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Stripes, strands or stipples: modelling the influence of three landscape banding patterns on resource capture and productivity in semi-arid woodlands, Australia

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Abstract

In the semi-arid open woodlands or savannas of eastern Australia banded vegetation is a common form of landscape patchiness. This banding can form relatively long strands or shorter stripes across the landscape, or small patches can occur in a stippled pattern. In degraded areas these patches can be completely removed from the landscape. This study addresses two related questions: does the type of patchiness (strands, stripes, or stipples) significantly influence how efficiently these semi-arid landscapes capture and store scarce soil resources; and how does this efficiency compare with landscapes that have lost all their patches? Results from a landscape simulation model, validated for a semi-arid woodland study site, demonstrated that the loss of landscape patchiness had the greatest influence on the capacity of the landscape to capture rainfall as soil water—reduced by about 25% compared to banded landscapes. This 25% loss of soil water reduced annual net primary productivity in these systems by about 40%. Banded patterns (stripes or strands) captured about 8% more rainfall as soil water than a stippled pattern; this increased their plant production by about 10%. However, these differences between banding patterns were relatively small compared to the impact of totally eliminating patchiness, which can occur with severe land degradation. This implies that preventing the loss of landscape patchiness is very important for managing savannas for production and conservation goals.

Keywords: Stripes; Strands; Stipples

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1. Introduction

In many arid and semi-arid environments around the world, limited rainfall and runoff–runon processes have lead to vegetation patchiness on many types of landscapes. Different terms have been used to described this phenomenon. For example, Archer (1990) has described patchy savanna parkland sites in southern Texas as ‘two-phase mosaics’. Belsky (1995) used this term to describe patchiness in some of the Serengeti grasslands of East Africa. Montaña (1992) described vegetation patches on the Mapimí Reserve in the southern Chihuahuan Desert, Mexico, as two-phase mosaics. This patchiness on Mapimí has also been described as ‘stripes’ (Cornet et al., 1992). Similar vegetation stripes in West Africa have been termed ‘brousse tigrée’ (Thiery et al., 1995), or ‘tiger bush’ in the more English-speaking East Africa. Vegetation ‘banding’ has been used to describe *Acacia aneura* grove–intergrove patterns in parts of arid Western Australia (Mabbutt and Fanning, 1987), Central Australia (Slatyer, 1961) and Eastern Australia (Boyland, 1973).

Vegetation banding can be of different forms even within a relatively small landscape area. For example, on a 200 ha study site in the semi-arid *Acacia* woodlands of Eastern Australia (Fig. 1), ribbon-like ‘strands’ of vegetation occur along minor, low-relief drainages (Fig. 2). In higher areas of the landscape, these more continuous strands are broken into shorter ‘stripes’, which are oriented along contours. Along low ridges, small patches or groves of *A. aneura* are ‘stippled’ across the landscape. These three banding patterns are related to soil-depth and fertility catenas, from shallower, poorer soils along

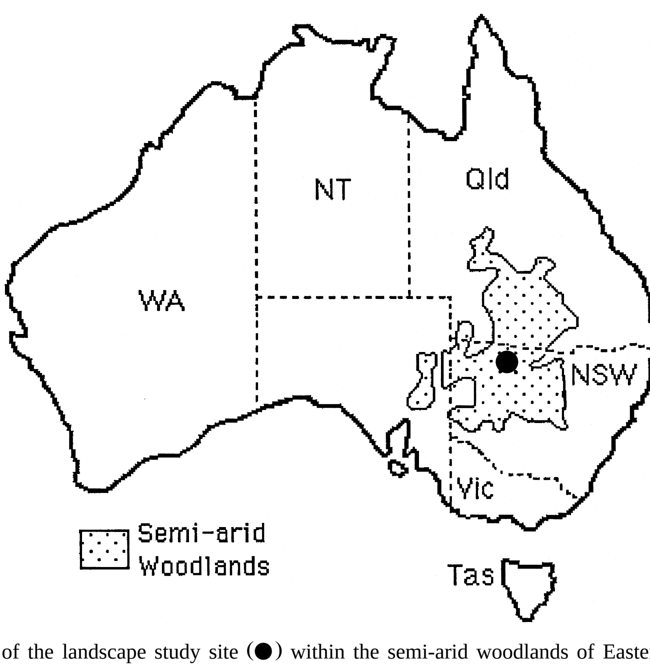

Fig. 1. Location of the landscape study site (●) within the semi-arid woodlands of Eastern Australia (after Harrington et al., 1984; Ludwig et al., 1994).

