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Long-term changes in semi-arid vegetation: Invasion of an exotic perennial grass has larger effects than rainfall variability

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Abstract

Questions: This paper examines the long-term change in the herbaceous layer of semi-arid vegetation since grazing ceased. We asked whether (1) there were differences in the temporal trends of abundance among growth forms of plants; (2) season of rainfall affected the growth form response; (3) the presence of an invasive species influenced the abundance and species richness of native plants relative to non-invaded plots, and (4) abundance of native plants and/or species richness was related to the time it took for an invasive species to invade a plot.

Location: Alice Springs, Central Australia.

Methods: Long-term changes in the semi-arid vegetation of Central Australia were measured over 28 years (1976–2004) to partition the effects of rainfall and an invasive perennial grass. The relative abundance (biomass) of all species was assessed 25 times in each of 24 plots (8 m × 1 m) across two sites that traversed floodplains and adjacent foot slopes. Photo-points, starting in 1972, were also used to provide a broader overview of a landscape that had been intensively grazed by cattle and rabbits prior to the 1970s. Species' abundance data were amalgamated into growth forms to examine their relationship with environmental variation in space and time. Environmental variables included season and amount of rainfall, fire history, soil variability and the colonization of the plots by the exotic perennial grass *Cenchrus ciliaris* (Buffel grass).

Results: Constrained ordination showed that season of rainfall and landscape variables relating to soil depth strongly influenced vegetation composition when *Cenchrus* was used as a covariate. When *Cenchrus* was included in constrained ordination, it was strongly related to the decline of all native growth forms over time. Univariate comparisons of non-invaded vs impacted plots over time revealed unequivocal evidence that *Cenchrus* had caused the decline of all native growth form groups and species richness. They also revealed a contrasting response of native plants to season of rainfall, with a strong response of native grasses to summer rainfall and forbs to winter rainfall. In the presence of *Cenchrus* these responses were strongly attenuated.

Discussion: Pronounced changes in the composition of vegetation were interpreted as a response to removal of grazing pressure, fluctuations in rainfall and, most importantly,

invasion of an exotic grass. Declines in herbaceous species abundance and richness in the presence of *Cenchrus* appear to be directly related to competition for resources. Indirect effects may also be causing the declines of some woody species from changed fire regimes as a result of increased fuel loads. We predict that *Cenchrus* will begin to alter landscape level processes as a result of the direct and indirect effects of *Cenchrus* on the demography of native plants when there is a switch from resource limited (rainfall) establishment of native plants to seed limited recruitment.

Keywords: Arid vegetation; Buffel grass; *Cenchrus ciliaris*; Grazing disturbance; Invasibility; Invasive species; Long-term dynamics; Vegetation change.

Nomenclature: Albrecht et al. (1997).

Introduction

Long-term measures of the floristic changes in vegetation composition provide insight into ecological processes that mediate vegetation change. Lack of experimental controls, however, often limit their interpretation; as does a commitment to maintain measurements at regular intervals over long periods of time (Turner et al. 2003). In particular, there is a paucity of published studies of long-term change in semi-arid vegetation in relation to invasive species (Lonsdale 1999; Anderson & Inouye 2001). Hence, little is known about the invasibility of arid and semi-arid vegetation, although the effects of invasive species on fire regimes are better understood (Mack & D'Antonio 1998).

Repeated sampling of semi-arid (rangeland) vegetation in Australia to quantify vegetation change is rare (see review by Lunt 2002) and only two published studies are well known (Crisp 1978; Crisp & Lange 1976); neither of which examined invasive species. More broadly, long-term changes in the composition of rangelands in Australia have mainly been reported from

temperate grassy ecosystems, as being caused by changed grazing regimes and altered nutrient status, and resulting in the invasion of exotic species (Trémont & McIntyre 1994; Yates & Hobbs 1997; Clarke 2000, 2003). In these, as in most other Australian landscapes, measurements of floristic change has mainly relied on analyses of spatial patterns to infer temporal change, rather than on long-term monitoring (Lunt 2002). Similarly, experimental manipulation using invasive species and disturbance are rare and the long-term outcome of these manipulations in semi-arid vegetation are known only from one example (McIvor 1998).

In arid and semi-arid environments the effects of disturbance regimes (intensity, frequency, season and extent) are difficult to disentangle from erratic climate fluctuations (Stafford-Smith & Morton 1990; Friedel 1991; Allen et al. 1995; Anderson & Inouye 2001). In these circumstances long-term data can be useful in detecting trends not only relating to fluctuations in climate but also variables such as fire, grazing and invasive plant species. Ideally, this would be in an experimental context where the variables of interest, such as invasive species, are manipulated so that the effects of climate could be partitioned. Large changes in the herbaceous layer of vegetation in Central Australia are thought to occur due to the effects of grazing and invasive plant species but there are few long-term data that enable these effects to be compared to climate fluctuations. In particular, the spread of an exotic perennial grass (*Cenchrus ciliaris*, Buffel grass) over the last decade is thought to have both direct competitive effects on biodiversity and indirect effects through altered fire regimes (Griffin 1993; Fairfax & Fensham 2000; Butler & Fairfax 2003; Franks 2002; Miller 2002).

This paper examines the long-term (28-year) change in the herbaceous layer of several plant communities near to Alice Springs in Central Australia since 1976. This study spans the period over which *Cenchrus* has colonized large areas of Central Australia and therefore provides a unique opportunity to assess its effects relative to other changes that have occurred over the same period. Firstly we present a summary of the visual change of sites since 1972 using photo-plot images and then examine quantitative changes in the composition of the herbaceous layer in relation to environmental variation in space and time. Next, we test whether (1) season of rainfall interacted with the presence of *Cenchrus* and affected the response of native plants to rainfall; (2) the presence of *Cenchrus* influenced the abundance and species richness of native plants relative to non-invaded plots; and (3) abundance of native plants and/or species richness was related to the time it took for *Cenchrus* to invade a plot.

