Grasses as invasive alien plants in South Africa

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Grasses are important, but often overlooked, elements of the South African alien flora. Current information shows that 15% of the grass genera and 12% of grass species in southern Africa are naturalized aliens. Many of these species are invasive in other parts of the world, where they are reducing the biodiversity of indigenous communities, changing ecosystem processes, retarding ecosystem restoration and reducing profits from ranching and arable agriculture. Their spread has been facilitated by domestic livestock, disturbance, long-distance transport and nitrogen addition to soils. Control is complicated by abundant seed production, persistent seed banks, positive response to disturbance, a dearth of biocontrol research and, in some cases, by herbicide resistance. This review of the impacts of alien grasses in other parts of the world suggests that alien grasses will become increasingly prevalent in South Africa, and that more research, aimed at identifying appropriate management responses, would be justified.

Introduction

This paper provides a brief overview of current knowledge of the distribution, invasion processes, impacts and control options for alien grasses in southern African ecosystems. Grasses are an important component of the naturalized alien flora in South Africa, but are often overlooked in reviews of the effects of invasive alien plants in southern Africa because of the major problems currently being experienced here with alien woody plant invasions.[1] By comparison with other parts of the world where alien grasses, particularly African species, are important transformers of ecosystems, grasses hardly feature on the 'big time' list of invasive species in this region. Nevertheless, problems caused by alien grasses in the subcontinent are likely to increase as a result of global change, so it is desirable to raise awareness of these significant plants, both to guide research and to formulate management priorities and responses.

Invasions by alien grasses have occurred worldwide as a result of seed introductions, and of tree and shrub clearing for pasture and grazing intensification. It has been proposed[2] that grass invasions are becoming important at local and global scales because grass flammability prevents recovery of woody vegetation, maintaining grass dominance, changing microclimate and causing nutrient losses. Grasses are exceptionally successful world travellers, particularly in livestock-based economies. Of the 580 species of alien grass in the British Isles, for example, 430 are believed to have been brought there in imported wool, 95 in imported grains and seeds, and only 55 as horticultural introductions.[3] In Australia, those plant species that persisted for several years without cultivation were found to be most likely to become invasive weeds.[4] The numerous, small, persistent seeds produced by many grasses extend their chances of persistence and eventual naturalization.

In southern Africa, only 12% of grasses (113 of 912 species) are naturalized aliens. These include 53 species in 29 alien genera and 60 alien species in 24 southern African genera (Table 1).[5,6] Many of these grasses were intentionally introduced to serve agricultural, horticultural or restoration functions. Europe, particularly the Mediterranean region, is the source of 60% (66 species) of naturalized alien grasses recorded in southern Africa, whereas 23 species are from central and southern America and the remainder (24 species) have diverse origins in Africa, Asia, North America and Australasia.

In southern Africa, alien grasses are seldom considered have the potential to reduce the biodiversity and productivity of natural ecosystems, despite the growing global evidence[7] that alien grasses can transform ecosystems. At present only five grass species, all large conspicuous perennials, are declared weeds in South Africa.[8] However, perennials and annuals are equally represented in the alien grass flora. The annuals, largely of European origin, are widespread and sometimes abundant in winter rainfall and arid parts of southern Africa, whereas the perennial species have successfully invaded both winter and summer rainfall regions, particularly in wetlands and riparian areas. Most alien grass species are too poorly known to evaluate their ecological and economic impact or to recommend control measures. This preliminary review of the processes and influences of perennial and annual grass invasions seeks to address this gap. Because of the dearth of local research on this topic, information is largely drawn from studies of invasive behaviour by the same (or related) grass species in Australia and North America.

Perennial grasses

Grasses are typically divided into annual and perennial species. Annual grasses (see later) complete their life cycles in a single year, and occur for at least part of the time only as seeds. Perennial grasses are long-lived, and can survive repeated fires or grazing pressure by sprouting, and can spread by vegetative means as well as by seeding. The distinction is useful in an ecological sense, as the impacts and potential control strategies would differ for these two broad types.

Seven perennial grasses — Spanish reed (*Arundo donax*), pampas grass (*Cortaderia jubata, C. selloana*), tussock-grass (*Nassella tenuissima, N. trichotoma*), fountain grass (*Pennisetum setaceum*) and feather-top (*P. villosum*) — are declared as Category 1 weeds in South Africa.[8] Another perennial, marram grass (*Ammophila arenaria*), although not a declared weed, has naturalized widely on coastal dunes[9] All these species have shown invasive behaviour in fire-driven or littoral ecosystems elsewhere in the world.[10–12] It is significant that all have wind-dispersed seeds, probably indicating that selection by large grazing mammals played a relatively minor role in their evolution.[13] On the other hand, African grasses (including species in the genera *Brachiaria, Eragrostis, Hyparrhenia, Sporobolus*)[14,15] are successful invaders in ecosystems in Australia, Brazil, Hawaii and North America that are naturally poor in large herbivores, but where domestic livestock have been introduced. African grasses are pre-adapted to survive in this situation because they are generally herbivore exploiters (being palatable to herbivores, recovering well after grazing, and having seeds adapted for dispersal in or on herbivores). In contrast, the wind-dispersed, alien invasive perennial grasses are unpalatable and flammable in the dry

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Table 1. Genera of grasses found in southern Africa that include naturalized alien (non-southern African) species.

