



Banded vegetation: survival under drought and grazing pressure based on a simple cellular automaton model

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In western NSW, Australia, banded vegetation communities in grassland and shrubland remain widespread after up to 150 years of livestock grazing and a number of severe droughts. A simple model based on cellular automata is employed to investigate the robustness of such communities. It is shown that grazing pressure, simulated by the loss of plants at random within the landscape, has little effect on survival of the banded structure, unless pressure is extreme. Drought, associated with the systematic loss of plants in the driest locations, results in more extensive band fragmentation. The model suggests that these seemingly sensitive runoff–runon systems are in fact quite robust, and may well have changed little morphologically since European settlement. Species composition and plant age structure may, however, have been affected.

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Introduction

Banded vegetation communities consist of generally contour-parallel groves of plants separated by areas that are largely bare (e.g. Macfadyen, 1950; Mabbutt & Fanning, 1987; Tongway & Ludwig, 1990). The width of groves and intergroves is commonly a few tens of metres. Banded plant communities have been described from semi-arid and arid grasslands, shrublands and woodlands. An example from a mixed grassland–shrubland is shown in Fig. 1. The landscape is a mosaic of runoff source areas and vegetated runon water sink areas. The runon zones have high infiltration capacities, efficiently retaining water from upslope, and thus manage to sustain a dense plant cover despite regional aridity. For example, Cornet *et al.* (1988) reported that in the Chihuahuan Desert of Mexico, groves received on average water totalling 150–250% of the mean rainfall, including water from runoff generated upslope. In detail, the vegetation mosaics contain more than the two broad elements or components just described. Often, there are recognisable sub-components within the vegetation, three being mapped by Cornet *et al.* (1988), including a ‘pioneer’ component at the upslope



Figure 1. Aerial photograph of banded vegetation in mixed grassland-shrubland in western NSW, Australia. The dark patches are cloud shadows.

margin of the vegetation. Deeper-rooted species may preferentially occur toward the downslope margin of a band. Likewise, within the unvegetated bands, there may be zonations such as a greater cover of surface stones toward the downslope margin.

Banded vegetation communities have a subdued microtopography associated with the runoff-runon processes. The upslope margin of the zones of plants occupies a break in slope where slope gradient is at its maximum of perhaps 0.5° . Below this, the slope profile flattens progressively toward the upslope margin of the next vegetation band, declining to perhaps 0.1° . The microtopography appears to reflect aggradation of the lower parts of the unvegetated zones, toward which water, sediment and organic detritus are washed by surface runoff. This ensures that the vegetated bands are steeper than the bare zones. Despite this, the vegetation creates a water sink, while the gentler bare areas are runoff sources. This comes about because of the strongly contrasting surface characteristics of these zones. Better soil structure and greater porosity arise from additional organic matter under the plants, and sealed, impermeable surfaces produced by raindrop impact on the bare soils are major contributors to the differences in infiltration behaviour.

Water shed from the bare zones trickles towards their very flat downslope margins, where deposition of detritus often creates a very subtle contour-parallel ridge. This impounds the runoff water, which gathers into shallow ponds that spread laterally across the slope. Even a few millimetres of rain has been observed to create such ponds in the landscape shown in Fig. 1. From these ponds, water slowly infiltrates and also trickles downslope among the plants, where it is absorbed so strongly that none appears to escape from the downslope margin of the band. The development of ponding at the upslope margin of vegetated bands favours the distribution of available water among the plants occupying the upslope margin of the grove and thence, by seepage, among the plants within the grove.

This gross hydrologic functioning of banded vegetation as a runoff-runon system is

relatively clear. The origin of banding itself has been disputed, a number of early ideas on the development of banding having been reviewed by Dunkerley & Brown (1995). These included the view that banding represents a pattern arising from the colonisation of an originally bare site, with seed lodgement and germination being related to the development of contour-parallel litter dams. Diametrically opposed to the colonisation view is the idea that the bands evolve as a denser plant cover is thinned out by climatic deterioration or by grazing pressure. Dunkerley & Brown (1995) concluded that banding in a chenopod shrubland north of Broken Hill in NSW predated European pastoralism at the site, and saw grazing pressure rather as a potential threat to the survival of the patterning. However, insufficient historical data exist to test these ideas, so a simple model was designed to begin the investigation into the links between grazing pressure and pattern survival.

