Effects of climate warming on the distributions of invasive Eurasian annual grasses: a South African perspective

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Abstract Threats posed by Eurasian annual grasses to ecosystem function have received little attention. Therefore, protocols for prioritising these alien annual species and likely future dimensions of their spread are urgently required. Here we modelled these grasses potential distribution and shifts in distribution ranges in South Africa under current and future climate scenarios. We applied a modelling framework (BIOMOD), which integrated a variety of parametric statistical and non-parametric rule based models to point distribution records of 29 invasive grass species. Correspondence between modelled and recorded distributions was calculated using the model accuracy criteria called the AUC (Area under the Curve). Based on this criteria 12 C₃ species were excellently modelled (AUC = 0.9-1), 11 C₃ species had good model accuracy (AUC = 0.7-0.8) and four C₃ and four C₄ species fell into the fair (AUC = 0.6-0.7) model accuracy class. Mean temperature of the coldest month was the strongest environmental parameter, for most of the alien grass distributions. Modelled distributions of the alien annual grasses projected into the future indicated range contractions in all C₃ species, except *Briza minor*, which were accompanied by shifts in species distribution ranges into higher altitudes. All C_4 species displayed habitat loss of relatively similar magnitude with climate warming and shifts in their distribution ranges also into higher elevations. These findings conclude that climate change will hinder the spread of European annual grasses in

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southern Africa. However, shifts in their distributions into pristine areas at higher elevations could pose a threat to the natural vegetation by altering fire regimes.

1 Introduction

There is general recognition that serious ecological, economic and social consequences result from the invasion of natural ecosystems by foreign biological organisms (McNeely et al. 2001; Perrings et al. 2000). Conservative estimates indicate that the global costs of alien invasive species impacts on natural ecosystems exceed the total economic output of the entire African continent (Pimentel et al. 2005), with such impacts predicted to intensify in the near future due to global climate change (Mooney and Hobbs 2000).

Grasses are one set of invasive species that collectively threaten regional and even global aspects of ecosystem function (D'Antonio and Vitousek 1992; Knapp 1996). In Africa, there are also examples of large-scale recipient invasions by alien grasses from other continents, or from other areas within the continent. These include the establishment of several European annual grasses in the South African Mediterranean climate region and the recent spread of perennial grasses of South American, Central and North African origin into South Africa (Milton 2004). These alien grasses are known to affect ecosystem structure, function and resources by accelerating wild fires, decreasing floral and faunal diversity and forage stability, altering soil food webs, soil moisture dynamics and decomposition cycles (Hobbs 2001; Lenz et al. 2003). The impacts of these alien grass invasions also bring about marked changes to the amount, distribution, and properties of combustible biomass, increased litterfall, and altered nutrient cycling patterns (Richardson and van Wilgen 2004; Yelenik et al. 2004). Also, the feedbacks between changes in ecosystem processes and changes in community structure following invasions by alien grass species (Vitousek 1990), lead to a further alteration in the function of ecosystems such as hydrology and fire regime (D'Antonio and Vitousek 1992). These shifts in function are of concern because of the potential to further increase the abundance of the invader (i.e. positive feedback; Vinton and Burke 1995). For example, the alien grass *Bromus tectorum* survives low intensity grass fires, which promotes its dominance in the post fire succession (Young and Allen 1997). Its high flammability prevents recovery of woody vegetation, thereby maintaining grass dominance, changing the microclimate and causing nutrient losses (D'Antonio and Vitousek 1992).

The problems posed by alien grasses in the South African Mediterranean-climate region have received little attention (Milton 2004; Musil et al. 2005) with most resources directed towards managing alien invasive woody plant infestations (Holmes and Cowling 1997a, b; Thuiller et al. 2006). However, there is increasing evidence that the natural flora in this region, unique in terms of its rich floristic diversity and endemism (Goldblatt and Manning 2000) and listed among 34 global biodiversity hot spots (Mittermeier et al. 2004), is under threat from competition by alien grasses. This based on reported increases in the abundance of alien annual grasses, especially on low-lying areas (Vlok 1988; Steinschen et al. 1996). The increase in alien grass abundance has been attributed to rangeland deterioration caused by ploughing, vegetation clearing and burning, to soil nutrient enrichment from fertilizer run-off and nitrogen-fixing leguminous species (Milton 2004), and to the dispersal of alien

grass seeds on the hides of grazing animals and in the dung of domestic livestock and wildlife (Malo and Suarez 1995; Shiponeni 2003). This increase is of concern, especially in terms of the wildflower diversity, which forms the basis of a growing lucrative nature-based tourist industry (Turpie and Joubert 2004).

Not only is the South African Mediterranean-climate region experiencing many anthropogenic changes, anticipated changes in global climate are expected to exacerbate non-native invasions (Dukes and Mooney 1999). This is of added concern in a region identified as especially vulnerable to biodiversity loss and species extinctions, as well as to distributional range changes with future warming and aridity trends (Midgley et al. 2002, 2003; Broennimann et al. 2006).

