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

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A B S T R A C T

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.

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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 ($\pm$ 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

F. albida roots had the greatest biomass at high water levels. Water stress decreased biomass of most plant parts, although *V. xanthophloea* foliar and root DW did not change in response to water, and *C. adenogonium* stems were uniformly small across levels of the water treatment (MANOVA; Table 2; Fig. 1).

A significant interaction in the profile analysis resulted from different responses of plant parts to water levels depending on the species. Root DW was more strongly reduced by medium and low water levels in *C. adenogonium* and *F. albida* than in *V. xanthophloea*, and *C. adenogonium* root mass declined less than in *F. albida*. *C. adenogonium* stem DW was not affected by water levels, although water stress reduced stem biomass in both *F. albida* and *V. xanthophloea*. Foliar DW was least responsive to water stress; it did not change at all in *V. xanthophloea* and decreased in the other two species only with severe water stress (Table 2; Fig. 1). The R:S of *C. adenogonium* did not respond to the water stress treatment ($F_{2,38} = 0.8$, $P = 0.4$). The average R:S of *C. adenogonium* was 5.0 ± 0.7 (SE). In contrast, the R:S of *V. xanthophloea* did differ with water ($F_{2,36} = 4.4$, $P = 0.02$), increasing from an average of 0.6 ± 0.07 (SE) under low water stress conditions to 0.9 ± 0.05 (SE) under medium and high water stress.

The only species in which seeds from both wet and dry populations germinated was *F. albida*. MANOVA showed water stress was the only significant factor affecting biomass, and DW declined overall with water stress (Table 3). Nonetheless, the profile analysis uncovered a significant interaction between populations and the water treatment due to different responses of leaves, stems, and roots. The DW of leaves from the wet population was highest under high water conditions, and leaves from the dry population were more resistant to diminished water, dropping in biomass only under severe water stress. In contrast, stems of individuals from the wet population maintained high biomass under medium water stress, while stems from the dry population decreased in biomass with medium water stress. Root DW declined with water stress in both populations, but roots from the dry population were slightly heavier with intermediate water stress (Fig. 2).

The R:S of *F. albida* seedlings was affected by an interaction between the seedlings' population (wet vs. dry) and the amount of water received. Seedlings from the wet population under the greatest water stress had slightly higher R:S than individuals from other treatment levels. One individual in particular had a very high R:S; when this seedling was removed from the analysis, the interaction was still significant, but the highest R:S were among individuals from the dry population exposed to moderate water stress. The lowest R:S was measured among seedlings from the wet population under moderate water stress (Table 4; Fig. 3).

4. Discussion

Overall, this experiment looked at the response of three widely distributed species to water stress to understand how recruitment and species distributions may change with increased drought. The study

Table 2
MANOVA and profile analysis of the DW of leaves, stems, and roots. The overall effect of species and water levels are explained by the MANOVA, and differences between response variables are described by the profile analysis.

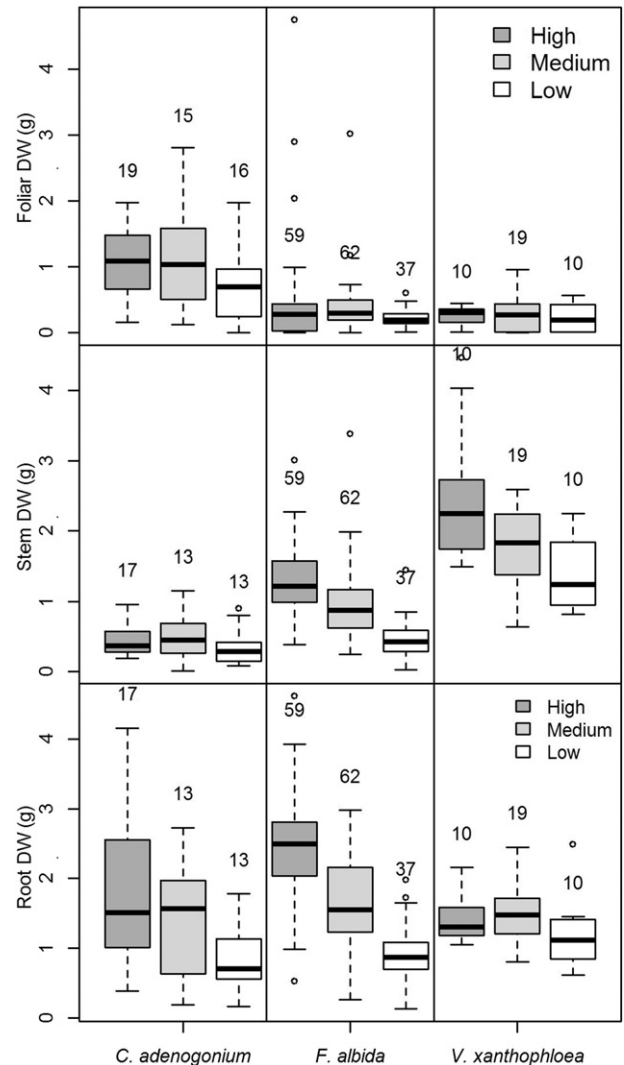| Variable	F	df	P
MANOVA			
Species	3.2	2	0.04
Water level	8.0	2	0.0005
Species * water	0.8	4	0.5
Profile analysis			
Species	58.7	2	<0.0001
Water level	5.1	2	0.007
Species * water	3.1	4	0.02

