7. Vegetation Dynamics: Recruitment and Regeneration in Two-Phase Mosaics

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Introduction

Banded landscapes are characterized by bands of dense perennial vegetation oriented parallel to the contour, separated by bare soil (Figures 1.1, 1.10, 1.12, this volume). They are widely distributed globally and have been studied in arid and semiarid climates of Sahelian Africa and the Middle East (White 1971; Wickens and Collier 1971), South Africa (van der Meulen and Morris 1979), Australia (Mabbutt and Fanning 1987; Tongway and Ludwig 1990), and North America (Cornet et al. 1992). White (1971) defined the common characteristics apparently necessary for the existence of a banded vegetation spatial structure. These characteristics are now well known and include a semiarid climate and rainfall runoff as sheet-flow on gently inclined surfaces (chapter 1, this volume). Commonly, the band and interband zones have a similar soil type and texture but not always. For example, some banded landscapes are located on soils with swell/shrink gilgai patterns and dynamics (Dunkerley and Brown 1995; Macdonald, Melville, and White 1999). The most common vegetation association in the bands is a mixture of grass and shrubs and/or trees (Slatyer 1961; Montaña, López-Portillo, and Mauchamp 1990; Seghieri et al. 1997) but can be dominated by grass (Worral 1959), trees alone (Worral 1960), or chenopod shrubs (Macdonald, Melville, and White 1999).

The origin of banded landscapes has been the subject of much conjecture (White 1971; Greig-Smith 1979). Boaler and Hodge (1964) postulated that bands developed from an initially evenly vegetated surface through gradual degradation due

to climatic or soil degradation. White (1971) and Boudet (1972) suggested that they originated from colonization of previously bare zones by concentrating resources upslope of natural obstacles to water movement. Mabbutt and Fanning (1987) and Cornet and associates (1992) proposed that the origin of banded landscapes lies in the geomorphic evolution of planar or very slightly convex or concave landforms so as to favor extensive sheet-flow runoff. All these explanations remain speculative because band initiation has not actually been observed. Modeling band initiation has been a major activity (chapter 9, this volume).

Hypotheses as to the overall functioning of banded landscapes have all been related to surface hydrological processes in which resources mobilized by rainfall runoff from the interband are effectively captured within the band and used by vegetation growing there (White 1970, 1971; Wickens and Collier 1971; Tongway and Ludwig 1990; chapter 5, this volume). This commonly results in denser, more perennial plants in the band than would be predicted from the average annual rainfall without spatial redistribution (Ludwig, Tongway, and Marsden 1994). These processes are dealt with in detail in chapters 4 and 5 of this volume. The underlying hypothesis exemplifies the Noy-Meir (1973) proposition that heterogeneous distribution of water in semiarid landscapes improves overall productivity than if water were evenly spread.

The objectives of this chapter are to discuss vegetation dynamics of banded landscapes in the light of the hydrological functioning of the landscape in terms of (1) the overall landscape vegetation structure, (2) the species composition and temporal dynamics at different locations within the bands, (3) the evidence provided by vegetation in upslope band migration, and (4) the effect of human activities on vegetation and band persistence. The data are drawn from the set of sites where formal vegetation studies have been carried out: Mapimi in Mexico, Banizoumbou in Niger, and Lake Mere in Australia, although smaller studies at other sites have also contributed.

Vegetation Band Structure

Band-Interband Patterns

The vegetation composition and structure of the bands proper are very variable between global locations (Table 7.1). White (1971) suggested three types of vegetation bands: those composed basically of grasses, those containing a mixture of grass and shrubs, and those composed of shrubs and trees. The wide range in lifeform suggests that there is an equivalent range in the availability of soil moisture over time and three-dimensional space in the soil. Different soil moisture regimes are caused by differences in the interaction of how much rain falls and its spatial redistribution. Theoretically, less frequent but deeply penetrating soil water additions might advantage trees, whereas grasses might be favored by frequent smaller showers.

