

Grasses as invasive plants in South Africa revisited: Patterns, pathways and management



Authors:

Vernon Visser^{1,2,3,4} 
 John R.U. Wilson^{3,4} 
 Kim Canavan⁵
 Susan Canavan³
 Lyn Fish⁶
 David Le Maitre^{3,7} 
 Ingrid Nänni⁴
 Caroline Mashau⁶
 Tim G. O'Connor³ 
 Philip Ivey⁴
 Sabrina Kumschick^{3,4} 
 David M. Richardson³ 

Affiliations:

¹SEEC – Statistics in Ecology, the Environment and Conservation, Department of Statistical Sciences, University of Cape Town, South Africa

²African Climate and Development Initiative, University of Cape Town, South Africa

³Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, South Africa

⁴Invasive Species Programme, South African National Biodiversity Institute, Kirstenbosch Research Centre, South Africa

⁵Department of Zoology and Entomology, Rhodes University, South Africa

⁶National Herbarium, South African National Biodiversity Institute (SANBI), South Africa

⁷Natural Resources and the Environment, Stellenbosch, South Africa

⁸South African Environmental Observation Network (SAEON), Pretoria, South Africa

Background: In many countries around the world, the most damaging invasive plant species are grasses. However, the status of grass invasions in South Africa has not been documented recently.

Objectives: To update Sue Milton's 2004 review of grasses as invasive alien plants in South Africa, provide the first detailed species level inventory of alien grasses in South Africa and assess the invasion dynamics and management of the group.

Method: We compiled the most comprehensive inventory of alien grasses in South Africa to date using recorded occurrences of alien grasses in the country from various literature and database sources. Using historical literature, we reviewed past efforts to introduce alien grasses into South Africa. We sourced information on the origins, uses, distributions and minimum residence times to investigate pathways and patterns of spatial extent. We identified alien grasses in South Africa that are having environmental and economic impacts and determined whether management options have been identified, and legislation created, for these species.

Results: There are at least 256 alien grass species in the country, 37 of which have become invasive. Alien grass species richness increased most dramatically from the late 1800s to about 1940. Alien grass species that are not naturalised or invasive have much shorter residence times than those that have naturalised or become invasive. Most grasses were probably introduced for forage purposes, and a large number of alien grass species were trialled at pasture research stations. A large number of alien grass species in South Africa are of Eurasian origin, although more recent introductions include species from elsewhere in Africa and from Australasia. Alien grasses are most prevalent in the south-west of the country, and the Fynbos Biome has the most alien grasses and the most widespread species. We identified 11 species that have recorded environmental and economic impacts in the country. Few alien grasses have prescribed or researched management techniques. Moreover, current legislation neither adequately covers invasive species nor reflects the impacts and geographical extent of these species.

Conclusion: South Africa has few invasive grass species, but there is much uncertainty regarding the identity, numbers of species, distributions, abundances and impacts of alien grasses. Although introductions of alien grasses have declined in recent decades, South Africa has a potentially large invasion debt. This highlights the need for continued monitoring and much greater investment in alien grass management, research and legislation.

Introduction

In many parts of the world, grasses are among the most damaging and widespread alien plant species (D'Antonio, Stahlheber & Molinari 2011; D'Antonio and Vitousek 1992; Gaertner et al. 2014). In the Americas, Australia and on many tropical islands, grasses have transformed ecosystems, usually by altering the natural fire cycle (D'Antonio and Vitousek 1992; Gaertner et al. 2014). By contrast, South Africa has fewer invasive grasses, and alien plant control efforts are dedicated primarily to combating woody plant invasions. The only grass species that has been widely targeted for control operations by the Working for Water Programme is *Arundo donax*,

Corresponding author: Vernon Visser, vervis@gmail.com

Dates: Received: 05 Sep. 2016 Accepted: 06 Dec. 2016 Published: 31 Mar. 2017

How to cite this article: Visser, V et al., 2017, 'Grasses as invasive plants in South Africa revisited: Patterns, pathways and management', *Bothalia* 47(2), a2169. <https://doi.org/10.4102/abc.v47i2.2169>

Copyright: © 2017. The Authors. Licensee: AOSIS. This work is licensed under the Creative Commons Attribution License.

Note: This paper was initially delivered at the 43rd Annual Research Symposium on the Management of Biological Invasions in South Africa, Goudini Spa, Western Cape, South Africa on 18-20 May 2016.

Read online:



Scan this QR code with your smart phone or mobile device to read online.

although < 0.5% of the total budget for alien plant control was allocated to managing this species (Table 2 in van Wilgen et al. 2012). Grasses also do not feature in the National Strategy for Dealing with Biological Invasions in South Africa (Department of Environmental Affairs [DEA] 2014). The relative paucity of grass invasions in South Africa might be because of high fire frequencies in African grasslands and savannas excluding alien grasses (Visser et al. 2016). It would, therefore, seem that grass invasions in South Africa are generally neither common nor widespread and that they do not pose a major risk. However, there are several reasons to be concerned about undetected and possible future grass invasions.

The last review of alien grasses in South Africa was published more than a decade ago (Milton 2004). This review highlighted major gaps in our knowledge. We do not know how many alien grasses are in South Africa nor their identity or status on the introduction-naturalisation-invasion (INI) continuum (Blackburn et al. 2011; Richardson and Pyšek 2012). While it appears that South Africa experienced lower introduction effort of alien grasses relative to other regions of the world, it was one of the countries most actively engaged in trialling alien grasses at pasture research stations (Visser et al. 2016). However, there is no consolidated inventory of species cultivated in these pasture research trials. Without a comprehensive (or as near as possible) inventory of alien grasses, it is impossible to ascertain all the risks.

We also have inadequate knowledge of the introduction pathways of alien grasses, which is needed to determine 'introduction debt', the number of species that are likely to be introduced to South Africa in the future (Rouget et al. 2016). Introduced but not yet naturalised or invasive grasses might also represent an invasion debt as they might invade in the future, while current invasions might spread to new areas and cause increasing negative impacts (Rouget et al. 2016). However, we need information on the origins of alien grasses, their residence times (Wilson et al. 2007) and propagule pressure to be able to estimate establishment and spread debts (Rouget et al. 2016). We also have very poor knowledge of alien grass impacts in South Africa, with Milton's (2004) review relying mostly on published impacts of alien grasses in other parts of the world.

We should be particularly wary of changes in invasions in the group in the face of rising atmospheric CO₂ levels and concomitant global climatic change. Grass species using the C₄ photosynthetic pathway have higher nitrogen-use efficiency relative to those that use the C₃ photosynthetic pathway (Taylor et al. 2010). It has been suggested that the competitive dominance of C₄ grasses across much of South Africa is because of this comparative advantage, but that at higher CO₂ levels, this advantage disappears and alien C₃ grasses will be more likely to invade South African grasslands in the future (Milton 2004; Richardson et al. 2000). Grasses have also been shown to exhibit strong phylogenetic conservatism of climatic niches (Edwards and Smith 2010)

and climate change could have differential consequences for grasses of particular phylogenetic clades.

Since 2004, an increasing amount of information on alien grass distributions, origins, traits and impacts in South Africa has become available from online databases, surveys and research projects. The legal framework for alien grass management in South Africa has also changed substantially with the introduction of the Alien and Invasive Species (A&IS) regulations under the *National Environmental Management: Biodiversity* (NEM:BA) Act 10 of 2004. A number of alien grasses were listed as invasive in 2014 (NEM:BA Alien and Invasive Species List 2016; A&IS regulations) and now have specific management requirements or are prohibited from being imported. Moreover, the A&IS regulations require the publication of a national status report on listed invasive species every 3 years, the purpose of which is to monitor the status of listed species and the effectiveness of the regulations and associated control measures (Wilson et al. 2017).

Given the demonstrated potential for alien grasses to become problematic invaders elsewhere in the world, the increased availability of data in South Africa and new legislation regarding alien species, we aim to provide an updated review of the status of alien grasses in South Africa. To this end, we collate the first detailed species-level inventory of alien grasses in South Africa. We use this inventory, together with other literature, to address some of the information gaps identified above, including investigating (1) minimum residence times (MRTs) of alien grasses in South Africa, (2) pathways of introduction and spread, (3) areas that are potentially being most impacted by alien grasses, (4) impacting species and the nature of their impacts and (5) information on management of alien grasses. This information is needed to make recommendations for future management of alien grasses in South Africa.

Methods

Inventory

We produced an inventory of alien grasses in South Africa (Online Appendix) using additional data sources to contribute to an already extensive inventory that we used for a recent publication (Visser et al. 2016). The inventory is based on an extensive search of the scientific and grey literature and of distribution databases (Appendix 1). We first checked species names from all sources against The Plant List (www.theplantlist.org) and corrected them to accepted species. We changed infra-specific names to the species level and removed hybrid species, but kept unresolved names. In a final refinement of the list, we flagged all species for which there was only one data source for its occurrence in South Africa, or for which there were fewer than five distribution records (see below for more information on distribution data). These species were manually checked by inspecting the original data source (either a reference or herbarium specimen). As measures of confidence in the presence of an alien grass species in South Africa, we flagged

all species (1) with only one data source for its occurrence in South Africa, (2) with no distribution data and (3) no herbarium records.

We also determined the status of each species on the INI continuum (introduced = species present outside of its native range either in cultivation or in the wild, but in the latter case, not yet reproducing. Hereafter, all references to species that are 'introduced' should be interpreted according to the aforementioned definition; naturalised = species that are reproducing in their alien range, but not spreading substantially; invasive = self-sustaining species that spread over large distances; Blackburn et al. 2011; Richardson and Pyšek 2012), relying on references to assign species' statuses (Appendix 1).

Minimum residence time

We obtained the earliest record of occurrence of a species in South Africa to calculate the MRT (Wilson et al. 2007). We checked GBIF (<http://www.gbif.org>), Plants of Southern Africa (POSA) and a number of historical and archaeobotanical studies for MRTs (Appendix 1), using the oldest date from all these databases for the MRT. Using these data, we created species accumulation curves for alien grasses in South Africa.

Pathways of introduction and spread

To investigate likely pathways of introduction and spread, we collected information on the uses of species (Quattrocchi 2006). Uses were assigned to one of the six categories (horticulture, animal food, food or beverage, raw material, soil stabilisation or none). We assumed that these uses will be correlated with both the initial reason for introduction and how and why species were spread by humans around South Africa (e.g. known pasture grasses were likely introduced as such and distributed to appropriate pasture lands). We investigated temporal patterns of alien grass introductions with respect to their primary uses, using the MRT for each species.

The origins of alien grasses can be useful for informing why species were introduced. We determined the native range of each species using the eMonocot database and manually assigned the native range of each species to one or more of six biogeographical realms: North America, South America, sub-Saharan Africa, temperate Eurasia, North Africa and Southeast Asia (Olson et al. 2001). We investigated temporal patterns of where species originated from using the same approach as for primary uses over time.

To test how the use and origin contribute to the progression of species across the INI continuum (from introduced to naturalised to invasive), we used ordinal logistic regression, with INI status as the response variable and use or origin as the predictor, using the R (R Core Team 2016) package ordinal (Christensen 2016).

To assess in more detail the role of the pasture industry in introducing alien grasses, we searched the literature for

information on (1) the existence of pasture research stations in South Africa, (2) the duration that these stations operated for, and (3) the species that were trialled at these stations. These data were used to complement our inventory of alien grasses.

Prevalence

We collated species distribution data from online databases and scientific publications on alien grasses in South Africa (Appendix 1). We downscaled all coordinates to the centroid of the nearest quarter-degree-grid-cell (QDGC). We also recorded the year in which each grass occurrence was made. We calculated total alien species richness and numbers of records across South Africa. Observed species richness patterns likely suffer from sampling bias towards roads and urban centres, and rarefaction has been shown to be the best at reducing this bias, although it tends to underestimate richness (Engemann et al. 2015). We used the R package 'vegan' to estimate species richness, excluding QDGCs with less than 20 samples, because rarefaction is inaccurate for small sample sizes. We also investigated whether particular biomes have more alien grasses and whether protected areas have records of alien grasses, by overlaying observed alien grass species distributions (actual localities as well as overlap with QDGCs occupied) on a high-resolution map of South African biomes (Mucina et al. 2005) and of protected areas (DEA 2016). We then calculated numbers of alien grasses in each biome and the number of protected areas with alien grass records.

We calculated the area occupied by each species by summing the number of QDGCs occupied. We examined the area occupied by each species with respect to whether species have been recorded as having impacts (see below), INI status and legal status (see below).

Impacts

Empirical measures of impact (e.g. Hawkins et al. 2015) are unavailable for alien grasses in South Africa, and so we focus here on establishing a baseline of current understanding. We did this by assimilating information from the literature gathered for our inventory of alien grasses (Appendix 1). We selected all references that mention any changes caused to the native environment (mainly biodiversity) or harm caused on the socio-economy attributable to the alien species (cf. Jeschke et al. 2014). Studies mentioning the dominance or invasiveness of a species without referring to changes to the native environment were not considered (e.g. Musil, Milton & Davis 2005; Sharma et al. 2010). For the studies referring to environmental changes, we assigned the most likely Environmental Impact Classification of Alien Taxa (EICAT) score for South Africa noting the confidence level (Blackburn et al. 2014; Hawkins et al. 2015). Only references included in Appendix 1 were considered for the EICAT classification, and no standardised literature review was performed.

Management of alien grasses

To evaluate gaps in research on control measures for alien grasses, we searched the literature used for compiling our

inventory (Appendix 1) and the Global Invasive Species Database (GISD; www.iucngisd.org/gisd/) for the 41 species that are either invasive or have impacts in South Africa. We grouped control measures into five categories: physical removal, fire, chemical, biocontrol and integrated control (based on the categories used in the GISD, with the addition of fire).

We used the prevalence and impact data collected in this study to evaluate the appropriateness of current NEM:BA categorisations (DEA 2016) of alien grass species [viz. prohibited species do not occur in the country and pose an unacceptable risk of invasion if they were to be introduced; category 1a species are those where eradication from the entire country is desirable and feasible (Wilson et al. 2013); category 1b species are those where ongoing control measures are required and all uses are prohibited; category 2 species can be used for commercial (or other) purposes provided that a permit is issued; otherwise, they are treated as category 1b species; finally, category 3 species are those where existing plantings can remain, but must be contained, no new plantings are allowed and a national management plan is required (DEA 2014)]. In brief, the differences between categories are because of whether an alien species is present in the country, whether eradication is feasible and some balance between benefits of plantings and risks of invasion. An accurate quantification for all species of both the feasibility of eradication and the net impact is beyond the scope of this study. Therefore, we used the spatial extent of each species as a proxy for eradication feasibility (Pluess et al. 2012a, 2012b; Rejmánek and Pitcairn 2002). Eradication feasibility is inversely proportional to the spatial extent (E), so we calculated a metric of relative invaded area (RIA) using the following formula:

$$RIA = 1 - \log(E)/\log(E_{\max}), \quad [\text{Eqn 1}]$$

where E_{\max} is the spatial extent of the species with the highest number of QDGCs occupied. RIA is 0 for species that are not present and 1 for the most widespread invasive grass. To estimate the net impact of each species (negative, neutral or positive), we used the data collected on impacts (previous paragraph) and on the uses of each species. Species with recorded impacts (Table 4) or that were found to be invasive in South Africa, and that have only one use, were given a 'negative' relative benefit. Species with a 'neutral' benefit were defined as those with recorded impacts or that are invasive, but have more than one use, or non-invasive species that have no or just one use. Species with a 'positive' benefit were defined as those that are non-invasive, do not have an impact and have more than one use.

The future and providing a framework for assessing the status of grass invasions in South Africa

We highlighted two areas of concern for potential grass invasions in the future: invasion debt and global change. We do not attempt to calculate all aspects of invasion debt as

defined in Rouget et al. (2016), but instead focus on one of the key components of these calculations: identifying species that are not yet invasive in South Africa, but which are known to be invasive elsewhere (this has been shown to be a useful indicator of a species becoming invasive in novel regions, e.g. Kumschick and Richardson 2013; Panetta 1993). We used the weed status in the Global Compendium of Weeds (GCW; Randall 2012) to identify species that are invasive anywhere in the world (species with a GCW status of 'environmental weed', 'invasive' or 'noxious weed'), but that are non-invasive in South Africa (introduced or naturalised).

To provide an indication of future grass invasions because of global change, we investigated relative frequencies of photosynthetic pathway type (C_3 , C_4 or intermediate C_3 - C_4) and of taxonomic affiliation as these have been shown to influence grass biogeographical patterns in relation to climate. We used Osborne et al. (2014) to assign grass species' photosynthetic type. To assign taxonomic affiliation, we used grass tribe information from GrassBase (Clayton et al. 2006 onwards) together with a recent phylogeny of grasses (Soreng et al. 2015) to assign species to one of the nine grass subfamilies (Aristidoideae, Arundinoideae, Bambusoideae, Chloridoideae, Danthonioideae, Ehrhartoideae, Micrairoideae, Panicoideae and Pooideae).

To assist with the NEM:BA A&IS regulations requirement for a national status report (due October 2017, see Wilson et al. 2017) and to provide simple, useful indicators of the status of alien grasses in South Africa, we have proposed a framework that can be regularly updated and improved on over time (Table 1). This framework covers all aspects of grass invasions covered in this paper (species presence, pathways, prevalence, impacts and management). Where possible, we compare the current situation with that in 2004. We also make recommendations for improved indicators for 2020, when the next national status report is due to be published.

