

Habitat distributions of 12 co-occurring wallaby grasses (*Rytidosperma* spp., Poaceae) and their response to a transition from pastoral to conservation land use

S. McIntyre^{A,B,*} , W. J. Müller^A  and Jon Lewis^B 

For full list of author affiliations and declarations see end of paper

***Correspondence to:**

S. McIntyre
Fenner School of Environment & Society,
The Australian National University, Acton,
ACT 2601, Australia
Email: sue.mcintyre@anu.edu.au

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ABSTRACT

The extent and abundance of *Rytidosperma* Steud. species in mixed woodland, forest and derived grassland was examined over a 15-year period following removal of long-term sheep grazing. Ground-layer vegetation in 73 permanent plots was surveyed five times between 2005 and 2020 in a 50-ha paddock on the southern tablelands of New South Wales. Sites were stratified over the slope positions and micro-habitats represented at the site. Of the 12 *Rytidosperma* species recorded, only *R. pallidum* was morphologically and ecologically distinct in the field. The remaining 11 species, termed ‘cryptic *Rytidosperma*’, were assessed using a novel sampling method developed for this group. *Rytidosperma pallida* was the only species strongly associated with sclerophyll forest habitat. The 11 other species varied in their habitat preferences but, as a group, were most dominant and persistent on upper slopes. Over the 15 years, the relative abundance of *R. pilosum*, *R. erianthum*, *R. monticola*, *R. carphoides* and *R. caespitosum* declined as annual exotics, native sub-shrubs and low-palatability graminoids became more dominant. But only one species (*R. pilosum*) significantly declined in overall frequency of presence (constancy) in the plots. The changes observed suggest that when pastoral land is converted to conservation management, reduced grazing pressure could affect the abundance of *Rytidosperma* species important to other species, such as the threatened moth *Synemon plana*.

Keywords: *Austroanthonia*, *Danthonia*, eucalypt grassy woodland, grazing, *Joycea pallida*, macropod, *R. auriculatum*, *R. laeve*, *R. monticola*, *R. penicillatum*, *R. racemosum*, *R. setaceum*, *R. tenuius*.

Introduction

Species of *Rytidosperma* Steud. (wallaby grasses) are unusual among temperate native grasses because of their persistence, palatability and productivity under livestock grazing, making them of great importance to the pastoral industry in south-eastern Australia (Whalley *et al.* 1978; Garden *et al.* 2001). Moreover, some species are tolerant of fertilisation (Whalley *et al.* 1978), a rare feature in the native ground flora (Dorrough *et al.* 2011), and can produce quantities of high-quality forage (e.g. Archer and Robinson 1988; Robinson and Archer 1988). In the New South Wales (NSW) southern tablelands, *Rytidosperma* is an important naturally occurring component of sown and fertilised pastures, and is particularly associated with sedimentary lithology and tolerant of acid soils (Munnich *et al.* 1991; Robinson *et al.* 1993). Pastures dominated by *Rytidosperma* can be stable under a range of livestock grazing regimes (Garden *et al.* 2000) and appear to have recolonised less stable sown pastures on the NSW central and southern tablelands where the genus is the most common dominant in pastures, and is strongly associated with sheep grazing (Garden *et al.* 2001).

Beyond its economic significance to livestock industries, the genus has relevance to conservation. The threatened golden sun moth (*Synemon plana* Walker) has been observed to be positively associated with occurrence (Richter *et al.* 2013), and amount and species number (Kutt *et al.* 2016), of *Rytidosperma*. O’Dwyer and Attiwill (1999)

found *S. plana* to be associated with four species in particular, whose roots were thought to be consumed by larvae of the moths. It is therefore important to understand the specific ecological characteristics of these species, as changes to management may affect existing habitat for golden sun moths.

There is widespread occurrence of reticulation in the sub-family Danthonioideae, explained by past hybridisation (Pirie *et al.* 2009), which results in a phylogenetic network rather than a more easily interpreted phylogenetic tree. Identification to species requires microscopic examination, but identifications are not always straightforward because the genus has a wide range of cytotypes, and continues to undergo both inter- and intra-specific hybridisation between cytotypes (Brock and Brown 1961; Waters *et al.* 2010). As a result, field researchers face major obstacles when conducting vegetation surveys when *Rytidosperma* is present. Understandably, vegetation surveys not specifically targeting this group tend to identify *Rytidosperma* only to genus at the plot level (e.g. Scott and Whalley 1982; Dowling *et al.* 1996; McIntyre 2008; Bryant *et al.* 2017), even though multiple taxa co-occur (Munnich *et al.* 1991; Waters *et al.* 2009). As wallaby grasses are broadly understood to be grazing tolerant and an important component of commercially grazed pastures, a transition to conservation management could result in changes to the component species. Moreover, as species of *Rytidosperma* vary in their ecological tolerances (Scott and Whalley 1982), some differences in response could be expected.

This paper documents changes in the extent and relative abundance of *Rytidosperma* species over 15 years, after a transition from long-term commercial sheep grazing to macropod grazing, in a heterogeneous paddock of 50 ha. More specifically we aim to:

1. further our understanding of the varying ecological characteristics within the genus through an investigation of their microhabitat preferences;
2. analyse the response of the species present to the removal of commercial livestock grazing;
3. interpret our observations in the context of the ecology of all *Rytidosperma* species in the region;
4. consider any implications for conservation management of the patterns and changes observed.

Materials and methods

Site characteristics and history

The study site is located on undulating hills and minor flats of the Yass River valley, on the southern tablelands of New South Wales. Permanent plots were established across a 50 ha paddock (centre 34°58'30'S, 149°12'23'E), covering an altitudinal range of 50 m (585–635 m). The soil parent materials are Ordovician sediments (Jenkins 2000) and the

clay-loam soils are acidic (pH 4–5) and highly erodible. The mean annual temperature is 20°C (maximum) and 6.5°C (minimum). Annual rainfall averages 644 mm, with monthly averages ranging from 45 mm (in May, June, July) to 66 mm (November). Extremely wet or dry conditions may be experienced in any month of the year and frosts are frequent in winter. The site has a 200-year history of livestock grazing. Stocking in the 25 years before the first vegetation assessment (2005) was 100 wethers, reduced to 65 from 2000 to 2004 during the Millennium Drought. Although this stocking rate of 2 dry sheep equivalent (DSE) ha⁻¹ is mid-range carrying capacity for native grassland in the region (Langford *et al.* 2004), one-third of the paddock was dry sclerophyll forest, which suggests higher grazing pressures.

