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Alien plant invasions in tropical and sub-tropical savannas: patterns, processes and prospects

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Abstract Biological invasions affect virtually all ecosystems on earth, but the degree to which different regions and biomes are invaded, and the quality of information from different regions, varies greatly. A large body of literature exists on the invasion of savannas in the Neotropics and northern Australia where invasive plants, especially African grasses, have had major impacts. Less has been published on

plant invasions in African savannas, except for those in South Africa. Negative impacts due to plant invasions in African savannas appear to be less severe than in other regions at present. As savannas cover about 60% of the continent, with tens of millions of people relying on the services they provide, it is timely to assess the current status of invasions as a threat to these ecosystems. We reviewed the literature, contrasting the African situation with that of Neotropical and Australian savannas. A number of drivers and explanatory factors of plant invasions in savannas have been described, mostly from the Neotropics and Australia. These include herbivore presence, residence time, intentional introductions for pasture improvements, fire regimes, the physiology of the introduced species, and anthropogenic disturbance. After comparing these drivers across the three regions, we suggest that the lower extent of alien plant invasions in African savannas is largely attributable to: (1) significantly lower rates of intentional plant introductions and widespread plantings (until recently); (2) the role of large mammalian herbivores in these ecosystems; (3) historical and biogeographical issues relating to the regions of origin of introduced species; and (4) the adaptation of African systems to fire. We discuss how changing conditions in the three regions are likely to affect plant invasions in the future.

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Introduction

Savannas form one of the world's largest biomes and are the dominant vegetation type in Africa (Scholes 1997), occupying about 65% of the continent (Huntley and Walker 1982). About a fifth of the global human population and a large proportion of the world's ungulates (wild and livestock) are found in savannas (Lehmann et al. 2009). A wealth of knowledge now exists on the composition and function of savannas, particularly in Africa (see Sinclair and Norton-Griffiths 1979; Huntley and Walker 1982; Bourlière and Hadley 1983; Cole 1986; Werner 1991; Scholes and Walker 1993; Sinclair and Arcese 1995; Solbrig et al. 1996; Cowling et al. 1997; Coe et al. 1999; du Toit et al. 2003; Sankaran et al. 2005, 2008; Furley 2006; Shorrocks 2007; Sinclair et al. 2008). This includes a growing understanding of the inherent complexity of savanna systems, and the extent that savannas depend on complex interactions of climatic and edaphic factors, and disturbance from both fire and herbivory (Sankaran et al. 2005, 2008). Globally, the tropical savannas are the second largest biome, extending over 15×10^6 km² (Long et al. 1989; Melillo et al. 1993).

Savannas are defined as a tropical vegetation type co-dominated by a largely continuous layer of grasses (generally below 2 m) and a discontinuous woody tree layer (Bourlière and Hadley 1983; Scholes 1997; Scholes and Archer 1997). A common feature of all savannas is the hot wet season and warm dry season (Scholes 1997), an usually high fire frequency (Huntley 1982; Scholes 1997), and high habitat heterogeneity (Pickett et al. 2003; Rogers 2003; Tongway and Ludwig 2005). Savannas vary spatially in composition and function across a number of scales (Bourlière and Hadley 1983). For example, there is high variation along soil gradients and associated vegetation at the scale of catenas, or across a variety of sub-savanna type habitats in the sub-Saharan region (see Fig. 1.9 in Shorrocks 2007). Within this spatial arrangement, savannas vary structurally, from a short grass layer with tall trees, to savannas with a range of shrub and tree sizes in between (e.g. Pivello et al. 1999a). Temporally, savannas and grasslands have varied in extent and distribution, from glacial/interglacial cycles (Dupont et al. 2000) to the last few hundred years (Gillson 2004).

Many millions of people depend on savannas for their livelihoods, leading to a wide range of land uses, such as agriculture, grazing and agroforestry, including fuel wood harvesting (Huntley 1982; Scholes 1997; van Wilgen et al. 2001). Therefore savannas are subject to many kinds of anthropogenic disturbances, as well as periodic natural disturbances (fire, drought, floods, mega-herbivores; Walker and Noy-Meir 1982; Scholes 1997). Anthropogenic disturbances create habitats and conditions suitable for invasions by alien plants, thus forming multiple sources for further invasions into savanna systems (van Wilgen et al. 2001). The Millennium Ecosystem Assessment (2005) assessed the past and current impact of five drivers of ecosystem change for a range of biomes. For the tropical grassland and savanna biome, invasive species were regarded to have had a relatively low impact over the last century, but a trend of very rapid increase of the impact for this biome was noted. The current low incidence and influence of invasive plants in savannas relative to some other terrestrial biomes may be related to the fact that disturbance, which generally favours invasions, is fundamental to savanna functioning. Savannas are generally resilient to changes in disturbance regimes (Walker and Noy-Meir 1982; Harrison and Shackleton 1999), possibly making them relatively resistant to biological invasions. Habitat modification has had a high impact and is increasing in importance; climate change has had a moderate but very rapidly increasing impact; over-exploitation a very high and continuing impact; and pollution a moderate but very rapidly increasing impact in these biomes (Millennium Ecosystem Assessment 2005). Although invasive species are not currently the main threat to the conservation of biodiversity and functioning of tropical grasslands and savannas, they may well become much more widespread and influential in the future. Therefore, it seems prudent to review the current status of plant invasions in the savanna biome.

Aims of the review and delimitation of terms

This paper collates available literature on plant invasions in savannas, with an emphasis on those in Africa and compares the situation in this region with savanna systems elsewhere. As there is no

over-arching global classification system for savannas (Scholes 1997), we contrast the situation in the African, Australian and Neo-tropical savannas using the broad definition of savanna (as described above). Finer scale classification systems are based on factors such as nutrient and moisture gradients and are frequently regionally specific (see Table 1 for definitions of various savanna systems). For example, in southern Africa, nutrient-rich, arid regions give rise to the fine-leaved (nanophyllous) savanna, while the nutrient poor, moister regions give rise to the broadleaved (mesophyllous) savannas (Scholes 1997 and Table 1). Although there may be differences in the presence of alien plants found in the different savanna types (for example in the fine-leaved or broadleaved savannas), the scale of this review and the dearth of information from the different regions precludes such fine-scale assessment at this stage. However, as this is the first assessment of alien plants in tropical savannas globally, the elucidation of broad patterns should be instructive.

To describe the levels of invasion of alien species invasions in savannas, we use the terms proposed by Richardson et al. (2000) and Pyšek et al. (2004). These include a range of terms which denote the status of introduced species at stages along the “naturalization-invasion continuum” (Pyšek and Richardson 2006), according to which species may be termed casual, naturalized, or invasive by invoking biogeographical criteria. Of most concern are *transformer* species, defined as a subset of invasive plants which change the character, condition, form, or nature of ecosystems over a substantial area relative to the extent of that ecosystem (Richardson et al. 2000).

