Buffel grass (Cenchrus ciliaris) as an invader and threat to biodiversity in arid environments: A review

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Review

Buffel grass (*Cenchrus ciliaris*) as an invader and threat to biodiversity in arid environments: A review

V.M. Marshall*, M.M. Lewis, B. Ostendorf

The University of Adelaide, Earth and Environmental Science, POB 1, Glen Osmond, South Australia 5064, Australia

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ABSTRACT

Popular pastoral species, Buffel grass (*Cenchrus ciliaris*) is receiving long overdue attention as an invasive weed that poses serious threats to biodiversity conservation worldwide. Most research focuses on the species as forage plant and is largely published in agricultural and grey literature. Meanwhile, there is a dearth of information about the species ecology in natural landscapes despite strong evidence from field workers and managers that the species is an aggressive invader and threat to biodiversity in many environments. We present a comprehensive review of the ecology, distribution and biodiversity impacts of Buffel grass when behaving as an invasive species. Foundations are laid for research into localised habitat requirements of the species that will aid in the management of Buffel grass invasions now and into the future.

1. Introduction

The global cost of controlling biological invasions is phenomenal. Typically, mitigation, containment or eradication of the invasive species is desired; however, control and eradication become controversial if the species is economically significant.

Buffel grass (*Cenchrus ciliaris L.*) is grown widely in tropical and sub-tropical arid rangelands around the globe because of its high tolerance to drought and capacity to withstand heavy grazing. Outside its natural range, Buffel grass can rapidly invade native vegetation, roadsides and urban landscapes, altering the wildfire regime and displacing the native flora and fauna. Due to the economic benefits of the species, eradication is controversial and weed management authorities are ill-informed to effectively target management actions. While over 400 research papers have been published relating to the improvement of Buffel pasture, less than 20 relate to its impact on biodiversity and even fewer describe its nature as an invader (Web of Science, June 2011). Strategic control of Buffel grass invasions requires knowledge of regions infested with or vulnerable to invasion, as well as a willingness from the community to be involved in controlling its spread, all of which are currently lacking.

Presented here is a review of the ecology, distribution and biodiversity impacts of Buffel grass in invaded environments, as well as a synthesis of physiological characteristics relevant to an understanding its behaviour as an invader. The paper aims to increase awareness about the ecological dangers of Buffel grass invasions continuing unchecked and to improve understanding about the ecology of Buffel grass for the purpose of managing invasions.

1.1. The controversy

The eradication of Buffel grass is controversial because the species is highly valued as a pastoral species and more recently for mine site rehabilitation and erosion control (Bhattarai et al., 2008; Guevara et al., 2009; Harwood et al., 1999; Praveen et al., 2005; Tefera et al., 2010; Walker and Weston, 1990). Buffel grass is uniquely suited to these purposes because it has high nutritional value for sheep and cattle, high tolerance to drought, an ability to withstand heavy grazing, a deep stabilising root system and responds quickly to rainfall events (Lazarides et al., 1997; Phillips, 1931). Buffel grass is also one of few pastoral species that is apomictic, meaning it can produce clones from seed, a trait which offers huge potential for the development and distribution of cultivars and agro-types specifically suited to pastoral grazing (Akiyama et al., 2005; Ozias-Akins and Van Dik, 2007). However, the characteristics which make Buffel grass so versatile and suited to a range of harsh conditions also make it an expert invader of non-target environments and from an environmental point of view it is important to prevent further spread of this weed. There is a lack of objective and quantitative research into the adverse impacts of Buffel grass invasions on biodiversity. Although this is changing, it

* Corresponding author. Tel.: +61 08 8303 6715.
E-mail address: victoria.marshall@adelaide.edu.au (V.M. Marshall).

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remains difficult to construct a compelling argument for the control of this highly valued pastoral species.

2. Origin and exotic distribution

Buffel grass occupies extensive areas of the globe within 45 degrees North and South of the Equator. We base this statement on a thorough examination of scientific literature as well as web-based publications and personal communications regarding the presence of the species across states and countries, the results of which are presented in Fig. 1. It should be noted that this map is based on sparsely distributed locational records. It is intended to indicate the expanse of states and countries that may be required to actively manage this weed, and is by no means a regionally accurate depiction of the species' extent. The grass is native to tropical and subtropical arid regions of Africa and western Asia; its exotic distribution spans parts of Australia, USA, Mexico and South America (Centre for Arid Zone Research, 2001; United States Department of Agriculture, 2010). The intercontinental dispersal of Buffel grass has been predominantly human-driven, thus understanding the species' dispersal history may be critical to control further spread (Pauchard and Shea, 2006).

2.1. History of intercontinental dispersal

Buffel grass is one of several African perennial grasses that were widely introduced around the world to better pastoral industries in the early 1900s. Considered to be a "wonder crop" (Hanselka, 1988) for its ability to withstand drought and rapidly respond to rains, Buffel grass was introduced into USA, Mexico, and Australia around 100 years ago and has since expanded into native ecosystems.

In Australia, Buffel grass was accidentally introduced by Afghan cameleers in the 1870s and it gradually naturalised in several areas in the north west of the country. The grass was intentionally introduced as a pastoral species in the 1920s (Centre for Arid Zone Research, 2001; Friedel and Wycott, 2007; Smyth et al., 2009). It was first sown in Queensland in Concurry in 1926, then Rockhampton in 1928 (Humphreys, 1967) and by the 1930s experimental sowing was made in several other Queensland districts (Eyre et al., 2009; Hall, 2000). Around 1950–60, after a period of prolonged drought in central Australia, Buffel was actively planted to prevent erosion and minimise dust storms around the airport at Alice Springs (−23.700297 S, 133.880510 E), where it has naturalised over the past 30 years (Cameron, 2004; Centre for Arid Zone Research, 2001). Concurrent with the introduction of the grass in central Australia, Australian pastoralists were importing new Buffel varieties from Northern Africa and India. These varieties displayed varying success in establishment depending on locality and climate (Friedel and Wycott, 2007). Buffel grass in its many forms now occupies extensive regions of the Australian mainland (Friedel and Wycott, 2007). It is the one of the most important pastoral species in Queensland, and covers vast expanses of native woodlands and grasslands (Cavaye, 1991). In New South Wales, Buffel grass is adapted to more northern, arid parts of the state (Nsw Department of Primary Industries, 2004).

