

Banded vegetation in some Australian semi-arid landscapes: 20 years of field observations to support the development and evaluation of numerical models of vegetation pattern evolution

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Abstract

Periodic vegetation patterns (PVPs) are striking features of many global drylands. Although they have attracted wide research study, resulting in many hypotheses, their origin and controlling factors remain unresolved. Theoretical works dominate a large literature seeking to account for the occurrence and properties of PVPs, especially banded vegetation patterns ('tiger bush'). In light of the plethora of theoretical studies, there is a need for more empirical observation and monitoring of PVPs, especially their responses to climatic variability and to foreshadowed climatic change. This paper highlights key results derived from more than 20 years of field study and monitoring of banded vegetation in arid New South Wales, Australia, where severe drought is a recurring feature. It advances the view that in this study area, and hence perhaps in other regions, local factors including plant physiology, soil properties, and climatic characteristics result in PVPs whose development and functioning might be quite unlike those of other regions. Importantly, these local characteristics appear to confer on the regional PVPs a considerable resilience to drought, and hence perhaps to climate change. The field evidence from the study area suggests that, despite predictions of a number of theoretical analyses, the PVPs are not facing imminent collapse. Generalised and non-specific models of PVPs require more realistic parameterisation and more thorough validation than has been customary, and this will require additional field evidence of the kind reviewed here.

Highlights:

- highlights results of field study of banded vegetation in the Broken Hill region of Australia over more than 20 years
- patterned vegetation in this area appears to be resilient in the face of drought and grazing pressure
- contrary to most model predictions, the vegetation bands do not migrate upslope, and do not undergo pattern change during severe drought
- direct observation of banded vegetation should increasingly accompany attempts at modelling responses of global drylands to climate change

Keywords: Patterned vegetation; Banded vegetation; Tiger bush; Fowlers Gap; Australia

1. Introduction

Periodic vegetation patterns (PVPs) are distinctive features of many global drylands (Debaluwe *et al.* 2008), and their origin is the subject of ongoing study (Kletter *et al.* 2009, Boonkorkuea *et al.* 2010, Sherratt 2010, Kealy & Wollkind 2012, Siteur *et al.* 2014, van der Stelt *et al.* 2015, Yizhaq & Bel 2016, Kohnke & Malchow 2017, Consolo *et al.* 2017, Dawes &

Williams 2017, Eigentler & Sherratt 2018, Wang & Zhang 2018, Sun *et al.* 2018). PVPs consist of virtually bare areas, 'intergroves', and more thickly vegetated areas or 'groves'. The ecohydrologic operation of these patchy landscapes involves a runoff-runon system, in which unvegetated parts of the landscape, where infiltrability is low, shed overland flow that passes downslope to nearby groves of plants, where runon infiltration boosts soil moisture. This community-level response to water scarcity supports more plant biomass than would be possible if the plant cover was unpatterned and plant growth relied on rainfall alone (Lejeune *et*

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al. 2002). Virtually all models seeking to understand banded vegetation identify overland flow occurring within runoff-runon systems as a key process. By garnering runoff water shed from bare intergrove soils upslope, vegetation groves can access more water than falls as direct rainfall. Most rainfall in drylands is consumed by evapotranspiration (ET), as reflected in common aridity indices (Arora *et al.* 2002), but the overall regional aridity is not constant at the scale of the patch structure of banded vegetation. Thus, Baudena *et al.* (2013) developed a model that estimated ET losses, and using an annual rainfall of 220 mm, estimated that bare zones (which suffer water loss via overland flow) had an ET loss of 0.54 times annual rainfall, whilst groves (which receive runoff water) had an ET of 2.1 times annual rainfall. These compare well to the values (0.61 and 2.87 times) observed in banded vegetation in Niger where mean annual rainfall was 228 mm (Galle *et al.* 1999). The ET flux from bare runoff sources is less than that of the vegetated groves not only because of the operation of the runoff-runon system redistributing moisture and the lack of transpiring vegetation; grove-intergrove differences in albedo, surface roughness, and vapour permeability of the soils also contribute (Haghighi *et al.* 2017).

PVPs occur in semi-arid grasslands, shrublands, and woodlands. Many theoretical works have sought general explanations for the occurrence of the different forms of PVP (spots, bands, and others), considering spatio-temporal patterns of soil moisture and vegetation biomass, as well as relationships with annual rainfall, slope form and gradient, and other factors that might have explanatory power. Several different approaches have been used in seeking such a unifying and widely-applicable explanation, including Turing-type analyses (involving interdependencies of biomass and water redistribution) and kernel-based approaches that embody facilitative and inhibitive interactions among plants that operate over different spatial scales. Analytical models dominate the literature, but approaches based on cellular automata and simple 'rules' describing water redistribution and plant growth have also been used (Dunkerley 1997a, 1997b, 1999, Esteban & Fairén 2006). Typically, facilitative influences are considered to include sheltering, shading and other beneficial effects of the clustering of aboveground plant parts, and the inhibitive effects are considered to result from competition for soil moisture among spreading root systems that may extend over a larger area than the plant canopy. Some approaches seek to

explain vegetation patterns in models that employ an unvarying mean annual rainfall (discussed further below), whilst other stress the importance of stochastic elements including the fluctuations of rainfall and soil moisture availability around the mean (the result of droughts and wet years) (Borgogno *et al.* 2007, D'Odorico *et al.* 2015, Chen *et al.* 2015). Guttal & Jayaprakesh (2007) showed that rainfall seasonality, often neglected in numerical models, may also be influential in patterned dryland vegetation, even in a model where seasonality was altered whilst keeping the mean annual rainfall fixed. Amounting to hundreds of papers, theoretical works on patterned vegetation now dominate the literature, and relevant field observations suitable for parameterisation and validation of numerical models remain scarce in comparison. Indeed, modellers in some cases attempt to validate their work by making comparisons with the output generated by the models of other workers, rather than with field evidence (e.g. Kealy & Wollkind 2012).

PVPs warrant scientific scrutiny for reasons beyond the academic challenge that they pose. An issue of particular importance in the context of global climate change is whether patterned vegetation in drylands, where water is a scarce resource, might be vulnerable to what has been termed 'catastrophic regime change' or 'catastrophic collapse' (Rietkerk *et al.* 2004; Scheffer *et al.* 2009, Tirabassi *et al.* 2014, Bathiany *et al.* 2018). The hypothesis has been advanced that diminished availability of water through changes in rainfall and/or evapotranspiration, together with environmental feedbacks, might lead to the rapid decline of plant cover in what some envisage to be an irreversible decline to an increasingly bare or even to a completely unvegetated condition (Chen *et al.* 2015, Vidiella *et al.* 2018). Thus, Sherratt (2013) argued on the basis of a numerical analysis that

"The author demonstrates via numerical simulations that a decrease in rainfall through the minimum level for patterns causes a transition to full-blown desert that cannot be reversed by increasing the rainfall again." (Sherratt 2013, Abstract).

According to some interpretations the occurrence of PVPs is a signal that the host ecosystem is on the path from fuller vegetation cover to a desertified or bare state (Barbier *et al.* 2006, Chen *et al.* 2015). Factors affecting the hypothesised collapse include the rapidity of climate change, and key ecological feedbacks. A principal feedback is thought to arise from the

effect of plants in enhancing the infiltrability of soils in their immediate vicinity. If plant cover declines, so too would the soil infiltrability, further reducing available soil moisture. The nature of collapse via such positive feedbacks was explored by Chen *et al.* (2015) using rates of rainfall change of 2 mm/a and 40 mm/a, and at the more rapid rate, which they took to be representative of the rapid onset of a drought, their model suggested irreversible collapse to an unvegetated state. In contrast, with the slower rate of rainfall change, taken to represent gradual climate change, stable periodic vegetation bands were predicted. Chen *et al.* (2015) showed that these could transition to become a complete vegetation cover if rainfall increased sufficiently. There is disagreement on whether ecosystem transitions in patterned vegetation are likely to occur, and if so, whether they are likely to be abrupt or gradual (Bel *et al.* 2012, Zelnik *et al.* 2013, Mohseni & Sepehr 2015). Some studies have indeed reported little change in PVPs over many decades, including in Somalia, where climatic stress and the pressure of human landuse are major perturbing factors (Gowda *et al.* 2017). Pattern changes have been considered by some to represent 'early warning signs' of collapse (Sankaran *et al.* 2018), but Kéfi *et al.* (2014) noted that there is so far no example of where 'early warning' signals were used to avoid an ecosystem shift.

The diversity of views about the possibility of catastrophic collapse may be partly a consequence of the fact that many workers have sought to explore general mechanisms accounting for PVPs, without regard to site-specific vegetation floristics, rooting depths, or soil types, and with little or no representation of the seasonal or inter-annual variability that is a universal feature of dryland rainfall. Rather than seeking to account for any particular patterned ecosystem, therefore, they have sought to understand some of the general principles or mechanisms that could be hypothesised to underlie the emergence of PVPs. There are a few exceptions to this generalisation, including Penny *et al.* (2013) and Stewart *et al.* (2014), who modelled the American SW desert and woody shrub invasion there, and Franz *et al.* (2012) who sought to account for vegetation patterns in Kenya, using local rainfall and other model conditions.

Given the global extent and importance of drylands, and the possible consequences of global climatic and environmental change for patterned vegetation, the correct diagnosis of possible regime shifts and loss of plant cover in dryland ecosystems is a worthwhile objective.

However, in this context, the plethora of numerical models of patterned vegetation (Borgogno *et al.* 2009, DeAngelis 2012), each reporting some degree of success in generating spatial patterns or other features that resemble what is seen in nature, is problematic. Not all approaches and modelling frameworks can be correct or fully complete (Pringle & Tarnita 2017). This means that we face a plethora of what Bokulich (2014) considered 'how possibly' hypotheses rather than the sought-after 'how actually' explanations of vegetation pattern development and maintenance. It appears that equifinality (Beven 1996, Brazier *et al.* 2001), especially when emergent spatial patterns are only qualitatively described (Mander *et al.* 2017), is readily possible in models of patterned vegetation. Given their diversity of assumption and approaches, it seems likely that multiple published models may yield plausible vegetation patterns and yet fail to reflect the true drivers and underlying mechanisms as they operate in nature. If this is so, then forecasts of resilience or of a tendency for catastrophic collapse in these ecosystems may be insecurely based, or misjudge the conditions under which a regime change could occur. Local environmental conditions, not reflected in any particular general model, may well be important for ecosystem resilience. This means that claims of a vulnerability to ecosystem collapse need to be set within the actual field conditions of particular landscapes, rather than based on general principles. Ideally, models and observational studies should both proceed, as they are mutually supportive (DeAngelis 2012).

A way in which the diversity of 'how possibly' explanations can be narrowed-down is to confront model predictions and model parameterisations with empirical data. The goal of the present paper is to highlight some relevant empirical observations from field studies of banded vegetation in the Australian drylands derived from more than 20 years of field monitoring and data collection, and to highlight ways in which these data suggest the need for numerical modelling of patterned vegetation that is more targeted to the properties of particular regional ecosystems. Regional ecosystems can be thought of as 'test cases', where model predictions can be judged against direct observation. In light of the importance of dryland environments, it is here argued that the search for understanding of particular ecosystems, with the capacity reliably to assess their vulnerability or resilience, should accompany the search for underlying general

explanations. These, if they exist, may well be subject to important local controls in particular environments or ecosystems, such as the particular physiology, phenology, and adaptations to water scarcity of key plant taxa.

The focus in the remainder of this paper is on banded vegetation, one of the most striking and extensive forms of PVP (Figure 1 and 2). In what follows, we begin by considering soil moisture and its temporal variation, since this is the critical resource for plant growth in drylands. This leads on to a discussion of how rainfall climatology and evapotranspiration

influence the accumulation of soil moisture. A series of related field observations bearing on patterned vegetation then follows: field evidence for pattern stability or migration, the role of clay mineralogy and soil development, fauna, and other influences commonly omitted from numerical models. The field data come from the drylands of far western New South Wales, Australia, where banded vegetation is widespread. Banded vegetation also occurs in adjoining parts of South Australia, including the Cockburn area (Figure 3).



