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ORIGINAL ARTICLE

Role of nurse rocks on woody plant establishment in a South African grassland

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ABSTRACT Many empirical studies have supported the facilitative effect of nurse plants, and several recent studies have reported similar phenomena with non-plant features, such as rocks. Few studies have explored the effect of rock height on plant establishment, although variation in height can affect establishment. This study examined whether rocky outcrops have positive effects on plant establishment, as do classic nurse plants, and explored the mechanisms involved in the nurse effects in a South African grassland. To answer these questions, we compared the number of individual woody plants at the edges of rocky outcrops and in the adjacent grassland matrix, as well as beneath a putative nurse plant (*Euclea crispa*) and in the adjacent grassland matrix. We also measured the heights of rocky outcrops and *E. crispa* and the proportions of grass cover. The results showed that larger numbers of woody seedlings occurred at the edges of rocky outcrops and beneath *E. crispa* compared with in the adjacent grassland matrix. A generalised linear model (GLM) showed that rock and *E. crispa* height positively affected the number of seedlings; the diaspores of most recorded species showed characteristics associated with dispersal by vertebrates. The GLM analysis showed that the proportion of grass cover had a negative effect on the number of seedlings. These results indicate that in addition to shrubs, rocky outcrops appear to have positive effects on the establishment of woody plants in South African grasslands, likely serving as perching structures for birds and providing favourable microhabitats.

Key words: Nurse object, seed dispersal, facilitation, Africa, Drakensberg

INTRODUCTION

The nurse plant effect is one of the most important processes in the survival, growth, and fitness of some plants, as well as in the diversity and dynamics of plant communities, especially in harsh ecosystems (Callaway 1995, Bruno et al. 2003). Over the last two decades, increasing numbers of studies have demonstrated the direct and indirect effects of nurse plants on plant establishment in biomes worldwide (Vieira et al. 1994, Gomez et al. 2005, Baumeister and Callaway 2006, Montesinos et al. 2007, Yoshihara et al. 2010, Fujita 2014). Recent studies have also suggested similar effects of non-plant elements, such as rocks (hereafter nurse rocks; Peters et al. 2008, Munguia-Rosas and Sosa 2008, Haussmann et al. 2010, Carlucci et al. 2011). However, studies on the effects of nurse rocks are very recent; consequently, our understanding of the rock effect on plant establishment is still in its infancy. Recent studies have recommended further research in this topic (Munguia-Rosas and Sosa 2008, Carlucci et al. 2011).

Microenvironment amelioration is one of the potential mechanisms involved in the nurse rock effect. For instance, the presence of rocky outcrops has been found to increase soil moisture retention and rainfall infiltration at the soil surface (Noy-Meir 2001, Steers 2011). Other processes might also contribute to the nurse effects, such as seed dispersal. Some frugivorous birds preferentially perch on rocky outcrops and deposit ingested seeds there (Martinez et al. 2008). These factors may change with rock height (Noy-Meir 2001, Carlucci et al. 2011), and variation in rock height may therefore affect plant establishment. As yet, little research has focused on the effect of variation in rock height on plant establishment.

The grassland biome of southern Africa is a very diverse ecosystem (O'Connor and Bredenkamp 1997). For example, South African grasslands support ca. 3,800 plant species and include globally significant centres of plant endemism (Cowling and Hilton-Taylor 1997). In this grassland biome, more woody plant individuals were found beneath shrubs such as *Acacia karoo* than in the grassland matrix, suggesting the importance of the nurse plant effect on plant establishment (O'Connor and Bredenkamp 1997). To our knowledge, however, no study has evaluated the role of nurse effects of rocky outcrops on woody plant establishment in this grassland. Sandstone outcrops of various sizes are found in the grasslands of the Drakensberg foothills in

South Africa. Thus, this grassland represents an ideal field site for testing nurse rock effects on plant establishment.

This study examined whether rocky outcrops have positive effects on plant establishment, as classic nurse plants do, and explored the mechanisms involved in the nurse effects. To answer these questions, we first compared the number of individual woody plants at the edges of rocky outcrops with the number in the adjacent grassland matrix; we also evaluated numbers beneath a putative nurse plant and in the adjacent grassland matrix. We chose *Euclea crispa* (Thunb.) Gürke (Ebenaceae) as a putative nurse plant, as it is the dominant shrub species in this grassland and has a dense crown, which can provide suitable habitat for the establishment of other woody plant species. We also measured the heights of rocky outcrops and *E. crispa* to analyse the effect of height variation on plant establishment. Additionally, the effect of grass cover on plant establishment was analysed, as numerous studies have shown that grass cover is an important factor in tree seedling establishment in grassland and savannah ecosystems (e.g. Holl 2002, Shararn et al. 2009).

