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Corrigenda

Impacts of level of utilisation by grazing on an *Astrebla* (Mitchell grass) grassland in north-western Queensland between 1984 and 2010. 1. Herbage mass and population dynamics of *Astrebla* spp. 2. Plant species richness and abundance

D. M. Orr and D. G. Phelps

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The co-ordinates for the experimental grazing site reported in these two papers were incorrectly published. The precise location of the northern corner of the experimental site (Toorak Research Station) in both the papers should be 21°0′49.49″, 141°46′59.54″. The typographical error is regretted.

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Impacts of level of utilisation by grazing on an *Astrebla* (Mitchell grass) grassland in north-western Queensland between 1984 and 2010. 2. Plant species richness and abundance

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Abstract. The occurrence of interstitial species in *Astrebla* grasslands in Australia are influenced by grazing and seasonal rainfall but the interactions of these two influences are complex. This paper describes three studies aimed at determining and explaining the changes in plant species richness and abundance of the interstitial species in a long-term sheep utilisation experiment in an *Astrebla* grassland in northern Queensland. In the first study, increasing utilisation increased the frequency of *Dactyloctenium radulans* (Button grass) and *Brachyachne convergens* (Downs couch) and reduced that of *Streptoglossa adscendens* (Mint bush). In the second study, seasonal rainfall variation between 1984 and 2009 resulted in large annual differences in the size of the seed banks of many species, but increasing utilisation consistently reduced the seed bank of species such as *Astrebla* spp. and *S. adscendens* and increased that of species such as *B. convergens*, *D. radulans*, *Amaranthus mitchellii* (Boggabri) and *Boerhavia* sp. (Tar vine). In the third study, the highest species richness occurred at the lightest utilisation because of the presence of a range of palatable forbs, especially legumes. Species richness was reduced as utilisation increased. Species richness in the grazing exclosure was low and similar to that at the heaviest utilisation where there was a reduction in the presence of palatable forb species. The pattern of highest species richness at the lightest grazing treatment was maintained across three sampling times, even with different amounts of seasonal rainfall, but there was a large yearly variation in both the density and frequency of many species. It was concluded that the maintenance of highest species richness at the lightest utilisation was not aligned with other data from this grazing experiment which indicated that the maximum sustainable wool production occurred at moderate utilisation.

Additional keywords: seasonal variation, soil seed banks, species frequency, utilisation.

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Introduction

Orr and Phelps (2013) reported that *Astrebla* spp. populations in *Astrebla* grasslands were sustainable over 26 years at 30% utilisation of the end of summer available forage. Furthermore, *Astrebla* spp. populations were able to recover from 14 years of 80% utilisation with above-average summer rainfall. While *Astrebla* spp. are the ecological matrix species (Grubb 1986), these grasslands also contain a diverse range of interstitial grass and forb species (Weston and Moir 1969; Lorimer 1978; Hall and Lee 1980; Orr 1981, 1986; Roe and Allen 1993; Phelps and Bosch 2002). The presence or absence of these interstitial species is strongly influenced by the distribution and trends in seasonal rainfall (Lorimer 1978; Orr 1981, 1986; Orr *et al*. 1988; Roe and Allen 1993). Summer rainfall results in the presence of a range of perennial grasses e.g. *Aristida latifolia*, annual grasses e.g. *Iseilema* spp. and summer forbs e.g. *Streptoglossa adscendens* while winter rainfall results in mainly winter forbs e.g. *Calotis scabiosa*. Rapid fluctuations in species presences occur over a short time period (Orr 1981; Orr *et al*. 1988; Roe and Allen 1993; Lewis *et al*. 2008, 2009). For example, Roe and Allen (1993) recorded a large number of species at Cunnamulla between 1941 and 1951, but many were present only occasionally and in small amounts. They concluded that any direct measurement of grazing impact on these species was not possible.

Sheep preferentially select forbs when they are available in *Astrebla* grasslands (Lorimer 1978; McMeniman *et al*. 1986; Pritchard *et al*. 1986; Orr *et al*. 1988). For example, Lorimer (1978) reported that ‘other species’ comprised only 10% of the pasture composition, but represented 57% of the sheep diet. This preferential defoliation of these species, in addition to their irregular presence, makes field identification and recording of many species challenging and it is not always possible to differentiate between species currently absent from the pasture and those removed by selective sheep grazing. Few data are available on the impacts of selective grazing on species richness and abundance, although Orr (1980) recorded desirable species such as *Rhynchosia minima* only under light grazing while less desirable species such as *Amaranthus mitchellii* and *Tribulus terrestris* were common under heavy grazing.

Orr and Phelps (2013) recorded the episodic recruitment of *Astrebla* spp. over 26 years in northern *Astrebla* grassland. Williams and Roe (1975) suggested that the lack of regular *Astrebla* spp. recruitment in these northern grasslands may be attributed to competition from high densities of the annual grass *Iseilema* spp. However, a glasshouse study of competition between *A. lappacea* and *Iseilema* spp. (Orr and Evenson 1993) suggested that this may occur only with high densities of *Iseilema* spp. because *A. lappacea* was more competitive than *Iseilema* spp. at comparable densities.

The long-term Toorak grazing experiment provided a unique opportunity to study the effects of utilisation on plant species richness and abundance (density and/or frequency of occurrence), particularly of the interstitial species. The difficulties of measuring these attributes in the field, as discussed above, led us to conduct glasshouse studies of the soil seed bank to provide an alternative approach. Glasshouse studies (1) remove the limitations imposed by selective grazing and (2) provide more favourable growth conditions than can occur in the field. Furthermore, repeated sampling of the soil seed bank over a range of seasonal conditions should provide an estimate of the effects of seasonal rainfall variability on potential species richness and abundance.

This paper reports three separate studies of plant species richness and abundance in the grazing experiment described by Orr and Phelps (2013). The first reports changes between 1989 and 2010 in the frequency in the grassland of those interstitial species, which were consistently identified during the BOTANAL sampling. The second measured the annual variation in soil seed banks between 1984 and 2009, particularly for *Astrebla* spp. and *Iseilema* spp., in those four treatments where permanent quadrats monitored *Astrebla* spp. populations (Orr and Phelps 2013). The third determined the total plant species richness in the soil seed bank across six grazing treatments for the years 2001, 2004 and 2007. Soil cores were collected in spring so that seed produced in the preceding summer had entered the soil seed bank but had not yet germinated in the following summer growing season.

Throughout these three studies we encountered a wide range of plant species and we are unable to present all these data in this paper. Nevertheless, we present data for the most regularly encountered species particularly *Astrebla* spp., the annual grasses *Iseilema* spp., *Brachyachne convergens* and *Dactyloctenium radulans* and the forb *S. adscendens*. We also present data for some of the less regularly encountered species where data indicated trends in relation to utilisation.

Materials and methods

Grazing study

A grazing experiment was established in 1984 (Orr and Phelps 2013) at Toorak Research Station (21.022°S, 142.785°E) in the Allaru land system (Turner and McDonald 1993) and which is described as 'flat to gently undulating plains; Mitchell grass open tussock grassland with other short grasses, occasional sparse forbland; moderately deep to deep, grey and brown cracking clays with strong self mulching surfaces'. The site is within Regional Ecosystem 4.9.1 (Sattler and Williams 1999). Botanical nomenclature in this paper is according to Bostock and Holland (2007).

