CSIRO PUBLISHING

www.publish.csiro.au/journals/trj *The Rangeland Journal*, 2009, **31**, 329–351

What drives plant biodiversity in the clay floodplain grasslands of NSW?

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Abstract. An assessment of the relative influences of management and environment on the composition of floodplain grasslands of north-western New South Wales was made using a regional vegetation survey sampling a range of land tenures (e.g. private property, travelling stock routes and nature reserves). A total of 364 taxa belonging to 55 different plant families was recorded. Partitioning of variance with redundancy analysis determined that environmental variables accounted for a greater proportion (61.3%) of the explained variance in species composition than disturbance-related variables (37.6%). Soil type (and fertility), sampling time and rainfall had a strong influence on species composition and there were also east–west variations in composition across the region. Of the disturbance-related variables, cultivation, stocking rate and flooding frequency were all influential. Total, native, forb, shrub and subshrub richness were positively correlated with increasing time since cultivation. Flood frequency was positively correlated with graminoid species richness and was negatively correlated with total and forb species richness. Site species richness was also influenced by environmental variables (e.g. soil type and rainfall). Despite the resilience of these grasslands, some forms of severe disturbance (e.g. several years of cultivation) can result in removal of some dominant perennial grasses (e.g. *Astrebla* spp.) and an increase in disturbance specialists. A simple heuristic transitional model is proposed that has conceptual thresholds for plant biodiversity status. This knowledge representation may be used to assist in the management of these grasslands by defining four broad levels of community richness and the drivers that change this status.

Additional keywords: cultivation, flooding, grassland composition, grazing, Mitchell grasslands, species richness.

Introduction

Awareness of the need to manage native grasslands to conserve biodiversity has grown in the past two decades (e.g. Lunt 1991, 1997; Howe 1994; McIntyre 1994; Prober and Thiele 1995; Nadolny 1998; Davidson *et al*. 2005; Hodgson *et al*. 2005; Knop *et al*. 2006). Grassland biodiversity research in Australia has concentrated on temperate grasslands and grassy woodlands, such as those on the NSW tablelands (e.g. Whalley *et al*. 1978; McIntyre *et al*. 1993; McIntyre and Lavorel 1994; Trémont and Whalley 1995; Clarke 2003) and on the basalt-derived soils of Victoria (e.g. Stuwe and Parsons 1977; Lunt 1990; Lunt and Morgan 1999; Morgan 1999). A body of research has also accumulated on subtropical woodlands and grasslands (e.g. Fensham 1998; Fensham *et al*. 1999; McIntyre and Lavorel 2001; McIntyre and Martin 2001) and tropical savannas of Queensland and the Northern Territory (e.g. Ash and McIvor 1998; Russell-Smith *et al*. 2003; Williams *et al*. 2003; Kutt and Woinarski 2007). An earlier generation of research in the subhumid and semi-arid floodplain grasslands (e.g. Orr 1980*a*, 1980*b*, 1981; Scanlan 1983; Orr and Holmes 1984; Roe and Davies 1985; Orr and Evenson 1991*a*, 1991*b*) focused on their pastoral value, rather than biodiversity *per se.* Information about management effects on biodiversity in the semi-arid floodplain grassland communities often dominated by Mitchell grass (*Astrebla* spp.) and Queensland bluegrass (*Dichanthium sericeum* (R.Br.) A.Camus) is sparse (Keith 2004). This is particularly so for the Moree Plains of NSW, where *Astrebla* species occur near the southern and eastern limits of their geographic distribution, and where native grasslands have been removed for irrigated and dryland farming. On these NSW floodplains, the present area of grasslands is ~7500–12 000 km^2 (Keith 2004), of which less than 100 km^2 are represented in conservation reserves, and the natural grasslands on basalt and fine-textured alluvial plains of northern NSW and southern Queensland are listed as an endangered ecological community under the *Environment Protection and Biodiversity Conservation Act* (1999).

The ability of cultivated and grazed grasslands to regain their pre-disturbance floristic composition is a critical issue for the maintenance of plant biodiversity where mixed farming is one of

10.1071/RJ08056 1036-9872/09/030329

the main land-uses. Although conversion to intensive cropping has removed up to 40% of the semi-arid floodplain grasslands in NSW, the structure of the remaining grasslands appears to be maintained under a range of livestock grazing and rotational cultivation regimes. The extent to which such management has modified the floristic composition and other biodiversity values of the Moree Plains may never be known, simply because there are few historic data and there are no grasslands that remain ungrazed by livestock (Clarke *et al.* 1998). Mitchell grasslands are thought, however, to be the most 'resilient' of the rangeland tussock pastures in Australia by having a strong tendency to return to their original state after disturbance (Harrington *et al.* 1984). Hence, Campbell (1989) concluded that permanent change in composition brought about by grazing regimes was unlikely. Nevertheless, changes in the floristic composition of these grasslands have been recorded in response to livestock grazing and cultivation, as well as to environmental drivers such as flood and drought (Beadle 1948; Everist 1964; Orr 1981; Campbell 1989; Bowman *et al.* 1997; Lewis *et al.* 2008).

Climate has an important influence on native grassland composition, and can mask and interact with the effects of agricultural management (Bellamy *et al.* 1996). Rainfall is a key variable in determining species composition and biomass in semi-arid grasslands (Roberts 1978; Foran and Bastin 1984; Orr and Holmes 1984; Campbell 1989; Orr and Evenson 1991*a*; Bowman *et al.* 1997; Fensham *et al.* 2000), and seasonal influences may have more profound impacts on species composition and abundance than livestock grazing (e.g. Orr 1981; Foran and Bastin 1984; Orr and Evenson 1985, 1991*a*; Bellotti *et al.* 1986; Lewis 2006). Temporal variation results not only from seasonal temperature and rainfall effects but also floods. Prolonged inundation can kill *Astrebla lappacea* tussocks, and a series of major floods in the 1970s (i.e. 1971, 1974, 1976) was attributed to the decline in *Astrebla* density in NSW (Campbell 1989). Hence, there is an urgent need to assess the relative contribution of grazing, cultivation, climate and flooding on the floristic composition of these grasslands to build a framework for management.

In this paper we use a space-for-time approach to examine the relative importance of disturbance-related variables (grazing, cultivation, flooding) and environmental variables (e.g. antecedent rainfall and soil type) in influencing species composition in the semi-arid, Moree Plains grasslands. We then develop a conceptual model to highlight how management influences plant diversity in these grasslands.

Materials and methods

Site selection and sampling methods

We surveyed grasslands on the Moree Plains in northern NSW (Fig. 1). Sites were chosen based on management history, in particular the history of cultivation, grazing, flooding and fire. Hence, sampling took place over a range of land tenures, including privately owned properties, reserves, travelling stock routes (TSRs) and other remnants (e.g. cemeteries). Sites were not evenly distributed over the study region due to the lack of rainfall in some areas. Areas that had not received rainfall in the months before sampling were generally avoided because species richness was lower and plant identification more difficult due to the lack of reproductive material. Sampling was undertaken in autumn (February–June) in 2002 and 2003. This is the best time to sample these grasslands (Clarke *et al.* 1998; Hunter and Earl 1999), as the warm temperatures combined with rainfall provide good conditions for germination and growth. However, once-off sampling at this time is unlikely to record all species because some are likely to be present only as seeds or underground buds. For example, several winter-growing annual species become part of the interstitial component of these grasslands following winter rainfall (Hunter and Earl 1999; Lewis 2006).

The selection of precise sampling locations within paddocks or section of stock route was based on being representative of the grassland in the surrounding management unit and being relatively homogeneous in structure. Certain areas were avoided, such as stock camps, wetlands, areas dominated by introduced pasture (i.e. >50% cover), areas cultivated within the previous year and areas with steep slopes. Up to four sites were surveyed on any one property in each year, but in most cases no more than one site was placed in a given paddock. An exception to this occurred when two contrasting methods of management, frequencies of flooding, or soil types occurred within the one paddock, in which case a maximum of two sites was placed in the paddock.

A range of native grassland communities was sampled over the landscape, although most sites were on clay soils (the most common soil type in the study region). Nine sites on non-clay soil types were sampled for comparative purposes. Areas that were dominated by, or that could potentially be dominated by, *Dichanthium sericeum* or *Astrebla* spp. were generally targeted in this survey, although not all sites fell into this broad category. Sites were chosen in areas of open grassland (sparse trees or shrubs, <5% cover of woody plants), shrubby grassland (5–25% cover of shrubs), and open grassy woodland (5–25% cover of trees). Areas with a dense cover of trees were avoided.

All vascular plants were recorded within 20 × 20 m quadrats. Each species was assigned a Braun-Blanquet cover abundance score using a six-point scale, by estimating its projected cover. Cover scores were: (1) <5% cover and <3 individuals per quadrat; (2) <5% cover and $\geq$3 individuals per quadrat; (3) 6–25% cover; (4) 26–50% cover; (5) 51–75% cover; and (6) >75% cover. Error in the cover estimate was minimised by a single observer (T. Lewis) making all estimates. The species richness per quadrat and cover of natives, introduced species, grasses (Poaceae), forbs, graminoids (non-grass monocotyledons), subshrubs, shrubs and trees were subsequently calculated.

Site information

A total of 52 private properties were visited during the survey. For sites on these properties, landholders were interviewed regarding the management history of their grassland. Questions addressed the history of cultivation, grazing, flooding and fire, and rainfall in the 4 months before sampling. Only variables that had a significant influence on species composition are described here (see '*Statistical analysis*'). Non-significant variables included time since fire, type of grazing animal, grazing management type (periodic or continuous), length of flood inundation, topsoil electrical conductivity and percentage bare

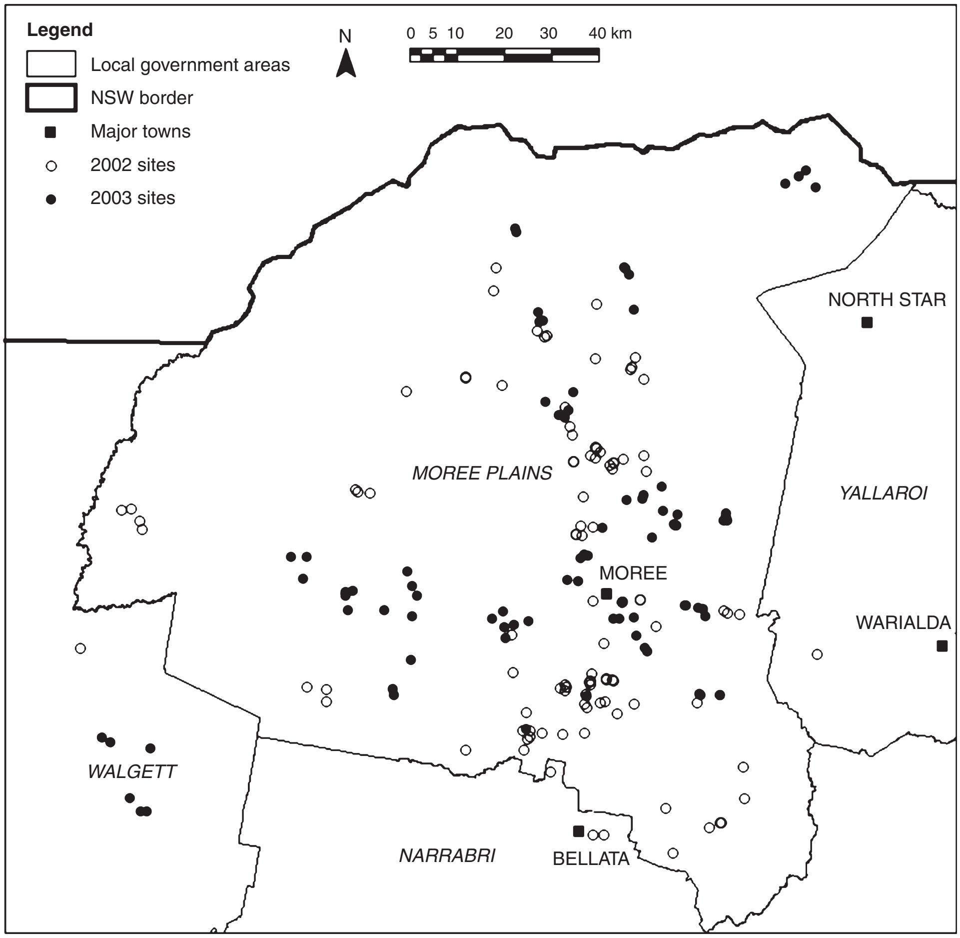


Fig. 1. Location of grassland quadrats sampled in 2002 and 2003 in the Moree Plains Local Government Area (northern NSW) and neighbouring local government areas (italics).

ground. Several other variables were recorded (e.g. time since livestock grazing, topsoil available sulfur, altitude and litter cover) but were not included in analysis due to high correlations with other variables.