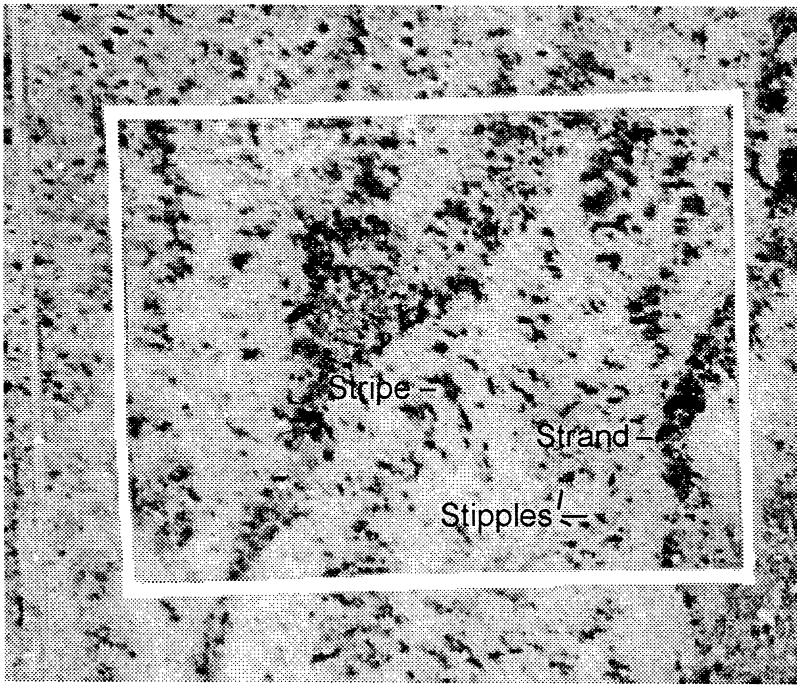

Fig. 2. A scanned aerial-photo of the 200 ha study site (within rectangle) showing *A. aneura* vegetation (dark areas) in different banding patterns (see text). A detailed description of the study site, including the direction of overland water flows, are given in Tongway and Ludwig (1990).

ridges to deeper, richer soils in the drainage bottoms (Tongway and Ludwig, 1990; Ludwig and Tongway, 1995).

Although vegetation banding has been extensively described and reviewed in reference to theory (e.g., Wiens, 1995), causes (e.g., Belsky, 1995), genesis (e.g., Thiery et al., 1995) and dynamics (e.g., Mauchamp et al., 1994), less attention has been paid to the function that patchiness plays in arid and semi-arid landscapes. One hypothesis is that patchiness functions to optimise the capture and storage of limited water and nutrients within these landscapes, and hence tends to maximise plant productivity within the system (Ludwig and Tongway, 1995). This hypothesis is based on the theory that many arid lands are source–sink or runoff–runon systems (Noy-Meir, 1973). This theory predicts that in environments with limited rainfall, plant productivity will be higher if rainwater is concentrated into patches rather than being uniformly dispersed over the landscape. This landscape function hypothesis has been confirmed by field data (Ludwig and Tongway, 1995, 1997) and simulation studies (Ludwig et al., 1994; Ludwig and Marsden, 1995).

In this study we extend these simulation studies to address two related questions. Firstly, compared to a landscape with no patchiness, how strongly does the presence of patches influence resource capture, and hence productivity? Secondly, in terms of resources and productivity, is it important whether patches are small and scattered over the landscape (stippled), or occur in short bands (stripes) or as long bands (strands)?

2. Methods

2.1. Semi-arid savanna landscape simulations

This simulation study was based on a semi-arid *A. aneura* open woodland or savanna landscape located in eastern Australia (Fig. 1). The banded *Acacia* groves, forming strands, stripes or stipples, are interspersed with open intergroves (Fig. 2). All three of these forms can be identified by focusing on different areas of the scanned aerial-photo. For the simulations, we assumed four areas, each 1 ha in size and with a uniform 1% slope. Three had patches dispersed as stipples, stripes or strands, occupying 25% of the 1 ha area, and one had no patches (Fig. 3). Each landscape area was gridded into 100 equal-sized units, and each unit was designated as being either a patch (black cell) or an interpatch (white cell) to form the desired patterns.