Genus	Number of alien species	Number of indigenous species	Origin*	Longevity	Carbon pathway	Reason for introduction	Distribution	Legal status
Agrostis	2	9	Australia, Europe	A, P	C_3	Accidental	Fynbos, savanna	None
Aira	1	0	Europe	A	C_3	Accidental	Fynbos, grassland	None
Ammophila	1	0	Europe	P	C_3	Dune stabilization	Coastal	None
Anthoxanthum	1	4	Malawi	P	C_3	Accidental	Fynbos, grassland	None
Arrhenatherum	1	0	Med. Europe	P	C_3	Pasture	Grassland	None
Arundo	1	0	Tropical Africa	P	C_3	Building	Wetland	1
Avena	5	0	Europe	A	C_3	Ornamental	Fynbos, succulent karoo, savanna	None
Axonopus	1	0	Tropical America	P	C_4	Pasture	Savanna	None
Bambusa	1	0	India	P	C_3	Ornamental	River banks	None
Brachiaria	1	19	Australia, Europe	P	C_4	Accidental	Grassland	None
Brachypodium	1	2	Med. Europe	A	C_3	Accidental	Fynbos, succulent karoo	None
Briza	3	0	Med. Europe, S. America	A	C_3	Ornamental	Fynbos, savanna	None
Bromus	10	6	Europe	A, P	C_3	Pasture, accidental	Fynbos, savanna	None
Catapodium	1	0	Med. Europe	A	C_3	Accidental	Fynbos	None
Cenchrus	3	1	Tropical America	A	C_4	Accidental	Savanna	None
Chloris	1	7	India	P	C_4	Pasture	Grassland, savanna	None
Coix	1	0	East Indies	A	C_4	Beads	Savanna	None
Cortaderia	2	0	S America	P	C_3	Ornamental, stabilization	River banks	1
Corynephorus	1	0	Europe	A	?	Accidental	Fynbos	None
Cynodon	2	6	Tropican Africa	P	C_4	Accidental	Savanna	None
Cynosurus	1	0	Europe	A	C_3	Accidental	Fynbos	None
Dactylis	1	0	Europe	P	C_3	Pasture	Fynbos, grassland	None
Deschampsia	2	0	Europe	P	C_3	Accidental	Grassland	None
Dichanthium	1	1	Asia	P	C_4	Accidental	Savanna	None
Digitaria	1	35	Europe	A	C_4	Accidental	All	None
Elusine	3	1	India, Tropical Africa	A	C_4	Food, accidental	Savanna	None
Elytrigia	1	0	Med. Europe	P	C_3	Accidental	Fynbos, grassland	None
Eragrostis	4	79	Med. Europe, N. Africa	A	C_4	Accidental	Savanna, grassland	None
Festuca	1	8	Europe	P	C_3	Pasture	Fynbos, grassland	None
Gasrtidium	1	0	Medit. Europe	A	C_3	Accidental	Fynbos, renosterveld	None
Hainardia	1	0	Medit. Europe	A	C_3	Accidental	Fynbos	None
Holcus	1	1	Europe	P	C_3	Pasture, accidental	Fynbos, savanna, forest	None
Hordeum	3	1	Europe, S. America	A, P	C_3	Accidental	Fynbos, Nama karoo	None
Lagurus	1	0	Med. Europe	A	C_3	Ornamental	Fynbos	None
Lamarckia	1	0	Med. basin	A	C_3	Ornamental	Fynbos	None
Lolium	4	0	Europe	A, P	C_3	Pasture, accidental	Fynbos, grassland, karoo, savanna	PW
Lophochloa	2	0	Europe	A	C_3	Accidental	Fynbos, succulent karoo, savanna	None
Microlaena	1	0	Australasia	P	?	Accidental	Forest	None
Nasella	5	0	S. America	P	C_3	Accidental	Fynbos, grassland	1
Panicum	1	40	N. America	P	C_3 or C_4	Accidental	Grassland	None
Parapholis	1	0	Europe	A	C_3	Accidental	Fynbos, succulent karoo, savanna	None
Paspalum	3	3	S. America	P	C_4	Pasture	Grassland, savanna, Nama karoo	None
Pennisetum	4	8	N. Africa	P	C_4	Ornamental	Fynbos, succulent karoo, grassland	1, PW
Periballia	1	0	Med. Basin	A	C_3	Accidental	Fynbos	None
Phalaris	6	0	Med Europe, Canary Island, U.S.A., S. America	A, P	C_3	Food, accidental	Fynbos, savanna	None
Poa	3	3	Europe	A,P	C_3	Ornamental	Fynbos, grassland, savanna, succulent karoo	None
Polypogon	2	2	Europe	A	C_3	Accidental	Fynbos, succulent karoo, Nama karoo, grassland, savanna	None
Puccinellia	2	2	Europe	P	C_3	Accidental	Wetland	None
Setaria	2	19	Tropical America	A, P	C_4	Pasture, food	Fynbos, savanna	None
Sorghum	2	1	Med. Europe, Tropical Africa	A, P	C_4	Pasture	Fynbos, grassland, savanna, succulent karoo	2
Sphenopus	1	0	Europe	A	C_3	Accidental	Wetland	None
Stipa	6	1	Med. Basin, Mexico, S. America, Australia	A, P	C_3	Accidental	Fynbos, Nama karoo	None
Vulpia	4	0	Europe	A	C_3	Accidental	All	None

*Origin, photosynthetic (carbon) pathway and distribution data extracted from Gibbs Russell *et al.*[5] and Fish.[6] Longevity: A = annual or ephemeral, P = perennial. Legal status from Henderson[8], where 1 = declared weed which must be controlled, 2 = declared invader to be controlled outside demarcated areas, and PW = proposed weed.

season because of a build-up of fibrous, unpalatable leaves and stems. Avoidance of these alien species by livestock and game may well give them an advantage over grazing-adapted indigenous species by substituting fire for grazing as the dominant disturbance regime.

