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A QUANTITATIVE STATE AND TRANSITION MODEL FOR THE MITCHELL GRASSLANDS OF CENTRAL WESTERN QUEENSLAND

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Abstract

Concerns of reduced productivity and land degradation in the Mitchell grasslands of central western Queensland were addressed through a range monitoring program to interpret condition and trend. Botanical and edaphic parameters were recorded along piosphere and grazing gradients, and across fenceline impact areas, to maximise changes resulting from grazing. The Degradation Gradient Method was used in conjunction with State and Transition Models to develop models of rangeland dynamics and condition. States were found to be ordered along a degradation gradient, indicator species developed according to rainfall trends and transitions determined from field data and available literature. *Astrebla* spp. abundance declined with declining range condition and increasing grazing pressure, while annual grasses and forbs increased in dominance under poor range condition. Soil erosion increased and litter decreased with decreasing range condition. An approach to quantitatively define states within a variable rainfall environment based upon a time-series ordination analysis is described.

The derived model could provide the interpretive framework necessary to integrate on-ground monitoring, remote sensing and geographic information systems to trace states and transitions at the paddock scale. However, further work is needed to determine the full catalogue of states and transitions and to refine the model for application at the paddock scale.

Key words: Astrebla; State and Transition Models; Degradation Gradient Method; range condition; Mitchell grasslands; grazing impacts, central western Queensland

Introduction

The Mitchell grasslands are the most extensive and productive native pastures of semi-arid western Queensland (Lee *et al.* 1980). They cover 33 million ha within Queensland, supporting 45% of the State's sheep and 10% of the cattle. The Northern Territory, Western Australia, New South Wales and South Australia share a further 11.8 million ha of Mitchell grasslands (Orr 1975).

The grasslands are dominated by the long-lived perennial *Astrebla* spp. (Mitchell grasses). The basal cover of these tussock grasslands is low (1 to 6%), and rainfall is highly variable, leading to fluctuations in both pasture yield and composition (Orr 1975, 1981). A change from summer to winter rainfall dominance, moving from the north to the south of Queensland also affects pasture yield and composition, particularly of inter-tussock annual and ephemeral species (Orr and Holmes 1984). This creates spatial and temporal differences when assessing rangeland condition within the Mitchell grasslands and led Everist and Webb (1975) to conclude that "the extrapolation from [vegetation] observations made at any one time can be misleading and inaccurate".

State and Transition Models (Westoby *et al.* 1989) have recently supplanted Clementsian successional theory (e.g. Clements 1916, 1936, Dyksterhuis 1949) in explaining vegetation based changes in rangeland condition. Reasons for this paradigm shift are given in recent publications (e.g. Whalley 1994, Brown 1994) and generally relate to the inability of succession to explain vegetational instability in the absence of disturbance.

Clementsian successional theory, however, formed the foundation of many modern techniques for interpreting changes in rangeland condition. The Degradation Gradient Method (DGM, Bosch and Gauch 1991) is Clementsian based, with thresholds and domains of attraction ordered along a singular gradient. Domains can be equated with major states in State and Transition Models (Bosch and Kellner 1991) and irreversible changes occur when domains of attraction are separated by a threshold. Models based on the DGM have been used in the New Zealand high country to help agency staff, graziers and funding bodies interpret vegetation monitoring results and serve as the basis for natural resource decision making within an adaptive management process (Bosch *et al.* 1996).

Successful implementation of sustainable best management practices ultimately rests with land managers. Watson *et al.* (1996) argue that the "mental models held by managers must acknowledge the value of continuous change. This provides the best opportunity for acquiring knowledge through experience". In this, they acknowledge the benefits of perceiving changes as a continuum, even if State and Transition event driven models provide a deeper ecological understanding.

This paper describes an approach by which both Clementsian and State and Transition theories were applied concurrently to develop models of the dynamics of the Mitchell grasslands in central western Queensland. Data were obtained from a pasture monitoring program established in 1989 in response to concerns by the pastoral industry and the scientific community about perceived declining productivity and rangeland degradation (e.g. Roberts and Crouch *ca.*1989, Tothill and Gillies 1992).

Materials and Methods

Data collection

Vegetation surveys

Fifty-seven sites of 30 by 30 m square were permanently marked to represent different conditional states (e.g. within existing grazing trials, fence line effects, piosphere and stock camp transects and sheepwalks) within a relatively homogeneous grazing area (RHGA, Bosch and Kellner 1991) of the central Mitchell grasslands (Fig. 1a). The RHGA study area was representative of the slightly concave flats dominant on the Undulating downs Land Zone of the central Mitchell grasslands (Fig. 1b, Turner *et al.* 1993). Further RHGA study areas (data not presented) were located within the northern Mitchell grasslands (Julia Creek – Richmond district) and southern Mitchell grasslands (Blackall district). These areas were deliberately separated to avoid broad differences in vegetation patterns along both north-south and east-west rainfall gradients (Fensham *et al.* 2000) unduly influencing potential grazing impacts.

The sites were initially surveyed in August 1989 and re-surveyed in January 1990, May 1991, May 1993 and May 1994. Site botanical composition was assessed using a modification of the nearest plant method (Evans and Love 1957), with the nearest plant within a 200 mm radius (instead of the nearest plant irrespective of distance) recorded at 200 points within each survey site. Similar methods capture at least 95% of the total mix of plant species in African rangelands (Hardy and Walker 1991, Stalmans and Mentis 1993).

Site descriptions

All sites were initially described (Table 1) based on Land Systems within the Undulating downs Land Zone (Turner *et al.* 1993), greater soil group (Northcote 1979, Northcote *et al.* 1975), general edaphic properties (e.g. soil depth, topography, and slope position) and evidence of disturbance (e.g. erosion activity). Bulked surface samples (0 - 10 cm) were analysed according to methods detailed by Bruce and Rayment (1982) to provide soil chemistry and particle size distribution (data not presented).

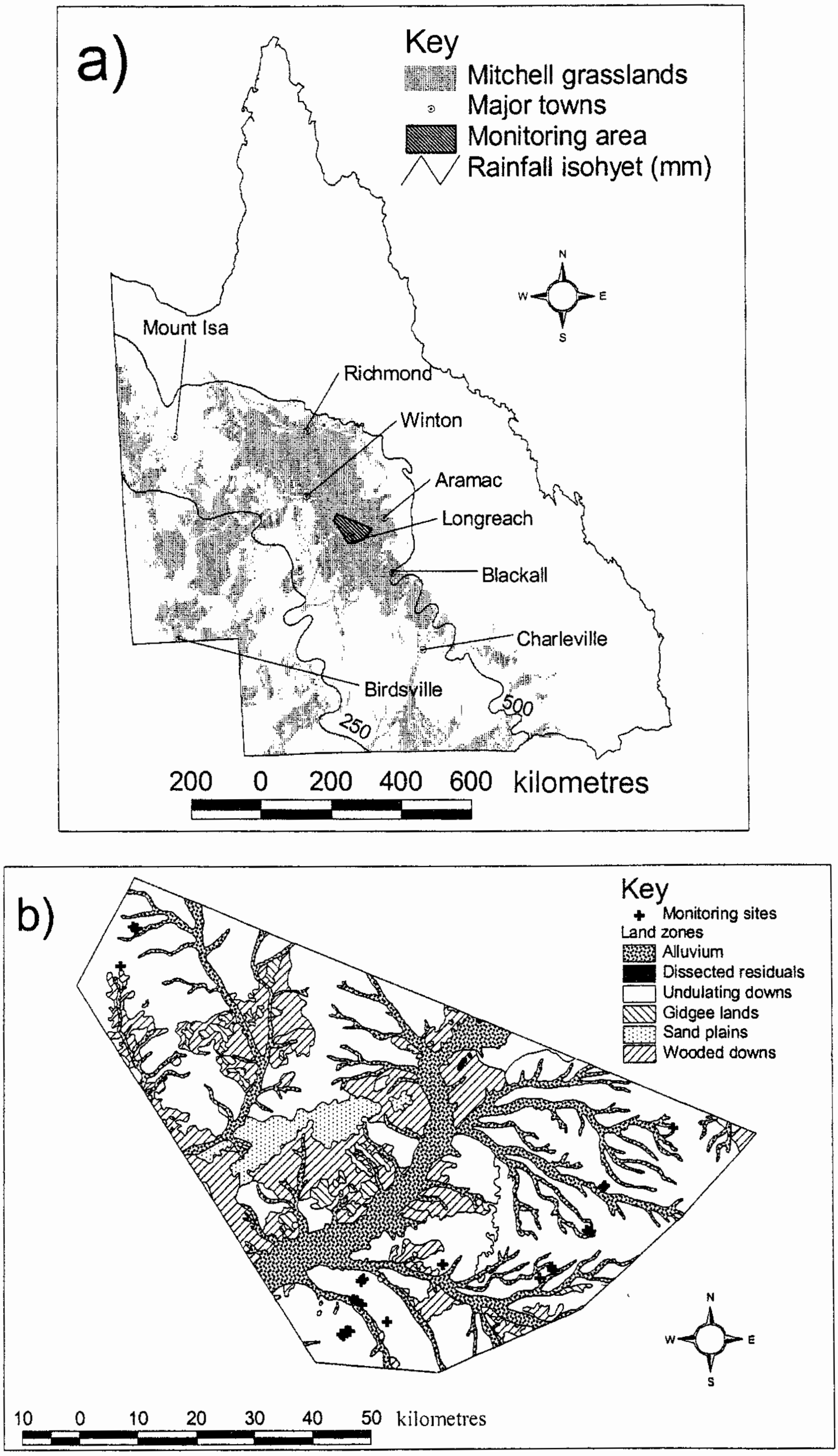

Fig. 1. The location of: a) the study area in relation to Longreach and the Mitchell grasslands of Queensland; and b) monitoring sites in relation to Land Zones (Turner *et al.* 1993) of the study area.