In savannas, the terms “invasion” and ‘bush encroachment’ are sometimes used interchangeably. Bush encroachment involves the increase in abundance and density of native woody plant species (Archer et al. 1995; Hoffmann and Todd 2000; Roques et al. 2001; Asner et al. 2003; Wigley et al. 2009). This phenomenon has often been related to poor land management practices such as overgrazing by domestic livestock (Walker et al. 1981), changes in land-use (Bond 2008), and increased CO₂ levels leading to tree encroachment and thickening in grass-dominated systems (Bond and Midgley 2000; Bond 2008). In this review we focus on invasions by alien (non-native) species (see Pyšek et al. 2004 for definition) and do not deal with bush encroachment,

where native woody species encroach to form dense, often monodominant, stands (for details on this phenomenon in North America, see Van Auken 2000).

It is also important to make a clear distinction between true savannas and artificial grasslands (pastures) in some cases when assessing plant invasions. For example, in Mexico artificial grasslands and natural savannas, from both tropical and temperate areas are usually lumped into a single category (pastizal). However, usually only artificial grasslands, created in places originally covered by woody vegetation, are heavily invaded by alien species (López-Olmedo et al. 2007).

Alien plant invasions in African savannas

The sparse information available in the literature on plant invasions in Africa suggests that invasions are not a major problem in these ecosystems (e.g. D’Antonio and Vitousek 1992). However, Henderson and Wells (1986) list 583 species of naturalised alien plants for tropical savannas in southern Africa, stating that 151 are known to be particularly aggressive invaders generally. More recently, 48 species were considered “prominent invaders” in the savanna biome of South Africa (Henderson 2007). *Lantana camara* L. was the most prominent species, followed by *Chromolaena odorata* (L.) R.M. King & H. Rob. and *Melia azedarach* L. The remaining of the top ten invasive species were, in order, *Solanum mauritianum* Scop., *Acacia mearnsii* De Wild., *Opuntia ficus-indica* (L.) Miller, *Ricinus communis* L., *Psidium guajava* L. and *Jacaranda mimosifolia* D. Don. However, of this list most species are usually only found along rivers flowing through savannas and are therefore not invaders of true savanna ecosystems. Some species definitely do invade savannas in South Africa: *Chromolaena odorata* in Hluluwe-Imfolozi (Macdonald 1983), *Opuntia stricta* in Kruger National Park (Fig. 1b; Foxcroft et al. 2004; Foxcroft and Rejmánek 2007), and *Prosopis* spp., *Schinus molle* and several other alien trees and shrubs in arid savanna around Kimberley (Milton et al. 2007). While most alien plant species that are currently invasive in South Africa arrived in the region in the 1800s, the invasion of grassland and savanna biomes by *O. ficus-indica* dates back to the 1770s (Henderson

Table 1 A typology of commonly used savanna related terminology

Term	Geographical distribution	Meaning
Cerrado	Brazil	The Brazilian cerrados comprise a gradient from the grassland form (named ‘campo limpo’) to a sclerophyllous woodland form (named ‘cerradão’), where the herbaceous layer gives place to arboreal elements, and the most apparent variation is in tree density and height. The intermediate ecotonal scrub forms are: ‘campo sujo’, ‘campo cerrado’ and ‘cerrado sensu stricto’, in an increasing density of trees. In cerradão, the canopy cover is ~30–60%; in cerrado sensu stricto ~30–40%; in campo cerrado, ~10%; in campo sujo, up to 1%, and there is no tree cover in campo limpo (Eiten 1972, 1983; Coutinho 1978, 1982 as in Pivello et al. 1999a; Huber and Riina 2003)
Caatinga	Brazil	Caatinga is found in northeastern Brazil and has a characteristic semiarid climate with average precipitation of 800 mm/annum. The vegetation is largely xerophytic, spiny and caducifoliate (Cavalcante and Major 2006). The term Caatinga is means “white forest”, and is often referred to as dry or scrub forest
Llanos	Colombia and Venezuela	Los Llanos (meaning the flat plains) is a vast tropical grassland plain situated at the east of the Andes in north-western South America. Because of infertile sandy soils and regular flooding, this area represents anomalously low plant species richness in the tropics (Barthlott et al. 1996; Huber and Riina 2003)
Pastizal	Mexico	In the most commonly used classification of Mexican vegetation, all grassland types, both natural and induced, from both tropical and temperate regions, were clumped together into a single category—pastizal—meaning grassland (López-Olmedo et al. 2007; Huber and Riina 2003)
Pine savanna	USA	Characterized by an open canopy of pines (<i>Pinus palustris</i> P. Mill. and/or <i>P. elliotii</i> Engelm.) and a diverse understorey of grasses and forbs maintained by frequent fires. Further characteristics include wet soils of low pH and relatively low nutrients (King and Grace 2000)
(Blue) Oak savanna	Coastal ranges and foothills of the Sierra Nevada in California	An oak savanna is a plant community with scattered “open-grown” oaks. Other terms for these savannas are “oak openings” and “oak barrens”. The savanna canopy ranges from about 10 to 50%. In such a habitat, the ground layer receives dappled sun and shade, which permits growth of a wide diversity of grasses and flowering plants. This is one of the Californian communities that is most invaded by alien plant species (Rejmánek et al. 2005, Fig. 13.2).
Mesic savanna	Southern Africa	Moist savanna systems, generally between 600 and 1500 mm rainfall per annum, found largely in the eastern parts of southern Africa; similar to fine leaved savanna (Scholes 1997)

Table 1 continued

Term	Geographical distribution	Meaning
Arid savanna	Southern Africa	Relatively arid regions with generally between 400 and 800 mm rainfall per annum, found largely in the western parts of southern Africa; similar to broad leaved savanna (Scholes 1997)
Fine leaved (nanophyllous)	Southern Africa	Nutrient rich, arid regions give rise to the fine leaved (nanophyllous) savanna (Scholes 1997)
Broad leaved (mesophyllous)	Southern Africa	Nutrient poor, moister regions give rise to the broadleaved (mesophyllous) savannas (Scholes 1997)
Grass and shrub savanna	North and eastern Africa	Savanna type stretching across northern Africa, from northern Senegal and Mauritania to Sudan. The northern border (the <i>Sahel</i>) is dominated by <i>Acacia</i> . It continues into the <i>Acacia-Commiphora</i> savanna of the horn of Africa, eastern Ethiopia, and east Africa as the <i>Somali-Masai</i> dry savanna (Shorrocks 2007)
Tree and shrub savanna	Central Africa	Two separated blocks of vegetation, lying north and south of the rainforest and miombo woodland savannas of central Africa. The northern area is dominated by <i>Terminalia</i> and <i>Combretum</i> trees and shrubs, and <i>Pennisetum purpureum</i> grass. The southern section is dominated by <i>Colophospermum mopane</i> tree and shrubs (Shorrocks 2007)
Woodland savanna	Central/South Africa	Two distinct blocks of savanna, namely, <i>Miombo</i> (central/south Africa), which is dominated by <i>Brachystegia boehmii</i> , and <i>doka</i> (in the north), which is dominated by <i>Isoberlinia doka</i> (Shorrocks 2007)
Forest-savanna mosaic	Africa	Encircles the tropical rainforest of the Congo basin, forming the edge of the 'true' savanna. Highly dynamic vegetation, interlacing forest, savanna and grassland (Shorrocks 2007)
Tropical savanna	Australia	The Australian tropical savannas are landscapes of dense grass and scattered trees that stretch across northern Australia from Broome to Townsville. They cover a huge area—around 1.9 million square kilometres—or around a quarter of mainland Australia's land area (Whitehead et al. 2000)

