


## ARTICLE

# Rainfall, fire and large-mammal-induced drivers of *Vachellia drepanolobium* establishment: Implications for woody plant encroachment in Maswa, Tanzania

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## Abstract

Worldwide, open grass areas of savannah ecosystems are being transformed into shrubland. This woody plant encroachment is likely a result of factors such as rainfall, fire and secondary dispersal by ungulate herbivory. However, few experiments have been conducted to disentangle and quantify the role of these factors for seed germination in savannahs. We assessed *in situ* germination success of *Vachellia drepanolobium* seeds under simulated rainfall variability patterns, fire treatments and dung experiments in Maswa Game Reserve, Tanzania. Fire reduced seed germination by more than 13%, whereas germination in buffalo and elephant dung increased by 1% and 3% respectively. Additionally, intermediate simulated rainfall was more beneficial for seedling emergence success than large, infrequent simulated rainfall amounts, while shoot growth was twice as high under frequent and intermediate simulated rainfall treatments than under large infrequent simulated rainfall. Our results provide insights that bush fires, drought stress, and large rainfall events can suppress *V. drepanolobium* seedling emergence and growth. Hence, bush encroachment may be linked to management practices such as fire regimes and climatic conditions, i.e., frequent low rainfall conditions. Our results can help predict future patterns of encroachment under varying rainfall and fire events.

## KEYWORDS

germination, root, seedling, Serengeti ecosystem, shoot, *Vachellia drepanolobium*

## Résumé

Partout dans le monde, les zones herbeuses ouvertes des écosystèmes de savane deviennent peu à peu des terres arbustives. Cet empiètement par des plantes ligneuses est probablement le résultat de facteurs tels que les précipitations, les incendies et la dispersion secondaire par l'herbivorie par les ongulés. Cependant, peu d'expériences ont été menées pour distinguer et quantifier le rôle de ces facteurs dans la germination des graines dans les savanes. Nous avons évalué le taux de germination *in situ* des graines de *Vachellia drepanolobium* dans le cadre de modèles de variabilité de précipitations simulés, de traitements par brûlage et d'expériences menées sur des bouses dans la réserve de Maswa, en Tanzanie. Le feu a réduit la germination des graines de plus de 13%, tandis que la germination sur les bouses de buffles et d'éléphants a augmenté respectivement de 1% et 3%. De plus, les pluies simulées intermédiaires ont été

plus bénéfiques pour le taux de levée des semis que les pluies simulées importantes et peu fréquentes, tandis que la croissance des pousses était deux fois plus élevée sous des pluies simulées fréquentes et intermédiaires que sous des pluies simulées importantes et peu fréquentes. Nos résultats indiquent que les feux de brousse, le stress hydrique et les fortes pluies peuvent empêcher l'émergence et la croissance des semis de *V. drepanolobium*. Par conséquent, l'empiètement sur la brousse peut être lié à des pratiques de gestion telles que les régimes de feu et les conditions climatiques, c'est-à-dire des conditions de faibles précipitations fréquentes. Nos résultats peuvent permettre de prédire les futurs modèles d'empiètement en cas de conditions de pluies et d'incendies variables.

## 1 | INTRODUCTION

There is currently a global shift of vegetation structure in savannah ecosystems due to transformation of open grassland to shrubland (Stevens et al., 2016; Auken, 2000). In sub-Saharan Africa, woody plant cover in the non-forest biome has increased by 7.5 million km<sup>2</sup> from 1986 to 2016 (Venter et al., 2018), whilst in the United States, 190,000 km<sup>2</sup> of grassland have been transformed to shrubland (Baez et al., 2012). This increase in woody vegetation is likely the result of multiple interacting factors such as increased CO<sub>2</sub> levels and nitrogen deposition in the atmosphere, changing herbivore population density, rainfall and fire suppression in savannah ecosystems (Reed et al., 2009; Stevens et al., 2016; Venter et al., 2018; Wigley et al., 2009). Tree–grass co-existence dynamics have been discussed in the framework of equilibrium, non-equilibrium and disequilibrium dynamics (Sankaran et al., 2004), in all of which tree–grass ratios can fluctuate in response to variables such as rainfall and disturbances by fire and grazing (Sankaran et al., 2004). Climatic variability, particularly rainfall pattern, is amongst the key potential drivers of tree–grass co-existence (Bond, 2008; Rugemalila et al., 2016). Increased rainfall enhances competitive pressure through grasses and grass fuel load, limiting tree seedling establishment due to resource competition at sapling stage and lower recruitment to adult trees due to frequent and intensive fire (February et al., 2013). However, seedling emergence and establishment are a key stage in tree–grass co-existence, and it is critical to explore factors that influence their survival and mortality. Most experimental precipitation studies have been conducted in the northern hemisphere (Beier et al., 2012; Fay et al., 2000), whereas little experimental work has been done in African savannah ecosystems (Beier et al., 2012; February et al., 2013; Tjelele et al., 2015).