Over the 50 ha, the vegetation comprises approximately equal amounts of Tablelands Sclerophyll Forest, Tablelands Grassy Woodland (Keith 2004) and grassland–open woodland mosaic derived from tree clearing. Although there is evidence of past ringbarking, most of the open areas resulted from pasture development in 1972–1974. Trees were bulldozed into windrows and burnt. The areas were chisel-ploughed, superphosphate was applied and sown to *Trifolium* spp. The entire site was burnt by wildfire in 1975. There have been no further pasture inputs, and soil sampling in 2006 indicated that available soil phosphorus had returned to 'native' levels (Colwell P, 5 mg kg⁻¹; see McIntyre 2008). Conversion from pastoral use to conservation management was initiated at the end of 2004 with the permanent removal of all livestock. The site has supported populations of macropods both before and after removal of livestock. During the study, the site was grazed by macropods, which move freely within and through numerous points on the boundary fence. These were, in the order of decreasing abundance, *Macropus giganteus*, *M. rufogriseus* and *Wallabia bicolor*. Hares were also present in very low numbers, with little grazing impact evident. The macropods were regarded as largely uncontrolled, there being no effective culling or known predators apart from the fox (*Vulpes vulpes* L.). The grazing regime after the removal of livestock was more selective, because the wild herbivores were unconstrained by fencing. This resulted in spatially variable grazing pressure, evident from the patchiness of sward height throughout the site (as described in McIntyre and Tongway 2005). The upper slopes were the most severely grazed part of the landscape before, and throughout, the study, because this is where sheep had previously camped and where kangaroos persistently congregated during the observation period. Pre-existing grazing lawns persisted more strongly here as a consequence. Rainfall variation resulted in grazing pressure also varying in time, although even at the lowest point of the 2017–2019 drought, grassland on the upper slopes supported an average biomass in the order of 1500 kg ha⁻¹.

Survey design

To monitor floristic changes, 73 permanent plots (5 × 6 m) were established and the first assessment was undertaken in spring 2005, 12 months after the removal of sheep. All plots were marked at two corners with sturdy metal stakes and were able to be accurately re-located in later surveys.

Plot locations were stratified to sample the range of environments over the site. These were categorised in terms of habitat and slope position (Table 1). All but the 'Forest' category were habitats that were in grassy woodland or grassland derived from grassy woodland:

1. Forest – in sclerophyll forest with continuous tree canopy characterised by *Eucalyptus rossii* and *E. mannifera*;
2. Open – cleared grassy woodland away from tree canopies;
3. Tree – under a well-developed tree canopy in grassy woodland;

For Habitats 1–3, upper slopes included hill crests and shoulders, lower slopes included break of slope and flats, whereas mid slopes were intermediate locations.

4. Sheep camp – these were physically equivalent to upper slope 'Tree' habitat but carried a nutrient legacy from their previous use by sheep as locations for habitual resting, resulting in dung and urine accumulation;
5. Drainage line – intermittent watercourses (first- and second-order) with scour ponds (Eyles 1977) and incised sections. Slope position for drainage lines was determined from the overall altitude at the study site as follows: upper (first-order drainage lines, >615 m), mid (first-order, 600–615 m) and lower (second-order drainage line, <600 m).

Assessments took place in late spring–early summer and were timed to allow for the flowering of cool-season grasses and *Rytidosperma* spp. The earliest commencement date was 20 November and latest finishing date 10 December. We avoided sampling in years when rainfall was low over the winter–spring growing period so as to maximise

Table 1. Stratification of survey design across habitat and slope position.

Habitat	Slope position			Total (N = 73)
	Upper	Mid	Lower	
Open	8	10	9	27
Tree	4	3	4	11
Forest	6	7	4	17
Drainage line	4	4	6	14
Sheep camp	4	0	0	4

Permanent plots (6 × 5 m) monitored on five occasions over 15 years (2005, 2010, 2013, 2016, 2020) stratified by habitat and slope position, totalling 73 plots.

apparency. Comparing annual rainfall totals with the long-term mean indicates slightly above-average rainfall over the 15-year observation period (Fig. 1). Variability in rainfall was high; observations started in the Millennium Drought, which broke 5 years later with a La Niña event in 2010–2011, and average to wet conditions continued until the short severe drought of 2017–2019. In summary, we observed emergence from two severe droughts with an intervening wet period of 7 years, including the record-breaking wet winter–spring of 2016, when 1.5 times the average rainfall was recorded.

Sampling and nomenclature

In the initial survey (2005), aspect was recorded, and ground surface cover was estimated in each plot according to the following categories: cryptogam, litter, rock, bare ground. Litter depth was measured at four fixed locations in each plot.

Full floristic surveys were conducted, recording the presence of all taxa (see notes below relating to *Rytidosperma*) by using the ranking system of Mannerje and Haydock (1963). Using this method, each species (or species combination) was ranked according to its relative contribution to the total biomass (including attached litter). The ranks were converted to proportional contribution using the following geometric series:

$$PR = (1 - k) \times k^{R-1}$$

where R is the rank order and k is the parameter, which was set at 0.3, as determined for pasture by Scott (1986). Species ranked 1 (70%), 2 (21%) and 3 (6%) are referred to as the dominants in a plot. On average, the top-three ranked species account for 97% of the total biomass in grassy vegetation (Scott 1986). Ranking was recorded down to 7. Species ranked 8 and below were given a nominal relative abundance of 0.01%. This ranking method gives a measure of relative abundance, represented as a percentage of the total sward biomass. All surveys were conducted by S. McIntyre and J. Lewis.

Taxonomic changes during the observation period

At the time of the first survey in 2005, *Joycea pallida* was taxonomically separate from other wallaby grasses (then *Austrodanthonia* spp.) and was morphologically distinct in the field. Accordingly, in recording the rankings, we assessed the relative amount of biomass of the following two entities: (1) *Joycea pallida* and (2) *Austrodanthonia* spp. (as described above). Linder et al. (2010) placed *Joycea pallida* and all *Austrodanthonia* species into *Rytidosperma*. In this paper, we have addressed the potential confusion this name change has made for communication, by using the current name for *Joycea pallida* as *R. pallidum*. Being unidentifiable to species level in the field, the collective entity assessed during surveys as *Austrodanthonia* spp. is referred to here as 'cryptic *Rytidosperma*'.

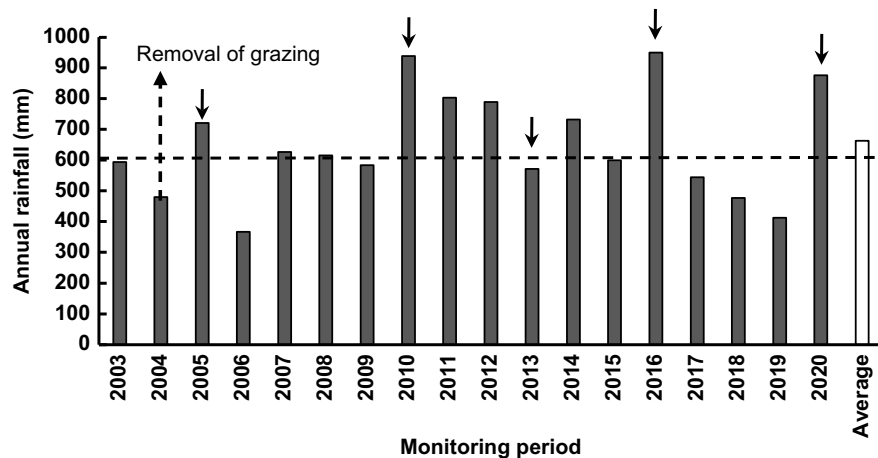


Fig. 1. Annual rainfall (mm) over the monitoring period 2005–2020. Data from 2003 to 2007 are from Ainslie Station 70000 (<http://www.bom.gov.au>; 31 km south), and thereafter, from the study site. The timing of the five surveys (in the spring of that calendar year) is indicated by downward arrows. The average received over the period 2003–2020 is represented by the open bar. The long-term average (Ainslie Station 70000 from 1935 to 2016) is indicated by the broken line. Upward broken arrow indicates the removal of livestock.