In this report, we do not use the term 'facilitation' to describe the effect of rocky outcrops on plant establishment. Facilitation is a type of biotic interaction in which an encounter between two organisms benefits at least one of them. However, a positive effect of an abiotic element on plants should not be regarded as a form of facilitation (Carlucci et al. 2011).

MATERIALS AND METHODS

The study site was located in a communal grassland in the Drakensberg foothills managed by the traditional council of Tsehseng, 11 km south of Phuthaditjhaba, South Africa (28°37′52″S, 28°49′58″ E; Fig. 1). The altitude is 1,850 m, and the vegetation is classified as eastern mountain escarpment grassland (O'Connor and Bredenkamp 1997). Sandstone outcrops are a common feature and are interspersed throughout the grasslands. *Themeda triandra* Forssk is the dominant grass species and *Euclea crispa* (Thunb.) Gürke is the dominant woody species, occurring as isolated individuals or in small stands in the grassland. *E. crispa* reaches a height of 1–2 m and is widely distributed throughout the grassland, often in rocky locations. At the base of terrace cliffs, we observed continuous woody vegetation consisting of *Gymnosporia heterophylla* (Eckl. & Zeyh.) Loes., *Myrsine africana* L., *E. crispa*, and *Diospyros whyteana* (Hiern) F. White. The climate is sub-humid sub-tropical, with a rainy summer (October to May) and dry winter (June to September). The mean annual precipitation over the previous 20 years was 1,197 mm, and the mean annual temperature was

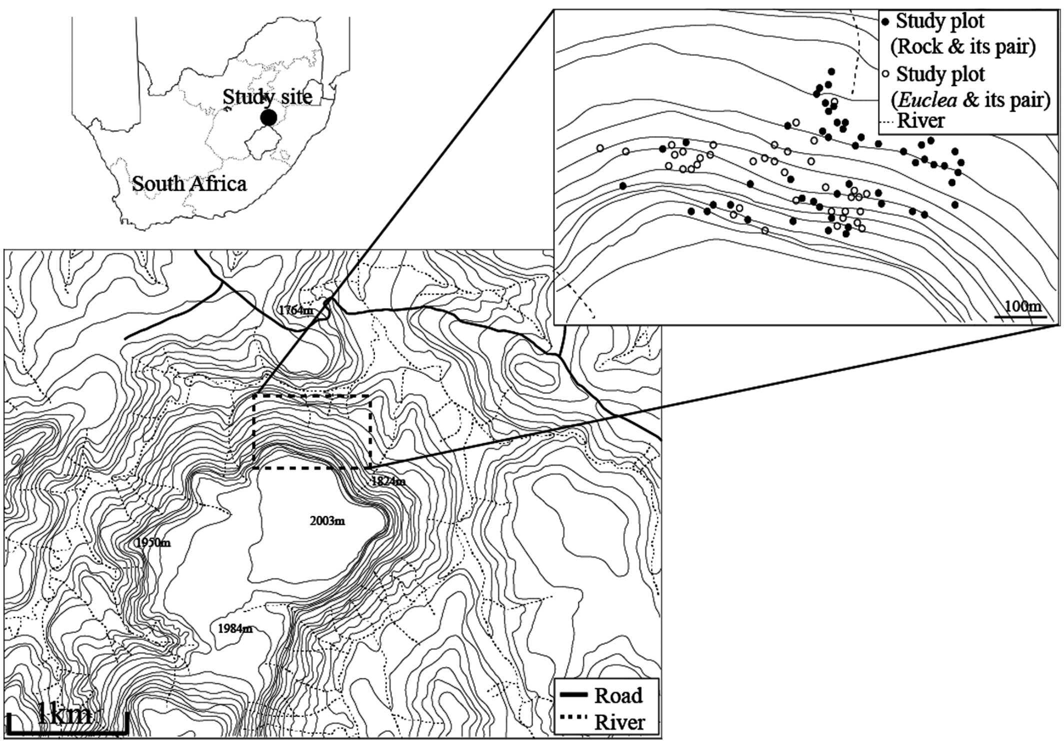

Fig. 1. Map of the study site and the position of paired studied plots.

9℃. Most of the communal grassland is burnt every year as result of human activity. Cattle and goats are often brought to the grassland to graze.