Above ground biomass (kg/ha) and grazing pressure (utilisation level, %) were estimated from photostandards (Phelps and Bates 1994, Orr 1978) at each site on each survey. Ground cover (%) was estimated in May 1991 from photographic slides of three random 1 m^2 quadrats within each site using a point intercept method on a projection screen (Day and Philp 1997). Rainfall data were interpolated from site positions (longitude and latitude) by the Climate Impacts and Natural Resource Systems Group (Natural Resource Sciences, Department of Natural Resources and Mines) from Bureau of Meteorology data (McKeon *et al.* 1998). This suite of habitat data was used for assessing the major factors influencing variation in vegetation composition.

Data analysis

Identifying vegetation states

Firstly, each recording date was ordinated independently in a time-series approach to avoid seasonal rainfall patterns unduly influencing the proportional plant abundance data. Outliers due to site habitat differences (e.g. extremes of pH, differences in Land System classifications) and species that occurred at less than 15% of the survey sites were removed prior to ordination to minimise noise in the data set (Gauch 1982). The software packages ISPD (an Integrated System for Plant Dynamics, Bosch *et al.* 1992) and PATN (Belbin 1987) were used to explore the best fit of data (through the analytical component of ISPD and by eye) within a range of ordination techniques (Gauch 1982). For each recording, an adapted PCA (Principal Components Analysis) centred ordination (Bosch and Gauch 1991) proved to be the most suitable, following initial clustering with DCA (Detrended Correspondence Analysis, Hill and Gauch 1980). Different vegetation groups were identified by eye in ISPD (Bosch *et al.* 1992) and these groups then defined as vegetation states (e.g. State A (1989) in Fig. 2) relative to the first ordination axis of PCA (a possible degradation gradient), with the second axis defined as a residual score (Bosch and Kellner 1991, Bosch and Gauch 1991).

Secondly, individual sites within each state were identified and their movement in ordination space from one state to another traced over time. This process provided evidence of generalised vegetation states, directions of change (or transitions) and the possible reversibility of the changes. The movement of groups of sites between similar vegetation states across sampling dates was taken as evidence of the presence of a single stable vegetation state (the solid arrows of Fig. 2). The movement of individual sites against a general trend was taken as evidence of transitions between vegetation states (the dashed arrows of Fig. 2). The combined evidence of stable vegetation states and the existence of transitions was utilised in defining a generalised, time independent, State and Transition Model (STM). For example, the same sites grouped together in ordination space on the basis of high proportions of *Malvastrum americanum*[1] and *Sida* spp. over the "average summer, wet winter" between August 1989 and January 1990, whilst another group of sites grouped on the basis of high proportions of *Astrebla* spp. and *Dichanthium sericeum* (Fig. 2). Details of site movements and vegetation states are provided in the results and discussion section.

Defining a degradation gradient and identifying indicator species

Edaphic factors and known management histories (e.g. protected sites, sites of known utilisation levels within grazing trials, sites close to watering points and stock camps) were plotted on the ordination diagrams at each date. This allowed the main ecological factor(s) responsible for the positioning of the states along the first axis to be defined, and to clarify or reject its status as a degradation gradient within each sampling date. The acceptance of the first ordination axis within each date specific data set as a degradation gradient was a prerequisite for condensing the quantified vegetation states into generalised vegetation states.

[1] See Table 2 for species nomenclature and descriptive information

Table 1. Site parameters measured during the study period.

Parameter	Recordings/Measurements conducted	Recording Dates
Vegetation composition	Plant species abundance (%)	all
Management history	Above ground biomass (kg/ha), grazing pressure (utilisation level, %) and evidence of disturbance	all
Daily rainfall	Interpolated daily rainfall (mm)	all
Photographic records	Landscape view photograph on slide film	all
Site location	Longitude and latitude (Global Positioning System), land system (e.g. F3 undulating downs), and site location in relation to landform elements (slope category e.g. gentle incline, landscape position e.g. mid-slope, shape e.g. convex, inclination e.g. waning, geomorphology agent e.g. sheet erosion, element e.g. hillslope, pattern e.g. undulating plain, relief (m), modal slope (%), slope (%), aspect (degrees), class e.g. gentle undulating plain)	August 1989
Site description	Physical parameters within the site including microrelief e.g. crab hole gilgai, vertical and horizontal intervals (m), erosion classes (state e.g. active, type e.g. sheet , degree of e.g. slight and evidence for e.g. accumulated fine sand), surface coarse fragments (aggregation e.g. fine sand accumulation, size in mm , shape e.g. rounded and lithology e.g. ironstone), rock outcrops (abundance, %, and lithology e.g. sandstone) and geology e.g. sandstone	August 1989
Soil classification	Greater soil group (e.g. brown cracking clay), soil depth (cm), colour e.g. DY brown, texture (e.g. medium clay, MC), structure (e.g. W4AB), consistency (e.g. moderate to weak) and coarse fragments (e.g. ironstone) through the profile (up to 1 m depth)	August 1989
Soil surface condition	Observable disturbance mechanisms, including type of grazing animal (cattle or sheep), grazing impact (disturbance level e.g. recently grazed), dominant surface condition (e.g. crusting) and rating (e.g. moderate), litter level rating (nil, some, moderate, high)	August 1989
Soil chemistry	pH and electrical conductivity (mS/cm) (1:5 soil:water), nitrogen (total, %, and nitrate-N, mg/kg), phosphorus (total, %, and bicarbonate extractable, mg/kg), potassium (total, %, and acid extractable, mg/kg), organic carbon (Walkley and Black, %), cation exchange capacity (milliequivalents/100g), chloride (mg/kg), calcium (%), magnesium (%), sodium (%), sulfur (%), DTPA extractable copper, zinc, manganese and iron (mg/kg), air dry moisture content (ADMC, % dry weight)	August 1989
Soil particle size distribution	Clay (%), silt, (%), fine sand (%), and coarse sand (%)	August 1989
Litter class	Ground cover (%)	May 1991

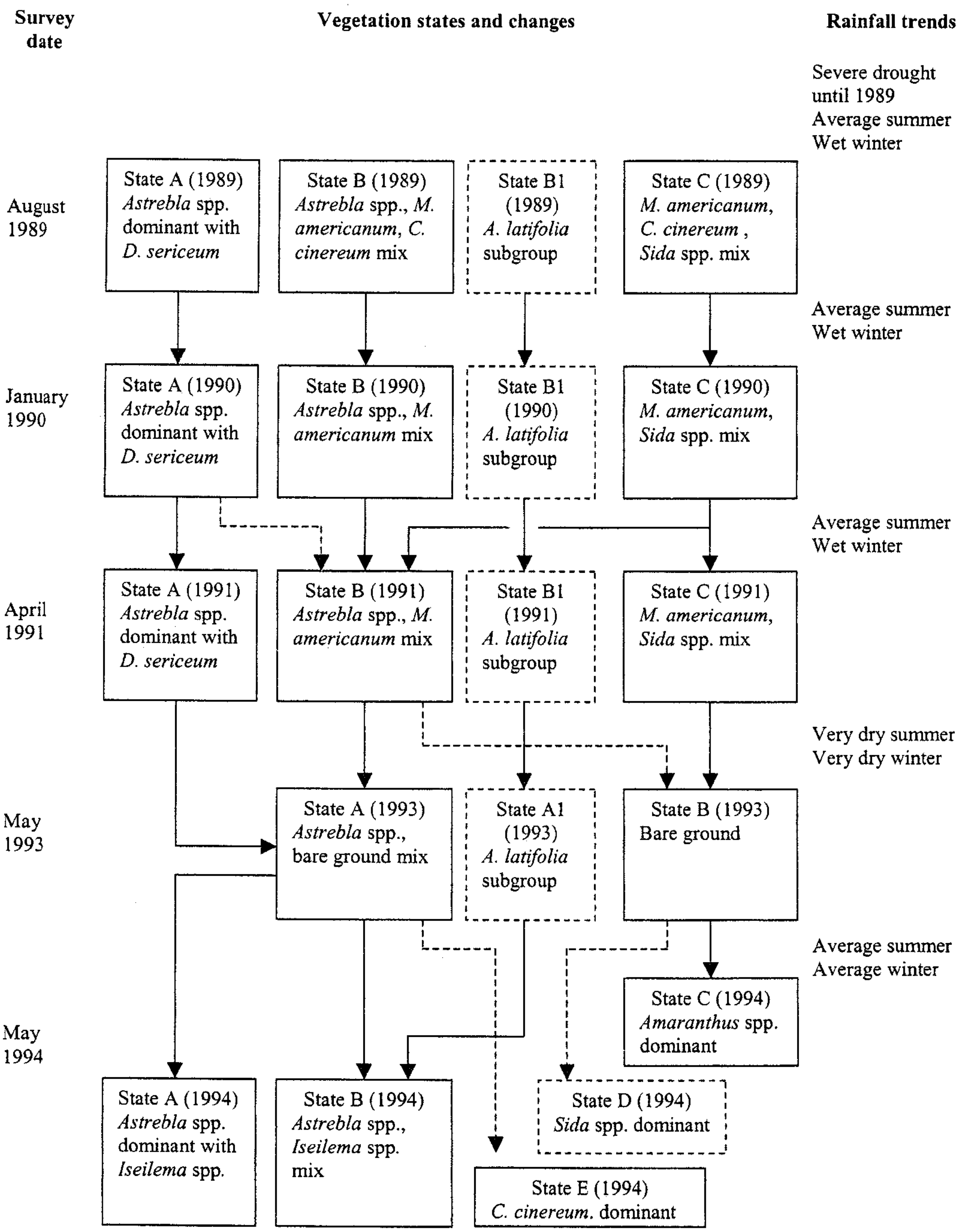

Fig. 2. Movement of sites between vegetation states formed from one date to another. Solid boxes represent well defined states (the grouping of a large number of sites), dashed boxes represent poorly defined states (the grouping of a small number of sites). Solid lines indicate a general movements of sites, dashed lines indicate the movement of individual (or a small proportion of) sites.

