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Source: *Invasive Plant Science and Management*, 13(2) : 41-58

Published By: Weed Science Society of America

URL: <https://doi.org/10.1017/inp.2020.11>

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Review

Cite this article: Wied JP, Perotto-Baldivieso HL, Conkey AAT, Brennan LA, and Mata JM (2020) Invasive grasses in South Texas rangelands: historical perspectives and future directions. *Invasive Plant Sci. Manag* **13**: 41–58. doi: [10.1017/inp.2020.11](https://doi.org/10.1017/inp.2020.11)

Received: 15 August 2019
Revised: 3 January 2020
Accepted: 3 April 2020
First published online: 13 April 2020

Associate Editor:
Kelly Lyons, Trinity University


Keywords:
Bermudagrass; buffelgrass; guineagrass; Lehmann lovegrass; Old World bluestems; remote sensing; tanglehead; unmanned aerial vehicles

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Invasive grasses in South Texas rangelands: historical perspectives and future directions

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Abstract

South Texas is home to a high diversity of species due to its location at the confluence of subtropical, desert, and coastal ecoregions. Historical overgrazing of South Texas rangelands transformed the savanna and prairie to a landscape dominated by woody plants and shrubs interspersed with low seral grass species and bare ground. During the first half of the 20th century, exotic grass species, coupled with the application of industrial agricultural practices appeared to be the future of forage production in South Texas and elsewhere. Several of these exotic species, namely King Ranch bluestem [*Bothriochloa ischaemum* (L.) Keng], Kleberg bluestem [*Dichanthium annulatum* (Forssk.) Stapf], Angelton bluestem [*Dichanthium aristatum* (Poir.) C.E. Hubbard], buffelgrass [*Pennisetum ciliare* (L.) Link], guineagrass [*Urochloa maxima* (Jacq.) R. Webster], Lehmann lovegrass (*Eragrostis lehmanniana* Nees), and Bermudagrass [*Cynodon dactylon* (L.) Pers.], have escaped pasture cultivation. Additionally, the native grass tanglehead [*Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult.] has begun displaying invasive behaviors. The monoculture growth habit of these species simplifies vegetation structure, reduces biodiversity, and decreases habitat for many species of wildlife. These grasses also alter natural fire regimes and nutrient cycling. This landscape-level transformation of vegetation composition and structure requires monitoring to quantify and assess the spatial and temporal distributions of invasive species as a basis to inform management practices. Current advances in remote sensing technologies, such as very high spatial resolution coupled with daily satellite imagery and unmanned aerial vehicles, are providing tools for invasive vegetation monitoring. We provide a synthesis of the natural history of these grasses, including their introductions, an overview of remote sensing applications in South Texas, and recommendations for future management practices.

Introduction

Throughout the world, invasive plant species decrease biodiversity and alter ecological processes such as nutrient cycling, hydrology, and disturbance regimes, cumulatively decreasing the proper function of ecosystems (D’Antonio and Vitousek 1992; Richardson et al. 2000; Simberloff et al. 2013; Vitousek 1990). Some species are accidental introductions, but many have been introduced for agronomic and erosion control purposes before becoming a nuisance in their new environments (Fulbright et al. 2013; Simberloff et al. 2013). Drought tolerance and high productivity make species attractive candidates for introduction and are the same traits that promote invasiveness (Fulbright et al. 2013).

South Texas (Figure 1) includes the area south of the Edwards Plateau from the Rio Grande at Del Rio east to San Antonio and southeast to the Gulf of Mexico at the mouth of Lavaca Bay (Carter 1958; Fulbright and Bryant 2002). The region historically consisted of midgrass coastal plains and inland savanna with the now-prevalent honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) relegated to riparian areas, washes, and other upland sites (Griffith et al. 2007; Jahrsdoerfer and Leslie 1988). South Texas’s variation in edaphic, geologic, and climatic factors, as well as the convergence of subtropical, eastern deciduous, and Chihuahuan desert species, creates a hyperdiverse region (Fulbright and Bryant 2002). The South Texas plains, exclusive of the coastal counties, are home to 514 resident native vertebrate species: 40 amphibians, 109 reptiles, 283 birds, and 82 mammals (Holt et al. 2000). Alone, the 76,006 ha of the South Texas Refuge Complex in the Lower Rio Grande Valley host 31 species of fish, 115 species of herpetofauna, 429 species of bird, and 44 species of mammal at some time during the year (Leslie 2016).

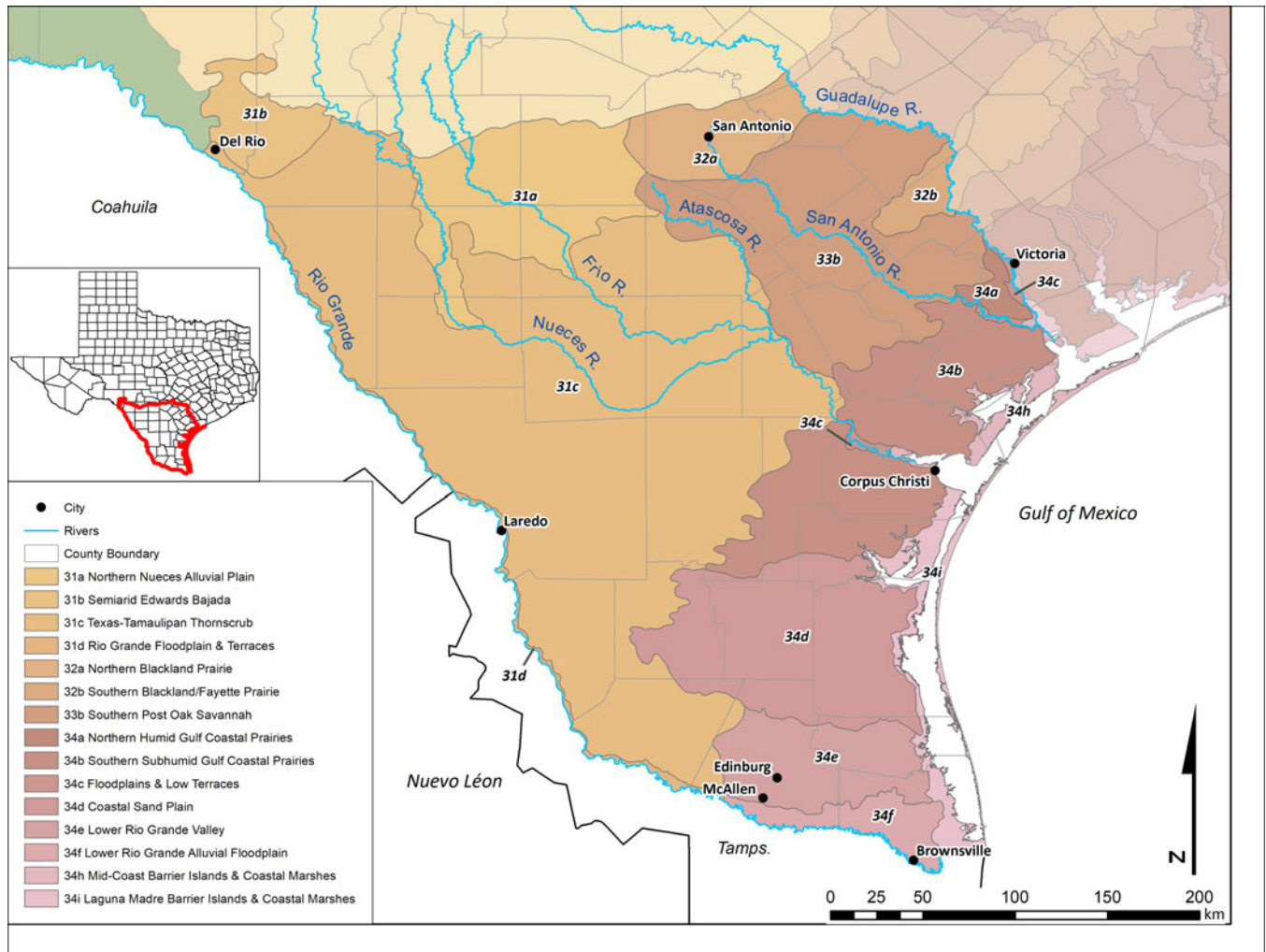


Figure 1. South Texas ecoregions based on Griffith et al. (2007).

