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The MANgrove-GroundwAter feedback model (MANGA) Describing belowground competition based on first principles

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Abstract

It is commonly accepted that the processes determining how plant-groundwater interactions influence vegetation patterns depend on subsurface properties, including groundwater availability, but not much is known about the underlying processes. We present a hybrid process-based simulation system to study the feedback between vegetation and subsurface hydrodynamics using mangroves as an example. Our approach relies on first principles rather than on empirical competition concepts. We develop a modular tool which dynamically couples an agent-based vegetation model to a continuum groundwater model. The vegetation model describes individual trees and their interactions within their environment and communities. We show the dependence of the salinity distribution on aquifer properties Within stylized case studies. Moreover, the model predicts varying tree allometries depending on variations of subsurface properties. Finally, we analyse the nature of belowground competition for fresh water as a direct consequence of the plant-soil feedback that is inherent to the modelling approach. The results show that the interaction of vegetation and subsurface hydrodynamics is crucial for vegetation zonation patterning in form of a pronounced distribution of tree allometry. We also discuss the benefits and disadvantages of our presented plant-soil feedback modelling approach, as well as its implications for future research.

Keywords: mangroves, groundwater, vegetation, subsurface, coupling, mechanistic, plant-soil feedback, belowground competition

1. Introduction

² 1.1. Motivation

³ Understanding the feedback mechanisms between vegetation structure and soil properties is a peren-

⁴ nial favorite in ecology since it is key to understand plant systems' functioning. Many studies have

⁵ shown that the spatial heterogeneity of resources in the soil, such as nutrients or water, controls

6 competitive or facilitative interactions between plants. Additionally, it influences both community

⁷ structure and zonation patterns which Robertson et al. (1993) expressed in gradual changes of

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⁸ species composition or allometry. It is reasonable to assume that plant-soil interactions are signifi-

⁹ cant in various environmental settings. However, they are particularly pronounced under conditions

 $_{10}$ $\,$ where a shortage of belowground resources controls observable vegetation patterns as in semiarid

habitats, peat bogs or coastal zones (see (Fowler, 1986; Thiery et al., 1995; Berger et al., 2008a,b;

¹² Rietkerk and van de Koppel, 2008; Getzin et al., 2016) and references within for example).

Empirical studies on plant-soil interactions, zonation and spatial self-organisation in real plant systems are still limited, despite the abundant theoretical literature on this topic. There is at least one exception to this: in mangrove forests, examples of pattern formations have been documented over many decades and it has been shown that regular patterns in this ecosystem are a frequent phenomenon rather than a peculiarity (see, (Lugo, 1980; Santos et al., 1997; Dahdouh-Guebas et al.,

¹⁸ 2004; Piou et al., 2006; Cohen et al., 2018; Ellison, 2000) and examples presented in the two reviews of Ellison (2000) and Kathimaga and Bingham (2001))

¹⁹ of Ellison (2000) and Kathiresan and Bingham (2001)).

The reason behind this exception in mangrove forests is a combination of factors: (i) Mangroves 20 occur in (sub)tropical intertidal zones often exposed to pronounced gradients in salinity due to the 21 inundation regime. (ii) Mangrove trees are physiologically adapted to inundation and can occur in 22 a wide range of the salinities (5 % to 90 %, (Ball, 1996)) mediated by changes in their hydraulic 23 architecture minimizing the risk of embolism under water stress conditions (Lovelock et al., 2006), 24 and the extension of roots into more favorable soil-water resources (Greaver and Sternberg, 2006) 25 to name a few. The strongest zonation pattern, however, either in species distribution or in tree 26 allometry and architecture observable in monospecific stands, emerges on steeper gradients (cf. 27 Figure 1*i*) or on the extreme ends of salinity or flooding gradients (Ball, 1998) suggesting that abiotic 28 factors are likely to be the most important drivers. Underlying factors and mechanism of zonation 29 suggested are geomorphology (Semeniuk, 1983; Thom, 1967), inundation classes (Watson, 1928), 30 physiological responses to gradients, propagule sorting (Rabinowitz, 1978), seed predation (Smith, 31 1987), and succession processes after disturbances such as hurricanes (Piou et al., 2006; Imai et al., 32 2006) all of which which often superimpose such that their particular impact is hard to be separated 33 from each other. 34 Since the site conditions (geomorphology, hydrological boundary conditions, and inundation fre-35

quency and amplitude) have a strong impact on the spatial distribution of porewater salinity distribution (Figure 1*i*), Smith (1992) suggested, these salinity gradients are the principal link between subsurface hydrology and mangrove zonation patterns on the single plant and plant community

³⁹ scale.

It is known that the plants' water use reduces with increasing salt stress (Yan and Guizhu, 2007; 40 Patel et al., 2010). Concurrently, the transpiration of the plants affects porewater salinities (Figure 41 1 ii). Consequently, the plant-soil feedback between porewater salinity and mangrove water uptake 42 represents an important interface between abiotic site conditions and plant growth patterns. The 43 emergence of species-specific or allometric zonation patterns can only be reliably modeled, when 44 the coupled ecosystem and these interactions are described with a mechanistically coupled hydro-45 dynamic groundwater-mangrove stand model. Using such a model, vegetation zonation patterns 46 and their disturbances should even be attributable to subsurface heterogeneity (Figure 1). 47 Within this work, we introduce the MANGA model that follows a concept based on first principles. 48

We verify the applicability of the model on a number of stylized setups showing the feasibility and benefits to use the mechanistical approach which inherently supports belowground competition for water without the necessity of any additional phenomenological description of competition effects as all existing models do. We also discuss the suitability of our approach to investigate the plant-porewater salinity feedbacks in mangrove forests. Due to the chosen mechanistic mod-



Figure 1: i) Typical zonation in a mangrove system: the hypothesized effect of the flooding gradient is modified by subsurface heterogeneity. ii) Plant-soil feedback model. By (fresh-)water uptake, mangroves locally increase porewater salinity and affect the water uptake ability for other individuals in the system. Belowground competition for water will be invoked by this coupling process.

elling approach and the fact that salinity stress has similar physiological effects on plant growth
 as drought stress, we are convinced that our model cannot only provide a versatile tool to support
 mangrove restoration and recovery projects in future, but stimulate further studies focusing on
 plant-groundwater feedbacks in other vegetation systems.

