**RESEARCH ARTICLE**

# The invasiveness of Guinea grass (*Megathyrsus maximus*) is characterized by habitat and differing herbivore assemblages in its native and invaded range

Aaron C. Rhodes[1], Robert M. Plowes[1], Dino J. Martins[2], Ivy Ng'Iru[2], Lawrence E. Gilbert[1]

**1** *Brackenridge Field Laboratory 2907 Lake Austin Blvd, University of Texas at Austin, Austin, USA* **2** *Mpala Research Centre, P.O. Box 555 - 10400, Nanyuki, Kenya*

Corresponding author: Aaron C. Rhodes (aaronrhodes@utexas.edu)

## Abstract

A significant challenge of global change is the human-mediated movement of pasture grasses and their subsequent impact on ecosystem processes when they become invasive. We must understand invasive grass ecology and their natural enemies in native and introduced ranges to mitigate these impacts. Guinea grass (*Megathyrsus maximus*) is a pantropically introduced pasture grass that escapes intended areas and invades native ecosystems – threatening biodiversity and ecosystem function. The success of invasive plants has often been attributed to ecological release from stressors, including natural enemies and resource availability. Our objective was to assess Guinea grass functional traits across three different habitat types in native and invaded ranges by documenting ungulate and arthropod abundance, diversity, and feeding guilds. Guinea grass functional traits were assessed in three habitat types: grassland, riparian, and woody thickets around nitrogen-fixing *Prosopis glandulosa* in its introduced range in Texas, USA, and *Senegalia mellifera* in its native range in Kenya. We characterized Guinea grass functional traits by measuring plant height, cover, biomass, root-to-shoot ratios, and reproductive traits. We then examined the phytophagous arthropod and ungulate abundance and feeding guild diversity across the three habitat types. We hypothesized that functional trait expression related to invasiveness would be associated with Guinea grass in its introduced range. Also, we hypothesized that the abundance and diversity of phytophagous arthropods and ungulates

would be lower in the invaded range. Finally, we hypothesized that Guinea grass functional traits would differ between the three habitat types, given the habitat types' innate differences in resource availability. We found that Guinea grass was 2.5 times taller and 3.3 times more productive and covered 2.5 times more area in its invaded versus native ranges. Introduced Guinea grass had higher reproduction rates with 2.5 times more reproductive tillers, while habitat type drove vegetative reproduction with 15 times more stoloniferous establishment in wooded and riparian sites than grasslands. Texan ungulate communities were less species-rich, less functionally diverse, and less abundant than the Kenyan ungulate community. The phytophagous arthropod diversity on plants was twice as high on Kenyan Guinea grass than on Texan Guinea grass. Total arthropod family richness was nearly double, with 15 families represented in Kenya and 8 in Texas. These results suggest that Guinea grass has escaped a rich assemblage of arthropods and ungulates and likely explains some of its spread in introduced ranges. This study demonstrates how the invasive success of Guinea grass can be understood in terms of its competitive ability and interaction with natural enemies in the introduced and native ranges and may inform future biological control.

## Introduction

Introducing perennial grasses for rangeland improvement has led to the pantropical distribution of highly invasive grasses (Marshall et al. 2012; Rhodes et al. 2021). Alarmingly, the traits beneficial to higher livestock yields are associated with invasiveness (Jank et al. 2014) and lead to human-mediated dispersal (Parsons 1972; Pyšek and Richardson 2007). Dozens of hypotheses have successfully explained biological invasions, each with its level of support and interconnectedness (Catford et al. 2009; Jeschke et al. 2012). Two prevalent hypotheses relevant to invasive grasses are the Enemy Release Hypothesis (Keane and Crawley 2002) and the Evolution of Increased Competitive Ability (Blossey and Notzold 1995). The mechanisms underlying these hypotheses are likely not mutually exclusive (Jeschke et al. 2012), and each mechanism leads to the expansion of realized niche spaces in invaded ranges. When released from biotic and abiotic factors that limit their productivity and reproductivity, nonnative species may become invasive (Cox and Ricklefs 1977; Torchin et al. 2003; Canavan et al. 2019). For example, the Enemy Release Hypothesis posits that specialist enemies will be absent from the new system and that generalists will prefer native plants (Keane and Crawley 2002). However, these hypotheses are often context-dependent, and generalities may not apply to particular species (Pyšek and Richardson 2007). Therefore, describing the mechanisms leading to invasion by focal organisms of management or agricultural interest is critical for understanding the invasion process and mitigating the negative consequences.

Life histories and functional traits are important indicators of plant success and often correlate with their invasiveness and dominance in a community (Cornwell and Ackerly 2010). Invasive species outcompete native plants for resources (Blossey and Notzold 1995; Davis et al. 2000) and win apparent competition by losing natural

enemies (Mlynarek et al. 2017). Several traits are associated with invasiveness: high reproductive output, reproductive mode (sexual vs. asexual), tolerance to herbivory, and height. Plant height often predicts invasiveness (Pyšek and Richardson 2007) through its impact on resource competition, correlation with biomass, and higher competitive ability to exploit resources (Canavan et al. 2019). Traits correlated to plant size are indicators of plant competition through their ability to disproportionately acquire resources such as light, water, and soil nutrients, which drive increased competitive ability and subsequent plant community composition (Lavorel et al. 2007; Dirks et al. 2017). Reproductive traits like clonality, increased flowering quantity, and increased flowering duration are indicators of invasiveness (Cadotte et al. 2006). Resource availability can drive interspecific differences in plant responses to herbivores (Coley et al. 1985). Likewise, intraspecific susceptibility to herbivores varies across resource availability (Fine et al. 2004). While a perennial grass in both its native and invaded range may have similar strategies, the release from natural enemies could alter these functional traits.

Guinea grass (*Megathyrsus maximus* syn. *Panicum maximum* (Jacq.) B.K. Simon & S.W.L. Jacobs) is consistently ranked among the most ecologically damaging invasive plant species globally (Best 2005; Randall 2017; CABI 2022). Guinea grass was first introduced to South Texas in the 1950s and has spread rapidly since the 1970s across a semi-tropical savanna dominated by the nitrogen-fixing trees honey mesquite *Prosopis glandulosa* Torr (Zitzer et al. 1996; Best 2005). Tree-grass interactions in these savannas include facilitation and competition for water and nutrient resources (Scholes and Archer 1997), and these primary associations mediate invasion at local scales (Colautti et al. 2006). Nitrogen-fixing trees promote improved nutrient availability, shade, and soil moisture (Zitzer et al. 1996; Scholes and Archer 1997) and facilitate Guinea grass invasion (Rhodes et al. 2022). Guinea grass is a tall-statured grass, often apomictic and polyploid, and is highly invasive pantropically (Kaushal et al. 2015; Canavan et al. 2019; Lambertini 2019). Tall-statured invasive grasses generally produce culms over 1.5 m in height and are noted for associating with invasiveness. They are commonly invasive outside their range (Lambert et al. 2010) and characterized by monodominance, high productivity, and reproductive rates (Canavan et al. 2019). Clonality, high flower count, and flowering throughout the season offer flexible life-history traits for invading Guinea grass (Rhodes et al. 2022). Comparing functional traits between naturally occurring invasive and native Guinea grass populations would improve our understanding of its invasion.

