

## Banded vegetation: development under uniform rainfall from a simple cellular automaton model

D. L. Dunkerley

Department of Geography and Environmental Science, Monash University, Clayton, Victoria, Australia

Received 21 November 1995; accepted in revised form 30 July 1996

*Key words:* Arid zone vegetation, Banded vegetation; Cellular automata, Runoff, Runon, Water partitioning

### Abstract

Banded vegetation communities are known from semi-arid and arid landscapes in many parts of the world, in grasslands, shrublands, and woodlands. The origin of the distinctive patterning has been the subject of speculation, a common view being that banding evolves through the decline of more complete vegetation cover because of climatic deterioration or through grazing disturbance. A simple model based on cellular automata is employed to test the hypothesis that plausible mechanisms of water partitioning in spatially unstructured plant communities can bring about the development of banding. It is shown that without any climatic change or external disturbance, strongly developed banding can emerge from an initially random distribution of plants. Physical processes underlying the water partitioning, some of which remain unresearched, are discussed, and management implications noted.

### Introduction

Banded vegetation communities are those in which multiple strips of the landsurface support a relatively dense cover of vascular plants, the intervening ground being much more open. According to most published descriptions (e.g. Macfadyen 1950; Mabbutt & Fanning 1987), the zones of denser plant cover run in bands parallel with the topographic contour, separated by unvegetated bands. The wavelength of a band-interband cycle is commonly a few tens of metres. Communities displaying strongly developed patterns of this kind have been described from semi-arid and arid grasslands, shrublands, and woodlands. An example from a mixed grassland-shrubland is shown in Figure 1. The structure produces a landscape that is fragmented into runoff source areas and vegetated runon water sink areas which have high infiltration capacities 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 may 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 margin of the vegetation. Deeper-rooted species may preferentially occur toward the downslope margin of a band.

### *Microtopography and the hydrology of banded vegetation*

Detailed studies of banded vegetation communities reveal a subtle associated microtopography, the upslope margin of the zones of plants occupying a break in slope where gradient steepens to perhaps 0.5°. Below this, the slope profile flattens progressively toward the upslope margin of the next vegetation band, declining to perhaps 0.1°. An example from western NSW is shown in Figure 2. 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. Overall, therefore, 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.





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

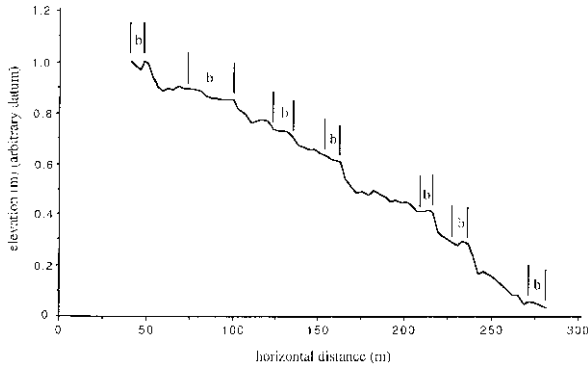


Figure 2. Detailed microtopographic profile across several cycles of the banded landscape shown in Figure 1. The b symbol denotes bare bands. The increase in slope onto the vegetation below is clearly evident. (Note extreme vertical exaggeration: 145×).

This comes about because of the strongly contrasting surface characteristics of these zones.

Despite having very low gradients, the bare areas are runoff source areas because their surfaces are quite

impermeable. Various characteristics contribute to this. Often, a surface veneer of stones occupies part of the surface, and this makes the covered fraction unavailable for water entry. More importantly, the unprotected surface develops surface sealing and crusting, as a result of disaggregation and puddling of the surface by raindrop impact. Finally, the strongly sealed surface acts to prevent the easy reciprocal escape of soil air as water infiltration occurs, and horizons of gas-filled vesicles develop which reduce the amount of water-conducting soil matrix.