Data collection

In September and October 2013, we randomly selected 40 rocky outcrops on sloped talus (Fig. 1). We studied only outcrops lacking woody plants over 1 m in height to control for potential nursing effect of these woody individuals. We measured the height of all study rocks. We used randomly placed 50 × 50-cm plots to sample the woody plants, with paired plots 2 m away in the adjacent grassland matrix. In placing plots, we randomly chose a direction from the centre of the rock and placed our plot along that edge of the rock (Fig. 2). Then, we moved 2 m in the same direction to place the paired plot, selecting a grassland matrix without direct rock or crown influence. If this was impossible, we randomly chose another direction. To characterise the microhabitat conditions in each plot, we visually estimated the proportion of grass cover using 10 % cover-class intervals. In each plot, we identified all woody seedlings < 20 cm in height, excluding current-year seedlings. We also identified all woody saplings 20–100 cm in height. We counted the numbers of seedlings and saplings in each species. The dispersal mode of each plant species was determined based on the morphology of its seeds and fruits (Friis 1992, Van Wyk and Van Wyk 1997) and from the literature (Smith and Goodman 1987, Castley et al. 2001, Senbeta and Teketay 2001, Githiru et al. 2002, Bleher et al. 2003, Chapman et al. 2003, Fourie 2008).

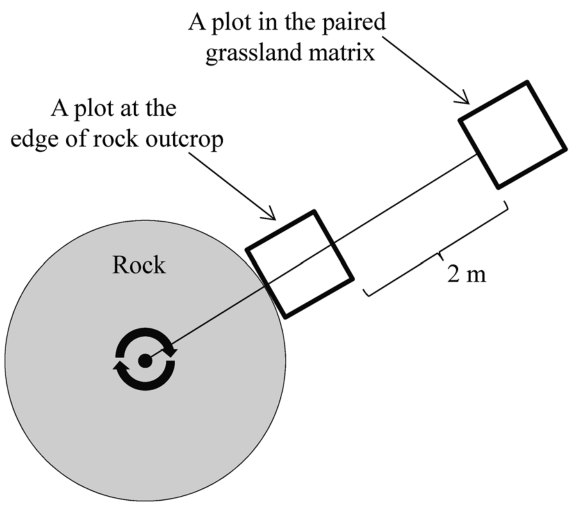

Fig. 2. Diagram of plots at the edge of rocky outcrops and in the paired grassland matrix. In placing plots, we randomly chose a direction from the centre of the rock and placed our plot along that edge of the rock.

In addition, we selected 40 *E. crispa* stands on sloped talus (Fig. 1). We did not select *E. crispa* that was growing next to rocky outcrops (50-cm radius from *E. crispa*) to control for any nursing effect of the rock. We placed plots (50 × 50 cm) beneath *E. crispa* and placed a paired plot 2 m away from the maximum extent of the crown in the grassland matrix. The heights of all study *E. crispa* stands were measured. Then, we sampled the plots using the above method. To avoid positive pattern associations between trees that resulted from the high occurrence of young individuals originating from the parent *E. crispa*, we excluded all *E. crispa* seedlings from plots beneath *E. crispa* and their paired grassland plots. The minimum distance separating experimental plots was 5 m. The total number of sampled plots was 160 (40 each for rocks and their paired grassland plots and 40 each for *E. crispa* and their paired grassland plots).

Data analysis

We compared the seedling abundance at the edges of the rocky outcrops with that in the paired grassland matrix plots using the Wilcoxon test. We also compared the seedling abundance beneath *E. crispa* with that in the paired grassland matrix. We did not find sufficient woody plant saplings for statistical analysis. Determinants of woody seedling abundance at the edge of rocky outcrops were examined using a generalised linear model (GLM) with a Poisson distribution and log-link function, and outcrop height and the proportion of grass cover as explanatory variables. Before performing the GLM analysis, we examined the extent of multicollinearity using a variance inflation factor (VIF). The two variables showed a VIF < 10 and were both included. The Akaike information criterion (AIC), which balances the fit of the model against the number of parameters, was used to select the best-fit model. The full model included two variables. To select the best-fit model, we removed explanatory variable (s) successively from the full model. The model with the lowest AIC was accepted as the best fit for the data. Determinants of woody seedling abundance beneath *E. crispa* were also examined using the GLM, and the tree height of *E. crispa* and proportion of grass cover were included as explanatory variables. The VIF for the two variables was < 10. We used R version 2.12.2 (R Development Core Team 2011) for the analyses.