Fig. 1. View downslope across Menindee banded vegetation. Trees on the horizon line an ephemeral stream

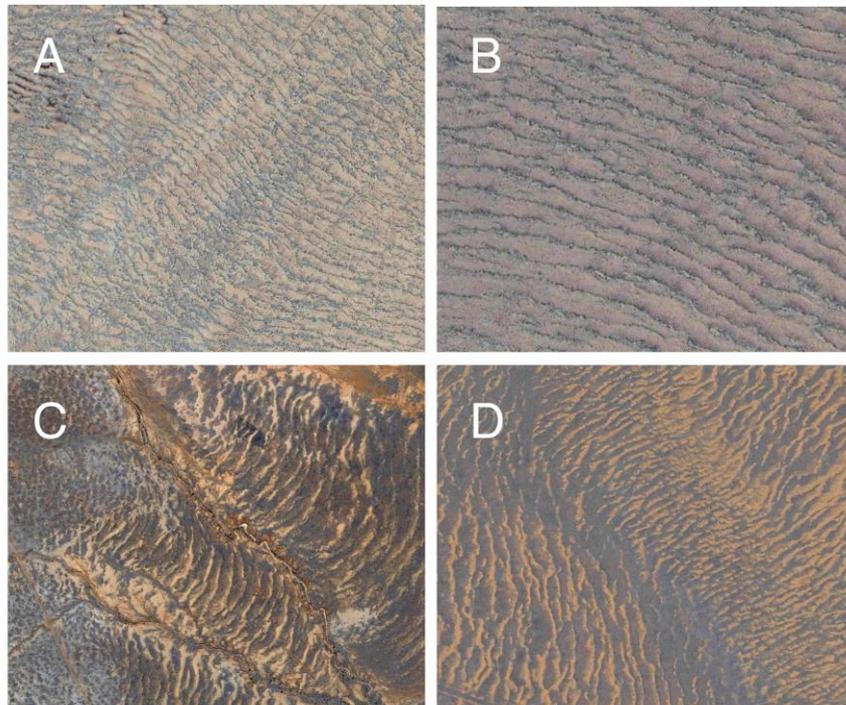


Fig. 2. Google Earth images of periodic vegetation patterns in western NSW and nearby South Australia. A. Cockburn area, SA. Width of image 1 km. B. Cockburn area, SA. Width of image 500 m. C. Fowlers Gap study site. Width of image 1 km. D. Menindee study site. Width of image 1 km

2. Materials and Methods

2.1. The field area – dryland western NSW

Observations in landscapes having striking banded vegetation were collected at two principal locations, the Fowlers Gap Arid Zone Research Station, located about 120 km north of the regional city of Broken Hill, and at a site about 40 km south-east of the city, in the direction of the town of Menindee. The two field study sites lie about 100 km apart (Figure 3). At Fowlers Gap, the banded vegetation occurs on a slope gradient of 0.5° , and is composed dominantly of small chenopod shrubs, including *Atriplex* and *Maireana* species (saltbushes and bluebushes) with some grasses, while the similarly sloping Menindee site is dominated by the perennial Mitchell grass (*Astrelba pectinata*) with some chenopod shrubs. *Atriplex vesicaria* has a shallow root system, interpreted as reflecting a typically shallow depth of soil wetting by rainfall (Jones

1969), and under grazing pressure, seed abundance and survival can be low (Hunt 2001). Depending on their size when drought commences, both *Atriplex vesicaria* and *Astrelba pectinata* can survive for some decades, though juvenile plants are more vulnerable than mature individuals, and may not survive severe drought (Hunt 2001, Orr & Phelps 2016). *Astrelba* species can respond rapidly to rainfall, and complete growth and seed production within six weeks (Wickens 1998). More evidence is needed of the effect of drought on long-lived shrubs and grasses, including the influence of drought timing, duration, and severity. In the case of Australian alpine grasses, Griffin & Hoffmann (2012) proposed that the season when drought occurs (especially in the case of summer drought) may be more important to plant survival than the drought duration. In the drylands, it may be that drought duration and severity are more important influences.

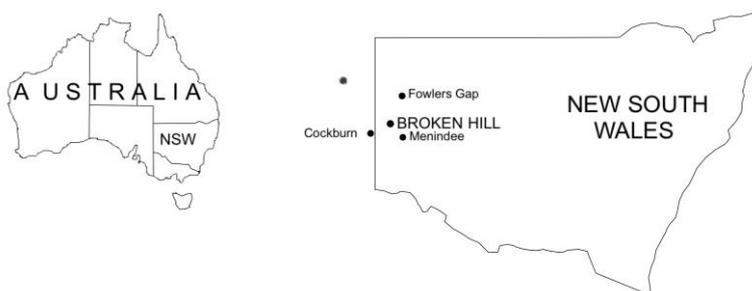


Fig. 3. Location map showing the study areas at Fowlers Gap and Menindee, in the far west of New South Wales, Australia

The average regional rainfall is about 220 mm, but there is a wide inter-annual variability, related to the El Niño – Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) phenomena; droughts are common (Verdon-Kidd & Kiem 2009). An annual rainfall close to the statistical mean annual rainfall does not occur very often; annual rainfalls are frequently significantly below or above the statistical average. The Millennium drought (van Dijk *et al.* 2013) affected the region from about 2001-2009, and ended with a period of above average rainfalls in 2010-2011. Rainfall conditions can be illustrated by 2006, a notably dry year, during which Fowlers Gap recorded 103 mm falling on 33 rain days; the largest daily amount was 17.8 mm. Following the drought, 2011 was a year of above-average rainfall at Fowlers Gap, when 526.2 mm fell on 65 rain days, the wettest recording 65.6 mm. This was undoubtedly sufficient to activate the runoff-runon system in this region, and may have resulted in integrated overland flow passing through multiple

wavelengths of the banded vegetation. In the last few years, drought conditions have returned, and in 2017, the yearly rainfall of 84.4 mm was lower than 2006 in the Millennium drought, falling over just 31 rain days, the wettest of which recorded 13.6 mm. These dry conditions have continued into 2018, such that in the year to the end of September, there were just 16 rain days, delivering a total of 13 mm, with a maximum daily amount of 3.2 mm. Undoubtedly, there has been no activation of the runoff-runon system regionally in 2018, and soils are very dry, with severe moisture stress. Drought conditions of this kind are a recurrent feature of the regional rainfall climatology. During the Federation drought of 1895-1902 (Ummenhofer *et al.* 2009) Broken Hill recorded rainfall of 91 mm in 1902, which is almost as dry as 2017. In 1940, during the ‘World War II’ drought, the yearly rainfall at Broken Hill was just 57.4 mm.

In the Broken Hill study area, summers are hot and dry, with daily maximum temperatures

often above 40° C. Streamflow is ephemeral, and the pastoral industry relies on the extraction of groundwater for stock watering. Sheep have been grazed on the unimproved native rangeland vegetation since the mid 19th Century. There are also native herbivores (kangaroos and related groups), as well as pest species including rabbits and goats, such that during droughts, the pressure on the surviving vegetation can result in severe overgrazing. The study sites have therefore experienced both periodic severe rainfall deficits and long-term grazing pressure. They consequently form a useful context for studying the vulnerability or resilience of banded vegetation.

Further details of the field sites can be found in Dunkerley & Brown (1995), Dunkerley (2002), and Dunkerley (2010).

2.2. Field methods

Long-term observations are needed to resolve ecosystem change, and therefore pairs of permanent benchmarks were established in 1995-1998, identifying the two endpoints of several transects 100 – 150 m in length spanning multiple wavelengths of the banded vegetation at both the Fowlers Gap and Menindee field sites. At intervals of a few years, soil moisture was recorded at 2 m intervals along these transects using an MP406 soil moisture sensor (ICT International). This device senses soil moisture only in the upper 6 cm of the soil, but Brutsaert (2014) has shown that root zone moisture generally correlates with surface soil moisture in the upper 5 cm or so. The unconfined compressive strength of the soils was determined at the same locations using a Proctor penetrometer. Bulk density was determined using the flexible-membrane method, with excavations of 0.3-0.5 L, and a needle gauge to set the pit water fill level accurately (Blake & Hartge 1986). Infiltrability of soils was estimated using cylinder infiltrometry (Bouwer 1986) with water level maintained with the aid of an electronic needle gauge, and lateral seepage correction as per Dunkerley (2000), or using rainfall simulation on small plots (Dunkerley 2012). Surveys of slope form and microtopography, and contour maps, were made with a laser total station. Repeat photography was collected from benchmarked photo points re-occupied every few years. At Fowlers Gap, high resolution rainfall data were collected using a 200 mm diameter tipping bucket rain gauge with 0.2 mm sensitivity, and a data logger that recorded the tip events using the Gregorian calendar, to the

nearest 1 sec (Dunkerley 2008). Official Australian Government monthly rainfall data for Broken Hill (<http://www.bom.gov.au/climate/data/>), where observations began in 1889, were also accessed to explore the longer-term record of droughts in the study area.

In evaluating what has been learned from the field observations, we first consider the field data on patterns of soil moisture in the banded vegetation landscapes, since soil moisture is the critical control on vegetation growth in the arid study landscapes. Patterns of soil moisture may reflect the operation of the runoff-runon mechanism, as well as moisture losses to evapotranspiration.

3. Results

3.1. Soil moisture patterns in banded vegetation, western NSW

In years when the runoff-runon systems have been activated (i.e., not drought years), the most prominent feature of the pattern of soil moisture within the banded vegetation is that the lowest soil moisture occurs in hard, dense, bare soils that are found in the lowermost intergroves, where, even after rain, the soil moisture can remain below 20% by volume, whilst groves have higher soil moisture in the range 30-35% (Figure 4). However, as Figure 4 shows, low soil moisture can also occur in the uppermost groves, where in fact it is generally reasoned that the highest soil moisture levels would arise from the absorption of runoff water. Depending on the time since rain, transpiration (and evaporation from the soil) can reduce the soil moisture. These ET losses are probably largest where the vegetation is most abundant (i.e., uppermost groves), despite the facilitative effects of plant clustering. Reduced soil moisture under denser vegetation cover has been reported (Yang *et al.* 2018), and seasonally reversing patterns of soil moisture between shrub sub-canopy and intercanopy spaces were reported by Li *et al.* (2010). At their desert field site in NW China, sub-canopy soils were wetter in April and May, but drier in June to September. Between the upslope and downslope grove margins at Fowlers Gap, soil moisture fluctuates erratically. At Menindee, similar but larger fluctuations are seen, and groves are often wettest near their upslope margin, and become drier toward their downslope margin (e.g. see Figure 2 in Dunkerley 2002). At least in days or years having sufficient rainfall to activate the runoff-runon system, therefore, observations at

both field sites are broadly consistent with the banded intergrove-grove patterned vegetation operating as a runoff-runon system through which the groves acquire higher levels of soil moisture. Soil moisture conditions have been

recorded during several droughts, and these are considered next in order to highlight the potential significance of ET losses from the banded ecosystems.

