



Oblique vegetation banding in the Australian arid zone: implications for theories of pattern evolution and maintenance

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This paper describes strongly developed vegetation bands that are not aligned along the contour. This previously unreported *oblique vegetation banding* is developed in an arid region of mixed tussock grasses and chenopod shrubs in western New South Wales, Australia.

In two of four contour-mapped, 0.5 ha quadrats, the vegetation bands are oriented at angles of 45–70° to the direction of slope. Various soil features indicative of a runoff and runon hydrology, very similar to those classically reported from contour-parallel vegetation banding, suggest that the oblique configurations have been stable for a considerable time.

In addition to the unusual band orientation, marked variations in the ratio of intergrove width to grove width were found within the study area, spanning the range 0.21–4.95, and there was generally no correlation between intergrove width and the width of the grove receiving runoff water from it. These findings cast doubt on the supposed close adjustment of intergrove dimensions to grove water requirements.

In nearby plots having ordinary contour-parallel vegetation banding, the absence of any upslope motion of the pattern was demonstrated using monuments installed at band margins 6 years previously.

These properties do not accord with the predictions of many models of the development of vegetation banding. However, soil changes associated with the runoff–runon system operating within vegetation bands may be involved in stabilizing their configurations. Thus, future investigations into the origin of vegetation banding must distinguish between their form and hydrologic *functioning* once established, and the fundamental *origin* of the vegetation pattern, which may be altogether different. In addition, pedologic and other processes which may inhibit free pattern adjustments must be incorporated into models addressing the development of vegetation banding.

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Introduction

Patterned vegetation, including bands, stripes, arcs and patches of plants with intervening barer soil, is a widely described plant community structure on gentle slopes within arid and semi-arid regions (Cornet *et al.*, 1988; Tongway & Ludwig, 1990). Recent thematic reviews have brought together much of what is known about this phenomenon (e.g. Valentin & Poesen, 1999; Tongway & Seghieri, 1999), especially in relation to the optimized harnessing of available rainfall that is one aspect of the runoff-runon mechanism operating within these landscapes (e.g. Bromley *et al.*, 1997).

There is continuing interest in attempting to understand the origin of vegetation banding (as distinct from its hydrologic operation once developed), with modelling being a common approach (Goodspeed & Winkworth, 1978; Thiery *et al.*, 1995; Dunkerley, 1997; Lefever & Lejeune, 1997; Lejeune *et al.*, 1999; Lejeune & Tlidi, 1999; Klausmeier, 1999). Below, we group these models into two broad classes, and distinguish between those whose subject is the hydrologic operation of vegetation banding and those which attempt to identify the origin of the pattern itself.

This study then analyses new field observations from an area of vegetation banding in arid western New South Wales, Australia, and focuses attention on the intra-regional variation in vegetation patterns there. We show that within a small study area, there is a range of vegetation patterns from classical, contour-parallel vegetation banding to a previously undescribed contour-oblique form. These differences in form suggest the existence of corresponding differences in hydrologic operation that appear to require modifications to current views of both the origin and the functioning of vegetation banding.

Ideas on the origin of vegetation banding

There are presently differing views about the origin and development of vegetation banding. A *mechanistic view* sees the phenomenon as the product of the different properties of bare and vegetated soils, in which bare surfaces develop crusts and become impermeable, directing surface runoff downslope to a neighbouring grove of plants where the water is absorbed into more permeable soils and there supports the relatively denser plant cover. Within the groves, synergistic effects like the mutual creation of sheltered microclimates, further benefit the plants. The resulting partitioning of the surface into water-scare and relatively water-rich zones is seen as the fundamental cause of the vegetation patterns.

In the *system behaviour* approach, vegetation banding is instead seen as belonging to the class of diverse patterns that arise in various systems, including chemical and biological ones, from the interactions among two or more processes operating at different spatial scales. A recent discussion of the processes involved has been provided by Barrio *et al.* (1999), and additional discussions of Turing instabilities can be found in Cressman & Vickers (1997) & Satnoianu *et al.* (2000).

An example of system instability related to vegetation banding proposed in the modelling of Lejeune *et al.* (1999) was the possibility that vegetation banding arises from simultaneous *competition* between plants (arising perhaps through the spread of root systems which draw water and nutrients from an area that may extend far beyond the limits of the above-ground plant canopy) and *co-operativity* among plants (perhaps from the advantageous local microclimate produced where plants cluster in groves), the two influences acting over different spatial scales. Canopy-related effects clearly act on a local scale, whilst root systems are known to extend widely into the interspaces between plants, and to play a role in determining plant spacing (Brisson &

Reynolds 1994; Schenk *et al.*, 1999). As shown by Lejeune *et al.* (1999), the development of a spatial pattern in which individuals are clustered into a repeating pattern is one possible outcome of the interplay of competition and co-operativity, but the particular pattern that emerges depends partly on the imposed conditions, including the presence of any anisotropy in the environment. Patterns arising from this kind of interaction, and belonging to a class of phenomena called Turing instabilities, can in principle arise even on completely level terrain, and hence need not involve a division of the surface into runoff and runon zones as is the case with the mechanistic view of vegetation banding. On sloping terrain however, an asymmetry in behaviour that arises because of the preferred flow direction may serve to fix the orientation of a pattern related to system behaviour, or to alter the form of the pattern (e.g. from patches to stripes). No clear mechanistic explanation for the occurrence of patches or stripes in particular areas has yet emerged.

These two views of vegetation banding are fundamentally different since in the mechanistic view, hydrologic behaviour accounts for the existence and continued operation of vegetation banding, whilst in the system behaviour view, the runoff–runon system is, to some extent at least, a consequence of the development of a spatial pattern in the vegetation whose origin lies not in hydrology but in other aspects of the ecology of the plant community. In addition, landscape models built using these two differing approaches diverge in their predictions about some key aspects of vegetation banding, but agree on others. The mechanistic, surface hydrology model of Dunkerley (1997) for example, suggested that once developed, vegetation banding could adopt a pattern in which grove–intergrove boundaries remained relatively fixed in space, undergoing only minor grove expansion and contraction in response to fluctuating annual rainfall, and this largely by advance and retreat of the downslope margin of each grove. The system behaviour models, however, predict continual upslope migration of the pattern of vegetation bands (see, for example, the animation provided in the world-wide-web-based supplementary materials accompanying Klausmeier, 1999). In contrast, there is agreement among both mechanistic and system-behaviour models that on gently sloping terrain, vegetation banding should adopt a contour-parallel alignment, at least when the pattern has existed for sufficiently long to have reached a stable configuration.

We consider these ideas later in relation to the interpretation of new field evidence from New South Wales (NSW), Australia, in which we examine the orientation of vegetation banding in relation to the direction of surface drainage, and the evidence for band migration judged against monuments installed at grove–intergrove boundaries and monitored for a period of years.