Spanish reed is apparently sterile in southern Africa, but spreads effectively by vegetative reproduction, often being washed downstream from numerous plantings as building material, windbreaks or for soil stabilization. Listed among the five worst invaders in the provinces of Gauteng and Limpopo (formerly Transvaal) in 1976,[16] Spanish reed was later recognized as a national problem because this and other fast-growing riparian invaders pose a threat to water security for South Africa's growing human population. Because of its large size and

Fig. 1. A dense stand of Spanish reed (*Arundo donax*) in the Huis River, between Oudtshoorn and Calizdorp in the Little Karoo. Such stands can change hydrological processes and may increase transpiration.

tendency to form dense stands on riverbanks (Fig. 1), Spanish reed also has potential to alter stream hydrology and sedimentology, to increase fire intensity,[10] and to reduce the diversity of riparian fauna and flora. Another grass that exploits an unstable habitat and moving water for dispersal is marram. This grass was widely planted on the South African coast to stabilize damaged dunes.[9] During high tides, viable rhizomes of this species can wash out of the sand and be transported hundreds of kilometres by near-shore sea currents.[17]

Tussock-grass invasions became evident in summer rainfall montane grassland pastures in the Eastern Cape, Free State and Mpumalanga provinces in the 1970s. These grasses reduce the forage value of natural pastures, and control by a combination of herbicide treatment, manual removal and improved grazing practice is costly.[18] The potential of this South American grass to transform large areas of natural pasture had been demonstrated in similar habitats in New Zealand in the 1940s.[19]

Fountain grass, a C_4 species from the arid Atlas Mountains of north Africa, has escaped from horticulture in arid and semi-arid Australia, Fiji, Hawaii, North America, Namibia, South Africa, Zambia and Zimbabwe.[20,21] It establishes best on denuded, fertile rocky soils,[21,22] and its increase in abundance is promoted by grazing because its barbed leaves are relatively unpalatable to ungulates.[23] The absence of natural seed predators gives the species a further advantage in Hawaii,[24] and possibly also in South Africa.[21] Through accumulation of unpalatable, fibrous dead leaf mass it suppresses dry forest regeneration[23] as well as increasing the frequency of fires in Hawaii.[20] Fountain grass can be found in abundance along road edges and on road cuttings on the outskirts of most Karoo towns,[25] where it has spread, presumably on vehicles, from gardens and street plantings. Although fountain grass is largely confined to disturbed habitats (such as mine dumps, road cuttings, and embankments) it has invaded other habitats. Examples include the tributaries of the Orange River at Augrabies, small drainage lines in natural veld in the southern Karoo and in erosion gullies in the Windhoek district of Namibia,[26] where it co-occurs with indigenous *Heteropogon contortus*, a grass that it out-competes in mesic habitats of Hawaii.[22,23] On the basis of fountain grass performance in Hawaii and on the Cape Peninsula,[21] it is most likely to spread into disturbed or sparse vegetation on fertile soils. Fynbos and renosterveld shrublands on shale and granite, and moist habitats such as drainage lines in the karoo, are therefore vulnerable to invasion, particularly after fire or disturbance such as woody plant clearing. The establishment of populations of fountain grass is likely to disadvantage indigenous plant species by increasing fire frequencies in fynbos shrublands or promoting fires in non fire-adapted vegetation, such as the succulent karoo. The underlying mechanism appears simple — stands of unpalatable invasive grass, rejected by grazing mammals, provide sufficient fuel to promote frequent fires, which allow the invasive grass to out-compete the indigenous vegetation (which is either not fire-adapted or adapted to longer fire cycles), and thereby to spread at the expense of indigenous vegetation.

At present the only way of reducing the densities of Spanish reed, pampas grass, tussock-grass and fountain grass is through mechanical and chemical removal.[27] However, biocontrol organisms, including insects and microbial pathogens, are presently under evaluation for Spanish reed, tussock grass and some other perennial grasses in Australia and the United States (H.G. Zimmermann and A. Witt, pers. comm.), and may soon offer a more cost-effective and sustainable management option for these and other perennials in South Africa.

Annual grasses

Annual grasses complete their life cycles in a single year. Their ephemeral lifestyle allows them to take advantage of rare favourable conditions, for example by invading arid areas following years of above-average rainfall.

In common with other alien organisms,[58] annual grasses are usually inconspicuous for many decades after their arrival in an ecosystem as they adapt to the local environment, and then increase exponentially in distribution and abundance (Fig. 2). Annual cheat grass (*Bromus tectorum*) was introduced to the United States from Eurasia in the 1800s, probably as a crop

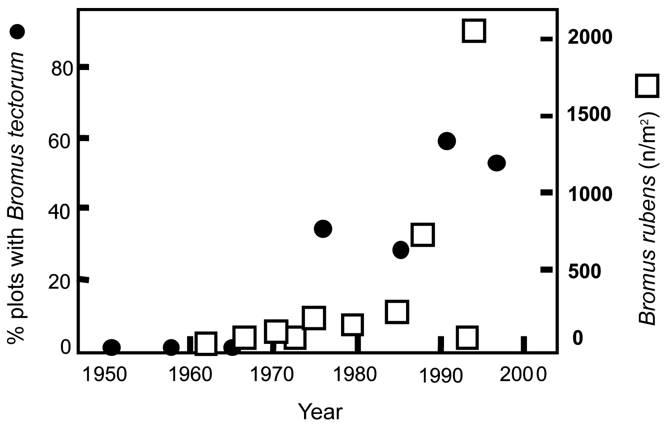

Fig. 2. An exponential increase in the abundance of alien annual Brome grasses took place in the 1980s in many parts of the United States. This graph shows the pattern of increase in *Bromus tectorum* (dots) in the ungrazed National Engineering and Environmental Laboratory, Idaho,[28] and in *B. rubens* (squares) at the Nevada test site.[29]

Table 2. Contribution of alien grass seedlings to plants emerging from the soil seed bank and from dung of indigenous herbivorous mammals foraging in a mixture of natural renosterveld vegetation and abandoned crop-land.