Fig. 1. Dry weights (g) of leaves, stems and roots of the three study species grown under high, medium, and low water conditions. Boxes include data between the lower and upper quartiles; lines represent the median; bars include all data except for outliers; circles represent outliers. *Faidherbia albida* and *V. xanthophloea* had statistically similar investments in root and leaf mass. Root and stem biomass differed across all levels of the water stress treatment, while leaf biomass was not affected. Sample sizes for *C. adenogonium* are 19 for the high water level, 15 for the medium water level, and 16 for the low water level. Sample sizes for *F. albida* are 59 for the high water level, 62 for the medium water level, and 37 for the low water level. Sample sizes for *V. xanthophloea* are 10 for the high water level, 19 for the medium water level, and 10 for the low water level.

species' present niches in GNP fall along a soil moisture gradient; *C. adenogonium* occupies drier areas, *V. xanthophloea* overlaps partially with *C. adenogonium* and also occurs in wetter habitats, and *F. albida* is found in the wetter range of *V. xanthophloea* but also occurs alone in the areas most likely to flood annually. The original hypothesis that these species would respond differently to water stress was supported, and analyzing these differences can help to formulate predictions regarding future changes in vegetation as Gorongosa's climate dries.

Along the Limpopo River in South Africa, *V. xanthophloea* is found in more mesic sites than is *F. albida* (O'Connor, 2010), but that is not true at GNP, which is wetter than other southern African sites where *V. xanthophloea* has been studied (O'Connor, 2010; Humphries et al., 2011). An examination of tree loss post-drought in South Africa showed 69.7% of *V. xanthophloea* mortality was due to drought, while just 31.8% of *F. albida* mortality could be ascribed to drought, suggesting *F. albida* is possibly more tolerant of water stress (O'Connor, 2010). These distributional and mortality data therefore suggest *F. albida* may be expected to

Table 3
MANOVA and profile analysis of *Faidherbia albida* leaves, stems and roots based on seed populations (wet vs. dry habitat) and watering regime.

Variable	F	df	P
MANOVA			
Population	0.0	1	0.9
Water level	31.6	2	<0.0001
Population * water	0.8	2	0.4
Profile analysis			
Population	1.9	1	0.2
Water level	18.8	2	<0.0001
Population * water	3.3	2	0.04

be more successful in a drier climate than *V. xanthophloea. Faidherbia albida* was also found to be prominent along the floodplain of the Zambezi River in Zimbabwe (Dunham, 1989) and the Limpopo River in South Africa (O'Connor, 2001).

However, the present study demonstrates the R:S of *V. xanthophloea* decreases under drought conditions, suggesting *V. xanthophloea* seedlings respond to water stress by allocating carbon belowground to support greater moisture acquisition. While this supports the hypothesis that *V. xanthophloea* may continue to successfully establish at GNP even in a drier climate, work from a more xeric region of Kenya found the R:S of *V. xanthophloea* does not change with water stress. Seedlings there had a R:S of 0.5 under conditions of both ample water and simulated drought (Otieno et al., 2001), while seedlings from GNP had an average R:S of 0.9 under well-watered conditions and a R:S of 0.6 with water stress. This may indicate that *V. xanthophloea* evolved greater plasticity where water is not limiting and will still be able to thrive as drought becomes more frequent in Gorongosa.

Even though *F. albida* appeared more drought tolerant than *V. xanthophloea* along the Limpopo (O'Connor, 2010), it occurs in the wettest areas where trees still manage to grow in GNP and is also prominent along the floodplain of the Zambezi River in Zimbabwe (Dunham, 1989) and the Limpopo River in South Africa (O'Connor, 2001). The present study suggests *F. albida* will be more affected by future drought than either *C. adenogonium* or *V. xanthophloea*. Leaves, stems, and roots of *F. albida* all lost considerable biomass with water stress. Interestingly, however, population level variation was detected, suggesting *F. albida* may be able to evolve to adapt to future climate conditions. Individuals from the dry population increased their R:S under moderate water stress relative to individuals from the wet population. This may be because they are better adapted to deal with soil moisture stress up to a point. With extreme water stress, the two populations have equivalent R:S if the outlier with a very high R:S is omitted. Alternatively, soil moisture may not be driving differences between the populations under study, perhaps because conditions are too similar to play a role in differential selection.