Once the first axis was confirmed as a degradation gradient, the abundances of species were plotted against PCA axis one, and Gaussian fit regression analyses performed using ISPD (Bosch *et al.* 1992, Bosch and Kellner 1991). Indicator species were defined as those with significant R^2 values ($P<0.05$) in relation to the first ordination axis, and with relatively high abundances in the Mitchell grasslands.

Data from sample dates with common indicator species displaying similar trends under similar rainfall conditions (e.g. the "average summer, wet winter" preceding August 1989, January 1990 and April 1991, Fig. 2) were grouped and re-analysed using PCA. As long as the same species and trends persisted, the combined model was used as a basis for more generalised indicator species curves (e.g. August 1989, January 1990 and April 1991 data were combined to become "Following major drought"). Where the same species and trends did not persist, the ability to combine data sets was rejected and individual data sets formed the basis of the indicator species curves. Consequently May 1993 and May 1994 became "During seasonal drought" and "Following seasonal drought" respectively. Details of combined models and indicator species curves are provided in "Determining Indicator species" within the results and discussion section.

The relative strength of indicator species as decreasers or increasers along the degradation gradient (axis one) was used to define the position of states (including sub-groups) within the generalised STM. Hence the high abundance of bare ground (a strong increaser species) in State VII, coupled with the absence of other species, suggested it to be the most degraded state. High abundances of *Cullen cinereum* within State III suggested it to be less degraded than State V, despite the strength of *M. americanum* as an increaser species. This evidence was reinforced through a tendency for degraded sites to be more common within States VII, VI and V.

Data availability

Data sets are available from the first author upon request, or can be found appended to Phelps (1999).

Results and Discussion

Identification of vegetation states

The main vegetation states identified from the ordination diagrams of each date are presented in Fig. 2. States were numbered for the individual ordinations at each field recording time. State A in August 1989 should thus not be considered as the equivalent to State A in May 1993, for example. The vegetation states are presented in the same order in which they appeared along the first ordination axis, although the relative length of each first axis is not provided. Vertical differences in May 1994 are for ease of presentation and do not reflect the second (residual) axis.

The general movement of sites through subsequent time specific ordinations is indicated by solid arrows, with August 1989 used as the baseline ordination. This general movement represents the creation of new ordinated vegetation groups at different times which may be similar to, or dissimilar from, the ordinated vegetation group in the preceding time and were assumed to represent time specific states. For example, the single arrow from State A (1989) to State A (1990) indicates that all the sites ordinated in this state in the August 1989 data were also ordinated in this state in the January 1990 data, reflecting stability over this time period. Stability of this kind was later used as evidence in determining generalised vegetation states.

The movement of a small proportion of sites against the general trend through subsequent ordinations is indicated by dashed arrows. For example, some sites moved from State C (1990) to State C (1991), whilst others were now ordinated in the State B (1991) group of sites. Instability of this kind was later used as evidence in determining transitions.

The temporal movement of sites to form new states is provided in the following descriptions:

Changes in State A (1989, Astrebla *spp. dominant with* D. sericeum*)*

This grassland, dominated by *Astrebla* spp. (primarily *A. lappacea* and *A. elymoides*, with some *A. pectinata* but rarely *A. squarrosa*), stayed the same during average to good rainfall years but by 1993 most of the *D. sericeum* (a palatable perennial grass, Table 2) had been lost following drought. After more favourable rainfall conditions over the 1993/94 summer period, bare ground was replaced by *Iseilema* spp. to form grassland dominated by *Astrebla* spp. with occurrences of *Iseilema* spp. A small number of sites in the grassland dominated by *Astrebla* spp. changed to grassland with *Astrebla spp.* mostly dominant between January 1990 and April 1991. Since this was against the general trend and rainfall conditions did not vary substantially (data not presented), it could be assumed that this resulted from increased grazing pressure at these sites. There was some evidence (data not presented) that the grouping of *A. squarrosa* with all other *Astrebla* spp. may cloud the correct interpretation of vegetation dynamics, especially given its relatively lower palatability (Table 2) and preference for run-on areas (Orr 1975). Its separation into a separate category would be recommended for future monitoring programs.

Changes in State B (1989, Astrebla *spp.,* M. americanum, C cinereum *mix)*

This grassland, mostly dominated by *Astrebla* spp., retained *M. americanum* but lost *C. cinereum* between August 1989 and January 1990. A change in rainfall patterns may have induced this vegetation shift. Bushell *et al.* (1993) found the density of both species declined in response to changed rainfall patterns, whilst *C. cinereum* increases are often associated with cool wet seasons. Alternatively, the change may reflect greater *M. americanum* persistence. *M. americanum* remained abundant until May 1993 when it was replaced with bare ground following dry conditions, with the exception of two sites which lost all plant cover (probably due to overgrazing during dry conditions). More favourable rainfall over the 1993/94 summer caused most of the sites to change into a mixed *Astrebla* spp. and *Iseilema* spp. state, whilst some changed to a *C. cinereum* dominant state.

Changes in State B1 (1989, A. latifolia *sub-group)*

This grassland, with a predominance of *Aristida latifolia*, formed a sub-group within State B in 1989, and remained the same until May 1993 when bare ground started to increase. This sub-group changed to an *Astrebla* spp. and *Iseilema* spp. mix by May 1994 (State B 1994). This followed improved rainfall conditions.

Changes in State C (1989, M. americanum, C. cinereum, Sida *spp. mix)*

This herbfield, dominated by *M. americanum, C. cinereum* and *Sida* spp. (primarily *S. fibulifera* and *S. trichopoda*), lost the *C. cinereum* component between August 1989 and January 1990. This shift in botanical composition coincided with the loss of *C. cinereum* from State B (grassland with *Astrebla spp.* mostly dominant). A small proportion of sites moved to State B (1991) following a reduction in *M. americanum* and *Sida* spp., but were generally returned in May 1993 following low summer and winter rainfall. This low rainfall (approximately 50% of mean rainfall) resulted in the complete loss of *M. americanum* and *Sida* spp. from all sites. This loss suggests a relatively unstable vegetation state which is more susceptible to drought conditions than either of the grassland states. The herbfield was dominated by *Amaranthus* spp. (primarily *A. mitchellii*) in May 1994 following improved rainfall conditions. The sites which had remained in a grassland state during 1991 and 1993 became dominated by *C. cinereum* in May 1994.

The analysis has indicated that rainfall was the dominant driving force for the major changes in botanical composition over time (represented by solid arrows in Fig. 2), a finding supported by other studies (e.g. Orr 1981, Roe and Allen 1993, Fensham *et al.* 2000). Within this dominant rainfall influence, other work has indicated that grazing can influence both short- and long-term

Table 2. Life form, longevity, palatability (Milson 1996, 2000) and nomenclature of species referred to in the text. Estimated longevity (in years) and palatability are provided as a guide for plant behaviour within the central Mitchell grasslands.

Species	Life form	Longevity	Palat-ability*
Abutilon malvifolium (Benth.) J.M.Black	Erect forb to 50 cm tall	Perennial (approx. 2-5years)	L
Amaranthus spp. L.	Erect forbs to 50 cm tall	Annual	L
Amaranthus mitchellii Benth.	Erect forb to 30 cm tall	Annual	L
Aristida latifolia Domin.	Erect tussock grass to 1.3 m tall	Perennial (approx. 5-8 years)	L
Astrebla spp. F.Muell. ex Benth	Erect tussock grasses to 1.5 m tall	Perennial (approx. 20–30 years)	H
Astrebla elymoides F.Muell ex Bailey	Erect tussock grass to 60 cm tall	Perennial	H
Astrebla lappacea (Lindl.) Domin.	Erect tussock grass to 60 cm tall	Perennial	H
Astrebla pectinata (Lindl.) F. Muell. ex Benth	Erect tussock grass to 1 m tall	Perennial	H
Astrebla squarrosa C.E. Hubbard	Erect tussock grass to 1.5 m tall	Perennial	M to H
Boerhavia diffusa L. (under revision, *B. diffusa* is no longer valid in Australia)	Prostrate (generally) to erect (occasionally) forbs	Perennial (approx. 2-3 years)	L to M
Cullen cinereum (Lindl.) J.W. Grimes	Erect forb to 60 cm tall	Annual (to facultative perennial)	L
Daucus glochidiatus (Labill.) Fisch., C.A.Mey. & Ave-Lall.	Erect forb to 20 cm tall	Annual	H
Desmodium campylocaulon F.Muell. ex Benth.	Prostrate (trailing) legume	Perennial (approx. 2-3 years)	H
Dichanthium sericeum (R.Br) A.Camus	Erect tussock grass to 60 cm tall	Perennial (approx. 5-8 years)	H
Digitaria spp. (F.Muell.) Hughes	Erect tussock grasses to 1 m tall	Perennial (possibly 5-10 years))	H
Digitaria coenicola (F.Muell.) Hughes	Erect tussock grass to 1 m tall	Perennial	H
Digitaria ctenantha (F.Muell.) Hughes	Erect tussock grass to 50 cm tall	Perennial	H
Eriochloa crebra S.T.Blake	Erect tussock grass to 1 m tall	Perennial (approx. 2-3 years)	M to H
Iseilema spp. R.Br.	Semi-erect grass to 70 cm tall	Annual/ephemeral	H
Iseilema membranaceum (Lindl.) Domin.	Semi-erect grass to 30 cm tall	Annual/ephemeral	H
Iseilema vaginiflorum Domin.	Semi-erect grass to 70 cm tall	Annual/ephemeral	H
*Malvastrum americanum*** (L.) Torr.	Erect forb to 50 cm tall	Perennial (possibly 2-5 years)	L
Panicum spp. L.	Erect tussock grasses to 1.5 m tall	Perennial (approx. 5-8 years)	M to H

