CSIRO PUBLISHING

The Rangeland Journal, 2014, **36**, 309
http://dx.doi.org/10.1071/RJ11068_CO

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

The Rangeland Journal, 2013, **35**(1) 1–15 and 17–28 doi:10.1071/RJ11068 and doi:10.1071/RJ11069

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.

CSIRO PUBLISHING

The Rangeland Journal, 2013, **35**, 1–15
http://dx.doi.org/10.1071/RJ11068

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.

D. M. Orr[A,C] *and D. G. Phelps*[B]

[A]Department of Agriculture, Fisheries and Forestry, PO Box 6014, Red Hill, Rockhampton, Qld 4701, Australia.
[B]Department of Agriculture, Fisheries and Forestry, PO Box 519, Longreach, Qld 4730, Australia.
[C]Corresponding author. Email: david.orr@daff.qld.gov.au

Abstract. Managing large variations in herbage production, resulting from highly variable seasonal rainfall, provides a major challenge for the sustainable management of *Astrebla* (Mitchell grass) grasslands in Australia. A grazing study with sheep was conducted between 1984 and 2010 on an *Astrebla* grassland in northern Queensland to describe the effects of a range of levels of utilisation of the herbage at the end of the summer growing season (April–May in northern Australia) on the sustainability of these grasslands. In unreplicated paddocks, sheep numbers were adjusted annually to achieve 0, 10, 20, 30, 50 and 80% utilisation of the herbage mass at the end of the summer over the ensuing 12 months. Higher levels of utilisation reduced both total and *Astrebla* spp. herbage mass because of the effects of higher utilisation on *Astrebla* spp. and this effect was accentuated by drought. The tussock density of *Astrebla* spp. varied widely among years but with few treatment differences until 2005 when density was reduced at the 50% level of utilisation. A major change in density resulted from a large recruitment of *Astrebla* spp. in 1989 that influenced its density for the remainder of the study. Basal area of the tussocks fluctuated among years, with increases due to rainfall and decreases during droughts. Seasonal rainfall was more influential than level of utilisation in changes to the basal area of perennial grasses. Drought resulted in the death of *Astrebla* spp. tussocks and this effect was accentuated at higher levels of utilisation. A series of three grazing exclosures were used to examine the recovery of the density and basal area of *Astrebla* spp. after it had been reduced by 80% utilisation over the preceding 9 years. This recovery study indicated that, although grazing exclusion was useful in the recovery of *Astrebla* spp., above-average rainfall was the major factor driving increases in the basal area of perennial grasses. Spring values of the Southern Oscillation Index and associated rainfall probabilities were considered to have potential for understanding the dynamics of *Astrebla* spp. It was concluded that *Astrebla* grassland remained sustainable after 26 years when grazed at up to 30% utilisation, while, at 50% utilisation, they became unsustainable after 20 years. Results from this study emphasised the need to maintain the population of *Astrebla* spp. tussocks.

Additional keywords: *Astrebla* spp., ecosystem processes, pasture dynamics, utilisation.

Received 17 October 2011, accepted 14 February 2013, published online 8 March 2013

Introduction

Astrebla (Mitchell grass) grasslands, which occupy 450 000 km^2 in Australia between the annual rainfall isohyets of 250 and 550 mm on cracking clay soils, where summer rainfall is dominant, are used for extensive grazing of domestic livestock. The grasslands can be virtually treeless and are dominated by one or more of the four *Astrebla* species, together with a wide range of other perennial and annual grasses and forbs. The species present at any given site are influenced by a range of factors including geographical location, recent rainfall history and utilisation by livestock (Orr 1975; Orr and Holmes 1984; Roe and Allen 1993; Phelps and Bosch 2002). Individual *Astrebla* spp. tussocks are long-lived (Williams and Roe 1975; Orr 1998) and are the ecological matrix species of the vegetation, while almost all other species are annual or short-lived perennials that fluctuate rapidly over a short time-period (interstitial species) (Grubb 1986; Orr 1986). In more northern *Astrebla* grasslands, where rainfall is strongly summer-dominant, the interstitial species tend to be annual grasses whereas further south, the interstitial species tend to be a wide range of grasses and forbs, because rainfall is more evenly distributed throughout the year. Specific rainfall sequences at any location can govern species composition (Orr 1981). Higher utilisation by livestock reduces the herbage mass of *Astrebla* spp. with consequent increases in the herbage mass of the interstitial species (Orr 1986).

Throughout its range, *Astrebla* grasslands are generally regarded as being stable and productive, although large variations in herbage production, resulting from high rainfall variability, provides a major challenge for their sustainable management (Orr 1975; Hall and Lee 1980; Orr and Holmes 1984; Roe and Allen 1993). One approach to managing this large variation in herbage production is to adjust livestock numbers to match the herbage mass at the end of the summer, which is the most reliable growing season (Ebersohn 1973). This approach prompts the question of what level of utilisation of herbage mass at the end of summer will maintain pasture productivity and what will be the corresponding productivity of livestock. Utilisation is defined as the annual grazing pressure set after the summer growing period by calculating the number of stock required to utilise a percentage of the herbage over the following year, in the absence of further growth.

Grazing studies, using the utilisation approach in south-western Queensland, suggested that a 30% utilisation of herbage of *Astrebla* grasslands (Beale *et al*. 1986; Orr *et al*. 1986) and 15% utilisation of *Acacia aneura* (Mulga) woodland (Orr *et al*. 1993) were sustainable. In both studies, 80% utilisation of herbage severely reduced the basal area of perennial grasses, which showed little increase in basal area following more favourable rainfall. Furthermore, total exclosure from grazing in the 80% utilisation treatment for 5 years in the *Astrebla* grassland study (C. J. Evenson, pers. comm.) failed to achieve any recovery in the basal area of perennial grasses. These are the only studies, which the authors are aware of, where the utilisation approach has been used. These results prompted the question of whether *Astrebla* grasslands in northern Queensland, where annual rainfall is strongly summer-dominant, may be more persistent than in southern Queensland where annual rainfall is more evenly distributed throughout the year.

A long-term grazing study was established at Toorak Research Station, Julia Creek in 1984 to determine the impact of utilisation of herbage on sustainable productivity in a northern *Astrebla* grassland. As with the studies of Orr *et al*. (1986, 1993), the philosophy behind this study design was that, with limited research resources, it was more effective to examine a broad range of unreplicated treatments rather than to replicate a limited range of treatments. While the treatments were not replicated, the study was conducted over 26 years in a landscape that is sufficiently uniform that results from one part of the landscape can be extrapolated: first, to the other parts of the landscape and second, to the northern *Astrebla* grasslands in general. The primary objectives of this study were to (i) determine the impacts of six levels of utilisation of herbage at the end of summer on the pasture and, therefore, livestock productivity in the northern *Astrebla* grasslands and (ii) quantify the role of rainfall variability and utilisation level on the processes of possible degradation of *Astrebla* spp. A secondary objective was to evaluate the processes of recovery of *Astrebla* spp. because, as with the two earlier utilisation studies, 80% utilisation substantially reduced the density and basal area of perennial grasses.

The use of the term 'utilisation' has evolved since the establishment of the Toorak study in 1984. McKeon *et al*. (1994) adopted the term to refer to the percentage of herbage consumed in relation to the total herbage produced in the daily time step model GRASP. Johnston *et al*. (1996) applied this as an average per cent utilisation over the growing season – an approach which has been extended across northern Australia (e.g. McIvor *et al*. 2010). Experimentally, utilisation has been more closely aligned to modelling approaches by matching stock numbers with short-term changes in pasture growth (e.g. Ash *et al*. 2011), but the same pragmatic approach, as used at Toorak, has also been recently applied i.e. annual adjustments based on a feed budget at the end of growing season (Hunt 2008).

In recent years, an increasing understanding of the ENSO (El Nino Southern Oscillation) phenomenon has provided an improved understanding of the association between rainfall variability and ecological events (McKeon *et al*. 2004). The Southern Oscillation Index (SOI), as a signal of the ENSO phenomenon, measures the difference in air pressure between Tahiti and Darwin with values generally between –30 and +30. High and low values of the SOI are associated with higher and lower probabilities of exceeding mean rainfall, respectively. The SOI is generally most useful when used as a 1- or 3-monthly mean and has been shown to have a relationship with rainfall occurrence in eastern Australia (Partridge 2001).

This paper reports the population dynamics of *Astrebla* spp. in north Queensland in response to a range of utilisation levels by sheep through a range of above- and below-average rainfall conditions and ENSO events between 1984 and 2010 and discusses the implications in relation to sustainable grazing management. This paper also reports management techniques of regeneration where grazing has been unsustainable. A further paper from this grazing study reports the impact of these treatments on plant species richness and abundance (Orr and Phelps 2013). There is also information on animal productivity and economic performance (D. G. Phelps, D. M. Orr, M. T. Sullivan, unpubl. data).

Materials and methods

Grazing study

A grazing study was established in 1984 at Toorak Research Station (21.02°S, 142.78°E) in the Allaru land system (Turner and McDonald 1993), 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). The Allaru land system is extensive throughout *Astrebla* grassland in Queensland where other research, e.g. Orr (1986), Orr *et al*. (1988), Orr and Evenson (1991*a*, 1991*b*) and Phelps (2006), has been conducted. 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 treatments U0, U10, U20, U30, U50 and U80) of the total herbage mass on a DM basis at the end of summer except in 1988 where the mass of the sub-shrub *Salsola kali* was excluded for animal welfare reasons. The months of April and May are generally used as the end of the summer growing period in northern Australia. Weathered grass stalks carried over from the previous growing seasons were excluded. Paddock sizes were 1, 54, 27, 18, 12 and 7 ha for treatments U0, U10, U20, U30, U50 and U80, respectively (Fig. 1), having been scaled to be grazed by 20 sheep each at the commencement of