Although not comprehensive of all terminology used in connection with savanna systems, these terms are commonly encountered in the literature. Although this list deals only with tropical and sub-tropical savannas, two commonly encountered savanna related terms from temperate North America are included for comparison

and Wells 1986). Within these biomes, river and stream banks which are frequently seasonally flooded are substantially more vulnerable to plant invasions than areas away from rivers (Henderson and Wells 1986; Foxcroft and Richardson 2003). Rivers and riparian habitats thus form important conduits of dispersal of alien plants from one area to another (Foxcroft et al. 2007; Richardson et al. 2007a). This

is further supported in an economic review of alien plant control programmes in South Africa; Turpie (2004) indicates that the grassland and savanna biomes are extensively invaded, but mostly in the moister regions and particularly along river courses.

The savanna ecosystems in South Africa's Kruger National Park (KNP; 20,000 km²), have been the subject of a long-standing scientific investigation

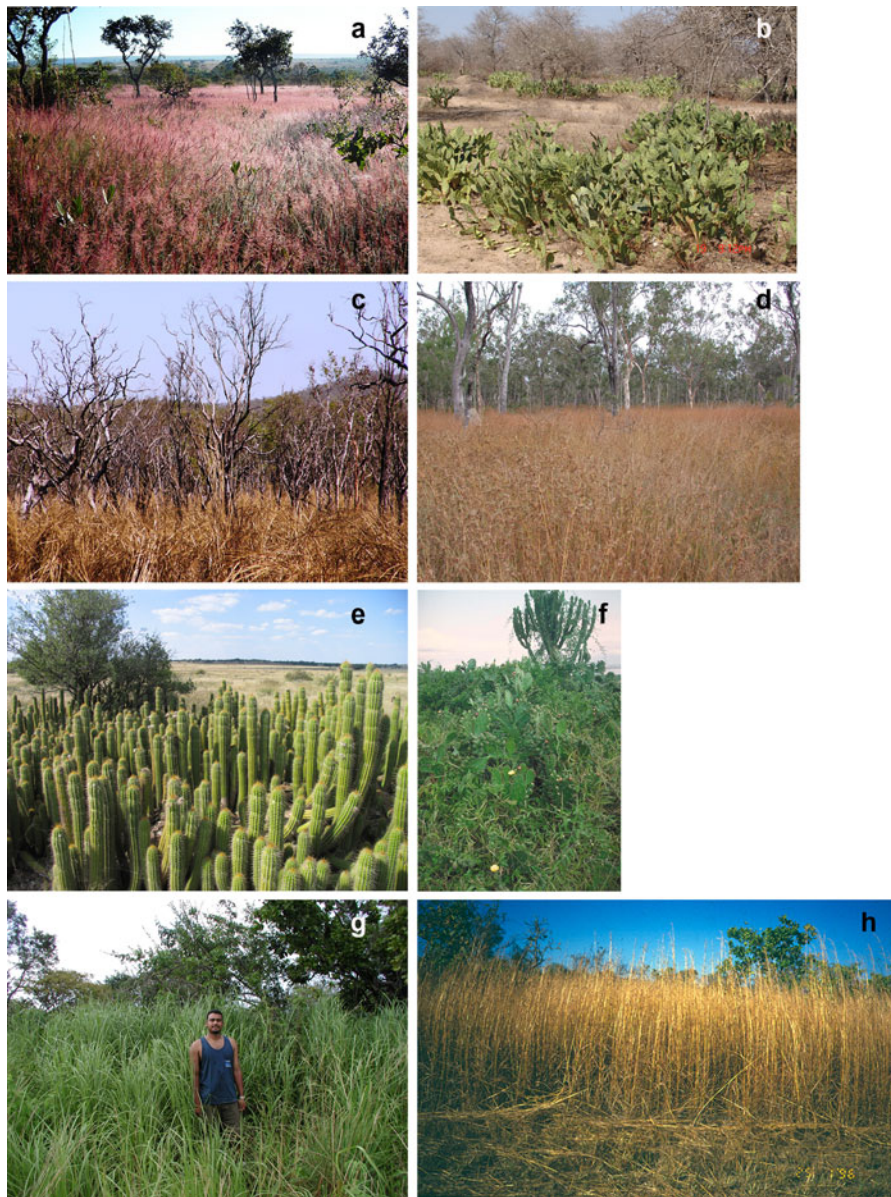


Fig. 1 Typical invasive species from the three regions covered in this review. **a** *Melinis minutiflora* (Poaceae; molasses grass) in the Neotropics. Photo M Carlos. **b** *Opuntia stricta* (Cactaceae; sour prickly pear) in Kruger National Park, South Africa. Photo LC Foxcroft. **c** *Andropogon gayanus* (Poaceae; gamba grass) in northern Australian savannas. Photo S Setterfield. **d** *Themeda quadrivalvis* (Poaceae; giant Kangaroo

grass) near Cairns, Australia. Photo M. Rejmánek. **e** *Echinopsis spachiana* (Cactaceae; torch cactus) invading arid savanna in South Africa. Photo DM Richardson. **f** *Opuntia monacantha* (Cactaceae; drooping prickly pear) in Queen Elizabeth National Park, Uganda. Photo M. Rejmánek. **g, h** *Hyparrhenia rufa* (Poaceae; thatch grass) in the central savannas of Venezuela. Photo Z. Baruch

(du Toit et al. 2003). Also, the invasion of alien plants in the KNP has been reasonably well studied (see e.g. Foxcroft and Richardson 2003; Freitag-Ronaldson and Foxcroft 2003; Foxcroft and Freitag-Ronaldson 2007 for a summary). The KNP currently maintains a

list of 373 alien plant species (Foxcroft et al. 2003, 2008; Foxcroft 2009), including invasive, aquatic, ruderal and ornamental species. However, Foxcroft et al. (2003) suggested that only 121 taxa were either invasive or potentially invasive, and more

importantly, only two (*L. camara* and *O. stricta*) species were regarded as transformer species at that point. This was based on observations of large impenetrable thickets of *L. camara* along rivers excluding all other species, and of large stands of *O. stricta* in the Skukuza region. However, current levels of alien plant abundance have been substantially reduced since 2003 and maintained at a low level due to the ongoing control activities by the Working for Water programme (see Foxcroft and Freitag-Ronaldson 2007).