Overstocking of sheep during the second half of the 19th century degraded range conditions and contributed to woody plant encroachment (Fulbright 2001; Lehmann 1969). Cattle ranching replaced sheep, but low carrying capacities required large tracts of rangeland (Fulbright 2001; Griffith et al. 2007). In the early 20th century, a search for grass species for forage and erosion control on degraded rangelands led to the introduction of several grass species to southern Texas (Fulbright et al. 2013). The extended droughts in the 1930s and 1950s in particular drove this search (Todd and Ogren 2016). Today, conservation of natural resources in South Texas is critical for property owners who increasingly earn their livelihood through outdoor recreation and are interested in wildlife management (Brennan et al. 2007; Fulbright and Bryant 2002; Smith 2010). Management strategies include brush management, decreased stocking rates, and restoration of pastures with native grass species. The increase of several invasive species (Table 1), such as tanglehead [*Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult.], King Ranch bluestem [*Bothriochloa ischaemum* (L.) Keng; also known as yellow bluestem] (NRCS 2019), Kleberg bluestem [*Dichanthium annulatum* (Forssk.) Stapf], Angleton bluestem [*Dichanthium aristatum* (Poir.) C.E. Hubbard], buffelgrass [*Pennisetum ciliare* (L.) Link], guineagrass [*Urochloa maxima* (Jacq.) R. Webster], Lehmann

lovegrass [*Eragrostis lehmanniana* Nees], and Bermudagrass [*Cynodon dactylon* (L.) Pers.], has become problematic for outdoor enthusiasts and conservationists (Smith 2010). *Pennisetum ciliare* and *C. dactylon* remain commonly planted exotic pasture grasses; however, the greater economic returns provided by fee-lease hunting are prompting landowners to provide suitable areas for wildlife habitat through conservation and ecological restoration. Restoration of native shrub species on abandoned cropland is impeded by the colonization of these grass species; this can be exacerbated by oil and gas infrastructure such as pad sites, pipelines, and rights-of-way (Cobb et al. 2016; Goertz 2013). Existing research has shown that grass invasions are likely to occur within 60 m of the abovementioned infrastructure. Changes in herbaceous vegetation restoration strategies with native ecotypic seed can provide resistance to exotic ingress (Falk et al. 2013; Twedt and Best 2004). In this review, we outline how these species have spread across South Texas. For each, we describe its natural history, uses, and impacts on rangelands and wildlife. Finally, we describe how we can use remote sensing methods to quantify the amount and spatial distribution of these species and monitor their spread across the landscape, as well as their potential effects on wildlife management in rangelands.

Table 1. Summary of key biological and ecological characteristics of the most common invasive grass species in South Texas.

Scientific name	Common synonymy	Common name(s)	Provenance	Life history	Growth form	Key ecological features	References
<i>Bothriochloa ischaemum</i> (L.) Keng	None	King Ranch bluestem, yellow bluestem	Temperate and subtropical Eurasia	Perennial	Caespitose	Fire-tolerant, highly grazing tolerant, drought resistant, associated with ecological disturbance	Celarier and Harlan 1955; Fulbright et al. 2013; Gabbard and Fowler 2007; Ortega-S et al. 2007; Shaw 2012
<i>Cynodon dactylon</i> (L.) Pers.	None	Bermudagrass	Subtropics and tropics of southeastern Africa and southern Asia	Perennial	Stoloniferous, rhizomatous	Moderately drought tolerant, grazing tolerant, little freeze tolerance, adaptable to many soil types, flooding tolerant	Anderson et al. 2002; Burton 1948; Fulbright et al. 2013; Shaw 2012; Tan et al. 2010; Way 2014
<i>Dichanthium annulatum</i> (Forssk.) Stapf	None	Kleberg bluestem	Tropical and subtropical eastern and southeastern Asia, tropical Africa	Perennial	Caespitose, weakly stoloniferous	Fire tolerant, highly grazing tolerant, moderately drought tolerant	Bhat et al. 2011; Celarier and Harlan 1955; Fulbright et al. 2013; Gabbard and Fowler 2007; Ortega-S et al. 2007; Shaw 2012
<i>Dichanthium aristatum</i> (Poir.) C.E. Hubbard	None	Angleton bluestem	Tropical and subtropical eastern and southeastern Asia	Perennial	Caespitose	Highly grazing tolerant, moderately drought tolerant	Bhat et al. 2011; Celarier and Harlan 1955; Fulbright et al. 2013; Shaw 2012
<i>Eragrostis lehmanniana</i> Nees	None	Lehmann lovegrass	Southern Africa	Annual, perennial	Caespitose	Fire tolerant, grazing tolerant, drought tolerant, adaptable to wide temperature range	Bock et al. 2007; Cox et al. 1988a; Fulbright et al. 2013; McGlone and Huenneke 2004; Shaw 2012; Williams and Baruch 2000
<i>Heteropogon contortus</i> (L.) P. Beauv. ex Roem. & Schult.	None	Tanglehead	Cosmopolitan tropics and subtropics	Perennial	Caespitose	Slow nutrient uptake, fire tolerant, grazing tolerant	Bielfelt and Litt 2016; Shaw 2012; Tothill and Hacker 1976; Wester et al. 2018
<i>Urochloa maxima</i> (Jacq.) R. Webster	<i>Panicum maximum</i> Jacq. <i>Megathyrsus maximus</i> (Jacq.) B.K. Simon & S.W.L. Jacobs	Guineagrass	Tropical and subtropical Africa	Perennial	Caespitose	Shade tolerant, resistant to short drought, fire tolerant, not freeze hardy, adaptable to many soil types	Fulbright et al. 2013; Langeland et al. 2008; Parsons 1972; Shaw 2012; Williams and Baruch 2000
<i>Pennisetum ciliare</i> (L.) Link	<i>Cenchrus ciliaris</i> L.	Buffelgrass	Tropics and subtropics of Africa and southwestern Asia	Perennial	Caespitose	Fire adapted, grazing resistant, drought resistant, not freeze hardy, intolerable to heavy soils	Fulbright et al. 2013; Marshall et al. 2012; Pinkerton and Hussey 1985; Shaw 2012; Williams and Baruch 2000

Natural Histories of Invasive Grasses

Heteropogon contortus (Tanglehead)

Heteropogon contortus is described as native in the southern Texas plains where midgrass prairies were common (Carter 1958; Johnston 1963). Its worldwide distribution is pantropical, with clusters in the southwestern United States, Central America, Hawai'i, the Indonesian archipelago, Australia, the Indian subcontinent, Madagascar, and southern Africa, which has led some to question its native status within North America (Correll and Johnston 1970; Tothill and Hacker 1976). Tothill and Hacker (1976) consider it a successful species based on its ability to thrive across varying habitats.

Heteropogon contortus is a C₄ perennial bunchgrass of the Andropogoneae tribe with erect culms typically growing to 1 m (Reilly et al. 2002; Soreng et al. 2015). Leaves occur along the length of culms, which end in inflorescences of spikate racemes. A long, twisted awn arises from each upper floret (Everitt et al. 2011). These awns collectively twist together along the raceme, giving the grass its common name. The florets are easily detachable, and the stiff awns attach to fur, clothing, and vehicles, which transport the seeds and facilitate dispersal. Reproduction is primarily apomictic, although sexual reproduction is known to occur (Reilly et al. 2002; Tothill and Hacker 1976). Flowering typically occurs from summer to early fall in southern Texas (Johnston 1963), but Tothill and Hacker (1976) suggested that flowering response may be adaptive due to the instability in subtropical climates. Because it takes in soil nutrients at a slower rate than other associated plant species, *H. contortus* can spread into areas with lower soil productivity (Bielfelt and Litt 2016). Slow absorption also allows established stands of *H. contortus* growing on more nutritive soils to persist longer than other herbaceous species that deplete soil nutrients more quickly (Bielfelt and Litt 2016). Thus, where *H. contortus* has become invasive, it is associated with a monoculture growth of closed canopy (Figure 2), which may decrease bare ground and light availability for other plants (Bielfelt and Litt 2016).

Heteropogon contortus has been considered a good native forage for livestock production during its growth phase; however, upon maturity, the coarse culms and decreased palatability reduce its preference among grazers (Reilly et al. 2002). Additionally, the stiff tangle of awns may cause physical injury to animals. Historically, *H. contortus* was a minor component of rangeland in southern Texas (Carter 1958), and likely not a major component of livestock diets. Johnston's (1963) data show a marked decrease in *H. contortus* abundance on grazed sites, indicating palatability to livestock. The decrease in grazing within South Texas has likely led to the proliferation of *H. contortus* (Wester et al. 2018). Many ranchers in South Texas have observed declining grazing preference by cattle when the plants reach maturity, which contrasts to other areas in western Texas and worldwide, where increasing grazing pressure decreases *H. contortus* abundance, regardless of its growth stage (Tjelmeland 2011).

Wester et al. (2018) proposed that changing land-use practices contributed to an increase of *H. contortus*. Early research on grazing reduction in southern Arizona likewise showed an increase in *H. contortus* production after removal of grazing pressure (Canfield 1948). Prescribed fire is a common tool for improving range through herbaceous renewal and brush removal, but *H. contortus* is naturally fire tolerant (Goergen and Daehler 2001; Tjelmeland 2011). Prescribed fire studies conducted in Jim Hogg County, TX, showed that small patches (<6.97 m²) of



Figure 2. Monoculture of *Heteropogon contortus* in a ranch pasture in Jim Hogg County, TX.

H. contortus increased in both burned and unburned patches 1 yr following a spring fire, but the increase was faster (50%) on burned sites compared with unburned plots (17%) (Wester et al. 2018). The resulting regrowth of surviving plants increased in crude protein 16% and decreased in crude fiber a month after burning, before decreasing with 52% livestock utilization in the burned patches compared with 1.8% in unburned patches (Wester et al. 2018). The use of prescribed burning can therefore make *H. contortus* a more desirable forage. However, Grace et al. (2016) found that fire can promote output up to 1,500 seedlings m⁻².

