# Buffel grass ( Cenchrus ciliaris ) eradication in arid central Australia enhances native plant diversity and increases seed resources for granivores

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RESEARCH ARTICLE

# Buffel grass (*Cenchrus ciliaris*) eradication in arid central Australia enhances native plant diversity and increases seed resources for granivores

Boyd R. Wright[1,2,3]  |  Peter K. Latz[3]  |  David E. Albrecht[4]  |  Roderick J. Fensham[5,6]

[1]Department of Botany, School of Environmental and Rural Science, The University of New England, Armidale, NSW, Australia

[2]School of Agriculture and Food Science, University of Queensland, St. Lucia, Qld, Australia

[3]Department of Land Resource Management, The Northern Territory Herbarium, Alice Springs, NT, Australia

[4]Australian National Herbarium, Centre for Australian National Biodiversity Research, (a joint venture between Parks Australia and CSIRO), Canberra, ACT, Australia

[5]School of Biological Sciences, University of Queensland, St. Lucia, Qld, Australia

[6]Queensland Herbarium, Toowong, Qld, Australia

**Correspondence**
Boyd Wright, Department of Botany, School of Environmental and Rural Science, The University of New England, Armidale, NSW 2350, Australia.
Email: bwright4@une.edu.au

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## Abstract

**Questions:** Buffel grass (*Cenchrus ciliaris* L.) is a drought-adapted invasive plant that has become a serious environmental weed in many arid and semi-arid systems. This paper examined whether eradication of buffel grass infestations: (i) increases frequency, richness and diversity of native vegetation and seed bank pools; and (ii) improves availability of seed resources for granivores.

**Location:** Alluvial ironwood/corkwood woodlands in arid central Australia.

**Methods:** We assessed differences in floristic and seed bank composition between buffel-infested sites and sites where buffel grass had been eradicated ca. 12 years previously. Plant species frequency data from nested-quadrat sampling were amalgamated into plant functional groups to examine their relationship to buffel treatment. A seed flotation method was employed to: (i) assess seed bank composition of functional groups at eradicated vs. infested sites; and (ii) test whether the mass of seeds available for granivores was higher at buffel-free sites.

**Results:** Buffel-eradicated sites supported richer and more diverse vegetation and seed banks across all functional groups except perennial grasses. The effect was strongest for perennial forbs, annual/short-lived forbs, and annual/short-lived grasses. The overall mass of seeds of non-buffel grass species was ca. 10-fold higher at buffel-removed sites. Numbers of seeds of species in the 0.001–0.009 9 g and 0.000 1–0.000 99 g size classes, both of which contain species with seeds consumed by granivores, were ca. 20- and 14-fold higher respectively at buffel-removed sites.

**Conclusions:** Buffel grass removal at localised scales provides islands of habitat with improved opportunities for native plant re-establishment and abundant foraging resources for granivores. Future research must disentangle the relative importance of dispersal vs. residual seed banks for community restoration after buffel grass invasion. Extended delays in eradication could allow seed bank reserves to deteriorate to a state that no longer permits regeneration.

**KEYWORDS**
arid vegetation, dispersal, disturbance ecology, grass-fire feedbacks, invasive plant, seed predation, seed bank

# 1 | INTRODUCTION

Introductions of invasive grass species have driven reductions in biodiversity in many arid and semi-arid ecosystems world-wide (DiTomaso, 2000; Bonney et al., 2017; Farrell and Gornish, 2019). In addition to displacing native species, exotic grass invasions can impair ecosystem function and cause major habitat changes by altering microclimates, changing disturbance regimes, and disrupting ecological interactions (e.g. interspecific mutualisms) among organisms (D'Antonio and Vitousek, 1992; Farrell and Gornish, 2019). Despite massive resource investments to control invasive plants in many arid areas, there remains inadequate documentation of restoration outcomes on native vegetation and seed banks in dryland regions (D'Antonio and Vitousek, 1992; Fairfax and Fensham, 2000; D'Antonio and Meyerson, 2002).

Buffel grass (*Cenchrus ciliaris* L., syn. *Pennisetum ciliare* (L.) Link), a perennial native of south and east Africa and southern Asia, is an invasive drought-tolerant grass that poses a serious threat to biodiversity in many arid and semi-arid ecosystems (Marshall et al., 2012; Olsson et al., 2012; Fensham et al., 2013, 2015, 2016; Bracamonte et al., 2017). Originally planted as a pasture grass in Australia and the Americas in the early 19th century, buffel grass has since aggressively invaded many native land systems that are well beyond pastoral zones (Tix, 2000; Clarke et al., 2005; Eyre et al., 2009; Cook and Grice, 2013). Several competitive traits promote buffel grass invasion into new habitats: its ability to establish and grow under low-rainfall conditions (Hodgkinson et al., 1989); prolific seed production with or without outcrossing (i.e. buffel grass is agamospermic) (De Lisle, 1963; Franks, 2002); the ability to chemically suppress the growth of native species via the leaching of allelopathic chemicals into soils (Cheam, 1984); bristly burrs that are easily dispersed over long distances by wind, water and/or animals (Goldsmith et al., 2008; Fensham et al., 2013); and the capacity to capture nutrient resources and rapidly regenerate from a deep root system after disturbance (Stevens and Fehmi, 2009; Young and Schlesinger, 2014).

