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Original article

Effects of plant-plant interactions and herbivory on the plant community structure in an arid environment of Saudi Arabia

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ABSTRACT

There is currently considerable evidence support that plant community structures are driven by plant-plant interactions (e.g., competition and facilitation). In contrast, there is also evidence demonstrating that plant community structure is affected by the impact of consumer pressure (e.g., grazing). In this study, 15 and 10 *Acacia gerrardii* nurse plants were selected inside and outside Sudyrah natural reserve (protected) area in western Saudi Arabia, respectively. The understory vegetation abundance (e.g. cover and density) was measured among quadrats around the nurse trees in both protected and unprotected areas to examine the impact of grazing and the positive interaction on the understory species. I found that understory vegetation associated with nurse trees (*A. gerrardii*) has been driven by both the positive impact of nurse plant and the grazing. Although the understory vegetation was positively affected by the impact of facilitation, the composition of such vegetation has been changed due to the impact of herbivory.

1. Introduction

Facilitation that is the positive plant-plant interaction enhances plant fitness, species richness, and plant biodiversity. Facilitation is especially common in stressful environments (e.g. arid environment), and its intensity increases along a stress gradient (Bertness and Callaway, 1994; Callaway & Walker, 1997; Brooker and Callaghan, 1998; Tewksbury and Lloyd, 2001; Flores and Jurado, 2003; Sthultz et al., 2007).

Although many studies have been conducted on plant-plant interactions along gradients of abiotic stresses, several studies recently proposed that such interactions could be driven by biotic stresses. Therefore, the plant community structure may be affected by complex interactions of biotic and abiotic factors (Olff and Ritchie, 1998; Catorci et al., 2016). A few studies have been conducted on the interactions among coexisting species along gradients of biotic stresses such as herbivory pressure (Brooker & Callaghan 1998; Brooker et al., 2006; Smit et al., 2007; Brooker et al., 2008).

According to the stress gradient hypothesis (SGH) (Bertness and Callaway, 1994), a biotic stress resulting from grazing pressure should have a positive impact on interactions between coexisting species. Experimentally, Callaway et al. (2005), Brooker et al. (2006), and Veblen (2008) found that the balance between plant-plant interactions (competition and facilitation) could be affected by the presence of herbivory. However, the impact of grazing by herbivores on the net outcome of interactions between coexisting species is certainly controversial. There are several studies that support the SGH hypothesis, suggesting that the presence of herbivory positively affect the interaction between coexisting species (Callaway et al., 2005; Smit et al., 2006; Eldridge et al., 2013; Howison et al., 2015; Filazzola et al., 2018). In contrast, a few studies oppose this hypothesis (e.g. Rousset and Lepart, 2002; Baraza et al., 2006). Moreover, several studies show that there is no impact of herbivory on the interactions between plant species (e.g. Rand, 2004; Smit et al., 2007; Howard et al., 2012).

The impact of grazing on the net outcome of the interaction between plant species depends on the intensity of grazing. For example, some studies (e.g. Smit et al., 2007; Vandenberghe et al., 2009) showed that the net outcome of interactions between the coexisting species shifted from a neutral to positive interaction (i.e. facilitation), then the positive interaction declined and disappeared with an increasing intensity of grazing. Under low grazing level, the impact of grazing on the net outcome of interactions between plant species can be very weak. Under moderate level of

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grazing, the positive interaction can be dominant between interacting plants, whereas under a high level of grazing, the positive interaction decreases and disappears (Smit et al., 2007; Vandenberghe et al., 2009; Eldridge et al., 2013). Moreover, the impact of grazing on the interactions between plant species also depends on the traits of interacting plants (e.g. palatable or unpalatable, see Smit et al., 2009).

Several studies suggest that unpalatable shrubs in degraded areas may act as nurse plants, and facilitate palatable species that are growing beneath them by protecting them from herbivory effect (Callaway et al., 2000). Further, an unpalatable facilitative plant can reduce environmental stress on its neighbour plant species, which contributes to increasing its compensation after herbivore damage (Maschinski and Whitham, 1989). Thus, a positive effect may occur due to the physical defence from possible herbivores (Villarreal-Barajas and Martorell, 2009) under an intermediate level of herbivory (Brooker et al., 2006) or high level of herbivory mediated by stress amelioration (Callaway et al., 2005). However, under a high level of grazing, the effect of grazing could have an indirect positive and negative impact on unpalatable and palatable species, respectively (Smit et al., 2009). This situation occurs when grazing reduces the impact of competition on unpalatable plant species by defoliation of its palatable neighbours.