F. albida seedlings invested more in root biomass than did the other species, and adults are known for developing deep root systems (Roupsard et al., 1999). The species' stomata are also very responsive to water stress, potentially mitigating the effects of drought (Roupsard et al., 1999). These characteristics may mean that, like *V. xanthophloea*, *F. albida* will be resistant to drought stress in GNP. Nonetheless, soil water stress does decrease the growth of *F. albida* seedlings, and even drought-induced investment in root growth has a limit when water stress is too great (Stave et al., 2005). In addition, because *F. albida* is strongly dependent on moisture deep within soils, light rains may not be sufficient to enable growth in the long term (Stave et al., 2005).

C. adenogonium grows much more slowly than the other two species, but it maintained a constant stem mass across treatments, and its root mass declined less than *F. albida*'s. *C. adenogonium* therefore appears to be the least affected by water stress overall, as it managed to support constant aboveground growth, and its root mass did not change enough
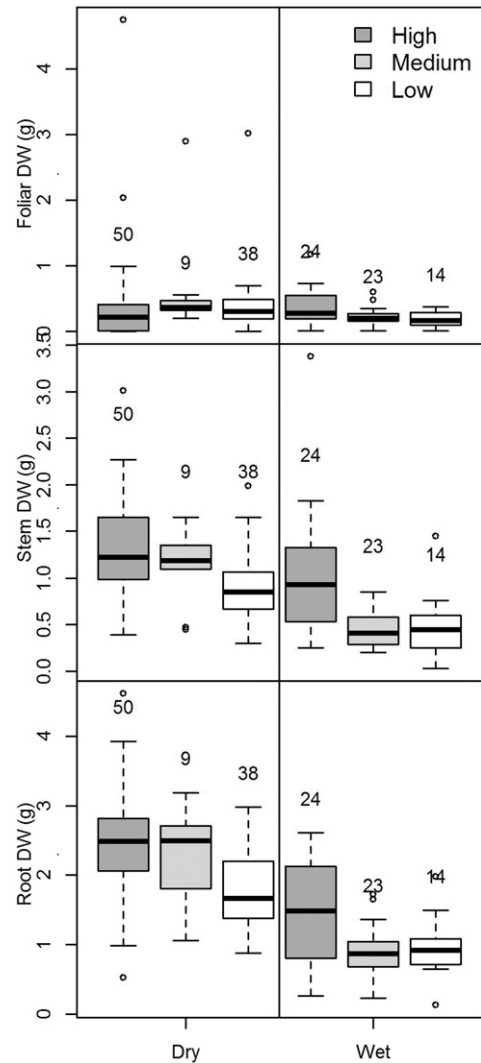

Fig. 2. Biomass of *Faidherbia albida* seedlings from populations found in frequently flooded (wet) vs. less frequently flooded (dry) areas. Box plots are as described in Fig. 1. Post hoc tests showed leaf biomass did not vary with treatment levels. Seedlings from the drier population invested more in roots. Root and stem biomass were greatest without water stress and reduced under the highest water stress. Sample sizes from the drier population are 50 for the high water level, 38 for the medium water level, and 23 for the low water level. Sample sizes from the drier population are 9 for the high water level, 24 for the medium water level, and 14 for the low water level.

to alter its R:S. This species may be expected to potentially expand rather than contract in distribution in a drying climate.

Climate will not operate in isolation, however. The combination of drought stress and high herbivory reduces tree growth and increases mortality (Birkett and Stevens-Wood, 2005). Herbivore populations are recovering in Gorongosa, and this, too, will affect seedling recruitment and species distributions. In Botswana, for example, increasing impala densities are limiting *F. albida* recruitment. This mesic species is being replaced in part by *Combretum mossambicense* (Moe et al.,

Table 4
ANOVA of *Faidherbia albida* root:shoot ratio based on seed populations (wet vs. dry habitat) and watering regime. Overall model: $F_{5,151} = 3.6$, $P = 0.004$.