58 1.2. Theoretical Background

⁵⁹ Plant-soil feedbacks in mangroves have been identified as important factors for ecosystem stability
 ⁶⁰ against environmental drivers like sea level rise (Kumara et al., 2010; Huxham et al., 2010). Re ⁶¹ cently, various studies aimed to advance insights about the underlying mechanisms governing those
 ⁶² feedbacks (Lovelock et al., 2015; McKee et al., 2007).

More specifically, a better understanding of the role of mangrove water uptake in the porewa-63 ter salinity distribution and the resulting feedback on mangrove forest zonation has been gained. 64 Hereby, considerable effort has been focused on the dependence of forest species composition and 65 tree allometry distribution on groundwater salinity. Various authors measure an influence of pore-66 water salinity gradients on species distribution (Joshi et al., 2003; Piou et al., 2006). Teh et al. 67 (2015) considered the influence of species-specific water uptake rates on resulting porewater salinity 68 and the possibilities of regime shifts from one species dominating the forest composition to another 69 species taking this role. Peters et al. (2014) were able to show salinity dependence of tree allometry 70 by introducing a mechanistic model for tree water uptake and tree growth behavior. Those results 71 are supported by empirical findings (Naidoo, 2006; Mitra et al., 2011). Other studies focus on 72 the implications of mangrove ecosystem characteristics on surface hydrology (Mazda et al., 2005). 73 Moreover, transport and dispersion of chemical and biological material and its consequences for 74 biomass and energy in the food web have been studied using a coupled model (Mazda and Wolan-75 ski, 2009). However, Mazda and Wolanski (2009) do not explicitly model individual tree growth, 76 which is necessary to study the implications of subsurface and surface hydrology on individual 77 mangrove growth. 78

To our knowledge a full mechanistic coupling approach between agent-based mangrove stand models 79 and porewater salinity dynamics is still missing in literature at this time, although some studies 80 have already introduced a feedback of individual plant water uptake and growth to groundwater 81

dynamics (Jiang et al., 2012; Sternberg et al., 2007; Teh et al., 2015). 82

Here, we apply agent-based modelling approaches and incorporate first principles to describe the 83 model dynamics. Use of first principles in agent-based modelling increases model flexibility, facil-84 itates predictions under new ecological conditions and allows insights to be gained regarding the 85 interplay of driving forces in an ecological system (Grimm and Berger, 2016). The aim of our new 86 model is to increase the understanding of the mechanistic interplay and the emerging feedback dy-87 namics of porewater salinity and mangrove vegetation zonation patterning. One possible outcome 88 of this approach is the emergence of tree-tree interactions such as competition for resources from 89 first principles rather than imposing those interactions implicitly. In this study, we subdivide the 90 feedback in two components. In the first component, the hydrological salinity dynamics in the 91 porewater is described and vegetation dynamics are grouped in the second component. 92

In hydrology, subsurface water in permanently saturated pore space is called groundwater, i.e. there 93 are only solid and liquid phases but without the presence of air. Within this study we assume 94 saturated conditions up to the soil surface. Consequently, the term groundwater is used syn-95 onymously for subsurface water. Finite element methods are widely applied in groundwater flow 96 process modelling after their first introduction into this research field in the 1980s (Narasimhan and 97 Witherspoon, 1982). Numerous sophisticated and well tested groundwater modelling software pack-98 ages are available, including MODFLOW (Harbaugh, 2005), or MODFLOW-based systems^{1,2}, FE-99 FLOW (Diersch, 2013), OpenGeoSys (OGS, www.opengeosys.org, Kolditz et al. (2012)), and Hy-100 droGeoSphere (Brunner and Simmons, 2012). We use OGS—an intensively tested and broadly ap-101 plied numerical simulation tool for coupled thermo-hydro-mechanical-chemical processes in porous 102 and fractured media—to model the abiotic hydrological dynamics of porewater salinity. In the past, 103 this tool has been successfully applied in studies dealing with water resource management (Kalbacher 104 et al., 2012) and for coupling with various additional simulation tools (Kalbacher et al., 2010; He 105 et al., 2015; Jing et al., 2018). Additionally, OGS has been used to investigate saltwater dynamics 106 in coastal aquifers (Walther et al., 2012, 2014). 107

Most mangrove models do not quantify single plant water uptake, although their variety is exten-108 sive. To our knowledge, only a few attempts exist to connect groundwater and vegetation models. 109 The MANHAM model (Sternberg et al., 2007; Jiang et al., 2012) is one of those attempts and 110 distinguishes between mangrove and (freshwater) hammock vegetation. It takes into account the 111 water balance at a vegetation patch by estimating precipitation, evaporation and transpiration. 112 The individual tree dynamics within the MANHAM model incorporate the approaches of the Kiwi 113 model (Berger and Hildenbrandt, 2000). Teh et al. (2015) combined the vegetation approach of 114 the MANHAM model and the SUTRA hydrodynamic groundwater flow model in their MANTRA 115 model. MANTRA allowed for a more realistic description of the subsurface processes and predic-116 tion of salinity distributions in a vegetation patch. Both models account for freshwater intrusion in 117 the vadose zone and the resulting change in porewater salinity distribution. Additionally, mixing 118 of vadose zone porewater and seawater by means of tidal dynamics is studied. These models also 119 consider plant transpiration dependence on porewater salinity. 120

¹https://www.waterloohydrogeologic.com/visual-modflow-flex/; last access: 18.09.2019 ²https://www.aquaveo.com/software/gms-groundwater-modeling-system-introduction; last access: 18.09.2019

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¹²² Competition for resources between neighboring trees in mangrove forests are typically treated via the Field Of Neighbourhood concept (FON), as introduced in Berger and Hildenbrandt (2000). ¹²⁴ Depending on its size, the plant is characterized by a rotationally symmetric field describing the ¹²⁵ strength of resource demand. Overlapping fields restrict the resource availability of competing ¹²⁶ plants.