Elucidation of the species of ‘cryptic *Rytidosperma*’

In addition to its biomass ranking, we sampled the available ‘cryptic *Rytidosperma*’ in each plot by collecting one inflorescence randomly from 10 plants. All plants were sampled if there were fewer than 10 plants flowering. There is no vegetative reproduction in these species and the tussocks are distinct. Plants were identified to species in the laboratory through microscopic assessment of floret morphology and indumentum by using the *Austrodanthonia* key and descriptions of Linder (2005). In total, 1959 individual plants were identified to species in this way. At the plot level, the percentage biomass of ‘cryptic *Rytidosperma*’ was allocated to the individual species in the proportion to which they were represented in the inflorescence sample from each plot.

Data analysis

The following 12 species were recorded in the surveys: *Rytidosperma auriculatum* (J.M.Black) Connor & Edgar, *R. caespitosum* (Gaudich.) Connor & Edgar, *R. carphoides* (F.Muell. ex Benth.) Connor & Edgar, *R. erianthum* (Lindl.) Connor & Edgar, *R. laeve* (Vickery) Connor & Edgar, *R. monticola* (Vickery) Connor & Edgar, *R. pallidum* (R.Br.) A.M.Humphreys & H.P.Linder, *R. penicillatum* (Labill.) Connor & Edgar, *R. pilosum* (R.Br.) Connor & Edgar, *R. racemosum* (R.Br.) Connor & Edgar, *R. setaceum* (R.Br.) Connor & Edgar, and *R. tenuius* (Steud.) A.Hansen & Sunding. Although distinct examples of *R. erianthum* and *R. monticola* were identified, and the former was more frequent, there were enough intermediate forms to require

a category combining both species for the analyses (*R. erianthum*–*R. monticola*).

2005 habitat analyses

Analyses of the floristic data were initially performed on the calculated percentage biomass for the 2005 survey of ‘cryptic *Rytidosperma*’ and each individual *Rytidosperma* species (but with *R. erianthum* and *R. monticola* combined). These species or species groupings fell into the following three categories for analysis:

1. ‘Cryptic *Rytidosperma*’, *R. erianthum*–*R. monticola*, *R. pilosum* – forward stepwise linear regression of percentage biomass in the 73 plots, examining the effects of plot environment (habitat and slope position), aspect, ground cover (estimated percentage cover of cryptogam, litter, rock, bare ground) and litter depth (average of five points in each plot), and interactions between all these categories and measurements.
2. *R. auriculatum*, *R. caespitosum*, *R. carphoides*, *R. pallidum* – forward stepwise logistic regression of presence or absence (also referred to as constancy) in the 73 plots, examining the effects of the same variables listed in (1).
3. *R. laeve*, *R. penicillatum*, *R. racemosum*, *R. setaceum*, *R. tenuius* – tabulation of numbers of occurrences in the 73 sites as their frequencies were too low for formal analysis.

For all the variables in (1), the data were log-transformed, $\ln(1 + \text{percentage biomass})$, before analysis. In (2), as the distribution of *R. pallidum* across the 73 plots was bimodal (i.e. present in large to moderate amounts, or in small

amounts or absent), the binary response analysed was dominant (biomass rank of 1–3) or not (rank of ≥ 4).

Analyses over time

Over the five survey times, analyses of percentage biomass and constancy of *Rytidosperma* were performed for each of the taxonomic entities listed in (1) and (2) above. These analyses were restricted to those plots where the entity being analysed was present on at least one of the survey times. This meant that not all habitat and slope position combinations were represented, so habitat and slope were collapsed into a single ‘environment’ factor. For percentage biomass, split plot in time repeated-measures analyses of variance were performed to compare environments, years and their interaction. As previously, the data were log-transformed before analysis. For constancy, two-way ANOVAs were performed on numbers of plots where the species was present for each environment in each year, to determine whether there was a significant change over time after adjusting for environment differences.

Results

Of the 365 plot assessments (5 surveys $\times$ 73 plots), 79% recorded ‘cryptic *Rytidosperma*’ being present and 34% recorded the presence of *R. pallidum*. Of the 73 plots, 63 had ‘cryptic *Rytidosperma*’ recorded in any of the years and the range was from 61 (in 2005) to 56 (in 2013, 2016, 2020). *Rytidosperma pallidum* was recorded in 27 of the plots in any of the years, with a range from 26 (in 2010) to 24 (in 2020). Up to five species of *Rytidosperma* co-occurred in a plot. Records of the species that were too infrequent to analyse statistically are summarised in Table 2.

Environmental patterns in 2005

Forward stepwise regression showed habitat, then slope position, to be the best explanatory variables for the seven taxonomic entities analysed, and these two terms accounted for 25–50% the variance (for total biomass) or deviance (for constancy) (Tables 3, 4; Supplementary Table S1). *Rytidosperma pallidum* was significantly linked to

sclerophyll forest and tree canopies, and there was little overlap in distribution between this and other species (Tables 4, 5). Cryptic *Rytidosperma* was strongly dominant on the upper slope plots, as was the common *R. erianthum*–*R. monticola* entity (Fig. 2). The other abundant species was *R. pilosum*, which had a more even distribution across slope positions, and tree and open plots (Fig. 2).

Among the moderately common taxa for which only constancy was analysed, open plots had a high likelihood of presence, with either no slope position preference (*R. carphoides*), upper slopes (*R. auriculatum*) or mid and upper slopes preferred (*R. caespitosum*) (Tables 4, 5). The latter species was as likely to occur under trees, or in drainage lines, as it was in the open.

Most taxa were recorded in drainage lines, but only on upper slopes (Table 4, Fig. 2), where the plots often included both wet areas and very dry microsites on the top of incised, eroded banks. Only one species, *R. racemosum*, was important on sheep camps, although *R. pilosum* was present in small amounts. The only species entirely restricted to one habitat type was *R. penicillatum*, which was recorded in five mid- and lower-drainage line plots.

Aspect was marginally significant for ‘cryptic *Rytidosperma*’, for which north-, east- and south-facing slopes were preferred, but only significant for one species, *R. caespitosum*, which was almost entirely restricted to eastern and southern aspects.

Ground cover attributes were significant in accounting for variability in occurrence for three of the seven taxa (or groups) analysed (Tables 3, 4), although much less important than habitat or slope position. *R. carphoides* was negatively associated with litter cover, consistent with its preference for open sites, and generally absent from beneath tree canopies. ‘Cryptic *Rytidosperma*’ and *R. erianthum*–*R. monticola* were positively associated with rock cover, which is consistent with their preference for upper slopes.

