The rhizomicrobiome of Sorghum ; impact on plant growth and stress tolerance

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Chapter 1

General introduction

Sorghum is an economically important cereal crop used for animal feed and human food worldwide, in particular for subsistence farmers in Sub-Saharan Africa. Due to the high demand for its different uses, development of new sustainable strategies that improve or safeguard sorghum production is needed. These strategies not only encompass plant breeding and agricultural management practices, but also harnessing beneficial microbe-crop relations which are key to the development of sustainable crop production. Despite the large number of studies addressing plant-microbiome interactions, little is known about the sorghum microbiome and how it affects sorghum growth and tolerance to biotic and abiotic stresses. The **overall objectives** of my thesis are to investigate the dynamics of the sorghum root microbiome and to explore the beneficial effects of the root microbiome on sorghum growth and stress tolerance. In this general introduction I will give a brief description of sorghum, its uses, characteristics and importance of this cereal worldwide. Then, I will provide background information on the composition, spatial distribution and dynamics of the root microbiome and its importance for plant growth and health. Furthermore, I will present the role of root exudates in the recruitment of the rhizosphere microbiome and will discuss other drivers of rhizosphere microbial community assembly. Additionally, I will provide examples on how the root microbiome can provide tolerance to the host plant against abiotic disturbances, in particular drought. Finally, I will provide insights into how microbial inoculants can impact plant growth and nutrient acquisition.

1 - Sorghum

Sorghum bicolor (L.) Moench. is a C4 plant belonging to *Poaceae* family that, based on anthropological evidences, has been consumed as early as 8000 BC and domesticated in Ethiopia and neighbouring countries around 4000-3000 BC (Smith & Frederiksen, 2000, Dillon *et al.*, 2007). Sorghum is currently the 5th most cultivated cereal worldwide (Ramu *et al.*, 2013). It has a short growth period and is relatively drought tolerant, which makes sorghum a preferred cereal in arid and semi-arid regions (Farre & Faci, 2006, Wu *et al.*, 2010, Funnell-Harris *et al.*, 2013). Sorghum serves as a food crop and is used for biofuel production (Dutra *et al.*, 2013), soil coverage (Bean *et al.*, 2013), beer production (Smith & Frederiksen, 2000) and silage (Pinho *et al.*, 2015). As food-grade, special attention is given to sorghum because it is gluten-free and contains high levels of health-promoting phytochemicals (Asif *et al.*, 2010). Due to the nutritional similarity of sorghum and maize, the gain in weight and milk production of cattle fed with sorghum is comparable to that of cattle fed with maize (Aydin *et al.*, 1999, Oliver *et al.*, 2004, Sauvant, 2004). For ethanol production, sorghum has a preference over other plant biomass sources such as corn, sugarcane and sugar beet due to the

reduced water requirement (Farre & Faci, 2006, Walker, 2011, Dutra *et al.*, 2013). In general, sorghum only needs one-third of the water required for sugarcane cultivation and only half of the water required for corn production (Wu *et al.*, 2010). Additionally, sorghum has a short growth period of 3-5 month compared to 9-12 month for sugarcane (Davila-Gomez *et al.*, 2011). Given these favorable characteristics and its diverse usages, it is highly relevant to identify sustainable methods for disease prevention and tolerance against abiotic stress (Funnell-Harris *et al.*, 2013). The problems associated with sorghum production are to some extent geographically determined. In Brazil, sorghum producers are often faced with unfertile soils low in available phosphate and high in aluminium (Ribeiro *et al.*, 2001, Magalhaes *et al.*, 2007) and with many fungal diseases (Rodrigues *et al.*, 2009, Cota *et al.*, 2012, Cota *et al.*, 2013). In Africa, producers often face problems with infection by the parasitic weed *Striga hermonthica* (Del.) Benth. causing substantial yield losses (Hassan *et al.*, 2009).