Among the models available in literature, only the single tree model BETTINA (Peters et al., 127 2014) accounts for dependence of individual tree allometry on groundwater salinity. Moreover, in 128 order to mechanistically describe the water fluxes within plants, Peters et al. (2014) introduce the 129 concept of plant water potential for quantifying tree water uptake. The osmotic potential of the 130 porewater controls the water uptake and thus the water extraction from the subsurface. BETTINA 131 is an agent-based mangrove model providing an intrinsic interface to a hydrodynamic groundwater 132 model. Further, the BETTINA model mechanistically describes the allometric plasticity depend-133 ing on the porewater salinity distribution. Peters et al. (2018) employed the model to show the 134 impact of the allometric plasticity on the self-thinning characteristics at varying porewater salinity 135 distributions. These features of BETTINA appear to be essential for i providing a plant feedback 136 on the subsurface water balance and ii) describing the tree allometry and modeling intra-specific 137 zonation patterns. 138

139 2. The MANGA Model

The process-based MANGA model³ consists of two components that simulate *i*) the abiotic environment using well-known and benchmarked processes from hydro-geological modelling (OpenGeoSys, **www.opengeosys.org**) and *ii*) the mangrove stand dynamics using an agent-based tree model (BET-TINA, Peters et al. (2014)). In the following section, we first introduce our coupling strategy and the two submodels. Then, the specific model coupling scheme is explained.

145 2.1. Model coupling and model documentation

The implementation of the mechanistically coupled simulation tool MANGA, including the feedback 146 between two very distinct types of systems, requires a flexible coupling framework. To facilitate 147 model development, we use already existing models by implementing them as submodules to our 148 software package. Modular approaches for simulation toolboxes are widely used in hydrogeological 149 modelling (e.g. Fischer et al. (2015); Horgue et al. (2014); Foglia et al. (2018)). This approach 150 allows developers to take advantage of performed work on model verification within each submodule. 151 Modular code structures also provide frameworks and allow future applications through exchange 152 or extension of individual modules. 153

¹⁵⁴ Sustainable model development has been proven crucial in the context of model reusability (Ram,
¹⁵⁵ 2013). In the past, ongoing effort on introducing standard protocols for model documentation was
¹⁵⁶ taken. Model reproducibility is one of the key motivations for acceptable model documentation.
¹⁵⁷ For agent-based population models, the ODD standard protocol is widely accepted and has been
¹⁵⁸ improved over more than a decade (Grimm et al., 2006, 2010; Grimm and Railsback, 2012; Grimm
¹⁵⁹ et al., 2017).

³https://github.com/jbathmann/pyMANGA_small/releases/tag/v1.0.0; last access 22.01.2019; DOI: 10.5281/zenodo.3621383

Additionally, transparent source code development facilitates model reproduction, application and 160 modification within the community. As a consequence, usage of version control software tools in 161 scientific modelling is increasing. A widely applied tool is the distributed version-control system 162 for tracking changes in source code during software development and coordination in collaborative 163 software development, GIT (Blischak et al., 2016; Ram, 2013). The aspects listed above and 164 regarded during MANGA model development align with the recommendations given in (Belete 165 et al., 2017). 166

The MANGA model is outlined in the following section. A full documentation following the ODD 167 standard is provided in the supplementary material. All source code is version controlled and 168 available to the community as an open source, GIT-version controlled project.⁴

169

2.2. Modelling approaches of the individual models 170

2.2.1. Porewater salinity dynamics—OGS 171

To explain the relationship between vegetation patterns and three-dimensional hydrodynamic pro-172 cesses, we have to consider temporal scales of decades up to at least some 100 years and spatial 173 dimensions of hectares. Porewater salinity distributions in turn, can vary on timescales of hours to 174 days. To keep the computational costs manageable, we consider saturated flow, i.e. the sediment 175 pores only contain water and no air. The limitations of this assumption in mangroves is discussed 176 later. 177

Following Diersch and Kolditz (2002), the porewater salinity dynamics are described by a system 178 of partial differential equations. Starting from mass and momentum conservation within the sys-179 tem, phenomenological laws of *Fickian type* dispersive mass flux, the *Bear-Scheidegger* dispersion 180 relationship and Newton's viscosity law are used. Additionally, porewater density is regarded as a 181 function of pressure and porewater salinity only. Moreover, the porewater is taken as incompressible 182 with constant dynamic viscosity. The interfacial drag term of momentum exchange is approximated 183 up to second order in bulk flow velocity. Within the momentum balance, inertia is neglected and 184 forces are accounted for up to linear order in bulk velocity. The resulting total porewater mass flow 185 in a three dimensional aquifer domain Ω reads 186

$$\phi \frac{\partial \rho_R}{\partial p} \frac{\partial p}{\partial t} + \phi \frac{\partial \rho_R}{\partial S} \frac{\partial S}{\partial t} - \nabla \left(\frac{\kappa}{\mu} \rho_R \left(\nabla p - \rho_R g \right) \right) + Q_p = 0, \tag{1}$$

and the evolution of porewater salinity in Ω is given by 187

$$0 = S\phi \frac{\partial \rho_R}{\partial p} \frac{\partial p}{\partial t} + S\phi \left(\frac{\rho_R}{S} + \frac{\partial \rho_R}{\partial S}\right) \frac{\partial S}{\partial t} - \nabla \left(\frac{\kappa}{\mu} \rho_R S \left(\nabla p - \rho_R g\right) + \rho_R \mathbf{D}_h \nabla S\right).$$
(2)