The Menindee field site

Field mapping was conducted in an area of vegetation banding where soils and plant cover have been described previously (Dunkerley & Brown, 1999). It is located about 40 km south-east of the city of Broken Hill, in western NSW (Fig. 1), in a landscape of gently undulating treeless plains that receive a highly variable annual rainfall averaging about 230 mm. Potential evapotranspiration exceeds 2.5 m a^{-1} , and surface water is absent. Over some hundreds of square kilometres, the landscape carries vegetation banding. This also extends across broad lowlands about 100 km to the west, in the easternmost parts of South Australia. The vegetation is dominated by chenopod shrubs such as *Maireana pyramidata* and *Atriplex vesicaria*, together with extensive growth of the Mitchell grass *Astrelba pectinata*. There is sporadic growth of the mulga tree *Acacia aneura* on rare rocky hillsides and of the river red gum *Eucalyptus camaldulensis* along the riparian corridors of major regional

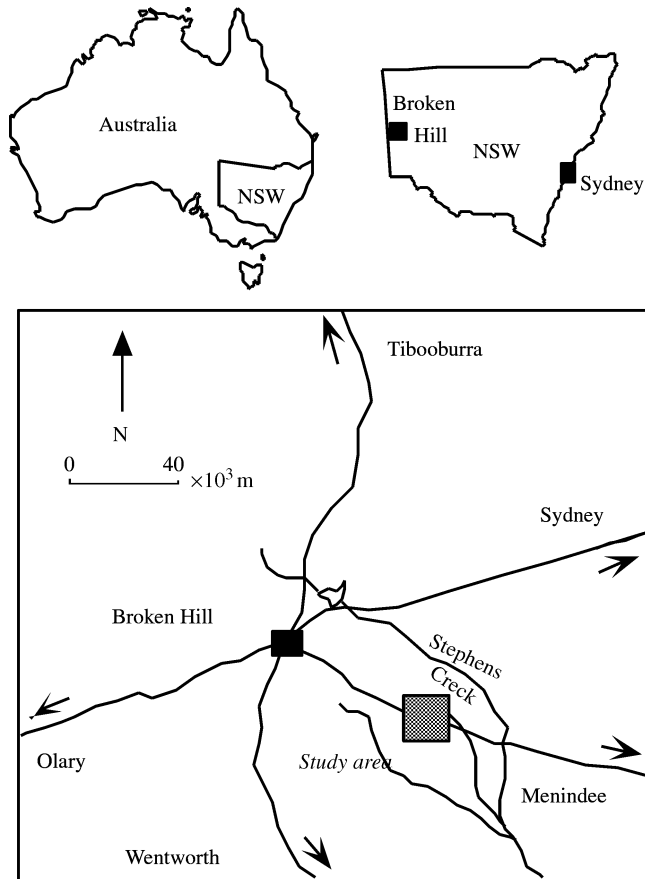


Figure 1. Location of the Menindee study area south-east of the city of Broken Hill.

drainage lines, all of which are ephemeral. The area has been grazed by sheep for about 150 years, and the vegetation cover is periodically reduced by drought or by outbreaks of the Australian plague locust, *Chortoicetes terminifera*, as well as other species, which can build up very large populations following seasons of good rainfall.

The surface soils exhibit only slight variation in texture across the undulating parts of the landscape where vegetation banding is developed, owing to the dominance of aeolian accretions of well-sorted material blown from desert country to the west, probably during times of marked aridity in cold periods of the Quaternary Era (Chartres, 1982; Greene *et al.*, 2001). Texturally, the surface soils are loams, and where bare, the surface is frequently colonized by lichens, algae, and cyanobacteria. Additionally, there are often scatters of quartz stones at the soil surface, but the subsoil is almost completely stone-free.

Intergroves are often completely devoid of vascular plants, and show surface soils that are extremely strong mechanically. Groves possess relatively soft and friable surface soils and often exhibit features indicative of marked shrink–swell phenomena in the subsoil, including soil collapse pipes and larger closed depressions, often encircled by tension cracks (Dunkerley & Brown 1999).

Data collection

On very gently sloping terrain, the orientation of vegetation banding can be difficult to judge by eye. Therefore, a digital theodolite incorporating laser distance measuring was used to map surface elevations and grove/intergrove margins within four 75 m × 75 m (approx. 0.5 ha) study plots, two of which were selected because the vegetation banding was known from prior surveys to be contour-parallel, and two at sites where the vegetation banding appeared to be aligned obliquely to the contour. All mapped plots were of sufficient size to include multiple wavelengths of the grove and intergrove pattern. The four plots were located within an area of about 4 km². Within each plot, up to 150 small marker pegs were set out at intervals of 3–5 m by a person walking along the grove–intergrove boundaries, which are generally very distinct. During the subsequent mapping, the location and elevation of each peg was recorded with the theodolite, and the pegs were progressively collected. This procedure proved necessary as the groves and intergroves form a confusing maze and without markers, sections of the study plot could inadvertently be mapped twice or not at all. The resulting (*X*, *Y*, *Z*) co-ordinates allowed the grove and intergrove boundaries to be plotted planimetrically, with the soil surface contoured at 5 or 10 cm intervals. This was carried out in the field on a portable computer the running the Surface III software (Kansas Geological Survey, 1995). Mean grove and intergrove widths as well as mean topographic slopes were determined from these maps by taking measurements along five evenly spaced transect lines oriented orthogonally to the contour, and spanning the mapped areas.

The contour maps were also used to derive numerical data on the relative orientations of the grove–intergroves boundaries and the topographic contours. Given that the study plots lay on essentially planar slopes, with little contour curvature, least-squares linear regression was applied to the co-ordinates of about ten locations evenly spaced along each contour line and each grove–intergrove boundary lying within each study plot. These fitted regression lines in effect provided best-fit trend lines for the vegetation boundaries and contours, smoothing minor irregularities. The mean orientation of the 5–8 vegetation boundaries and 5–8 contours on each plot were then found by averaging the fitted regression slopes, and the difference between the orientations tested using a standard *t*-test.

In addition, more detailed topographic information, together with the locations of grove boundaries, were obtained by determining elevations at 1 m intervals along linear transects oriented at right angles to the vegetation boundaries, and spanning multiple grove–intergrove cycles, and by direct measurement with tapes. Several tape transects were run for up to 0.5 km, in order to obtain data on 15–20 wavelengths of the banded pattern. These are used to look for relationships between intergrove and grove dimensions.

The projected cover of foliage and fallen litter were estimated by point-counting at 1 m intervals along multiple 50 m line-intercept transects oriented haphazardly within the groves.

Soil samples were collected along the transects used to map detailed microtopography. At 2 m intervals, a steel core cutter was used to remove samples of 100 cm³. These were sealed in bags and later dried at 105°C for 24 h and gravimetric water content determined from the weight loss. Bulk density was then calculated from the dry soil weight, following the procedure of Blake & Hartge (1986). Additionally, at 1 m intervals along the same transects, a Proctor penetrometer with a calibrated spring was used to determine the unconfined compressive strength (penetration resistance) of the soils.