Whilst plant germination and early seedling growth are highly susceptible to changes in climatic conditions, particularly water availability (O'Brien et al., 2013), there is a need to understand how the early plant successional stages are affected by rainfall (Midgley & Bond, 2001; Morrison et al., 2018). However, little is known about how precipitation and soil moisture variation may influence seedling establishment, which is the critical first step in woody plant encroachment (Beier et al., 2012; Morrison et al.,

2018; Wilson & Witkowski, 1998). Another potential factor influencing seed germination and seedling establishment is consumption or seed gut passage (seed scarification), and seed deposition in different herbivore species dung. Herbivore species and guilds produce dung with microclimates that differ from soil and from one another, so each will likely have different rates of seed germination and establishment (Tjelele et al., 2015; Vega et al., 2010). Seed germination and establishment success in dung of various herbivores species depend on its nitrogen concentration, fibrous texture, moisture content, colour and temperature (Wilson & Witkowski, 1998). Hence, higher seed germination success might be observed in dung of browsers and mixed feeders such as elephant (*Loxodonta africana*), which has relatively low nitrogen concentrations, is more fibrous and retains moisture for longer time, compared to dung of grazers such as buffalo (*Syncerus caffer*) and cattle (*Bos taurus*) (Tjelele et al., 2015; Wickens, 1969). Whilst herbivore dung contains significant concentrations of nutrients, it also retains heat and loses moisture more rapidly than soil due to its black colour, and thus may limit seed germination (Wilson & Witkowski, 1998). Bush fires which are common in African savannah ecosystem may affect seedling establishment and their survival (Calabrese et al., 2010; Frost & Robertson, 1987). Fires can cause seed scarification for hard-seeded coat, directly kill seeds for soft seeded coat and seedlings, but they can also reduce grass abundance and, thus, resource competition, thereby promoting tree seedling establishment indirectly (Calabrese et al., 2010; Walters et al., 2004). Fire intensity depends on timings of fires and respective fuel loads, and hotter fires are more likely to kill tree seeds and seedlings than cooler fires (Walters et al., 2004). Further, seeds buried in the ground might be less strongly affected by fire compared to those lying on the surface (Tozer, 1995).

To better understand the key processes, which control seed germination and seedling establishment, we experimentally manipulated soil moisture (irrigation levels), micro-habitat through herbivore dung (elephant and buffalo dung) and fire (hot and cool) in a savannah biome. We conducted our work in Maswa Game Reserve (MGR), a grassland savannah adjacent to Serengeti National Park of northern Tanzania. Here, woody plant species, particularly *Vachellia drepanolobium* (Previously known as *Acacia drepanolobium*), have

been increasing in densities and become dominant over the past two decades (Niboye, 2010), which is a growing concern for wildlife conservation and a potential source for ecological and economic losses. Particularly in areas of MGR, where fire practices have been reduced since 2008, open grassland has rapidly been converted into thick bushes of *V. drepanolobium* (Ishengoma, pers. Com 2018).

We expected higher germination success of *V. drepanolobium* seeds under irrigation treatments simulating high rainfall events compared to lower but regular irrigation. We further hypothesised that seeds buried in the ground as well as surface soil seeds exposed to cooler fire will germinate better compared to surface soil seeds exposed to hot fires. In addition, we expected that the presence of herbivore dung (both elephant and buffalo) as growing medium would enhance germination success of *V. drepanolobium* seeds compared to soil medium alone.

Our study provides insights into early-stage recruitment processes of *V. drepanolobium*, a woody encroacher species that has been reported to increase across various eastern African savannah systems in recent decades (Okello, 2007; Okello & Young, 2009; Yassin, 2019).