Methods

Study sites and sampling

The study sites were located in the former Simpson Gap grazing lease, now situated in the West MacDonnells National Park ca. 11 km west of Alice Springs, Central Australia. The climate is semi-arid with variable rainfall (mean = 285 mm.a⁻¹). Prior to the 1970s the area was used for cattle grazing and much of the area was severely degraded with little ground cover and incipient signs of soil erosion (see App. 1 and 2). Monitoring sites were established in the early 1970s with photo-plots; data collection began in 1976 when relative abundance estimates of each ground layer species were recorded by Peter Latz (PKL). Since 1976, 25 recordings of abundance were made for each plot by the same person (PKL).

Two sites were established that together consisted of 24 (8 m × 1 m) plots in which the relative abundance of species was recorded. One of the sites, with 11 plots (Boundary transect), was located perpendicular to creeks and the other, with 13 plots (East Bore transect), was located near a bore 4 km to the east. The plots were spaced at intervals approximately 50 m apart to account for spatial variability within a physiographic land unit. Five vegetation types were sampled, which are typical of the plains and foothills adjacent to the MacDonnell Ranges and correspond to those recognized in a vegetation survey of an adjacent area (Albrecht & Pitts 2004):

1. Ironwood (*Acacia estrophiolata*) and Fork-leaved Corkwood (*Hakea divaricata*) on alluvial flats;
2. Saline patches on alluvial flats;
3. Rocky or sandy creek lines with Tea-tree (*Melaleuca* spp.);
4. Sandy Red Gum (*Eucalyptus camaldulensis* var. *obtusata*) creek lines;
5. Witchetty Bush (*Acacia kempeana*) and *Acacia aneura* on rocky hills and gravelly rises.

The number of samples (plots × time) for each vegetation type and the proportion of invaded plots by *Cenchrus* is shown in Table 1.

The Percentage Rank method was used to record the relative abundance of species on each of 25 occasions for each of the 8-m² plots (Tothill et al. 1992). Timing of data collection was primarily determined by above average rainfall events both in winter and summer that produced some ground layer biomass response. Ground layer species were grouped into nine growth form classes, four grasses (short-lived native, longer-lived native, persistent native and *Cenchrus* and five non-grass groups (ferns, short-lived exotic forbs, short-lived native forbs, suffrutescent shrubs and perennial forbs, and native shrubs < 1 m). Note that larger shrubs such as *Acacia aneura* (mulga) were not included in the plots because the sample plots were spaced between trees and large

Table 1. Environmental variables for constrained ordination and their conditional effects (F values) for redundancy analysis (RDA) and partial redundancy analysis (partial RDA) with the abundance of *Cenchrus ciliaris* as a covariate. Number of samples (plots \times time) and proportion of plots invaded by *Cenchrus* over all sample times and plots given for each vegetation type sampled.

Variable	Type of variable	RDA F -value	Partial RDA F -value
Time	Continuous (years)	115.5***	10.81***
Rainfall			
Annual	Continuous (mm)	3.3**	3.6**
Previous 4 months	Continuous (mm)	0.9 ns	0.3 ns
Seasonal rainfall	Categorical	10.6 ***	6.9***
Fire			
Frequency	Count	3.9**	3.6***
Recency	Categorical (recent or not)	1.8 ns	1.8 ns
Rabbits	Categorical (recent or not)	2.6**	3.5***
Soil depth	Continuous	9.3***	17.1***
Soil base content	Continuous	15.2***	7.6**
Vegetation type			
Mulga rises (124 samples, 22% buffel)	Categorical	53.9***	5.1**
Alluvial flats (Ironwood) (250 samples, 62% <i>Cenchrus</i>)	Categorical	5.9**	6.8***
Alluvial flats (Saline) (100 samples, 63% <i>Cenchrus</i>)	Categorical	14.7***	9.5**
Creek lines (Tea-tree) (75 samples, 81% <i>Cenchrus</i>)	Categorical	8.7**	7.7**
Creek line (Redgum) (50 samples, 72% <i>Cenchrus</i>)	Categorical	6.5**	6.8**
Distance to creek line	Continuous (m)	22.9***	8.6**

shrubs. Short-lived species included ephemeral and annual species whilst longer-lived species are those that survive more than one year but do not persist. The species recorded, their respective total abundance, frequency and growth form group are listed in App. 3.

Photo-points

A series of photo-points was established along each of the transects and colour slides of each photo-point were taken at irregular intervals since 1972 with prominent landmarks in the background. Selected photo-points were digitized and aligned for comparison of changes of ground cover and the presence of *Cenchrus* through time. A representative subset of the slides has been reproduced in black and white in an appendix to represent visual changes in the dominance and composition of the ground cover and shrub layer along the transects.

Multivariate analyses

Initial exploratory analyses used multivariate methods to examine the relationship of sample sites through time in terms of their floristic relatedness and to correlate these patterns with environmental change using ordination (ter Braak 1987). Redundancy analysis RDA and partial RDA (CANOCO) was used in constrained ordination on major environmental factors after comparison with correspondence analysis (CA) because the gradient lengths were less than three and the eigenvalues were higher than analyses with canonical correspondence analysis (CCA). There were 600 samples (24 plots \times 25 times) and 75 species in the species matrix. All

species were analysed using their untransformed abundances and rare species were not downweighted. Nineteen environmental variables were initially used in the environmental matrix and was reduced to 15 for the final analysis after forward selection (Table 1). The major growth form groups (see App. 3) were used as passive (supplementary) variables. Statistical tests of the significance of the relationship used Monte Carlo simulations with 999 permutations within CANOCO. Partial RDA was used with the abundance of *Cenchrus* as a covariate to better examine the effects of environmental variables on the floristic composition through time independent of *Cenchrus*. Following this analysis the abundance of major growth forms was plotted against time for plots not affected by *Cenchrus* to detect trends associated with post-grazing recovery.