Vegetation cover on the interbands was so low at all sites that its dynamics have been largely ignored in the literature. At the Lake Mere site in Australia, vegetative

Table 7.1. Common Aspects of the Vegetation Structure in Several Sites of
Banded Vegetation

	Niger site	Burkina Faso site	Mexico site	Australia site
Dominant in thicket core, backbone of the banded pattern	*Combretum micranthum* (shrub)	*Combretum micranthum* (shrub)	*Hilaria mutica* (perennial grass)	*Acacia aneura* (tree)
Dominant upslope the thicket core	*Guiera senegalensis* (shrub)	Tall annual community (mainly grasses)	*Flourensia cernua* (shrub)	*Thyridolepis mitchelliana* (perennial grass)
Distributed independently from the banded pattern	—	*Pterocarpus lucens* (shrub)	*Prosopis glandulosa* (shrub)	*Eragrostis eriopoda* (perennial grass)

cover on the interband was never more than 10%, whereas the mulga band exceeded 50% foliar cover and the upslope grassy fringe or ecotone had 25% cover (Tongway and Ludwig 1990).

In the Sahel, Couteron, Mahamane, and Ouedraogo (1996) and Couteron, and co-workers (2000) studied the differences in band structures at sites at Banizoumbou (Niger) and Bidi (Burkina Faso) by examining the distribution of woody species. The rainfall distribution is similar, and the dominant species at both sites is *Combretum micranthum*. The soil texture at Bidi is sandier and lacks the cemented ironstone gravel present at Banizoumbou, so that the infiltration rates are higher and the soil water more evenly distributed across the landscape. As a consequence, the vegetation banding, as assessed by measuring the density of juveniles of *C. micranthum* across the vegetation band at Bidi, is not as strongly differentiated as at Banizoumbou and has a lower overall biomass per unit area. These vegetation data illustrate variations in intrinsic banded landscape runoff/runon processes (function).

Within-Band Patterns

The vegetated bands can be divided into three basic sections (Figure 7.1): (1) the upslope fringe, (2) the main body of the band, and (3) the downslope fringe (Cornet et al. 1992; Montaña 1992; Couteron et al. 2000). One would expect the upslope fringe to receive a higher frequency of runon events and more water overall than the downslope fringe, which would receive only ambient rain plus rare runon from exceptional events. This expectation is supported by vegetation data.

For example, at Lake Mere, the upslope fringe was composed of perennial grass cover of 20.2% that is composed of nine species and a two-species shrub cover of 7.4%. The main body of the band comprised 12.4% perennial grass cover that is
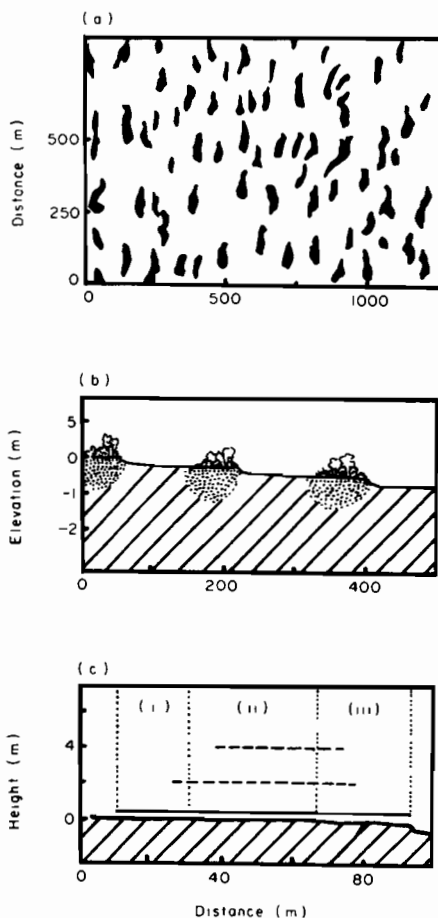
Figure 7.1. Schematic representation of banded vegetation patterns from the southern Chihuahuan Desert (Mexico). (a) Aerial view at 1:25,000 scale showing the vegetation bands (in black) surrounded by almost bare areas. (b) Idealized cross-section of the landscape showing the distribution of vegetation and soil water moisture after rain (dotted areas in the soil profile). (c) Idealized cross-section of a vegetated band. Horizontal straight lines indicate the range vegetated and the height of herbaceous species (continuous line), shrubs (lower dashed line), and small trees (upper dashed line). Dotted vertical lines indicate the three subdivisions of the bands used in this work: (i) upslope, (ii) main body, and (iii) downslope. (Modified from Fig. 1, Montaña 1992.) Permission courtesy of Blackwell Science Ltd.

composed of nine species and 40.1% shrub/tree cover composed of two species. There was no downslope fringe (Tongway and Ludwig 1990), implying that resource availability there was too low to support plant populations. This accords with the comparative hydrological analysis in chapter 5 of this volume.