Treatments were 0, 10, 20, 30, 50 and 80% utilisation (subsequently referred to as U0, U10, U20, U30, U50 and U80) of total pasture biomass available at the end of summer. Paddock sizes were 1, 54, 27, 18, 12 and 7 ha for U0, U10, U20, U30, U50 and U80, respectively, having been scaled to graze 20 sheep each at the commencement of grazing in June 1984. Sheep numbers within each treatment were changed at the end of each summer growing period based on the pasture biomass measured annually, usually in May. Merino weathers were weighed, stratified on bodyweight, and allocated to treatment paddocks using the formula $N_S = Y/I_S \times U \times P_S$ where: N_S = sheep number, Y = pasture biomass, I_S = sheep intake (kg/dry sheep equivalent and assumed to be 400 kg), U = utilisation and P_S = paddock size (ha). Grazing commenced in July 1984. (Further details are provided in Orr and Phelps 2013).

Study 1 – Species frequency

Species composition was based on frequency of occurrence measured at the end of the summer growing season between 1989 and 2010 using BOTANAL (Tothill *et al*. 1992). In the BOTANAL sampling, the three species contributing most were used to determine yield while the presence of up to five extra species were recorded and used to calculate frequency of occurrence. Four to nine trained operators assessed a minimum of 60, 250, 200, 150, 140 and 80 quadrats, each 0.5 × 0.5 m, in U0, U10, U20, U30, U50 and U80, respectively. Between 1989 and 1992 the major species involved were selected in the field according to presence in the general site area; and subsequently based on a standard species list. A large number of species were recorded and their frequencies varied widely throughout this study. However, this paper presents the frequency of six species which were consistently recorded throughout the study. Data are presented as mean frequencies across years with no statistical analyses because there was no estimate of error due to the unreplicated nature of this study.

Study 2 – Annual seed banks

Commencing in 1984, seed banks were monitored annually in spring by germinating soil samples collected at random from U10, U30, U50 and U80. Between 1984 and 1995, 15 samples were collected each as a single core of 12 × 12 cm to a depth of 5 cm in each of the four treatments. Between 1996 and 2009, 15 samples were collected as five individual cores each 5 cm diameter and 5 cm deep and bulked to comprise each sample. In the subsequent summer, each of these 15 samples from each treatment was spread on top of compacted sand in 20 cm diameter, drained plastic pots which were then randomly distributed in a plant house and seed in these samples was germinated by capillary watering (Jones and Bunch 1988). Emerged seedlings were identified and counted over one germination cycle (Orr 1999) of 8 weeks. The numbers of seeds m^{-2} in the field were then calculated from the numbers of seedlings germinating in the pots. In this paper, we present data for the most commonly recorded grass and forb species between 1984 and 2009.

Seed density (seeds m^{-2}) from annual seed bank data were log-transformed before analysis using residual maximum likelihood (REML) (Genstat 2002) with fixed effects of utilisation treatment and years within treatment and random effects of paddocks and samples within paddocks.

Study 3 – Detailed seed bank studies

In spring 2001, 2004 and 2007, the soil seed bank was assessed using a 60 × 60-m grid across the whole 115-ha experimental site. This grid size was selected to provide 20 soil samples in the U80 (the smallest grazed treatment) and 16, 162, 69, 49, 36 samples in U0, U10, U20, U30 and U50, respectively. The centre of each grid cell was located using a Geographic Positioning System and one bulked soil sample was collected within each cell. Each of these bulked soil samples comprised four individual cores, each of 5 cm diameter and 5 cm depth, collected along four cardinal transects and within 5 m of the centre of the grid cell. Within each grid cell, visual estimates were also made of total pasture biomass, *Astrebla* spp. utilisation (Orr 1980), *Astrebla* spp. density and *Astrebla* spp. basal area (Phelps and Orr 2003).

In the summer after collection, cores were spread on compacted sand in 15 cm diameter drained pots. Pots were randomly assigned among four blocks in a plant house where they were watered daily by overhead sprinkler for 30 min (Orr *et al*. 1996). Emerging seedlings were identified, counted and removed over a 10-week period ensuring that no plant produced seed before removal. To account for residual seed dormancy (Orr 1999), this process was repeated in the second and third summers after collection. Soil samples were allowed to dry out after the first and second samplings, stored in a cool, dry environment and the soil core above the sand thoroughly mixed in each pot before the second and third wetting cycles. Data presented are combined for the three wetting cycles.

High densities of *Iseilema* spp. (>50 seeds/pot), particularly in the 2001 sampling, necessitated the removal of these plants after identification to genus level, but before inflorescence development making individual species identification impossible. Similarly, we grouped three individual *Astrebla* species, *A. lappacea*, *A. elymoides* and *A. pectinata*, into the group *Astrebla* spp. because of the need for an inflorescence to distinguish these species, while *A. squarrosa* is readily identifiable as a seedling.

The number of different species recorded from the soil seed bank in pots from the grid sampling over the three sampling periods was determined. Seed density (seeds m^{-2}) and frequency (%) (frequency of occurrence in pots) for the major species in each sampling period were log-transformed before analysis using REML with the fixed effect of utilisation treatment and random effects of paddocks and samples within paddocks. Soil seed bank frequencies (%) for the most commonly occurring grasses and forbs were expressed as presence/absence data and modelled as a Generalised Linear Model with binomial error and logit link function.

Results

Rainfall

Summer rainfall between 1984 and 2010 varied from 60% below to 100% above the long-term mean of 384 mm for Toorak Research Station (Fig. 1). For Study 3, the 2001 cores were collected following 3 years of above-average summer rainfall while the 2004 and 2007 cores were collected in a period of generally below average rainfall. The long-term mean winter (April–September) rainfall is 56 mm and above-average winter rainfalls of 175, 122, 217 and 182 mm were received in 1990, 1998, 2006 and 2007, respectively.

Study 1 – Species frequency

Frequency of *D. radulans* was highest generally at U80 between 1998 and 2003 before increasing at U50 to be highest in 2006, 2007 and 2009 (Fig. 2*a*). *Brachyachne convergens* had high frequencies at U80 between 1994 and 2001 and in 2010 and also at U50 between 2006 and 2009 (Fig. 2*b*). Frequency of *S. adscendens* tended to be highest at U80 until 1993, after which

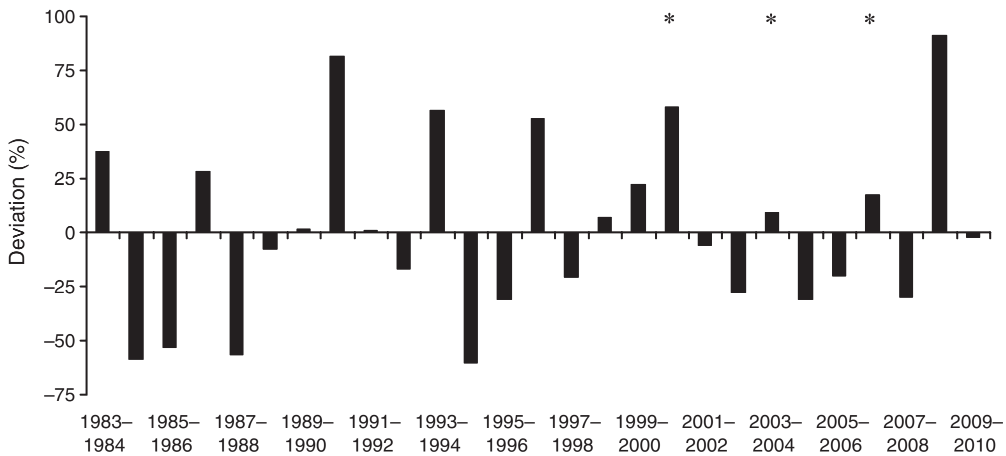

Fig. 1. Deviation of summer rainfall from the long-term mean between 1984 and 2010 at Toorak. Asterisks indicate years of seed bank sampling for Study 3.