Effect of time and space on the abundance of *Cenchrus ciliaris*

The hypotheses to be tested were that the abundance of *Cenchrus* (1) increased through time, (2) was consistent over time in each vegetation type and (3) did not respond to season of rainfall. The effect of time was tested in a one-factor (ANOVA) with time as a fixed factor using all sample plots. A two-factor ANOVA using vegetation type as a fixed factor (six levels) and before and after 1990 as a fixed factor tested the consistency of change in each vegetation type. Finally, a two-factor ANOVA using vegetation type as a fixed factor (six levels) and season of rainfall as a factor (three levels) tested the effect of season of rainfall on the abundance of *Cenchrus* across all vegetation types. The

dependent variables (growths form groups) were transformed to arcsin squareroot of the variable used. All data were checked for homogeneity of variance by plotting the residuals vs predicted values as recommended by Quinn & Keough (2002).

*Effect of abundance of *Cenchrus ciliaris* on growth forms and species richness*

The first hypothesis was that growth form abundance and species richness varied with season of rainfall and was affected by the presence of *Cenchrus*. This was tested using a two-factor ANOVA with season of rainfall and presence of *Cenchrus* as fixed factors. Season of rainfall had three levels: winter rainfall (April – September), summer rainfall (October – March), and no seasonal rainfall. The non-invaded sites were defined as those plots with 1% or less rank abundance of *Cenchrus* whereas invaded sites were defined as > 1% rank abundance of *Cenchrus*. The second hypothesis to be tested was that growth form class abundance and species richness varied with time and was affected by the presence of *Cenchrus* independent of rainfall. This was tested using a two-factor analysis of covariance (ANCOVA) with time and presence of buffel as fixed factors and four month rainfall prior to sampling as the covariate.

Time had two levels: pre-1990 sampling and post-1990 sampling. The non-invaded sites were defined as those plots with 1% or less rank abundance of *Cenchrus* whereas buffel presence was defined as > 1% rank abundance of *Cenchrus*. The dependent variables (growths form groups) were transformed to arcsin squareroot of the variable used. Where the covariate interactions were not significant in the original model, each interaction term was removed and the model refitted sequentially. All data were checked for homogeneity of variance by plotting the residuals vs predicted values as recommended by Quinn & Keough (2002).

*Correlations with time to colonization by *Cenchrus ciliaris**

The relationship between the time taken for *Cenchrus* to reach > 5% rank abundance in individual plots and: (1) the species richness of plots the year prior to colonization, (2) species richness average for all years prior to colonization, (3) abundance of native plants, and (4) distance to creek lines were compared using pair wise correlation and the significance determined by Fisher's *r* to *z* test. The initial date was set at 1972 when the plots were established and *Cenchrus* was within 10 km of all plots.

Results

Photo-plots

Ground cover changes can be observed in the photo-plots as can shifts in the composition of the ground stratum and the presence of *Cenchrus* tussocks. On the alluvial plain, typical of half the plots, there was a rapid transition from a sparse cover of weedy annuals in 1972 (App. 1a) to a dominance of native perennial grasses following the exceptional rainfall in 1974–1976 (App. 1b). Fires and droughts after this period reduced the cover of grasses in the early 1980s following which *Cenchrus* became dominant across the plain and has maintained its dominance (App. 1c, d). Creek line plots were also denuded of vegetation in the early 1970s and rapidly responded to rainfall in the 1970s (App. 2a). However, by 1983 *Cenchrus* had become well established along the creek lines (App. 2b) and maintained dominance for the past 20 years (App. 2c, d).

Multivariate analyses

Constrained ordination showed strong relationships between the environmental variables of time, vegetation types, distance from creek lines, soil depth and base content, and season of rainfall and floristic composition (Table 1). Rainfall, fire related effects and rabbit presence had much smaller effects (Table 1).

Constrained ordination showed that the first two axes accounted for 32% of the variance in the abundances of species. The global model with all environmental variables produced a multivariate regression coefficient of 0.93 for axis 1 and 0.81 for axis 2. A biplot of the main environmental variables, growth form groups, and the abundance of *Cenchrus* show the overriding influence of time and buffel abundance on floristic composition (Fig. 1a). Consequently, most growth form groups are negatively associated with time, but distance from creek lines and soil depth also influenced the composition of the vegetation.

The effects of environmental factors on the composition of the vegetation were more clearly shown when *Cenchrus* was used as a covariate in a partial RDA. In this analysis soil depth, time, season of rainfall, soil base content and vegetation type were strongly related to floristic composition (Table 1). In addition the relationships between growth form groups and environmental factors are more explicit (Fig. 1b). Short-lived native forbs are associated with winter rainfall whilst longer-lived native grasses are associated with summer rainfall and total rainfall. Ferns are associated with rises in the landscape whilst short-lived grasses are associated with deeper soils that have been burnt (Fig. 1b). Over time

there appears to have been an increase in dicots (forbs and shrubs) whilst the relative abundance of short-lived native grasses has decreased (Fig. 1b).

Plots of temporal trends, in the absence of *Cenchrus*, revealed non linear trends in the abundance of life form groups over time (Fig. 2). Short-lived exotic forbs decreased in relative abundance whilst the abundance of short-lived native forbs was highly variable through time with peaks corresponding to major winter rainfall events in 1978, 1986, 1992, and 1993 (Fig. 2b). Ferns showed an increasing abundance through time (Fig. 2c), whilst short-lived native grass showed the converse (Fig. 2d). The relative abundance of longer-lived native grasses has fluctuated greatly through time (Fig. 2e) with major decreases following the droughts in the early 1990s.