Seedling type	Seedlings emerged per m² top soil	Seedlings emerged per kg air-dry dung				
		Zebra	Eland	Wildebeest	Other*	Average
Total seedlings	121 600	1170	228	286	947	657
Briza species	8 372	11	3	1	28	22
Bromus diandrus	3 028	38	0	6	0	11
Bromus pectinatus	0	3	0	0	0	1
Vulpia myuros	53 800	492	80	32	30	159
Lolium species1	572	14	7	2	3	26
Lolium species 2	0	2	0	0	0	1
Poa annua	543	29	1	31	12	18
Total alien grass (%)	55	50	40	25	8	31
Indigenous grass (%)	19	40	45	11	76	50
Forbs & geophytes (%)	26	9	14	64	17	18
Shrubs (%)	0	0	1	0	0	1

*'Other herbivores' included bontebuck, red hartebeest and springbok. Data from Shiponeni.[41]

contaminant.[28] Being adapted to disturbance, it spread rapidly with infrastructure and domestic livestock and now dominates the 40 million ha of the inter-montane western areas of the U.S.A.[29] Once established, its advance into semi-desert shrublands was rapid[30,31] and exacerbated by over-grazing that reduced perennial grass cover.[28]

Although initially welcomed as alternative forage, its yield is too variable for an economically sustainable livestock industry. In dry years there is zero production because the grass fails to germinate, whereas high biomass production in wet years promotes fire.[28] Flammable, fine cheat grass fuel has increased the incidence and average extent of fires,[32] and reduced fire-return intervals from 60 to five years.[29] Whereas infrequent hot fires in woody fuel reduce cheat grass seedbanks, soil-stored cheat grass seeds survive low intensity grass fires.[28] Post-fire succession towards indigenous perennials is prevented by the fast-growing annual grasses which out-compete seedlings of perennial plants.[28] The addition of nitrogen through fertilizers[33] or nitrogen-fixing plants[34] increases the growth and abundance of this and other annual grasses relative to perennials. The grass–fire cycle[2] has transformed millions of hectares from shrubland with a perennial grass understorey to annual grassland, increasing fire hazard, and reducing grazing security and biodiversity.[35]

Fragmentation of natural vegetation by roads and transformation for crop production facilitates alien grass invasion through nitrogen runoff from agricultural land and movement of domestic livestock between fields and natural vegetation[36]. In south-western Australia, grazing is a major contributor to the invasion of mixed shrubland and woodland by annual alien grasses and forbs. As in the case of cheat grass, these herbaceous plants out-compete and prevent the establishment of seedlings of native woody plants.[36] Biological 'soil crusts' inhibit cheat grass establishment[37], but both livestock and fire reduce cryptogram cover on friable soil surfaces,[29] facilitating invasion. The only way to reverse annual grass invasions appears to be re-seeding of invaded areas with perennial plants, combined with the exclusion of fire and grazing animals.[30,38]

Most of the annual alien grasses in South Africa belong to the Pooidea (species in the genera *Avena, Briza, Bromus, Hordeum, Lolium, Phalaris, Poa, Stipa,* and *Vulpia)* and originated in fire-prone, grazed ecosystems around the Mediterranean basin. Once introduced as seed contaminants in croplands, they are efficiently transported by grazing mammals into natural vegetation. Most have seeds with barbed awns and are transported on the hide or hair of grazing animals.[39] Viable seeds are also dispersed in large quantities in the dung of domestic livestock[40] and wildlife, particularly zebras.[41] A study has shown that alien annual grasses constituted 31% of all seedlings emerging from the dung of indigenous African ungulates grazing in fragmented renosterveld shrublands and on abandoned croplands in the Western Cape (Table 2).[41] The indigenous winter-growing grasses of the Western Cape are generally perennials of the tribe Arundinoidea. Adapted for drought tolerance rather than avoidance, they exclude the annual invaders where the vegetation remains undisturbed.[42] Alien annual grasses, although often evident only on small-scale disturbances in natural vegetation,[43] become more prevalent at a landscape scale following fire or heavy grazing.[44] They produce abundant seed (for example, an Australian pasture with a cover of *Vulpia* grasses of 13% produced 265 000 seeds per square metre) and may dominate soil seedbanks in disturbed Western Cape vegetation (Table 2). Some of the seed that remains ungerminated in the soil seed bank enables most annual grasses to persist and re-appear after further disturbances[45] such as vegetation clearing, fire, drought and heavy grazing.

In common with cheat grass, there is evidence that the annual grasses invasive in the fynbos, renosterveld and strandveld vegetation types of the Western Cape benefit from nutrient enrichment. This can originate from land use in the surrounding area, or through woody plant invasion. When alien nitrogen-fixing leguminous species such as Port Jackson willow (*Acacia saligna*) and lupins *(Lupinus luteus)* invade nutrient-poor soils, soil organic matter and mineralization rates increase, and more nitrogen is available.[46–48] In nursery trials the alien grasses *Briza maxima* and *Bromus diandrus* grew better on soils taken from beneath alien wattles (*Acacia* species) than on soils from native fynbos shrublands.[47] Alien grasses thus tend to dominate areas cleared of alien legumes and other trees that increase soil organic matter.[49] Whereas soil nitrogen additions benefit alien annuals, they may decrease species richness of indigenous flora that evolved with low soil nitrogen levels.[50]The densest alien grass stands occur in native vegetation fragments that receive runoff from surrounding wheatlands. One such example is the Tienie Versfeld Geophyte Reserve, where the National Botanical Institute, in collaboration with the Working for Water programme, introduced grass control trials in 2003 (Fig. 3).

The effects of annual alien grass invasions on southern African ecosystems have not been investigated to any significant degree. In lowland fynbos shrublands, indigenous herbaceous plant diversity was negatively related to the density of alien annuals.[43] Similarly, in the succulent karoo, annual *Stipa capensis*

Fig. 3. A Working for Water team establishing alien grass removal experiments at the Tienie Versfeld Geophyte Reserve near Darling in the Western Cape. Grass was experimentally removed by hoeing, cutting, burning and the use of herbicides. The response of indigenous plants, particularly rare bulbs, will be compared among treatments.

