

Characterizing invasiveness through a descriptive study of Guinea grass (*Megathyrsus maximus*) growing in three habitat types and differing herbivore assemblages in both Kenya and Texas.

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Abstract

Guinea grass (*Megathyrsus maximus* syn. *Panicum maximum*) is an important pasture grass that has been introduced pantropically, yet in many cases has escaped cultivation and is invading native rangelands – threatening biodiversity at multiple trophic levels. An increasing challenge of rangeland management is balancing the importance of pasture grasses with their negative impact on ecosystem processes. Given this challenge, it is critical to understand the mechanisms that underlie grass invasion. In this descriptive study, our objective was to assess the ecological stress release hypothesis by comparing the relative abundance and functional traits of Guinea grass in Kenya's home range with its introduced range in Texas, USA. To characterize Guinea grass dominance in Texas vs. Kenya, we measured plant height and cover and examined the associated arthropod and ungulate abundances. We characterized these associations across three habitat types of differing resource availability; 1) Under woody legumes with higher soil moisture and soil nitrogen, 2) grasslands with higher light yet drier soils, 3) riparian areas with higher soil water moisture and light. We found that Texas Guinea grass was 50% taller than Kenyan Guinea grass except for riparian environments comparable to its introduced range. Texan Guinea grass occupied 50% more area than Kenyan Guinea grass and was especially abundant under woody legumes. Texas ungulate communities were less diverse and abundant. The arthropod herbivore diversity was twice as high on Kenyan Guinea grass. These results suggest that Guinea grass has escaped a rich assemblage of herbivores and likely explains some of its spread in nonnative ranges. The interaction between resource environment and herbivory may elucidate mechanisms important for Guinea grass escaping cultivation in its introduced range and lays the foundation for future ecological studies and a search for biological control.

Introduction

The introduction of perennial grasses for rangeland improvement has led to the pantropical distribution of highly invasive grasses (Marshall, Lewis et al. 2012, CABI 2020). Intended and unintended release of invasive grasses has detrimental impacts on ecosystem processes (D'Antonio and Vitousek 1992). A proposed mechanism for exotic plant invasions is the Ecological Release Hypothesis, which posits that specialist enemies will be absent from the new system and that generalists will prefer native plants (Keane and Crawley 2002). A second mechanism arises from theoretical community ecology, which relies on disturbance (Shea and Chesson 2002). It is critical to understand these patterns and processes in the context of both the native and introduced ranges in order to explain the underlying mechanisms of invasion (van Kleunen, Dawson et al. 2010). This foundational understanding will lead to a general understanding of how an invasive grass's ecology and biology differ in its native and introduced range and open opportunities for directed management.

Two popular hypotheses surrounding the success of invasive species deal with a plant's ability to outcompete native plants for resources (Blossey and Notzold 1995, Davis, Grime et al. 2000) or through apparent competition by losing natural enemies (Mlynarek, Moffat et al. 2017). Together these ideas predict a landscape's invasibility due to the availability of resources and the higher invasiveness due to improved performance with less natural enemies. For both invasibility and invasiveness, species life histories and functional traits are important indicators of plant success and are often highly correlated with their invasiveness and dominance in a community (Cornwell and Ackerly 2010). This would lead to the expectation that high reproductive output, mode, tolerance to herbivory, and growth rates would be important indicators. While it is expected for perennial grasses in both the native and invaded range to have similar strategies, release from natural enemies would alter the phenology of functional traits.

Nutrient and water availability vary greatly across vegetation types. In savanna systems, woody vegetation and riparian patches integrate with a connected grassland matrix. Differing light environment, nutrient turnover in woody legumes, and water availability have essential impacts on grass growth (Zitzer, Archer et al. 1996, Ludwig, Dawson et al. 2004). Therefore, a gradient of available resources may be inferred by proxy through these areas and inference to Guinea grass response to resources.

Here we evaluate Guinea grass productivity through cover and height in its introduced range, and native range differed across resource availability gradients in three different environments. We quantified the species richness of arthropods, and ungulates, in Guinea grass's introduced and native range and examined their impact on Guinea grass functional traits and reproductive output. We hypothesize that there will be higher richness and diversity of ungulate herbivores, and arthropod herbivores on Guinea grass in native ranges versus the introduced range. We hypothesize that this will be correlated with overall functional traits related to production, resistance, and reproductive output.