Water shed from the bare zones trickles toward their very flat downslope margins, where deposition of detritus often creates a subdued contour-parallel ridge. This impounds the runoff water, which gathers into shallow ponds that are laterally extensive across the slope. Even a few mm of rain has been observed to create such ponds in the landscape shown in Figure 1. From these ponds, water 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. Sedimentation associated with the ponding creates a depositional environment that could favour colonisation by plants, though this has not been documented in the field. Elsewhere (e.g. Thiéry et al. 1995) it has been argued that colonisation of such upslope areas, and a resulting diminution of resources reaching the downslope margin of the grove, may produce a net upslope migration of the banding. Such upslope migration has not been demonstrated from Australia, and remains an hypothesis requiring testing.

The vegetated bands, though they are on average steeper, absorb water strongly because they possess better-structured soils. This character arises because of the additional organic matter from the plants and soil fauna. Burrowing soil fauna may also increase soil porosity. Zones of highest infiltration capacity are located around plant bases, where water may be delivered by stemflow (e.g. Pressland 1976). Vegetated surfaces often have a rougher surface arising from enhanced shrink-swell phenomena and associated collapse pipes (crabholes), shrub mounds, tussock bases, and regolith mounds produced by animal burrowing (Dunkerley & Brown, forthcoming). The rougher vegetated surface undoubtedly retards any surface runoff that does occur there, increasing the opportunity time for infiltration as the water moves slowly over the surface. Further, because of canopy and litter protection, crusting and sealing are undeveloped within the zones of plants. There are undoubtedly many factors like these which distinguish the components of a vegetation mosaic. Additional effects probably arise from differential surface colonisation by microphytes, differing albedo and near-surface airspeed, and non-uniform distribution of effects such as desiccation cracking. Many of these remain to be explored in the field.

Despite these uncertain details, the gross hydrologic functioning of banded vegetation as a runoff-runon system is relatively clear. The origin of banding itself remains in dispute, and there may be several distinct causes for pattern development. The general contour-parallelism of the bands, though, suggests in all cases that gravity-driven surface water movement plays a key role in pattern development. Some of the existing ideas on the origin of banding are considered briefly below as a prelude to the description of the new model.

### *The origin of banded vegetation communities*

A number of early ideas on the development of banding were reviewed by Dunkerley & Brown (1995). These include 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. However, litter dams, though common on the gentle topographic gradients typical of banded vegetation, are spaced far more closely together than vegetation bands, and so an unspecified process is then required in order to eliminate some strips and increase mean band spacing. Additionally, litter dams are rarely laterally continuous over the hundreds of metres typical of banded vegetation patterns, being really very small-scale features that might be expected to develop within unvegetated bands. 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. This latter view was not supported by the results of Dunkerley & Brown (1995). They investigated downslope trends of grain-size in surface stone mantles within the unvegetated bands in an arid shrubland in western NSW Australia. Finding downslope size decline but little probability of downslope stone transportation or sorting under present conditions, they concluded that the banding was of Holocene age, clearly pre-dating the modern introduction of grazing animals. In yet another view of the nature of pattern development, Cornet et al. (1988) argued that banding developed as a consequence of the cessation of rill and gully development during slope evolution, with sheetwash processes replacing concentrated flow, and interacting with vegetation colonising the broader surface from locations along former drainage lines. The geomorphic components of this model have not been formalised or tested.