As noted earlier, some models of vegetation banding suggest that continual upslope migration of the pattern should be exhibited. In 1995, we had erected permanent

monuments to mark the upslope borders of several groves at the field site. Monuments were also erected to mark the end points of two long transects crossing many grove–intergrove cycles. These have been re-visited and photographed episodically since, in order to document any shift in the position of the vegetation boundaries.

Results

The contour maps of the 0.5 ha plots (Figs 2–5), confirm the existence in the study area of both contour-parallel and oblique vegetation banding. The characteristics of each are summarized briefly below.

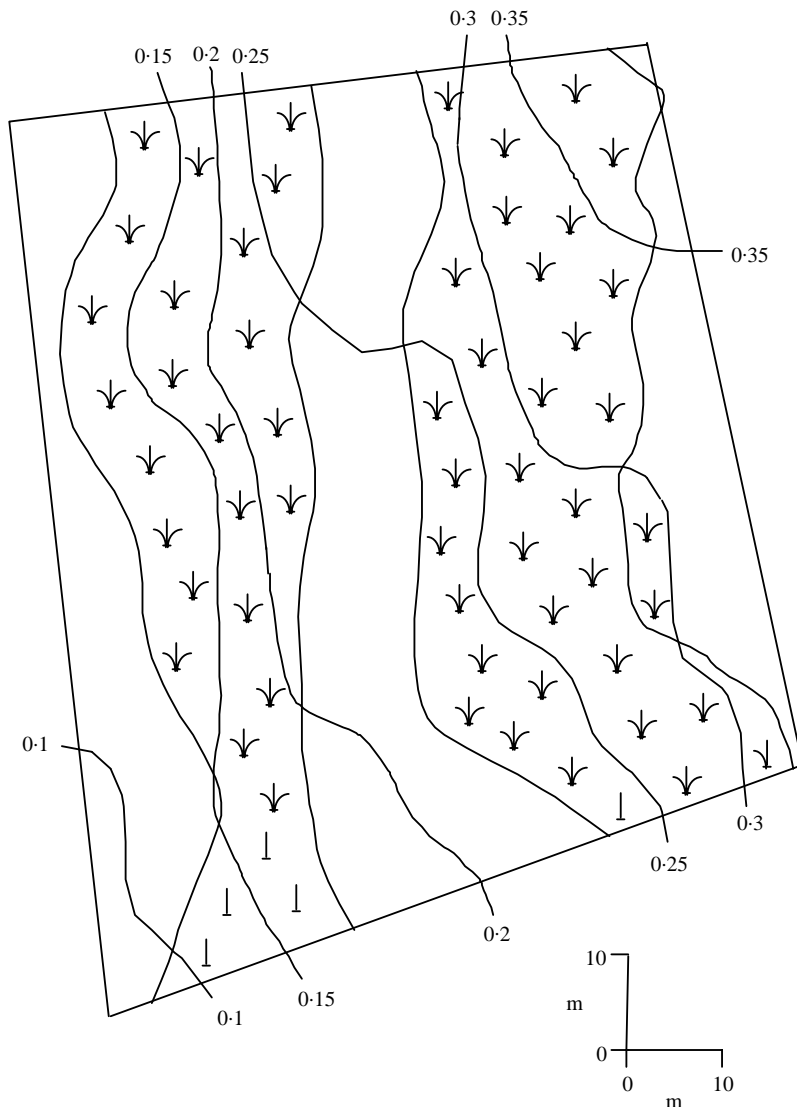


Figure 2. Contour map (with grove boundaries) of quadrat 1 at Menindee (contour-parallel banding). Contour datum is arbitrary.

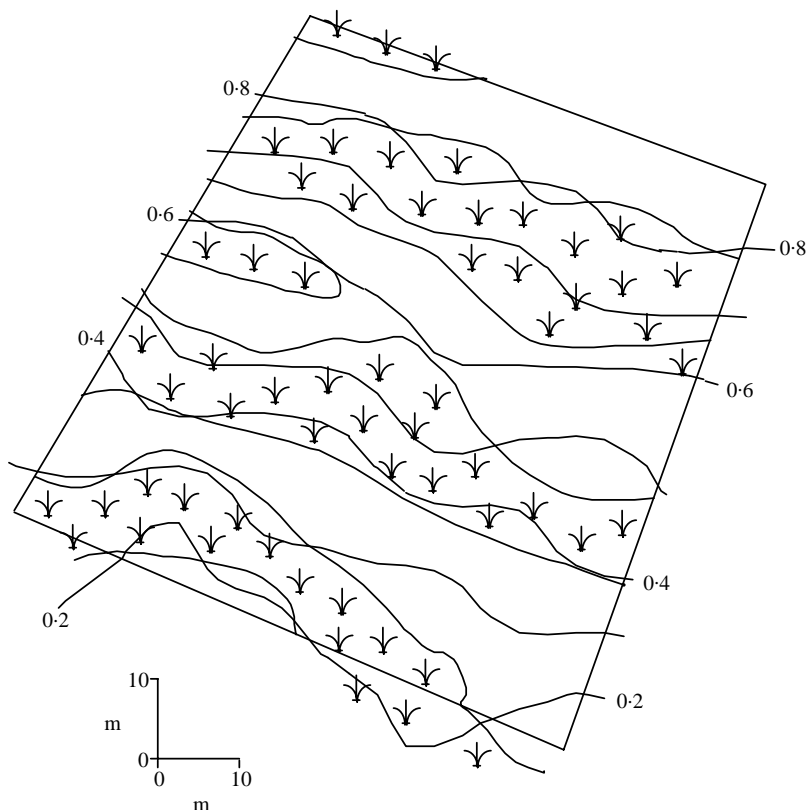


Figure 3. Contour map (with grove boundaries) of quadrat 2 at Menindee (contour-parallel banding). Contour datum is arbitrary.

Contour-parallel vegetation bands

These take the form conventionally regarded as typifying vegetation banding. Figures 2 and 3 show that individual boundaries do not remain precisely contour-parallel, though departure from contour parallelism is <10 cm over 75 m, so that the approximation to contour parallelism is close. Despite these small deviations, the vegetation bands as a whole are clearly oriented in a cross-slope direction. The numerical assessment of contour and vegetation band orientation employing linear regression demonstrated that at both sites, the mean trend of the bands was not significantly different from the orientation of the contours so that the grove boundaries are demonstrably contour-parallel (Table 1). The relatively large mean angular divergence of vegetation borders and the contour for site 1 is the result of marked contour curvature in one corner of the study plot. The study plot shown in Fig. 2 is very close to the site where the alignment of a boundary was surveyed by Dunkerley & Brown (1999), who found a mean departure from fixed elevation of 2.3 cm in a 100 m segment of the upslope edge of a single test grove. This figure is comparable to the <3 cm departure from fixed elevation of upslope grove margins surveyed in Western Australian groved mulga woodland by Mabbutt & Fanning (1987).