The impact of global warming or climate change on natural ecosystems has received considerable international attention in recent decades, with various modelling techniques devised and employed. Large-scale climatic factors acting as surrogates for physiologically relevant variables are commonly used in various parametric statistical and non-parametric rule based bioclimatic models to predict plant distributions (Frescino et al. 2001; Thuiller 2003) and to project future distributions, species turnover, range expansion and contraction under climate change scenarios (Duckworth et al. 2000; Bakkenes et al. 2002). In South Africa, such bioclimatic models have been applied to assess areas climatically suitable for 71 species of major plant invaders comprising predominantly woody trees and shrubs (Rouget et al. 2004). However, this modelling approach was applied to only one alien annual grass species, *Briza maxima* (Richardson et al. 2000).

A fundamental assumption for modelling ecological niches as stable constraints on a species' geographical distribution potential is the equilibrium concept, which presumes that modelled species are at equilibrium with their environment (Guisan and Zimmerman 2000; Guisan and Thuiller 2005). However, this concept does not strictly apply to alien species whose geographical range is still expanding. This assumption seems improbable for many alien grass species in South Africa as their recorded dates of earliest collection (based on herbarium specimens) signify introduction during the 19th century and possibly even earlier for some species, e.g. 1659 for *Lolium temulentum* (Bromilow 2001), thereby allowing them adequate time to infiltrate a wide range of available habitats. However, in some alien grass species where human or other biotic aided dissemination have not afforded them the opportunity to infiltrate all potentially invasive habitats, modelled prospective distributions might be underestimated. The converse applies to those species with scattered distribution patterns over a wide region. Here patterns possibly reflecting human induced-disturbances rather than inherent climatic features.

Other potential environmental constraints on species distributions not incorporated into bioclimatic models included fecundity, evolutionary change, soil physical and chemical properties, local pathogens, land transformation caused by human activity and natural disturbance (Hulme 2003; Mitchell and Power 2003; Blumenthal 2006). Despite these limitations to the bioclimatic model approach (Pearson and Dawson 2003; Pearson et al. 2006), it still provides a good initial assessment of the potential distribution of a species that may aid in the development of protocols for prioritising harmful species and the likely future dimensions of spread. Therefore, this study's objectives were to model potential distributions of different alien grass species in South Africa and project future changes and shifts in their distribution ranges with climate warming.

2 Materials and methods

2.1 Databases and species selection

The databases used for establishing environmental limits of the alien invasive grass species were ACKDAT comprising 12,000 species listings spread across 3,000 sites in South Africa at a $1 \times 1'$ grid resolution (approximately 1.5×1.8 km) or one arc minute resolution (McDonald 1997). PRECIS (Germishuizen and Meyer 2003) data was also used containing location data of ca 21,660 South African species at a spatial resolution of $15 \times 15'$ grid resolution. The SAPIA database (Henderson 1999) was not utilized because its invasive species distribution listings were not all authenticated by archived herbarium specimens, and also because of its bias towards woody invasive species. Distribution records of 60 species of alien annual grasses listed by Milton (2004) were extracted from the two databases, at the level of quarter degree grid square. Analyses concentrated on those alien annual species with 20 or more occurrences to lessen the likelihood of computing unreliable bioclimatic limits (Stockwell and Peterson 2002). Also a realized species niche is more likely to approximate its fundamental niche where the species is distributed over multiple diverse landscapes with a wide range of diverse competitors (Cao 1995).

2.2 Environmental parameters

Six climatically derived environmental parameters relevant to physiological function and survival of alien grass species but with differing influences across species were selected as environmental determinants. They were obtained from the CRU CL 2.0 dataset averaged for the period 1961–1990 (New et al. 2000) at a spatial resolution of $10 \times 10'$ grid resolution (c. 16×16 km) and included mean minimum temperature (T_{min}) during the coldest month (monthly means of daily values), mean maximum temperature of the hottest month (T_{max}) , mean annual temperature (T_{mean}) mean annual precipitation (MAP), annual potential evaporation (PE) and growth days (GD) expressed as annual sum of daily temperatures exceeding 10° C. The parameter that contributed the most to the overall bioclimatic model was selected on the basis of explained deviance.

Predictions of future climates in the year 2050 (averages for the period 2036–2065) were based on two scenarios, namely A2-High (4.5° C temperature increase) and B2-Mid (2.5° C temperature increase) based upon draft emission scenarios prepared for the Intergovernmental Panel on Climate Change's Third Assessment Report (Nakicenovic and Swart 2000; Hulme et al. 2001). The climatic data corresponding with each scenario were generated by general circulation models (GCM) at the Hadley Centre for Climate Prediction and Research (HadCM3) downscaled for South Africa at a spatial resolution of $10 \times 10'$ grid resolution (10 arc min). Downscaling defines the development of regional scale projections of change from the global models used to simulate the global response of the climate system (Midgley et al. 2005).