In the Americas, Buffel grass was first introduced to the USA in 1917 as a trial pasture species. Initial trials, located on the heavy clays of northern Texas failed (Hanselka, 1988). Thirty years later, in 1947, it was grown successfully in lower brush country of San Antonio, Texas (Hanselka, 1988). The variety, taken from the Turkan Deset of Nothern Kenya, established readily from seed (Halvorson, 2003) and by the 1950s when Texas was in its seventh year of drought, it became commercially available and flourished under the dry conditions (Hanselka, 1988). By 1985 ranchers in southern Texas had established the grass over 4 million hectares of US farming land (Cox et al., 1988). The grass was introduced into Arizona by the US Soil Conservation Service in the 1940s and spread out from plantings by 1954. By the early 1980s, after several wet

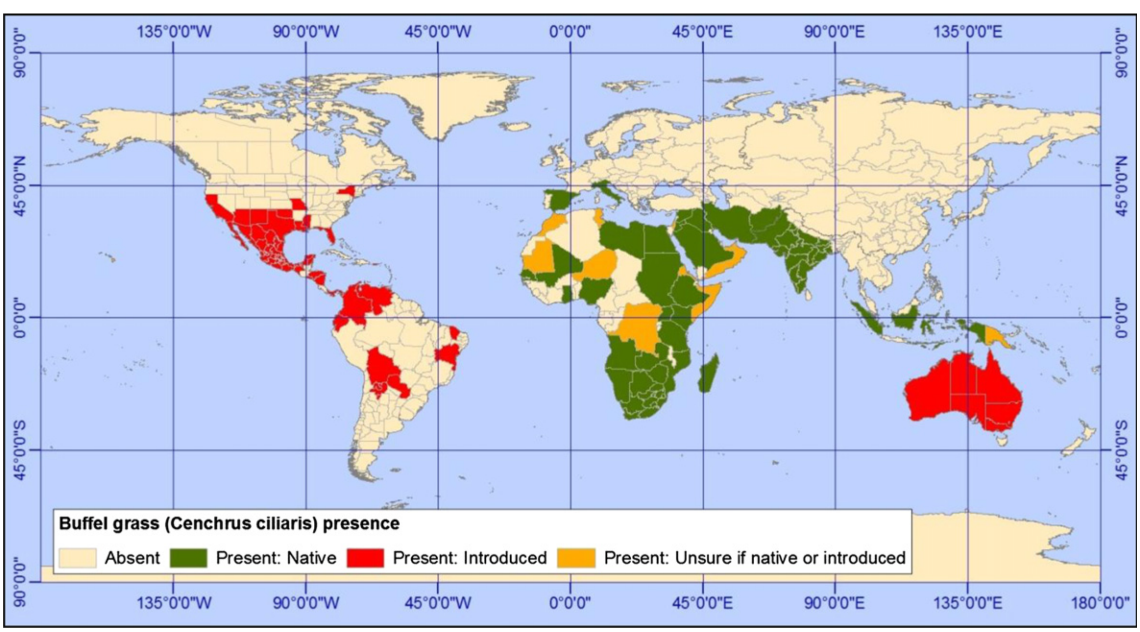

Fig. 1. The native and exotic distribution of Buffel grass to state or country level compiled from published and internet sources. Buffel grass is native (green) to Afghanistan, Angola, Botswana, Canary Islands , Egypt, Ethiopia, Ghana, India, Indonesia, Iran, Iraq, Israel, Italy, Jordan, Kenya, Libyan Arab Jamahiriya, Mali, Madagascar, Mozambique, Namibia, Nigeria, Pakistan, Saudi Arabia, Senegal, Spain, Sudan, Swaziland, Syrian Arab Republic, Tanzania, Uganda, Zambia, and Zimbabwe (Arizona-Sonora Desert Museum Staff and Volunteers, 2008). The species is exotic (red) in Australia, the United States (incl. Hawaii (1932), Arizona (1946), California, Florida, Louisiana, Mississippi, Missouri, New Mexico New York and Texas (1940s), Virgin Islands, and Oklahoma), and parts of central and south America including Mexico (Centre for Arid Zone Research, 2001; United States Department of Agriculture, 2010). Buffel grass is present, but may be native or introduced (yellow), in Central African Republic, Mauritania, Niger, Oman, Somalia, Yemen and Zaire. Buffel grass is shown as "Absent" (beige) where there is a lack of data confirming its presence and thus does not truly represent absence of the species.

summers, it extensively naturalised in the Santa Rita Experimental Range of Tucson, Arizona (Halvorson, 2003). In the 1970s or 80s it was discovered on the Organ Pipe Cactus National Monument (Rutman and Dickson, 2002), an important site created to preserve a representative area of Arizona's Sonoran Desert. Buffel grass spread to cover as much as 625 square miles of the site by 1994 (Rutman and Dickson, 2002). The grass was also introduced into the US state of Hawaii, where 33% of native grasslands were displaced by *Cenchrus* dominated grasslands within 30 years of its introduction to the island (Warren and Aschmann, 1993). Restoration of Hawaiian native grasslands has begun, and success has been demonstrated over a 4 year period (Daehler and Goergen, 2005).

In the 1970s Buffel grass was introduced into Sonora, Mexico from the US to bolster the cattle industry (Cox et al., 1988; De La Barrera and Castellanos, 2007; Franklin et al., 2006). From 1973 to 2000 Buffel grass pastures in Mexico increased from 7700 ha to 140,000 ha (Franklin et al., 2006). It is estimated to have the potential to cover 53% of Sonora and up to 12% of Mexico overall (Arriaga et al., 2004). The Mexican government promotes the use of Buffel grass, which is actively planted to this day (Lyons et al., 2009) and it is unlikely to regulate its spread because cattle ranching drives so much of the economy (Tix, 2000).

In the 1950s Buffel grass was introduced into the Paraguayan Chaco, South America, from Texas. It was sown on a large scale for about 30 years until Buffel blight and other foliar diseases that attack the species were introduced (Glatzle, 2003). The grass was difficult to establish on sandy soils in this region and since the 1980s it has been gradually replaced by Gatton panic (*Panicum maximum* Jacq.), another African perennial, which is easier to establish and harvest in this area (Glatzle, 2003).

According to the Global Biodiversity Information Facility Buffel grass is also present in Central American countries Colombia, Nicaragua, El Salvador and Honduras as well as Brazil, Bolivia, French Guiana, Panama and Venezuela in South America and some Caribbean islands, although there is little documentation regarding its introduction to these locations (Global Biodiversity Information Facility, 2011).