Panicum decompositum R.Br.	Erect tussock grass to 1 m tall	Perennial	M
Plantago spp. L.	Erect forbs to 30 cm tall	Annual	H
Plantago debilis R.Br.	Erect forb	Annual	H
Portulaca sp. L.	Prostrate forb	Annual	M
Rhynchosia minima (L.) DC.	Prostrate (twining) legume	Perennial (approx. 2-3 years)	M
Salsola kali L.	Erect forb to 70 cm tall	Annual	L to M
Sida spp. L.	Erect forbs to 1 m tall	Perennial	L
Sida fibulifera Lindl.	Prostrate, shrubby, forb	Perennial	L
Sida filiformis A.Cunn.	Erect forb to 50 cm tall	Perennial	L
Sida trichopoda F.Muell.	Erect forb to 60 cm tall	Perennial	L
Solanum esuriale Lindl.	Erect forb to 30 cm tall	Perennial	L

* ranked as high (H), moderate (M) or low (L) palatability
** cryptogenic species

changes in botanical composition (e.g. Orr 1980a, 1980b). This may be especially true at specific sites, and may be reflected in the deviations from the general pattern of change (represented by dashed lines in Fig. 2). For example, most sites within State A (1989) remained in this state until 1993 where drought conditions lead to the loss of *D. sericeum*. Some sites, however, went directly to State B in 1991. This deviation may have resulted from high grazing pressure at these sites and the subsequent removal of highly palatable *D. sericeum* plants. The change of sites from State B (1991) to State B (1993) and State A (1993) to State E (1994) may have resulted from high grazing pressure, with a decline in *Astrebla* spp. offset by an increase in less palatable plants or bare ground in each instance (Fig. 2). However, the shift of individual sites from State B (1993) to State D (1994) is difficult to explain. Whilst most bare ground sites were populated by *Amaranthus* spp. (generally regarded as a coloniser of bare ground), a few had high abundances of *Sida* spp. (generally regarded as a benign species), perhaps reflecting differing rainfall patterns, grazing pressure or initial soil seed banks.

Some individual sites had known grazing and rainfall histories that enabled the successful definition of disturbance gradients. For most sites, exact management practices (e.g. the timing and duration of grazing and numbers and types of animals) and rainfall data (e.g. timing and intensity of rainfall) which would have influenced changes were not recorded, necessitating the use of interpolated rainfall data and assumptions of grazing histories based on pasture measurements. A monitoring program which sought to fully involve land managers from the outset would have helped capture the detailed data required.

Generalised vegetation states

The generalised vegetation states (Fig. 3) represent a condensing (outside of ordination space) of the 20 date dependent states (Fig. 2) into a STM independent of time and rainfall, based on a consistent movement of sites and the existence of a degradation gradient at each sampling date. The continuity of sites dominated by *Astrebla* spp. for four out of five monitoring dates, across a range of seasonal rainfall patterns, provided evidence for the existence of one generalised *Astrebla* spp. dominated state (State I, Fig. 3). The continuity of sites with *Astrebla* spp. mostly dominant, but mixed with other species, provided evidence for the formation of State II.

Date specific grassland states were also associated with vegetation inseparable from the main groupings in ordination space (e.g. the *A. latifolia* sub-group, State B1 1989 to 1991 and State A1 1993). These are reflected as sub-groups within the generalised states. State I and State II were subdivided into two and four sub-groups, on the basis of the sub-dominance of *D. sericeum*, *A. latifolia*, *M. americanum*, bare ground or *Iseilema* spp. These generalised states are supported by evidence from McArthur *et al.* (1994) and Partridge (1996). State I is similar to a climax sere suggested by Roberts (1972) but at odds with some suggested pioneer species (e.g. *A. latifolia* and *Iseilema* spp.).

The general similarity between herbfield states identified under each set of seasonal circumstances (particularly the absence of perennial grasses) creates the temptation to form one generalised herbfield state. The lack of temporal species continuity, particularly with the separation of sites dominated by bare ground in May 1993 into three separate vegetation states in May 1994, provides insufficient evidence to justify this grouping. The evidence, instead, points to five separate vegetation states (States III through State VII) to be used within a monitoring framework. Pragmatically, a simplification to sub-groups within a single herbfield state ("State III") for presentation to range managers may be justifiable, if not strictly correct based on the evidence.

Some potential vegetation states were not identified over the monitoring period. One expectation from observations and anecdotal evidence was a *Salsola kali* dominant state similar to States IV or VI. Other dominant plants recorded in the literature include *Boerhavia diffusa* (under

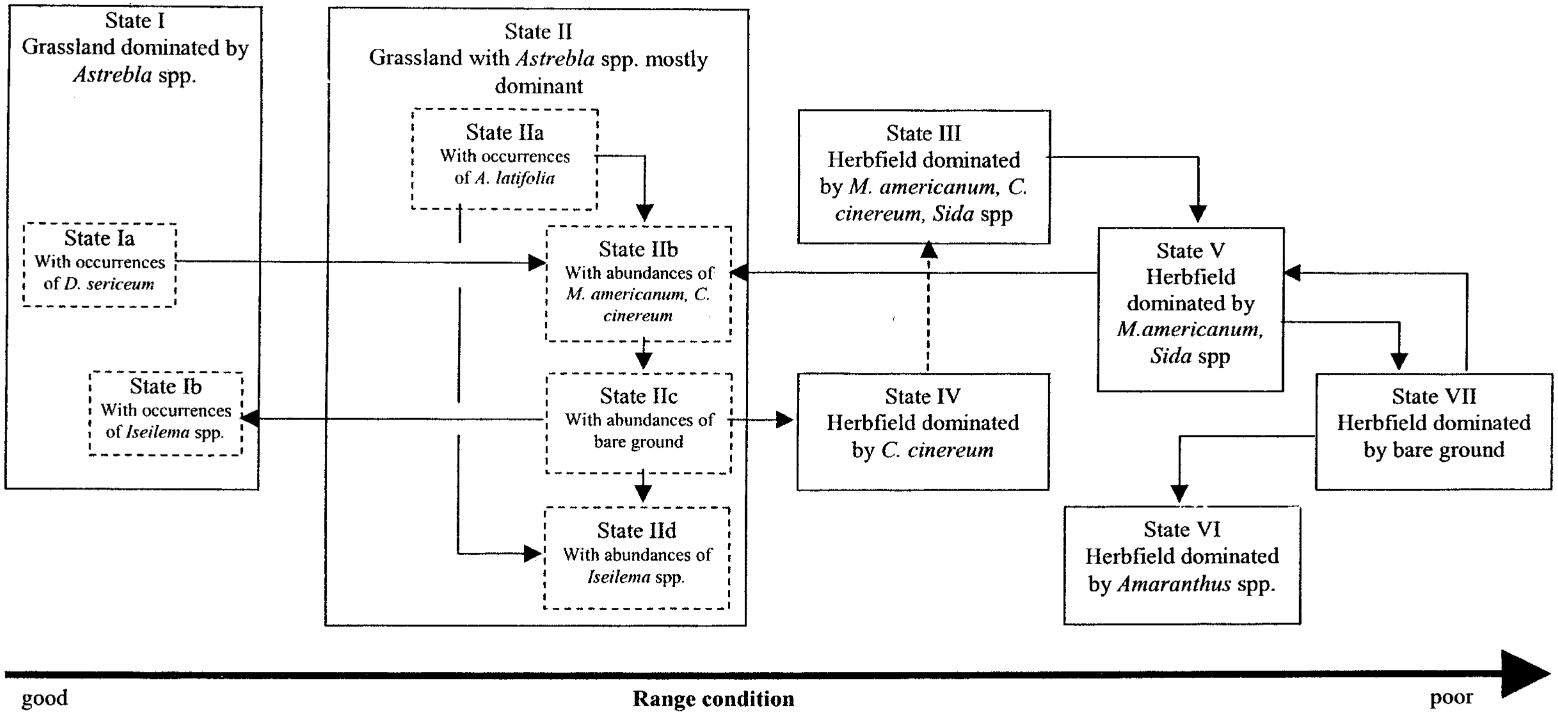

Fig. 3. A generalised, time independent, STM for the central Mitchell grasslands of Queensland, Australia, derived from pasture monitoring between August 1989 and May 1994. (Solid boxes represent well defined states, dashed boxes indicate sub-groups within states. Solid lines represent well defined Transitions; dashed lines indicate Transitions with weak supporting evidence. The horizontal separation of states reflects their relative position along the first ordination axis; vertical separation is for ease of presentation).

revision, *B. diffusa* is no longer valid in Australia), *Plantago debilis* and *Solanum esuriale* (Davidson 1954). There is, however, insufficient evidence to include these plants within states in the current model. This suggests that a longer period of monitoring was required to capture a wider range of rainfall conditions and hence a fuller overview of the potential states within the central Mitchell grasslands. The emphasis should be placed on a time frame sufficient to capture a suite of different rainfall trends whilst being able to compare grazing management. Jones *et al.* (1995) suggested a minimum of 10 years when monitoring experimental grazing sites. Phelps *et al.* (1993) suggested monitoring 10 to 15 major climatic events over whatever time was necessary to encapsulate rainfall induced vegetation changes in the Mitchell grasslands.