Although facilitation is common in stressful environments (Bertness and Callaway, 1994; Callaway and Walker, 1997; Brooker and Callaghan, 1998; Tewksbury and Lloyd, 2001; Flores and Jurado, 2003; Sthultz et al., 2007), the impact of facilitation has not been detected in stressful environments in Saudi Arabia. Perhaps, in a stressful environment, chronic overgrazing negatively influences the impacts of facilitation and promotes the net outcome of the interactions between neighbouring species to switch to a negative interaction. For example, *Acacia tortilis* trees have a positive interaction with their understory herbaceous species but the intensity of the positive interaction decreases in the presence of grazing (Abdallah et al., 2008).

The canopy of a tall plant provides shade environment that may attract herbivores as a shelter that leads them to overgraze understory herbaceous plants. Therefore, the net outcome of interactions between coexisting plant species is affected by the herbivore grazing (Murray and Illius, 2000; Arsenault and Owen-smith, 2002). The intensity of facilitation between plant species may disappear with an increasing ferocity of grazing due to a decline in the abundance and performance of herbaceous species that grow under the canopy of the nurse plant. Thus, the impact of facilitation is unnoticeable in such arid environments that suffer from overgrazing.

Although plant-plant interactions control the structure of plant community (Al-Namazi et al., 2016), we believe that the impact of grazing in the arid environment also plays a key role in the plant community structure because unpalatable species will be more dominant and frequent in this environment, whereas palatable species will be inferior.

In this study, I attempted to show that overgrazing is the main cause behind the disappearance of the facilitation effect in the stressful environment in Saudi Arabia. I predict that (1) the facilitation impact will be negatively affected by herbivores pressure in grazed areas. (2) The plant composition will vary among grazed versus protected areas because unpalatable species will be dominant in the plant community of grazed areas.

2. Materials and methods

2.1. Study site

The study was conducted inside (protected) and outside (grazed) of Sudyrah nature reserve which belongs to the National Wildlife Research Centre (NWRC). It is located on the arid Najd plains of western Saudi Arabia, about 45 km southeast of Taif Governorate in southwestern Saudi Arabia (21°14′55.6″N, 40°43′44.8″E) (Fig. 1). This reserve area (4 km^2 in total) was declared as a scientific nature reserve centre and fenced since 1986 by NWRC. Since that time, grazing by domestic livestock was excluded, allowing the vegetation inside the protected area to recover from overgrazing. The grazed area outside the reserve is grazed by various livestock animals such as sheep, goat, and camel. The study was conducted at the end of summer and beginning of autumn from August to October 2016. The average annual rainfall in the reserve is about 85 mm per year. The mean annual maximum air temperature is about 37 °C, whereas the mean annual minimum air temperature is about 15.7 °C. The mean annual medial air temperature is about 23 °C.

2.2. Experimental design

The study was conducted at two sites differing in grazing intensity (protected versus heavily grazed). The protected area was inside the nature reserve of Sudyrah, whereas the grazed area was outside the reserve. Both sites share the same soil type and topography. Within each site, two transects of 8 m long were established from the centre of 15 *Acacia gerrardii* Benth. trees canopies inside the reserve and 10 trees canopies outside the reserve, in two directions (north and south). Six quadrates (1 m × 1 m) were distributed along each transect: 2 quadrats under, 2 at the edge, and 2 outside the *Acacia* canopy. A species list was compiled in each quadrat. The mean abundance of species (the number of individuals per species) was recorded for the three micro-habitats (under, at the margin, and outside the canopy) in each grazed and protected study site. Some other community attributes were also estimated including species richness and species cover. Species richness was calculated as the total number of species occurring per unit area (1 m^2).