Grazing

Sites were sampled across four different land tenures with differing grazing histories: (1) privately owned property (131 sites); (2) public land (i.e. travelling stock routes and reserves) (43 sites); (3) nature reserves (seven sites); and (4) cemeteries (three sites). Stocking rates (dry sheep equivalents per hectare, DSE/ha) were obtained or calculated for all sites with a history of recent grazing. For sites on private property, stocking rates were provided by landholders. An average stocking rate for the year before sampling was calculated for each site, by taking into account periods of no grazing. For sites on travelling stock routes, stocking rates were calculated using Rural Lands Protection Board permit records in the months before sampling. Long-term stocking rates (i.e. stocking rates over the last century) were not calculated due to the lack of reliable records for most sites. Given that cattle and sheep have different metabolic requirements, stocking rates had to be converted for cattle-grazed sites by assuming that one cow, bull or steer was equivalent to 10 DSE and one calf was equivalent to 5 DSE.

Cultivation

Sites that had been cultivated or cropped within 1 year of sampling were avoided as such areas were generally lacking native species. Sites that had been cultivated were most commonly sown with cereal crops such as wheat, barely, oats and sorghum. Four cultivated sites were sown with introduced grasses or legumes (often after the last cereal crop cultivation) and two sites were sown with *Astrebla lappacea* (Lindl.) Domin in the 1980s, after the last cultivation. Number of years since last cultivation was obtained from landholders. A score for length of cultivation was devised as follows: (1) never cultivated (121 sites); (2) cultivated for $\leq$5 years consecutively (20 sites); or (3) cultivated for >5 years consecutively (42 sites).

Flooding

A score for frequency of flooding was devised as follows: (1) not flooded, or very rarely flooded (perhaps once in 30 years) (94 sites); (2) flooded, but <1 flood every 2 years on average (53 sites);

and (3) flooded at least once every 2 years on average (37 sites). A flood was defined as a period of time when the site would have been completely submerged by flowing water (usually from a nearby watercourse). Localised waterlogging after heavy rainfall did not constitute a flood.

Rainfall

The amount of rainfall that had fallen in the 4 months before sampling, as well as average annual rainfall for the property, was obtained from most landholders. For sites that were not on private property, rainfall in the months before sampling and average annual rainfall were estimated using data obtained from the nearest rainfall recording station provided by the Commonwealth Bureau of Meteorology, and nearby properties for which rainfall was known. The average annual rainfall for all sites ranged from 443 to 660 mm (mean of 560 mm); although in the 4 months before sampling at each site, rainfall ranged from 75 to 357 mm (mean of 168 mm).

Sampling time and location

A total of 184 individual sites were surveyed, 98 in autumn 2002 and 86 in autumn 2003. Sampling date for each site was converted to Julian time (day 1 = 1 January 1900) for analysis. In 2002, sampling was concentrated towards the east of the study region, due to lack of rainfall in the west. The location of each site (northing and easting coordinates) was included in analysis since sites were not randomly distributed across the study area and there is known variation in species assemblages from east to west (Hunter and Earl 1999).

Soil variables

Soil type was broadly categorised in the field as either: (1) grey to black clay (132 sites); (2) brown clay (43 sites); or (3) other (sandy loams, red earthy soils, etc., nine sites). A soil sample was collected at each site using an auger with a 10-cm diameter to 10 cm depth. Two soil samples were taken at random points along the northern edge of each vegetation sampling quadrat, and were thoroughly mixed. After field collection, soils were dried in an oven at 40°C for ~48 h, or until dry. Immediately before analysis, samples from each site were repeatedly split using a sample divider until ~100 g remained. This sample was then placed through a sieving machine to ensure grain sizes <2 mm. The sieved sample was placed in a separate, airtight, labelled container for analysis. Soil samples were analysed for available phosphorous, organic carbon, pH and electrical conductivity.

Soil pH was measured in water, with a soil to solution ratio of 1 : 5 at 25°C, after 1 h of shaking and a 20–30 min settling time. The pH reading was taken using a standardised pH meter. A measure of the amount of phosphorus available to plants was determined using the fluoride-extractable phosphorus, Bray method (Bray and Kurtz 1945, cited by Rayment and Higginson 1992). This method uses an extraction solution of 0.03 M ammonium fluoride in 0.025 M hydrochloric acid (HCl) and a very short extraction time (60 s) (Rayment and Higginson 1992). Some soil variables (e.g. total nitrogen and available sulfur) were not analysed, as these variables are likely to be correlated with other soil elements (i.e. phosphorus).

Soil organic carbon was estimated by loss on ignition and follows the method by Allen *et al*. (1986). This provides a crude measure of the amount of organic matter in the soil. Soil (~1 g) was weighed and placed in a muffle furnace at 550°C for 2 h. The sample was removed and allowed to cool to room temperature before reweighing. Loss in weight was calculated as a percentage of the dry weight and converted to percentage of organic carbon.

Tree cover

A tree cover score at each site was devised as follows: (1) no trees in close proximity to the plot (144 sites); (2) trees shading at least part of plot, but not within the plot (35 sites); or (3) trees within the plot (five sites).

Taxonomy

Nomenclature for vascular plants generally followed work by Harden (1992, 1993, 2000, 2002) and Wheeler *et al*. (2002) for grasses. An exception was the Asteraceae genus *Ixiolaena*, which has been revised to *Leiocarpa* (Wilson 2001). Voucher specimens for most species were collected so that identifications could be verified. Introduced species are indicated by an asterisk throughout the paper.

Statistical analysis

Ordination analysis was chosen to provide insights into the effects of disturbance-related variables and environmental variables on species composition. Multivariate analyses were conducted using the program CANOCO, version 4.5 (ter Braak and Šmilauer 2002). Ordination involved two steps: indirect gradient analysis (unconstrained ordination) and direct gradient analysis (constrained ordination) (Lepš and Šmilauer 2003). Indirect gradient analysis was used initially to search for major gradients in the plant species data, irrespective of independent variables. Direct gradient analysis was then used to explain the vegetation data in terms of specific explanatory variables of interest (e.g. disturbance-related and environmental variables).

Indirect gradient analysis using detrended correspondence analysis (DCA) produced a gradient length of 2.76 (after deletion of non-clay soils) and no unmeasured gradient was detected. The relatively short gradient length suggested species were responding roughly linearly to the explanatory variable gradients, hence, redundancy analysis (RDA) was selected as the most appropriate ordination technique.

Species cover data were transformed since the data contained many zeros, by taking logarithms, using the transformation ln $(10 \times (x+1))$, where x = species cover score. Infrequent species (with two occurrences or less) were deleted from the dataset before analysis. Categorical variables (i.e. land tenure, occurrence of cultivation and soil type) were coded as 'dummy variables' within the data spreadsheet, where the dummy variable takes the value of one if the site belongs to that category, and zero if not. Automatic forward selection was used to rank each explanatory variable and its relative importance in determining the species cover data and to reduce the number of variables in the dataset and manual selection was used to determine the variance explained by individual variables (ter Braak and Šmilauer 2002). Monte Carlo permutation tests were used to test the significance of each variable, by repeatedly shuffling the samples and comparing the generated test statistics with the test statistic generated from the null hypothesis, which suggests species are unrelated to the explanatory variables. Each permutation leads to a new dataset from which a test statistic can be calculated (ter Braak and Šmilauer 2002). The default option of 499 permutations was chosen, which is adequate for a test at the 5% significance level (ter Braak and Šmilauer 2002).

The strong influence of non-clay soils on species composition was taken into account when determining the influence of other variables on species composition, by only comparing sites located on clay soils ($n = 175$). After removing sites with non-clay soils, variables that were not significant ($P > 0.05$) after forward selection were removed from the dataset before re-analysis. All variables that had a significant influence on species composition are shown in Table 1. The reduced dataset consisted of ten environmental variables (with eleven categories), four disturbance-related variables (with six categories), 175 sites and 260 species. To further reduce the number of variables to assist in interpretation, we conducted a correlation analysis between all environmental variables and removed any variables that were highly correlated ($P < 0.001$) with the others. The final set of variables used ordination comprised of available phosphorus, annual rainfall, Julian time, cultivation, stocking rate and frequency of flooding.

Partitioning of variance was used to determine the variance uniquely described by disturbance-related variables and environmental variables. The method involved the use of partial ordination by 'factoring out' certain variables (e.g. all environmental variables) by setting them as covariates in the analysis (Borcard *et al.* 1992). Three RDA runs were conducted to determine: (A) pure effect of environmental variables alone; (B) pure effect of disturbance variables alone; and (C) combined variation due to the joints effects disturbance variables and environmental variables. The remaining variation was unexplained. The RDA runs were: (1) RDA constrained by environmental variables, with disturbance variables as covariables; (2) RDA constrained by disturbance variables, with environmental variables as covariables; and (3) RDA constrained by disturbance variables and environmental variables, with no covariables.

Species richness variables (total, native, introduced, forb, grass, graminoid, sub-shrub, shrub and tree richness) were defined as supplementary variables in CANOCO and were added *post hoc* to the ordination by projection (by regressing the data on to ordination axes) (ter Braak and Šmilauer 2002). Correlations between species richness variables and other variables (disturbance-related and environmental) were tested using Spearman rank tests. Student's *t*-statistic was used to determine whether correlations differed significantly from zero (i.e. no correlation).

Results

General floristics

A total of 364 plant taxa were recorded, of which 77% (280) were native and 23% (84) were introduced. The 364 taxa belonged to 55 different plant families. Families with the greatest

Table 1. Significant variables (disturbance-related, and environmental variables) used in multivariate analysis after forward selection and their categories (if qualitative)

A correlation matrix was used to identify significant correlations ($P < 0.001$) between variables. Positive (+) and negative correlations (–) were obtained using Spearman's rank tests and are useful in interpreting the ordination diagram. Qualitative variables can have both positive and negative correlations because one category may be positively correlated with a variable and another category may be negatively correlated with the same variable

Variable	Category	Correlations
		Disturbance variables
Land tenure[A]	Privately owned	Julian time (+), northing (+), recent rainfall (–), flood frequency (+), cultivation (+)
	Public land	Stocking rate (+), flood frequency (–), cultivation (–)
	Nature Reserve	Stocking rate (–)
Cultivation	Cultivated	Julian time (+), land tenure (+ and –), tree cover (–)
	Not cultivated	
Stocking rate	Continuous	Land tenure (+ and –)
Flood frequency score	Continuous	Land tenure (+ and –), northing (+)
		Environmental variables
Annual rainfall	Continuous	Recent rainfall (+), pH (–), easting (+)
Recent rainfall (in 4 months before sampling)[A]	Continuous	Annual rainfall (+), northing (–), land tenure (–)
Julian time	Continuous	Land tenure (+), cultivation (+)
Soil type[A]	Grey to black clay	Available P (–), organic carbon (–), easting (+)
	Brown clay	Organic carbon (+), available P (+), easting (–)
Available soil phosphorus	Continuous	pH (–), organic carbon (+), soil type (+ and –)
Soil organic carbon[A]	Continuous	Available P (+), soil type (+ and –), easting (–), soil pH (–)
Soil pH[A]	Continuous	Available P (–), northing (+), organic carbon (–), annual rainfall (–)
Tree cover score[A]	Continuous	Cultivation (–)
GPS easting[A]	Continuous	Soil type (+ and –), organic carbon (–), annual rainfall (+)
GPS northing[A]	Continuous	Land tenure (+), pH (+), flood frequency (+), recent rainfall (–)

[A] Not included in final ordination model.

number of taxa were Poaceae (97), Asteraceae (54), Fabaceae (35), Chenopodiaceae (30), Malvaceae (14) and Cyperaceae (9). Eleven taxa occurred in ≥50% of the 184 sites. In order of decreasing frequency, these were *Dichanthium sericeum* (sample frequency 75%), *Panicum decompositum* (R.Br.) (75%), *Enteropogon acicularis* ((Lindl.) Lazarides) (73%), *Solanum esuriale* (Lindl.) (63%), *Chloris truncata* (R.Br.) (61%), **Acacia farnesiana* ((L.) Willd.) (60%), *Sclerolaena muricata* var. *villosa* ((Benth.) Ulbr.) (60%), *Boerhavia dominii* (Meikle & Hewson) (57%), *Neptunia gracilis* (Benth.) (57%), *Sida trichopoda* (F.Muell.) (55%) and **Rapistrum rugosum* (L.) All. (50), where * indicates introduced species. Many taxa were recorded only once or twice in the survey: 19% occurred only once and 10% were recorded twice.