2.3 Bioclimatic model projections

Future prospective habitats of alien invasive grass species were projected using the BIOMOD application in S-Plus version 7.0 (Insightful Corporation, Seattle, USA) which maximizes the predictive accuracy of current species distributions and the reliability of future potential distributions using different types of statistical modelling methods (Thuiller 2003, 2004). BIOMOD computes for each species and in the same package the four most widely used modelling techniques, with the best model being identified. These include generalized linear models (GLM), generalized additive models (GAM), classification and regression tree analysis (CART) and artificial neural networks (ANN). In this study, we restricted our analysis to the former three models.

2.4 Model calibration and evaluation

The modelled dataset was randomly divided into two subsets in order to determine the quality of predictions for each grass species. These included the initial calibration (70% of data) dataset and the remaining evaluation (30% of data) dataset. Model accuracy was assessed using the Area Under the Receiver Operating Characteristic (ROC) curve (AUC index) on the evaluation dataset (Pearce and Ferrier 2000). A rough guide for classifying the accuracy of the models being: AUC 0.9–1 = excellent; 0.8-0.9 = good; 0.7-0.8 = fair; 0.6-0.7 = poor; 0.5-0.6 = fail (Swets 1988). To transform the probabilities values from the models into presence or absence of the selected species, a threshold value was applied which maximizes jointly the amount of correctly predicted presence and absence (Thuiller 2003). This threshold reduces the risk of identifying areas not environmentally suitable for a species.

2.5 Habitat suitability

Altered distribution ranges of each species were analysed by calculating the percentage of stable, climatically suitable habitats. This was defined as the grid cells suitable for the species both at present (current climate) and under each of the two scenarios of climate change (future climate). The percentage of lost habitat was defined as habitat that was suitable under current climate conditions but predicted to become unsuitable under future climate scenarios. Of the presently suitable habitats, the grid cells predicted to become unsuitable designated the percentage of lost habitat. Conversely, the percentage of new climatically suitable habitat was defined as habitat that was unsuitable in the present but predicted to become suitable under future scenarios. An altitudinal background layer was also applied to the data, to derive a visual assessment of the direction of species range change. No formal analysis was conducted with altitude.

3 Results

3.1 Species attributes and model accuracy classes

Of the 60 listed species of alien invasive annual grasses, 29 had more than 20 records. Twenty-five of these species possessed a C_3 photosynthetic pathway and 4 of these species a C_4 photosynthetic pathway (Table 1). Three classes of model accuracy were apparent. The first, the "excellent model accuracy" class comprised 12 exclusively C_3

	ΡP	DEC	Calib	ration data	Evaluation	data		Threshold	Envire	onmenta	l variab	les		
				AUC	Presence	Absence	AUC	probability	T_{\min}	$T_{\rm max}$	$T_{\rm mean}$	GD	MAP	PE
Excellent model accuracy														
Hordeum murinum (L.)	ű	1,896	347	0.94	86.6	86.8	0.92	0.16	б	7		4	1	
Briza maxima (L.)	ű	1,872	260	0.95	89.6	90.0	0.95	0.06	4	1		б	2	
Aira cupaniana (Guss.)	ű	1,814	237	0.97	91.7	92.1	0.96	0.09	4	7		б	1	
Bromus diandrus (Roth)	ű	1,897	201	0.95	86.0	86.0	0.93	0.07	б	1		4	2	
Briza minor (L.)	ű	1,830	175	0.94	88.3	88.3	0.92	0.05	4	1		б	2	
Phalaris minor (Retz.)	ű	1,907	172	0.93	85.7	85.3	0.90	0.06	4	1		б	2	
Brachypodium distachyon (L.) P.Beauv.	ű	1,894	159	0.98	91.9	92.0	0.97	0.07	4	7		б		1
Lolium rigidum (Gaudin)	ű	1,897	135	0.94	88.9	89.3	0.94	0.05	4	7		б	1	
Parapholis incurva (L.) C.E.Hubb.	ű	1,948	93	0.96	91.3	91.6	0.96	0.04	4	2		б		
Lophochloa cristata (L.) Hyl.	ű	1,897	69	06.0	85.7	84.8	0.97	0.03	б	1		7		4
Lagurus ovatus (L.)	ű	1,916	68	0.98	95.2	94.1	0.99	0.03	4		1		2	3
Bromus hordeaceus (L.)	ű	1,927	61	0.94	88.0	88.0	0.96	0.02	3	4		2		
Good model accuracy														
Bromus catharticus (Vahl.)	ű	1,846	765	0.85	77.1	77.1	0.84	0.26	2		4		Э	1
Polypogon monspeliensis (L.) Desf.	ű	1,891	453	0.84	76.4	76.3	0.84	0.14	б	0	4		1	
Poa annua (L.)	ů	1,900	370	0.85	76.0	76.1	0.83	0.11	7	4	1		3	

 Table 1
 Species attributes and bioclimatic model statistics of 29 grass species grouped into three classes based on model accurateness