Plant breeding programs make considerable progress by engineering sorghum varieties resistant to specific diseases and adverse environmental conditions and varieties with improved nutrient acquisition. Next to plant breeding, soil and plant-associated microbiomes are receiving increasing interest for their untapped potential to contribute to plant growth, development and health (Raaijmakers *et al.*, 2009, Bulgarelli *et al.*, 2015). In this context, combining plant breeding and microbiome-based crop production strategies is potentially a powerful strategy, realising that breeding programs typically do not consider the interaction with the soil and plant-associated microbiomes. Dangl *et al.* (2013) and Schlaeppi & Bulgarelli (2015) argued that selection and development of plants based on a combination of functional genes and plant responsiveness to beneficial soil microorganisms are expected to provide highly durable protection against diseases.

2 – The Soil Microbiome

Soil is a large reservoir of microorganisms interacting with plants in a variety of ways. For example, soil microorganisms play a crucial role in biogeochemical processes such as the decomposition of organic matter and the regulation of C and N cycles (Maul & Drinkwater, 2010, Nielsen *et al.*, 2011, Lavecchia *et al.*, 2015). They also play key roles in the growth of plants and strongly regulate plant nutrient uptake (Nielsen *et al.*, 2015). The interaction between plants and soil microorganisms can be positive, neutral or negative (Rasmussen *et al.*, 2013). Positive interactions include symbiotic associations of plants with arbuscular mycorrhizal fungi (AMF) and microbes that promote plant growth, whereas negative interactions include pathogenesis and competition for nutrients (Bais *et al.*,

2006). The result of the interaction depends on many factors such as plant species and genotype, soil type, soil microbial community diversity and abiotic factors (Philippot *et al.*, 2013, Van der Putten *et al.*, 2013). For example, the study by Govindasamy *et al.* (2017) indicated that the soil plays a crucial role in the rhizobacterial endophyte composition of four sorghum cultivars. Moreover, inorganic and organic fertilizers can influence the composition of soil bacterial communities (Marschner *et al.*, 2001) and in turn the plant rhizosphere microbiome assembly. In this sense, Lavecchia *et al.* (2015) found that the taxonomic composition of bacterial communities inhabiting the sorghum rhizosphere are more affected by organic fertilization with compost than by inorganic fertilization with urea.

3 – The Root Microbiome

Plant roots can be divided into three main compartments, i.e. the rhizosphere, rhizoplane and endosphere. The rhizosphere is defined as the small zone surrounding and influenced by the plant root via the release of root-derived compounds that select and activate members of the soil microbial community (Hiltner 1904). The rhizoplane is the surface of the plant roots, whereas the endosphere represents internal root tissue, including the vascular system. Nunan et al. (2015) suggested that the influence of plant root-derived compounds on the microbial community is likely to be greater in the rhizoplane than in the rhizosphere (Nunan *et al.*, 2005). In this regard, as the rhizosphere microbial community is considered to be a subset of the microbial community of the bulk soil (Mendes *et al.*, 2014, Lima *et al.*, 2015, Cipriano *et al.*, 2016, Yan *et al.*, 2016), the rhizoplane microbial community is a subset selected from the rhizosphere. A second level of selection from the root microbiome occurs when going from the rhizoplane into the endosphere (Edwards *et al.*, 2015). Studying the structure and assembly of root-associated microbes in rice, Edwards *et al.* (2015) found that the bacterial diversity decreased going from rhizosphere to endosphere. Once inside the host, endophyte communities change their metabolism and become adapted to the internal environment (Turner *et al.*, 2013, Mitter *et al.*, 2017). Microbial endophytes may accelerate seedling emergence, modify root morphology, help plants to remove contaminants, solubilize phosphorus, enhance uptake of other plant nutrients and promote plant growth (Dudeja *et al.*, 2012).