At Mapimi, a greater number and diversity of species were found on the upslope fringe compared with downslope (Figure 7.2). The upslope fringe had much higher species richness (5.43 ± 0.51; range, one to 18 species) than the downslope fringe of the vegetation band (1.72 ± 0.12; range, zero to four) as measured in 2 × 1-m quadrats (Montaña 1992). Seedlings growing in full sunlight grew larger than those in shade. There was a distinct senescence zone on the downslope side of the band.

There is a diversity of germination strategies among the commonly found plant species. Some plants germinate in multiple locations, whereas others appear to
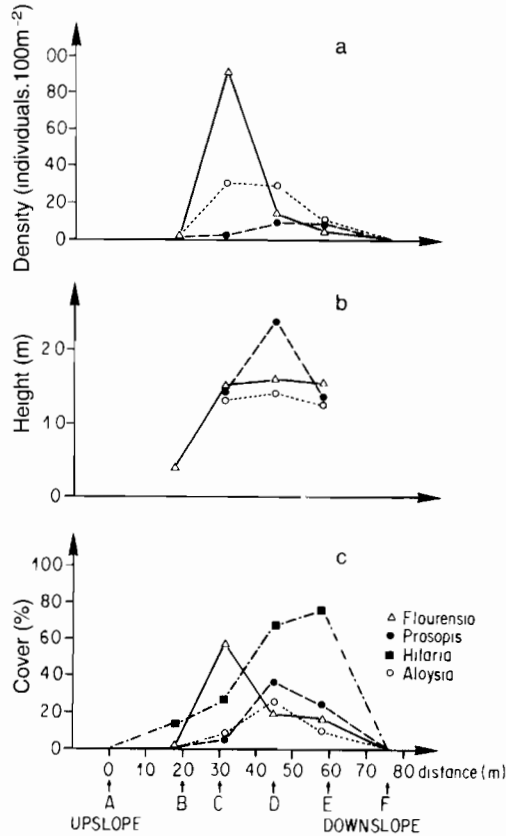
Figure 7.2. Density (a), height (b), and cover (c) of the most abundant shrubs and small trees in a vegetation band from the southern Chihuahuan Desert (Mexico). (Modified from Fig. 16.6, from Cornet et al 1992.) Permission courtesy of Blackwell Science Ltd.

favor a restricted set. For example, in Mexico, *Prosopis glandulosa* seedlings were recorded both in the band and in the bare area, whereas *Flourensia cernua* seedlings were dominantly found in the upslope fringe (Montaña, López-Portillo, and Mauchamp 1990; Mauchamp et al. 1993). In Niger, 50% of *C. micranthum* seedlings were in the core, and similar proportions of the remainder were in the upslope and downslope fringes, whereas *Guiera senegalensis* specialized in either core or upslope fringe sites (93%) and only 7% in the downslope fringe (Couteron, Mahamane, and Ouedraogo 1996; Couteron et al. 2000). These observations are consistent with the notion that the future floristic composition (and hence the vegetation structure), at a specific site, are mainly influenced by the availability of safe sites and the ability of seeds to reach them (Harper et al. 1961; Harper, Williams, and Sagar 1965; Harper 1977) and also by the biotic and abiotic conditions for plant establishment (Grubb 1977).

Vegetation Band Dynamics

A greater part of published vegetation studies in banded landscapes has been concerned with the dynamics of the vegetated bands, mainly in the upslope fringe or ecotone, where the dynamics are greatest. Indeed, the dynamics of the long-lived vegetation in the core of the band have had little attention due to the long time-frame needed to study these organisms effectively (Tongway and Ludwig 1990; Montaña 1992; Galle, Seghieri and Mounkaila 1997). For example, Mulga (*Acacia aneura*) is believed to live for about 250 years (Crisp 1978), implying that successful establishment of new plants need not be a frequent event. The vegetation dynamics studies were mainly undertaken to investigate the basic processes of colonization and plant species succession and to provide information about possible upslope migration processes. These studies accepted the controlling influence of runoff/runon hydrological processes in principle but looked in finer detail at the consequences for vegetation.

