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Investigating possible effects of climate change on tree recruitment: Responses of abundant species to water stress in Gorongosa National Park

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ABSTRACT

Climate change is predicted to manifest in more extreme droughts in large parts of Africa. Investigating how species' distributions may change in response to drought is therefore necessary for understanding ecosystem functioning, and it will also help inform land managers regarding changes in resource availability. This work can be approached at the species and population levels with greenhouse studies that demonstrate changes in plant growth and allocation patterns in response to water stress. The present study contributes to this research need by investigating the effects of water stress on seedlings of three abundant tree species at Gorongosa National Park (GNP). GNP is the site of intense conservation efforts and is predicted to suffer from increased drought in the near future. *Combretum adenogonium*, *Vachellia xanthophloea*, and *Faidherbia albida* are abundant trees in the park and are found across a moisture gradient. A water stress treatment showed that seedlings of *C. adenogonium* may be least affected by future drought, and *V. xanthophloea* may be able to adapt to drought by maintaining root biomass even as aboveground growth decreases. *F. albida* is found in the wettest areas of the park where trees grow, and population level differences show individuals from a drier region invest more in roots under moderate water stress. Together, these data suggest that these three species may continue to establish under drought conditions, but if water stress is prolonged, the ranges of *V. xanthophloea* and *F. albida* may contract.

1. Introduction

Climate change is predicted to affect the African continent in diverse ways. Northern and southern regions may experience greater drought while eastern Africa is expected to become wetter (Boko et al., 2007; Niang et al., 2014). Mozambique will be uniquely affected by changes in precipitation as the country stretches across the climatic divide between what will be the wetter East and the drier South. The northern half of Mozambique is expected to receive more rain, while the south is predicted to suffer from increased drought (McSweeney et al., 2010a). In reality, the future tense is misused here as Mozambique has been experiencing measurable climatic changes since the 1960's. Temperature rose 0.6 °C, and average precipitation decreased 6.3 mm per month of the country's rainy season between 1960 and 2006 (McSweeney et al., 2010a, 2010b). Rising temperatures and increased water stress are therefore very real phenomena in Mozambique, and understanding their effects on the nation's ecology is of critical importance to conservation.

Mozambique was once home to vast numbers of wildlife, but the abundance of large mammals was reduced by more than 90% in many cases during the country's protracted civil war (Lindsey and Bento, 2012). Although Mozambique now has an impressive amount of protected areas (encompassing ~16% of the nation's territory; CBD, 2015), ensuring the future security of these ecosystems will depend in part upon mitigating and adapting to climate change. This is particularly true in Gorongosa National Park (GNP); impressive conservation efforts underway there are successfully restoring the park's rich fauna (Stalmans et al. in prep). However, modeling exercises for the region encompassing GNP show it will likely experience a delay in the onset of the rainy season by one month, a 10% decrease in precipitation, and a 1.5–2 °C rise in temperature between 2021 and 2050 (Andersson et al., 2011). Understanding changes in vegetation resulting from these climatic extremes will help inform the park's future adaptive management.

The present study was therefore undertaken to investigate the regenerative success of three of the park's abundant tree species, *Combretum adenogonium* (Combretaceae), *Faidherbia albida* (Fabaceae), and *Vachellia xanthophloea* (Fabaceae). Seedlings are particularly vulnerable just after germination, so this work focuses on the first months of seedling establishment (Fenner, 2000). To understand potential changes in the survival of these three dominant species as climate becomes more xeric, this study addressed the hypothesis that seedlings of the focal species may respond differently to water stress, with

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C. adenogonium being most resistant to drought conditions, while *F. albida* may be most susceptible to water stress. It was also hypothesized that populations may already be differentially adapted to local soil water conditions. The broader aim of this work is to generate data that can inform projections regarding possible changes in the spatial distribution and abundance of dominant woody species in GNP.

2. Material and methods

2.1. Study site

Gorongosa National Park is at the southernmost end of Africa's Great Rift Valley (18°58′04.84″ S, 34°21′41.64″ E). It encompasses vast ecological diversity ranging from Afromontane rainforest, miombo, riverine forest, wooded savannas, to open floodplain. The center of the park (primarily wooded savanna and floodplain with riverine forests) received an average of 824 (±354 SD) mm of rain annually since 2000. Rainfall is highly seasonal with a pronounced wet season between December and February. Seeds of the three study species were collected from wooded savannas (*C. adenogonium* and the drier population of *V. xanthophloea*), riverine forest (the wetter population of *V. xanthophloea*), and the wet edges of the floodplain (*F. albida*).