Within the root microbiome, plant growth-promoting rhizobacteria (PGPR) are functionally highly relevant microbial groups. PGPR are defined as rhizosphere microbiota that, in association with their host plants, directly or indirectly stimulate root and/or shoot growth (Bhattacharyya & Jha, 2012). PGPR can promote plant growth by facilitating resource acquisition or modulating plant hormone levels, decreasing the inhibitory effects of pathogenic agents on plant development,

increasing the availability of nutrients in the rhizosphere, increasing root surface area, and enhancing beneficial symbiosis (Bhattacharyya & Jha, 2012, Glick, 2012). For sorghum, recent studies focused on the mechanisms of sorghum root microbiome recruitment and composition (Lavecchia *et al.*, 2015, Mareque *et al.*, 2015), whereas other studies investigated the potential effects of PGPR on sorghum growth, yield, nutrient uptake and abiotic stress alleviation (Ali *et al.*, 2009, Cobb *et al.*, 2016, Dhawi *et al.*, 2016, Dos Santos *et al.*, 2017).

3.1. - Root Microbiome Assembly by Rhizodeposition

Through a variety of mechanisms such as exudation, secretion, mucilage production, and cell debris, roots provide a variety of compounds such as carbohydrates, amino acids, phenolic compounds, sugars and inorganic ions to their surrounding soil microbiome (Haas & Défago, 2005, Haichar *et al.*, 2008, Bever *et al.*, 2012). Also communication between plant and soil microorganisms often begins by root exudation with a subsequent recognition and response by microorganisms at community and individual levels (Singh *et al.*, 2008). The structure of the bacterial and fungal members of the root microbiome changes with the quantity and quality of rhizodeposition. For example, studying the spatial and temporal dynamics and composition of the rhizosphere microbiome of white lupin roots, Marschner *et al.* (2002) found that the fungal community composition correlated with citric acid exudation, whereas the bacterial community composition correlated with cis-aconitic, citric and malic acid exudation.

The outcome of the chemical interplay between the plant roots and the recruitment of specific members of the soil microbiome depends, in part, on the ability and efficiency of these microbiome members to utilize specific root deposits for growth and activity (Bais *et al.*, 2006). The same root compounds that attract beneficial microorganisms may also attract plant pathogens (Mendes *et al.*, 2013) or parasitic plants (Bouwmeester *et al.*, 2007). This is the case for strigolactones which play an essential role in the establishment of AMF symbiosis but are also (mis)used by parasitic plants of the genera *Striga*, *Orobanche* and *Phelipanche* (Cavar *et al.*, 2015). Moreover, the same root exudates that increase the abundance of a specific group of bacteria could decrease others. For example, Huang *et al.* (2017) recently observed that *Sorghum halepense* [L.] Pers. secretes the phenolic compounds p-hydroxybenzoic acid (p-HBA) and p-hydroxybenzaldehyde (p-HBAL). The addition of p-HBAL to soil significantly increased the abundance of members of the Acidobacteria, Chloroflexi, Verrucomicrobia and Cyanobacteria but decreased the relative abundance of members of the Proteobacteria.

3.2. Other Drivers of Root Microbiome Assembly

Various other biotic and abiotic factors determine root microbiome assembly, including root architecture (Berg & Smalla, 2009, Lindedam *et al.*, 2009, Pérez-Jaramillo *et al.*, 2017), soil factors (Smalla *et al.*, 2001, Girvan *et al.*, 2003, Kuramae *et al.*, 2012, Serna-Chavez *et al.*, 2013), land use (Wakelin *et al.*, 2013), plant genotype (Miethling *et al.*, 2000, Smalla *et al.*, 2001, Kowalchuk *et al.*, 2002), and plant growth stage (van Overbeek & van Elsas, 2008). As soil has a wide range of properties that may, independent or in combination, influence the growth and activities of microorganisms, soil is often reported as the major factor in shaping the rhizosphere microbiome (Singh *et al.*, 2007, Xu *et al.*, 2009, Kuramae *et al.*, 2012). Soil factors that influence the root microbiome composition include soil moisture, pH, organic matter content and nutrient availability (Kuramae *et al.*, 2012, Serna-Chavez *et al.*, 2013), soil type (Girvan *et al.*, 2003) and soil history (Smalla *et al.*, 2001).