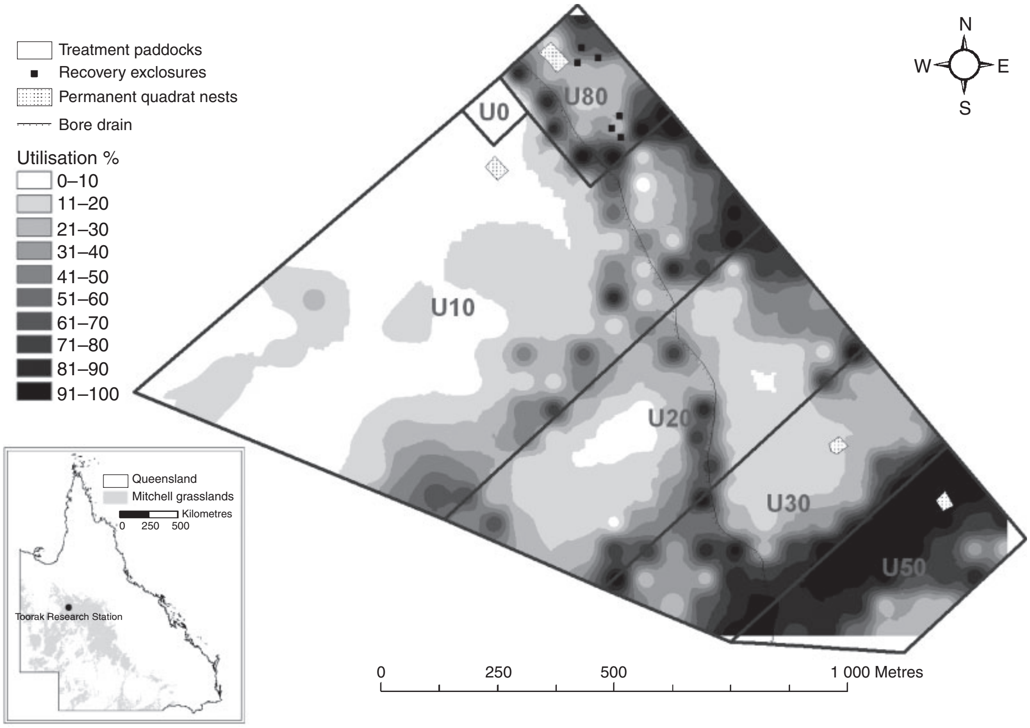

Fig. 1. Layout of Toorak grazing study showing the layout of the six treatment paddocks. The distribution of utilisation is as mapped by Phelps and Orr (2003). The location of the permanent quadrats and the recovery quadrats are also indicated.

grazing in June 1984. At the end of each summer (April or May), Merino wethers with a fat score of 2.5 or higher were stratified on shorn liveweight and allocated to treatment paddocks using the formula $N_S = Y/I_S \times U \times P_S$ where: N_S is sheep numbers, Y is herbage mass (kg DM ha^{-1}), I_S is the intake by sheep (kg dry sheep $equivalent^{-1}$ and assumed to be 400 kg), U is utilisation level (%) and P_S is paddock size (ha). Grazing commenced in July 1984.

Herbage mass

Herbage mass was estimated at the end of the summer growing season in 1984 and 1985 using a tied rank technique (Halls and Dell 1966) and in subsequent years using BOTANAL (Tothill *et al*. 1992). Only total herbage mass was recorded in 1984 and 1985. Since May 1986, herbage mass and species composition were measured by between four and nine trained operators who assessed a minimum of 60, 250, 200, 150, 140 and 80 quadrats (not permanent quadrats), each 0.5 × 0.5 m, in the U0, U10, U20, U30, U50 and U80 treatments, respectively. The calibration data of individual operators were used to adjust their individual rankings to herbage mass of the different species. *Astrebla* spp. were combined at the genus level until 1993 when *A. squarrosa* was recorded separately following observations that its occurrence was declining on the high levels of utilisation treatments. This paper reports total herbage mass and that of *Astrebla* spp. and *Iseilema* spp. (pasture dominants) while plant species richness and abundance is reported in Orr and Phelps (2013). Data on total herbage mass were log-transformed before analysis using REML (Genstat 2002) with fixed effects of utilisation level and years within utilisation level and random effects of paddocks and quadrats within paddocks.

Astrebla *spp. dynamics*

The dynamics of *Astrebla* spp. was studied in 25 permanent quadrats, each 1 × 1 m, established at random in one nest in each of the U10, U30, U50 and U80 treatments. In 1984, the position of individual *Astrebla* spp. tussocks in each quadrat was located by dividing each quadrat into 16 grid units, each 0.25 × 0.25 m, and charting the position and diameter of each tussock within each grid cell. The diameter of each plant was measured. Where tussocks were not circular or where plants had fragmented, the living plant diameter was measured first along the widest diameter and second the diameter in the perpendicular direction to this widest diameter. Subsequent recordings were made annually in autumn when the survival and size (see below) of existing plants were recorded along with any seedling recruitment (Orr *et al*. 2004, 2010*a*). Basal area of *Astrebla* spp. was calculated on an individual quadrat basis as the area occupied by all *Astrebla* spp. tussocks in that quadrat (expressed as a percentage). Individual plant size for both the original plants and annual cohorts was determined as the area covered by each plant of that cohort and was calculated by dividing the total basal area (in cm^2) of that cohort per quadrat by the number of individual plants (incorporating the number of segments making up each of these tussocks) in that quadrat (Orr *et al*. 2004, 2010*a*).

Spatial estimation of utilisation in each paddock in spring 2001, 2003 and 2007 (Phelps and Orr 2003) suggested that the permanent quadrats in treatments U10, U30 and U50 were representative of the utilisation rate of these treatments (Fig. 1). Utilisation where the quadrats were located in the U80 treatment was lower than anticipated (30–50% utilisation).

Density and basal area of *Astrebla* spp. over time were analysed as repeated-measures of the quadrats using REML and by modelling the variance-covariance matrix to account for the correlation structure induced by the repeated-measures. The variance-covariance matrix for both variables was modelled as an unstructured matrix. Density data were log-transformed and basal area data arcsine-transformed before analysis. Since many of the original tussocks of *Astrebla* spp. died in the 1984–88 drought, only data from 1989 onwards were included in the survival analysis. Survival profiles for both the 1984 and 1989 cohorts for the four levels of utilisation (treatments U10, U30, U50 and U80) were compared by applying a proportional hazard model (Cox 1972) with the U10 treatment as the baseline hazard.

Pasture recovery

By 1993, the U80 treatment had become unsustainable with a substantial reduction in the basal area of *Astrebla* spp. Consequently, in 1994, a recovery study commenced within the U80 treatment to evaluate the potential for *Astrebla* spp. to recover from 9 years of continuous heavy utilisation. Three treatments of different starting times of exclosure of all sheep, spring 1994, spring 1995 or spring 1996, were designed as a randomised block experiment within the paddock of the U80 treatment. Six plots (two replicates of three treatments), each 13×7 m, were established in spring 1994 with each plot containing 12 permanent quadrats, each 1×1 m, to monitor *Astrebla* spp. One plot from each replicate was exclosed randomly each spring. All permanent quadrats were recorded annually between 1994 and 2000 as outlined above. All treatments continued until 2000.

Density, recruitment, survival and basal area and plant size of *Astrebla* spp. within each sampling date were analysed using REML based on the six plots (12 quadrats per plot) of the three exclosure treatments and a seventh plot (25 quadrats outside the exclosures).

Results

Rainfall

Summer (October–March inclusive) rainfall variedly widely between 1984 and 2010 and ranged from 60% below to 100% above the long-term mean of 384 mm (Fig. 2). There were three extended droughts (24 months of rainfall continuously in the lowest 10th percentile, Clewett *et al*. 2003) in 1984–86, 1987–89 and 1994–96; five major droughts (12 months of rainfall continuously in the lowest 10th percentile) in 1984–85, 1987–89, 1991–92, 1994–95 and 2002–03, and two summers, 1990–91 and 2008–09 where summer rainfall was > than 80% above the mean (Fig. 2*a*). The long-term mean winter (April–September) rainfall was 56 mm and above-average winter rainfalls of 175, 122, 217 and 182 mm were received in 1990, 1998, 2006 and 2007, respectively.

Mean spring (September–November) SOI values varied between –15 and +20 (Fig. 2*b*) and values greater than +5 or more negative than –5 were statistically related to summer rainfall [based on the Kolmogorov–Smirnov test, Clewett *et al*. (2003)]. Spring SOI values, which were low in 1985–86 to 1987–88 and high in 1988–89, 1998–99 and 1999–2000, were associated with substantial changes in the plant dynamics *Astrebla* spp., as reported below.

Total herbage mass

Total herbage mass at the end of the summer growing season fluctuated in response to variation in rainfall with low herbage masses in the drought years of 1985, 1986, 1988 and 2005 (Fig. 3*a*). Total herbage mass profiles across time differed ($P < 0.001$) with utilisation treatment (i.e. a significant year × utilisation treatment interaction) with herbage mass

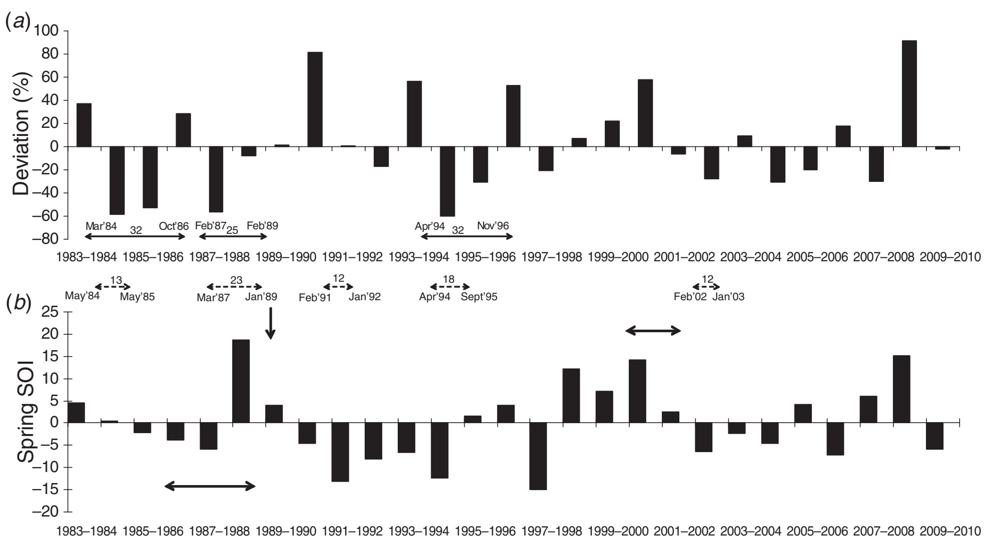

Fig. 2. (*a*) Deviation from mean summer rainfall at Toorak between 1983–84 and 2009–10 with durations (months) and dates of extended (—) and major (- - -) droughts as defined by RAINMAN (Clewett *et al*. 2003) and (*b*) mean spring (September–November) Southern Oscillation Indices (SOI) between 1983 and 2009. Periods when significant vegetation effects were recorded are indicated with arrows.