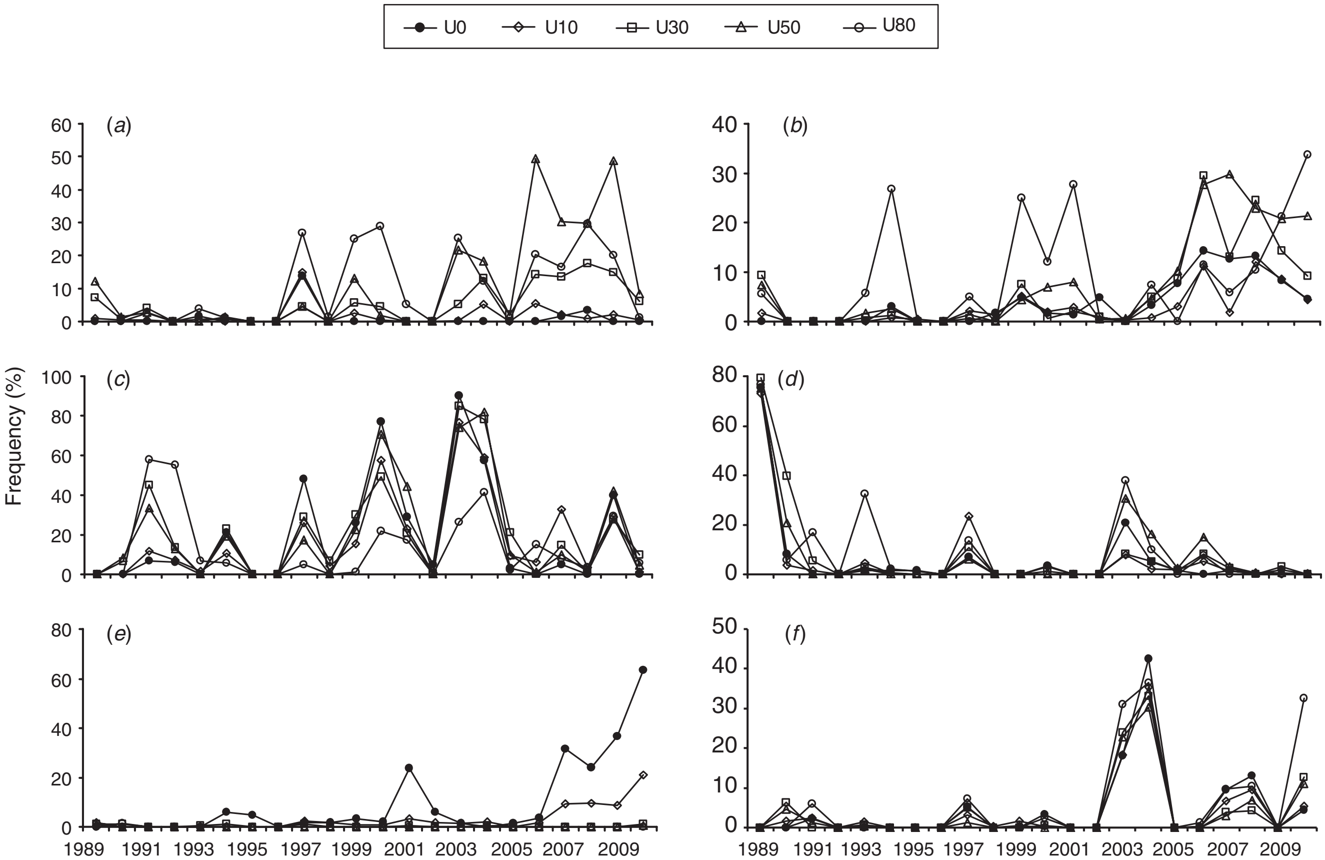

Fig. 2. Frequency (%) in the field of (*a*) *Dactyloctenium radulans*, (*b*) *Brachyachne convergens*, (*c*) *Streptoglossa adscendens*, (*d*) *Amaranthus mitchellii*, (*e*) *Rhynchosia minima* and (*f*) *Cleome viscosa* at five levels of utilisation in *Astrebla* grassland at Toorak between 1984 and 2010. (U20 data were excluded to improve the clarity of presentation.) Note differences in the *y*-axis scales.

time it tended to be consistently lower and vary more in relation to seasonal conditions than to utilisation (Fig. 2*c*). The ephemeral forb *Am. mitchellii* tended to vary more in relation to seasonal trends than to utilisation with highest frequencies corresponding with drought years e.g. 1993, 1997 and 2003 (Fig. 2*d*). The legume *Rhynchosia minima* tended to increasingly high frequencies at U0 and U10 (Fig. 2*e*). Frequency of the annual forb, *Cleome viscosa* showed a strong seasonal response with frequencies of 20–40% in all treatments in 2003 and 2004 but usually being 10% or less in most other years (Fig. 2*f*).

Study 2 – Annual seed banks

Germinable seed banks for six species varied widely among years as indicated by a significant ($P < 0.01$) utilisation × year interaction (Fig. 3). The seed bank of *Astrebla* spp. ranged from 0 seeds m^{-2} (all four treatments) in 2009 to 110 seeds m^{-2} at U10 in 2006 and were lower at U50 than the other treatments after 2002 (Fig. 3*a*). *Iseilema* spp. ranged from 0 seeds m^{-2} at U80 in 1986 during drought to 3430 seeds m^{-2} at U50 in 1992 following above-average rainfall over the 1990–91 summer and average rainfall over the 1991–92 summer and then tended to be lower at U50 and U80 from 1999 (Fig. 3*b*). *Brachyachne convergens* was absent from the seed bank in 1986 and 1988 but persisted to be highest at 55 seeds m^{-2} at U50 in 2005 following a series of drought years and tended to be higher at U50 and U80 in most years, especially after 1991 (Fig. 3*c*). *Dactyloctenium radulans* remained low with few treatment differences until 2004 when it increased particularly at U50 to be highest at 260 seeds m^{-2} at U50 in 2008 following a series of drought years (Fig. 3*d*). *Streptoglossa adscendens* ranged from 0 seeds m^{-2} at U50 in 1989 to 450 seeds m^{-2} at U10 in 2003 following drought over the 2001–02 and 2002–03 summers and tended to be lowest at U80 between 2000 and 2007 (Fig. 3*e*). *Gomphrena breviflora* was generally absent until 2002 and was then highest at U50 in 2005, 2007 and 2008 (Fig. 3*f*). The seed bank of *Boerhavia* spp. generally remained low at U50 while it tended to increase at the other three treatments between 2004 and 2006 (Fig. 3*g*). The seedbank of *Tribulus terrestris* was generally low but was highest at U50 and U80 in 2008 and also in 2004 and 2005 (Fig. 3*h*).