This dichotomy of Guinea grass is its economic success and ecological damage, which can be attributed to several core traits; its ability to grow in variable precipitation (400 mm – 1700 mm), high tolerance to herbivory (Sukhchain 2010), high reproductive rates (Rhodes et al. 2022) and strong competitive ability in its invaded range (Ho et al. 2016). Much of our current understanding of Guinea grass reproduction, production, and function is through its development as a pasture grass (Jank et al. 2014; Euclides et al. 2018; Maciel et al. 2018) or as a noxious weed (Alves and Xavier 1986; Best 2005; Ammondt and Litton 2012). However, few studies leverage

an understanding of Guinea grass characteristics and interactions with natural enemies and stressors to understand the success of Guinea grass as an invasive species. Given that resource availability is a driver of invasion processes (Davis et al. 2000; Hui et al. 2016), understanding how resources alter Guinea grass production, reproduction, and interaction with the herbivore community is essential for mitigating Guinea grass invasion and evaluating prospective biological control programs.

Invasive plants alter the structure and function of arthropod communities (Van der Colff et al. 2015). Generally, invasive plants reduce arthropod diversity and abundance, leading to the collapse of trophic links (Herrera and Dudley 2003). However, the response of arthropod functional groups to invasive plants is mixed. Litt et al. (2014) found that abundance and taxonomic richness decreased in around half of the 87 studies reviewed, with the most significant increases in detritivores in 67% of the studies and herbivorous arthropods reduced by 48%. Plant community phylogenetic, phytochemical, and species richness can all impact an insect's ability to feed on plants (Salazar and Marquis 2022). Therefore, many phytophagous arthropods may fail when plant communities change to invasive dominants, which may promote invasion.

Ungulates may be used to manage invasive plants, improving ecological restoration and maintenance outcomes with the added benefit of contributing to livestock yields (Frost and Launchbaugh 2003; Bailey et al. 2019). Grasses escaping from highly abundant and diverse ungulate communities will likely have higher productivity and reproductivity, competing well in invaded ranges. However, ungulates have differential impacts on plant species depending on their feeding guild and the physiology of the plant, such that the functional diversity of herbivores reduces plant establishment success (Rhodes et al. 2018). Targeted grazing of palatable grasses has shown promise for reducing the invasiveness of plants (Gaskin et al. 2021), but sustainable management is expected to entail arthropod associates. Thus, characterizing the arthropod and ungulate diversity in the native range of an invasive grass plays a critical role in understanding the ecological importance of those arthropods and developing efficient biological control programs.

The primary objective of this project was to evaluate Guinea grass functional traits across three habitat types in the native and invaded ranges and document the arthropod and ungulate herbivore community assemblages. To achieve this objective, we; first quantified Guinea grass functional traits and reproductive output across three habitat types. Second, we measured the richness and diversity of phytophagous arthropods and ungulate herbivores on Guinea grass in native ranges versus the invaded range. Third, we characterized these communities by their relative abundance and feeding guild diversity. Fourth, we developed a list of the arthropod community attached to Guinea grass to understand their impact. We hypothesized that functional trait expression related to invasiveness would be associated with Guinea grass in its introduced range. We hypothesized that functional traits would differ between the three habitat types, given the habitat types' innate differences in resource availability. Finally, we hypothesized that the abundance and diversity of phytophagous arthropods and ungulates would be lower in the invaded range, consistent with the Enemy Release Hypothesiss.

## Methods

We established field sites to examine Guinea grass occurring naturally in two savanna systems; 1) the native range in Laikipia Province, Kenya, and 2) the invaded range in South Texas, where Guinea grass is spreading rapidly. Ten locations were selected in both Kenya and Texas. Each location had three habitat types: woody mottes (thickets), open grassland, and riparian zones. Three 1 × 1 m subplots were randomly established within each habitat type for 180 subplots. Mottes were under woody legumes with higher soil moisture and soil nitrogen. We selected two major tree species, each native to the study area; *Senegalia mellifera* (Benth.) Seigler & Ebinger, common in the red soils of Laikipia, and *P. glandulosa* in Texas a common species. The grassland sites for each grouping were approximately halfway between the thicket (motte) and riparian habitat types. Riparian areas were defined as the upland portion of ephemeral creeks that fed into the main waterway (Los Olmos Creek in Texas and Ewaso Ng'iro River in Kenya).

In Kenya, field sites were selected along the Ewaso Ng'iro River. West of the river is Mpala Research Centre, an active cattle ranch with approximately 3000 livestock grazing at low to moderate stocking intensities on 19,500 hectares, including Zebu/Boran mix-breed of cattle, camel, goat, and sheep. Mottes were maintained naturally by large ungulate and fire disturbances. In Texas, the study was conducted at two ranches with active brush and cattle management activities in the semi-arid mesquite thorn tree savanna of the South Texas Plains ecoregion. A 1600-ha ranch pasture in Kenedy, Kleberg & Brooks Counties on Palobia loamy fine sand was brush-chained in the 1970s and then partly root-plowed in 1998 to form residual stands of *P. glandulosa* in a grassland matrix and a 1000-ha ranch pasture in Brooks County, on Padrones fine sand. Cattle regularly graze both sites and feed on Guinea grass. Stocking densities were generally low to moderate using resident longhorn cattle (*Bos primigenius*) and common stocker cattle (*Bos tauru*s).

### Guinea grass productivity, functional traits, and reproduction

Within each 1 × 1 m subplot, we measured Guinea grass height to the highest leaf and visually estimated the percent foliar cover at each site to understand how functional traits vary across habitat types and invaded vs. native range. We used the height as a functional indicator that provides a relative indicator of the competitive potential of Guinea grass in its native and invaded range across habitat types. We uprooted one Guinea grass clump from each subplot by tossing the quadrat and selecting the central individual to estimate productivity and resource allocation to above and belowground tissues (three in total from each site). The plants were cut to separate aboveground tissues (leaves, culms, and inflorescences) from the belowground tissues (roots and rhizomes). Belowground tissue was soaked in water overnight and then washed over a 1 mm sieve to remove soil and soil organic matter. The aboveground tissue was dried in a drying oven for 72 hours at 50 °C. Root clumps were broken up over a sieve to remove

the remaining soil. The above and belowground tissue was summed to calculate total biomass, and then root tissue biomass (mg) was divided by shoot biomass (mg) to calculate root to shoot ratio. Finally, in each of the three 1 m² plots, the total numbers of seed heads and stolons were recorded. The mean of the three plots was then used in the analyses. Seedheads were defined as panicles with mature seeds, noted by the ease of dislodging seeds. Stolons were characterized by lateral shoots that had established a rooted node with at least five leaves and a height of 20 cm. These definitions ensured that the stolon had been successfully established.

## Ungulate associates

Six camera trap locations along the south, central, and northern portions of Mpala Research Centre and ten camera trap locations were used at the Texas ranch. The camera survey was conducted from January 2019 to June 2019 until the Guinea grass sampling was completed. At each study site, we placed a trail camera (HyperFire 2 Professional Covert Camera Trap) (Reconyx, Holmen, WI, USA) to estimate relative use by ungulate species (O'Brien 2011) within an approximate 30 m detection range and 40° field of view. Cameras were set at very high sensitivity to capture three photos at five-second intervals with a five-minute rest period between triggers. Each ungulate that appeared at least once in the three-photo set was counted, and these counts were summed and divided by the number of active camera days. Counts of each ungulate species were scored and converted into an index of ungulates per camera day. Ungulate species were then grouped into feeding guilds based on their behavior and physiology to grazer, mixed-feeder, and browser, following Kingdon (2015) in Kenya or based on physiology following Hanley (1982) and Holechek et al. (1989) in Texas. These data represent general patterns of ungulate activity (ungulate camera$^{-1}$ day$^{-1}$) and are presented as descriptive data.