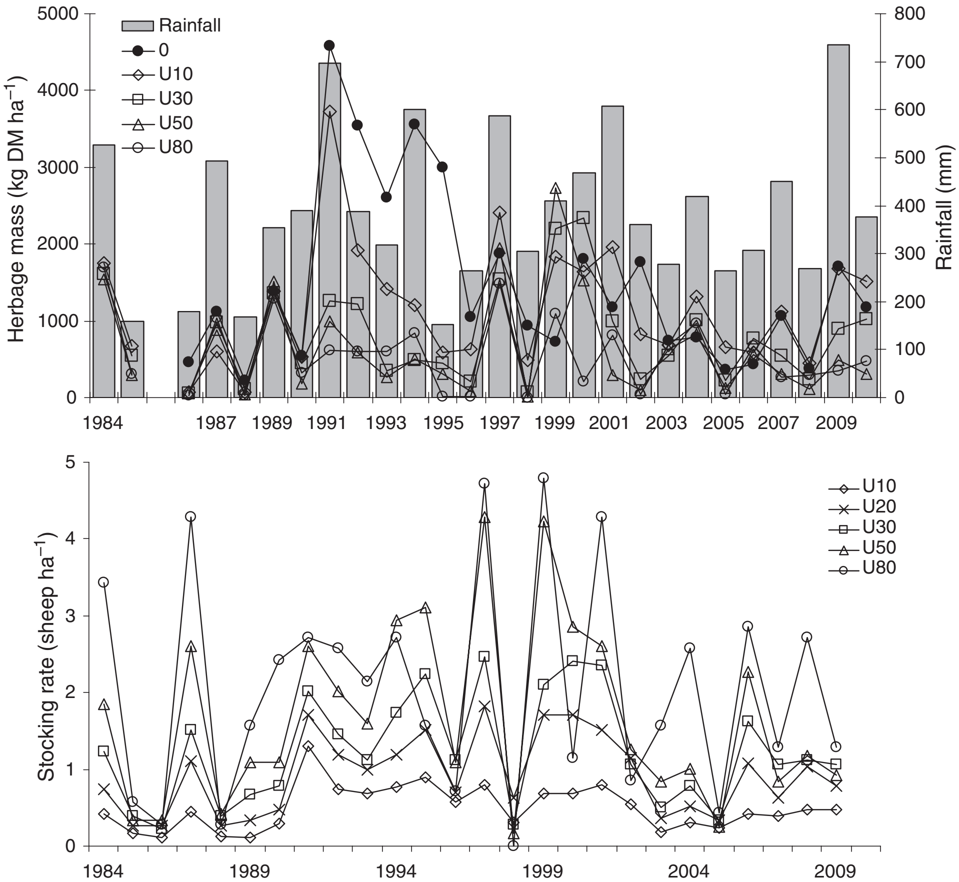

Fig. 3. (*a*) Total herbage mass (kg DM ha^{-1}) at five levels of utilisation in relation to summer rainfall. Data for treatment U20 were excluded to improve clarity of presentation and analysis for 1986–2010 was performed on log-transformed data. (*b*) Annual stocking rates (sheep ha^{-1}) used to achieve five levels of utilisation in an *Astrebla* grassland at Toorak between 1984 and 2010.

differing least across years in treatment U10 and most in treatment U80. In treatment U0, total herbage mass was greatest between 1987 and 1996, but declined to be between U10 and U30 treatments in most years thereafter. In the grazed treatments, total herbage mass was consistently greatest on treatment U10 and reduced proportionately as treatments increased in level of utilisation. For clarity of presentation, data for treatment U20 are not included but these data were consistently intermediate between the U10 and U30 treatments.

Stocking rate of sheep

Stocking rates (sheep ha^{-1} and sheep kg^{-1} DM of herbage) increased with increasing utilisation. For example, the average stocking rate over the 26 years of the study was 0.5 sheep ha^{-1} in treatment U10 and 2.1 sheep ha^{-1} in treatment U80. Stocking rates fluctuated widely in response to variable rainfall throughout the study, from 0.1 sheep ha^{-1} in treatment U10 in 1986, 1988 and 1989 to 4.8 sheep ha^{-1} in treatment U80 in 1999 (Fig. 3*b*). Stocking rate was also more sensitive to fluctuations in herbage mass on the higher utilisation treatments as higher sheep intakes ha^{-1} were required to achieve these levels of utilisation. For example, the standard error of mean varied least for treatment U10 ($\pm$0.06 sheep ha^{-1}) and most for treatment U80 ($\pm$0.29 sheep ha^{-1}) with intermediate values of 0.10, 0.14 and 0.24 sheep ha^{-1} for treatments U20, U30 and U50, respectively.

From 1995 onwards, total herbage mass in treatment U80 was dominated by annual grasses and forbs which were often unable to support a full 12 months of grazing. Sheep numbers in this treatment were reduced or the treatment completely destocked due to low herbage mass and sheep losing liveweight before the start of the subsequent wet season. When possible, new sheep from a reserve pool were substituted for the existing sheep to maintain the utilisation level of the treatment. This was not always possible and there were occasions when utilisation was below the planned utilisation on the U80 treatment at the break-of-season rainfall and the start of the wet-season growing period. In 1998, the herbage mass at the end of summer was only able to support a stocking rate of 0.5 sheep ha^{-1} and the treatment remained ungrazed over the 1998–99 season.

Herbage mass of species

The herbage mass of *Astrebla* spp., estimated in April–May each year, ranged from 15 kg DM ha^{-1} in treatment U80 in May 1998 to 4800 kg DM ha^{-1} in treatment U0 in 1991 and was higher in treatment U0 than all the grazed treatments between 1990 and 1996. Thereafter, the herbage mass of *Astrebla* spp. in treatment U0 declined substantially between 1997 and 2003 (Fig. 4*a*) and this coincided with a reduced frequency of *Astrebla* spp. (data not presented). In treatment U0, tussocks of *Astrebla* spp. became moribund over the dry 1994–96 period, produced little new growth, failed to produce inflorescences and then died over the wet season of 1995–96. The herbage mass of *Astrebla* spp. gradually increased to be highest in 2010 and this increase was associated with an increased frequency of *Astrebla* spp., albeit not to the pre-1996 levels. In the grazed treatments, the herbage mass of *Astrebla* spp. was consistently highest on the lower utilisation treatments and was reduced by increasing utilisation until 1998 when the U80 treatment could not be restocked. Although after 2000, the herbage mass of *Astrebla* spp. in treatment U80 fluctuated widely (this treatment remained ungrazed over the 1998–99 year), for the other grazed treatments, there was a continuation of the overall trend for a reduced herbage mass of *Astrebla* spp. with increasing utilisation.

The herbage mass of *Astrebla squarrosa* ranged from 0 kg DM ha^{-1} in drought years to 1860 kg DM ha^{-1} in treatment U30 in 2001 (Fig. 4*b*). The herbage mass of *A. squarrosa* in treatment U0 was initially high between 1993 and 1996 but declined in 1997 and, thereafter, generally remained intermediate. In the grazed treatments, the herbage mass of *A. squarrosa* was consistently highest in treatments U10 and U30 and also initially in treatment U50 until 2003, after which time the herbage mass in treatment U50 was similar to that in treatment U80. The herbage mass of

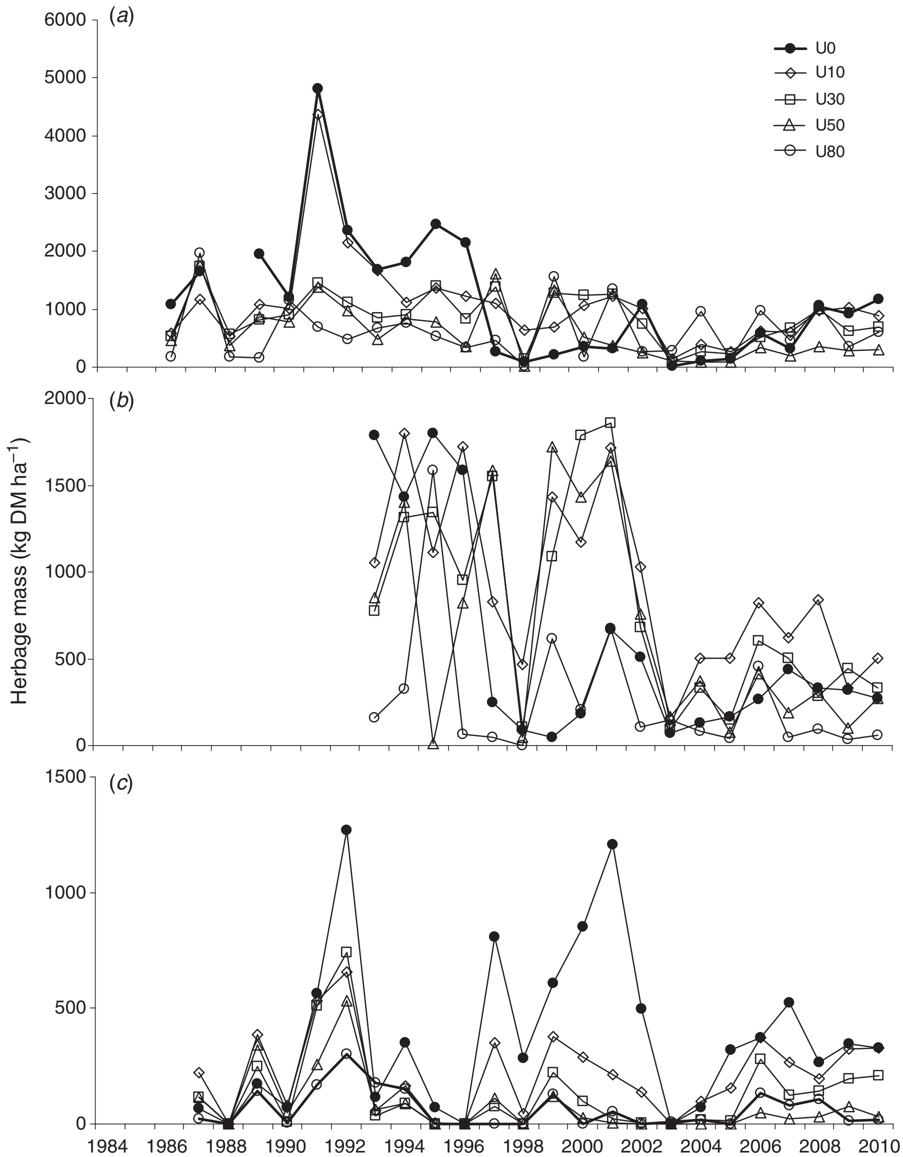

Fig. 4. Herbage mass (kg ha^{-1}) of (*a*) *Astrebla* spp., (*b*) *A. squarrosa* and (*c*) *Iseilema* spp. at five levels of utilisation in an *Astrebla* grassland at Toorak between 1984 and 2010. Data for treatment U20 were excluded to improve clarity of presentation.

Iseilema spp. ranged from 0 kg DM ha^{-1} in drought years to 1280 kg DM ha^{-1} in treatment U0 in 1992 (Fig. 4*c*). From 1990 onwards, the herbage mass of *Iseilema* spp. was consistently highest on the U0 treatment and declined on treatments with increasing levels of utilisation.