$ \begin{array}{llllllllllllllllllllllllllllllllllll$	upua promotues (L.) O.1 ay Olypogon virtidis (Gouan) Breistr. (ulpia myuros (L.) C.C.Gmel. Jolium temulentum (L.) Jophochloa pumila (Desf.) Bor Avena fatua (L.) Avena sativa (L.)	చి చి చి చి చి చి చి	$\begin{array}{c} 1,813\\ 1,896\\ 1,829\\ 1,812\\ 1,811\\ 1,811\\ 1,830\\ 1,826\end{array}$	$173 \\ 152 \\ 93 \\ 58 \\ 58 \\ 40 \\ 29 \\ 29 \\ 29 \\ 29 \\ 29 \\ 29 \\ 20 \\ 20$	$\begin{array}{c} 0.92\\ 0.87\\ 0.91\\ 0.86\\ 0.94\\ 0.87\\ 0.72\end{array}$	83.3 78.6 84.4 74.5 85.7 78.9 65.2	83.3 78.5 84.5 84.4 78.9 65.5	$\begin{array}{c} 0.88\\ 0.87\\ 0.87\\ 0.83\\ 0.83\\ 0.83\\ 0.83\\ 0.83\\ 0.89\end{array}$	$\begin{array}{c} 0.06\\ 0.06\\ 0.02\\ 0.02\\ 0.01\\ 0.01\end{array}$	4 ω ω ω 4 4	0 44 4	40 m	n 00	1 7 1 1 m	
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	agrostis barrelieri (Daveau)	C_4	1,902	119	0.70	63.2	62.5	0.63	0.05		4				

species with a diverse range of occurrences (61-347 listings) and dates of earliest record (1814-1948). The second the "good model accuracy" class comprised ten also exclusively C₃ species with a relatively larger diverse range of occurrences (29-765 listings) but similar range of dates of earliest record (1811-1900). The third the "fair model accuracy" class comprised three C₃ species with low occurrences (34-74 listings) and relatively more recent dates of earliest record (1897-1947), and also four C₄ species with moderate occurrences (113-245 listings) and intermediary dates of earliest record (1874-1902). One of these C₄ species, *Eragrostis barrelieri*, had the lowest level of model accuracy (AUC = 0.63) of all species (Table 1).

3.2 Assessment of potential and observed distributions

Species included in the excellent model accuracy class exhibited modelled potential distributions in close proximity to their observed values with virtually all the observed records enclosed within the modelled potential distribution areas (Thuiller et al. 2003). This pattern was apparent in both widespread species, e.g. *Hordeum murinum* (Fig. 1a), as well as those, e.g. *Lagurus ovatus* (Fig. 1b), with more localised distribution in the south western and south eastern regions of South Africa. However, the widespread and more localised species in the good and fair model accuracy classes which included species with both the C₃ photosynthetic pathway, e.g.



Fig. 1 Recorded (*black dot*) and modelled potential distributions (*gray dot*) for **a** *Hordeum murinum* (C₃), **b** *Lagurus ovatus* (C₃), **c** *Polypogon monspeliensis* (C₃), and **d** *Eragrostis tef* (C₄)

Polypogon monspeliensis (Fig. 1c) and C_4 photosynthetic pathway, e.g. *Eragrostis tef* (Fig. 1d). displayed a higher fraction of outliers at the periphery of their modelled potential distribution areas.

Pooled results for C_3 and C_4 grass species distributions were also mapped under current and future climate conditions (Fig. 2a and b). C_3 grass species showed a prevalence in the south western and south eastern regions and C_4 grasses a prevalence in the north-eastern and north-western regions of South Africa under current climate conditions with these distributions shifting southwards and eastwards in the C_3 and C_4 grasses respectively with future climate warming.

3.3 Environmental correlates of species distributions

Mean temperature of the coldest month (T_{min}) was the main environmental constraint for species with the C₃ photosynthetic pathway, particularly those included in the excellent model accuracy class (Table 1), with growth-days of secondary importance. In contrast, mean temperature of the warmest month (T_{max}) , mean annual temperature (T_{mean}) and mean annual precipitation (MAP) were environmental constraints of importance for species with the C₄ photosynthetic pathway (Table 1).



Fig. 2 Current and modelled potential distributions (under the A2 scenario) for **a** all 29 C_3 grass species under current climate conditions (*gray dot*) **b** projected distributions of all 29 C_3 (*gray dot*) grass species under future climate conditions **c** four C_4 (*black dot*) grass species under current climate conditions of all C_4 (*black dot*) grass species under current climate conditions of all C_4 (*black dot*) grass species under current climate conditions of all C_4 (*black dot*) grass species under future climate conditions of all C_4 (*black dot*) grass species under future climate conditions of all C_4 (*black dot*) grass species under future climate conditions of all C_4 (*black dot*) grass species under future climate conditions of all C_4 (*black dot*) grass species under future climate conditions defined all clim