At both contour-parallel sites (Figs 2 & 3), groves were wider than intergroves, the mean ratio of intergrove/grove width being 0.76. Both quadrats have gentle slope

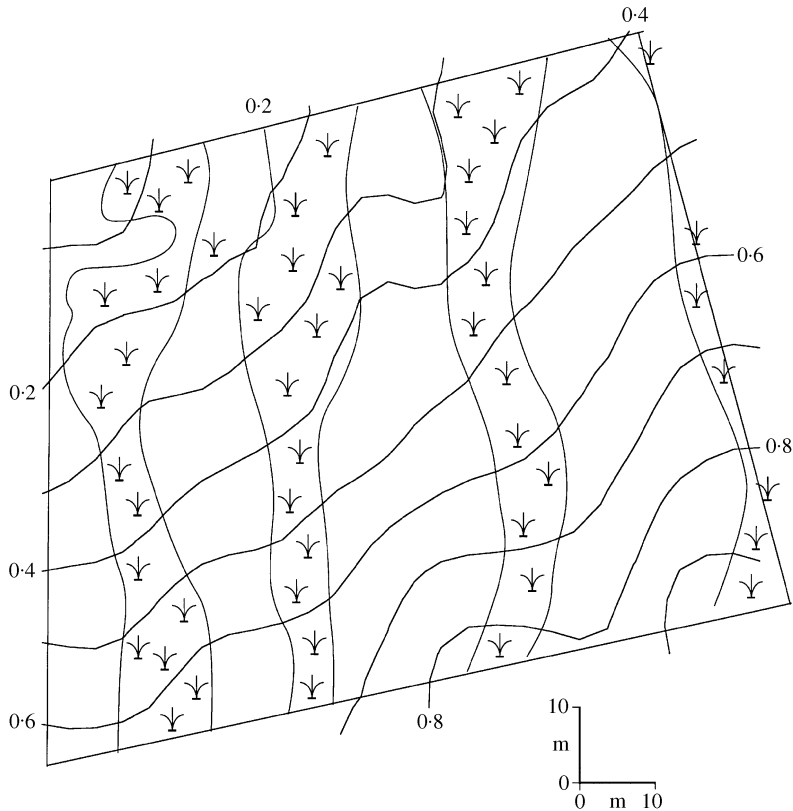


Figure 4. Contour map (with grove boundaries) of quadrat 3 at Menindee (oblique banding). Contour datum is arbitrary.

gradients, with the relative dimensions of intergroves and groves being quite variable (Table 2). Grasses and shrubs provided a foliar cover of 31–39% within the groves, whilst 21–23% of grove surfaces was bare (Table 3). Remaining areas carried a litter of fallen leaves. Intergroves have no vascular plant cover.

Oblique vegetation bands

Two study plots proved to contain oblique vegetation banding (Figs 4 & 5). These show quite a different configuration of groves and intergroves from the contour-parallel sites (Figs 2 & 3), and the regression analysis indicated that the orientation of the bands was significantly different from that of the contours (and in places grove borders were essentially orthogonal to the contour), so that these features warrant the name *oblique vegetation banding* (Table 1). The mean differences in the orientation of the grove boundaries and contours for the oblique banding plots were 10° and 42° . Furthermore, on the basis of the five evenly spaced transects measured along the runoff paths at each site (i.e. orthogonally to the contour, as for the contour-parallel sites, but here crossing the grove borders obliquely) the ratio of mean intergrove/grove widths is > 1 (Table 2), the mean being 1.39, which is in contrast to the mean of 0.76 at the contour-parallel sites. Thus, whilst in the contour-parallel sites, groves are notably wider than the intergroves, the reverse applies in the oblique vegetation

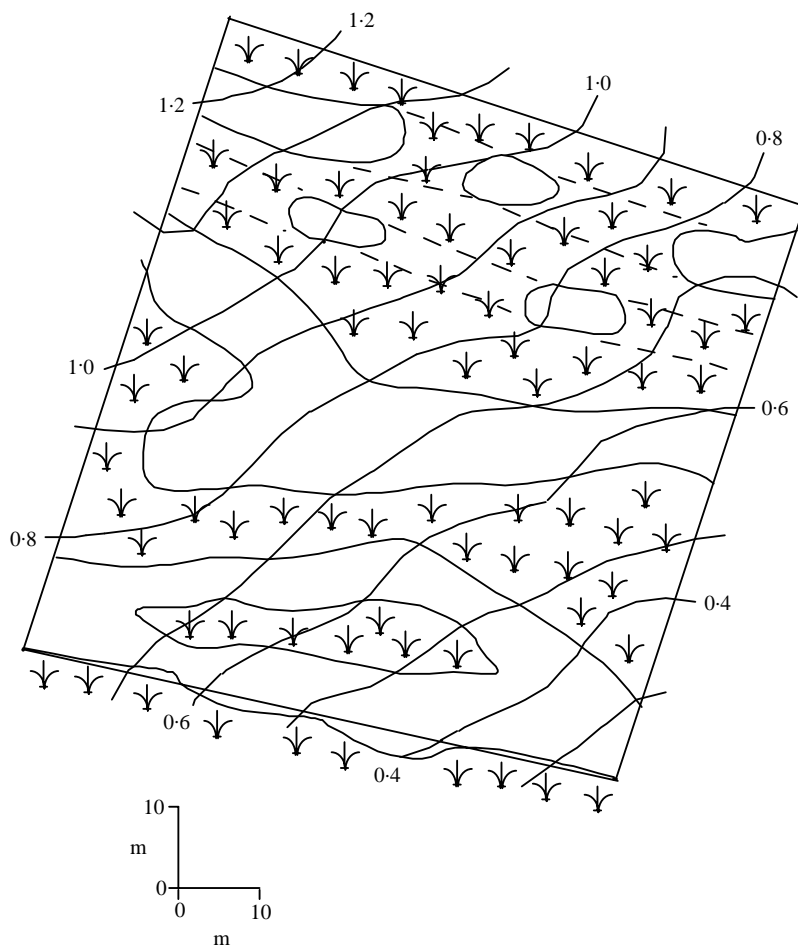


Figure 5. Contour map (with grove boundaries) of quadrat 4 at Menindee (oblique banding). Dashed lines indicate possible prior location of intergroves now partially vegetated. Contour datum is arbitrary.

banding. There are also evident differences in the pattern of vegetation bands, with a considerably higher variability of intergrove widths (and a somewhat larger variability of grove widths) in the oblique banding (Table 2).

Foliar cover was slightly higher in the contour-parallel vegetation bands than in the oblique bands (Table 3), and the mean difference is statistically significant at $\alpha = 0.05$ (small-sample *t*-test, Freund, 1974).