The rhizosphere microbial community composition may vary during plant growth and development (Chaparro *et al.*, 2014). Different factors may be responsible for this temporal change, including seasonality. For example, in spring and summer due to the higher temperatures, the soil microbial community often increases its metabolic activity in conjunction with the accelerated mineralization of soil organic matter and accelerated root growth (Grayston *et al.*, 2001). During plant growth, rhizodeposition changes as well as root architecture (Marschner *et al.*, 2004). Chaparro *et al.* (2013) observed higher exudation of sugars and sugar alcohols at early stages of plant growth than at later growth stages, whereas the content of amino acids and phenolics increased with plant age. Micallef *et al.* (2009) found that with plant age, the bulk soil and rhizosphere community converged to a similar community, which coincides with the expected reduction in root exudation when plants are close to the end of their life cycle.

Also plant genotype is an important factor driving root microbiome assembly (Ettema & Wardle, 2002, Berg & Smalla, 2009). Several studies have shown that plant genotypes can recruit beneficial microorganisms to help plants against pathogenic attacks (Rudrappa *et al.*, 2008, Berendsen *et al.*, 2012, Yoon *et al.*, 2016). Therefore, plant genotype selection has been proposed as a means to stimulate the frequency and/or activities of PGPR (Cook, 2007, Picard & Bosco, 2008). Aiming to find bacterial isolates that significantly inhibited sorghum fungal pathogens, Funnell-Harris *et al.* (2013) found that the sorghum genotype affected the selection and persistence of *Pseudomonas* spp., which have the potential to ameliorate sorghum diseases. Yoon *et al.* (2016) found that the efficiency of *Gluconacetobacter diazotrophicus* in colonizing sorghum roots varied among

different genotypes, being higher in sweet sorghum genotypes than in grain genotypes. Dos Santos *et al.* (2017) further found that grain and forage sorghum genotypes exhibited superior nutritional and productivity responses to inoculation with a mixture of the PGPB bacteria *Herbaspirillum* and *Burkholderia* as compared with sweet sorghum.

The mechanisms underlying compatibility between the plant genotype and the indigenous microbial community or introduced microbial inoculants are not well understood yet, but differences in rhizodeposition between different plant species and genotypes are most likely a key determining factor. For sorghum it is know that a variety of root derived products is genotype specific (Czarnota *et al.*, 2003). For example, Mohemed *et al.* (2016) showed that sorghum genotypes Korokollow, Fakimustahi and Wadfahel exuded the highest amounts of the strigolactone 5-deoxystrigol while the genotypes Wadbaco and SRN-39 produced the highest amount of orobanchol. Akiyama *et al.* (2010) suggested that both orobanchol and 5-deoxystrigol induce hyphal branching of the arbuscular mychorrizal fungi *Gigaspora margarita*. Moreover, Tesfamariam *et al.* (2014) found that different sorghum genotypes produced different amounts of sorgoleone that plays a predominant role in the inhibition of nitrification in the rhizosphere. Sorgoleone inhibited the activity of *Nitrosomonas*, which is one of the bacterial groups responsible for the nitrification process (Tesfamariam *et al.*, 2014). Despite these effects on specific root-associated microorganisms, however, little is known about the overall effect of strigolactones on the sorghum root microbiome.