Other species to record significant ($P < 0.01$) utilisation × year interactions included the annual grasses *Chloris pectinata*, *Digitaria ctenantha*, and *Panicum laevinode* and the annual forbs *Amaranthus mitchellii*, *Flaveria trinervia*, *Sida* spp. and *Portulaca oleracea*. The seed bank of *F. trinervia* tended to be highest at U10 whereas all other species tended to be highest at U50 and U80.

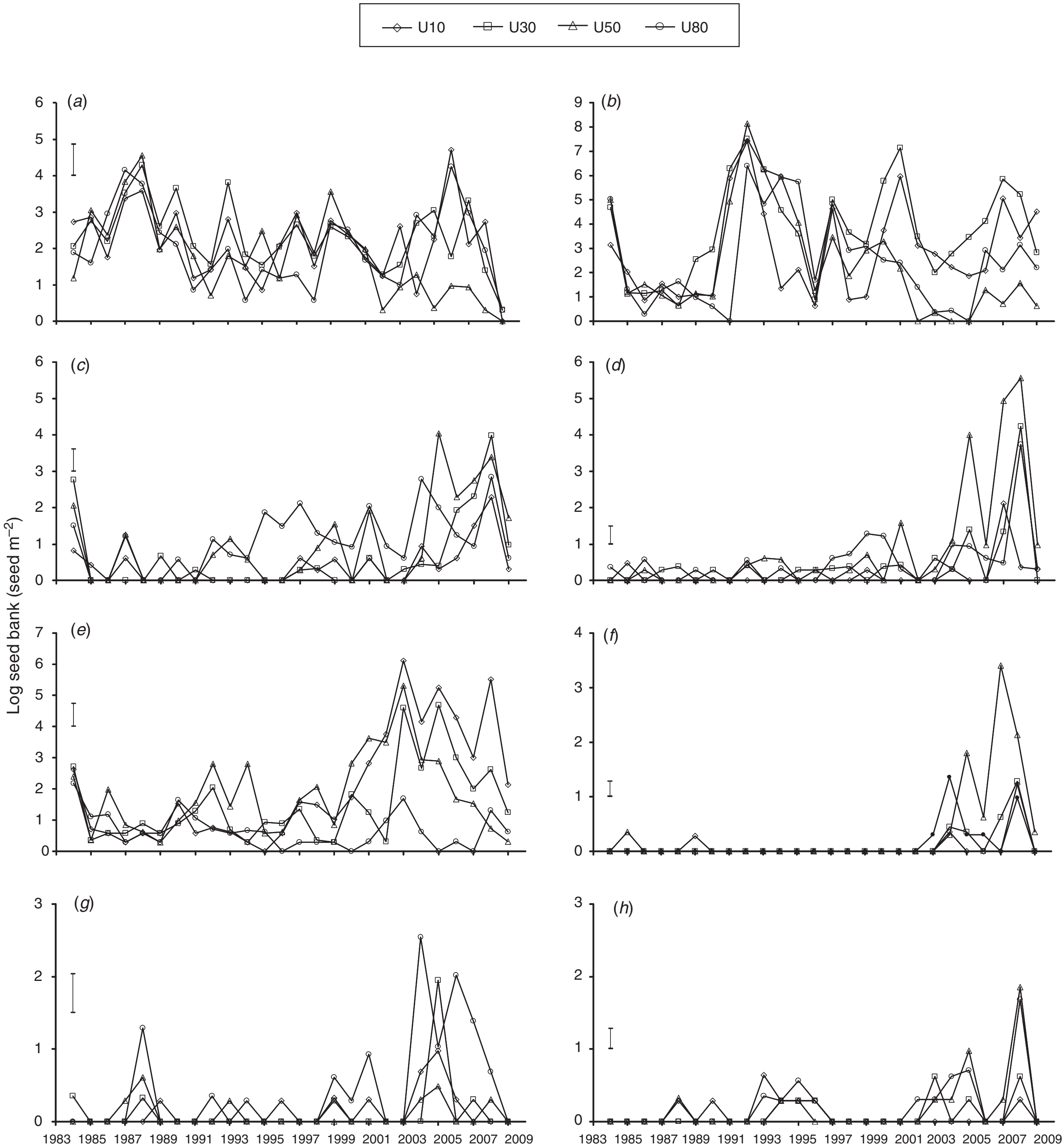

Fig. 3. Soil seed bank density (seeds m^{-2}) of (*a*) *Astrebla* spp., (*b*) *Iseilema* spp., (*c*) *Brachyachne convergens*, (*d*) *Dactyloctenium radulans*, (*e*) *Streptoglossa adscendens* and (*f*) *Gomphrena breviflora*, (*g*) *Boerhavia* sp., and (*h*) *Tribulus terrestris* at four levels of utilisation between 1984 and 2009 in *Astrebla* grassland at Toorak. (Analysis performed on log-transformed data; vertical bars are standard errors. Note differences in the *y*-axis scales).

Study 3 – Detailed seed bank studies

Number of species

A total of 74 species, 18 grasses and 56 forbs (including two sedges), were recorded in the soil seed bank over the three sampling periods (Table 1). The highest number of species occurred consistently at U10 with 44, 47 and 38 species in 2001, 2004 and 2007, respectively (Fig. 4). The lowest number of 18 species occurred at U0 in 2004 and at U80 in 2007. The high number of species recorded at U10 was dominated by forbs with

Table 1. Mean frequency of occurrence of grasses and forbs recorded in the soil seed bank in *Astrebla* grassland at Toorak between 2001 and 2007