Population dynamics of Astrebla *spp.*

Density and recruitment

The effect of utilisation treatment on plant density differed ($P < 0.001$) with year (Fig. 5*a*). From 1990 to 1993, density decreased more in treatments U50 and U80, was greatest in treatment U50 from 1999 to 2002 and least from 2003 to 2010. There was a very large recruitment event in 1989 (Fig. 5*b*), which was associated with average summer rainfall, but followed a spring 1988 SOI value of 18 after 3 years with negative SOI values (Fig. 2*b*). Smaller recruitment events occurred in 1987, 1991, 1994, 1999, 2000, 2006 and 2007. The events in 1987, 1989 and 2001 showed no treatment trends while seedling density in 1999 and 2000 tended to be higher in treatments U50 and U80.

Survival

Survival of the original, 1984 *Astrebla* spp. tussocks depended on their initial size. All tussocks with a diameter <5 cm in 1984 died in the 1984–88 drought (data not presented). Some initial tussocks with a diameter ≥5 cm in 1984 persisted throughout the study despite substantial mortality in both the droughts of 1984–88 and 2003–05 (Fig. 6*a*). Survival hazards for the 1984 cohort with diameters >5 cm and based on the number of plants in 1984 differed ($P < 0.05$) among utilisation treatments. Plants in treatment U30 were 1.6 times more likely to survive than those in treatments U10 and U50 while plants in treatment U80 were half as likely to survive as plants in treatment U10. Maximum life span for the 1984 cohort was >26 years. The hazard profiles for plants of the 1989 cohort differed ($P < 0.05$) among all treatments with a decreasing chance of survival as utilisation increased (hazard coefficients of 0.7, 0.6 and 0.3 for treatments U30, U50 and U80, respectively) (Fig. 6*b*). Maximum life span for the 1989 cohort was >21 years. Survival of the 1991, 1994, 1999, 2000, 2006 and 2007 cohorts, pooled across the four treatments, differed markedly among starting years. The number of plants established in 1991 declined sharply in the drought of 1991–92, whereas plants from the other five cohorts had much higher initial survival when each subsequent summer had above-average rainfall (Fig. 6*c*).

Basal area of Astrebla *spp.*

There was a significant ($P < 0.001$) utilisation × year interaction for basal area (Fig. 7). Basal area collapsed in 1984–89; in 1986 and 1988 it was not measurable and it was virtually zero in 1989 as a consequence of the 1984–86 and 1987–88 droughts (Fig. 2*a*). It increased greatly between 1989 and 1994 and again between 1998 and 2002 with generally favourable rainfall, but declined greatly again in the 2003–05 drought, before recovering steadily following the return of more favourable seasonal rainfall after 2005. The high utilisation

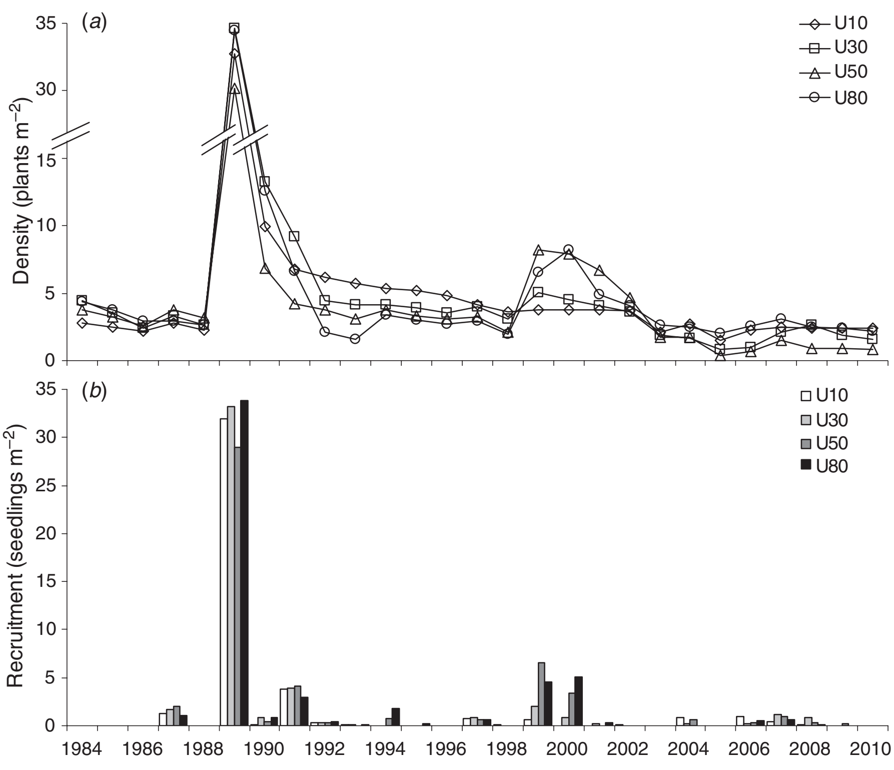

Fig. 5. (*a*) Density (plants m^{-2}) (analysis performed on log-transformed data) and (*b*) seedling recruitment (seedlings m^{-2}) of *Astrebla* spp. at four levels of utilisation in an *Astrebla* grassland at Toorak between 1984 and 2010.

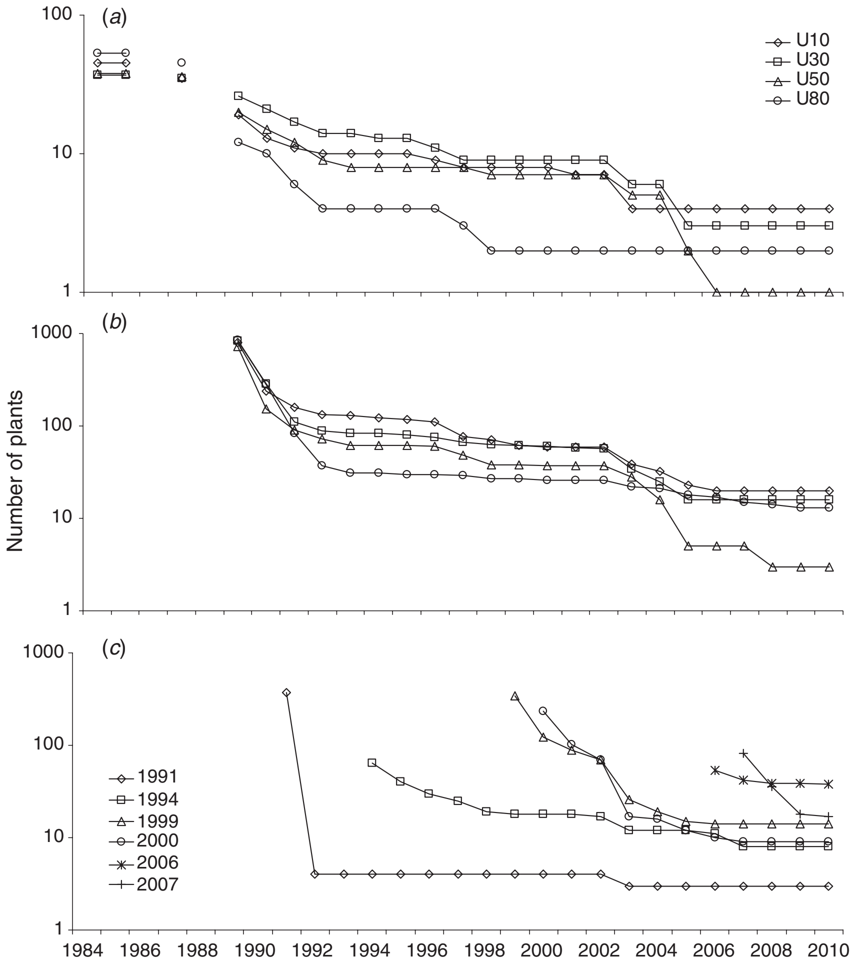

Fig. 6. Survival of *Astrebla* spp. (number of plants) of (*a*) original plants (>5 cm diameter in 1984) at four levels of utilisation, (*b*) 1989 cohort at four levels of utilisation and (*c*) six annual cohorts, averaged across four utilisation treatments, in an *Astrebla* grassland at Toorak between 1984 and 2010. (Note log scales).

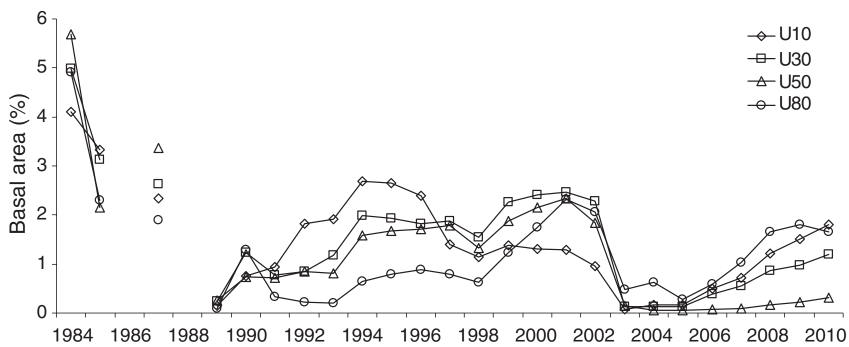

Fig. 7. Total basal area of *Astrebla* spp. (%) at four levels of utilisation in an *Astrebla* grassland at Toorak between 1984 and 2010. Analysis performed on arcsine-transformed data.

treatments mostly reduced the basal area of *Astrebla* spp. and it was generally lower in treatment U80 than in the other treatments until 1999, immediately after this treatment was forcibly spelled over the 1998–99 summer. Subsequently, the basal area in treatment U80 was consistently higher than that of the other treatments. Since 2005, basal area in treatment U50 failed to increase despite favourable rainfall. These changes in basal area reflected similar changes in individual plant size.

Plant size

Changes in tussock size for all cohorts showed similar trends as basal area with all tussocks, irrespective of cohort, increasing in size in response to above-average rainfall and declining during droughts (Fig. 8). In 1984, the size of the tussocks in treatment U80 was reduced relative to the other three treatments until a rapid increase following spelling over the summer of 1998–99. Tussocks also expanded faster in treatment U80 than the other three treatments after 2007, especially in comparison with tussocks in treatment U50 which expanded least (Fig. 8*a*). Tussock sizes for the 1989 cohort increased steadily until 2001, except for treatment U10 which ceased expanding after 1995 (Fig. 8*b*). After 2001, all tussocks were reduced in size by the drought of 2002–03. All survivors then showed an increase in tussock size on all utilisation treatments with increased rainfall from 2005 to 2010, but from 2007 the recovery in treatment U50 slowed so that tussocks were consistently smaller than those of the other three utilisation treatments. Tussock sizes for the 1991, 1994, 1999, 2000, 2006 and 2007 cohorts failed to show any treatment effects and data presented were pooled across the four treatments (Fig. 8*c*). Tussock sizes for the 1999 and 2000 cohorts increased only slightly until 2005 because of the 2002–03 drought, but then increased rapidly with favourable rainfall until 2010. In contrast, tussock sizes for the 2006 and 2007 cohorts increased rapidly in response to favourable rainfall years.