Total species richness ranged from seven to 56 species per quadrat, with an average of 31 ± 0.64. Average native and introduced species richness was 26.3 ± 0.58 and 4.7 ± 0.20 per quadrat, respectively. Sites were composed mostly of forbs (15.3 species per quadrat), grasses (9.8 species per quadrat) and subshrubs (2.9 species per quadrat).

General ordination output

Redundancy analysis after forward selection produced eigenvalues for the first four ordination axes of 0.041, 0.026, 0.023 and 0.015. The 14 explanatory (disturbance and environmental) variables explained 19.3% of the variance in species cover data. Soil type (grey to black clay or brown clay) and sampling time were the most important explanatory variables for predicting species composition, explaining 13.5 and 10.9% of the total explained variance, respectively.

After removing correlated variables, the reduced dataset explained 9.3% of the variance in species cover data. Forward selection of the species cover data showed that all variables in the reduced dataset had a significant ($P < 0.05$) influence on species composition (Table 2). Environmental variables accounted for 61.3% of the explained variance and disturbance-related variables accounted for 37.6% of the explained variance (Fig. 2). A small proportion (1.1%) of the variance was explained by the intersection of environmental and disturbance variables.

Disturbance-related determinants of composition

Stocking rate had an important influence on species composition, accounting for 12.9% of the explained variance. Some common species (e.g. *Sclerolaena birchii* (F.Muell.) Domin, *Dactyloctenium radulans* (R.Br.) P.Beauv. and *Salsola kali* var. *kali*) tended to occur at sites with higher stocking rates (Appendix 1), although other species tended to be more abundant at ungrazed sites (e.g. *Eulalia aurea* (Bory) Kunth, *Ptilotus semilanatus* (Lindl.) J.M.Black and *Vittadinia cuneata* DC, Appendix 1). Ordination suggested that introduced species richness was associated with sites with greater stocking rates (Fig. 3), although this correlation was not significant with univariate Spearman correlation. Moreover, no species richness variables were correlated with stocking rate.

Species composition was also influenced by the occurrence of cultivation, which accounted for 11.8% of the explained variance. Examination of the species matrix identified certain species

Table 2. Forward selection results, showing conditional effects and marginal effects for significant ($P < 0.05$) variable categories in the RDA for species cover scores

Only uncorrelated variables were used in this ordination model and only sites on clay soils were analysed ($n = 175$). ME, marginal effects; CE, conditional effects; λ, eigenvalues. Note: a probability of $P = 0.002$ is the lowest achievable given the number of permutations

Variable category	ME λ	CE λ	*F*	*P*
Julian time	0.02	0.02	3.80	0.002
Annual rainfall	0.02	0.02	3.60	0.002
Available P	0.02	0.02	2.97	0.002
Stocking rate	0.01	0.01	2.37	0.002
Occurrence of cultivation	0.01	0.01	2.07	0.002
Flood frequency	0.01	0.01	1.96	0.002

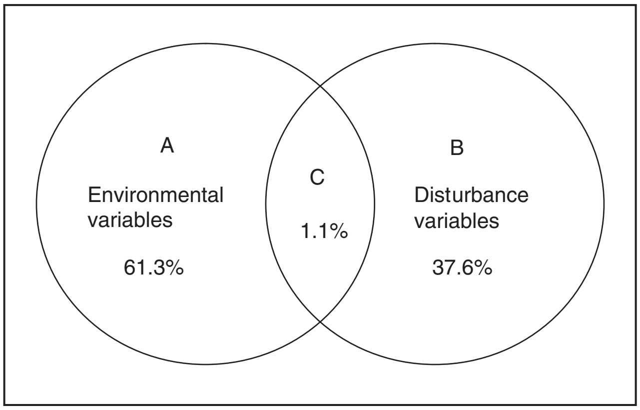


Fig. 2. Results of variance partitioning with partial redundancy analyses. Variation in the species data is explained by: (A) environmental variables; (B) disturbance variables; and (C) their joint effects. Values are percentages of total variation explained by the species data.

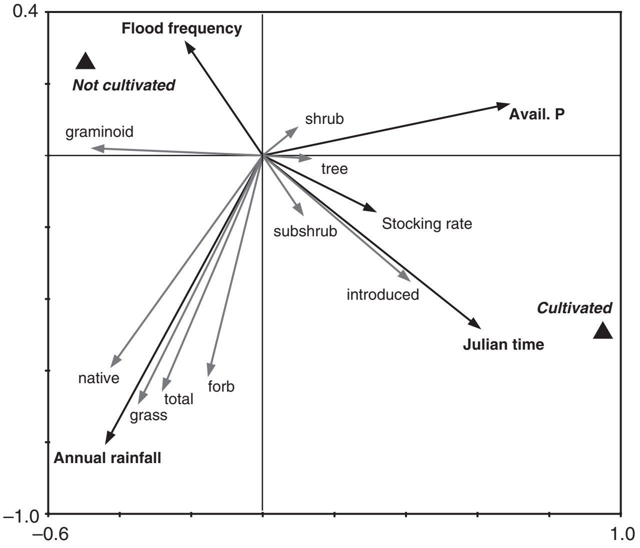


Fig. 3. Ordination (RDA) biplot for the reduced set of variables showing trends in species richness (supplementary variables in grey font). All variables are continuous, except the occurrence of cultivation (plotted as triangles, rather than arrows).

associated with cultivation (e.g. **Medicago polymorpha* L. and *Salsola kali* var. *kali*, Appendix 2). Some common species tended to be negatively associated with repeated cultivation, including **Acacia farnesiana*, *Astrebla elymoides* F.Muell. ex F.M.Bailey, *A. lappacea*, *Einadia nutans* subsp. *nutans* (R.Br.) A.J.Scott, *Eulalia aurea*, *Maireana decalvans* (Gand.) PaulG.Wilson, *Ptilotus semilanatus* and *Rhagodia spinescens* (R.Br.) (Appendix 2). Total, native, forb, shrub and sub-shrub richness were positively correlated with increasing time since cultivation (total, $t = 4.1$, d.f. = 173, $P < 0.001$; native, $t = 4.3$, d.f. = 173, $P < 0.001$; forb, $t = 2.9$, d.f. = 173, $P = 0.005$; shrub, $t = 6.0$, d.f. = 173, $P < 0.001$; and subshrub, $t = 5.3$, d.f. = 173, $P < 0.001$).

Flood frequency also had a significant influence on grassland composition, accounting for 12.9% of the explained variance in species cover. Examination of the species matrix identified some species that tended to be more abundant at frequently flooded sites (e.g. *Cyperus bifax* C.B.Clarke, *Eleocharis pallens* S.T.Blake, *Marsilea drummondii* A.Braun, and *Paspalidium jubiflorum* (Trin.) Hughes) and others that were more abundant at sites that did not flood (e.g. *Astrebla lappacea*, *Austrodanthonia bipartita* (Link) H.P.Linder , *Austrostipa aristiglumis* (F.Muell.) S.W.L.Jacobs & Everett and *Paspalidium constrictum* (Domin) C.E.Hubb., Appendix 3). Flood frequency was positively correlated with graminoid species richness ($t = 4.7$, d.f. = 173, $P < 0.001$) and was negatively correlated with total and forb species richness ($t = -2.2$, d.f. = 173, $P = 0.027$ and $t = -3.3$, d.f. = 173, $P = 0.001$, respectively).

General impacts of management disturbances

Sites with lower native species richness tended to have histories of recent or extended cultivation, or were affected by a combination of factors such as sustained heavy grazing, a high frequency of flooding or drought. Introduced species that were often present at such sites included **Urochloa panicoides* P.Beauv., **Echinochloa colona* (L.) Link, **Rapistrum rugosum*, **Physalis lanceifolia* Nees, **Cucumis myriocarpus* Naudin, **Cirsium vulgare* (Savi) Ten., **Polygonum aviculare* L., **Tribulus terrestris* L. and **Xanthium occidentale* Bertol. Certain native species were also common at such sites, including *Salsola kali* var. *kali*, *Sclerolaena muricata* var. *muricata* (Moq.) Domin, *Chloris truncata*, *Portulaca oleracea* L., *Convolvulus remotus* R.Br., *Sida trichopoda* and *Boerhavia dominii*. Not all of these species were present at a given disturbed site, and some of these species also occurred at undisturbed sites (i.e. they were generalist species).

Several native species were more frequently abundant at sites that had not been subject to severe management-related disturbances, for example *Ptilotus semilanatus*, *Themeda avenacea* (F.Muell.) Maiden & Betche, *Vittadinia cuneata*, *Astrebla lappacea*, *Maireana* spp. and *Eulalia aurea* (Appendices 1–3).

Environmental determinants of composition

Environmental variables accounted for ~61.3% of the explained variance in the species cover data. Species composition was influenced by several environmental variables (Table 2) mostly related to soil type (and, hence, topsoil chemistry), time of sampling, rainfall and plot location (easting and northing). Species associated with higher available phosphorus (and, hence, brown clay soils) included *Astrebla lappacea*, **Tribulus* spp., *Dactyloctenium radulans*, **Urochloa panicoides*, *Paspalidium constrictum*, *Cucumis myriocarpus*, *Erodium crinitum* Carolin, *Sclerolaena birchii* (F.Muell.) Domin, *Digitaria brownii* (Roem. & Schult.) Hughes and *Amaranthus macrocarpus* Benth. Species negatively associated with available phosphorus (i.e. associated with grey to black clay soils) included *Dichanthium sericeum*, *Aristida leptopoda*, *Chloris truncata*, *Neptunia gracilis* and *Goodenia fascicularis* F.Muell. & Tate.

Sites on grey to black clay soils were more common in the east of the region and sites on brown clay soils were more common in the west of the study region (Table 1). Grasslands in the east of the study region were often dominated by grasses such as *Aristida leptopoda*, *Dichanthium sericeum*, *Panicum decompositum*, *Austrodanthonia bipartita* and *Austrostipa* spp. Although some of these species were also dominant further west, *Astrebla lappacea*, *Enteropogon acicularis*, *Paspalidium jubiflorum* and **Urochloa panicoides* appeared only to be dominant in the west of the study region.

Total, native, grass and forb species richness trended in a similar direction in ordination and were correlated with the annual rainfall vector (Fig. 3). Further, univariate analysis suggested annual rainfall was positively correlated with these richness variables (total, $t = 2.6$, d.f. = 173, $P = 0.010$; native, $t = 1.8$, d.f. = 173, $P = 0.070$; and grass, $t = 3.4$, d.f. = 173, $P < 0.001$). Spearman's rank tests also recognised positive correlations between available phosphorus in the topsoil and introduced species richness ($t = 3.7$, d.f. = 173, $P < 0.001$) and sub-shrub species richness ($t = 2.4$, d.f. = 173, $P = 0.020$). Available phosphorus was negatively correlated with native species richness ($t = -2.7$, d.f. = 173, $P = 0.008$) and grass species richness ($t = -2.5$, d.f. = 173, $P = 0.014$).

The occurrence of past cultivation influenced some soil variables. Percentage organic carbon in the topsoil was significantly lower at cultivated sites ($F_{1,168} = 4.54$, $P = 0.035$), as was electrical conductivity ($F_{1,168} = 6.40$, $P = 0.012$).