2.3. Data analyses

Collected data were analysed using the generalized linear model (GLM) to test the interaction between factors of the microsite (under the canopy, the edge of the canopy, and open or outside the canopy) and treatment nested within the grazed/protected treatment. Post hoc comparisons were conducted using a Tukey's HSD test to compare vegetation attributes among treatments. The statistical analyses were implemented using SPSS software ver. 16.0 for Windows. Indicator species analysis (Dufrene and Legendre, 1997) was carried out to identify the species uniquely associated with the microsites.

3. Results

The results show a significant effect of microsites (df = 2, F = 7.872, $P \leq 0.0001$) but no significant effect of grazing factor was observed on the plant composition based on density among the two areas (the grazed versus protected) (df = 1, F = 0.459, P = 0.498; Table 1). In contrast, there were significant effects of both grazing and microsite factors on the plant composition based on the cover (Table 2). The species composition based on the cover shows that the composition of plants was significantly affected by grazing (df = 1, F = 11.37, P = 0.001) and microsite (df = 2, F = 5.677, P = 0.004) among the two areas. The data analysis of plant composition based on the plant density showed that the interaction between grazing and microsite factors was not significantly different between the two areas (df = 2, F = 0.119, P = 0.888). However, the interaction between grazing and microsites was

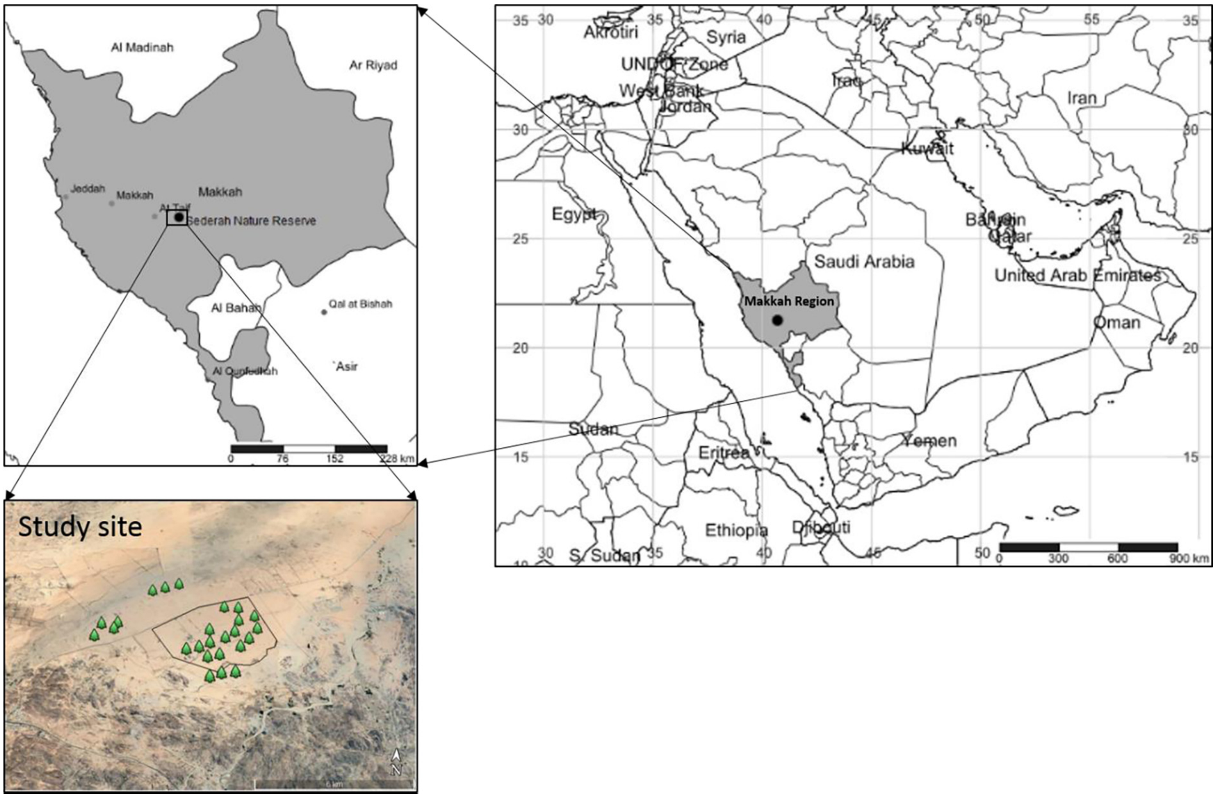

Fig. 1. Map of the study site.