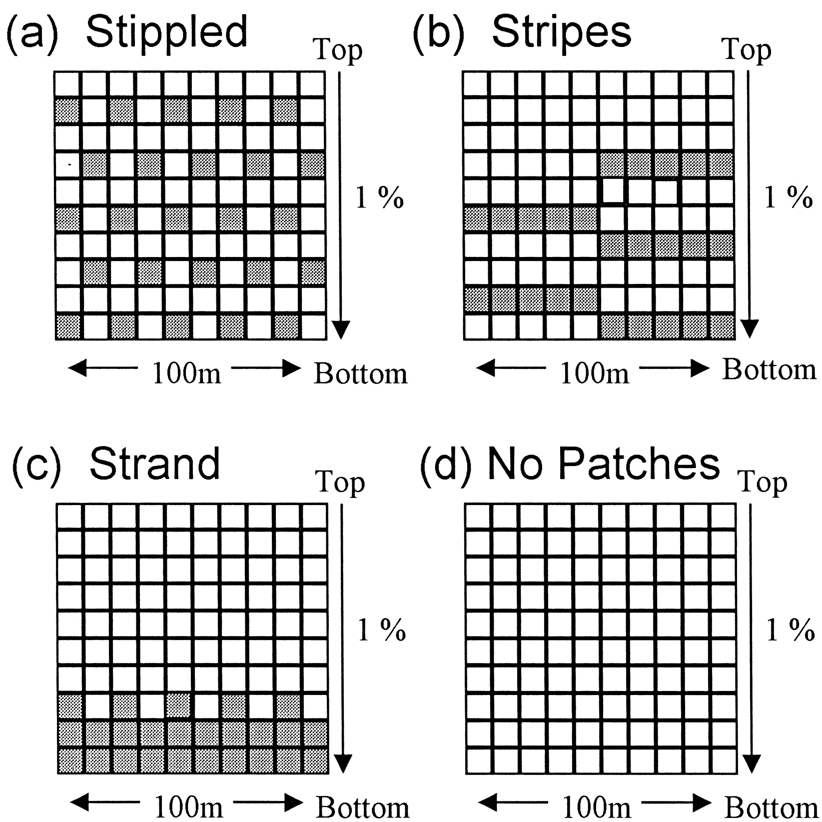

Fig. 3. Top-view schematics of patches (solid grid cells) and interpatches (open grid cells) for the four landscape patchiness patterns simulated in this study: (a) stippled—dispersed patches; (b) stripes—larger, elongated patches; (c) strands—long linear, basal patches; and (d) no patches.

Simulations were used to describe how water, as the primary limiting resource, flows down the landscape, through the units, and possibly out the bottom of the system (Fig. 3). If the amount of rainfall (R), and its intensity, exceeds the water storage capacity (SC) or the infiltration rate (IR) of the soil within an interpatch area then runoff (ROff) occurs (Fig. 4). This ROff can be captured by down-slope patches, or run out (ROut) of the landscape system. If the IR or SC of a patch is exceeded then ROff occurs from the patch, to the next down-slope interpatch, patch or out of the system. Computation details are provided in Appendix A.

ROut from the 1 ha landscape following a rainfall event at time (t) in functional form was:

$$\mathrm{ROut}_t = f(R,\mathrm{IR},\mathrm{SC})_t \tag{1}$$

Rainfall (R) amounts and intensities, and temperatures, used in the simulations were taken from a 31.5 year record obtained from a Class A weather station located at Cobar, New South Wales, in the centre of the semi-arid woodlands. Total ROut from the bottom of each of the four landscape systems, averaged over the 31.5 years, was taken as the measure of resource loss.

Based on data from soil studies on the study site (Greene, 1992; Greene and Ringrose-Voase, 1992), soil infiltration rates (IR) for patches and interpatches were set at 60 and 10 mm/h. Soil depths are about 100 and 45 cm for patches and interpatches, respectively. Total soil water storage capacities (SC) for patches and interpatches are dependent on their soil depths and the water holding capacities of their soils, which are 42% and 35%, respectively. The soils on the site are Xerollic Haplargids.

2.2. Landscape simulation model

A ‘flow-filter’ landscape model has been developed to quantify how semi-arid open woodlands or savannas function to ‘filter-out’ resources ‘flowing’ about these land-

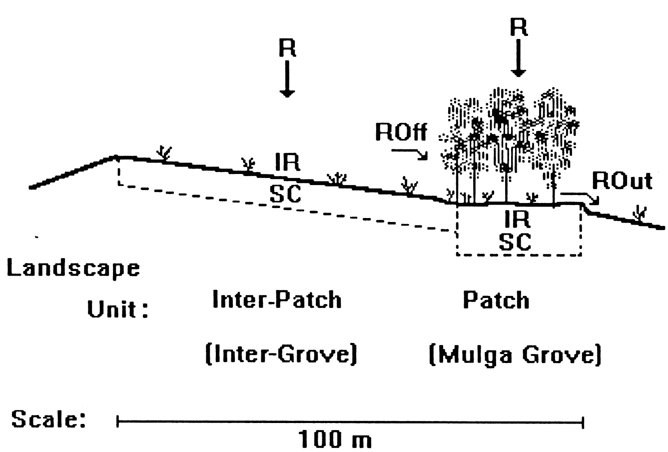

Fig. 4. Side-view schematic of a semi-arid landscape showing how water from rainfall (R) may runoff (ROff) when amounts and intensities exceed the infiltration rate (IR) or water storage capacity (SC) of the soil in the interpatch. Runoff not captured and stored by patches will run out (ROut) of the landscape system (after Ludwig et al., 1994).

scapes (Ludwig et al., 1994). Annual net plant production (NPP) for the four landscape systems with different banding patterns was estimated by using a simulation model, called SEESAW (a simulation of the ecology and economics of semi-arid woodlands; Ludwig et al., 1992, 1994). This model has a modular structure, going from climatic inputs to financial outputs (Fig. 5). For the purposes of this landscape simulation, which focuses on ROut and NPP, outputs from the sheep production (SHEEPSAW) and financial (ECONOSAW) modules were not required.

Each module of SEESAW is deterministic, and mechanistic. For example, the WATDYN module, adapted from Walker and Langridge (1996), uses a modified Penman–Monteith equation to estimate daily transpiration and evaporation soil water losses (Raupach, 1991). It also estimates a number of resistances to soil water losses, such as plant canopy aerodynamic drag, and soil surface sealing or crusting (details in Walker and Langridge, 1996). For our purposes, WATDYN was used to compute total ROut as a yearly average from each of the four landscape systems based on the soil water dynamics in each landscape unit across each system.

