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Review of the Invasive Forage Grass, Guinea Grass (*Megathyrsus maximus*): Ecology and Potential Impacts in Arid and Semi-Arid Regions

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Abstract

Several introduced African grasses are known to present recurring patterns of invasiveness and cause a severe impact on the diversity and functioning of ecosystems worldwide. *Megathyrsus maximus* (Guinea grass), a forage grass species native to South Africa, is reported to be highly invasive and pose a serious threat to native biodiversity in the introduced range. Despite the severe ecological threats posed by *M. maximus* worldwide, there is a dearth of information on the ecological and agroecological impact of *M. maximus* when growing in unintended areas. In this review, we present general information on *M. maximus*, its distribution and ecological threats it poses, particularly in arid and semi-arid regions. We highlight the gaps in current knowledge on the impact on recipient communities, challenges in effective management, and potential impacts due to climate change, particularly changes in rainfall patterns. We also stress the need for public awareness about the threats posed by *M. maximus* to prevent its invasion in unintended areas.

Keywords: biological invasion, African forage grasses, semi-arid subtropics, habitat degradation, Guinea grass

Introduction

With the introduction of species outside their native range, humans have caused a significant impact on the composition of biological communities worldwide. While a significant portion of introduced species do not get established in proportions that can have ecological impacts, a few become highly successful in invading recipient habitats. These invasive non-native species pose a serious threat to native species and potentially alter the ecosystem functions. Invasive plants are known to threaten biodiversity, reduce carbon storage, and influence the fundamental ecosystem processes such as fire regimes and nutrient cycling. Invasive species not only pose considerable harm to the native ecosystem and biodiversity but also have a significant economic impact. For example, Pimentel *et al.* (2005) estimated the annual cost of invasive plants in the United States to be at least US$27B. A recent study by Diagne *et al.* (2021) reported the total cost of biological invasion world-wide to be a minimum of US $1.288 trillion (2017 dollars) over the past few decades. While the high cost of invasive species control is one of the challenges faced by land managers, researchers have also acknowledged the social dimensions of invasive species management (Pimentel *et al.* 2005). This challenge is further compounded when invasive plant species have commercial value. For example, managing invasive grasses with agronomic value for farmers results in conflicts between farmers who want to exploit them as grazing grasses and conservationists who are concerned about ecological impacts (CABI 2019).

Invasive non-native grasses, originally introduced as forage grasses, are known to cause a significant impact on the functioning and stability of ecosystems (D'antonio and Vitousek, 1992). They also pose a threat to agriculture as major agronomic weeds (Parker *et al.* 2013). Invasive grasses of African origin are particularly known to cause a severe impact on the diversity and functioning of ecosystems worldwide. These grasses have evolved under the high pressure of herbivory (Cerling *et al.* 2015) and adapted to a wide range of environmental conditions (Baruch, 1994) which gives them a competitive advantage against the native plants in terms of colonizing ruderal habitats. The life history traits (e.g., high growth rates and tolerance to herbivory, soil nutrient status, pH, and salinity) that make them valuable as forage grasses are also the ones that promote invasiveness in these grasses (Overholt and Franck, 2017).

Here we present the ecology, economic and ecological threats, and challenges in the management of *Megathyrsus maximus*, [Jacq.] B.K. Simon & S.W.L. Jacobs (Poaceae), previously *Panicum maximum* and *Urochloa maxima* [Jacq.]) (Guinea grass), introduced to the tropics and subtropics as a forage grass. In the introduced regions, *M. maximus* has escaped from the cultivated rangelands and invaded disturbed sites, roadsides, untended areas, and grazing pastures at alarming rates. Despite the severe ecological threats posed by *M. maximus*, there is limited information on the ecology of and potential threats posed by *M. maximus* in the invaded regions, particularly in the tropical and sub-tropical regions around the globe, where it poses a significant threat in both agricultural fields and natural areas. The aim of this review is to highlight the potential threats posed by *M. maximus* in the introduced range if the grass grows out of confinement in ranches and pastures and infests nearby areas.