## 2 | MATERIAL AND METHODS

### 2.1 | Study area

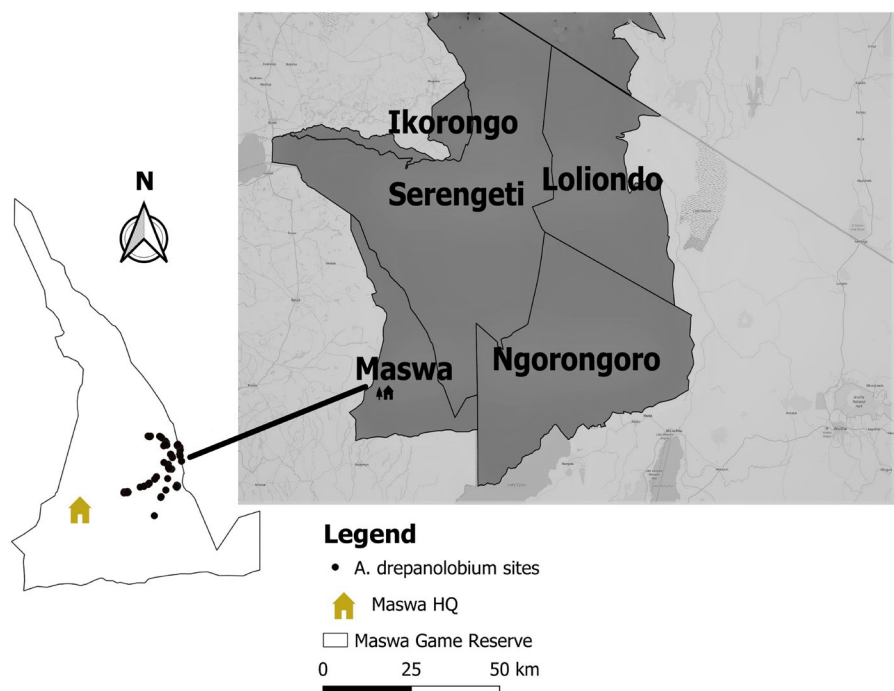
The study was conducted in East of Maswa Game Reserve (MGR), Tanzania ( $34^{\circ} 35' 49.6''$  E and  $3^{\circ} 17' 3.7''$  S), from June to August 2018. MGR occupies an area of 2,200 km<sup>2</sup> and acts as an important buffer zone (Figure 1) between Serengeti National Park and Ngorongoro Conservation Area (TAWA, 2018). The area acts as

herbivore refuges for the great wildebeest migration in Serengeti-Maasai Mara Ecosystem (Borner, 1981; Makacha et al., 1982). Common wildlife species present include African elephants, buffalo, wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), topi (*Damaliscus korrigum*), zebra (*Equus quagga*), baboon (*Papio anubis*), leopard (*Panthera pardus*), hyaena (*Crocuta crocuta*) and lion (*Panthera leo*) and a variety of antelopes and bird species (Makacha et al., 1982; TAWA, 2018). Soils are classified as Vertisol (WRB), composed of amorphous minerals (Jager, 1982). Main vegetation types of the area include grasslands interspersed with kopjes, *Vachellia* woodlands and thorn scrub (TAWA, 2018). In recent years, vegetation change (from grassland to scrubland) has been observed in MGR, as well as in other parts of Serengeti ecosystem, including Makundusi grazing land, Ikorongo – Grumeti Reserves and Loliondo (N. Mbise, pers. Com, 3 February 2017; S. Jozeph, pers. Com, 1 March 2018). Average temperatures in MGR range from 9°C to 22°C in May to August, and 23°C to 35°C in October to April (Jager, 1982). The MGR has two wet seasons, that is the short rains from November to December and the long rains from January to May, with an annual average rainfall ranging from 600 to 1,150 mm (Bartzke et al., 2018; Poelchau & Mistry, 2006).

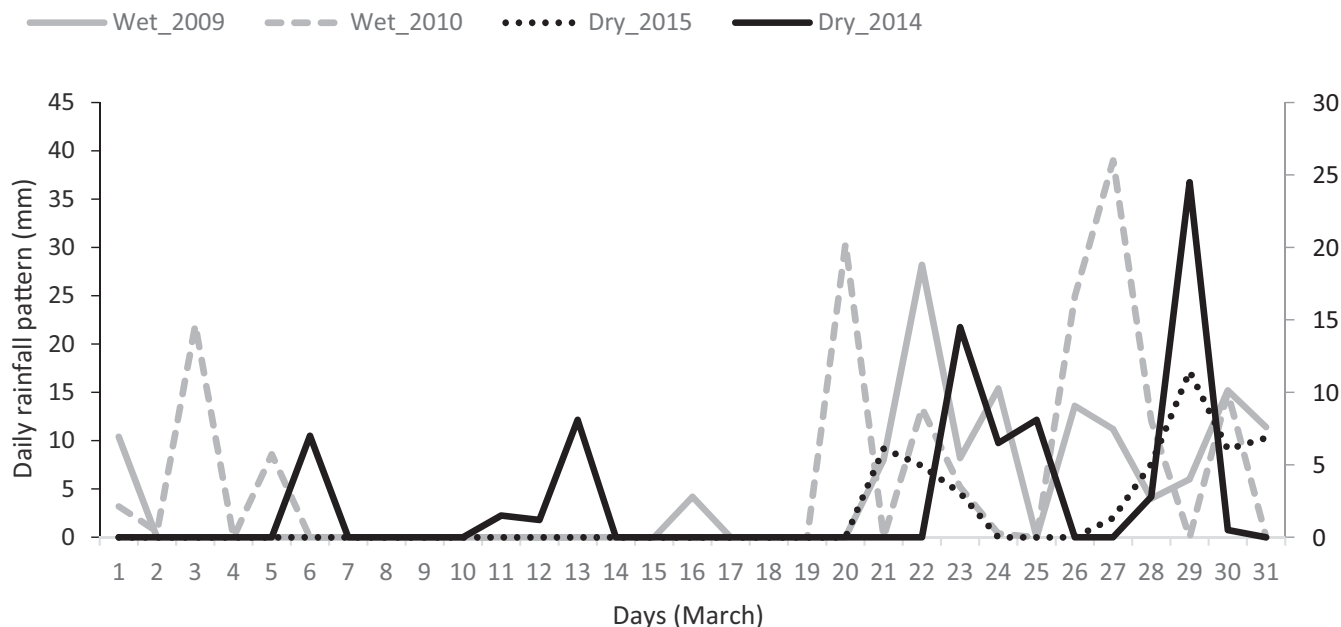
The long rain season reaches the peak in March, with an average total rainfall of 127 mm per month in past 9 years, a maximum daily precipitation observed in March was 39 mm per day in wet years and 24.5 mm per day in dry years (Figure 2).