Discussion

The relative importance of disturbance-related and environmental variables

Floristic composition of Moree Plains grasslands was explained more by environmental variables (61.3% of explained variance) than by disturbance-related variables (37.6%). This supports the findings from similar grasslands, where environmental variables have a greater influence on species composition than management-related variables at both the local scale and regional scale (e.g. Orr 1981; Fensham *et al*. 2000). The greater influence of environmental variables is probably related to the strong temporal influence on composition, as it is well known that Mitchell grasslands respond strongly to rainfall and its interaction with temperature (Orr 1981; Orr and Holmes 1984; Campbell 1989; Orr and Evenson 1991*a*; Lewis 2006).

Environmental variables

Rainfall was an important variable in explaining grassland species composition (Table 2). This is consistent with the findings of previous studies in Mitchell grasslands in Queensland where the longest floristic gradient was aligned with climatic variables associated with rainfall (Fensham _et al._ 2000). Changes in Mitchell grasslands brought about by seasonal rainfall and drought have also been reported by Orr and Holmes (1984), Campbell (1989), Orr and Evenson (1991_a_), Bowman _et al._ (1997) and Phelps and Bosch (2002).

The influence of sampling time on composition is not unexpected given that sites sampled on any given day were often geographically close; up to four sites were sampled on any one property and nearby properties were often sampled on the same day. Hence, nearby sites had usually experienced similar climatic conditions before sampling. The effect of sampling time on species composition was also influenced by differences between the 2 years of sampling, as differing seasonal conditions (e.g. a winter drought in 2002) in the lead-up to sampling likely influenced composition. Previous studies have shown that there can be significant variations in species composition and richness in these grasslands among years and seasons, depending on

Fig. 4. Transitional model for plant biodiversity status in native grasslands on clay soils of the Moree Plains, northern NSW. High, moderate and low biodiversity levels are defined by composition and richness (based on sampling 20 × 20 m quadrats in autumn), with detailed definitions provided below. Native grassland is defined as >50% of the vegetative ground cover composed of native herbaceous species, over half of the total number of species are native, and where there is at least 10% standing vegetation cover. Extirpated sites are no longer considered native grassland and have very low plant diversity due to elimination of most species from above and below-ground (e.g. cultivated paddocks). Vertical arrows represent changes (reversible and irreversible) in biodiversity status that are driven by a combination of management influences and environmental influences. Rainfall regime (SOI, southern oscillation index) is represented as a horizontal arrow as rainfall can have an overriding influence on plant richness and influence grassland response to management drivers and other environmental drivers (e.g. the impacts of grazing are likely to be greater during periods of low rainfall when plants are physiologically stressed). Transitions between diversity levels (i.e. vertical arrows) are based on the current study, Lewis _et al._ (2008), other literature and hypothesised changes that could not be determined from this study (Table 3). Curved broken lines represent the boundaries between plant diversity levels. Biodiversity status definitions: ‘High’, high native species richness in autumn (at least 30 native species per 0.04-ha quadrat) with a low number (≤7) and cover (<10%) of introduced species, occurrence of rare species (listed for NSW or nationally), ≥3 native herbaceous species with ≥6% cover and good structural diversity with a mix of forbs, grasses, sub-shrubs and graminoids. Typical grasses might include: _Astrebla elymoides_, _A. lappacea_, _Dichanthium sericeum_, _Aristida leptopoda_, _Austrodanthonia bipartita_, _Chloris truncata_, _Enteropogon acicularis_, _Panicum decompositum_, _P. buncei_ F.Muell. ex Benth., _P. queenslandicum_ Domin, _Digitaria divaricatissima_ (R.Br.) Hughes, _Eragrostis parviflora_ (R.Br.) Trin., _Eriochloa pseudoacrotricha_ (Stapf ex Thell.) J.M.Black, _E. crebra_ S.T.Blake, _Eulalia aurea_, _Paspalidium globoideum_ (Domin) Hughes, _P. constrictum_, _Sporobolus caroli_ Mez, _Thellungia advena_ Stapf and _Themeda avenacea_. Typical forbs might include: _Alternanthera denticulate_ R.Br., _Asperula cunninghamii_ Airy Shaw & Turrill, _Boerhavia dominii_, _Brachycome ciliaris_ (Labill.) Less., _Calotis scabiosifolia_ Sond., _Chamaesyce drummondii_ (Boiss.) D.C.Hassall, _Convolvulus erubescens_ Sims, _Crotalaria dissitiflora_ Benth., _Cullen tenax_ (Lindl.) J.W.Grimes, _Desmodium campylocaulon_ Benth., _Eclipta platyglossa_ F.Muell., _Einadia nutans_ (R.Br.) A.J.Scott, _Eryngium plantagineum_ F.Muell., _Glycine latifolia_ (Benth.) Newell & Hymowitz, _Goodenia fascicularis_, _Hibiscus trionum_ L., _Marsilea drummondii_, _Mimulus gracilis_ R.Br., _Minuria integerrima_ (DC) Benth., _Neptunia gracilis_, _Oxalis perennans_ Haw., _Phyllanthus virgatus_ G.Forst., _Ptilotus semilanatus_, _Pycnosorus globosus_ Benth., _Rhynchosia minima_ (L.) DC, _Rostellularia adscendens_ (R.Br.) R.M.Barker, _Sida trichopoda_, _Solanum esuriale_, _Verbena gaudichaudii_ (Briq.) P.W.Michael, _Vittadinia cuneata_ and _Wahlenbergia communis_ Carolin. Typical graminoids include: _Juncus aridicola_ L.A.S.Johnson, _J. usitatus_ L.A.S.Johnson, _Fimbristylis dichotoma_ (L.) Vahl, _Eleocharis pallens_, _Cyperus bifax_ other _Cyperus_ spp., _Caesia calliantha_ R.J.F.Hend., _Carex inverse_ R.Br. and _Crinum flaccidum_ Herb. Typical subshrubs include: _Atriplex semibaccata_ R.Br., _Eremophila debilis_ (Andrews) Chinnock, _Leiocarpa websteri_ (S.Moore) Paul G. Wilson, _Maireana aphylla_ (R.Br.) Paul G. Wilson, _M. decalvans_, _M. microphylla_ (Moq.) Paul G. Wilson, _Sclerolaena muricata_ var. _villosa, Swainsona_ spp. and _Einadia hastata_ (R.Br.) A.J.Scott. Assuming winter rainfall occurs, several annual species (mostly introduced species) become part of the interstitial component (see list of winter annuals below). ‘Moderate’, moderate native species richness in autumn (15–30 native species per 0.04 ha) with a relatively low number (<10) and cover (<25%) of introduced species, and often dominated by <3 native herbaceous species. Although many of the species typical of ‘High’ biodiversity sites may be present, some dominant perennial grass species have been removed due to certain forms of disturbance and others have become more abundant. Grasses that rapidly disperse (i.e. by wind or livestock) will be common at sites recovering from severe disturbances like cultivation. Typical grasses might include: _Dichanthium sericeum_, _Aristida leptopoda_, _A. latifolia_ Domin, _Chloris truncata_, _Enteropogon acicularis_, _Eriochloa pseudoacrotricha_, _Panicum decompositum_, _Sporobolus caroli_, _S. mitchellii_ (Trin.) C.E.Hubb. ex S.T.Blake, _Dactyloctenium radulans_, *_Echinochloa colona_, _Eragrostis parviflora_, _E. setifolia_ Nees, _Leptochloa divaricatissima_ S.T.Blake, _Paspalidium jubiflorum_ and *_Urochloa panicoides._ In addition to some of the common (i.e. disturbance-tolerant) forbs, graminoids and sub-shrubs listed above for ‘High’ biodiversity sites, other species include: *_Tribulus terrestris_, _T. micrococcus_ Domin, _Sclerolaena muricata_ var. _muricata_, _Portulaca oleracea_, *_Medicago_ spp., _Salsola kali_ var. _kali_, *_Xanthium_ spp., *_Rapistrum rugosum_, _Cucumis_ spp., *_Malvastrum americanum_ (L.) Torr., *_Physalis lanceifolia_, _Polymeria pusilla_ R.Br. and _Ipomoea lonchophylla_ J.M. Black. Native taxa (e.g. grazing-sensitive species) such as _Ptilotus semilanatus_, _Themeda avenacea_, _Eulalia aurea_, _Vittadinia cuneata_, _Asperula cunninghamii_, _Desmodium campylocaulon_, _Glycine_ spp. and _Swainsona murrayana_ Wawra are less likely to be recorded in this stage. ‘Low’, low native species richness in autumn (<15 native species per 0.04 ha), often with a high number (≥10) or cover (≥25%) of introduced and annual species, poor structural diversity (i.e. mostly annual forbs and grasses), no rare species (listed for NSW or nationally) and often dominated by <3 herbaceous species. Although some of the species typical of ‘High’ biodiversity sites may be present (i.e. disturbance-tolerant species), many species have been removed. Annual grasses and forbs, and introduced species are likely to be abundant. Typical grasses include: *_Urochloa panicoides_, _Chloris truncata_, _Dichanthium sericeum_, _Sporobolus caroli_, _Panicum decompositum_, _Enteropogon acicularis_, *_Echinochloa colona_, *_Avena fatua_ L. (winter only) and *_Phalaris paradoxa_ L. (winter only). Other typical species include: _Salsola kali_ var. _kali_, *_Tribulus terrestris_, _T. micrococcus_, _Sclerolaena muricata_ var. _muricata_, _S. birchii_, _Portulaca oleracea_, *_Rapistrum rugosum_, *_Cucumis_ spp., *_Cirsium vulgare_, *_Polygonum_ spp., _Convolvulus remotus_, _Sida trichopoda_, _Solanum esuriale_, *_Malvastrum americanum_, _Boerhavia dominii_, _Verbena gaudichaudii_ and *_Lactuca_ spp. ‘Winter annual species’: a group of annual species that increase in abundance, or usually only occur in late autumn, winter or spring on the Moree Plains. The species include: *_Rapistrum rugosum_, *_Sonchus oleraceus_ L., _Plantago cunninghamii_ Decne., *_Hedypnois rhagadioloides_ (L.) F.W.Schmidt, _Erodium crinitum_, *_Medicago polymorpha_, *_Medicago truncatula_ Gaertn., *_Medicago minima_ (L.) Bartal. other *_Medicago_ spp., *_Conyza bonariensis_ (L.) Cronquist, *_Phalaris paradoxa_, _Daucus glochidiatus_ (Labill.) Fisch _et al._, *_Avena fatua_, _Calotis hispidula_ (F.Muell.) F.Muell., *_Hordeum leporinum_ Link, *_Calendula arvensis_ L., *_Centaurea melitensis_ L., *_Cirsium vulgare_, *_Ciclospermum leptophyllum_ (Pers.) Sprague, *_Echium plantagineum_ L., _Lachnagrostis filiformis_ (G.Forst.) Trin., *_Lolium perenne_ L., *_Aster subulatus_ Michx., *_Bromus cartharticus_ Vahl, *_Silybum marianum_ (L.) Gaertn., and *_Solanum nigrum_ L. Some of these species may be recorded in any of the above biodiversity levels but are likely to be more common at sites with a ‘Low’ or ‘Moderate’ biodiversity status.