Few studies have been conducted on the effects of *H. contortus* on wildlife in southern Texas. Bielfelt (2013) reported that increasing density of *H. contortus* increased density of breeding pairs among three obligate grassland species: Cassin's sparrow (*Peucaea cassinii* Woodhouse), Eastern meadowlark (*Sturnella magna* Linnaeus), and grasshopper sparrow (*Ammodramus savannarum* J. F. Gmelin). Mourning dove (*Zenaidura macroura* Linnaeus) density increased with rising *H. contortus* density, though the presence of scissor-tailed flycatchers (*Tyrannus forficatus* Gmelin) decreased. The growth form of *H. contortus* likely provides some ground-foraging and ground-nesting bird species improved protection from predation (Bielfelt 2013). Buelow et al. (2011) found that northern bobwhite (*Colinus virginianus* Linnaeus) used sites dominated by *H. contortus* for nesting in similar proportion (i.e., without preference) to available patches across the landscape; however, they avoided *H. contortus* patches during times spent off-nest. Presumably, the dense nature of *H. contortus* monocultures hampers the movement of ground foragers and may decrease the availability of a diverse diet (Buelow et al. 2011). Similarly, Edwards et al. (2017) detected fewer coveys of *C. virginianus* where invasive grasses, including *H. contortus*, reached >20% canopy cover. This correlated to areas of decreased bare ground and forb production. Where *H. contortus* is prevalent, grassland birds seem to be trapped in a trade-off between improved nesting conditions and less diverse food resources.

Old World Bluestems

The term "Old World bluestems" is applied to agronomic grasses in the Americas imported from Eurasia and Africa. These species belong to a monophyletic, agamic complex of species within the genera *Bothriochloa*, *Dichanthium*, and *Capillipedium* (Harlan et al. 1958; Mathews et al. 2002; Soreng et al. 2015). Specifically, the species encountered in South Texas are *B. ischaemum* (King Ranch bluestem, also known as yellow bluestem), *D. annulatum*

(Kleberg bluestem), and *D. aristatum* (Angleton bluestem) (NRCS 2019). They are distantly related to the native bluestem species within the *Andropogon* and *Schizachyrium* genera with which they form sister clades (Arthan et al. 2017; Mathews et al. 2002). The native range of *B. ischaemum* is temperate and subtropical Eurasia (Celarier and Harlan 1955; Todd and Ogren 2016). *Dichanthium annulatum* and *D. aristatum* are both found from India to southeast and eastern Asia, with *D. annulatum* also occurring in tropical Africa (Celarier and Harlan 1955; Bhat et al. 2011; Todd and Ogren 2016).

The Old World bluestems are C_4 perennial species (Soreng et al. 2015). Hybridization can occur between species in *Dichanthium* and *Bothriochloa* (Singh 1965). Diploids of each species reproduce sexually, whereas polyploids are facultative or obligate apomicts (Harlan and de Wet 1963). Apomictic reproduction is common within both genera and among their hybrids, though vegetative reproduction by stolons occurs (Gould and Shaw 1983; Harlan et al. 1964; Hatch et al. 1999). A plasticity in growth form coupled with hybridization makes identification to the species level difficult, though a groove on the pedicellate spikelets is a defining character of *Bothriochloa* (Best 2006; Celarier and Harlan 1955).

In the United States, several species of *Dichanthium* and *Bothriochloa* were investigated for use in forage production beginning in the early 20th century. *Dichanthium aristatum* and hurricane grass [*Bothriochloa pertusa* (L.) A. Camus] appear to have been accidental introductions to the Western Hemisphere, via the Caribbean Islands (Celarier and Harlan 1955). *Dichanthium annulatum* also appears to have been an accidental introduction (Alderson and Sharp 1994; Novosad and Pratt 1959). Caucasian bluestem [*Bothriochloa bladonii* (Retz.) S.T. Blake] and *B. ischaemum* arrived in the New World for use as potential forage producers (Celarier and Harlan 1955).

Bothriochloa ischaemum is usually recorded as an accidental introduction to the United States (Harlan 1951). The earliest record of *B. ischaemum* in the United States was traced back to a shipment from the U.S. consulate in Amoy (modern Xiamen), Fujian, China, to the California Agriculture Experiment Station in Berkeley (Alderson and Sharp 1994; Celarier and Harlan 1955). Similar material was shipped to the Texas Agriculture Experiment Station in Angleton in 1914 by the U.S. Bureau of Plant Industry (Alderson and Sharp 1994). This species was found growing unexpectedly in a pasture of the King Ranch (Nueces County, TX) by Soil Conservation Service agronomist Nick Díaz in 1939 (Lea 1957). From this material, 34 kg of seed was sent to the Soil Conservation Service nursery in San Antonio, TX, for production investigations (Nixon 1949). Commercial release of *B. ischaemum* began in 1949 (Alderson and Sharp 1994). This year also marks the first accession to a herbarium of a *B. ischaemum* sample collected in Kleberg County (South Texas) and not associated with experiment stations or grass nurseries (Gabbard and Fowler 2007).

Dichanthium annulatum was noticed growing on King Ranch by agronomist Nick Díaz (Lea 1957). The original source of this population is unknown. Beginning around 1915, the King Ranch began experimental plantings of Rhodes grass (*Chloris gayana* Kunth) with an eventual 12,282 ha in production by 1940 (Lea 1957). It is possible seeds or stolons of *D. annulatum* were accidentally mixed with the *C. gayana* material, as both occur in South Africa. Seeds were collected from this population and sent to the Soil Conservation Service nursery in San Antonio, where the grass was increased for production with an informal release of grass seed to producers in the 1940s (Alderson and Sharp 1994).

Dichanthium aristatum plants were donated to the Texas Agriculture Experiment Station in Angleton in 1915 by the USDA Office of Forage-Crop Investigation from materials sent from the Poona Agriculture College (modern Pune Agriculture University) in India (Hafner 1926; Novosad and Pratt 1959). By the 1950s, two cultivars of *D. aristatum*, 'Gordo' and 'Medio', were created from source plants from South Africa and Bee County, TX, respectively, at the Soil Conservation Service nursery in San Antonio. A third cold-hardy cultivar named 'T-587' was released in 1981 from worldwide-sourced stock in the 1950s (Alderson and Sharp 1994).

By the late 1940s, the desire for improved pasture grasses grew, and Old World bluestem production increased, with nearly 55,000 kg of *B. ischaemum* seed harvested for sale in Texas and Oklahoma (Nixon 1949). The Old World bluestems were seen as superior to the native bluestem species due to their grazing resistance and ability to thrive under high fertilizer regimens (Ahring et al. 1978). In the 1950s, work to create improved varieties was undertaken by the Oklahoma Agriculture Experiment Station (Celarier and Harlan 1956). King Ranch instituted a seeding program of planting *B. ischaemum* and *D. annulatum*, among other introduced grasses such as *P. ciliare* and *C. dactylon*, in pastures cleared of brush (Lea 1957; Schnupp and DeLaney 2012). By the 1970s, Old World bluestems were investigated for erosion and weed control along highway rights-of-way by the Texas Highway Department (later Texas Department of Transportation; McCully et al. 1970). In addition, trials were conducted on *B. ischaemum* to test its use as a reclamation grass on former oil well reserve pits in the 1980s (McFarland et al. 1987). An estimated 1 million ha of Texas and Oklahoma rangeland has been seeded with nonnative bluestems since the mid-1980s (Ruffner and Barnes 2012).

Ecosystem disturbances appear to have neutral to positive feedbacks to the spread of these grass species. Root growth is deep, especially in *B. ischaemum*; Allred and Nixon (1955) note that roots reached a depth of 2 to 3 m in a heavy clay soil with roots comprising two times the vegetation growth, improving drought resistance. The exotic bluestems are highly tolerant of grazing, especially in comparison to native grass species (Gabbard and Fowler 2007; Ortega-S et al. 2007). *Bothriochloa bladonii*, *B. ischaemum*, and *D. annulatum* appear to tolerate prescribed fire applications (Gabbard and Fowler 2007; Grace et al. 2001). Fires occurring in the mid-growing season have shown negative effects on *B. ischaemum*, notably when tillers are composed of pre-reproductive and reproductive tillers (Ruckman et al. 2012; Simmons et al. 2007). Similarly, postdrought fires during the growing season were found more successful than dormant-season fires in promoting growth of native forbs without increasing spread of *B. ischaemum* (Twidwell et al. 2012). Encroachment of woody plants appears to indirectly facilitate establishment of *B. ischaemum* by creating disturbances, and thus pathways for invasion within the landscape (Alofs and Fowler 2013).

Shaw (2012) classified *D. annulatum* as poor livestock forage, and Pacheco et al. (1983) found it has a low nutritive value with low protein content and high levels of fiber and silica. It is palatable to cattle and important in late summer when other grasses become dormant (Meyer and Brown 1985). *Bothriochloa ischaemum* is listed as fair forage for livestock and wildlife (Shaw 2012). Palatability of this species is high, though stems cure quickly late in the growing season, thus deterring grazing (Davis 2011; Powell 1994). Old World bluestem forage is capable of supporting gains in livestock weight early in the summer, but this capability declines by August (Coleman and Forbes 1998). Crude protein content



Figure 3. Characteristic yellow color of reproductive stage of *Bothriochloa ischaemum* in Nueces County, TX.

of *B. ischaemum* can decrease from 19% with immature growth to 3.7% with mature growth (National Research Council 1971). Crude protein can be increased in Old World bluestems by maintaining pasture at a short height and applying nitrogen fertilizer (McCullum 2000).