Methods and Study Site

Study sites

We established field sites to examine Guinea grass occurring naturally in two savanna systems; 1) Laikipia, Kenya, representing part of Guinea grass's native range, 2) South Texas, part of its current introduced range. We established locations across precipitation gradients (439 mm - 639 mm in Kenya and 736 mm in South Texas). In Kenya, field sites were selected along the Ewaso Nyiro River on a North-South and Low-High, precipitation gradient in Laikipia, Kenya. On the west side of the river is Mpala Research Centre, an active cattle ranch with approximately 2000-3000 livestock grazing at low to moderate stocking intensities on 19500 hectares, including Zebu/Boran mix-breed of cattle, camel, goat, and sheep. On the east side of the river are communal tribal lands where cattle grazing is less structured and is often grazed at high stocking densities. Ten locations were selected in both Kenya and Texas, and at each study location (20 in total). Three samples were taken in woody mottes (thickets), open grassland matrix, and riparian zones. A total of 30 locations, each subdivided into 3 study sites (mott/grassland/riparian) in Kenya and Texas, a total of 180 study sites.

Guinea grass height and percent cover

To understand how functional traits vary across land use, environmental gradients, and introduced vs. native range, we measured the height and percent cover at each site. We sampled three 1 m² quadrats in Guinea grass patches for percent cover and selected the largest plant from each quadrat for measuring the height. The average value of the three plots was used in the analysis.

Arthropod associates

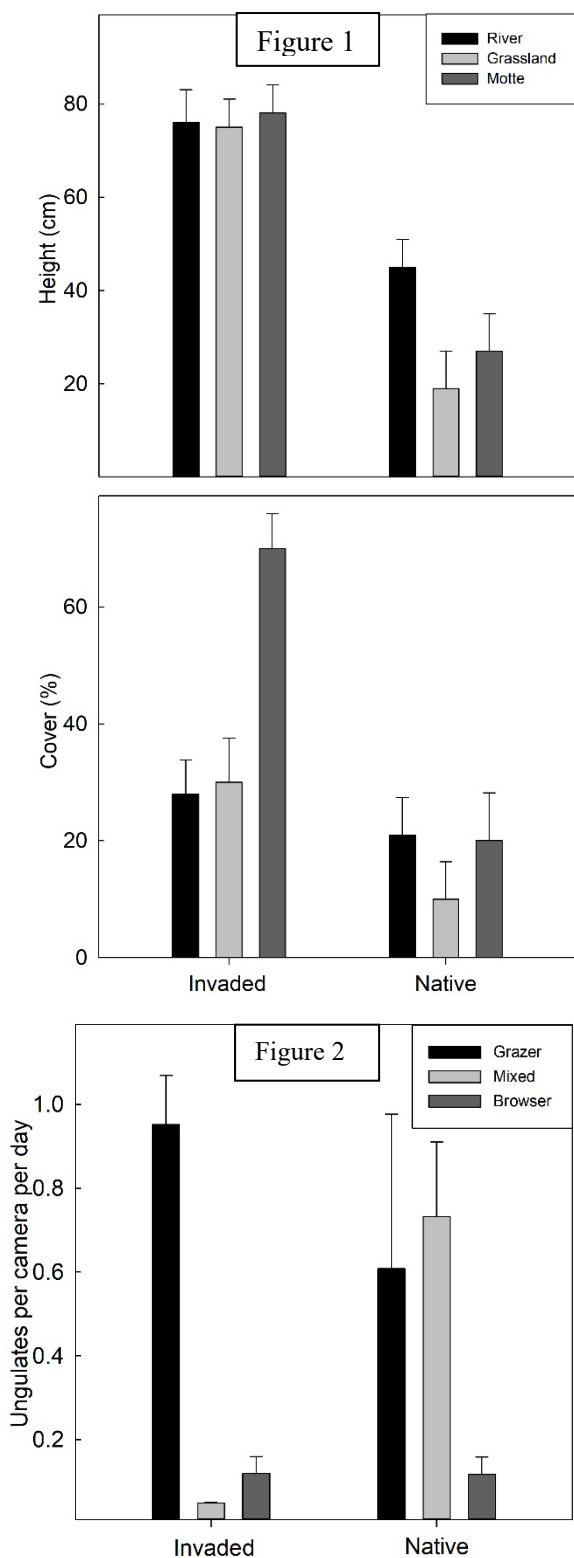
Three Guinea grass plants from each site were uprooted and placed in 20 l buckets before being transported back to the lab. Five culms were selected from each grass clump were examined under a microscope for arthropod presence and damage. Arthropod specimens were collected and assigned morphospecies reference names, then identified to the family level using CO1 barcodes. Unique morphospecies identifiers were used to estimate species richness. Family level identification was used to estimate feeding guilds. Feeding guilds are leaf mining, leaf chewing, Stem-boring, fruit boring, granivorous, sap-sucking, gallobionts, rhizophagous, detritivorous, saprophagous. Arthropod abundance was estimated by recording the number of arthropods by morphospecies per gram of wet plant tissue measured. Specimens were collected, cataloged, and then stored in ethanol in a 2ml microtube.