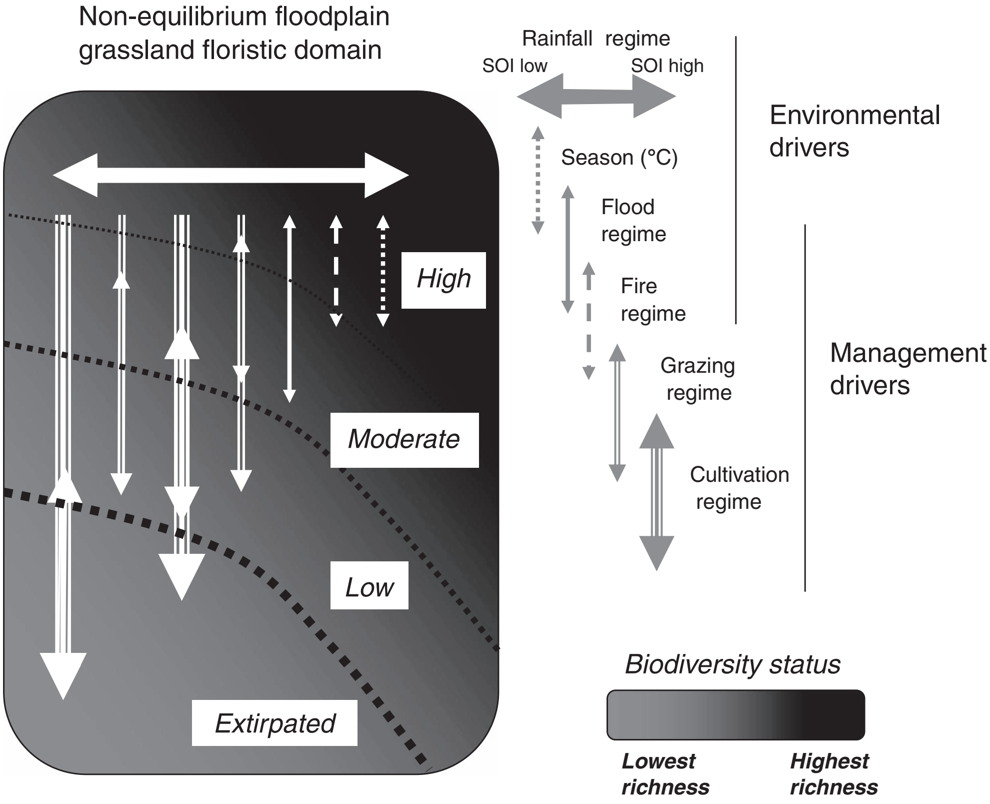
recent rainfall and seasonal timing of rainfall (Orr 1981; Orr and Evenson 1985; Hunter and Earl 1999; Lewis 2006; Lewis *et al.* 2008). For example, at plots that were sampled in 2002 and revisited in 2003, *Astrebla elymoides* increased in abundance, although *Dichanthium sericeum* decreased (data not shown). Fluctuation in the dominance of *Astrebla* spp. and *Dichanthium sericeum* among years was also reported by Williams and Roe (1975). The seasonal conditions that may favour one of these species over the other are still uncertain, although previous studies suggest *D. sericeum* responds well in years of higher rainfall (Roberts 1978; Hunter and Earl 1999).

Differences in composition from east to west across the study region were obvious. Hunter and Earl (1999) also reported longitudinal variations in floristic composition in the region, with chenopod shrublands more common in the west and grasslands in the east. Floristic variation has also been reported for an east–west gradient in grassy woodlands in central NSW (Prober and Thiele 2004). Variations from east to west are probably related to gradients in soil type and climatic conditions (e.g. effective rainfall) across the region.

Soil type and fertility had an important influence on grassland composition (Table 2), with sites on brown clay soils associated with a soil fertility gradient (Table 1). Soil chemistry was also recognised as an important factor influencing species associations in Mitchell grasslands in north-west Queensland (Hall 1982), and is an important determinant of species composition in other Australian grasslands. On the southern tablelands of NSW, Prober *et al.* (2002) reported the dominance of introduced annuals in grassy remnants with nutrient-rich topsoils, with a high correlation between topsoil nitrate and the abundance of introduced annuals. In the current study, topsoil percentage organic carbon and available phosphorus were both positively correlated with introduced species richness ($t = 6.7$, d.f. = 173, $P < 0.001$ and $t = 3.7$, d.f. = 173, $P < 0.001$, respectively). This is not surprising given that introduced species are often more competitive than natives under conditions of enhanced soil fertility (Wijesuriya and Hocking 1999), with traits favouring rapid colonisation and effective reproduction (Trémont and McIntyre 1994). Similarly, in the Walgett region, Bowman *et al.* (1997) reported that paddocks in 'poor' condition (i.e. with lower densities of *Astrebla* spp.) had higher organic carbon and nitrogen, which was correlated with a greater component of annuals such as **Medicago* spp.

Disturbance-related variables

Although environmental variables explained more of the variance in species composition in these grasslands than disturbance-related variables, management effects were discernible. The effects of grazing on grassland species composition have been widely reported (e.g. McIntyre and Lavorel 2001; McIntyre *et al.* 2003; Barbaro *et al.* 2004), with the importance of grazing varying between studies and grassland types. For example, grazing was an important variable in south-east Queensland grasslands, accounting for 4% of the explained variation in species composition (McIntyre *et al.* 2003), and grazing intensity was the strongest influence on composition of temperate grassy woodlands in northern NSW (Clarke 2003). Another study of temperate grasslands on the northern tablelands of NSW using a sampling approach different from Clarke (2003), found lithology,



altitude and soil disturbance to be the most important variables in explaining floristic composition, with grazing being of lesser importance (McIntyre and Lavorel 1994). In the current study we could determine only the effects of recent grazing intensity. However, it is likely that long-term grazing history has had an influence on the present grassland composition (e.g. Lunt 1997; Lunt *et al*. 2007). Intense livestock grazing for long periods of time (i.e. over-grazing) could result in the loss of dominant grasses, such as *Astrebla lappacea*, *Astrebla elymoides*, *Dichanthium sericeum*, *Eulalia aurea* and *Themeda avenacea* (Beadle 1948; Williams and Mackey 1983; Phelps and Bosch 2002; Lewis 2006), as well as several grazing-sensitive species (Appendix 1; Lewis *et al*. 2008).

Species composition and richness was also influenced by past cultivation. Differences in species composition and richness between previously cultivated areas and nearby uncultivated areas were also recorded at an *Astrebla–Dichanthium sericeum* grassland reserve (Kirramingly Nature Reserve), 13–22 years after the last cultivation (Lewis *et al*. 2008). Studies elsewhere (e.g. tall-grass prairie, Mediterranean steppe and calcareous grassland) suggest it might take decades or even centuries for richness and composition to return to a pre-disturbance condition after several decades of cultivation (Kindscher and Tieszen 1998; Römermann *et al*. 2005; Fagan *et al*. 2008). The decreases in species richness and changes in composition at previously cultivated sites are probably related to the differing abilities of species to colonise disturbed land (e.g. through wind dispersal) and cope with changes in abiotic conditions. Given that seed banks of many perennial grasses, including *Astrebla* spp. have limited long-term viability in the soil (<5 years) (O'Connor and Pickett 1992; Morgan 1998) continuous cultivation for a longer period will lead to local extinction of such perennial grasses, necessitating dispersal and recruitment from surrounding areas. Some species (e.g. *Dichanthium sericeum*) are able to recolonise previously cultivated paddocks relatively quickly (especially with the aid of careful grazing management to spread seed) although other species (e.g. *Astrebla* spp.) may be more difficult to recolonise after several years of cultivation (Appendix 2). Changes in the measured soil properties were observed in the current study with decreases in organic carbon and electrical conductivity at cultivated sites. Although a return of organic carbon to cultivated areas might encourage recovery of species composition in these grasslands, such management intervention could also encourage introduced species (see above and also McIntyre and Martin 2001).

Most of the species that were more abundant at frequently flooded sites in these grasslands are known to thrive in wet conditions (e.g. *Cyperus bifax*, *Eleocharis pallens*, *Marsilea drummondii* and *Paspalidium jubiflorum*). There was no indication of a reduction in perennial grass abundance at frequently flooded sites, as has been reported for similar grasslands in north-west Queensland (Hall 1982). However, *Astrebla lappacea* abundance was negatively associated with frequent flooding (Appendix 3; also see Campbell 1989; Bowman *et al*. 1997) and total species richness was negatively correlated with flooding frequency (also observed by Dick 1993). Although flooding in our study did not have a major influence on composition, the response of different grassland species to varying degrees of flooding and inundation requires further investigation, given the potential changes in natural flooding regimes brought about by irrigated and dryland farming development. Season of flooding may also influence species composition as flooding during the active growth phase (i.e. summer) perhaps has a more severe effect on perennial summer-growing grasses, than flooding at other times of the year. There may also be complex interactions between the timing of flooding and grazing, as suggested by Hall (1982).

Severe disturbances in these grasslands can result in the removal of the dominant perennial grasses (i.e. matrix species, such as *Astrebla* spp.) that are able to tolerate natural disturbances (e.g. fire, macropod grazing and drought). Such disturbances reduce the conservation value of these grasslands because some matrix species (e.g. *Astrebla* spp.) and intolerant interstitial species are replaced by disturbance specialists and invasion of such species may influence the recovery of severely disturbed areas (Belsky 1986; Graham and Hutchings 1988; Bowman *et al*. 1997; Römermann *et al*. 2005). McIntyre and Lavorel (1994) proposed a similar model for temperate grasslands in northern NSW, although the relative proportion of tolerant species to intolerant species appears to be higher for the grasslands in the current study. This tolerance of the Moree Plains grasslands to management disturbances may be related to the severity of natural disturbances (e.g. frequent drought and water stress, periodic flooding, shrinking and swelling of the clay soils) in this environment during the period of their evolution. The tolerance of these grasslands is fortunate given the extent of landscape modification in the study region through a long history of grazing and large areas of cultivation for cereal crops. Intensive agricultural uses (e.g. cotton farming) that were not investigated in this study could have a greater influence on the persistence of native grassland species than occasional dryland cropping, and it cannot be assumed that native grasslands will re-establish a natural composition after such intensive landscape modification.

Transitional model cf. *states and transitions*

Conceptual models (e.g. McArthur *et al*. 1994) that depict changes in composition are useful in management (Westoby *et al*. 1989; Whalley 1994). Mitchell grasslands are widely regarded as having the capacity to regain their structure and composition after natural and management-imposed disturbances (Harrington *et al*. 1984; Orr and Holmes 1984). Therefore, defining a series of quasi-stable states for these grasslands may be inappropriate in the context of their changes in floristic composition in response to periodic droughts and floods. Although state-and-transition models have previously been proposed for *Astrebla* spp. and *Dichanthium* spp. grasslands (McArthur *et al*. 1994; Phelps and Bosch 2002), these models are of limited use in terms of grassland biodiversity status. In north-west NSW, it is unlikely that all of the states defined by McArthur *et al*. (1994) are stable, where a system is considered stable if it persists despite perturbations (Westoby *et al*. 1989). Furthermore, some of the compositional states defined for central-western Queensland do not seem to apply in NSW (e.g. the herbfield states in Phelps and Bosch 2002). The ability to define stable states may be further complicated by variations in the abundance of different matrix species in response to rainfall events both within and among years. Therefore, we propose a conceptual model where the floristic domain of the

Table 3. Known and hypothesised causes for transitions in biodiversity status (defined by species composition and richness) in Fig. 4, and for Mitchell grasslands elsewhere

Known causes are based on findings in the current research and other research conducted in the Moree Plains grasslands (Clarke *et al.* 1998; Lewis 2006; Lewis *et al.* 2008). Hypothesised causes are based on literature from elsewhere (e.g. other Mitchell grasslands)

Status change	Known causes	Hypothesised causes
Minor decrease	Drought, certain livestock grazing regimes, altered flooding regime, resulting in increased flooding frequency	Certain fire regimes (e.g. repeated burning in autumn or during droughts, or in combination with heavy livestock grazing) (Roberts 1978; Leigh and Holgate 1979; Scanlan 1980; Mulham 1985)
Minor increase	Complete removal of livestock (e.g. Kirramingly Nature Reserve), adequate rainfall for plant growth during the growing season (spring, summer or autumn)	Conservative livestock grazing regimes (Everist 1964; Orr 1980*b*; Cunningham and Milthorpe 1981; Williams and Mackey 1983; Foran *et al.* 1985; Orr and Evenson 1991*a*; Bowman *et al.* 1997; Fensham *et al.* 1999), fire after a series of good seasons (i.e. when grass cover is high) (Wright 2001)
Moderate decrease	Cultivation, extended periods of over-grazing	Extended periods of drought often in combination with livestock grazing (Francis 1935; Williams and Roe 1975; Orr 1981), increased flooding frequency during growing season (Hall 1982; Bowman *et al.* 1997)
Moderate increase	Removal of livestock grazing (e.g. Kirramingly Nature Reserve), although this may not be sufficient after extended periods of cultivation	Careful grazing management involving rests from grazing and low stocking rates to allow recruitment of all native species (including long-lived perennial grasses) (Campbell 1989; Roe and Allen 1993; Campbell *et al.* 1996; Bowman *et al.* 1997), a series of good seasons (i.e. with above average summer rainfall) (Orr 1981; Orr and Holmes 1984; Fensham *et al.* 2000)
Major decrease	Extended periods of cultivation (>10 years consecutive)	Extended periods of over-grazing (Francis 1935; Beadle 1948; Williams and Roe 1975; Orr 1980*a*; Bowman *et al.* 1997; Phelps and Bosch 2002), note: recovery from such disturbance from the seed bank is more likely than following extended periods of cultivation
Major increase	Careful management after a short period of cultivation (<5 years), involving grazing at strategic times to aid in seed dispersal from neighbouring grasslands and favourable seasons for plant growth	Restoration of degraded grassland involving addition of native seed and removal of introduced species (e.g. Pywell *et al.* 2002; Martin and Wilsey 2006; Gibson-Roy *et al.* 2007)

grassland transitions is between high, moderate and low plant biodiversity status (Fig. 4). These broad classes are explicitly defined by species composition and richness and are driven by both environmental and management factors (Fig. 4). This model is based on the correlations in this study and observations from the literature and field work (Table 3). There needs to be further investigation in order to understand the shifts in botanical composition over longer time frames, and the thresholds required to produce major shifts in botanical composition of these grasslands.