## Arthropod associates

Three Guinea grass plants from each site were uprooted and transported back to the lab. Three culms and the associated roots from each grass clump were examined for arthropods under a microscope, the stem was dissected, and the leaf, inflorescence, culm, and roots. We assumed that arthropods still attached to the plant after this process were more likely to be associated with this plant rather than transient. Arthropod abundance was estimated by recording the number of arthropods per gram of wet plant tissue measured for each morphospecies recognized by morphological differences. Specimens were collected, cataloged, and stored in ethanol in a 2 ml microtube. Each morphospecies was barcoded at the CO1 locus. A region of approximately 450 bp targeting the CO1 locus was amplified with degenerate primers (ZBJ-ArtF1c, ZBJ-ArtR2c (Alberdi et al. 2018), followed by Sanger sequence analysis. Sequence similarity searches were conducted against the NCBI GenBank database to score the family taxonomic assignments. The family level of each morphospecies was used to estimate feeding guild assignments using a standard reference (Simpson 2013). Feeding guilds

were defined as: leaf mining, leaf chewing, stem boring, fruit boring, granivorous, sap-sucking, gallobionts, rhizophagous, detritivorous, and saprophagous. Arthropods with no association with phytophagous families were not used in the analysis but were submitted to GenBank.

## Statistics

The height of the tallest culm, total biomass, foliar cover (%), root-to-shoot ratio, stolon count, and reproductive tiller counts were analyzed using mixed-effects regressions. Arthropod morphospecies counts were also analyzed using a mixed-effects regression. For all regressions, the fixed effects were the habitat type and invasion status and their interaction. The heterogeneity of variance was assessed by visually assessing the distribution of model residuals. Invasion status (native vs. invaded) was used as an identity variance structure to deal with variance heterogeneity and site as a random effect to account for spatial autocorrelation. Normality was assessed by visually inspecting a histogram of model residuals and was analyzed as normally distributed data. Feeding guilds for ungulates and arthropods are reported as the raw averages with their standard error. Ungulate camera data is presented as descriptive, given that no direct correlation could be made between ungulate abundance and specific use of Guinea grass. All regression analyses were done in R (R Core Team 2021) using the nlme package for mixed-effects modeling (Pinheiro et al. 2021).

# Results

## Guinea grass productivity and functional traits

Guinea grass in its invaded range had productivity and functional traits consistent with a successful invader. Guinea grass in its invaded range was taller, had 3.3 times higher biomass per plant, covered 2.5 times more area, and had twice as much shoot production over root production (Fig. 1). Guinea grass height was 2.5 times taller in its invaded range ($F_{(1,10)}$= 42, $p$ < 0.001) and interacted with habitat ($F_{(2,44)}$ = 4.67, $p$ = 0.014), such that Guinea grass growing in riparian zones of its native range was statistically similar to its invaded range (Fig. 1A). Similarly, Guinea grass plants had higher biomass production in its invaded range ($F_{(1,10)}$ = 78, $p$ = < 0.001) and an interactive effect was driven by the low biomass in Kenyan grassland habitats ($F_{(2,44)}$ = 7.0, $p$ = .002) (Fig. 1B). Anecdotally, Kenyan grassland Guinea grass had more evidence of grazing than other habitats. Foliar cover (%) was 2.5 times higher in the invaded range ($F_{(1,10)}$ = 14, $p$ = 0.004) and the motte habitat type ($F_{(1,44)}$ = 12, $p$ < 0.001). Further, invasion status had a significant interaction, driven by high cover in invaded mottes ($F_{(1,10)}$ = 30 $p$ = < 0.001) (Fig. 1C). The root-to-shoot ratio in the invaded range was half that of the native range ($F_{(1,10)}$ = 7.3, $p$ = 0.02) (Fig. 1D) but did not vary significantly by habitat type, nor was there an interaction ($F_{(1,42)}$ = 0.99, and $F_{(2,42)}$ = 0.92). Guinea grass produced twice as much aboveground biomass in the invaded range.
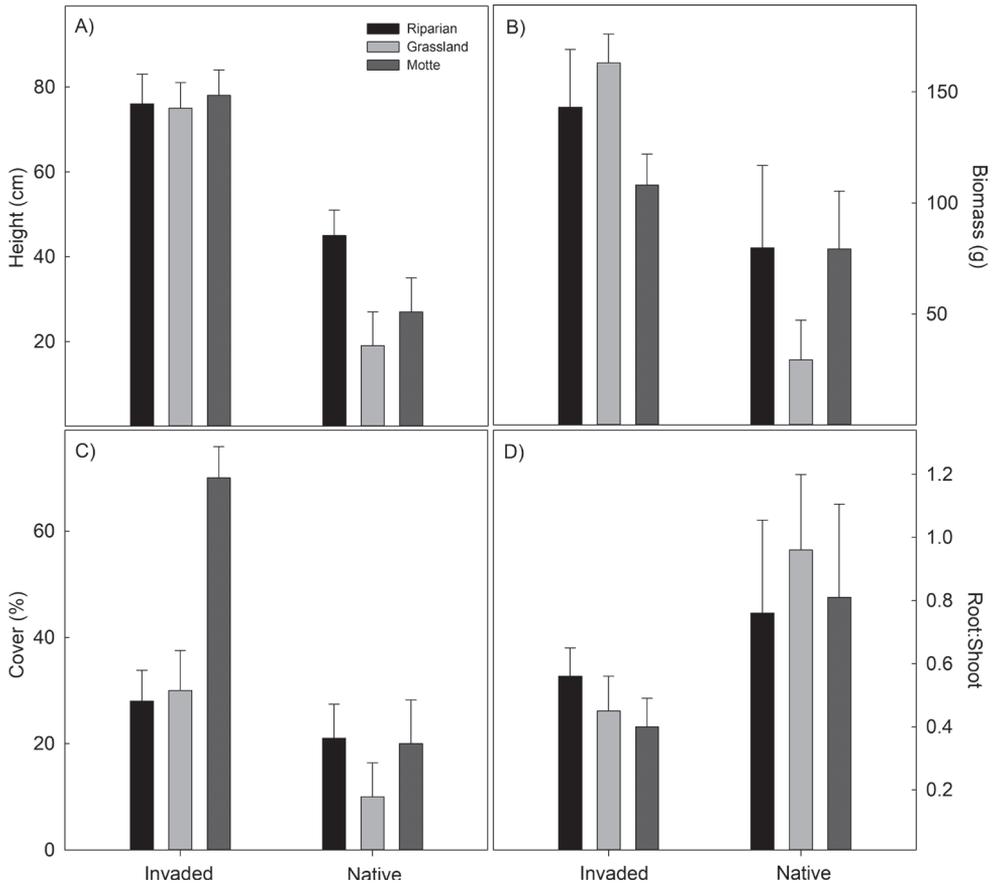
**Figure 1.** Guinea grass's morphological and physiological traits across three habitat types in native and invaded ranges. The morphological and physiological traits of Guinea grass are presented in four panels **A** height (cm) **B** Biomass dry weight (g) **C** percent foliar cover, and **D** root-to-shoot ratio. The bar's colors represent the ephemeral riparian, grassland, and motte portions of the matrix. Habitat type is nested within invaded (Texas) or native range (Kenya). The bar heights are calculated from the model predictions, and the error bars are the standard error.