### 2.2 | Irrigation experiment

*Vachellia drepanolobium* pods (with an average weight of 1.54 g  $\pm$  0.13) were collected from beneath *V. drepanolobium* trees in Maswa



**FIGURE 1** Study site in Maswa Game Reserve, northern Tanzania. Black circles represent surveyed sites, at which fire and dung experiments were conducted, and that were occupied by *V. drepanolobium*



**FIGURE 2** Daily precipitation (in mm) for the month of March, which is the peak of the long rainy season. We selected daily values for two wet years (2009 & 2010) and two dry years (2014 & 2015), to show variation in daily rainfall in Maswa Game Reserve, Tanzania. Source: Maswa Game Reserve headquarters

from June to July 2018. Only visibly healthy individual seeds were hand-selected, and seed maturity was checked by opening 5–10 seeds and ensuring that the radicle was fully formed (O'Brien et al., 2013). Furthermore, seed health was checked by using water, that is seeds that sank in a basin of water were deemed healthy (O'Brien et al., 2013). In total, approximately 825 seeds were placed in germination trays with 55 pots per tray and pot sizes of  $5.2 \times 5.2$  cm, filled with black cotton soil (clay soil), collected from *V. drepanolobium* encroached sites (O'Brien et al., 2013; Wilson & Witkowski, 1998). Each tray was randomly assigned one of three irrigation treatments (i.e. 275 seeds per treatment) (O'Brien et al., 2013). Treatments were frequent (4 ml), intermediate (9 ml) and infrequent (30 ml) rainfall per pot for daily, 2-day and 7-day irrigation frequencies, respectively. The water treatments were based on dividing the 127 mm of rainfall in March by 30 days to get the frequent rainfall treatment on a daily basis. Thus, the frequent water treatment amounted to 4.23 mm, the intermediate treatment to 8.46 mm and the infrequent treatment to 29.61 mm, which were rounded to frequent = 4, intermediate = 9 and infrequent = 30 mm, respectively. These amounts represent precipitation variation patterns based on the average precipitation in March for Maswa Game Reserve collected via rain gauge over the last 9 years (Maswa Weather Stations). The simulated rainfall pattern treatments differed in raining frequency whilst sustaining an approximately equal monthly rainfall amount of  $127 \pm 19$  mm, as is usually expected for this region in March, that is during the long rainy season (see also Figure 2). The frequent water treatment represented consistent low amounts of water available to seedlings per raining event, which often occurs in the area. The intermediate watering treatment was done every 2 days, representing relatively

more water at a time, whilst the infrequent watering treatment represented extreme rainfall conditions (Nejad, 2011). Seeds were placed on their side on the soil surface to replicate natural seed position, and pots with soil were watered to saturation prior to planting. The germination trays were placed inside a wooden cage covered by a polythene net to provide slight shade and exclude rainfall and potential seed predators (Fay et al., 2000; O'Brien et al., 2013). During the experiment, average recorded temperature was  $24.1^\circ\text{C}$ . Starting 7 days after planting (Razeek et al., 2016; Wilson & Witkowski, 1998), seedlings were monitored daily for germination (radicle emergence), mortality and seedling development over 35 days, and seedling shoot height data were collected every 7 days. At the end of the experiment, total length of each seedling root and shoot was measured and recorded.

### 2.3 | Large-mammal dung experiment

In total, 75 and 70 fresh ( $\leq 1$ -day old) dung piles of elephants and buffalo, respectively, were randomly located within the study site and five *V. drepanolobium* seeds (removed from the pods) were inserted in each dung pile (Table 1). The full experiment included a total of 375 and 350 seeds, for elephant and buffalo dung, respectively. The dung piles were covered by thorny branches of *Vachellia* and *Commiphora* trees (creating  $2 \times 2$  m cage) to prevent a potential destruction and seed predation by larger wild animal species and birds. However, few dung piles, mostly from buffalo, were decomposed by termites and some seeds had been eaten. No watering treatment was done, and the experiment was left undisturbed

**TABLE 1** Large-mammal dung experimental design, *Vachellia drepanolobium* seeds were planted in elephant and buffalo dung piles, and the control treatment seeds were planted in soil

Attribute	Treatments		
	Elephant dung	Buffalo dung	Control
Number of dung piles	75	70	–
Total number of seed used	375	350	385

Note: Observation for the seedling emergence was done in 14 days' period.