The effects that Old World bluestems have on wildlife have been studied for a wide variety of species and topics. As a component of herbivore diets, *B. ischaemum* and *D. annulatum* have been analyzed for white-tailed deer (*Odocoileus virginianus* Zimmermann) in Texas. *Odocoileus virginianus* are primarily browsing animals, but use of grass increases when the quality of other components decrease or when fresh regrowth occurs after grazing by livestock (Arnold and Drawe 1979; Bryant et al. 1979; Chamrad and Box 1968; Everitt and Drawe 1974). Bryant et al. (1981) confirmed this seasonal use of *B. ischaemum* in central Texas *O. virginianus*. *Bothriochloa ischaemum* is consumed by *O. virginianus* as succulent growth or when woody browse is not preferred, but its preference index values are low compared with other available grass species. Similarly, Meyer et al. (1984) found *O. virginianus* used *D. annulatum* in the summer, accounting for 14% of their seasonal diet. Despite the high usage, the in vitro digestible energy of *D. annulatum* was among the lowest at 1.85 kcal g⁻¹ which would require 246 g to provide a daily maintenance level of digestible energy of 3,252 kcal g⁻¹ to a 55-kg lactating doe (Meyer et al. 1984). Mean percent crude protein values of *D. annulatum* samples are 6.7% (SE = 0.7%) and only provide sufficient protein >13% for *O. virginianus* growth and reproduction during spring and autumn (Meyer and Brown 1985). These results indicate a low utility of these exotic bluestem grasses by *O. virginianus*.

The tendencies (Figure 3) of *Bothriochloa* and *Dichanthium* to develop monocultures create changes in habitat suitability for various wildlife species. For example, mounds of maritime pocket gophers (*Geomys personatus maritimus* Davis) are less likely to be found on sites containing *D. annulatum* (Cortez et al. 2015). A study of *B. ischaemum* impacts on rodent communities in the Edwards Plateau of Texas found hispid cotton rat (*Sigmodon hispidus* Say and Ord) densities to be similar between native vegetation and invaded sites, but fulvous harvest mice (*Reithrodontomys fulvescens* J.A. Allen) and northern pygmy mice (*Baiomys taylori* Thomas) were only captured in native vegetation (Sammon and

Wilkins 2005). Similarly, the species richness of a rodent community decreased in north-central Oklahoma grasslands with 40% to 60% Old World bluestem cover compared with native grassland controls, with *S. hispidus* again becoming the most prevalent species (Greer et al. 2014). Kamler et al. (2003) and Pavur (2016) hypothesized that swift foxes (*Vulpes velox* Say) avoided Conservation Reserve Program grasslands seeded to Old World bluestems where taller and denser vegetation decreased prey abundance and reduced vision, which increases susceptibility to predation by coyotes (*Canis latrans* Say).

Lesser prairie-chicken (*Tympanuchus pallidicinctus* Ridgway) hens require areas of abundant bare ground for brood rearing, while males require short vegetation for lek sites, both of which can be lacking within Old World bluestem-dominated grasslands (Ripper et al. 2008). As with *V. velox*, Conservation Reserve Program fields planted with exotic species did not provide more benefit to *T. pallidicinctus* over native prairie (Wolfe et al. 2016). Where the structure and plant diversity between native prairie and Conservation Reserve Program grassland greatly differs, a smaller abundance of grassland songbirds are benefited (Chapman et al. 2004). *Ammodramus savannarum* are one of the few grassland songbirds whose breeding density increased in Old World bluestem fields, though high breeding densities have been negatively correlated with individual reproductive success (George et al. 2009, 2013a). The vegetation structure between native prairie and *B. ischaemum*-dominated grasslands were similar enough to support dickcissel (*Spiza americana* J. F. Gmelin) and *S. magna* nesting sites (George et al. 2009). While wintering birds may use Old World bluestem fields for structural cover, there may exist a trade-off for lower food abundance in these fields (George et al. 2013b). Dense growth of Old World bluestems on Conservation Reserve Program fields provided scaled quail (*Callipepla squamata* Vigors) with some cover, but they avoided dense vegetation and favored more diverse structure and plant species composition (Kuvlesky et al. 2002). Similarly, *C. virginianus* was less abundant in Conservation Reserve Program fields (George et al. 2013a), although, Arredondo et al. (2007) found that *C. virginianus* did use *D. annulatum* for nesting cover, though at lower percentages compared with other grass species.

Old World bluestems simplify arthropod diversity, which decreases nutrient cycling, prey abundance, and pollination services (Kuvlesky et al. 2012; Litt and Steidl 2010). Biomass of arthropods was significantly lower (Kruskal-Wallis H = 307, P < 0.001) in *B. ischaemum* sites (0.3 g sample⁻¹) compared with native prairies (1.3 g sample⁻¹; Hickman et al. 2006). Arthropod abundance in *D. annulatum* grasslands remained similar to that of native grasslands but differed by species richness (Cord 2011; Mitchell and Litt 2016; Woodin et al. 2010). The Shannon diversity index for insects on a native grassland site was 1.4 with evenness of 0.7, whereas these values were 1.0 and 0.5, respectively, on a *D. annulatum*-dominated site in Nueces County, TX (Woodin et al. 2010). Exotic bluestems had a simplifying effect on several arthropod functional guilds, including herbivorous, predatory, and detritivorous groups. Relative abundances of hemipteran and homopteran species increased relative to other herbivorous species such as orthopterans (Cord 2011; McIntyre and Thompson 2003; Mitchell and Litt 2016; Woodin et al. 2010). Detritivorous insects were least abundant among *D. annulatum* (Cord 2011), and isopods decreased on exotic grasslands, presumably due to changes in amounts and composition of litter (Mitchell and Litt 2016). The simplification of these arthropod groups appears to affect the distributions of predatory arthropod species, namely arachnids (Cord 2011; Woodin et al. 2010). Ants were absent from Old

World bluestem sites, particularly harvester ants (*Pogonomyrmex* spp. Mayr), which are a primary prey species for the threatened Texas horned lizard (*Phrynosoma cornutum* Harlan; McIntyre 2003). Grassland birds are typically granivorous but include arthropods in their diets, especially during breeding and brood rearing, with insects from the orders Lepidoptera, Orthoptera, and Coleoptera being most important to their diets (McIntyre and Thompson 2003; Wiens 1973). These orders decreased in abundance in Old World bluestem sites.

Pennisetum ciliare (Buffelgrass)

Pennisetum ciliare is native to tropical and subtropical Africa and southwestern Asia, with South Africa being the likely geographic origin of the species (Burson et al. 2012; Marshall et al. 2012). It was initially introduced to four sites in Texas for investigation as a pasture grass; however, soil conditions in Angleton and cold winters in Temple, Chillicothe, and Tyler prevented survival of these plantings (Hanselka 1988; Pinkerton and Hussey 1985). A second accession of plant material, this time from the Turkana Basin of Kenya and Ethiopia, was successfully established at the Soil Conservation Service nursery in San Antonio in 1946 (Alderson and Sharp 1994; Cox et al. 1988a). The USDA Soil Conservation Service has success with field trials in southern Texas and informally released a variety for production in 1949 (Cox et al. 1988a; Hanselka 1988). Commercial production began in the 1950s, coinciding with a period of severe drought in Texas (Marshall et al. 2012). Several cultivars were developed during this period through the 1980s (Alderson and Sharp 1994). By 1985, *P. ciliare* was established on over 4 million ha in southern Texas, accounting for 90% of seeded pasture in the state south of San Antonio (Cox et al. 1988a; Mayeux and Hamilton 1983). Overall it is the dominant herbaceous cover on 10 million ha in southern Texas and northeastern Mexico (Williams and Baruch 2000). It was similarly promoted in Arizona and Sonora, Mexico, for improved pastures in the 1940s and 1950s, respectively (Franklin et al. 2006; Marshall et al. 2012; Martin-R et al. 1995). The spread in Sonora has reached more than 1 million ha (Arriaga et al. 2004).

Pennisetum ciliare is a perennial within the Paniceae taxonomic tribe that uses C₄ carbon fixation in photosynthesis (Marshall et al. 2012; Shaw 2012). Plants grow tufted to 120 cm in height with spikelets subtended by soft hairs on a spike-like panicle (Everitt et al. 2011). The species is highly plastic in its growth form (Marshall et al. 2012). It is an aposporous apomict, with tetraploidy being the most common genotype; sexual reproduction is known in some genotypes (Akiyama et al. 2005; Burson et al. 2012; Ozias-Akins and Van Dijk 2007). Seed dormancy appears to change according to the provenance of the parent material (Hacker and Ratcliff 1989). Winkworth (1971) found 10% of sown seed remained viable after 2 yr, while seed maintained in dry storage appeared to enter a second dormancy and emerge with 60% germination. *Pennisetum ciliare* can also reproduce vegetatively via rhizomes and stolon production (Marshall et al. 2012). Seed is spread via attachment to animal fur, vehicles, runoff, and wind (Ortega-S et al. 2013). Some studies suggest *P. ciliare* may have allelopathic qualities (Franks 2002; Fulbright and Fulbright 1990).

Persistence of *P. ciliare* stands requires frost-free winters and medium-textured, low-salinity soils (Hanselka 1988). Roots can grow to 2.4 m deep in the soil, but the low and high water-holding capacities of coarse- and fine-textured soils, respectively, retard growth, as do high water tables (Hanselka 1988; Marshall et al.

2012). There is comparable production of aboveground biomass on sandy- and loamy-textured soils, but *P. ciliare* becomes a predominant species and spreads more easily on loams and sandy clays (Johnson and Fulbright 2008). Establishment occurs more readily on more alkaline soils than acidic soils (Johnson and Fulbright 2008). Wet winters can destroy seed released during the growing season, and hard freezes can damage established plants (Cox et al. 1988a). *Pennisetum ciliare*, especially the cultivar 'T-446', most commonly grown in North America, persists where precipitation ranges from 330 to 550 mm but dies when precipitation reaches >600 mm (Ibarra-F et al. 1995). Despite these limitations, cultivars have been produced that better tolerate unfavorable conditions by breeding an apomict with desirable traits with a sexual reproductive plant (Burson et al. 2012; Cox et al. 1988a; Marshall et al. 2012).