Few formal models of the development of banding have been designed. Goodspeed & Winkworth (1978) presented a grid-based computer simulation of grove development in banded communities of the mulga tree (*Acacia aneura* F. Muell.) that have been described from several locations in semi-arid Australia (e.g. Tongway & Ludwig, 1990). According to Goodspeed & Winkworth (1978), their model yielded a two-cycle grove-intergrove pattern aligned across the slope at about 45° to the contour. However, only 37 plants from the original 2500 survived in their 180-year-old distribution, and banding is not revealed in their published figures. Their model, in which plant reorganisation was driven by a steadily declining rainfall, indeed appears not to have accounted for the development of vegetation banding.

Dunkerley (in press) presented a model based upon a more physically realistic conception of runoff-runon behaviour and soil water recharge. A similar cellular automaton (CA) model was employed for this purpose. This model generated strongly developed banding without the requirement for climatic deterioration or grazing pressure. The conclusion drawn was that banding may represent the normal pattern of plant growth to be expected on low-gradient landscapes where aridity is too great for a uniform plant cover to exist. The banding was shown to provide better water retention on the slope, and to permit a greater vegetation cover than would otherwise be supported.

In the light of this conclusion, grazing pressure, and perhaps also drought, must be regarded as potentially capable of disrupting established banding. Two modified CA models are employed here to examine the robustness of established banded vegetation under such stresses.

The cellular automaton (CA) model: a brief description

Models based upon cellular automata are widely used in the study of spatial patterns and their development (Hogeweg, 1988; Green, 1994). In such models, the landscape is modelled as a tessellation or mosaic of rectangular cells. The evolution of the cell properties, such as the presence or absence of vegetation, is required to follow a set of rules which reflect the properties of neighbouring cells. The utility of this kind of model comes about because the exact physical processes underlying the water partitioning, some of which were mentioned above, are not yet documented in sufficient detail for their operation to be described in a process-based model. The model contained a tessellation of 2500 cells (50 × 50). A variable initial fraction of these, located at random, was denoted as occupied by plants, the remainder being bare. In each iteration, 100 mm of rainwater was distributed uniformly to all cells. Each iteration represents the aggregate effects of a notional 'year'. Individual storm events were not modelled. The rules for water partitioning were as follows: for a bare cell, 10% of the rainfall was absorbed but no runoff water, all of which was passed on to the cells downslope. This reflects what has been seen in the field, where the first few

millimetres of rain wet up the regolith surface, all other water (including any later runoff water from upslope) passing across the surface with little or no absorption. For cells containing plants, complete water absorption was specified. This was shared both laterally and downslope. Along the contour, the nearest neighbouring cells were each allocated 10% and the cells two removed were allocated 5% of the water received by the donor cell. Water was allocated according to the same rules to the two cells in the rows immediately downslope.

In developing the model, each cell was thought of as representing one square metre of surface. In the banded site near Broken Hill referred to earlier, and shown in Fig. 1, each square metre contains 5–10 grass tussocks and associated litter, rather than a single plant. Representing this in the model as a vegetated cell thus seems reasonable. For mulga, Pressland (1976) showed that the zone of increased infiltration rate around the tree base extended for a radius of at least 2 m, again in accord with the scale of spatial influence adopted in the present model.

In each iteration, all cells were inspected for soil wetness, represented by accumulated water depth. Cells too dry for plant growth were those with less than 1.2–3.5 times the annual rainfall (the value was varied as explained below). These became bare. Bare cells that were sufficiently moist were allocated plants, simulating successful germination and plant growth. This was done for soil moisture levels of 0.6–1.2 times the annual rainfall (the value was varied as explained below). It is necessary to permit colonisation at lower levels of soil water availability than found beneath established plants, since otherwise colonisation of unoccupied sites could not occur. The entire tessellation was dried out at the end of each iteration, bare cells totally, and cells carrying plants to 10 mm water depth. This procedure represents the annual loss of water by evaporation and transpiration.

Once an initial plant cover fraction was set out by random numbers, the model ran solely under the control of the water partitioning and plant survival rules just specified.