**TABLE 2** Fire experimental design, *Vachellia drepanolobium* seeds were placed in cool, hot, sub-soil hot (sub-soil) fire treatments and control treatment

Attribute	Treatments			
	Cool	Hot	Sub-soil	Control
Total number of seed	201	220	40	220

Note: Cool = green grassland patch was burned, hot = dry grassland patch was burned, sub-soil = seeds were located in 1 cm depth within the soil and burned, control = no fire.

under ambient temperature conditions, checked regularly over 14 days before data collection. As a control, a total of 385 seeds were collected from *V. drepanolobium* trees and planted in germination trays, watered (20 ml) daily over 14 days to resemble optimal wet season growing conditions in soil. Data collected after 14 days included the number of seeds germinated as well as shoot height and root length of the seedlings that emerged in the treatments.

## 2.4 | Fire experiment

Pods of *V. drepanolobium* were collected in the field, making a total count of 681 seeds, which were subjected to three fire treatments and a control treatment (Table 2); 201 seeds were laid out on the soil surface, exposed to cool fire (cool), 220 seeds to hot fire (hot) and 40 seed to hot fire in sub-soil. Fire plots were a 15 × 15 m grassland patch covered with relatively green grasses (cool fire) or dry grasses (hot fire), ignited and burned for 30 min. The third treatment contained 40 seeds that were buried in sub-soil (1 cm depth – treatment = sub), and cut dry grasses were added in a quadrat of 90 × 70 × 25 cm and burned for 10 min. All seeds were collected after 30 min when fire had ceased and planted in germination trays, watered with 20 ml daily and monitored for seed germination over a period of 30 days. As a control, 220 seeds not subjected to fire treatment were planted in germination trays, followed by daily watering (20 ml) for 30 days. Seeds emerging from germination trays were counted and recorded.

## 2.5 | Data analysis

Analyses were performed using R environment for two-way ANOVA and Tukey's HSD (v.3.4.1 The R Foundation for Statistical Computing 2017) and PALEontological STatistics (PAST) version 3.20 for Kruskal–Wallis test, Dunn's test and chi-square test (Hammer et al., 2001). Data were checked for normality and two-way ANOVA was used to test for the mean difference of seedling shoot heights amongst three irrigation treatments over the 5-week period. For non-normally distributed data, Kruskal–Wallis test was used to test whether seedling root length differed across the three irrigation treatments. Dunn's and Tukey's HSD post hoc analysis were performed to test significant differences across means. We tested for difference of the number of successfully germinated seeds against planted seeds amongst treatments, that is seed germination success in large-mammal dung piles and fire regime treatment using chi-square test and binomial proportions test, respectively, at a 95% confidence interval and statistical significance level of  $\alpha = 0.05$ .

## 3 | RESULTS

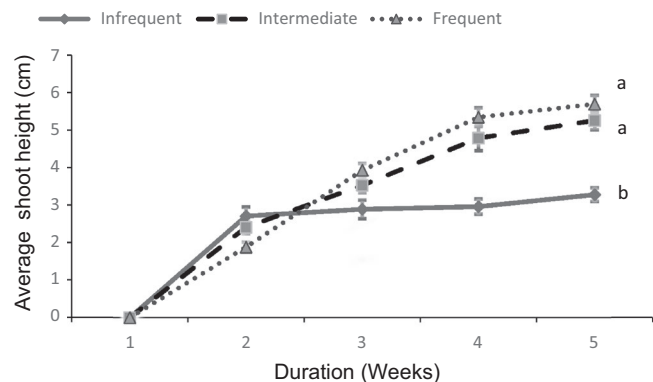
### 3.1 | Seed germination success and seedling survival

Across all three irrigation treatments, a total of 114 (14%) of all 825 planted seeds germinated within the 5-week-long experiment. However, seed germination did not vary significantly across water treatments ( $\chi^2 = 1.268$ ,  $p = 0.4091$ ), with 37 (14%) seeds germinating under the infrequent water treatment, 43 (16%) at the intermediate water treatment and 34 (13%) seeds germinating at the frequent water treatment. Only the infrequent water treatment had 6 (16%) dying seedlings.