In Macdonald and Frame's (1988) synthesis of five protected areas in tropical savannas, few alien species were recorded. In the Serengeti-Ngorongoro ecosystem (Tanzania) the authors listed 12 introduced vascular plant species, of which they considered four to be substantial problems. The most problematic species at that time appears to have been *Tagetes minuta* L., which had replaced native grasses over an area of 10–15 ha. *Euphorbia tirucalli* L., which was listed among alien species (presumed to be introduced from India), has more recently been shown to be native to east and southern Africa (Carter and Radcliffe-Smith 1988; Germishuizen and Meyer 2003) and introduced to west Africa and India (Mies et al. 1996; Pandey 2000). In general it was thought that introduced plants were unimportant in the Serengeti ecosystem (Macdonald and Frame 1988). However, Lyons and Miller (1999) and Henderson (2002) listed 43 species of alien plants for the Ngorongoro crater. Belsky (1987) wrote that there was no indication that introduced weeds were colonizing natural disturbances or invading the undisturbed grassland community in Serengeti National Park. Foxcroft (2003) recorded 10 species of alien plants in the Seronera and western corridor areas of the Serengeti National Park. These included widespread stands of *Opuntia stricta* var. *dillenii* (Ker Gawl.) L. D. Benson and *O. monacantha* Haw. Among the approximately 1,300 vascular plant species known from the Mkomazi Game Reserve (Tanzania; 3,250 km², see Coe et al. 1999), only eight naturalized plant species were reported (Table 2).

Very little is known from other parts of Africa. However from published phytosociological studies it appears that savannas in the other regions of Africa are also only very rarely invaded by non-native plant species. For example, Schmitz (1971) reported *Ageratum conyzoides*, *Amaranthus spinosus*, *Bidens*

pilosa, *Sonchus asper*, *Solanum nigrum*, *Conyza bonariensis*, *Physalis peruviana*, *Eclipta prostrata*, and *Galinsoga parviflora* as occasional aliens in disturbed savannas of Congo. Jeník and Hall (1976) reported only *Azadirachta indica* as occasionally growing in Accra Plains savannas, Ghana. Sillans (1958, p. 67) provided a short list of about 30 species introduced in savannas of western equatorial Africa. Unfortunately, it is impossible to say whether individual species are just casual, persisting after cultivation, or clearly naturalized. However, it is clear that none of them are transformer or dominant species.

To conclude, the picture that emerges from a study of the literature and our observations (see above and Table 2) suggests that in African savannas, despite the range of potentially invisable habitats, many forms of anthropogenic landuse over a long period (Bourlière and Hadley 1983), and high levels of frequent disturbances, invasive alien plants are not yet very widespread or common, and are a relatively minor component of habitat degradation and biodiversity loss. An important caveat however is that many woody alien species were introduced and widely planted for agroforestry only in last few decades, and many of these species are already naturalized and/or known to be invasive in some part of the world. Although problems with invasive species originating from agroforestry are not yet well reported, such problems are widespread throughout the tropics, including many parts of Africa (see Richardson et al. 2004 for a review). Species selected for agroforestry and practices associated with this landuse combine to create a perfect recipe for increasing invasions (e.g. mainly traits clearly associated with invasiveness; high propagule pressure, increasing time since introduction, improved climate matching; increased availability of mutualists, especially mycorrhizal fungi and nitrogen-fixing bacteria; Richardson et al. 2004).

Alien plant invasions in Neotropical savannas

Much work has been done on assessing the invasion of intentionally introduced species in the Neotropics, and data indicate that savannas in the New World are, at least locally, highly invaded (Parsons 1972). For example, Baruch and Bilbao (1999) report how African C₄ grasses, introduced into Neotropical

Table 2 Naturalized vascular plant species recorded across the African savannas

Species	Family	Native range	Uganda			South Africa		Tanzania	
			Lake Mburu National Park ¹	Murchinson Falls National Park ²	Queen Elizabeth National Park ³	Hluhluwe-Imfolozi Game Reserve ⁴	Kruger National Park ⁵	Serengeti National Park ⁶	Mkomazi Game Reserve ⁷
<i>Agave sisalana</i> Perrine	Agavaceae	Central America					1	1	
<i>Agave</i> sp.	Agavaceae	Central America	1						
<i>Ageratum conyzoides</i> L.	Asteraceae	C. & N. America	1		1		2		
<i>Amaranthus dubius</i> Mart.	Amaranthaceae	C. & S. America		1	1				
<i>Amaranthus hybridus</i> L.	Amaranthaceae	C. & S. America		1					
<i>Amaranthus spinosus</i> L.	Amaranthaceae	C. & S. America		1			P		
<i>Argemone mexicana</i> L.	Papaveraceae	C. America			1		1		
<i>Austrocyllindropuntia subulata</i> (Muehlenpfordt) Backeberg 1941	Cactaceae	Ecuador, Peru						1	
<i>Bidens pilosa</i> L.	Asteraceae	Americas					3		1
<i>Bryophyllum delagoense</i> Harv.	Crassulaceae	Madagascar			1–2		1		
<i>Cannabis sativa</i> L.	Cannabaceae	Asia			1		P		
<i>Capsicum frutescens</i> L.	Solanaceae	S. America		1			P		
<i>Cardiospermum halicacabum</i> L.	Sapindaceae	Origin uncertain, but thought to be N and tropical America					Riparian only	2	
<i>Catharanthus roseus</i> (L.) G. Don	Apocynaceae	Madagascar		1	1		River beds only		
<i>Chromolaena odorata</i> (L.) R.M. King & H. Rob.	Asteraceae	SE USA to NE Argentina and West Indies				4	Riparian only		
<i>Conyza sumatrensis</i> (C. albidia) Willd. Ex Spreng.	Asteraceae	S. America	2	2	2		P		
<i>Datura stramonium</i> L.	Solanaceae	C. America			2		1		P
<i>Duranta repens</i> L.	Verbenaceae	S. America			2				
<i>Eclipta prostrata</i> (L.) L.	Asteraceae	Americas		1			P	1	1
<i>Gainsoga parviflora</i> Cav.	Asteraceae	S. America			1				
<i>Ipomoea hederifolia</i> L.	Convolvulaceae	S. America			1				