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Class/Species	Current range size	Potential range $\times 10^3 \text{ km}^2$	Overall rar	ige change %	Habitats lo	st %	Habitats ga	ined %
			A2-High	B2-Mid	A2-High	B2-Mid	A2-High	B2-Mid
Excellent model accuracy								
Hordeum murinum	823	210.7	-59.2	-54.1	59.9	54.2	0.4	0.1
Briza maxima	583	149.2	-22.8	-20.2	29.8	23.8	4.0	3.6
Aira cupaniana	517	131.6	-35.0	-34.3	35.6	34.3	0.6	0.0
Bromus diandrus	737	111.1	-46.9	-49.2	54.4	52.1	4.5	2.8
Briza minor	627	159.7	4.0	32.4	44.2	35.4	48.2	68.4
Phalaris minor	801	205.1	-18.1	-11.0	26.1	19.2	8.0	8.2
Brachypodium distachyon	422	108.0	-56.6	-45.4	54.3	49.3	0.4	3.5
Lolium rigidum	576	139.8	-38.0	-32.1	50.3	41.4	12.3	9.5
Parapholis incurva	415	106.2	-22.6	-2.2	36.1	23.1	13.5	21.0
Lophochloa cristata	658	168.4	-35.6	-21.1	42.9	30.8	4.3	9.4
Lagurus ovatus	271	61.7	-21.8	-4.4	50.2	40.2	28.4	35.8
Bromus hordeaceus	574	139.3	-68.5	-56.4	40.4	59.8	1.9	3.3
Good model accuracy								
Bromus catharticus	1,433	366.8	-63.8	-54.3	63.8	54.3	0.0	0.0
Polypogon monspeliensis	1,302	333.3	-28.6	-25.0	31.3	28.0	2.4	2.9
Poa annua	1,279	319.7	-42.4	-26.2	43.8	30.2	1.1	4.0
Vulpia bromoides	848	217.1	-38.9	-31.2	41.4	32.9	2.8	1.6
Polypogon viridis	1,028	263.2	-63.4	-51.4	69.0	54.5	5.2	6.1

Table 2 Current and potential range of alien grasses, including fractional changes in overall range and in habitats lost and gained under two climate scenarios (A2-Hioh and B2-Mid)

Vulpia myuros	771	112.9	-36.4	-31.6	43.4	34.2	4.0	5.6
Lolium temulentum	1,177	292.9	-28.4	-10.5	35.0	25.3	9.9	14.8
Lophochloa pumila	744	113.7	-2.4	0.8	15.0	9.8	12.6	10.6
Avena fatua	943	241.4	-52.6	-34.1	65.4	51.4	12.8	14.6
Avena sativa	1,213	310.5	-24.1	-24.4	81.4	62.9	54.6	41.5
Fair model accuracy								
Lolium multiflorum	1,082	277.0	-58.8	-41.0	59.6	41.4	0.8	0.4
Vulpia muralis	635	162.6	-52.8	-34.5	56.4	39.1	3.6	1.6
Agrostis avenacea	982	251.4	-66.6	-50.3	42.4	59.6	6.1	9.3
Eragrostis tef	1,299	332.5	-54.8	-44.5	58.0	44.1	3.2	2.6
Digitaria sanguinalis	1,451	371.5	-45.4	-34.1	50.4	38.2	4.4	4.1
Eragrostis pilosa	1,044	267.3	20.0	22.0	38.4	39.5	58.4	61.5
Eragrostis barrelieri	1,543	395.0	1.9	14.1	44.0	30.3	45.9	44.4
Species grouped and sorted	on the same criteri	a as in Table 1						

3.4 Modelled species distributions with climate warming

Almost all species with the C₃ photosynthetic pathway displayed contractions in their overall distribution ranges with future climate warming (Table 2). These range contractions were consistently greater under the A2-High than the B2-Mid climate scenario and differed in magnitude between species, genera, tribes and subfamilies. Members of the genus Bromus exhibited the largest range contraction overall (49-56%), followed by the genus Polypogon (25-51%), Vulpia (31-35%), Avena (24-34%) and Lolium (11–41%). These range contractions were accompanied by shifts in species distribution ranges into areas of higher elevation. Among C₃ species, the largest shifts in distribution range (41–55% of habitats gained) was evident in Avena sativa (Fig. 3b) followed by Lagurus ovatus (28-36% of habitats gained) with modest shifts in distribution range (10-21% of habitats gained) apparent in Parapholis incurva, Lolium temulentum, Avena fatua, Lophochloa pumila andLolium rigidum. Briza minor was the exception in that it displayed a small to moderate range expansion (4–32%) accompanied by a substantial shift (48–68% of habitats gained) in its distribution range (Fig. 3a) These range contractions and shifts in distribution ranges with future climate warming were less consistent among species with the C₄



Fig. 3 Predicted future distributions for **a** *Briza minor* (C₃), **b** *Avena fatua* (C₃), **c** *Eragrostis pilosa* (C₄), and **d** *Eragrostis barrelieri* (C₄), under an A2-high climate scenario. Habitats unchanged (*plus sign*), habitats lost (*multiplication sign*) and habitats gained (*black dot*). The distributions are plotted against a background altitudinal layer, with the *darker shades* indicating areas of higher elevation

photosynthetic pathway. Two of the C₄ species, namely *Erogrostis tef* and *Digitaria* sanguinalis, displayed considerable range contractions (34–55%) but trivial shifts (2–4% of habitats gained) in their distribution ranges. This seemingly contrasted with the other two C₄ species, namely *Erogrostis pilosa* (Fig. 3c) and *Erogrostis barralieri* (Fig. 3d) which exhibited small to moderate range expansions (2–22%) but comparatively large shifts (44–62% of habitats gained) in their distribution ranges. However, collectively both C₃ and C₄ grass species displayed overall range contractions with future climate warming (Fig. 2c and d).