Pasture recovery

Density, recruitment and size of *Astrebla* spp. were similar among exclosure treatments between 1994 and 1998. Density and recruitment were greater ($P < 0.05$) in treatment U80 (not grazed in the 1998–99 year) than the three exclosure treatments in 1999 and 2000 (Fig. 9*a*, *b*) and plant size tended ($P < 0.10$) to be greater in the 1994 exclosure than the other treatments in 1999 and 2000 (Fig. 9*e*). Basal area was similar among exclosure

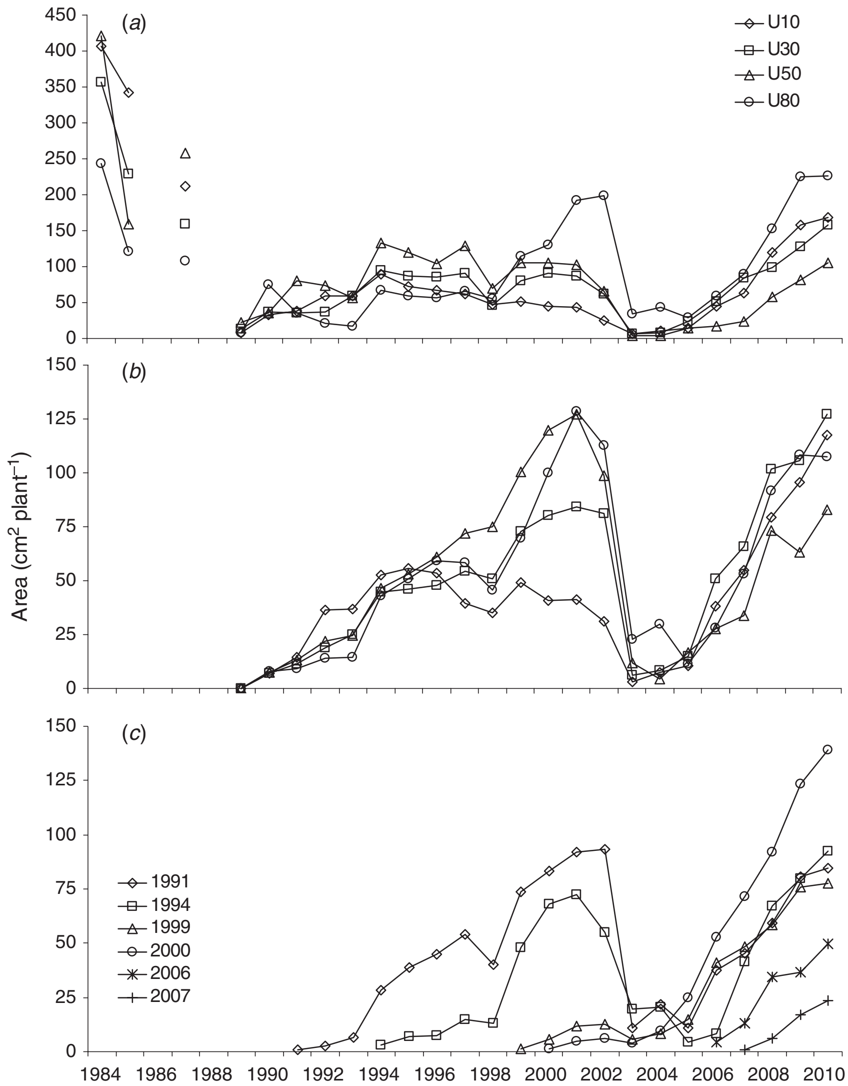

Fig. 8. Size (cm^2 plant^{-1}) of *Astrebla* spp. of (*a*) original plants (>5 cm diameter in 1984), (*b*) the 1989 cohort at four levels of utilisation and (*c*) six annual cohorts averaged across four utilisation treatments in an *Astrebla* grassland at Toorak between 1984 and 2010.

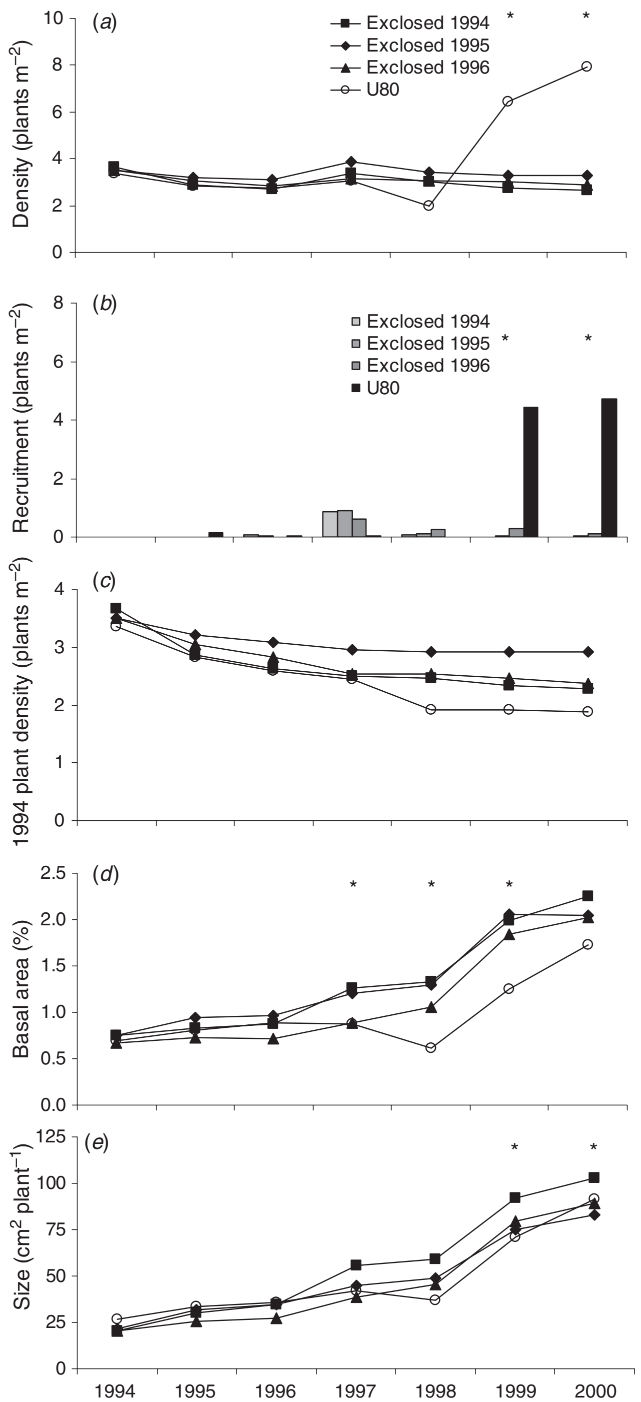

Fig. 9. (*a*) Density (plants m^{-2}), (*b*) recruitment (seedlings m^{-2}), (*c*) survival (number of plants), (*d*) basal area (%) and (*e*) size (cm^2 $plant^{-1}$) of *Astrebla* spp. plants in relation to three exclosures and one utilisation treatment in an *Astrebla* grassland at Toorak between 1994 and 2000. Within years, asterisks indicate differences ($P < 0.05$) among treatments.

treatments between 1994 and 1996 but separated in 1997, 1998 and 1999 with treatment U80 having a lower basal area (Fig. 9*d*). Plant survival was unaffected by exclosure in any year with a tendency ($P = 0.092$) for a difference in 1998 with survival in treatment U80 less than the 1995 exclosure treatment (Fig. 9*c*).

Discussion

Astrebla grassland remained sustainable and productive after 26 years of grazing, throughout a range of rainfall extremes when grazed by sheep at up to 30% utilisation of the total herbage mass at the end of the summer. Productivity in treatment U80 could not be maintained after 14 years of grazing because the basal area and density of *Astrebla* spp. declined sharply and the pasture became dominated by annual species. In treatment U50, however, grazing was maintained despite a marked decline in the presence of *Astrebla* spp. suggesting there is a level of grazing at which land degradation may not become apparent for decades, and prompting the question of when intervention is necessary to commence pasture recovery. This study experienced two severe droughts, 1987–88 and 2002–05, which both impacted on the vegetation independently of utilisation. However, vegetation recovery was more rapid on treatments with lower levels of utilisation possibly due to a combination of lower pre-drought stress and lower post-drought utilisation. Overall these results are consistent with those of the effects of differing utilisations on pasture productivity in both *Astrebla* grassland (Beale *et al*. 1986; Orr *et al*. 1986) and *Acacia aneura* woodland (Orr *et al*. 1993). Despite prolonged heavy utilisation (treatments U50 and U80), surviving tussocks of *Astrebla* spp. were able to recover rapidly following above-average rainfall. In terms of modern utilisation terminology, the figure of 30% utilisation in this study for long-term safe carrying capacity equates to 22%.

Results for the U80 treatment failed to reflect the full impact of this very heavy grazing treatment and need to be interpreted carefully. The high stocking rates used to achieve treatment U80 were unsustainable, especially towards the end of the dry season in drought years, and sheep were removed and not returned until after the start of the wet season. This ensured that this treatment was effectively rested early in the wet season in many years, when heavy grazing has a major impact on perennial grasses (Mott *et al*. 1992). In addition, this treatment was fully rested over the 1998–99 year and this rest was further enhanced by above-average rainfall over the summer of 1998–99. Therefore, results from this nominal U80 treatment after 1999 reflected a large *Astrebla* spp. recruitment in 1989 and a full season of rest which coincided with favourable rainfall.

The mean stocking rate used to achieve treatment U30 was 1.2 sheep ha^{-1} and this was higher than the 'district average' stocking rate of 0.62 sheep ha^{-1} cited by Lorimer (1978) and 0.5 sheep ha^{-1} cited by Hall and Lee (1980). The increasing variability of stocking rate with increasing utilisation (Fig. 3*b*) reflected higher numbers of sheep to achieve such high levels of utilisation after a wet season and was reflected, in turn, with higher input costs of maintaining higher sheep numbers.