We use hydrostatic pressure (p), porewater salinity (S), the parameters bulk density (ρ_R) , perme-188 ability (κ), dynamic viscosity (μ), the constant gravitation vector (g), medium porosity (ϕ), and 189 hydrodynamic dispersion (\mathbf{D}_h) . 190

Let Γ be the boundary of the domain Ω . Then the Dirichlet-type boundary conditions are im-191 posed on $\Gamma_D \subset \Gamma$, and Neumann-type boundary conditions on Γ_N , such that $\Gamma = \Gamma_D \cup \Gamma_N$ and 192 $\Gamma_D \cap \Gamma_N = \emptyset.$ 193

⁴https://github.com/jbathmann/pyMANGA_small/releases/tag/v1.0.0; last access: 22.01.2019

¹⁹⁴ Our particular definitions of the boundary condition functions g_i^j are explained in detail in sec-¹⁹⁵ tion 3. For the hydrostatic pressure boundary conditions, we note that flow boundary conditions ¹⁹⁶ are equivalent in their form to Neumann-type boundary conditions:

$$p - g_D^p = 0 \text{ on } \Gamma_D \text{ (Dirichlet)},$$

$$\left\langle \frac{\kappa}{\mu} \rho_R \left(\nabla p - \rho_R g \right) \left| n \right\rangle + g_N^p = 0 \text{ on } \Gamma_N \text{ (Neumann)},$$
(3)

with the scalar product denoted by $\langle \cdot | \cdot \rangle$. For the component concentration, the boundary conditions are given by:

$$S - g_D^S = 0 \text{ on } \Gamma_D \text{ (Dirichlet)},$$

$$\left\langle \left(\frac{\kappa}{\mu} \rho_R S \left(\nabla p - \rho_R g\right) + \rho_R \mathbf{D}_h \nabla S\right) \left| n \right\rangle + g_N^S = 0 \text{ on } \Gamma_N \text{ (Neumann)}.$$
(4)

The hydro component transport process implementation has been intensively benchmarked, including the Goswami (Goswami and Clement, 2007) and the Elder (Elder et al., 2017) problem. The results have been compared to the results of other numerical software packages. Documentation on benchmarks performed and the OGS project is available online⁵.

203 2.2.2. Mangrove model—BETTINA

The general interplay of allometric tree measures, physiological parameters, and resource limitation within BETTINA is given in the supplementary material. Water dynamics within single trees in BETTINA are modeled as follows: The water uptake Q is calculated starting from Darcy's law for laminar flow of water volume

$$Q = \frac{\Delta\Psi}{R},\tag{5}$$

with potential difference $(\Delta \Psi)$ and flow resistance along the flow path (R). Here, $\Delta \Psi$ is the difference between the leaf water potential and the sum of height potential of the leaf and osmotic potential of the porewater. Hence, environmental factors, tree allometry, and species-specific parameters are considered.

BETTINA does not explicitly model salt absorption and exclusion mechanisms, thus there is no
 species-specific consideration. This implies the assumption of negligible effect of those mechanisms
 on considered temporal and spatial scales.

So far, BETTINA parametrization is based on Avicennia germinans. The resistance R in turn is a function which depends on tree geometry such as stem height, stem radius, root zone, and crown geometry, as well as on species-specific parameters such as xylem conductivity and fine root permeability.

Resources are distributed through a specified ratio. Hence, the available resources for the tree are attributed to a limiting resource: either water uptake Q or the available light. BETTINA does not account for the influence of nutrient availability. The available resources are used for maintenance of the living biomass (proportional to the trees' volume) and growth. Within tree growth, resources available for growth are allocated in order to optimize resource uptake by facilitating uptake of

⁵https://www.opengeosys.org/docs/; last access: 27.12.2019

the limiting kind of resource. For more detailed explanations see Peters et al. (2014), Peters et al. (2018) and the supplementary material.

In order to model tree populations, we combine several trees which are described by the BETTINA model. The interaction of trees within our approach can only manifest itself in competition for resources. Shadowing effects between different individuals are taken into account. We do not explicitly introduce a competition scheme for water uptake, since trees indirectly compete by local change of environmental conditions (porewater salinity) in the vicinity of their roots, which is modeled in detail by the coupling to OGS.

232 2.3. Implementation of the Model Coupling



Figure 2: MANGA coupling scheme as explained in section 2.3: *i)* Plant model BETTINA. *ii)* Information on setup for groundwater simulations. *iii)* Dynamic porewater salinity model OGS. *iv)* States of porewater salinity distribution within the aquifer.

Mangrove stand and porewater salinity dynamics have distinct temporal scales. Groundwater dy-233 namics on the spatial scales of several hectares take place on timescales from seconds to hours. 234 Vegetation dynamics is typically modeled with time steps varying from months to years. In our 235 approach, the latter defines the frequency of transfer of information between the two distinct mod-236 els. OGS often requires finer time stepping than BETTINA. Between BETTINA timesteps, all 237 information about the mangrove population (i.e. the boundary conditions within the OGS setup) 238 stays constant while OGS is calculating the change in porewater salinity distribution. BETTINA 239 then uses the calculated information on porewater salinity distribution to update the mangrove 240 population in its next time step. 241

- ²⁴² The implemented coupling cycle for system dynamics after setup initialization reads:
- 1. BETTINA evolves and updates every tree (Figure 2i).

Information on plant distribution and individual specific allometric measures is saved in distinct boundary grids, which are passed to OGS. Hereby, equation (5) is applied to dynamically update the Neumann-type boundary conditions for bulk flow velocity (Equation (3)) defined at the tree root meshes. Abiotic external drivers can also be included using boundary grids (Figure 2 *ii*).

OGS calculates the development of porewater salinity within the setup under consideration
 of all biotic and abiotic external drivers (Figure 2 *iii*).