Changes over time

Rytidosperma pallidum

The distinctiveness of *R. pallidum* is the large size of the coarse, unpalatable tussocks, which are rarely grazed.

Table 2. Constancy of least frequent *Rytidosperma* species recorded over five surveys.

Species	Overall (N = 365)	2005 (N = 73)	2010 (N = 73)	2013 (N = 73)	2016 (N = 73)	2020 (N = 73)	Any year (N = 73)
<i>R. racemosum</i>	29	4	6	6	7	6	7
<i>R. laeve</i>	9	3	1	1	1	3	4
<i>R. penicillatum</i>	7	0	3	1	2	1	5
<i>R. tenuius</i>	7	1	1	0	1	4	4
<i>R. setaceum</i>	4	1	0	1	0	2	2

Constancy (number of plots in which a species was present) of five *Rytidosperma* species in 73 monitoring plots over five monitoring surveys. These species were too infrequent for statistical analyses. Number of plots assessed is given in parentheses. ‘Overall’, total number of records of species in plots; ‘Any year’, the total number of plots in which the species was recorded in any of the survey years.

Table 3. Order of fitting terms and percentage of variance explained in the analysis of percentage total biomass.

Number of sites present in 2005 (N = 73)	<i>Cryptic Rytidosperma</i> 61	<i>R. erianthum, monticola</i> 35	<i>R. pilosum</i> 50
Habitat	1 (P < 0.001)	2 (P < 0.001)	1 (P < 0.001)
Slope position	2 (P < 0.001)	1 (P < 0.001)	2 (P = 0.02)
Habitat × Slope	3 (P = 0.002)	3 (P < 0.001)	3 (P = 0.2)
Aspect	4 (P = 0.04)	6 (P = 0.06)	–
log(litter depth)	–	–	–
log(percentage cryptogam cover)	–	–	–
log(percentage litter cover)	–	–	–
log(percentage rock cover)	5 (P = 0.007)	4 (P < 0.001)	–
log(percentage bare ground)	–	–	–
Rock × Habitat	–	5 (P = 0.001)	–
Rock × Aspect	6 (P = 0.02)	–	–
Percentage variance explained after			
1 term	27.8	17.3	18.7
2 terms	49.9	44.8	25.8
3 terms	57.6	52.3	29.1
4 terms	60.3	58.9	–
5 terms	63.9	66.7	–
6 terms	68.9	69.2	–
Final model terms	1 to 6	1 to 5	1 and 2

Best-fitting models to describe the response of 'cryptic *Rytidosperma*', and the two most frequently occurring taxonomic entities to landscape factors and ground cover variables in the 2005 survey. Forward stepwise regression was used to determine fitting order and interactions. Terms significant at the 5% level are in bold.

Table 4. Order of fitting terms and percentage of deviance explained in the analysis of constancy.

Number of sites present (N = 73)	<i>R. auriculatum</i> 12	<i>R. caespitosum</i> 15	<i>R. carphoides</i> 10	<i>R. pallidum</i> 19
Habitat	1 (P = 0.003)	1 (P = 0.02)	1 (P = 0.02)	1 (P < 0.001)
Slope position	2 (P = 0.002)	2 (P = 0.03)	–	–
Aspect	–	3 (P = 0.01)	–	2 (P = 0.2)
log(litter depth)	–	–	–	–
log(percentage cryptogam cover)	–	–	–	–
log(percentage litter cover)	3 (P = 0.13)	–	2 (P = 0.04)	–
log(percentage rock cover)	–	–	–	–
log(percentage bare ground)	–	–	–	3 (P = 0.1)
Percentage deviance explained after				
1 term	24.0	16.3	19.9	39.4
2 terms	42.6	26.1	27.1	47.3
3 terms	46.0	43.8	–	50.4
Final model terms	1 and 2	1 to 3	1 and 2	1

Best-fitting models to describe the response of four *Rytidosperma* species to landscape factors and ground cover variables in 2005. Forward stepwise logistic regression was used to determine fitting order and interactions. Response variable is constancy (presence or absence) at a site, except for *R. pallidum*, which was analysed as dominant (biomass rank of 1–3) or not (rank of ≥ 4). Terms significant at the 5% level are in bold.

Over the 15 years, this species maintained its constancy and dominance in sclerophyll forest plots on all slope positions (Fig. 3), but where it occurred under individual tree

canopies, it was more dominant during the wet years (2010–2016) and was significantly reduced after droughts (i.e. in 2005 and 2020; data not shown).

Table 5. Summary of constancy responses of moderately common taxa in 2005.

Parameter	Probability	s.e.
<i>R. auriculatum</i>		
Habitat		
Camp	0	0
Drainage	0.31	0.10
Forest	0	0
Open	0.33	0.08
Tree	0	0
Slope position		
Lower	0.12	0.06
Mid	0.04	0.04
Upper	0.37	0.08
<i>R. caespitosum</i>		
Habitat		
Camp	0	0
Drainage	0.40	0.13
Forest	0	0
Open	0.27	0.08
Tree	0.28	0.13
Slope position		
Lower	0.08	0.05
Mid	0.23	0.08
Upper	0.36	0.09
<i>R. carphoides</i>		
Habitat		
Camp	0	0
Drainage	0.08	0.07
Forest	0	0
Open	0.31	0.09
Tree	0.09	0.08
<i>R. pallidum</i>		
Habitat		
Camp	0	0
Drainage	0	0
Forest	0.82	0.09
Open	0.07	0.05
Tree	0.28	0.13

Mean probabilities of presence and standard errors determined as predictions from forward stepwise logistic regression models. Slope position means are not presented for *R. carphoides* and *R. pallidum* because differences between positions were not significant. For *R. pallidum*, presence means present as a dominant species (rank 1–3). Bold indicates values that are significantly greater than zero.

‘Cryptic *Rytidosperma*’

The ‘cryptic *Rytidosperma*’ group similarly maintained its constancy, but representation in the sward declined progressively (Fig. 3). There were significant interactions with habitat and slope position. In open plots on upper slopes, progressive decline as a percentage of biomass occurred during the wet years, with some recovery in 2020 following three drought years. In other favoured habitats, ‘cryptic *Rytidosperma*’ declined after 2005, and did not recover in 2020 (e.g. upper-slope tree and drainage lines, mid slopes open and drainage lines, and lower slopes