Buffel grass invasion can have major impacts on ecological processes and population dynamics of organisms that occupy invaded systems. Typically, invasion leads to the capture of large proportions of light, water and nutrient resources by buffel grass plants. This results in competitive displacement of native vegetation and a general reduction in plant diversity (Saucedo-monarque et al., 1997; Jackson, 2004, 2005; Stevens and Fehmi, 2011; Castellanos et al., 2016; Farrell and Gornish, 2019). Invasion can also lead to negative impacts on wildlife, causing reductions in dietary variety, altering wildlife foraging behaviour, and changing the structure of habitats (Franks, 2002; Smyth et al., 2009; Young and Schlesinger, 2014; Bonney et al., 2017; Dittmer and Bidwell, 2018). Fire regimes can also be altered by buffel grass invasion, as the biomass and continuity of fuels generally increases after invasion (Albrecht and Pitts, 2004; Clarke et al., 2005; McDonald and McPherson, 2011). Consequently, buffel-invaded systems often burn hotter and more regularly than native vegetation, and this can have detrimental effects on biodiversity in systems not adapted to high intensities or frequencies of pyric perturbation (Miller et al., 2010; McDonald and McPherson, 2011).

Despite the abundant literature inferring that buffel grass removal should be implemented where biodiversity maintenance is a management objective (Franks, 2002; Friedel et al., 2006; Grice et al., 2013), there is little empirical evidence to demonstrate that eradication helps native vegetation communities to recover (Farrell and Gornish, 2019). Additionally, it is unclear whether ecosystem restoration subsequent to buffel grass invasion can restore food resources for the diverse granivorous ant, bird and small-mammal fauna that typically occupy arid vegetation communities (Morton 1985; Smyth et al., 2009; Grice et al., 2013; Young and Schlesinger, 2014). Among arid fauna assemblages, granivores may be particularly negatively affected by buffel grass invasion as reductions in the variety and density of seeds in seed banks would be expected to accompany post-invasion declines in plant diversity. Nevertheless, there are currently no empirical data to verify this hypothesis, and there is a dearth of literature quantifying the impacts of buffel grass invasion on native seed banks. Addressing these research shortfalls is urgently needed, given that the distribution of buffel grass infestation is still expanding, and that buffel grass eradication is being attempted in many arid and semi-arid conservation reserves in North America and across inland Australia (Schlesinger et al., 2013; Dittmer and Bidwell, 2018; Young and Schlesinger, 2018; Farrell and Gornish, 2019).

The objectives of the current study were to quantify the effects of buffel grass eradication on extant vegetation and soil-borne seed banks in alluvial woodland habitat in arid central Australia. Specifically, we aimed to test the hypotheses that buffel grass eradication would: (i) lead to increased native plant species richness and diversity across plant growth forms; (ii) replenish native seed bank pools; and (iii) increase the mass of seeds of species in seed size classes known to be consumed by granivores.

# 2 | METHODS

## 2.1 | Study site

All sites were in alluvial woodland habitats at the base of the Ilparpa Range (also known as the Blatherskite Range), 10–13 km southwest of Alice Springs, central Australia. The average annual rainfall of the region is 282.8 mm, with the majority falling over summer months (December–February) (Australian Government Bureau of Meteorology 2020 [Alice Springs Airport annual rainfall records 1941–2020]). Summers are typically hot, with mean daily maximum and minimum temperatures during the warmest month (January) being 36.5 and 21.6°C, respectively (Australian Government Bureau of Meteorology 2020). Winters are cold, with mean maximum and minimum temperatures during the coldest month (July) being 19.9 and 4.0°C, respectively (Australian Government Bureau of Meteorology 2020). The predominant land

use in the area is rural residential properties (generally 20 acres) with adjoining conservation reserve and uncommitted crown (public) land. Prior to the 1980s, the area was part of a large pastoral lease and much of the area had apparently been severely overgrazed during this period (Clarke et al., 2005).