RESULTS

The mean height of the surveyed rocks was 1.1 (range 0.2–3.6) m. We found no significant difference in the proportion of grass cover between rocky outcrops (median = 50 %, range = 0–90 %) and their paired grassland matrix plots (median = 60 %, range = 10–90 %; $P = 0.17$; Wilcoxon test).

The mean height of the surveyed *E. crispa* was 2.0 (range 1.2–3.1) m. Again, we found no significant difference in the proportion of grass cover between beneath *E. crispa* (median = 40 %, range = 0–80 %) and the paired grassland matrix plots (median = 50 %, range = 10–90 %; $P = 0.25$; Wilcoxon test).

In all, 21 of 40 rocky outcrops had at least one woody plant seedling, and 181 individuals from 11 woody species were found at the edges of the rock outcrops (Table 1; Fig. 3). Only three of the 40 paired plots in the grassland matrix contained woody individuals, with a total of 15 individuals from four species. We found that significantly more seedlings were established at the edges of rocky outcrops than in the paired grassland matrix plots (Fig. 4-a; Wilcoxon test, $P < 0.001$). For saplings, seven of the 40 rocky outcrops surveyed contained at least one individual, with a total of 29 individuals of four species (Table 1). Conversely, no woody plant saplings were found within the paired grassland matrix plots.

We found similar trends in seedling distribution beneath *E. crispa*. In all, 17 of 40 *E. crispa* surveyed sheltered at least one woody plant seedling, and we found 120 individuals from eight woody species overall. Three of the 40 grassland matrix plots contained woody individuals, comprising ten individuals from three species. Significantly more seedlings established beneath *E. crispa* than in the paired grassland matrix plots (Fig. 4-b; Wilcoxon test, $P < 0.001$). Five of the 40 *E. crispa* surveyed contained at least one sapling of a woody plant species, with a total of 22 individuals, belonging to five species (Table 1). Again, saplings of woody plant species were not found within the paired grassland matrix plots.

The most abundant species was *M. africana* both at the edge of rock outcrops and beneath *E. crispa*, accounting for 46 % and 82 %, respectively. Most recorded species were vertebrate-dispersed diaspores, which are small and brightly coloured (Table 1).

The GLM analysis showed that both outcrop height and the proportion of grass cover influenced seedling distribution (Table 2). The best-supported model according to the AIC included outcrop height and the proportion of grass cover, which together explained 34.3 % of the deviance. The model indicates that seedling number was positively associated with outcrop height and negatively associated with the proportion of grass in all models that selected this variable.

The best-supported model for seedling number beneath *E. crispa* included the tree height and proportion of grass

Table 1. List of woody plant seedling and sapling

Species	Fruit type	Diaspore size (mm)	Diaspore color	Disperser agent	Number of seedling				Number of sapling			
					RO	GM	BE	GM	RO	GM	BE	GM
Searsia dentata (Thunb.) F.A.Barkley	Drupe	4	Red	Bird[a]	7	2	2	1	1	0	1	0
Asparagus cooperi Baker	Berry	4	Red	Unknown	1	0	0	0	0	0	0	0
Gymnosporia heterophylla (Eckl. & Zeyh.) Loes.	Capsule	5	Brown	Unknown	4	0	2	0	0	0	2	0
Eulea crispa (Thunb.) Gürke	Berry	5	Black	Bird[b]	61	7	—	—	9	0	—	—
Diospyros whyteana (Hiern) F.White	Drupe	13	Brown	Bird, Mammal[c]	2	0	2	0	4	0	1	0
Calpurnia intrusa (R.Br.in W.T.Aiton) E.Mey.	Legume	Unknown	Unknown	—	0	0	1	0	0	0	0	0
Myrsine africana L.	Berry	4	Red	Bird, Mammal[d]	84	3	98	3	15	0	17	0
Canthium ciliatum (Klotzsch) Kuntze	Drupe	13	Black	Bird[e]	4	0	8	0	0	0	0	0
Osyris lanceolata Hochst. & Steud.	Drupe	10	Black	Unknown	1	0	0	0	0	0	0	0
Halleria lucida Jaub. & Spach	Berry	10	Black	Bird[f]	1	0	0	0	0	0	0	0
Rhoicissus tridentata (L.f.) Wild & R.B.Drumm.	Berry	10	Black	Bird[g]	15	3	1	6	0	0	0	0
Other spp.					1	0	6	0	0	0	1	0

RO: at edge of rocky outcrop. GM: Grassland matrix. BE: Beneath *Euclea crispa*.
a: Castley et al. (2001) for similarly diaspore size *Searsia crenata* (4 mm) in South Africa. b: Smith and Goodman (1987) for similarly diaspore size *Euclea divinorum* (7 mm) c: Chapman and Chapman (2003) for similarly diaspore size *Diospyros abysinnica* (10 mm) in Uganda. d: Senbeta and Teketay (2001). e: Githiru et al. 2002 for *Canthium oligocarpum* (15mm) in Ethiopia. f: Fourie (2008). g: Bleher et al. (2003).