Although the rhizosphere microbiome composition changes according to the plant species, plant genotype, soil type and developmental stage, there is also a group of microbiome members that remains stable for the aforementioned factors and is referred to as the core microbiome (Lundberg *et al.*, 2012, Yeoh *et al.*, 2016, Pfeiffer *et al.*, 2017). Yeoh *et al.* (2016) found that despite striking differences in the composition of two soil microbial community investigated, sugarcane root microbiome showed a bacterial core enriched by *Bradyrhizobium, Rhizobium, Burkholderia, Herbaspirillum, Bacillus* and *Streptomyces* relative to bulk soil. Pfeiffer *et al.* (2017) suggested that the bacterial taxa *Microvirga zambiensis*, *Bradyrhizobium* sp., *Sphingobium vermicomposti*, the genus SMB53 of the *Clostridiaceae* family and the actinobacterial species *Blastococcus* sp. were tightly associated with potato rhizosphere irrespective of site and vegetation stage. Lundberg *et al.* (2012) observed that from 256 OTUs identified in the root compartments rhizosphere and endosphere and in soil, 164 OTUs were defining the *Arabidopsis thaliana* endophytic compartment core microbiome. It should be emphasized, however, that core microbiome data reported to date are mostly based on taxonomy and not on functional traits of the microbiome.

3.3. Impact of Disturbances on Root Microbiome Assembly

Disturbances are defined here as events that alter environmental conditions such that a microbial community is impacted. Disturbances are generally classified as *pulses* or *presses*. While a pulse disturbance is short-term disturbance that rapidly diminishes, a press disturbance is characterized as a continuous event maintained over longer periods of time (Bender *et al.*, 1984, Lake, 2000). Many biotic and abiotic disturbances may alter the soil microbial community, which in turn influence the functioning of the soil ecosystem (Lavecchia *et al.*, 2015, Suleiman *et al.*, 2016). Because of its sensitivity to disturbances, soil and root microbial communities are considered as bioindicators of soil quality (Mendes *et al.*, 2013). Under the influence of an abiotic disturbance, microbial communities can be resilient, tolerant, resistant or susceptible (Shade *et al.*, 2012). Microbes that can cope with abiotic disturbances might be beneficial to plants by alleviating stress conditions through diverse mechanisms like enhanced water and nutrient uptake, stimulation of plant growth by hormones such as indole acetic acid (IAA) and by triggering the plants' defense systems to biotic and abiotic stresses (Kavamura *et al.*, 2013, Rolli *et al.*, 2015).

Some bacterial genera are able to withstand drought better than others. To overcome stress effects, microbes rely on different physiological and morphological strategies such as dormancy, spore formation, growth rate changes and exopolysaccharide production (Sandhya *et al.*, 2009, Vurukonda *et al.*, 2016, Naylor *et al.*, 2017). Under moisture stress conditions, Actinobacteria have been reported to enrich in soil (Bouskill *et al.*, 2013), rhizosphere (Taketani *et al.*, 2017) and endosphere (Naylor *et al.*, 2017). In soils of the Brazilian semi-arid region, Taketani *et al.* (2017) determined the rhizosphere bacterial community composition of two different leguminous tree species: *Mimosa tenuiflora* and *Piptadenia stipulacea* during the dry and rainy season. They found that during the dry season the abundance of Actinobacteria increased in the rhizosphere of the two tree species whereas their abundance decreased during the rainy season. Barnard *et al.* (2013), studying the responses of soil bacterial communities to extreme desiccation and rewetting, showed that Actinobacteria (Actinomycetales order) strongly increased in relative abundance when exposed to water stress which was reversed again after rewetting. Actinobacteria have the capability to produces spores in response to drought stress which allows them to remain in a dormant state for a long period of time (Fang *et al.*, 2017).