Indeed, few formal models of the development of banding appear to have been developed. Goodspeed & Winkworth (1978) presented a computer simulation of grove development in communities of the mulga tree (*Acacia aneura*), a vegetation type that has been described from several locations in semi-arid Australia (e.g. Tongway & Ludwig 1990). They used a 50 × 50 array of cells, each of which initially contained a tree. Rainwater was distributed among these cells during a 200-year simulation. In this time, the 'annual' rainfall was reduced from 40 mm to zero, to provide an impetus for the thinning and re-arrangement of the plant cover. Rain and upslope runoff water not absorbed by a plant

was redistributed to the next row of cells downslope, 70% to the cell immediately below and 15% to each of the cells adjacent to it. 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 convincingly revealed in their published figures. Their model indeed appears not to have accounted for the development of vegetation banding. A potential flaw in it is the adopted pattern of water redistribution, which is entirely downslope from a plant. No lateral wetting of the soil adjacent to a plant was permitted, despite the known three-dimensional migration of water within the soil matrix, such as that mapped beneath shrubs in a Western Australian heath by Specht (1957). Further, the Goodspeed & Winkworth model contained no representation of the effects of extensive lateral surface water ponding.

Much greater success in simulating the development of banding was achieved by Thiéry et al. (1995). These authors employed a cellular model based upon two sets of effects. Competition was modelled to exist when upslope, and also diagonally upslope, plants hampered plant development of a downslope neighbour. Synergy (a combination of beneficial effects) was in contrast modelled when lateral and downslope neighbours favoured plant development through effects on the immediate plant environment. Thiéry et al. were able to produce banded patterns with a restricted set of model parameters. However, their model did not incorporate any physical process, and generated rapid upslope migration of the banded patterns, which, as noted before, has yet to be demonstrated in the field.

The goal of the work reported here was thus to investigate whether a model based upon a more intuitively reasonable conception of runoff-runon behaviour and soil water recharge was sufficient to account for band development. A simple cellular automaton model was employed for this purpose.

### **Runoff-runon behaviour in the cellular automaton (CA) model**

Models based upon cellular automata are widely used in the study of spatial patterns and their development (Hogeweg 1988; Green 1994; Thiéry et al. 1995). 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 vegeta-

tion, is required to follow a set of rules which reflect the properties of neighbouring cells. In the present case, for example, an empty cell can be set to increase the volume of runoff water received by the next cell downslope. If the downslope cell carries plants, and is thus strongly water-absorbing, the next cell downslope will experience no runoff and will thus be an inhospitable site for plant survival. However, a vegetated cell can supply water to an adjacent bare one, through surface ponding or subsurface seepage. Surface ponding, and lateral surface water flow, seem likely to be especially important, since the hydraulic conductivity of dry subsoils can be very low.

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. Similar benefits from cellular modelling have been demonstrated in the case of the Japanese fir-waves (Shimagare) by Iwasa et al. (1991) and Sato & Iwasa (1993). These authors were able to explore the processes affecting tree death and regrowth and successfully modelled the wave phenomenon within the cellular model paradigm. The main alternative form of modelling, embodying much more detailed process mechanisms (e.g. Mauchamp et al. 1994) can represent the ongoing operation of banded landscapes but has not yet been employed to generate banded patterns.

### *Model construction*

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 empty. In each iteration, 100 mm of rainwater was distributed uniformly to all cells. It seemed improbable that every site where banding has been described has suffered steadily diminishing annual rainfall, as employed in the Goodspeed & Winkworth (1978) model. Therefore the present work was developed with constant rainfall, except for some trials (described below) in which declining rainfall was introduced in order to investigate the effects of climatic deterioration. 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 mm of rain wet up the regolith surface, all other water (including any later runoff water from upslope) passing across the sur-

face with little or no absorption. For cells containing plants, complete water absorption was specified. This was shared among the two neighbouring cells along the contour on either side (i.e., among four neighbouring cells). 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. Very minor edge effects arose in the model, since border cells lacked adjacent cells on one or other side, and thus received no water from those cells by seepage or ponding. These effects are very slight and do not significantly perturb the model operation over the bulk of the tessellation.

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 Figure 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 all runs of the model, the same tessellation of 2500 cells was employed.

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 was free-running under the control of the water partitioning and plant survival rules just specified.

## Results

Within a reasonably broad range of model conditions, vegetation banding was very clearly and strongly developed. Up to 7 or 8 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, in contrast, were relatively diffuse, with only a minority of cells containing plants. These features accord with those observed in the field. Though of the correct order of magnitude, band- interband wavelength was somewhat underestimated in the model.