(dubiously indigenous but probably of Mediterranean origin) dominated sites with reduced perennial shrub cover and herbaceous diversity.[44] Although it has been inferred from these studies that dense stands of grasses appear to pose a direct threat to the growth and reproduction of indigenous annuals and geophytes through competition, the hypothesis remains to be tested. At this stage it is uncertain how indigenous species and life-forms are responding to the novel cocktail that includes altered grazing and fire regimes, fragmentation, nutrient enrichment, alien grasses, climate and atmospheric change. There is also debate as to whether the colonization by annual alien grasses of areas cleared of woody legumes should be viewed as an asset or a hazard. Given adequate rain for their germination, these plants provide rapid cover following clearing or burning of alien wattles (*Acacia* species),[51] controlling soil movement, possibly out-competing wattle seedlings and changing the appearance of denuded landscapes. On the other hand, it is possible that they might be reducing the survival of the few indigenous plants that emerge from seed-banks long suppressed by woody invaders.

There appear to be no quick fixes for annual grass invasions. Annual grass weeds that cause economic losses in crop and pasture systems worldwide are killed by herbicides, provided that they are applied thoroughly enough to preclude re-invasion in subsequent years. Not only is this plant-killing approach expensive, but thoroughness has selected for multiple herbicide resistance in some species of *Avena, Lolium* and *Vulpia* in Australia,[45,52,53] Chile, France, Israel and South Africa.[54] A more sustainable approach to annual grass weed reduction is the prevention or reduction of seeding by microbial pathogens (such as smut fungus) or other organisms.[52,55] An alternative approach, more suitable for use in natural vegetation, is nitrogen immobilization through the application of carbon in the form of a mulch of sawdust (95%) and sucrose (5%). In Minnesota, this treatment facilitated the establishment of perennial prairie plants by reducing the growth of annual weeds.[56] In the United States this approach is supplemented by the planting of indigenous plants that will out-compete the annuals, as well as by weeding or burning and grazing in the early spring before indigenous species start to grow, so as to reduce competition from annual grasses.[57] Follow-up management usually involves protection from fire and grazing. Although control of alien annual grasses in indigenous vegetation has been attempted in small nature reserves at Nieuwoudville and Darling (in the Western Cape) using a combination of herbicides and grazing, as yet no rigorous comparison of various methods has been published.

Global change and grass invasions

The photosynthetic pathways of grasses are either of the C_3 type (a carbon-fixing pathway that is most efficient where the growing season is cool — in temperate and high altitude environments) or the tropical C_4 type that is more efficient where the growing season is warm. Most of southern Africa's grass species are of the C_4 type, whereas all the annual invasive alien species, and some of the most invasive perennials (pampas, tussock and feather-top grasses and Spanish reed), are C_3 (Table 1). C_4 grasses use nitrogen more efficiently[11] so can out-compete C_3 grasses in undisturbed vegetation. However, global change is likely to change this competitive balance. Vegetation clearing, the addition of fertilizers and increases in atmospheric nitrogen all increase nitrogen availability in the soil, giving C_3 grasses an advantage over C_4 plants. Furthermore, an increase in atmospheric CO_2 will improve nitrogen-use efficiency of C_3 grasses, giving them an even greater advantage over C_4 grasses.[11]

The advance of annual and perennial C_3 grass invasions from patch to landscape scales is clearly driven by disturbance and exacerbated by nutrient enrichment (Fig. 4). Biome-wide invasions by alien grasses, where the alien species become an integral part of the vegetation of a given biome and alter its composition and functioning, have not yet occurred in southern Africa. However, given global change scenarios, including increased atmospheric nitrogen,[59] warmer conditions and greater variability in rainfall quantity and seasonality, all of which would disadvantage the indigenous plants of the fynbos and succulent karoo biomes,[60] and the tendency of alien grasses to facilitate frequent, low-intensity fires, annual grasses do have potential to take control of processes in winter rainfall biomes. Moreover, increasing atmospheric carbon dioxide and nitrogen would tend to disadvantage C_4 grasses and enable C_3 aliens to establish within grassland and savanna.[61,62]

It is therefore predicted that global changes of this type will reduce the ability of indigenous C_4 grasses to block invasions by C_3 species and lead to an increase in alien annual and unpalatable C_3 perennial grasses in all our rangeland biomes. These are likely to increase fire frequency and reduce grazing

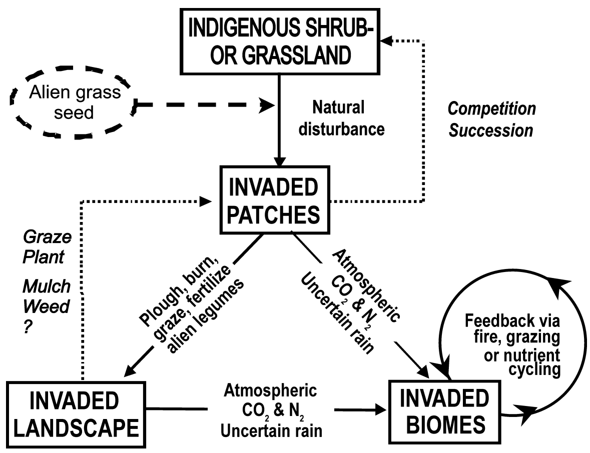

Fig. 4. Process of C_3 invasive alien grass introduction, establishment, spread, and persistence in shrublands or C_4 grasslands . Adapted from Richardson *et al.*[11]

value, further disadvantaging C_4 African grasses that evolved with grazing mammals. As rangeland transformations of this type would have major economic consequences, further investigation into the effects of global change on interactions between C_3 and C_4, alien and indigenous grasses is needed as well as pre-emptive research on biocontrol options for grass species that have potential to transform southern African ecosystems.