Drought and grazing pressure were modelled by adding a set of rules that resulted in the loss of vegetation cover. Prior to applying these plant eradication rules, which are explained below, the model was run for 20 iterations. This was sufficiently long for a stable pattern of vegetation banding to emerge, and was taken to represent processes prior to the introduction of stock, or a period free of severe drought.

Grazing simulation

The effect of heavy grazing pressure was simulated by the elimination of plants from a variable fraction of the cells at each model iteration. The cells were selected at random, so that no spatial pattern of effect was imposed. From 10% to 80% of plants were eliminated during various model runs. Very extensive devegetation has been observed in western NSW during dry years, under the combined pressure of stock, rabbits and goats. After stabilisation of the model, grazing pressure was eliminated to observe the trends in recovery of the banding.

Drought simulation

In contrast to the random plant loss in the simulation of grazing pressure, plants were eliminated in drought according to the available soil moisture in cells. In various model runs, the rainfall was reduced to 60 mm or less per iteration, resulting in the driest cells becoming devegetated. This applied a spatial unevenness to the devegetation, plants at the ends of bands, which relied on water derived laterally from neighbours, or plants at the downslope margin of a band, which received least runoff water, being most

prone to eradication. The drought conditions were sustained for up to two–five iterations to reflect the duration of persistent drought in the ENSO-moderated eastern Australian rainfall regime (Nicholls, 1991). The model results presented here were derived to reflect the conditions in the grassland shown in Fig. 1. For the case of shrublands or woodlands, with better drought resistance, the plant loss would not be as rapid as that invoked here, where death occurred after 1 year with inadequate soil moisture. As for the simulation of grazing pressure, the process of recovery in the plant community was observed during iterations following the return of rainfall to its pre-drought value.

Results

Contour-parallel vegetation banding was very clearly and strongly developed in the model during the first 20 iterations, when conditions were not varied. Up to seven or eight cycles of the grove–intergrove pattern were evident. The bands generally displayed quite sharp upslope margins, along which most cells contained plants. The downslope grove margins were more diffuse, both aspects matching those observed in the field.

Grazing impact

Grazing impact involving the spatially random elimination of up to 50% of the plant cover in each iteration had no sustained effect. The small random gaps in bands were rapidly recolonised in subsequent iterations. At higher levels of plant loss, more lasting effects became evident.

With 60% of cover eliminated at each iteration, the banding became slightly less regular, and plant cover became quite fragmented. Plant cover declined through about 20 or 30 iterations to a stable value about 5% lower than that with no grazing. For 70% elimination, the decline occurred more rapidly, in 15–20 iterations, and plant cover stabilised at 10% below the ungrazed level. In both cases, bare patches caused by grazing were located sufficiently closely that recovery was possible within 10 iterations.

Under even higher levels of grazing, plant cover declined dramatically. With 80% loss in each iteration, the vegetation cover fell to less than 2% within 50 iterations. At 85% loss per iteration, cover was eliminated completely, leaving a bare surface, in 15 iterations.

These results are illustrated in Fig. 2 which shows the trends in plant cover through a model run with 60% of plants removed by grazing at each iteration.

Interestingly, the results (e.g. compare iteration 50 with the original pattern at iteration 20) show that the banding pattern after recovery may be more regular than the initial pattern prior to grazing impact. Isolated small patches of plants evidently become eliminated by the overgrazing, and the linearity and lateral extent of the redeveloped bands is enhanced.

Drought impact

The impact of moderate drought on the banding was somewhat different. In all cases, the rather uneven downslope margin of the bands was subject to plant loss, so that the bands became narrower. Likewise, plants which had colonised the slightly less favourable areas between patches of plants, where lateral water sharing by seepage or surface ponding was vital to survival, were also prone to elimination. The vegetation

thus tended to break up into increasingly isolated but still contour-aligned patches, rather than continuous bands. This is illustrated in Fig. 3. Fragmentation of the bands was notably less severe than in the case of grazing impact described above, and some remnants of the upslope margins of bands persisted. However, the gaps produced in the bands were larger.