4 Discussion

The findings of this study indicate that future climate warming will hinder the spread of Eurasian annual grasses in South Africa. Of the 29 species that were modelled, all the C₃ grass species, with the exception of one, showed contractions in their distribution range with warmer climate conditions projected for the middle of the century. Modelled range contractions were associated with shifts of variable magnitude in the distributions of all C₃ species into areas of higher elevation mainly in the south-eastern regions of the country and Drakensberg mountains in Lesotho. Habitat loss among C_3 species occurred mainly in the warmer central interior and/or at lower altitudes in the north-western and south eastern regions of country. Noteworthy, was the range contraction of 20% predicted for Briza maxima for a mean annual temperature increase of 2.5°C. Similarly (Richardson et al. 2000) predicted a 13% range contraction under a 2°C rise in mean annual temperature reported in a separate study applying an environmental envelope model. The latter study also predicted habitat loss for *B. maxima* in the north-western regions of South Africa and a shift in its distribution into higher elevations in the south-eastern regions of the country (Richardson et al. 2000). These findings concur that C_3 grasses are most active under cooler climate conditions during winter with peak growth temperatures ranging between 15°C and 25°C (Bewley and Black 1994). Therefore, an increase in temperature may be expected to negatively impact on these cooler climate C_3 grasses.

South African grasses are geographically separated from one another, with C_4 grasses predominating over most of the country. However only in the winter rainfall areas of the south-western regions, and along the summits of the south-eastern regions and Drakensberg mountains do C_3 species increase in abundance (Vogel et al. 1978). This distribution pattern suggests an increase of T_{min} may prevent the expansion of alien C_3 grasses but favour expansion of C_4 grasses especially aspartate forming sub types if such climate warming is accompanied by reduced precipitation and/or soil moisture.

The selection by the bioclimatic model of mean temperature of the coldest month (T_{\min}) , as the principle environmental constraint for alien grass species with the C₃ photosynthetic pathway concurred with analyses of large-scale patterns of grass distributions in South Africa, Namibia (Vogel et al. 1978; Ellis et al. 1980) and in the desert regions of Sinai, Negev, and Judea in Israel (Vogel et al. 1986). These studies all indicated that minimum temperature (T_{\min}) during the growing season is the environmental parameter having the strongest correlation with the relative abundance of C₃ grasses with precipitation (MAP) ranked as a less important

determinant of the relative success of such grasses (Vogel et al. 1978; Ellis et al. 1980).

Minimum temperature is also important in "dormancy breaking" of the seed once certain conditions are met. This process is experienced by the majority of non tropical species, where the seed must experience certain environmental factors or must undergo certain metabolic changes. Some seeds are commonly released from dormancy by being chilled. Since such temperatures are only available during the winter, seeds that rely on this means for dormancy breaking must await the passage of the cold season to germinate (Bewley and Black 1994). The rate of activity of C₃ grasses is reduced at temperatures below 15°C and above 25°C. Thus increased temperatures, such as those associated with climate change, will invariably lead to less areas of climate suitability for grasses adapted to cool moist temperate habitats (Jones 1992).

In contrast, mean annual precipitation (MAP), mean temperature of the hottest month (T_{max}) and mean annual temperature (T_{mean}) were ranked more or less equally in terms of their total contribution to the explained deviance as environmental constraints for species with the C₄ photosynthetic pathway. Again, this concurred with grass distribution patterns in North America (Teeri and Stowe 1976), Costa Rica (Chazdon 1978) and Kenya (Tieszen et al. 1979) which have all indicated higher proportions of C_4 grasses in areas with high temperatures during the growing season and low precipitation. Similarly, grass distribution patterns in South Africa, Namibia and Israel also indicate that high temperatures during the growing season favour C₄ grasses with aspartate forming subtypes, which include the *Eragrosteae* (Ellis 1977), attaining their greatest abundance in xeric areas of low rainfall (Ellis et al. 1980; Vogel et al. 1986). In contrast, malate forming subtypes of C_4 grasses which include some Digitaria species (Ellis et al. 1980), are not well represented in arid regions. These grasses attain their maximum abundance under conditions of increased moisture or lower water stress, given suitably high temperatures (Ellis et al. 1980; Vogel et al. 1986). Interestingly T_{max} in terms of explained deviance was ranked as the most important environmental variable for Digitaria sanguinalis and precipitation the least important.