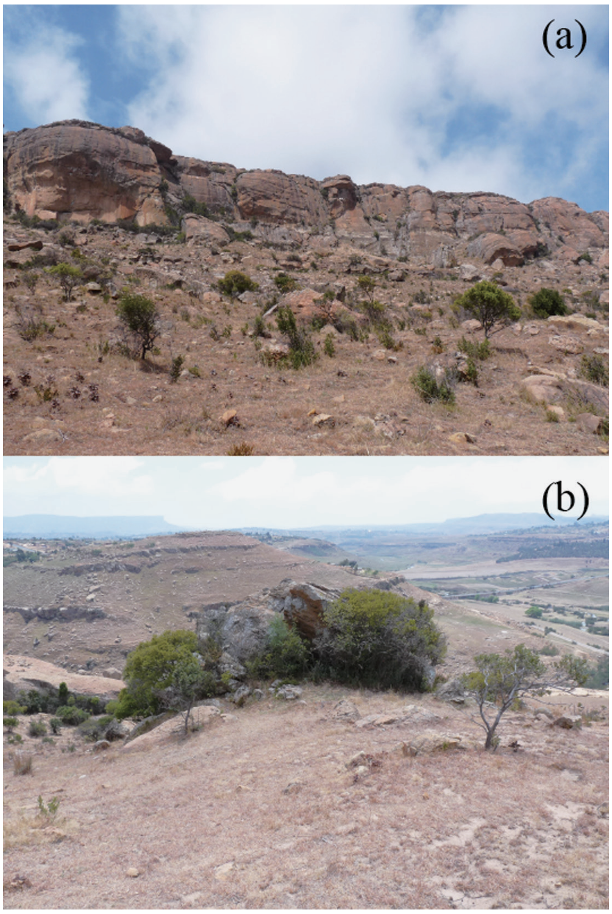

Fig. 3. Studied grassland dominated by *Themeda triandra* with sandstone outcrops and scattered *Euclea crispa* (a). Sandstone outcrops in the grassland (b). Note woody plant seedling established at the edge of rocky outcrops. Photographs by T. Fujita in September 2013.

cover (Table 3). The model also indicated that seedling number was positively associated with outcrop height. Again, seedling number was negatively associated with the proportion of grass in all models that selected this variable.

DISCUSSION

In addition to the area beneath *E. crispa*, the edges of rocky outcrops were also shown to have substantially more seedlings compared with the adjacent grassland matrix (Table 1). This result supports the idea that, as with classic nurse plants, rocky outcrops have positive effects on the establishment of woody plants in harsh ecosystems. Smit et al. (2005) reported similar results, showing that the distribution of *Picea abies* seedlings was positively associated with rocky outcrops and nurse plants in a wooded pasture in Switzerland.

The GLM analysis showed that the height of both the rock outcrops (Table 2) and *E. crispa* (Table 3) had positive effects on the number of seedlings. We attribute this result at least partly to the perch effect, which leads to increased seed deposition by frugivorous birds because (1) most seedlings recorded at the edges of rocky outcrops and beneath *E. crispa* had characteristics associated with dispersal by birds (Table 1), and (2) it is known that tall structures receive more seed rain from bird-dispersed plant species than do short ones (Holl 1998, Toh et al. 1999). For instance, Toh et al. (1999) found that bird-dispersed seeds were more abundant under artificial perches that were 6 m tall than under 3 m tall perches.