Results

Inventory

A total of 256 alien grass species were found to have been introduced to South Africa by human activity (Table 1; Online appendix). Of these species, 122 (48%) are considered naturalised, and 37 of these naturalised species have become invasive (representing ~14% of all introduced alien grass species and 30% of naturalised species; Table 1). For many species, there was little confidence regarding their presence in South Africa: 33% of species only had one record of occurrence in South Africa, 42% of species had no distribution data, 30% of species had only one reference and no distribution data, 30% had no herbarium record and 26% were lacking in all the aforementioned aspects (Table 1). A further 29 species are potentially native species, but we classified these as extra-limital because they are native to one of South Africa's neighbouring countries, but alien to South Africa based on our data sources (Online appendix). Some of these could potentially represent intra-African spread (Faulkner et al., 2017).

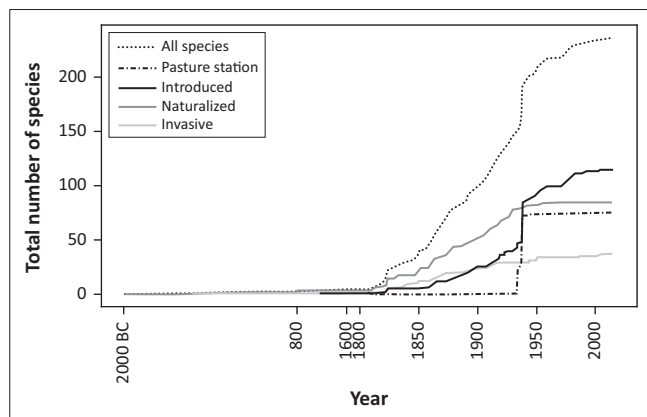
TABLE 1: Framework for monitoring alien grass invasions in South Africa.

Category	Indicator	Status in 2004	Status in 2016	Recommendation for monitoring and reporting status in 2020
Species	Lists	113 <i>naturalised</i> species	256 species in total 122 <i>naturalised</i> species 37 <i>invasive</i> species	Change in number that is invasive over time. Status as per Blackburn et al. (2011).
	Confidence in presence	Not recorded	Measures of confidence in presence: 83 species (33% of all alien grasses) have (A) only one reference for occurrence in South Africa. 106 species (42% of all species) have (B) no distribution data. 77 species (30% of all species) have (C) no herbarium records. 75 species (30% of all species) conform to both (A) and (B). 65 species (26% of all species) conform to (A), (B) and (C)	100% with at least one distribution record. 100% with herbarium records. Revisit sites with low confidence in presence.
Pathways	New introductions	Not recorded	Not recorded	Number of import permits issued, number of interceptions
	Total area occupied	330/462 QDGCs (71%) in South Africa with alien grasses	351/462 QDGCs (76%) in South Africa with alien grasses	Estimate of area of occupancy and extent of occurrence across spatial scales
Impacts.	Occupancy of key sites (protected areas)	Not recorded	148 of 1097 protected areas with alien grass records	As above at protected areas
	Abundance.	Not recorded	Not recorded.	Percentage covers for A&IS listed species.
Areas by impacts	Impact scores for species.	Qualitative description of the impacts of ~12 species.	11 species with recorded impacts, 7 with impacts quantified.	Quantification of (global) impacts of all alien grasses that have recorded impacts elsewhere in the world.
	Number of QDGCs for species with impacts	Not recorded	333/462 QDGCs (72%)	As previous
Efficacy of management and regulation.	Number of species listed.	CARA 2001 Listed: 9 species Prohibited: 33 taxa	NEM:BA A&IS regulations: 14 species listed; 38 species prohibited (3 of which are possibly already introduced).	Confirmation that all prohibited species are not in the country. Evidence for categorisation of listed species.
	Management spending.	Not recorded	0.33% of the total budget for Working for Water alien plant control between 1995 and 2008 spent on <i>Arundo donax</i> L. (van Wilgen et al. 2012).	Control costs for all alien grasses.
Research efforts	Number of theses on alien grasses.	Not recorded	16 theses up until July 2016 (out of ~254 on alien plants; 6%)	Amount of money invested in alien grass research.

Provided are various indicators covering all aspects ('category') of grass invasions addressed in this paper. For each indicator we provide a status for 2004, 2016 (current) and recommendations for improvements in reporting for 2020. Results for 2004 are from our own results and from Milton (2004), when available.

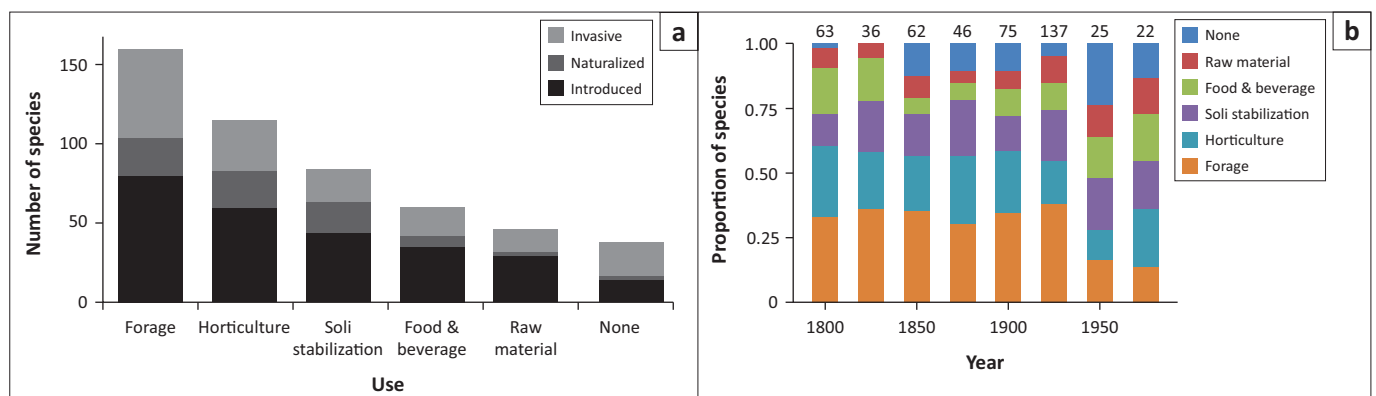
Minimum residence time

The first alien grasses in South Africa were crops, such as *Eleusine coracana*, *Pennisetum glaucum* and *Sorghum bicolor*, which were brought to the region by Iron Age farmers early in the first millennium (Antonites and Antonites 2014). Maize (*Zea mays*) was introduced much later, sometime in the 17th or 18th centuries (Antonites and Antonites 2014). The oldest alien grass herbarium records were collected just over 200 years ago (in 1811) for *Arundo donax* near Tulbagh in the Western Cape and *Rostraria pumila* near Fraserburg in the Northern Cape (Online appendix). The number of alien grasses recorded in South Africa increased rapidly until about 1940 (90% of species were recorded before 1955); for many species, the first record of occurrence is 1938 because of introductions by pasture research stations (Figure 1, see discussion below). There are far fewer first records after 1940 (Figure 1). Species that have naturalised or become invasive have much longer residence times in South Africa than



Note the scale on the x-axis is different before and after 1800. The total number of alien grass species is indicated by the dotted line. Species introduced by pasture research stations are indicated by the dot-dash line. The remaining solid lines represent species grouped by their status on the introduction-naturalisation-invasion continuum. The dark solid line represents species that are not yet naturalised or invasive, that is, 'introduced' on the introduction-naturalisation-invasion continuum. Naturalised, but not yet invasive species are represented by the slightly lighter solid line, and invasive species by the lightest solid line. New species were introduced at a relatively constant rate until 1938 when many species were introduced by pasture research stations. Most of the novel species introductions in 1938 did not result in new invasions as evidenced by the relatively constant total number of naturalised and invasive species after this date. After 1938 the rate of introductions has gradually slowed until the present day.

FIGURE 1: Cumulative number of alien grass species recorded in South Africa over time.



(b), The total number of species introduced in each interval is shown at the top of each bar.

FIGURE 2: (a) Uses of alien grasses in South Africa, with numbers of species per use category indicated by bar size. Each use category is further subdivided by species' statuses along the introduction-naturalisation-invasion continuum. (b) Trends over time (as deduced from earliest records of occurrence), per 25-year interval (apart from the first interval which represents the period 2000 BC to 1825), in the proportions of species being introduced to South Africa relative to use categories.

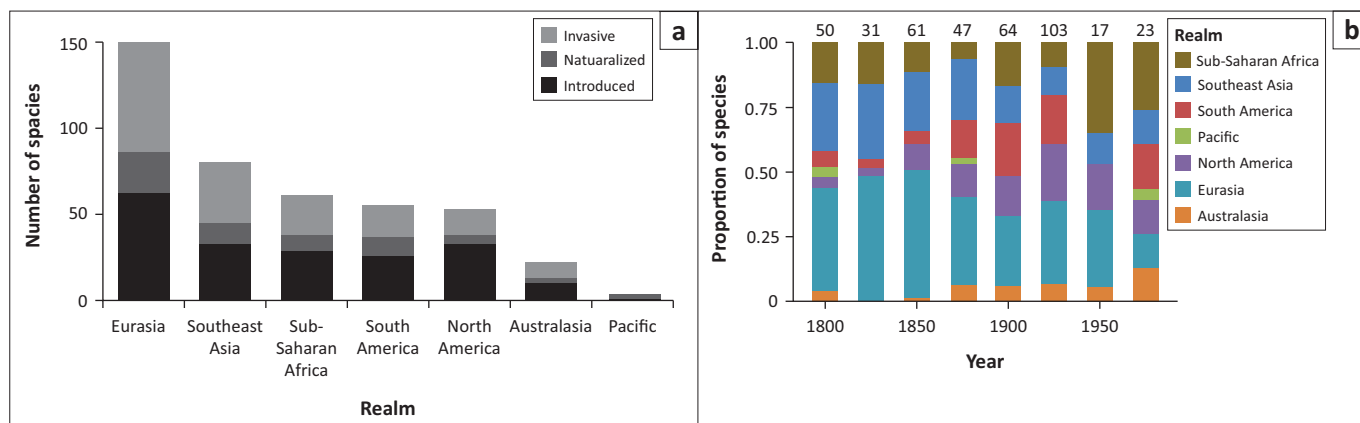
species that are not recorded as naturalised or invasive (mean MRT in years: introduced = 86, naturalised = 131, invasive = 123; one-way ANOVA, $F = 38.62$, $n = 234$, d.f. = 2, $P < 0.0001$; Figure 1).

Pathways of introduction and spread

Forage represents the most common use of alien grasses in South Africa (62.2%; Figure 2a). The other most common use categories are horticulture, soil stabilisation, food and beverages, raw materials and lastly those with no known use (Figure 2a). Species with no use ('none') were the most likely to be invasive, followed closely by species used for forage (Figure 2a; Appendix 2, Table 1-A2). Fewer species used for forage have been introduced into South Africa since about 1950 (as a proportion of all use categories; Figure 2b). Concomitantly, there has been an increase in species being introduced that have no use (Figure 2b).

Alien grasses in South Africa are native to (in decreasing order of contribution) Eurasia, Southeast Asia, sub-Saharan Africa, South America, North America, Australasia and the Pacific (Figure 3a). Species native to South America were proportionally the most likely to be invasive, followed by species native to Eurasia (Figure 3a; Appendix 2, Table 2-A2). Species native to North America were proportionately the least likely to be invasive (Figure 3a; Appendix, Table 2-A2). The proportion of species being introduced that are native to Eurasia has steadily declined over time, with a relative increase in the introduction of grasses native to Australasia (Figure 3b). More recently, since about the 1950s, an increasing proportion of introductions has been of species native to sub-Saharan Africa (Figure 3b, cf. Faulkner et al. 2017).

We found evidence of 14 different pasture research stations being active at some point in South Africa (Appendix 3, Table 1-A3), although some of these appear not to have existed for very long, or they cultivated very few alien grass species. Five stations (Prinshof, Athole, Leeuwkuil, Estcourt and Cedara) were responsible for introducing 95% of the 81 alien grass species cultivated at these stations, with Prinshof alone having cultivated 63 species (Appendix 3, Table 2-A3).



(b). The total number of species introduced in each interval is shown at the top of each bar.

FIGURE 3: (a) Origins of alien grasses in South Africa, with numbers of species per realm indicated by bar size. Each realm is further subdivided by species' statuses along the introduction-naturalisation-invasion continuum. **(b)** Trends over time (as deduced from earliest records of occurrence), per 25-year interval (apart from the first interval which represents the period 2000 BC to 1825), in the proportions of species being introduced to South Africa relative to their realms of origin.

Pasture research stations were responsible for introductions of 40 alien grass species in South Africa (~16% of all alien species), a conclusion reached because the starting date of trials at pasture stations involving these species preceded any other records of them in South Africa.

Prevalence

At present about 76% of QDGCs in South Africa have recorded occurrences of alien grasses, compared with 71% in 2004 (Table 1). The raw species occurrence data show that QDGCs with the most number of alien grass species are in the south-west of the country and that there are other notable pockets of high species richness around the major cities of Johannesburg and Port Elizabeth, and across much of the eastern escarpment (Figure 4a). A slightly different pattern emerges when we examine the *number of records* in QDGCs of these same species: the south-west of the country once again has the highest values, with the rest of the country generally having low numbers of records, apart from the areas around Johannesburg, Port Elizabeth and Durban (Figure 4b). However, as with most herbarium data, it is evident that there has been much more intensive collection of alien grasses along roads and around major urban centres (Figure 4a,b). After attempting to correct for sampling bias, it appears that alien grass species richness is still high in the Fynbos, but is possibly higher in the east of the country – in the grasslands of the Free State and in the southern Lowveld (Figure 4c). However, alien grass sampling was insufficient in many QDGCs, resulting in a much more restricted overview of alien grass species richness across the country compared with the raw data (Figure 4). When examining observed alien grass spatial patterns over time, we see that the high number of species and records in the south-west of the country is a fairly recent phenomenon, which has increased greatly in the last ~50 years, but is possibly the result of greater collection effort in this area during this time period (Appendix 4, Figure 1-A4).

In contrast to the high percentage of QDGCs occupied by alien grasses, only 148 of 1097 protected areas recorded the

presence of alien grasses (Table 1). However, 195 protected areas occur in QDGCs where alien grasses were recorded. Alien grasses were recorded for the first time between 2004 and 2016 in an additional 24 protected areas.

In terms of the extent of individual species, we found that relatively few alien grasses occur across large areas of South Africa. Most alien grasses occupy relatively limited areas (Appendix 4, Figure 2-A4), although invasive grasses were much more widespread than other alien grasses (mean number of QDGCs \pm SE: invasive = 88.08 ± 24.19 , naturalised = 29.10 ± 7.67 , introduced = 3.79 ± 2.44 ; Appendix 4, Figure 2-A4).

The results in terms of presence and abundance in the different biomes of South Africa are presented in detail in Appendix 4.

Impacts

We found recorded impacts for only 11 alien grass species in South Africa (Table 2). Of these, two species have major impacts (MR), two have moderate impact (MO), two minor impacts (MN) and five were data deficient (DD) according to our scoring of the EICAT due to a lack of environmental impact and the availability of only records of socio-economic impact (Table 2; Blackburn et al. 2014; Hawkins et al. 2015). Species with notable impacts were widespread, being recorded in 72% of QDGCs in South Africa (Table 1), although this is largely because of widespread species such as *Arundo donax* and *Pennisetum setaceum* – other species with notable impacts are not widespread (Appendix 4, Figure 2-A4). There was a great deal of uncertainty about ecological and socio-economic impacts caused by alien grasses in South Africa. Numerous studies have described alien grasses as dominant or invasive, without specifying the changes to the native environment (e.g. Musil et al. 2005; Rahlao et al. 2009; Sharma et al. 2010). However, few direct data exist: the EICAT score of only two species was with medium certainty and the rest with low certainty (Table 2).

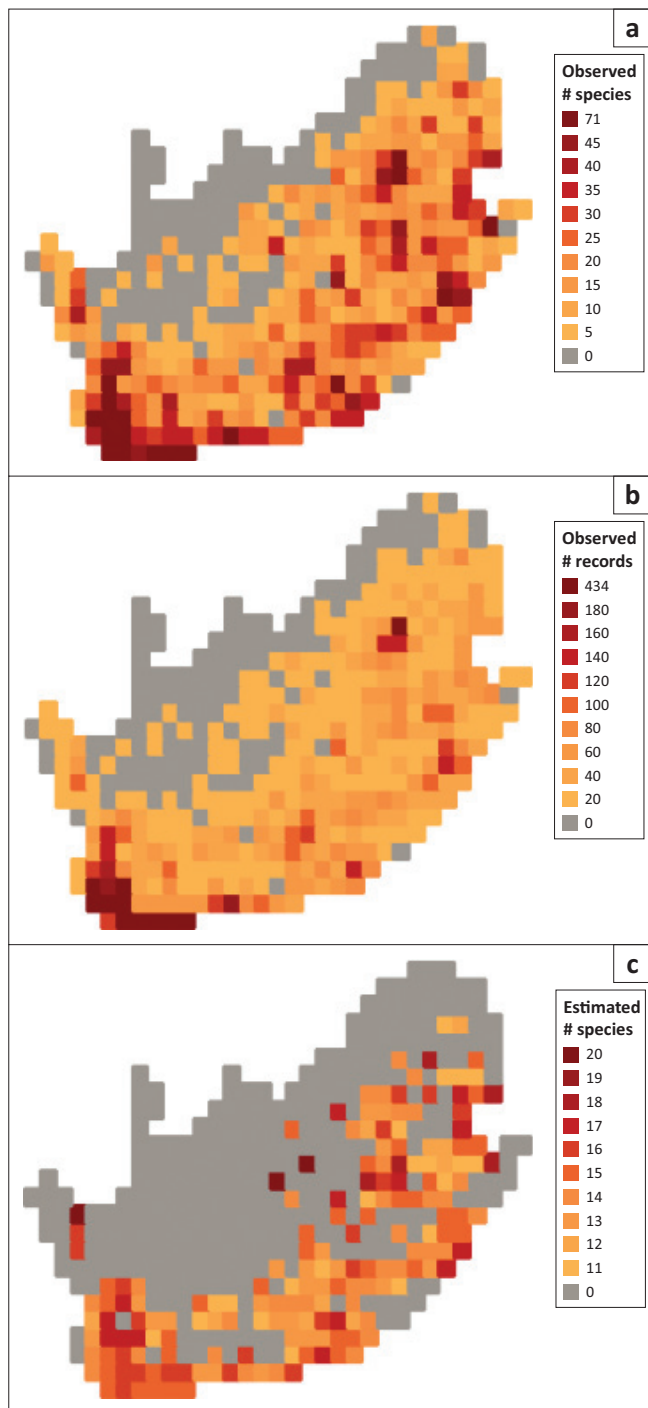


FIGURE 4: (a) Observed alien grass species richness, (b) observed numbers of records of alien grasses, and (c) estimated species richness in quarter-degree grid-cells (QDGCs) across South Africa. Darker reds indicate higher species richness or numbers of records. Estimated species richness was calculated using rarefaction (see methods).