The FORSAW module of SEESAW computes net primary production (NPP) of forage through time (t) as a function of plant available moisture (PAM), available nitrogen (AN) in the soil, air temperatures (TEMPS), incoming solar radiation (SOLRAD) and atmospheric carbon dioxide concentrations (CO_2):

$$\mathrm{NPP}_t = f(\mathrm{PAM},\mathrm{AN},\mathrm{TEMPS},\mathrm{SOLRAD},\mathrm{CO}_2)_t \tag{2}$$

PAM was estimated from soil water dynamics (i.e., WATDYN). Soil available nitrogen (AN) dynamics was based on nutrient relationships in arid lands (Charley and

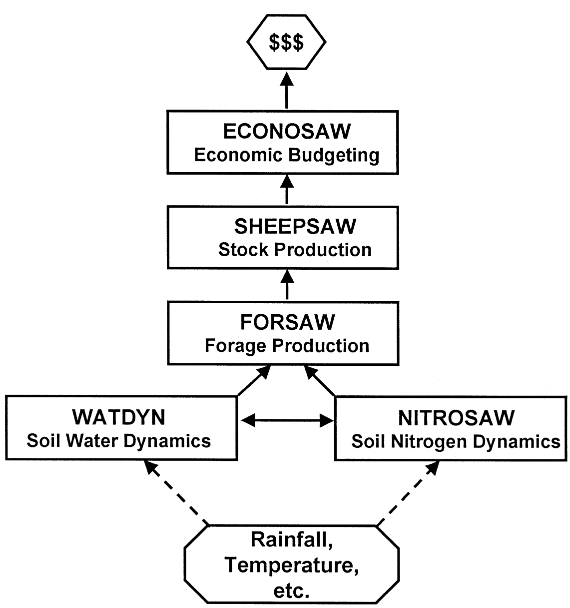

Fig. 5. The modular and flow structure of the SEESAW simulation model, from environmental inputs to financial outputs (after Ludwig and Marsden, 1995).

Cowling, 1968), where pools of mineralizable nitrogen tend to build-up during droughts, then produce 'flushes' of available nitrogen with drought-breaking rains.

Forage production by seven plant guilds (ephemeral forbs, perennial forbs, ephemeral grasses, palatable C3 perennial grasses, palatable C4 perennial grasses, fibrous C4 perennial grasses and palatable shrubs) was simulated. Given initial biomass of leaves, stems and roots for each guild, the daily rate of fixation of new photosynthetic biomass was calculated using a scheme in wide usage by plant growth modellers (e.g., Hanson et al., 1988). First a maximum photosynthetic fixation rate per day (dependent on the genetic potential of the plants in each guild) is computed based on available radiant energy (SOLRAD). Then this maximum rate is adjusted by rate enhancing or limiting factors (PAM, AN, TEMPS and CO_2), resulting in a daily rate. The impact of these factors differs between the guilds.

The concentration of CO_2 has been increasing at a rate of about 1.5 ppmv (0.4%) per year (Pearman, 1988). Increased CO_2 is known to enhance the yield of C3 crops due to increased net photosynthesis, but not in C4 crops (Gifford, 1988). This production enhancement due to increasing CO_2 appears to be linear up to about 700 ppmv. In FORSAW, maximum photosynthetic rates for each guild were adjusted by increasing CO_2 concentration changes over the 31.5 year simulated, the C3 plant guilds being enhanced while C4s were unaffected.

For each plant guild, maximum photosynthetic rate occurs at a temperature optimum, with 'bell-shaped' functions limiting this rate at temperatures lower or higher than this optimum. The minimum and maximum temperatures at which net photosynthesis becomes negative (i.e., daily respiration losses exceed photosynthetic gains) also differs among plant guilds (e.g., C4s have higher optimums, minimums and maximums than C3s).

Plant available moisture (PAM) is that factor that most strongly limits the maximum photosynthetic rate. For example, under the warm and windy conditions of spring and summer, soil water in soil surface layers can quickly become limiting, particularly to those plant guilds with shallow roots systems (e.g., ephemeral forbs and grasses). As soils dry, PAM can quickly drop below a threshold, below which soil water is limiting. The function relating the limitation of maximum photosynthetic rate to PAM, expressed as volumetric soil water contents (e.g., cm^3 H_2O/cm^3 soil) can be taken as sigmoidal, with asymptotes at zero when contents are low and at one when contents are high. A similar function can be used for the rate limitation due to available nitrogen (AN) in the soil, as derived from the NITROSAW module, but the threshold below which the rate drops off is generally quite low. In other words, the plant guilds in these semi-arid woodlands are well adapted to growing under conditions of low soil nutrients (Charley and Cowling, 1968).

In simulating the production of new plant biomass, or its decline, the FORSAW module of SEESAW estimates a number of other growth processes. The translocation and assimilation of new photosynthate to new leaf, stem and root biomass depends on the 'internal' demands for maintaining a 'balance' between these plant organs (i.e., a shoot to root ratio). It assumes that these ratios remain relatively constant within a plant guild, but differ between guilds, depending on the life form of the guild (i.e., forb, grass, shrub, tree). For example, if the shoot to root ratio increases (i.e., above the constant), then photosynthate will be translocated down from shoots to roots, thus re-establishing the balance. If shoot biomass is consumed by stock, lowering the shoot to root ratio, then photosynthate will be used to grow new shoots.