4. States of porewater salinity distribution within the aquifer are saved at dynamical adapting frequencies, which orient on the change rate of porewater salinity distribution (Figure 2 iv).

253 3. Model application

We study the mechanism connecting mangrove water uptake and porewater salinity distribution in stylized scenario setups. Subsequently, we investigate the effect on resource acquisition of tree communities emerging from the implemented plant-soil feedback.

A simple vegetation setup consists of one tree located at a point \vec{r} on the surface of a three dimensional aquifer domain Ω . Environmental factors like tidal activity and precipitation are not considered since we focus on the implications of plant water use. Additionally, the aquifer domain Ω is defined to be homogeneous with respect to the aquifers permeability κ . Introducing a hydraulic gradient i_x leads to a constant groundwater flow. Using this setup, the dependence of the groundwater salinity distribution and tree model dynamics on the parameters i) aquifer permeability and ii) hydraulic gradient, can be investigated by parameter variation.

The smallest possible setup of interacting trees consist of two individuals. Hence, we add a second tree to the scenario described above, to examine the tree-tree interactions. Both trees are located in one streamline. By variation of the distance between the two trees, the strength and nature of competition for belowground resources is analyzed (Figure 3).



Figure 3: **MANGA application setup.** Groundwater recharge on the landward boundary, open flow conditions on the seaward boundary. Tree freshwater uptake affects salinity distribution within the aquifer.

The aquifer domain Ω (extensions $\vec{x} \in \{[0, L_x], [0, L_y], [-L_z, 0]\}$) is represented using a 3-dimensional grid with resolution of a characteristic length scale of 1 m in the x-y plane. In the vicinity of trees, the grid is refined, up to the characteristic length scale of $0.3 r_R$, with r_R denoting the root radius. In the vertical direction, five layers are considered with a four times higher resolution at the surface

²⁷² than at the bottom of the aquifer.

- Within this stylized case study, we update the tree population monthly, i.e. information between the two submodels is exchanged every month.
 - The initial distributions for pressure (p_I) and salinity (S_I) are set as

$$S_I(\vec{x}) = S(x, y, z, t = 0) = S_0$$
 and (6)

$$p_I(\vec{x}) = p(x, y, z, t = 0) = -\rho g z,$$
(7)

where g is the gravitational constant.

For both scenarios, no flow boundary conditions for both variables, pressure and salinity, are imposed along the y-, and z-axis. A constant horizontal hydraulic gradient i_x induces background bulk flow. Pressure boundary conditions (g^p) for the left (uppercase L) and right (uppercase R) boundaries are given as $g_D^{L,p} = p_I(x = 0, y, z)$ (8)

$$g_N^{R,p} = \frac{\kappa}{\mu} \rho_R^2 g i_x,\tag{9}$$

with constant dynamic viscosity μ and homogeneous permeability tensor κ . Salinity boundary conditions g^S read

$$g_D^{L,S} = S_0 \tag{10}$$

283

$$g_D^{R,S} = S_0. (11)$$

²⁸⁴ The boundary conditions describing tree (fresh-)water uptake at the root (uppercase T) read

$$g_N^{T,p} = \rho_R \frac{\Delta \Psi}{R} \quad . \tag{12}$$

This boundary condition represents the extraction of fresh water from the saline water body as described in Peters et al. (2018). In our setup, the boundary conditions $g_D^{L,S}$, $g_D^{R,S}$, $g_D^{L,p}$ and $g_N^{R,p}$ fully define the environmental conditions for the groundwater dynamics: $g_D^{L,p}$ defines the pressure 285 286 287 on the left boundary of the setup domain representing a constant pressure head on the landward boundary of a saturated groundwater body. $g_N^{R,p}$ denotes the bulk flow out of the domain over its 288 289 right boundary. This boundary condition is applied in order to impose groundwater flow velocities 290 resulting from the gravitational force. The salinity values on those two boundaries are set as constant using $g_D^{L,S}$ and $g_D^{R,S}$ representing the inflow of water with a certain salinity and the outflow to a 291 292 similar water body, e.g. the outflow of water into the open sea. In general, one can incorporate 293 other environmental factors such as tidal activity and precipitation by defining additional boundary 294 conditions, representing those phenomena. For the sake of simplicity and conceptual analysis, our 295 setup only incorporates the background flow as described above. 296

Values for OGS parameterization, i.e. the parameters defining groundwater flow, used to generate 297 the following example simulations, are given in Table 1 and are inspired using the results of Schwen-298 denmann and Riecke (2006) and Tait et al. (2016). In this stylized model application, we choose an 299 aquifer depth of 1.5 m in order to represent a shallow mangrove aquifer as observed in Schwenden-300 mann and Riecke (2006). Values for molecular diffusion, dynamic viscosity and reference density are 301 aligned with standard values for distilled water at room temperature. We simplify the groundwater 302 dynamics by assuming salinity-independent groundwater density. Values for the permeability and 303 the hydraulic gradient vary within the range of measurement results presented in Schwendenmann 304

Symbol	Parameter	Value/Range
d	Tree distances	0 m to 10 m
L_x	Aquifer length	$20\mathrm{m}+d$
L_y	Aquifer width	$10\mathrm{m}$
L_z	Aquifer depth	$1.5\mathrm{m}$
D_m	Molecular Diffusion coefficient	$1 \times 10^{-9} {\rm m}^2/{\rm s}$
β_T	Transversal dispersion coefficient	0.2
β_L	Longitudinal dispersion coefficient	1
$ ho_0$	Reference density	$1 imes 10^3 \mathrm{kg/m^3}$
μ	Dynamic viscosity	$1 \times 10^{-3} \mathrm{Pa/s}$
κ	Permeability tensor	$5 \times 10^{-12} \mathrm{m}^2$ to $50 \times 10^{-12} \mathrm{m}^2$
i_x	Horizontal pressure difference ratio	2×10^{-4} to 20×10^{-4}
S_0	Initial salinity	35~%

Table 1: Input parameters for OpenGeoSys.

and Riecke (2006). We designed the horizontal extent of our setup in a way that boundary effects on the trees are minimized. The order of magnitude for transverse and longitudinal dispersion coefficients is given by numerical restrictions and are adapted from (Pool and Carrera, 2011).