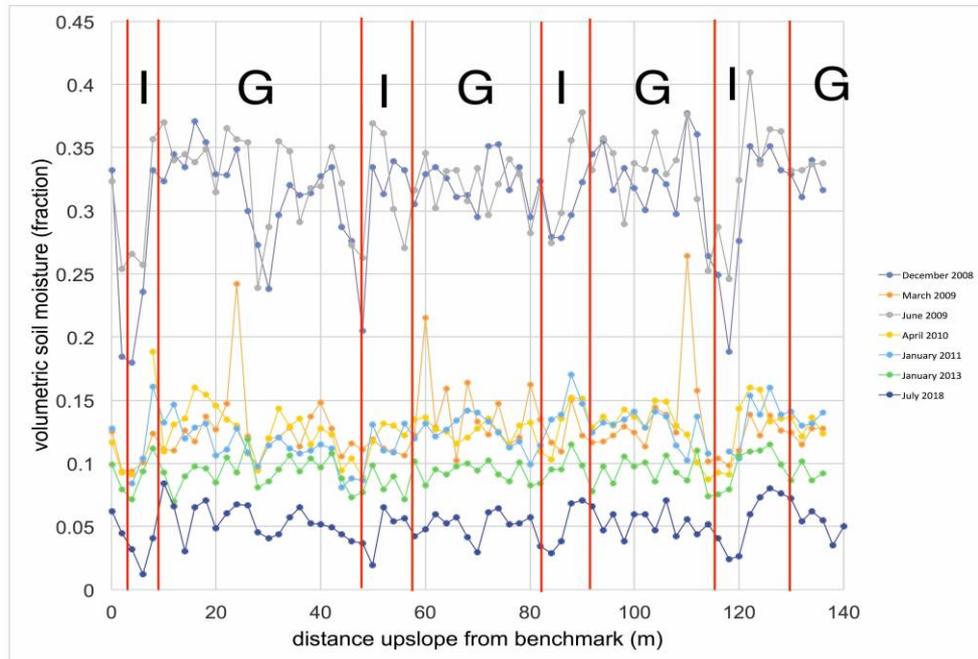


Fig. 4. Transects of soil moisture data collected at the Fowlers Gap field site from December 2008 to July 2018. Data were collected every 2 m along a permanently benchmarked transect. See text for details

3.1.1. Soil moisture patterns as affected by severe drought

At Fowlers Gap in July 2018, following more than 21 months of drought, soils were very dry, averaging ~ 5% soil moisture. The data of Figure 4 show that highest soil moisture levels were found in the mid-intergroves, reaching 8-9% by volume, but were drier in the lowermost intergroves or uppermost grove, at 1-2%. Remarkably, within groves, which are always modelled as being wetter than intergroves, the soil moisture in some places is lower than in the mid-intergroves, averaging only ~ 5%. At Menindee, the same feature was seen (data were collected in drought during July and again in October 2018): maximum soil moisture of ~ 10% was seen in the mid-intergroves, with lowest soil moisture of ~ 2-3% in the lowermost intergroves (Figure 5). Within the groves, soil moisture was lowest at the upslope margins (~4%), rising to a maximum at the downslope margins (~6%). These features are quite unexpected: highest soil moisture in the mid-intergroves (from which overland flow is shed), and rising soil moisture with distance

downslope through the groves are not incorporated in any models of patterned vegetation known to the writer. Since both field sites had experienced prolonged drought that was ongoing when these field observations were collected, the soil moisture patterns just described are reasoned to reflect residual soil moisture after prolonged soil evaporation (active transpiration by severely moisture-stressed vegetation having already ceased). The observed peaks of soil moisture in the intergroves are hypothesised to reflect limited bare soil evaporation through the dense, hard, and crusted soils there. Thin soil crusts have been shown to restrict vapour diffusion, limiting the reciprocal escape of air that is required to allow infiltration of water into the soil pore network (McIntyre 1958a, 1958b). Lower soil moisture in groves may reflect more rapid soil evaporation there, owing to the more friable and open-textured soils of the groves. Much of the soil evaporation is likely to have been slow phase 3 evaporation, which is governed by upward vapour transport from wetter subsoils to the uppermost soil layers (top few cm) from which the vapour is lost to the atmosphere from

the soil pore system (Haghighi 2017, Quinn 2018). The presence of root and biological macropores within grove soils may assist in upward vapour transport, but to the writer's knowledge, this possibility has not been investigated. The important point, however, is that during severe drought, the uppermost groves are drier than the lower groves, and hence plants in the upper grove face more severe moisture stress. In this way, droughts may result in the death of plants that might have colonised the uppermost groves, and in so doing, mitigate against the upslope migration of groves that is suggested by many numerical models of banded vegetation (Lefever & Lejeune 1997). Most models presume that plants at the downslope margins of groves are those which suffer the greatest moisture stress

and consequent mortality. The pattern of soil moisture reported here, however, also appears to reduce the likelihood of the death of plants in the lowermost groves, which is almost universally incorporated into models of banded vegetation. Since the soil moisture patterns in droughts just described have not to the best of the writer's knowledge previously been reported, this finding may assist in the more complete modelling of banded vegetation. If indeed plant death occurs upslope, and plant survival downslope in groves, this may help to account for the lack of upslope migration seen in models that do not adequately incorporate the consequences of drought and grove-intergrove differences in soil evaporation for plant survival.

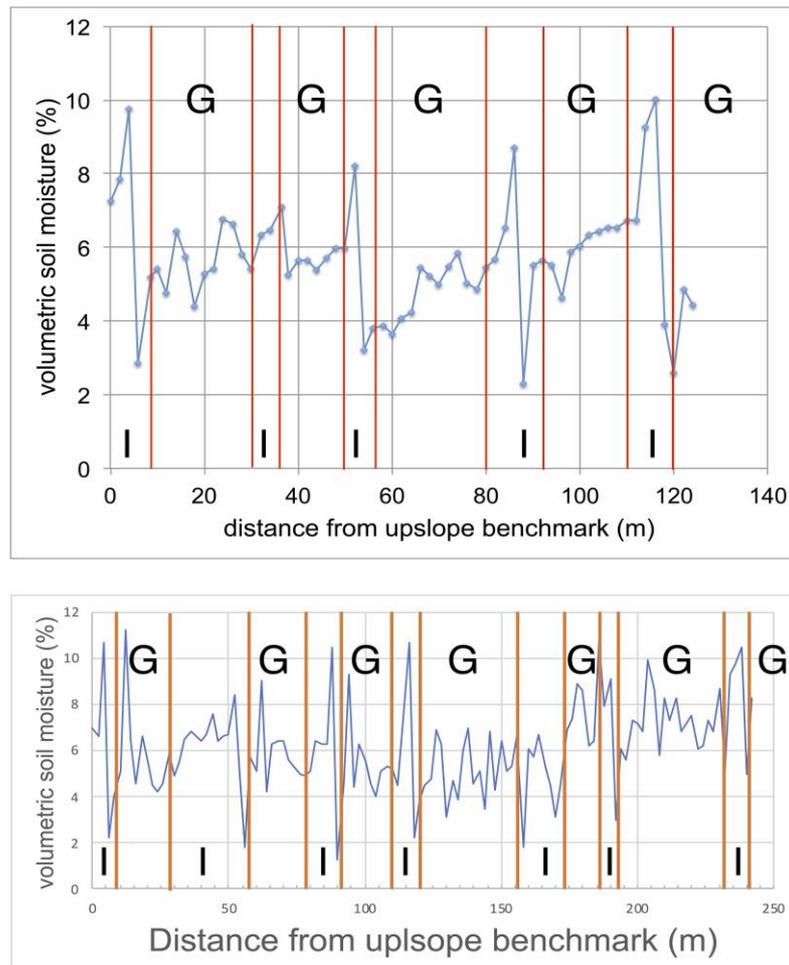


Fig. 5. Transects of soil moisture data collected at the Menindee field site. Upper: detail of transect showing data collected in July 2018. Lower: full transect showing data collected in October 2018, two weeks after a fall of 34 mm of rain. See text for details

Figure 6 shows part of the Menindee field site following a period of rain. Greening of the upslope margins of the groves is evident, with little runoff apparently having reached the lower groves. However, it is also evident that plants

growing at the extreme upslope edges of the groves are not green and actively growing. Thus, even when the runoff-runon system has clearly been active, the upper edge of the groves is not a favourable location for plant growth. It

may be that at the extreme edge of the grove, root access to moisture upslope is reduced by the adjacent dry and hard soils of the lowermost

intergrove, whilst plants within the grove can access moisture in all radial directions.



Fig. 6. Photo showing upper edge of a grove of Mitchell grass at the Menindee field site. Photo taken after a rainfall event that delivered water to the upper grove, but which was insufficient to reach the lower groves. Downslope is to the right of the image

3.2. Rainfall and its influence on the PVPs

The soil moisture data of Figure 4 show that there are wide temporal variations in soil moisture levels, attributable to the frequency with which rainfall sufficient to activate the runoff-runon system occurs, and to the lengths of intervening rainless periods when transpiration and bare soil evaporation progressively reduce soil moisture. It is appropriate therefore to consider the temporal occurrence of rainfall in the banded vegetation in more detail.

In many models seeking to understand banded vegetation, rainfall is taken to be constant at a rate that is typically ~ 1 mm/day, with no seasonal or inter-annual variation (Rietkerk *et al.* 2002, Esteban & Fairen 2006, Thiery *et al.* 1995, Lejeune & Tlidi 1999, Thompson *et al.* 2008, Ursino & Callegaro 2016, Roitberg & Shoshany 2017). The neglect of rainfall variability in time is justified on the basis of the observation that banded vegetation pattern geometry does not change dramatically over time periods of one or a few years. This is reasoned (e.g. Foti & Ramirez 2013) to indicate that the vegetation patterns are adapted to the long-term average characteristics of the soil-climate system. However, D'Odorico *et al.* (2006, 2007) have shown that the changing temporal occurrence of rainfall is important to patterned systems, including the seasonality of rainfall. Intermittency effects have also been explored by Kletter *et al.* (2009). D'Odorico *et al.* (2015) have moreover argued that climatic fluctuations are in fact of critical importance,

and result in a form of 'noise-induced stability', tending to hold the patterned vegetation in a state intermediate between bare and fully vegetated. Importantly, they reasoned that this mechanism results in a diminished probability of a catastrophic shift to full desert conditions. In related work, Cueto-Felgueroso *et al.* (2015) explored the role of inter-storm waiting times, which allow soils to dry out, as well as related aspects of the temporal arrival of rainfall. They concluded that to understand the temporal evolution of plant biomass it is necessary to consider both aggregate amounts of precipitation and the patterns of inter- and intra-annual rainfall variability. The latter may of course alter under climate change, and so influence the likelihood of wholesale ecosystem shifts.

These studies suggest that reliance of models on a constant annual rainfall may be overlooking important ecosystem processes. This conclusion also arises from the empirical soil moisture data presented above, which showed previously undescribed soil moisture patterns attributable to severe drought. These are times when there is an increased risk of plant mortality, which may be probably event at the uppermost groves (Figure 6). This bears on the issue of upslope migration of banded patterns, considered below. Because scenarios of future rainfall in a warmer world suggest the more frequent occurrence of intense rainfalls (Trenberth 2011), and the likelihood that these may activate the runoff-runon system more often, it becomes necessary to consider the nature of dryland rainfall events. Understanding

the origin of PVPs under presumed conditions of fixed annual rainfall appears not to be an adequate basis for identifying risks of catastrophic ecosystem shifts, not least because changes in climate might in fact prove to be beneficial to these ecosystems, rather than detrimental. In addition, CO₂ fertilisation and other effects need to be considered when evaluating the risks faced by particular ecosystems (Lu *et al.* 2016).

Small showers, especially if of low intensity, are entirely absorbed by even intergrove soils, or lost to evaporation. They generate no overland flow, and hence do not benefit the groves. It has been argued that small falls might in fact deliver more soil moisture to intergroves than to groves, since intergroves lose little or nothing to canopy and litter interception. On the other hand, it is possible that large falls generate sufficient runoff to yield integrated overland flow able to pass through one or more groves. If so, their contribution to soil moisture in individual groves may be proportionally less than in smaller rainfalls which may be entirely captured within a single wavelength of the runoff-runon system. Additionally, wet years or large individual periods of rain (over multiple days) may be sufficient to supply all plant water needs, and thus eliminate – and mask – any facilitative effects of groves, such as sheltering and shading (Cipriotti & Aguiar 2015). Equally, it could be argued that extremely dry periods such as prolonged droughts, when root zone soil moisture is effectively unavailable (recall the 2018 soil moisture patterns, presented above), eliminate any competitive interactions of plants via laterally extended root systems, since little soil moisture is available, and plant growth may be suppressed across entire landscapes (Barbier *et al.* 2008). This conceptual analysis suggests that groves may garner more water than intergroves principally from events of some limited range of rainfalls of intermediate size, sufficient to generate downslope-directed overland flow from intergrove to adjacent grove, but not sufficiently large to result in integrated downslope flow crossing multiple grove-intergrove cycles, and not so small that the rainfall is fully absorbed everywhere. The consequent masking of facilitative or competitive plant interactions would have both a temporal variability (wet and dry years; ENSO cycles) and a spatial variability (such as contrasting soil water distributions between phases of the vegetation mosaic, such as upper grove or lower intergrove). Just what the range of grove-supporting rainfall characteristics is remains unclear. As noted previously, many

authors attempt to relate properties of patterned vegetation such as band wavelength, to mean annual rainfall, but in light of the foregoing, this may sacrifice important details of ecosystem processes that are needed to forecast outcomes in a warmer future climate.