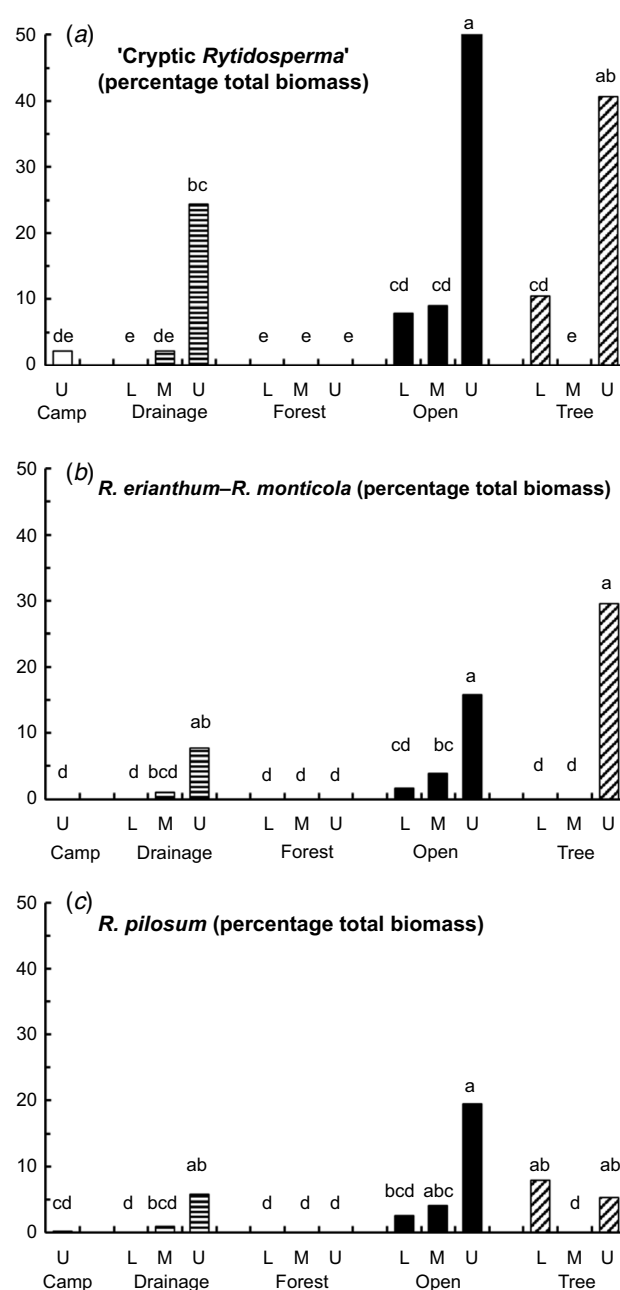


Fig. 2. Observed percentage total biomass of the three most frequently occurring taxonomic entities, (a) ‘cryptic *Rytidosperma*’ (excluding *R. pallidum*), (b) *R. erianthum*–*R. monticola* and (c) *R. pilosum*, over the range of habitat and slope position combinations sampled over 50 ha. Slope positions: lower (L), mid (M), upper (U); Habitats: ‘Camp’, sheep camp; ‘Drainage’, drainage line; ‘Forest’, dry sclerophyll forest; ‘Open’, open grassland in cleared areas; ‘Tree’, under mature tree canopy in woodland. Different letters denote significant differences between the means ($P < 0.05$).

open). On camps, ‘cryptic *Rytidosperma*’ persisted for at least 8 years, but percentage biomass was very low in 2016 and 2020.

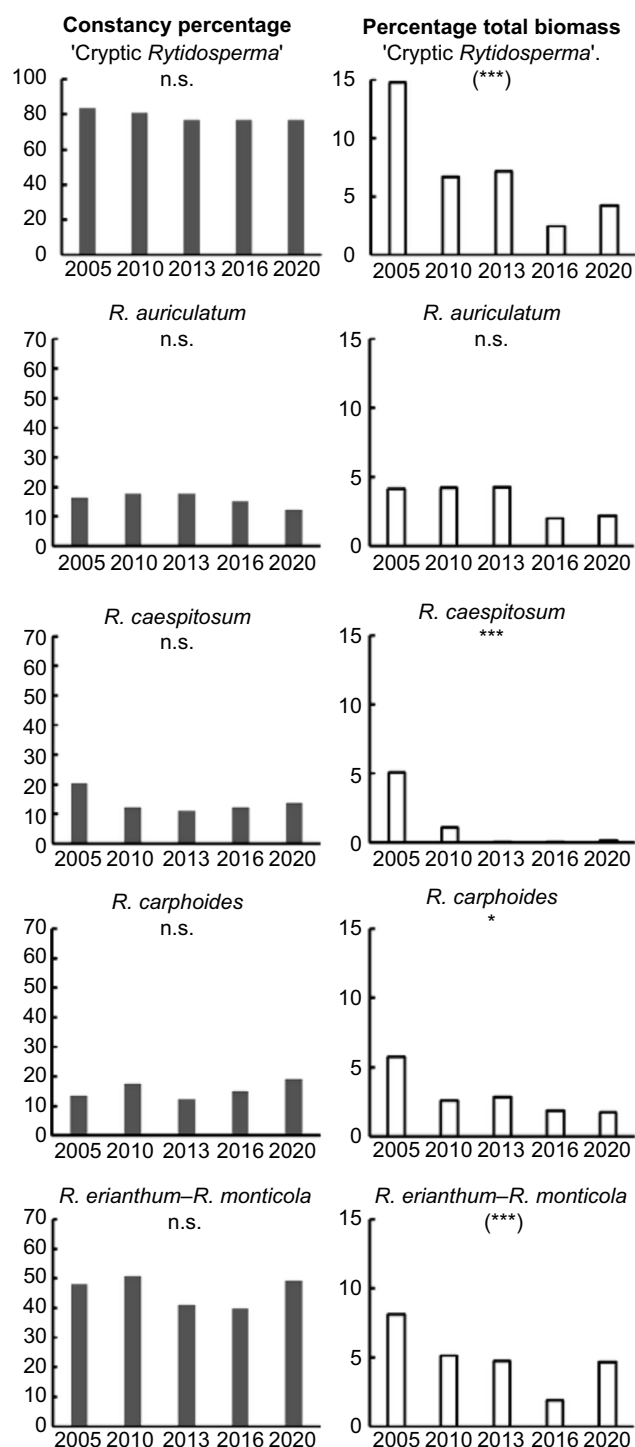


Fig. 3. Changes in constancy (percentage of the 73 sites where the taxon was present) and percentage of total biomass (at sites where present in 1 year or more) of *Rytidosperma* over 15 years from 2005 to 2020. Results of ANOVA are indicated as: n.s., no significant change over time; significant at *, $P < 0.05$; significant at **, $P < 0.01$; significant at ***, $P < 0.001$. Parentheses around asterisks indicate interactions with habitat and slope position discussed in the text. 'Cryptic *Rytidosperma*' represents the species assessed in the field collectively with the exception of *R. pallidum*, which was assessed separately.

Fig. 3. (Continued).

Common *Rytidosperma* species

Of the five other *Rytidosperma* entities analysed, constancy was maintained in four (*R. auriculatum*, *R. caespitosum*, *R. carphoides*, *R. erianthum-R. monticola*), whereas relative abundance was maintained only in *R. auriculatum*. The other three declined significantly over time (Fig. 3). One species, *R. pilosum*, declined in both constancy and dominance, most dramatically after the first survey in 2005 (Fig. 3). There was greater persistence on upper slopes (open) and lower slopes (open and tree), but not in any mid-slope habitats.