Identifying a degradation gradient

The existence of a degradation gradient from State I (good condition) to State VII (poor condition) was tested through plotting known grazing histories, surface litter cover, erosion activity and bare ground within the generalised vegetation states of the proposed STM. It would be expected that declining ecological condition along a degradation gradient would be associated with factors such as increasing erosion resulting from increasing grazing intensity (expressed as utilisation) and the loss of soil surface cover. The lack of such a relationship would be sufficient to reject the presence of a degradation gradient, and to reject the proposed STM.

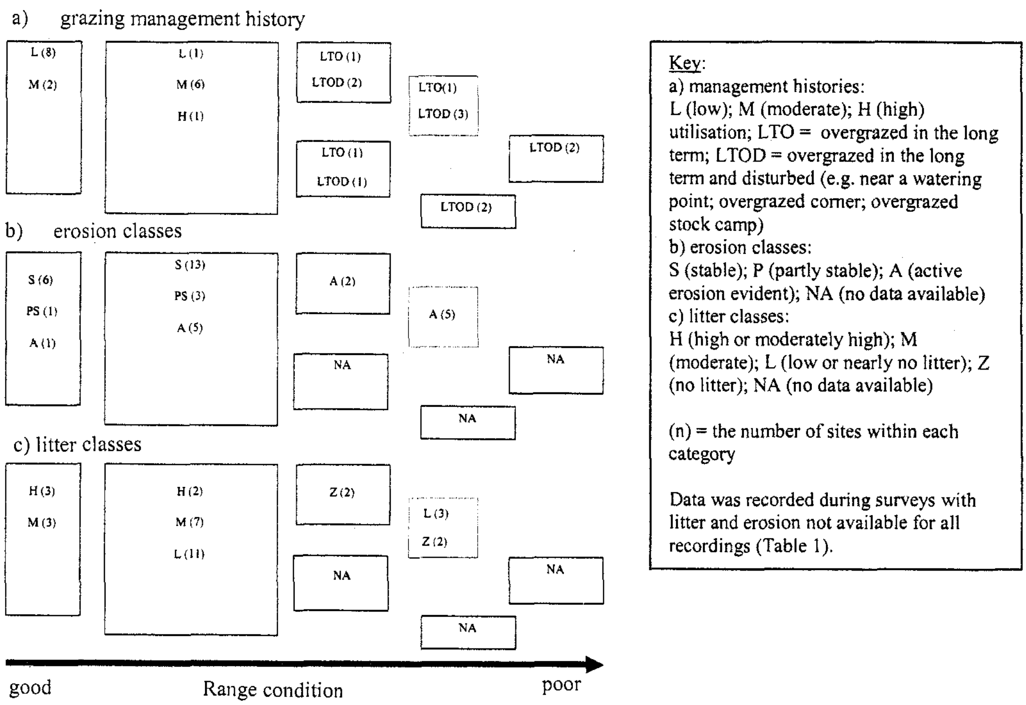

Fig. 4. Evidence for a degradation gradient within the STM for the central Mitchell grasslands: a) grazing management history; b) erosion classes; and c) litter classes.

The general trend present was for grazing intensity and erosion to increase and for surface litter levels to decline from State I to VII (Fig. 4). State I was dominated by sites with low utilisation (8 out of 10 of sites with known management histories), stable erosion (6 out of 8 sites) and high to moderate levels of litter (all sites). There were minor incidences of moderate utilisation and active erosion at sites within these vegetation states. State II was dominated by sites with moderate utilisation (6 out of 8 sites, with one low and one high), stable erosion (13 out of 21 sites) and moderate to low levels of litter (18 out of 20 sites). There were occurrences of active erosion (five sites). The herbfield states (States III to VII) exclusively contained sites that were overgrazed in the long term, or overgrazed and disturbed (those close to watering points, near stock camps and in overgrazed corners), were actively eroding and had low to zero surface litter present.

Other authors have deliberately ordered States and Transitions along degradation gradients, or in some cases, along two axes representing different aspects of degradation. For example, Ash *et al.* (1994) presented a model for northern Australian tropical tallgrass communities with States placed along axes for disturbance and risk of accelerated soil erosion. They also discussed the value of recognising key pasture species to indicate positive or negative change. Orr *et al.* (1994) presented two axes relating to degradation in their model for the southern black speargrass zone, animal productivity and soil stability. They also included a "Management Restoration Threshold" below which major alterations to management would be required to effect change to range condition. This threshold is similar in nature to the border between domains of attraction along a degradation gradient presented by Bosch (1989) and Bosch and Kellner (1991).

Grice and Macleod (1994), in a discussion on the practical use of STMs, ordered their model for the woodlands/grasslands of western New South Wales along a degradation gradient, albeit without defining the gradient as such. Jones and Burrows (1994) defined the relative degradation of states within their mulga zone STM, again suggesting the value of retaining this basic element of Clementsian theory. McIvor and Scanlan (1994) presented a model for the northern speargrass zone, in which transitions were acknowledged to be accompanied by changes in soil stability and pasture productivity. They did not define a degradation gradient although states were ordered in a way which could be interpreted as a degradation gradient. McArthur *et al.* (1994) explicitly divided their model for the Mitchell grass, bluegrass-browntop and Queensland bluegrass pasture zones into sustainable, deteriorating and degraded categories along a degradation gradient.

These examples indicate that whilst STMs are now well accepted in Australia, aspects of Clements (1916) and Dyksterhuis (1949) have been retained, albeit generally not explicitly stated. Specifically, perceived degradation gradients, management thresholds and key plant species are still presented as tools in interpreting range condition. This seems sensible. The introduction of a new system of modelling range condition should not mean all previous attempts have nothing to offer. Rather, the combining of the best elements of each would seem appropriate. This appears to be the unwritten intent of many rangeland researchers.

Determining indicator species

The definition of degradation gradients in both the generalised vegetation states and the time specific vegetation states made it possible to determine indicator species along the first ordination axis. The time specific vegetation states were initially analysed for indicator species, to reduce noise from differing rainfall patterns. Where rainfall patterns were similar at different dates (e.g. rains following a seasonal drought) similarities were also found in both species abundance and behaviour. This made it possible to summarise the indicator species according to rainfall patterns (Fig. 5). Whilst indicator species are presented individually, it is the combined abundances of all species which serve to group sites in ordination space. When assessing the placement of new sites relative to existing groups along the degradation gradient (i.e. states), all indicator species should be considered in the context of the descriptions included in the catalogue of states (see section "A quantitative State and Transition Model" for comprehensive descriptions).