Figure 3 shows model results for a 2-year drought with rainfall 40% below normal (at 60 mm year^{-1}). At iteration 22, the end of the drought, the vegetation is fragmented into about 40 patches of varying size. The larger patches retain a strong cross-slope orientation, but the smaller ones are composed of only a single vegetated cell. When rainfall returns to normal, these patches extend laterally, producing strong banding, though less well structured than the pre-drought condition, within 10 iterations. By iteration 50, 28 'years' after the drought, banding is again strongly developed.

In a more severe droughts, when rainfall was lower or the drought duration greater, the plant cover was decimated. Often no vegetation survived. In the final year of a 5-year drought of 40 mm year^{-1} , only three small patches remained. However, by iteration 50 (25 'years' later), strongly developed banding had re-emerged, though only three bands were present. Some large remaining bare regions (and hence decline in overall plant cover fraction), at the top of the slope and elsewhere, were an artefact of the model, which does not incorporate upslope colonisation. In the field site, wind and other agencies would undoubtedly disperse seeds across such an area, and some reserve would also remain in the soil. In this case, essentially complete recovery of the vegetation could be expected. The actual timing of such recovery in years cannot be seen from the model, and would of course depend upon the actual wetness of the drought and subsequent years. The model incorporates only a stepwise return to a

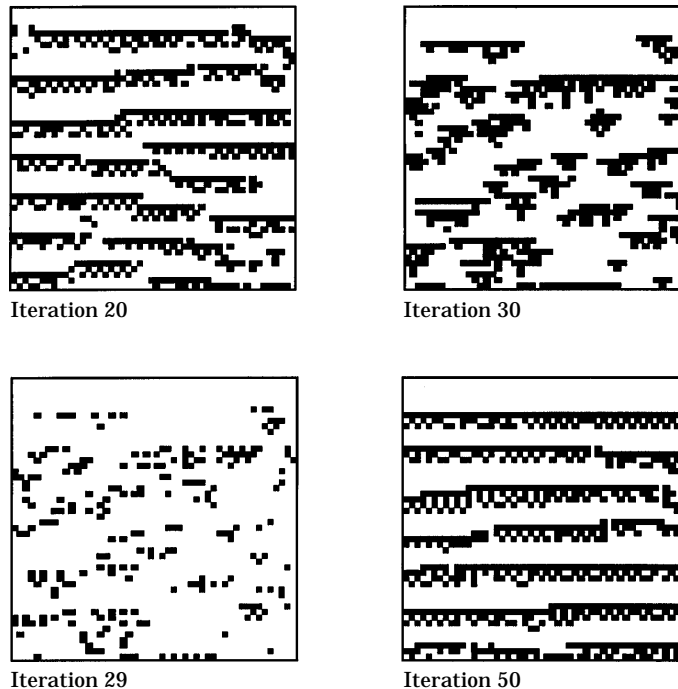


Figure 2. Sequence of CA modelled vegetation cover distributions. Well-developed banding at iteration 20 is replaced by a dispersed pattern after 10 'years' of grazing pressure (iteration 29). Rainfall 100 mm per iteration.

steady 100 mm of rain per iteration, and incorporates no processes such as deflation of the surface during the drought, which could well act to retard recovery.

Thus, according to the present model, drought is potentially more destructive of vegetation banding than is grazing pressure. But in droughts that are not severe, the efficient water use achieved in banded vegetation permits fragments of the bands to survive, with recovery of the original degree of patterning within 25 years.

The decline in plant cover for the grazing pressure and drought cases as shown in Fig. 4. This reveals that a 2-year drought with rain 40% below normal, and grazing pressure eliminating 60% of plants annually, each yield a decline of about 15% in plant cover. At their most devegetated, both models display about 10% remaining plant cover, but the structural arrangement clearly differs between the drought- and grazing-induced cases. In each case the recovery phase is the slowest, water retention gradually improving as the banded patterning is redeveloped.