Table 1
Mixed-model analysis of variance results on the impact of grazing factor (grazed versus protected), and canopy position (microsite) on plant density. df and MS stands for degrees of freedom and mean squares, respectively.

Source of variation	Sum of squares	df	MS	F	P
Grazing Effect (GE)	0.438	1	0.438	0.459	0.498
Microsite Effect (ME)	15.043	2	7.521	7.872	<0.0001
GE × ME	0.227	2	0.114	0.119	0.888
Error	1255.397	1314	0.955		
Total	1579.250	1320			

Table 2
Mixed-model analysis of variance results on the impact of grazing factor (grazed versus protected), and canopy position (microsite) on plant cover. df and MS stands for degrees of freedom and mean squares, respectively.

Source of variation	Sum of squares	df	MS	F	P
Grazing Effect (GE)	296.296	1	296.296	11.37	0.001
Microsite Effect (ME)	295.898	2	147.949	5.677	0.004
GE × ME	286.630	2	143.315	5.499	0.004
Error	34243.830	1314	26.061		
Total	36420.636	1320			

significantly variable regarding the plant cover (df = 2, F = 5.499; P = 0.004).

The density of understory herbaceous species was significantly higher under the canopies of nurse trees than that at the edge of canopies in both grazed and protected areas (Fig. 2). In contrast, plant cover was significantly higher in the microhabitat under the canopy than that in other two microhabitats (at the edge and the open) in the protected area, whereas regarding the plant cover, there were no significant variations among the three microhabitats in the grazed area (Fig. 3). The species richness was found to be higher in the protected area than that in the grazed area, particularly at the microhabitat under the canopy (Fig. 4).

The indicator of species analysis (Table 3) shows that the most dominant species under canopy in the grazed area is *Euphorbia granulata* Forrsk; (an unpalatable species) and *Aizoon canariense* L., which is favoured by disturbance. The most common species at the edge of canopies in the grazed area are *Commicarpus grandiflorus* (A. Rich.) Standl (an unpalatable species) and *Tribulus terrestris* L. (a disturbance species).

4. Discussion

Findings of this study indicate that herbivory has a negative impact on the plant cover of understory species but has no impact

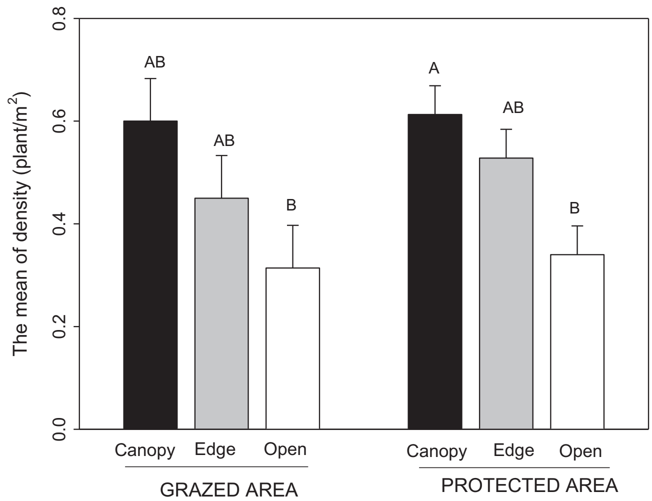

Fig. 2. The mean values of plant density among three microhabitats in two areas with different grazing effects (e.g., grazed versus protected areas). Bars showing by the same letter are not significantly different at $P \geq 0.05$, based on Tukey's HSD post hoc tests.