A space-for-time substitution study (Pickett, 1989) was conducted to compare alluvial woodland vegetation that was currently infested with buffel grass with vegetation that had been subject to buffel grass eradication measures ca. 12 years previously. The study design allowed for inferences to be made about the way alluvial woodland communities regenerate after buffel grass eradication by assuming that between-site environmental differences were minimal. This assumption was tested via soil sampling and site assessment (see section 2.2 *Vegetation* and Appendix S1). The specific sampled woodland type is recognised as ironwood (*Acacia estrophiolata* F.Muell.) and fork-leaved corkwood (*Hakea divaricata* L.A.S.Johnson) on alluvial flats (Albrecht and Pitts, 2004). Aside from buffel grass, the extant vegetation and seed banks at all sites were completely free of non-native plant species.

Buffel grass eradication measures at the buffel-removed sites were conducted using two methods. At the Purdie site, buffel grass tussocks were removed manually using crow bars and shovels in ca. 2005/6. At the Albrecht block and the Latz northern and Latz southern sites, buffel grass was killed in ca. 2005 via the application of herbicide (glyphosate) and plants were left to decompose. Ongoing management had occurred at all sites after removal, with buffel grass seedlings removed or spot-sprayed with herbicide when they emerged. It is acknowledged that the differing removal treatments applied by the owners of the different blocks was a limitation that may have influenced vegetation composition early in the post-eradication period. Nevertheless, after ca. 12 years (i.e. in 2017, when the sampling for our study occurred), it is likely that buffel grass eradication per se would have been the overriding effect on native vegetation composition, rather than the type of buffel control measure originally employed. The buffel-infested sites included two residential blocks, a nature reserve and a recreation reserve on crown land. In 2014, two of the six plots on the recreation reserve were observed to have been slashed (i.e. mowed). Despite introducing an unintended disturbance to these plots, the plots were retained in the analysis as the buffel grass appeared to have recovered community dominance rapidly after the slashing (BRW pers. obs.).

## 2.2 | Vegetation

To examine changes in plant community composition following buffel eradication, field surveys were conducted in June 2017 at the previously described buffel-infested and buffel-removed sites. Species nomenclature of vegetation recorded during surveys followed Albrecht et al. (2007) and was updated for some species using the Australian Plant Census (2020) (Appendix S2 and S3). Four replicate sites were selected to represent buffel-infested localities and four were selected to represent buffel-cleared areas

(hereafter referred to as infested and removed sites). The sites were chosen based on habitat similarity and the willingness of landholders to allow ecological studies to take place on their land. At each of the eight sites, six sampling plots were randomly selected, resulting in 48 plots in total.

Rainfall during the preceding summer was 203.4 mm from Dec 2016 to Feb 2017 (Australian Bureau of Meteorology, 2020), which provided good conditions for growth and flowering (and seeding) of species that are summer-germinating/growing. The vegetation composition of the plots was assessed using the nested-quadrat technique of Morrison et al. (1995). For this technique, a square compound quadrat was employed that comprised eight concentric square subquadrats of the following areas: 2, 4, 8, 16, 32, 64, 128, and 256 $m^2$. The centroid of the compound quadrat was randomly located, and the vegetation of subquadrats was surveyed progressively from the smallest to the largest subquadrat. A species was allocated a "frequency of occurrence" score within the compound quadrat based on the number of subquadrats that contained part of the basal and above-ground part of at least one plant of that species. Plants were grouped according to six combinations of growth form and longevity: perennial forbs, annual/short-lived perennial forbs (i.e. lifespan <2 years), perennial native grasses, annual/short-lived perennial native grasses (i.e. lifespan <2 years), buffel grass and shrubs/trees. The species that were recorded, their growth forms and longevity are given in Appendix S2.

Soil samples were collected from each plot to be used in subsequent multi- and univariate analyses to account for potentially confounding edaphic effects on vegetation composition (see seed bank extraction section below for soil sampling methodology). These samples were analysed for sand, silt and clay sediment fractions in a laboratory at the Botany Department, University of New England. This analysis was done by agitating soil samples in a slurry with de-ionised water in test tubes for 5 min and then allowing them to settle for 24 hr. The relative proportions of sand, silt and clay were then assessed by measuring the heights of each soil component in the test tubes. No statistical differences in mean sand, silt or clay content were observed between buffel-infested and buffel-removed sites, which provided evidence that the assumption of between-site habitat similarity was robust (Appendix S1).