Discussion and conclusions

In both the simulation of grazing and drought impacts, the loss of vegetation cover resulting from applied stress is rapid, declining by 10–15% in just a few iterations. Upon removal of the stress, recovery proceeds, though slowly. Time intervals of up to 15 or more iterations are needed for the re-linking of scattered patches of vegetation, even in the simulated case of an instantaneous and permanent removal of stress. The model suggests that plant cover levels return to their former values after this time, and that the strongly banded patterns are also redeveloped. Evidently, stresses of either kind can eliminate small patches of vegetation that formerly produced irregularities in

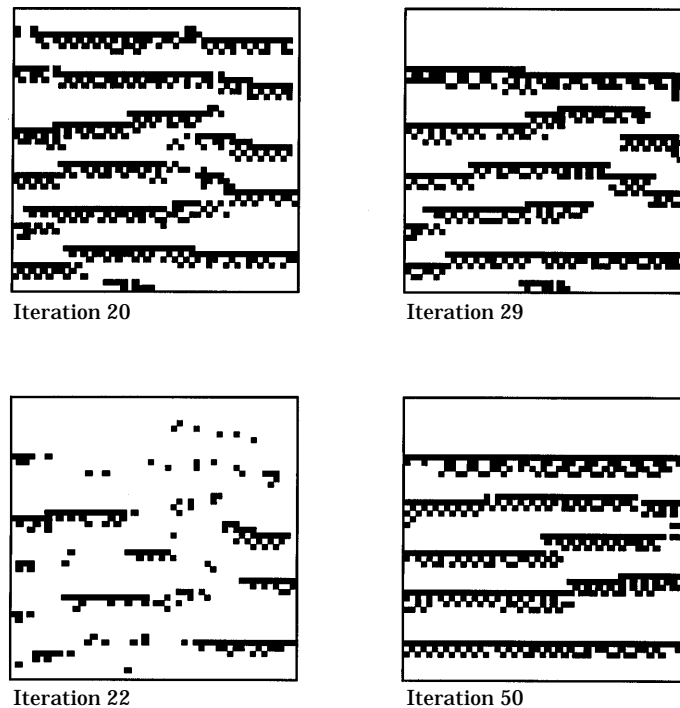


Figure 3. Sequence of CA modelled vegetation cover distributions. Contour-parallel patch pattern at iteration 22 resulted from 2 'years' of drought with a rainfall of 60 mm per iteration. Rainfall then returned to 100 mm per iteration.

the banded patterns, leaving the post-stress pattern more regular. If this behaviour applies in the field site portrayed in Fig. 1, as seems likely, then some of the strikingly regular and spatially extensive patterning evident there may have arisen from repeated episodes of stress in the periodic ENSO-related droughts that typify the environment of eastern Australia. Such periods of stress evidently favour the survival of plants within well-structured bands that trap available water most efficiently.

The results derived here depend upon assumptions inherent in the model, but not explicit within its simple structure. Foremost among these is that an adequate seed reserve exists within the soil, or that sufficient wind-transported seed can be dispersed across the site for germination of new plants wherever soil wetness is sufficient. The other inbuilt assumptions relate to the water partitioning rules. These rely on a tendency for surface sealing in soils not protected by a plant canopy, such that the soil surface becomes impermeable and generates surface runoff. This is certainly the case with the soils in the area shown in Fig. 1, which seal and shed runoff in as little as a few millimetres of rain. Finally, the model can only represent a surface of low gradient, where velocities reached by the surface runoff are insufficient to cause rill or gully cutting. If developed, such features would carry water rapidly beyond the site and disrupt the functioning of the runoff-runon mosaic. Low gradients are also conducive to surface ponding and lateral water sharing, as embodied in the model.