3. Nomenclature and morphology

Buffel grass (*Cenchrus ciliaris* L.) is a robust, deep-rooted C4 perennial tussock grass native to tropical and sub-tropical arid environments (Sharif-Zadeh and Murdoch, 2001). The species has highly varied morphological and physiological characteristics, which when combined with its wide geographic distribution, have led to considerable taxonomic uncertainty, with many synonyms evolving as a result (Table 1). The common name *Buffel grass* is widely accepted and generally refers to *Cenchrus ciliaris* or *Pennisetum ciliare*. Adding uncertainty to any accounts of Buffel grass is that the genera *Cenchrus* and *Pennisetum* are not easily distinguishable, and caution should be taken to ensure that records of the species are credible (Pers. Comm. Helen Vonow, South Australian Herbarium).

Table 1
Buffel grass synonyms.

Common	Buffel grass, African Fox-tail Anjan grass, koluk katai Buffel sandbur, Zacate buffel, pasto buffel
Scientific	*Cenchrus ciliaris*, *C. Setigerus* Vahl., *C. aequiglumis* Chiov., *C. anjana* Ham., *C. bulbosus* Fresen., *C. digynus* Ehrenb., *C. aequiglumis* Chiov., *C. anjana* Ham., Ex Wallich, *C. bulbosus* Fresen., *C. digynus* Ehrenb. Ex Boiss., *C. echinoids* Wight Ex Steud., *C. glaucus* Mudaliar & Sundaraj, *C. lappaceus* Tausch, *C. longifolius* Hochst. Ex Steud., *C. mutabilis* Wight ex Hook., *C. pennisetiformis* Hochst. & Steud., *C. pubescens* L. ex B.D. Jacks., *C. Rigidifolius*, *Pennisetum ciliare*, *P. cenchroides* Rich. ex Pers., *P. distylum* Guss., *P. incomptum* Nees ex Steud., *P. longifolium* Fenzl ex Steud., *P. petraeum* Steud., *P. polycladum* Chiov., *P. prieurii* A. Chev., *P. rangei* Mez, *P. rufescens* (Desf.) Spreng., *P. rufescens* Hochst. ex Steud., *P. teneriffae* Steud (Tu, 2002)

Morphological and physiological differences between Buffel grass varieties have been studied on several occasions (Gutierrez-Ozuna et al., 2009; Jacobs et al., 2004; Jorge et al., 2008; Mnif et al., 2005a; Morales-Romero and Molina-Freaner, 2008). These studies describe the range of dimensions to which the grass grows (Table 2). A Pakistani study on the morpho-genetic variability between 20 Buffel grass accessions (Arshad et al., 2007) showed that most (38.7%) of the morphological variance between accessions used in the study were associated with the height of the plant, leaf area, number of leaves on the main tiller, part of internodes covered by leaf sheath, the number of branches per plant and the number of reproductive branches per plant (Arshad et al., 2007).

Intra-species variation has arisen both naturally and from the commercial development of new strains to improve productivity of pastoral land. Cultivars have been developed with increased growth rates, disease resistance and tolerance to a range of environmental conditions. Consequently, knowledge about the suitability of various strains in different environments may be critical for effective control of infestations. The provenance, exotic distribution, conditions for growth and characteristic traits of some commonly sown *C. ciliaris* cultivars are therefore presented in Table 3.

Commercial cultivars may be grouped into tall, medium and short varieties. Tall varieties (growing up to 1.5 m) are suited to heavier soils and higher rainfall and are generally used for cattle production. These usually display bluish-green coloured leaves, and develop rhizomes. Smaller varieties (<90 cm), generally used for sheep production and erosion control, are typically suited to lighter textured soils, are less tolerant of flooding, and have poor rhizome development (Table 3).

Generally, Buffel grass is apomictic (Bray, 1978), although rare sexual individuals have been identified (Akiyama et al., 2005). Seed spreads easily by wind, along water courses and human or animal traffic. Some varieties can also reproduce vegetatively through rhizomes and stolons. The result of this is that a range of plant forms occur and can be observed growing in dense monotypic stands, as well as in small clumps or even lone tussocks throughout the landscape.

To thoroughly assess the threats posed by Buffel grass invasion, we must ask whether the invasive capacity also varies between sub-species. This has been studied in Mexico (Gutierrez-Ozuna et al., 2009) and Tunisia (Mnif et al., 2005b). Both studies concluded that invasion success is not directly linked to genotypic variation, and that other factors such as phenotypic plasticity and propagule pressure could be major determinants of the invasion success of Buffel grass. However, Humphreys (1967) reports that shorter Buffel varieties are less competitive against native grasses than taller Buffel varieties in sub-tropical climates, and may be better suited to semi arid conditions. Further research is required for a conclusive answer to this question (Humphreys, 1967).

Table 2
Approximate range of dimensions of Buffel grass morphology as described in the literature.

Trait	Dimensions
Plant height	20–150 cm
Stem thickness	1–3 mm
Leaf	1.5–30 cm long, 3–8 mm wide
Ligules	0.5–2 mm
Inflorescences	Yellow–purple–grey
Time to flowering	Approximately 3 months from germination
Roots	Up to 2.4 m deep

Table 3
The provenance, exotic distribution, conditions for growth, and characteristic traits of some commonly sown *Cenchrus ciliaris* cultivars (Food and Agriculture Organization of the United Nations, 2011).

Height	Cultivar/variety	Provena-nce	Exotic distribution	Environmental tolerances	Characteristic traits	Rhizomes
Tall	Biloela	Dodoma in Tanzania 1937 (CSIRO)	Rockhampton, Queensland Australia	Tolerant of flooding (more so than shorter varieties) Suited to a range of soils, can survive on heavier clays Suited to higher rainfall High salt tolerance (Griffa et al., 2010)	Straw coloured seed head with red tinge	Yes
Tall	Boorara A-12a-3	Kenya	Cattle ranch in central Queensland	Will grow in infertile soils Suited to higher rainfall		Yes
Tall	Nunbank A-12a-5			Suited to higher rainfall		Yes
Tall	Bella		Australia	Suited to higher rainfall	Good resistance to Buffel Blight	Yes
Tall	Viva		Australia	Suited to higher rainfall	Good resistance to Buffel Blight	Yes
Tall	Tarewinnabar	Kenya	Queensland	Greater frost tolerance than other cultivars (exp. Molopo)	Scarce seed production	Yes
Tall	Molopo A-12a-2	Molopo River, Western Transvaal, South Africa	NSW	Good frost tolerance More tolerant of flooding than sorter varieties	Low seed production	Yes, good development
Tall	Lawes	Pretoria, Africa			Identical to American cultivar T3782, blue Buffel and Molopo	Commercial seed N/A
Tall	Zeerust			500–625 mm rainfall area in Africa	Tall, leafy	
Tall	Edwards	Kenya	Several hybrids being tested in the US and Australia	Withstands heavy grazing	Robust habit, minimal seed	
Medium	G636 Kongwa 531	Kongwa, Tanzania		Best results on red Barth veiled at Kongwa, Tanzania under annual rainfall 561 mm	Fine leaved, erect, ample seed	
Short- medium (90 cm)	Gayndah, CPI73386, A-12a-7	Kenya	Australia		Short, suitable for sheep grazing Leafier and more tillers than other cultivars (Cameron, 2004) Straw coloured seed head (Primary Industries and Fisheries (Qld, Australia), 2010)	No
–	Chipinga	Zimbabwe			Fine leafy variety	
Short	American A-12a-9	American	Australia	Suitable for sheep but its high palatability may lead to its overgrazing and disappearance High salt tolerance (Griffa et al., 2010)	Identical to American material T.4464 Leafier and more tillers than other cultivars (Cameron, 2004) Red to purple coloured seed head	No
Short	Higgins	Texas			True breeding apomictic variety developed from a sexual variety	
Short	West Australian A-12a-8	Afghanistan	1870–80 Australia on Afghan cameleers	Least drought tolerant of all, nutritionally valuable Grows well on cleared gidgee in Queensland	High shoot/root ratio, increased by phosphorus application (Humphreys, 1967)	
Dwarf	Manzimnyarna and Sebungwe	Semi-arid conditions in Africa				