Model parameters for the tree, modeled by BETTINA, are given in the supplementary material and taken from the original BETTINA single tree model parametrization (Peters et al., 2014) for

310 Avicennia germinans.

311 3.1. Single tree scenario

At simulation start, a tree sapling is planted at the domain surface with five meters distance to the inflow and the lateral boundaries and 15 meters distance to the outflow boundary (Figure 3). In order to investigate the influence of aquifer permeability values and the hydraulic gradient, N = 30numerical experiments have been performed varying those parameters.

After 50 years simulation time, the salinity along the flow direction at 15 cm depth is observed. A characteristic shape for the salinity distribution within the aquifer as shown in Figure 4i is observed for all parameters tested. Directly in the root zone, the salinity increases along flow direction. Downstream to the tree, an effect of increased salinity in the porewater occurs until the effect of the Dirichlet boundary condition dominates the measurements at the outflow boundary.

Increase of salinity within the root region is observed for all used parameter setups after 50 years 321 simulation time, as shown in Figure 4 *ii-iii*. The root zone is defined by the intersection of the 322 aquifer domain Ω and cylinder around the tree center with radius $r_s = r_R$, with r_R denoting the 323 trees' root radius. Lower mean salinities within the root zone are observed with the increase of both 324 aquifer permeability and hydraulic gradient (Figure 4ii). Hereby, within the range of parameters 325 tested, a five times larger permeability leads to a decrease of salinity by roughly 25 %. Additionally, 326 a three fold increased hydraulic gradient reduces the root zone salinity by approximately 10%. An 327 increase of initial salinity S_0 leads to an increase in root zone salinity (Figure 4 *iii*). Trees in a setup 328

with $S_0 \ge 95 \%$ do not persist for 50 years.

In Figure 4*iv* the result for tree height measurements are presented. As shown, increasing permeabilities or increasing hydraulic gradients lead to an increase in total tree height after 50 years simulation time. The measure is sensitive to both parameters tested. Increase of hydraulic gradi-



Figure 4: Stylized case study scenario for one tree. *i*) Visualization of results for model run with initial salinity $S_0 = 35 \text{ ppt}$, $\kappa = 2.5 \times 10^{-11} \text{ m}^2$ and $i_x = 1.2 \times 10^{-3}$ after t = 50 years simulation time. The red rectangle depicts the plane shown in the transect view below. Salinity shown is observed along the transect line at 15 cm depth (red line along transect plane). The intersection of the aquifer with the gray cylinder depicted within the transect view defines the root zone. *ii*) Mean salinity within the root zone after 50 years simulation time in dependence of varying parameter values for κ and i_x . *iii*) Mean salinity S_0 . *iv*) Tree height after 50 years simulation time in dependence of varying parameter values for κ and i_x . *v*) Ratio of crown area to root area after 50 years simulation time in time in dependence of varying parameter values for κ and i_x . *vi*) Ratio of crown area to root area after 50 years simulation time in time in dependence of varying parameter values for κ and i_x . *vi*) Ratio of crown area to root area after 50 years simulation time in time in dependence of varying parameter values for κ and i_x . *vi*) Ratio of crown area to root area after 50 years simulation time in time in dependence of varying parameter values for κ and i_x . *vi*) Ratio of crown area to root area after 50 years simulation time in time in dependence of varying parameter values for κ and i_x . *vi*) Ratio of crown area to root area after 50 years simulation time in time in dependence of varying parameter values for κ and i_x . *vi*) Ratio of crown area to root area after 50 years simulation time in time in dependence of varying parameter values for κ and i_x . *vi*) Ratio of crown area to root area after 50 years simulation time in time in dependence of varying parameter values for κ and i_x . *vi*) Ratio of crown area to root area after 50 years simulation time in time in dependence of varying parameter values for κ and i_x . *vi*) Ratio

ents leads to an increase in reached total tree height. Similarly, the correlation between total tree height and permeability is positive.

³³⁵ Comparison of the crown area with root area shows an allometric response of the tree growth to ³³⁶ varying subsurface properties (Figure 4v-vi). With lower permeability as well as low hydraulic ³³⁷ gradients, the tree allocates more resources into root growth than into crown growth leading to ³³⁸ an decreasing fraction between the respective areas. Higher initial salinities lead to more resource ³³⁹ allocation in root growth resulting in a lower crown to root area fraction.

340 3.2. Two tree scenario

As second application, a second tree is added to the setup described above. The tree located upstream is called first tree in the following, the other tree is called second tree. The second tree is located downstream to the first with varying distance d (Figure 5*i*). The groundwater flow domain is extended by d in the flow direction, such that the distance between the absorbing Dirichlet boundary and the second tree stays constant. N = 40 numerical experiments have been performed with distances varying from 0.25 m to 10 m. The values for aquifer permeability $\kappa = 2.5 \cdot 1 \times 10^{-11} \text{ m}^2$, hydraulic gradient $i_x = 1.2 \times 10^{-3}$ and simulation time t = 50 years are kept constant.

 $_{348}$ An example for resulting salinity distributions measured after 50 years simulation time in 15cm

 $_{349}$ depth on the transect plane is shown in Figure 5 *i*. A characteristic shape has been observed for

 $_{350}$ all tested values of d, showing the resulting shape as the combination of the individual salinity distributions induced by each individual tree.



