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Variation in woody plant species establishment according to nurse plant size in the South African grassland

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ABSTRACT: The nurse plant effect has been highlighted in a large number of studies, especially in harsh ecosystems. This positive effect may vary with the size of the nurse plant. The present study examined the effects of nurse plant size and grass cover on the pattern of plant establishment in the South African grassland. We compared the number of woody plant seedlings beneath a putative nurse plant (*Euclea crispa*) with that in the adjacent grassland matrix, and measured the canopy area and heights of *E. crispa* and the proportions of grass cover. Factors affecting the abundance of woody seedlings beneath *E. crispa* stands were examined using a generalized linear mixed model (GLMM); Akaike's information criterion was used to select the best-fit model. The best-supported model included tree height and the proportion of grass cover, but did not include canopy area. Tree height positively affected the number of seedlings, and the diaspores of most recorded species showed characteristics associated with dispersal by vertebrates. The GLMM also showed that the proportion of grass cover had a negative effect on the number of seedlings. These results suggest that *E. crispa* plants have positive effects on the establishment of woody plants in South African grasslands, likely by serving as perching structures for birds and providing less competitive microhabitats with a grass layer beneath their canopies.

KEY WORDS: Africa, Facilitation, Nurse plant, Perch effect.

INTRODUCTION

The nurse plant effect (i.e., the positive effect of a plant on the establishment of another one through amelioration of abiotic stress and/or increased seed deposition) has been highlighted in a large number of studies, especially in harsh ecosystems (Callaway, 1995; Yang *et al.*, 2010; Fujita, 2014; Fujita, 2016). This positive effect may vary with the size of the nurse plant (e.g., canopy area and tree height). Several studies have analyzed the relationship between nurse plant size and seedling establishment (e.g., Tewksbury and Lloyd, 2001; Azihou *et al*., 2013). Some studies found a significantly positive relationship between nurse plant size and seedling establishment (Tewksbury and Lloyd, 2001; Vieira *et al*., 2013), whereas another found no clear relationship (Azihou *et al*., 2013). To understand the mechanism of the nurse plant effect fully, further research is necessary.

The grassland biome of southern Africa is rich in species, community, and ecosystem diversity. For example, South African grasslands support approximately 3800 plant species and comprise globally significant centers of plant endemism (Cowling and Hilton-Taylor, 1997). These species-rich landscapes hold high conservation value, but are now severely threatened by anthropogenic activities (O'Connor, 2005). A better understanding of the vegetation dynamics in this grassland is crucial for sustainable management and conservation.

The grasslands in the Drakensberg foothills of South Africa can be described as *Themeda triandra* Forssk (Poaceae) grasslands with scattered shrubs (O'Connor and Bredenkamp, 1997). *Euclea crispa* (Thunb.) Gürke (Ebenaceae) is the dominant shrub species in this grassland (O'Connor and Bredenkamp, 1997). With the dense foliage and rounded form of *E. crispa*'s canopy, this shrub may act as a nurse plant for other woody plant species in the grassland. In this study, we examined whether *E. crispa* had positive effects on plant establishment and analyzed how the size of *E. crispa* affected the pattern of plant establishment by observing spatial distributions of woody plant seedlings. The effect of grass cover on plant establishment was also examined, as numerous studies have shown that grass cover is an important factor in tree seedling establishment in grassland and savannah ecosystems (Holl, 2002; Shararn *et al*., 2009). Specifically, our research questions were: (1) Is seedling abundance beneath *E. crispa* higher than that in the open grassland matrix? (2) If so, does seedling abundance beneath *E. crispa* increase as the canopy area and tree height increase? and (3) Does seedling abundance beneath *E. crispa* decrease as the proportion of grass cover beneath *E. crispa* increases?

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MATERIALS AND METHODS

Study Area

The study site was located in a communal grassland in the Drakensberg foothills managed by the traditional council of Tsheseng, located 11 km south of Phuthaditjaba, South Africa (28°37′52″S, 28°49′58″E), at 1850 m elevation. The mean annual precipitation calculated for the last 20 years is 1197 mm, and the mean annual temperature is 9°C (climate data were obtained from the South African weather bureau for Royal National Park, located 90 km southeast of the study area). Cattle and goats are generally brought up to the grassland to graze, and the region is burned every year by local people. Sandstone outcrops, a common feature of the landscape, are interspersed throughout the grassland. *Themeda triandra* is a dominant grass species at the study site, and *E. crispa* is the dominant woody plant species, occurring as isolated individuals or in small stands in the grassland. *Euclea crispa* reaches a height of 1–2 m and is widely distributed throughout the grassland, often in rocky locations. The fleshy berries (5 mm in diameter) of *E. crispa* are black when ripe and dispersed primarily by frugivorous birds. At the base of terrace cliffs, the grassland contains continuous stands of woody plants such as *Gymnosporia heterophylla* (Eckl. & Zeyh.) Loes., *Myrsine africana* L., *E. crispa* and *Diospyros whyteana* (Hiern) F. White. These woody species, except *E. crispa*, rarely occur on slope taluses in grasslands.