The composition of the root microbiome of plants growing under drought conditions can be different according to the plant genotype or growth stage. For example, Naylor et al. (2017) found that bacterial communities associated with the rhizosphere of 18 plant species, including two sorghum

varieties, exposed to drought can change bacterial community composition at later stages of plant growth. Furthermore, bacterial species like *Pseudomonas* and *Rhizobium,* often found in the sorghum rhizosphere (Matiru & Dakora, 2004, Funnell-Harris *et al.*, 2013), appeared to be well adapted to stress conditions possibly due to the production of exopolysaccharides (EPS) (Sandhya *et al.*, 2009, Alves *et al.*, 2014). Casanovas *et al.* (2002) and Marasco *et al.* (2012) further showed that representatives of the bacterial genera *Azospirillum, Achromobacter, Klebsiella and Citrobacter* have the potential as PGPR to alleviate plant drought stress. Yandigeri *et al.* (2012) showed that the drought-tolerant endophytic actinobacteria promote growth of wheat under water stress conditions. Similarly, Sandhya *et al.* (2009) showed that *Pseudomonas putida* strain GAP-P45 inoculated onto sunflower seedlings relieved drought stress, increased plant survival and plant biomass through the production of exopolysaccharides. Also sorghum inoculated with *Rhizobium* showed increased yields under drought stress, although these effects were genotype dependent (Rashad *et al.*, 2001). Govindasamy *et al.* (2017) studied the functional and phylogenetic diversity of culturable rhizobacterial endophytes of sorghum growing at different moisture conditions and found a dominance of *Bacillus* species among the isolates identified to present at least one PGPR trait that could alleviate water stress. Interestingly, sorghum inoculated by four *Bacillus sp.* strains isolated from sorghum rhizosphere cropped at semi-arid locations, showed a higher relative water content of leaves and soil moisture content compared to the non-inoculated control treatment (Grover *et al.*, 2014). In this context, the authors proposed that microorganisms isolated from stressed ecosystems may be ideal candidates to be applied as bio-inoculants in crops susceptible to the respective stress condition (Grover *et al.*, 2014).

4 –Microbial Inoculants

Following detailed plant microbiome analyses, numerous bacterial and fungal genera have been isolated from rhizosphere, rhizoplane and endosphere and tested for their beneficial effects on plant growth and health (Berendsen *et al.*, 2012, Funnell-Harris & Sattler, 2014, Vasanthakumari & Shivanna, 2014). Indeed, application of microbial inoculants to plants has been shown to be a promising practice to increase plant growth, crop yield, and resistance to plant pathogen (Dutta *et al.*, 2014, da Silveira *et al.*, 2016). Microbial inoculants have also been employed as part of integrated nutrient management systems (Richardson *et al.*, 2011). To date, PGPR and AMF are the most common microorganisms used for plant inoculation. PGPR can be applied to seeds or seedlings prior to be transferred to their growth substrates (e.g. rockwool, soil) (Cipriano *et al.*, 2016) or applied to

the substrate after seeds or seedlings have been transferred (Malusa *et al.*, 2012, Dos Santos *et al.*, 2017). For sorghum, several studies over the past five years have indicated that PGPR treatment reduced diseases caused by fungal pathogens, increased plant biomass, nutrient uptake and yield (Funnell-Harris *et al.*, 2013, Yoon *et al.*, 2016, Dos Santos *et al.*, 2017)

While most studies to date focused on microbial inoculants with one single microbial strain, there is an increased interest in designing consortia of microorganisms with different synergetic modes of action (Rajasekar & Elango, 2011, Dos Santos *et al.*, 2017). Consortia containing different microorganisms with supplementary or synergistic characteristics are presumed to be more effective or more consistent than single microbial inoculants (Mendes *et al.*, 2013). For example, Artursson *et al.*, (2006) and Bonfante & Anca (2009) showed a beneficial effect of PGPR and AMF co-inoculation on AMF symbiosis. Hameeda *et al.* (2007) found that application of bacterial isolates together with AMF provided in 45 days the same or greater plant and root growth and mycorrhizal colonization than provided by the AMF inoculum alone in 90 days. Also Dhawi *et al.* (2016) found that the combination of PGPR with AMF increased sorghum biomass more than the treatment with AMF alone. Similarly, Duponnois *et al.* (2006) observed that strains of fluorescent pseudomonads in combination with AMF, increased heavy metal tolerance, mycorrhizal colonization and shoot length of sorghum.