3.2.1. *Effects of wet and dry years on the character of rainfall events*

A full representation of rainfall pulses as typically occur in drylands has not to date been included in models of banded vegetation. Both rainfall event characteristics, such as depth and intensity, and the nature of the dry waiting periods between rainfalls, are important. For Fowlers Gap, Dunkerley (2008) reported that dry intervals between rainfall events averaged 9.6 days but extended to a maximum of almost 102 days (~ 3 months). As will be shown below, there is evidence that longer-term variations in rainfall, related to ENSO and IOD cycles and the sequence of wet and dry years, also influence the functioning of banded vegetation.

Dunkerley (2013) explored the nature of rainfall events in wet and dry years at Fowlers Gap. This showed that small rainfall events (< 2 mm) are common in all years, but that events are on average larger and more intense in wet years. The major cause of the difference in event averages is that wet years exhibit a small number of very large events (> 60 mm) which were not experienced at all in dry years during the >10 years of data analysed (2002-2012). An additional difference was seen in the intensity profile of rainfall events. More Q1 events were seen in dry years than in wet, and these are associated with infiltration rather than runoff (Dunkerley 2012). In wet years, the proportion of Q3 events is larger, and these are associated with less infiltration and more partitioning into surface runoff. Among rainfall events, the 90th percentile of rainfall rate was 8.3 mm/h during dry years, but 13.3 mm/h (60% larger) during wet years. Given that intergrove infiltration rates, estimated using low-intensity simulated rainfall on small plots, are 7-10 mm/h (Dunkerley 2012), many small and low-intensity rainfall events can be absorbed without activating the runoff-runon system. In events with average intensities > 10 mm, the runoff-runon system becomes active, especially during and after short intensity bursts which may only last for 5 – 20 minutes or so. These bursts can be an order of magnitude more intense than the mean intensity of the enclosing event, and can hence generate runoff within groves that would otherwise not occur.

It is apparent that both rainfall event properties, and the infiltrability of the soils, influence the operation of the runoff-runon system. Dunkerley (2002) showed that within groves at Menindee, infiltrability reached almost 70 mm/h, though importantly the maximum value was seen not at the upper margin of the grove, but at about 5-7 m into the grove, that is, about 0.3 of the total width of a grove from upslope to downslope margins. Similarly, at Fowlers Gap infiltrability within groves has been measured by cylinder infiltrometry, with rates generally in the range 30-45 mm/h. Of course, the peak in soil infiltrability does not necessarily indicate the location of the peak in actual water uptake within groves. Rather, accumulated soil moisture depends on the frequency with which

overland flow actually reached the 0.3 distance or other location within a grove. However, high infiltrability values like those just noted would ensure that most rainfall arriving at the soil surface within a grove would be absorbed there. Likewise, shallow overland flow would be delayed in transit across both intergrove and grove, and arrive at locations inside a grove sometime after the intense rainfall that triggered it, or even as afterflow once rain had ceased. In that situation, the infiltrability of groves would probably be sufficiently high to absorb the runoff water (Figure 7). More field data are required to document the conditions under which integrated overland flow occurs, passing through multiple wavelengths of the runoff-runon system, rather than being trapped within the grove immediately downslope.



Fig. 7. Two views taken looking upslope at the Fowlers Gap field site, showing intergrove runoff being absorbed as runoff within chenopod shrub groves. Upper: intergrove and grove boundaries, with flow direction marked. Lower: view of runoff-runon in a second part of the Fowlers Gap field site. Note ponding in intergrove but absence of ponding in the grove, where higher infiltrability is shown

3.3. Absence of upslope migration of the vegetation bands

Most numerical models of banded vegetation predict that the groves move incrementally

upslope, as a result of a presumed abundant moisture supply to the upslope margin of the grove and moisture stress toward the downslope edge. Infiltration near the upslope grove border is reasoned to facilitate plant establishment, and

by widening the grove, this in turn limits the water reaching the downslope margins, where plant cover is progressively lost.

As Deblauwe *et al.* (2012) noted, the issue of upslope migration remains incompletely resolved; whilst numerical models frequently exhibit upslope migration (e.g. Esteban & Fairen 2006), field evidence to support this claim remains scarce and equivocal. Klausmeier (1999) reported model predictions of upslope migration at rates of 0.4-0.6 m/a (for trees) and 1.4-1.9 m/a (for grasses); however, his model relied on an unvarying rainfall of 300 mm/a making these results problematic to apply to any actual dryland ecosystem. Consolo *et al.* (2017) predicted upslope band migration at rates of 0.5-1.6 m/a, but in a model that neglects the temporal variability of rainfall. Deblauwe *et al.* (2012) reported multi-decade mean rates judged from repeat imagery at three locations in the range 0.2 – 0.8 m/a. Chappell *et al.* (1999) inferred rates of 0.19 – 0.27 m/a for banded vegetation in Niger. In a study of the fragmentation of banded vegetation in Niger in the period 1960-1992, Wu *et al.* (2000) attributed loss of vegetation cover to the growing human population, with associated pressures from grazing and firewood collection. Whilst they were able to show patchy loss of vegetation, they only located very minor instances where new colonisation had occurred, and no overall upslope migration of entire vegetation bands.

In contrast, the permanent monuments at upslope grove margins at the Menindee site have been monitored for 23 years, with repeat survey of grove-intergrove boundaries and photo points re-occupied opportunistically during that time (Figure 8). Though the photographs show major fluctuations in vegetation cover, vigour and greenness, they show no detectable net shift in the grove-intergrove boundary position, and this is confirmed by surveys along the transects of groves at this site (Figure 9). The few shifts in boundary location evident in Figure 9 reflect the scant vegetation cover remaining in parts of the drought-affected landscape, and the resulting difficulty in defining grove margin positions, and especially lower grove margins, where the individual plants become widely scattered. During very high rainfall years, the Menindee site has shown an extensive cover of ephemeral plants within normally bare intergroves (Figure

10). However, when dry conditions return, these ephemerals are lost, and bare intergrove conditions become re-established, without any shift in the grove-intergrove boundaries. Likewise, despite the occurrence of La Lina years with above-average rainfall, there has been no upslope expansion of the groves.

The pattern stability recorded at Menindee is striking, because as noted above, this area experiences a strong ENSO influence, with rainfalls both well above and well below the long-term mean, and prolonged and repeated droughts; it has also been grazed by stock for more than 150 years. Local residents have reported (pers. comm.) that the vegetation is resilient and becomes re-established even after severe drought.

The Menindee field evidence is not consistent with the kinds of model upslope migration rates listed previously, since those rates would require that the grove margin had shifted upslope by at least 5 - 15 m during the 23 years of direct observation. The results presented above concerning the effects of drought on soil moisture (which yield a pattern that is the reverse of what is commonly assumed) provide a partial explanation for the observation that upslope pattern migration does not occur at Menindee. Soil properties, considered shortly, also mitigate against upslope migration. Without further evidence, this result cannot be generalised to the different field conditions at other banded vegetation sites beyond the Broken Hill region. However, there are other field studies that have reported stable, non-migrating banded vegetation. For instance, Coueron *et al.* (2000) reported stable patterns in Niger and Burkina-Faso (W Africa), and offered some hypotheses accounting for the stable patterns. Since the lack of upslope migration at Menindee and the W African sites contrasts with the relatively fast movement predicted by many numerical models, these models may also incorrectly represent other aspects of the PVPs, such as their resilience. Importantly, if the groves do not move, then soil differentiation between intergroves and groves can be cumulative through time. The density and hardness of lowermost intergroves, for example (discussed in the following section) can increase with time, providing another factor reducing the probability of upslope migration of groves.



Fig. 8. Time series of photos of a benchmarked grove boundary at the Menindee field site, from 1995 to 2018. Note changes in vigour of the vegetation but no apparent movement of the grove-intergrove boundary. Flow direction is shown. Two photos from 2018 indicate effects of grazing stock between date of bottom left photo (July 2018) and bottom right photo (October 2018)

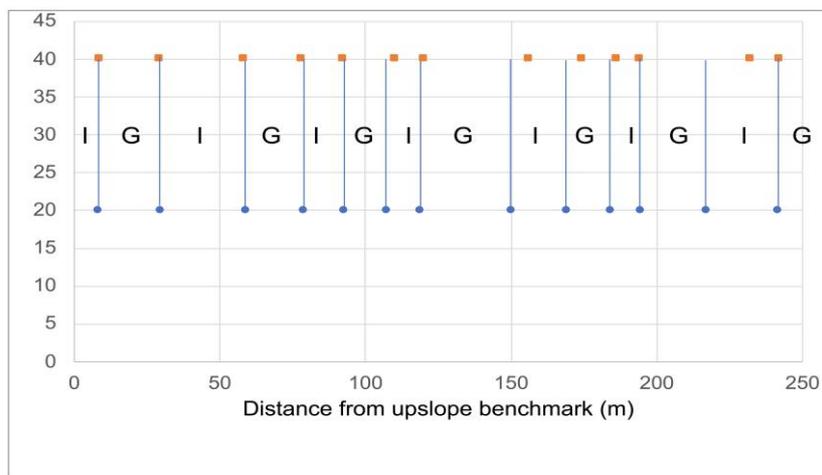


Fig. 9. Locations of grove and intergrove boundaries on a permanently benchmarked transect of 240 m, at the Menindee field site. Positions shown were surveyed in 2001 (lower data points) and 2018 (upper data points). Lines marking the boundary positions in 2001 are extended upward for comparison with the 2018 data. See text for details



Fig. 10. View along the contour at the Menindee field site (downslope is to the right). Photo taken in 1999 when conditions were sufficiently wet for the normally bare intergroves to be infilled by ephemeral plants (these are green; the Mitchell grass groves are a pale buff colour)

3.4. Pedologic development in the banded vegetation

In their investigation of banded mulga in Western Australia, Mabbutt & Fanning (1987) showed that hardpan occurred at a greater depth beneath groves than beneath intergroves, and interpreted this to indicate that the groves and intergroves had been in their current positions for sufficiently long for this pedologic differentiation to develop (possibly since the late Quaternary). Dunkerley (2002) reported higher bulk density in lower intergrove soils ($> 1.7 \text{ g/cm}^3$) than in grove soils (1.2 g/cm^3). Replicate determinations in lower intergrove and grove yielded mean and standard deviation values of 1.7 (std dev 0.23, $n=10$) (intergrove) and 1.3 (std dev 0.09, $n=10$) (grove). Correspondingly, the unconfined compressive strength was extremely high in lower intergroves ($> 2000 \text{ kPa}$) but much weaker soils within groves (200-500 kPa). Such dense and mechanically strong soils offer sufficient resistance to slow or prevented root extension altogether (Kirby & Bengough 2002, Clark *et al.* 2003). A likely explanation for the high strength of lower intergrove soils is that a subtle microtopography is associated with banded vegetation, presumed to result when overland flow slows and ponds on the lower intergroves, before the local slope steepens into the uppermost grove. As a result of infiltration and eventual drying-out of those ephemeral ponds, it is hypothesised that dissolved salts including carbonates, as well as translocated clays, enter the soils there. Having been precipitated within the soils, these materials both increase the bulk density and the mechanical strength of the soils. The soil shear strength is so high that it is frequently extremely difficult to embed even the

sharp metal prongs of soil moisture probes. Within groves, the larger flux of infiltrating runoff water seems likely to carry any dissolved salts to greater depths within the soil, especially during large rainfall events.