Management of alien grasses

A literature search revealed that of the 41 species identified as being invasive or having recorded impacts, management options have been described for only 11 species (27%) (Appendix 5). The most commonly suggested management strategy is physical removal (11 species), followed by chemical control (10 species), integrated control (8 species), using fire (6 species) and biological control (3 species) (Appendix 5).

Prior to 2004, only nine grass species were legislated for management and 33 taxa were prohibited from being introduced (Table 1; Appendix 6). Currently, under NEM:BA 14 species are legislated for management and 38 species are prohibited from being introduced (Table 1; Appendix 6). The current NEM:BA categorisation of species (NEM:BA Alien and Invasive Species List, 2016) is for the most part in accordance with our evaluation based on the spatial extent of a species' invaded area and the relative benefits of alien grasses in South Africa (Figure 5b). The one category 1a species (*Paspalum quadrifarium*), six of the eight category 1b species and the one category 3 species (*Ammophila arenaria*) were correctly categorised based on our scheme (Figure 5b). However, only 14 species, or 5.5% of all alien grass species in South Africa, are listed under the A&IS regulations (Figure 5b; Online appendix; Appendix 6). Based on our analysis, at least one other uncategorised species (*Bromus madritensis*) should be in category 1a; another 11 species in category 1b; 29 in category 2; 52 in category 3 and for 20, our analysis does not support their listing (Figure 5b). Some unlisted species are common agricultural grasses (e.g. wheat, *Triticum aestivum* etc.) and, therefore, do not require any regulation, but these only account for a small proportion of unlisted species. There is also one A&IS listed species where it is not clear whether it is present in South Africa [we could find no references for *Sasa ramosa* being present, but it is listed as category 3 (Appendix 6)]. We also found that 3 of 38 species on the NEM:BA A&IS prohibited list are already present in South Africa (*Panicum antidotale*, *Pennisetum polystachion* and *Themeda quadrivalvis*) (Appendix 6). However, they do not appear to have naturalised and are not yet widespread (Figure 5b; Online appendix).

The future and providing a framework for assessing the status of grass invasions in South Africa

To provide an indication of possible invasion debt, we investigated the number of non-invasive (introduced and naturalised) grasses in South Africa that are invasive elsewhere in the world. We found that 118 species (66% of 180 non-invasive species) are invasive elsewhere in the world (Online appendix). Of these species, 67 have naturalised in South Africa.

We also investigated the type of photosynthetic pathway used by alien grass species, and the taxonomic affinity of these species, as possible indicators of future invasion trends. Most alien grasses in South Africa use the C_3 photosynthetic pathway (61.4%; Appendix 7, Figure 1-A7), and these species are more common in the south-west of the country (Appendix 7, Figure 2-A7). However, most C_3 species belong to the subfamily Pooideae, with the next largest C_3 clade being represented by the clade Bambusoideae (Appendix 7, Figure 3-A7). There are only six C_3 alien grass species in South Africa in the largely C_4 Panicoideae clade (Appendix 7, Figure 3-A7).

TABLE 2: Alien grass species in South Africa with recorded impacts.

Species	Impacts	References	INI status	NEM:BA A&IS category 2016	Potential EICAT classification for South Africa	Certainty
<i>Ammophila arenaria</i>	Although indigenous species are able to co-exist with this species, these are a subset of the native dune flora (mostly smaller herbaceous plants) and the same species co-exist with <i>A. arenaria</i> across its entire distribution, unlike native dune communities which change in composition	Hertling and Lubke (1999)	Naturalised	3	MO	medium
<i>Arundo donax</i>	Dominates riparian areas, outcompeting native species and facilitating the establishment of other alien species. <i>A. donax</i> predicted to have greater impacts in drier, colder habitats where dry material can accumulate	Guthrie (2007)	Invasive	1b	MR	medium
	<i>A. donax</i> is thought to promote fires. Also causes accumulation of sediments and widening of river channels and locally excludes native species	Holmes et al. (2005)	-	-	MR	low
<i>Avena barbata</i>	Dominates old fields and disturbed habitats in lowland fynbos	Heelemann et al. (2013)	Invasive	None	MO	low
<i>Avena fatua</i>	Dominates old fields and disturbed habitats in lowland fynbos	Sharma et al. (2010)	Invasive	None	MN	low
<i>Glyceria maxima</i>	Outcompetes native wetland species	Mugwedi (2012)	Invasive	1b†	MR	low
<i>Hordeum murinum</i>	The long awns are especially a problem as they can cause injury to livestock by puncturing the mouth and throat and entering the skin and eyes as well as contaminating wool	Todd (2008)	Invasive	None	DD	-
<i>Lolium multiflorum</i>	Mentions highly competitive characteristics	Holmes (2008)	Invasive	None	MN	low
<i>Nassella tenuissima</i>	Poor grazing value so when dominant, decreases livestock productivity	Milton (2004)	Invasive	1b	DD	-
<i>Nassella trichotoma</i>	Poor grazing value so when dominant, decreases livestock productivity	Milton (2004)	Invasive	1b	DD	-
	The fine sharp seeds can contaminate wool	Esler, Milton and Dean (2006)	-	-	DD	-
<i>Pennisetum setaceum</i>	The leaves are barbed and unpalatable and the build-up of dead leaves increases the risk of veld fires	Esler, Milton and Dean (2006)	Invasive	1b‡	DD	-
<i>Stipa capensis</i>	Reduces grazing capacity and damages wool and hides	Steinschen, Gorne and Milton (1996)	Introduced	None	DD	-

Both, ecological and socio-economic impacts were considered as reported, but only negative changes are considered (cf. Jeschke et al. 2014). EICAT scores and certainty levels (according to Blackburn et al. 2014; Hawkins et al. 2015) are purely based on the studies performed on environmental impacts in South Africa (socio-economic impacts were not classified) and on references provided in this table rather than a standardised literature search. For full references see Appendix 1.

MR, major; MO, moderate; MN, minor; DD, data deficient.

†, 1b in protected areas and wetlands. Not listed elsewhere; ‡, Sterile cultivars or hybrids are not listed.

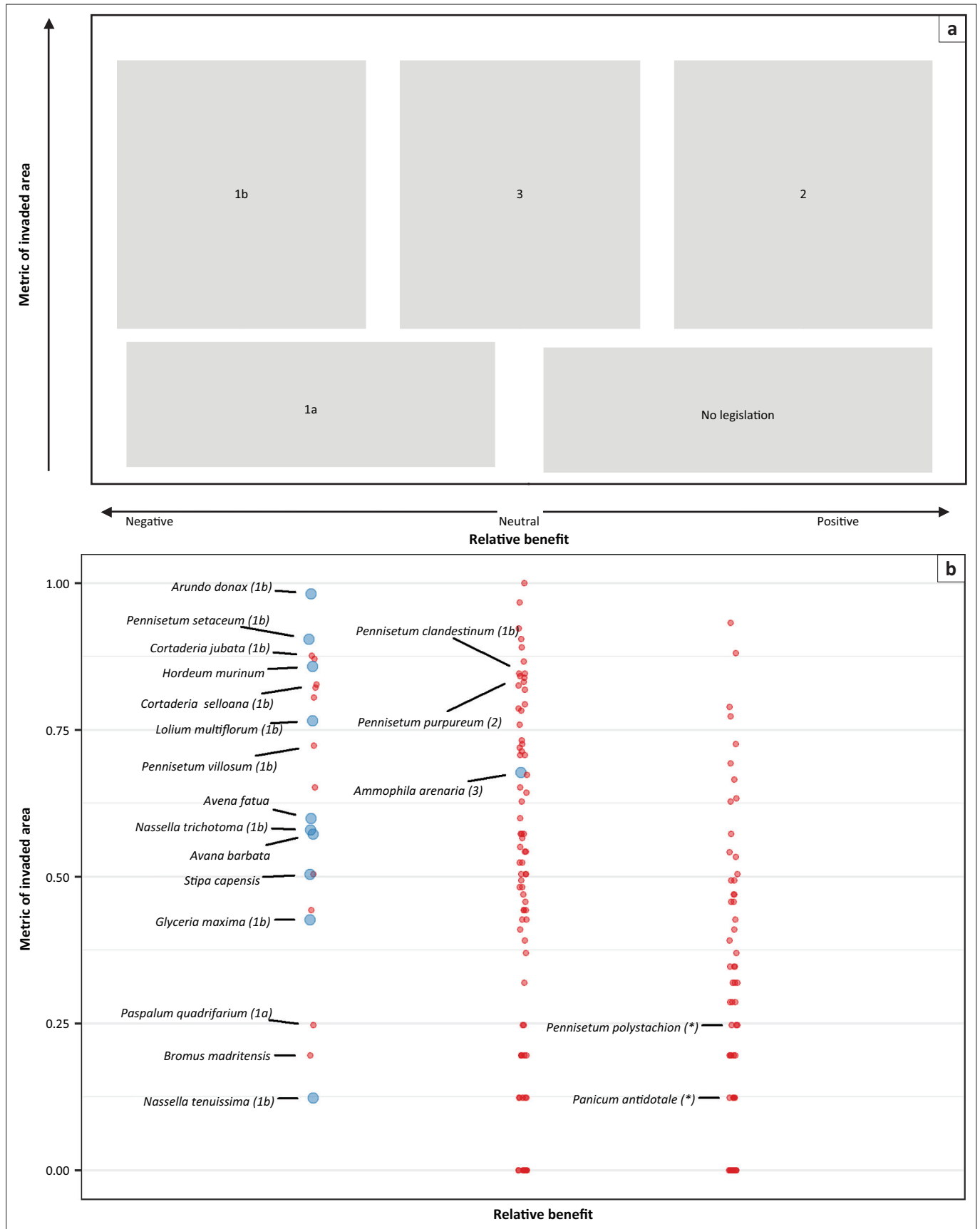


FIGURE 5: (a) Alien species in South Africa are regulated by the Alien and Invasive Species (A&IS) Regulations (2016) under the *National Environmental Management: Biodiversity (NEM:BA) Act 10 of 2004*. Guidelines for the categorisation of species (1a, 1b, 2 or 3) are primarily based on the spatial extent of the invaded area and the relative benefits of species. These two factors alone can possibly be used to provide an objective method of providing a NEM:BA category for alien species as shown in this figure. (b) Alien grass species plotted in relation to their spatial extent and relative benefit (see methods for details). Also provided are species names for species categorised under NEM:BA and their associated categories (in parentheses). An asterisk represents species that are on the NEM:BA prohibited list, but were found to occur in South Africa. Species with recorded impacts are shown in blue.

Discussion

This study provides a much needed reassessment and improved clarity on the status of alien grass species in South Africa. Based on our inventory (Online appendix), at least 256 alien grass species have been introduced to the country. This list and its ancillary data can help inform alien grass research and management, as we shall discuss here.

In both absolute and relative terms, the number of invasive grasses in South Africa is lower than in many other countries (Visser et al. 2016). Around 14% of alien grasses introduced into South Africa have become invasive (Table 1), which is lower than Europe (19%) or the USA (34%) (Visser et al. 2016). Our knowledge of alien grasses in South Africa is generally very patchy; only 70% have herbarium records (Table 1). The identity of many alien grasses in South Africa is therefore uncertain. Moreover, the status of species on the INI continuum is often based solely on anecdotal published information. We might therefore be greatly underestimating the number of invasive grasses in the country. For a third of all alien grass species, we found one reference for their occurrence in South Africa; this, together with the large number of species with no herbarium records or distribution data (Table 1), makes it difficult to be certain that these species are indeed in the country. We suggest that future evaluations of alien grasses should make a concerted effort to address some of these shortcomings (Table 1).

Alien grasses are present throughout most of South Africa (Figure 4). However, this pattern is biased at least in part, by *ad hoc* botanical collections, with extensive sampling bias, for example, towards major urban centres (Figure 4c; see Engemann et al. 2015 and Richardson et al. 2005 for discussion on these collection biases and the implications for analyses). Nevertheless, it appears that the Fynbos Biome has among the highest number of alien grass species and that alien grasses in the fynbos tend to be more abundant and widespread than in other biomes (Figure 4; Appendix 4, Figure 4-A4). Of the 11 species with recorded impacts, six affect the Fynbos Biome. There is also considerable anecdotal evidence to suggest that alien grasses are having large impacts in the Fynbos Biome (Musil et al. 2005; Sharma et al. 2010; Vlok 1988), but these impacts have been poorly quantified. Our knowledge of alien grass impacts in South Africa in general is very poor (Table 2), and further research is needed. Interestingly, protected areas were mostly free of alien grasses (in terms of actual records of occurrence; Table 1; see also Foxcroft et al. 2017). One possible interpretation of this result is that protected areas are somehow more resistant to alien grass invasions, possibly because it is more difficult to invade undisturbed vegetation, or because fire and/or herbivores prevent the establishment of alien grasses (Mack and Thompson 1982; Visser et al. 2016). Another possibility is that sampling of alien grasses in protected areas has been poor. There is some justification to suspect the latter reason because of recent publications describing grass invasions in South African National Parks,

which are perhaps better monitored than other protected areas (Spear et al. 2011).

It is difficult to predict what the future holds with regard to grass invasions, but some trends are apparent. New introductions into South Africa have declined steadily over the last 70 years; although probably because of poor data, no new alien species have been recorded since 2004 (Figure 1). This suggests that the socio-economic factors that led to the introduction of many alien grasses in the past have changed and that the risk of this introduction pathway causing major problems in the future has been greatly reduced. It seems that South African ecosystems are inherently less open to invasion by alien grasses than those in many other parts of the world (Visser et al. 2016). However, it is likely that some of the species already present in South Africa will become naturalised or invasive in the future, representing a considerable invasion debt (~66% of non-invasive alien grass species in South Africa are known to be invasive elsewhere in the world). More than half (57%) of these species have naturalised and some are possibly on their way to becoming invasive. This is all the more likely because recent introductions were from regions with similar climates to South Africa, for example, Australia and sub-Saharan Africa (Figure 3b). Recent introductions were also relatively more likely to be of species with no known use (Figure 2b), those species that tended to be the mostly likely to become invasive. Pasture grasses were also more likely to be invasive than were species in other usage categories (Appendix 2, Table 1-A2). We found that the most common use for grasses in South Africa was for forage (Figure 2a), and that pasture research stations were responsible for introducing many novel alien grass species. Similar situations with regard to pasture grasses have been observed elsewhere in the world, for example, Australia and the USA (Cook and Dias 2006; Lonsdale 1994; Ryerson 1976; Visser et al. 2016). Australia is notable for the number of grass species that were introduced (~1600 species; Cook & Dias 2006; Visser et al. 2016) and also the subsequent number of problematic pasture grass invaders (Cook & Dias 2006). Of the 118 grass species that are not invasive in South Africa, but are invasive elsewhere, 74% are used for pasture, and 32% were trialled at pasture research stations. This suggests that pasture grasses present a considerable invasion debt for South Africa, as exemplified by the recent observation of a pasture species, *Glyceria maxima*, invading wetlands in KwaZulu-Natal (Mugwedi 2012). Another consideration for predicting future invasions is changing trends in the purposes for which grasses are used. We found few changes over the last two centuries in this regard (Figure 2b). However, recently there has been considerable interest in introducing grasses for novel uses such as biofuels (Blanchard et al. 2011) or for species that are thought to have potential for multiple purposes (e.g. bamboos; Canavan et al. 2016). Propagule pressure is likely to be high for these species, because they are likely to be cultivated in large-scale agricultural settings, and the chances of these species then naturalising in adjacent areas is all the more likely

(Simberloff 2009). Natural and human-mediated spread of introduced grasses between South Africa and Africa also represents a potentially increasing threat (Faulkner et al. 2017).