4. Establishment and growth

Understanding requirements for germination, growth and development is important for identifying fundamental habitat requirements of a species. In arid landscapes, the most critical life history stages in the development of any plant community are seed germination and seedling emergence (Call and Roundy, 1991). There have been numerous studies of the seed longevity and germination rates of Buffel grass, due to its popularity as a pasture species (Bhattarai et al., 2008; Sharif-Zadeh and Murdoch, 2001; Winkworth, 1971). In this section we explore some of the key findings from these studies.

Soil moisture is critical for germination (Ward et al., 2006; Winkworth, 1971). For Buffel grass, the minimum rainfall for seedlings to emerge from loam soils is 6.3 mm (3.14 mm on two consecutive days). This was determined by Ward et al. (2006) in a greenhouse experiment designed to simulate conditions during the summer rainy season of Tucson, Arizona where Buffel grass is prevalent. They found that the probability of new emergence was highest on days 3 and 4 for seedlings that received 3 and 4 consecutive days of simulated precipitation. Probability for new emergence dropped substantially after day four. Based on the results from this experiment Ward et al. (2006) determined that conditions required for emergence of 50% viable Buffel grass had occurred in Tucson in 1 of 2 years over the summer rainy season. In central Australia periods suitable for perennial grasses to germinate are suggested to occur about once a year on average (Winkworth, 1971).

Buffel grass withstands infrequent germination opportunities, in part due to the extreme longevity of its seed bank, estimates of which range from 2 to 30 years (Friedel et al., 2007). Seeds may lay dormant in the ground for up to 8 months, while retaining the original seed viability (Winkworth, 1963). Beyond 12 months, germination rates drop to less than 12%, and remain at 10% for around a two years after that (Winkworth, 1963b).

Buffel seed has been shown to germinate between 10–40 °C with optimal germination rates at 30 °C/20 °C day/night temperatures. These figures were obtained in continuous light, continuous dark and for light/dark alterations (Winkworth, 1971). Germination is influenced by substrate, with the highest germination rates in potting mix, followed by clay followed by paper towelling in study of germination in these three substrates (Bhattarai et al., 2008).

Buffel grass appears to perform particularly well at elevated CO_2 levels and it demonstrates increased biomass, plant height, leaf length, leaf width and improved overall growth performance, as is usual for tropical C4 grasses (Bhatt et al., 2007). CO_2 uptake and water use efficiency of the plant, are greatest at day/night air temperatures 30/20 °C and decrease at higher temperatures until death at 45/35 °C day/night temperatures (De La Barrera and Castellanos, 2007). The optimum temperature for photosynthesis is 35 °C (Tix, 2000). The species is drought resistant (Phillips, 1931) and does not tolerate extended periods of flooding or subfreezing temperatures (2008, Lazarides et al., 1997). Buffel grass can tolerate soils with low levels of nutrients. However, it does show increased water use efficiency (WUE), crude protein and dry forage yields with increased nitrogen (Patidar et al., 2008) and widened shoot/root ratio with increased phosphorus (Christie, 1974; Humphreys, 1967). Buffel grass has a moderate salt tolerance: the varieties Americana and Biloela have higher salt tolerance than other cultivars (Griffa et al., 2010).

5. Adaptations and environmental constraints in arid ecosystems

C4 grasses, such as Buffel grass, typically dominate tropical savannas, a biome characterised by a summer growing season (when high temperatures coincide with high rainfall), open-canopies, and dense grassy understoreys that fuel frequent fires. By contrast, arid and semi-arid ecosystems are characterised by low, erratic and infrequent rainfall events, high evapo-transpiration rates and sparse vegetation due to insufficient soil moisture to promote seedling emergence and further plant growth (Reynolds et al., 2004). Consequently, arid systems are relatively resistant to alien invasions (Usher, 1988). Yet, Buffel grass thrives in them.

Buffel grass demonstrates several qualities that make it uniquely suited to survive harsh arid conditions. These include the accumulation of carbohydrates at the base of its stems for slow release when needed, a deep root system (up to 2.5 m in deep soils) (Halvorson, 2003) that enables it to access water supplies faster and for longer than most native herbs and forbs, as well as extended seed longevity and opportunistic germination (Centre for Arid Zone Research, 2001; Sharif-Zadeh and Murdoch, 2001; Winkworth, 1971). Additionally, arid environments may present Buffel grass with less competition, disease and predation. For example, in most cases, anecdotal evidence indicates that Buffel grass, by virtue of its presence, outcompetes native plants for water, light and nutrients. However, it can struggle for dominance against other exotic grasses of similar provenances such as the such as Parthenium weed (*Parthenium hysterophorus*), native to subtropical North and South America (Nsw Department of Primary Industries, 2004). Furthermore, in arid climates, Buffel grass may be less affected by tropical diseases including Buffel Blight (*Magnaporte grisea*), Ergot, Smut, Rust, and Blast and the Paralid moth, which help to suppress the species in the tropics (Food and Agriculture Organization of the United Nations, 2011; Nsw Department of Primary Industries, 2004; Qld Primary Industries and Fisheries, 2010).