Conclusions

Alien grasses, both annual and perennial, are a costly problem for agriculture, biodiversity conservation, fire and water management and rehabilitation following disturbance or clearing of woody weeds. They are efficiently dispersed by wind, vehicles and animals, produce many seeds and generally maintain persistent seed banks with few, if any, specialized seed predators. Because they benefit from anthropogenic land transformation, and from various aspects of global change, and because they alter ecosystems to their own advantage, the problems they pose are likely to increase. In South Africa, alien grasses have become increasingly prevalent over the past three decades. Conservation managers need to know what grass invasions are doing to indigenous plant and animal species, how current grazing and fire management affects their abundance, and how to and whether to control grasses in natural vegetation and as part of rehabilitation management.

This review of the effects of alien grasses in other parts of the world suggests that alien grasses will become increasingly prevalent in South Africa, and that more research, aimed at identifying appropriate management responses, would be justified.

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1. Richardson D.M. and van Wilgen B.W. (2004). Invasive alien plants in South Africa: How well do we understand the ecological impacts? *S. Afr. J. Sci.* **100**, 45–52.
2. D'Antonio C.M. and Vitousek P.M. (1992). Biological invasions by exotic grasses the grass/fire cycle and global change. *Annu. Rev. Ecol. Syst.* **23**, 63–87
3. Ryves T.B., Clement E.J. and Foster M.C. (1996). *Alien Grasses of the British Isles.* Botanical Society of the British Isles, London.
4. Lonsdale W.M. (1994). Inviting trouble: introduced pasture species in northern Australia. *Austral. J. Ecol.* **19**, 345–54.
5. Gibbs Russell G.E., Watson L., Koekemoer, M., Smook L., Barker N.P., Anderson H.M. and Dallwitz M.J. (1990). Grasses of Southern Africa. *Mem. Bot. Surv. S. Afr.* **58**, National Botanical Institute, Pretoria.
6. Fish L. (2000). Poaceae. In *Seed plants of southern Africa. Strelitzia* **10**, 659–762, ed. O.A. Leistner. National Botanical Institute, Pretoria.
7. Richardson D.M., Rundel P.W. and van Wilgen B.W. (2002). Impacts of invasive alien plants on fire regimes. In Abstracts. *The Ecological Society of America 87th Annual Meeting,* p. 44. Ecological Society of America, Tucson, Arizona.
8. Henderson L. (2001). *Alien Weeds and Invasive Plants — A complete guide to declared weeds and invaders in South Africa.* Plant Protection Research Institute Handbook no. 12, Agricultural Research Council, Pretoria.
9. Hertling, U.M. and Lubke, R.A. (2000). Assessing the potential for biological invasion — the case of *Ammophila arenaria* in South Africa. *S. Afr. J. Sci.* **96**, 520–527.
10. D'Antonio C.M. (2000). Fire, plant invasions, and global changes. In *Invasive Species in a Changing World,* eds H.A Mooney and R.J. Hobbs, pp. 65–93. Island Press, Washington, D.C.
11. Richardson D.M., Bond W.J., Dean W.R.J., Higgins S.I., Midgley G.F., Milton S.J., Powrie L.W., Rutherford M.C., Samways M.J. and Schulze R.E. (2000). Invasive alien organisms and global change: a South African perspective. In *Invasive Species in a Changing World,* eds H.A. Mooney and R.J. Hobbs, pp. 303–349. Island Press, Washington, D.C.
12. Low T. (1999). *Feral Future.* Viking-Penguin Books, Victoria, Australia.
13. Milton S.J., Siegfried W.R. and Dean W.R.J. (1990). The distribution of epizoochoric plant species: a clue to the prehistoric use of arid karoo rangelands by large herbivores. *J. Biogeog.* **17**, 25–34.
14. McClaran M. and Anable M.E. (1992). Spread of introduced Lehman lovegrass along a grazing intensity gradient. *J. Appl. Ecol.* **29**, 92–98.
15. Witt A.B.R and McConnachie A.J. (in press) The potential of classical biological control of invasive grass species with special reference to invasive *Sporobolus* spp. (Poaceae) in Australia. *Proc. XI International Symposium on Biological Control of Weeds,* Canberra, 27 April – 2 May 2003.
16. Wells M.J.; Duggan K. and Henderson L. (1980). Woody plant invaders of the central Transvaal. *Proc. 3rd National Weeds Conference, South Africa,* 11–23.
17. Aptekar R. and Rejmánek M. (2000). The effect of sea-water submergence on rhizome bud viability of the introduced *Ammophila arenaria. J. Coastal Cons.* **6**, 107–111
18. Viljoen D.B. (1987). Pasture recovery after nasella tussock control with tetrapion. *Appl. Plant Sci.* **1**, 18–22.
19. Healy A.J. (1945). Nasella tussock: field studies and their agricultural significance. *New Zealand Dept. Sci. Ind. Res. Bull.* **91**, 5–90.
20. Williams D.G., Mack R.N. and Black R.A. (1995). Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. *Ecology* **76**, 1569–1580.
21. Milton S.J., Hoffmann J.H., Bowie R.C.K., D'Amico J.D., Griffiths M., Joubert D.F., Loewenthal D., Moinde N.N., Seymour C., Toral-Grande M.V. and Wiseman R. (1998). Invasive fountain grass on the Cape Peninsula. *S. Afr. J. Sci.* **94**, 57–58.
22. Goergen E. and Daehler C.C. (2001). Reproductive ecology of a native Hawaiian grass (*Heteropogon contortus*; Poaceae) versus its invasive alien competitor (*Pennisetum setaceum*; Poaceae) *Int. J. Plant Sci.* **162**, 317–326.
23. Cabin J.R., Weller G.S., Lorence H.D., Flynn W.T., Sakai K.A., Sandquist D. and Hadway J.L. (2000). Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. *Conserv. Biol.* **14**, 439–453.
24. Goergen E. and Daehler C.C. (2001). Inflorescence damage by insects and fungi in native pili grass (*Heteropogon contortus*) versus alien fountain grass (*Pennisetum setaceum*) in Hawaii. *Pacific Sci.* **55**, 129–136.
25. Milton S.J. and Dean W.R.J. (1998). Alien plant assemblages near roads in arid and semi-arid South Africa. *Diversity and Distributions* **4**,175–188.
26. Joubert D.F. and Cunningham P.L. (2000). The distribution and invasive potential of *Pennisetum setaceum* (Fountain Grass) in Namibia. *Technical Report: NR/2000/1,* School of Natural Resources and Tourism, Polytechnic of Namibia, Windhoek.
27. Bromilow C. (2001). *Problem Plants of South Africa — a guide to identification and control of more than 300 invasive plants and other weeds.* Briza Publications, Pretoria.
28. Young J.A. and Allen F.L. (1997). Cheat grass and range science 1930–1950. *J. Range Mngnt* **50**, 530–535.
29. Whisenant S.G. (1990). Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. In *Proc. Symposium on Cheatgrass Invasion, Shrub Die-off and Other Aspects of Shrub Biology and Management.* Intermountain Research Station General Technical Report INT-276, eds E.D. McAurthur, E.M. Romney, S.D.Smith.and P.T Tueller, pp. 4–10. Ogden, Utah.
30. Anderson J.E. and Inouye R.S. (2001). Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecol. Monogr.* **71**, 531–556.
31. Hunter R. (1990). Recent increase in *Bromus* populations on the Nevada test site. In *Proc. Symposium on Cheatgrass invasion, shrub die-off and other aspects of shrub biology and management. Intermountain Research Station General Technical Report* INT-276, eds E.D. McAurthur, E.M. Romney, S.D.Smith.and P.T Tueller, pp. 22–25. Ogden, Utah.
32. Pyke D.A and Knick S.T. (2003). Plant invaders, global change and landscape restoration. In *Rangelands in the New Millennium. Proc. 7th Int. Rangel. Congr.,* eds N. Allsopp, A.R. Palmer, S.J. Milton, K.P Kirkman, G.I.H. Kerley, C.R. Hurt and C.J. Brown, pp. 278–287. Document Transformation Technologies, Pretoria.
33. Paschke M.W., McLendon T. and Redente E.F. (2000). Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosystems* **3**, 144–158.
34. Maron J.L. and Connors P.G. (1996). A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* **105**, 302–312.
35. Knapp P.A. (1996). Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert: history, persistence, and influences to human activities. *Global Environ. Change* **6**, 37–52.
36. Hobbs R.J. (2001). Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. *Conserv. Biol.* **15**, 1522–1528.
37. Wicklow-Howard M., Serpe M., Orm J., Stokes J. and Rosentreter R. (2003). Effects of biological soil crusts on seed germination of *Bromus tectorum.* In *Rangelands in the New Millennium. Proc. 7th Int. Rangel. Congr.,* eds N. Allsopp, A.R. Palmer, S.J. Milton, K.P Kirkman, G.I.H. Kerley, C.R. Hurt and C.J. Brown, pp. 1276–1278. Document Transformation Technologies, Pretoria.
38. Pellant M (1990). The cheatgrass–wildfire cycle. Are there any solutions? In *Proc. Symposium on Cheatgrass Invasion, Shrub Die-off and Other Aspects of Shrub biology and Management.* Intermountain Research Station General Technical Report INT-276, eds E.D. McAurthur, E.M. Romney, S.D.Smith.and P.T Tueller, pp. 11–18. Ogden, Utah.
39. Shmida A. and Ellner S. (1983). Seed dispersal on pastoral grazers in open Mediterranean chaparral, Israel. *Israel J. Bot.* **32**, 147–159.