Effect of time and space on the abundance of *Cenchrus ciliaris*

Cenchrus abundance significantly increased in time from an average abundance score of less than five in 1976 to an abundance score of more than 60 throughout 2000–2004, $F_{24, 575} = 15.0, p < 0.0001$ (Fig. 3). A decrease in abundance was prominent in 1986, 1992 and 1993 corresponding to a period of winter rains (Fig. 3). Pre- and post-1990 changes in *Cenchrus* abundance were also significant, $F_{1, 564} = 88.0, p < 0.0001$ (Fig. 3) and the abundance of *Cenchrus* varied among plant community types pre- and post-1990 $F_{1, 564} = 25.7, p < 0.0001$ (Fig. 4). *Cenchrus* was most abundant in the creek line communities and least abundant on the rock hillsides (Fig. 4). Season of rainfall, four months prior to sampling, had no significant effect on the abundance of *Cenchrus* $F_{2, 558} = 1.65, p > 0.19$. There was also no significant difference in the mean rainfall (four months prior to sampling) pre- and post-1990, $F_{1, 20} = 2.4, p > 0.1$, or among season of rainfall, $F_{1, 20} = 1.3, p > 0.1$. However, prior to 1990 only 22% of rainfall records fell in winter whereas post-1990 50% of rainfall records were in winter.

Effect of *Cenchrus* abundance on growth form groups

Season of rainfall had significant effects on the abundance of both exotic and native growth form groups as well as overall species richness (Table 2, Fig. 5). In addition the presence of *Cenchrus* reduced the abundance of most native growth form groups whereas the exotic species were less suppressed (Table 2, Fig. 5). The effect of season varied markedly among native growth form groups with short-lived native and exotic forbs showing a pronounced response to winter rainfall whereas the native grasses responded more strongly to summer rainfall (Fig. 5). Species richness in plots was generally higher after prolonged rainfall in winter (Fig.

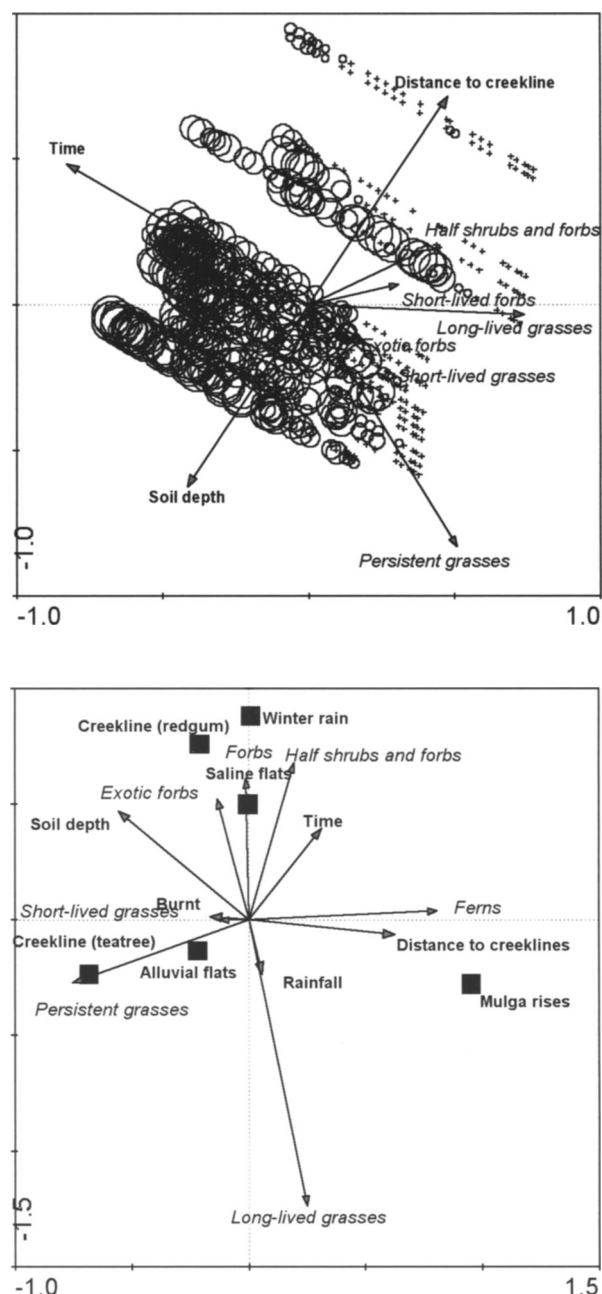


Fig. 1. Ordination diagrams for redundancy analysis (RDA) of 600 samples (24 plots \times 25 times) and 75 species. Sites and species removed from the diagram to enable the relationship between main environmental variables and growth form groups to be plotted clearly. **a.** RDA, *Cenchrus ciliaris* plotted with size of symbol corresponding to abundance, vegetation types removed from the diagram for clarity; **b.** Partial RDA with *Cenchrus* included as a covariate. Continuous environmental variables shown as solid lines and arrows, categorical variables shown as filled squares. Growth form groups (supplementary variables) shown in italics.

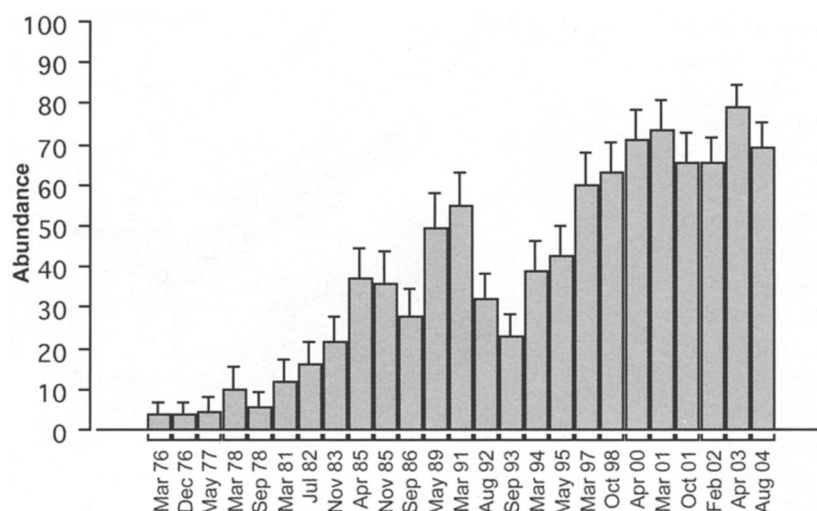


Fig. 3. Mean (+ SE) abundance score of *Cenchrus ciliaris* for all plots at each sample time.