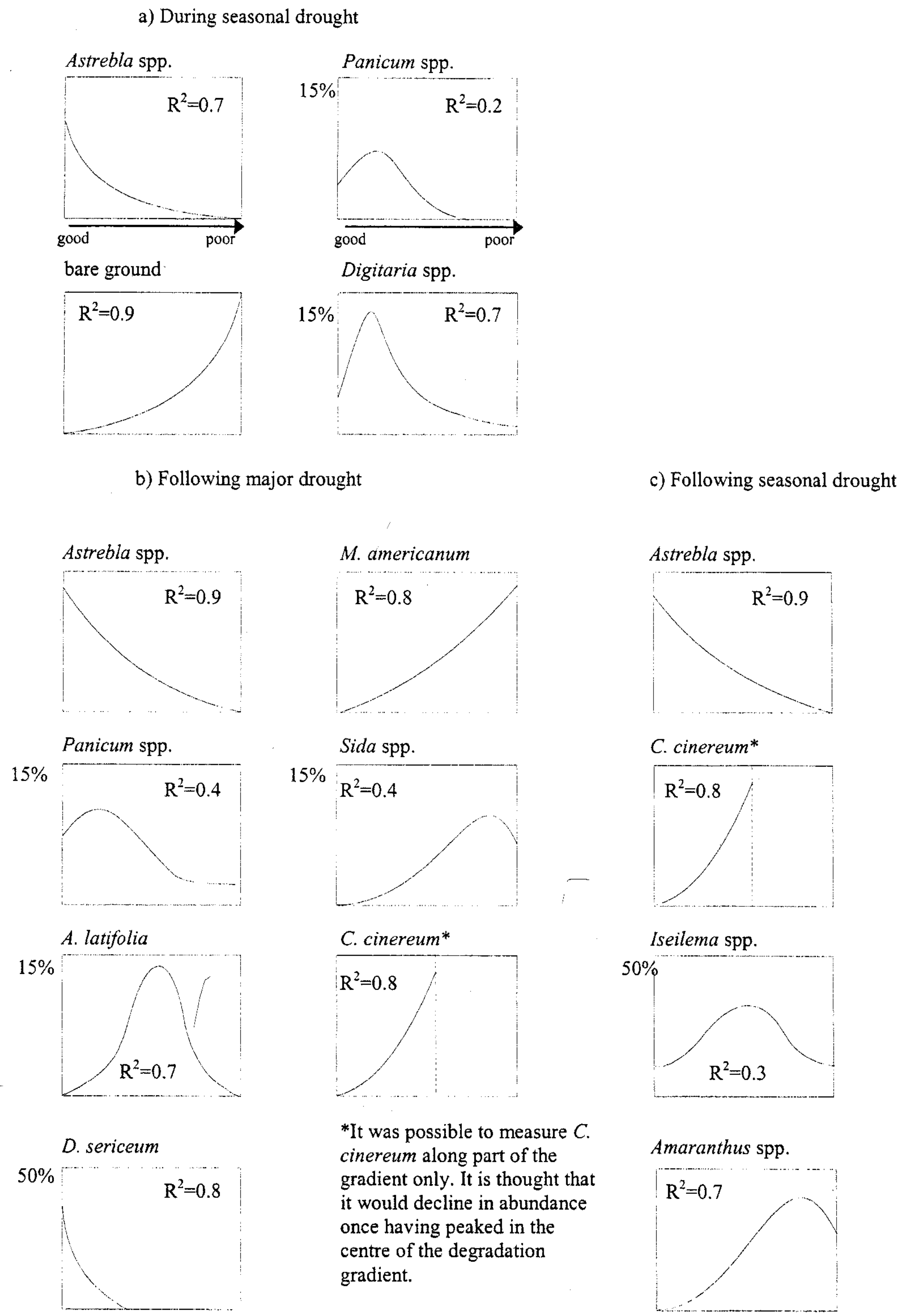

Fig. 5. Stylised response curves of indicator species along the degradation gradient (PCA axis one) for the central Mitchell grasslands within rainfall pattern groups: a) during seasonal drought; b) following major drought; and c) following seasonal drought. Maximum abundances (vertical axis) are 100% unless otherwise indicated.

During seasonal drought (Fig. 5a), bare ground was the strongest indicator (R^2=0.9) of degraded range condition (equating to State VII of Fig. 3), while *Astrebla* spp. was the strongest indicator (R^2=0.7) of non-degraded range condition (equating to States I and II). *Digitaria* spp. (a combination of *D. coenicola* and *D. ctenantha*) (R^2=0.7) and *Panicum* spp. (primarily *P. decompositum*) (R^2=0.2) were associated with State II at low abundances (Fig. 5) with high to moderate abundances of *Astrebla* spp. and low to moderate abundances of bare ground.

Analysis of the sites surveyed following drought-breaking rains (Fig 5b) indicated that *Astrebla* spp. again had its highest abundance in the non-degraded vegetation states (States I and II). The relatively high abundance of *D. sericeum* in association with *Astrebla* spp. was a good indicator of State Ia. The combined presence of *Astrebla* spp., *M. americanum* and *C. cinereum* was a good indicator of State II, forming State IIb under these circumstances. *Panicum* spp. provided an indication (R^2=0.4) of State II, albeit only reaching low abundances (less than 10%). High abundances of *A. latifolia* distinguished State IIa within the overall confines of State II. Both *M. americanum* and *C. cinereum* were good indicators (R^2=0.8) of the degraded forb states following major drought (particularly State III). *Sida* spp. abundances were less than 15%, contributing as an indicator (R^2=0.4) of State III.

Following seasonal drought (Fig. 5c), *Amaranthus* spp. dominated State VI in response to favourable rainfall and is therefore a good indicator (R^2=0.7) of severely disturbed states in a process of recovery. Sites in good condition were associated with high abundances of *Astrebla* spp., providing a good indicator (R^2=0.9) for State I. Sites dominated by *Astrebla* spp. but with abundances of *C. cinereum* (R^2=0.8) or *Iseilema* spp. (R^2=0.3) indicated State II following seasonal drought, particularly States IIb and IId. Other species associated with State II under these conditions included *Eriochloa crebra*, *Digitaria* spp. and *Sida* spp.

The ability to identify indicator species along a degradation gradient allows quantitative (using thresholds within ISPD, Bosch and Kellner 1991) or qualitative (using indicator species proportions as a guide) positioning of new sites into the central Mitchell grassland STM based on botanical composition and seasonal conditions. The use of indicator species from different times, representing a range of rainfall-induced botanical compositions, reduces the need to extrapolate from dissimilar seasons, and should provide a degree of certainty not previously available.

The concerns of Everist and Webb (1975) are thus partially satisfied through a model incorporating seasonal impacts, with a single recording event interpreted in context of both spatial and temporal variability. The prerequisite of success in this approach is adequate coverage of temporal variability, to ensure confidence in capturing all major vegetation states and transitions.

A quantitative State and Transition Model (STM)

The identification of vegetation states, degradation gradients and indicator species has allowed a quantitative STM to be developed (Fig. 3) and described (Box 1) for the central Mitchell grasslands. Supplementary information from other sources has allowed transitions to be better defined and described than from the pasture monitoring evidence alone. This new model enhances information previously presented by McArthur *et al.* (1994) by refining the area of applicability and utilising more recent evidence. This process could be considered useful in determining quantitative STMs in other rangeland ecosystems where monitoring programs have been undertaken or are current.

Box 1. Catalogue of States and Transitions for the central Mitchell grasslands

Catalogue of States

State I. Grassland dominated by *Astrebla* spp., typically 50-90% relative abundance (50-70% during seasonal drought, 50-90% following seasonal or major drought). A stable state generally with low erosion, high litter, high projected foliage cover, high pasture yields (with a small forb yield component), drought dormant *Astrebla* spp. tussocks obvious but difficult to discern if living or dead. Animal productivity stable but may only be moderate due to a lack of forbs. State Ia exists only under better rainfall conditions, with *D. sericeum* relative abundances of 10-40%. State Ia generally exists following seasonal drought, with *Iseilema* spp. relative abundances of 10-15%.

State II. Grassland with *Astrebla* spp. mostly dominant, typically 5-50% relative abundance (5-50% during major drought, 15-50% following seasonal or major drought). A less stable state because of the lower perennial grass component, generally with low to moderate erosion, moderate to high litter, moderate to high projected foliage cover, moderate to high pasture yields (with a higher forb yield component), drought dormant *Astrebla* spp. tussocks may be obvious but difficult to discern if living or dead. Animal productivity fluctuates depending on rainfall but generally higher than State I because of a higher forb component. State IIa generally exists under better rainfall conditions with *A. latifolia* relative abundances of 5-15%. Paradoxically State IIa may be most apparent following seasonal drought before annual species occupy bare areas. State IIb generally follows drought or overgrazing, with *M. americanum* and/or *C. cinereum* relative abundances of 5-30%. State IIc generally occurs during drought with bare ground relative abundances of 10-30%. State IId generally occurs following drought with *Iseilema* spp. relative abundances of 10-30%. Animal production would be the lowest of State II (Lorimer 1978).

State III. Herbfield dominated by *M. americanum*, *C. cinereum* and *Sida* spp., typically 0-30% *Astrebla* spp. relative abundance. Identifiable from State V as *C. cinereum* relative abundance will be high (20-80%). A highly unstable state generally with moderate to high erosion, low to moderate litter, low to moderate projected foliage cover, low to moderate pasture yields (with a very high forb yield component), drought dormant *Astrebla* spp. tussocks not obvious. Animal productivity fluctuates widely depending on rainfall but generally low because of low grass component and inability to carry stock through drought conditions.

State IV. Herbfield dominated by *C. cinereum*, typically 0-30% *Astrebla* spp. relative abundance. Identifiable from State III as *C. cinereum* relative abundance will be high (20-80%) but *M. americanum* and *Sida* spp. will be low (less than 20%). A highly unstable state as per State III.

State V. Herbfield dominated by *M. americanum* and *Sida* spp., typically 0-20% *Astrebla* spp. relative abundance. Identifiable from States III and IV as *C. cinereum* is absent or present in minor abundances only (less than 10%). A highly unstable state as per State III.

State VI. Herbfield dominated by *Amaranthus* spp., typically 0-15% *Astrebla* spp. relative abundance. Generally exists following seasonal drought. A highly unstable state as per State III.

State VII. Herbfield dominated by bare ground, typically 0-10% *Astrebla* spp. relative abundance and a lack of other species. Generally exits during seasonal or major drought. Identifiable from State IIc as bare ground abundance is high (30-100%). A highly unstable state as per State III.

Catalogue of Transitions

Transition I, II. (from State I to State II). Whilst not recorded, would occur with a reduction in *Astrebla* spp. density resulting from overgrazing, severe drought or possibly flooding or wildfire. Transition Ia, IIb would result from drought, unfavourable rainfall patterns or overgrazing which lead to a reduction in *D. sericeum* abundance.