Species	2001	2004	2007
Grasses			
Aristida latifolia	4.4	0	0
Astrebla spp.	20.3	28.9	27.8
Astrebla squarrosa	7.1	1.9	2.6
Brachyachne convergens	30.9	23.8	42.1
Chionachne hubbardiana	0	0.2	0.4
Chloris pectinata	7.9	2.3	2.0
Cynodon dactylon	0.5	0.6	0
Dactyloctenium radulans	24.6	27.8	42.3
Dichanthium sericeum	2.6	0	0
Digitaria ctenantha	26.2	18.7	24.6
Echinochloa colona	0.7	1.2	0.2
Eragrostis parviflora	0	0.2	0
Eragrostis tenellula	41.8	45.6	31.7
Eriochloa crebra	6.5	0.9	2.9
Iseilema spp.	75.1	53.4	61.0
Panicum laevinode	6.8	8.6	18.6
Paspalidium constrictum	0.2	0	0
Sporobolus australasicus	15.0	6.2	3.5
Forbs			
Abelmoschus ficulneus	0.2	0.1	0.7
Abutilon malvifolium	0.8	0.2	1.1
Acalypha australis	9.8	0	0
Alternanthera nodiflora	0	0	0.1
Alysicarpus muelleri	3.9	2.1	1.1
Amaranthus mitchellii	6.3	20.4	13.9
Boerhavia spp.	8.2	31.9	7.8
Chamaesyce drummondi	18.5	16.1	4.3
Centipeda minima	0.3	1.0	2.4
Chenopodium cristatum	0.7	0	0
Cleome viscosa	4.5	16.5	11.7
Citrullus colocynthis	0.2	1.1	0.2
Corchorus trilocularis	5.1	5.2	4.6
Crotalaria dissitiflora	1.0	0	0
Crotalaria medicaginea	0	0	0.2
Crotalaria sp.	1.3	0	0
Crotalaria sp.	0	0	0.6
Cullen cinereum	1.2	1.2	0.8
Desmodium muelleri	0.9	0.1	0
Desmodium sp.	0.2	0	0
Flaveria trinervi	1.3	14.0	9.0
Glycine falcata	0.2	0.2	0.2
Gomphrena breviflora	2.1	7.8	20.0
Goodenia fascicularis	0	0	0.3
Heliotropium tenuifolium	0.7	0.1	0
Indigastrum parviflora	0.1	0	0
Ipomoea diamantinensis	1.0	0.2	0.1
Ipomoea lonchophylla	0.3	0.2	0.1
Indigofera trita	0	0	1.2
Isotoma gulliveri	0.7	0	0
Josephinia eugeniae	1.7	0	0.8
Malvastrum americanum	0.6	0.1	0.2
Oldenlandia caerulescens	5.0	24.5	13.9
Peripleura hispidula	5.3	6.4	3.0
Phyllanthus maderaspatensis	17.3	6.8	4.0
Phyllanthus virgatus	0	0.4	0
Pimela decora	0.2	0.3	0
Portulaca oleracea	6.8	4.5	1.8
Rostellularia adscendens var. clementii	0	0	1.1
Rhynchosia minima	5.5	1.5	1.7
Sida fibulifera	0.3	0	1.0
Sida spinosa	3.3	2.9	2.3
Solanum esuriale	2.1	0	0
Streptoglossa adscendens	57.0	57.3	25.4
Tephrosia rosea	1.0	1.6	1.0
Teucrium integrifolium	0	0	0
Tribulus terrestris	1.9	3.7	3.4
Wedelia asperrima	0.1	0	0
Cyperus bifax	10.2	5.1	7.2
Cyprus difformis	2.7	2.4	4.7
Indet. 1	0	1.1	0
Indet. 2	0	0.2	0
Indet. 3	0	0	0.3
Indet. 4	0	0	1.1
Indet. 5	0	0	0.3
Indet. 6	0	0	0.5

31, 33 and 26 in occurring in 2001, 2004 and 2007, respectively, and was higher than at any other utilisation. Included in those forb species which were recorded predominantly at low utilisation were the palatable legumes *Alysicarpus muelleri*, *Glycine falcata* and *Rhynchosia minima* and the palatable forb *Ipomoea lonchophylla*. None of these four species occurred at U50 or U80 in any of the three samplings. Grass species numbers were slightly higher at 13, 14 and 14 at U10 compared with 11, 8 and 9 at U80 in 2001, 2004 and 2007, respectively. *Aristida latifolia* and *Dichanthium sericeum* were present following the relatively wet 2000–01 summer but were absent following the relatively dry 2003–04 and 2006–07 summers.

Germinable seed bank density

Differences in germinable seed bank density occurred among the three sampling periods. For example, the highest density of *Iseilema* spp. (1850 seeds m^{-2} at U10) occurred in 2001, the wettest of the three years, and was lower in both 2004 and 2007 (Fig. 5*a*) whereas the density of *D. radulans* seeds increased from being lowest in 2001 to highest in 2007 (Fig. 5*b*). Lowest *Astrebla* spp. seed densities occurred in 2001, the wettest year and were higher in 2004 and 2007 when rainfall was less than in 2001 (Fig. 5*d*). Within years for each species, seed bank density differed ($P < 0.01$) among utilisations. *Iseilema* spp. was consistently highest at U10 and U30 and lowest at U50 and U80 with a decline at U0 in 2004 and 2007 (Fig. 5*a*). In contrast, density of *D. radulans* seeds increased ($P < 0.01$) with increasing utilisation reaching 230 seeds m^{-2} at U50 in 2007 (Fig. 5*b*). Similarly, *B. convergens* seed densities in 2001 were similar between U0 and U30 but increased ($P < 0.01$) at U50 and U80, in 2004 there were no differences ($P > 0.05$) but in 2007 it was lowest at U80 (Fig. 5*c*). *Astrebla* spp. were absent from U0 at all samplings (Fig. 5*d*). In the grazed treatments, seed density was similar ($P > 0.05$) in 2001 but was reduced ($P < 0.01$) at U50 in both 2004 and 2007. *Streptoglossa adscendens* seed density in 2001 was highest ($P < 0.01$) at U0 and U50 although, by 2004, it was lowest ($P < 0.01$) at both U50 and U80 and seed densities were similar ($P > 0.05$) in 2007 (Fig. 4*e*). *Amaranthus mitchellii*

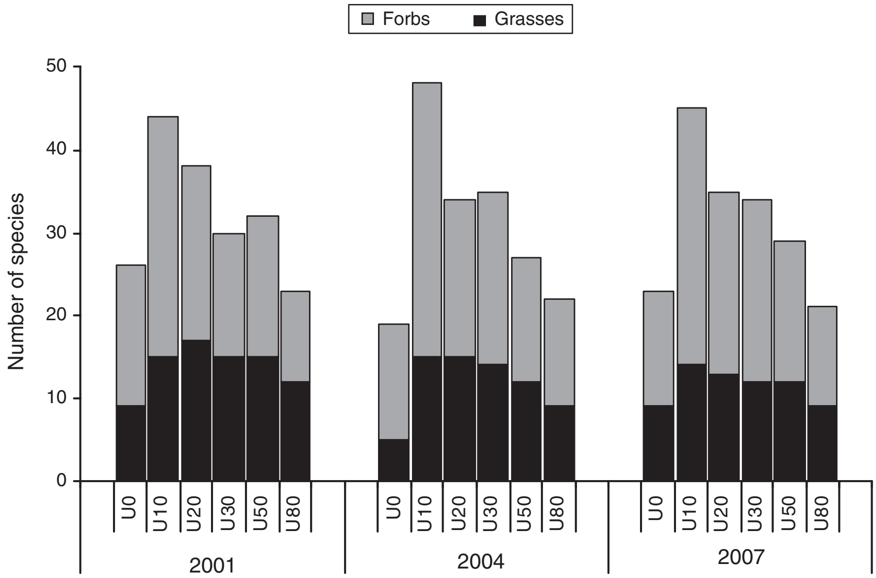

Fig. 4. Number of grass and forb species recorded in the soil seed bank at six levels of utilisation in spring 2001, 2004 and 2007 in *Astrebla* grassland at Toorak.

seed density was similar between U0 and U30 but increased ($P > 0.05$) at U50 and U80, particularly in 2004 and 2007 (Fig. 4*f*).

Eragrostis tenellula seed density was highest ($P < 0.01$) at U50 in all 3 years although in 2001, density at U0 was similar to that at U50 (data not presented). The seed density of *D. ctenantha* was highest at U0 although this trend was significant only in 2004 and 2007. *Gomphrena breviflora* was absent from U0 at all samplings although its seed density increased ($P < 0.01$) with grazing pressure in all 3 years but in 2007, its density at U80 was less than that at U20 and U30.