Typical model output is shown in Figure 3. The model was observed on a computer monitor as it ran. It was generally observed that the cells at the upslope border of the model became bare within a relatively few iterations, since they received no runoff water. Thus, plant cover rapidly thinned out here, but the runoff water that was consequently shed downslope permitted plants receiving this water to survive. This process could be seen occurring in patches over the whole slope. Through successive iterations, the patches became linked and the cross-slope banding pattern emerged. Strong banding was generally developed within 10–30 iterations, though in some runs pattern evolution was slower.

Banding was generally aligned across the slope (contour- parallel). In some model runs, however, departures were noted. Chance linking of growing patches sometimes formed banding that displayed some sinuosity, or bands that divided into two across the slope. This kind of pattern is also evident in the field, and can be seen in the map presented as Figure 1 in Dunkerley & Brown (1995). It was also reported by Thiéry et al. (1995), both from the field and from their cellular model. In some runs, small partial bands survived, persisting as patches of vegetation. Though this has not been fully explored, it appeared that band irregularity was promoted by beginning the model with a low fraction (less than 20%) of cells occupied by plants.

Apart from the tendency to greater sinuosity when the model was run from an initially low plant cover, little sensitivity to this parameter was evident. Simulations were run for initial cover values from 1% to 90%. From low initial values, the plant cover increased as banding developed, while from dense initial cover, plant loss occurred during band development. A stable cover fraction, able to be maintained in equilibrium with the applied rainfall amount, evolved in all cases.

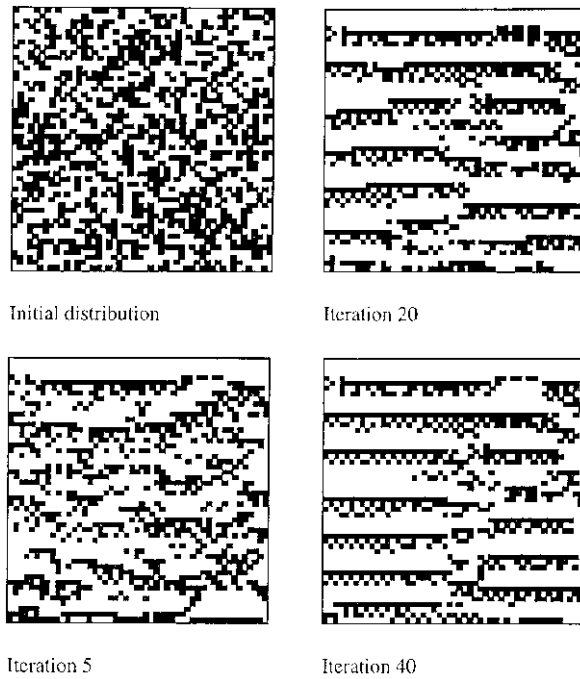


Figure 3. Typical banded patterns produced from the CA model. The initial random pattern and the plant distribution at three later iterations of the model are shown. Germination moisture 70 mm; plant death moisture 260 mm. Annual rainfall 100 mm.

Successive profiles of plant cover fraction down the modelled slope are shown in Figure 4. These are averages of all cross-slope cells. The initial distribution of plants, having in this case a mean cover amount of 40%, was replaced by seven cycles of banding, the sixth downslope being an incomplete band containing a gap of about 10 m. The cover fraction in the vegetated bands reaches 65–70%, while the bare zones are either completely bare or have 6% or less plant cover.