Transition II, I. Not recorded but would occur with the recruitment of *Astrebla* spp. from at least 100 mm summer rainfall (Austin and Williams 1988) with follow up rains coupled with high germinable seed banks. Only restricted by grazing under exceptional conditions. Transition IIc, Ib would result from summer rainfall conditions which favour *Iseilema* spp. recruitment. Transition IIa, IIb/IId would result from drought followed by early summer or summer rainfall favouring forb or annual grass recruitment. Transition IIb, IIc would result from drought reducing forb abundance, with IIc, IId following summer rainfall conditions favouring *Iseilema* spp.

Transition II, III/IV. Were not recorded, but would occur with a reduction in *Astrebla* spp. density coupled with winter and summer rainfall which favours forb recruitment. Transition IIc, IV specifically resulted from late winter rainfall which favoured *C. cinereum*.

Transition IV, III. There was only weak evidence for this transition, but resulted from an increase in *M. americanum* and *Sida* spp. following summer rainfall.

Transition III, V. Resulted from the loss of *C. cinereum*, probably due to unfavourable winter rainfall.
Transition V, VII. Resulted from the loss of *M. americanum* and *Sida* spp. during drought.
Transition V, VII. Resulted from the recruitment of *Astrebla* spp. and reduction in forbs
Transition VII, V. Resulted from the increase of *M. americanum* and *Sida* spp. following summer drought breaking rains.
Transition VII, VI. Resulted from the increase of *Amaranthus* spp. following summer drought breaking rains. The differences in transitions from State VII to either States V or VI are not clear. These species have only moderate to poor palatability so it is unlikely that grazing would affect their relative increase, which may depend only upon the timing of rainfall.

Opportunities and Hazards

The major hazard is overgrazing which leads to *Astrebla* spp. abundances of less than 30%. Any of the herbfield states represent low productivity, increased erosion risk, the loss of desirable species and a real difficulty in returning to a desirable state. State VII is the worst in condition but, paradoxically, may return to State II more rapidly than the other herbfield states. The probability of this occurring, however, would be small with rains required to fall in a way that soil moisture is maintained over the whole of summer to enable *Astrebla* spp. seedlings to reach maturity in the same summer. This has been observed in the northern Mitchell grasslands, and may not occur as readily in the herbfield states where soil moisture competition from mature forbs exists. Grazing management would have no impact on a massive recruitment, but continued heavy grazing would decrease the survival of the new mature tussocks. Similarly, newly matured *Astrebla* spp. tussocks in the other herbfield states require light to moderate grazing to enhance growth and survival. It is at this stage that grazing management is crucial, with all of the evidence suggesting that rainfall alone drives recruitment events per se.

Opportunities exist within State II to optimise productivity by maintaining a balance of both perennial grasses and annual forbs and grasses. The type and quantity of annual species to grow will depend upon rainfall patterns and soil moisture, but the opportunity for their growth can be provided through reducing projected foliage cover (Orr 1980a) at moderate grazing pressures. Any increases in *M. americanum*, *C. cinereum* or *Iseilema* spp. should be treated with caution and grazing pressure reduced to enable pasture recovery. The major hazard to recovery is the long time frame which may be required before *Astrebla* spp. recruitment occurs. Recovery following drought (e.g. State IIc) should also be accompanied with light grazing pressure to avoid the possibility of creating a herbfield state. If a projected foliage cover reduction strategy is adopted, standing dry matter is also reduced and drought susceptibility is increased. Observation suggests that most country is in State II, with some tending towards a herbfield state.

State I is the most stable, and provides a degree of drought proofing through high standing dry matter yields that is not found within State II. Whilst productivity may be lower than State II, income is generally more stable. For this reason, light grazing and fodder retention is a strategy practiced by many graziers in the central Mitchell grasslands.

Allied situations

The Mitchell grasslands occupy 45 million ha in Australia. States I and II could be expected to occur in all situations, but the herbfield states and sub-groups would vary, especially along the north-south summer rainfall gradient. Differences could also be expected towards the more arid western Mitchell grasslands where *Astrebla* spp. density is typically lower. A band of looser ("ashy") soils with a fine ped structure, high porosity and strongly slaking surface run from the McInlay district through to the Muttaburra district in the north of Queensland. These soils may be associated with the Makunda (Klm) and Allaru (Kla) Formations of the Rolling Downs Group formed from Lower Cretaceous parent material (Vine 1970, Casey 1966, Casey 1968 and Vine 1963). Observation suggests *Astrebla* spp. tussocks are more prone to dislodgment under drought and overgrazing in these ashy soils. These soils may also be more suited to *Iseilema* spp. growth.

Implications of differing conditional states

Data presented in this paper indicate that the states can be arranged along a degradation gradient, with the best ecological condition at State I and the worst at State VII (Fig. 4). Direct observation, experience and other published evidence (Bushell *et al.* 1993, Phelps *et al.* 1993) suggest grazing, rainfall and vegetation data have been interpreted correctly in placing the herbfield states along the degradation gradient, although the spacing in Fig. 3 is not necessarily indicative of the relative severity of degradation of each state. It is likely that a management threshold exists between State II and the herbfield states (States III to VII), as few sites from latter states returned to a grassland state during the survey period. It is also likely that animal productivity in the herbfield states would be both reduced in the long-term and highly variable in the short-term.

The herbfield states, lacking perennial grasses, would have little feed on offer for livestock during dry periods. Perennial grasses comprise a significant proportion of the diet of sheep between (Lorimer 1978), as well as immediately following (Orr *et al.* 1988), pasture growth initiating rainfall events. This enables livestock to be carried longer into dry periods than pastures consisting of forbs alone would allow. However, animal nitrogen and energy balances may be lower on diets dominated by grasses (Norton *et al.* 1978, McMeniman *et al.* 1989), with forbs reported to have higher nutrient levels than green leaf of grasses (McMeniman *et al.* 1986). It is likely that animal productivity would vary considerably within the herbfield states and that a high risk of liveweight loss and animal mortality (or the need for agistment or supplementary feeding during drought) result.

The supposition that animal productivity is much reduced in states in the worst ecological condition (e.g. the herbfield states) is also supported by the findings of Roe and Allen (1993) and Phelps and Orr (1998). Both have reported that stocking sheep at levels which maintain good conditional states (i.e. moderate stocking rates) provided improved monetary returns over levels which lead to degraded states (i.e. high stocking rates) in the southern and northern Mitchell grasslands respectively.

Mechanisms of transitions

As with states, not all expected transitions were identified during the study period and cannot easily be determined from the literature. For example, changes directly from State I to State II and State II to the herbfield states (e.g. State IV) were recorded only within sub-groups (there were transitions from State Ia to IIb and from State IIc to IV but transitions were not recorded from State I to II). Whilst such transitions may be expected, they are not presented within Fig. 3. Where there was clear evidence that a transition existed during the study period, it is represented as a solid arrow. Transitions with only weak evidence (e.g. only one or two sites which moved in that direction) are represented with a dashed line.

The mechanisms of transitions were not clear from the current study, with both the literature and observations used to define the processes involved. Any movement from good to poor condition would necessarily involve the loss of *Astrebla* spp. (Fig. 3 and Box 1). Orr (1975) cites the reasons for the depletion of *Astrebla* spp. in Mitchell grass pastures as:

i) the removal of seedlings by gross overstocking;
ii) excessive grazing during active growth;
iii) grazing dormant plants close to ground level; and
iv) burrowing for roots.

Within the context of variable rainfall, and associated variable pasture growth and botanical composition, i) would most likely occur following drought when the pasture biomass is low and there are few existing *Astrebla* spp. tussocks, or potentially over winter (Roe and Davies 1985);

ii) would most likely occur during periods of below average rainfall or drought recovery; iii) would most likely occur during either winter or periods of drought; and iv) would most likely occur during periods of extreme drought.

Catastrophic climatic events, such as flooding, prolonged drought and wildfire may also lead to the loss of *Astrebla* spp. tussocks. Bowman *et al.* (1997) reported that flooding can lead to the large scale disappearance of *A. lappacea* in New South Wales. *A. squarrosa* and *A. elymoides*, however, often grow in flooded areas (Orr 1975), and flooding during dormancy may not have as severe an impact (personal observation). Williams and Roe (1975) reported that *Astrebla* spp. tussocks can be killed by drought, and local knowledge suggests that wildfire in the heat of summer can lead to the loss of *Astrebla* spp. Grazing management may also play a role in these extreme events. A transition from State I directly to a herbfield State would probably require a catastrophic event to reduce *Astrebla* spp. abundances from 50 to 90% to less than 30%.

Declining range condition could be avoided through the prevention of conditions which lead to a net loss of *Astrebla* spp., through either the protection of existing tussocks or the promotion of new plants through recruitment. Recruitment is generally both small and irregular (Williams and Roe 1975), and insufficient to compensate for high tussock mortality. This suggests that the maintenance of a site within either of the grassland states would be dependent on existing *Astrebla* spp. tussock survival.

Any improvement in range condition would necessarily involve a net gain of *Astrebla* spp. (Fig. 3 and Box 1) through rare large recruitment events, and depend upon both favourable summer rainfall patterns and a high germinable seed bank at the start of summer (Orr 1991, Orr and Evenson 1991), although seedlings recruited towards the end of summer may survive if soil moisture is maintained over winter (Austin and Williams 1988).