Origins and Distribution

Megathyrsus maximus, a forage grass native to tropical and sub-tropical Africa, was introduced across Asia, Europe, North America, and South America for hay and silage production but has caused significant ecological impacts. *Megathyrsus maximus* has become an invasive species in tropical areas and warm temperate areas including the United States, India, Australia, and Brazil (Daehler *et al.* 1998; Sarkar *et al.* 2018) (Fig. 1). By 1915, *M. maximus* was present in the United States, Mexico, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Trinidad, Bermuda, Bahama, Cuba, Jamaica, and Haiti (Hitchcock and Chase, 1917). In the United States, *M. maximus* was first introduced to Florida and across the Gulf Coast in the early 1800s as grazing fodder for cattle and sheep, which then further spread into Southern Mexico (Vasey,1887). By 1907, *M. maximus* was reported to grow along the coast of Alabama, Mississippi, and Texas as a forage grass. *Megathyrsus maximus* was cited to have been growing along the bank of the Guadeloupe river in Texas as early as 1984 (Arthur, 1894). It is now a prominent invasive plant in south Texas (Soti *et al.* 2020) and all major islands of Hawaii (Ammondt *et al.* 2013).

Morphology and Seed Biology

Megathyrsus maximus is a deep-rooted C4 perennial bunchgrass. It grows in erect clumps with a clump radius ranging from 0.21 m to 2.89 m. Stems are cylindrical and 2.5m -3.5m tall (Aganga and Tshwenyane, 2004; Everitt, 2011) with a slightly flattened base. However, the height is dependent on other habitat conditions such as soil moisture, nutrients, shade, etc. Stems are streaked with white wax at the nodes and internodes with leaf blades growing from the lower nodes (Moore, 2010). Leaf-blades are clustered, 20-35cm long and 7-20mm wide, with few appressed hairs. When the leaves are older, the ends curl and dry (Gould, 1975; Everitt, 2011). Roots are dense and fibrous with extensive root hairs near the surface but continue to grow deeper, up to 4.5m (Sumiyoshi, 2012). The dense rhizomes and roots, which can grow up to 1m deep, allow *M. maximus* to survive drought conditions (Aganga and Tshwenyane, 2004) and tolerate fire.

Reproduction occurs through seed as well as vegetative propagation. It is a prolific seed producer, with each plant producing up to 9000 seeds, however, seed yields are low due to seed shattering and small seed size (Sidhu, 1992). While plant biomass is reported to be significantly higher under shade, seed production is reported to be low (Sidhu, 1992). The germination rate of *M. maximus* seeds is reported to be relatively low (Mishra *et al.* 2008). However, the seed viability may be well over 80% if they are dried gradually to 10% moisture (Muir and Jank 2004). The seeds have been reported to experience dormancy for more than 3 years. Optimal seeding depth for *M. maximus* varies by soil type, 1cm in heavy soils and 1.5 cm in sandy soils (Muir and Jank 2004).

Habitat preferences

In its native range, subtropical southern Africa, *M. maximus* is adapted to grow under trees. It is reported to grow well under 25-50% shading, but growth declines at 75% shading (Malaviya *et al.* 2020). Under shaded conditions, *M. maximus* is reported to have a higher nitrogen concentration in the tissue (Paciullo *et al.* 2017). In south Texas, it does well under both shade and open canopy (authors' personal observation). This could potentially explain high *M. maximus* growth under mesquite trees, a leguminous plant. *Megathyrsus maximus* tolerates a wide range of temperature, 12.2 – 27.8^{o}C. The optimum temperature for seed germination is estimated at 19.1-22.9°C but plant growth and biomass accumulation are higher in higher temperatures, with temperature having a strong positive correlation with root biomass (Muir and Jank, 2004). *Megathyrsus maximus* grown under high temperatures is also reported to have a strong association with mycorrhizal fungi, leading to higher phosphorus uptake (Řezáčová *et al.* 2018).