Plant Dynamics in Response to Available Moisture

Herbaceous Plants

At the scale of the band upslope fringe, soil moisture dynamics influence both germination and establishment of herbaceous plants (Cornet et al 1992; Montaña 1992); over time, the species composition implies successional development. This pattern is characterized by the presence of annual or ephemeral plants at the extreme upslope edge of the ecotone followed in a downslope sequence: short-lived perennials and then long-lived perennials more closely resembling the species composition of the core of the band. For example, at Mapimi, between 1982 and 1986 in the upslope fringe there was a decrease of herbaceous perennials (forbs) and an increase of both perennial grasses and saplings of woody species (Cornet et al.1992). Further, Montaña (1992), studying the spatial distribution of plants along a transect from the upslope edge of the fringe to the main body, found (1) a gradual increase in species richness up to a peak and then a decrease (as would be expected within an ecotone), (2) changes in both the lifeform and the floristic dominance spatially matched this peak, and (3) a change in the distribution of species abundance from geometrical to log-normal, as would be expected in a successional process (May 1981).

Woody Plants

The above findings for herbaceous vegetation do not extend to woody plants, where the age distribution of *P. glandulosa*, a long-lived woody plant was used to seek evidence for progressive upslope migration (López-Portillo and Montaña 1999). The hypothesis underlying this study was that if upslope migration were a continuous process, both the age and size classes of *P. glandulosa* would increase systematically downslope within a band. An inventory of plants showed this not to be true. In particular, younger plants were not more abundant in the upslope loca-

tions, and larger individuals were not found in downslope locations within the bands. Some *P. glandulosa* close to the upslope edge appeared to be greater than 50 years old. However, dead trees in the contiguous bare areas up and down slope of the band suggest that some sections of the downslope part of the bands have contracted, the rest of the population remaining stable (López-Portillo and Montaña 1999). *P. glandulosa* is known to have a strong invasive propensity (Brown and Archer 1990), particularly into landscapes where grass competition has been reduced by grazing (Bush and van Auken 1990). Its seeds are dispersed widely by large herbivores, so it may be a poor indicator for the upslope migration of "natural" bands.

Seed Dispersal

There appear to be no specific studies of seed production as such in banded landscapes. The few studies made on seeds relate to dispersal and indicate that the seed bank is patchily distributed and concentrated mainly in the vegetated patches. Mauchamp and associates (1993) showed that 90% of seeds were beneath the crown of adult plants in the surface soil layer for the shrub *F. cernua,* the dominant vegetation cover on the upslope edge of bands in Mexico. Montaña, López-Portillo, and Mauchamp (1990) recorded most *F. cernua* seedlings less than 3 m away from the nearest adult and not any more than 5 m distant. Moreover, conditions for *F. cernua* recruitment are met only in the upslope ecotone between the main body of the band and the bare area (i.e., in the colonization front). These characteristics of *F. cernua* recruitment, coupled with the observation that some bands have a dense grass cover upslope of the *F. cernua* populations, led Mauchamp and associates (1993) to the conclusion that *F. cernua* populations persist in vegetation bands by metapopulational dynamics involving successive colonizations and local extinctions (Pulliam 1988). This is consistent with conventional seed dispersal and establishment observations: primary and secondary dispersal and seed density decrease with distance from the source plant (Harper 1977; Nelson and Chew 1977; Schaal 1980; Howe and Smallwood 1982; Boyd and Brum 1983; Green 1983; Chambers and MacMahon 1994).

The vegetation bands have microtopographic features that favor seed accumulation. Reichman (1984) and Ellner and Shmida (1981) showed that seed trapping in natural and artificial depressions in the soil surface is common in arid lands generally. In desert ecosystems, Chambers and MacMahon (1994) stated that few long-lived perennials have persistent seed banks, whereas annual species range from high to transient (Kemp 1989). In banded landscapes, seed may be washed or blown by wind across the bare interband zone and accumulated by the vegetation band. Seghieri and colleagues (1997) found a 180-fold difference between the annual soil seed bank at the core of the band compared with the bare area. The transport of seeds between vegetation bands, by runoff water or wind, may be a source of regeneration in degraded bands (Mauchamp et al. 1993). They found that *F. cernua* seedlings germinated all over the band after rain, strongly suggesting redistribution and concentration of seeds in the band by sheet-flow.

As mentioned above, domestic and wild animals may also disperse seeds, as in the case of *P. glandulosa*, as the distribution of seedlings was clumped in animal camps. This manner of dispersion might increase the probability of seed survival in the landscape as a whole because of the high predation of seeds by insect larvae close to parent plants (Montaña, López-Portillo, and Mauchamp 1990). *P. lucens* in Burkina Faso may also have dispersal mechanisms not related to the runoff/runon banded landscape processes (Couteron et al. 2000).