Table 2 continued

Species	Family	Native range	Uganda			South Africa		Tanzania	
			Lake Mburo National Park ¹	Murchinson Falls National Park ²	Queen Elizabeth National Park ³	Hluluwe-Imfolozi Game Reserve ⁴	Kruger National Park ⁵	Serengeti National Park ⁶	Mkomazi Game Reserve ⁷
<i>Lantana camara</i> L.	Verbenaceae	C. & S. America	2	2	2	1 (4 in riparian areas)			
<i>Opuntia ficus-indica</i> (L.) Mill.	Cactaceae	S. America				1			
<i>Opuntia monacantha</i> (Willd.) Haworth.	Cactaceae	S. America	2	4	4	P	4	4	
<i>Opuntia stricta</i> var. <i>dillenii</i>	Cactaceae	Florida, Texas, Cuba					4	4	
<i>Panicum trichoides</i> Sw.	Poaceae	Americas		1					
<i>Phyla nodiflora</i> (L.) Greene	Verbenaceae	Americas						1	
<i>Phyllanthus amarus</i> Schum. & Thonn.	Euphorbiaceae	C. & S. America		1					
<i>Pityrogramma calometanos</i> (L.) Link	Pteridaceae	C. & S. America		2—Along rivers	1—Along rivers				
<i>Portulaca grandiflora</i> Hook.	Portulacaceae	S. America			2				
<i>Ricinus communis</i> L.	Euphorbiaceae	Tropical E and NE Africa						4—Dry riverbeds only	
<i>Senna alata</i> (L.) Roxb.	Fabaceae	S. America			2				
<i>Senna bicapsularis</i> (L.) Roxb.	Fabaceae	S. America			2			P—dry riverbeds only	
<i>Senna septentrionalis</i> (Viv.) Irwin & Barneby	Fabaceae	S. America			1			P—dry riverbeds only	
<i>Senna siamea</i> (Lam.) Irwin & Barneby	Fabaceae	Asia	3	P	P			P—dry riverbeds only	
<i>Senna spectabilis</i> (DC) Irwin & Barneby	Fabaceae	S. America		1	1				
<i>Solanum seeforhitanum</i> Andr.	Solanaceae	C. & S. America			1			4	
<i>Sonchus oleraceus</i> L.	Asteraceae	Eurasia		1	1			P	

Table 2 continued

Species	Family	Native range	Uganda			South Africa		Tanzania	
			Lake Mburo National Park ¹	Murchinson Falls National Park ²	Queen Elizabeth National Park ³	Hluluwe-Imfolozi Game Reserve ⁴	Kruger National Park ⁵	Serengeti National Park ⁶	Mkomazi Game Reserve ⁷
<i>Stachytarpheta urticifolia</i> Sims	Verbenaceae	Central Mexico, S. America					Ornamental only		1
<i>Syndrella nodiflora</i> (L.) Gaertn.	Asteraceae	C. & S. America	1	1	1				
<i>Tagetes minuta</i> L.	Asteraceae	C. America	4	2	2		3—Mainly along rivers	P	
<i>Tecoma stans</i> HBK.	Bignoniaceae	C. & S. America			4		2		
<i>Tridax procumbens</i> L.	Asteraceae	C. & S. America		2	1		P		1
<i>Zinnia peruviana</i> (L.) L.	Asteraceae	C. America (southern Arizona)					3—Often in disturbed sites		

Although by no means a complete species list, the following is compiled from various field observations by the authors and other published sources. The list provides an indication of the kinds of species which have been introduced, and where possible, an indication of the abundance. Abundance values: 1—naturalized only locally, 4—very invasive, either widespread or dense local infestations. P—present, but abundance unknown

^{1–3} Based on collections made by M. Rejmánek and E. Rejmánková in 1991 and 1993

⁴ Macdonald and Frame (1988)

⁵ Based on Foxcroft et al. (2003, 2009). The list includes notes where applicable, but generally excludes species invading river courses, tourist camps and staff villages (ornamental species)

⁶ Reported by Foxcroft (2003), Macdonald and Frame (1988; only for *Tagetes minuta* L.), and Hoeck (2009, unpublished report; only for *Datura stramonium* L.)

⁷ Based on Vollesen et al. (1999)

savannas to improve forage quality, have successfully spread and displaced native species. Assessing the physiological attributes of the *Hyparrhenia rufa* (Nees) Stapf. (Fig. 1g, h), a successful invader, they suggest that its success is due to its water-stress evasion strategy, larger biomass allocation to leaves, high germination rates and fast seedling growth. Additionally, C₄ grasses are also known to have higher nitrogen-use efficiencies (NUE) than C₃ species (Brown 1978; Snaydon 1991), thus adding further competitive ability.

In assessing the effects of invasive alien plants on fire regimes, Brooks et al. (2004) discuss the role of African grasses in Venezuelan savannas, which increase biomass by up to 50%. Similarly, *Imperata cylindrica* (L.) P. Beauv. in south-eastern USA pine savannas increases fuel loads enormously (Richardson et al. 2007b). Rejmánek et al. (2005) state that savannas, especially disturbed deforested areas in the Neotropical regions, are very often dominated by African grasses such as *Hyparrhenia rufa* and *Melinis minutiflora* P. Beauv., while similar tropical habitats in Africa (specifically the east African savannas) and Asia are dominated by Neotropical woody plants, such as *Lantana camara* and *Opuntia* spp.

In Brazil, a number of African grasses selected for high forage and seed production potential (Klink 1996) were intentionally introduced—a practice which was still encouraged in the late 1990s (Pivello et al. 1999a). Additionally, large areas were disturbed by ploughing, which provided opportunities for the introduced grasses to invade (Klink 1996). In an assessment of the impact of alien grasses in Brazilian savannas, Pivello et al. (1999a, b) contend that these introduced species had spread to such a magnitude that they are present and dominant in almost all cerrado fragments. The dominant species include *Melinis minutiflora*, *Brachiaria (Urochloa) decumbens* Stapf., *Hyparrhenia rufa*, *Andropogon gayanus* Kunth (Fig. 1c) and *Panicum maximum* Jacq. Some African grasses were reported to inhibit regeneration of trees in Neotropical savannas (Hoffman and Haridasan 2008). Further, in Columbia, Venezuela, and Brazil, Williams and Baruch (2000) reported that about 4 million km² were transformed to pasture by using, to a large extent, African C₄ grasses. The tree *Calotropis gigantea* R.Br. (Crown flower) is described as “the most aggressive phytoinvader” in

the Caatinga biome of Brazil (Cavalcante and Major 2006).