3.5. Obliquity, not contour-parallelism, of some band orientations

On the basis of field mapping using a laser theodolite, the writer has described vegetation banding from the Menindee field site that is not aligned with the contour, but oblique to the slope (Dunkerley & Brown 2002). The mean angle of divergence of band margins from the topographic contour lay in the range 15° - 40° . A regional tendency to oblique band orientation was confirmed by Deblauwe (pers. comm. 2012), using remotely-sensed data on band orientation and slope direction. The presence of oblique vegetation banding is as yet unexplained. At their Menindee site, Dunkerley & Brown (2002) reported that the relative widths of intergrove and grove differed among local instances of contour-aligned banding and oblique banding, developed under the same climate (this can be seen in Figure 2). These findings suggest that an additional factor or factors exerts a major influence on band orientation. More importantly, it suggests that the hydrology of oblique banding is sufficient to maintain these regular features, and that contour-parallelism is not a requirement for banded vegetation to persist within the landscape. It would be expected, for instance, that runoff water draining orthogonally to the contour would be deflected at the oblique upslope grove margins, perhaps to drain obliquely downslope there, with implications for seed, organic matter and sediment transport,

and perhaps affecting the movement of water from intergrove to grove. Berg & Dunkerley (2004) also reported oblique vegetation banding in mulga woodlands in the Northern Territory, Australia. Given the very low slope gradients characteristic of sites carrying banded vegetation (0.2° - 0.5° , Dunkerley & Brown 1995, Dunkerley & Brown 1999), additional precise ground surveys appear necessary to further explore the occurrence of oblique vegetation banding. Since the origin of such features remains unexplained, it is difficult to evaluate the likely vulnerability of these landscapes to climate change and ecosystem shifts.

3.6. The role of clay mineralogy and bedrock composition on hydrology of the PVPs

Mabbutt & Fanning (1987) showed that mulga (*Acacia aneura*) band dimensions in Western Australia varied with underlying bedrock lithology. Though this has not been further explored, it presumably reflects differences in regolith and soil properties driven by the underlying bedrock. A further instance of the role of soil properties was reported by Dunkerley & Brown (1995) and Dunkerley (2013), who reported that soil collapse features locally known as ‘crabholes’ (see Figure 11 and Upton 1983) were abundant within vegetation groves at Fowlers Gap, but completely absent from intergroves. These features are reasoned to operate as follows. Subsoils have a high content of illite-family clay minerals, which shrink when dry. Thus, during prolonged droughts, the

subsoil materials contract and surface soil material falls into the resulting cracks, so opening crabholes to the surface. At the same time, the vegetation cover declines owing to drought, which would otherwise enhance overland flow when rain occurred. Crabholes close and the soil surface heals during runs of years with adequate rainfall, presumably by erosion of the friable soil materials, and splash transport of surrounding soil into the crabhole pits. Scattered throughout the groves during major drought, the crabholes are runoff, seed, and sediment traps when overland flow does occur, perhaps during rare thunderstorm rainfalls. In this way, through the periodic occurrence of drought (often linked to the ENSO phenomenon), soil behaviour enhances the runoff trap efficiency within groves. Dunkerley (2014) explored this is a simple cellular automaton model and showed that the presence of crabholes results in a smaller decline in vegetation cover during droughts than when the same rainfall conditions are applied to a landscape lacking crabholes. This is another instance of the potential for characteristics of the local climate, including the occurrence of runs of dry years, to interact with local landscape and soil conditions, in ways that may be important to the development (and resilience) of vegetation patterning. Phenomena such as this cannot be captured when only mean annual rainfalls are used in attempts to understand the variation in vegetation patterning, or when the clay mineralogy of soils, with consequences such as cracking or crabhole formation, are overlooked.



Fig. 11. Photos of typical soil collapse pipes (‘crabholes’) that are found within the vegetation groves at both field sites after prolonged dry conditions, or after recent rain. These features promote the trapping of overland flow shed from intergroves upslope

3.7. *The role of fauna and their effect on trapping of overland flow within the PVPs*

Numerical modelling has to date focussed on the influence of vegetation on the surface hydrology of PVPs. Relatively neglected influences include the roles of fauna: ants, termites, mammals, marsupials, and other groups (Eldridge *et al.* 2001). Whitford (1998) showed that in Australian banded mulga landscapes, shallow foraging pits dug by goannas (*Varanus spp.*) were most numerous in the interception zone just upslope of the mulga groves, and contributed to the trapping of water, seeds, and sediment in that phase of the vegetation mosaic. Though detailed hydrologic effects were not investigated, Berg & Dunkerley (2004) reported that termite activity was more abundant in intergroves than within groves, in banded mulga woodland in the Northern Territory, Australia. In their study area NW of Alice Springs, intergroves were not unvegetated but rather carried a dense cover of grasses. In this area, there were also abundant ant nests which, by providing infiltration pathways into the deeper soil, seem likely also to be involved in the hydrology of the patterned vegetation.

In the specific case of spotted patterns in dryland vegetation, Bonachela *et al.* (2015) proposed that termite activity resulted in increased robustness of dryland ecosystems to climate change, by creating favourable habitats. This view has been further explored by Tarnita *et al.* (2017), in a model of patterned vegetation that included both the facilitative effects of plants and the role of termites and perhaps other territorial animals in creating the regular divisions of the landscape. The effects of biota through burrowing and macropore creation are presumably specific to individual banded vegetation landscapes; their importance to pattern evolution remains an area in need of additional study.

3.8. *Persistence of enhanced infiltrability following loss of plant cover*

Many models estimate soil infiltrability from plant cover or biomass, since it is known that vegetated soils develop better structure and greater porosity. The enhancement of infiltrability can extend beyond the limits of the plant canopy, into the surrounding interspace (Dunkerley 2000). However, it is not clear how rapidly infiltrability declines through time when the vegetation becomes dormant or dies. At the Fowlers Gap and Menindee field sites, much of the vegetation remains during drought, even

though some plants are either dormant or dead. Woody shrubs may take many years to decay, and hence the effects of the root systems, and of porous shrub mounds (Ravi *et al.* 2007), which are widely developed at Fowlers Gap, will persist in the landscape (Daryanto *et al.* 2012). Soulard *et al.* (2013) noted that shrub mounds persisted even after fire in shrublands of dryland Arizona. Although they found evidence of mound erosion in the short term, the longer-term fate of the mounds was not resolved. Persistence of plant parts and/or shrub mounds suggests that, when modelled rainfall is too low to support plant growth, and the modelled biomass-dependent infiltrability is reduced (e.g. Saco *et al.* 2007) it may in fact remain elevated until the rainfall increases in subsequent years. Correctly modelling the decline in infiltrability requires knowledge of the rate of vegetation decomposition, and this may differ between the aboveground and root system components. Coefficients are used in some models (e.g. Saco *et al.* 2007) to express the rate of biomass loss, but no models, to the writer's knowledge, consider above and belowground components separately, nor do any employ field data to parameterise biomass loss coefficients.

There are no available empirical data on the rates of root decay in the study area. However, using buried litter bags in the Chihuahuan Desert in New Mexico, Kemp *et al.* (2003) found that root material only lost 20% of its mass in 3-4 years. For the Negev, Steinberger *et al.* (1995) estimated that the time required for 95% loss of root mass was 15.9 years. These slow rates of mass loss (presumably extended further during drought conditions) suggest that soil porosity and infiltrability could be maintained through even a long drought. This raises uncertainty about the validity of models in which living plant biomass is linked to infiltrability (e.g. HilleRisLambers *et al.* 2001) or in which biomass loss is adjusted in steps, such as annually (the time-step used for rainfall in most models), and then determines the estimated infiltrability of the model cell where vegetation cover has declined (e.g. Esteban & Fairen 2006). Furthermore, Steinberger *et al.* (1995) suggested that root decomposition was slower in the Negev, owing to a lack of termite activity, than in the Chihuahuan Desert, where termites were important. This observation again suggests that a single model of the change in soil infiltrability after plant death will not be applicable to all banded vegetation ecosystems, and that instead, predictions of resilience will need to be based on local, site-specific process knowledge. In the context of future climates,

much remains to be learned about how root systems may respond. However, a suggestion has been made from rain exclusion experiments, that a moderate decline in rainfall may result in an increase in the extent of root systems, as plants seek to maximise available water (Padilla *et al.* 2015). No such effects have been incorporated in models that foreshadow PVP regime shifts in response to future climate change, but it seems likely that this is overlooking another ecosystem mechanism that might well bear on the issue of resilience or vulnerability to catastrophic change.

4. Discussion: Banded vegetation, drought, and resilience or vulnerability under future climate change

It was noted above that some authors view the occurrence of patterned vegetation as a signal of vegetation stress, and on the basis of numerical models, have foreshadowed that rapid collapse PVPs is possible under future climate change (Rietkerk *et al.* 2004, Mayor *et al.* 2013, Kéfi *et al.* 2007, Kéfi *et al.* 2014). In light of the evident robustness of the PVPs in the Broken Hill district, two questions then arise. Are the numerical models of banded ecosystem behaviour sufficiently developed to allow confidence in forecasts that there is a risk of regime change and ecosystem collapse? Are the available descriptions of possible future climatic conditions, and of vegetation responses to them, adequate for application to scenario modelling of PVPs?

Future environmental conditions will include higher levels of atmospheric CO₂, and the consequences of this were explored by Kéfi *et al.* (2008). However, their model did not consider any particular plant taxa, and only employed annual rainfall. Kéfi *et al.* (2014) pointed to the lack of empirical data to validate measures of pattern change that might be linked to a trend toward desertification, while Zelnik *et al.* (2013) showed that different classes of model dealing with patterned vegetation, with different parameterisations of key drivers and feedbacks, differ in their responses to climatic change. The difficulty, in light of the need for site-specific conditions to be reflected in model structure, is that most models are not process-oriented. Rather, they express processes in probabilistic terms, assigning a likelihood to the colonisation of bare area as a function of the extent of unvegetated surface upslope, or the likelihood of plant survival as a function of the density of surrounding vegetation. Weissmann *et al.* (2017) have demonstrated both positive

and negative feedbacks related to vegetation abundance, in a remote-sensing study of a large area of the Sahel, and it is evident that detailed ecological study is needed to understand the dynamics of biomass in particular landscapes.

As noted above, few models of PVPs include realistic parameterisations of rainfall. Most assume a constant daily rainfall, frequently of about 1 mm/d, to represent semi-arid conditions. Some have explored the effects of drought in numerical models, but with many generalisations and assumptions whose bearing on the model results is not straightforward to assess. For instance, Konings *et al.* (2011) used simplifications that include all rainfall events being of 2 h duration, no rainfall at night, and droughts in which the rainfall declines more-or-less monotonically in each year of modelled 10 year droughts. Realistic annual fluctuations in rainfall during droughts were not included. In their model, the soil infiltrability was taken to be proportional not to biomass but to the amount of surface water, estimated as rainfall minus ET and seepage losses. Ancillary influences such as the effects of soil crusts on soil evaporation were not incorporated, and the particular plant physiology for the taxa present in the field (e.g. root characteristics, physiological adaptations to drought) were not represented. Models of this kind seem likely to fail when applied to any actual ecosystem, such as the Menindee or W African sites referred to earlier, and to be insufficient for judging vulnerability of PVPs under scenarios of future climate change.

Limited modelling has suggested that rainfall intermittency may enhance vegetation resilience (Kletter *et al.* 2009), and analyses of the temporal structure of rainfall events, including the distributions of dry intervals between rainfall, have suggested that the temporal structure exerts a stronger influence on the soil moisture-vegetation system than does the mean precipitation rate (Cueto-Felgueroso *et al.* 2015, Zhang *et al.* 2016). Likewise, Puigdefabregas (2005) showed that in patterned drylands, the temporal variation of rainfall intensity during storms exerts a dominant influence on runoff lengths and patterns of runoff infiltration. Scenarios of future climate remain divided about how an invigorated hydrological cycle will affect annual or seasonal rainfalls. The Clausius-Clapeyron scaling is evidently not achieved at higher temperatures if moisture availability is limiting (Skirris *et al.* 2016), as it is likely to be in patterned drylands. Moreover, there are no securely-based estimates of probably future changes in the temporal patterns

of dryland precipitation, such as the amount of rain per event, event duration and intensity, or the rainless waiting time between events. Ecological data suggest that the duration of moisture pulses is critical to ecosystem response (Ratajczak *et al.* 2017), and field studies suggest that rainfall intensity and amount are both influential in the runoff-runon system, differing for instance between frontal and convective rainfalls (Magliano *et al.* 2015). In locations such as the study sites discussed here, the operation of the ENSO and IOD mechanisms under future climatic conditions remains unresolved. This casts considerable doubt over forecasts of ecosystem collapse or of major regime shifts in the banded vegetation, whose continued existence and striking geometric regularity argue for resilience rather than vulnerability.

