



Changes in allometric relations of mangrove trees due to resource availability – A new mechanistic modelling approach



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ABSTRACT

Models based on allometric responses to competing neighbours and environmental conditions in mangrove forests are increasingly available. However, the improvement of these models requires a mechanistic understanding of how individual trees allocate biomass. This study introduces a new tree model (BETTINA) focusing on this issue. It is designed to investigate the response of trees in terms of biomass allocation patterns to environmental conditions. Additionally, it is suitable as a component of an individual-based mangrove stand model. BETTINA describes the plasticity of trees in growth patterns depending on their below-ground resource uptake. In contrast to the existing mangrove stand models, BETTINA focusses explicitly on the processes leading to variation in resource availability. Based on the physical principle of osmotic potential of solutions, the direct influence of salinity on plant water availability is considered. Allometric model parameters are not restricted to only the above-ground measures of trees' traits (such as stem diameter and height), but also characterize below-ground biomass. Within BETTINA these measures are not limited to predefined empirical maximum values, but are the result of and depend on environmental conditions.

The model is suitable to explain allometric measures and relations in dependence on total plant size and environmental conditions (for now salinity and light), and has a great potential for a physiologically and physically based improvement of plant component related biomass estimations.

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1. Introduction

Mangroves cover roughly 75% of the tropical and subtropical coasts of the world (representing 2.4% of tropical forests, Spalding et al., 2010) and are therefore recognized as one of the most productive ecosystems worldwide, with productivity rates compared to those of the tropical rain forests (Aburto-Oropeza et al., 2008; Blaber, 2007; Holguin et al., 2001; Primavera, 1998; Twilley, 1988). Understanding the patterns of biomass accumulation of forests requires accurate estimates of biomass. An assessment of the relevant processes is essential for realistic estimations of the potential consequences of environmental change (Castañeda-Moya et al., 2011; Comley and McGuinness, 2005; Komiyama et al., 2000).

To date, substantial literature is available on the above-ground biomass of mangrove forests. Since the mid 1980s, over 43 allometric equations have been developed to estimate the standing biomass of mangroves around the world (Komiyama et al.,

2005, 2008). While Soares and Schaeffer-Novelli (2005) describe a strong species-specific trait allometry, later studies find that allometric relations can vary more within species growing in different locations (Comley and McGuinness, 2005). Comley and McGuinness (2005) found that stem diameter (DBH) is negatively correlated to root biomass, while positively correlated to above-ground biomass. Nevertheless, due to the difficulties of measuring below-ground biomass, few studies integrate both above- and below-ground estimations of biomass production.

Unfortunately, methodological difficulties in the measurement of below-ground biomass estimations result in uncertainties regarding mangrove forests biomass estimations (Bouillon et al., 2008; Comley and McGuinness, 2005). To improve the understanding of the processes it is necessary to detect the critical factors leading to these allometric variations and to attribute this variation to the underlying physical and physiological principles.

Some authors point at salinity as the major regulator of growth in shape or size of mangrove individuals or their components: Despite the fact that mangrove species are well adapted to dominate under saline conditions (Burchett et al., 1984; Lawton and Todd, 1981; Sobrado and Ball, 1999), growth is reduced as

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salinity increases (Naidoo and Chirkoot, 2004; Suárez and Medina, 2006). Further, there is evidence that more resources are allocated into root biomass when below-ground resources are limited (Castañeda-Moya et al., 2011; Naidoo, 2009; McKee, 1995). Leaf growth, leaf area and xylem conductivity are also affected by increasing salinities (Parida et al., 2004). We therefore conclude that there is enough evidence suggesting a strong influence of salinity on allometric relations.

Plants adjust their biomass allocation so that their growth is equally limited by all resources (Bloom et al., 1985). Growth dynamics respond to gradients of resources, regulators and hydro-periods (Castañeda-Moya et al., 2011). In this way, plants growing under light limitation will tend to allocate more biomass to the crown to develop leaf biomass, capable of compensating for light resource limitation, while below-ground biomass responds to a limitation of soil resources. In other words, plants in nutrient-poor soils will allocate more biomass to roots, thereby maximizing efficiency for gathering the most strongly limiting resources and increasing the root:shoot ratio (Castañeda-Moya et al., 2011). Access to limited resources can lead to distinct phenotypic forms, for example the shrub forms of dwarf mangroves (e.g., Lovelock et al., 2004).

Measurements of pressure gradients in mangroves between leaf and soil matrix have been carried out by Lovelock et al. (2006a and 2006b), where variation in soil water potential was almost completely explained by variation in osmotic potential. Thus, salinity could limit the plant's water access. Further, these pressure gradients suggest that physical mechanisms are the background for the description of the water uptake within the presented BETTINA-model.