Another possible contributor to future grass invasions is global change (climate, atmospheric CO₂, N pollution, land-use change, etc.). One of the reasons that C₄ grasses are thought to dominate South African grasslands is their higher nitrogen-use efficiencies at pre-industrial CO₂ levels (Milton 2004; Richardson et al. 2000). Rising atmospheric CO₂ levels could, therefore, contribute to increased invasions by C₃ grasses (Milton 2004; Richardson et al. 2000). Moreover, altered nitrogen cycles because of nitrogen pollution or from nitrogen-fixing invasive species would similarly favour C₃ grass species. Weedy native and alien grasses have been documented to dominate nitrogen-enriched soils in fynbos and renosterveld (Sharma et al. 2010; Yelenik, Stock & Richardson 2004). However, C₄ grasses are also thought to be dominant in South African grasslands (and many other grasslands around the world) because of their higher water-use efficiencies under high light and low moisture and CO₂ conditions (Edwards et al. 2010; Edwards and Smith 2010; Osborne and Sack 2012). Therefore, reduced precipitation because of anthropogenic climate change would maintain the competitive advantage of native C₄ species, but perhaps allow for the establishment of alien C₄ species. Warmer temperatures would therefore also favour C₄ species. However, grasses have been shown to exhibit strong phylogenetic conservatism of climatic niches, principally in relation to temperature (Edwards and Smith 2010). The occurrence of C₃ grasses in cooler climes and C₄ grasses in warmer climes is now thought to be largely an artefact of the large number of species within the C₃ grass subfamily Pooideae and the large number of C₄ species in the subfamilies Panicoideae, Aristidoideae and Chloridoideae (Edwards & Smith 2010). Most grasses introduced into South Africa and most of the current invasive species belong to the subfamily Pooideae (Appendix 7). Given these species' affinity for cooler climates, it is unlikely that many new invaders will emerge from this clade and that these species will expand their distributions as the climate warms. Using a climate-envelope approach to predict the future distributions of grass invaders in South Africa, Parker-Allie, Musil & Thuiller (2009) provided support for such a notion. Overall, given the combination of the above factors (nitrogen-use efficiency, water-use efficiency and phylogenetic niche conservatism), we suggest that the alien grasses most likely to be favoured in South African by global change are C₃ Panicoideae species. Only six species in this group are known to have been introduced to South Africa (Appendix 7), which is possibly a contributing factor to the relative paucity of invasive grasses. Other aspects of global change such as land-use change and changing invasion pathways are also likely to affect possible future grass invasions. Transformation of natural environments can aid the establishment of invasive species, particularly many grass species (e.g. Rahlao et al. 2014; Veldman et al. 2009). Alien grasses are also commonly

used for revegetation, particularly along roadsides (*pers. obs.*), and sometimes after mining operations have ended (Rahlao et al. 2014). We might therefore expect increasing land transformation to aid the spread and establishment of invasive grasses in South Africa. Novel invasion pathways, such as the introduction of grasses for biofuels or in carbon mitigation schemes, could also cause new grass invasions (Blanchard et al. 2011; Canavan et al. 2016).

Our results suggest numerous avenues for improved alien grass management in South Africa. Mechanical and chemical controls are the most commonly employed techniques for alien grass control (albeit for only a few species; Appendix 5), though biological control is used much less frequently when compared with other taxa (Hill and Coetzee 2017; Zachariades et al. 2017). These techniques are already widely employed by the Working for Water programme (van Wilgen et al. 2012). However, very few resources are being allocated to alien grass management (Table 1), and the current NEM:BA categorisations of grasses do not encourage much more investment, as only 14 species are listed (Figure 5). Our scheme to evaluate NEM:BA categorisations for species suggests that only about 8% of the 256 alien grasses in South Africa probably *do not* need to be on the NEM:BA A&IS 2016 list, but currently only 5.5% of species that should be listed *are* on this list. Further research in providing a simple, but objective and scientifically defensible method for categorising alien species is therefore urgently needed.

Conclusions

There are many alien but few invasive grass species in South Africa. Much uncertainty exists with respect to their identity, numbers of species, distributions, abundances and impacts. Given the potentially large grass invasion debt in South Africa, continued monitoring of alien grass distributions and abundances and much greater engagement with authorities is needed to limit future problems.

Acknowledgements

V.V. received funding from the South African National Department of Environmental Affairs through its funding of a South African National Biodiversity Institute's Invasive Species Programme post-doctoral fellowship, and a National Research Foundation Scarce Skills post-doctoral fellowship, and a research fellowship funded by the African Climate Development Initiative. D.L.M. was funded by the Natural Resource Management programmes, Department of Environmental Affairs, Cape Town. S.K. was funded by the South African National Biodiversity Institute's Invasive Species Programme and the DST-NRF Centre of Excellence for Invasion Biology.

Competing interests

The authors declare that they have no financial or personal relationship(s) that may have inappropriately influenced them in writing this article.

Authors' contributions

All authors conceived the idea and contributed to data collection. V.V. led the data analysis together with D.M.R. and J.R.U.W., with contributions from S.C. and S.K. V.V. led the writing of the article together with J.R.U.W. and D.M.R., with contributions from D.L.M., I.N., T.G.O'C. and S.K.

References

- Antonites, A. & Antonites, A.R., 2014, 'The archaeobotany of farming communities in South Africa', in C.J. Stevens, S. Nixon, M.A. Murray & D.Q. Fuller (eds.), *Archaeology of African plant use*, pp. 225–232, UCL Institute of Archaeology Publications, Left Coast Press, Walnut Creek, CA.
- Blackburn, T.M., Essl, F., Evans, T., Hulme, P.E., Jeschke, J.M., Kühn, I. et al., 2014, 'A unified classification of alien species based on the magnitude of their environmental impacts', *PLoS Biology* 12, e1001850. <https://doi.org/10.1371/journal.pbio.1001850>
- Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V. et al., 2011, 'A proposed unified framework for biological invasions', *Trends in Ecology and Evolution* 26, 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Blanchard, R., Richardson, D.M., O'Farrell, P.J. & von Maltitz, P., G., 2011, 'Biofuels and biodiversity in South Africa', *South African Journal of Science* 107, 19–26. <https://doi.org/10.4102/sajs.v107i5/6.186>
- Canavan, S., Richardson, D.M., Visser, V., Le Roux, J.J., Vorontsova, M.S. & Wilson, J.R.U., 2016, 'The global dissemination of bamboos (Poaceae: Bambusoideae): A review', *AoB Plants* 9, plw078. <https://doi.org/10.1093/aobpla/plw078>
- Christensen, R.H.B., 2016, *Ordinal – Regression models for ordinal data*, R package, viewed 1 October 2016, from <https://cran.r-project.org/>
- Cook, G.D. & Dias, L., 2006, 'It was no accident: Deliberate plant introductions by Australian government agencies during the 20th century', *Australian Journal of Botany* 54, 601–625. <https://doi.org/10.1071/BT05157>
- D'Antonio, C.M., Stahlheber, K. & Molinari, N., 2011, 'Grasses and forbs', in D. Simberloff & M. Rejmánek (eds.), *Encyclopedia of biological invasions*, pp. 280–290, University of California Press, Berkeley and Los Angeles, California.
- D'Antonio, C.M. & Vitousek, P.M., 1992, 'Biological invasions by exotic grasses, the grass/fire cycle, and global change', *Annual Review of Ecology and Systematics* 23, 63–87. <https://doi.org/10.1146/annurev.es.23.110192.000431>
- Department of Environmental Affairs (DEA), 2016, *South Africa Protected Areas Database (SAPAD_OR_2016_Q1)*, viewed 12 April 2016, from <http://egis.environment.gov.za/>
- Edwards, E.J., Osborne, C.P., Strömberg, C.A.E., Smith, S.A. & C. Grasses Consortium, 2010, 'The origins of *C₄* grasslands: Integrating evolutionary and ecosystem science', *Science* 328, 587–591. <https://doi.org/10.1126/science.1177216>
- Edwards, E.J. & Smith, S.A., 2010, 'Phylogenetic analyses reveal the shady history of *C₄* grasses', *Proceedings of the National Academy of Sciences* 107, 2532–2537. <https://doi.org/10.1073/pnas.0909672107>
- Engemann, K., Enquist, B.J., Sandel, B., Boyle, B., Jørgensen, P.M., Morueta-Holme, N. et al., 2015, 'Limited sampling hampers "big data" estimation of species richness in a tropical biodiversity hotspot', *Ecology and Evolution* 5, 807–820. <https://doi.org/10.1002/ece3.1405>
- Faulkner, K.T., Hurley, B.P., Robertson, M.P., Rouget, M. & Wilson, J.R.U., 2017, 'The balance of trade in alien species between South Africa and the rest of Africa', *Bothalia* 47(2), a2157. <https://doi.org/10.4102/abc.v47i2.2157>
- Foxcroft, L.C., van Wilgen, N., Baard, J. & Cole, N., 2017, 'Biological invasions in South African National Parks', *Bothalia* 47(2), a2158. <https://doi.org/10.4102/abc.v47i2.2158>
- Gaertner, M., Biggs, R., Beest, M., Hui, C., Molofsky, J. & Richardson, D.M., 2014, 'Invasive plants as drivers of regime shifts: Identifying high-priority invaders that alter feedback relationships', *Diversity and Distributions* 20, 733–744. <https://doi.org/10.1111/ddi.12182>
- Hawkins, C.L., Bacher, S., Essl, F., Hulme, P.E., Jeschke, J.M., Kühn, I. et al., 2015, 'Framework and guidelines for implementing the proposed IUCN Environmental Impact Classification for Alien Taxa (EICAT)', *Diversity and Distributions* 21, 1360–1363. <https://doi.org/10.1111/ddi.12379>
- Henderson, L., 2007, 'Invasive, naturalized and casual alien plants in southern Africa: A summary based on the Southern African Plant Invaders Atlas (SAPIA)', *Bothalia* 37, 215–248. <https://doi.org/10.4102/abc.v37i2.322>
- Hill, M.P. & Coetzee, J.A., 2017, 'The biological control of aquatic weeds in South Africa: Current status and future challenges', *Bothalia* 47(2), a2152. <https://doi.org/10.4102/abc.v47i2.2152>
- Jeschke, J.M., Bacher, S., Blackburn, T.M., Dick, J.T.A., Essl, F., Evans, T. et al., 2014, 'Defining the impact of non-native species', *Conservation Biology* 28, 1188–1194. <https://doi.org/10.1111/cobi.12299>
- Kumschick, S. & Richardson, D.M., 2013, 'Species-based risk assessments for biological invasions: Advances and challenges', *Diversity and Distributions* 19, 1095–1105. <https://doi.org/10.1111/ddi.12110>
- Lonsdale, W.M., 1994, 'Inviting trouble: Introduced pasture species in northern Australia', *Australian Journal of Ecology* 19, 345–354. <https://doi.org/10.1111/j.1442-9993.1994.tb00498.x>
- Mack, R.N. & Thompson, J.N., 1982, 'Evolution in steppe with few large, hooved mammals', *American Naturalist* 119, 757–773. <https://doi.org/10.1086/283953>
- Milton, S.J., 2004, 'Grasses as invasive alien plants in South Africa', *South African Journal of Science* 100, 69–75.
- Mucina, L., Rutherford, M.C., Powrie, L.W. & Rebelo, A.G., 2005, *Vegetation map of South Africa, Lesotho and Swaziland*, South African National Biodiversity Institute, Pretoria.
- Mugwedi, L.F., 2012, 'Invasion ecology of *Glyceria maxima* in KZN rivers and wetlands', M.Sc. thesis, University of the Witwatersrand.
- Musil, C.F., Milton, S.J. & Davis, G.W., 2005, 'The threat of alien invasive grasses to lowland Cape floral diversity: An empirical appraisal of the effectiveness of practical control strategies: Research in action', *South African Journal of Science* 101, 337–344.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C. et al., 2001, 'Terrestrial ecoregions of the world: A new map of life on Earth. A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity', *BioScience* 51, 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)
- Osborne, C.P. & Sack, L., 2012, 'Evolution of *C₄* plants: A new hypothesis for an interaction of CO₂ and water relations mediated by plant hydraulics', *Philosophical Transactions of the Royal Society B: Biological Sciences* 367, 583–600. <https://doi.org/10.1098/rstb.2011.0261>
- Osborne, C.P., Salomaa, A., Kluyver, T.A., Visser, V., Kellogg, E.A., Morrone, O. et al., 2014, 'A global database of *C₄* photosynthesis in grasses', *New Phytologist* 204, 441–446. <https://doi.org/10.1111/nph.12942>
- Panetta, F., 1993, 'A system of assessing proposed plant introductions for weed potential', *Plant Protection Quarterly* 8, 10–14.
- Parker-Allie, F., Musil, C.F. & Thuiller, W., 2009, 'Effects of climate warming on the distributions of invasive Eurasian annual grasses: A South African perspective', *Climatic Change* 94, 87–103. <https://doi.org/10.1007/s10584-009-9549-7>
- Pluess, T., Cannon, R., Jarošík, V., Pergl, J., Pyšek, P. & Bacher, S., 2012a, 'When are eradication campaigns successful? A test of common assumptions', *Biological Invasions* 14, 1365–1378. <https://doi.org/10.1007/s10530-011-0160-2>
- Pluess, T., Jarošík, V., Pyšek, P., Cannon, R., Pergl, J., Breukers, A. et al., 2012b, 'Which factors affect the success or failure of eradication campaigns against alien species?', *PLoS One* 7, e48157. <https://doi.org/10.1371/journal.pone.0048157>
- Quattrocchi, U., 2006, *CRC world dictionary of grasses: Common names, scientific names, eponyms, synonyms, and etymology – 3 volume set*, CRC Press, Boca Raton, FL.
- R Core Team, 2016, *R: A language and environment for statistical computing*, viewed 1 October 2016, from <http://www.r-project.org/>
- Rahlao, S.J., Milton, S.J., Esler, K.J. & Barnard, P., 2014, 'Performance of invasive alien fountain grass (*Pennisetum setaceum*) along a climatic gradient through three South African biomes', *South African Journal of Botany* 91, 43–48. <https://doi.org/10.1016/j.sajb.2013.11.013>
- Rahlao, S.J., Milton, S.J., Esler, S.J., van Wilgen, B.W. & Barnard, P., 2009, 'Effects of invasion of fire-free arid shrublands by a fire-promoting invasive alien grass species (*Pennisetum setaceum*) in South Africa', *Austral Ecology* 34, 920–928. <https://doi.org/10.1111/j.1442-9993.2009.02000.x>
- Randall, R.P., 2012, *A global compendium of weeds, 2nd edition*, Department of Agriculture and Food, Perth, Western Australia.
- Rejmánek, M. & Pyšek, P., 2002, 'When is eradication of exotic pest plants a realistic goal?', in C.R. Veitch & M.N. Clout (eds.), *Turning the tide: The eradication of invasive species, Proceedings of the international conference on eradication of island invasives*, pp. 249–253, IUCN, Cambridge, UK.
- Richardson, D.M., Bond, W.J., Dean, W.R.J., Higgins, S.L., Midgley, G., Milton, S.J. et al., 2000, 'Invasive alien species and global change: A South African perspective', in H.A. Mooney & R.J. Hobbs (eds.), *Invasive species in a changing world*, pp. 303–350, Island Press, Washington, DC.
- Richardson, D.M. & Pyšek, P., 2012, 'Naturalization of introduced plants: Ecological drivers of biogeographical patterns', *New Phytologist* 196, 383–396. <https://doi.org/10.1111/j.1469-8137.2012.04292.x>
- Richardson, D.M., Rouget, M., Ralston, S.J., Cowling, R.M., Van Rensburg, B.J. & Thuiller, W., 2005, 'Species richness of alien plants in South Africa: Environmental correlates and the relationship with indigenous plant species richness', *Ecoscience* 12, 391–402. <https://doi.org/10.2980/1195-6860-12-3-391.1>
- Rouget, M., Robertson, M.P., Wilson, J.R.U., Hui, C., Essl, F., Renteria, J.L. et al., 2016, 'Invasion debt – quantifying future biological invasions', *Diversity and Distributions* 22, 445–456. <https://doi.org/10.1111/ddi.12408>
- Ryerson, K.A., 1976, 'Plant introductions', *Agricultural History* 50, 248–257.
- Sharma, G.P., Muhl, S.A., Esler, K.J. & Milton, S.J., 2010, 'Competitive interactions between the alien invasive annual grass *Avena fatua* and indigenous herbaceous plants in South African Renosterveld: The role of nitrogen enrichment', *Biological Invasions* 12, 3371–3378. <https://doi.org/10.1007/s10530-010-9730-y>
- Simberloff, D., 2009, 'The role of propagule pressure in biological invasions', *Annual Review of Ecology, Evolution and Systematics* 40, 81–102. <https://doi.org/10.1146/annurev.ecolsys.110308.120304>
- Soreng, R.J., Peterson, P.M., Romaschenko, K., Davidse, G., Zuloaga, F.O., Judziewicz, E.J. et al., 2015, 'A worldwide phylogenetic classification of the Poaceae (Gramineae)', *Journal of Systematics and Evolution* 53, 117–137. <https://doi.org/10.1111/jse.12150>
- Spear, D., McGeoch, M.A., Foxcroft, L.C. & Bezuidenhout, H., 2011, 'Alien species in South Africa's national parks', *Koedoe* 53, Art. #1032, 4 pages. <https://doi.org/10.4102/koedoe.v53i1.1032>
- Taylor, S.H., Hulme, S.P., Rees, M., Ripley, B.S., Ian Woodward, F. & Osborne, C.P., 2010, 'Ecophysiological traits in *C₄* and *C₃* grasses: A phylogenetically controlled screening experiment', *New Phytologist* 185, 780–791. <https://doi.org/10.1111/j.1469-8137.2009.03102.x>