Figure 5: Stylized case study scenario with two trees. *i*) Visualization of results for t = 50 years, $\kappa = 2.5 \times 10^{-11} \text{ m}^2$, $i_x = 1.2 \times 10^{-3}$ and d = 6.25 m. t, κ and i_x are constant throughout the whole figure. The red rectangle depicts the plane shown in the transect view below. Salinity shown is measured along the transect line at 15 cm depth (red line along transect plane). The root zone is defined in Figure 4. *ii*) Tree height over the tree height from the setup for one tree (Figure 4) with varying distance d. *iii*) Mean salinity within the root zone over the reference value obtained from the corresponding one tree setup in dependence of tree distance d. *iv*) Allometric ratio over the reference value obtained from the one tree setup in dependence of tree distance d.

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Figure 5 *ii* shows the mean salinity within the root zone (defined above) vs. the reference value obtained from the corresponding results of the one tree setup. For both trees, the mean salinity is increased. A range of approximately 4 m can be observed for the first tree until the effect of salinity increase by the presence on the second tree is negligible. A small jump in the root zone salinities for both trees can be observed at the same distance. Mean salinity within the root zone of the second tree is increased for all tested values of *d* relative to the reference tree, with the maximum of root zone salinization at approximately 4 m distance between the tree centers. The reduction in total reached tree height is shown in Figure 5 *ii*. A reduction of tree growth for the first tree can be observed. Within the range of 4 m, the effect of tree growth reduction is decreasing with increasing distance between the trees from a reached height of 83 % of the reference measure at distance d = 0.25 m, to a vanishing effect, e.g. same total tree height as measured in the reference setup. Decrease of tree growth varying from 77 % to 88 % of the reference value for the second tree is observed within the results of all performed numerical experiments. This effect is decreasing with increasing distance between the trees.

The measured crown to root ratio of both trees is divided by the reference ratio in Figure 5 *iv*. For both trees, a reduction of this allometric measure is observed. A value below one indicates increased resource allocation to root growth relative to the reference tree. For the first tree, the same range of effect of tree distances up to 4 m can be observed. The minimum value for the allometric measure of the first tree is 75%. Increased allocation of resources to root growth is observed for all tested values of d for the second tree. Here, the minimum of the fraction of 68% is measured at d = 1 m.

372 4. Discussion

To the best of our knowledge, the MANGA model is the first simulation model which describes plantgroundwater feedbacks according to first principles and is thus explicitly mechanistic. The model is a hybrid linking an agent-based vegetation model (BETTINA) with a continuous groundwater model. The model was firstly applied to mangroves because this ecosystem is characterized by pronounced zonation patterns in both species distributions and patterns in the allometry of one particular species, which provides extraordinary possibilities to evaluate the suitability of the model to capture the underlying mechanisms correctly.

Allometric patterns were addressed by the simulation experiments performed. The single tree setup showed an influence of subsurface properties on groundwater salinity distributions and tree growth behavior. Results obtained using the two tree model system provide insights into the mechanisms governing belowground competition for resources in mangroves.

Based on first principles, following emerging effects of soil parameters on the modelled plant-soil
 feedback have been shown within the single tree setup:

• Aquifers with low soil permeabilities result in higher mean salinities in the root zones. With increasing soil permeabilities, higher groundwater flow velocities occur and, therefore, the salt accumulated at tree roots is carried away more easily. Hence, the established equilibrium salt concentration decreases with higher values of subsurface permeability. The same mechanism explains reduced mean salinity values within the root zone for higher hydraulic gradients.

With increasing permeability and increasing hydraulic gradients, equally parameterized trees
 become taller within the same amount of time. The tree growth is reduced by increasing
 groundwater salinity, which is a result of soil-parameter-dependent equilibrium groundwater
 salinities.

An effect of subsurface properties on the emerging allometry of our model trees has been shown. The reduced ratio of crown area to root area with reduced ground water flow velocities (low hydraulic gradients and/or low permeability values) and therefore higher salinities within the root zones of the trees can be understood by analyzing the growth behavior of the BETTINA model. In situations, where the porewater salinity is high, a tree within the BETTINA model allocates resources such that porewater is more accessible, e.g. a larger root

area facilitates water uptake. This observation is also in line with the original description of the solitaire BETTINA model (Peters et al., 2014).

• Within the model framework, qualitative agreement with the observed relations between the growth behavior of trees and initial salinities (i.e. different mangrove systems like delta systems or tropical dry regions) are reproduced. Due to the growth dynamics within the BETTINA model, trees directly react to salinity by variation of their growth behavior. Hence, trees allocate more resources in root growth within saline than in brackish conditions.

The model presented here shows effects of the positioning of a tree within its environment by analyzing the emerging interaction of two trees:

Resulting pore water salinity distributions within a two-tree setup emerge partly from the superposition of their individually induced effects on water uptake. In the presented ground-water salinity distribution along a transect line at 15 cm depth (Figure 5 i), two maxima can be observed. Each of those maxima represents the peak of the groundwater salinity distribution induced by individual trees. In this numerical experiment, the water uptake of the second tree, and therefore the increase in groundwater salinity, is lower due to the higher background salinity within its root zone induced by the first tree.

• The increase of salinity within the root zone for the two trees shown in Figure 5ii shows 417 dependence of the tree positioning relative to each other. For the first tree, the presence of 418 the second tree can only be measured up to a distance corresponding to approximately two 419 times the root radius. In contrast, the root zone of the second tree has increased salinity 420 for all tested distances between the trees. Since less saline water from the inflow boundary 421 reaches the first tree firstly, the effect of increased salinity is always lower for this tree. After 422 a threshold distance between the trees is reached, the increasing effect of the second tree 423 on porewater salinity is not affecting the region of the first tree by means of diffusion and 424 dispersion. Hence, the second tree's presence has no influence on the porewater salinity 425 distribution within the first tree's root zone (Figure 5 *iii*, *iv*). 426

427 Some shortcomings within the model design exist due to simplifications. Here, we explicitly discuss
 428 some of the model's assumptions listed in the main body and the appendix of this work.