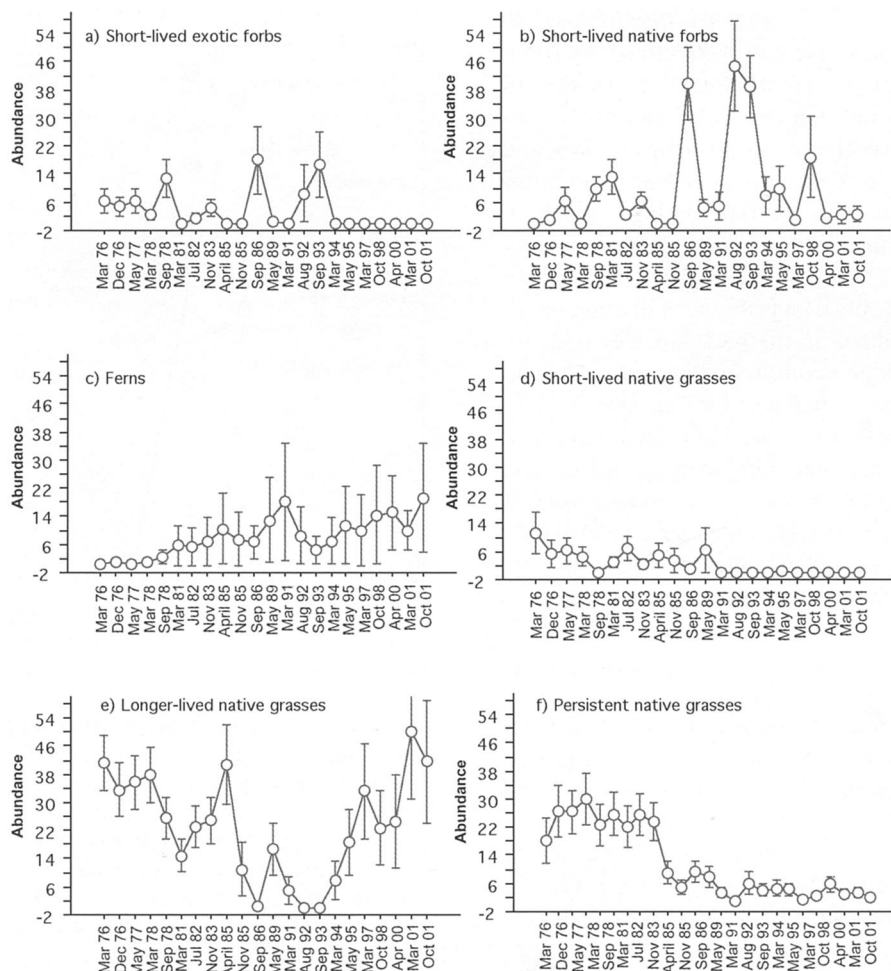


Fig. 2. Mean (+ SE) abundance score in plots where *Cenchrus ciliaris* was absent each sample time for: (a) short-lived exotic forbs, mostly annuals; (b) short-lived native forbs, mostly annuals; (c) ferns; (d) short-lived native grasses, mostly annuals; (e) longer-lived native grasses; (f) persistent native grasses. Recent data excluded because *Cenchrus ciliaris* was present in all plots.

5f). The presence of *Cenchrus* reduced species richness in both summer and winter (Table 2, Fig. 5f).

The presence of *Cenchrus* (> 1% rank abundance) in plots significantly reduced the abundance of most growth form groups both before and after 1990 relative to non-invaded sites with little or no *Cenchrus* (Table 3, Fig. 6). Short-lived native forbs, and suffruticose shrubs and forbs were generally more abundant post-1990 whereas native grasses were more abundant prior to 1990 (Fig. 6). Rainfall was significant as a covariate for longer-lived native grasses and suffruticose shrubs and forbs but not for other growth forms (Table 3). The effect size between non-invaded and *Cenchrus* plots was greater post-1990 than before 1990 for short-lived native forbs, native shrubs, and suffruticose shrubs and forbs. Conversely, the effect size was greater before 1990 for native grasses (Fig. 6). Species richness was not affected by the presence of *Cenchrus* prior to 1990 but after 1990 species richness was higher in the non-invaded plots relative to those with *Cenchrus* (Fig. 7). Species richness varied considerably with time corresponding to periods of high winter rainfall although overall rainfall was not a significant covariate (Table 3).

Correlations with time to colonization by *Cenchrus ciliaris*

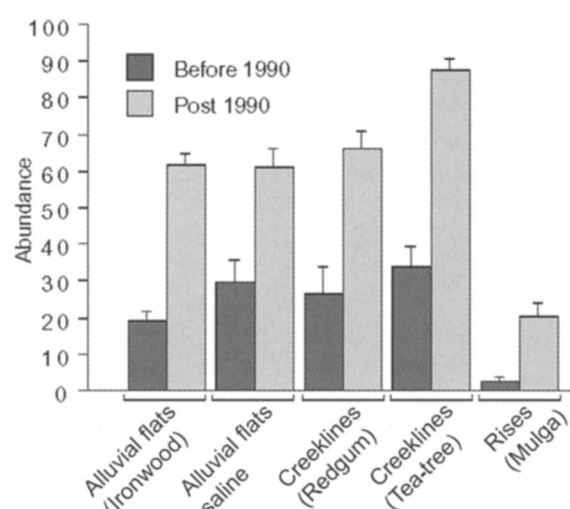


Fig. 4. Mean (+se) abundance score of Buffel grass (*Cenchrus ciliaris*) for all plots in each of five vegetation types before and after 1990 sampling dates. Ironwood (*Acacia estrophiolata*), Redgum (*Eucalyptus camaldulensis* var. *obtusata*), Tea-tree (*Melaleuca* spp.), Mulga (*Acacia aneura*)

Table 2. Summary results for analyses of variance (ANOVA) for the effect of the presence of *Cenchrus* and season of rainfall for ten response variables.