Megathyrsus maximus is generally reported as a drought-tolerance species. However, soil moisture is reported as the major limiting factor for *M. maximus* growth. It grows well in areas with a total annual rainfall of 87-100 cm and grows moderately in drier soils. Under low soil moisture conditions, leaf biomass production declines significantly (Viciedo *et al*. 2019). *Megathyrsus maximus* is known to grow well in a wide range of soil conditions. It prefers well-drained light-textured soils, sandy loams, or loams (Holm *et al.* 1977). *Megathyrsus maximus* is reported to tolerate seasonal inundation and the seeds can survive some flooding, but prolonged water logging can reduce seed viability and germination rate (Muir, 2004). In Malaysia, *M. maximus* is reported to grow on peat (Gajaweera, *et al.* 2011), while in Sri Lanka, it is reported to do well in low humic gley soils with very high-water holding capacity. *Megathyrsus maximus* also has a wide pH tolerance range, with optimal growth at soil pH 5-7. In south Texas, it grows in soils with pH greater than 8, while in Sri Lanka it grows in pH 5.5-7.7, and in Malaysia in 3.0-3.5 (Chew *et al.* 1980). Though it has a wide pH tolerance range, biomass production in *M. maximus* is reported to decline in soil pH >8 and <4 (Bernardes *et al.* 2018). It has high nitrogen demand and is highly competitive in nitrogen-rich soils, producing higher biomass than the cooccurring natives.

Ecological impact

Megathyrsus maximus invades both agricultural fields and natural areas, causing a significant impact on the ecosystem functioning and processes by altering the fire regime and soil quality as well as attracting pests and diseases of crops (Mantoani *et al.* 2016). It has been reported to be a major pest in both annual and perennial crops such as rice, corn, sugarcane, coffee, citrus, and other fruit orchards causing a major reduction in crop yield (Table 1). *Megathyrsus maximus* has been associated with agronomic pests such as *Bipolaris yamadae*, a leaf spot disease infecting sugarcane, serving as a refuge during the otherwise fallow season.

Not only is *M. maximus* fire resistant but it is also reported to alter fire regime in the dry tropical forests of Hawaii (Ellsworth *et al.* 2014) and other tropical and subtropical landscapes. Tall *M. maximus* plants growing under trees add a high fuel load and can act as fire ladders carrying fire from the surface to tree canopies during the dry season causing lasting damage in the invaded systems (Best, 2006). Because *Megathyrsus maximus* is fire-tolerant and can rapidly regenerate from rhizomes after fires, it creates a positive feedback loop favoring its own growth in post-fire, high nutrient ash beds (Aganga and Tshwenyane, 2004). In Queensland, Australia, the dense tussocks of *M. maximus* growing along rivers and floodplains are known to outcompete the native species and displace them (Calvert 1998). In south Texas, the native plant restoration project in the Tamaulipan thornscrub has been significantly impacted by the extensive invasion by *M. maximus*. *M. maximus*, which can grow up to 2 meters tall, can overgrow and shade out the transplanted seedlings of native plants and outcompete them (Dick 2015).

While there is not much information on the impact of *M. maximus* on wildlife, it has been reported to degrade the northern bobwhite (*Colinus virginianus*) habitat in Texas. It also displaces native seed producing plants eaten by Gambel's quail (*Callipepla gambelii*) and other bird species (Kuvlesky *et al.* 2012). In addition, the shift in fire regime causes a decline in native arthropod communities in the habitats nearby (Warren *et al.* 1987). In Puerto Rico, *M. maximus* is known to cause a decline in ground-dwelling insects, while in Australia, it is reported to reduce the larval survival rates of *Mycalesis* spp butterflies feeding on its leaves (See Table 1).

Table 1. Summary of ecological and agronomic impacts of *M. maximus* in the introduced range.