At certain temperatures and daylengths, depending on the plant guild, photosynthate may be translocated to flowers, fruits and seeds, or other types of propagules (e.g., new tillers or buds in plants that reproduce vegetatively). The processes of seed germination and senescence and death are also simulated in FORSAW. Seeds will germinate and seedlings will establish with favourable moisture and temperatures conditions. When conditions are unfavourable, senescence and death of plant parts, or entire plants, will occur. The drop of dead plants, or parts thereof, to litter, and the subsequent breakdown and decomposition of this litter, was also simulated. The consumption of plant parts is computed by the SHEEPSAW module. The details of these plant growth, death and consumption functions, as used in SEESAW, are beyond the scope of this paper, but this information is available from the authors.

3. Results

The SEESAW model was validated before running the simulations on the four artificial landscape systems (of fixed size, shape and slope) with different patch patterns

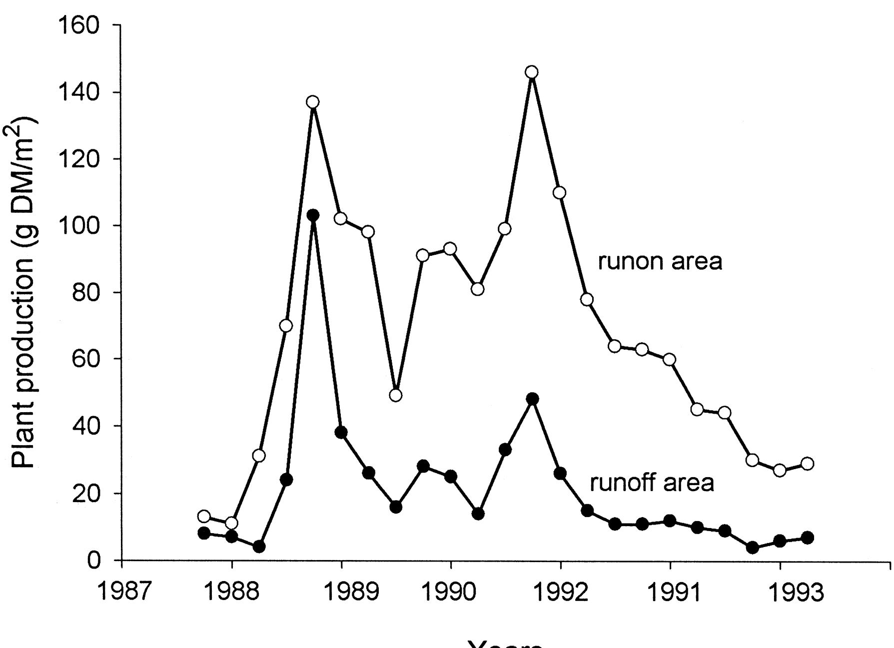

Fig. 6. Forage production (g/m^2) in landscape patches (runon areas) and interpatches (runoff slopes) over 6 years (1988 to 1993) on the semi-arid woodland study site (after Hodgkinson and Freudenberger, 1997).

(stippled, stripes, strands and no patches) over 31.5 years. Validation was based on 6 years of forage production and rainfall data from the study site (Hodgkinson and Freudenberger, 1997). The patches (runon areas or landscape sinks) consistently had higher plant production (all guilds combined) than interpatches (runoff areas or source zones) (Fig. 6). Clearly, spatial redistribution of water and nutrients across landscapes drives spatial heterogeneity in plant production (Noy-Meir, 1981). However, the temporal patterns of production over the 6 years were similar with high forage growth peaks during good years (e.g., 1988). On both runoff and runon areas total forage production steadily declined with the drought that started in 1991, but less so for the runon patches. Although not shown here for brevity, production data for each plant guild over the 6 years was used to validate the ability of SEESAW to simulate plant growth and death patterns.

The loss of runoff (ROut) from the simulated landscape systems with no patches was about 25% greater than for those with patches (Fig. 7). The stripe and strand banded patterns were about 8% more efficient at capturing runoff than the stippled pattern. Run-out from the stippled system maybe higher because runoff from rains probably flows between and around the smaller patches. As striped and strand patterns capture and conserve the most rainwater, these systems had an annual net primary production (NPP) of nearly 500 kg/ha (Fig. 8). The landscape system with no patches only had an NPP of about 280 kg/ha, about 40% lower than that for stripe and strand patterned

