow}}{k_f \cdot A_{x.section}} = \frac{l_{flow}}{k_f \cdot \pi \cdot r_{stem}^2} \quad (8)$$

L_P [m s⁻¹ Pa⁻¹] is the root surface permeability. To our knowledge, there are very few measurements of this parameter for mangroves. Field (1984) estimated 3.3×10^{-15} m s⁻¹ Pa⁻¹ for *Avicennia marina* at sea water salinity. We used this value for the simulations. In contrast to k_f , this parameter includes the flow length of this part, i.e., the thickness of the root surface layer. If the fine roots are equally distributed within the root radius, the root surface area $A_{root.surface}$ can be described by the root radius and a constant “Root Area Index“ ($RAI_{fine.root}$) analogous to the Leaf Area Index (LAI) [m² m⁻²].

In eq. (8), the flow path length l_{flow} was determined by allometric relations (see Peters et al., 2014, 2018). The hydraulic conductivity k_f has been estimated in several field studies for a variety of species (e.g., Melcher et al., 2001 for *Rhizophora mangle*; Lovelock et al., 2006 for *Avicennia germinans* and *Laguncularia racemosa*). The values in the literature cover quite a wide range, and there is evidence that the parameter also depends on salinity (Sobrado, 2007). For this study, we used 0.104×10^{-9} m² s⁻¹ Pa⁻¹, as estimated by Sobrado (2001) for *Avicennia germinans* at 39 ppt.

According to the applied pipe theory, the area of the flow cross-section $A_{x,section}$ is a function of the stem radius, which we assume as constant along the flow path.

205 Water uptake and feedback on porewater salinity

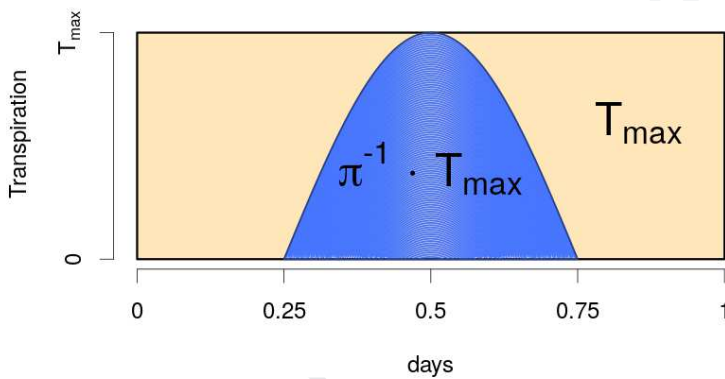
Finally, with eq. 1 and the two resistances (eq. 7 and 8) in a series connection, the water uptake of a single tree can be described explicitly as:

$$210 \quad Q = \frac{-\Delta\Psi}{R_1 + R_2} \quad (9)$$

As described above, the driving force of that water uptake is the leaf water potential. The minimum water potential is only reached in the daytime and sap flow/transpiration follows an approximately sinusoidal course over the day. For *Avicennia marina*, this has been measured by Steppe et al. (2018). Previous model versions of BETTINA did not consider the sinusoidal pattern and overestimated daily transpiration values. Since we want to estimate a realistic feedback on porewater, we included an improved quantification of daily water fluxes. Hence, to consider this daily cycle, we modified eq. (9) to eq. (9b)

$$215 \quad Q = \frac{T_{max}}{\pi} = \frac{-\Delta\Psi_{min}}{\pi \cdot (R_1 + R_2)} \quad (9b)$$

220 with $\Delta\Psi_{min}$ being the lowest potential difference (highest absolute value but, negative) at midday and T_{max} the corresponding transpiration. The derivation is illustrated in Fig. 3. Assuming leaf water potential is continuously at its minimum value, daily transpiration would correspond to the area of the yellow filled rectangle (T_{max}). Assuming a sinusoidal daily cycle with a maximum transpiration rate at midday, daily transpiration corresponds to the blue area (Fig. 3). The ratio of the blue and the yellow area is π^{-1} .