- Van Wilgen, B., 2014, *A national strategy for dealing with biological invasions in South Africa*, DEA, Pretoria, South Africa.
- van Wilgen, B.W., Forsyth, G.G., Le Maitre, D.C., Wannenburgh, A., Kotzé, J.D., van den Berg, E. et al., 2012, 'An assessment of the effectiveness of a large, national-scale invasive alien plant control strategy in South Africa', *Biological Conservation* 148, 28–38. <https://doi.org/10.1016/j.biocon.2011.12.035>
- Veldman, J.W., Mostacedo, B., Peña-Clarosa, M. & Putz, F.E., 2009, 'Selective logging and fire as drivers of alien grass invasion in a Bolivian tropical dry forest', *Forest Ecology and Management* 258, 1643–1649. <https://doi.org/10.1016/j.foreco.2009.07.024>
- Visser, V., Wilson, J.R.U., Fish, L., Brown, C., Cook, G.D. & Richardson, D.M., 2016, 'Much more give than take: South Africa as a major donor but infrequent recipient of invasive non-native grasses', *Global Ecology and Biogeography* 25, 679–692. <https://doi.org/10.1111/geb.12445>
- Vlok, J., 1988, 'Alpha diversity of lowland fynbos herbs at various levels of infestation by alien annuals', *South African Journal of Botany* 54, 623–627. [https://doi.org/10.1016/S0254-6299\(16\)31264-9](https://doi.org/10.1016/S0254-6299(16)31264-9)
- Wilson, J.R.U., Gaertner, M., Richardson, D.M. & van Wilgen, B.W., 2017, 'Contributions to the national status report on biological invasions in South Africa', *Bothalia* 47(2), a2207. <https://doi.org/10.4102/abc.v47i2.2207>
- Wilson, J.R.U., Ivey, P., Manyama, P. & Nänni, I., 2013, 'A new national unit for invasive species detection, assessment and eradication planning', *South African Journal of Science* 109, 1–13.
- Wilson, J.R.U., Richardson, D.M., Rouget, M., Procheş, S., Amis, M.A., Henderson, L. et al., 2007, 'Residence time and potential range: Crucial considerations in modelling plant invasions', *Diversity and Distributions* 13, 11–22. <https://doi.org/10.1111/j.1366-9516.2006.00302.x>
- Yelenik, S., Stock, W. & Richardson, D., 2004, 'Ecosystem-level impacts of invasive alien nitrogen-fixing plants. Ecosystem and community-level impacts of invasive alien *Acacia saligna* in the fynbos vegetation of South Africa', *Restoration Ecology* 12, 44–51. <https://doi.org/10.1111/j.1061-2971.2004.00289.x>
- Zachariades, C., Paterson, I.D., Strathie, L.W., Hill, M.P. & van Wilgen, B.W., 2017, 'Assessing the status of biological control as a management tool for suppression of invasive alien plants in South Africa', *Bothalia* 47(2), a2142. <https://doi.org/10.4102/abc.v47i2.2142>

Appendix start on the next page →

Appendix 1

TABLE 1-A1: Online and published sources used to compile a checklist of alien grass species in South Africa

Reference	Introduced	Naturalised	Invasive	Distribution	Date
Adams et al. (2012)	-	-	✓	-	✓
Baard and Kraaij (2014) INI status was assigned based on species' status in this reference †	-	✓	✓	-	-
Bromilow (2010)	-	✓	-	-	-
CABI (2016) INI status was assigned based on species' status in this reference †	✓	✓	✓	-	-
Clayton et al. (2006 onwards)	-	-	-	-	-
Cowan and Anderson (2014)	-	✓	-	✓	✓
Davies (1975)	-	-	-	-	✓
Department of Agriculture & Forestry (1940)	✓	-	-	-	✓
Foxcroft et al. (2008)	-	✓	✓	-	-
GBIF (2016)	✓	-	-	✓	✓
Glen (2002)	✓	-	-	-	-
GISD (2016) INI status was assigned based on species' status in this reference †	✓	✓	✓	-	-
Grootfontein Agricultural Development Institute (2016)	✓	-	-	✓	✓
Guthrie (2007)	-	-	✓	-	-
Harding (1982)	-	-	-	✓	✓
Heelemann et al. (2013)	-	✓	✓	✓	✓
Henderson (2007) Invasive if species recorded as being abundant or very abundant at more than one locality †	-	✓	✓	✓	✓
Hertling & Lubke (1999)	-	-	-	✓	✓
Holmes (2008)	-	-	✓	✓	✓
Joubert (1984)	-	-	✓	✓	✓
Lesoli et al. (2013)	-	✓	-	-	-
Maggs and Ward (1984)	-	-	-	-	✓
Manning and Goldblatt (2012)	✓	-	-	-	-
Masubelele et al. (2009)	-	✓	-	✓	✓
Milton et al. (1998)	-	✓	-	✓	✓
Mugwedi (2012)	-	-	✓	-	-
Musil et al. (2005)	-	-	✓	✓	✓
PlantsinStock (2016)	✓	-	-	-	-
Powrie (2012)	✓	-	-	✓	✓
Rahlao et al. (2010)	-	-	✓	-	-
Randall (2012) INI status was based on the statuses in this reference, as described in the relevant columns here †	Species occurring in SA with statuses in Randall (2012) that are not any of those listed for naturalised or invasive species	Species occurring in SA with statuses in Randall (2012) of: Cultivation Escape, Environmental Weed, Garden Escape, Invasive, Naturalised, Noxious Weed	Species occurring in SA with statuses in Randall (2012) of: Environmental Weed, Invasive, Noxious Weed	✓	-
Ratnasingham & Herbert (2007)	✓	-	-	-	-
SANBI (2009a) Naturalised, if described as such. †	✓	✓	-	-	-
SANBI (2009b)	✓	-	-	✓	✓
Scott (1982)	-	-	-	-	✓
Sharma et al. (2010)	-	-	✓	✓	✓
Shiponeni & Milton (2006)	-	-	-	✓	✓
Steinschen et al. (1996)	-	-	✓	✓	✓
Thunberg (1823)	-	-	-	-	✓
Todd (2008)	-	-	✓	✓	✓
USDA, ARS, National Genetic Resources Program (2016) Naturalised in South Africa, if described as such. †	✓	✓	-	-	-
Viljoen (1987)	-	-	-	✓	✓

Indicated are the references used to determine species' statuses along the introduction-naturalisation-invasion continuum (Blackburn et al. 2011). References with a ✓ indicate that the reference was used to assign that specific status to a species. References that were used as sources of distribution data are indicated with ticks in the 'Distribution' column, and those for obtaining dates of occurrences (and ultimately minimum residence times) in the 'Date' column.

To clarify the alien status of all species in South Africa we first compared our initial list of species against a list of native grasses obtained from the Plants of Southern Africa database (POSA; <http://newposa.sanbi.org/>). Thereafter, we further refined the list using distribution information on the native range of each species from the eMonocot database (<http://emonocot.org>) and the Germplasm Resources Information Network (<http://ars-grin.gov/cgi-bin/npgs/html/taxgenform.pl?language=en>). We flagged species that were possibly native to South Africa, but not recorded as such in POSA, and manually checked whether these are in fact native.

†, indicate special conditions.

References

- Adams, J.B., Grobler, A., Rowe, C., Riddin, T., Bornman, T.G. & Ayres, D.R., 2012, 'Plant traits and spread of the invasive salt marsh grass, *Spartina alterniflora* Loisel., in the Great Brak Estuary, South Africa', *African Journal of Marine Science* 34, 313–322. <https://doi.org/10.2989/1814232X.2012.725279>
- Baard, J.A. & Kraaij, T., 2014, 'Alien flora of the Garden Route National Park, South Africa', *South African Journal of Botany* 94, 51–63. <https://doi.org/10.1016/j.sajb.2014.05.010>
- Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., et al., 2011, 'A proposed unified framework for biological invasions', *Trends in Ecology & Evolution* 26, 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Bromilow, C., 2010, *Problem plants of South Africa*, 3rd edn., Briza Publications, South Africa.
- CABI, 2016, *Invasive species compendium*, CAB International, Wallingford, viewed 10 May 2016, from <http://www.cabi.org/isc/>
- Clayton, W.D., Vorontsova, M.S., Harman, K.T. & Williamson, H., 2006 onwards, *GrassBase – The Online World Grass Flora*, The Board of Trustees, Royal Botanic Gardens, Kew, viewed 10 May 2016, from <http://www.kew.org/data/grasses-db.html/>
- Cowan, O.S. & Anderson, P.M.L., 2014, 'The Peninsula Shale Renosterveld of Devil's Peak, Western Cape: A study into the vegetation and seedbank with a view toward potential restoration', *South African Journal of Botany* 95, 135–145. <https://doi.org/10.1016/j.sajb.2014.09.003>
- Davies, O., 1975, 'Excavations at Shongweni South Cave: The oldest evidence to date for cultigens in Southern Africa', *Annals of the Natal Museum* 22, 627–662.
- Department of Agriculture & Forestry, 1940, *Pasture research in South Africa. Progress report no. 2*, Government printer, Pretoria.
- Foxcroft, L.C., Richardson, D.M. & Wilson, J.R.U., 2008, 'Ornamental plants as invasive aliens: Problems and solutions in Kruger National Park, South Africa', *Environmental Management* 41, 32–51. <https://doi.org/10.1007/s00267-007-9027-9>
- GBIF, 2016, *Global biodiversity information facility: Free and open access to biodiversity data*, Global Biodiversity Information Facility, Copenhagen, viewed 10 May 2016, from <http://www.gbif.org/>
- Glen, H.F., 2002, *Cultivated plants of Southern Africa: Botanical names, common names, origins, literature*, Jacana Media.
- GISD, 2016, *Global invasive species database*, Invasive Species Specialist Group, viewed 10 May 2016, from <http://www.issg.org/database/welcome/>
- Grootfontein Agricultural Development Institute, 2016, *Grootfontein herbarium*, viewed 10 May 2016, from <http://gadi.agric.za/herbarium/her-general.php>
- Guthrie, G., 2007, 'Impacts of the invasive reed *Arundo donax* on biodiversity at the community-ecosystem level', M.Sc. thesis, University of the Western Cape.
- Harding, G.B., 1982, 'The autecology of *Stipa trichotoma* Nees (nassella tussock) on the Rhodes Estate, in the S.W. Cape', M.Sc. thesis, University of Cape Town.
- Heelemann, S., Krug, C.B., Esler, K.J., Reisch, C. & Poschod, P., 2013, 'Soil seed banks of remnant and degraded Swartland Shale Renosterveld', *Applied Vegetation Science* 16, 585–597. <https://doi.org/10.1111/avsc.12026>
- Henderson, L., 2007, 'Invasive, naturalized and casual alien plants in southern Africa: A summary based on the Southern African Plant Invaders Atlas (SAPIA)', *Bothalia* 37, 215–248. <https://doi.org/10.4102/abc.v37i2.322>
- Hertling, U.M. & Lubke, R.A., 1999, 'Use of *Ammophila arenaria* for Dune stabilization in South Africa and its current distribution – perceptions and problems', *Environmental Management* 24, 467–482. <https://doi.org/10.1007/s002679900247>
- Holmes, P.M., 2008, 'Optimal ground preparation treatments for restoring lowland Sand Fynbos vegetation on old fields', *South African Journal of Botany* 74, 33–40. <https://doi.org/10.1016/j.sajb.2007.08.005>
- Joubert, D.C., 1984, 'The soil seed bank under nassella tussock infestations at Boschberg', *South African Journal of Plant and Soil* 1, 1–3. <https://doi.org/10.1080/02571862.1984.10634099>
- Lesoli, M.S., Gxasheka, M., Solomon, T.B. & Moyo, B., 2013, Integrated plant invasion and bush encroachment management on southern African rangelands, in A.J. Price & J.A. Kelton (eds.), *Herbicides – Current research and case studies in use*, InTech, Rijeka, pp. 259–313.
- Maggs, T. & Ward, V., 1984, 'Early Iron Age sites in the Muden area of Natal', *Annals of the Natal Museum* 26, 105–140.
- Manning, J. & Goldblatt, P., 2012, *Plants of the Greater Cape Floristic Region. 1: The Core Cape flora. Strelitzia 29*, South African National Biodiversity Institute, Pretoria, South Africa.
- Masubelele, M.L., Foxcroft, L.C. & Milton, S.J., 2009, 'Alien plant species list and distribution for Camdeboo National Park, Eastern Cape Province, South Africa', *Koedoe* 51, 1–10.
- Milton, S.J., Hoffmann, J.H., Bowie, R.C.K., D'Amico, J., Griffiths, M., Joubert, D., et al., 1998, 'Invasive fountain grass on the Cape Peninsula', *South African Journal of Science* 94, 57–58.
- Mugwedi, L.F., 2012, 'Invasion ecology of *Glyceria maxima* in KZN Rivers and wetlands', M.Sc. thesis, University of the Witwatersrand.
- Musil, C.F., Milton, S.J. & Davis, G.W., 2005, 'The threat of alien invasive grasses to lowland Cape floral diversity: an empirical appraisal of the effectiveness of practical control strategies: research in action', *South African Journal of Science* 101, 337–344.
- National Environmental Management: Biodiversity Act (10/2004): Alien and Invasive Species List, 2016, Government notice #864, Government Gazette #40166, 29 July 2106.
- Plantsinstock, 2016, *Plantsinstock*, viewed 10 May 2016, from <http://www.plantsinstock.co.za/>
- Powrie, L.W., 2012, *Les Powrie extensions for Arcview 3.x v.18*, Unpublished guide, South African National Biodiversity Institute, Cape Town. Les Powrie extensions for Arcview 3.x v.18.docx downloaded from www.sanbi.org on 25 June 2015.
- Rahlao, S., Milton, S.J., Esler, K.J. & Barnard, P., 2010, 'The distribution of invasive *Pennisetum setaceum* along roadsides in western South Africa: The role of corridor interchanges', *Weed Research* 50, 537–543. <https://doi.org/10.1111/j.1365-3180.2010.00801.x>
- Randall, R.P., 2012, *A global compendium of weeds*, 2nd edn, Department of Agriculture and Food, Western Australia.
- Ratnasingham, S. & Hebert, P.D., 2007, 'BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>)', *Molecular Ecology Notes* 7, 355–364. <https://doi.org/10.1111/j.1471-8286.2007.01678.x>
- SANBI, 2009a, *Plants of southern Africa: an online checklist*, Version 3, South African National Biodiversity Institute, Pretoria, viewed 10 May 2016, from <http://posa.sanbi.org/searchspp.php>
- SANBI, 2009b, *SIBIS portal*, South African National Biodiversity Institute, Pretoria, viewed 10 May 2016, from <http://sibis.sanbi.org/>
- Scott, L., 1982, 'Late quaternary fossil pollen grains from the Transvaal, South Africa', *Review of Palaeobotany and Palynology* 36, 241–278. [https://doi.org/10.1016/0034-6667\(82\)90022-7](https://doi.org/10.1016/0034-6667(82)90022-7)
- Sharma, G.P., Muhl, S.A., Esler, K.J. & Milton, S.J., 2010, 'Competitive interactions between the alien invasive annual grass *Avena fatua* and indigenous herbaceous plants in South African Renosterveld: The role of nitrogen enrichment', *Biological Invasions* 12, 3371–3378. <https://doi.org/10.1007/s10530-010-9730-y>
- Shiponeni, N.N. & Milton, S.J., 2006, 'Seed dispersal in the dung of large herbivores: Implications for restoration of Renosterveld shrubland old fields', *Biodiversity & Conservation* 15, 3161–3175. <https://doi.org/10.1007/s10531-005-6317-5>
- Steinschen, A.K., Gorne, A. & Milton, S.J., 1996, 'Threats to the Namaqualand flowers: Outcompeted by grass or exterminated by grazing?', *South African Journal of Science* 92, 237–242.
- Thunberg, C.P., 1823, *Flora Capensis*, J.G. Cottae, Stuttgart.
- Todd, S., 2008, 'The abundance and impact of alien annual grasses on Hantam-Roggeveld Dolerite Renosterveld vegetation at Nieuwoudtville, Northern Cape, South Africa', Unpublished report, Plant Conservation Unit, Botany Department, University of Cape Town.
- USDA, ARS, National Genetic Resources Program, 2015, Germplasm Resources Information Network – (GRIN), National Germplasm Resources Laboratory, Beltsville, Maryland, viewed 10 May 2016, from <https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysimple.aspx>
- USDA, NRCS, 2015, The PLANTS Database, National Plant Data Team, Greensboro, NC 27401–4901 USA, viewed 10 May 2016, from <http://plants.usda.gov>
- Viljoen, B.D., 1987, 'Effect of rate and time of application of tetrapion on nassella tussock (*Stipa trichotoma* Nees) in South Africa', *South African Journal of Plant and Soil* 4, 79–81. <https://doi.org/10.1080/02571862.1987.10634945>

Appendix 2 start on the next page →

Appendix 2

TABLE 1-A2: Statistical summary of differences among use categories in relation to the numbers of alien grass species of different statuses across the introduction-naturalisation-invasion continuum as determined by an ordinal logistic regression.

Use category	β	2.5%	97.5%	LRT	<i>P</i>
None	1.15	0.23	2.10	5.984	< 0.05
Forage	0.70	0.03	1.41	4.205	< 0.05
Horticulture	0.51	-0.05	1.08	3.125	0.07
Raw material	-0.53	-1.32	0.23	1.838	0.18
Soil stabilisation	0.27	-0.30	0.83	0.884	0.35
Food and beverage	-0.13	-0.83	0.56	0.135	0.71

A likelihood-ratio test (LRT) was used to test whether the association of each use category with introduction-naturalisation-invasion status was significantly different from zero. Significant *P*-values shown in bold. Also shown are correlation coefficients (β) and upper and lower 95% confidence intervals.

TABLE 2-A2: Statistical summary of differences among realms to which species are native in relation to the numbers of alien grass species of different statuses across the introduction-naturalisation-invasion continuum as determined by an ordinal logistic regression.

Realm	β	2.5%	97.5%	LRT	<i>P</i>
South America	2.23	1.26	3.27	21.61	< 0.0001
Eurasia	1.52	0.80	2.30	18.19	< 0.0001
North America	-1.29	-2.22	-0.42	8.73	< 0.01
Southeast Asia	0.25	-0.33	0.83	0.71	0.40
Australasia	0.34	-0.73	1.36	0.40	0.53
Pacific	0.55	-2.71	3.26	0.15	0.70

A likelihood-ratio test (LRT) was used to test whether the association of each use category with introduction-naturalisation-invasion status was significantly different from zero. Significant *P*-values shown in bold. Also shown are correlation coefficients (β) and upper and lower 95% confidence intervals.