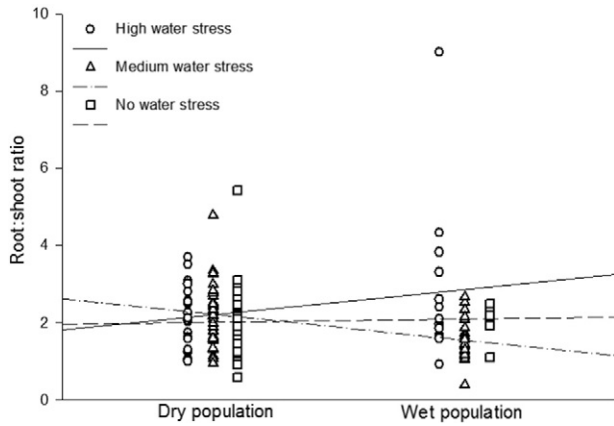| Variable	F	df	P
Population	0.6	1	0.4
Water level	3.2	2	0.04
Population * water	5.7	2	0.004

Fig. 3. Root:shoot ratios *of Faidherbia albida* seedlings from populations found in frequently flooded vs. less frequently flooded areas exposed to different levels of water stress.

2009), a sister species to *C. adenogonium*. Impala densities increased dramatically in GNP between 2014 and 2015 (Massad, pers. obs.), and it will be of interest to ecologists and restoration practitioners to understand how interactions between herbivores and climate will affect the distribution of Gorongosa's vegetation in the future. The greenhouse data generated by this experiment illustrate different responses between dominant species to water stress and can be used to design field experiments that realistically address species' responses to climate change and herbivore pressure.

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References

Andersson, L., Samuelsson, P., Kjellstrom, E., 2011. Assessment of climate change impact on water resources in the Pungwe river basin. Tellus 63A, 138–157.

Birkett, A., Stevens-Wood, B., 2005. Effect of low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya. African Journal of Ecology 43, 123–130.

Boko, M., Niang, I., Nyong, A., Vogel, C., Githeko, A., Medany, M., Osman-Elasha, B., Tabo, R., Yanda, P., 2007. Africa. climate change 2007: impacts, adaptation and vulnerability. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, C.E. (Eds.), Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge UK, pp. 433–467.

Convention on Biological Diversity, 2015. https://www.cbd.int/countries/profile/default.shtml?country=mz#measures [Accessed 8 December 2015].

Dunham, K.M., 1989. Vegetation-environment relations of a middle Zambezi floodplain. Vegetatio 82, 13–24.

Fenner, M., 2000. Seeds: The Ecology of Regeneration in Plant Communities. second ed. CABI Publishing, New York.

Humphries, M.S., Kindness, A., Ellery, W.N., Hughes, J.C., Bond, J.K., Barnes, K.B., 2011. Vegetation influences on groundwater salinity and chemical heterogeneity in a freshwater, recharge floodplain wetland, South Africa. Journal of Hydrology 411, 130–139.

Lindsey, P., Bento, C., 2012. Illegal hunting and the bushmeat trade in central Mozambique. A Case-Study from Coutada 9, Manica Province. TRAFFIC East/Southern Africa, Harare, Zimbabwe.

McSweeney, C., New, M., Lizcano, G., 2010a. UNDP climate change country profiles: Mozambique. Available: http://country-profiles.geog.ox.ac.uk/ (Accessed 3 December 2015).

McSweeney, C., New, M., Lizcano, G., Lu, X., 2010b. The UNDP climate change country profiles improving the accessibility of observed and projected climate information for studies of climate change in developing countries. Bulletin of the American Meteorological Society 91, 157–166.

Moe, S.R., Rutina, L.P., Hytteborn, H., du Toit, J.T., 2009. What controls woodland regeneration after elephants have killed the big trees? Journal of Applied Ecology 46, 223–230.

Niang, I., Ruppel, O.C., Abdrabo, M.A., Essel, A., Lennard, C., Padgham, J., Urquhart, P., 2014. Africa. In: Barros, V.R., Field, C.B., Dokken, D.J., Mastrandrea, M.D., Mach, K.J., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1199–1265.

O'Connor, T.G., 2001. Effect of small catchment dams on downstream vegetation of a seasonal river in semi-arid African savanna. Journal of Applied Ecology 38, 1314–1325.

O'Connor, T.G., 2010. Transformation of riparian forest to woodland in Mapungubwe National Park, South Africa, between 1990 and 2007. Austral Ecology 35, 778–786.

Otieno, D.O., Kinyamario, J.I., Omenda, T.O., 2001. Growth feature of *Acacia tortilis* and *Acacia xanthophloea* seedlings and their response to cyclic soil drought stress. African Journal of Ecology 38, 126–132.

Roupsard, O., Ferhi, A., Granier, A., Pallo, F., Depommier, D., Mallet, B., Joly, H.I., Dreyer, E., 1999. Reverse phenology and dry-season water uptake by *Faidherbia albida* (Del.) A. Chev. in an agroforestry parkland of Sudanese west Africa. Functional Ecology 13, 460–472.

Stave, J., Oba, G., Eriksen, A.B., Nordal, I., Stenseth, N.C., 2005. Seedling growth of *Acacia tortilis* and *Faidherbia albida* in response to simulated groundwater tables. Forest Ecology and Management 212, 367–375.