How important is it to incorporate fuller rainfall climatology in models of PVPs?

Because many models of dryland PVPs neglect many of the distinctive aspects of the climatology of dryland rainfalls, it is worth considering whether this is an important limitation on the confidence that can be placed in the models, and particularly their application to forecasts of future resilience or vulnerability of PVPs.

Interannual rainfall fluctuations are a prominent feature of most locations where PVPs have been described, and are especially large in some locations, such as the field sites discussed here, because of the influence of various teleconnection mechanisms such as ENSO and IOD. The occurrence of drought, including multi-year drought, is a related phenomenon. These aspects of rainfall climatology are undoubtedly ecologically important, with increased plant mortality occurring in extended periods of soil moisture restriction. Just how important this is to pattern evolution and maintenance awaits proper field-based monitoring. At finer temporal scales, the intensity and duration of falls of rain, and their internal intensity profile, are known to affect the partitioning of water at the soil surface, and hence the ecologically-important flux of overland flow from intergrove to grove. However, here again, we lack the observational data that would be needed to link the water balance of groves to the detailed event-scale aspects of rainfall climatology.

This situation presents a challenge for model validation that needs to be addressed. Validation is a complex and much-debated issue in ecological modelling (Power 1993, Ryliel 1996, Augusiak *et al.* 2014). Certainly, models based

on an unvarying annual rainfall are capable of generating emergent PVPs, and in that sense, a kind of model validation can be based on the assessment of this ability against empirical data on PVPs. The problem for a validation of such models in process terms, however, is that there are no dryland PVPs in locations with unvarying annual rainfall, so that the ecological components of models cannot be validated against any field data. In the absence of this kind of validation, there is a likelihood that these models only suggest a group of 'how possibly' explanations for environments that do not occur in any actual ecosystem. More importantly, how adequately such models might capture the influence on PVPs of prolonged, severe drought or the changed rainfall in a future warmer world consequently remains an open question. As argued here, evaluations of these aspects of model performance would need to be set within the context of a specific ecosystem, because the sensitivity of plants to drought or rainfall occurrence varies among the grasses, shrubs, or trees making up particular regional instances of PVPs. Importantly, forecasts of the future resilience or vulnerability of PVPs under climate change and landuse pressure go beyond the simple capacity to 'nowcast' the morphology of PVPs, and in principle require a much more complete basis in ecological and ecohydrological processes.

In summary, uncertainty must remain about the validity of conclusions drawn from models of PVPs that rely on unvarying annual rainfalls. These models must be formally validated, and either accepted or refined in light of the outcomes of the validation process. It is argued here that the challenge for the research community is to set such validation in the context of empirical data on real regional instances of PVPs, since soil, rainfall, and ecosystem character vary significantly among global PVPs. Ecological and environmental data, and observations of the dynamics of PVPs through many years, will be required for model testing and evaluation. This is both a significant challenge, but also an opportunity to link the potential power of numerical models with observation-based parameterisation and validation data, in ways that have the potential to support genuine advances in our understanding of dryland PVPs.

Ecological knowledge should increasingly be incorporated into models of PVPs. For instance, Cook *et al.* (2005) showed that in the case of Australian mulga trees, individuals isolated in intergroves show higher water use efficiency than those clustered in groves. This kind of

plant physiological detail is lacking from almost all published models of PVPs.

5. Conclusions

The field-based study of banded vegetation in the Broken Hill region suggests that the particular regional instances of emergent patterned vegetation reflect local conditions including floristics, soils, and climate, that are unlikely to be the same in any other areas of banded vegetation. In the study region, which imposes severe drought in combination with grazing pressure, the banded ecosystems appear to be resilient. Additional study would be required to fully understand how and with what relative importance climatic conditions, microtopography, plant physiology, and other factors account for this apparent resilience. Importantly, the field data and their interpretation highlight several issues:

- That soil evaporation during drought may be an important influence on the spatial distribution of soil moisture stress, and that evaporation reduces soil moisture levels more in groves than in intergroves;
- That plant dormancy or death may not immediately reduce soil infiltrability;
- That upslope migration of the banded patterns need not occur for stable patterns to exist over periods of decades;
- That banded patterns can occur that are oblique to the contour;
- That stable band patterns can allow pedologic developments, such as hardening of lower intergrove soils, that effectively lock the patterns in a fixed position;
- The small tussocks of perennial Mitchell grass do not exhibit widely-spreading root systems, and hence in forming striking banded patterns, seem unlikely to reflect long-range competition on a different scale to the close-range facilitation.

The plethora of models of PVPs are in need of more demanding testing and validation, though in light of the periods of time involved in the evolution of PVPs, this may prove to be demanding. It is appropriate to consider a few instances of model predictions. Sherratt (2005) predicted that the upslope migration speed of vegetation bands should be independent of hillslope gradient. Deblauwe *et al.* (2011, p.999) argued that during drought, bare gaps in dryland vegetation cover should coalesce such that banded structures emerge on the steepest slopes. Yizhaq *et al.* (2005) suggested that banded vegetation showing higher wavenumber (more bands per unit length of hillslope) should be less

resilient to drought that areas of lower wavenumber. Additional observational study of pattern migration and of the response of PVPs to drought should be capable of testing hypotheses such as these. Presently, there are simply too few field or empirical observations of PVPs, especially over extended periods of time. Likewise, the antiquity of PVPs remains largely unknown. Both Mabbutt & Fanning (1987) and Dunkerley & Brown (1995) reasoned that Australian PVPs must have been in existence for long periods to allow soil differentiation and development, perhaps since the early Holocene. On the other hand, on the basis of an analytical model, Sherratt (2015) reasoned that in the Sahel, vegetation bands were no older than 150-250 years, and had resulted from the colonisation of bare ground. Such issues are more difficult to resolve, and it may be that PVPs in different regions are of different ages.

The principal conclusion of the present study is therefore that increasingly, empirical observation and model development should be more closely linked. There is a plethora of analytical and numerical models, but too few data with which to parameterise and validate them. If it is to contribute to debates about PVPs in these useful ways, direct observation and monitoring of actual PVPs needs to be more extensively undertaken. Baseline data against which to judge the impact of climate change appear to be especially necessary.

References

- Arora, VK., 2002. The use of the aridity index to assess climate change effect on annual runoff. *Journal of Hydrology*, 265; 164-177.
- Barbier, N., P. Couteron, J. Lejoly, V. Deblauwe, O. Lejeune, 2006. Self-organised vegetation patterning as a fingerprint of climate and human impact on semi-arid ecosystems. *Journal of Ecology*, 94; 537-547.
- Barbier, N., P. Couteron, J. Lejoly, V. Deblauwe, O. Lejeune, 2008. Self-organized vegetation patterning as a fingerprint of climate and human impact on semi-arid ecosystems. *Journal of Ecology*, 94; 537-547. doi: 10.1111/j.1365-2745.2006.01126.x .
- Bathiany, S., M. Scheffer, EH. Van Nes, MS. Williamson, TM. Lenton, 2018. Abrupt climate change in an oscillating world. *Nature Scientific Reports*, 8, 5040, DOI:10.1038/s41598-018-23377-4.
- Baudena, M., J. von Hardenberg, A. Provenzale, 2013. Vegetation patterns and soil-atmosphere water fluxes in drylands. *Advances in Water Resources*, 53; 131-138.
- Bel, G., A. Hagberg, E. Meron, 2012. Gradual regime shifts in spatially extended ecosystems. *Theoretical Ecology*, DOI 10.1007/s12080-011-0149-6.
- Berg, SS., DL. Dunkerley, 2004. Patterned Mulga near Alice Springs, central Australia, and the potential

- threat of firewood collection on this vegetation community. *Journal of Arid Environments*, 59; 313-350. doi:10.1016/j.jaridenv.2003.12.007.
- Beven, K., 1996. Equifinality and uncertainty in geomorphological modelling. Chapter 12, pp.289-313 in BL Rhodes & CE Thorn (Eds.) *Proceedings of the 27th Binghampton Symposium in Geomorphology*, 27-29 September 1996. Wiley & Sons Ltd.
- Blake, GR., KH. Hartge, 1986. Bulk density. Chapter 13, pp.363-375 in A. Klute (Ed.) *Methods of Soil Analysis, Part 1. Physical and mineralogical methods*. American Society of Agronomy, Agronomy Monograph 9.
- Bokulich, A., 2014. How the tiger bush got its stripes: 'how possibly' vs. 'how actually' model explanations. *The Monist*, 97; 321-338.
- Bonachela, JA., RM. Pringle, E. Sheffer, TC. Coverdale, JA. Guyton, KK. Caylor, SA. Levin, CE. Tarnita, 2015. Termite mounds can increase the robustness of dryland ecosystems to climatic change. *Science*, 347; 651-655. doi: 10.1126/science.1261487.
- Boonkorkuea, N., Y. Lenbury, FJ. Alvarado, DJ. Wollkind, 2010. Nonlinear stability analyses of vegetative patterns formation in an arid environment. *Journal of Biological Dynamics*, 4; 346-380. DOI: 10.1080/17513750903301954.
- Borgogno, F., P. D'Odorico, F. Laio, L. Ridolfi, 2007. Effect of rainfall interannual variability on the stability and resilience of dryland plant ecosystems. *Water Resources Research*, 43, doi:10.1029/2006WR005314.
- Borgogno, F., P. D'Odorico, F. Laio, L. Ridolfi, 2009. Mathematical models of vegetation pattern formation in ecohydrology. *Reviews of Geophysics*, 47, paper No. 2007RG000256.
- Bouwer, H., 1986. Intake rate: cylinder infiltrometer. Chapter 32, pp.825-844 in A. Klute (Ed.) *Methods of Soil Analysis, Part 1. Physical and mineralogical methods*. American Society of Agronomy, Agronomy Monograph 9.
- Brazier, RE., KJ. Beven, SG. Anthony, JS. Rowan, 2001. Implications of model uncertainty for the mapping of hillslope-scale soil erosion predictions. *Earth Surface Processes and Landforms*, 26; 1333-1352. DOI: 10.1002/esp.266.
- Brutsaert, W., 2014. Daily evaporation from drying soil: universal parameterization with similarity. *Water Resources Research*, 50; 3206-3215. doi: 10.1002/2013WR014872.
- Chappell, A., C. Valentin, A. Warren, P. Noon, M. Charlton, JM. d'Herbes, 1999. Testing the validity of upslope migration in banded vegetation from southwest Niger. *Catena*, 37; 217-229.
- Chen, Y., T. Kolokolnikov, J. Tzou, C. Gai, 2015. Patterned vegetation, tipping points, and the rate of climate change. *European Journal of Applied Mathematics*, www.pnas.org cgi doi 10.1073/pnas.0502884102.
- Cipriotti, PA., MR. Aguiar, 2015. Is the balance between competition and facilitation a driver of the patch dynamics in arid vegetation mosaics? *Oikos*, 124; 139-149. doi: 10.1111/oik.01758.
- Clark, LJ., WR. Whalley, PB. Barraclough, 2003. How do roots penetrate strong soil? *Plant and Soil*, 255; 93-104.
- Consolo, G., C. Curro, G. Valenti, 2017. Pattern formation and modulation in a hyperbolic vegetation model for semiarid environments. *Applied Mathematical Modelling*, 43; 372-392. <http://dx.doi.org/10.1016/j.apm.2016.11.031>.
- Cook, GD., TZ. Dawes-Gromadzki, 2005. Stable isotope signatures and landscape functioning in banded vegetation in arid-central Australia. *Landscape Ecology*, 20;649-660. DOI 10.1007/s10980-005-0069-1.
- Couteron, P., A. Mahamane, P. Ouedraogo, J. Seghieri, 2000. Differences between aneded thickets (tiger bush) at two sites in West Africa. *Journal of Vegetation Science*, 11; 321-328.
- Cueto-Felgueroso, L., M. Dentz, R. Juanes, 2015. Regime shifts in bistable water-stressed ecosystems due to amplification of stochastic rainfall patterns. *Physical Review E*, 91, 052148, DOI:10.1103/PhysRevE.91.052148.
- Daryanto, S., DJ. Eldridge, TB. Koen, 2012. Soil nutrients under shrub hummocks and debris mounds two decades after ploughing. *Plant Soil*, 351; 405-419. DOI 10.1007/s11104-011-0978-5.
- Dawes, JHP., JLM. Williams, 2016. Localised pattern formation in a model for dryland vegetation. *Mathematical Biology*, 73; 63-90. DOI 10.1007/s00285-015-0937-5.
- DeAngelis, DL., 2012. Self-organizing processes in landscape pattern and resilience: a review. *ISRN Ecology*, Vol. 2012, Article ID 274510. doi:10.5402/2012/274510.
- Deblauwe, V., N. Barbier, P. Couteron, O. Lejeune, J. Bogaert, 2008. The global biogeography of semi-arid period vegetation patterns. *Global Ecology and Biogeography*, 17; 715-723.
- Deblauwe, V., P. Couteron, O. Lejeune, J. Bogaert, N. Barbier, 2011. Environmental modulation of self-organized periodic vegetation patterns in Sudan. *Ecography*, 34; 990-1001. doi: 10.1111/j.1600-0587.2010.06694.x.
- Deblauwe, V., P. Couteron, J. Bogaert, N. Barbier, 2012. Determinants and dynamics of banded vegetation pattern migration in arid climates. *Ecological Monographs*, 82; 3-21.
- D'Odorico, P., F. Laio, L. Ridolfi, 2006. Vegetation patterns induced by random climate fluctuations. *Geophysical Research Letters*, 33, doi:10.1029/2006GL027499.
- D'Odorico, P., F. Laio, A. Porporato, L. Ridolfi, N. Barbier, 2007. Noise-induced vegetation patterns in fire-prone savannas. *Journal of Geophysical Research*, 112, G02021, doi:10.1029/2006JG000261.
- D'Odorico, P., F. Laio, L. Ridolfi, 2015. Noise-induced stability in dryland plant ecosystems. *PNAS*, 102; 10819-10822. www.pnas.org cgi doi 10.1073/pnas.0502884102.
- Dunkerley, D.L., 1997a. Banded vegetation: development under uniform rainfall from a simple cellular automaton model. *Plant Ecology*, 129; 103-111.
- Dunkerley, D.L., 1997b. Banded vegetation: survival under drought and grazing pressure from a simple cellular automaton model. *Journal of Arid Environments*, 35; 419-428.
- Dunkerley, DL., 1999. Cellular automata: the exploration of spatial phenomena in ecology. pp.145-183 in A.H. Fielding (Ed.) *Machine learning methods for ecological applications*, Boston: Kluwer Academic, 261pp.