The significance of the lateral water sharing process built into the model was investigated by reducing the lateral sharing to the two cells immediately adjoining a vegetated cell and the single cell downslope. This had the effect of narrowing the resulting bands in the downslope direction, but did not inhibit the development of the contour-parallel banding. Indeed, this development was at least as strong as with water sharing among two neighbouring cells in each direction. When lateral water sharing was excluded and only downslope flow was permitted (as in the model of Goodspeed and Winkworth (1978)), the result was entirely different. No advantage exists under these rules for adjacent cells both occupied by vegetation, and no linking of cells to form bands was observed. A

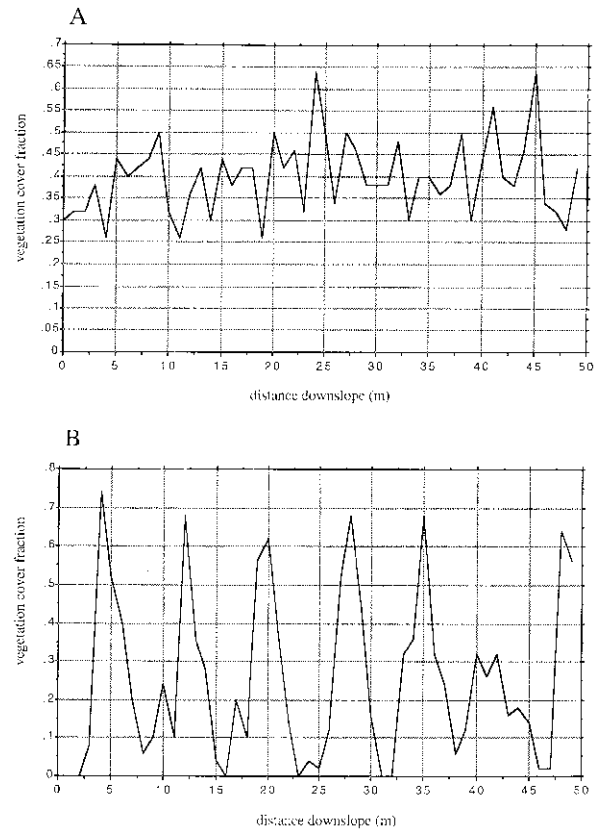


Figure 4. Downslope trends in mean vegetation cover fraction in the CA model (averaged across the whole tessellation of cells). A: initial distribution, with 40% of cells vegetated. B: cyclic pattern of cover evolved after 20 iterations of the model. The plant cover in the bands exceeds that of the initial random distribution, while that in the bare zones is very low or zero. Model conditions as for Figure 3.

typical simulation, after 30 iterations, is shown in Figure 5. As can be seen, the vegetated cells are scattered across the slope with little evident pattern. Further, the aggregate vegetation cover over the tessellation is only 14%, compared to about 23% for the same rainfall but with lateral water sharing. Clearly, in the absence of banding, more of the rain water leaves the slope foot as runoff, with the soil thus remaining drier and able to support fewer plants.

Sensitivity of model operation to the level of soil wetness specified for plant death or the growth of a new plant was investigated by repeated trials during which these parameters were varied. The minimum soil wetness specified for plant survival appeared primarily to influence the spacing of the vegetated bands. For higher levels of required water, more bare runoff source area is required upslope. Adjustment of this paramet-

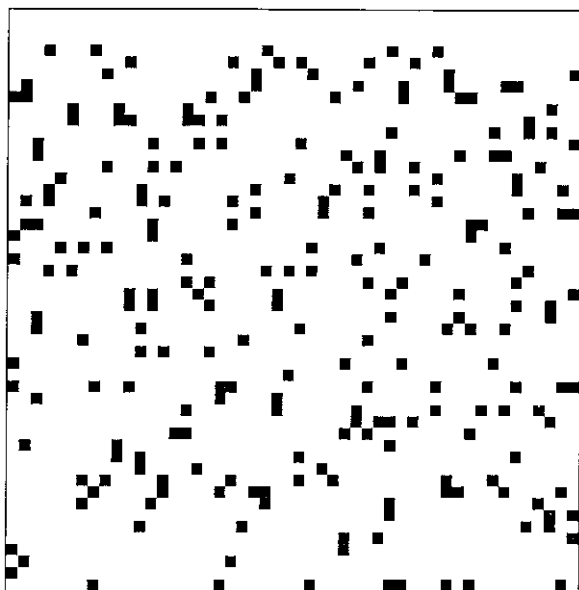


Figure 5. Output of the CA model with lateral moisture transfer eliminated. The pattern of surviving plants after 30 iterations (14% cover) reveals no development of banding. Model conditions as for Figure 3.