Conclusions

Environmental influences (e.g. soil and rainfall) explained a greater proportion of the variance in species composition than disturbance-related variables in the Moree Plains grasslands. Nevertheless, past cultivation, stocking rate and flooding frequency all influenced species composition to a small but significant degree (together explaining 37.6% of the variation in species composition). Although Mitchell grasslands are resilient to natural disturbances, severe anthropogenic disturbances (e.g. cultivation for several years) can remove dominant grass species and encourage disturbance specialists. Both long-term floristic monitoring and manipulative experiments are needed to further unravel the dynamics of these endangered grasslands.

Acknowledgements

This work was undertaken for a PhD degree for T. Lewis who was supported by an Australian Postgraduate Award. Financial support was received from The Grassy Ecosystems Grant Program (a joint initiative of the World Wide Fund for Nature Australia and the National Heritage Trust); the NSW National Parks and Wildlife Service; and the University of New England. We are grateful to all the landholders that let us onto their properties. Staff at the Moree RLPB office were helpful in providing access to permit records and with management information regarding stock routes and reserves.

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Manuscript received 14 October 2008; accepted 24 December 2008

Appendix 1

Mean species abundance score (1–6) for species recorded at sites with different grazing regimes in the year prior to sampling: (1) ungrazed sites (*n* = 24); (2) light to moderately grazed sites (*n* = 119); and (3) heavily grazed sites (*n* = 37). Ungrazed sites had not been grazed for at least 1 year prior to sampling; light to moderately grazed sites had stocking rates of ≤5 DSE/ha; and heavily grazed sites had stocking rates of >5 DSE/ha. Only species with 10 occurrences or more across 184 sites have been listed. Introduced species are indicated by an *

Species	Ungrazed		Light-moderate stocking rate		High stocking rate	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
*_Acacia farnesiana_	1.21	0.26	1.19	0.12	1.57	0.20
Alternanthera denticulata	0.46	0.16	0.81	0.08	0.76	0.15
Amaranthus macrocarpus var. _pallidus_	0.00	0.00	0.18	0.05	0.11	0.08
Aristida leptopoda	1.46	0.31	1.08	0.12	1.16	0.21
Aristida platychaeta	0.29	0.19	0.17	0.06	0.05	0.05
Aristida ramosa	0.54	0.26	0.23	0.07	0.49	0.23
Asperula conferta	0.00	0.00	0.33	0.06	0.14	0.08
Astrebla elymoides	0.79	0.32	1.38	0.16	1.30	0.25
Astrebla lappacea	0.50	0.22	0.82	0.14	1.22	0.28
Atriplex semibaccata	0.29	0.14	0.24	0.05	0.35	0.12
Atriplex species B	0.08	0.08	0.10	0.04	0.30	0.11
Austrodanthonia bipartita	0.46	0.17	0.33	0.06	0.32	0.11
Austrostipa aristiglumis	0.38	0.22	0.18	0.06	0.59	0.19
Boerhavia dominii	1.79	0.19	0.90	0.09	1.16	0.16
Bothriochloa decipiens	0.63	0.27	0.06	0.04	0.32	0.16
Brachyscome ciliaris var. _ciliaris_	0.08	0.08	0.08	0.03	0.19	0.09
Brachyscome heterodonta var. _heterodonta_	0.33	0.16	0.03	0.02	0.19	0.09
Calotis scabiosifolia var. _scabiosifolia_	0.13	0.09	0.24	0.06	0.11	0.08
Carex inversa	0.04	0.04	0.09	0.04	0.11	0.06
*_Centaurea melitensis_	0.29	0.14	0.06	0.03	0.19	0.09
Chamaesyce drummondii	0.71	0.19	0.65	0.08	0.46	0.14
Chloris truncata	1.00	0.21	1.42	0.11	1.32	0.18
Chloris ventricosa	0.08	0.08	0.07	0.03	0.41	0.15
*_Cirsium vulgare_	0.21	0.13	0.08	0.03	0.08	0.06
Convolvulus erubescens	0.83	0.20	0.85	0.09	0.73	0.15
Convolvulus remotus	0.08	0.08	0.15	0.05	0.32	0.15
*_Conyza bonariensis_	0.67	0.21	0.18	0.05	0.59	0.14
Crinum flaccidum	0.29	0.14	0.11	0.04	0.14	0.08
Cucumis melo subsp. _agrestis_	0.21	0.12	0.10	0.03	0.14	0.06
*_Cucumis myriocarpus_ subsp. _leptodermis_	0.00	0.00	0.08	0.03	0.03	0.03
Cullen tenax	0.58	0.19	0.57	0.08	0.62	0.15
Cyperus bifax	1.13	0.23	1.12	0.11	1.08	0.22
Dactyloctenium radulans	0.00	0.00	0.33	0.07	0.49	0.16
Daucus glochidiatus	0.33	0.16	0.10	0.04	0.03	0.03
Desmodium campylocaulon	0.25	0.14	0.38	0.07	0.57	0.17
Dichanthium sericeum	2.29	0.33	2.36	0.16	2.32	0.25
Digitaria brownii	0.13	0.09	0.00	0.00	0.16	0.09
Digitaria divaricatissima	0.50	0.17	0.57	0.09	0.43	0.14
Digitaria porrecta	0.17	0.12	0.18	0.06	0.08	0.06
*_Echinochloa colona_	0.00	0.00	0.26	0.06	0.11	0.08
Eclipta platyglossa	0.21	0.12	0.20	0.05	0.27	0.11
Einadia hastata	0.21	0.12	0.18	0.05	0.03	0.03
Einadia nutans subsp. _linifolia_	0.29	0.14	0.18	0.05	0.35	0.13
Einadia nutans subsp. _nutans_	0.67	0.20	0.20	0.05	0.35	0.12
Einadia polygonoides	0.25	0.11	0.34	0.06	0.41	0.12
Eleocharis pallens	0.08	0.08	0.42	0.09	0.32	0.15
Elymus species B	0.08	0.08	0.05	0.03	0.22	0.10
Enteropogon acicularis	1.63	0.25	1.70	0.13	1.89	0.21
Eragrostis alveiformis	0.21	0.12	0.14	0.05	0.22	0.10
Eragrostis parviflora	0.58	0.19	0.62	0.09	0.43	0.14
Eremophila debilis	0.21	0.12	0.08	0.03	0.19	0.09
Eriochloa crebra	0.63	0.21	0.63	0.09	1.00	0.19
Eriochloa pseudoacrotricha	0.50	0.22	0.28	0.07	0.30	0.13
Erodium crinitum	0.00	0.00	0.17	0.05	0.19	0.09
Eryngium plantagineum	0.13	0.09	0.10	0.04	0.16	0.09
Euchiton sphaericus	0.63	0.19	0.12	0.04	0.05	0.04

Appendix 1 (*continued*)

Species	Ungrazed		Light-moderate stocking rate		High stocking rate	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
Eulalia aurea	0.50	0.22	0.26	0.07	0.14	0.10
Fimbristylis dichotoma	0.17	0.12	0.23	0.06	0.00	0.00
Glycine latifolia	0.21	0.12	0.08	0.04	0.00	0.00
Glycine tabacina	0.21	0.12	0.11	0.04	0.05	0.05
Goodenia fascicularis	0.58	0.18	0.89	0.09	0.70	0.16
Hibiscus trionum	0.17	0.12	0.27	0.06	0.22	0.10
Ipomoea lonchophylla	0.13	0.13	0.21	0.06	0.22	0.11
Iseilema membranaceum	0.25	0.14	0.27	0.06	0.27	0.11
Juncus usitatus	0.33	0.13	0.24	0.05	0.70	0.15
**Lactuca saligna*	0.29	0.14	0.08	0.04	0.11	0.08
Leiocarpa brevicompta	0.00	0.00	0.25	0.06	0.16	0.09
Leiocarpa websteri	0.71	0.21	0.68	0.08	0.70	0.15
Leptochloa divaricatissima	0.92	0.23	0.51	0.08	1.11	0.18
Maireana aphylla	0.25	0.12	0.18	0.06	0.08	0.05
Maireana decalvans	0.33	0.16	0.20	0.05	0.38	0.12
Maireana microphylla	0.17	0.08	0.06	0.02	0.08	0.06
**Malvastrum americanum*	1.00	0.20	0.82	0.09	0.49	0.13
Marsilea drummondii	0.42	0.18	0.52	0.08	0.70	0.15
**Medicago polymorpha*	0.42	0.17	0.86	0.10	0.59	0.15
**Medicago truncatula*	0.17	0.12	0.18	0.06	0.19	0.09
Minuria integerrima	0.21	0.12	0.24	0.05	0.35	0.12
Neptunia gracilis	1.00	0.19	1.05	0.09	1.14	0.16
**Opuntia stricta*	0.08	0.06	0.03	0.02	0.19	0.09
Oxalis perennans	1.17	0.20	0.87	0.09	0.78	0.16
Panicum buncei	0.46	0.17	0.29	0.06	0.38	0.12
Panicum decompositum	1.50	0.29	1.54	0.10	1.65	0.16
Panicum queenslandicum	0.38	0.16	0.31	0.06	0.22	0.10
Paspalidium constrictum	0.42	0.21	0.24	0.06	0.24	0.10
Paspalidium globoideum	0.38	0.23	0.22	0.05	0.27	0.11
Paspalidium jubiflorum	0.25	0.17	0.30	0.08	0.30	0.13
**Phyla canescens*	0.21	0.15	0.13	0.05	0.11	0.08
Phyllanthus virgatus	0.42	0.17	0.43	0.07	0.38	0.12
**Physalis lanceifolia*	0.04	0.04	0.14	0.04	0.00	0.00
Plantago cunninghamii	0.13	0.09	0.12	0.04	0.03	0.03
**Polygonum aviculare*	0.25	0.14	0.10	0.04	0.05	0.05
Polymeria pusilla	0.17	0.12	0.25	0.06	0.05	0.05
Portulaca oleracea	0.58	0.16	0.92	0.09	0.84	0.16
Pratia concolor	0.08	0.08	0.32	0.07	0.11	0.08
Ptilotus semilanatus	0.42	0.16	0.19	0.05	0.05	0.05
Pycnosorus globosus	0.21	0.12	0.45	0.07	0.03	0.03
**Rapistrum rugosum*	1.08	0.24	0.92	0.09	1.08	0.17
Rhagodia spinescens	0.21	0.10	0.24	0.06	0.38	0.12
Rhynchosia minima	0.50	0.19	0.39	0.07	0.41	0.14
Rostellularia adscendens	0.04	0.04	0.08	0.03	0.00	0.00
Rumex brownii	0.38	0.13	0.13	0.04	0.19	0.09
Rumex tenax	0.21	0.12	0.11	0.03	0.05	0.05
Salsola kali var. *kali*	0.08	0.06	0.16	0.04	0.16	0.09
Sclerolaena birchii	0.00	0.00	0.03	0.02	0.19	0.09
Sclerolaena muricata var. *muricata*	0.75	0.22	0.83	0.09	0.86	0.17
Sclerolaena muricata var. *villosa*	0.75	0.19	1.10	0.09	0.95	0.15
Sida cunninghamii	0.04	0.04	0.12	0.04	0.11	0.06
Sida spinosa	0.25	0.12	0.07	0.03	0.11	0.08
Sida trichopoda	0.83	0.19	1.11	0.08	0.62	0.15
Solanum esuriale	1.29	0.21	1.21	0.09	1.11	0.17
**Sonchus oleraceus*	0.63	0.19	0.35	0.07	0.41	0.13
Sporobolus caroli	0.54	0.18	0.68	0.08	0.54	0.16
Sporobolus mitchellii	0.08	0.08	0.28	0.08	0.11	0.08
Swainsona queenslandica	0.25	0.12	0.06	0.02	0.05	0.05
Thellungia advena	0.50	0.17	0.66	0.10	0.62	0.15
Themeda avenacea	0.29	0.15	0.10	0.04	0.16	0.10