- Dunkerley, DL., 2000. Hydrologic effects of dryland shrubs: defining the spatial extent of modified soil water uptake rates at an Australian desert site. *Journal of Arid Environments*, 45; 159-172.
- Dunkerley, DL., 2002. Infiltration rates and soil moisture in a groved mulga community near Alice Springs, arid central Australia: evidence for complex internal rainwater redistribution in a runoff-runon landscape. *Journal of Arid Environments*, 51; 199-219.
- Dunkerley, DL., 2008. Identifying individual rain events from pluviograph records: a review with analysis of data from an Australian dryland site. *Hydrological Processes*, 22, 5024-5036. DOI: 10.1038/srep38752.
- Dunkerley, DL., 2010. Ecogeomorphology in the Australian drylands and the role of biota in mediating the effects of climate change on landscape processes and evolution. In Bishop P. and Pillans B. (eds.) *Australian Landscapes*, Geological Society, London, Special Publication 346; 87-120.
- Dunkerley, DL., 2012. Effects of rainfall intensity fluctuations on infiltration and runoff: rainfall simulation on dryland soils, Fowlers Gap, Australia. *Hydrological Processes*, 26; 2211-2224. DOI: 10.1002/hyp.8317.
- Dunkerley, DL., 2013. Sub-daily rainfall events in an arid environment with marked climate variability: Variation among wet and dry years at Fowlers Gap, New South Wales, Australia. *Journal of Arid Environments*, 96; 23-30. <http://dx.doi.org/10.1016/j.jaridenv.2013.04.002>.
- Dunkerley, DL., 2014. Vegetation mosaics of arid western New South Wales, Australia: considerations of their origin and persistence. Chapter 12, pp. 315-345 in EN Mueller *et al.* (Eds.) *Patterns of Land Degradation in Drylands: Understanding Self-Organised Ecogeomorphic Systems*, DOI 10.1007/978-94-007-5727-1 12, Springer Science+Business Media Dordrecht 2014.
- Dunkerley, DL., KJ. Brown, 1995. Runoff and runon areas in patterned chenopod shrubland, arid western New South Wales, Australia: characteristics and origin. *Journal of Arid Environments*, 30; 41-55.
- Dunkerley, DL., KJ. Brown, 1999. Banded vegetation near Broken Hill, Australia: significance of soil surface roughness and soil physical properties. *Catena*, 37; 75-88.
- Dunkerley, DL., KJ. Brown, 2002. Oblique vegetation banding in the Australian arid zone: implications for theories of pattern evolution and maintenance. *Journal of Arid Environments*, 51; 163-181.
- Eigentler, L., JA. Sherratt, 2018. Analysis of a model for banded vegetation patterns in semi-arid environments with nonlocal dispersal. *Mathematical Biology*, 77; 739-763. <https://doi.org/10.1007/s00285-018-1233-y>.
- Eldridge, DJ., M. Lepage, MA. Bryannah, P. Ouedraogo, 2001. Soil biota in banded landscapes. Chapter 6, pp.105-131 in DJ Tongway, C Valentin & J Seghier (Eds.) *Banded vegetation patterning in arid and semiarid environments*, New York: Springer, 251pp.
- Esteban, J., V. Fairén, 2006. Self-organised formation of banded vegetation patterns in semi-arid regions: a model. *Ecological Complexity*, 3; 109-118.
- Foti, R., JA. Ramírez, 2013. A mechanistic description of the formation and evolution of vegetation patterns. *Hydrology and Earth System Sciences*, 17; 63-84. doi:10.5194/hess-17-63-2013.
- Franz, TE., KK. Caylor, EG. King, JM. Nordbotten, MA. Celia, I. Rodríguez-Iturbe, 2012. An ecohydrological approach to predicting hillslope-scale vegetation patterns in dryland ecosystems. *Water Resources Research*, 48, W01515, doi:10.1029/2011WR010524.
- Galle, S., M. Ehrmann, C. Peugot, 1999. Water balance in a banded vegetation pattern. A case study of tiger bush in western Niger. *Catena*, 37; 197-216.
- Gowda, K., S. Iams, M. Silber, 2017. Dynamics and resilience of vegetation bands in the Horn of Africa. arXiv, 1705.053082.2.
- Griffin, PC., AA. Hoffmann, 2012. Mortality of Australian alpine grasses (*Poa* spp.) after drought: species differences and ecological patterns. *Journal of Plant Ecology*, 5; 121-133. doi: 10.1093/jpe/rtr010.
- Guttal, V., C. Jayaprakash, 2007. Self-organization and productivity in semi-arid ecosystems: implications of seasonality in rainfall. *Journal of Theoretical Biology*, 248; 490-500. doi:10.1016/j.jtbi.2007.05.020.
- Haghighi, E., JW. Kirchner, 2017. Near-surface turbulence as a missing link in modeling evapotranspiration-soil moisture relationships. *Water Resources Research*, 53; 5320-5344. doi: 10.1002/2016WR020111.
- HilleRisLambers, R., M. Rietkerk, F. van den Bosch, H.H.T. Prins, H. de Kroon, 2001. Vegetation pattern formation in semi-arid grazing systems. *Ecology*, 82; 50-61.
- Hunt, LP., 2001. Low seed availability may limit recruitment in grazed *Atriplex vesicaria* and contribute to its local extinction. *Plant Ecology*, 157; 53-67.
- Jones, RM., 1969. Soil moisture and salinity under bladder saltbush (*Atriplex vesicaria*) pastures in the New South Wales Riverine Plain. *Australian Journal of Experimental Agriculture and Animal Husbandry*, 9; 603-609.
- Kealy, BJ., DJ. Wollkind, 2012. A Nonlinear Stability Analysis of Vegetative Turing Pattern Formation for an Interaction-Diffusion Plant-Surface Water Model System in an Arid Flat Environment. *Bulletin of Mathematical Biology*, 74; 803-833. DOI 10.1007/s11538-011-9688-7.
- Kéfi, S., V. Guttal, WA. Brock, SR. Carpenter, AM. Ellison, VN. Livina, DA. Seekell, M. Scheffer, EH. van Nes, V. Dakos, 2014. Early warning signals of ecological transitions: methods for spatial patterns. *PLoS ONE*, 9(3): e92097. doi:10.1371/journal.pone.0092097.
- Kéfi, S., M. Rietkerk, C.L. Alados, Y. Pueyo, V.P. Papanastasis, A. ElAich, P.C. de Ruiter, 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449; 213-218.
- Kemp, PR., JF. Reynolds, RA. Virginia, WG. Whitford, 2003. Decomposition of leaf and root litter of Chihuahuan desert shrubs: effects of three years of summer drought. *Journal of Arid Environments*, 53; 21-39. doi:10.1006/jare.2002.1025.
- Kirby, JM., AG. Bengough, 2002. Influence of soil strength on root growth: experiments and analysis using a critical-state model. *European Journal of Soil Science*, 53; 119-128.
- Klausmeier, CA., 1999. Regular and irregular patterns in semiarid vegetation. *Science*, 284; 1826-1828.
- Kletter, AY., J. von Hardenberg, E. Meron, A. Provenzale, 2009. Patterned vegetation and rainfall