er in no case prevented the development of banding. However, setting this parameter to very high values (up to 600 mm) resulted in bands with an incomplete plant cover even at the uppermost border of the grove, as a result of competition among neighbouring cells. Bands with this character have not been encountered in western NSW.

In contrast, the soil wetness required for plant colonisation of a formerly bare cell is critical. It must lie within the range of wetness actually achieved by bare cells, or no colonisation is possible. This makes it almost essential for the required wetness to be little more than the annual rainfall, since a bare cell lying between two vegetated ones absorbs 10% of the rain and receives 10% of the water held in each adjacent cell. If each of these held 250% of the rainfall (by gathering runoff water) then the water supply to the bare cell amounts to 60% of the annual rainfall. In various model runs plant colonisation of any cell with wetness greater than this amount was permitted. When this value was increased to and beyond the annual rainfall, the downslope width of bands decreased, because the amount of water passing through the band did not provide adequately high soil wetness. Lower values, of 90%, 80%, and 70% of the annual rainfall permitted increasingly wide bands to develop.

### *Effect of climatic deterioration*

The influence of declining moisture availability was investigated briefly. This was done by permitting the development of banding in the model, for 10 or more iterations. Then the rainfall in each successive iteration was reduced by 2 mm. The outcome was consistent in all trials. Vegetation bands at the top of the slope began to break up, gaps appearing in what was formerly continuous vegetation. Eventually, whole bands disappeared. The disappearance of an upslope band releases more runoff water to sustain plants further down the slope, but as the drying continues, bands there also disintegrate. In some trials, rainfall was eventually stabilised at 30 mm. In this case, after the disintegration and disappearance of some bands, more widely spaced bands became stable, with the available water thus partitioned among fewer plants. At rainfalls of 10-20 mm the surface was left devoid of plants. If the simulated slope were more than 50 m in length, one would expect to see plant survival lower down, but in the extreme only plants along the watercourse would survive, in the 'contracted' distribution seen in arid areas. The conclusion from these trials is that vegetation banding can develop and remain stable provided that the rainfall is also sustained. Declining rainfall is associated with the disintegration of the banding and with increasing band spacing, and is certainly not a factor driving the creation of the pattern, at least in this model. Stages in a typical simulated climatic deterioration are shown in Figure 6.

### **Discussion and conclusions**

The very simple CA model presented here does not embody a detailed knowledge of particular field processes. Rather, it expresses their combined action in a manner that accords with observed field conditions in banded landscapes. The model nonetheless enables some interesting conclusions to be reached. The principal conclusion is that the enhanced absorption of surface water in the vicinity of plants, followed by the sharing of this water by seepage from surface ponds and by lateral subsoil seepage, is sufficient by itself to account for the remarkably ordered structure seen in banded vegetation.

Some restrictions must be placed on the field conditions where this is likely to apply. The slope must be sufficiently gentle that the ponding can occur. On steeper gradients, more direct downslope flow paths