230 Figure 3: The transpiration during one day corresponds to the blue area (sine-wave shape) with a maximum transpiration rate (in litre per day) at midday coincident with minimum leaf water potential. The ratio of the blue area and the rectangular area, which represents a constant maximum transpiration rate over 24 hours is π^{-1} .

When the tree is growing, the allometric measures develop in a way that the relationship $R_1=R_2$ is maintained (Peters et al., 2014). While growing, the tree decreases both resistances by continually increasing the flow cross-sections and increasing water uptake. Salt exclusion in the root zone increases the soil porewater salinity in the coupled model (Passioura et al., 1992). Consequently, hydraulic processes in the sediment must counteract this process to establish an equilibrium state. For this study, we design a straightforward approach to simulate this effect. A single tree starts growing in the center of a squared patch of soil with 5 m edge length and according to a water reservoir of $1 \text{ m}^3 \text{ m}^{-2}$. The initial salinity is 40 ppt, and superficial (tidal) water has a salinity of 35 ppt. The salinity of the soil porewater is regulated when a similar amount of superficial water compensates for plant freshwater uptake. The dilution of porewater with superficial water (with a salinity of 35 ppt) is simulated by exchanging over three days 8% of the porewater with superficial water to mimic the effect of tidal flushing and a subsequent decline in salinity — the prevailing salinity at any given time results from these two processes (see Fig. 4A).

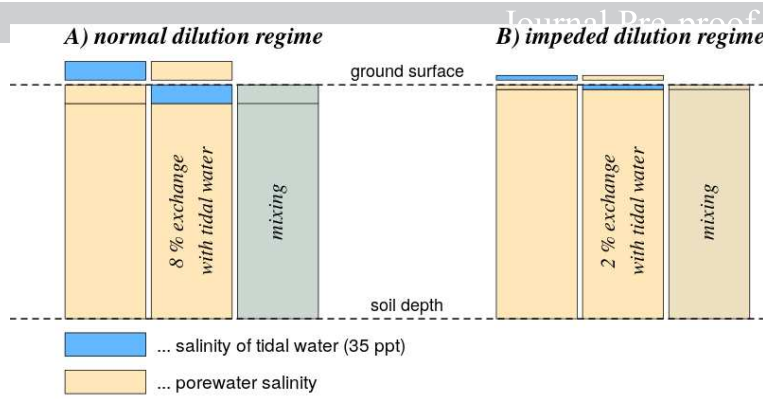


Figure 4: Scheme of the implementation of dilution of saltwater in the soil column, A) normal dilution regime: 8% of the water was exchanged with tidal water (35 ppt); B) impeded dilution regime: only 2% exchange.

Partial canopy loss

Partial canopy loss will occur only when the water supply is below the amount required for biomass maintenance since the total living tree volume cannot exceed the volume maintained by the resources taken up by the tree. In this case, the unitless factor K_{reduc} to determine the reduction of the tree volume is:

$$K_{reduc} = \frac{Res_{maint} - Q}{Res_{maint}} \quad (10)$$

with Res_{maint} resources needed for maintenance and Q water uptake as the available below-ground resource [all in $m^3 s^{-1}$]. K_{reduc} describes the share of the biomass that cannot be maintained with the available resources. The K_{reduc} factor applies to different tree components (Fig. 5). As a consequence of the cylindrical shape of the components, the surface areas will also be reduced by the same proportion.

$$r_{crown, reduc} = r_{crown} \cdot \sqrt{1 - K_{reduc}} \quad (11a)$$

$$r_{root, reduc} = r_{root} \cdot \sqrt{1 - K_{reduc}} \quad (11b)$$

Since stem height and radius cannot decrease, a sector of the stem cross-section will die (Fig. 5).