## 2.3 | Seedbanks

During the vegetation sampling, 10 cm × 5 cm deep-soil cores were extracted at each plot using a 5 cm diameter soil corer (i.e. ca. 980 $cm^3$ soil were collected per plot). The cores were collected by randomly placing the centre of a 20-m transect within the nested quadrats of the vegetation surveys and then sampling soil cores at 2-m intervals along the transect. Following collection, the soil samples were bulked and then bagged and stored in polyethylene bags. Seed extraction from the samples took place in March 2019 using the flotation method of Malone (1967). The bulked samples were first split using a soil cutter into 0.5 kg representative samples. The samples were then immersed

in potassium carbonate solution (140 g potassium per 200 ml of deionised water) and stirred vigorously for 30 s using a plastic spatula. The solution was then left to sit for 5 min and the floating organic matter was decanted through a series of fine sieves (1, 0.5 and then 0.1 mm). The extracted material was then washed under running water and dried overnight in a drying oven at 60°C. Extraction and identification of seeds from the organic material was performed using a stereo microscope and a propagule reference set. Viability of smaller seeds (<1 mm diameter) was assessed by applying light pressure to the seeds with forceps. If the seeds resisted this pressure, they were deemed viable. Larger seeds were cut open using a scalpel and examined for the presence of healthy white endosperm.

Following extraction and identification of seeds, ten seeds of each species were weighed out using an analytical lab balance that was accurate to the nearest 0.000 01 g. Where less than 10 seeds were extracted from the soil samples, additional seeds were obtained from a reference set of seeds collected by BRW. From these replicate seed batches, the average mass of individual seeds was calculated for each species. Where the dispersed propagule of a species consisted of a woody fruit (e.g. those of *Tribulus* and *Sclerolaena* spp.), the fruits were dissected, and the enclosed seeds were extracted and weighed. Following weighing, seeds were assigned to the following seed size classes: >0.01 g (or "large"), 0.001–0.009 9 g (or "medium"), 0.000 1–0.000 99 g (or "small"), and 0.000 01–0.000 099 g (or "very small"). Buffel grass was given its own category because when it invades communities it dominates habitats and we were interested to determine how much food resources for granivores are provided by buffel grass following invasion. The mass of seeds within each size class at each plot was calculated by grouping the seeds into classes and then summing the product of species-specific seed masses and the number of seeds of each species at each plot. This figure was then scaled up to give an approximation of the mass of seeds in each size class at the hectare scale (kg/ha).

## 2.4 | Statistical analysis

Multivariate analyses in CANOCO (Ter Braak and Smilauer, 2012) were used to examine the effects of buffel grass eradication on floristic composition and seed banks. Unconstrained ordinations using Detrended Correspondence Analysis (DCA) were used over Principal Components Analysis (PCA) as gradient lengths were more than three. Species variables for both the vegetation and seed bank analyses were ordinated using untransformed frequency scores at plots. Rare species were down-weighted. Abundances of the six floristic and seed bank growth form/longevity classes were plotted as supplementary variables. The supplementary variables did not contribute directly to the calculation of the ordination axes, but their relationship to plots could be interpreted from their position on the axes.

The effects of buffel grass eradication and buffel grass density on floristic and seed bank abundance, richness and diversity

(Shannon) were assessed using linear models (i.e. ANOVA) and generalised linear models (GLM) in R (R Core Team 2018). Prior to analysis, data exploration was carried out following the protocol of Zuur et al. (2010). Buffel grass eradication was treated as a categorical variable with two levels — removed and infested. Poisson GLMs were initially used for the abundance and richness analyses as the data sets for these analyses comprised count data. When initial modelling indicated underdispersion, quasi-poisson GLMs were used to account for the underdispersion (Zuur et al., 2013). When initial modelling indicated overdispersion, negative binomial models were used (Zuur et al., 2013). ANOVA was used for the vegetation and seed bank diversity analyses as the data sets for these analyses comprised continuous data. Following all analyses, graphical model validations were carried out.

For the seed mass data set, a generalised least squares (GLS) analysis was applied because initial general linear models showed heteroscedastic residuals (evident on plots of standardised residuals vs. the seed class covariate). Taking a GLS approach meant that a heterogeneous variance structure could be specified in the model, thereby allowing for variable residual spread among the different seed classes. Post-hoc tests using Bonferroni corrections were conducted using the emmeans package (Lenth, 2016) to assess the significance of differences in seed masses between the various seed classes across infested and removed plots.

Soil parameters (sand, silt, and clay content) were analysed using ANOVA. These analyses were conducted to determine whether underlying between-site edaphic differences could exist that could be driving vegetation dynamics. Data exploration and model validation procedures for the soil analyses followed the protocols used for the other ANOVA analyses.

## 3 | RESULTS

### 3.1 | Vegetation

Buffel grass eradication had a strong effect on plant species composition, with the first axis of the vegetation DCA strongly correlated with removal treatment and accounting for 19.98% of variation in the data set. From the biplot of this analysis (Figure 1a), there was a clear separation of buffel-infested and buffel-removed sites, indicating strong floristic differences between the two treatments. Also from the biplot, the abundance of all plant growth forms except perennial grasses and buffel grass were strongly associated with buffel-free sites (Figure 1a).