Germinable seed bank species frequency

Differences in seed bank frequency of occurrence for most species were apparent among the three samplings. *Iseilema* spp. and *S. adscendens* were the two most frequent species recorded, peaking at 100 and 94%, respectively, at U0 in 2001. Given that the soil samples were collected within an evenly spaced grid, this indicates a very even spatial distribution of the seeds of each species in the absence of grazing. Mean frequencies of the three palatable legume species (*A. muelleri*, *G. falcata* and *R. minima*) and the palatable forb *I. lonchophylla* at U10, were 3.5, 3.1, 0.8 and 1.4%, respectively. Within years for each species, seed bank frequency differed among utilisations. *Iseilema* spp. frequency generally was similar at U0–U30 but declined ($P < 0.01$) at U50 and U80 (Fig. 6*a*). *Dactyloctenium radulans* frequency increased ($P < 0.01$) with utilisation in all years (Fig. 6*b*). *Brachyachne convergens* frequency in 2001 was similar U0 to U30 but increased ($P < 0.01$) at U50 and U80 while in 2004 there were no differences ($P > 0.05$). In 2007, *B. convergens* frequency was lower ($P < 0.01$) at U80 compared with that at U0, U20, U30 and U50 (Fig. 6*c*). *Astrebla* spp. was absent from U0 in all 3 years. In the grazed treatments, *Astrebla* spp. frequency was similar ($P > 0.05$) in all five treatments in each of the years although in both 2004 and 2007, it tended to be lower at U50 than the other treatments (Fig. 6*d*). *Streptoglossa adscendens* frequency in 2001 was highest ($P < 0.01$) at U0 and U50 although, in 2004 and 2007, it was lowest at U50 and U80 (Fig. 6*e*). *Amaranthus mitchellii* frequency was similar between U0 and U30 but increased ($P < 0.05$) at U50 and U80, particularly in 2004 and 2007 (Fig. 6*f*).

Eragrostis tenellula seed bank frequency was highest ($P < 0.05$) at U50 in all 3 years although in 2001 it was similar to that at U80. In 2001, *G. breviflora* was present only at U30, U50 and U80, but in 2004 it increased ($P < 0.05$) to be highest at U80 while in 2007, it increased ($P < 0.05$) from U10 up to U50 but was reduced at U80 (data not shown).

Discussion

Both utilisation and rainfall affected species richness and abundance in the *Astrebla* grassland studied whether estimated by extant plants or using the seed bank flora as a surrogate. This finding is consistent with other studies in *Astrebla* grasslands indicating that both utilisation (Orr 1980) and trends in seasonal rainfall (Orr 1981) influence species composition. Despite the importance of utilisation, few comparative studies of its impacts on plant species richness and abundance are available. O'Connor *et al*. (2011) reported that although stocking rate was known to affect grassland plant richness and abundance, few studies in either South Africa or the USA had directly examined the effect of livestock management on these grassland attributes. Our study contributes directly to this understanding.

Highest species richness at the lowest level of utilisation in our study provided support for the 'intermediate disturbance' hypothesis (Connell 1978) whereby maximum species richness and abundance occurs at some intermediate level of disturbance. In our study, maximum species richness occurred at U10 with both decreasing and increasing utilisation progressively reducing it – particularly for forbs (Fig. 4).

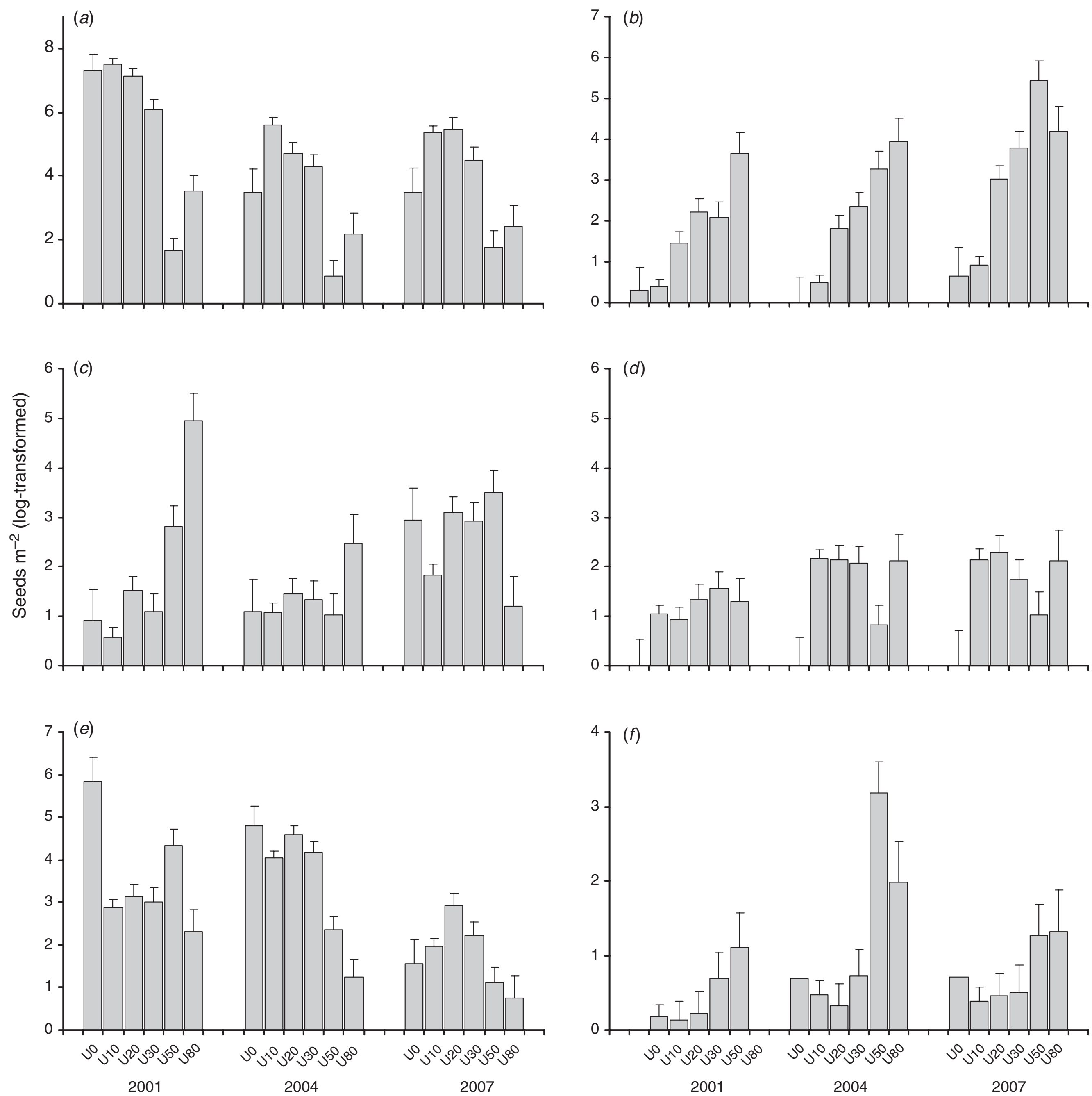

Fig. 5. Soil seed bank density (seeds m^{-2}) of (*a*) *Iseilema* spp., (*b*) *Dactyloctenium radulans*, (*c*) *Brachyachne convergens*, (*d*) *Astrebla* spp., (*e*) *Streptoglossa adscendens* and (*f*) *Amaranthus mitchellii* at six utilisations in 2001, 2004 and 2007 in *Astrebla* grassland at Toorak. (Analysis performed on log-transformed data; vertical bars are standard errors. Note differences in the *y*-axis scales).