Spring (September–November) SOI values and associated rainfall probabilities, along with RAINMAN software indication of drought periods, proved useful in understanding the impacts of variable rainfall on the vegetation changes measured in this study. Low spring SOI values associated with two extended droughts between March 1984 and February 1989 resulted in a major reduction in the basal area and survival of tussocks of *Astrebla* spp. However, a large reduction in the basal area of *Astrebla* spp. between 2002 and 2003 was not associated with extended drought. Nevertheless, Stone *et al*. (2007) reported that high annual maximum temperature and low humidity during 2002–03 resulted in high deficits of vapour pressure, which amplified the effects of low rainfall. A high spring SOI in 1988 and average rainfall over the summer of 1988–89 was associated with the major recruitment event in 1989, while similar high values in 1998 and 1999 were associated with a large increase in the basal area of *Astrebla* spp.

Higher levels of utilisation reduced total herbage mass mainly because of the greater defoliation of *Astrebla* spp., consistent with earlier reports of the effects of grazing on *Astrebla* grassland (Hall and Lee 1980; Orr 1986; Roe and Allen 1993). Very high total herbage masses of 5250 kg DM ha^{-1} were recorded in 1991 while the mean of 2000 kg DM ha^{-1} in U10 was at the upper range of values recorded in central (Orr and Evenson 1991*a*) and southern *Astrebla* grassland (Roe and Allen 1993). The high values in this study were similar to earlier recordings at Toorak (Lorimer 1978; Hall and Lee 1980) and probably reflected the strongly summer-dominant rainfall as evidenced by high values of herbage mass of *A. squarrosa* and *Iseilema* spp., which are both more common in the northern than the central and southern *Astrebla* grasslands (Orr 1986; Roe and Allen 1993).

In the absence of grazing (treatment U0), the highest total herbage mass was recorded between 1987 and 1996, but then declined to be intermediate between those in treatments U10 and U30. This decline mirrored an observed decline in the density of *Astrebla* spp. Absence of disturbance is unnatural in these grasslands: before European settlement, these grasslands were grazed by kangaroos and subjected to intermittent fire. The decline in total herbage mass with continued exclosure is consistent with the suggestion that under-utilisation causes the death of tussocks of *Astrebla* spp. (Everist 1964) and the suggestion of Everist and Webb (1975) that total exclosure from grazing results in 'the evolution of plant communities other than *Astrebla* grasslands'. This suggestion is further supported by changes in plant species richness and abundance reported in the second paper of this series (Orr and Phelps 2013).

Astrebla *spp. dynamics*

Density and recruitment

Large variation in the density of *Astrebla* spp. throughout this study was consistent with data from the southern *Astrebla* grasslands (Roe and Davies 1985; Roe 1987), which these authors attributed to the failure of seedling recruitment. At Toorak, a large change in density occurred as a direct consequence of the large 1989 recruitment event. The resultant 30 seedlings m^{-2} was one of only three large, and apparently episodic, recruitment events recorded in the *Astrebla* grasslands and was associated with a large (220 seeds m^{-2}) seed bank of *Astrebla* spp. and a low (35 seeds $^{-2}$) seed bank of *Iseilema* spp. in the spring of 1988 (Orr and Phelps 2013). Analysis of rainfall patterns, associated with these three episodic recruitment events (Orr and Silcock 2010), inferred a 3-year rainfall sequence; above-mean rainfall in the first summer (to produce seed), below-mean rainfall in the second year (preventing seed germination) followed by above-mean rainfall in the third summer (promoting germination and establishment in the more open pasture). Furthermore, all three events were associated with a particular drought phase of the ENSO weather phenomenon and also low densities of *Iseilema* spp. (Williams and Roe 1975). Such episodic recruitment is consistent with the suggestion (Roe 1987) that the period between large recruitment events in *Astrebla* grasslands 'may exceed 40 years'.

Recruitment in 1999 and 2000 was higher in treatments U50 and U80 compared with treatments U10 and U30 and the three exclosures in the recovery study within treatment U80. By this time, accumulation of herbage after 3–5 years of exclosure would have provided high herbage cover which retards recruitment (Orr 1986). Furthermore, both plant density and basal area were lower in treatments U50 and U80 compared with the exclosures, suggesting that competition from existing tussocks of *Astrebla* spp. may limit recruitment. Further analysis of individual quadrats indicated that recruitment was generally higher where either density and/or basal area were low. This suggested that seedling recruitment of *Astrebla* spp. was more likely to be associated with recovery from drought, provided a suitable seed bank was present, rather than a series of summers with favourable rainfall. The occurrence of three documented large recruitment events, associated with a drought phase of the ENSO weather phenomenon, supports this suggestion. Further study is warranted to develop procedures for predicting large recruitment events.

Plant growth and basal area

In favourable rainfall summers, such as 1998–99 and 1999–2000, tussocks of *Astrebla* spp. from all cohorts expanded in size rapidly, irrespective of utilisation. This expansion resulted from new main tillers on basal nodes and from the rhizome (Everist 1964; Jozwik *et al*. 1970). The accompanying increase in herbage mass resulted from axillary tillers on lower nodes (Jozwik *et al*. 1970), which were also likely to increase seed production (Orr and Evenson 1991*b*). Similar large increases in plant size through tillering with favourable rainfall have been recorded in other C_4 perennial grasses such as *Heteropogon contortus* (Orr *et al*. 2004, 2010*a*) and *Bothriochloa ewartiana* (Jones *et al*. 2009; Orr and O'Reagain 2011).

Despite the documented capacity to produce new tillers, even under heavy utilisation, little is known of the tiller bud dynamics of *Astrebla* spp. Scanlan (1983) suggested that individual tillers of *Astrebla* spp. survive for up to 3 years. The longevity of both tillers and tiller buds could provide valuable management information, especially for formulating drought management and recovery strategies. Hendrickson and Briske (1997) studied the dynamics of axillary buds in two diverse North American perennial grasses and reported that both species retained substantial numbers of dormant and viable buds, which exceeded parental tiller longevity by at least 12 months, and these buds comprised a substantial meristematic source. Given the persistence of tussocks of *Astrebla* spp. and the absence of regular seedling recruitment, the tiller bud bank of *Astrebla* spp. probably represents a major source for tussock growth and further research is required to better understand the contribution of the tiller bud bank to *Astrebla* spp. persistence.

Drought caused tiller mortality, probably of older tillers, and resulted in reduced tussock size and basal area. Severe drought, such as 1984–86, reduced both the size and survival of original large (diameter >5 cm in 1984) tussocks and those tussocks that did survive were observed to have only one or two live tillers while smaller (diameter <5 cm in 1984) tussocks died completely. Recovery of basal area after 1989 from these original plants highlights the importance of maintaining a residual population of *Astrebla* spp. tussocks through drought periods. These surviving tussocks are then vital in allowing *Astrebla* spp. to recover following the resumption of favourable summer rainfall. Fair *et al*. (2001) concluded that the continuing dominance of the long-lived North American grass *Bouteloua gracilis* was related to its ability to survive despite partial plant mortality due to drought. A similar persistence mechanism has been reported for the long-lived *Bothriochloa ewartiana* in northern Australian (Orr and O'Reagain 2011). Similarly, Wright and Van Dyne (1976) reported that long-term drought plays an important role in the mortality or otherwise of long-lived plants.

Large variation in the basal area of *Astrebla* spp. over time resulted from large variations in tussock size, as density was relatively stable. Few data are available on the plant size of *Astrebla* spp. although the largest sizes of 125 cm^2 $plant^{-1}$ (treatment U30, 1989 cohort in 2010) and 140 cm^2 $plant^{-1}$ (2000 cohort in 2010) are similar to the maximum size of 160 cm^2 $plant^{-1}$ for *Bothriochloa ewartiana* (Orr and O'Reagain 2011). However, the original tussocks of *Astrebla* spp. were 400 cm^2 $plant^{-1}$ in 1984, declined to 10 cm^2 $plant^{-1}$ in 1989 and then increased to up to 200 cm^2 $plant^{-1}$ in 2010. This large range in plant size indicates the great capacity of tussocks of individual *Astrebla* spp. to expand in response to favourable rainfall conditions following contraction during drought.

Survival and life spans

Some original tussocks of *Astrebla* spp. survived throughout the 26 years of this study. This is consistent with Williams and Roe (1975) who reported a maximum life span of 23 years. Such longevity is similar to the calculated 30 years for *Bothriochloa ewartiana* elsewhere in northern Australia (Orr and O'Reagain 2011); 39 years for *Bouteloua curtipendula* and *Schizachyrium scoparium* in Kansas (Lauenroth and Adler 2008) and 28 years for *Bouteloua eriopoda* in New Mexico (Wright and Van Dyne 1976). Despite this longevity, survival of tussocks was clearly reduced by drought and then further reduced by increasing utilisation as was evident with the original plants between 1984 and 1989 (Fig. 6*a*).

Survival of annual cohorts differed among years, highlighting the importance of favourable rainfall during establishment (Lambert *et al*. 1990). Higher levels of utilisation further reduced the survival of annual cohorts with survival for the 1989 cohort after 2 years being 20, 13, 12 and 10% and plant size being 14, 11, 12 and 9 cm^2 for treatments U10, U30, U50 and U80, respectively. Such survival is within the range of 5–45% survival recorded for two seedling cohorts at Blackall (Orr and Evenson 1991*a*), but higher than the 4–5% survival for the large, 1941 recruitment at Cunnamulla (Roe and Davies 1985). Similarly, Orr and O'Reagain (2011) reported large differences in survival of young grass plants due to differences in seasonal rainfall.

Increased mortality in treatment U80 up until 1998, and of both the original and 1989 tussocks in treatment U50 after 2003, reflect the unsustainable nature of this level of utilisation, despite treatment U50 appearing sustainable for almost 20 years. This result supports the suggestion (Orr *et al*. 2010*b*) of there being a time lag before the effects of a grazing treatment are reflected in changes in pasture composition. The overall importance of the longevity of tussocks of *Astrebla* spp. in maintaining sustainable grassland is highlighted by the fact that, of the total basal area in 2010, 14 and 40% were contributed by the 1984 and 1989 tussocks, respectively.

Pasture recovery

The overall effects of exclosure on degraded pasture were unclear. Exclosure tended to halt the decline in tussock survival and basal area that was apparent in treatment U80 due to drought between 1994 and 1996. However, it prevented seedling recruitment which occurred under heavy grazing during the above-average rainfall summers of 1998–99 and 1999–2000. Exclosure did result in the recovery of basal area between 1996 and 1998 but the major influence on recovery was above the average rainfall in the summers of 1998–99 and 1999–2000. *Astrebla* spp. responded rapidly to this rainfall even in treatment U80 (ungrazed over the 1998–99 summer) and further reflected the ability of *Astrebla* spp. to respond to favourable rainfall even under heavy grazing. Continuous exclosure limited recruitment and so suggests that wet-season spelling (Mott *et al*. 1992), combined with dry-season grazing, may be more beneficial to the recovery of *Astrebla* spp. The collapse of the herbage mass of *Astrebla* spp. after 12 years of exclosure further supports this suggestion. Questions on the duration and frequency of wet season spelling were not addressed in this study and require further research.