## Reproduction – Seed heads and stolons

Seedborne reproduction by Guinea grass, measured by seedhead count, was nearly three times as abundant in the invaded range ($F_{(1,10)}$ = 14, $p$ = 0.004). Still, it did not vary significantly across habitat types or the interaction between native and invaded provenance and by habitat type ($F_{1,42)}$ = 1.3 and $F_{2,42)}$ = 0.6, respectively) (Fig. 2A). Stolon production was no different in the invaded range compared to the native range, nor was there an interaction between habitat type or invasion status. However, stolon production differed significantly by habitat type, with the grassland habitat type having around 1/10th to 1/20th the mean number of stolons (Fig. 2B) compared to mottes or riparian sites.
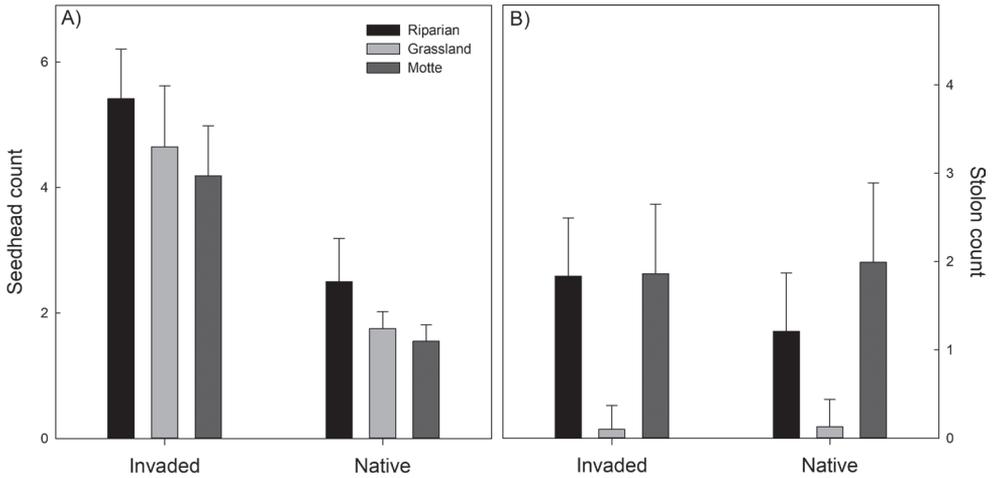
**Figure 2.** Guinea grass's reproductive output and mode across three habitat types in native and invaded ranges. The reproductive outputs by seedhead and stolon counts of Guinea grass are presented in two panels **A** seedhead count and **B** stolon count. The bar's colors represent the ephemeral riparian, grassland, and motte (woody portion) for each vegetation type, which is nested within invaded (Texas) or native range (Kenya). The bar heights are calculated from the model predictions, and the error bars are the standard error.

## Ungulate associates

In Texas, we observed five ungulate species: *Bos taurus* Linnaeus, 1758, *Odocoileus virginianus* Zimmermann, 1780, *Pecari tajacu* Linnaeus, 1758, *Sus scrofa* Linnaeus, 1758, *Boselaphus tragocamelus* Pallas, 1766. According to their behavior and physiology, these species were classified into their respective feeding guilds, one grazer, three mixed feeders, and one browser (Hanley 1982; Holechek et al. 1989). In Kenya, we observed 18 ungulate species (in order of abundance): *Bos taurus* Linnaeus, 1758, *Equus quagga* Boddaert, 1785, *Aepyceros melampus* Lichtenstein, 1812, *Loxodonta africana* Blumenbach, 1797, *Giraffa camelopardalis reticulata* De Winton, 1899, *Equus quagga burchellii* Gray, 1824, *Syncerus caffer* Sparrman, 1779, *Equus grevyi* Oustalet, 1882, *Ovis aries* Linnaeus, 1758, *Madoqua guentheri* Thomas, 1894, *Kobus ellipsiprymnus* Ogilby, 1833, *Tragelaphus strepsiceros* Pallas, 1766, *Taurotragus oryx* Pallas, 1766, *Phacochoerus africanus* Gmelin, 1788, *Capra hircus* Linnaeus, 1758, *Nanger granti* Brooke, 1872, *Raphicerus campestris* Thunberg, 1811, and *Hippopotamus amphibius* Linnaeus, 1758. According to their behavior and physiology, nine grazers, six mixed-feeders, and four browsers were assigned to their respective feeding guilds (Kingdon 2015). The native range presented a similar abundance of grazers yet considerably more abundant mixed-feeders and browsers. Total ungulate relative abundance across feeding guilds was 1.5 (ungulate camera$^{-1}$ day$^{-1}$) in the native range versus 1.1 (ungulate camera$^{-1}$ day$^{-1}$) in the invaded range (Fig. 3).
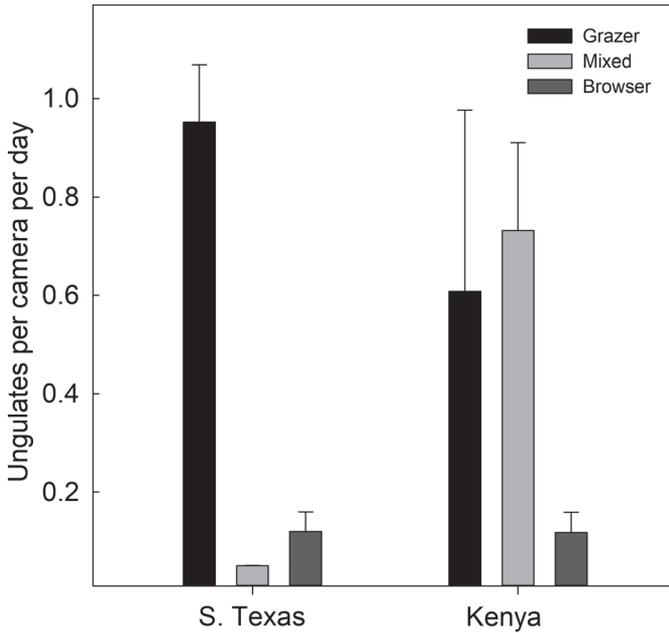
**Figure 3.** Ungulate feeding guild abundances in Texas and Kenya. Ungulate counts per camera day$^{-1}$ are divided into feeding guilds and presented in their invaded (South Texas) and native (Kenya) range. The data are raw means and standard errors.

## Arthropod associates

Guinea grass from Texas had less than half the phytophagous morphospecies of arthropods, with an average of 1.01 morphospecies per sample. In contrast, Guinea grass samples from Kenya had 2.14 ($F_{(1,10)}$ = 12 $p$ = 0.006). However, there was no significant association between habitat types or interaction between habitat type and invasion status ($F_{(1,42)}$ = 0.19, $F_{(2,42)}$ = 1.46, respectively) (Fig. 4). When standardized by the mass of sampled Guinea grass, there were on average 0.28 ± 0.06 morphospecies per gram of wet material in Kenya and 0.169 ± 0.03 morphospecies per gram in Texas. In Kenya, we described 27 unique morphospecies across 15 families whose members comprise nine feeding guilds: leaf mining, leaf chewing, stem-boring, fruit-boring, granivorous, sap-sucking, gallobionts, rhizophagous, detritivorous, saprophagous. Ten morphospecies from 8 families and six potential feeding guilds were identified in Texas. In Texas, three morphospecies of oribatid mites were the most abundant, and they primarily decompose organic material (Fig. 5) (Table 1).