The variability of intergrove and grove widths on long downslope transects

Results of the 0.5 km tape measure surveys across multiple wavelengths of the vegetation banding were examined for the presence of any systematic relationship between intergrove width (taken to be no more than a general indicator of the volume of runoff, given that there may be variations in the efficiency with which runoff is shed from individual intergroves) and the width of the following grove (which should be

Table 1. *Results of the analysis of relative orientation of grove–intergrove boundaries and topographic contours for the four study plots*

Field site	Number of grove–intergrove borders digitized	Number of contour lines digitized	Mean angular divergence between grove–intergrove borders and contours (deg)	Probability of observed difference in mean orientations
Contour-parallel 1	3	4	16.6	0.07
Contour-parallel 2	5	7	2.9	0.19
Oblique 1	7	6	41.8	<0.0001*
Oblique 2	8	8	9.7	0.03*

*Indicates a difference statistically significant at $\alpha=0.05$.

wider when more runoff water is available), by regressing grove widths against upslope neighbouring intergrove widths. Regression is used as a suitable tool with which to explore the dependence (if any) of grove width on the upslope neighbouring intergrove. Sample sizes in this analysis are set out in Table 4, and included on the longest transect 21 intergroves and the following 21 groves. These transects did not span the entire length of gentle slopes in the study area, some of which extend for kilometres. In only one case from the five long transects analysed was a statistically significant relationship found (small-sample *t*-test, Freund, 1974; Table 4), in which a positive correlation was shown. In the remaining cases, no relationship between intergrove width and grove width was exhibited.

Soil properties—evidence of redistribution of materials in runoff

The study sites were observed only during rainless weather. In order to infer whether there is commonly a runoff source upslope and a runoff sink within the groves of the oblique banding, as is known to be the case in contour-parallel banding, selected soil properties were examined. It has been shown previously from contour-parallel banding in this area (Dunkerley & Brown, 1999) that the bulk density and compressive strength of the soils tend to increase toward the lowermost parts of

Table 2. *Dimensions of intergroves and groves within the four Menindee study quadrats. All widths were measured along the runoff path (normal to the contour)*

Site	Mean (S.D.) of intergrove width (m)	Mean (S.D.) of grove width (m)	Ratio of mean intergrove/grove widths
Contour-parallel 1	15.02 (5.00)	21.85 (3.00)	0.687
Contour-parallel 2	9.63 (4.82)	11.48 (4.11)	0.836
Oblique 1	26.51 (11.48)	15.82 (4.75)	1.675
Oblique 2	13.44 (12.23)	12.11 (6.08)	1.109

Table 3. *Details of slope gradient, foliar cover, and other surface conditions at the four Menindee study quadrats*

Site	Mean projected foliar cover (%)	Mean projected litter cover (%)	Mean projected bare soil cover (%)	Mean slope gradient (deg)
Contour-parallel 1	39.0	38.8	21.1	0.23
Contour-parallel 2	—	—	—	0.55
Oblique 1	30.6	45.6	23.8	0.57
Oblique 2	35.3	43.7	21.0	0.61

each intergrove. It has been inferred that this reflects the delivery of clays, salts, or other binding materials carried with the runoff water arriving from upslope. Future work will be directed to a fuller analysis of soil composition, and an investigation of the controls on bulk density.

Figure 6 shows these soil properties from the detailed transect across the oblique banding of Fig. 4. There is a very clear and coincident peak in bulk density and compressive strength in the lowermost intergrove or uppermost grove soils, and these peaks appear in each wavelength of the repeating pattern. Indeed, the systematic variation in soil properties is more marked and more consistently present in the oblique bands than at contour-parallel sites studied previously (e.g. see data in Dunkerley & Brown, 1999). It is not clear why the peak in compressive strength is sometimes located in the lowermost intergrove but may also occur in the uppermost grove. We speculate that this may relate to the position of occasional preferred pathways along which water passes from the intergrove into the grove, carrying with it suspended clays and/or dissolved salts, which modify the properties of the receiving grove soils.

Observations of shifts in the position of grove boundaries at Menindee

The time-series of photographs of the monumented locations (Fig. 7) showed no detectable shift in the position of individual grove–intergrove boundaries since 1995.

Table 4. *Relationship between intergrove and grove dimensions from five long transects crossing multiple wavelengths of vegetation banding at Menindee*

Transect number	Mean grove width (m)	Mean intergrove width (m)	Number of cycles of vegetation banding (length of transect, m)	Correlation coefficient, intergrove width with grove width
1	13.4	12.5	19 (493 m)	0.022*
2	17.3	14.9	11 (354 m)	0.088
3	17.5	11.7	16 (466 m)	0.504
4	21.9	11.5	13 (435 m)	0.238
5	8.0	14.3	21 (468 m)	0.171

*Indicates statistically significant regression relation at $\alpha=0.05$.

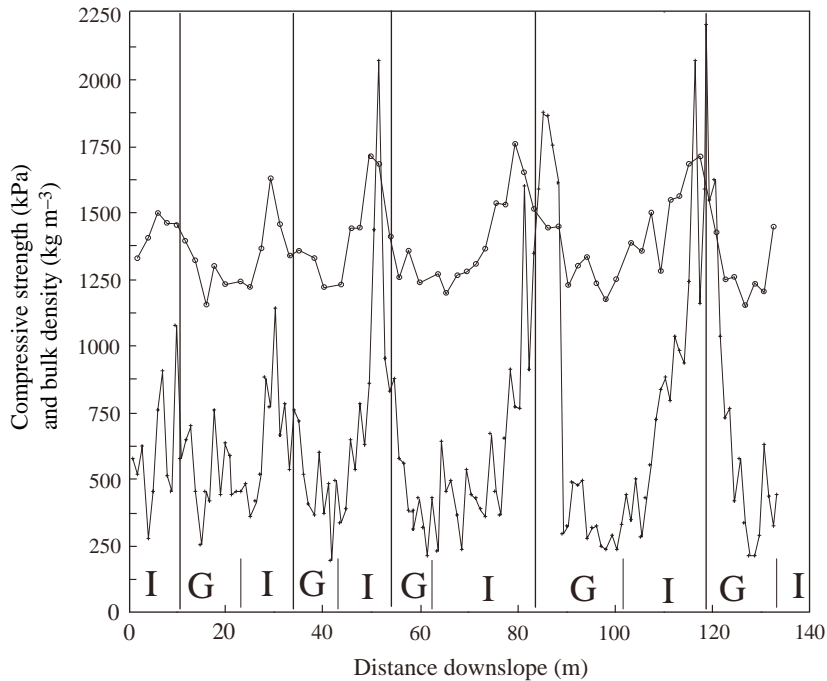


Figure 6. Soil bulk density and compressive strength results from a transect across Menindee quadrat 3 (oblique vegetation banding). G indicates grove, I indicates intergrove. (○) compressive strength, (+) bulk density.

Indeed, the same grass tussocks can be identified along the grove margin in both photos. In 2001, we extended these results by re-measuring two long profiles first surveyed in 1995, that spanned multiple cycles of grove and intergrove. Results (Fig. 8) show no evidence of systematic migration of grove–intergrove boundaries, the majority of which remained in place within the limits of measurement accuracy (typically, <0.5 m). The upslope edge of grove 4 (Fig. 8) was displaced downslope in 2001, but this small motion could be accounted for by the death of one or two shrubs close to the line of the transect. The shrubs here can be quite widely spaced, so that the death of one, with a resulting gap in the grove border, would have been mapped as an indentation in that boundary.