One key reason for the rapid recovery in basal area from the drought of 1984–1986 was the high initial density of *Astrebla* spp. resulting from the large recruitment in 1989. This rapid recovery, through seed produced by existing tussocks, contrasts with other possible recovery mechanisms where, for example, heavy grazing and/or extended drought have greatly reduced tussock density of *Astrebla* spp. For example, total exclosure between 1984 and 1989, following 9 years of 80% utilisation, failed to recover the basal area of perennial grasses in a southern *Astrebla* grassland (C. J. Evenson, pers. comm.). This failure to recover the basal area of perennial grasses was due to the absence of tussocks of *Astrebla* spp. [at that site in February 1984, *Astrebla* spp. contributed 20 kg DM ha^{-1} to a total perennial grass biomass of only 50 kg ha^{-1} (Orr 1986)]. In this situation, recovery would require substantial recruitment to achieve a suitable density of tussocks of *Astrebla* spp. and this recovery process is currently being monitored in another study (D. G. Phelps, unpubl. data). These considerations further emphasise the need to develop a better understanding of those factors which contribute to successful seedling recruitment.

Implications for long-term experiments

This study was conducted over a very long time-frame compared with most national and international studies but still failed to follow a single *Astrebla* spp. cohort for its full life-span (Jones and Mott 1980). Maintaining long-term experiments is difficult especially when continuous resources are required to monitor livestock welfare and to commit to regular measurements of key variables. If this study had ceased, say after 12 years, it would not have discovered:

- A collapse of the herbage mass of *Astrebla* spp. under exclosure, which had implications for the health of *Astrebla* grasslands;
- A collapse of the herbage mass and basal area of *Astrebla* spp. in treatment U80 in 1998 and the important role of spelling in promoting recovery; and
- The collapse of the basal area and tussock survival of *Astrebla* spp. in treatment U50 following 19 years of grazing and the implication that degradation may not be expressed for decades.

It is likely that the density of *Astrebla* spp. in treatment U50 would have been further reduced with a continuation of this treatment, eventually leading to having to spell this paddock to achieve pasture recovery. However, would treatment U50 have recovered with spelling, as did treatment U80, or would recovery become reliant on the recruitment of further *Astrebla* spp.? Would the next major recruitment event have occurred before the death of all existing plants? It is difficult to predict what further discoveries may have been made but this study has further highlighted the importance of long-term studies (Jones *et al*. 1995).

Sustainable management of Astrebla *grasslands*

This study indicated that 30% utilisation of the herbage mass at the end of summer was sustainable and that higher utilisation levels were unsustainable. Economic analysis of animal productivity data (D. G. Phelps, D. M. Orr, M. T. Sullivan, unpubl. data) indicates that financial returns were higher in treatment U50 for the short to medium term, but never in treatment U80. This situation further highlights the conundrum outlined by Burrows *et al*. (2010), whereby producers have to forgo income in the short to medium term to achieve long-term, sustainable outcomes. Unsustainable use of *Astrebla* grasslands, under normal rainfall conditions, are indicated by lack of appreciable tussock density and basal area of *Astrebla* spp., high frequencies of annual grasses, such as *Dactyloctenium radulans* and *Brachyachne convergens*, and changes in other interstitial species (Phelps and Bosch 2002; Orr and Phelps 2013).

Rainfall variability, in addition to utilisation, is the major driver of vegetation change of rangelands and sustainable management practices need to respond to this variability. Drought clearly reduces the basal area of perennial grasses, irrespective of level of utilisation, although higher levels of utilisation further reduce tussock size and survival. Reducing utilisation during such drought periods will maximise the survival of tussocks which, in turn, become pivotal in pasture recovery following drought. Recognising periods of above-average rainfall will allow the recovery of the basal area of perennial grasses which can be rapid given two or more summers of above-average rainfall. Spring SOI values may be useful in developing management strategies associated with such recovery periods. The rapid recovery recorded in the current study, even at high levels of utilisation, highlights the importance of maintaining a residual population of existing tussocks to allow recovery to occur. Any severe reduction in the tussock density of *Astrebla* spp. will inevitably reduce long-term herbage production, economic profitability and pasture sustainability.

A feature of this long-term grazing study was the occurrence of a major recruitment event and the subsequent increase in tussock density over the next 20 years. Although such events are very infrequent, their impact on maintaining tussock density has long-term implications. Recognising recruitment events and then managing to maximise seedling survival can result in maintaining high tussock density over a very long period. The exclosures in this recovery study prevented seedling recruitment after 2–4 years without grazing compared with grazed treatments. This was probably due to accumulated dead herbage in the exclosures suppressing seedling growth. This finding suggests that year-long exclosure from grazing may not be an effective strategy to achieve recovery. Resting during the early part of the growing season may be more effective because this is the critical period when perennial grasses are most susceptible to defoliation (Mott *et al*. 1992).

This paper has focussed on the dynamics of *Astrebla* spp., which are the ecological matrix species of the vegetation in the *Astrebla* grasslands, and identifies that recovery of the basal area of *Astrebla* spp. can be achieved through judicial management in conjunction with favourable summer rainfall. A companion paper from this grazing study (Orr and Phelps 2013) reports major differences in both the density and frequency of the interstitial species in these grasslands and, unlike *Astrebla* spp., recovery of these species may not be as readily achievable.

Conclusions

This study provides important, long-term data on the grazing management of *Astrebla* spp. in *Astrebla* grasslands in northern Australia and indicates that 30% utilisation of the herbage at the end of summer is sustainable in the long-term. Utilisation higher than 30% results in reduced basal area and survival of *Astrebla* spp. and, with time, becomes unsustainable. This study has also highlighted the importance of maintaining the population of the tussocks *of Astrebla* spp. Rainfall variability had a major impact on the dynamics of *Astrebla* spp. and spring values of the SOI may provide an indication of the potential for vegetation change.

Acknowledgements

The Toorak study was established with funding from the Australian Wool Corporation, which then supported the study until 2001. This study received financial support from BHP Cannington mine between 2004 and 2006 for community and biodiversity outcomes. The study was also a component of larger projects supported by the Natural Heritage Trust, the National Landcare Program, Land water and Wool and Meat and Livestock Australia. Nearly 100 staff, too many to mention individually, provided valuable support for pasture and sheep sampling over many years. However, particular acknowledgement is made to Andrew Coward, Tony Barnes, Peter Connolly, Steven O'Connor and Peggy Olsson who oversaw the maintenance of the grazing study and animals.

References

Ash, A. J., McIvor, J. G., Corfield, J. P., and Ksiksi, T. (2011). Grazing management in tropical savannas: utilisation and rest strategies to manipulate rangeland condition. *Rangeland Ecology and Management* **64**, 223–239. doi:10.2111/REM-D-09-00111.1

Beale, I. F., Orr, D. M., Holmes, W. E., Palmer, N., Evenson, C. J., and Bowly, P. S. (1986). The effect of forage utilisation levels on sheep production in the semi arid south west of Queensland. *In*: 'Rangelands: a Resource under Siege'. (Eds P. J. Joss, P. W. Lynch and O. B. Williams.) p. 30. (Australian Academy of Science: Canberra.)

Bostock, P. D., and Holland, A. E. (2007). 'Census of the Queensland Flora.' (Queensland Herbarium, Environmental Protection Agency: Brisbane.)

Burrows, W. H., Orr, D. M., Hendricksen, R. E., Rutherford, M. T., Myles, D. J., Back, P. V., and Gowen, R. (2010). Impacts of grazing management options on pasture and animal productivity in a *Heteropogon contortus* (black speargrass) pasture in central Queensland. 4. Animal production. *Animal Production Science* **50**, 284–292. doi:10.1071/AN09145

Clewett, J. F., Clarkson, N. M., George, D. A., Ooi, S., Owens, D. T., Partridge, I. J., and Simpson, G. B. (2003). 'Rainman StreamFlow (version 4.3): a Comprehensive Climate and Streamflow Analysis Package on CD to Assess Seasonal Forecasts and Manage Climate Risk.' (Department of Primary Industries Queensland: Brisbane.)

Cox, D. R. (1972). Regression and life tables. *Journal of the Royal Statistical Society. Series B. Methodological* **34**, 187–220.

Ebersohn, J. P. (1973). Environmental limitations and their role in stability of low rainfall grazing lands. A case history and viewpoint. *In*: 'Proceedings III World Conference on Animal Production'. pp. 2(d): 6–8. (World Conference on Animal Production: Melbourne.)

Everist, S. L. (1964). The Mitchell grass country. *Queensland Naturalist* **17**, 45–50.

Everist, S. L., and Webb, L. J. (1975). Two communities of urgent concern in Queensland: Mitchell grass and tropical forests. *In*: 'National System of Ecological Reserves in Australia'. Report No. 19. (Ed. F. Fenner.) pp. 39–52. (Australian Academy of Science: Canberra.)

Fair, J. L., Peters, D. P., and Lauenroth, W. K. (2001). Response of individual *Bouteloua gracilis* (Gramineae) plants and tillers to small disturbances. *American Midland Naturalist* **145**, 147–158. doi:10.1674/0003-0031(2001)145[0147:ROIBGG]2.0.CO;2

Genstat (2002). 'Genstat for Windows. Release 6.1.' (VSN International: Oxford.)

Grubb, P. J. (1986). Problems posed by sparse and patchily distributed species in species-rich plant communities. *In*: 'Community Ecology'. (Eds J. M. Diamond and T. J. Case.) pp. 207–225. (Harper and Row: New York.)

Hall, T. J., and Lee, G. R. (1980). Response of an *Astrebla* spp. grassland to heavy grazing by cattle and light grazing by sheep in north-west Queensland. *Australian Rangeland Journal* **2**, 83–93. doi:10.1071/RJ9800083

Halls, L. D., and Dell, T. R. (1966). Trials of ranked set sampling for forage yields. *Forest Science* **12**, 22–26.

Hendrickson, J. R., and Briske, D. D. (1997). Axillary bud banks of two semi-arid perennial grasses: occurrence, longevity and contribution to population persistence. *Oecologia* **110**, 584–591. doi:10.1007/s004420050199

Hunt, L. P. (2008). Safe pasture utilisation rates as a grazing management tool in extensively grazed tropical savannas of northern Australia. *The Rangeland Journal* **30**, 305–315. doi:10.1071/RJ07058

Johnston, P. J., McKeon, G. M., and Day, K. A. (1996). Objective 'safe' carrying capacities for south-west Queensland, Australia: development of a model for individual properties. *The Rangeland Journal* **18**, 244–258. doi:10.1071/RJ9960244

Jones, R. M., and Mott, J. J. (1980). Population dynamics in grazed pastures. *Tropical Grasslands* **14**, 218–224.