There was seemingly greater disparity among the C_4 grasses in their modelled distributions with climate warming. Two species, namely *E. pilosa and E. barrelieri*, displayed moderate overall range expansions/shifts but substantial habitat gained with the converse apparent in the two other species, namely *E. tef* and *D. sanguinalis*. However all four species displayed habitat loss of relatively similar magnitude with climate warming, this most apparent in the drier and warmer savannas in the northwestern and north eastern regions of the country. They also exhibited similar shifts in their distribution ranges into predominantly cooler and moister grasslands at higher elevations in the countries interior, though these shifts were of substantially greater magnitude in *E. pilosa* and*E. barrelieri* than in *E. tef* and *D. sanguinalis*.

In conclusion these findings collectively point to a reduced expansion of European annual grasses in South Africa with future climate warming. However, the predicted shifts in distributions of these grasses into pristine regions at higher elevations with climate warming, particularly in floristically rich Mediterranean-climate ecosystems, could pose a threat to the natural vegetation by altering fire regimes. Also, rising atmospheric CO_2 levels could mitigate the negative impacts of climate warming by allowing especially C_3 grasses to persist in more arid nutrient impoverished lowland fynbos ecosystems by improving their photosynthetic water use and nitrogen use efficiencies (Richardson et al. 2000). However, ultimately human caused land use change and other disturbances will most likely drive the spread of invasive European annual grasses into natural habitats (D'Antonio and Vitousek 1992; Milton 2004).

References

- Bakkenes M, Alkemade JR, Ihle F, Leemans R, Latour JB (2002) Assessing the effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Glob Chang Biol 8:390–407
- Bewley JD, Black M (1994) Seeds—physiology of development and germination, 2nd edn. Plenum Press, New York
- Blumenthal DM (2006) Interactions between resource availability and enemy release in plant invasion. Ecol Lett 9:887–895
- Broennimann O, Thuiller W, Hughes GO et al (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? Glob Chang Biol 12:1079–1093
- Bromilow C (2001) Problem plants of South Africa: a guide to the identification and control of more than 300 invasive plants and other weeds. Briza, Pretoria
- Cao G (1995) The definition of the niche by fuzzy set theory. Ecol Model 77:65-71
- Chazdon RL (1978) Ecological aspects of the distribution of C₄ grasses in selected habitats of Costa Rica. Biotropica 10:265–269
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Ann Rev Ecol Syst 23:63–87
- Duckworth JC, Bunce RGH, Molloch AJC (2000) Modelling the potential effects of climate change on calcareous grasslands in Atlantic Europe. J Biogeogr 27:347–358
- Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? TREE 14:135–139
- Ellis RP (1977) Distribution of the Kranz syndrome in the Southern African Eragrostoideae and Panicoideae according to bundle sheath anatomy and cytology. Agroplantae 9:73–110
- Ellis RP, Vogel JC, Fuls A (1980) Photosynthetic pathways and the geographical distribution of grasses in South Africa/Namibia. S Afr J Sci 76:307–314
- Frescino TS, Edwards TC Jr, Moisen GG (2001) Modelling spatially explicit forest structural attributes using generalised additive models. J Veg Sci 12:15–26
- Germishuizen G, Meyer NL (2003) Plants of southern Africa: an annotated checklist. Strelitzia 14:1– 1231
- Goldblatt P, Manning J (eds) (2000) Cape plants. A conspectus of the Cape flora of South Africa. Strelitzia 9. National Botanical Institute, Pretoria
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009
- Guisan A, Zimmerman HG (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186
- Henderson L (1999) The Southern African Plant Invaders Atlas (SAPIA) and its contribution to biological weed control. Afr Entomol 1:159–163
- Hobbs RJ (2001) Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. Conserv Biol 15:1522–1528
- Holmes PM, Cowling RM (1997a) The effects of invasion by Acacia saligna on the guild structure and regeneration capabilities of South African fynbos shrublands. J Appl Ecol 34:317–332
- Holmes PM, Cowling RM (1997b) Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien invaded South African shrublands. Pl Ecol 133:107–122
- Hulme PE (2003) Winning the science battles but losing the conservation war? Oryx 37:178–193

Hulme M, Doherty R, Ngara T et al (2001) African climate change: 1900-2100. Clim Res 17:145–168 Jones HG (1992) Plants and microclimate. A quantitative approach to environmental plant physiol-

ogy, 2nd edn. Cambridge University Press, Cambridge, 428 pp

Knapp PA (1996) Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert: history, persistence, and influences to human activities. Glob Environ Change 6:37–52