Infrequent species

Although no analyses could be performed on five species, the data suggest increasing presence of *R. tenuius* and persistence of the other four species (Table 2).

Replacement dominants

'Cryptic *Rytidosperma*' declined in dominance ranking in 74% of the plots where it was initially a dominant (i.e. a biomass ranking of 1, 2 or 3) in 2005. It did not become more dominant in any plot (Table S2). Dominance was greatest in the open grassland on the upper slopes, where *R. erianthum-R. monticola*, *R. auriculatum*, *R. carphoides* and *R. pilosum* formed short swards. These areas also tended to retain these species as a dominant over the 15 years (Fig. 4), with the exception of *R. pilosum*, which had disappeared from the upper slopes by 2020.

Where dominance was lost, 'cryptic *Rytidosperma*' was most frequently displaced or outgrown by three life-forms (Table S2, 6):

- (a) Native perennial graminoids – e.g. *Lomandra filiformis* (21 plots), *Aristida ramosa* (5 plots),

(a) 2005



(b) 2010



(c) 2020



Fig. 4. General view of open habitat on upper slopes at (a) the commencement of the survey period (2005), (b) 5 years and (c) 15 years after removal of sheep grazing. This area was the least productive part of the landscape studied. It remained the most heavily grazed area, and was where *Rytidosperma* best retained its dominance. During the study, *Lomandra filiformis* and *Melicrus urceolatus* shrubs were becoming more frequent dominants across the landscape and their presence at this site is evident in the foreground in 2020.

- (b) Annual exotics – e.g. *Trifolium* spp. (8 plots), *Briza maxima* (7 plots), *Vulpia* spp. (5 plots), *Hypochoeris glabra* (4 plots), *Aira* spp. (4 plots).
 (c) Native shrubs – e.g. *Melicrus urceolatus* (7 plots), various Fabaceae (12 plots).

Although the ‘cryptic *Rytidosperma*’ species tended to retain their constancy in the plots, there is evidence of decline that is both relative (as assessed by ranking) and absolute. There was an obvious reduction in plant numbers observed when sampling in the field, consistent with the reduced number of flowering plants available for sampling (Table 7), particularly in 2013 (the driest sampling year) and 2016 (the wettest sampling year, Fig. 1).

Discussion

Regional representation

Of the 17 lowland *Rytidosperma* species occurring on the southern tablelands, 12 were identified in this study (Table 8). These are the same 12 species recorded in a survey of 1300 ha with a similar management history, i.e. long-term livestock grazing with limited pasture improvement (McIntyre *et al.* 2010). These two sites are 20 km distant and share vegetation types (a mosaic of southern tableland grassy woodland and sclerophyll forest). In a survey of 68 natural and improved pastures in an adjacent district centred 50 km NE of the study site, Munnich *et al.* (1991) recorded nine species of *Rytidosperma*, representing a subset of those reported here. Relative abundances were comparable to those at our study site, with the exception of our common *R. erianthum* not being recorded by Munnich *et al.*, whereas *R. monticola* was frequent. Difficulties delineating these species have been experienced by other researchers in the region (D. L. Garden, pers. comm.) and it is possible that *R. erianthum* material was differently interpreted by Munnich *et al.*

Ecological differentiation within the genus

Within the study site, the variables ‘habitat’ and ‘slope position’ represented a readily discernible categorisation of the landscape, integrating environmental (soil attributes, soil moisture) and biotic factors (nutrients relocated by livestock, eucalypt presence and identity). On average, one or both of these variables accounted for 38% of the variation in the grasses analysed (range 20–58%; Tables 3, 4). The strongest differentiation was between the sclerophyll forest (dominated by *R. pallidum* on all slope positions) and the remaining habitats (camp, drainage, open, tree). The latter habitats represented variations within the grassy woodland vegetation type, and supported most of the ‘cryptic *Rytidosperma*’ populations. Within the grassy formation, we

Table 6. Life-forms replacing cryptic *Rytidosperma* at sites where it was a previous dominant.

Site	Number of occurrences of cryptic <i>Rytidosperma</i> being out-ranked				
	Annual exotics	Perennial exotics	Native shrubs	Native forbs	Native graminoids
Open, upper slope (eight sites)	10	2	5	0	9
Open, mid slope (eight sites)	9	3	7	2	12
Open, lower slope (four sites)	5	0	3	2	4
Under tree, upper slope (three sites)	2	1	4	0	6
Under tree, lower slope (three sites)	1	1	1	1	8
Drainage line (three sites)	4	2	1	0	5
Sheep camp (three sites)	8	2	0	0	3
All occurrences	39	11	21	5	47

Data are summarised from the 32 sites where *Rytidosperma* was a dominant (ranked 1–3) in any of the five surveys (detailed in Table S2). The species that displaced cryptic *Rytidosperma* from a dominance ranking of either 1, 2 or 3 between any two surveys were classified by life-form and origin, and tallied over all 32 sites.

Table 7. Number of *Rytidosperma* inflorescences obtained in samples.

Parameter	Year of survey (number of sites present)					
	2005 (n = 61)	2010 (n = 59)	2013 (n = 56)	2016 (n = 56)	2020 (n = 56)	Sum of all years (n = 288)
Potential number of inflorescences	610	590	560	560	560	2880
Actual number collected	480	450	313	301	415	1959
Percentage of potential	79	76	56	54	74	68

Expressed as a percentage of the potential number of inflorescences that could have been collected from each plot in which 'cryptic *Rytidosperma*' was present (we aimed to collect one inflorescence from each of up to 10 plants per plot when available). *Rytidosperma pallidum* was not included in these samples.

detected subtle patterns of habitat preference among individual species.

Aspect was significant for the 'cryptic *Rytidosperma*' group, and one species (*R. caespitosum*) demonstrated a preference for protected eastern- and southern-facing slopes. Few ground-cover variables proved important once habitat and slope position were taken into account. Open sites on upper slopes had the highest proportion of rock cover and lowest litter cover, but 'cryptic *Rytidosperma*' and '*R. erianthum*–*R. monticola*' were positively associated with rock cover within those sites. Although *R. carphoides* differed from the group broadly in not being significantly associated with upper slopes, it was linked to the low litter cover that is characteristic of the open upper slope habitats. On the whole, tree canopies were not a favoured habitat, although on the less protected upper slopes, 'cryptic *Rytidosperma*' was as abundant under the widely scattered trees as in the open (Fig. 2). Only *R. caespitosum* and *R. pilosum* tolerated tree canopies on the mid and/or lower slopes (Table 5, Fig. 2).