## Discussion

In South Texas, Guinea grass has pronounced functional and reproductive traits associated with invasiveness. Our results show that Guinea grass in South Texas was taller, dominated a larger area, produced more biomass (especially aboveground), and
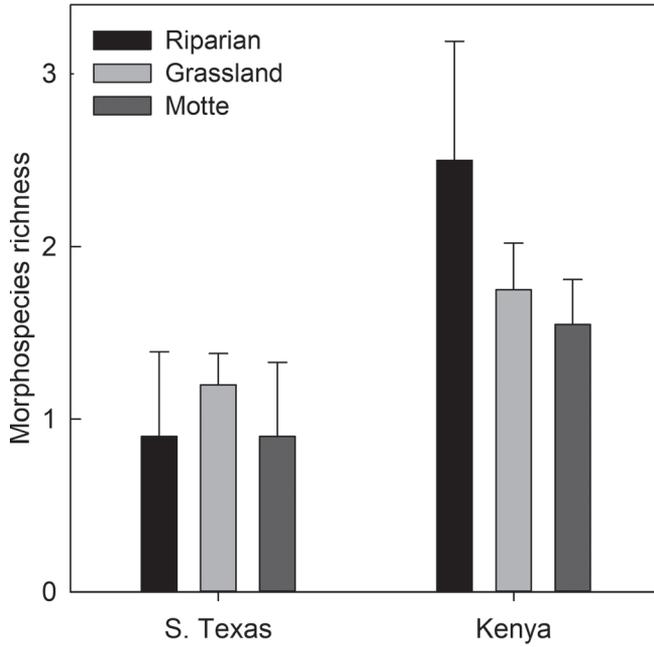
**Figure 4.** Guinea grass-associated arthropod morphospecies in three habitat types in the invaded and native ranges. The bar's colors represent the ephemeral riparian, grassland, and motte (woody) vegetation types. The habitats are nested within invaded (Texas) or native ranges (Kenya). The bar heights are calculated from the model predictions, and the error bars are the standard error.
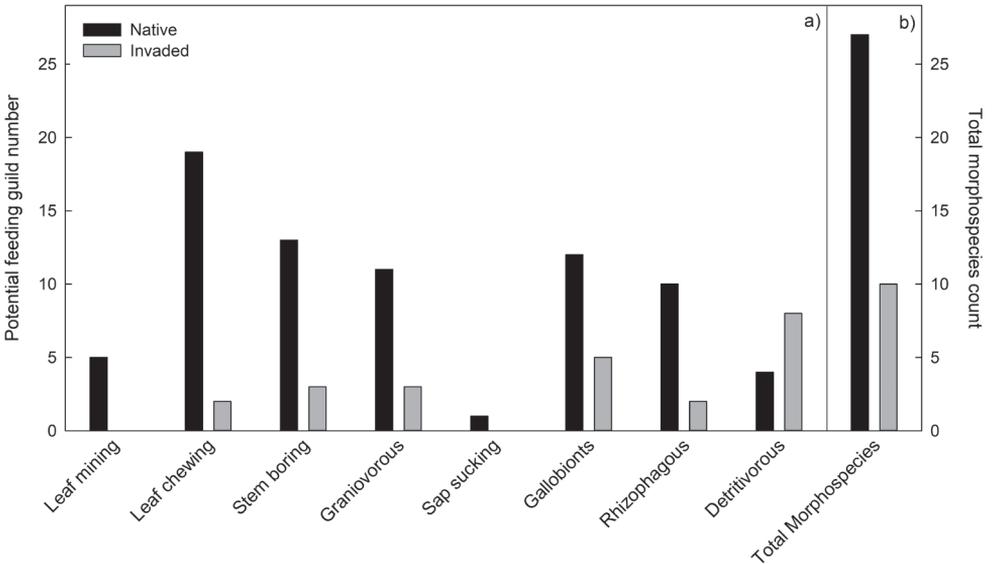


**Figure 5.** The potential feeding guilds from the total morphospecies in native and invaded ranges. Panel A compares potential feeding guilds given a given family's known feeding guild types. Panel B sums the total morphospecies count. The bar's colors represent native (dark) or invaded (Texas). The bar heights are the total sum of morphospecies that potentially belong to a particular feeding guild.

**Table 1.** Diversity of arthropod morphospecies collected from Guinea grass in Kenya and Texas.

| Kenya families | Species count* | Texas families | Species count* |
|---|---|---|---|
| *Agaonidae* | 1 | *Cecidomyiidae* | 1 |
| *Cecidomyiidae* | 3 | *Chloropidae* | 1 |
| *Chloropidae* | 6 | *Cicadellidae* | 1 |
| *Chrysomelidae* | 2 | *Haplozetidae* | 3 |
| *Crambidae* | 1 | *Mordellidae* | 1 |
| *Curculionidae* | 1 | *Nymphalidae* | 1 |
| *Geometridae* | 2 | *Oppiidae* | 1 |
| *Hydraenidae* | 1 | *Pyralidae* | 1 |
| *Lygaeidae* | 1 | | |
| *Noctuidae* | 2 | | |
| *Phlaeothripidae* | 1 | | |
| *Phycitinae* | 1 | | |
| *Pyralidae* | 3 | | |
| *Tenebrionidae* | 1 | | |
| *Tortricidae* | 1 | | |
| Total | 27 | | 10 |

*Species count is the number of morphospecies in that family.

reproduced sexually at higher rates than in its native range. These differences likely have cascading impacts on Guinea grass's competition with native species (Ammondt and Litton 2012; Ho et al. 2016; Espinosa-Garcia and Villasenor 2017; CABI 2022). Guinea grass's release from ecological stressors and enemies has likely contributed to the highly successful expansion of Guinea grass in the three different habitat types in South Texas. In contrast, the three habitat types in Kenya corresponded to heterogeneous and lower productivity and reproduction capacity compared to the heterogeneity of its invaded range. Likewise, Guinea grass's escape from abundant and functional diverse phytophagous arthropods and ungulates has likely contributed to its success across these variable environments. This study represents an essential step in describing differences in the breadth of Guinea grass's natural enemies in its native and invaded ranges and the niches it can occupy, which improves our understanding of Guinea grass invasion.

The morphology and productivity of invasive plants are functional traits that can predict invasiveness (Pyšek and Richardson 2007). Greater height and biomass influence resource competition and invasiveness (Canavan et al. 2019), indicating faster growth rates, resource acquisition, and reproductive potential. Our results suggest that Guinea grass is becoming dominant in its invasive range by producing taller plants, higher biomass per plant, and higher foliar cover (Fig. 1) (Canavan et al. 2019). This productivity correlates to Guinea grass's ability to compete for light and soil resources which have cascading effects on nutrient cycling and fire cycles (D'Antonio and Vitousek 1992). Tall-statured grasses disproportionately outcompete and become invasive compared to short-statured grasses (Canavan et al. 2019). Reproductive output and mode are associated with the invasiveness of plants (Pyšek 1997; Pyšek and Richardson

2007). In Guinea grass, seed-borne and vegetative reproduction likely leads to an effective invasion across different habitat types and resource availability (Rhodes et al. 2022).

Vegetative reproduction is associated with a higher competitive ability (Pyšek 1997), and the reproductive mode plays a critical role in sustaining local populations and dispersing propagules (Benson and Hartnett 2006; Simberloff 2009). Thus, reproductive traits play an important role in plant community assembly and subsequent invasion (Dirks et al. 2017). Guinea grass's propagule pressure and reproductive plasticity are critical factors for its establishment in novel and resource-available habitat types in its expanding range (Rhodes et al. 2022). In an established perennial grass community, asexual reproduction can represent up to 99% of the population turnover, while sexually reproduced individuals can be near 1% (Benson and Hartnett 2006). The higher reproduction through seedheads in the invaded range and stoloniferous reproduction was important in mottes in the native and invaded range. Guinea grass will likely have more successful establishment events in the invaded range without significant herbivore pressure.