$$A_{X.section} = \pi \cdot r_{stem}^2 \cdot (1 - K_{reduc}) \quad (11c)$$

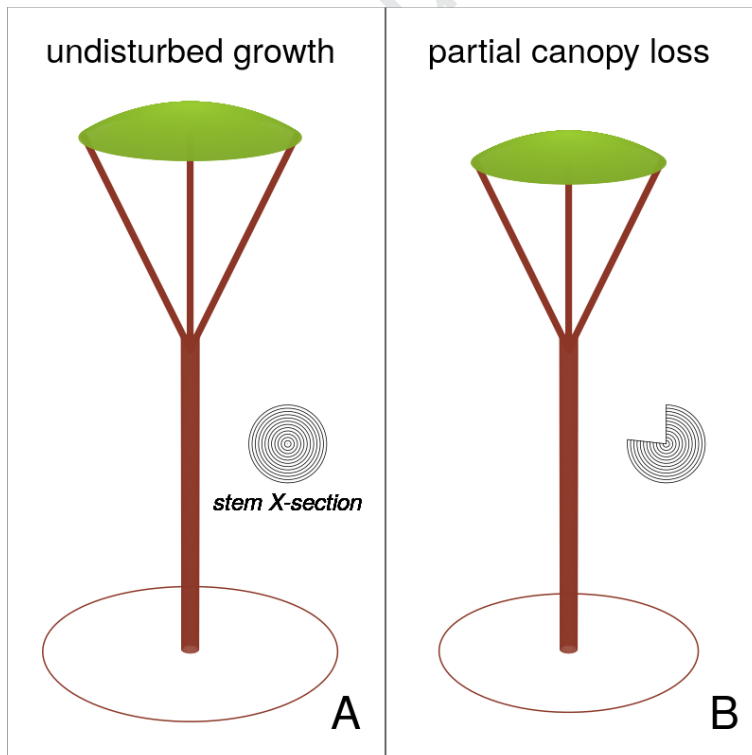


Figure 5. A, Shape of the tree before partial canopy loss; B, Shape of the tree with partial canopy loss, decreased root, crown radii (eq. 11a, b), and reduced stem cross-section (eq. 11c).

Scenario of drought stress

To simulate a scenario of drought stress leading to partial canopy loss (referred to below as “disturbance”), we reduced the dilution of porewater with superficial water by limiting superficial (tidal) water supply from 8% to 2% during four years (see Fig 4B), as can occur during a relatively dry period (e.g., Krauss et al., 2007; Eslami-Andargoli et al., 2009; Santini et al., 2015). Consequential increasing salinity leads via a lower potential gradient to a decreased water uptake and provokes a reduction of tree volume (eq. 11 a,b,c). After the disturbance, tree growth will be re-established until the end of the simulation time after 100 years.

Results

Figure 6 shows the transpiration and soil porewater salinity for the model run. A constant dilution of 8% of the pore water in a time step of three days (see above) in combination with increasing transpiration rates (due to increasing tree heights) over the first 80 years of development led to continuously rising salinity values. With this initial exchange rate between surface and tidal water, the salinity reached 57 ppt.

The disturbance of the dilution regime (reduction from 8% to 2% in the years 81-84, analogous to a decrease in tidal flushing) impeded the exchange with the surface water and salinity increased suddenly to 71 ppt. This led to the water uptake falling below the living tissue maintenance demand and to a partial loss of biomass in the canopy and other plant components. Transpiration was limited to the value which occurred when the tree was smaller and growing under much more mesic conditions (Fig. 6, green dashed line, after 25 years at 44 ppt). Table 1 shows the dimensions of the model tree before the disturbance and with the impeded dilution regime.

Table 1: Tree characteristics before (80 years) and after the impeded dilution regime (84 years).

Simulation Year	Crown Radius [m]	Stem Radius [m]	Dead part of Cross section	Root Radius [m]	Stem Height [m]	Total Height [m]	Transpiration [L / day]	Salinity [ppt]
80	2.59	0.20	0.00	2.59	5.49	10.68	42.4	57
84	2.08	0.20	0.36	2.08	5.49	9.65	17.3	71

After another four years, the original dilution regime of 8% per three days was re-established. As a consequence, porewater salinity was relaxed, transpiration increased again, and growth was re-established. After that, transpiration and salinity slowly rose.