Alien plant invasions in Australian savannas

African bunchgrasses and European annual grasses are common alien species in Australia (D’Antonio and Vitousek 1992), with the history of planned plant introductions (Lonsdale 1994) dating back to the 1880s (Mott 1986). Lonsdale (1994) reports that 466 pasture species were intentionally introduced into the savannas of northern Australian and at least 13% of these species have become invasive. Their invasiveness is most likely due to these species being predominantly selected as vigorous competitors, hardy and mostly of savanna origin. Thus, the intentional introduction of species has greatly enhanced the status of invasive species in particular areas. However, it appears that the estimate by Lonsdale (1994) might be an underestimate, as Cook and Dias (2006) show that over 70 years more than 8,200 species were introduced into cultivation in the country by Australia’s Commonwealth Plant Introduction Scheme.

Andropogon gayanus (Fig. 1c) is one of the most noxious invasive plant species in Australian tropical savannas; this invasion has led to several-fold increases in the fuel load and fire intensity in northern Australian savannas (Rossiter et al. 2003). Introduced as a pasture grass in about the 1930s, *A. gayanus* has spread across the northern areas of Australia (Flores et al. 2005). It inhibits soil nitrification and thereby depletes total soil nitrogen from the already nitrogen-poor soils and promotes fire-mediated nitrogen loss (Rossiter-Rachor et al. 2009). Combined with the altered fire regime, it forms self-perpetuating positive feedback loops (Rossiter-Rachor et al. 2009). We return to the role of fire as a mechanism of invasion in a later section. Besides fire regime altering grasses from Africa or Asia (e.g., *Andropogon gayanus*, *Cenchrus ciliaris*, *Pennisetum polystachion*, *Themeda quadrivalvis*—Fig. 1d), several woody species are also invading Australian savannas (*Acacia nilotica* from Africa, *Cryptostegia grandiflora* from Madagascar, *Jatropha gossypifolia* from C. America, *Lantana camara* from the Neotropics, *Mimosa pigra* from S. America, *Parkinsonia aculeata* from S. America, *Prosopis* spp.

from Americas, *Ziziphus mauritiana* from India) (Fenshaam et al. 1994; Grice et al. 2000; Grice 2004). However, perhaps the most difficult are more than 10 cactus species introduced from Central and South America (Hosking et al. 1988).

Mechanisms at play: reasons for lower rates of invasion in Africa

Biological invasions are increasing in extent and impact globally, threatening the integrity and functioning of ecosystems (Sala et al. 2000; Millennium Ecosystem Assessment 2005; Mooney et al. 2005), yet little scientific evidence of naturalization and impacts has emanated from African savannas. D'Antonio and Vitousek (1992) stated that, for example, alien grass invasions could be found on all continents, although examples from Africa (and Eurasia) are rare. Much of what has been written is based on observations mainly in southern Africa and South Africa in particular (for example, Brown and Gubb 1986; Henderson and Wells 1986; Freitag-Ronaldson and Foxcroft 2003). This could be contrasted with the book *World Savannas* (Mistry 2000) where invasive plants are discussed in four places: invasive African grasses in Brazilian cerrado, African grasses in Venezuelan llanos, and invasive plants in Australian savannas. There is, however, also a short discussion about invasive plants in South African savannas, based on Henderson and Wells (1986) chapter in Macdonald et al. (1986) and on Richardson et al. (1997). Invasive plants are not even mentioned in the chapter on savannas in West or East Africa.

In the volume *Biodiversity and Savanna Ecosystem Processes* (Solbrig et al. 1996), plant invasions are discussed in two chapters. One chapter discusses ecophysiological aspects of the invasion by African grasses, and their impact on biodiversity (Baruch 1996) and the other biodiversity and stability in tropical savannas (Silva 1996). Importantly however, only invasions in Neotropical savannas are discussed in both cases. Interestingly, Baruch (1996) states that African grasses had been introduced since colonial times, both accidentally and deliberately. He however attributed the widespread invasions to the more recent introductions of grasses introduced for pasture 'improvement'. He further contends that the species richness and structural diversity of the natural

grasslands had been lost and turned into "closed, species-poor, homogeneous stands" (Baruch 1996).

Does this mean that Africa savannas are more resistant to plant invasions (i.e. do particular features of the habitat confer resistance), or that the particular species that have been introduced are less aggressive invaders? Surely some areas or patches must be as invulnerable as in other savannas? Similarly, a wide range of species have been introduced, into a range of areas, many of which are known invaders elsewhere in similar habitats. Therefore it is unlikely that there are no species that possess the traits needed to invade in some areas. Alternatively, invasions may be widespread, but not adequately reported across much of Africa, where invasions have been markedly understudied with the exception of South Africa (Pyšek et al. 2008). Species introduced recently for agroforestry are an example of where species are known to be potentially invasive, or have already started spreading, but such invasions are too recent to be well covered in the literature. Moreover, we should remember that, in general, much less is known about plant invasions in the tropics than in temperate zones (Ramakrishnan 1991; Rejmánek 1996; Denslow and DeWalt 2008). In the next section (also see Table 3) we offer some potential explanations for the patterns described above.

Herbivore presence/absence

In temperate grassland biomes, those areas that are more vulnerable to alien plant invasions lack large mammalian grazers to affect selection in perennial grasses (Mack 1989). These include Australia, South America and parts of the USA. Native grasses in the New World were not adapted to heavy mammalian grazing pressure and associated disturbances, having had a long absence of mammalian grazers (Mack 1989). Thus, under the influence of cattle introduced during human colonization, grasses introduced from Eurasia which had adapted to large, congregating mammalian grazers over a long period, were well suited to invading the New World territories (Kimball and Schiffman 2003). In North America, bison occurred in large herds in the Great Plains, but were absent from a number of areas such as California's central valley since the late Pleistocene (12,000 years ago; Edwards 1992). Additionally, bison have been functionally absent from American savannas and

Table 3 A summary of the roles of seven factors potentially influencing alien plant invasions in three major savanna systems

Factor	Africa	Neotropics	Australia
Herbivore presence	Very high	Very low	Low
Time since introduction (lag phase)	Most in last 100 years, but <i>Opuntia ficus-indica</i> dates back to 1770s	Long, dating back to 1500s	Recent (since about 1850s for northern Australia)
Intentional introduction (pasture planting)	None	High	Very high
Widely planted for pasture	None	Very high	High
Fire	Very high frequency. Vegetation fire adapted	Low, minor role in ecosystem	Frequent but with low intensity fire; but <i>Andropogon gayanus</i> significantly increases fuel load, fire intensity and frequency of fires
Resistance; resistance to species naturalisation is probably conferred by increased numbers of barriers to invasion	Unknown; <i>Opuntia</i> spp. well adapted to invasion in arid African systems due to CAM photosynthesis	Unknown; but possibly overcome by ploughing disturbance, widespread planting, and preadaptation of African grasses (e.g., <i>Hyparrhenia rufa</i>)	Unknown, but possibly overcome by pasture planting. Also, <i>Andropogon gayanus</i> forms positive self-reinforcing feedback loops in the N cycle
Anthropogenic disturbance	High levels of grazing by cattle and goats. Fire was used frequently for providing fresh grass and other reasons	High	Livestock grazing
Physiology of introduced species	CAM photosynthesis of <i>Opuntia</i> spp. introduced to Africa	The success of introduced African C4 grasses is suggested to be due to their water-stress evasion strategy, larger biomass allocation to leaves, high germination rates, fast seedling growth and higher nitrogen use efficiencies	Bunch grass growth form