Appendix 1 (*continued*)

Species	Ungrazed		Light-moderate stocking rate		High stocking rate	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
Trianthema triquetra	0.00	0.00	0.16	0.05	0.19	0.09
Tribulus micrococcus	0.63	0.24	0.45	0.09	0.30	0.12
**Tribulus terrestris*	0.00	0.00	0.29	0.08	0.11	0.08
**Urochloa panicoides*	1.13	0.25	0.39	0.09	0.57	0.15
Verbena gaudichaudii	1.21	0.21	0.56	0.08	0.76	0.15
Vittadinia cuneata	1.29	0.22	0.48	0.07	0.38	0.14
Wahlenbergia communis	0.63	0.18	0.50	0.08	0.38	0.12
**Xanthium occidentale*	0.17	0.10	0.12	0.04	0.05	0.05

Appendix 2

Mean species abundance score (1–6) for species recorded at sites with different cultivation regimes: (1) uncultivated sites ($n = 121$); (2) sites cultivated for $\leq$5 years consecutively ($n = 20$); and (3) sites cultivated for >5 years consecutively ($n = 42$). Only species with 10 occurrences or more across 184 sites have been listed. Introduced species are indicated by an *

Species	Uncultivated		Cultivated ≤5 years		Cultivated >5 years	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
**Acacia farnesiana*	1.54	0.11	1.00	0.35	0.52	0.13
Alternanthera denticulata	0.76	0.08	1.00	0.21	0.55	0.14
Amaranthus macrocarpus var. *pallidus*	0.13	0.05	0.33	0.16	0.05	0.05
Aristida leptopoda	1.23	0.13	0.86	0.33	1.21	0.21
Aristida platychaeta	0.16	0.06	0.00	0.00	0.24	0.11
Aristida ramosa	0.33	0.09	0.29	0.24	0.29	0.13
Asperula conferta	0.25	0.06	0.29	0.16	0.19	0.08
Astrebla elymoides	1.55	0.16	0.76	0.29	0.64	0.19
Astrebla lappacea	1.10	0.15	0.86	0.33	0.14	0.10
Atriplex semibaccata	0.29	0.06	0.33	0.16	0.14	0.08
Atriplex species B	0.20	0.05	0.05	0.05	0.00	0.00
Austrodanthonia bipartita	0.36	0.06	0.24	0.14	0.36	0.13
Austrostipa aristiglumis	0.43	0.09	0.24	0.17	0.05	0.03
Boerhavia dominii	1.21	0.09	1.29	0.21	0.64	0.15
Bothriochloa decipiens	0.22	0.07	0.14	0.14	0.10	0.10
Brachyscome ciliaris var. *ciliaris*	0.12	0.04	0.10	0.10	0.05	0.05
Brachyscome heterodonta var. *heterodonta*	0.14	0.04	0.00	0.00	0.05	0.05
Calotis scabiosifolia var. *scabiosifolia*	0.19	0.05	0.24	0.14	0.19	0.09
Carex inversa	0.07	0.03	0.14	0.10	0.12	0.07
**Centaurea melitensis*	0.18	0.05	0.00	0.00	0.02	0.02
Chamaesyce drummondii	0.62	0.08	0.52	0.19	0.64	0.14
Chloris truncata	1.22	0.10	1.38	0.36	1.55	0.18
Chloris ventricosa	0.16	0.06	0.10	0.07	0.10	0.06
**Cirsium vulgare*	0.07	0.03	0.05	0.05	0.21	0.09
Convolvulus erubescens	0.80	0.08	1.05	0.21	0.69	0.14
Convolvulus remotus	0.12	0.04	0.19	0.13	0.33	0.13
**Conyza bonariensis*	0.34	0.06	0.10	0.10	0.38	0.13
Crinum flaccidum	0.16	0.05	0.14	0.10	0.07	0.05
Cucumis melo subsp. *agrestis*	0.12	0.04	0.10	0.10	0.17	0.07
**Cucumis myriocarpus* subsp. *leptodermis*	0.04	0.02	0.14	0.08	0.05	0.03
Cullen tenax	0.60	0.08	0.57	0.19	0.55	0.14
Cyperus bifax	1.13	0.12	1.33	0.26	0.83	0.16
Dactyloctenium radulans	0.33	0.08	0.38	0.18	0.21	0.09
Daucus glochidiatus	0.14	0.04	0.00	0.00	0.10	0.07
Desmodium campylocaulon	0.36	0.07	0.29	0.16	0.52	0.16
Dichanthium sericeum	2.07	0.14	2.00	0.37	3.17	0.25
Digitaria brownii	0.07	0.03	0.00	0.00	0.02	0.02
Digitaria divaricatissima	0.44	0.08	0.52	0.21	0.76	0.16
Digitaria porrecta	0.08	0.03	0.19	0.11	0.36	0.14
**Echinochloa colona*	0.17	0.05	0.52	0.22	0.07	0.05
Eclipta platyglossa	0.26	0.06	0.10	0.07	0.12	0.06
Einadia hastata	0.14	0.04	0.19	0.13	0.17	0.08
Einadia nutans subsp. *linifolia*	0.26	0.06	0.29	0.16	0.07	0.05
Einadia nutans subsp. *nutans*	0.37	0.07	0.19	0.13	0.10	0.07
Einadia polygonoides	0.37	0.06	0.57	0.18	0.10	0.05
Eleocharis pallens	0.36	0.08	0.29	0.16	0.33	0.15
Elymus species B	0.15	0.05	0.00	0.00	0.00	0.00
Enteropogon acicularis	1.82	0.12	1.86	0.35	1.38	0.22
Eragrostis alveiformis	0.21	0.06	0.19	0.13	0.02	0.02
Eragrostis parviflora	0.48	0.08	0.67	0.25	0.76	0.16
Eremophila debilis	0.17	0.05	0.00	0.00	0.00	0.00
Eriochloa crebra	0.74	0.10	0.67	0.22	0.55	0.15
Eriochloa pseudoacrotricha	0.26	0.07	0.52	0.24	0.33	0.11
Erodium crinitum	0.17	0.05	0.33	0.14	0.00	0.00
Eryngium plantagineum	0.14	0.04	0.10	0.10	0.05	0.05
Euchiton sphaericus	0.12	0.04	0.05	0.05	0.38	0.12
Eulalia aurea	0.34	0.08	0.33	0.21	0.00	0.00

Appendix 2 (_continued_)

Species	Uncultivated		Cultivated ≤5 years		Cultivated >5 years	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
Fimbristylis dichotoma	0.17	0.05	0.24	0.17	0.12	0.08
Glycine latifolia	0.13	0.05	0.10	0.10	0.05	0.05
Glycine tabacina	0.14	0.04	0.10	0.10	0.02	0.02
Goodenia fascicularis	0.84	0.09	0.71	0.21	0.69	0.14
Hibiscus trionum	0.25	0.06	0.14	0.10	0.26	0.10
Ipomoea lonchophylla	0.21	0.06	0.48	0.20	0.12	0.07
Iseilema membranaceum	0.19	0.05	0.29	0.16	0.45	0.13
Juncus usitatus	0.23	0.06	0.24	0.17	0.07	0.05
*Lactuca saligna	0.41	0.07	0.10	0.07	0.24	0.08
Leiocarpa brevicompta	0.14	0.05	0.00	0.00	0.14	0.08
Leiocarpa websteri	0.73	0.08	0.57	0.18	0.57	0.14
Leptochloa divaricatissima	0.69	0.09	0.33	0.16	0.79	0.18
Maireana aphylla	0.24	0.06	0.10	0.07	0.00	0.00
Maireana decalvans	0.36	0.07	0.00	0.00	0.05	0.05
Maireana microphylla	0.12	0.03	0.00	0.00	0.02	0.02
*Malvastrum americanum	0.78	0.09	1.00	0.24	0.62	0.13
Marsilea drummondii	0.60	0.09	0.48	0.18	0.36	0.12
*Medicago polymorpha	0.57	0.08	1.29	0.23	0.95	0.19
*Medicago truncatula	0.20	0.06	0.19	0.13	0.12	0.07
Minuria integerrima	0.21	0.05	0.52	0.19	0.24	0.10
Neptunia gracilis	1.13	0.08	1.10	0.21	0.74	0.14
*Opuntia stricta	0.09	0.03	0.00	0.00	0.05	0.03
Oxalis perennans	0.98	0.09	0.76	0.19	0.67	0.15
Panicum buncei	0.38	0.07	0.33	0.16	0.14	0.08
Panicum decompositum	1.46	0.09	1.57	0.26	1.76	0.20
Panicum queenslandicum	0.33	0.07	0.05	0.05	0.31	0.10
Paspalidium constrictum	0.29	0.07	0.14	0.10	0.24	0.12
Paspalidium globoideum	0.26	0.06	0.19	0.11	0.26	0.11
Paspalidium jubiflorum	0.32	0.09	0.19	0.13	0.24	0.12
*Phyla canescens	0.07	0.04	0.10	0.10	0.31	0.13
Phyllanthus virgatus	0.50	0.08	0.05	0.05	0.31	0.10
*Physalis lanceifolia	0.06	0.03	0.19	0.11	0.17	0.08
Plantago cunninghamii	0.08	0.03	0.19	0.13	0.10	0.07
*Polygonum aviculare	0.06	0.03	0.00	0.00	0.31	0.11
Polymeria pusilla	0.15	0.05	0.10	0.10	0.38	0.12
Portulaca oleracea	0.86	0.08	1.52	0.18	0.50	0.13
Pratia concolor	0.27	0.06	0.24	0.14	0.14	0.08
Ptilotus semilanatus	0.29	0.06	0.00	0.00	0.00	0.00
Pycnosorus globosus	0.36	0.07	0.19	0.11	0.29	0.10
*Rapistrum rugosum	0.96	0.09	1.29	0.21	0.83	0.15
Rhagodia spinescens	0.33	0.06	0.19	0.11	0.10	0.07
Rhynchosia minima	0.40	0.07	0.29	0.17	0.48	0.13
Rostellularia adscendens	0.09	0.04	0.00	0.00	0.00	0.00
Rumex brownii	0.16	0.04	0.19	0.13	0.19	0.08
Rumex tenax	0.13	0.04	0.10	0.07	0.05	0.03
Salsola kali var. _kali_	0.11	0.03	0.14	0.10	0.31	0.10
Sclerolaena birchii	0.07	0.03	0.05	0.05	0.05	0.03
Sclerolaena muricata var. _muricata_	0.70	0.08	1.19	0.32	0.98	0.16
Sclerolaena muricata var. _villosa_	1.20	0.09	0.81	0.22	0.67	0.13
Sida cunninghamii	0.15	0.04	0.00	0.00	0.02	0.02
Sida spinosa	0.09	0.04	0.24	0.14	0.05	0.05
Sida trichopoda	1.04	0.09	1.24	0.19	0.62	0.13
Solanum esuriale	1.43	0.08	0.76	0.21	0.76	0.15
*Sonchus oleraceus	0.42	0.07	0.29	0.16	0.36	0.11
Sporobolus caroli	0.64	0.08	0.95	0.22	0.40	0.12
Sporobolus mitchellii	0.31	0.08	0.10	0.10	0.00	0.00
Swainsona queenslandica	0.10	0.03	0.00	0.00	0.07	0.05
Thellungia advena	0.74	0.10	0.52	0.19	0.29	0.10
Themeda avenacea	0.21	0.06	0.00	0.00	0.00	0.00
Trianthema triquetra	0.16	0.05	0.24	0.14	0.05	0.05