Jones, R. M., Jones, R. J., and McDonald, C. K. (1995). Some advantages of long-term grazing trials with particular reference to changes in botanical composition. *Australian Journal of Experimental Agriculture* **35**, 1029–1038. doi:10.1071/EA9951029

Jones, P., Filet, P., and Orr, D. M. (2009). Demography of three perennial grasses in a central Queensland Eucalypt woodland. *The Rangeland Journal* **31**, 427–437. doi:10.1071/RJ09035

Jozwik, F. X., Nicholls, A. O., and Perry, R. A. (1970). Studies on the Mitchell grasses (*Astrebla* F. Muell.). *In*: 'Proceedings 11th International Grassland Congress'. Surfers Paradise, Australia. (Ed. M. J. T. Norman.) pp. 48–51. (Australian National University Press: Canberra.)

Lambert, F. J., Bower, M., Whalley, R. D. B., Andrews, A. C., and Bellotti, W. D. (1990). The effects of soil moisture and planting depth on emergence and seedling morphology of *Astrebla lappacea* (Lindl.) Domin. *Australian Journal of Agricultural Research* **41**, 367–376. doi:10.1071/AR9900367

Lauenroth, W. K., and Adler, P. B. (2008). Demography of perennial grasslands plants: survival, life expectancy and life span. *Journal of Ecology* **96**, 1023–1032. doi:10.1111/j.1365-2745.2008.01415.x

Lorimer, M. S. (1978). Forage selection studies 1. The botanical composition of forage selected by sheep grazing *Astrebla* spp. pasture in north-west Queensland. *Tropical Grasslands* **12**, 97–108.

McIvor, J. G., Bray, S. G., Grice, A. C., and Hunt, L. (2010). 'Grazing Management Guidelines for Northern Australia: Scientific Rationale and Justification.' Final Report Project B.NBP.0579. (Meat and Livestock Australia: Sydney.)

McKeon, G. M., Brooke, K. D., Carter, J. O., Day, K. A., Howden, S. M., Johnston, P. W., Scanlan, J. C., and Scattini, W. J. (1994). Modelling utilisation rates in the black speargrass zone of Queensland. *In*: 'Clean Country, Clean Product, Clear Profit. Working Papers. 8th Biennial Australian Rangelands Conference'. Katherine, NT. pp. 128–132. (Australian Rangeland Society: Cottesloe, WA.)

McKeon, G. M., Hall, W. B., Henry, B. K., Stone, G. S., and Watson, I. W. (2004). 'Pasture Degradation and Recovery in Australia's Rangelands: Learning from History.' (Queensland Department of Natural Resources, Mines and Energy: Brisbane.)

Mott, J. J., Ludlow, M. M., Richards, J. H., and Parsons, A. D. (1992). Effects of moisture supply in the dry season and subsequent defoliation on persistence of the savanna grasses *Themeda triandra*, *Heteropogon contortus* and *Panicum maximum*. *Australian Journal of Agricultural Research* **43**, 241–260. doi:10.1071/AR9920241

Orr, D. M. (1975). A review of *Astrebla* (Mitchell grass) pastures in Australia. *Tropical Grasslands* **9**, 21–36.

Orr, D. M. (1981). Changes in the quantitative floristics in some *Astrebla* spp. (Mitchell grass) communities in south-western Queensland in relation to trends in seasonal rainfall. *Australian Journal of Botany* **29**, 533–545. doi:10.1071/BT9810533

Orr, D. M. (1986). Factors affecting the vegetation dynamics of *Astrebla* grasslands. PhD Thesis, University of Queensland, Brisbane, Australia.

Orr, D. M. (1998). A life cycle approach to population ecology of two tropical grasses in Queensland, Australia. *In*: 'Population Biology of Grasses'. (Ed. G. Cheplick.) pp. 366–389. (Cambridge University Press: New York.)

Orr, D. M., and Evenson, C. J. (1991*a*). Effects of sheep grazing *Astrebla* grasslands in central Western Queensland III. Dynamics of *Astrebla* spp. under grazing and exclosure between 1975 and 1986. *The Rangeland Journal* **13**, 36–46. doi:10.1071/RJ9910036

Orr, D. M., and Evenson, C. J. (1991*b*). Effects of a single clipping on the seed production response of *Astrebla* spp. *The Rangeland Journal* **13**, 57–60. doi:10.1071/RJ9910057

Orr, D. M., and Holmes, W. E. (1984). Mitchell grasslands. *In*: 'Management of Australia's Rangelands'. (Eds G. N, Harrington, A. D. Wilson and M. D. Young.) pp. 241–254. (CSIRO: Melbourne.)

Orr, D. M., and O'Reagain, P. J. (2011). Managing for rainfall variability: impacts of grazing strategies on perennial grass dynamics in a dry tropical savanna. *The Rangeland Journal* **33**, 209–220. doi:10.1071/RJ11032

Orr, D. M., and Phelps, D. G. (2013). 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. *The Rangeland Journal* **35**, 17–28.

Orr, D. M., and Silcock, R. G. (2010). The occurrence and causes of episodic recruitment of *Astrebla* spp. *In*: 'Rain on the Rangelands. Proceedings of the 16th Biennial Conference of the Australian Rangeland Society'. (Ed. D. J. Eldridge.) (Australian Rangeland Society: Bourke.)

Orr, D. M., Bowly, P. S., and Evenson, C. J. (1986). Effects of grazing management on the basal area of perennial grasses in *Astrebla* grassland. *In*: 'Rangelands: a Resource under Siege'. (Eds P. J. Joss, P. W. Lynch and O. B. Williams.) pp. 56–57. (Australian Academy of Science: Canberra.)

Orr, D. M., Evenson, C. J., Jordan, D. J., Bowly, P. S., Lehane, K. J., and Cowan, D. C. (1988). Sheep productivity in an *Astrebla* grassland of south-west Queensland. *Australian Rangeland Journal* **10**, 39–47. doi:10.1071/RJ9880039

Orr, D. M., Evenson, C. J., Lehane, J. K., Bowly, P. S., and Cowan, D. C. (1993). Dynamics of perennial grasses with sheep grazing in *Acacia aneura* woodlands in south-west Queensland. *Tropical Grasslands* **27**, 87–93.

Orr, D. M., Paton, C. J., and Reid, D. J. (2004). Dynamics of plant populations in *Heteropogon contortus* (black speargrass) pastures on a granite landscape in southern Queensland 1. Dynamics of *H. contortus* populations. *Tropical Grasslands* **38**, 17–30.

Orr, D. M., Yee, M. C., Rutherford, M. T., and Paton, C. J. (2010*a*). Impacts of grazing management options on pasture and animal productivity in a *Heteropogon contortus* (black speargrass) pasture in central Queensland. 2. Population dynamics of *Heteropogon contortus* and *Stylosanthes scabra* cv. Seca. *Crop & Pasture Science* **61**, 255–267. doi:10.1071/CP09194

Orr, D. M., Burrows, W. H., Hendricksen, R. E., Clem, R. L., Back, P. V., Rutherford, M. T., Myles, D. J., and Conway, M. J. (2010*b*). Impacts of grazing management options on pasture and animal productivity in a *Heteropogon contortus* (black speargrass) pasture in central Queensland. 1. Pasture yield and composition. *Crop & Pasture Science* **61**, 170–181. doi:10.1071/CP09193

Partridge, I. J. (2001). 'Will it Rain? The Effect of the Southern Oscillation and El Nino on Australia.' Information Series Q101016. (Department of Primary Industries: Brisbane.)

Phelps, D. G. (2006). Controlling *Aristida latifolia* (Feathertop wiregrass) in *Astrebla* spp. Mitchell grasslands with fire and grazing. PhD Thesis, University of New England, Armidale, Australia.

Phelps, D. G., and Bosch, O. J. H. (2002). A quantitative state and transition model for the grasslands of central western Queensland. *The Rangeland Journal* **24**, 242–267. doi:10.1071/RJ02014

Phelps, D. G., and Orr, D. M. (2003). A GIS approach to determining vegetation patterns in small paddocks. *In*: 'Rangelands in the New Millennium. Proceedings of the VII International Rangelands Congress'. (Eds N. Allsop, A. R. Palmer, S. J. Milton, K. P. Kirkman, G. I. Kerley, C. R. Hurt, and C. J. Brown.) pp. 98–99. (International Rangeland Congress: Durban.)

Roe, R. (1987). Recruitment of *Astrebla* spp. in the Warrego region of south-western Queensland. *Tropical Grasslands* **21**, 91–92.

Roe, R., and Allen, G. H. (1993). Studies on the Mitchell grass association in south-western Queensland 3. Pasture and wool production under different rates of stocking and continuous or rotational grazing. *The Rangeland Journal* **15**, 302–319. doi:10.1071/RJ9930302

Roe, R., and Davies, H. I. (1985). Long-term variation in the density of *Astrebla* spp. in the Warrego region of south-western Queensland. *Tropical Grasslands* **19**, 87–95.

Sattler, P. S., and Williams, R. D. (1999). 'The Conservation Status of Queensland's Bio-regional Ecosystems.' (Environmental Protection Agency: Brisbane.)

Scanlan, J. C. (1983). Changes in tiller and tussock characteristics of *Astrebla lappacea* (curly Mitchell grass) after burning. *Australian Rangeland Journal* **5**, 13–19. doi:10.1071/RJ9830013

Stone, G., Bruget, D., Carter, J., Hassett, R., McKeon, G. M., and Rayner, D. (2007). 'Pasture Production and Condition Issue. The State of Environment in Queensland: Land.' (Environmental Protection Agency, Queensland Government: Brisbane.)

Tothill, J. C., Hargreaves, J. N. G., Jones, R. M., and McDonald, C. K. (1992). 'BOTANAL – a Comprehensive Sampling and Computing Procedure for Estimating Pasture Yield and Composition. 1. Field Sampling.' CSIRO Australia Division of Tropical Crops and Pastures, Tropical Agronomy Technical Memorandum No. 78. (CSIRO: St Lucia.)

Turner, E. J., and McDonald, W. J. F. (1993). Land systems. *In*: 'Western Arid Region Land Use Study – Part V'. Technical Bulletin No. 30. (Eds E. J. Turner, W. J. F. McDonald, C. R. Ahern and M. B. Thomas.) pp. 139–158. (Queensland Department Primary Industries, Division of Land Utilisation: Brisbane.)

Williams, O. B., and Roe, R. (1975). Management of arid grasslands for sheep: plant demography of six grasses in relation to climate and grazing. *Proceedings of the Ecological Society of Australia* **9**, 142–156.

Wright, R. G., and Van Dyne, G. M. (1976). Environmental factors influencing semi-desert grassland perennial grass demography. *The Southwestern Naturalist* **21**, 259–274. doi:10.2307/3669712