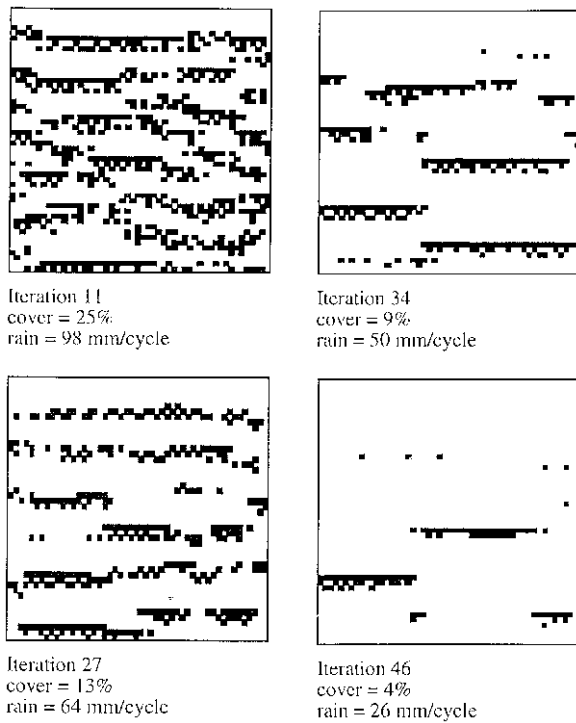


Figure 6. Output of the CA model in which the rainfall declines by 2 mm per iteration. Band fragmentation, and an increase in band spacing, are evident. See text for description.

might be possible, and this may be part of the reason that banding is not developed on gradients of more than about  $0.5^\circ$ . The higher water flow velocities that could be developed on steeper slopes would also reduce the opportunity time for infiltration, and might be associated with more channelised flow. Another requirement for banding to develop seems to be regolith materials that become highly impermeable when left bare. Strong tendencies to surface sealing and crust development, for example, enhance the generation of runoff from bare patches, and the shelter afforded by plants restricts this development where plants grow. This kind of contrast then results in strongly differing water absorbency over quite small distances, and within the same overall soil type. The final evident requirement for banding to develop is a rainfall regime that delivers too little available moisture for plants to colonise the entire surface. Thus, banding is clearly a phenomenon peculiar to dry climates.

Banding of the general character of that simulated here has been described from many locations, including Niger and Mexico. Floristic differences among these sites may be important in generating particular

small-scale hydrologic features at each site. It appears likely, however, that the aggregate hydrologic operation of banded sites must involve the beneficial effects of lateral water sharing embodied in the model presented here. A feature which is distinctly different among the various banded vegetation communities globally is the surface microtopography. The location where ground slope is steepest seems to vary: in Australia, this lies within the active vegetation grove, and in Niger, in the degraded zone below the grove. The role of the microtopography, and reasons for these evident differences, are topics in need of further study both in the field, and with models incorporating a sediment transport component.

Management of drylands, especially rangelands, is of great concern. The CA model presented here emphasises the potential sensitivity of banded vegetation communities within these rangelands. The plant cover is only able to remain as extensive as it is because of the efficient water shedding and trapping that takes place within the runoff-runon system. Heavy trafficking by hard-hoofed animals within the bare bands could increase water absorption there, starving plants downslope of water. Likewise, heavy grazing of the vegetated bands could reduce plant canopy cover and increase the likelihood of soil surface sealing, with consequent limiting of water entry. Together, these effects could disrupt the surface hydrology. This would be marked by a decrease in overall plant cover, this in turn increasing grazing pressure on a diminishing fodder source, resulting in a potentially accelerating tendency for the site to become badly degraded. Because suitable records have not been kept, the impact of 150 years of grazing on banded communities in NSW is impossible to judge. Certainly, banded communities exist over large areas today. It may be that the very low stocking rates in these arid rangelands have not caused disruption to the hydrological processes. Alternatively, the banded landscapes might have been significantly altered, perhaps in subtle ways, since the commencement of grazing. Floristic changes may have taken place of which we are unaware. Certainly, in the face of this uncertainty, it is important that the functioning of these landscapes be understood with a view to conserving their productivity and landscape role, a view stressed by Ludwig et al. (1994) and Ludwig & Tongway (1995).

## Acknowledgements

The writer thanks Kate Brown, Ellyn Cook and Kath Jerie for their field assistance.

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