Appendix 2 (*continued*)

Species	Uncultivated		Cultivated ≤5 years		Cultivated >5 years	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
Tribulus micrococcus	0.45	0.09	0.95	0.30	0.21	0.10
**Tribulus terrestris*	0.21	0.07	0.19	0.13	0.19	0.14
**Urochloa panicoides*	0.50	0.09	0.62	0.23	0.55	0.16
Verbena gaudichaudii	0.83	0.09	0.24	0.14	0.57	0.14
Vittadinia cuneata	0.54	0.08	0.29	0.14	0.74	0.14
Wahlenbergia communis	0.50	0.08	0.48	0.19	0.50	0.13
**Xanthium occidentale*	0.08	0.03	0.00	0.00	0.24	0.10

Appendix 3

Mean species abundance score (1–6) for species recorded at sites with different flooding regimes: (1) not flooded, or very rarely flooded (perhaps once in 30 years) (94 sites); (2) flooded, but with less than one flood every 2 years on average (53 sites); and (3) flooded at least once every 2 years on average (37 sites). Only species with 10 occurrences or more across 184 sites have been listed. Introduced species are indicated by an *

Species	Not flooded		Flooded infrequently		Flooded frequently	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
*_Acacia farnesiana_	1.23	0.13	1.15	0.17	1.41	0.20
Alternanthera denticulata	0.64	0.09	0.74	0.12	1.00	0.15
Amaranthus macrocarpus var. _pallidus_	0.13	0.05	0.25	0.09	0.00	0.00
Aristida leptopoda	1.45	0.15	0.75	0.16	1.14	0.22
Aristida platychaeta	0.19	0.07	0.15	0.09	0.08	0.06
Aristida ramosa	0.48	0.12	0.19	0.11	0.08	0.08
Asperula conferta	0.23	0.06	0.26	0.09	0.22	0.10
Astrebla elymoides	1.06	0.16	1.49	0.24	1.41	0.29
Astrebla lappacea	1.09	0.17	0.74	0.19	0.43	0.18
Atriplex semibaccata	0.28	0.06	0.23	0.08	0.27	0.11
Atriplex species B	0.12	0.04	0.25	0.10	0.03	0.03
Austrodanthonia bipartita	0.46	0.08	0.28	0.09	0.14	0.07
Austrostipa aristiglumis	0.45	0.11	0.21	0.09	0.16	0.08
Boerhavia dominii	1.18	0.10	1.13	0.13	0.78	0.17
Bothriochloa decipiens	0.29	0.10	0.13	0.09	0.00	0.00
Brachyscome ciliaris var. _ciliaris_	0.14	0.05	0.00	0.00	0.14	0.08
Brachyscome heterodonta var. _heterodonta_	0.06	0.03	0.17	0.07	0.11	0.08
Calotis scabiosifolia var. _scabiosifolia_	0.18	0.06	0.23	0.08	0.19	0.09
Carex inversa	0.06	0.03	0.13	0.07	0.08	0.06
*_Centaurea melitensis_	0.14	0.05	0.19	0.08	0.00	0.00
Chamaesyce drummondii	0.72	0.10	0.51	0.11	0.49	0.15
Chloris truncata	1.29	0.13	1.11	0.15	1.68	0.19
Chloris ventricosa	0.11	0.05	0.11	0.07	0.24	0.11
*_Cirsium vulgare_	0.12	0.05	0.08	0.05	0.08	0.05
Convolvulus erubescens	0.94	0.10	0.57	0.12	0.81	0.15
Convolvulus remotus	0.06	0.04	0.23	0.10	0.38	0.13
*_Conyza bonariensis_	0.39	0.08	0.32	0.10	0.14	0.07
Crinum flaccidum	0.03	0.02	0.36	0.11	0.08	0.05
Cucumis melo subsp. _agrestis_	0.17	0.05	0.15	0.06	0.00	0.00
*_Cucumis myriocarpus_ subsp. _leptodermis_	0.04	0.03	0.08	0.04	0.05	0.04
Cullen tenax	0.63	0.10	0.47	0.11	0.62	0.15
Cyperus bifax	0.69	0.11	1.55	0.16	1.43	0.22
Dactyloctenium radulans	0.37	0.08	0.32	0.12	0.14	0.08
Daucus glochidiatus	0.17	0.06	0.09	0.06	0.00	0.00
Desmodium campylocaulon	0.37	0.09	0.40	0.11	0.43	0.13
Dichanthium sericeum	2.29	0.17	2.42	0.22	2.24	0.29
Digitaria brownii	0.07	0.04	0.04	0.04	0.00	0.00
Digitaria divaricatissima	0.70	0.10	0.21	0.08	0.51	0.15
Digitaria porrecta	0.22	0.07	0.11	0.07	0.05	0.05
*_Echinochloa colona_	0.21	0.07	0.21	0.09	0.11	0.06
Eclipta platyglossa	0.22	0.06	0.15	0.06	0.27	0.10
Einadia hastata	0.18	0.05	0.04	0.03	0.24	0.10
Einadia nutans subsp. _linifolia_	0.24	0.07	0.28	0.09	0.08	0.06
Einadia nutans subsp. _nutans_	0.28	0.07	0.32	0.10	0.27	0.11
Einadia polygonoides	0.38	0.07	0.45	0.10	0.03	0.03
Eleocharis pallens	0.18	0.07	0.42	0.14	0.68	0.21
Elymus species B	0.16	0.06	0.06	0.03	0.00	0.00
Enteropogon acicularis	1.62	0.14	1.98	0.19	1.62	0.22
Eragrostis alveiformis	0.22	0.07	0.17	0.08	0.00	0.00
Eragrostis parviflora	0.57	0.09	0.42	0.11	0.76	0.20
Eremophila debilis	0.17	0.05	0.06	0.04	0.05	0.05
Eriochloa crebra	0.73	0.12	0.53	0.12	0.81	0.18
Eriochloa pseudoacrotricha	0.31	0.08	0.28	0.10	0.32	0.14
Erodium crinitum	0.18	0.05	0.11	0.06	0.11	0.08
Eryngium plantagineum	0.15	0.05	0.08	0.05	0.08	0.06
Euchiton sphaericus	0.20	0.06	0.19	0.08	0.05	0.05
Eulalia aurea	0.28	0.09	0.19	0.09	0.32	0.13

Appendix 3 (*continued*)

Species	Not flooded		Flooded infrequently		Flooded frequently	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
Fimbristylis dichotoma	0.16	0.06	0.23	0.10	0.11	0.08
Glycine latifolia	0.21	0.07	0.00	0.00	0.00	0.00
Glycine tabacina	0.16	0.05	0.06	0.04	0.05	0.05
Goodenia fascicularis	0.78	0.10	0.60	0.12	1.11	0.16
Hibiscus trionum	0.26	0.07	0.30	0.10	0.11	0.06
Ipomoea lonchophylla	0.16	0.06	0.42	0.12	0.08	0.08
Iseilema membranaceum	0.17	0.05	0.38	0.11	0.32	0.12
Juncus usitatus	0.16	0.06	0.19	0.08	0.30	0.12
**Lactuca saligna*	0.27	0.06	0.49	0.12	0.30	0.09
Leiocarpa brevicompta	0.14	0.05	0.19	0.08	0.00	0.00
Leiocarpa websteri	0.64	0.09	0.60	0.12	0.86	0.16
Leptochloa divaricatissima	0.59	0.09	0.72	0.15	0.84	0.18
Maireana aphylla	0.24	0.07	0.09	0.06	0.08	0.06
Maireana decalvans	0.26	0.07	0.21	0.08	0.30	0.12
Maireana microphylla	0.13	0.04	0.02	0.02	0.05	0.04
**Malvastrum americanum*	1.01	0.10	0.53	0.12	0.49	0.13
Marsilea drummondii	0.31	0.08	0.70	0.13	0.86	0.18
**Medicago polymorpha*	0.79	0.10	0.55	0.12	0.89	0.20
**Medicago truncatula*	0.31	0.08	0.04	0.04	0.05	0.05
Minuria integerrima	0.19	0.06	0.30	0.09	0.35	0.12
Neptunia gracilis	0.94	0.10	1.11	0.13	1.19	0.16
**Opuntia stricta*	0.10	0.04	0.08	0.05	0.00	0.00
Oxalis perennans	0.87	0.10	0.87	0.13	0.92	0.16
Panicum buncei	0.39	0.08	0.15	0.07	0.38	0.12
Panicum decompositum	1.45	0.11	1.47	0.17	1.89	0.16
Panicum queenslandicum	0.27	0.07	0.21	0.08	0.49	0.14
Paspalidium constrictum	0.44	0.09	0.06	0.04	0.11	0.08
Paspalidium globoideum	0.33	0.07	0.25	0.11	0.05	0.04
Paspalidium jubiflorum	0.04	0.03	0.32	0.12	0.86	0.23
**Phyla canescens*	0.02	0.02	0.11	0.06	0.43	0.16
Phyllanthus virgatus	0.47	0.09	0.34	0.10	0.35	0.12
**Physalis lanceifolia*	0.15	0.05	0.02	0.02	0.08	0.06
Plantago cunninghamii	0.11	0.04	0.04	0.04	0.16	0.09
**Polygonum aviculare*	0.06	0.03	0.11	0.06	0.22	0.10
Polymeria pusilla	0.22	0.06	0.17	0.07	0.16	0.08
Portulaca oleracea	0.90	0.10	0.87	0.13	0.70	0.15
Pratia concolor	0.20	0.06	0.25	0.09	0.32	0.12
Ptilotus semilanatus	0.23	0.06	0.09	0.06	0.22	0.10
Pycnosorus globosus	0.30	0.07	0.38	0.10	0.30	0.11
**Rapistrum rugosum*	1.18	0.10	0.72	0.13	0.78	0.17
Rhagodia spinescens	0.32	0.07	0.26	0.09	0.11	0.06
Rhynchosia minima	0.44	0.09	0.34	0.10	0.41	0.14
Rostellularia adscendens	0.07	0.03	0.00	0.00	0.11	0.08
Rumex brownii	0.16	0.05	0.11	0.05	0.27	0.11
Rumex tenax	0.09	0.04	0.17	0.07	0.08	0.05
Salsola kali var. *kali*	0.17	0.05	0.09	0.04	0.22	0.10
Sclerolaena birchii	0.10	0.04	0.02	0.02	0.03	0.03
Sclerolaena muricata var. *muricata*	0.79	0.11	0.83	0.13	0.89	0.15
Sclerolaena muricata var. *villosa*	1.00	0.10	1.11	0.13	1.00	0.15
Sida cunninghamii	0.14	0.04	0.06	0.04	0.08	0.06
Sida spinosa	0.12	0.05	0.09	0.06	0.05	0.05
Sida trichopoda	0.97	0.10	0.91	0.12	1.05	0.15
Solanum esuriale	1.33	0.10	1.17	0.14	0.92	0.16
**Sonchus oleraceus*	0.50	0.09	0.26	0.09	0.30	0.12
Sporobolus caroli	0.76	0.10	0.47	0.11	0.49	0.14
Sporobolus mitchellii	0.13	0.05	0.30	0.13	0.30	0.15
Swainsona queenslandica	0.09	0.04	0.09	0.06	0.05	0.04
Thellungia advena	0.67	0.10	0.58	0.14	0.51	0.15
Themeda avenacea	0.17	0.06	0.09	0.07	0.11	0.06
Trianthema triquetra	0.16	0.05	0.13	0.06	0.11	0.08

Appendix 3 (*continued*)

Species	Not flooded		Flooded infrequently		Flooded frequently	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
Tribulus micrococcus	0.41	0.09	0.68	0.18	0.24	0.11
**Tribulus terrestris*	0.34	0.10	0.11	0.08	0.00	0.00
**Urochloa panicoides*	0.56	0.11	0.58	0.14	0.32	0.14
Verbena gaudichaudii	0.74	0.10	0.77	0.13	0.51	0.14
Vittadinia cuneata	0.68	0.10	0.38	0.10	0.49	0.13
Wahlenbergia communis	0.59	0.09	0.28	0.09	0.57	0.14
**Xanthium occidentale*	0.11	0.04	0.06	0.04	0.19	0.09