In savanna systems, woody vegetation and riparian patches integrate with a grassland matrix creating gradients of light environment, nutrient turnover, and water availability that have vital impacts on grass growth (Zitzer et al. 1996; Ludwig et al. 2004). The interaction between herbivores and resources significantly impacts community structure and plant production (Olff and Ritchie 1998; Fine et al. 2004; Wan et al. 2014). Plant species in different habitat types may express variable intraspecific traits (Pyšek 1997; Cadotte and Lovett-Doust 2001). Phenotypic plasticity may improve outcomes for invasiveness, and grasses invading multiple habitat types often achieve similar negative impacts on each habitat, despite their different resource availability (Richards et al. 2006). Our study found that in its native range, Guinea grass had different morphometrics and reproductive characteristics across habitat types. In Kenya, Guinea grass height in riparian areas was similar to the height in habitat types of Texas (Fig. 1A). These differences are partly due to increased water resources in riparian environments and nutrients and shade in mottes (Zitzer et al. 1996) that improve outcomes for germination and growth in the critical early stages of development (Rhodes et al. 2022).

Losing natural enemies can increase biomass compared to native populations (Torchin et al. 2003). Guinea grass's escape from a comprehensive assemblage of natural enemies is correlated with these increases in primary production and reproductive capacity. Further, in this study, higher productivity translated into higher seedhead production, which could further accelerate the invasion of Guinea grass in South Texas savannas through enhanced dispersal and propagule pressure (Rhodes et al. 2022). The increase in productivity correlates to the lower number of arthropod herbivores in the invaded range, which is indicative of a reduction in natural enemies (Torchin et al. 2003; Lucero et al. 2020). Aggregated with this loss of phytophagous arthropods is the abundance and diversity of ungulate herbivores, which may contribute to lower productivity in the invaded range. The feeding guilds of both groups of organisms may differentially impact invasion success.

The differences between Kenya and Texas's arthropod and ungulate communities were stark. Several arthropod species encountered in Kenya are from feeding guilds known to tend toward specialization, including stem borers and mites (Rhodes et al. 2021). While invasive species can acquire novel enemies in their invaded range (Torchin et al. 2003; Rhodes and St. Clair 2018), they do so to a lesser degree. Therefore, the acquisition of generalist herbivores in Texas has likely not replaced the top-down impact on Guinea grass dominance and height in its native range, similar to the general results of enemy release (Lucero et al. 2020). However, Kenyan Guinea grass was similar to Texas's in resource-rich environments (riparian areas and mottes). This pattern may be due to increased tolerance to herbivory through resource availability (Coley et al. 1985) or growth-defense trade-offs (Lind et al. 2013). In addition, we documented that the phytophagous arthropod community varies drastically between the native and invaded ranges. In the case of invasive species that are important for forage and livestock yields, breeding programs select to heighten resistance to pathogens (Savidan et al. 1989; Maciel et al. 2018). Together, the arthropod and ungulate communities likely restrict Guinea grass to high-resource habitats and represent a barrier to its spread in Kenya. Yet, when released from these enemies, Guinea grass spreads well in a broader ecological niche in South Texas.

Utilizing natural enemies has formed the basis for classic biological control. The potential for classic biological control has been known for decades (Dodd 1940) as a self-sustaining management practice. However, invasive species management is also context-dependent, and a single organism may not be sufficient to contain an invasive organism. Therefore, more recent biological control programs often include a functionally diverse introduction of natural enemies, grasses such as *Arundo donax* (Goolsby et al. 2011; Goolsby et al. 2016), or control of invasive ants (Porter and Gilbert 2004). A renewed interest in controlling invasive grasses through biological control may lead to substantive improvements in the mitigation of grass invasion (Sutton et al. 2019).

## Conclusion

This study represents an essential step in describing the productivity and reproduction of Guinea grass in three resource environments and its association with natural enemies in its native and invaded ranges. Guinea grass achieved high productivity and reproductivity across the range of habitat types in its invaded range when released from native enemies. However, in its native range, when subjected to natural enemies, the potential of Guinea grass was significantly reduced. In addition, the diversity of specialist and generalist arthropods in Kenya is high compared to the few generalist arthropods in Texas. This information improves our understanding of opportunities to develop impactful and sustainable biological control agents (Sutton et al. 2019). Further, since release from a single enemy may not drive increased invasiveness, using a suite of organisms across feeding guilds may be more appropriate in biological control (Porter and Gilbert 2004; Goolsby et al. 2011; Goolsby et al. 2016).

Grasses are a critical group of organisms that make up most food crops and are translocated for pasture development, yet are also among the most pervasive invaders (Linder et al. 2018; Sutton et al. 2019). Given these two competing interests, an important goal is to search for sustainable biological control specific to the problematic grass species (Rhodes et al. 2021). Understanding how Guinea grass's ecology and biology differ in its native and introduced range may open opportunities for directed management. A troubling predicament is an enormous effort spent controlling Guinea grass as a weed and a similar effort developing Guinea grass as a pasture grass, encouraging invasive traits (Rhodes et al. 2021). Guinea grass represents an economically valuable forage species for livestock globally (Jank et al. 2014) yet often escapes to degrade ecosystem function and diversity. While traditional means of controlling invasive grasses may not be effective at landscape scales (Rhodes et al. 2021), a renewed focus on biological control for grasses could prove critical for controlling invasive grasses globally (Sutton et al. 2019).

## Acknowledgements

## References

Alberdi A, Aizpurua O, Gilbert MTP, Bohmann K (2018) Scrutinizing key steps for reliable metabarcoding of environmental samples. Methods in Ecology and Evolution 9(1): 134–147. https://doi.org/10.1111/2041-210X.12849

Alves A, Xavier FE (1986) Major perennial weeds in Brazil: *Panicum maximum* Jacq., *Paspalum maritimum* Trin., *Brachiaria purpurascens* Hens., *Senecio brasiliensis* Less.

Ammondt SA, Litton CM (2012) Competition between Native Hawaiian Plants and the Invasive Grass *Megathyrsus maximus*: Implications of Functional Diversity for Ecological Restoration. Restoration Ecology 20(5): 638–646. https://doi.org/10.1111/j.1526-100X.2011.00806.x

Bailey DW, Mosley JC, Estell RE, Cibils AF, Horney M, Hendrickson JR, Walker JW, Launchbaugh KL, Burritt EA (2019) Synthesis Paper: Targeted Livestock Grazing: Prescription for Healthy Rangelands. Rangeland Ecology and Management 72(6): 865–877. https://doi.org/10.1016/j.rama.2019.06.003

Benson EJ, Hartnett DC (2006) The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. Plant Ecology 187(2): 163–178. https://doi.org/10.1007/s11258-005-0975-y

Best C (2005) Fighting weeds with weeds: battling invasive grasses in the Rio Grande delta of Texas. In: Van Devender T, Espinosa-García, FJ, Harper-Lore, BL, Hubbard T (Eds) Invasive plants on the move: controlling them in North America. Tucson, Arizona, 307–317.

Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive non-indigienous plants - A hypothesis. Journal of Ecology 83(5): 887–889. https://doi.org/10.2307/2261425

CABI (2022) Megathyrsus maximus In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc

Cadotte M, Lovett-Doust J (2001) Ecological and taxonomic differences between native and introduced plants of southwestern Ontario. Ecoscience 8(2): 230–238. https://doi.org/10.1080/11956860.2001.11682649

Cadotte MW, Murray BR, Lovett-Doust J (2006) Evolutionary and ecological influences of plant invader success in the flora of Ontario. Ecoscience 13(3): 388–395. https://doi.org/10.2980/i1195-6860-13-3-388.1

Canavan S, Meyerson LA, Packer JG, Pyšek P, Maurel N, Lozano V, Richardson DM, Brundu G, Canavan K, Cicatelli A, Čuda J, Dawson W, Essl F, Guarino F, Guo W-Y, van Kleunen M, Kreft H, Lambertini C, Pergl J, Skálová H, Soreng RJ, Visser V, Vorontsova MS, Weigelt P, Winter M, Wilson JRU (2019) Tall-statured grasses: A useful functional group for invasion science. Biological Invasions 21(1): 37–58. https://doi.org/10.1007/s10530-018-1815-z

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity & Distributions 15(1): 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: A null model for biological invasions. Biological Invasions 8(5): 1023–1037. https://doi.org/10.1007/s10530-005-3735-y

Coley PD, Bryant JP, Chapin III FS (1985) Resource availability and plant antiherbivore defense. Science 230(4728): 895–899. https://doi.org/10.1126/science.230.4728.895

Cornwell WK, Ackerly DD (2010) A link between plant traits and abundance: Evidence from coastal California woody plants. Journal of Ecology 98(4): 814–821. https://doi.org/10.1111/j.1365-2745.2010.01662.x

Cox GW, Ricklefs RE (1977) Species diversity and ecological release in Caribbean land bird faunas. Oikos 28(1): 113–122. https://doi.org/10.2307/3543330

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. Annual Review of Ecology and Systematics 23(1): 63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: A general theory of invasibility. Journal of Ecology 88(3): 528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

Dirks I, Dumbur R, Lienin P, Kleyer M, Grünzweig JM (2017) Size and reproductive traits rather than leaf economic traits explain plant-community composition in species-rich annual vegetation along a gradient of land use intensity. Frontiers in Plant Science 8: 891. https://doi.org/10.3389/fpls.2017.00891

Dodd AP (1940) The biological campaign against Prickly-Pear. Commonwealth Prickly Pear Board, Brisbane, [ii +] 117 pp.

Espinosa-Garcia FJ, Villasenor JL (2017) Biodiversity, distribution, ecology and management of non-native weeds in Mexico: a review. Revista Mexicana De Biodiversidad 88: 76–96. https://doi.org/10.1016/j.rmb.2017.10.010

Euclides VPB, Carpejani GC, Montagner DB, Nascimento D, Barbosa RA, Difante GS (2018) Maintaining post-grazing sward height of *Panicum maximum* (cv. Mombaca) at 50 cm led to higher animal performance compared with post-grazing height of 30 cm. Grass and Forage Science 73(1): 174–182. https://doi.org/10.1111/gfs.12292

Fine PVA, Mesones I, Coley PD (2004) Herbivores promote habitat specialization by trees in Amazonian forests. science 305: 663–665. https://doi.org/10.1126/science.1098982

Frost RA, Launchbaugh KL (2003) Prescription grazing for rangeland weed management. Rangelands 25(6): 43–47. https://doi.org/10.2458/azu_rangelands_v25i6_frost

Gaskin JF, Espeland E, Johnson CD, Larson DL, Mangold JM, McGee RA, Milner C, Paudel S, Pearson DE, Perkins LB, Prosser CW, Runyon JB, Sing SE, Sylvain ZA, Symstad AJ, Tekiela DR (2021) Managing invasive plants on Great Plains grasslands: A discussion of current challenges. Rangeland Ecology and Management 78: 235–249. https://doi.org/10.1016/j.rama.2020.04.003

Goolsby JA, Kirk AA, Moran PJ, Racelis AE, Adamczyk JJ, Cortés E, Marcos García M, Martinez Jimenez M, Summy KR, Ciomperlik MA (2011) Establishment of the armored scale, *Rhizaspidiotus donacis*, a biological control agent of *Arundo donax*. The Southwestern Entomologist 36(3): 373–374. https://doi.org/10.3958/059.036.0314

Goolsby JA, Moran PJ, Racelis AE, Summy KR, Jimenez MM, Lacewell RD, Perez de Leon A, Kirk AA (2016) Impact of the biological control agent *Tetramesa romana* (Hymenoptera: Eurytomidae) on *Arundo donax* (Poaceae: Arundinoideae) along the Rio Grande River in Texas. Biocontrol Science and Technology 26(1): 47–60. https://doi.org/10.1080/09583157.2015.1074980

Hanley TA (1982) The nutritional basis for food selection by ungulates. Rangeland Ecology & Management/Journal of Range Management Archives 35: 146–151. https://doi.org/10.2307/3898379

Herrera A, Dudley TL (2003) Invertebrate community reduction in response to *Arundo donax* invasion at Sonoma Creek. Biological Invasions 5(3): 167–177. https://doi.org/10.1023/A:1026190115521

Ho CY, Tsai MY, Huang YL, Kao WY (2016) Ecophysiological factors contributing to the invasion of *Panicum maximum* into native *Miscanthus sinensis* grassland in Taiwan. Weed Research 56(1): 69–77. https://doi.org/10.1111/wre.12186

Holechek JL, Pieper RD, Herbel CH (1989) Range management. Principles and practices. Prentice-Hall.

Hui C, Richardson DM, Landi P, Minoarivelo HO, Garnas J, Roy HE (2016) Defining invasiveness and invasibility in ecological networks. Biological Invasions 18(4): 971–983. https://doi.org/10.1007/s10530-016-1076-7

Jank L, Barrios SC, do Valle CB, Simeao RM, Alves GF (2014) The value of improved pastures to Brazilian beef production. Crop & Pasture Science 65(11): 1132–1137. https://doi.org/10.1071/CP13319

Jeschke J, Aparicio LG, Haider S, Heger T, Lortie C, Pyšek P, Strayer D (2012) Support for major hypotheses in invasion biology is uneven and declining. NeoBiota 14: 1–20. https://doi.org/10.3897/neobiota.14.3435

Kaushal P, Paul S, Saxena S, Dwivedi KK, Chakraborti M, Radhakrishna A, Roy AK, Malaviya DR (2015) Generating higher ploidies (7× and 11×) in guinea grass (*Panicum maximum* Jacq.) utilizing reproductive diversity and uncoupled apomixis components. Current Science 109: 1392–1395.

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17(4): 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0

Kingdon J (2015) The Kingdon field guide to African mammals. Bloomsbury Publishing.