Factor	df	Exotic forbs	Exotic shrubs	Native short-lived forbs	Native ferns	<i>Fimbri-stylis</i>	Long-lived native grass	Persistent native grass	Short-lived native grass	Suffruticose shrubs/ forbs	Richness
		F p	F p	F p	F p	F p	F p	F p	F p	F p	F p
<i>Cenchrus</i>	1	0.8 ns	0.3 ns	17.5 ***	9.3 ***	7.2 **	24.1 ***	8.2 **	1.1 ns	0.6 ns	3.6 *
Season of rainfall	2	30.6 ***	1.0 ns	74.0 ***	0.1 ns	3.6 *	11.9 ***	8.9 **	4.4 *	0.1 ns	20.2 ***
Buffel × Season	2	0.2 ns	1.1 ns	22.4 ***	0.2 ns	0.8 ns	6.1 **	1.3 ns	1.2 ns	1.5 ns	0.2 ns
Residual df	570										
Transform		Arc sin	Arc sin	Arc sin	Arc sin	Arc sin	Arc sin	Arc sin	Arc sin	Arc sin	Arc sin

Table 3. Summary results for analyses of covariance (ANCOVA) for the effect of the presence of *Cenchrus ciliaris* and time for ten response variables. All ANCOVA models were refitted if the covariate interactions were non significant. Four month rainfall prior to sampling was the covariate.

Factor	df	Exotic forbs	Exotic shrubs	Native short-lived forbs	Native ferns	<i>Fimbri-stylis</i>	Long-lived native grass	Persistent native grass	Short-lived native grass	Suffruticose shrubs/ forbs	Richness
		F p	F p	F p	F p	F p	F p	F p	F p	F p	F p
<i>Cenchrus</i>	1	1.1 ns	1.7 ns	43.7 ***	29.9 ***	9.5 ***	61.6 ***	8.8 ***	1.5 ns	2.9 ns	15.9 ***
Time (before vs after 1990)	1	0.3 ns	1.8 ns	21.8 ***	7.3 **	0.1 ns	17.4 ***	44.6 ***	8.4 **	11.8 ***	4.1 ns
<i>Cenchrus</i> × Time	1	0.1 ns	1.9 ns	16.8 ***	5.3 *	0.1 ns	9.2 *	0.3 ns	2.9 *	3.5 *	24.2 ***
Rainfall	1	0.1 ns	0.1 ns	13.6 ***	0.1 ns	2.2 ns	7.0 *	0.15 ns	1.9 ns	5.0 *	0.1 ns
Residual df	568										
Transform		Arc sin	Arc sin	Arc sin	Arc sin	Arc sin	Arc sin	Arc sin	Arc sin	Arc sin	Arc sin

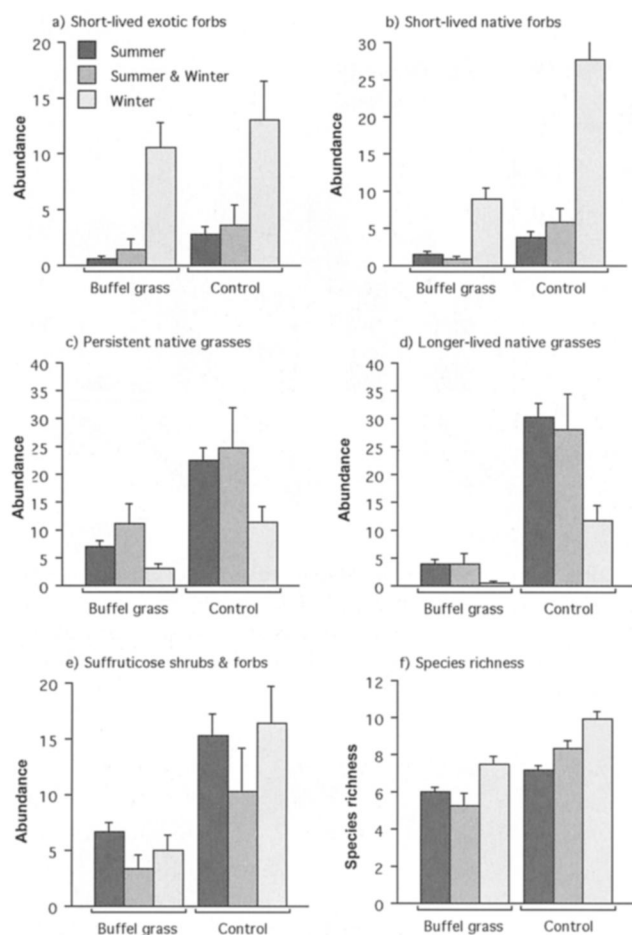


Fig. 5. Mean (se) abundance score for non-invaded vs. *Cenchrus ciliaris* plots among three seasons of rainfall. **a.** short-lived exotic forbs, mostly annuals; **b.** short-lived native forbs, mostly annuals; **c.** persistent native grasses; **d.** longer-lived native grasses; **e.** suffrutescent shrubs and perennial forbs; **f.** species richness.

Time to *Cenchrus* presence in a plot was positively correlated with both the mean richness at times before and the richness in the year prior to colonization ($r = 0.65$, $p < 0.05$, $r = 0.77$ $p < 0.01$) respectively, but was not well correlated with abundance of native plants prior to colonization ($r = 0.25$, $p > 0.1$). Distance to creek lines was also positively correlated with time to colonization ($r = 0.61$, $p < 0.05$) as was distance to creek lines and species richness ($r = 0.67$, $p < 0.05$).