Location/Region	Ecological and Agronomic Impacts	References
Australia	Reduction in the larval survival rates of *Mycalesis* spp butterflies.	Braby *et al.* 1995
Argentina	Major weed in sugar cane fields leading up to 60% crop loss.	Cabrera *et al.* 2020
Brazil	Aggressive invader of annual and perennial crops, including rice, sugarcane, coffee, citrus, and other fruit orchards.	Durigan, 1992
Ecuador	Reduction in biodiversity of the Northern Ecuadorian Amazon area.	González *et al*. 2021
India	Host of a major pest, fall armyworm (*Spodoptera frugiperda*)	Maruthadurai and Ramesh, 2020
Sri Lanka	Invades naturals areas such as forests and scrublands and disturbed degraded lands negatively impacting forestry and agriculture.	Weerawardane and Dissanayake, 2005
Hawaii	Reduction of native grasses and woody plant communities. Adds fuel to brush fires.	Cabin *et al.* 2002; Ellsworth, 2014

	Pose a threat to crops such as *Jatropha curcas* i.e Barbados nut directly by influencing the fire regime and indirectly by changing soil nutrient status.	
Florida, Texas, and Louisiana	Major weed in cotton and sugarcane. Serves as an alternate host for sugarcane aphid *Melanaphis sacchari.* Serves as host for *Bipolaris yamadae,* leaf spot disease, which infects sugar cane crops. Degradation of the northern bobwhite *Colinus virginianus* habitat.	Overholt and Franck, 2017; Schenck and Lehrer, 2000; de Souza *et al.* 2019 Adhikari *et al.* 2020; Moore, 2010
Puerto Rico	Decrease in the abundance of ground-dwelling arthropods.	Moreno *et al.* 2014

Economic and Environmental Value

Megathyrsus maximus was universally introduced as a fodder species for its high protein content and high tolerance to grazing and environmental stresses (Habermann *et al.* 2019). Because it is one of the most productive forage grasses and highly palatable to cattle, it is frequently planted by ranchers. Since it is a perennial bunchgrass with dense root growth, it has the potential to reduce soil erosion (Maass *et al*. 1988; Mishra *et al*. 2008) and add soil organic matter. *Megathyrsus maximus* has also been reported to be a moderate metal accumulator and has the potential to be used as a phytoremediation/phytoextraction candidate in soil and wastewater treatment projects (Olatunji *et al.* 2014, de Sousa *et al*. 2019, Anigbogu *et al.* 2020). In low rainfall areas in Africa, *M. maximus* mulch is used as a drought management strategy (Wade and

Sahchez, 1983; Manu *et al.* 2017). In addition, *M. maximus* incorporated into the corn-legume cropping cycle is reported to increase soybean yields, improve forage quality, minimize nutrient loss, and thus maintain soil fertility in tropical conditions (Costa *et al.* 2021). *Megathyrsus maximus* can also potentially host predatory arthropods including earwigs and spiders and could be utilized as a trap plant in maize fields to reduce spotted stem borer, *Chilo partellus,* eggs and larva (Koji *et al.* 2017).

Climate Change and Range Expansion Potential

Given the agronomic value of *M. maximus*, human mediated dispersal and propagule pressure are two major factors for its range expansion. However, climate change, which is projected to influence the rainfall pattern and temperatures leading to increased temperatures and prolonged drought periods, particularly in the sub-tropics, can also influence the distribution of *M. maximus* in this region. While *M. maximus* is reported to be tolerant to drought and high temperatures, there is some evidence that the above ground biomass growth is limited by soil moisture levels (Viciedo *et al.* 2019). These results show a mixed outcome for *M. maximus* under climate change scenarios. It can potentially both increase and or decrease suitable habitats for *M. maximus*. Under increasing temperatures, combined with drought conditions, *M. maximus* might reduce its expansion in natural areas in the arid and semi-arid regions. There is also a possibility of decrease in habitat suitability in arid and subtropical regions as well as the northward expansion of the species. However, irrigated agricultural fields, which are rich in soil nitrogen, are at a higher risk of *M. maximus* invasion in the topical, subtropical, and warm temperature regions (Kariyawasam *et al.* 2021). There is also a possibility of decrease in the suitable habitats in the arid and semi-arid tropics and subtropics and northward expansion. Thus, further species distribution models projecting the potential response of *M. maximus* to changes in rainfall and temperature could be important in developing long-term management plans.