From the univariate vegetation analyses, buffel-removed sites had significantly higher abundance (deviance = 107.04, $df = 1$, $p < 0.001$), richness (deviance = 107.47, $df = 1$, $p < 0.001$) and diversity ($F_{1,46} = 93.87$, $p < 0.001$) of perennial forbs; higher abundance (deviance = 124.06, $df = 1$, $p < 0.001$) and richness (deviance = 43.94, $df = 1$, $p = 0.018$) of annual/short-lived perennial forbs; higher abundance (deviance = 145.14, $df = 1$, $p < 0.001$) and richness (deviance = 110.39, $df = 1$, $p < 0.001$) of annual/short-lived perennial grasses; and higher
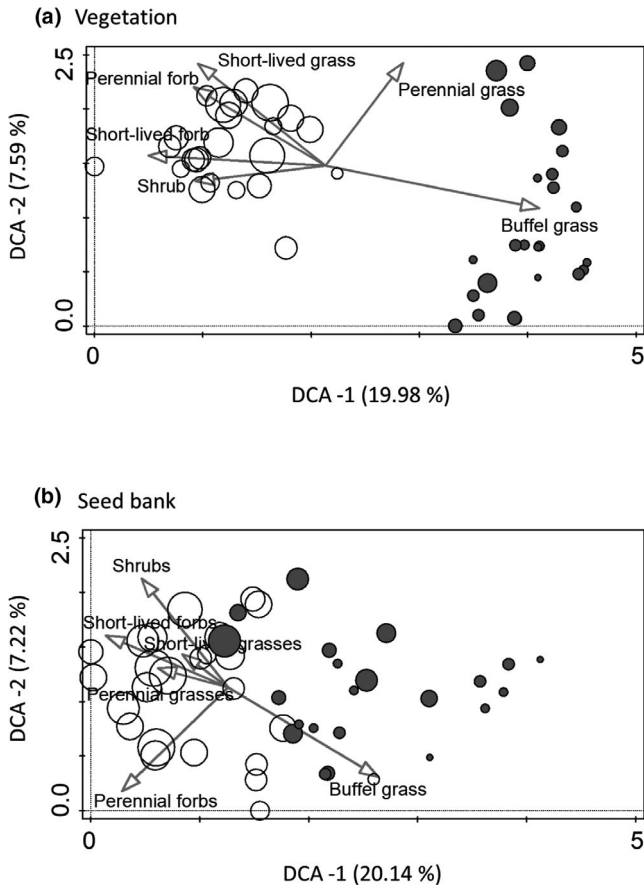
**(a) Vegetation**

**(b) Seed bank**

**FIGURE 1** Vegetation abundance (a) and seed bank abundance (b) biplots with supplementary variables plotted passively. Shaded circles represent buffel-infested plots, open circles are plots where buffel grass was eradicated. Circle size corresponds to relative species richness within plots. Supplementary life form variables are represented by arrows. Direction and length of arrows in the plots indicates the relative strength of association between the plant growth-form groups and plots within the ordination space



**(a) Vegetation**

**(b) Seedbank**

**FIGURE 2** Effects of buffel eradication treatment on mean (+ standard error) vegetation abundance (a) and seed bank density (b) across plant growth forms (Abbreviations: ASL, annual/short-lived; P, perennial). Results from generalized linear model analyses are presented above group means. Significance of the tested parameters is given by the significance codes: ***, $p < 0.001$; n.s., not significant

abundance (deviance = 108.92, $df = 1$, $p < 0.001$) and richness (deviance = 45.88, $df = 1$, $p < 0.001$) of shrubs (Figure 2a, Appendix S4).

Numerically common perennial forb species that were more abundant in removed than infested sites were primarily from the family Chenopodiaceae, including *Einadia nutans*, *Maireana scleroptera* and *Sclerolaena* spp. (Appendix S2). Annual grass species that were more abundant in removed than infested sites included *Aristida* spp., *Dactyloctenium radulans*, *Enneapogon polyphyllus* and *Urochloa piligera* (Appendix S2). Shrub species that had increased abundance at buffel-removed sites were *Acacia victoriae* and *Rhagodia spinescens* (Appendix S2). Some species, including *Calocephalus* sp., *Chrysocephalum apiculatum*, and *Wahlenbergia* sp., were unaffected or had increased abundance at buffel-infested sites (Appendix S2).