When mature plants are removed from a site, seedlings can quickly reestablish themselves if seed vigor is high (Tjelmeland et al. 2008). Lyons et al. (2013) demonstrated that removal of *P. ciliare* increased cover of native herbaceous species in the Sonoran Desert in northern Mexico. The species is fire adapted, with a combination of a deep root system, the capacity for rapid regrowth after defoliation, and responsiveness to nitrogen addition in the soil (Lyons et al. 2013, Marshall et al. 2012). Unlike most native grass species, following defoliation, *P. ciliare* regrows from nodes along lower stems rather than from the crown (Van Devender et al. 1997). *Pennisetum ciliare* has been shown to alter soil carbon and nitrogen across multiple climate regions across Mexico and has been demonstrated to significantly contribute to aboveground carbon losses in the Sonoran Desert (Abella et al. 2012; Williams and Baruch 2000). However, Lyons et al. (2013) found that replacing nitrogen through fertilizer supplementation improved the response of *P. ciliare* over native vegetation cover in test plots.

Pennisetum ciliare responds better to grazing pressure than most native grass species, a factor that is likely due to lateral growth of tillers (Fensham et al. 2013). Its drought tolerance and response to grazing has made it an attractive livestock forage (Marshall et al. 2012). Within Tamaulipan brushland, aboveground primary production was reported to be 7,025 kg ha⁻¹ (Martin-R et al. 1995). *Pennisetum ciliare* is a preferred grass species for both cattle and domesticated sheep (Everitt et al. 1981; Ramírez et al. 1995). Nutritional values of *P. ciliare* often outperform those of native grasses (Hanselka 1989). Temporary increases in crude protein and phosphorus were noted after prescribed burning of *P. ciliare*, and burned patches were grazed more heavily due to improvements in palatability and forage quality (Hanselka 1989). Cattle-stocking rates increased in South Texas from approximately 12 ha AU⁻¹ (animal unit) on native range to 4 ha AU⁻¹ on *P. ciliare* pasture (Hanselka 1988). Similarly, Sonoran Desert stocking rates increased from 27 to 40 ha AU⁻¹ (animal unit year) on native range to 9 to 15 ha per AU⁻¹ on *P. ciliare* pasture (Martin-R et al. 1995). However, high stocking rates may weaken stands of *P. ciliare* and decrease its spread (Ortega-S et al. 2013).

Pennisetum ciliare has been studied as a forage component of *O. virginianus* and mule deer (*Odocoileus hemionus* Rafinesque) diets. Both deer species were shown to use the grass, mostly fresh green growth, as forage in Sonora (Ortega-S et al. 2013). Additionally, *O. hemionus* used *P. ciliare* sites in a manner similar to native range as long as water and thermal cover were provided (Ortega-S et al. 2013). Levels of crude protein were below winter requirements of *O. virginianus* in South Texas, but the grass contributed significantly to winter diets (Everitt and Gonzalez 1979).



Figure 4. Early spring growth of *Pennisetum ciliare* on a pipeline right-of-way in Jim Hogg County, TX.

Lagomorphs in Sonora showed between 70% and 80% use of *P. ciliare* in areas where native grasses were available (Ortega-S et al. 2013).

The presence of stands of *P. ciliare* (Figure 4) appears to decrease the usable space of habitat for several species of birds (Grahmann et al. 2018). Food production is lower on these sites, with a decrease in the cover, density, and diversity of forbs and decreased abundance and diversity of arthropods (Flanders et al. 2006; Sands et al. 2009). Specifically, arthropods from the orders Hymenoptera, Coleoptera, and Araneae, all important protein components of brooding birds, were less abundant (Flanders et al. 2006). The trophic structure appears to be simplified through simplified vegetation communities (Sands et al. 2009). Flanders et al. (2006) discovered that the abundance of lark sparrows (*Chondestes grammacus* Say), black-throated sparrows (*Amphispiza bilineata* Cassin), northern mockingbirds (*Mimus polyglottos* Linnaeus), *C. virginianus*, and *P. cassinii* were all greater on sites with native vegetation. Species that form resident breeding populations preferred native vegetation to *P. ciliare*-dominated sites (Flanders et al. 2006). In South Texas, *C. virginianus* abundance decreases with increases in the percentage of *P. ciliare*, and quail use declines where the grass composes >20% of cover (Hernández and Guthery 2012). *Colinus virginianus* do use the grass as screening cover and nesting sites, but this may be an artifact of lack of preferred vegetation; however, the lack of bare ground produces a barrier to brood use (Hernández and Guthery 2012). Grahmann et al. (2018) found that cool-season prescribed burns combined with continuous grazing improved usable space for *C. virginianus*. Masked quail (*Colinus virginianus ridgwayi* Brewster) in Sonora, Mexico, used *P. ciliare* as cover during a drought, but their use of these sites declined once native herbaceous vegetation recovered (Kuvlesky et al. 2002). Overall, Flanders et al. (2006) found that pastures dominated by *P. ciliare* supported only about half of the biomass of arthropods and half the density of *C. virginianus* compared with pastures dominated by native grasses. Thus, *P. ciliare* has the potential to reduce carrying capacity for *C. virginianus* by about 50%.

The frequent management practices of cool-season prescribed burns and disking to increase forb production for quail may increase the density of a stand of *P. ciliare* (Kuvlesky et al. 2002;

Tjelmeland et al. 2008). The species is a noted colonizer of disturbed areas, and these disturbances increase the recruitment of seedlings whose success is contingent on bare ground (McIvor 2003; Sands et al. 2009). Disking may be a method of spreading *P. ciliare* into areas with loamy soils, and root-plowing brush in southern Texas increased the frequency of *P. ciliare* compared with control sites (Johnson and Fulbright 2008; Ruthven et al. 1993). On infertile, arid sites, fire itself may not expand *P. ciliare* so much as the lack of native vegetation (Fensham et al. 2013). The intensity at which the species burns is high (Cohn 2005). Fires do not occur frequently on the Hawai'ian Islands or in the Sonoran Desert, and as a result, the native vegetation lacks adaptations to fire (McDonald and McPherson 2011; Simonson et al. 2004). *Pennisetum ciliare* creates a landscape more akin to subtropical grasslands than a desert, and the fuel load induces fires in the Sonoran Desert that are more severe; this places species such as saguaro [*Carnegiea gigantea* (Engelm.) Britton & Rose] and organ-pipe cactus [*Stenocereus thurberi* (Engelm.) Buxbaum] at a higher risk of mortality (McDonald and McPherson 2011). Similarly, Hawai'ian grasslands of *H. contortus* burned more slowly with a small spread compared with areas invaded by *P. ciliare* (Daehler and Carino 1998). The greatest risk to biodiversity in Mexico posed by *P. ciliare* may be anthropogenic; for example, conversion of native rangeland to improved pasture has been implicated in the clearing of >100,000 ha of land (Brenner 2010, 2011).

Urochloa maxima (Guineagrass)

Urochloa maxima is native to tropical and subtropical Africa with a longer history of establishment in the Americas than the other species described here (Akiyama et al. 2008; Parsons 1972). In its native range, it inhabits conditions from grasslands to open woodlands, with tolerance for shady conditions (Duke 1983; Skerman and Riveros 1990). The species was first recorded in the Caribbean Islands in the late 17th century, presumably introduced from ships engaging in the slave trade between western Africa and European colonies (Parsons 1972). It was present in Mississippi by the 1810s and southern Mexico by the 1860s, where it increased the productivity of grazing lands (Parsons 1972). *Urochloa maxima* had become naturalized in Hawai'i by 1871 and spread throughout the islands' *H. contortus* grasslands (Ammond et al. 2013; Daehler and Carino 1998). Production was investigated near Wollangbar, New South Wales, Australia, in the 1890s and spread north along the coast to tropical areas of Queensland (McCosker and Teitzel 1975). The grass was studied at a Soil Conservation Service Plant Materials Center in Wailuku, Hawai'i, in 1957, and though a cultivar was not released publicly, it was distributed for field trials across the state (Alderson and Sharp 1994). The arrival of *U. maxima* in southern Texas and northeastern Mexico is relatively recent, with a rapid expansion evident from the 1970s; however, repeated introductions before 1970 did not result in lasting populations (Best 2006; Correll and Johnston 1970). The current range is approximately from the central Gulf Coast near Victoria, TX, to Monterrey, Nuevo León, Mexico (Best 2006). This population is presumed to have escaped from an unauthorized planting of *U. maxima* in the Rio Grande Valley with seeds obtained from the agriculture experiment station in Weslaco, TX (Best 2006). The species has now been identified rapidly expanding along the southern reach of the San Antonio River within the city limits of San Antonio (KG Lyons, personal communication).