40. Malo J.E. and Suarez F (1995) Herbivorous mammals as seed dispersers in a Mediterranean dehesa. *Oecologia* **104**, 246–255.
41. Shiponeni N.N. (2003). *Dispersal of seeds as a constraint in revegetation of old fields in Renosterveld vegetation in the Western Cape, South Africa.* M.Sc. thesis, University of Stellenbosch.
42. Linder H.P. (1989). Grasses in the Cape Floristic Region: phytogeographical implications. *S. Afr. J. Sci.* **85**, 502–505.
43. Vlok J.H.J. (1988). Alpha diversity of lowland fynbos herbs at various levels of infestation by alien annuals. *S. Afr.J. Bot.* **54**, 623–627.
44. Steinschen A.K., Görne A. And Milton S.J. (1996). Threats to the Namaqualand flowers: outcompeted by grass or exterminated by grazing? *S. Afr. J. Sci.* **92**, 237–242.
45. Dowling P.M. (1996).The ecology of *Vulpia. Plant Protection Quarterly* **11** Suppl. 1, 204–206
46. Stock W.D., Wienand K.T. and Baker A.C. (1995). Impacts of invading N_2 fixing *Acacia* species on patterns of nutrient cycling in two Cape ecosystems: evidence from soil incubation studies and ^{15}N natural abundance values. *Oecologia* **101**, 375–382.
47. Yelenik S.G., Stock W.D. and Richardson D.M. (in press). Ecosystem-level impacts of invasive *Acacia saligna* in the South African fynbos. *Restoration Ecology.*
48. Van der Berckt T. (2002). *The ecological effects of* Acacia saligna *in a Sand Plain Fynbos ecosystem of the Western Cape, South Africa.* M.Sc. thesis, University of Stellenbosch.
49. Richardson D.M. and van Wilgen B.W. (1986). Effects of thirty-five years of afforestation with *Pinus radiata* on the composition of mesic mountain fynbos near Stellenbosch. *S. Afr. J. Bot.* **52**, 309–315.
50. Brooks M.L. (2003). Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *J. Appl. Ecol.* **40**, 344–353.
51. Euston-Brown D.I.W., Botha S. and Bond W.J. (2002). *The influence of fire severity on post fire vegetation recovery on the Cape Peninsula.* Unpubl. Report, Department of Water Affairs and Forestry: Working for Water programme, Cape Town.
52. Medd R.W. (1996). Ecology of wild oats. *Plant Prot. Quart.* **11**, Suppl.1, 185–187.
53. Gill G.S. (1996). Why annual ryegrass is a problem in Australian agriculture. *Plant Prot. Quart.* **11** Suppl.1, 185–187.
54. Cairns A. and Eksteen E. Group G/9 resistant rigid ryegrass (*Lolium rigidum*), South Africa. Website: Weeds Science Society of America — International Survey of Herbicide-resistant weeds. Http://www.weedscience.org (accessed: September 2003).
55. Hetherington S.D. and Auld B.A. (1996). Biological control of annual grass weeds — progress and prospects. *Plant Prot. Quart.* **11** Suppl. 1, 215–216.
56. Blumenthal D.M., Jordan N.R. and Russelle M.P. (2003). Soil carbon addition controls weeds and facilitates prairie restoration. *Ecol. Appl.* **13**, 605–615.
57. Pellant M. (2003). The Great Basin restoration initiative: challenges and tools to restore a desert landscape in the Western United States. In *Rangelands in the New Millennium., Proc. 7th Int. Rangel. Congr.*, eds N. Allsopp, A.R. Palmer, S.J. Milton, K.P. Kirkman, G.I.H. Kerley, C.R. Hurt and C.J. Brown, pp. 1241–1243. Document Transformation Technologies, Pretoria.
58. Dean W.R.J. (2000). Alien birds in southern Africa: what factors determine success? *S. Afr. J. Sci.* **96**, 9–14.
59. Jefferies R.L. and Maron J.L. (1997). The embarrassment of riches: atmospheric deposition of nitrogen and community ecosystem processes. *Trends Ecol. Evol.* **12**, 74–78.
60. Hannah L., Midgley G.F., Lovejoy T., Bond W.J., Bush M., Lovett J.C., Scott D. and Woodward F.I. (2002). Conservation of biodiversity in a changing climate. *Conserv. Biol.* **16**, 264–268.
61. Dukes J.S. (2000). Will the increasing atmospheric CO_2 concentration affect the success of invasive species? In *Invasive Species in a Changing World.* eds H.A. Mooney and R.J. Hobbs, pp. 95–113. Island Press, Washington, D.C.
62. Wand S.J.E, Midgley G.F. and Stock W.D. (2002). Response to elevated CO_2 from a natural spring in a C_4-dominated grassland depends on seasonal phenology. *Afr. J Range Forage Sci.* **19**, 81–92.