Appendix 3 start on the next page →

Appendix 3

TABLE 1-A3: Pasture research stations established in South Africa.

Station	Establishment year	Closure year	Number species cultivated	Reference
Skinners Court, Pretoria	1903	1912	?	Smith and Rhind (1984)
Groenkloof, Pretoria	1912	1923?	2	Smith and Rhind (1984)
Burttholm, Vereeniging	1913	1919	3	Gunn and Codd (1981)
Prinshof, Pretoria	1923	1940?	63	DAF (1940); Smith and Rhind (1984)
Athole Research Station, Amsterdam, Mpumulanga	1934	?	26	Donaldson (1984)
Towoomba, Bela-Bela, Limpopo	1934	?	2	Donaldson (1984)
Albany Museum Herbarium, Grahamstown	1934	1937	1	Smith and Rhind (1984)
Rietondale, Pretoria	1934	1972	?	Smith and Rhind (1984)
Leeuwkuil, Vereeniging	1934	1938?	24	Donaldson (1984); Story (1938)
Potchefstroom	1946	< 1956?	2	Smith and Rhind (1984)
Cedara, Pietermaritzburg	1951	Still operational	13	Smith and Rhind (1984)
Rietvlei, Pretoria	1954	< 1956?	?	Smith and Rhind (1984)
Koolbank Grass Seed Station, Pretoria	1954	< 1956?	?	Smith and Rhind (1984)
Estcourt	1936	?	18	Scott (1966)

Source: Department of Agriculture & Forestry (DAF), 1940, *Pasture research in South Africa: Progress report no. 2. Division of soil and veld conservation*, Government Printer of the Union of South Africa, Pretoria

Provided for each station are the establishment year, closure year (when available) and supporting references.

References

- Donaldson, C.H., 1984, 'Fifty years of pasture research in South Africa', *Journal of the Grassland Society of Southern Africa* 1, 4.
- Gunn, M. & Codd, L.E., 1981, *Botanical exploration of southern Africa*, Botanical Research Institute, Cape Town.
- Scott, J.D., 1966, 'Pasture research in Natal', *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa* 1, 27–32.
- Smith, A. & Rhind, J.M.L.C., 1984, 'Eight decades of pasture plant improvement in South Africa', *Journal of the Grassland Society of Southern Africa* 1, 25–28.
- Story, R., 1938, 'Leeuwkuil-weiveldnavorsingstasie', in *Departement van Landbou en Bosbou, Weiveldnavorsing in Suid-Afrika: Vorderingsverslag no. 1*, p. 69, Staatsdrukker, Unie van Suid-Afrika,

Appendix continued on the next page →

TABLE 2-A3: Introduced grass species cultivated at pasture research stations in South Africa.

Station	Species	Year	Novel introduction	Reference
Prinshof	<i>Aegilops cylindrica</i> Host	1938	Yes	DAF (1940)
Estcourt	<i>Agropyron cristatum</i> (L.) Gaertn	1937	Yes	DAF (1940)
Leeuwkuil	<i>Agropyron cristatum</i> (L.) Gaertn	1938	-	DAF (1940)
Prinshof	<i>Agropyron cristatum</i> (L.) Gaertn	1938	-	DAF (1940)
Prinshof	<i>Agropyron desertorum</i> (Fisch. ex Link) Schult	1938	Yes	DAF (1940)
Prinshof	<i>Agropyron fragile</i> (Roth) P.Candargy	1938	Yes	DAF (1940)
Cedara	<i>Agropyron</i> spp.	1951	-	Smith and Rhind (1984)
Athole	<i>Agrostis capillaris</i> L.	1934	Yes	DAF (1940)
Estcourt	<i>Agrostis capillaris</i> L.	1937	-	DAF (1940)
Leeuwkuil	<i>Agrostis capillaris</i> L.	1938	-	DAF (1940)
Prinshof	<i>Agrostis capillaris</i> L.	1938	-	DAF (1940)
Cedara	<i>Agrostis</i> spp.	1951	-	Smith and Rhind (1984)
Athole	<i>Agrostis stolonifera</i> L.	1934	-	DAF (1940)
Estcourt	<i>Agrostis stolonifera</i> L.	1937	-	DAF (1940)
Leeuwkuil	<i>Agrostis stolonifera</i> L.	1938	-	DAF (1940)
Prinshof	<i>Andropogon gerardii</i> Vitman	1938	Yes	DAF (1940)
Prinshof	<i>Andropogon hallii</i> Hack	1938	Yes	DAF (1940)
Athole	<i>Arrhenatherum elatius</i> (L.) P.Beauv. ex J.Presl & C.Presl.	1934	-	DAF (1940)
Leeuwkuil	<i>Arrhenatherum elatius</i> (L.) P.Beauv. ex J.Presl & C.Presl.	1938	-	DAF (1940)
Prinshof	<i>Arrhenatherum elatius</i> (L.) P.Beauv. ex J.Presl & C.Presl.	1938	-	DAF (1940)
Prinshof	<i>Astrebula</i> spp.	1938	-	DAF (1940)
Prinshof	<i>Avena nuda</i> L.	1938	Yes	DAF (1940)
Athole	<i>Axonopus compressus</i> (Sw.) P.Beauv.	1934	-	DAF (1940)
Prinshof	<i>Bothriochloa saccharoides</i> (Sw.) Rydb.	1938	Yes	DAF (1940)
Prinshof	<i>Bouteloua chondrosioides</i> (Kunth) Benth. ex S.Watson	1938	Yes	DAF (1940)
Prinshof	<i>Bouteloua curtipendula</i> (Michx.) Torr.	1938	-	DAF (1940)
Prinshof	<i>Brachiaria mutica</i> (Forssk.) Stapf	1938	Yes	DAF (1940)
Athole	<i>Bromus catharticus</i> Vahl	1934	-	DAF (1940)
Cedara	<i>Bromus catharticus</i> Vahl	1951	-	Smith and Rhind (1984)
Estcourt	<i>Bromus catharticus</i> Vahl	1937	-	DAF (1940)
Leeuwkuil	<i>Bromus catharticus</i> Vahl	1938	-	DAF (1940)
Prinshof	<i>Bromus catharticus</i> Vahl	1938	-	DAF (1940)
Athole	<i>Bromus inermis</i> Leyss.	1934	-	DAF (1940)
Cedara	<i>Bromus inermis</i> Leyss.	1951	-	Smith and Rhind (1984)
Estcourt	<i>Bromus inermis</i> Leyss.	1937	-	DAF (1940)
Leeuwkuil	<i>Bromus inermis</i> Leyss.	1938	-	DAF (1940)
Prinshof	<i>Bromus inermis</i> Leyss.	1938	-	DAF (1940)
Prinshof	<i>Buchloe dactyloides</i> (Nutt.) Engelm.	1938	-	DAF (1940)
Prinshof	<i>Chondrosium eriopodum</i> Torr.	1938	Yes	DAF (1940)
Prinshof	<i>Chondrosium gracile</i> Kunth	1938	-	DAF (1940)
Prinshof	<i>Chondrosium hirsutum</i> (Lag.) Sweet	1938	Yes	DAF (1940)
Prinshof	<i>Coix lacryma-jobi</i> L.	1938	-	DAF (1940)
Athole	<i>Cynosurus cristatus</i> L.	1934	Yes	DAF (1940)
Prinshof	<i>Cynosurus cristatus</i> L.	1938	-	DAF (1940)
Athole	<i>Dactylis glomerata</i> L.	1934	-	DAF (1940)
Cedara	<i>Dactylis glomerata</i> L.	1951	-	Smith and Rhind (1984)
Estcourt	<i>Dactylis glomerata</i> L.	1937	-	DAF (1940)
Leeuwkuil	<i>Dactylis glomerata</i> L.	1938	-	DAF (1940)
Prinshof	<i>Dactylis glomerata</i> L.	1938	-	DAF (1940)
Leeuwkuil	<i>Echinochloa esculenta</i> (A.Braun) H.Scholz	1938	Yes	DAF (1940)
Athole	<i>Elymus caninus</i> (L.) L.	1934	-	DAF (1940)
Leeuwkuil	<i>Elymus caninus</i> (L.) L.	1938	-	DAF (1940)
Prinshof	<i>Elymus elongatus</i> (Host) Runemark	1938	Yes	DAF (1940)
Prinshof	<i>Elymus repens</i> (L.) Gould	1938	-	DAF (1940)
Prinshof	<i>Elymus smithii</i> (Rydb.) Gould	1938	Yes	DAF (1940)
Estcourt	<i>Elymus trachycaulus</i> (Link) Gould ex Shinnars	1937	Yes	DAF (1940)
Prinshof	<i>Elymus trachycaulus</i> (Link) Gould ex Shinnars	1938	-	DAF (1940)
Leeuwkuil	<i>Eragrostis tef</i> (Zucc.) Trotter	1938	-	DAF (1940)
Athole	<i>Festuca arundinacea</i> Schreb.	1934	-	DAF (1940)
Burttholm	<i>Festuca arundinacea</i> Schreb.	1914	-	Burt-Davy (1920)
Cedara	<i>Festuca arundinacea</i> Schreb.	1951	-	Smith and Rhind (1984)

Appendix table continued on the next page →

TABLE 2-A3 (Continues...): Introduced grass species cultivated at pasture research stations in South Africa.

Station	Species	Year	Novel introduction	Reference
Estcourt	<i>Festuca arundinacea</i> Schreb.	1937	-	DAF (1940)
Groenkloof	<i>Festuca arundinacea</i> Schreb.	1912	-	Smith and Rhind (1984)
Leeuwkuil	<i>Festuca arundinacea</i> Schreb.	1938	-	DAF (1940)
Prinshof	<i>Festuca arundinacea</i> Schreb.	1938	-	DAF (1940)
Athole	<i>Festuca ovina</i> L.	1934	Yes	DAF (1940)
Leeuwkuil	<i>Festuca ovina</i> L.	1938	-	DAF (1940)
Leeuwkuil	<i>Festuca pratensis</i> Huds.	1938	Yes	DAF (1940)
Athole	<i>Festuca rubra</i> L.	1934	Yes	DAF (1940)
Estcourt	<i>Festuca rubra</i> L.	1937	-	DAF (1940)
Leeuwkuil	<i>Festuca rubra</i> L.	1938	-	DAF (1940)
Prinshof	<i>Festuca rubra</i> L.	1938	-	DAF (1940)
Athole	<i>Holcus lanatus</i> L.	1934	-	DAF (1940)
Cedara	<i>Holcus lanatus</i> L.	1951	-	Smith and Rhind (1984)
Leeuwkuil	<i>Holcus lanatus</i> L.	1938	-	DAF (1940)
Prinshof	<i>Holcus lanatus</i> L.	1938	-	DAF (1940)
Prinshof	<i>Leymus angustus</i> (Trin.) Pilg.	1938	Yes	DAF (1940)
Prinshof	<i>Leymus chinensis</i> (Trin.) Tzvelev	1938	Yes	DAF (1940)
Prinshof	<i>Leymus ramosus</i> (C.Richt.) Tzvelev	1938	Yes	DAF (1940)
Athole	<i>Lolium multiflorum</i> Lam.	1934	-	DAF (1940)
Cedara	<i>Lolium multiflorum</i> Lam.	1951	-	Smith and Rhind (1984)
Cedara	<i>Lolium multiflorum</i> Lam.	1951	-	Smith and Rhind (1984)
Estcourt	<i>Lolium multiflorum</i> Lam.	1937	-	DAF (1940)
Leeuwkuil	<i>Lolium multiflorum</i> Lam.	1938	-	DAF (1940)
Prinshof	<i>Lolium multiflorum</i> Lam.	1938	-	DAF (1940)
Athole	<i>Lolium perenne</i> L.	1934	-	DAF (1940)
Cedara	<i>Lolium perenne</i> L.	1951	-	Smith and Rhind (1984)
Estcourt	<i>Lolium perenne</i> L.	1937	-	DAF (1940)
Leeuwkuil	<i>Lolium perenne</i> L.	1938	-	DAF (1940)
Prinshof	<i>Lolium perenne</i> L.	1938	-	DAF (1940)
Athole	<i>Lolium rigidum</i> Gaudin	1934	-	DAF (1940)
Prinshof	<i>Oryzopsis hymenoides</i> (Roem. and Schult.) Ricker ex Piper	1938	Yes	DAF (1940)
Prinshof	<i>Panicum acrotrichum</i> Hook.f.	1938	Yes	DAF (1940)
Prinshof	<i>Panicum miliaceum</i> L.	1938	-	DAF (1940)
Prinshof	<i>Panicum obtusum</i> Kunth	1938	Yes	DAF (1940)
Athole	<i>Panicum phragmitoides</i> Stapf	1934	Yes	DAF (1940)
Towoomba	<i>Panicum phragmitoides</i> Stapf	1934	-	DAF (1940)
Prinshof	<i>Panicum plenum</i> Hitchc. and Chase	1938	Yes	DAF (1940)
Prinshof	<i>Panicum prolutum</i> F.Muell.	1938	Yes	DAF (1940)
Prinshof	<i>Panicum virgatum</i> L.	1938	Yes	DAF (1940)
Prinshof	<i>Paspalidium flavidum</i> (Retz.) A.Camus	1938	Yes	DAF (1940)
Athole	<i>Paspalum dilatatum</i> Poir.	1934	-	DAF (1940)
Cedara	<i>Paspalum dilatatum</i> Poir.	1951	-	Smith and Rhind (1984)
Estcourt	<i>Paspalum dilatatum</i> Poir.	1937	-	DAF (1940)
Leeuwkuil	<i>Paspalum dilatatum</i> Poir.	1938	-	DAF (1940)
Prinshof	<i>Paspalum dilatatum</i> Poir.	1938	-	DAF (1940)
Prinshof	<i>Paspalum notatum</i> Flügge	1938	-	DAF (1940)
Cedara	<i>Paspalum urvillei</i> Steud.	1951	-	Smith and Rhind (1984)
Athole	<i>Paspalum virgatum</i> L.	1934	Yes	DAF (1940)
Leeuwkuil	<i>Paspalum virgatum</i> L.	1938	-	DAF (1940)
Prinshof	<i>Paspalum virgatum</i> L.	1938	-	DAF (1940)
Athole	<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	1934	-	DAF (1940)
Burtholm	<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	1915	-	Burt-Davy (1915a)
Groenkloof	<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	1912	-	Smith and Rhind (1984)
Prinshof	<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	1938	-	DAF (1940)
Leeuwkuil	<i>Pennisetum glaucum</i> (L.) R.Br.	1938	-	DAF (1940)
Potchefstroom	<i>Pennisetum glaucum</i> (L.) R.Br.		-	Smith and Rhind (1984)
Prinshof	<i>Pennisetum polystachion</i> Schult.	1938	-	DAF (1940)
Athole	<i>Pennisetum purpureum</i> Schumach.	1934	-	DAF (1940)
Burtholm	<i>Pennisetum purpureum</i> Schumach.	1915	-	Burt-Davy (1915)
Cedara	<i>Pennisetum purpureum</i> Schumach.	1951	-	Smith and Rhind (1984)
Potchefstroom	<i>Pennisetum purpureum</i> Schumach.		-	Smith and Rhind (1984)

Appendix table continued on the next page →

TABLE 2-A3 (Continues...): Introduced grass species cultivated at pasture research stations in South Africa.