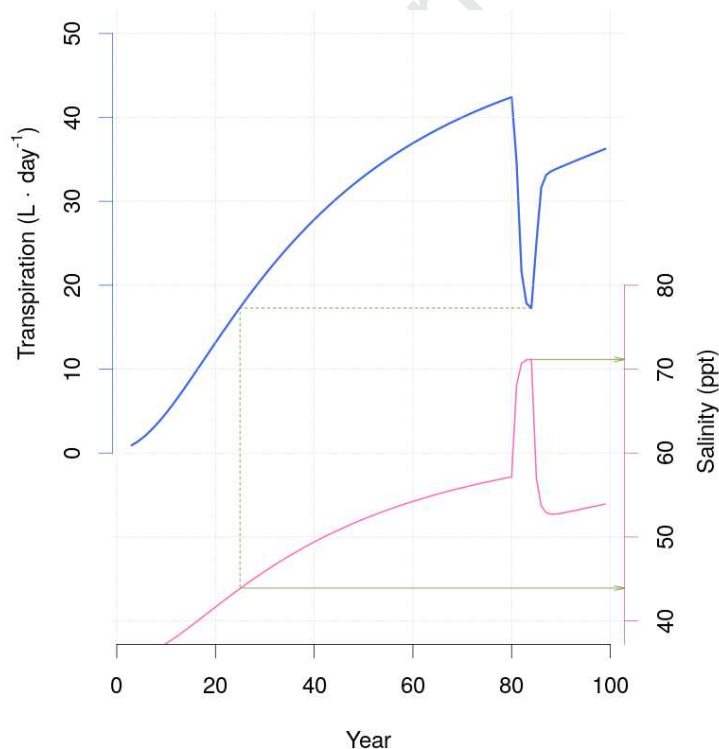


Figure 6. Blue, left y-axis: tree transpiration with increasing tree size vs. time until disturbance and partial canopy loss after 80 years; Pink, right y-axis, salinity increases with water uptake, disturbance of porewater dilution after 80 years leads to increased salinity, and release of disturbance after four years decreases salinity.

This behaviour illustrates the impact of the tree water use on soil porewater salinity and vice versa. To better understand the link between plant water use and porewater salinity, we compared the states just before partial canopy loss occurs and while the dilution with seawater is impeded. The main effects of partial canopy loss are: (i) a reduced water uptake which diminishes porewater salinisation; (ii) shorter branches which downsize the flow path length, facilitating water uptake, and (iii) a lower tree height which decreases the height potential (eq. 5).

Reduced salinisation

The model allows investigation of the links between transpiration and salinisation of soils at different stages of tree development. The transpiration drop with the disturbance of the dilution regime (81 years) is a result of the canopy loss and biomass reduction due to lacking water for maintenance and a decreased water potential gradient by increased salinity (57 to 71 ppt). Water flow after partial canopy loss appears just enough to maintain the surviving biomass and in equilibrium with the dilution regime.

Fig. 7 illustrates the effect of biomass loss. Before the disturbance (Fig. 7A), the model shows higher total water uptake than that required for maintenance, and the difference (a surplus) can be allocated to plant growth. In contrast, water uptake becomes insufficient to maintain the plant when porewater salinity increases with the reduced dilution of porewater salinity (Fig. 7B). Finally, partial loss of biomass decreases both water required for maintenance and water uptake by reduced flow cross-sections (Fig. 7C) until an equilibrium is reached, allowing for tree survival. The decreased water uptake by reduced flow cross-sections limits the salinisation effect (drop from 42.7 to 17.5 L day⁻¹ from A to C) to counteract the limited dilution with surface water.