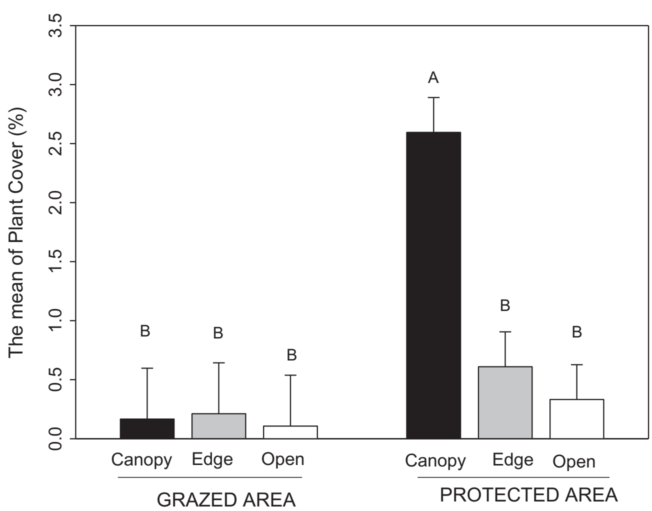

Fig. 3. The mean values of plant cover among three microhabitats in two areas with different grazing effects (e.g., grazed versus protected areas). Bars showing by the same letter are not significantly different at $P \geq 0.05$, based on Tukey's HSD post hoc tests.

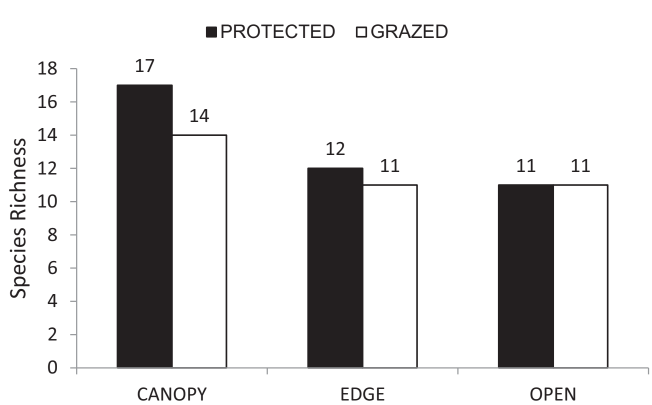

Fig. 4. Species richness of beneficiary understory species in the different microsites among the two locations (protected versus grazed).

on their density (Tables 1, 2). The results based on plant density illustrate that there is no significant impact of grazing on the positive interaction between the nurse plant and the beneficiary understory herbaceous species (Fig. 2). Although the density of an understory species (i.e. the number of species per area unit) has not been affected by herbivory, overgrazing has a significant effect on the understory plant community composition (see also Al-rowaily et al., 2015). Our results, therefore, are against the studies suggesting grazing negatively affected facilitation (Murray and Illius, 2000; Arsenault and Owen-smith, 2002; Abdallah et al., 2008), but in agreement with studies stating that there is no impact of herbivory on plant-plant interactions (Rand, 2004; Smit et al., 2007; Howard et al., 2012).

The results demonstrate that there was a positive effect for the nurse plant in both grazed and protected areas when the density is used to indicate the performance of understory species. However, when the plant cover is used as an indicator of the performance, the positive effect of the nurse plant appeared only in the protected area but disappeared in the grazed area. Although there was a significant variation in the plant cover among the three microhabitats in the protected area, there was no significant variation in the plant cover among the three microhabitats in the unprotected (grazed) area (Fig. 3). The results based on the plant density demonstrate that facilitative impact of nurse plant on understory species is apparent and exists in both in grazed and protected areas because the plant density under the canopy is higher than that in the open area (outside the canopies of nurse trees) (Fig. 2). These results, therefore, illustrate that the positive interaction of the nurse plant is not affected by the grazing factor.

Nevertheless, the impact of grazing on species composition is clear according to the results if the plant richness in the protected area is compared with that in the grazed area (Fig. 4). Although the vegetation composition based on the density of plant species is significantly higher under the canopy in both protected and grazed areas, the structure of community differs among these two areas and this result is in an agreement with Eldridge et al., 2016. This result may be attributed to the selection of herbivores for palatable plant species. If a plant species is selectively grazed, its fitness might be declined, and consequently, a modification for competitive dynamics may occur among the plant community, and unpalatable species can outcompete weak palatable species (i.e. because of grazing pressure) (Gurevitch et al., 2000; Fowler, 2002). Therefore, in the grazed area, species most benefiting from the facilitation are unpalatable plants. The indicator of species analysis shows that there is a variation in plant structure among the two treatments of grazing and three microsites (Table 3).