Station	Species	Year	Novel introduction	Reference
Prinshof	<i>Pennisetum purpureum</i> Schumach.	1938	-	DAF (1940)
Prinshof	<i>Pennisetum setaceum</i> (Forssk.) Chiov.	1938	-	DAF (1940)
Athole	<i>Phalaris aquatica</i> L.	1934	-	DAF (1940)
Estcourt	<i>Phalaris aquatica</i> L.	1937	-	DAF (1940)
Leeuwkuil	<i>Phalaris aquatica</i> L.	1938	-	DAF (1940)
Prinshof	<i>Phalaris aquatica</i> L.	1938	-	DAF (1940)
Estcourt	<i>Phalaris arundinacea</i> L.	1937	-	DAF (1940)
Prinshof	<i>Phalaris arundinacea</i> L.	1938	-	DAF (1940)
Prinshof	<i>Phalaris coerulescens</i> Desf.	1938	Yes	DAF (1940)
Athole	<i>Phleum pratense</i> L.	1934	-	DAF (1940)
Estcourt	<i>Phleum pratense</i> L.	1937	-	DAF (1940)
Leeuwkuil	<i>Phleum pratense</i> L.	1938	-	DAF (1940)
Prinshof	<i>Phleum</i> sp.	1938	-	DAF (1940)
Prinshof	<i>Poa compressa</i> L.	1938	Yes	DAF (1940)
Athole	<i>Poa pratensis</i> L.	1934	-	DAF (1940)
Estcourt	<i>Poa pratensis</i> L.	1937	-	DAF (1940)
Leeuwkuil	<i>Poa pratensis</i> L.	1938	-	DAF (1940)
Prinshof	<i>Poa pratensis</i> L.	1938	-	DAF (1940)
Athole	<i>Poa trivialis</i> L.	1934	-	DAF (1940)
Prinshof	<i>Poa trivialis</i> L.	1938	-	DAF (1940)
Estcourt	<i>Psathyrostachys juncea</i> (Fisch.) Nevski	1937	Yes	DAF (1940)
Prinshof	<i>Rytidosperma pilosum</i> (R.Br.) Connor and Edgar	1938	Yes	DAF (1940)
Athole	<i>Rytidosperma semiannulare</i> (Labill.) Connor and Edgar	1934	Yes	DAF (1940)
Prinshof	<i>Rytidosperma semiannulare</i> (Labill.) Connor and Edgar	1938	-	DAF (1940)
Estcourt	<i>Schedonnardus paniculatus</i> (Nutt.) Trel.	1937	Yes	DAF (1940)
Prinshof	<i>Schizachyrium scoparium</i> (Michx.) Nash	1938	Yes	DAF (1940)
Albany Museum	<i>Setaria</i> spp.		-	Smith and Rhind (1984)
Prinshof	<i>Sorghastrum nutans</i> (L.) Nash	1938	-	DAF (1940)
Leeuwkuil	<i>Sorghum × drummondii</i> (Nees ex Steud.) Millsp. and Chase	1938	-	DAF (1940)
Prinshof	<i>Sorghum × drummondii</i> (Nees ex Steud.) Millsp. and Chase	1938	-	DAF (1940)
Prinshof	<i>Sorghum halepense</i> (L.) Pers.	1938	-	DAF (1940)
Towoomba	<i>Sorghum halepense</i> (L.) Pers.	1934	-	DAF (1940)

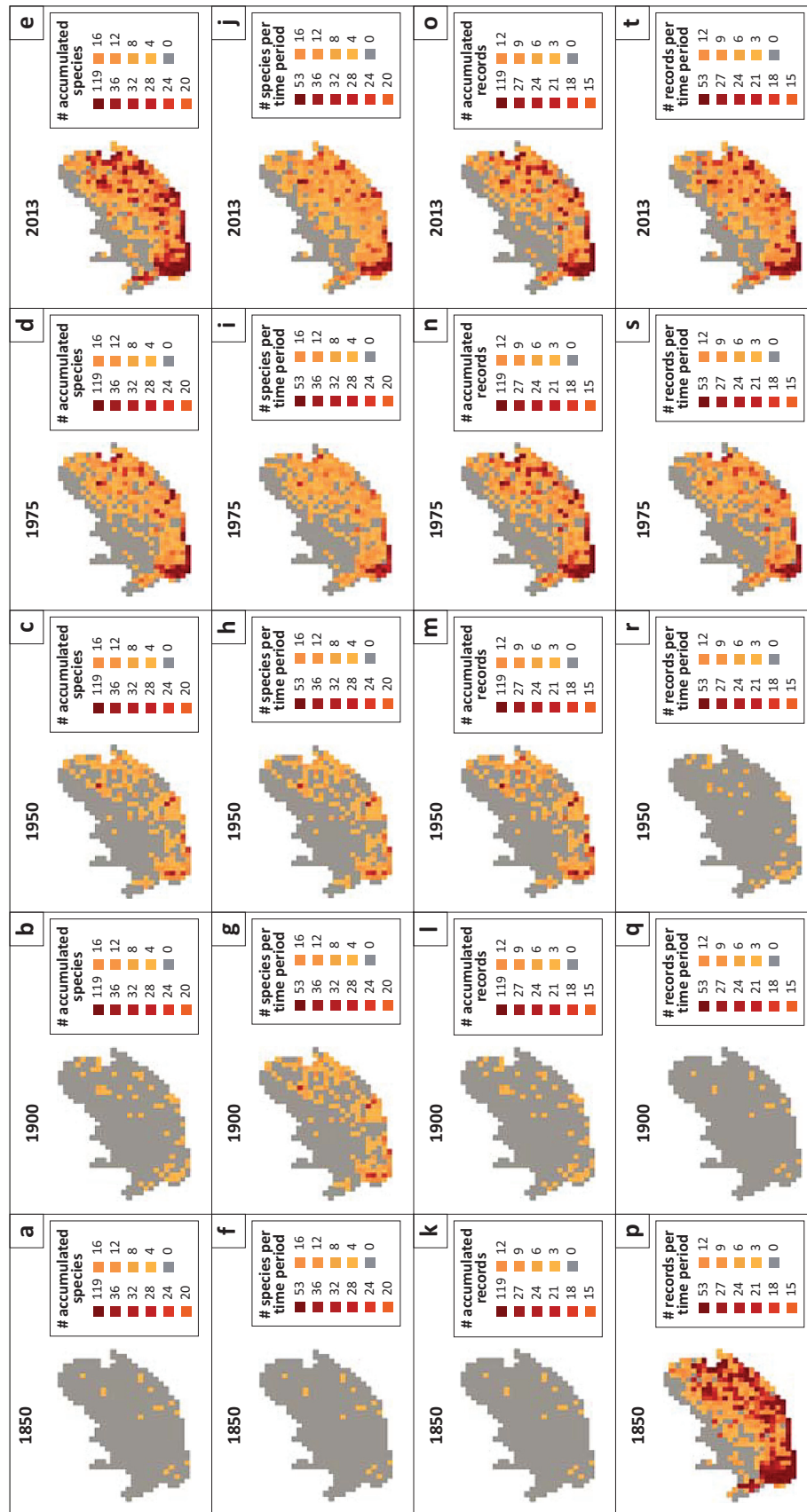
Provided for each species are the station at which it was trialed, the year the species was trialed (or the pasture station establishment year if trial date unavailable), whether the species was previously not in South Africa (novel introduction), and supporting references.

References

- Burt-Davy, J., 1915, 'Napier grass. A new and valuable fodder-grass for South Africa', *The Agricultural Journal of South Africa* 1, 362–366.
- Burt-Davy, J., 1920, 'New Zealand tall fescue. *Festuca Arundinacea*', *The Sun & Agricultural Journal of South Africa* 1, 114–116.
- Department of Agriculture & Forestry (DAF), 1940, *Pasture research in South Africa: Progress report no. 2. Division of soil and veld conservation*, Government Printer of the Union of South Africa, Pretoria.
- Smith, A. & Rhind, J.M.L.C., 1984, 'Eight decades of pasture plant improvement in South Africa', *Journal of the Grassland Society of Southern Africa*, 1, 25–28.

Appendix 4 start on the next page →

Appendix 4



(a–e) accumulated alien grass species richness. (f–j) alien grass species richness per time interval (1811 to 1900, 1901 to 1950, 1951 to 1975, and 1976 to 2013). (k–o) accumulated number of alien grass records and (p–t) numbers of records of alien grasses per time interval. Species richness and numbers of records are aggregated to quarter-degree-grid-cells (QDGCs). Darker reds indicate higher species richness or numbers of records.

FIGURE 1-A4: Patterns over time.

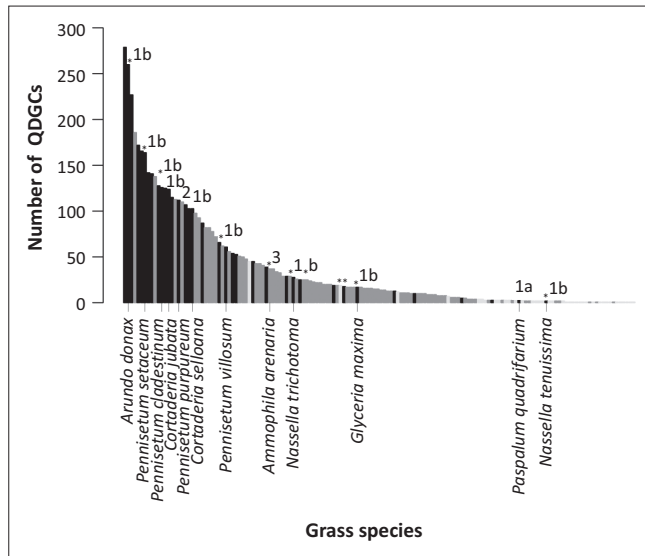


FIGURE 2-A4: Area occupied by alien grass species (measured in number of quarter-degree-grid-cells, QDGCs, occupied), plotted in descending order. The status of species on the introduction-naturalisation-invasion continuum is indicated by bar colour (light grey = introduced, dark grey = naturalised and black = invasive). Species with recorded impacts are indicated by an asterisk above the bars (see Table 2). Species that currently have legal requirements for their management are named and their legal status is indicated above the bars (see Appendix 5 for further details).

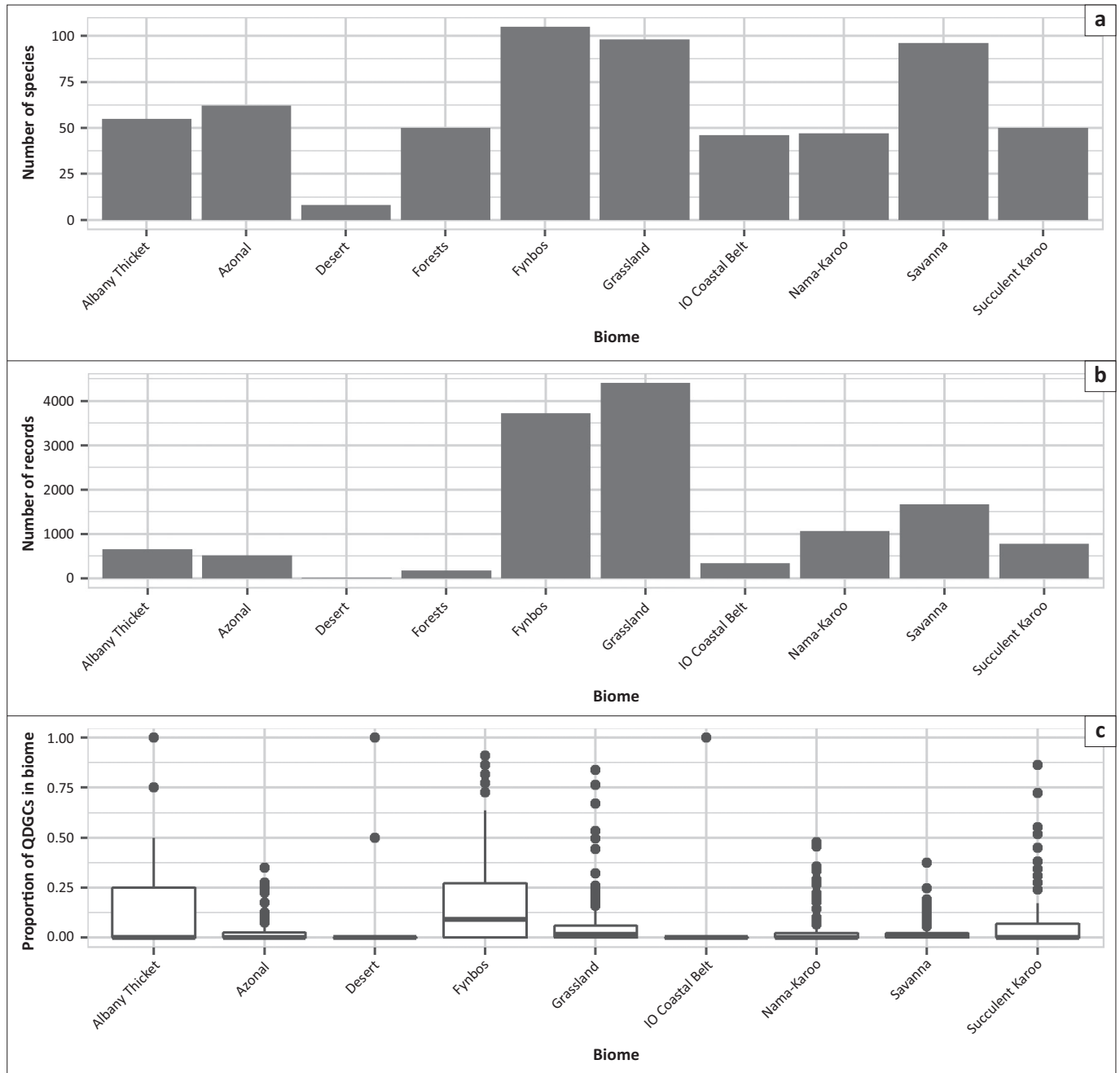
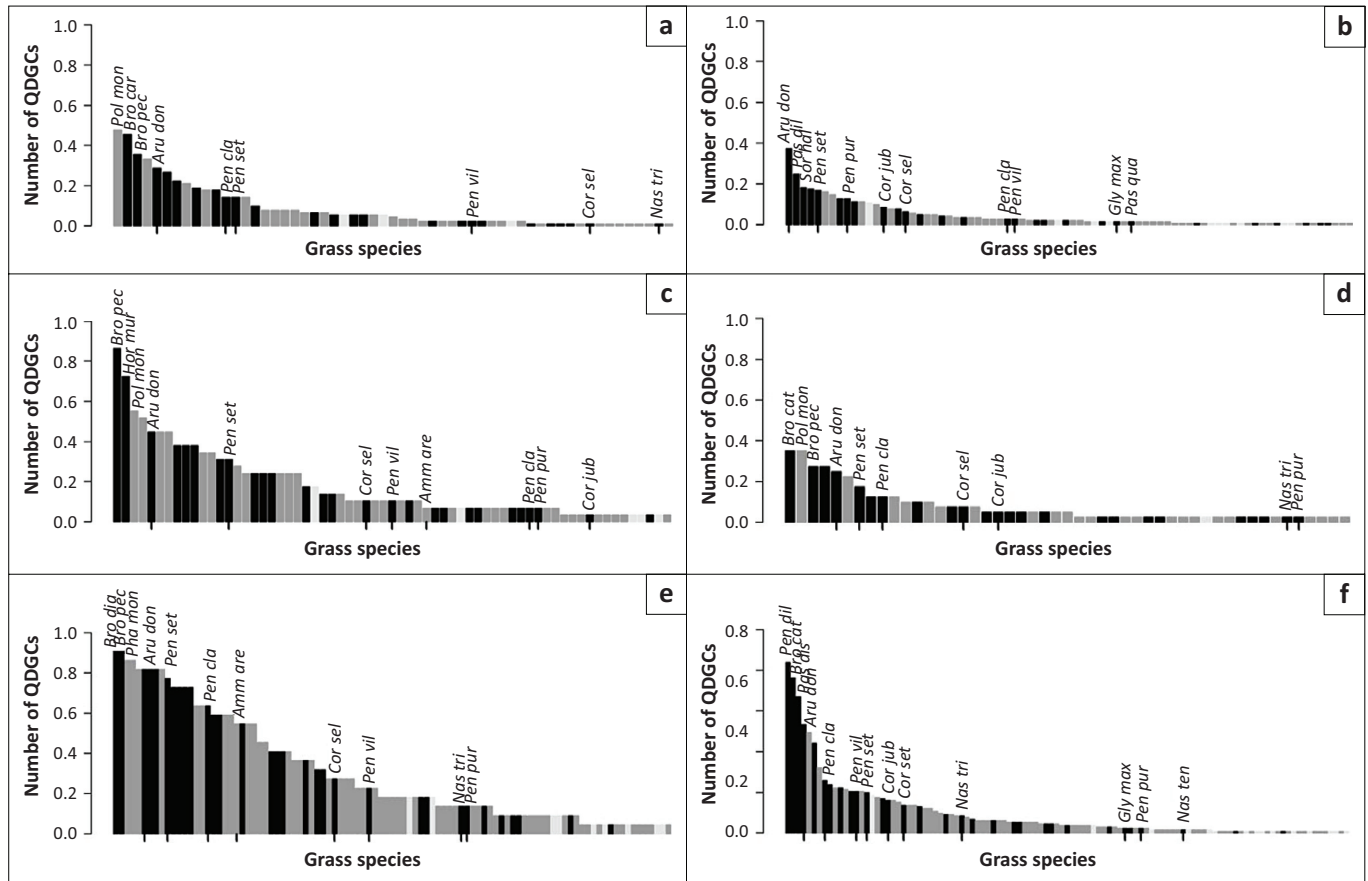


FIGURE 3-A4: (a) The number of alien grass species in each biome of South Africa. (b) The number of occurrence records of alien grass species in each biome of South Africa. (c) Area occupied by alien grass species in each biome of South Africa [measured as the proportion occupied by each species of quarter-degree-grid-cells (QDGCs) available in each biome]. The Fynbos, Grassland and Savanna biomes have the most alien grass species. The Grassland and Fynbos biomes also have the most occurrence records.



The status of species on the introduction-naturalisation-invasion continuum is indicated by bar colour (light grey = introduced, dark grey = naturalised and black = invasive). Species that currently have legal requirements for their management are named and indicated by a rug mark below the relevant bar (see Appendix 5 for further details). Also named are the three species with the greatest proportion of quarter-degree-grid-cells occupied in each biome. The Grassland and Succulent Karoo biomes also have some species that occur across almost all of these biomes, but these were far fewer in number than in the Fynbos Biome. The Fynbos Biome was exceptional in having a much higher number of species that occur across large areas of the biome.

FIGURE 4-A4: Area occupied by alien grass species as a proportion of quarter-degree-grid-cells in each biome (total number of quarter-degree-grid-cells in each biome provided in parentheses after biome name). (a) Nama-Karoo (90); (b) Savanna (142); (c) Succulent Karoo (29); (d) Azonal (40); (e) Fynbos (22); (f) Grassland (131).

Appendix 5

TABLE 1-A5: Management options for the 41 species that are either invasive or have impacts in South Africa.