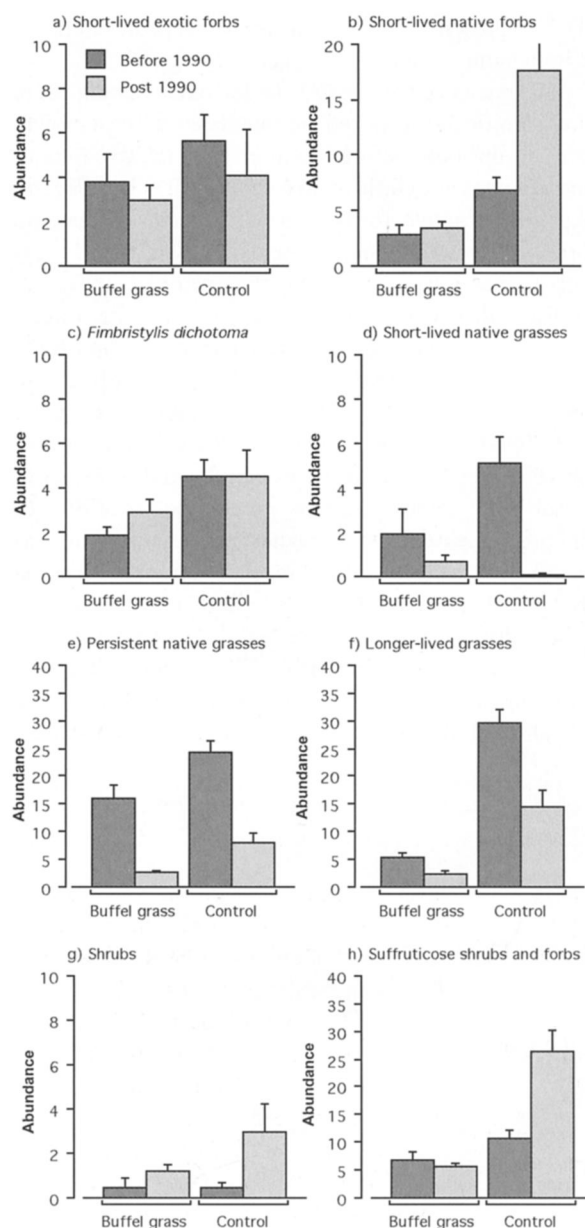


Fig. 6. Mean (se) abundance score for non-invaded vs. *Cenchrus ciliaris* plots pre- and post-1990 sample dates. **a.** short-lived exotic forbs, mostly annuals; **b.** short-lived native forbs, mostly annuals; **c.** *Fimbristylis dichotoma*, a graminoid; **d.** short-lived native grasses, mostly annuals; **e.** persistent native grasses; **f.** longer-lived native grasses; **g.** native shrubs; **h.** suffrutescent shrubs and persistent forbs.

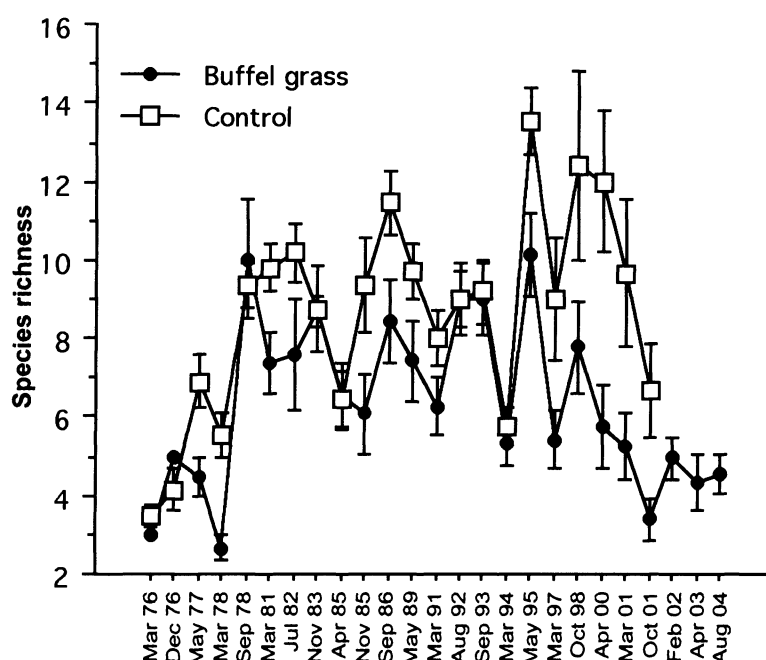


Fig. 7. Species richness (\pm se) in plots with either *Cenchrus ciliaris* present or absent for each of the sample times. Recent sample times do not have enough replication of plots without *Cenchrus* to be included.

Discussion

Long-term changes in the absence of Cenchrus ciliaris

We found pronounced changes in the composition of the herbaceous layer in plots where *Cenchrus ciliaris* was absent. These changes appear to be related to the removal of grazing pressure and fluctuations in seasonal rainfall. Prior to the spread of *Cenchrus* in the 1970s, the area was used intensively for cattle grazing and was widely recognized as being in a degraded state. There were large areas of bare ground due to the combined effects of rabbits and pastoralism. This is reflected in the photo records of early 1972; bare ground was common despite rainfall every month in 1968. Similarly, in 1973, rain fell in all months and rainfall was above average through to the beginning of plot sampling. In 1976, species richness in sites was the second lowest recorded and there were relatively low abundances of ferns, short-lived native forbs, suffrutescent shrubs, and persistent forbs; these low abundances may reflect the residual effects of total grazing pressure (Friedel 1991; Wilson 1990; Grice & Barchia 1992). Grazing pressure could also explain the lack of a positive relationship between rainfall and short-lived native forb abundance. The grazing hypothesis is supported by the findings of Kinloch & Friedel (2005), who detected depleted native seed banks adjacent to stock watering points in Central Australia. Alternatively, the increased perennial native grass abundance following summer rains may have suppressed the response of forbs to rainfall events in the 1970s. The

drought event of the mid-1980s had a marked effect on the abundance of native grasses. Perennial (persistent) native grasses never regained their dominance compared to longer-lived native grasses. By the 1990s, both short-lived exotic forbs and short-lived native grasses were rarely recorded, which possibly indicates that strong residual effects of grazing had ceased.