The plant community in the protected area is more diverse because the nurse plants (*Acacia* trees) increase the biodiversity (Noumi et al., 2015). In the absence of grazing impact, the plant diversity (i.e. higher species richness) includes species from both palatable and unpalatable plants (Fig. 4). In contrast, in the grazed area, the plant community structure contains mainly unpalatable species and a few species of palatable species (e.g. species that have an ability to resist grazing pressure) (Table 3). Thus, herbivory acts as an ecological filter and reduces the species richness by eliminating palatable species. Therefore, the plant community structure changes due to the interplay of plant-plant interactions and herbivory (Catorci et al., 2012).

In the protected area, at the centre of the canopy, the most dominant species are competitor species such as *Lycium shawii* Roem & Schult. (which is very common in this microsite). Although this species is palatable for camel and sheep, it has also a high competitive ability. This species, therefore, takes advantage of the protection against grazing in the protected area through its high competitive ability and high seed dispersal by birds living on the canopy of *A. gerrardii*. *Salvia aegyptiaca* L. is also one of the most

Table 3
The indicator of species analysis among three microhabitats in two areas vary in term of grazing factor (grazed versus protected).

Group	Species	Traits	IV	p*
Grazed canopy	*Euphorbia granulata*	Unpalatable succulent	38.8	0.021
Grazed canopy	*Aizoon canariense*	Unpalatable	34.8	0.033
Grazed edge	*Tribulus terrestris*	Thorny disturbance herb	60.9	0.008
Grazed edge	*Commicarpus grandiflorus*	Unpalatable	33.8	0.041
Protected canopy	*Lycium shawii*	Thorny shrub edible by camels	85.0	0.0002
Protected canopy	*Salvia aegyptiaca*	Aromatic unpalatable	57.0	0.024
Protected edge	*Stipagrostis plumosa*	Palatable grass	52.6	0.019
Protected edge	*Indigofera spinosa*	Palatable legume	37.5	0.028

dominant canopy species because it has shade preference and receives facilitation from the nurse plant (*A. gerrardii*). It is also a competitor species and therefore, a dominant species in this microsite (see Al-Namazi et al., 2016). At the edge of the canopy in the protected area, the most dominant species are palatable and stress-tolerant species such as *Indigofera spinosa* Forssk and *Stipagrostis plumosa* (L) Munro ex T. Anders. These species have low competitive ability but they have high stress-tolerance ability. Therefore, they are dominant in more stressful microhabitats at the edge of the canopy.

On the contrary, in the grazed area, at the centre of the canopy, the canopy of nurse plant provides shade for herbivores (Dean et al., 1999) which contribute to an increasing grazing pressure on the palatable plant species growing under the canopy of the nurse plant. Herbivores (e.g. livestock) seek the canopies of nurse trees and use them as shelter to avoid the sun heat and radiation. Therefore, herbivores clear all palatable species, disturb the soil, and reduce the habitat suitability for plants. As a result, unpalatable species such as *Euphorbia* species (which is a Poisonous species) are dominant in this microsite. At the edge of the canopy, the grazing pressure is less effective than that under the canopy microsite. In this microhabitat, the unpalatable species (e.g. *Commicarpus* sp.) were also dominant. However, several species that are relatively palatable (e.g. *Cynodon dactylon*) existed in this microhabitat as well. Considering that these species are high yielding palatable species and very resistant to grazing and trampling (Chaudhary and Al-Jowaid, 1999). Such species at the edge microsite benefit from facilitation by *A. gerrardii* (the nurse plant) because they are far away from grazing pressure and less susceptible to animal disturbance. Moreover, some dominant species (such as *Tribulus* sp) at the edge microsite in the grazed area are protected against grazing by having thorny seeds.

The results of this study indicate that the plant community structure is formed by biotic interaction between associated species and abiotic stress in the protected area under no herbivore impact. The competitor species are dominant in the benign environment under the canopy of nurse plant, whereas stress tolerant species (such as *I. spinosa* and *S. plumosa*) are more common in more stressful microsite at the edge of the canopy (see Al-Namazi et al., 2016).

In the grazed area, grazing plays a key role in forming the plant community structure because the plant community structure is driven by grazing selectivity. Palatable species in this area experience grazing pressure with an increasing intensity of grazing. This pressure negatively affects the growth and survival of palatable species, whereas it positively affects the growth and survival of unpalatable species by relieving the competitive stress caused by palatable species. Therefore, unpalatable and disturbance-dependent species are more common in this grazed area.

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