A change in microenvironment conditions with the height of the rock outcrops and of *E. crispa* may also ex-

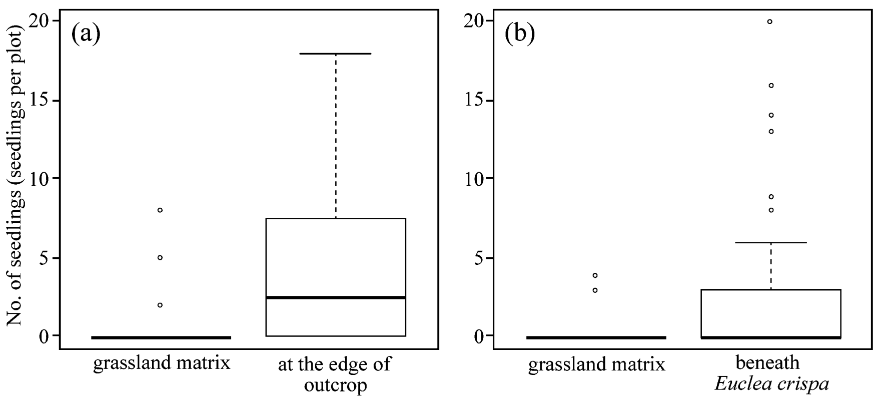

Fig. 4. Seedling abundance at the edge of rocky outcrops and in the paired grassland matrix plots (a) , and beneath *Euclea crispa* in the paired grassland matrix plots (b). See text for plot definitions. Maximum and minimum values are respectively shown by the upper and lower ends of the vertical bars; 75 % and 25 % quartiles are shown by the upper and lower edges of the boxes, respectively; and the middle line represents the median value.

Table 2. Comparison of the generalized linear models of seedling number response to two explanatory variables at the edge of rocky outcrops

Parameter estimate and standard error (SE) of explanatory variables						AIC	Percentage deviance explained
(Intercept)	SE	Rock height	SE	Proportion of grass cover	SE		
1.746	0.177	0.579	0.101	− 0.024	0.003	270.7	34.3
2.453	0.121	—	—	− 0.024	0.003	295.3	24.5
0.829	0.141	0.575	0.090	—	—	329.8	12.0
Null model							
1.510	0.074	—	—	—	—	360.4	—

Table 3. Comparison of the generalized linear models of seedling number response to two explanatory variables beneath *Euclea crispa*

Parameter estimate and standard error (SE) of explanatory variables						AIC	Percentage deviance explained
(Intercept)	SE	Tree height	SE	Proportion of grass cover	SE		
− 1.562	0.577	1.601	0.212	− 0.025	0.005	218.4	44.8
− 3.153	0.479	1.944	0.196	—	—	239.9	36.3
2.433	0.167	—	—	− 0.040	0.005	273.8	24.1
Null model							
1.098	0.091	—	—	—	—	338.6	—

plain the observed pattern of plant establishment. Noy-Meir (2001) found that soil water content was positively correlated with the height of the nearest outcrop due to shading and a reduction in wind speed. Martens et al. (2000) showed that as tree height increased, the mean understory light decreased, which can reduce water stress in nursed seedlings. The amelioration of microenvironment conditions is likely important for plant establishment in stressful environments with high irradiance, temperatures, and soil water deficits. Future studies should examine the changes in environmental variables such as soil water content, light condition, and air temperature with nurse height and their effects on the fate of nursed seedlings.

Seedling establishment was more likely at the edges of rocky outcrops and beneath *E. crispa* with less grass cover (Table 2 and Table 3). This indicates that a reduction in the grass layer is prerequisite for the establishment of woody plant species in this grassland. Grasses can affect tree seedling survival and growth in a number of ways, including shading, below-ground competition for water and nutrients, or by altering fire frequency and intensity (Holl 2002). In the KwaZulu-Natal Drakensberg grassland, fire-exclusion experiments have led to the establishment of woody plants, including forest pioneers and forest species such as *M. africana* and *D. whyteana* (de Villiers and O'Connor 2011). Consequently, suppressed fire might be particularly important for the survival of woody plant species in this grassland.

In addition to shrubs, rocky outcrops appear to have a positive effect on the establishment of woody plants in South African grasslands, likely serving as perching structures for birds and providing favourable microhabitats. However, the number of sapling were substantially lower compared to seedling both at the edge of rock outcrops and beneath *E. crispa* (Table 1). This results indicate that nurse effect from rocky outcrops and *E. crispa* are crucial for seedling establishment but have limited impact on later persistence. To clarify this, future study should conduct long-term monitoring of post establishment phase. In addition, it will be important to determine which nurse structures (rocky outcrops vs. *E. crispa*) are most important for woody plant establishment in grasslands. Although both structures promoted plant establishment, they may differ in their interactions with nursed species in some aspects. For example, previous studies have indicated that belowground competition by nurse plants negatively affects nursed species survival (Callaway 1992), but this would not occur with rock-nursed species. To address this, seedling performance near nurse rocks and nurse plants should be compared, and the factors contributing to seedling performance should be assessed.

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