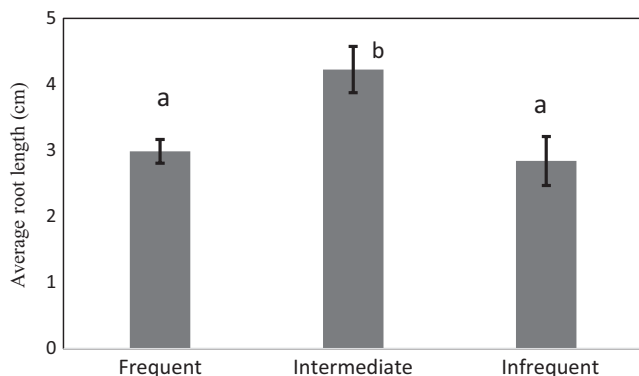
Seedling shoot heights differed across treatments between the first week and fourth week; particularly seedlings from infrequent water treatment (2.71 cm  $\pm$  0.24) grew slowly compared to the frequent water treatment (1.88 cm  $\pm$  0.13) as the experiment continued ( $F_{3,362} = 71.31$ ,  $p < 0.001$ , Figure 3). At the end of experiment, seedling shoot heights of frequent and intermediate water treatments (5.7 cm  $\pm$  0.23 and 5.26 cm  $\pm$  0.25, respectively) were almost twice as tall than those under infrequent water treatment (3.28 cm  $\pm$  0.18, Figure 3). Intermediate water treatment (4.23 cm  $\pm$  0.35) had a significant effect on seedling root length than frequent (2.99 cm  $\pm$  0.18) and infrequent water treatments (2.84 cm  $\pm$  0.37,  $\chi^2 = 9.118$ ,  $p = 0.0103$ ). Intermediate water treatment roots were almost twice as long as infrequent and frequent water treatment roots (Figure 4). Further, average root–shoot length ratio increased from frequent to infrequent water treatment (Figure 5).

### 3.2 | Seed germination under large-mammal dung and fire treatments

Slightly more seeds, that is 63 (17%) and 50 (14%), out of 375 and 350 seeds inserted in elephant and buffalo dung, respectively, germinated



**FIGURE 3** Average ( $\pm$ SE) seedling shoot heights over the entire duration of the experiment (5 weeks) across three different irrigation treatments. Infrequent = 30 ml in 7 days' period (solid line), intermediate = 9 ml in 2 days' period (dashed line), frequent = 4 ml every day (dotted line). Different letters show significant differences across treatments according to Tukey's HSD at 95% significance level)



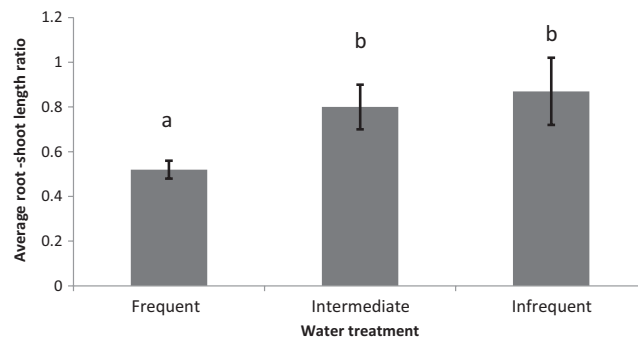
**FIGURE 4** Average ( $\pm$ SE) seedling root length across irrigation treatments over a 5-week period. Infrequent = 30 ml in a 7-day period. Intermediate = 9 ml in a 2-day period, Frequent = 4 ml every day. Different letters show significant differences after Dunn's test and a significance level of 95%

whilst in the control 51 (13%) out of 385 seeds germinated, although not significant ( $\chi^2 = 2.009$ ,  $p = 0.74$ ). None of 40 planted sub-soil hot fire treatment seeds germinated (Figure 6) whilst in the hot fire experiment, 5 (2%) of the 220 seeds germinated, in the cool fire treatment 3 (1%) of the 201 seeds germinated, and in the control treatment, 31 (14%) of 220 seeds germinated ( $\chi^2 = 37.692$ ,  $p < 0.001$ , Figure 6).

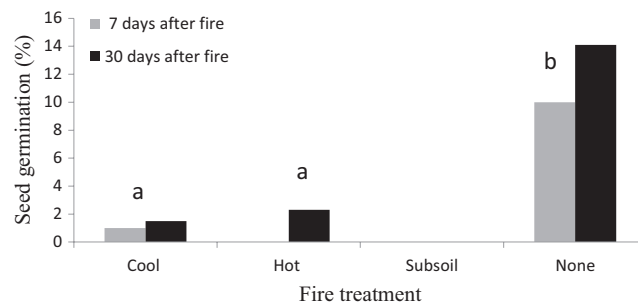
## 4 | DISCUSSION

### 4.1 | Seed germination and seedling growth under irrigation treatment

Our intermediate water treatment had the highest seed germination success, which might have been enough water to mechanically break the seed coat/wall, that is regular contraction and expansion



**FIGURE 5** Average ( $\pm$ SE) root: shoot length ratio across different irrigation treatments. Infrequent = 30 ml in a 7-day period, intermediate = 9 ml in a 2-day period, frequent = 4 ml every day. Different letters show significant differences according to Dunn's test and a significance level of 95%