The processes behind, however, act on the level of individual plants. Salinity, e.g., alters root anatomy (Cheng et al., 2010, 2012). Lignin and suberin significantly contribute to the formation of an apoplastic transport barrier influencing the radial transport of gas, water and dissolved ions in the apoplast and play important roles in protecting plants from biotic and abiotic stress (Cheng et al., 2012). Performances of this barrier are strongly regulated by the environmental conditions surrounding the roots (Laskov et al., 2006), such as water logging (Gibberd et al., 1999; McDonald et al., 2002), salt (Krishnamorthy et al., 2009; Shannon et al., 1994) and nutrients (Schreiber et al., 2005). Higher salinities will induce the roots to lignify more than roots submitted to lower salinities (Cheng et al., 2012), protecting the root and plant from absorbing too much salt, but also preventing it from absorbing all the necessary nutrients. As a compensation reaction, more biomass will be allocated into roots, improving their ability to absorb nutrients and affecting the proportion of biomass in stem, branches and crown.

Despite weaknesses in a mechanistic understanding of the regulators (such as salinity) influencing the patterns of plant growth and biomass allocation, it is generally accepted that the interactions among resources (nutrients), regulators (soil salinity, sulphides) and hydro-period (duration, frequency and depth of flooding, Castañeda-Moya et al., 2011; Twilley and Rivera-Monroy, 2005) define the types of mangrove forests and their ecosystem functions (Feller et al., 2010; Ewel et al., 1998; Lugo and Snedaker, 1974; Thom, 1982).

Individual-based models describing mangrove stands have been proven to be suitable for analysing the influences of the performance, behaviour and interactions of individual trees on the stand characteristics (see e.g., Chen and Twilley, 1998, Berger and Hildenbrandt, 2000, Kautz et al., 2011, or Vogt et al., 2013). None of the existing forest stand models, however, provide a mechanistic description of the above- and below-ground biomass allocation of individual trees (Berger et al., 2008), which is essential for a better understanding of biomass allocation patterns and carbon storage

in general, and for the forest dynamics in a given environmental situation in particular.

In this work we introduce an individual-based model (BETTINA) addressing this issue. It hinges on the hypothesis that mangrove plants (regardless of their species) react to salinity stress in such a way that trees modify their patterns of biomass allocation in order to cope with environmental constraints. Plants will invest more energy into root biomass when salinity becomes a stressing factor that limits water and, hence, nutrient uptake. Under light resource limitation, plants tend to allocate more biomass to crown and height growth (Martínez-Garza et al., 2013). These assumptions define the allometric relationships and contribute to an improved understanding of biomass budgets and patterns in the vegetation composition of a stand.

The BETTINA-model thus represents a novel tool to assess mangrove biomass and its distribution over the plant components in relation to plant responses to the environment. Within this article we present the model design of a single individual and the behaviour of the model over variation in salinity.

2. Methodology

2.1. General concept

The goal of the BETTINA-model is to describe the mechanisms and driving forces of biomass allocation and, thus, the plasticity of the mangrove plant due to environmental conditions. Using underlying physical and physiological principles for resource uptake, the 'bottleneck' of the resource uptake can be detected and the growth allocation can be performed in terms of improving the access to resources. Thus, the model plant will be able to reproduce a plastic adaptation to environmental conditions as salinity or competition with neighbours is varied.

For the model design the following basic assumptions have been made:

- The resources are strictly divided into above-ground (light) and below-ground (water) resources.
- The use of above- and below-ground resources is proportional. Thus, on the individual scale, either below-ground or above-ground resources are limiting (see also Lin et al., 2013).
- Resources used for maintenance are proportional to the total biomass. The difference between available resources and these maintenance costs is used for plant growth.
- The plant's individual growth allocation is focussed on improving the uptake of the limited resource (Bloom et al., 1985; Castañeda-Moya et al., 2011). That means that the model identifies the current bottleneck of resource availability and uses the allocation of biomass to widen these bottlenecks and improve access to the limiting resource.
- For now, by means of simplicity, only water will be considered as the limiting below-ground resource. We consider water the key element in any resource uptake (except for light). Certainly, nutrient availability might differ strongly according to site conditions. Nevertheless, nutrients are diluted in water, and, thus, – considering the presumptions of the model – the plant's nutrient access is closely related to the water availability. We are aware, that nutrient shortage would increase water demand (because water is the transport medium). But a consideration of nutrients would not change the principles of the model. Rather, it would increase the complexity of the problem and the number of unknown parameters. Nevertheless, describing water uptake within the model does to some degree account for nutrient uptake.

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