A recent study identified effective rainfall and rainfall seasonality as the most significant factors influencing the distribution of savannas at a global scale (Lehmann et al., 2011). At a regional scale, the researchers explore how topography, soils and disturbance interact with rainfall to impact woody vegetation growth and fire frequency, which reduce and promote the growth of C4 grasses, respectively. They conclude that woody vegetation growth should be considered as a potential surrogate for identifying the potential limits of the savanna biome (Lehmann et al., 2011).

Here, we review the factors that promote and constrain the geographic extent of Buffel grass distribution. We report on the four factors identified as key distribution determinants of C4 grasses worldwide: climate, edaphic characteristics, topography and fire/disturbance. We acknowledge that due to large intra-species variation there may be some differences in apparent environmental tolerances of the grass; however our discussion refers to the species as a whole. Specific climate and landscape features that are reported to influence Buffel grass distribution are summarised in Table 4.

5.1. Climate

Buffel grass occupies a diverse range of climates. It can tolerate extremely high temperatures approaching 50 °C (De La Barrera and Castellanos, 2007), but it will not establish where the mean annual minimum drops to below 5 °C (Cox et al., 1988). It tolerates wide ranging annual rainfall averages, establishing in regions that receive anywhere from less than 250 mm to 2670 mm of rainfall, annually (Nsw Department of Primary Industries, 2004; Tix, 2000). Temperature appears to be a stronger limiting factor to the species global extent than annual average rainfall. However, it has been observed that episodic advances in invasion fronts typically follow early summer rainfall events (Friedel et al., 2006; Mnif and Chaieb, 2010).

Rainfall seasonality is a key factor influencing the distribution of the savanna biome worldwide (Lehmann et al., 2011). Savanna, categorised as a habitat with a C4 grass layer, such as Buffel grass, shows the greatest response to summer rainfall. In sub-tropical parts of Queensland, Australia, for example, Buffel grass is primarily sown in areas where 60% of annual rainfall reliably occurs during the summer months. However, rainfall seasonality is linked to the probability of drought, tree survival, woody vegetation growth rates and thus the probability of disturbance; therefore its

Table 4
Summary of the landscape features that may influence Buffel grass distribution.

Environmental factor		Location, climate	Comment	Reference
Climate	Temperature	Semi-arid Queensland, Australia	30 degrees Celsius optimum in the region for Buffel grass growth	(Christie, 1975)
		Kenya, Southern Africa, Southern Texas, Mexico, and Australia	Survives at minimum annual average temperatures of between 5 and 25 °C	(Cox et al., 1988)
	Rainfall	Central Australia	Buffel grass abundance higher after summer rains than winter rains	(Clarke et al., 2005)
		Mexico	Predicted distribution is between 0–800 mm annual rainfall	(Arriaga et al., 2004)
		Kenya, Southern Africa, Southern Texas, Mexico, and Australia	0–800 mm annual rainfall	(Cox et al., 1988)
	Illuminance	Semi-arid Queensland, Australia	Small effect on the growth of Buffel grass	(Christie, 1975)
Geology and soils	Soil texture and fertility – increased phosphorus and Ph		Affects the efficacy of Buffel grass spread into adjacent ecosystems	(Eyre et al., 2009)
	Phosphorus	Central Australia	High P levels results in high Buffel grass growth	(Christie, 1975; Humphreys, 1967; Winkworth, 1964)
	Soil water potential	Semi-arid Queensland, Australia		(Christie, 1975)
	Soil mineral deficiency	Central Australia	May be a limiting factor	(Winkworth, 1964)
	Soil type	Arizona, USA and Sonora, Mexico	Buffel grass appears to grow mainly on soils derived from volcanc, gneissic and limestone where chemistry and mineralogy vary greatly	(Van Devender and Dimmitt, 2006)
	Soil texture	Kenya, Southern Africa, Southern Texas, Mexico, and Australia	Buffel grass persists well in well drained loam, sandy loam, clay loam and sandy clay loam soils, and will lose vigor and die when established in silt, silt loam, silty clay loam, silt clay and clay soils	(Cox et al., 1988; Humphreys, 1967; Van Devender and Dimmitt, 2006)
Topography, land systems and vegetation associations	Woody vegetation	Poplar box community, Queensland, Australia	Higher retained vegetation, lower Buffel grass, suggested as result of propagule pressure, competitive capacity of BG	(Eyre et al., 2009)
	Leaf litter	Queensland Eucalypt woodlands, Australia	Higher leaf litter, lower BG	
	Ground cover		Buffel grass readily colonises	
	Modified landscapes	Central Australia	Buffel grass can be observed more frequently and at higher densities in modified landscapes	
	Vegetation type	Mexico	Desert scrub most at risk of invasion, followed by Mesquite woodlands, Abandonded agricultural land and Tropical deciduous forests	(Arriaga et al., 2004)
	Elevation		Potential distribution ranges from sea level to 900 m ASL.	
	Aspect	Arizona, USA and Sonora, Mexico	Hillside concentrations of Buffel grass are typically found on steeper south, wouth eash and south west slope aspects	(Van Devender and Dimmitt, 2006)
	Slope	North eastern Sonora	Correlated with slopes of 14-19 degrees on relict clay soils	
	Creek lines (red gum)	Central Australia	50 samples, 72% Buffel grass	(Clarke et al., 2005)
	Creek lines (tea tree)		75 samples, 81% Buffel grass	
	Saline alluvial flats		100 samples, 63% Buffel grass	
	Iron wood alluvial flats		250 samples 62% Buffel grass	
	Mulga rises		124 samples, 22% Buffel grass	
	Drainage systems, alluvial plains	Central Australia arid climate		(Eyre et al., 2009)
Disturbance Zones	Stocking routes and grazed sites	Queensland Eucalypt woodlands, Australia	Highest mean Buffel grass cover on stocking routes, compared to national parks and state forest where it is not detected Higher Buffel grass cover where grazing occurs	(Eyre et al., 2009)

Table 4 (*continued*)

Environmental factor		Location, climate	Comment	Reference
	Burnt sites	Queensland Eucalypt woodlands, Australia	Buffel grass abundance highest on site that experience "low intensity fire" as compared to "high intensity fire" or no fire.	
	General	Mexico	Disturbance increases the chances of Buffel grass colonising a site and becoming invasive	(Arriaga et al., 2004)
	Roads and highways	Arizona, USA and Sonora, Mexico	Buffel grass range expands along major freeways, especially on those that have been repeatedly bladed	(Van Devender and Dimmitt, 2006)

influence on Buffel grass distribution should not be considered in isolation from these factors.