- intermittency. *Journal of Theoretical Biology*, 256; 574-583. doi:10.1016/j.jtbi.2008.10.020.
- Köhnke, MC., H. Malchow, 2017. Impact of parameter variability and environmental noise on the Klausmeier model of vegetation pattern formation. *Mathematics*, 5, 69, doi:10.3390/math5040069.
- Konings, AG., SC. Dekker, M. Rietkerk, GG. Katul, 2011. Drought sensitivity of patterned vegetation determined by rainfall-land surface feedbacks. *Journal of Geophysical Research*, 116, G04008, doi:10.1029/2011JG001748.
- Lefever, R., O. Lejeune, 1997. On the origin of tiger bush. *Bulletin of Mathematical Biology*, 59; 263-294.
- Lejeune, O., M. Tlidi, 1999. A model for the explanation of vegetation stripes (tiger bush). *Journal of Vegetation Science*, 10; 201-208.
- Lejeune, O., M. Tlidi, P. Couteron, 2002. Localized vegetation patches: a self-organized response to resource scarcity. *Physical Review E* 66, DOI: 10.1103/PhysRevE.66.010901.
- Li, J., CY. Zhao, YJ. Song, Y. Sheng, H. Zhu, 2010. Spatial patterns of desert annuals in relation to shrub effects on soil moisture. *Journal of Vegetation Science*, 21; 221-232. DOI: 10.1111/j.1654-1103.2009.01135.x.
- Lu, X., L. Wang, MF. McCabe, 2016. Elevated CO₂ as a driver of global dryland greening. *Nature Scientific Reports*, 6:20716. DOI: 10.1038/srep20716
- Mabbutt, JA., PC. Fanning, 1987. Vegetation banding in arid Western Australia. *Journal of Arid Environments*, 12; 41-59.
- Magliano, PN., DD. Breshears, RJ. Fernández, EG. Jobbágy, 2015. Rainfall intensity switches ecohydrological runoff/runon redistribution patterns in dryland vegetation patches. *Ecological Applications*, 25; 2094-2100.
- Mander, L., SC. Dekker, M. Li, W. Mio, SW. Punyasena, TM. Lenton, 2017. A morphometric analysis of vegetation patterns in dryland ecosystems. *Royal Society Open Science*, 4: 160443. <http://dx.doi.org/10.1098/rsos.160443>.
- Mayor, AG., S. Kéfi, S. Bautista, F. Rodríguez, F. Cartení, M. Rietkerk, 2013. Feedbacks between vegetation pattern and resource loss dramatically decrease ecosystem resilience and restoration potential in a simple dryland model. *Landscape Ecology*, 28; 931-942. DOI 10.1007/s10980-013-9870-4.
- McIntyre, DS., 1958a. Permeability measurements of soil crusts formed by raindrop impact. *Soil Science*, 85; 185-189.
- McIntyre, DS., 1958b. Soil splash and the formation of surface crusts by raindrop impact. *Soil Science*, 85; 261-266.
- Mohseni, N., A. Sepehr, 2015. Self-organized vegetation patterns: early warning signals for prediction of ecosystem transitions. *Journal of Environmental Studies*, 41(1), Spring 2015.
- Orr, DM., DG. Phelps, 2016. Impacts of level of utilisation by grazing on an *Astrelba* (Mitchell grass) grassland in north-western Queensland between 1984 and 2010. 1. Herbage mass and population dynamics of *Astrelba* spp. *The Rangeland Journal*, 35; 1-15. <http://dx.doi.org/10.1071/RJ11068>
- Padilla, FM., J. de Dios Miranda, C. Armas, FI. Pugnaire, 2015. Effects of changes in rainfall amount and pattern on root dynamics in an arid shrubland. *Journal of Arid Environments*, 114; 49-53. <http://dx.doi.org/10.1016/j.jaridenv.2014.11.005>
- Penny, GG., KE. Daniels, SE. Thompson, 2013. Local properties of patterned vegetation: quantifying endogenous and exogenous effects. *Philosophical Transactions of the Royal Society A.*, 371: 20120359. <http://dx.doi.org/10.1098/rsta.2012.0359>
- Pringle, RM., CE. Tarnita, 2017. Spatial self-organization of ecosystems: integrating multiple mechanisms of regular-pattern formation. *Annual Reviews of Entomology*, 62; 359-377. 10.1146/annurev-ento-031616-035413.
- Puigdefábregas, J., 1995. The role of vegetation patterns in structuring runoff and sediment fluxes in drylands. *Earth Surface Processes and Landforms*, 30; 133-147. DOI: 10.1002/esp.1181
- Quinn, R., A. Parker, K. Rushton, 2018. Evaporation from bare soil: Lysimeter experiments in sand dams interpreted using conceptual and numerical models. *Journal of Hydrology*, 564; 909-915. <https://doi.org/10.1016/j.jhydrol.2018.07.011>
- Ratajczak, Z., P. D'Odorico, SL. Collins, BT. Bestelmeyer, FI. Isbell, JB. Nippert, 2017. The interactive effects of press/pulse intensity and duration on regime shifts at multiple scales. *Ecological Monographs*, 87; 198-218.
- Ravi, S., P. D'Ordorico, GS. Okin, 2007. Hydrologic and aeolian controls of vegetation patterns in arid landscapes. *Geophysical Research Letters*, 34, L24S23, doi:10.1029/2007GL031023
- Rietkerk, M., MC. Boerlijst, F. van Langevelde, R. HilleRisLambers, J. van de Koppel, L. Kumar, HHT. Prins, AM. de Roos, 2002. Self-organization of vegetation in arid ecosystems. *The American Naturalist*, 160; 524-530.
- Rietkerk, M., SC. Dekker, PC. de Ruiter, J. van de Koppel, 2004. Self-organised patchiness and catastrophic shifts in ecosystems. *Science*, 305; 1926-1929. DOI: 10.1126/science.1101867.
- Roitberg, E., M. Shoshany, 2017. Can spatial patterns along climatic gradients predict ecosystem responses to climate change? Experimenting with reaction-diffusion simulations. *PLoS ONE.*, 12, e0174942. <https://doi.org/10.1371/journal.pone.0174942>
- Saco, PM., GR. Willgoose, GR. Hancock, 2007. Ecogeomorphology of banded vegetation patterns in arid and semi-arid regions. *Hydrology and Earth System Sciences*, 11; 1717-1730.
- Sankaran, S., S. Majumder, S. Kéfi, V. Guttal, 2018. Implications of being discrete and spatial for detecting early warning signals of regime shifts. *Ecological Indicators*, 94; 503-511. <https://doi.org/10.1016/j.ecolind.2017.11.040>
- Scheffer, M., J. Bascompte, WA. Brock, V. Brovkin, SR. Carpenter, V. Dakos, H. Held, EH. van Nes, M. Rietkerk, G. Sugihara, 2009. Early-warning signals for critical transitions. *Nature*, 461; 53-59. doi:10.1038/nature08227
- Sherratt, JA., 2005. An analysis of vegetation stripe formation in semi-arid landscapes. *Journal of Mathematical Biology*, 51; 183-197. doi:10.1073/pnas.1420171112
- Sherratt, JA., 2010. Pattern solutions of the Klausmeier Model for banded vegetation in semi-arid environments I. *Nonlinearity*, 23; 2657-2675. doi: 10.1088/0951-7715/23/10/016.
- Sherratt, JA., 2013. Pattern solutions of the Klausmeier model for banded vegetation in semiarid

- environments V: the transition from patterns to desert. *SIAM Journal of Applied Mathematics*, 73; 1347-1367.
- Sherratt, J.A., 2015. Using wavelength and slope to infer the historical origin of semiarid vegetation bands. *PNAS.*, 112; 4202-4207. Doi:10.1073/pnas.1420171112.
- Siero, E., A. Doelman, M.B. Eppinga, J.D.M. Rademacher, M. Rietkerk, K. Siteur, 2015. Striped pattern selection by advective reaction-diffusion systems: Resilience of banded vegetation on slopes. *Chaos*, 25, 036411, <http://dx.doi.org/10.1063/1.4914450>
- Siteur, K., E. Siero, M.B. Eppinga, J.D.M. Rademacher, A. Doelman, M. Rietkerk, 2014. Beyond Turing: the response of patterned ecosystems to environmental change. *Ecological Complexity*, 20; 81-96. <http://dx.doi.org/10.1016/j.ecocom.2014.09.002>
- Skliris, N., J.D. Zika, G. Nurser, S.A. Josey, R. Marsh, 2016. Global water cycling amplifying at less than the Clausius-Clapeyron rate. *Nature Scientific Reports*, 6:38752. DOI: 10.1038/srep38752
- Soulard, C.E., T.C. Esque, D.R. Bedford, S. Bond, 2013. The role of fire on soil mounds and surface roughness in the Mojave Desert. *Earth Surface Processes and Landforms*, 38; 111-121. DOI: 10.1002/esp.3264
- Steinberger, Y., R. Degani, G. Barness, 1995. Decomposition of root fitter and related microbial population dynamics of a Negev Desert shrub, *Zygophyllum dumosum*. *Journal of Arid Environments*, 31; 383-399.
- Stewart, J., A.J. Parsons, J. Wainwright, G.S. Okin, B.T. Bestelmeyer, E.L. Fredrickson, W.H. Schlesinger, 2014. Modeling emergent patterns of dynamic desert ecosystems. *Ecological Monographs*, 84; 373-410.
- Sun, G.Q., C.H. Wang, L.L. Chang, Y.P. Wu, L. Li, 2018. Effects of feedback regulation on vegetation patterns in semi-arid environments. *Applied Mathematical Modelling*, 61; 200-215. <https://doi.org/10.1016/j.apm.2018.04.010>
- Tarnita, C.E., J.A. Bonachela, E. Sheffer, J.A. Guyton, T.C. Coverdale, R.A. Long, R.M. Pringle, 2017. A theoretical foundation for multi-scale regular vegetation patterns. *Nature*, 541; 398-401. doi:10.1038/nature20801
- Thiery, J.M., J.M. D'Herbes, C. Valentin, 1995. A model simulating the genesis of banded vegetation patterns in Niger. *Journal of Ecology*, 83; 497-507.
- Thompson, S., G. Katul, S.M. McMahon, 2008. Role of biomass spread in vegetation patterns formation within arid ecosystems. *Water Resources Research*, 44, W10421, doi:10.1029/2008WR006916
- Tirabassi, G., J. Viebahn, V. Dakos, H.A. Dijkstra, C. Masoller, M. Rietkerk, S.C. Dekker, 2014. Interaction network based early-warning indicators of vegetation transitions. *Ecological Complexity*, 19; 148-157. <http://dx.doi.org/10.1016/j.ecocom.2014.06.004>
- Trenberth, K.E., 2011. Changes in precipitation with climate change. *Climate Research*, 47; 123-138. doi: 10.3354/cr00953
- Ummenhofer, C.C., M.H. England, P.C. McIntosh, G.A. Meyers, M.J. Pook, J.S. Risbey, A. Sen Gupta, A.S. Tascheyo, 2009. What causes southeast Australia's worst droughts? *Geophysical Research Letters*, 36, doi:10.1029/2008GL036801.
- Upton, G., 1983. Genesis of crabhole microrelief at Fowlers Gap western New South Wales. *Catena*, 10; 383-392.
- Ursino, N., C. Callegaro, 2016. Diversity without complementarity threatens vegetation patterns in arid lands. *Ecohydrology*, 9; 1187-1195. DOI: 10.1002/eco.1717
- Van Dijk, A.J.M., H.E. Beck, R.S. Crosbie, R.A.M. de Jeu, Y.Y. Liu, G.M. Podger, B. Timbal, N.R. Viney, 2013. The Millennium Drought in southeast Australia (2001-2009): Natural and human causes and implications for water resources, ecosystems, economy, and society. *Water Resources Research*, 49; 1040-1057. doi:10.1002/wrcr.20123
- Verdon-Kidd, D.C., A.S. Kiem, 2009. Nature and causes of protracted droughts in southeast Australia: Comparison between the Federation, WWII, and Big Dry droughts. *Geophysical Research Letters*, 36; L22707, doi:10.1029/2009GL041067
- Vidiella, B., J. Sardanyés, R. Solé, 2018. Exploiting delayed transitions to sustain semiarid ecosystems after catastrophic shifts. *Interface*, 15, 20180083. <http://dx.doi.org/10.1098/rsif.2018.0083>
- Wang, X., G. Zhang, 2018. Vegetation pattern formation in seminal systems due to internal competition reaction between plants. *Journal of Theoretical Biology*, 458; 10-14. <https://doi.org/10.1016/j.jtbi.2018.08.043>
- Weissmann, H., R. Kent, Y. Michael, N.M. Shnerb, 2017. Empirical analysis of vegetation dynamics and the possibility of a catastrophic desertification transition. *PLoS ONE* 12, <https://doi.org/10.1371/journal.pone.0189058>
- Whitford, W.G., 1998. Contribution of pits dug by goannas (*Varanus gouldii*) to the dynamics of banded mulga landscapes in eastern Australia. *Journal of Arid Environments*, 40; 453-457.
- Wickens, G.E., 1998. *Ecophysiology of economic plants in arid and semi-arid lands*. Berlin: Springer, 343pp.
- Wu, X.B., T.L. Thurow, S.G. Whisenant, 2000. Fragmentation and changes in hydrologic function of tiger bush landscapes, south-west Niger. *Journal of Ecology*, 88; 790-800.
- Yang, T., M. Ala, Y. Zhang, J. Wu, A. Wang, 2018. Characteristics of soil moisture under different vegetation coverage in Horqin Sandy Land, northern China. *PLoS ONE.*, 13, e0198805. <https://doi.org/10.1371/journal.pone.0198805>
- Yizhaq, H., E. Gilad, E. Meron, 2005. Banded vegetation: biological productivity and resilience. *Physica, A* 356; 139-144.
- Yizhaq, H., G. Bel, 2016. Effects of quenched disorder on critical transitions in pattern-forming systems. *New Journal of Physics*, 18, doi:10.1088/1367-2630/18/2/023004
- Zelnik, Y., S. Kinast, H. Yizhaq, G. Bel, E. Meron, 2013. Regime shifts in models of dryland vegetation. *Philosophical Transactions of the Royal Society A.*, 371: 20120358. <http://dx.doi.org/10.1098/rsta.2012.0358>.
- Zhang, D.H., X.R. Li, F. Zhang, Z.S. Zhang, Y.L. Chen, 2016. Effects of rainfall intensity and intermittency on woody vegetation cover and deep soil moisture in dryland ecosystems. *Journal of Hydrology*, 543; 270-282. <http://dx.doi.org/10.1016/j.jhydrol.2016.10.003>.