A rapid assessment of the invasive status of *Eucalyptus* species in two South African provinces

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Gum trees, or eucalypts (*Eucalyptus* species), have been targeted for invasive alien plant clearing programmes in many parts of South Africa. This has caused some dissatisfaction where the species concerned also have useful characteristics, and stakeholders contend that some of these useful species are not invasive. A rapid assessment of the invasive status of *Eucalyptus* species at 82 sites in South Africa (54 in the Western Cape and 28 in Mpumalanga) indicated that only Red River gum (*E. camaldulensis*) and flooded gum (*E. grandis*) are clearly invasive. Surveys were not undertaken in parts of the Western Cape known to be invaded by spider gum (*E. lehmannii*); the invasive status of this species is well known and is not contested. Red River gum has transformed long stretches of rivers and its importance as a major weed has been underestimated in previous reviews of alien plant invasions in South Africa. Most other species were naturalized. We recommend that projects aimed at clearing eucalypts should focus on riparian areas and nature reserves (where all eucalypts have deleterious effects), but that clearing projects outside these areas should only target species known to be invasive until such time as the invasive status of the other eucalypts (notably sugar gum, *E. cladocalyx*, and karri, *E. diversicolor*) can be ascertained with a greater degree of confidence.

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Introduction

Gum trees, or eucalypts, in the genus *Eucalyptus* number approximately 400 species, almost all of them endemic to Australia.[1] In their native range they occupy a wide variety of habitats and bioclimates. Eucalypts have been very widely planted worldwide.[2] By 1940, approximately 149 *Eucalyptus* species had been established in South Africa. Early introductions took place mainly through the colonial forest administration of the Cape Colony in the late 19th century.[3] In South Africa, eucalypts are now used for timber, poles, firewood, as shelterbelts and ornamentals, and are valuable sources of nectar and pollen necessary for the production of honey.[4,17]

Although eucalypts deliver many benefits to South African society, they also have undesirable influences. Eucalypt plantations use large amounts of water — for example, the afforestation of catchments in Mpumalanga province with eucalypts resulted in the total drying-up of streams 6–12 years after planting.[5] In addition, some eucalypts are considered invasive with potentially negative effects on natural habitats.[6,7]

In terms of the regulations under the Conservation of Agricultural Resources Act (Act No. 43 of 1983), landowners in South Africa are legally responsible for the control of invasive alien plants (including seven species of eucalypts) on their properties. These regulations define three categories of declared weeds and invaders. Category 1 refers to prohibited weeds that must be controlled in all situations. Category 2 includes plants with commercial value that may be planted in demarcated areas subject to a permit, provided that steps are taken to control spread, and planting is prohibited in riparian areas and wetlands. Category 3 includes ornamental plants that may no longer be planted or traded. Specimens may remain in place provided a permit is obtained and steps taken to control their spread.

Recently, concern was raised by beekeepers that extensive clearing of eucalypts would result in a significant reduction in pollen and nectar resources on which the apiculture industry depended. It was argued that this could also have potentially serious consequences for the deciduous fruit industry due to the