Lambert AM, Dudley TL, Saltonstall K (2010) Ecology and impacts of the large-statured invasive grasses *Arundo donax* and *Phragmites australis* in North America. Invasive Plant Science and Management 3(4): 489–494. https://doi.org/10.1614/IPSM-D-10-00031.1

Lambertini C (2019) Why are tall-statured energy grasses of polyploid species complexes potentially invasive? A review of their genetic variation patterns and evolutionary plasticity. Biological Invasions 21(10): 3019–3041. https://doi.org/10.1007/s10530-019-02053-2

Lavorel S, Díaz S, Cornelissen JHC, Garnier E, Harrison SP, McIntyre S, Pausas JG, Pérez-Harguindeguy N, Roumet C, Urcelay C (2007) Plant functional types: are we getting any closer to the Holy Grail? Terrestrial ecosystems in a changing world. Springer, 149–164. https://doi.org/10.1007/s10530-019-02053-2

Lind EM, Borer E, Seabloom E, Adler P, Bakker JD, Blumenthal DM, Crawley M, Davies K, Firn J, Gruner DS, Stanley Harpole W, Hautier Y, Hillebrand H, Knops J, Melbourne B, Mortensen B, Risch AC, Schuetz M, Stevens C, Wragg PD (2013) Life-history constraints in grassland plant species: A growth-defence trade-off is the norm. Ecology Letters 16(4): 513–521. https://doi.org/10.1111/ele.12078

Linder HP, Lehmann CER, Archibald S, Osborne CP, Richardson DM (2018) Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. Biological Reviews of the Cambridge Philosophical Society 93(2): 1125–1144. https://doi.org/10.1111/brv.12388

Litt AR, Cord EE, Fulbright TE, Schuster GL (2014) Effects of Invasive Plants on Arthropods. Conservation Biology 28(6): 1532–1549. https://doi.org/10.1111/cobi.12350

Lucero JE, Arab NM, Meyer ST, Pal RW, Fletcher RA, Nagy DU, Callaway RM, Weisser WW (2020) Escape from natural enemies depends on the enemies, the invader, and competition. Ecology and Evolution 10(19): 10818–10828. https://doi.org/10.1002/ece3.6737

Ludwig F, Dawson TE, Prins HHT, Berendse F, de Kroon H (2004) Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. Ecology Letters 7(8): 623–631. https://doi.org/10.1111/j.1461-0248.2004.00615.x

Maciel GA, Braga GJ, Guimaraes Jr R, Ramos AKB, Carvalho MA, Fernandes FD, Fonseca CEL, Jank L (2018) Seasonal Liveweight Gain of Beef Cattle on Guineagrass Pastures in the Brazilian Cerrados. Agronomy Journal 110(2): 480–487. https://doi.org/10.2134/agronj2017.05.0262

Marshall VM, Lewis MM, Ostendorf B (2012) Buffel grass (*Cenchrus ciliaris*) as an invader and threat to biodiversity in arid environments: A review. Journal of Arid Environments 78: 1–12. https://doi.org/10.1016/j.jaridenv.2011.11.005

Mlynarek JJ, Moffat CE, Edwards S, Einfeldt AL, Heustis A, Johns R, MacDonnell M, Pureswaran DS, Quiring DT, Shibel Z, Heard SB (2017) Enemy escape: A general phenomenon in a fragmented literature? Facets 2(2): 1015–1044. https://doi.org/10.1139/facets-2017-0041

O'Brien TG (2011) Abundance, density and relative abundance: a conceptual framework. In: O'Connell AF, Nichols JD, Karanth KU (Eds) Camera Traps in Animal Ecology. Springer, Tokyo, 71–96. https://doi.org/10.1007/978-4-431-99495-4_6

Olff H, Ritchie ME (1998) Effects of herbivores on grassland plant diversity. Trends in Ecology & Evolution 13(7): 261–265. https://doi.org/10.1016/S0169-5347(98)01364-0

Parsons JJ (1972) Spread of African pasture grasses to the American tropics. Rangeland Ecology & Management/Journal of Range Management Archives 25: 12–17. https://doi.org/10.2307/3896654

Porter SD, Gilbert LE (2004) Assessing host specificity and field release potential of fire ant decapitating flies (Phoridae: *Pseudacteon*). Assessing host ranges for parasitoids and predators used for classical biological control: a guide to best practice: 152–176.

Pyšek P (1997) Clonality and plant invasions: can a trait make a difference. The ecology and evolution of clonal plants, 405–427.

Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? Biological Invasions. Springer, 97–125. https://doi.org/10.1007/978-3-540-36920-2_7

Randall RP (2017) A global compendium of weeds. RP Randall, Perth, Australia.

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rhodes AC, St. Clair SB (2018) Measures of browse damage and indexes of ungulate abundance to quantify their impacts on aspen forest regeneration. Ecological Indicators 89: 648–655. https://doi.org/10.1016/j.ecolind.2018.02.013

Rhodes AC, Larsen RT, Clair SBS (2018) Differential effects of cattle, mule deer, and elk herbivory on aspen forest regeneration and recruitment. Forest Ecology and Management 422: 273–280. https://doi.org/10.1016/j.foreco.2018.04.013

Rhodes AC, Plowes RM, Goolsby JA, Gaskin JF, Musyoka B, Calatayud P-A, Cristofaro M, Grahmann ED, Martins DJ, Gilbert LE (2021) The dilemma of Guinea grass (*Megathyrsus maximus*): A valued pasture grass and a highly invasive species. Biological Invasions 23(12): 1–17. https://doi.org/10.1007/s10530-021-02607-3

Rhodes AC, Plowes RM, Lawson JR, Gilbert LE (2022) Guinea grass establishment in South Texas is driven by disturbance history and savanna structure. Rangeland Ecology and Management 83: 124–132. https://doi.org/10.1016/j.rama.2022.04.003

Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters 9(8): 981–993. https://doi.org/10.1111/j.1461-0248.2006.00950.x

Salazar D, Marquis RJ (2022) Testing the role of local plant chemical diversity on plant–herbivore interactions and plant species coexistence. Ecology 103(9): e3765. https://doi.org/10.1002/ecy.3765

Savidan YH, Jank L, Costa JCG, Dovalle CB (1989) Breeding *Panicum maximum* in Brazil 1. Genetic-resources, modes of reproduction and breeding procedures. Euphytica 41(1–2): 107–112. https://doi.org/10.1007/BF00022419

Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28(1): 517–544. https://doi.org/10.1146/annurev.ecolsys.28.1.517

Simberloff D (2009) The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution, and Systematics 40(1): 81–102. https://doi.org/10.1146/annurev.ecolsys.110308.120304

Simpson SJ (2013) Mouthparts and feeding. In: Simpson SJ, Douglas AE (Eds) The Insects. Structure and Function, 5th edn. Cambridge University Press, Cambridge, 15–45. https://doi.org/10.1017/CBO9781139035460.005

Sukhchain (2010) Breeding Guinea grass - A review. Range Management and Agroforestry 31: 109–115.

Sutton GF, Canavan K, Day MD, Den Breeyen A, Goolsby JA, Cristofaro M, McConnachie A, Paterson ID (2019) Grasses as suitable targets for classical weed biological control. BioControl 64(6): 605–622. https://doi.org/10.1007/s10526-019-09968-8

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421(6923): 628–630. https://doi.org/10.1038/nature01346

Van der Colff D, Dreyer LL, Valentine A, Roets F (2015) Invasive plant species may serve as a biological corridor for the invertebrate fauna of naturally isolated hosts. Journal of Insect Conservation 19(5): 863–875. https://doi.org/10.1007/s10841-015-9804-3

Wan HY, Rhodes AC, St. Clair SB (2014) Fire severity alters plant regeneration patterns and defense against herbivores in mixed aspen forests. Oikos 123: 1479–1488. https://doi.org/10.1111/oik.01521

Zitzer SF, Archer SR, Boutton TW (1996) Spatial variability in the potential for symbiotic N-2 fixation by woody plants in a subtropical savanna ecosystem. Journal of Applied Ecology 33(5): 1125–1136. https://doi.org/10.2307/2404692