Although these examples indicated additive and synergistic effects of the interaction of PGPR and AMF, it remains a challenge to establish compatibility and enhanced activity within a microbial consortium. Furthermore, the costs and technical complexity involved in the creation of single and combined microbial inoculants, together with legislative and regulatory obstacles, is a major impediment in the development of this microbial technology. Hence, alternative techniques to large-scale microbial inoculant production and registration are needed. An alternative that contemplates inoculum production in a broad perspective is microbiome transplantations (Gopal *et al.*, 2013). In this sense, mixing small amounts of naturally disease suppressive soil into a disease-conducive soil has been shown to be a successful alternative pathogen abatement (Weller *et al.*, 2002, Mendes *et al.*, 2011). Understanding the keystone microbial taxa involved in the transferability and predictability of these microbiome-associated plant phenotypes (Oyserman *et al.*, 2018) is an essential element of future research to construct microbial inoculants that provide effective and consistent effects under diverse field conditions.

Outstanding Questions in this thesis

What is the relative importance of plant genotype, plant growth stage and soil type on the composition of the sorghum rhizobacterial community?

Are fungal-bacterial interactions in the sorghum rhizosphere modulated by plant genotype, plant growth stage and/or soil type?

Can rhizobacterial communities contribute to drought tolerance of sorghum?

Are bacterial communities recruited from soil with a history of sorghum cultivation and drought more effective in conferring drought tolerance?

Are endophytic strains, characterized as PGPB in sugarcane, able to provide beneficial effects on sorghum performance?

Thesis outline

In **Chapter 2,** I describe the differences in rhizobacterial community composition of seven different sorghum cultivars grown in the greenhouse in two different soil types at four different plant growth stages. The aim of this work was to evaluate the relative impact of each factor (soil type, cultivar, plant growth stage) on the sorghum rhizobacterial community composition. The rhizobacterial taxonomic composition was assessed by high-throughput 16S rRNA amplicon sequencing. Also, the profile of strigolactones exuded by roots of the different sorghum cultivars was assessed and correlated with rhizobacterial community composition.

The goal of the work described in **Chapter 3** was to study the co-occurrence of bacterial and fungal communities in the rhizosphere of different sorghum cultivars. For this purpose, I selected a subset of the DNA samples from the rhizosphere of two sorghum cultivars, two soils and three plant growth stages from the initial mesocosm experiment described in Chapter 2. The taxonomic composition of rhizobacterial and fungal communities was assessed by high-throughput 16S and 18S rRNA amplicon sequencing, respectively. Subsequently, I investigated if fungal-bacterial interactions in the sorghum rhizosphere are modulated by soil type, plant genotype and plant growth stage.

Chapter 4 addresses the effects of different rhizobacterial community compositions on growth and drought tolerance of sorghum. I aimed to pinpoint possible bacterial taxa associated with plant water stress alleviation. For that, we used a microbiome transplantation approach to minimize the effects of abiotic characteristics on plant growth and plant stress alleviation. I analysed the

diversity and relative abundance of rhizobacterial communities from two sorghum cultivars (drought susceptible, drought tolerant) that were pre-cropped in five microbiologically and physico-chemically different soils and subsequently transplanted to a standardized soil and exposed to drought stress.

In **Chapter 5**, the effects of five endophytic bacterial strains on the growth of four sorghum cultivars are described **.** These bacterial strains were originally selected as PGPB of sugarcane and were tested here for their beneficial effects on sorghum growth. Dry biomass and root architecture were evaluated as indicators of plant growth. Furthermore, I checked if their PGPB effects could be linked to the plant genotype and bacterial isolate identity.

In **Chapter 6,** I provide a general discussion of the main findings of this thesis and highlight the importance of sorghum-microbiome interactions. I discuss the approaches used in this thesis to give future directions and perspectives for fundamental research as well as for practical application of the knowledge obtained.