Data collection

In September and October 2013, 40 *E. crispa* stands were randomly selected in the grassland (ca. 1 × 0.5-km) along the slope talus. We defined an *E. crispa* stand as having at least one *E. crispa* individual over 1 m tall that exhibited no overlap with the crowns of other woody species and lacked other woody plant species over 1 m in height beneath the crown. The number of *E. crispa* individuals within a stand ranged from one to five, and the heights and canopy areas of all study *E. crispa* stands were measured. We estimated the canopy area as an ellipse using the maximum length and maximum width of stands. In each stand, woody plant seedlings were sampled in a 50 × 50-cm randomly placed plot beneath *E. crispa* and in a 50 × 50-cm paired plot (2 m away) in the adjacent grassland matrix. To establish plots beneath *E. crispa* stands, a direction from the centre was randomly chosen, and the plot was placed at the midpoint between the tree trunk and the canopy projection limit. We then used the same direction to establish the paired plot 2 m away from the canopy projection, selecting a grassland matrix with no direct canopy cover. If that was not feasible, we randomly chose another direction. In each plot, we identified all woody plant seedlings less than 50 cm in height, with the exception of current-year seedlings with a cotyledon that were not lignified. We counted the number of each seedling species. To characterize microhabitat conditions in each plot, the proportion of grass cover was estimated visually using 10% cover-class intervals in each plot. The minimum distance separating experimental paired plots was 5 m, and the total number of sampled plots was 80.

Data analysis

To avoid positive spatial associations resulting from the high occurrence of young individuals originating from each parent *E. crispa*, we excluded all *E. crispa* seedlings from the analyses. The numbers of seedlings as well as the proportion of grass cover beneath *E. crispa* stands and within the paired grassland matrix were compared using Wilcoxon tests. The factors affecting the abundance of woody seedlings beneath *E. crispa* stands were examined using a generalized linear mixed model (GLMM) with Poisson distribution and a log-link function. The canopy area of the *E. crispa* stands, stand height, and the proportion of grass cover were included as explanatory variables and the directions used to place the paired plots were included as a random effect. Akaike's information criterion (AIC) was used to select the best-fit model. The full model included all three variables. To select the best-fit model, we successively deleted explanatory variable(s) from the full model. Then, the model with the lowest AIC was accepted as best for the data. We used R version 2.12.2 for all analyses.

RESULTS

The mean canopy area of the surveyed *E. crispa* stands was 5.1 m^2, ranging from 0.5 to 12.2 m^2. The mean height of the *E. crispa* stands was 2.0 m, ranging from 1.2 to 3.1 m. The proportion of grass cover did not differ between *E. crispa* stands (median = 40%, range = 10–80%) and the paired grassland matrix plots (median = 50%, 10–90%; $P = 0.25$; Wilcoxon test).

Overall, 130 seedlings of 8 woody species (height ≤50 cm) were found (Table 1). Most of these seedlings (92%) were found beneath *E. crispa* stands. The seedling numbers were significantly more abundant beneath *E. crispa* stands than in paired plots within the grassland matrix ($P < 0.001$; Wilcoxon test). Most of the recorded species beneath *E. crispa* stands represented vertebrate-dispersed diaspores, which are small and brightly colored (Table 1).

The best-supported model according to AIC included the stand height and the proportion of grass cover, but did not include the canopy area (Table 2). Four of the top five models selected stand height, and all of these models indicated a positive correlation between seedling abundance and tree height. By contrast, the proportion of grass cover was negatively correlated with the seedling abundance in all models that selected this variable (Table 2).

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Table 1 List of woody plant seedlings (H < 50 cm).

Familiy	Species	Life form	Palatability	Fruit type	Diaspore size (mm)	Diaspore color	Disperser agent	Number of seedlings	
								Beneath Euclea	Grassland matrix
ANACARDIACEAE	*Searsia dentata*	S	Palatable	D	4	Red	Bird[a]	2	1
CELASTRACEAE	*Gymnosporia heterophylla*	S	Spine	C	5	Brown	Unknown	2	0
EBENACEAE	*Diospyros whyteana*	S	Palatable	D	13	Brown	Bird・Mammal[b]	2	0
FABACEAE	*Calpurnia intrusa*	S	Unknown	L	Unknown	Unknown	Unknown	1	0
MYRSINACEAE	*Myrsine africana*	S	Palatable	B	4	Red	Bird・Mammal[c]	98	3
RUBIACEAE	*Canthium ciliatum*	S	Spine	D	13	Black	Bird[d]	8	0
VITACEAE	*Rhoicissus tridentata*	C	Palatable	B	10	Black	Bird[e]	1	6
	one unidentified sp.							6	0