Aside from rainfall seasonality, another limiting factor is effective rainfall (Lehmann et al., 2011). Effective rainfall is the amount of rainfall available for plant uptake, and is influenced by a range of factors such as temperature, soil and topography. Effective rainfall is particularly important where rainfall is infrequent or erratic, such as in arid environments (Lehmann et al., 2011).

5.2. *Edaphic characteristics*

Buffel grass grows on a wide range of soil types but long term persistence appears to be dependent on specific textural types (Cox et al., 1988). For instance, seedlings emerge in sandy, silty and clayey soils, but emergence declines as either sand, silt or clay content approach 100% (Cox et al., 1988). Meanwhile, they gradually lose vigour and die when established in silt, silt loam, silty clay loam, silt clay and clay soils (Cox et al., 1988). It persists in well drained loam, sandy loam, clay loam and sandy clay loam soils and actively spreads by seed in north west Australia in sandy loam soils (Humphreys, 1967). The grass prefers sandy and sandy loam soils (Centre for Arid Zone Research, 2001; Van Devender and Dimmitt, 2006) but will colonise loam soils, provided it experiences approximately 90 days growth in the summer and relatively warm, dry winters (Cox et al., 1988).

The importance of soil texture on plant growth is typically linked to the capacity of the soil to retain moisture (Reynolds et al., 2004). Several Buffel cultivars have been developed to withstand flooding, and thus are more likely to be able to establish on heavier soils which retain moisture. In dry areas Buffel grass will adapt to heavy clay soils that become too water-logged in tropical regions (Cameron, 2004). It is generally slow to establish on black cracking clay, but does well once established (Food and Agriculture Organization of the United Nations, 2011). More rhizomatous varieties are believed to show superior adaptation to heavier soils (Humphreys, 1967).

In the Sonoran Desert of Mexico, Buffel grass distribution is limited to a few well defined geomorphic settings (Van Devender and Dimmitt, 2006). It occurs on soils derived from volcanic deposits (rhyolite and basalt), gneiss (granite) and limestone, where soil chemistry and mineralogy vary greatly, thus its distribution does not relate in any simple way with standard soil types (Van Devender and Dimmitt, 2006). The species preference for soils derived from volcanic deposits is also observed in the MacDonnell Ranges of central Australia where Buffel grass readily grows on granitic geomorphic settings and is absent from adjacent quartzite and sandstones (Pers. Comm., Peter Latz). In southern Queensland soils most suitable for Buffel grass establishment include red earths with friable surface (ironbark and poplar box country), Lighter Brigalow and Brigalow /Belah clays, sandy soils with moderate phosphorus (river frontage sands and some Cypress pine country), as well as, soil once under gidgee or softwood scrub (Cavaye, 1991). The observation that Buffel grass growth is strong on red earths (Cavaye 1991) should be noted with caution, for in central Australia, Buffel grass only grows on red earths in localised depressions (Pers. Comm., Peter Latz).

The species can establish on soils of low fertility, provided nitrogen and phosphorus are sufficient (Bhati and Mathur, 1984). Several studies illustrate that high levels of phosphorus in particular results in greater Buffel grass yield (Humphreys, 1967; Winkworth, 1964). The importance of soil fertility may vary with respect to rainfall (Lehmann et al., 2011), and in arid locations soil of high fertility may be especially important for Buffel grass to establish. Buffel grass is intolerant of high levels of available soil aluminium and manganese (Cook, 2007). According to a study conducted in Tanzania, the seed spreads well in soils with a soil pH ranging from 7–8 (Cook, 2007).

5.3. *Topography, land systems and vegetation associations*

Buffel grass distribution can range from sea level to 2000 m in altitude (Global Biodiversity Information Facility, 2011). At a local scale, the grass tends to establish in natural depressions across the landscape. This is particularly true in arid environments, as depressions provide a moist environment for establishment as well as protection from grazing (Johnson, 2010). In arid Australia, Buffel grass often displays strongest growth along creek lines and embankments (Centre for Arid Zone Research, 2001). This is consistent with global observations that river systems are a major means for the spread of weeds (Johansson et al., 1996).

On the Plains of Sonora the species exists in large areas that are flat and also up adjacent slopes. On slopes the distribution is tightly correlated to slope angles of 14–19 degrees with relict clay soils, and can be absent from nearby slopes with different conditions of percent to rock cover, depth to hardpan and slope angle (Van Devender and Dimmitt, 2006). The grass is less common on gently sloping bajadas of Sonora where it tends to clump in the shade of trees, larger shrubs and prickly pears (Van Devender and Dimmitt, 2006). Conversely, at a broad scale, C4 species tend to flourish in open environments where ample light is available, and are physiologically incapable of dominating closed-canopy ecosystems (Sage and Kubien, 2003).

In the MacDonnell Ranges of central Australia Buffel grass is prevalent on the low-lying, rich soils of the alluvial plains beneath ironwood and fork-leaved corkwood trees. It can also be seen growing throughout rocky granitic hills, beneath *Acacia* open woodlands, yet it can be completely absent from adjacent outcrops of alkaline dolomite or amphibolites that support hummock grassland communities of native C4 grass, *Triodia* (Pers. Comm., Peter Latz).

5.4. Fire and other disturbances

Disturbance has long been recognised as a facilitator for the spread of invasive species (Lonsdale, 1999). Disturbance, causing soil surfaces to loosen, may be natural or anthropogenic in nature. Commonly, anthropogenic causes include human road and foot traffic. For instance, Buffel grass often establishes along disturbed rights of way such as highways and larger paved roads that have been repeatedly bladed (Van Devender and Dimmitt, 2006). Natural disturbances may relate to occurrences such as the upturn of sediments along watercourses, wildfire and the movement of animals, reptiles or birds. Establishment of the species has been associated with burrowing animals such as endangered Australian marsupial, the Northern Hairy-nosed Wombat (*Lasiorhinus kreftii*), and the European Rabbit (*Oryctolagus cuniculus*), which is a significant pest in arid regions of Australia (Department of the Environment, 2009).

Perhaps the most damaging act of disturbance is fire. Buffel grass produces a high fuel load that supports more frequent and intense fires than arid landscapes are otherwise likely to be exposed to (D'antonio and Vitousek, 1992). It is often first to remerge on ash beds, hence forming a positive feedback loop which favours its own regeneration, and modifies the invaded system irreversibly (Miller et al., 2010). There are several physiological characteristics of Buffel grass that enable it to respond so quickly to fire and rain, including a deep penetrating root system, and a long lifespan of individual tussocks, which mean that it can re-sprout from established tussocks following fire. There is some evidence to suggest that the more severe the fire, the more rapid the post-fire recovery of above ground biomass (Miller et al., 2010), with one study suggesting that Buffel grass cover doubles after fire (Butler and Fairfax, 2003). The degree of disturbance necessary for establishment may be closely linked to the competitive situation of the surrounding flora (Humphreys, 1967). Fire immediately reduces competition with surrounding vegetation, and hinders recruitment of juvenile woody vegetation, preventing future recovery of the landscape and making it more vulnerable to rapid colonisation by fast growing species such as Buffel grass. Fire also temporarily increases available phosphorus in the soil (Bennett et al., 2003) which Buffel grass may be able to rapidly exploit (Miller et al., 2010).