Discussion

Several new findings were encountered in the field results just presented. To our knowledge, the contour maps (Figs 2–5) are the first precise field data analysing the orientation of multiple wavelengths of vegetation bands in relation to the slope on which they are developed, and showing oblique vegetation bands. These data also appear to be the first examination of variation in the detailed morphology of vegetation banding within the same local climate and soil environment.

The existence of both contour-parallel and oblique vegetation banding in the study area poses several questions. First, in bands oriented obliquely to the contour, all water flow paths across intergroves and groves are longer, in proportion to $\cos(\alpha)$, where α is the angle between the contour and the grove margin, than would be the case

if those same bands were rotated to become contour-parallel. Oblique bands thus in effect provide wider intergroves with a longer runoff fetch, as well as longer flow paths through groves. Thus, at oblique site (1), the mean intergrove width measured along the runoff path was 26.5 m, which exceeds by 77% the mean width at contour-parallel

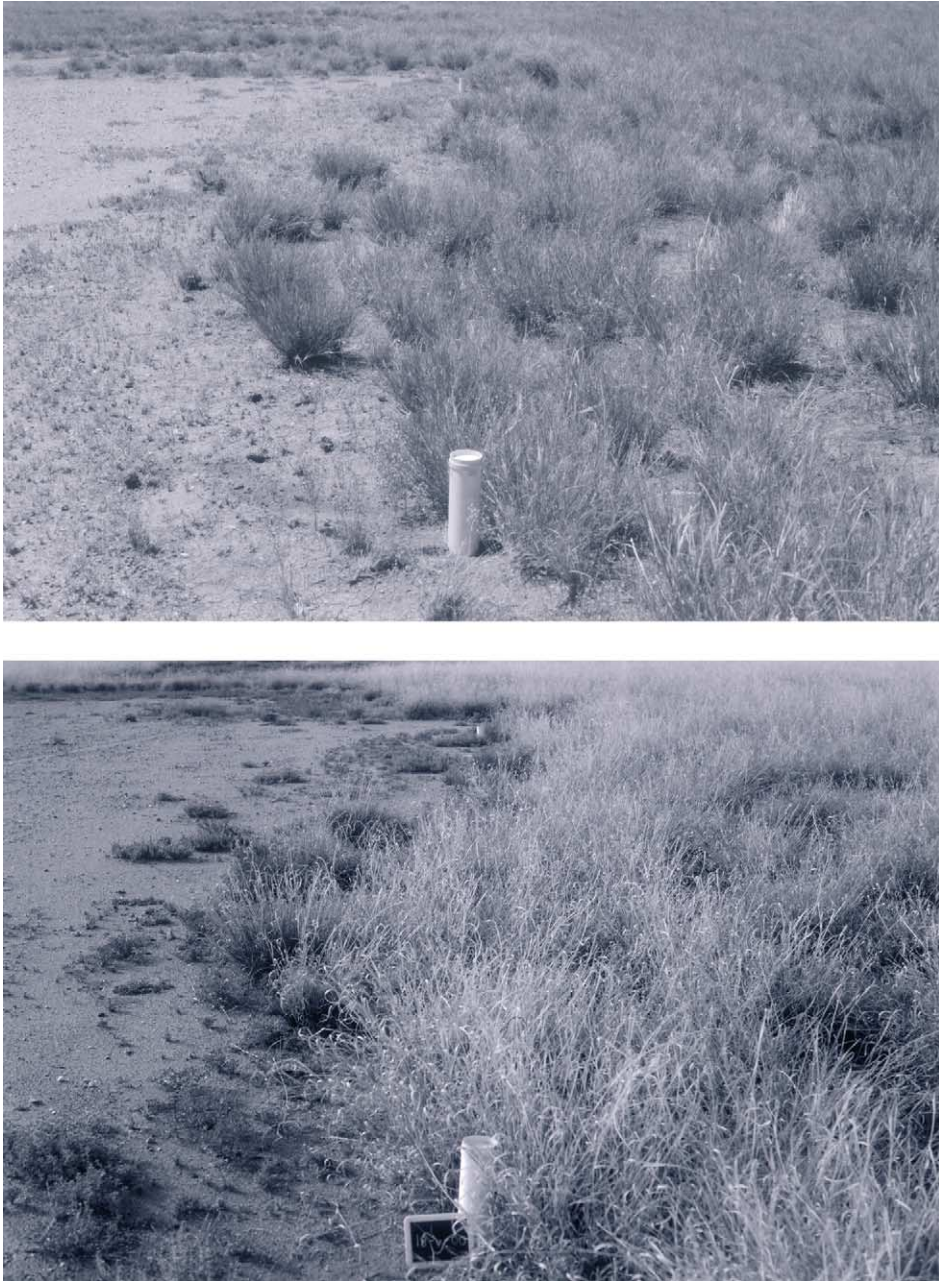


Figure 7. Photos of a monumented grove margin in contour-parallel vegetation banding at Menindee taken in 1995 (upper) and in 2001 (lower). Downslope is to the right of the photo. The two marker cairns are 15 m apart.

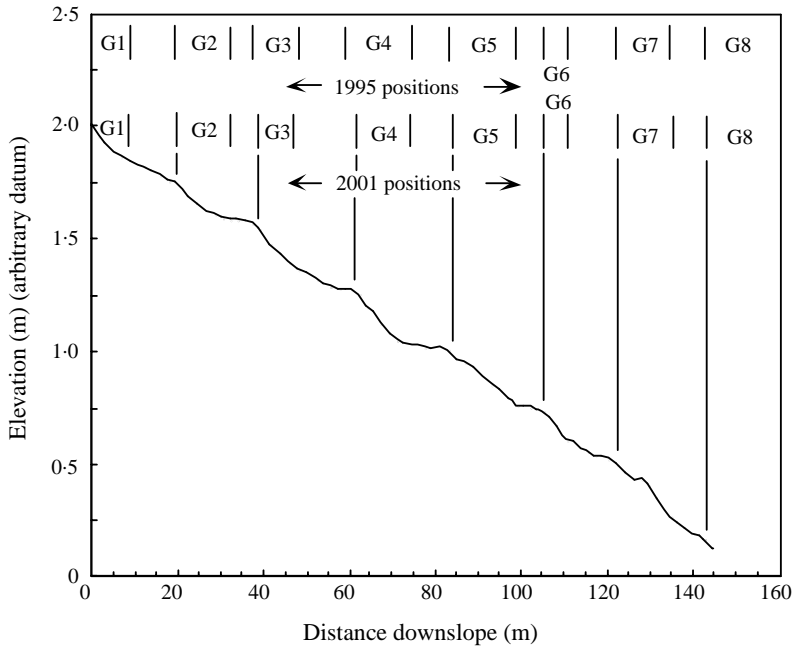


Figure 8. Grove margins plotted on a 150 m transect across contour-parallel vegetation at Menindee, showing positions in 1995 and in 2001. Note the only major shift in the position of a boundary is the downslope displacement of the upslope edge of grove 4. The lower part of the diagram indicates the slope form, based upon 88 points fixed with a digital theodolite. This shows how slope typically flattens toward lower intergrove, and steepens in the uppermost grove.