Species	Physical removal	Fire	Chemical	Integrated	Biocontrol	Number of control measures	References
<i>Ammophila arenaria</i> (L.) Link	✓	✓	✓	✓	-	4	GISD (2016)
<i>Arundo donax</i> L.	✓	-	✓	✓	✓	4	GISD (2016); Guthrie (2007)
<i>Avena barbata</i> Pott ex Link	-	-	-	-	-	0	
<i>Avena fatua</i> L.	✓	✓	✓	✓	-	4	Musil et al. (2005); Todd (2008)
<i>Bambusa balcooa</i> Roxb.	-	-	-	-	-	0	
<i>Bambusa vulgaris</i> Schrad.	-	-	-	-	-	0	
<i>Brachypodium distachyon</i> (L.) P. Beauv.	-	-	-	-	-	0	
<i>Briza maxima</i> L.	-	-	-	-	-	0	
<i>Briza minor</i> L.	-	-	-	-	-	0	
<i>Bromus catharticus</i> Vahl	-	-	-	-	-	0	
<i>Bromus diandrus</i> Roth	✓	✓	✓	✓	-	4	Holmes (2008); Musil et al. (2005)
<i>Bromus madritensis</i> L.	-	-	-	-	-	0	
<i>Bromus pectinatus</i> Thunb.	✓	✓	✓	✓	-	4	Holmes (2008); Musil et al. (2005)
<i>Bromus rigidus</i> Roth	-	-	-	-	-	0	
<i>Bromus rubens</i> L.	-	-	-	-	-	0	
<i>Bromus tectorum</i> L.	-	-	-	-	-	0	
<i>Cortaderia jubata</i> (Lemoine ex Carrière) Stapf	-	-	-	-	-	0	
<i>Cortaderia selloana</i> (Schult. & Schult.f.) Asch. & Graebn.	-	-	-	-	-	0	
<i>Glyceria maxima</i> (Hartm.) Holmb.	-	✓	✓	-	-	2	GISD (2016); Mugwedi (2012)
<i>Hordeum murinum</i> L.	✓	-	-	-	-	1	Musil et al. (2005)
<i>Lagurus ovatus</i> L.	-	-	-	-	-	0	
<i>Lolium multiflorum</i> Lam.	✓	✓	✓	✓	-	4	Holmes (2008)
<i>Lolium perenne</i> L.	-	-	-	-	-	0	
<i>Lolium rigidum</i> Gaudin	-	-	-	-	-	0	
<i>Nassella tenuissima</i> (Trin.) Barkworth	-	-	-	-	-	0	Viljoen (1987)
<i>Nassella trichotoma</i> (Nees) Hack. & Arechav.	✓	✓	✓	✓	✓	4	Viljoen (1987)
<i>Paspalum dilatatum</i> Poir.	-	-	-	-	-	0	
<i>Paspalum distichum</i> L.	-	-	-	-	-	0	
<i>Paspalum quadrifarium</i> Lam.	-	-	-	-	-	0	
<i>Paspalum urvillei</i> Steud.	-	-	-	-	-	0	
<i>Paspalum vaginatum</i> Sw.	-	-	-	-	-	0	
<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	✓	-	✓	✓	✓	4	GISD (2016)
<i>Pennisetum purpureum</i> Schumach.	-	-	-	-	-	0	
<i>Pennisetum setaceum</i> (Forssk.) Chiov.	✓	-	-	-	-	1†	Rahlao et al. (2014)
<i>Pennisetum villosus</i> Fresen.	-	-	-	-	-	0	
<i>Phalaris aquatica</i> L.	-	-	-	-	-	0	
<i>Poa annua</i> L.	✓	-	✓	-	-	2	GISD (2016)
<i>Poa pratensis</i> L.	-	-	-	-	-	0	
<i>Sorghum halepense</i> (L.) Pers.	-	-	-	-	-	0	
<i>Stipa capensis</i> Thunb.	-	-	-	-	-	0	
<i>Vulpia myuros</i> (L.) C.C.Gmel.	-	-	-	-	-	0	
Total number of species against which each control measure has been used	11	6	11	8	3		

†, Suggested control is to reduce seed production and establishment of *P. setaceum* through revegetation with native species.

All references as in Appendix 1.

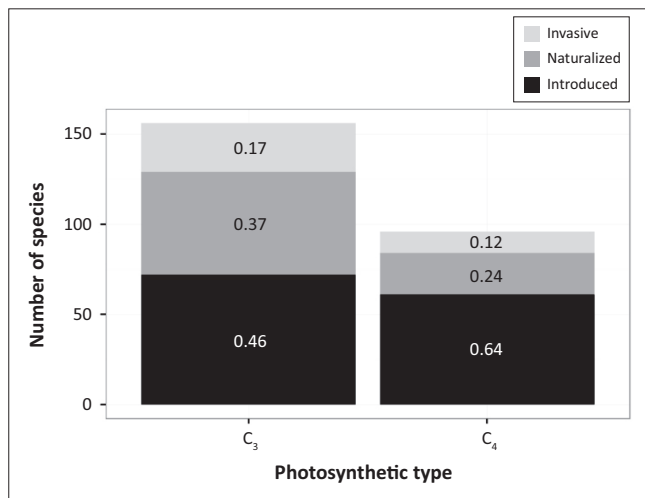
Appendix 6

TABLE 1-A6: Grasses listed under the NEM:BA Alien and Invasive Species (A&IS) 2016 Regulations (excluding Marion and Prince Edward islands).

Name in NEM:BA A&IS 2016 regulations	The Plant List accepted name	NEM:BA A&IS status
<i>Ammophila arenaria</i> (L.) Link	<i>Ammophila arenaria</i> (L.) Link	3
<i>Arundo donax</i> L.	<i>Arundo donax</i> L.	1b
<i>Cortaderia jubata</i> (Lemoine ex Carrière) Stapf	<i>Cortaderia jubata</i> (Lemoine ex Carrière) Stapf	1b
<i>Cortaderia selloana</i> (Schult.) Asch. & Graebn.	<i>Cortaderia selloana</i> (Schult. & Schult.f.) Asch. & Graebn.	1b. Sterile cultivars or hybrids are not listed.
<i>Glyceria maxima</i> (Hartm.) Holmb.	<i>Glyceria maxima</i> (Hartm.) Holmb.	1b in protected areas and wetlands.
<i>Nassella tenuissima</i> (Trin.) Barkworth	<i>Nassella tenuissima</i> (Trin.) Barkworth	1b
<i>Nassella trichotoma</i> (Nees) Hack. ex Arechav.	<i>Nassella trichotoma</i> (Nees) Hack. & Arechav.	1b
<i>Paspalum quadrifarium</i> Lam.	<i>Paspalum quadrifarium</i> Lam.	1a
<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	1b in Protected Areas and wetlands in which it does not already occur.
<i>Pennisetum purpureum</i> Schumach.	<i>Pennisetum purpureum</i> Schumach.	2
<i>Pennisetum setaceum</i> (Forssk.) Chiov.	<i>Pennisetum setaceum</i> (Forssk.) Chiov.	1b. Sterile cultivars or hybrids are not listed.
<i>Pennisetum villosus</i> R.Br. ex Fresen.	<i>Pennisetum villosus</i> Fresen.	1b
<i>Sasa ramosa</i> (Makino) Makino & Shibata	<i>Sasa ramosa</i> (Makino) Makino & Shibata	3
<i>Spartina alterniflora</i> Loisel.	<i>Spartina alterniflora</i> Loisel.	1a
<i>Achnatherum brachychaetum</i> (Godr.) Barkworth	<i>Stipa brachychaeta</i> Godr.	Prohibited.
<i>Achnatherum caudatum</i> (Trin.) S.W.L.Jacobs & J.Everett	<i>Stipa caudata</i> Trin.	Prohibited.
<i>Aegilops cylindrica</i> Host	<i>Aegilops cylindrica</i> Host	Prohibited.
<i>Aegilops geniculata</i> Roth	<i>Aegilops geniculata</i> Roth	Prohibited.
<i>Aegilops species</i>	<i>Aegilops species</i>	Prohibited.
<i>Aegilops triuncialis</i> L.	<i>Aegilops triuncialis</i> L.	Prohibited.
<i>Andropogon bicornis</i> L.	<i>Andropogon bicornis</i> L.	Prohibited.
<i>Andropogon virginicus</i> L.	<i>Andropogon virginicus</i> L.	Prohibited.
<i>Arundinaria</i> Michx. species	<i>Arundinaria</i> Michx.; <i>Pleioblastus</i> Nakai; <i>Sasa</i> Makino & Shibata; <i>Pseudosasa</i> Makino ex Nakai	Prohibited.
<i>Cenchrus echinatus</i> L.	<i>Cenchrus echinatus</i> L.	Prohibited.
<i>Cenchrus longispinus</i> (Hack.) Fernald	<i>Cenchrus longispinus</i> (Hack.) Fernald	Prohibited.
<i>Chrysopogon aciculatus</i> (Retz.) Trin.	<i>Chrysopogon aciculatus</i> (Retz.) Trin.	Prohibited.
<i>Cortaderia richardii</i> (Endl.) Zotov	<i>Cortaderia richardii</i> (Endl.) Zotov	Prohibited.
<i>Cymbopogon refractus</i> (R.Br.) A.Camus	<i>Cymbopogon refractus</i> (R.Br.) A.Camus	Prohibited.
<i>Hymenachne amplexicaulis</i> (Rudge) Nees	<i>Hymenachne amplexicaulis</i> (Rudge) Nees	Prohibited.
<i>Imperata brasiliensis</i> Trin.	<i>Imperata brasiliensis</i> Trin.	Prohibited.
<i>Imperata brevifolia</i> Vasey	<i>Imperata brevifolia</i> Vasey	Prohibited.
<i>Ischaemum rugosum</i> Salisb.	<i>Ischaemum rugosum</i> Salisb.	Prohibited.
<i>Miscanthus floridulus</i> (Labill.) Warb. ex K.Schum. & Lauterb.	<i>Miscanthus floridulus</i> (Labill.) Warb. ex K.Schum. & Lauterb.	Prohibited.
<i>Muhlenbergia schreberi</i> J.F.Gmel.	<i>Muhlenbergia schreberi</i> J.F.Gmel.	Prohibited.
<i>Nassella charruana</i> (Arechav.) Barkworth	<i>Nassella charruana</i> (Arechav.) Barkworth	Prohibited.
<i>Nassella hyalina</i> (Nees) Barkworth	<i>Nassella hyalina</i> (Nees) Barkworth	Prohibited.
<i>Nassella leucotricha</i> (Trin. & Rupr.) R.W.Pohl	<i>Nassella leucotricha</i> (Trin. & Rupr.) R.W.Pohl	Prohibited.
<i>Neyraudia reynaudiana</i> (Kunth) Keng ex Hitchc.	<i>Neyraudia reynaudiana</i> (Kunth) Keng ex Hitchc.	Prohibited.
<i>Oryza rufipogon</i> Griff	<i>Oryza rufipogon</i> Griff.	Prohibited.
<i>Panicum antidotale</i> Retz.	<i>Panicum antidotale</i> Retz.	Prohibited.
<i>Pennisetum alopecuroides</i> (L.) Spreng.	<i>Pennisetum alopecuroides</i> (L.) Spreng.	Prohibited.
<i>Pennisetum pedicellatum</i> Trin.	<i>Pennisetum pedicellatum</i> Trin.	Prohibited.
<i>Pennisetum polystachion</i> (L.) Schult.	<i>Pennisetum polystachion</i> (L.) Schult.	Prohibited.
<i>Saccharum spontaneum</i> L.	<i>Saccharum spontaneum</i> L.	Prohibited.
<i>Setaria faberi</i> R.A.W.Herrm.	<i>Setaria faberi</i> R.A.W.Herrm.	Prohibited.
<i>Setaria palmifolia</i> (J.Koenig) Stapf	<i>Setaria palmifolia</i> (J.Koenig) Stapf	Prohibited.
<i>Sorghum</i> hybrid 'Silk'	<i>Sorghum</i> hybrid 'Silk'	Prohibited.
<i>Sorghum x alnum</i> Parodi	<i>Sorghum x alnum</i> Parodi	Prohibited.
<i>Sporobolus indicus</i> (L.) R.Br. var. major (Buse) Baaijens	<i>Sporobolus fertilis</i> (Steud.) Clayton	Prohibited.
<i>Themeda quadrivalvis</i> (L.) Kuntze	<i>Themeda quadrivalvis</i> (L.) Kuntze	Prohibited.
<i>Themeda villosa</i> (Pair.) A.Camus	<i>Themeda villosa</i> (Pair.) A.Camus	Prohibited.
<i>Zizania latifolia</i> (Griseb.) Turcz. ex Stapf	<i>Zizania latifolia</i> (Griseb.) Turcz. ex Stapf	Prohibited.

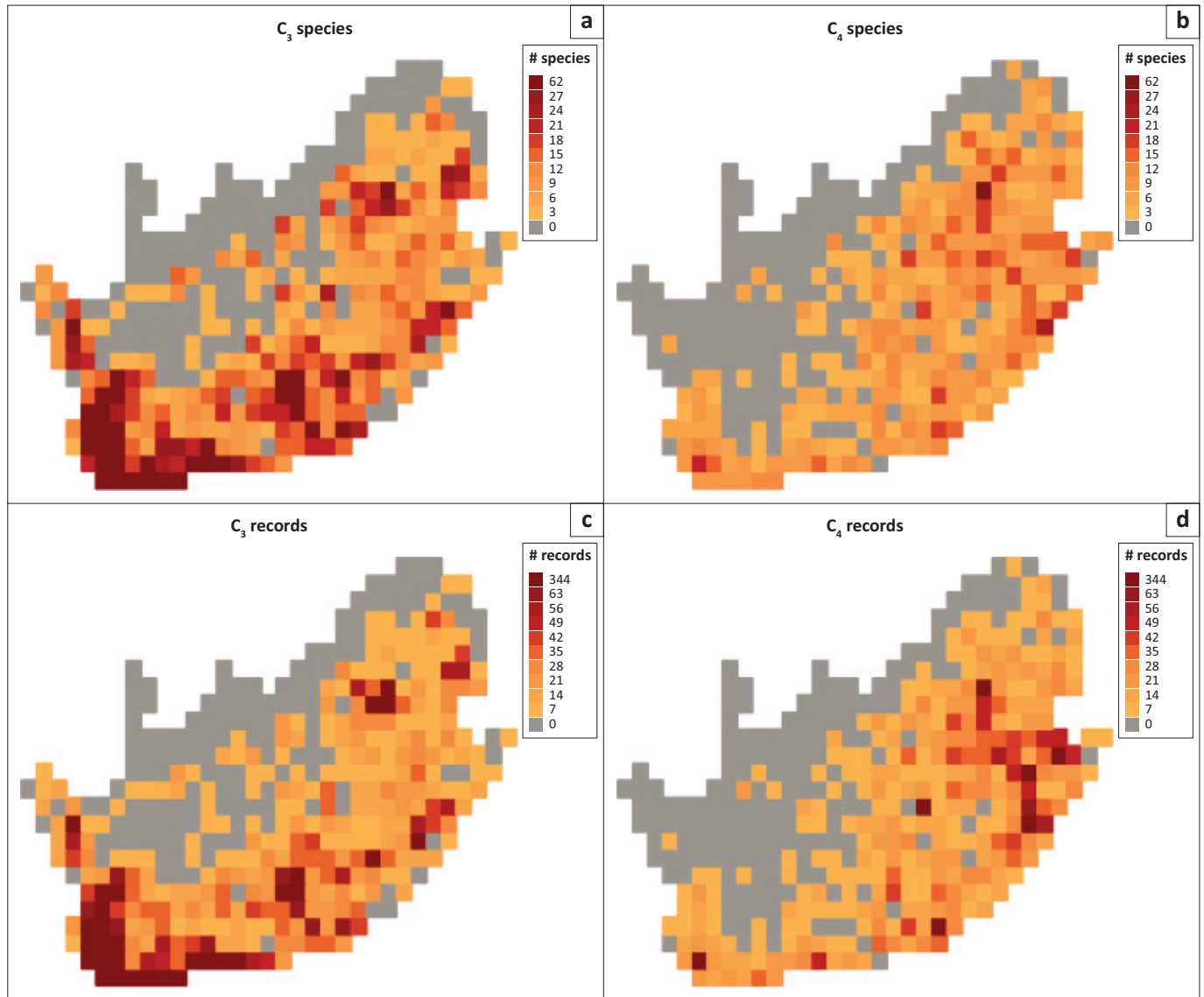
Provided are the species names, the type of management suggested (physical removal, use of fire, chemical control, integrated control – a combination of other management measures or biological control), the total number of control measures suggested and the references for these.

Appendix 7



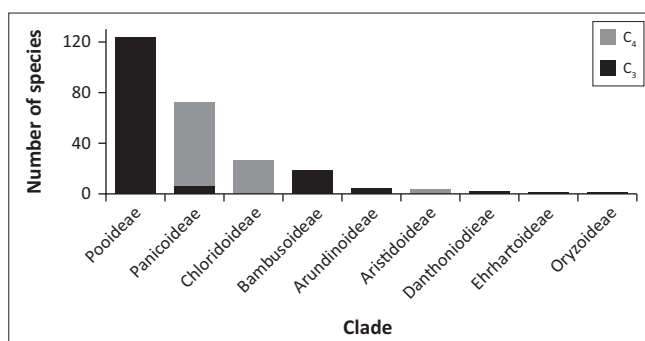
Within each photosynthetic pathway, the numbers of species of each status across the introduction-naturalisation-invasion continuum are shown (as well as the proportion, indicated by the numbers in each bar).

FIGURE 1-A7: Numbers of alien grass species using the C_3 or C_4 photosynthetic pathway.



The geographical distribution of (a, b) species richness or (c, d) numbers of records of alien grasses using the (a, c) C₃ photosynthetic pathway or (b, d) the C₄ photosynthetic pathway. C₃ species richness and numbers of records are higher in the south-west of the country; C₄ species richness and numbers of records are higher in the eastern part of the country.

FIGURE 2-A7: Geographical distribution of grass species.



This figure clearly shows the strong phylogenetic signal of the type of photosynthetic pathway (C₃ or C₄). Most alien grasses in South Africa belong to the clade Pooideae, which only has species using the C₃ photosynthetic pathway and contributes the largest number of C₃ species to South Africa. The next most speciose clade of alien grasses in South Africa is Panicoideae, which mostly has species using the C₄ photosynthetic pathway, with only six species using the C₃ photosynthetic pathway in this clade. The clades Chloridoideae and Aristidoideae are completely C₄ dominated, and the remaining clades are completely C₃ dominated.

FIGURE 3-A7: Phylogenetic signals of the type of photosynthetic pathways.