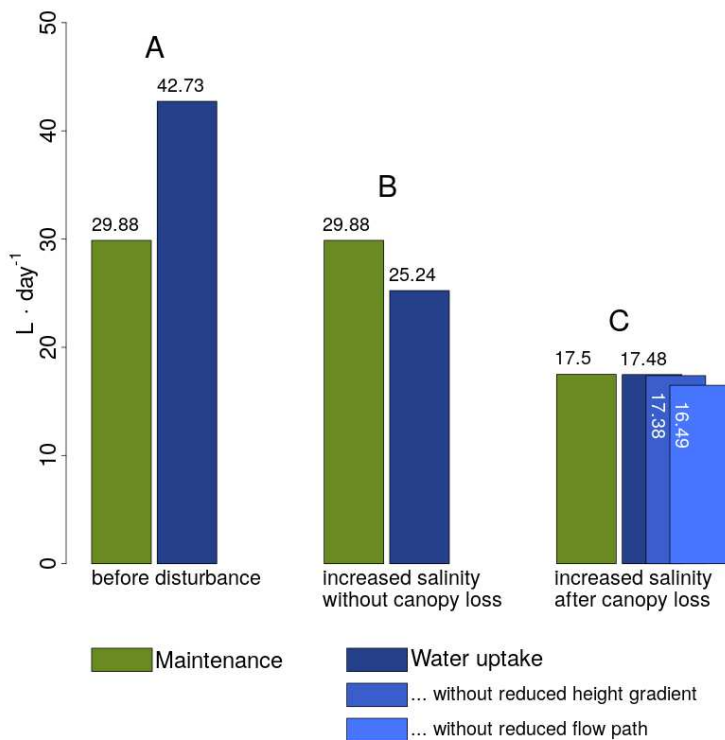


Figure 7. Tree maintenance costs (green) and water uptake (blue) for the model run. A, 80 years after the initial model run and before disturbance by increasing salinity; B, with increased salinity but without canopy loss; C, with increased salinity after canopy loss.

Physiological effects of biomass loss

The living tree volume decreased from 1.7 to 1.0 m³. As described above, this biomass loss resulted in reduced maintenance requirements (Fig. 7B and C, green columns). Further, with partial canopy loss, which reduced branch length and root radius, the flow path decreased from 12.5 to 11.1 m, and tree height from 10.7 to 9.7 m. With eq. 5 and 6, we assessed how the reduction in tree height and flow path length influenced water uptake and allocation (Fig. 7C). In this case, water uptake was underestimated by 0.5% and 3.2%, respectively. Both effects are associated with a decreased crown radius (i.e., a reduced branch length).

Discussion

The mechanistic description of water uptake linked to allometric measures in the BETTINA model allows for a quantification of several benefits of partial canopy loss to survive temporary increases in porewater salinity, which are associated with reduced water availability.

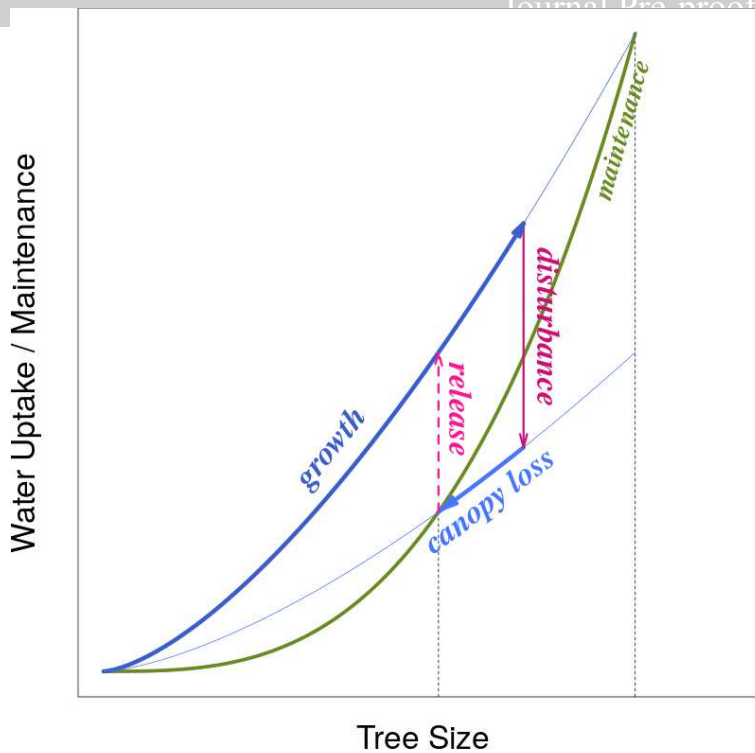
One of the advantages of this modelling approach is the use of hydraulic parameters that have been known and studied for a long time (e.g., root surface permeability, Field, 1984). Parametrising the model with these values provides benefits of greater transparency and results that are less biased by model calibration efforts. On the other hand, different parameters may be taken from different studies, authors, and experimental contexts. Model errors without calibration may be large, but there is a significant potential to generalise findings yielded with models using empirically derived parameters.