## 3.2 | Seed banks

Similar to the vegetation DCA, the seed bank DCA showed a strong positive effect of buffel grass removal on non-buffel grass species
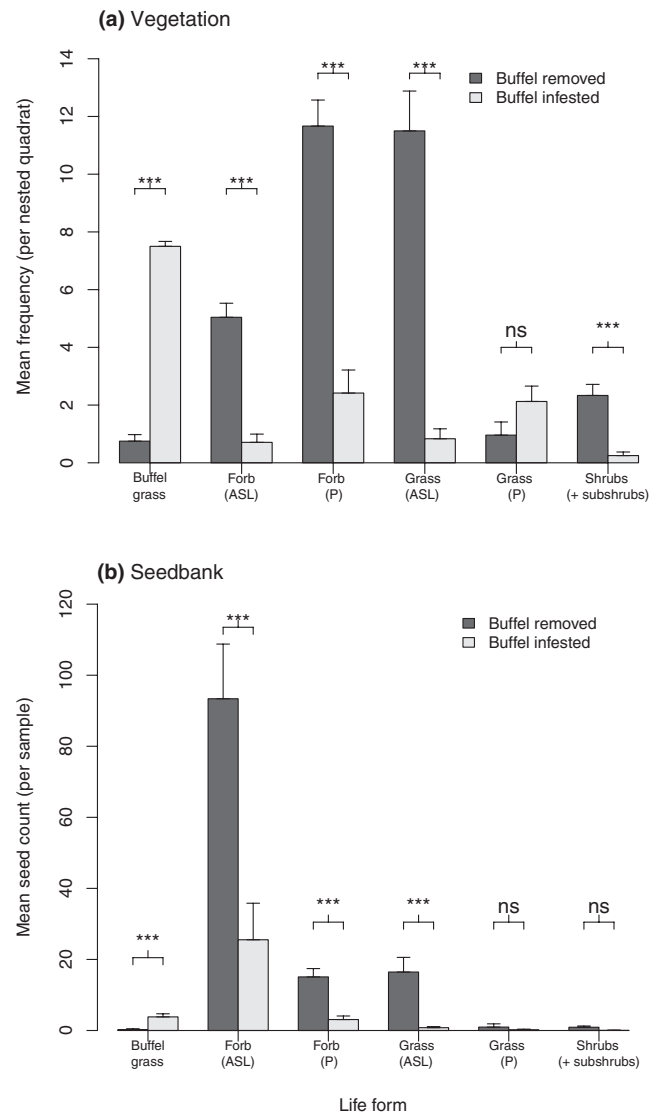
abundance, with the first axis of the seed bank DCA accounting for 20.14% of variation in the data set. Seed abundances of all plant growth forms other than buffel grass strongly increased at buffel-free sites (Figure 1b). Separation of the buffel-removed vs. infested sites was not as complete for the seed bank DCA as for the vegetation DCA. This suggests that while the above-ground component at infested sites had been almost completely transformed into a buffel grass monoculture, seed banks in these areas had sustained some remnant of the original system.

From the univariate seed bank analyses, seed bank abundance and richness of all non-buffel grass life form groups except perennial grasses and shrubs (which could not be analysed due to insufficient data points) were significantly higher at buffel-free compared

to buffel-infested sites (all $p < 0.001$) (Figure 2b, Appendix S3 and S5). Seed bank diversity of the annual/short-lived perennial forbs ($F_{1,46} = 10.14$, $p = 0.003$) and annual/short-lived perennial grasses ($F_{1,46} = 37.54$, $p < 0.001$) was also significantly higher at buffel-removed sites compared to infested sites (Appendix S5).

From the analysis of seed size classes, there was a significant interaction between buffel grass removal treatment and seed size class (likelihood ratio test = 45.30, $df = 4$, $p < 0.001$), indicating that the different seed classes were affected differently by buffel grass eradication. This interactive effect is illustrated in Figure 3, which shows that buffel grass eradication had a strong positive effect on all seed size classes of non-buffel grass species except the very small seed size class (where it had no effect), but had a negative impact on the total mass of buffel grass seeds.

The total mass of non-buffel grass seeds in the seed bank was ca. 10× higher at buffel-removed sites (46.26 kg/ha) than at buffel-infested sites (4.15 kg/ha). Non-buffel grass seeds in the medium size class (0.001–0.009 9 g) were ca. 20× higher at buffel-removed sites (14.26 kg/ha) compared to buffel-infested sites (0.72 kg/ha) ($t[220] = 2.79$, $p = <0.006$) (Figure 3). Similarly, non-buffel grass seeds in the small size class (0.000 1–0.000 99 g) were ca. 13.5× higher at buffel-cleared plots (18.24 kg/ha) compared to buffel-infested plots (1.35 kg/ha) ($t[220] = 5.074$, $p = <0.00 1$) (Figure 3). There was no significant difference between the mass of non-buffel grass seeds in the very small size class (0.000 01–0.000 099 g) between buffel-removed and infested sites (Figure 3). The mass of buffel grass seeds was approximately 15× higher at buffel-infested sites (1.2 kg/ha) compared to buffel-removed sites (0.08 kg/ha) ($t[220] = −3.95$, $p = <0.00 1$) (Figure 3).