Urochloa maxima is a member of the Paniceae tribe that uses the C_4 photosynthetic pathway (Reinheimer et al. 2005; Shaw 2012). The species is a caespitose perennial, generally growing up to 2.5 m with a many-branched panicle inflorescence (Shaw 2012). Two phenotypes appear in southern Texas: one of tropical provenance with an upright growth habit and a second of subtropical provenance with geniculate growth and shade tolerance (Best 2006). Reproduction may occur apomictically or sexually (Akiyama et al. 2008). Sexual reproduction occurs among diploid individuals, with apomixis occurring in polyploid individuals (Savidan 1980). Propagation is primarily through seed dispersal by wind, water, and animal movements (Ansari et al. 2008; Best 2006). Veldman and Putz (2010) demonstrated that motor vehicles carry the seeds, which established on disturbed logging sites in a tropical dry forest in Bolivia. The species tolerates a variety of soil types, though production decreases on less fertile soils (Duke 1983; Skerman and Riveros 1990). Water-logged soils, saline soils, and hard frost damage the plant (Duke 1983; Langeland et al. 2008). A variety of cultivars have been produced with varying growth forms and adaptations to tolerate different environments (McCosker and Teitzel 1975). A deep root system provides resistance to short periods of drought by accessing water down to 1 m in the soil profile (Langeland et al. 2008). The robust root system was shown by Schaller et al. (2003) to restrict the lateral growth of the root system of young rainbow eucalyptus (*Eucalyptus deglupta* Blume) trees in Costa Rica. The species burns readily and is fire tolerant, regenerating following fire disturbance from below-ground rhizomes (Ellsworth et al. 2014; Langeland et al. 2008; Skerman and Riveros 1990). *Urochloa maxima* has shown allelopathic qualities in laboratory experiments (Chou and Young 1975).

Urochloa maxima is a productive livestock forage worldwide, especially for beef and dairy cattle, but also for sheep (Aganga and Tshwenyane 2004; McCosker and Teitzel 1975). The grass is often used for hay and silage production (Skerman and Riveros 1990). It is considered a highly palatable forage (Best 2006). Continuous grazing of *U. maxima* pasture can lead to mortality, but frequent grazing leaving a standing crop of >0.35 m produces continuous fresh growth (Skerman and Riveros 1990). Due to its worldwide use and differing agronomic practices (e.g., fertilizer application), the nutrient content of *U. maxima* varies widely among localities (Skerman and Riveros 1990). However, crude protein is highest and crude fiber lowest in fresh growth (McCosker and Teitzel 1975). Barbosa et al. (2012) recommend grazing management practices that promote a high tiller population renewal to increase the production of younger growth and thereby increase growth rates and nutritional values. Ramirez-Yañez et al. (2007) found that cattle use of *U. maxima* pastures increased following prescribed burning, presumably from the flush of regrowth in South Texas. The seeds of this species show some ability to germinate after passing through the gastrointestinal tract of cattle (Gardener et al. 1993).

The population of subtropical *U. maxima* in southern Texas has become invasive in croplands, rangelands, and urban areas (Best 2006). *Urochloa maxima* and, to an extent, *P. ciliare* comprise the dominant herbaceous layer along many sites on the Rio Grande river corridor, where they have become impossible to remove (Lonard and Judd 2006). A study of seven sites along the Rio Grande found that *U. maxima* was the dominant species in the ground layer, particularly those sites with a dense shrub and tree canopy cover (Lonard and Judd 2002; Figure 5). The two sites where it was absent were dominated by salt-tolerant species (Lonard and Judd 2002). Restoration of Tamaulipan thornscrub



Figure 5. *Urochloa maxima* growing under the canopy of *Prosopis glandulosa* and sweet acacia [*Vachellia farnesiana* (L.) Wight & Arn.] in Kleberg County, TX.

in southern Texas has been hampered by invasion of *M. maximus* (Dick 2015; Twedt and Best 2004; Vela 2015). Additionally, it competes with the endangered Tamaulipan kidneypetal (*Ayenia limitaris* Cristóbal) for partial shade under shrubs (USFWS 2014).

The tall and lanky growth and shade tolerance of *U. maxima* has made it a problem species for citrus growers in Florida and Texas (Hall et al. 1998; Sauls 1995). During drought conditions, the presence of dry tillers in shrubs can create ladders that carry fire from the ground to shrub and tree canopies (Best 2006). Changes in fire behavior and return intervals are blamed for ecosystem changes to dry tropical forests in Hawai'i by clearing native forest species and allowing trees and shrubs to invade (Ellsworth et al. 2014). Additionally, *U. maxima* invades native Hawai'ian *H. contortus* grasslands and remnant dry lowland forests, causing a reduction in plant diversity (Ammond et al. 2013; Daehler and Carino 1998).

There are few studies investigating the effects of *U. maxima* on wildlife. Moore (2010) investigated *C. virginianus* use of *U. maxima* sites and found that nest success decreased by 4% for every 1% increase of *U. maxima* cover, presumably from reductions in diversity and production of forb and grass seeds. Selection of *U. maxima* for loafing cover may be related to the shade tolerance of the grass and its growth within brush (Moore 2010). A study of grass seed selection among pen-raised *C. virginianus* found preferred selection for *U. maxima* and switchgrass (*Panicum virgatum* L.) seeds compared with Texas millet [*Urochloa texana* (Buckley) R. Webster] and plains bristlegrass [*Setaria leucopila* (Scribn. & Merr.) K. Schum.] seeds (Larson et al. 2012). The seeds of *U. maxima* are large relative to their mass and provide 18% protein and 3.58 kcal g⁻¹ of energy; however, in wild *C. virginianus* harvested in Kenedy County, TX, only 11 of 260 crops from necropsied quail contained *U. maxima* seeds, comprising <2% of total grass seeds (Larson 2008; Larson et al. 2012). Displacement of native grasses by *U. maxima* is causing declines in grass skipper butterflies (subfamily Hesperinae), whose caterpillars feed on native grasses (USFWS 2008).

Eragrostis lehmanniana (Lehmann Lovegrass)

Eragrostis lehmanniana is native to the southern Kalahari Desert and the Karoo of South Africa, where it is considered an early successional species (Cox et al. 1988b; Humphrey 1994). In 1932, seed was imported from the Griqualand West region by Franklin Crider



Figure 6. Dense stand of *Eragrostis lehmanniana* growing alongside a ranch road in southwestern Texas.

and planted near Superior, AZ, at the Boyce Thompson Arboretum (Cox et al. 1988a). Testing of the grass was conducted at the Soil Conservation Service nursery in Tucson, AZ, beginning in 1935, and a refined accession, 'A-68', was selected for seed production in 1937 (Alderson and Sharp 1994; Cox et al. 1988b). Approximately 135 kg of seed produced at the Tucson nursery was planted on Soil Conservation Service plots from Arizona to west Texas, and in 1950, the Arizona Agriculture Experiment Station and Soil Conservation Service released seed for commercial production (Alderson and Sharp 1994; Cox et al. 1988b). Approximately 70% of commercially produced seed was sown on rangelands and along highway rights-of-way in Arizona, New Mexico, and Texas, with the remaining seed planted in the northern Mexican states of Chihuahua, Coahuila, and Sonora (Cox et al. 1988a, 1988b). Seeds from diploid individuals were imported from Northern Cape, South Africa, to allow genetic insertion of preferred traits, and a second variety labeled 'TEM-SD' was commercially released as germplasm by the Texas Agriculture Experiment Station and USDA Agriculture Research Service in 1991 (Alderson and Sharp 1994).

Eragrostis lehmanniana is a caespitose perennial (Figure 6) within the Eragrostideae tribe that utilizes C_4 carbon fixation (Shaw 2012; Soreng et al. 2015). Culms grow to 80-cm tall with a profusion of 7- to 15-cm-long layered leaves that create a clump up to 92 cm across (Crider 1945; Shaw 2012). Plants are weakly stoloniferous with many culms decumbent or geniculate along lower nodes (Burson and Voigt 1996; Zeid et al. 2011). Roots are fine textured and only reach shallowly into soil, with 80% occurring in the top 30 cm of the soil profile (Cox et al. 1992). Asexual reproduction via apomixis occurs in polyploidy individuals, though diploid individuals ($2n = 2x = 20$) produce seed sexually (Alderson and Sharp 1994; Burson and Voigt 1996). Apomictic individuals predominate in its native African range and in the southwestern United States (Burson and Voigt 1996;

Schussman et al. 2006; Zeid et al. 2011). Despite lower genetic variability from nonsexual reproduction, *E. lehmanniana* exhibits a high phenotypic plasticity that allows it to survive multiple ecological sites (Schussman et al. 2006). Established stands of *E. lehmanniana* can produce two seed crops each year, a heavy yield in early summer and a lighter yield in late summer to early autumn (Crider 1945). Seedling emergence appears to decrease in soil textures with higher fractions of clay, and germination is inhibited when seeds are below 5 mm in the soil profile (Cox and Martin 1984; Cox et al. 1988b).

Eragrostis lehmanniana is adapted to climates with temperature ranges between 0 and 38 C and requires 130 to 160 mm of precipitation during active growth (Cox et al. 1988a). The species persists but seldom spreads with summer precipitation between 100 and 160 mm and persists and spreads with precipitation between 160 and 220 mm. Stands may produce as much as 2,695 kg ha⁻¹ of dry matter during favorable conditions (Anderson et al. 1953). Where it is the dominant species, net aboveground production increases, with pure stands having up to four times that amount (McGlone and Huenneke 2004). Cox et al. (1990) reported that *E. lehmanniana* annually produced three to four times more green forage than native grasses in southeastern Arizona. Palatability of *E. lehmanniana* is low, and cattle prefer native perennial grasses during summer (Cable 1971). During other seasons, utilization increases in relation to native grasses due to *E. lehmanniana*'s prolonged green forage (Cox et al. 1988b). Crude fiber constitutes 35% of fresh forage and provides 3.6% and 3.2% digestible protein for cattle and sheep, respectively (National Research Council 1971). The protein content of *E. lehmanniana* is higher in winter compared with native forages such as Arizona cottontop [*Digitaria californica* (Benth.) Henr.] (Cable 1976). *Eragrostis lehmanniana* is considered resistant to defoliation, as it evolved to withstand high grazing pressures (Anable et al. 1992; Bock et al. 2007). Disturbance, especially grazing, does not appear to be necessary for the spread of *E. lehmanniana* as much as proximity to seed sources (Bock et al. 2007; Geiger and McPherson 2005; McClaran and Anable 1992).