grasslands since about 1880 (Knapp et al. 1999), and their numbers declined substantially before this date. Not only did this result in a loss of herbivory pressure, but a substantial shift in the functioning of these savanna ecosystems (Knapp et al. 1999). This period coincides with some prominent invasions of Eurasian grasses in North American perennial grasslands and shrublands, such the invasion of *Bromus tectorum* L. This annual grass was disseminated during the building of the transcontinental railway and it is estimated that 200,000 km² were invaded between 1890 and 1930s (Mack 1989). In Australia the largest indigenous grazers are the eastern grey and red kangaroos, and South America also lacks large congregating grazers.

This is certainly not the case across the savannas of Africa. Large herds of a variety of species are characteristic features of African savannas, and include substantial numbers of mega-herbivores and

bulk grazers (Sinclair and Norton-Griffiths 1979; Owen-Smith 1988; Sinclair and Arcese 1995; du Toit et al. 2003). Thus herbivores could conceivably suppress naturalization of alien plant species. In addition to ungulates and mega-herbivores, insect herbivory and effect of pathogens are likely to be important. Insect and pathogen damage on alien plants in African savannas may not differ from that of other savanna systems, but may act in concert with the pressure from large mammals. In a controlled study, Agrawal and Kotanen (2003) showed that alien plants suffered leaf attack levels that were the same, or higher, than those experienced by congeneric native plants. Similarly, Maron and Vilà (2001) suggested that native herbivores can reduce the likelihood of plant growth of the introduced species, as well as seed set and survive.

Another important consideration is whether the changes in herbivory pressure, both in space and time,

are likely to impart increased or decreased resistance to invasion. However, because so little is known of the role of herbivores in influencing invasibility of ecosystems, any attempts to discuss the changes in herbivory would be conjecture at this stage.

Propagule pressure: intentional introductions and widespread pasture plantings

One of the most striking features of the invasion of Australian savannas is the abundance of species that were intentionally introduced for pasture enhancement and other reasons (Lonsdale 1994; Cook and Dias 2006). Similar patterns exist for the Neotropics (Baruch and Bilbao 1999). These species were not only intentionally introduced in high numbers, but actively dispersed and sown in a wide range of areas. Further, in many cases species selected for importation were selected for the same traits that would promote invasion (Anderson et al. 2006). However, there are no records of the same trend in the African savanna systems. This is probably as a result of the already abundant forage and browse (of sufficiently good quality) present to maintain large numbers of wild ungulates and domestic stock. Thus repeated introductions of large quantities of propagules were unlikely. This also presents a rare opportunity for African countries to ensure that policies are put in place to prevent similar introductions. Although the continent's rich grass flora, which is also adapted to the pressures of the region (herbivory by large mammals and fire), is unlikely to be invaded by grasses from other areas due caution is however still required. Milton (2004) suggests that, for South Africa at least, the winter rainfall and arid regions already show signs of increasing grass invasions, while the summer rainfall areas are likely to be invaded in wetlands and riparian areas.

Economic pressures are an enormous additional factor driving the intentional introduction of pasture grasses and other species. For example, intensive cattle grazing practices could not be sustained in the tropical America's without the introduction of African grasses (D'Antonio and Vitousek 1992). This is another likely cause of differences in the levels of invasion between Africa and South America (and probably also Australia). Tropical South American savannas are among the most important resources in the region, and probably globally, for cattle production (Lascano 1991).

However, the soils are commonly extremely acidic and have low nutrient levels (Sánchez and Isabell 1979). The higher productivity of African C_4 grasses is derived from their tolerance to high temperatures, drought, and ability to grow on acid, nutrient poor soils that are typical of most of tropical America (D'Antonio and Vitousek 1992). In areas of improved pasture (using alien species), production per unit area (typically beef cattle production) can be increased by as much as 10 times (Lascano 1991). Therefore the economic incentive to extend the areas sown with alien species was and still is high.

The role of herbivory in preventing or at least limiting the invasion by alien plants has not been well studied in the tropics (Dawson et al. 2009). The 'enemy release hypothesis' states that highly invasive alien plants suffer less herbivory than less invasive plants (Dawson et al. 2009). Ungulate herbivory (the role of insect herbivores was generally under-appreciated) was considered an important factor in limiting plant invasions in South Africa's Kruger National Park (Macdonald 1988). For example, Macdonald (1988) observed that *Nicotiana glauca* R.C. Graham and *Ricinus communis* only occurred in the KNP in areas protected from heavy grazing. Also, Macdonald (1988) reported that a small population of *Acacia dealbata* Link. growing along the banks of the Sabie River was eventually eliminated from the park through browsing pressure. Vegetation in African savannas has evolved with humans (and their livestock), high grazing and browsing pressure by wild ungulates, and fire (D'Antonio and Vitousek 1992), thus becoming highly adapted and tolerant to fire (see van Wilgen et al. 2007 for a discussion of the effects of fire).

The time since introduction (residence time) and the potential "lag-phase" that often precedes widespread invasions cannot be excluded as a possible explanation for the lower levels of invasion in African savannas to date. Residence time has shown to be a crucial factor in determining a species' abundance and distribution (Rejmánek 2000; Pyšek and Jarošík 2005; Wilson et al. 2007). However, as it appears that intentional introductions were kept to a minimum, and information on accidental introductions is largely unknown, it is difficult to factor in the role of residence time as even approximate dates of introduction are not known for most regions.

In a global review of plant invasions Lonsdale (1999) stated that savannas are among the least

invaded biomes globally. However, there was considerable within-group variation. Further, work by Humphries et al. (1991) in Australia, and Lonsdale (1999; a global review) suggests that there are real differences in the degree of invasion between biomes, which might lead one to conclude, for example, that deserts and savannas are less invasible. However, Lonsdale (1999) additionally suggests that these results cannot be interpreted without, at least, rough estimates of propagule pressure.

History and biogeography

A general pattern that emerges at this time is that Africa and Australia have mostly been invaded by Cactaceae from the Neotropics, whereas Australia and the Neotropics have been mainly invaded by African C₄ grasses. This is probably proportional to species pools (Cactaceae are, with exception of one species, the New World family and there are very likely more C₄ grass species in Africa than in any other continent), pre-adaptation of CAM photosynthesis in the Cactaceae to dry tropics, the physiological attributes of African C₄ grasses and, the extent of savanna systems in Africa. In comparison, Australia did not provide many invasive species to other parts of the world, except for *Acacia* spp. in Africa (and elsewhere), but these are mostly invasive in temperate regions of the continent, and mostly in South Africa (Nel et al. 2004).

