



# Plant drought resistance is mediated by soil microbial community structure and soil-plant feedbacks in a savanna tree species



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## ARTICLE INFO

### Keywords:

Climate change  
Phospholipid fatty acid analysis  
Plant functional traits  
Plant-soil (below-ground) interactions  
Soil microbes  
Savanna ecosystems

## ABSTRACT

Soil microbial communities have the potential to modify plant performance and condition plant species responses to environmental change, but the role of soil microorganisms for plant drought responses remains unclear. We used a novel experimental approach to examine the interactive effects of drought and presence of soil microbes on biomass production and plant traits in a savanna tree species. Seedlings of *Bauhinia brachycarpa* were grown in sterilized or 'live' soil, with or without drought, during a 24-week greenhouse experiment. Soil microbial community structure was assessed with phospholipid fatty acid analysis and soil-plant feedback effects were measured. Both drought and the presence of soil microbes decreased plant growth and biomass produced per gram nitrogen (a proxy for N use efficiency) but increased biomass allocation to roots. However, the presence of soil microbes increased plant drought resistance, driven by weakened soil-plant feedbacks under dry conditions. Experimental drought was associated with an increase in the Gram positive: Gram negative bacteria ratio, but did not affect the fungi: bacteria ratio or total microbial biomass. Our results suggest that soil microbes mediate plant responses to drought via soil-plant feedbacks and drought-induced changes in microbial community structure. These findings highlight the importance of plant-soil interactions for improved mechanistic understanding of savanna function, and confirm that characteristics of the soil microbial community could have significant implications for ecosystem stability in a changing environment.

## 1. Introduction

Savannas are a widespread and diverse tree-grass ecosystem, providing important services such as carbon sequestration, livestock production and biodiversity (Scholes and Archer, 1997; Baudena et al., 2015). Within these systems, changes in tree cover can have significant consequences for ecosystem function and earth-atmosphere feedbacks (Druce et al., 2008; Baudena et al., 2015). Along with fires and land-use change, water availability is considered to be a key driver of tree abundance in savanna systems (Bond, 2008). As precipitation patterns are expected to shift in the future (IPCC, 2007), understanding the mechanisms of drought tolerance in savanna tree species is central to predicting future savanna ecosystem function and resilience to climate change (Craine et al., 2013).

Impacts of drought on plant physiology and growth are well documented, and numerous studies have examined the role of plant traits for plant drought tolerance (Chaves et al., 2003; van der Molen et al., 2011; Zwicke et al., 2015). However, growing evidence suggests that plant

species responses to environmental change may also be mediated by soil microorganisms (Yang et al., 2009; Bloor and Bardgett, 2012; Fuchslueger et al., 2014; Kannenberg and Phillips, 2017; Fry et al., 2018). Soil microbial communities have the potential to influence plant growth and functional traits via changes in soil properties and the accumulation of soil pathogens or mutualists (Friesen et al., 2011; Smith-Ramesh and Reynolds, 2017). Although soil feedback effects are often negative, microbial effects on plants can also be neutral or positive depending on the different microbial groups involved (Kulmatiski et al., 2008; van der Putten et al., 2013). For example, mycorrhizal fungi may be of benefit to water-stressed plants by increasing access to soil water, improving plant hydraulics and gas exchange, whereas fungal pathogens may exacerbate plant vulnerability to drought (Aroca and Ruiz-Lozano, 2009; Kannenberg and Phillips, 2017). Disentangling the contribution of soil microorganisms for plant drought responses is complicated as it requires the use of sterile growing medium in experiments. To date, the majority of studies on plant responses to drought have been carried out in the presence of soil microbes (but see Kannenberg and

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<https://doi.org/10.1016/j.envexpbot.2018.08.013>

Received 21 May 2018; Received in revised form 25 July 2018; Accepted 12 August 2018

Available online 15 August 2018

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**Table 1**

Effects of water treatments, soil treatments and their interaction on plant biomass and functional traits.

	df	Water treatment		Soil treatment		Water × soil	
		F	P	F	P	F	P
Total biomass	1, 20	169.7	< 0.001	315.2	< 0.001	49.79	< 0.001
Relative growth rate	1, 20	109.56	< 0.001	230.45	< 0.001	7.06	0.015
Shoot biomass	1, 20	67.02	< 0.001	29.28	< 0.001	12.69	0.002
Root: shoot ratio	1, 20	18.00	< 0.001	22.31	< 0.001	2.33	0.142
Specific leaf area	1, 20	0.66	0.426	0.75	0.396	2.10	0.163
Specific root length	1, 20	1.34	0.260	22.43	< 0.001	0.13	0.727
Plant N content	1, 20	82.36	< 0.001	50.90	< 0.001	0.86	0.366
Biomass: N ratio	1, 20	0.37	0.548	32.67	< 0.001	12.28	0.002

Phillips, 2017), and thus the importance of soil microbial communities for plant sensitivity to environmental fluctuations remains poorly understood.