Eragrostis lehmanniana is considered a fire-tolerant species and recovers more quickly than native species (McGlone and Huenneke 2004). This has a 2-fold effect on enhanced propagation of the species. The earlier recovery over native grasses allows for higher seed production within a year after a fire event, and removal of litter, whether by fire or mechanical means, enhances seedling emergence by increasing red light penetration and temperature fluctuations at the ground level (McGlone and Huenneke 2004; Roundy et al. 1992; Ruyle et al. 1988). McGlone and Huenneke (2004) described a higher quantity of litter accumulation in *E. lehmanniana* stands, which may alter fire intensity and encourage further establishment of the species.

Little research has been conducted on the effects of *E. lehmanniana* on wildlife. Several studies of grassland birds indicate that *E. lehmanniana* decreases food and shelter resources (Bock and Bock 1992; Flanders et al. 2006; Whitford 1997). At the Santa Rita Experimental Range, Gambel's quail (*Callipepla gambelii* Gambel) and *C. squamata* both avoided *E. lehmanniana* sites in favor of mesquite grasslands and less dense perennial grass cover with high forb diversity, respectively (Medina 2003). In South Texas, *E. lehmanniana* was used by *C. virginianus* for nesting but generally avoided for forage areas (Sands et al. 2012). *Eragrostis lehmanniana* decreases abundance of Palmer's century plant (*Agave palmeri* Engelm.), which is an important nectar source for Mexican long-tongued bats (*Choeronycteris*



Figure 7. Monoculture sod of *Cynodon dactylon* during anthesis in coastal South Texas.

mexicana Tschundi) and lesser long-nosed bats (*Leptonycteris yerbouanae* Martínez and Villa-R.; Lindsay et al. 2011).

Cynodon dactylon (Bermudagrass)

Cynodon dactylon has a cosmopolitan distribution with likely origins in southeastern Africa and south Asia, though it has been culturally significant in India since at least 1500 BCE due to its ability to provide productive forage for livestock (Kneebone 1966; Way 2014). It is one of the most widely distributed plants in the world (Harlan et al. 1970). *Cynodon dactylon* first arrived in the Western Hemisphere on one of the voyages of Christopher Columbus to the Caribbean Islands (Way 2014). The first likely introduction to North America occurred between 1733 to 1738, when botanist Robert Miller brought material to Savannah, GA, and within 50 yr, it was recorded in South Carolina as well (Kneebone 1966). Intentional plantings were used for pasture, but spread is also attributed to movement of livestock and the use of hay as packing material (Kneebone 1966). The first cultivar, ‘Coastal’, was released in 1943 as a cross between a productive strain discovered near Tifton, GA, and two tall strains of southern African provenance (Burton 1948; Kneebone 1966; Way 2014). Many seeded cultivars have since been developed, as well as hybrids that are essentially sterile and require propagation by sprigging (Corriher and Redmon 2009).

Cynodon dactylon is a rhizomatous and stoloniferous sod-forming grass (Figure 7) of the Cynodonteae tribe that utilizes C₄ photosynthesis (Shaw 2012; Soreng et al. 2015). Besides being used for pasture and hay production, it is a common lawn grass in the southern United States (Way 2014). The most frequently encountered varieties outside cultivation are the diploid ($2n = 2x = 36$) ‘common’ and the tetraploid ‘Coastal’, which is larger and more resistant to foliage removal, drought, frost, and disease (Alderson and Sharp 1994; Harlan et al. 1970; Rouquette et al. 2011). Both varieties are adaptable to many soil textures and pH ranges, but heavy clays and sands reduce production without fertilizer application (Burton 1948; Corriher and Redmon 2009; Marsalis 2004). *Cynodon dactylon* has little freeze tolerance, which limits its distribution (Anderson et al. 2002). The species exhibits a high degree of phenotypic plasticity, with many naturally occurring ecotypes (Harlan et al. 1970; Hoveland 1960; Rouquette et al. 2011). It is considered drought resistant, though the degree varies depending on ecotype or cultivar, and it is able to withstand

submergence, both at depth and of long duration (Tan et al. 2010; Zhou et al. 2013).

Cynodon dactylon has a history of use for livestock production in the southern United States since the late 19th century (Way 2014). It withstands defoliation well (Grace et al. 2001). Fresh, mature *C. dactylon* forage provides 28.5% crude fiber, 5.8% protein, and energy levels of 2.72 Mcal kg⁻¹ for cattle, while its hay provides 29.4% crude fiber, 7.9% protein, and energy of 2.20 Mcal kg⁻¹ for cattle (National Research Council 1971). Average annual crude protein from South Texas samples was 11.4%, which meet the needs for dry cows across all seasons and for lactating cows all seasons but winter (Gonzalez and Everitt 1982).

Dense growth of *C. dactylon* has been shown to be highly utilized forage of black-bellied whistling ducks (*Dendrocygna autumnalis* Linnaeus) and Canada geese (*Branta canadensis* Linnaeus) in South Texas (Bolen and Forsyth 1967; Glazener 1946). However, this growth decreases survivability of *C. virginianus* chicks by impeding movement and increasing temperatures up to 4 C compared with forb-dominated sites (Martin et al. 2015). Furthermore, *C. dactylon* provides poor nesting cover, and it outcompetes other plants, subsequently decreasing seed and arthropod availability to *C. virginianus* (Bond et al. 2005; Crouch 2017). Gust and Schmidly (1986) observed a change in rodent diversity and hypothesized that the monoculture habit of *C. dactylon* decreases food availability of small mammals.

Cynodon dactylon is considered an early successional species and is closely associated with disturbed rangelands (Barnes et al. 2013; Grace et al. 2001). Way (2014) suggests it seldom exists naturally as a component of climax vegetation. It has been found to be an early colonizer of formerly submerged land in the Texas Gulf prairies (Scifres and Mutz 1975). The affinity for disturbance by *C. dactylon* could prove problematic for habitat restoration projects; however, drought has been shown to be a factor aiding in removal of *C. dactylon* during a restoration in South Texas (Crouch 2017). This suggests that the spread of this species in South Texas may be restricted to the more mesic coastal prairies and riparian zones farther inland.

Monitoring Invasive Species: Remote Sensing Approaches

Understanding the spatial and temporal dynamics of invasive grasses is critical to the effective monitoring and management of rangelands (Villarreal et al. 2019). Monitoring of rangeland conditions was first systematically established under a range succession model based on Clementsian succession theory (Westoby et al. 1989). This model allowed changes in vegetation along a single axis and did not account for encroachment of shrubs and trees or the introduction of exotic species (Briske et al. 2005). State and transition models were developed wherein the ecosystem may occupy one of multiple potential stable states (Briske et al. 2005; Westoby et al. 1989). Autogenic or allogenic triggers may modify ecological structure and function during transitions between states creating a threshold, with return to a previous state requiring intervention (Young et al. 2014). This model has since become useful for describing many types of terrestrial ecosystems (Bestmeyer et al. 2011). It is under this framework that we hypothesize that invasive grass species have transitioned rangelands in South Texas into a new stable state.

Past monitoring in rangelands relied on subjective measurements of ground observations (Booth and Tueller 2003). Remote sensing technologies have played an increasing role in the estimation of standing yields and canopy heights, mapping