- Lenz TI, Moyle-Croft JL, Facelli JM (2003) Direct and indirect effects of exotic annual grasses on species composition of a South Australian grassland. Austral Ecol 28:23–32
- Malo JE, Suarez F (1995) Herbivorous mammals as seed dispersers in a Mediterranean dehesa. Oecologia 104:246–255
- McDonald DJ (1997) VEGMAP: a collaborative project for a new vegetation map of southern Africa. S Afr J Sci 93:424–426
- McNeely JA, Mooney HA, Neville LE et al (2001) A global strategy on invasive alien species. IUCN, Gland, Switzerland and Cambridge, UK. In collaboration with the Global Invasive Species Programme
- Midgley GF, Hannah L, Millar D et al (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. Glob Ecol Biogeogr 11:445–451
- Midgley GF, Hannah L, Millar D et al (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. Biol Conserv 112:87–97
- Midgley GF, Chapman RA, Hewitson B et al (2005) A status quo, vulnerability and adaptation assessment of the physical and socio-economic effects of climate change in the western cape. Report of the Western Cape Government. Cape Town
- Milton SJ (2004) Grasses as invasive alien plants in South Africa. S Afr J Sci 100:69-75
- Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421:625-627
- Mittermeier RA, Robles Gil P, Hoffmann M et al (2004) Hotspots revisited. CEMEX, Mexico
- Mooney HA, Hobbs RJ (eds) (2000) Invasive species in a changing world. A project of SCOPE: the Scientific Committee on Problems of the Environment. Island Press, Washington DC
- Musil CF, Milton SJ, Davis GW (2005) The threat of alien invasive grasses to lowland Cape floral diversity: an empirical appraisal of the effectiveness of practical control strategies. S Afr J Sci 101:337–344
- Nakicenovic N, Swart R (2000) Emissions scenarios: a special report of working group III of the intergovernmental panel on climate change. Cambridge University Press, Cambridge
- New M, Lister D, Hulme M et al (2000) A high-resolution data set of surface climate over global land areas. Clim Res 21:1–25
- Pearce J, Ferrier S (2000) Evaluating the predictive performance of habitat models developed using logistic regression. Ecol Model 133:225–245
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob Ecol Biogeogr 12:361–371
- Pearson RG, Thuiller W, Araújo MB et al (2006) Model-based uncertainty in species' range prediction. J Biogeogr 33:1704–1711
- Perrings C, Williamson M, Dallmazzone S (2000) The economics of biological invasions. Edward Elgar, Cheltenham
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52:273–288
- Richardson DM, Bond WJ, Dean RJ et al (2000) Invasive alien species and global change: a South African perspective. In: Mooney HA, Hobbs R (eds) Invasive species in a changing world. Island Press, California, pp 303–350
- Richardson DM, van Wilgen B (2004) Invasive alien plants in South Africa: how well do we understand the ecological impacts? S Afr J Sci 100:45–52
- Rouget M, Richardson DM, Nel JL et al (2004) Mapping the potential ranges of major plant invaders in South Africa, Lesotho and Swaziland using climatic suitability. Divers Distrib 10:475–484
- Shiponeni NN (2003) Dispersal of seeds as a constraint in revegetation of old fields in Renosterveld vegetation in the Western Cape, South Africa. Dissertation (M.Sc.), University of Stellenbosch
- Steinschen AK, Görne A, Milton SJ (1996) Threats to the Namaqualand flowers: outcompeted by grass or exterminated by grazing? S Afr J Sci 92:237–242
- Stockwell DRB, Peterson AT (2002) Effects of sample size on accuracy of species distribution models. Ecol Model 148:1–13
- Swets KA (1988) Measuring the accuracy of diagnostic systems. Science 240:1285–1293
- Teeri JA, Stowe LG (1976) Climatic patterns and the distribution of C₄ grasses in North America. Oecologia 23:1–12
- Thuiller W (2003) BIOMOD—optimizing predictions of species distributions and projecting potential future shifts under global change. Glob Change Biol 9:1353–1362
- Thuiller W (2004) Patterns and uncertainties of species' range shifts under climate change. Glob Chang Biol 10 2020–2027

- Thuiller W, Vayreda J, Pino J et al (2003) Large-scale environmental correlates of forest tree distributions in Catalonia (NE Spain). Glob Ecol Biogeogr 12:313–325
- Thuiller W, Richardson DM, Rouget M et al (2006) Interactions between environment, species traits and human uses describe patterns of plant invasions. Ecology 87(7):1755–1769
- Tieszen LL, Senyimba MM, Imbamba SK et al (1979) The distribution of C_3 and C_4 grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. Oecologia 37:337-350
- Turpie J, Joubert A (2004) The value if flower tourism on the Bokkeveld Plateau—a botanical hotspot. Dev South Afr 21:645–662
- Vinton MA, Burke IC (1995) Interactions between individual plant species and soil nutrient status in shortgrass steppe. Ecology 76:1116–1133
- Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7–13
- Vlok JHJ (1988) Alpha diversity of lowland fynbos herbs at various levels of infestation by alien annuals. S Afr J Bot 54:623–627
- Vogel JC, Fuls A, Ellis RP (1978) The geographical distribution of Kranz grasses in South Africa. S Afr J Sci 74:209–215
- Vogel JC, Fuls A, Danin A (1986) Geographical and environmental distribution of C₃ and C₄ grasses in the Sinai, Negev, and Judean deserts. Oecologia 70:258–265
- Yelenik SG, Stock WD, Richardson DM (2004) Ecosystem level impacts of invasive acacia saligna in the South African Fynbos. Res Ecol 12:44–51
- Young JA, Allen FL (1997) Cheat grass and range science 1930–1950. J Range Manag 50:530–535