Life form S: Shrub. C: Climber. Fruit type D: Drupe. C: Capsule. L: Legume. B: Berry. (a) Castley *et al*. (2001) for similar diaspore size *Searsia crenata* (4 mm) in South Africa. (b) Chapman *et al*. (2003) for similarly diaspore size *Diospyros abysinnica* (10 mm) in Uganda. (c) Senbeta and Teketay (2001) for *Myrsine africana* in Ethiopia. (d) Githiru *et al*. (2002) for similar diaspore size *Canthium oligocarpum* (15 mm) in Ethiopia. (e) Bleher *et al*. (2003) for *Rhoicissus tridentata* in South Africa.

Table 2 Comparison of the generalized linear mixed models of seedling number response to three explanatory variables under *Euclea crispa*. Models were selected according to the value of Akaike's information criterion (AIC). The null model in which all three explanatory variables were removed.

Parameter estimate and standard error (±SE) of explanatory variables				AIC
(Intercept)	Stand height	Proportion of grass cover	Canopy area	
-3.53±0.80	2.25±0.29	-0.02±0.01		121.4
-3.67±0.82	2.45±0.37	-0.02±0.01	-0.04±0.04	122.6
-4.72±0.75	2.48±0.29			128.8
-4.72±0.77	2.48±0.36		0.00±0.04	130.8
0.67±0.45		-0.02±0.01	0.14±0.03	172.8
-0.61±0.41			0.19±0.03	189.3
1.74±0.35		-0.03±0.01		190.1
Null model				
0.48±0.37				224.7

DISCUSSIONS

In this study, no clear relationship between the *E. crispa* canopy area and seedling abundance beneath *E. crispa* was found (Table 2). This pattern contrasts with that of previous studies, which showed a positive correlation between the nurse plant canopy area and plant abundance beneath nurse plants (e.g., Tewksbury and Lloyd, 2001; Vieira *et al.*, 2013). A large canopy can provide favorable microhabitats that are crucial for later persistence; however, this effect may have limited impact on early establishment, which was the focus of the present study (Azihou *et al.*, 2013). Azihou *et al*. (2013) found that the abundance of saplings (>1.3 m in height) was positively correlated with the nurse plant canopy area, but found no association between seedling abundance (≤1.3 m in height) and canopy area in African grasslands. Alternatively, the lack of a canopy area effect could be explained by the low variation in this variable (0.5–12.2 m^2) compared with that in earlier studies (1.5–162.0 m^2 in Tewksbury and Lloyd (2001) and 1.4–64.3 m^2 in Vieira *et al*. (2013)).

Unlike the size of the canopy area, the height of the *E. crispa* stands was positively correlated with woody seedling occurrence beneath *E. crispa* stands (Table 2). This result could be due to the perch effect, which leads to increased seed deposition by frugivorous birds under tall trees (Holl, 1998; Toh *et al*., 1999). Indeed, the species we found established beneath *E. crispa* stands had small, brightly colored diaspores, which are indicative of dispersal by birds. Frugivorous birds preferentially perch on taller trees probably to gain better calling sites or better protection from predators (McDonnell, 1986; Aukema and Martinez del Rio, 2002). Common frugivores in this region, including the dark-capped bulbul (*Pycnonotus nigricans*), the Cape rock thrush (*Monticola rupestris*) and the red-winged starling (*Onychognathus morio*), are potential dispersers of the seeds of woody plant species beneath *E. crispa*.

Seedling establishment was more likely to occur beneath *E. crispa* stands where the grass cover was diminished (Table 2), suggesting that suppression of grass cover is a prerequisite for the establishment of woody plant species in grasslands (Shararn *et al.*, 2009). Grasses can affect seedling establishment in a number of ways, including above- and below-ground competition for light, water, and nutrients. The suppression of fire

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following reduced grass cover may also be crucial for the establishment of woody plant species in grasslands that are burned annually by local people. Future studies should examine the relative importance of these factors through manipulative experiments.

Tall individuals of *E. crispa* appear to enhance the establishment of other woody plant species in South African grasslands, possibly by offering perching structures for frugivorous birds. Suppression of grass cover is also a prerequisite for the establishment of woody plant species. The explanation provided in this study for the observed pattern of plant establishment is mainly speculative at this point. Additional studies of other biogeographic regions as well as experimental approaches are needed to fully understand how nurse plant size affects the pattern of plant establishment.

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