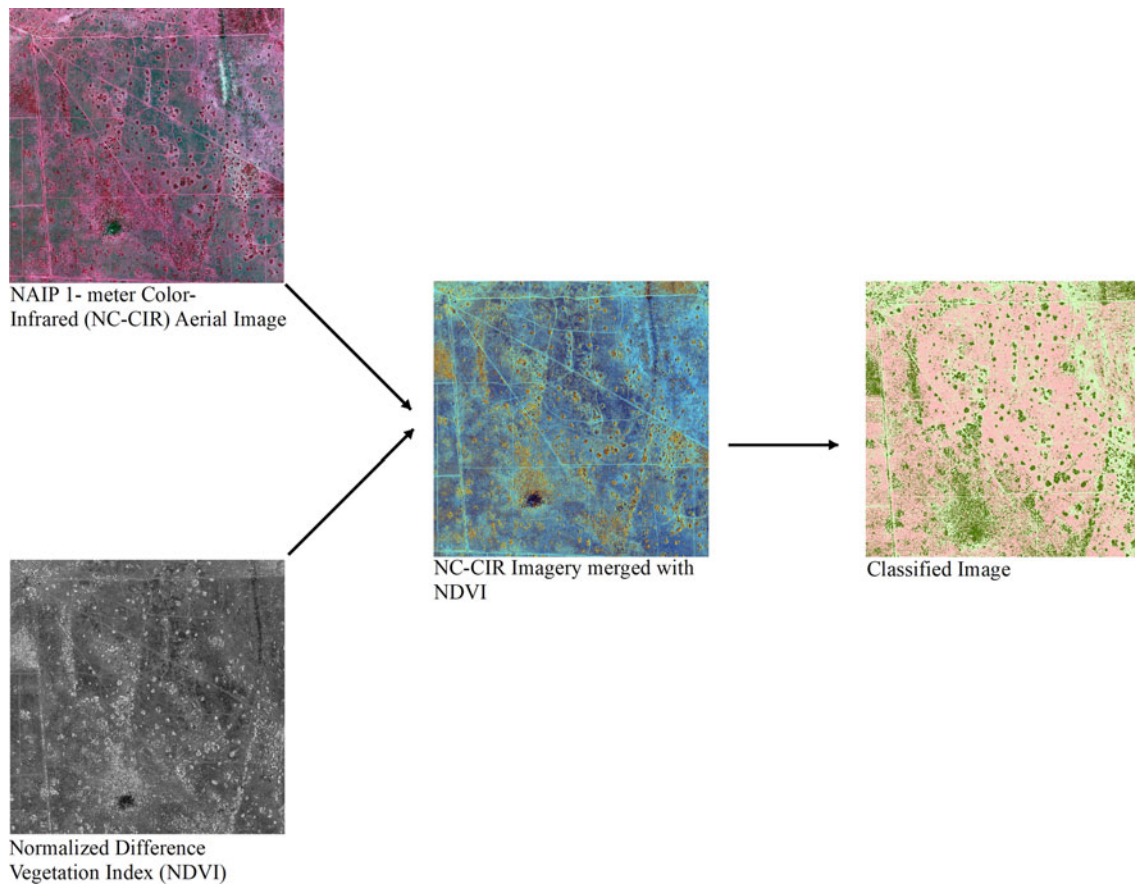


Figure 8. Workflow of unsupervised classification of 2014 National Agriculture Imagery Program aerial photography with normalized difference vegetation index layer stack (adapted from Mata et al. 2018).

of vegetation distributions, and detection of invasive plant species (Bradley and Mustard 2006; Everitt and Deloach 1990; Everitt et al. 1995, 1996; Franklin et al. 2006; Hestir et al. 2008; Hunt et al. 2003; Piñeiro et al. 2006). Since 1972, Landsat satellites have provided the longest record of Earth observation and have been used to classify invasive grasses (Roy et al. 2014). Knight (2004) successfully classified Landsat imagery to distinguish *B. ischaemum* and *B. bladhii* from native grasslands and croplands in Oklahoma. Image classification, combined with habitat models, has been applied to quantify *P. ciliare* environments where invasion is likely (Brenner et al. 2012; Young et al. 2013). Coarser spatial and high-spectral resolution satellites, such as the Moderate Resolution Imaging Spectroradiometer (MODIS), have been used to map the distribution and phenological status of *P. ciliare* in the Sonoran Desert of Arizona (Wallace et al. 2016). Using higher spatial resolutions (<5-m pixel size) than MODIS and Landsat, aerial photography has also been used to detect the phenological responses of *P. ciliare* to water stress in South Texas (Everitt et al. 1987). More recently, Mata et al. (2018) classified National Agriculture Imagery Program images to assess the spatial and temporal distribution of *H. contortus* (Figure 8) between 2008 and 2014 and observed an increase from 4% to 20% in *H. contortus* cover. Although aerial photography provides higher spatial resolution for lower cost, it lacks the spectral resolution of satellite imagery, usually providing only bands in the visible and near-infrared spectra (Huang and Asner 2009; Underwood et al. 2003). Additionally, imagery lacks consistent data acquisition,

with very low temporal revisit times that can limit its usefulness for monitoring studies (Underwood et al. 2003).

Recently launched satellites have included hyperspectral sensors that detect a continuous spectrum of visible and shortwave electromagnetic radiation divided into hundreds of small bands (Huang and Asner 2009; Toth and Józków 2016). Production of microsatsellites has allowed for constellations producing <10-m resolution multispectral data at weekly or shorter time intervals (Toth and Józków 2016). These microsatsellites lack the spectral resolution of the larger satellites, but some platforms, such as RapidEye, include a red edge band, which has improved vegetation mapping accuracies and allowed for detection of foliar nitrogen estimation (Ramoelo et al. 2012; Schuster et al. 2012). Operating a constellation of small satellites allows reductions in revisit times to days compared with the large Earth-observing satellites (Butler 2014). Deployment of unmanned aerial vehicles (Figure 9) has allowed production of low-cost on-demand imagery with spatial scales <2 cm (Anderson and Gaston 2013; Rango et al. 2006). These high spatial resolutions allow the identification of individual patches using mounted digital cameras and ground control points to create mosaicked, georeferenced imagery (Hill et al. 2017; Lu and He 2017). This data-acquisition process can also be used to construct digital elevation models and digital surface models to quantify canopy height comparable with more expensive Lidar data (Ni et al. 2015).

While remote sensing has advanced significantly in terms of platforms, classification algorithms, and access to data and

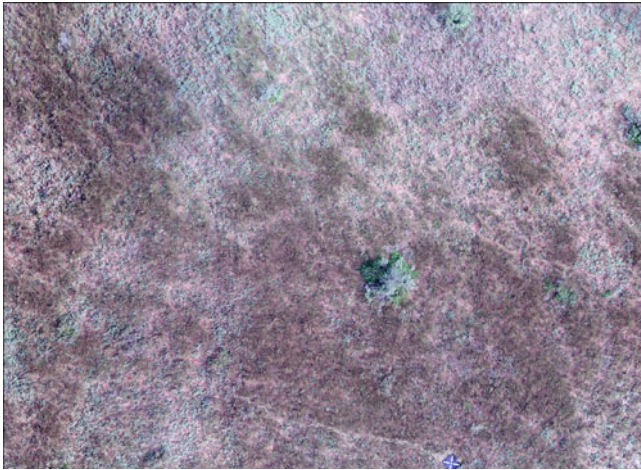


Figure 9. Natural color orthoimagery acquired by an unmanned aerial vehicle of a pasture containing *Heteropogon contortus* in South Texas. Dark areas in the image correspond to patches of *H. contortus*. Pixel resolution is 1.4 cm.

classification approaches through the cloud, there is a need to improve accuracy and the delivery of information to end users (e.g., ranchers, land managers). Traditional image classifications have allowed the classification of invasive monocultures of *H. contortus* in South Texas with accuracies greater than 85% (Mata et al. 2018). However, there is a need to develop classification approaches for the other species in South Texas. This may require the combination of unmanned aerial vehicle platforms combined with satellite platforms to improve both temporal and spatial resolution (Rango et al. 2006). Development of classification approaches and very-high-resolution multispectral imagery in different seasons may also prove useful to improve identification of invasive grasses in South Texas. New approaches such as deep learning and artificial intelligence can potentially improve accuracies to greater than 95% (Zeng et al. 2019). The use of multiple periods and time-series analyses can be used to inform the temporal dynamics of invasive grasses at local and regional scales (Mata et al. 2018; Villarreal et al. 2019). The use of landscape metrics to assess patch dynamics can be used to evaluate the spread of invasive grasses across the landscape (Mata et al. 2018). Young et al. (2014) used remote sensing information and combined it with landscape metrics to quantify thresholds among states in UK peatlands. Image classification, combined with wildlife observation data, can provide a useful framework to develop spatially explicit habitat suitability models to prioritize management and restoration of wildlife habitat. Hence, developing approaches that integrate image classification, soil information, wildlife data, and other environmental variables can help translate remote sensing products from image classifications to management tools for land managers in rangelands as part of their geospatial technology tools.

Future Directions

Land use in South Texas has changed in the last 100 yr from dedicated livestock operations to a combination of livestock and wildlife conservation. The introduction of grasses, once very beneficial to livestock operations, may now have become problematic for wildlife conservation and habitat management. The spread of invasive grasses as a result of changes in land-use practices, such as reduced grazing and oil and energy development, may pose new

challenges in South Texas landscapes (Smith 2010; Wester et al. 2018). The extent that invasive species have spread precludes complete eradication as a practical conservation option. Some exotics like *P. ciliare* and *C. dactylon* are still planted and actively managed by some landowners. Approaches to manage invaded areas may include the introduction of pyric herbivory (Grahmann et al. 2018; Walther 2019). Depending on management objectives, reintroducing native species through fire or native reseeding may improve habitat for wildlife and provide a more sustainable livestock production, with potentially more resilient and profitable ecosystems in the long term. There is a need to develop state and transition models for South Texas rangelands and determine whether these rangelands have transitioned beyond a threshold to a new potentially stable state. Quantifying the spatial and temporal distribution and monitoring the spread of these species will best inform management practices moving into the future. We have already been able to quantify the spatial and temporal dynamics of *H. contortus* (Mata et al. 2018), but it is important to develop regional models to assess potential areas of *H. contortus* invasions. Research into creating methods to quantify the distribution of *B. ischaemum* and *D. annulatum* with daily, high spatial resolution satellite imagery may provide the framework for local and regional image classifications. Similar studies need to be conducted for *D. aristatum*, *P. ciliare*, *M. maximum*, *E. lehmanniana*, and *C. dactylon*. These approaches, combined with fieldwork, would provide a road map to understanding the biology and ecology of invasive grasses in South Texas. The results of these studies will provide conservationists and landowners the tools to preserve and maintain the Last Great Habitat.

Acknowledgments. Funding for this project was provided by the South Texas chapter of the Quail Coalition. An additional grant was awarded from NASA and the Center for Systems Integration and Sustainability at Michigan State University to JPW. LAB was supported by the C.C. “Charlie” Winn Endowed Chair in the Richard M. Kleberg, Jr. Center for Quail Research. We are grateful to F. S. Smith, A. D. Falk, K. G. Lyons, and the two anonymous reviewers who helped us improve this article. Figures 6 and 7 were provided by F. S. Smith. No conflicts of interest have been declared. This is manuscript number 19-118 from the Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, Kingsville, TX.

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