Photo-plots also revealed increases in larger woody species throughout the study area corresponding to an increase in abundance of highly palatable shrubs in plots where *Cenchrus* was absent. Long-term photo-plot data from semi-arid savanna in the Northern Territory also show a similar trend (Bastin et al. 2003) as does other studies in semi-arid regions of Australia (Noble 1997) where exotic perennial grasses are absent. Whilst the larger woody shrubs (*Acacia* and *Senna* species) were not sampled in plots, an increase in shrub abundance may be linked to their increase because they have fleshy seeds dispersed by birds. Hence, increases in perch sites may have enhanced the dispersal and recruitment of shrubs in the absence of *Cenchrus*.

Seasonality of rainfall in the absence of Cenchrus ciliaris

Seasonality of rainfall had strong effects on the abundance of native forbs and grasses. Both native and exotic forbs responding more strongly to winter rainfall than summer rainfall. In contrast, the native grasses were more abundant after summer rainfall, which may account for the co-existence of these groups in time.

This seasonal effect of rainfall is widely reported in arid and semi-arid vegetation in southern Australia (e.g. Maconochie 1982; Friedel et al. 1993), but the herbaceous response has rarely been measured over sequences of winter rainfall events. Changes in the seasonality of large rainfall events during the 28 years of survey may account for shifts in the abundance of herbaceous growth forms over time. Prior to 1990, short-lived native forb abundance was much lower than in the years after 1990; whilst the converse pattern was detected in perennial native grasses in plots where *Cenchrus* was absent. Both mean annual rainfall and season of rainfall were not significantly different pre- and post-1990. Prior to 1990, however, only 22% of rainfall records fell in winter whereas post-1990 50% of rainfall records were in winter. These winter rainfall patterns may account for the decreased native grass abundance over time.

The spread and effects of Cenchrus ciliaris

We have shown that *Cenchrus* is invasive in a semi-arid environment and that it changes the floristic composition of the vegetation. Invasibility appears to be related to both propagule pressure from sources along drainage and resource availability but the role of disturbance remains equivocal. *Cenchrus* has progressively colonized the study site since 1976 when there were only a few records of its presence and its abundance was less than 5% in those plots. Since then, *Cenchrus* has steadily increased its presence in plots and its abundance regularly exceeds 80%. This measured spread across two floodplains is mirrored in qualitative observation throughout floodplains of Central Australia, including the iconic landscapes of Uluru - Kata Tjuta and Watarrka National Parks (Puckey et al. 2004). Long-term studies of European impacts on Australian vegetation have attributed changes to altered fire regimes, grazing, vegetation clearance and agriculture (Lunt 2002). Our study is the first to quantify floristic change, relative to non-invaded plots, due to an invasive plant species over time.

Cenchrus has a pronounced effect on the seasonal growth response of native forbs and native grasses by reducing both winter growth, in forbs, and summer growth in grasses. This can be seen in the differences in the effect of *Cenchrus* has on the abundance of forbs and grasses pre- and post-1990. Native grass abundance was more strongly affected by *Cenchrus* prior to 1990 because more effective summer rain fell during that period. Post-1990, short-lived native forbs, suffruticose shrubs and perennial forbs were more strongly suppressed relative to non-invaded plots because of more effective winter rain. These rainfall effects suggests *Cenchrus* makes use of both summer and winter rainfall

resulting in the long-term competitive exclusion of native herbaceous species whenever there is effective rainfall for growth. Thus, species richness is more strongly depressed when there is both summer and winter rainfall compared to other seasons and non-invaded plots. Our species richness results are consistent with space for time studies in other semi-arid region (Fairfax & Fensham 2000; Franks 2002; Butler & Fairfax 2003) that showed the cover of *Cenchrus* was negatively associated with species richness. We predict that reductions in species richness will become more pronounced over time because the seed banks of native forbs and grasses will gradually be depleted and the scope for metapopulation dynamics via dispersal from unaffected patches decreases.

The indirect effect of invasive grasses on floristic composition, by changing fire regimes, is widely recognized as a significant ecological factor (D'Antonio & Vitousek 1992; Brooks et al. 2004; Rossiter et al. 2003; Zedler 1983). *Cenchrus* has the potential to alter fire regimes in arid and semi-arid areas because of increased fuel load and fuel continuity. Thus, a combination of frequent ignitions, high fuel loads and fuel continuity induced by *Cenchrus* is likely to be increasing the intensity and frequency of fires and cause the decline of some woody species. This change in fire regimes can be seen in the low abundance of native shrubs (< 1 m high) in plots dominated by *Cenchrus* compared with non-invaded plots after 1990. In our plots, the frequency of fires has increased since the spread of *Cenchrus*; however, non-invaded plots may also be affected because they are interspersed with areas dominated by *Cenchrus*. We predict that if the spread of *Cenchrus* continues unabated, landscape changes will begin to occur, resulting from both the direct competitive effects and the indirect effects of changed fire regimes. The reversibility of these changes is likely to depend on whether the system has shifted from a resource limited (rainfall) recruitment to a seed limited recruitment as a result of *Cenchrus* changing the ability of native plants to persist in space and time.

This long-term study has shown the complex nature of vegetation change in Central Australia driven by both fluctuations in climate and the spread of an invasive grass. Overall, the influence of the rapid increase in *Cenchrus* biomass had the greatest impact on the herbaceous layer and may also be affecting the woody component through changed fire regimes. Whether the structure and composition of our study site will be permanently altered by the invasion of an exotic perennial grass will depend on its persistence and only continued monitoring will detect this change.

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