Soil microbial effects on plants may be driven by microbial activity and microbial community structure, both of which are under the influence of abiotic factors (Lau and Lennon, 2011; van der Putten et al., 2016). In the case of drought, reduced soil water availability may directly depress soil microbial activity and biomass production (Schimel et al., 2007). Moreover, soil microbial communities may change under dry conditions due to the selection of drought-tolerant groups such as fungi (with lower nutrient requirements and a higher water acquisition capacity) or Gram+ bacteria (with a thicker peptidoglycan cell wall layer) (Williams and Rice, 2007; Manzoni et al., 2012). In theory, drought-induced shifts in soil microbial activity and community structure should modify plant-soil interactions for nitrogen (N) (Bloor and Bardgett, 2012) and the relative abundance of pathogenic fungi (van der Putten et al., 2013), with cascading effects on soil-plant feedbacks. In practice, few studies have simultaneously investigated above- and belowground responses to water availability and the consequences of soil-plant interactions for plant resistance to drought (Karlowsky et al., 2017).

Here we examine the effects of reduced water availability on plant growth and functional traits in seedlings of a savanna tree species, *Bauhinia brachycarpa*, growing in sterilized or unsterilized soil medium. The main objective was to investigate the linkages between plant drought resistance, soil microbial community structure and soil-plant feedbacks. We focus on the seedling stage since this is a bottleneck for successful tree recruitment in natural communities, and woody seedlings are known to show high sensitivity to biotic and abiotic conditions (Bloor et al., 2009; Comita et al., 2014). We hypothesize that: 1) presence of soil microbes has negative effects on plant growth; 2) plant drought resistance is modified in the presence of soil microbes. We also assess whether drought alters soil feedback effects due to drought-induced changes in either microbial biomass or community structure.

## 2. Material and methods

### 2.1. Experimental design

The greenhouse experiment was performed at the Xishuangbanna tropical botanical garden, Chinese Academy of Sciences, China (21°41'N, 101°25'E, 570 a.s.l.). The experiment consisted of two treatments in a factorial design: soil treatment ('live', sterile) and water treatment (wet, dry). Each of the four treatment combinations was replicated six times.

In May 2016, we collected *Bauhinia brachycarpa* seeds in a nearby savanna ecosystem (23°28'N, 102°10'E, 480 m a.s.l.); *Bauhinia brachycarpa* is a drought-tolerant species with small leaves and deep roots that dominates in the dry savanna ecosystem of the Yuanjiang valley, Yunnan, China. Seeds were surface-sterilized (1 min 75% ethanol, 3 min 2% NaOCl, 1 min 75% ethanol, 3 min distilled water), germinated in plug trays filled with sterilized sands, and left to grow for two weeks.

One week prior to seedling transplanting, field soil in the 0–15 cm soil layer was collected beneath mature *B. brachycarpa* trees in the Yuanjiang savanna ecosystem. Field soil was pooled and homogenized to avoid effects of soil heterogeneity. Half of the soil was kept at 5 °C whereas the remainder was steam-sterilized for 3 h at 121 °C and then kept at 5 °C prior to the start of the experiment.

Pots (14 cm diameter × 16 cm height) were filled with a sand, peat and soil mix (volume ratio of 6: 3: 1). All sand and peat used in the pots was steam-sterilized and soil used was either sterilized field soil (sterile soil treatment) or live field soil (live soil treatment). On 27 August 2016, one tree seedling was transplanted into each pot, and all seedlings were left to grow with regular watering in the greenhouse conditions for nine weeks. Pots were randomly located in the greenhouse and re-arranged weekly to avoid possible positioning effects. From 29 October 2016 onwards, seedlings allocated to the 'wet' treatment received water addition based on the precipitation regime in the Yuanjiang savanna ecosystem during the wet season, whereas seedlings in the 'dry' treatment had an 85% reduction in watering regime, equivalent to the average precipitation regime during the dry season. In the 'wet' treatment, pots received two or three watering events per week, resulting in a total water addition of 348 ml (equivalent to the average rainfall of 589.9 mm in the wet season i.e. May–October, based on long-term weather records). 'Dry' treatments received 61 ml of water weekly (equivalent to the average rainfall of 104.1 mm in the dry season i.e. November–April). Plants were left to grow for a further 15 weeks under these watering regimes. Over the total experimental period, the average air temperature was 24 °C, and the average air humidity was 67% (consistent with long-term weather records for the Yuanjiang valley).

### 2.2. Plant sampling and calculations

Initial seedling dry mass was determined at the date of seedling transplantation for 13 individual seedlings by harvesting, oven-drying (70 °C for 72 h) and then weighing. All remaining experimental plants were harvested in mid-February 2017 and separated into shoots and roots. Roots were washed to remove soil and organic debris. Specific leaf area (SLA, the one-sided area of a fresh leaf divided by its oven-dry mass, m<sup>2</sup> g<sup>-1</sup>) and specific root length (SRL, the ratio of root length to dry mass of fine roots, m g<sup>-1</sup>) were determined following standard protocols (Pérez-Harguindeguy et al., 2013). We chose specific leaf area and specific root length, as they are key plant traits in predicting plant-soil feedbacks (Baxendale et al., 2014; Cortois et al., 2016). SLA was measured on 2–4 fully expanded fresh leaves per individual. Leaf area was determined using ImageJ software after scanning with a flatbed scanner (Canon Lide 120, Canon, Japan). SRL was measured on a subsample of fine fresh roots per individual. Root length was measured using SmartRoot software (Lobet et al., 2011) and a flatbed scanner (Canon Lide 120, Canon, Japan). All shoots and roots were then oven-dried at 70 °C for 72 h to determine dry mass. Shoot biomass, root biomass and total biomass were used as measures of plant growth. Dried shoot and root material were ground and analysed for whole-

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