Comparing the transpiration in the model with published studies shows similarity to typical daily transpiration and sap flow values. For example, in the model, a tree after 80 years (before the disturbance) with a dbh of 39.9 cm has a daily transpiration of 42.7 litres. Lovelock et al. (2016) estimated for mangroves based on sap flow data an average transpiration of 1.1 litres per day per cm of dbh, which correspond to 44 litres per day for our model tree. Additionally, for *A. germinans* growing at moderately high salinities (30-50 ppt in the surface, 61-74ppt at 20 cm depth) Muller et al. (2009) measured sap flow of around 30 litres per day for medium sized trees (dbh about 24 cm) and for larger trees (dbh about 45 cm) 30-60 litres per day in the dry season and 50-80 in the wet season.

Using the BETTINA model, we detected two types of effects of partial canopy loss: (i) enhanced individual adaptation to high porewater salinity, and (ii) benefits through the feedback of reduced water uptake and transpiration on porewater salinity.

Partial canopy loss reduced both maintenance costs and water uptake, but reduced maintenance costs to a greater extent. This effect is summarised in Fig. 8, which is an idealised scheme to demonstrate this principle. The blue lines mark the trajectories of the relationship between plant size (neglecting the change of allometric relations under different environmental conditions) and water uptake (neglecting the feedback of plant water uptake on salinity). The trajectory is steeper as salinity decreases, and plant water uptake will be higher. If water uptake is greater than the maintenance needs, the plant will grow until water uptake equals plant maintenance (Fig. 8, dashed line). A temporary reduction in soil porewater dilution will lead to increased salinity, and the plant will switch to a lower growth trajectory. On this lower trajectory, the biomass exceeds maximum tree size; partial canopy loss occurs at this point in the curve, and the biomass is set back to a lower value. The first three arrowheads in Figure 8 conform to the three conditions displayed in Fig. 7. Thus, partial canopy loss may be the primary mechanism by which plants adapt to high soil porewater salinity and, potentially, to other environmental conditions that reduce water availability. The model behaviour is consistent with canopy losses observed during drought and low sea-level events in Australia (Duke et al., 2017; Lovelock et al., 2017)

In addition to shrinking maintenance costs, there was an additional but small effect of partial canopy loss, a result of the reduced xylem flow path length and tree height gradient. Following eq. 8, the flow length in the modelled tree is proportional to xylem resistance. Assuming $R_1 = R_2$, a 10% reduction of the flow path length would lead to a water uptake increase of > 5% (eq. 9). The effect of the reduced height gradient is much lower: with eq. 5, there is only a 0.01 MPa with a 1-m height reduction, which is equivalent to a salinity reduction of 0.12 ppt (eq. 4). To validate these secondary benefits of loss of branches to potentially improving the overall tree water balance is challenging because many processes do not act independently. However, future work could assess whether flow path length reduction has a more significant effect on tree water balance than the decrease in the height potential, which can be tested in field studies by assessing whether crowns die from the outside towards the stem, rather than from the top down.