site (1) (mean 15.0 m). Given that these two plots were only about 1 km apart and likely to experience almost identical annual rainfalls, this finding does not accord with the suggestion noted earlier that, in a mechanistic view of vegetation banding, the intergrove width is adjusted to provide a runoff volume adequate to support the groves. Instead, the oblique intergroves would be expected to shed about 77% more runoff into the associated groves than would the nearby contour-parallel intergroves. This indicates a need for more formal measures of intergrove width incorporating a measure of intra-site variance, to provide a sound basis for assessment of whether indeed intergrove dimensions change systematically along climatic gradients. Only with such data can we be sure that a putative climatically determined trend in intergrove widths actually exceeds the within-region variability.

The intra-regional variability of intergrove widths just noted poses difficulties for the widely accepted view that banded vegetation is a community-level adaptation to the limited availability of soil moisture in the landscape. The ratio of grove to intergrove width at the contour-parallel sites was 0.76, but 1.39 at the oblique sites. In other words, the wide oblique intergroves were associated with narrow groves, whilst the narrower contour-aligned intergroves appear to support much wider groves. This is difficult to reconcile with the observation that the same storms would pass across both sites and, given the similarity in surface soils, that a square metre of intergrove at both sites should shed about the same volume of runoff to the neighbouring grove. This difficulty is increased by the finding that at the oblique sites, where there should be more runoff water available to each square metre of grove, the foliar cover (reflective of tussock density within the grove) is actually lower, despite the greater volumes of runoff water potentially able to support plant growth (Table 3).

Finally, the long tape-measure transects revealed that the majority of sites exhibited no systematic relation of intergrove width to grove width, based on many more wavelengths of the banded pattern. Indeed, these results show that individual intergrove/grove width ratios range widely (4.95–0.21). These transect-based width measurements neglect any flow convergence or divergence related to contour curvature, and this might account for some of the evident lack of accord between the dimensions of presumed intergrove runoff sources and the groves that depend on the runoff water delivered from upslope. Nonetheless, we believe that added to the results already presented, these data pose significant difficulties for any mechanistic view of vegetation banding.

Careful studies of the water balance of banded vegetation have also suggested results not completely in accord with the mechanistic, hydrologic view. For example, Seghieri & Galle (1999) performed a multi-year experiment on banded vegetation in Niger. They found that runoff water was not essential to the life cycle of shrubs in parts of the grove, but rather escaped to deep drainage, and was lost to the plants.

Overall, our findings do not accord well with the mechanistic view of vegetation banding as a phenomenon arising primarily from the water requirements of groves and the intergrove dimensions (runoff source area size) required to meet these needs. The Menindee vegetation banding shows, within an area of only 4 km², intergroves narrower than their associated groves (at the contour-parallel sites) and intergroves considerably wider than their associated groves (the oblique vegetation banding), as well as large fluctuations in intergrove–grove width ratios (and in general, no significant correlation between intergrove and grove widths) in long transects in both forms of banding. Soil surface features, including infiltration properties, in the intergroves and groves seem likely to be very similar, given their common parent material, close proximity, and floristically closely similar plant cover. The direct observation of runoff and infiltration is difficult in this remote location, where major rain events are rare. Nevertheless, this appears necessary in order to verify that the runoff behaviour of intergroves at the contour-parallel sites is indeed similar to that at the oblique sites. On the presumption that the intergroves are similar in their hydrologic behaviour at the parallel and oblique sites, the findings just discussed are more in accord with a system instability conception of vegetation banding, where surface hydrology is not the primary determinant of pattern creation and can therefore vary in response to some other influencing factor (as yet not known), than of a mechanistic model in which band dimensions are supposedly attuned sensitively to the local climate, and to maximizing water availability to grove plants. One of us (DLD) recently visited the Menindee field site a few weeks after heavy rains had fallen there. In the oblique banding, there were abundant signs of runoff leaving the downslope edges of many groves, as well as of water flow within the groves. Sediment plumes, small proto-rills, and litter dams all suggested that there had been integrated runoff passing through the oblique banding. However, in the nearby contour-parallel banding, no signs of surface runoff were observed. This suggests that the wider intergroves and narrower groves in the oblique banding may have generated more surface runoff than could be absorbed within the groves, leading to a loss of water from the system, whilst the contour-parallel bands trapped all runoff. This provides a further example of significant intra-site variability in hydrology that is not in accord with the idea that these systems are adjusted to maximize water derived from local rainfall. Unfortunately, owing to the lack of any meteorological recording stations in the vicinity of the study site, we have no data on the size of the rain events that produced the runoff just described, or on the distribution of rain event magnitudes that influence the growth patterns of the local vegetation.

On the other hand, the finding that the grove–intergrove boundaries have remained absolutely fixed for nearly 6 years, does not accord with the system instability models that require continuing upslope progression of the pattern. For example, the model of

Klausmeier (1999) required that grass bands migrate upslope by $1.4-1.9 \text{ m year}^{-1}$, or by a distance of 8–10 m during the period of our observation of the Menindee sites, whilst our field observations have detected no systematic displacement whatsoever.

One possible interpretation of this lack of accord is that the model of Klausmeier (1999) requires some modification in order to correspond better with actual field conditions. However, this lack of accord between model prediction and our field data may simply reflect the perturbing role of pedologic development in a runoff–runon system. In the field, soils of the intergroves undergo progressive loss of materials carried away with runoff water, and these build up where the water ponds and is absorbed, in the lowermost intergrove and adjacent upper grove, where very high bulk densities and compressive strengths consequently arise (see Fig. 6). Thus, as pointed out by Dunkerley & Brown (1999), soils that are extremely dense and hard develop just above the intergrove–grove boundary. These pose an obstacle to the lodgement and germination of seeds. The soils of the lowermost intergroves were shown above to exhibit penetration resistances of $>2 \text{ MPa}$, and Dunkerley & Brown (1999) reported values in this same area of $>4 \text{ MPa}$. Though we are aware of no data on the ability of the roots of chenopod shrubs or the local tussock grasses to extend through soils having such high penetration resistance, these values do exceed those known to inhibit the root development of crop and pasture species (Taylor *et al.*, 1966; Blanchar *et al.*, 1978), and may provide some similar inhibition for the vegetation at Menindee. Additionally, a small surface ridge resulting from sediment deposition is built up at the lower intergrove, and becomes a factor promoting ponding of runoff water and its gradual redistribution by overflow into the grove. In other words, the presence of an intergrove and a following grove, together with runoff, sediment translocation and re-deposition, modify the local soil and hydrologic environment in ways that would mitigate against any free upslope migration of the vegetation pattern which might otherwise occur. In their pioneering study of mulga grove country in Western Australia, Mabbutt & Fanning (1987) showed that there were differences in depth to soil hardpans beneath intergrove and grove. The period of time likely to be required for this kind of deep soil differentiation led them to infer that the pattern might have had its origin in the late glacial or Holocene, and thus that there was a ‘... considerable stability of banding patterns...’ (Mabbutt & Fanning, 1987, p. 58). Similar conclusions were suggested by comparing co-registered aerial photographs of vegetation banding in chenopod shrubland at Fowlers Gap, 115 km north of Broken Hill NSW, taken 20 years apart, and in photographs of groved mulga NW of Alice Springs, Northern Territory, Australia, taken 22 years apart, where no evidence of systematic pattern migration could be detected, judged against reference points (roads, fencelines) visible in both sets of images (Dunkerley, unpublished). Likewise, Mougnot *et al.* (1996) were not able to confirm consistent upslope migration in a study of time-sequence aerial photographs of vegetation banding in Niger, though they did report a pattern in which shrubs and trees were younger toward the upslope parts of groves, and older downslope.