A survey of over 900 randomly located trees was undertaken along more than 134 km of the park's road network; this encompassed multiple habitats in the Rift Valley sector of the park and a small stretch of the park's miombo. Along these roads, the three focal species accounted for over 36% of individuals; 11.4% of all trees were *C. adenogonium*, 10.5% were *F. albida*, and 14.5% were *V. xanthophloea*. Only two other species were comparable in terms of their abundance, *Philenoptera violacea* and *Acacia robusta* (Massad, unpublished data). *Combretum adenogonium* grows in the park's drier regions, outside its seasonally flooded zones. *V. xanthophloea* is widely distributed throughout the section of the Rift Valley contained in the park and is dominant in mesic regions that do not necessarily flood. *F. albida* grows in nearly monospecific stands in areas that flood with close to annual regularity.

2.2. Experimental methods

Seeds were collected between September and October 2014, as species were fruiting. Seeds were collected from beneath five different trees in a population (distance between adult trees <100 m) in areas expected to represent wetter and drier extremes of their range to test for local adaptations to different soil moisture regimes. These designations were based on elevation, proximity to a river, and proximity to the floodplain; hereafter, populations are described as 'wetter' or 'drier.' Six soil samples were taken from around each adult tree, three at about 10 cm depth and three at about 40 cm depth. Samples were weighed wet and then oven dried at 50 °C and reweighed to determine soil moisture. This information was used to examine differences in soil moisture content at the collection sites of the wetter and drier populations.

Seeds were planted in January 2015 in 3 L seedling bags. To break dormancy, *V. xanthophloea* seeds were submerged in just boiled water over night before planting, and *F. albida* seeds were manually scarified. *C. adenogonium* seeds were planted without any preparation. Planting soil came from a single location near the center of the park removed from the sites of seed collection, but each seedling bag was also inoculated with a small amount of soil collected from around the adult trees to support the presence of appropriate mycorrhizae and other soil microbes. Upon planting, seeds were watered with 1 L of water, soil was maintained humid until the experimental treatment began. Seedlings were grown in an open air greenhouse covered with clear 180 μm greenhouse film that prevented rain from entering the greenhouse. The seedlings' positions on the greenhouse tables were randomly switched several times during the course of the experiment.

Once seedlings had developed their first true leaves, they were subjected to different levels of a water stress treatment. Levels of water stress were based on historic rainfall data from GNP. Monthly average precipitation between 1999 (when regular record collection began after the civil war) and 2004 (ten years before the initiation of the experiment) was calculated and applied to seedlings over the course of five watering events per month. Seedlings therefore received different amounts of water each month, concordant with historic levels of monthly precipitation. Plants in the high water (no water stress) level received a quantity of water equal to the monthly average rainfall. Plants subject to moderate water stress received a monthly amount of water equal to the first quartile of the historic monthly average. Plants under high water stress received half the amount of water as those in the moderate water stress level (Table 1). Seedlings were allowed to grow through May 2015, roughly four months after germinating and three months after the water stress treatment began. Due to the poor germination of many seeds, the hypothesis regarding local adaptation to soil moisture conditions could only be tested for *F. albida*.

Seedlings were harvested in June 2015. They were dried at 50 °C, and dry weights (DW) were obtained for leaves, stems, and roots. Root: shoot ratios (R:S) were also calculated. DW of the different plant parts were analyzed using MANOVA followed by profile analysis. Profile analysis allows for differences between multiple response variables to be explored. Predictor variables included were the water stress treatment, species, and their interaction. A separate MANOVA of *F. albida* tested the effects of population and the water stress treatment as well as their interaction. Post hoc tests to examine differences between treatment levels were done with ANOVA followed by Tukey's Studentized Range Test for each response variable separately.

R:S were analyzed to determine the effect of the water stress treatment on the different species with ANOVA. When species were combined in a single model, differences between them obscured the effect of the water stress treatment, so they were analyzed separately. Population was included in the model for *F. albida*. Sample sizes were at most 10 individuals per half-sib family (seeds from the same mother tree) per water stress level, but due to poor germination, sample sizes varied between species (minimum sample size for a species by water stress level = 10; maximum = 62 for wet and dry populations combined in the MANOVA). DW and R:S were log transformed for normality; Type III sum of squares results are used because of unequal sample sizes (means, medians, ranges and sample sizes are available in Supplementary Table 1). All analyses were done with SAS/STAT® software (Version 9.3, Copyright 2011, SAS Institute Inc., Cary NC).

3. Results

Only seeds from the drier ranges of *C. adenogonium* and *V. xanthophloea* germinated (mainly due to insect damage), limiting an examination of population level differences to *F. albida*. At the time of seed collection (in the middle of the dry season), soils around the wetter and drier seed provinces were statistically equal ($F_{1,178} = 0.4$, $P = 0.5$).

Species invested differently in foliar, stem, and root biomass. Young *C. adenogonium* leaves had the highest DW across levels of the water treatment, and *V. xanthophloea* stems were consistently heaviest.

Table 1
Experimental watering regime. The values are mL water applied to the seedlings five times per month.

Month	No water stress (control)	Moderate water stress	High water stress
January	395	326	163
February	461	265	133
March	385	207	103
April	187	90	45
May	51	39	20