Synthesis of published observations of *Rytidosperma* growth rates and habitat through the C–S–R strategy framework (Grime 1979; Table 8) suggests that the species of the southern tablelands cover one primary strategy, stress tolerance (e.g. *R. pallidum*), as well as the four secondary strategies (S–R, C–R, C–S, C–S–R). Competitive ruderals (C–R) are fast-growing, grazing-tolerant species of

productive habitats and were absent from the study site, with the exception of *R. racemosum*, which was uncommon, and largely restricted to remnant sheep camps. The species hypothesised to have the S–R and C–S–R strategies, based on published information of stature, growth rates, grazing tolerance and habitat productivity, were the most common species in our study (Table 8). These largely matched our own data, in which the S–R species occupied the most stressed sites (open, upper slopes, low litter cover, rocky), and the putative C–S–R species extended further into the more productive mid and lower slopes. Three of the southern tableland species 'missing' from our survey are reported in the literature to be associated with fertile soils of generally high pH (*R. fulvum*, *R. bipartitum* and *R. richardsonii*; Table 8), a sufficient reason for their absence from the predominantly infertile, acidic soils of the study site.

Decline and persistence

The relatively heavy sheep grazing on the study site in the 25 years preceding livestock removal would have been favourable to *Rytidosperma* generally (Langford et al. 2004; Dorrough et al. 2011), as reflected in the dominance of 'cryptic *Rytidosperma*' in the first 2005 survey, when it was ranked 1, 2 or 3 in 52% of the grassy woodland sites. By 2020, this proportion was reduced to 12%. This loss of dominance was also evident as significant declines in

Table 8. Ecological summary of *Rytidosperma* spp. occurring on the southern tablelands of NSW.

Literature summary of ecological preference	Observations this study
<i>R. tenuius</i> (Strategy: S) Restricted to a narrow range of undisturbed, unfertilised habitats on low-fertility soils. ^{1,2}	Uncommon – no decline Dry sclerophyll forest and woodland upper slopes; increased from one to four sites.
<i>R. pallidum</i> (Strategy: S) Highly unpalatable and grazing intolerant. Large statured. ^{2,3,5} Restricted to unfertilised, low-fertility acid soils, associated with dry sclerophyll forest. ^{3,4,5}	Common – no decline Restricted to dry sclerophyll forest and beneath trees; highly unpalatable and rarely grazed.
<i>R. longifolium</i> (Strategy: S) Open forest on rocky sites, ^{4,27} sandy soils, ⁴ rarely in damp places. ⁴	Not recorded
<i>R. leaeve</i> (Strategy: S) Tends to be associated with intact native vegetation rather than pastures and agricultural development. ^{1,2,6} Wide range of soils, grazing levels and habitats tolerated. ^{6,7,8}	Rare – no decline Fugitive species in the range of grassy woodland habitats, absent from sheep camps, dry sclerophyll forest.
<i>R. auriculatum</i> (Strategy: S–R) Short-statured species of low-fertility sites with wide grazing tolerance. ^{6,10} Slow-growing and not responsive to P or N additions. ^{9,10} Associated with sun moth. ¹¹ Intolerant of fertilised pasture. ² On scalped, disturbed and eroded roadsides. ⁵ Palaeozoic sediments. ¹¹	Moderately common – no decline Open, upper slopes and eroded edges of drainage lines. Absent from dry sclerophyll forest and beneath trees.
<i>R. carphoides</i> (Strategy: S–R) Short-statured species of low-fertility sites with wide grazing tolerance. ^{6,10} Slow-growing and not responsive to P or N additions. ^{9,10} Associated with sun moth. ¹¹ Intolerant of fertilised pasture. ^{2,5} Tolerates range of pH. ^{7,8} Palaeozoic sediments. ¹¹	Moderately common – declined Strongly associated with open sites, and low litter cover. Absent from dry sclerophyll forest.
<i>R. erianthum</i> (Strategy: S–R) Slow-growing species on low-fertility, acid soils ^{5,7,9,13} with higher fertility also tolerated. ^{10,12,15} In pastures ⁵ with moderate grazing tolerance. ¹⁵ Varied but dry habitats, with distribution centred on NSW southern tablelands and Victoria, with wide range of habitats. ^{1,4,13}	Common – declined (analysed as ' <i>R. erianthum</i> – <i>R. monticola</i> ') Strongly associated with upper slopes in open, rocky areas, beneath trees and in drainage lines. See also <i>R. monticola</i> .
<i>R. monticola</i> (Strategy: C–S–R) Associated with sandy, granitic ⁴ and acid soils. ^{1,7} Range of fertilities ^{2,6} and grazing levels. ⁶ Exposed, disturbed habitats. ⁴	Less common than <i>R. erianthum</i> but with many intermediate forms present, these two species had to be merged in the analyses.
<i>R. setaceum</i> (Strategy: C–S–R) Medium-sized species with moderate growth response to added P. ⁹ Tolerates a range of grazing levels and pH. ^{5,6,7,8,13,14} Seems to be most consistently associated with dryness, natural pastures and unfertilised sites. ^{5,6,8,13,14} Some occurrences in high fertility. ¹²	Rare – no decline Intermittently recorded at two open sites.
<i>R. pilosum</i> (Strategy: C–S–R) Wide range of soils and habitats ^{1,4,8} , from unfertilised ^{5,6} to fertilised pastures ² , but no cultivation. ¹ Moderate stature and growth rate and unresponsive to high P. ⁹ Wide grazing tolerance ¹⁶ but prefers moderate-heavy grazing. ^{6,15,16} Associated with acid soils, ⁷ cooler climate ¹ and the NSW southern tablelands. ^{2,17}	Very common – major decline All slope positions in open and under trees. Absent from dry sclerophyll forest, and lower drainage lines. Some presence in sheep camps.
<i>R. caespitosum</i> (Strategy: C–S–R) Extremely wide range of habitats ^{4,8} , soils ^{8,11,13} and grazing levels ^{6,18,19} . Moderate tolerance of acidity, ^{7,22} grazing ^{15,21} and fertility. ^{6,15} Different ploidy between and within populations. ^{20,23} Morphology and flowering variable over range. ²³ More common on NSW slopes and plains than tablelands. ^{1,17}	Moderately common – declined Mid and upper slopes in open, drainage lines, and under trees. Not in dry sclerophyll forest or sheep camps. On south- and east-facing slopes.

(Continued on next page)

Table 8. (Continued).

Literature summary of ecological preference	Observations this study
<i>R. richardsonii</i> (Strategy: C–S–R) Medium-sized ²⁴ fast-growing species ⁹ responsive to higher P ^{1,9} and N ²⁴ or not. ¹⁰ On poorly drained ¹ , lower slopes ¹ , and moderately fertile soils of higher pH. ^{1,7} Range of grazing levels and other disturbances tolerated. ¹	Not recorded
<i>R. duttonianum</i> (Strategy: C–S) Medium-sized ²⁴ fast-growing species that is variably responsive to P ⁹ and pasture fertilisation. ^{6,10,12,15} Variable grazing response. ^{6,15} Prefers acidic soils ^{5,7} and favours poor drainage. ^{4,5}	Not recorded
<i>R. fulvum</i> (Strategy: C–R) Productive, fast-growing ²⁵ species on high-fertility soils. ^{4,13} Responsive to increasing nutrients. ^{9,10,24} On heavy soil of higher pH. ^{4,7} Warmer and wetter sites within central-western NSW. ¹³ Grazing insensitive. ⁶	Not recorded
<i>R. bipartitum</i> (Strategy: C–R) Tall-growing species of fertile soils ^{1,4,22} and fertilised sites ¹ with wide grazing tolerance. ¹ Productive, high quality forage ²⁵ , warm temperatures. ¹³ On sheep camps, eroded, trampled, cultivated sites. ^{1,5}	Not recorded
<i>R. racemosum</i> (Strategy: C–R) Tall, fast-growing productive grass ^{9,10,28} sometimes associated with higher fertility levels ^{2,5,6,29} higher pH ^{5,7} and good drainage ^{1,11} . On all parent materials ^{1,26,22} associated with tree cover ^{1,30} . Grazing insensitive ^{1,5,6}	Uncommon – no decline Main wallaby grass at all sheep camp sites.
<i>R. penicillatum</i> (Insufficient ecological information) Associated with grassland and open woodland. ⁴	Uncommon – no decline Recorded only in lower drainage lines.