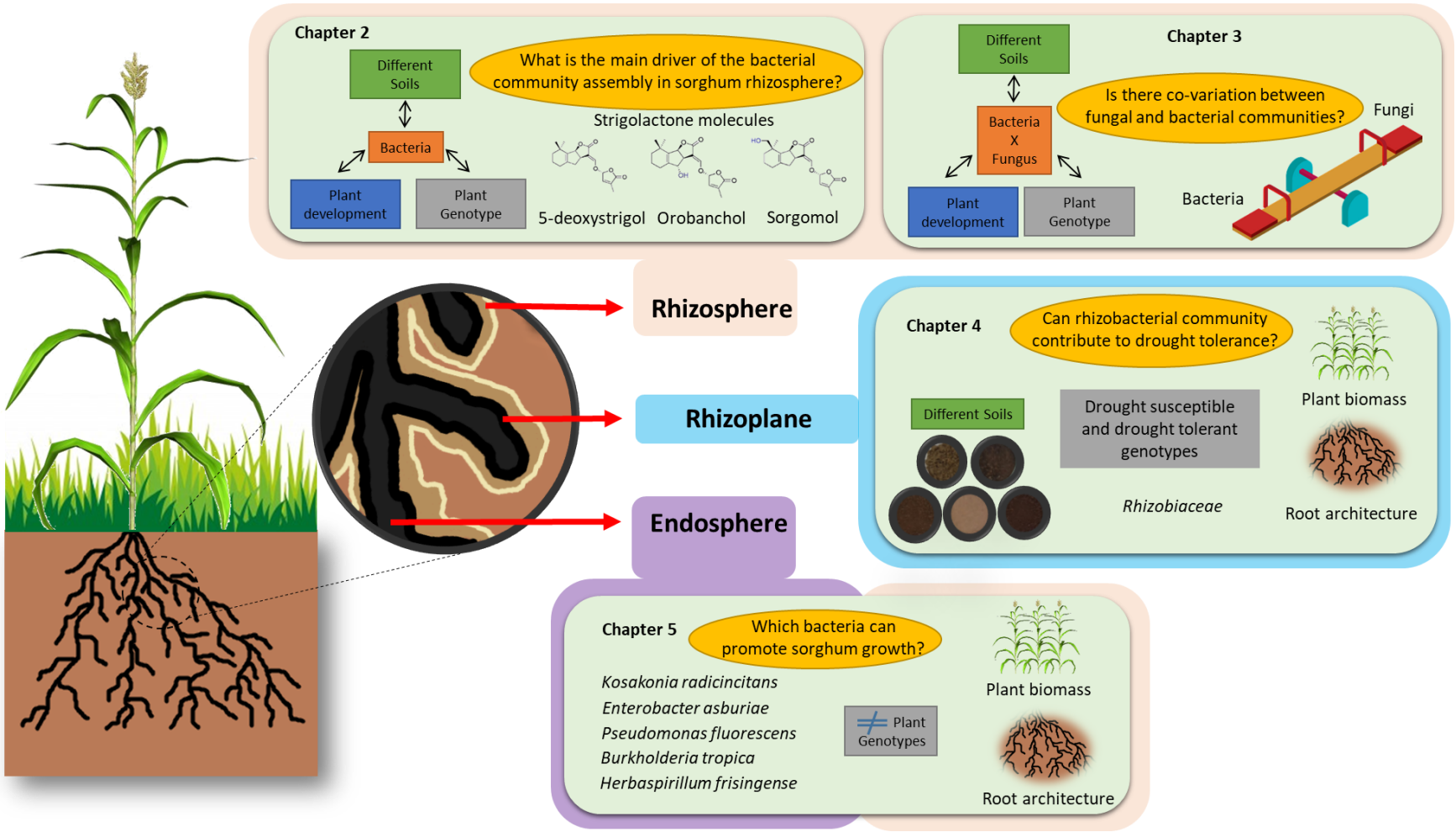

Figure 1. Schematic overview of the chapters presented in this thesis.