**FIGURE 6** Seed germination (in %) of *A. drepanolobium* for different fire treatments. Grey = germination over a normal germination period (7 days); black = germination at the end of the experiment. Cool = green grassland patch was burned, hot = dry grassland patch was burned, sub-soil = seeds were located in 1 cm depth within the soil, none = no fire. Different letters show significant differences (for both grey and black colors) according to binomial proportion test at 95% confidence interval

of seeds due to water absorption in a short period of time (Schopfer, 2006; Steinbrecher & Leubner-Metzger, 2016). Seed germination success of *Vachellia tortilis* and *Vachellia robusta* was found to increase with rainfall in Serengeti (Morrison et al., 2018). In a similar study, an intensive watering treatment (16 ml administered every 2 days) resulted in higher seed germination of *Vachellia karoo*, *Vachellia nilotica* and *Vachellia tortilis* than other water treatments (i.e. 2 ml, 8 ml and 16 ml administered every 4 and 8 days) (Wilson & Witkowski, 1998). In another study, intermediate moisture stimulated seed germination, presumably because the extremes of too little or too much water limited germination (Razeek et al., 2016). Our results emphasise the importance of consistency of soil water availability for *V. drepanolobium* seed germination.

In our study, seedling shoot heights were highest in frequent low water treatments over time. These results suggest that frequent low rainfall events are more important for seedlings than the actual amount of water supplied, which is in agreement with Ferreira et al. (2015) and Wilson and Witkowski (1998). Thus, in addition to

changes in total precipitation, changes in the temporal distribution of rainfall events may also influence germination success and establishment of *V. drepanolobium* seedlings.

Whilst it has been reported that under limited resources, plants are able to alter their growth patterns by investing particularly in root growth (Bouteillé, 2011), we found shortest roots under frequent low rainfall treatment and root-shoot length ratios increasing from frequent water treatment to infrequent water treatments, that is the plants did not seem stressed (Harris, 1992). Hence, we suggest that *V. drepanolobium* seedlings are sensitive to water availability at the levels were applied and can easily adapt to water stress situations within a short period of time. In MGR, the year 2012 had the lowest rainfall records of all years, during which a wide establishment of *V. drepanolobium* saplings seemed to have taken place in the grasslands (unpublished data). These findings are advocating for the role of bottom-up process in regulating tree-grass co-existence (Staver & Koerner, 2015). And one possibility is that, *V. drepanolobium* recruitment is maximised when rainfall is low, thus grass productivity is low, leading to low competition for soil moisture between grasses and seedlings (Coughenour et al., 1985; Morrison et al., 2018). This phenomenon was also observed in other savannah ecosystems across the world (Fensham et al., 2005), particularly in the absence of fire (Jager, 1982).

Our field observation during the experiment and survey showed that water was readily absorbed and disappeared from the topsoil, which was mainly black cotton soil with deep wide cracks. Woodland and grassland distribution are correlated with infiltration rate and depth of soil moisture (Jager, 1982). Infiltration is positively influenced by cracks in the soil, with more moisture being available in deeper soil layers rather than upper soil (Jager, 1982). Thus, more water will be readily available to woody plant saplings rather than grasses in soils that crack, such as the black cotton soils used in this study (Sankaran et al., 2004). We observed that most *V. drepanolobium* encroachment sites were located in black cotton soil (Personal observation, 2018), which is in agreement with previous findings suggesting that soil types influence seed germination and seedling establishment of *V. drepanolobium* (Okello, 2007; Okello & Young, 2009). As these soils dry, they fracture and put stress on woody plants, which *V. drepanolobium* can likely cope with in contrast to other woody plant (Pringle et al., 2016). Further studies should focus on seedling establishment and woody plant encroachment under different soil type characteristics as it could help in a deeper understanding and more precise predictions of woody encroachment processes.

## 4.2 | Seed germination under large-mammal dung

Our results show that seed germination success in elephant and buffalo dung was not statistically significant compared to the control. In Cameroon, a similar study also reported that germination success of fresh seeds did not differ between seeds sown in elephant dung and forest soil (Nchanji & Plumptre, 2003). Wickens (1969) suggested that seed germination is more favoured in fibrous dung piles due to lower nitrogen content, which might explain our slightly higher

germination success in elephant compared to buffalo dung. Some studies also reported a reduced seed germination success in dung due to a lack of sufficient moisture to support seed germination, due to its often hard crust and potential competition amongst plant species seeds on limited resources within a dung pile (Miller, 1995; Wickens, 1969; Wilson & Witkowski, 1998). Contrarily to our findings, Tjelele et al. (2015) have reported herbivore dung as a suitable and nutritive growth medium for seedling emergence, establishment and recruitment into adult trees.