Findings reported by other authors are compared with those observed in this study. Species are ordered by their ecological strategy (Grime 1979), as determined from measurements of growth characteristics, habitat and morphology reported in the cited literature. Alpine species (*R. indutum*, *R. gracile*, *R. nudiflorum*) are not included. Note that observations for rare and uncommon species in this study were not supported by statistical analysis. References cited: (1) Scott and Whalley (1982); (2) Munnich et al. (1991); (3) McIntyre et al. (2010); (4) PlantNET (<http://plantnet.rbg.gov.au>); (5) Doing (1972); (6) Dorrough et al. (2011); (7) Dowling et al. (1996); (8) Fensham (1989); (9) Waddell et al. (2016); (10) Bolger and Garden (1999); (11) Benson (1994); (12) Bryant et al. (2017); (13) Waters et al. (2009); (14) Price et al. (2010); (15) Hamilton (2001); (16) Biddiscombe (1953); (17) Prober and Thiele (2004); (18) Austin et al. (1981); (19) Williams (1969); (20) Abele (1959); (21) Hodgkinson (1976); (22) Williams (1979); (23) Waters et al. (2011); (24) Harradine and Whalley (1978); (25) Robinson and Archer (1988); (26) Prober et al. (2002); (27) Linder (2005); (28) Robinson (1976); (29) Robinson and Dowling (1976); (30) Chilcott et al. (1997). S, stress-tolerant strategy; R, ruderal strategy; C, competitive strategy; P, phosphorus; N, nitrogen.

percentage of total biomass for ‘cryptic *Rytidosperma*’, *R. caespitosum*, *R. carphoides*, *R. pilosum* and ‘*R. erianthum*–*R. monticola*’. Nonetheless, presence in the plots (constancy) did not decline, except in the case of *R. pilosum* (Fig. 3). A ranking of less than three indicates an average representation of less than 3% of the total biomass in grassy vegetation (Scott 1986), so that regardless of the variation in total biomass over the survey period, these changes in rankings represent proportionately very large changes in abundance. That the populations in the study declined over the 15 years was very evident from ongoing and frequent field observations, and was supported by the reduced availability of flowering individuals in the 2013 and 2016 surveys (Table 8). We attribute the proportional decline (percentage total biomass) to the growth of native shrubs and native perennial graminoids, and pulses of annual exotic growth in wet seasons (as noted by Langford et al.

2004), and conclude that these were having a competitive effect on the reproductive output of *Rytidosperma*.

When macropod-only grazing replaced sheep and macropod grazing after 2004, the grazing pressure became lighter and the following broad changes could be expected: reduced trampling (Albon et al. 2007), a reduction in the pool of rapidly recycled nutrients (Ruess and McNaughton 1987), and a shift in species abundance in favour of more stress tolerance and its related conservative leaf economics, expressed as higher leaf dry matter content or reduced specific leaf area (McIntyre 2008; Pierce et al. 2017). These trends were evident in the reduced dominance of ‘cryptic *Rytidosperma*’ with S–R and C–S–R strategies, the lack of decline in the stress tolerators (S strategy, including *R. pallidum*) and the increasing dominance of species with high leaf dry matter content (LDMC), most notably *Lomandra filiformis*, *Aristida ramosa*, *Melichrus urceolata*, and

Fabaceae sub-shrubs (see McIntyre 2008). These represent typical strategies for the site overall, whereas local-scale factors such as disturbance, fine-scale soil patterns, and biotic interactions enable a range of species with different traits to co-exist (Bruehlheide *et al.* 2018). For example, the competitive ruderal species *R. racemosum* persisted in sheep camps, where historical nutrient inputs of sheep dung and urine remained high.

Implications for conservation

The removal of livestock in the interests of biodiversity conservation has resulted in the increased representation of native shrubs and graminoids in the ground layer at the study site. A wider survey of multiple sites under different land uses in the district suggests that this is a general response that could be expected if fertiliser inputs cease and grazing is removed (McIntyre 2008). This increase in structural diversity of the ground layer both reflects and promotes more varied grazing intensities spatially, which has benefits for both faunal and plant diversity (McIntyre *et al.* 2003; Howland *et al.* 2014, 2016).

With their tolerance for grazing and drought, *Rytidosperma* spp. overall appear robust and able to persist in the wider landscape, providing existing natural, low-input pastures are not replaced by cultivation and heavy fertiliser use (e.g. see McIntyre 2008). In that sense, their decline under conservation land use may not be an issue. However, we have shown that conservation management may disadvantage some short-statured species with a grazing requirement, including species with which the endangered golden sun moth has been associated (*R. erianthum*, *R. auriculatum*, *R. carphoides*, *R. setaceum*; O'Dwyer and Attiwill 1999). In our study, these species occurred on open sites in the upper slopes, the habitat in which *Rytidosperma* dominance was best retained. We attribute this to the preferential use of this part of the landscape by eastern grey kangaroos who have largely maintained these areas as grazing lawns over the 15 years (Fig. 4). In other conservation settings, grass, tree and shrub encroachment may have a greater impact on these short-statured species when livestock are removed. Managers aiming to conserve golden sun moth populations in reserves need to be aware of the grazing requirements of the food plants that nurture the moth larvae, and manage total grazing appropriately, whether it be macropod, livestock or feral species.

Two species reported in our study (*R. tenuius* and *R. penicillatum*; Table 8) are of unknown conservation status. Despite wide geographical ranges, they are not widely reported in the literature (Table 8) and appear to have somewhat restricted habitats. Without random field collection and subsequent microscopic examination, they would not have been detected at the study site or recorded in the surveys. Our method of sampling inflorescences, and determining the proportions of the different species present,

could be applied to any method in which *Rytidosperma* abundance is collectively assessed. It is based on the assumption that flowering activity is proportionate to the abundance of that species which, while not ideal, represents a significant advance on the more common practice of grouping several disparate species into a single category.

Supplementary material

Supplementary material is available [online](#).

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Author affiliations

^ACSIRO Land and Water, GPO Box 1700, Canberra, ACT 2601, Australia.

^BAustralian National University, Fenner School of Environment and Society, Canberra, ACT 0200, Australia.