## 4 | DISCUSSION

The current study indicates that buffel grass removal enhances native vegetation and seed bank diversity. This finding supports a small, but growing body of international literature showing that successful native re-establishment can occur even after long-standing buffel grass infestations (Funk et al., 2013; Farrell and Gornish, 2019). The strong positive effect we observed of buffel grass removal on native plant life form groups most likely reflects, at least partially, release from competition and increased light and moisture resources after removal (Eilts and Huxman, 2013; Mganga et al., 2015). Interestingly, within the annual/short-lived perennial forb life form, the vegetation of several species, including *Wahlenbergia* sp. and *Calocephalus* sp., was unaffected or even favoured by dense buffel grass infestations. It may be that these plants, which are small-statured and generally have smaller seeds than perennials, are less affected, or even favoured, by shady habitat conditions under dense buffel grass swards.

Enhanced shrub diversity after buffel eradication in our study was driven primarily by increased abundance of the shrub *Rhagodia spinescens* and seedlings of *Acacia victoriae*. Like the native forbs and
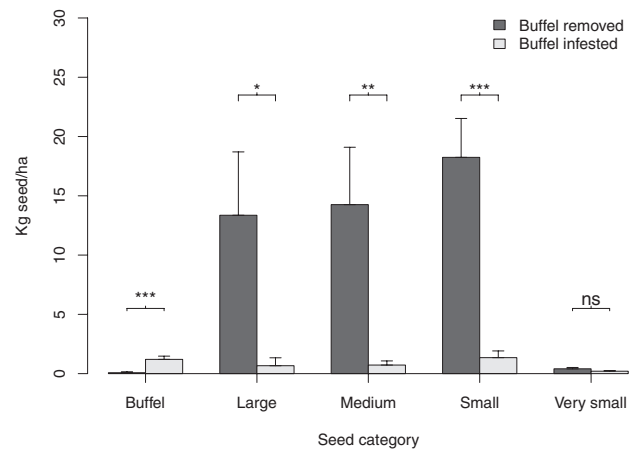
**FIGURE 3** Observed mean seed masses (+ standard error) of seed size classes at buffel-removed and buffel-infested sites. The large seed class consists of seeds weighing >0.01 g, the medium seed class consists of seeds weighing 0.001–0.009 9 g, the small seed class consists of seeds weighing 0.000 1–0.000 99 g, and the very small seed class consists of seeds weighing 0.000 01–0.000 099 g. Differences in seed mass between groups according to buffel treatment are given by the significance codes: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; n.s., not significant

grasses, shrub seedlings may have benefited following buffel grass eradication from improved light conditions and less competition. Additionally, recent research suggests that allelopathic compounds in buffel grass vegetation cause a reduction in *Acacia victoriae* seed viability and reduce germination rates of another *Acacia* species, *Acacia tetragonophylla* (common name: dead finish) (Edwards et al., 2019). Consequently, it could be that a combination of release from competition and removal of allelopathic effects explains the increased abundance of shrubs at our buffel-cleared sites.

Buffel grass removal also led to an increase in shrubs and subshrubs of the family Chenopodiaceae. From a management perspective, this is an important outcome as chenopod shrubs and subshrubs often have fire-retardant characteristics, and their dominance may reduce the likelihood of wildfires (Montgomery and Cheo, 1969). In this way, broadscale buffel removal programmes might interrupt fire invasion feedbacks that convert fire-sensitive shrub- and tree-dominated native vegetation to pyrophilic exotic grassland (Clarke et al., 2005; Miller et al., 2010; McDonald and McPherson, 2011).

It is unclear whether recovery of the vegetation in our study was from persistent on-site seed banks that were extant at the time of buffel removal, or from propagules that had dispersed in from surrounding areas. Recruitment from dispersed seeds as a primary source of regeneration seems unlikely, as all sites in our study were, at the time of buffel removal, largely surrounded by other buffel-infested blocks. However, this does not preclude the possibility that some seeds could have been brought in from long distances by animals, as many species observed at our sites are adapted for animal dispersal (e.g. the fleshy-fruited *Enchylaena tomentosa* and *Einadia nutans*, spiny-fruited *Tribulus* and *Sclerolaena* spp., and sticky-fruited *Boerhavia* spp.).

Buffel grass burrs were absent from all except one of the 24 buffel-cleared sites. This suggests that buffel grass seed banks at buffel-cleared areas had become exhausted since clearing via germination, predation and seed decay. It also suggests that observations at buffel-cleared sites by PKL and DEA of recurrent waves of buffel recruitment after rainfall was from seed that had dispersed in from nearby extant swards, rather than from residual seed banks. If this was the case, then fine netting placed on fencing around buffel-cleared sites may reduce the need for regular management by minimising wind and animal dispersal of buffel seed into these areas. That a large fraction of the buffel seed bank could have decayed since removal is supported by previous research by Winkworth (1971) and Silcock and Smith (1990), who found that buffel grass seeds are relatively short-lived under field conditions and maintain ≤10% viability after two years.