The assumption of saturated soil conditions is important to keep computation cost for the ground-429 water submodel low. This simplification implies that water saturation in the soil does not limit 430 plant growth which we can assume in mangrove ecosystems. In principle, it would be possible to 431 extend the current model coupling such that both sub-models calculate and evaluate water sat-432 uration in the soil. Extensions to the groundwater model further increase model runtimes. Our 433 approach to use a deterministic model to depict belowground dynamics, however, already leads 434 to increased model runtimes compared to traditional belowground competition approaches (e.g. 435 FON), thus reducing model usability. Furthermore, we currently do not consider geochemical reac-436 tions (e.g. redox-reactions) and multi-component transport reaction processes (e.g. transformation 437 of nutrients). In the presence of nutrient scarcity or important geochemical reactions, however, 438 modifications for both the tree and groundwater model are possible (see e.g. He et al. (2015)). Due 430 440 to the modularity of our coupling approach, it is even possible to exchange the tree or groundwater model for an approach that is capable to meet aforementioned potential requirements, i.e. variable 441 saturated soil or geochemical reactions. 442

The current setups also do not account for any dilution effect at the ground surface (e.g. precipitation or tidal dynamics and the role of crab burrows for water infiltration). The incorporation of

precipitation and tidal dynamics is neglected here in order to be able to directly analyze the feedback 445 model, although those drivers also influence the manifestation of the analyzed plant-soil feedback. 446 For preliminary investigations on how changes in tidal amplitude and incursion into the mangrove 447 forest affect the plant-soil feedback, time-dependent boundary conditions⁶ can be included in the 448 groundwater model. Furthermore, our model could be extended by incorporating models available 449 in the literature as provided by Mazda and Wolanski (2009), taking advantage of our modular 450 approach. Mazda and Ikeda (2006) proposed how crab burrows affect soil permeabilities. Using 451 their results, the influence of crab burrows can be explicitly modelled with inhomogeneous soil 452 permeability distributions within our approach in future investigations. 453

⁴⁵⁴ Using first principles, less assumptions drawn from empiric measurements are used, eventually re⁴⁵⁵ sulting in more reliable model results. We can use more mechanistic relations and rely less on
⁴⁵⁶ empirical-based but phenomenological assumptions. Still, model parametrization remains challeng⁴⁵⁷ ing.

The emerging interaction between the trees and the porewater dynamics provides insights into the 458 mechanisms driving the plant-soil feedback. Based on first principles (Grimm and Berger, 2016), 459 only plant water uptake and the associated salinity increase was imposed. The emerging interaction 460 of trees can be interpreted as outcome of competition for water which is usually modelled implicitly 461 (Berger and Hildenbrandt, 2000). We were able to show that competition for resources, fresh water 462 in this case, is a direct consequence of the mechanism described by the model. For this reason, we 463 are convinced that the developed hybrid modelling approach is an important step forward towards 464 the description of plant-water-feedbacks beyond the chosen mangrove system. 465

466 5. Conclusions

This work presents the coupling of an agent-based mechanistic tree model to a complex groundwater 467 flow and transport model. So far, recent approaches to model the plant-groundwater salinity feed-468 back in mangrove ecosystems have used plant models which did not consider varying tree allometry 469 (Jiang et al., 2012; Sternberg et al., 2007; Teh et al., 2015). The semi-mechanistic approach by 470 Peters et al. (2014) was able to explain varying tree allometry, but it did not account for dynamic 471 environmental conditions as a result of tree water uptake or explain plant-soil feedbacks. By using 472 an approach based on first principles, we were able to address these shortcomings. The introduced 473 model delivers a novel approach to study the characteristics of different types of mangrove zonation 474 patterns, e.g. species- and allometric zonation. 475

More specifically, we were able to explain the allometric response of trees to different subsurface 476 properties providing new insights into the mechanisms governing plant-soil feedback. Most impor-477 tantly, the influence of subsurface properties on subsurface resource distribution is explained by 478 the model without the explicit use of competition models: Within the introduced MANGA model, 479 no belowground competition concept such as FON (Berger and Hildenbrandt, 2000) has been im-480 posed. Still, competition for belowground resources emerges and the model predicts an asymmetric 481 competition behavior. As such, the presented approach does not depend on additional empirical 482 parameters that would be required to describe competition with the currently available models. 483 Our approach, thus, provides a more robust approach to simulate mangrove communities. 484

⁶https://www.opengeosys.org/docs/benchmarks/python-bc/hertz-contact/hertz-contact/; last access: 20.12.2019

In other models, the dominance in asymmetric competition for water (Teh et al., 2015; Berger and 485 Hildenbrandt, 2000) depends on tree and root size. With a systematic analysis of our approach 486 using stylized setups, we could firstly show that allometric properties of the trees are governed by 487 subsurface properties (single tree model). Furthermore, unlike other models available in the liter-488 ature, the groundwater salinity distribution in our model depends on the geometrical arrangement 489 of the two individual trees and we could show how the resource distribution between competing 490 trees also depends on the tree position (two tree model). Our tool is therefore helpful to develop 491 a better understanding of the processes defining belowground competition for resources and aid to 492 design more robust belowground competition concepts. 493

The MANGA model provides indication of the importance of the plant-soil feedbacks on the ap-494 pearance of mangrove stand zonation. Future works may want to focus on the development of 495 a novel competition concept as a surrogate approach to the current methods such as FON. As a 496 continuation to this study, the model will be used to further investigate the nature of species and 497 allometry zonation in mangrove ecosystems. Due to the modular design of MANGA, other envi-498 ronmental drivers such as tidal activity or precipitation can be incorporated to the groundwater 499 model easily in order to obtain realistic stand patterns. Even more, after considering one species 500 allometry zonation in dependency of environmental factors, the interface to the BETTINA model 501 also allows to extend model setups for more mangrove species. We are confident that our approach 502 goes so far that it lays the basis for a wholly new concept of plant-soil interaction models that can 503 be adjusted flexibly to individual requirements also in non-mangrove environments with different 504 driving components than salinity. 505

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516 7. Declaration of interest

517 None

518 References

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