Tree Size

Figure 8: Idealised trajectories of the tree size – water uptake relation for different salinities (blue) and of maintenance of living tissues (green). The dashed vertical lines define maximum tree size for these two salinities when water uptake equalises maintenance. Partial canopy loss occurs when tree size exceeds the maximum size for a particularly salinity, which shifts to a lower trajectory with partial canopy loss. After the release of the disturbance, the water uptake may switch back to the old trajectory (dashed arrow).

Partial loss of tree canopy also had a benefit through feedback from water uptake on the porewater salinity, where reduced transpiration decreases salinisation. The release of salinisation (or increased water availability) with reduced canopy transpiration has been observed in field studies, where lower porewater salinity has been reported in canopy gaps in mangroves (Amir, 2012) as can be inferred from Passioura et al. (1992). However, in our model, the hydrodynamic processes have been reproduced in a simplified way, but the results suggest that reduced salinisation in mangrove forests should be explored further. Taking into account subsurface water flow and dilution processes or groundwater inflow in mangroves can improve the understanding of this process and its ecological effects.

In our model, the hydraulic parameters of mangrove trees L_p and k_f are assumed to be constant and species-specific. However, some of the literature points towards a salinity-dependent variation in these parameters. For example, the root hydraulic conductivity of *A. marina* decreased by half when salinity increased (Field, 1984) and xylem conductivity was reduced at high compared to low salinity for mangroves (Melcher et al., 2001; Lovelock et al., 2006; Hao et al., 2009) and in plants from drought-prone environments (Abrams, 1990; Bucci et al., 2005). Further evidence is that the hydraulic traits and the short stature of scrub or dwarf mangrove plants that grow under osmotic stress reduced the risk of hydraulic failure (e.g., xylem cavitation), but at the cost of decreased water transport efficiency (Melcher et al., 2001, Lovelock et al., 2005).

In summary, trees growing at sites with higher salinity develop decreased xylem conductivity and root permeability, which implies both a physiologically limited water supply under highly saline conditions but also a higher resistance to damage by drought. Developing knowledge about these links could add further to our understanding of the adaptation strategies of the mangrove trees to changing environments and help to improve the predictability of our models.

Further, recent studies have suggested mangroves may have a range of alternative strategies to deal with water shortage. Reef and Lovelock (2015) review leaf temperature regulation and the uptake of respired CO_2 as water- saving strategies. The absorption of atmospheric water through canopy tissues has been documented as an important pathway to acquire additional water for photosynthesis and growth (Nguyen et al. 2017). Steppe et al. (2018) and Schreel et al. (2019) investigated rainwater uptake by mangroves and observed a strong link with tree stem growth. Strategies that reduce water loss, as well as those that access additional water sources, may interact with partial canopy loss. For example, decreased foliage may reduce the capacity for foliar uptake of rainwater. The availability of atmospheric water sources to plant canopies is important for hydraulic function (Nguyen et al. 2017) but is not linked to porewater salinity and thus is not included in our model. However, including access to atmospheric water sources in future models increases the potential for explaining the diversity of different biological phenomena with hydraulic mechanisms in the future.

425 The interrelation between hydraulic flow processes in the subsurface, competition for water among trees, porewater
 salinity and water uptake was explored by Bathmann et al. (2020) using a coupled approach (MANGA) with the
 BETTINA model and the hydrodynamic numerical groundwater model OpenGeoSys (OGS, www.opengeosys.org,
 Kolditz et al., 2012). The results indicate that neighbourhood relations within the forest stand have an impact on water
 430 availability for individual trees, and suggest that partial canopy loss may also be affected by the mangrove stand
 structure. A future implementation of the partial dieback of biomass in the MANGA model using different
 parameterisations for different species (including diverse capabilities of partial biomass loss) could facilitate
 investigation of the impacts of stand structure and composition on canopy dieback.

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- Partial canopy loss is accompanied by an equal loss of living tissue in other parts
- Reduction of water uptake reduces porewater salinisation
- Reduction of living biomass reduces water need for tissue maintenance
- Lower canopy promotes water availability by reducing flow path length and height

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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