Recolonisation of the surface after drought also depends upon the action of many

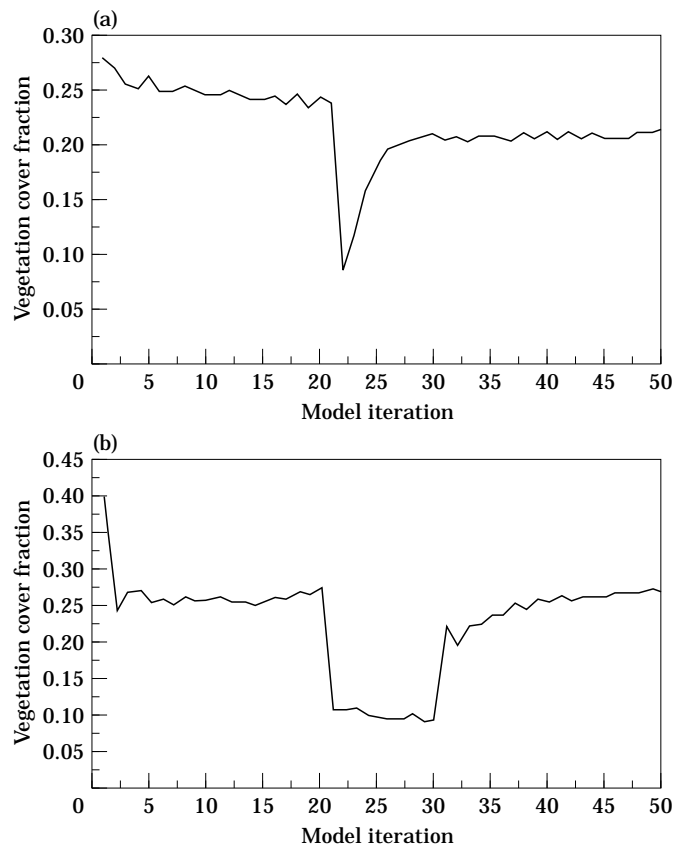


Figure 4. Time sequence plots of vegetation cover from the CA models of (a) 2-'year' drought having 60 mm rainfall per iteration and (b) 10 'years' of grazing pressure eliminating 60% of plants in each iteration. Rainfall 100 mm per iteration.

processes not made explicit in the model. Seed lodgement on bare surfaces is assumed to be readily possible. In the field, the prospects for this are probably enhanced by the provision of lodgement sites in desiccation cracks, against the residue of grass tussocks, and the like. The recolonisation process in the model proceeds only on the basis of the adequate availability of soil moisture. Thus, while trends may be adequately represented in the model, specific rates of processes such as recolonisation cannot be inferred from it.

Despite the several limitations of the CA model employed here, it nonetheless seems reasonable to conclude that banded vegetation patterning may be quite resilient in the face of drought or grazing stress. The effects of the two forms of stress are quite distinct, much more of the banded pattern evidently persisting in the face of moderate drought than under spatially random grazing pressure. In a study made in a banded shrubland about 120 km north-west of the site shown in Fig. 1, Dunkerley & Brown (1995) concluded from field evidence that banding considerably pre-dated the introduction of grazing stock. Thus, the banding was deemed to have persisted despite both drought and grazing pressure. In non-banded plant communities on floodplains flanking major creeks in that area, severe overgrazing at the turn of the century resulted in scalding whose effects persist today. These communities have thus been less resilient than the banded communities lying on the gentle footslopes above. This is consistent with the idea that banded vegetation is more efficient at retaining runoff water onsite, and hence at supporting plant cover under difficult conditions. Banded saltbush was recorded in the field area of Dunkerley & Brown (1995) during surveys carried out in 1968 (Mabbutt *et al.*, 1974). These patterns have thus persisted through several severe droughts. However, this does not establish that the banding was present prior to European settlement. It is surprising in this context that Beadle (1948), who carried out extensive field surveys of pasture condition in western NSW, did not refer to the banding, though he did make passing reference to the microrelief that is associated with it. It must still therefore be seen as possible that the patterns have perhaps become more extensive since the beginning of pastoralism.

The model results presented here are nonetheless consistent with the conclusion of Dunkerley & Brown (1995) that banding north of Broken Hill has persisted despite 150 years of pastoralism. Landscapes such as these thus seem to be structured in ways that make them suitable for sustained low-intensity grazing use, despite the arid external climate and the inter-annual unreliability of the rainfall.

Remaining uncertainties about the banded vegetation of western NSW are considerable. The present study sheds no light upon possible changes in species composition of the vegetation, nor upon possible effects of pastoralism on the distribution of plant ages. It seems possible that both of these parameters, as well as others, such as soil nutrient status, have been affected by European use of the landscape. Detailed field studies may illuminate some of these issues. Additionally, further field studies of these landscapes will assist in the identification of the actual field processes through which, for example, a seed reserve survives times of drought and heavy grazing pressure, and by which plant growth re-establishes the banded patterns. Finally, because the maintenance of fodder in the extensive banded landscapes of the arid and semi-arid zones depends upon the integrity of the runoff-runon systems, programmes of long-term monitoring of the condition of these communities seem warranted.

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