Ungulate associates

Six camera trap locations along the south, central, and northern portion of Mpala Research Centre and in one of the two pastures at the Texas ranch were used to estimate the relative abundance of ungulates and species richness. Counts of each ungulate species were made and converted into ungulates per camera day to index their relative abundance. Ungulate species were then grouped into feeding guilds based on their behavior and physiology to grazer, mixed-feeder, and browser.

Statistics

Cover and height were analyzed using mixed-effects analysis with invasion status as an identity variance structure to deal with the heterogeneity of variance and site as a random effect to account for spatial autocorrelation. Arthropod and ungulate species richness are reported as raw values.



Results

Guinea grass height and cover

Texas Guinea grass of more than 50% taller than Guinea grass in its native range, yet there was an interactive effect of Guinea grass growing in the riparian areas where heights were closer to the invaded range (**Figure 1**).

Ungulate diversity

In Texas, we observed five ungulate species: *Bos taurus*, *Odocoileus virginianus*, *Pecari tajacu*, *Sus scrofa*, *Boselaphus tragocamelus*. Collapsed into their respective feeding guilds, there were one grazer, three mixed feeders, and one browser.

In Kenya, we observed 22 ungulate species: *Giraffa camelopardalis reticulata*, *Oreotragus oreotragus*, *Tragelaphus scriptus*, *Tragelaphus strepsiceros*, *Alcelaphus buselaphus lelwel*, *Bos taurus*, *Equus burchelli*, *Hippopotamus amphibius*, *Ovis aries*, *Phacochoerus africanus*, *Syncerus caffer*, *Aepyceros melampus*, *Camelus dromedarius*, *Capra aegagrus*, *Equus grevyi*, *Gazella granti*, *Kobus ellipsiprymnus*, *Loxodonta africana*, *Madoqua guentheri*, *Oryx beisa*, *Raphicerus campestris*, *Taurotragus oryx*. There were 11 grazers, seven mixed feeders, and four browsers when collapsed in their respective feeding guilds.

The relative abundance of these feeding guilds as measured by camera traps are presented in **Figure 2**.

Arthropod diversity

In Kenya, we described 25 unique morphospecies across 17 families whose members comprise nine feeding guilds: leaf mining, leaf chewing, Stem boring, fruit boring, granivorous, sap-sucking, gallobionts, rhizophagous, detritivorous, saprophagous. In Texas, seven total morphospecies from 5 families, whose most diverse were detritivorous mites found in Guinea grass's roots. Per plant sample, Guinea grass from Kenya had an average of 1.01 morphospecies, while grass samples from Kenya had 2.14. When standardized by the mass of sampled Guinea grass, native morphospecies were on average 0.28 ± 0.06 species per gram of wet material, and 0.169 ± 0.03 arthropod species per gram.

Discussion

In this descriptive study, we show differences in the height and cover of Guinea grass across native and invaded ranges yet these measurements interact with areas of variable resource availability. Further, we document that the arthropod community varies drastically between the native and invaded range. This is also true for the total species richness of

ungulates on the native versus invaded range and the relative abundance as binned into feeding guilds. Generally, the functional diversity of ungulates and arthropods was much higher in Kenya when compared to Texas.

Motte, grassland, and riparian areas represent different resource environments for plants (Zitzer, Archer et al. 1996), and the interaction between herbivore and resources in arthropods has an essential impact on community structure and, therefore, plant production (Fine, Mesones et al. 2004). Our study suggests that Guinea grass was likely limited by nutrient resources available in mottes and not by ungulates or arthropod herbivores in an introduced range. However, in Kenya, height in rivers was much higher, and cover in rivers and mottes was more similar to Guinea grass in its invaded range. These differences are likely due to increased water resources in riparian environments and nutrients and shade in mottes (Zitzer, Archer et al. 1996). Also, we observed that

Guinea grass growing in open areas in Kenya was anecdotally subjected to higher grazing rates, which translated into large differences in cover and height (Rhodes Obs.). Similarly, in Texas, the correlation between heavy rainfall and the lack of impact that cattle have on Guinea grass, whereas in milder conditions, the cattle can reduce Guinea grass height, cover, and dominance (Unpublished data).

In conclusion, Guinea grass represents a vital forage species for livestock globally (Jank, Barrios et al. 2014), yet often escapes to degrade ecosystem function and diversity. This study represents an essential step in describing Guinea grass's breadth of natural enemies in its native and invaded ranges. We are beginning to connect ungulate impact on Guinea grass and leverage cattle for targeted grazing of invasive African grasses in Texas. We are also beginning to document the ecological association of arthropods in Kenya and identify arthropods' generalists in Texas. Together these projects will help develop targeted grazing tools and the search for a species-specific biological control.

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