It is unlikely that differences in recruitment would exist between States I and II, as seedling recruitment and yearling mortality is higher under moderate grazing pressure than under no grazing, resulting in net similarities (Orr and Evenson 1991). However, if rainfall conditions favour *Iseilema* spp., recruitment of *Astrebla* spp. may be restricted (Orr and Evenson 1993). *Iseilema* spp. abundances reached 30% within State IId. Consequently, high grazing pressure within State IId could result in a transition to a herbfield state, similar to the removal of seedlings by gross overstocking. Orr (1980b) also suggested that the recovery of *Astrebla* spp. following drought depends largely upon recruitment. An increase in *Iseilema* spp. following drought could therefore reduce the proportion of *Astrebla* spp., potentially leading State IIc to a herbfield state, or preventing State VII from recovering.

Populations of both *D. sericeum* and *A. latifolia* increase with above average summer rainfall (Blake 1938, Lee *et al.* 1980, Orr 1980a), the latter increasing mainly under lighter grazing pressure. As with *Astrebla* spp., their abundance is a result of recent rainfall history over the past one to three years (Orr 1981). A decline in *D. sericeum* and *A. latifolia* results from drought conditions. High grazing pressure may also reduce the abundance of the highly palatable *D. sericeum.* The Transitions of State Ia to State IIb and State IIa to State IIb or State IId resulted from dry conditions. The return of favourable rainfall at these sites would likely see the return of these sites to the compositions recorded in 1989.

Other grasses and forbs occupy the spaces between the tussocks of the perennial species and their dynamics are the most difficult to predict. This is reflected in the small proportion of forbs which were useful indicator species (Fig. 5). The abundance of the annual and short lived perennial forbs is a result of immediate rainfall history (Orr 1981) and dependent upon the germinable seed bank, the bare space available and the projected foliage cover of the perennial grasses (Orr 1980a). The low basal areas found in the Mitchell grasslands (1 to 6%) suggests that space is rarely limiting, although increases in the abundance of perennial grasses can be at the expense of annual species (Orr 1981). Root competition from the perennial grasses may also limit moisture availability and restrict the abundance of annual species.

A wide range of annual forbs and grasses can be found following rains immediately after drought. Botanical composition under these conditions is determined by the timing of the rainfall e.g. *Daucus glochidiatus* and *Plantago* spp. respond to increased winter rainfall, whilst *Desmodium campylocaulon* and *Sida* spp. were recorded in highest abundance following summer rainfall (Orr 1981). *Iseilema membranaceum* was found to increase with increasing summer rainfall, as were *B. diffusa* and *Rhynchosia minima*. (Orr 1981, 1986). *M. americanum* increased with late or early summer rainfall (Orr 1986, Bushell *et al.* 1993, Phelps *et al.* 1993) but it survives for only two to three years before dying during dry or drought conditions.

Some forbs and annual grasses have been reported to occur only under different grazing pressures. Hall and Lee (1980) reported *Abutilon malvifolium, M. americanum, Portulaca* sp., *S. kali, Sida filiformis* and *C. cinereum* to occur only under heavy grazing with cattle in the northern Mitchell grasslands. Some *Sida* spp. were found to occur under both heavy and light grazing (e.g. *S. trichopoda*), but none were confined to light grazing alone. *Iseilema* spp. tended to increase under moderate grazing (Fig. 5). This is consistent with Foran and Bastin (1984) who reported *Iseilema vaginiflorum* density and biomass to be greater at 1.6 km than at either 0.8 or 3.2 km from water in a cattle grazing area, but differs from Hall and Lee (1980) who found that *Iseilema* spp. tended to increase under heavy grazing by cattle.

Transitions from and between any of the herbfield states are therefore difficult to predict. It is likely that the Transitions from State III to State V and from State V to State VII resulted from dry conditions and subsequent high forb mortality, rather than from grazing pressure. The formation of State IV, however, probably resulted from a combination of high grazing pressure, high *Iseilema* spp. density and rainfall conditions which favoured the germination of *C. cinereum*. The few sites which moved from State IV to State III probably received rainfall favouring the establishment of *M. americanum* and *Sida* spp. The Transition of State VII to either of States V or VI is probably dependent on rainfall patterns, similar to the findings of Orr (1981). The transition from State IIc to State Ib probably resulted from summer rainfall allowing *Iseilema* spp. to fill the bare spaces, but may have been accompanied by light grazing pressure. The return of any of the herbfield states to a grassland State would require the large scale recruitment of *Astrebla* spp., with a direct change from a herbfield State to State I very unlikely.

Application of the central Mitchell grassland STM at the paddock scale

The introduction of this paper asserted that "the successful implementation of sustainable best management practices ultimately rests with land managers". Whilst a quantitative STM has been developed to describe vegetation changes and their causes at specific sites, land managers require tools to monitor changes at relevant scales. In central western Queensland, the basic natural resource management unit is the grazed paddock, which ranges in size from small holding paddocks of 25 to 100 ha (used to infrequently hold stock for short periods of time during husbandry activities) to main paddocks of 2500 ha or greater. It is at this scale that land managers make decisions concerning stock numbers (grazing intensity), grazing initiation and grazing duration in relation to factors such as animal husbandry, market forces, labour supply and rainfall. It is thus at this scale that the largest impact on sustainability is realised.

In theory, paddocks can be mapped into conditional states within county types (e.g. Land Zones or Land Systems) using on-ground monitoring and remote sensing technology through GIS or paper-based cartography. For instance, Orr (1978, 1980a) defined grazing pressure and vegetation condition patterns through the on-ground monitoring of *Astrebla* spp. basal area and botanical composition in the Blackall district of Queensland. Bellamy *at al.* (1996) and Bastin *et al.* 1993 are two examples of the application of GIS and remote sensing technologies at the paddock scale to identify changes in vegetation states and grazing patterns for the interpretation of range condition. However, satellite technology has limitations in determining vegetation composition changes for some soil types or at fine scales (e.g. Bastin *et al.* 1998) and on-ground monitoring programs have failed to gain general acceptance within the grazing community.

In practice, basing a monitoring program upon the central Mitchell grassland STM (to provide an interpretational framework), on-ground monitoring sites (to provide site specific data) and satellite imagery (to enable scaling up of site specific data and assist in monitoring site selection) could provide the capacity to trace the expansion or contraction of conditional states over time at the paddock scale. Paddock scale transitions could be hypothesised or developed from expert knowledge as an aid to on-ground management decisions. Such an approach may provide the "common ground" required for successful dialogue between researches, policy makers, funding bodies and rangeland managers and may be best approached within existing group structures (e.g. Landcare groups).

Scaling the central Mitchell grassland STM up to application within paddocks could introduce an additional layer of complexity, with the possibility of attempting to trace changes between seven states over time. For simplicity at the paddock scale, the model may need to be summarised through the pragmatic removal of the grassland sub-groups and the condensing of the herbfield states into "State III Herbfield (IIIa dominated by forb species following rainfall, IIIb dominated by bare ground during drought)". This may provide a more acceptable and practical model for graziers who have not yet been exposed to State and Transition Models and overcome difficulties relating to data and mapping complexity when attempting to categorise paddocks into states. It should not, however, be confused with the more definitive central Mitchell grassland STM. It should also not be confused with possible models for other regions, but may be useful in providing a framework for developing experiential based models for other regions.

Further work

The six years of data collection reported here is short relative to reported botanical fluctuations in Mitchell grasslands (e.g. Orr 1981, 1986). Consequently, this relatively short monitoring period has probably failed to identify all possible states and transitions. However, the major states reported do conform well to existing local and published knowledge (McArthur *et al.* 1994, Partridge 1996, Roberts 1972). Continuation of this monitoring would be invaluable to unravel the many transitions that are possible under varying climatic and management conditions. It is doubtful whether researchers alone could refine such a complex system. The active involvement of land managers to provide detailed management information and their observations to help explain transitions, would be essential. Land managers are actively "experimenting" in their day to day management of the resources by applying "treatments" (management practices) and observing or monitoring the outcomes of their actions. The first six years of monitoring by scientists in this study have made tools (models and indicators) available for helping land managers to more formally assess and interpret the condition of their rangelands. Putting these in practice through the establishment of a long term monitoring program for land managers could play an important role in the further refinement of states and indicator species, and the explanation of transitions between states. Such a community-based monitoring program that is designed to be an integral part of rangeland management will also directly benefit the development and evaluation of sustainable management practices, through the capturing and sharing of monitoring information with other land managers and researchers (Allen *et al.* 1995, Bosch *et al.* 1996).

There is no reason to assume that STMs supplant models of rangeland ecosystem dynamics based on Clementsian successional theory. Westoby *et al.* (1989) provided examples in their defining paper on State and Transition Models that could easily be arranged along a degradation gradient. However, the long held assumption of singular climax has been discredited. Other authors have come to question this aspect of successional theory, often presenting their own alternatives and compromises (see Glenn-Lewin and van der Maarel 1992 for many examples) that suggest succession goes beyond a self repairing ecological sliding scale.

Conclusions

State and Transition Models (Westoby *et al.* 1989) and the Clementsian based Degradation Gradient Method, which acknowledges the existence of thresholds (Bosch and Kellner 1991), were successfully combined to produce a quantitative STM for the central Mitchell grasslands of Queensland. Vegetation states were identified using ordination techniques and tracing the movements of individual monitoring sites through time. Similarities within these states across rainfall patterns allowed a generalised (temporally independent) model to be developed. Both the time specific and generalised vegetation states were found to occur along a degradation gradient. It was therefore possible to identify indicator species and to develop a STM which includes quantitative descriptors to place new sites within the predefined states. Using these two theories in combination it was possible to develop a tool by which land managers can interpret both current range states and transitions for monitoring sites on their own properties.

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