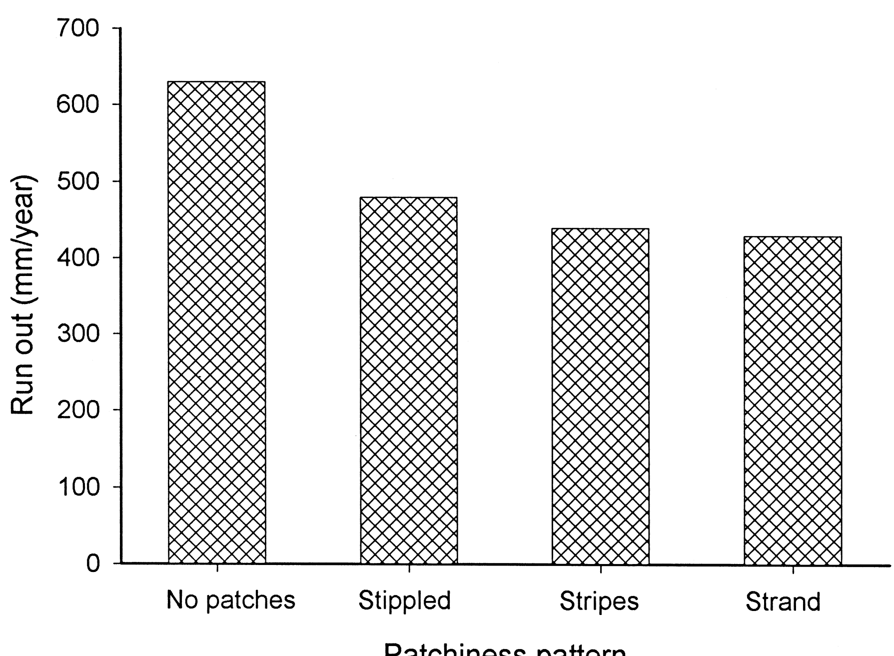

Fig. 7. Average losses of water as run out (mm/year) from the four simulated landscapes: no patches compared to stippled, stripped or strand patch patterns (see Fig. 3 for patterns).

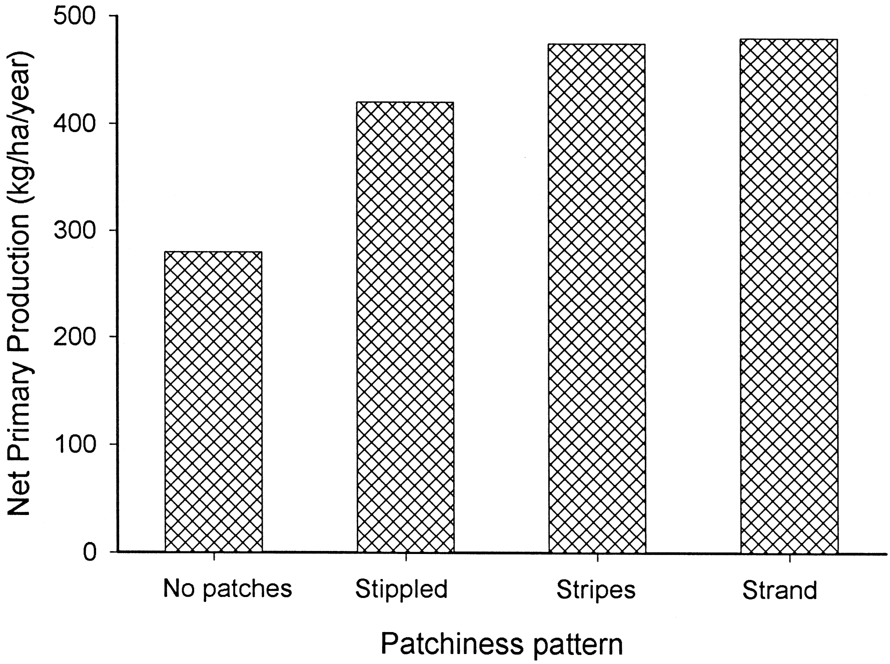

Fig. 8. Annual net primary production (kg/ha per year) from simulated landscapes for three patch-pattern types and no patches (see Fig. 3 for examples of these patterns).

landscapes. Because these banded patterns captured about 8% more soil water than the stippled pattern, their NPP was by about 10% higher.

4. Discussion

4.1. Impacts of patch loss

These simulations demonstrate that the loss of landscape patchiness can result in a dramatic reduction in a limited resource (soil water) and, hence, reduce productivity by 40%. This loss of landscape patches also impacts on soil fertility. Patches are known to be 'islands of fertility' (e.g., Garner and Steinberger, 1989). The concentration of nutrients within such patches, particularly in soil layers near the surface, are often many times those in the interpatch spaces (Tongway et al., 1989; Tongway and Ludwig, 1990, 1994). For example, areas of landscape with intact patches had significantly higher concentrations of soil nitrogen and organic carbon, water infiltration rates, and plant production, compared to landscapes with degraded patches (Table 1). Thus, the main message is that the loss of patches means the loss of the rich soils, and the plants, that constitute these patches.