Grazing effects

The reduction in interstitial species richness and abundance with increasing utilisation reflected the ability of sheep to select individual species in their diet even when that species has a low frequency of occurrence in the pasture. Lorimer (1978) reported that the 'other species' component – mainly forb species – rarely exceeded 10% of the pasture but constituted up to 57% of the sheep's diet, with legumes especially selected. In our study, the high species richness and abundance at U10 included the legumes *A. muelleri*, *G. falcata* and *R. minima* and the palatable (Orr *et al*. 1988) forb, *I. lonchophylla.* The general absence of palatable forbs in pastures grazed above U20 suggested that these species were reduced to undetectable levels in the soil seed bank through long-term selective grazing by sheep. The most consistently recorded, palatable forb in the BOTANAL estimations was *R. minima*. It was often recorded

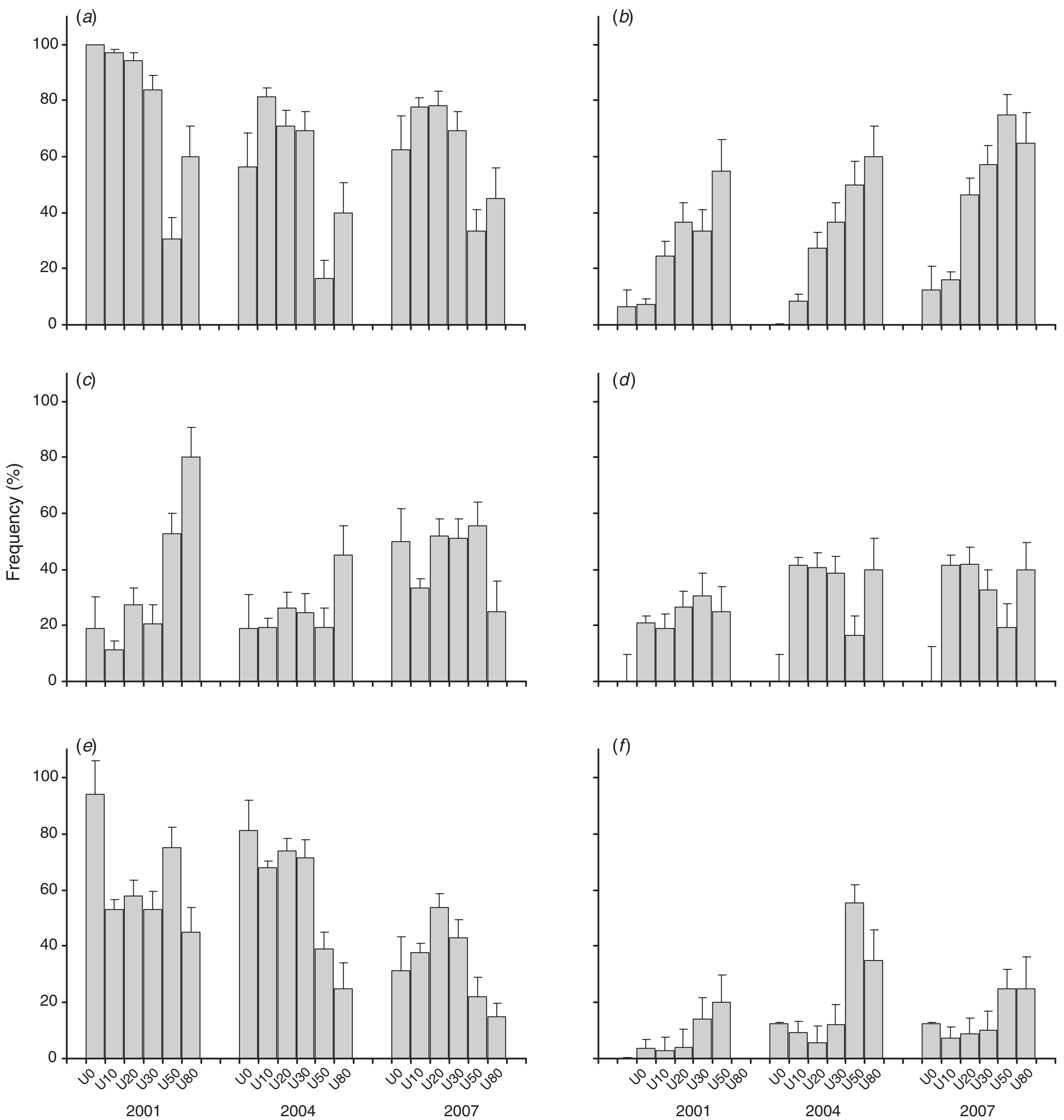

Fig. 6. Frequency of seedlings from the seed bank in glasshouse pots (%) of (*a*) *Iseilema* spp., (*b*) *Dactyloctenium radulans*, (*c*) *Brachyachne convergens*, (*d*) *Astrebla* spp., (*e*) *Streptoglossa adscendens* and (*f*) *Amaranthus mitchellii* in relation to six utilisations in 2001, 2004 and 2007 in *Astrebla* grassland at Toorak. (Analysis performed on log-transformed data; vertical bars are standard errors).

but only at U0 and U10 suggesting that long-term continuous grazing has depleted some palatable interstitial species. This contrasts with the conclusion of Everist and Webb (1975) that there was no evidence suggesting that any forb or annual grass species has been eliminated by moderate sheep grazing.

Astrebla spp. density and frequency in the soil seed bank declined with utilisation above our U30 treatment and was undetectable after 26 years of exclosure. *Astrebla* spp. seed production occurs rapidly following summer rainfall (Everist 1964) and Weston and Moir (1969) reported that sheep select some *Astrebla* spp. seed in their diet during the late wet and early dry season. It follows then that increasing utilisation probably leads to this measured reduction in seed production. Nonetheless, seedling recruitment occurred at U50 and U80 in this study (Orr and Phelps 2013) suggesting that the reduced amount of *Astrebla* spp. seed set under high utilisation was still adequate for recruitment, given suitable summer rainfall.

Increasing utilisation also reduced the occurrence of *Iseilema* spp. This finding contrasted with the suggestion (Milson 2000; Phelps and Bosch 2002) that a dominance of *Iseilema* spp. indicates overgrazing. It also contrasted with the findings of Hall and Lee (1980) that it occurred at a higher density under heavy grazing with cattle compared with light grazing with sheep. There are conflicting reports about the selection of *Iseilema* spp. by sheep in *Astrebla* grasslands. Lorimer (1978) reported that *Iseilema* spp. made its greatest contribution to sheep diets while green and immature during the wet season and contributed little during the subsequent dry season. Weston and Moir (1969) and Pritchard *et al*. (1986) reported that *Iseilema* spp. formed a large part of the diet throughout the year, except late in the dry season.

Less palatable, toxic or annual species tended to increase with increasing utilisation. For example, the annual grasses *B. convergens*, *D. radulans* and *E. tenellula* and the forbs *Am. mitchellii*, *Boerhavia* spp., *G. breviflora*, *P. oleracea* and *T. terrestris* are reported to increase with heavy grazing (Everist 1974; Orr 1986; Milson 2000) and these species were more frequent under heavy grazing in our study. There are few reports of reduced species richness and abundance under heavy grazing as occurred in our study although Oliva *et al*. (1998) reported reduced species richness and abundance following 10 years of heavy grazing in Argentina.