The historical context is also important; people from Africa were transported to the Americas as early as the 1500s and 1600s as slaves, and undoubtedly transported various plants with them (Kull and Rangan 2008). For example, African grasses were used as bedding in slave ships (Parsons 1972) and food crops such as African rice accompanied these movements (Carney 2003). Thus, species such as *Melinis minutiflora* and *Hyparrhenia rufa* were first described from Brazil and not from their native areas.

Fire

Fire is an important process in savanna ecosystems (van Wilgen et al. 2007), where it removes high amounts of fast accumulating material (Bond and Keeley 2005), and facilitates the coexistence of trees and grasses (Higgins et al. 2000). The evolution of African savannas with fire (of both natural and

anthropogenic ignition sources), has long been accepted by ecologists as a predictable and common feature (Bond et al. 2005; Sankaran et al. 2008). Fire has further been suggested as an important evolutionary force shaping biomes (Bond and Keeley 2005) and a key factor in splitting species into fire tolerant and intolerant areas, and thereby maintaining C₄ grasslands and savannas in their state (Bond et al. 2005).

Fire can filter and suppress those potentially invasive species that are poorly adapted to the fire regime into which they are moved. Alternatively, fires may promote invasions by disadvantaging native grasses (Grace et al. 2001). For example, many of the grasses which were introduced to and subsequently invaded the Neotropics and Australia are C₄ bunchgrasses which are well adapted to fire. There are many examples of how invasive alien grasses interacted with fire to alter various ecosystem processes (for example see Vitousek 1990; D'Antonio and Vitousek 1992; D'Antonio 2000). In the northern Australian savannas the invasion of *Andropogon gayanus* has increased fuel loads, the intensity, extent and frequency of fires (Rossiter-Rachor et al. 2009). These impacts further resulted in a four-fold increase in biomass and the above-ground pools of nutrients, and therefore a general depletion of soil nutrients, specifically nitrogen (Rossiter-Rachor et al. 2009). Other mechanisms of invasion-fire mediated changes include the establishment of new plant forms (from wooded savanna to grassland) which may have intrinsic fuel properties that differ from those of native species (Brooks et al. 2004). This may change the window of fire activity by either shortening or lengthening the fire season, as well as change surface to canopy fire patterns (and vice versa).

Conclusions: Are African savannas resistant to plant invasions?

Our review suggests that African savannas are less severely invaded than those on other continents. Likely reasons for this are (1) the lack of intentional grass species introductions in most areas of Africa compared to the Neotropics and Australia, where introductions for 'pasture improvement' were major contributors to invasions in savanna ecosystems; (2) resistance of native African grasses to grazing and disturbances associated with grazing, acquired during

evolutionary history by selection from large herbivores that were missing from analogous Neotropical and Australian ecosystems; (3) historical and biogeographical reasons of the origin of introduced species, and (4) the adaptation of African systems to fire (Table 3). Among the key differences between the seasonally dry vegetation of Africa and the Neotropics are the longer history of human occupation and animal domestication and the greater frequency of fire in Africa and the much more diverse mammal fauna in Africa that did not suffer major extinctions during Pleistocene (Lock 2006).

However, it needs to be borne in mind that invasions by alien species are poorly reported across Africa, besides South Africa and other localised areas (Pyšek et al. 2008). The lack of complete species lists, distribution data and information on introduction dates and history of individual invasions makes generalization difficult. For example, data on naturalised woody species, which are likely to be increasing in extent, is highly fragmented (Richardson et al. 2004). Since the invasibility of an ecosystem cannot be rigorously evaluated without accounting for confounding factors such as propagule pressure (Lonsdale 1999; Chytrý et al. 2008a, b; Pyšek et al. 2010), it is even more difficult to draw conclusions of whether African savannas are inherently more resistant to invasion by alien species.

It is also possible that the invasions described in the literature on savannas focus on densely invaded areas with substantial impacts, which might be limited in extent. Therefore, to obtain deeper insight into the global patterns of invasions in savannas, further research is needed to (1) obtain accurate and objective inventories of alien plant species from representative regions within the savanna biomes; (2) assess the role that these species play in savanna ecosystems, also in relation to native species diversity; and (3) develop proxies for propagule pressure based on historical and economic data to assess the relationship between introduction intensity and extent of invasion. Such data would facilitate rigorous testing of hypotheses associated with the observed patterns and pave the way for an unbiased picture of the invasibility of savanna ecosystems in different parts of the world.

The review would not be complete without speculating on how global environmental change may alter the status and dynamics of plant invasions in savannas.

Changing levels of CO₂ are likely to be important drivers of change. Atmospheric CO₂ has already risen by 30% in the past century, from ~275 ppm to about 370–375 ppm in 2005 (Keeling and Whorf 2001; Solomon et al. 2007) and ~430 ppm currently (Stern 2007). Concentrations of around 550 ppm are expected by 2035 (Stern 2007), with 700 ppm predicted by the end of the current century (Houghton et al. 1996). Although there is little data on the expected changes in the invasiveness of alien species specifically (Ziska 2003; Walther et al. 2009), recent studies provide us with indications that changes will be momentous. C₄ plants are thought to have evolved in hot regions of the world in response to decreasing atmospheric CO₂ (Ehleringer 2005; Sage 2004). By the middle of this century, CO₂ concentrations will have exceeded the threshold at which C₄ plants have a photosynthetic advantage over C₃ species (Bond 2008). This potentially means that the invasion of African C₄ grasses in the Neotropics and Australian savannas could become less important. In grasslands and savannas across Africa, rapid increase in the use of woody alien species for commercial forestry and especially agroforestry, suggests that a number of species already introduced and widely dispersed are likely to become highly invasive (see for example Table 13.1 in Richardson et al. 2000). In combination with the traits of many of these species which make them inherently invasive (Richardson et al. 2004), elevated CO₂ could greatly improve their persistence in the ecosystems they invade, exacerbating their negative impacts. However, there are other factors that should be considered. For example, the recent analysis of 161 savanna sites in Africa (Sankaran et al. 2008) concluded that there is a strong negative dependence of woody cover on soil nitrogen availability, suggesting that increased anthropogenic N-deposition may cause shifts in savannas towards more grassy communities. The only conclusion possible at this point is that altered precipitation regimes, elevated levels of CO₂, and N-enrichment will often end with opposing and interacting influences on the tree-grass balance in savannas. Whether native or exotic species will profit from such changes will be likely highly site specific.

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