Further, once a landscape has lost its patches, it significantly losses its ability to capture, store and recycle any *new* materials (e.g., soil sediments, litter, seeds) that are washed or blown into the system (Ludwig and Tongway, 1995). Such degraded

Table 1
Differences in nitrogen and organic carbon in the 0–1 cm soil layer, in water infiltration rates and plant production between two landscape areas, one with intact patches and the other with degraded patches. Data from areas of semi-arid woodland on 'Trafalgar' station, near Cobar, New South Wales (for details, and other examples, see Tongway and Smith, 1989; Tongway and Ludwig, 1997a,b)

Characteristic	Landscapes patches	
	Intact	Degraded
Soil nutrients		
Available nitrogen (ppm)	75.4[a]	22.4[b]
Organic carbon (%)	1.5[a]	0.8[b]
Infiltration rate (mm/h)	49.2[a]	7.8[b]
Plant production (g/m^2)	231.2[a]	13.6[b]

Characteristics with different superscript letters are significantly different ($P = 0.05$), based on Tukey's HSD test.

landscape systems can be termed dysfunctional (Tongway and Ludwig, 1997b). In other words, the system has become 'leaky'. Rainwater and nutrients are no longer efficiently captured and stored within the landscape—runoff becomes run-out, carrying away valuable rainwater, sediments and organic matter out of the system (e.g., into creeks, rivers, pans and lakes). This also means less plant production, or none at all, if levels of available water and nutrients remain below critical thresholds and plants fail to respond to rainfall because of loss of patches (Hodgkinson and Freudenberger, 1997). Thus, under degradation pressures, dysfunctional landscapes become poor in nutrients, lose water infiltration potential, and have significant declines in plant production.

The signs of decline or loss of landscape patchiness are often very obvious (Tongway and Ludwig, 1997b). For example, in some of the patchy woodlands near the study site, it is not uncommon to observe *Acacia* groves where every tree is dead and the ground is bare within the groves, and across the intergroves. Also, log-mounds, formed when dead trees fall over, show signs of breakdown and erosion, with logs exposed above an eroded surface. Typically, such logs are buried by a mound of fertile soil, which is covered with perennial plants (Tongway et al., 1989). Thus the signs are clear, but what about the causes?

Basically, the answer to this question is overgrazing. Although there are different types of overgrazing (Freudenberger et al., 1997), the loss of landscape patches is caused by an excessive consumption of the plants (e.g., perennial grasses) that form patches. Over time, and especially during droughts, excessive defoliation of plants can lead to their deaths (Hodgkinson, 1992), resulting in reduced patch size and density. Thus, overgrazing leads to landscape dysfunction, often within specific areas such as along fences and near watering points—a pattern observed around the world (Coughenour, 1991). Of course, other factors can contribute to loss of landscape patchiness. For example, high intensity fires in old, dense Mediterranean forest will completely consume the vegetation, producing smooth, homogeneous or non-patchy surfaces which have high rates of soil erosion after such fires (Lavee et al., 1995). They found that more open forest with more frequent, but cooler fires, have naturally patchy surfaces which do not erode.

Another question is why has overgrazing only occurred since pastoral settlement? In Australia's rangelands this was about 150 years ago (Noble and Tongway, 1986). The likely answer is that pastoralism brought more consumers, e.g., domestic sheep and cattle, and feral camels, horses, donkeys, rabbits, goats and pigs. All of these have been introduced to landscapes that since ancient time had only been grazed by macropodid marsupials (Freudenberger et al., 1997). Stock watering points were extensively developed, with the effect that kangaroo populations have greatly increased, especially in places where its natural predator, the dingo, has been controlled to protect stock. The net result is a 'total grazing pressure' that eventually destroys landscape patchiness. How can such degraded landscapes be fixed?

4.2. Landscape rehabilitation

The rehabilitation of dysfunctional landscapes can be achieved only by restoring landscape patches, that is, by rebuilding the structures that trap and store limited soil resources (Tongway and Ludwig, 1993). Experimental work has demonstrated that new patches can be restored on bare slopes by simply building piles of brush of about 10 m^2 (Tongway and Ludwig, 1996). It was found that these brush piles functioned to trap runoff, sediments and litter flowing or blowing around the landscape. After only 3 years, soil sediments and litter had significantly accumulated within the brush piles. Compared to controls, nitrogen and carbon levels were 30% higher, water infiltration rates increased 10-fold and the abundance of soil invertebrates increased four-fold. Perennial grasses and forbs re-established within the brush piles, but not in the controls, even though the experimental plots were being subject to moderately high grazing pressures by sheep and kangaroos (Ludwig and Tongway, 1996). The 'spiky' branches of the brush pile protected new plants from grazing.

Some rangeland managers in the semi-arid *Acacia* woodlands of eastern Australia already make brush piles when they cut branches from *Acacia* during droughts to 'emergency' feed their sheep (Harrington et al., 1984). However, rather than leaving branches next to the trees they are cut from, managers should be encouraged to build brush piles in places where rehabilitation is most needed, and with piles orientated along contours to increase their efficiency for trapping runoff.

Larger brush piles can be built by using bulldozers to 'thin' shrubs, where a chain is pulled between two bulldozers working parallel to the contours (Noble et al., 1997). At an appropriate spacing between strips, chaining creates large piles of uprooted trees (i.e., large patches) that are very efficient at trapping soil and litter. These strips or piles of brush and trees also provide refuge sites for fauna such as small mammals and lizards. Of course, landscape restoration using the chaining method must be very carefully planned (i.e., no chaining on steep landscapes).