Management

The characteristics of *M. maximus*, such as high growth rate and tolerance to heavy grazing, shade, drought, salinity, and soil pH, which make it preferred forage grass species, also make it an aggressive invader in non-target habitats. In addition, prolific seed production and ability to rapidly regrow from rhizomes after fire make this species difficult to manage in the arid and semi-arid regions where prescribed burning is typically used for invasive species control (Johnson and Di Tomaso, 2006). Mechanical removal/mowing is reported to be ineffective as the plant can grow back from rhizomes. At a local scale, when the growth is limited, manual removal can be effective, but in larger areas it is expensive and labor intensive. Furthermore, because of its high agronomic value, complete eradication of *M. maximus* from introduced regions is impossible and/or highly controversial. Clearly, there is no single strategy to effectively manage this invasive grass. Several efforts to introduce biological control agents for *M. maximus* management have had mixed results. While the fungal pathogens *Dreshclera gigantean, Exserohilum rostratum, and E. longirostratum* have shown promising results in managing *M. maximus* in sugarcane fields in Florida (Chandramohan *et al.* 2004), a recent effort to introduce stem boring moths, *Buakea kaeuae* Moyal et al., which is specific to small *M. maximus* of south-central Kenya, was reported to be unsuccessful (Vacek *et al.* 2021). Along with biocontrol, treating with 1% glyphosate is reported to be effective *M. maximus* management (Smith *et al.* 2012). However, there are conflicting reports on successful management with glyphosate treatment. While treatment with glyphosate only is reported be effective for spot control when the plants are at a younger stage, glyphosate mixed with flazasulfuron is reported to provide up to 95% *M. maximus* control in citrus groves (Singh *et al*. 2012). In south Texas, management strategies have generally involved a combination of cattle grazing and prescribed burning. It has been reported to reduce *M. maximus* density and increase native plant species richness (Ramirez-Yanez, 2005; Ramirez-Yanez *et al.* 2007). Thus, effective management of *M. maximus* in the introduced range, particularly in the semi-arid tropics and subtropics, can be achieved through a combination of public awareness and integrated pest management including cattle grazing, post emergent herbicides, and prescribed burning followed by pre-emergent herbicides.

Conclusions

M. maximus is a forage grass species with high agronomic value, widely distributed in the tropics and sub-tropics where it is now considered as a highly invasive species. Given its high tolerance for biotic and abiotic stresses, it is likely to further expand its distribution. Because of its agronomic value and extent of spread, complete eradication of *M. maximus* from the introduced range is not desirable nor possible. Thus, the primary strategy for *M. maximus* management should be to reduce its impact on native communities and crops in agricultural fields. Site specific strategies based on the habitat environmental conditions need to be developed for the effective management of *M. maximus*. In areas where *M. maximus* has not extensively invaded cropping fields and native grasslands, it can be managed by well-planned grazing. In areas where *M. maximus* is already established, management can potentially be achieved through the integration of biocontrol (including planned grazing) as well as cultural, chemical, and mechanical methods. While the effectiveness of habitat manipulation has mixed results and is site dependent (Huston 2004), its invasion in agricultural fields can be prevented and/or minimized through proper management of nitrogen fertilizer and precision irrigation. Further comprehensive studies on seed viability, germination, and site-specific *M. maximus* physiology and growth analysis are necessary for effective management. In addition, habitat modeling, incorporating habitat preferences to identify potential impacts of changes in climatic variables, could be important in preventing further spread of *M. maximus* while still allowing for economic uses where feasible.

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