These considerations suggest that models of vegetation banding should incorporate a module to account for the pedologic changes that follow the partitioning of the surface into runoff and runon zones. In particular, if high penetration resistance in the lowermost intergrove does inhibit plant growth there, then upslope migration may not be required, bringing the system–instability models into agreement with our field evidence that at Australian sites, vegetation banding does not migrate upslope.

The soil bulk density and compressive strength data showed very clear patterns related to position in the intergrove–grove cycle that are further indicative of stability in the location of the pattern components. Notably, both bulk density and compressive strength reached local peaks toward the bottom of the intergrove and/or in the immediately adjacent parts of the following grove. This pattern was particularly clear and well developed in comparison with similar data from contour-parallel vegetation

banding. This suggests that there has been more systematic sorting of materials, or perhaps a greater delivery of clays and other materials to the lowermost intergroves, in the oblique case. This might be expected, since the intergroves here are relatively wide (and the groves narrow) in comparison with the contour-parallel site. This would provide a larger contributing area from which clays and salts could be sourced and carried to the lower intergroves by surface runoff.

It therefore seems likely that processes of soil differentiation, and the attendant consequences for seed lodgement and germination, may inhibit any tendency for pattern migration in some banded vegetation communities. Therefore, one hypothesis to account for the contour-parallel and oblique Menindee vegetation bands is that their origin relates to a system instability, perhaps of the competition-co-operativity type. Numerical models of band development (e.g. Klausmeier, 1999) show greater divergence of band orientation from contour-parallelism in the early iterations of the model. These irregularities in the pattern are progressively eliminated from the model as repeated iterations are run. No scale of real time is attached to these models. However, Dunkerley & Brown (1995) suggested an antiquity of some millennia for chenopod shrubland vegetation banding in western NSW, the development having commenced when glacial aridity began to be replaced by early Holocene warmth and higher rainfalls. If the differentiation of soils across intergroves became sufficiently marked in the early phases of this development, then it may be that the pattern of groves at the Menindee site has been fixed at the form developed early in the developmental process, so that morphological development was in effect halted. The evaluation of this hypothesis requires more evidence than we currently possess. The implications are potentially important, however. If the scenario just outlined is valid, then observations of modern hydrology in the oblique vegetation banding at Menindee can do no more than describe the behaviour of a system that is not fully developed, and it will prove difficult from the results to understand the true origin of the vegetation banding. Indeed, this may also apply to the classical, contour-parallel vegetation banding. If soil differentiation also anchors these systems so that no upslope progression is possible, then these also may have failed to develop to what would otherwise have been their equilibrium morphology. Indeed, vegetation banding commonly exhibits irregularities such as Y-junctions between adjacent bands. Various models of vegetation banding predict this, but only in the early stages of pattern development (e.g. Dunkerley, 1997; Klausmeier, 1999). Therefore, the persistence of such irregularities in the Menindee area and elsewhere may suggest that the pattern of banding has been prevented from advancing to a fully developed condition.

The lack of upslope migration at Menindee raises a number of possibilities. It may be that some instances of vegetation banding do exhibit upslope migration, or the evidence may be confused with temporary plant growth following good rains. Alternatively, as suggested above, it may be that vegetation banding patterns are able to migrate, but only until pedologic changes, including the development of extreme soil penetration resistance, prevent this, fixing the groves in position. In some soils, perhaps those of sandy texture, this stage may not be reached, allowing upslope migration to proceed.

Conclusions

Investigation of the diverse vegetation banding in the Menindee region of New South Wales has demonstrated that much in the origin and functioning of these landscapes remains to be understood. Considerable intra-regional variability in intergrove-grove width ratios was shown. This is not consistent with the widely supported view that the dimensions of intergroves are sensitively adjusted to supply the additional runoff water

required to support the neighbouring grove, as a community-level adjustment to dry environmental conditions. Nor is the fixed position of the contour-parallel banding consistent with many models that suggest that patterns should undergo continual upslope migration. Finally, no secure explanation can yet be offered for the development of the oblique vegetation banding reported from Menindee.

It appears that in order to make further progress in understanding vegetation banding, more multi-year studies quantifying pattern migration (or the lack of it) are required. Alongside these, we require more detailed mapping of pattern orientation and more evaluations of the intra-regional variation in pattern geometry. Verification in other areas of sizeable intra-regional variability of intergrove-grove width ratios as documented here will cast additional doubt on the appropriateness of the mechanistic, hydrologic view of vegetation banding. We believe that these systematic aspects of landscape ecology are of sufficient significance to warrant the additional investigative effort.

The evidence presented from Menindee raises the classical issues of the unravelling of form, process, and evolution. This is a common stumbling block in the study of landscapes and their evolution, and the principle of *equifinality* expresses the notion that different developmental pathways may result in the same final form. Describing the form and its operation once fully developed clearly does not necessarily serve to identify the developmental pathway that was followed. For example, Goudie *et al.* (1992) described a landscape of strikingly parallel tree groves with intervening grassland in the Kimberley region of Western Australia. However, these were developed on a level surface, with no evident runoff-runon pathways. The hypothesis raised to account for these was that the groved distribution of plants reflected initial differences in the underlying soil materials, perhaps related to the positions of former wind-blown dunes that had been eroded from the landscape. Clearly in this case, understanding present-day landscape hydrology cannot serve to indicate the origin of the groves.

The identification of developmental pathways is made more challenging if the development process involves regenerative mechanisms (positive feedback), and this appears to be the case with vegetation banding. If such processes are important, then the boundary conditions, or initial form that provides the 'starting-point' for the development, can become highly critical, and subtle changes in this can lead to very different outcomes. The possibility that vegetation banding becomes fixed at any early stage of development, rather than proceeding to a mature state, further complicates attempts to resolve the actual origins of this widespread community structure.

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