4.3. Soil condition and biodiversity

Semi-arid landscapes used for grazing must be managed wisely to avoid the loss of patches. Land managers need to acknowledge the significance of patches and incorporate this knowledge into property management plans. This includes having an understanding of why overgrazing reduces patchiness, soil surface condition and productivity, thus leading to landscape dysfunction, desertification, and losses of biodiversity.

Maintaining landscape patchiness is vital for maintaining biodiversity, and vice versa, as the two are closely linked. For example, if biologically derived soil pores (i.e., those >0.75 mm) are closed, then the infiltration of water virtually stops (Greene, 1992). These biopores are formed by soil fauna such as ants and termites burrowing within favourable patchy habitats (Noble and Tongway, 1988; Whitford et al., 1992; Eldridge, 1993a; Greenslade and Smith, 1994). The cover of plants and cryptogams on a landscape are also important for slowing runoff and erosion (Eldridge, 1993b; Greene et al., 1994); this cover also protects biopores from raindrop impacts that tends to collapse them (see Greene, 1992, for details). The type and nature of soil surface stone and rock cover can also greatly influence runoff (Lavee and Poesen, 1991). For example, they found that landscapes with small (3 cm) stones resting on top of the soil surface consistently produced less runoff than bare soil at stone covers ranging from 30 to 88%.

Thus, the management of soil surfaces and patches is of critical importance in maintaining landscape function; that is, the capturing and storing of limited soil resources and producing good plant growth (Tongway and Ludwig, 1997a,b), and therefore conserving soil biotic diversity. Grazing land management must integrate both production and conservation goals (Foran et al., 1990). Morton et al. (1995) and Stafford Smith (1994) provide some guidelines for assessing whether a pastoral property is being managed sustainably. Ludwig and Freudenberger (1997) provide a landscape perspective on semi-arid grazing land sustainability, which is not achieved by managing only for landscape patchiness, but involves responding to many social, economic, ecological and political factors. Therefore, a knowledge of how landscapes function, and the importance of patches in this function, whether in stripes, strands or stipples, can contribute to the formation of policies and programs to achieve a goal of sustainable integration of production and conservation activities and values in rangelands.

Acknowledgements

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Appendix A. Algorithm for the computation of runoff (ROff) between landscape units and run out (ROut) of the landscape system

The aim of this landscape simulation study was to investigate how three patch patterns, stipples, stripes and strands, influence the amount of water flowing out of a hypothetical landscape system and, hence, its potential productivity. Therefore, a number of other factors which could influence run out and productivity were held constant, and a number of simplifying assumptions were made. For this study of patch pattern slope, patch area and interpatch area were held constant at 1%, 25% and 75%, respectively. Patch size was set at 100×100 m, and stripe and strand patches were consistently located towards the bottom of the simulated hillslope (Fig. 3). For simplicity, it was assumed that lateral or reticulate flows were not significant in our simulations because the landscape was assumed to be a flat planar surface of uniform 1% slope.

Computations were spatial and temporal. Runoff and run out were computed temporally for each rainfall event over a 31.5 year record from Cobar, New South Wales, Australia, given:

1. If no rain occurs (the usual case), soil water balance for each landscape patch pattern unit (see Fig. 3) was computed using the WATDYN model (Walker and Langridge, 1996).
2. If rain occurs and if the amount of rainfall (R), and its intensity, exceeds the water infiltration rate (IR) or the water storage capacity (SC) of the soil within a landscape
   unit, then runoff (ROff) occurred from that unit (see Fig. 4).

The spatial computations were as follows:

1. Runoff, ROff_z, was first computed for each landscape unit (z) in the row at the top of the landscape (Fig. 3) as:

   $$\mathrm{ROff}_{1z} = R_{1z} - \mathrm{IR}_{1z},$$

   that is, rainfall inputs, (R_{1z}), less infiltration, IR_{1z}, in mm/h, summed over the 24 h/day. Soil water storage for each unit was then computed given the amount of water infiltrated into the soil, balanced against other relationships within WATDYN.
2. Second, ROff_{2z} was computed for the second row of landscape units, that is those immediately downslope of the first row. For the second row of landscape units, runoff was computed as:

   $$\mathrm{ROff}_{2z} = \mathrm{SR}_{2z} - \mathrm{IR}_{2z}$$

   where $\mathrm{SR}_{2z} = R_{2z} + \mathrm{ROn}_{2z}$, that is, the supply rate of water to unit z in row 2 is the sum of rainfall inputs and runon, ROn_{2z}, which equals the runoff from the unit above ($\mathrm{ROn}_{2z} = \mathrm{ROff}_{1z}$). Note that these calculations do not apply to the first row since it is at the top of the landscape and does not receive runon.
3. Third, the above computations were repeated for each of the rows in the landscape system—10 in our four different simulated landscape systems (Fig. 3).
4. Last, run out (ROut) from the landscape system was equal to the sum of the amount of runoff computed for the last row of landscape units (i.e., $\mathrm{ROut}_z = \mathrm{ROff}_{10z}$).

Finally, note that as computations proceed down the rows of landscape units, that some units are designated as 'runon patches' (Fig. 3), which have significantly higher infiltration rates than runoff units (3 vs. 25 mm/h). It is the effect of patterning of these patches that was investigated in this simulation study.

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