At buffel-removed sites, the ca. 20-fold and 13.5-fold increase in the mass of seeds in the medium and small seed size classes respectively indicates that community restoration subsequent to buffel removal increases the availability of seed resources for granivores. Unfortunately, there is a dearth of information on the dietary preferences of arid Australian vertebrate and invertebrate granivores. Consequently, it is difficult to speculate on exactly which granivore guilds are most likely to benefit from the improved seed resources that occur after buffel grass eradication. Nevertheless, from the available literature, it can be speculated that important seeds for granivores in the small seed size class of our study would include those of the grass genera *Enneapogon*, *Dactyloctenium* and *Aristida*. These genera are known to be consumed by zebra finches (*Taeniopygia guttata*) and flock bronzewing pigeons (*Phaps histrionica*) (Morton and Davies, 1983; Dostine et al., 2014; Young and Schlesinger, 2018). Potentially important seeds in the medium size class of our study include those of the genera *Abutilon* (family Malvaceae) and *Urochloa* (family Poaceae), which are consumed by rock rats (Edwards, 2013) and flock bronzewing pigeons (Dostine et al., 2014). Seeds of the genus *Tribulus* (family Zygophyllaceae), also in the medium size class, are a favoured food source of the red-tailed black cockatoo (*Calyptohynchus banksii*) (DEA, PKL, BRW pers. obs.). Although seeds of some species in the very small seed size class are known to be consumed by granivores (e.g. *Portulaca oleracea* [family Portulaceae] [Dostine et al., 2014]), the overall mass of seeds in this size class was small compared to the other seed size classes in our study, and hence unlikely to contribute greatly to granivore diet composition.

The results do not support the possibility that buffel-infested areas provide comparable seed resources for granivores relative to intact native vegetation communities. The estimated mean mass of buffel grass seed at infested sites (1.2 kg/ha) was much lower than the combined mass of non-buffel grass seeds at buffel-removed sites (46.26 kg/ha). This finding may partially explain previous observations that link buffel invasion to depauperate populations of granivore guilds of birds, harvester ants and rodents (Ludwig et al., 2000; Friedel et al., 2006; Smyth et al., 2009; Young and Schlesinger, 2014). However, it is possible that results from these studies also reflect that granivores benefit from the generally more open site attributes of native plant communities, which may facilitate easier foraging and/or better nesting or breeding sites than weed-invaded habitats (Antos and Williams, 2015).

## 5 | CONCLUSION

The current study demonstrated long-term (12 years post removal) biodiversity benefits following the eradication of buffel grass in an arid woodland system. Nevertheless, the detection of occasional buffel grass seeds and seedlings at buffel-removed sites indicates that ongoing site monitoring and removal of emerging seedlings is necessary to prevent re-invasion in these systems. Discussions with landholders indicated that mechanical removal was very labour-intensive and time-consuming. Therefore, future efforts aimed at providing cost-effective, large scale buffel grass eradication will presumably rely on refining herbicide control methods (e.g. see Dixon et al., 2002 for an informed examination of buffel grass eradication techniques using herbicide spraying on Airlie Island, Western Australia). A key area of future research, not just in buffel-infested systems, but in invaded ecosystems generally, will be to disentangle the relative importance of seed dispersal vs. residual seed banks for native plant community regeneration after invasion. If residual seed bank pools are identified as important, it will be vital to determine the time taken after invasion for seed bank reserves to deteriorate to a state where they can no longer sustain vegetation regeneration. This will provide managers with a threshold timeframe within which to conduct eradication before native plant regeneration is prevented by a lack of seed availability. Comprehensive studies on seed longevities in soils of individual species will be crucial.

### CONFLICTS OF INTEREST
The authors have no conflicts of interest to declare.

### AUTHOR CONTRIBUTIONS
BRW, PKL, DEA conceived and designed the research; BRW, PKL, DEA performed the experiments; BRW analysed the data; BRW, PKL, DEA, RF wrote and edited the manuscript.

### DATA AVAILABILITY STATEMENT
Data from this study are located at DRYAD digital repository (https://doi.org/10.5061/dryad.000000020).

## ORCID

*Boyd R. Wright* https://orcid.org/0000-0002-6322-4904

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**Appendix S1.** ANOVA results from analyses of soil sand, silt and clay content

**Appendix S2.** List of species abundances and life history attributes from vegetation study

**Appendix S3.** List of species and life history attributes from seed bank study

**Appendix S4.** Generalized linear model and ANOVA results showing effects of buffel eradication on vegetation richness and diversity across plant growth forms

**Appendix S5.** Generalized linear model and ANOVA results showing effects of buffel eradication on seed bank richness and diversity across plant growth forms