We have observed that once established, it may not require disturbance to spread and consider that rhizomes may be an agent for this, though further research is required to confirm this.

6. Impacts on ecosystem function and biodiversity

Invasive species are recognised as the primary cause of global biodiversity loss, homogenising the world's flora and fauna (Ustin et al., 2002). Grass invasions can be particularly devastating, impacting ecological organisation of populations to ecosystems, and in their aggregate may be sufficiently widespread to alter global aspects of ecosystem function (D'antonio and Vitousek, 1992). Buffel grass is no exception.

Buffel grass invasion can devastate local ecosystems by altering wildfire regimes, soil erosion rates, ground surface temperatures and supply of vital resources to surrounding life forms, compromising biodiversity (D'antonio and Vitousek, 1992). Significant invasions have been reported in arid communities throughout Australia, the USA, Mexico and South America and many species and ecosystem functions have been impacted (Table 5).

Several studies illustrate a negative relationship between Buffel grass occurrence and general species richness (Bestelmeyer and Schooley, 1999; Blanco et al., 2005; Clarke et al., 2005; Collins and Glenn, 1991; Fairfax and Fensham, 2000; Flanders et al., 2006; Franklin et al., 2006; Hannah et al., 2007; Jackson, 2005; Janice, 2005). Clarke et al. (2005) conducted an important investigation into the long term changes in semi-arid vegetation of central Australia, which demonstrated that Buffel grass had a more significant impact on herbaceous species richness than rainfall variability.

Flora and fauna impacted by Buffel grass are summarised in Table 5. Most of these examples are reported in grey literature and further research is needed in order to conclusively link Buffel grass to loss of particular species. Included in the list are keystone species the Saguaro Cactus (Schiermeier, 2005) and the River Red Gum (Centre for Arid Zone Research, 2001) which characterise the deserts of Arizona and Australia, respectively. Species such as the Saguaro Cactus, the River Red Gum and other woody perennials do not withstand repeated fires as they have slow juvenile recruitment compared with Buffel grass.

Buffel grass produces large volumes of standing dead matter which burns hotter and faster than most grasses native to Australia and the Americas (D'antonio and Vitousek, 1992; Martin-R et al., 1999; Schiermeier, 2005; Smyth et al., 2009). The result is increased wildfire frequency and intensity in ecosystems not adapted to fire. Additionally, it regenerates quicker than many natives on ash beds, creating a positive feedback loop that favours Buffel grass regeneration (D'antonio and Vitousek, 1992; Miller et al., 2010). An alarming aspect of Buffel grass invasions is that they can occur quite suddenly. Areas apparently devoid of Buffel grass may be rapidly dominated by the species following the rains that trail a period of prolonged drought or fire, with this dominance often maintained for decades (Clarke et al., 2005).

The impact of Buffel grass on arid ecosystem function is significant. This is because creek lines typically act as a blockade to the spread of fire, even when dry, because the soils lining the creek do not support the growth of dense, fire-fuelling grasses. Anecdotal evidence indicates that Buffel grass thrives along creek lines in dry environments (Miller et al., 2010). Thus, a feature that should prevent the spread of fire can transport it, effectively acting as the "wick for the fire" (Humphries et al., 1992 as cited in D'antonio and Vitousek, 1992) and the fear, however sensationalised, is that Buffel grass will transform arid environments such as the Sonora Desert into African-style savannas.

The overall impact of Buffel grass invasions on biodiversity is not fully known, although it is likely that we are seeing only the beginning of its potential to encroach into new ecosystems. The extent of Buffel grass invasions will continue to expand until new equilibriums have been reached within invaded ecosystems (Dullinger et al., 2009).

6.1. Is Buffel grass a true "invader"?

The apparent dependence of Buffel grass establishment on disturbed soil surfaces makes its ecological label as an "invader" controversial. Invasive species are considered such when they can successfully establish, become naturalised and spread to new natural habitats apparently without further assistance from humans and are generally new introductions into an eco-region (Radosevich et al., 2007). So, the question becomes whether Buffel grass could expand its range without human disturbance. One example that suggests it cannot is that of the Centro Ecologico de Sonora housing development in Mexico. Environmental conditions in the region are and always were suitable for Buffel grass, yet establishment in the area was triggered only by major disturbances caused during the development of the new housing project (De La Barrera, 2008). Mcivor (2003) also attempted to answer our question, and concluded that while Buffel grass is able to colonise bare areas it is not able to invade dense vegetation suggesting it is not invasive (Mcivor, 2003). Whether Buffel grass behaves as a *true* invader appears to depend on

Table 5
Flora and fauna impacted by the introduction of Buffel grass to their native habitats.