Exclusion of grazing resulted in the complete absence of *Astrebla* spp. seed in the soil seed bank and much reduced *Astrebla* spp. biomass in the herbage (Orr and Phelps 2013). The poor overall pasture performance of the exclosure treatment supported the suggestion (Everist and Webb 1975) that complete exclosure results in the evolution of plant communities other than *Astrebla* grassland. Similarly, Hickman *et al*. (2004) reported reduced species richness in ungrazed compared with grazed prairie in North America. However, reduced species richness and abundance with removal of grazing in our study conflicted with results in another Australian grassland at Kirramingly Nature Reserve, New South Wales, where *Astrebla* spp. were present (Lewis *et al*. 2008). There, disturbance in the form of livestock grazing was not necessary to maintain plant species richness. In Argentina, Oliva *et al*. (1998) reported that species richness and abundance improved within an exclosure which had been excised from a formerly moderately grazed area.

The relationship between the total number of species recorded and utilisation remained similar for each of the three samplings (Fig. 4). Nevertheless, there were some notable differences in density and frequency of individual species between samplings. This result is consistent with the finding (Lewis *et al*. 2008) that differences between grazed and ungrazed sites remain constant despite large fluctuation in species relative richness through time.

These *Astrebla* grasslands have been grazed predominantly by Merino sheep for wool production since European settlement in the 1860s and, as a result, we used sheep in our grazing study commencing in 1984. However, a steady economic decline of the wool industry since the 1970s has lead to cattle grazing progressively replacing sheep. *Astrebla* grasslands in the 2010s are used predominantly for cattle production, particularly in the northern region. Filet (1990) compared the diets of sheep and cattle grazing *Astrebla* grassland in southern Queensland and reported that sheep diets consistently contained a much higher composition of forbs, when they were available in the pasture, than cattle. This finding suggested that, at the same utilisation percentage, species richness and abundance in these grasslands could be higher under cattle grazing than under sheep.

Seasonal effects

Many species displayed large variations in both density and frequency despite few major differences in their presence/absence between the three samplings. Nevertheless, some species were present in some years but not others. For example, the perennial grasses *A. latifolia* and *D. sericeum* were present only in 2001. This result was consistent with other reports that both species occur mainly during periods of above-average rainfall in western Queensland (Williams and Roe 1975; Orr 1981).

The most apparent fluctuations in densities and frequencies occurred with *Iseilema* spp. in response to differing rainfall patterns in 2001, 2004 and 2007. This is consistent with fluctuation in *Iseilema* spp. measured in an earlier study at Toorak Research Station (Hall and Lee 1980). In our study, the highest germinable *Iseilema* spp. soil seed bank density of 3100 seeds m^{-2} was more than 10-fold greater than the highest measured density of *Astrebla* spp. of 220 seeds m^{-2}. Such large differences, particularly for *Iseilema* spp., give credence to the suggestion (Williams and Roe 1975) that high densities of *Iseilema* spp. can prevent the establishment of *Astrebla* spp. Furthermore, *Iseilema* spp. density was only 35 seeds m^{-2} in 1989 when the large *Astrebla* spp. recruitment of 30 seedlings m^{-2} was recorded (Orr and Phelps 2013). Large *Astrebla* spp. recruitment events can be associated with a drought phase of ENSO during which times *Iseilema* spp. densities are normally low. However, because of this large seed production potential of *Iseilema* spp. relative to *Astrebla* spp., it is possible to speculate that a large *Astrebla* spp. recruitment event during ENSO drought phases is, by default, associated with low *Iseilema* spp. densities and maybe other species as well.

Our study recorded a total of 74 species of which 18 (including *Astrebla* spp., *A. squarrosa* and *Iseilema* spp.) were grasses and 56 were forbs of which 11 were legumes. This number is about the same as the 20 grasses, 58 forbs (including 14 leguminous forbs) in *Astrebla* grassland at Cunnamulla (Roe and Allen 1993) and much lower than the 194 taxa and 49 plant families (Lewis *et al*. 2008) and the 364 plant taxa (Lewis *et al*. 2009) at Kirramingly Nature Reserve, Moree, New South Wales. One major reason for these differences may be related to low incidence of winter rainfall at Toorak relative to more southern regions (Lewis *et al*. 2008). Other reasons were our grouping of plant species and restricted seed germination procedure with only summer germination times. In our study, we grouped three individual species into the group *Astrebla* spp. and we were unable to identify up to nine individual species of *Iseilema* spp. (Milson 2000).

Seed bank methods

The two wetting methods used in this study – capillary wetting for annual seed banks and overhead spraying for species richness and abundance – resulted in substantial differences in seed bank values for the same sampling period. For example, the seed bank of *Iseilema* spp. in 2001 ranged 95–1625 seeds m^{-2} using the capillary method whereas the same range for the overhead spraying method was 175–2450 seeds m^{-2}. These differences support the claim (Orr *et al*. 1996) that the overhead spraying method is a superior method, particularly for clay soils.

Sustainable management of Astrebla grasslands

This study indicated that the highest species richness and abundance was maintained at the lightest utilisation under continuous grazing. Other results from this grazing study indicate that first, the *Astrebla* grasslands remained sustainable when utilisation was maintained at up to 30% of end of summer available forage (Orr and Phelps 2013) and second, that maximum sustainable and economic wool production also occurred at 30% utilisation (D. G. Phelps, D. M. Orr, M. T. Sullivan, unpubl. data). On the other hand, if the aim in managing these grasslands is to maximise species richness and abundance such as in a grassland nature reserve, then the use of carefully managed livestock grazing is essential.

In terms of maintaining species richness and abundance, Everist and Webb (1975) suggested 'arrangements' with experienced graziers to manage their *Astrebla* grasslands primarily for the maintenance of the vegetation. Our results support this suggestion as a way of managing future *Astrebla* grassland nature reserves to ensure the maintenance of species richness and abundance. Our results also support the establishment of such nature reserves in several areas that represent the diverse regional variation throughout the broad range of *Astrebla* grasslands in northern Australia. Nevertheless, such areas may represent poor reference points for monitoring changes in species occurrences.

Orr and Phelps (2013) demonstrated that recovery of *Astrebla* spp. basal area was possible by excluding domestic livestock, particularly during periods of above-average summer rainfall. Such recovery was possible because *Astrebla* spp. tussocks remained before implementing recovery management. However, recovery of some forb species may be difficult and require re-introduction of seed, because we detected no seed of these species in the soil seed bank. Nevertheless, Lewis *et al*. (2008) suggested that grasslands at Kirramingly Nature Reserve, which contains *Astrebla* spp., can recover in terms of native species richness following heavy grazing. Given the substantial differences in species richness and abundance among our wide range of utilisation rates, we suggest that the ecological status of *Astrebla* grasslands may be better assessed by including both annual grass and forb species richness and abundance in addition to the status of *Astrebla* spp.

Conclusions

This study provides important data on the impact of utilisation on plant species richness and abundance in northern *Astrebla* grasslands. Plant species richness and abundance in the seed bank was highest at the lightest utilisation and was progressively reduced with increasing utilisation rates. Species richness and abundance in an exclosure was numerically similar to that at the heaviest utilisation used in this study, but differed noticeably in the species present. Differences in rainfall patterns and totals among years resulted in fluctuations in both the frequency and seed density of many species, although there was little variation in the species that were present. Continuous grazing to achieve maximum sustainable wool production will result in some reduction in plant species richness and abundance.

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