From our unpublished data, one elephant dung pile carried on average  $204 \pm 15$  seeds of *V. drepanolobium*, similar to findings by Brahmachary (1980), who found that up to 100 tree seedlings germinated per elephant dung pile. This highlights the potential role of elephants as seed-dispersal agent (Harich et al., 2016; Lieberman et al., 1987). During our large-mammal dung experiment, we observed that only few seeds decay in large-mammal dung piles whilst other few seeds were eaten, possibly by termites and small mammals. Generally, we retrieved almost all planted seeds back that had not germinated. Hence, we conclude that seed predation was negligible, probably because seeds were planted (inserted) inside herbivore dung piles and covered by thorn branches to limit access by most seed predators. However, our seed germination study might not have been conducted at the right season since we had to actively search for seeds and plant them in dung, that is they did not pass the digestive tract. The latter can increase seed germination potential due to seed scarification (Goheen et al., 2010; Miller, 1995; Rugemalila et al., 2017), though was not part of our experimental design.

## 4.3 | Bush fires suppress *V. drepanolobium* seed germination success

In addition to rainfall and herbivory, fire is one of the major regulatory mechanisms shaping vegetation structure and composition in savannah ecosystems, and in the Serengeti ecosystem in particular (Beale et al., 2013; Strauch & Eby, 2012). Our fire experiment showed that seed germination was reduced by 13% in burned treatments, which is in accordance with (Okello, 2007), who showed that fire significantly reduced seed germination success of *V. drepanolobium* in Kenya. In our study, both cool and hot fire treatments suppressed germination of *V. drepanolobium* seeds placed on surface soil, thus highlighting the negative effect of fires on seed germination. Further, none of the seeds germinated in the sub-soil hot fire treatment, in contrast to Okello (2007) who found higher germination success in buried seed compared to surface soil seed. Though the number of seeds was relatively small for this treatment compared to other treatments, these results reflect the negative impact intensive fire might have on the soil seedbank of *V. drepanolobium* (Tozer, 1995). Fire impact on the soil seedbank varies with the amount of fuel burnt and soil depth, with finely ground fuel loads burning hotter and killing seeds near the soil surface (Tozer, 1995). Contrary to our expectation, we found no significant difference in seed germination success between

hot and cool fire treatments, suggesting a general intolerance of *V. drepanolobium* seeds to fire. Our fire experiment results are inconsistent with a previous study (Walter et al., 2004), who found no difference in seed germination in burnt seeds and unburnt seeds of *Vachellia karroo*. Fires can also enrich soil nutrients through ash and kill damaging insects, thereby promoting seed germination, seedling growth and survival (Sabiiti & Wein, 1987; Tozer, 1995; Walters et al., 2004).

Seasonally prescribed fires are usually a management tool in protected areas, particularly in Serengeti-Maasai Mara ecosystem (Dempewolf, 2007). However, reduced bush fires, as experienced in some parts of MGR, could have led to bush encroachment as was observed in Ethiopia (Lemenih et al., 2011; Yusuf et al., 2011). Bush-encroached areas in MGR experience reduced grass fuel load due to significantly increased bare ground cover (Kimaro et al., 2019), which has also been reported elsewhere in Africa (Angassa & Oba, 2007; Smit & Prins, 2015; Yusuf et al., 2011). Reduced fuel loads decrease the frequency and intensity of fire, favouring establishment of tree seedlings and saplings, which in turn leads to woody plant encroachment (Estes et al., 2008). Further, bush encroachment often provides decreased food quality and quantity, limited access to food and an increased landscape of fear for large mammalian herbivores (Yassin, 2019). Thus, bush-encroached areas are likely to promote further woody plant encroachment processes due to a continuously reduced competition from grasses, less predation and trampling effect from herbivores, and low fire intensity and/or frequency, all of which favour tree seedling establishment (Lemenih et al., 2011).

## 5 | CONCLUSION

We conclude that frequent low rainfall will lead to lower seed germination but will positively support the growth of already established seedlings, whilst few large rainfall events appear to suppress *V. drepanolobium* germination. Moreover, we found that hot and cool bush fires can strongly suppress *V. drepanolobium* seed germination as well as the soil seedbank (our sub-soil treatment) and, thus, reduces potential woody plant encroachment. Rainfall and fire interact in savannah environment, as large rainfall events, lead to greater fuel loads and, thus, more intense fires. In addition, large mammals contribute in early establishment *V. drepanolobium* as their dung piles support seed germination in the dry season prior to rainfall, which might give woody species a competitive advantage over the grass layer. Our results suggest that management tools to suppress *V. drepanolobium* encroachment in MGR should include prescribed fire to prevent further woody plant seedling establishment. In addition, mechanical intervention such as timely uprooting should be considered for areas that have been heavily encroached, as these areas cannot easily support fires. Further, our results on seedling success under different rainfall regimes can help predict future patterns of encroachment using models on climate change scenarios.

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## CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest regarding the publication of this manuscript.

## RESEARCH INVOLVING HUMAN PARTICIPANTS AND/OR ANIMALS

The authors affirm that neither human participants nor animals have been involved in this research.

## DATA AVAILABILITY STATEMENT

The data can be provided up on request.

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