Species/community; location	Observed impact of Buffel grass invasion on named species	Reference
River Red Gum (*Eucalyptus camaldulensis Dehnh*); Australia	BG growing in creek lines where River Red Gums are found – withstands hot fires in winter and spring that RRG may not recover from	(Centre for Arid Zone Research, 2001)
Mulga (*Acacia aneura*); Australia	More frequent wildfires, reducing numbers in just decades	
Northern Hairy-nosed wombat (*Lasiorhinus krefftii*); Queensland, Australia	Disturbed soils around burrow promote/facilitate Buffel grass establishment displacing native grasses and forcing the burrow occupant to travel further to feed	(Centre for Arid Zone Research, 2001; Friedel et al., 2007)
Pili grass (*Heteropogon contortus*); Hawaii, USA	One of several non-indigenous grasses displacing Pili grass in most dry, leeward habitats of the Hawaiian Islands	(Daehler and Goergen, 2005)
Various endemic species; Australia	Buffel grass is displacing native species from mesic islands in arid ecosystems	
Species richness	Declines in the presence of Buffel grass	(Butler and Fairfax, 2003, Clarke et al., 2005, Jackson, 2005)
Ground dwelling bird guilds and "hot climate specialist" ants; central Australia	Composition of guilds/community groups varies	(Smyth et al., 2009)
Various reptiles; Queensland, Australia	Both increaser and decreaser responses to Buffel grass presence	(Eyre et al., 2009)
Forbs; Queensland, Australia	Minimally effected by Buffel grass, but may be due to low rainfall at time of experiment	
Various native grasses, Australia	Winter growth is reduced when competing with Buffel grass	(Clarke et al., 2005; Eyre et al., 2009)
Various herbaceous species; Australia	Buffel grass leachates shown to reduce seed germination of various Australian herbaceous species under laboratory conditions	(Eyre et al., 2009)
Forbs (*Cyperus* gracilis, and *Radscondons*), Australia	10% less abundant in Buffel grass pasture	
Many-headed Wiregrass (*Aristida caput-medusae*), Slender Chloris (*Chloris divaricata*), Fairy grass (*Sporobulus caroli*)	Increaser response to Buffel grass infestation	
Cryptoblephaus pannous	Decreaser response to Buffel grass infestation	
Trees, Peachwood shrub, False Sandlewood (*Eremophila mitchellii*); *Australia*	Following exposure to Buffel grass fuelled fire Tree canopy shows recovery in the form of epocormic shoots, Peachwood resprouts but does not fare so well as neighbouring trees, False Sandlewood did not re sprout	(Butler and Fairfax, 2003)
Shortlived forbes, suffruticose shrubs	More abundant when Buffel grass is present	(Clarke et al., 2005)
Woody layer	Negatively affected by Buffel grass fuelled fires	(Clarke et al., 2005)
Desert tortoise (*Gopherus agassizii*) and Mule deer (*Odocoileus hemionus*); Sonoran Desert Ecoregion	Habitat is threatened by Buffel grass fuelled fires	(Arizona-Sonora Desert Museum Staff and Volunteers, 2008)
Giant Saguaro Cactus (*Carnegiea gigantea*); Arizona and Texas, USA and Mexico	Species devastated by Buffel grass fuelled fires, and competition for water	(Schiermeier, 2005, Arizona-Sonora Desert Museum Staff and Volunteers, 2008)
Cactus ferruginous pygmy owl (*Glaucidium brasilianum cactorum*); Arizona, USA	Threatened as a result of Buffel grass fuelled fires devastating cacti in which the pygmy owl lives	(Defenders of Wildlife, 2010)
Columnar cactus (Pachycereus pectin-aboriginum); Sonora, Mexico	Growth examined in thorn scrub and in Buffel grass pastures – no significant effect on plant abundance but a major difference on size distribution. All seedlings that emerged on pasture died within one year. Data shows that adult populations persist but cannot replace and will face local extinction	(Morales-Romero and Molina-Freaner, 2008)

different environmental factors. In Australia, Buffel grass displays the characteristics of both invaders and colonisers; in the tropical north of the Northern Territory (the "Top End") Buffel grass spreads from sown pastures either slowly or not at all. Conversely, in central Australia and western Queensland it spreads readily (Cameron, 2004). This may relate to the nature of soil surfaces or soil type; Top End soils form a crust following rain that prevents seedlings from establishing, while soils of the arid inlands possess the crumbly/ loose surfaces required for Buffel grass establishment (Cameron, 2004).

Overall, there is consensus in the literature that disturbances facilitate the establishment of the species and human are a frequent cause of disturbances. However, there is little evidence from the literature that human disturbances are necessary to facilitate spread at broad scales and once established, anecdotal evidence indicates that the species can often invade into adjacent areas unaided.

7. Management

Management of Buffel grass throughout invaded environments is crucial to conserve natural ecosystem structure, composition and function. Due to the many benefits of its cultivation, eradication of Buffel is not desired, nor is it likely that it could be achieved due to the extent of invasion. Therefore, control of invasions is conducted a local scale. At present, there are several options for control of Buffel grass in infested land systems, including the application of herbicides, manual removal, prescribed burning and controlled animal grazing. Chemical controls can be effective, but application must be strategically timed to coincide with the species' period of peak growth (Arizona-Sonora Desert Museum Staff and Volunteers, 2008; Daehler and Goergen, 2005; Dixon et al., 2002; Johnson and Kendall, 2008). Manual methods of control are costly, time consuming and therefore restricted to local removal efforts. To be effective, the entire plant must be removed; mowing is not effective. Prescribed burning followed by the application of herbicides and sowing of native grasses has been highly effective at suppressing Buffel grass while promoting the regeneration of native flora (Daehler and Goergen, 2005). Additionally, while not the desired control mechanism from an environmental point of view, grazing can be effective at controlling the spread of Buffel grass (Pers. Comm. Peter Latz). Of course, economic and ecological analysis of the process of eradicating or controlling invasive species indicates that the most cost-effective and least environmentally damaging method is spread *prevention*.

8. Conclusions

Buffel grass (*Cenchrus ciliaris* L.) is grown widely in tropical and sub-tropical arid rangelands around the globe because of its high drought tolerance and capacity to withstand heavy grazing. However, in certain situations, particularly in arid to semi-arid environments, Buffel grass has the ability to rapidly invade the surrounding environment. Consequences of invasion can be significant as Buffel grass alters wildfire regimes and displaces native flora and fauna. Effective, strategic control of Buffel grass invasions requires knowledge of regions infested with or vulnerable to invasion, as well as a willingness of the community to be involved in its control.

At a global scale, temperature emerges as the primary factor restricting spread, with the species not surviving at average monthly temperatures below 5 °C (Cox et al., 1988). Rainfall seasonality and effective rainfall are influential, and a consistent summer rainy season is particularly important for growth. However, these factors can not be considered in isolation from variables such as vegetation and topography. Seedling emergence is reliant on soil disturbance. Consequently, the species regional distribution is likely to coincide with disturbed environments such as creek lines and roadsides. Soil texture influences germination rates and establishment. Once established it may be less selective with regard to soils. Successful population establishment may depend on appropriate soil moisture, soil texture, phosphorus/ nitrogen availability, topography and sun exposure. Phosphorus deficiency in soils is a particularly strong barrier to establishment in arid locations.

Arid and semi-arid environments are particularly prone to Buffel grass invasion and do not tolerate the increased frequency and intensity of wildfires that accompany increased biomass of the grass. Buffel grass fuelled fires are believed to be responsible for declining numbers of characteristic arid zone plants, the Saguaro Cactus (Arizona, USA) and River Red Gum (Australia). Arid landscapes worldwide stand out as requiring urgent control of Buffel grass.

Effective control of Buffel grass populations will require global action at local and regional scales. This paper has highlighted the morphological characteristics, environmental tolerances and biodiversity impacts of Buffel grass to facilitate predictive habitat modelling and identification of regions requiring urgent control as well as raise concern for control of this invasive weed.

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