Upslope Band Migration

The notion of upslope migration or movement of the vegetation bands has been a common thread in all studies of banded landscapes (White 1971; Greig-Smith 1979; Mabbutt and Fanning 1987; Montaña, López-Portillo, and Mauchamp 1990; Tongway and Ludwig 1990; Montaña 1992). Most of the evidence for the movement of whole bands is circumstantial and collected over short time spans relative to the functioning of the landscape. In particular, observations of dead trees just downslope of the band provided strong prima facie evidence of band movement. When linked with the accepted runoff/runon processes for band-interband pattern maintenance, these plant observations provide a hypothesis worthy of testing. Upslope migration of vegetation bands has been extensively modeled (chapters 8 and 9, this volume), and several plausible scenarios exist.

There is a little evidence of the upslope migration of whole bands, but it is not compelling in a global sense. In Mexico, the edge of the band moved 4 m upslope between 1982 and 1987 and thereafter remained static. Upslope retraction of the vegetation in the downslope fringe did not commence until 1988 (Montaña 1992). This suggests that any upslope movement of the band as a whole is not a steady whole-of-band migration. There may be a time lag of a number of years between upslope edge advance and the downslope edge retraction, depending on seasonal conditions. These spatial dynamics of species succession also reflect the gradual development of appropriate edaphic habitat in the upslope fringe. In Niger, large tree roots found in the interband zone (J. Rajot, pers. comm.) imply that trees once occupied this zone.

The relative dearth of actual measurements of genuine upslope migration, as opposed to periodic expansion/contraction of either the upslope or downslope fringe in response to alternating weather regimes, implies that the process is probably intermittent rather than continuous. The evidence also suggests asynchronous movement of the respective edges (Montaña 1992). Measuring a rate of migration has therefore not been fruitful. Perhaps a study of long-term climatic variation would be able to shed more understanding on the dynamics of band migration in that there could be periods when migration was active and rapid and a time when it was quiescent. In some systems, soil biogeochemical processes are implicated in the form of siliceous hardpan formation (Mabbutt and Fanning 1987), implying near-geologic time spans in any movement of the vegetated bands. There are no observations on banded landscapes over the century time scales that can be used to confirm or refute the basic notion.

Degradation of Vegetation Bands due to
Human Activities

Most research on banded landscapes has been concerned with the basic nature of their functioning, and the application of this knowledge to examining the effects of stress and disturbance on managed banded landscapes is essential. At Lake Mere, a range of grazing pressures was experimentally applied to a site where the band comprised a perennial grassland ecotone and a mulga woodland (Anderson and Hodgkinson 1997). They found that the perennial grass sward that dominated the ground layer of the ecotone served an important functional role in that the grass slowed and obstructed the flow of runoff water from the interband (Tongway and Ludwig 1997), capturing a greater proportion of runoff compared with a treatment in which domestic and wild herbivores had consumed the greater part of the grass, permitting runoff water to run through the band. As a consequence, both the grass and the mulga were moisture-deficient, as shown by predawn water potential measurements, threatening their survival (Anderson and Hodgkinson 1997). This is a clear example of the role of perennial vegetation in directly contributing to landscape function. Without this resource-capturing process, the existence of mulga banding would be threatened, as the banded mulga landscapes are intrinsically less resource capturing than either the Mexico or Niger banded landscapes (chapter 5, this volume).

Wu and associates (2000) found similar effects of degradation to the Australian work. Their retrospective remote-sensing study in Niger showed that between 1960 and 1992, the bands near Hamdallaye (13° 34' N, 2° 35' E) became seriously fragmented due to human activity (Figure 1.8, this volume). The period of the photographic review coincides with a massive build-up of stock numbers (Cisse 1981). Firewood harvesting also increased over this period, with tracks being made to both collect and transport the wood. Fragmentation took several forms. The bands broke up into shorter sections, permitting runoff water to bypass the band and become lost from the system. Wu suggested that lacunarity analysis is an appropriate tool to quantify this process. In addition, the downslope boundary of the bands retracted upslope over the period, also indicating that the water relations in the downslope fringe of the band had been adversely affected. López-Portillo and Montaña (1999) also recognize overgrazing as a vector of change in band functioning.

The consequences for management are clear. Increasing human pressure limits plant establishment everywhere, but the least favorable sites are more adversely affected (e.g., the downslope fringe). The effect of human pressure is to restrict or limit the capture of resources by the bands. Water, topsoil, litter, and seeds flow around or through degraded bands and out of the system, so that resource capture by less favored sites is even more restricted (Ludwig et al. 1997). These stresses might favor upslope expansion of some band fragments in the short term but would accelerate the disorganization of the banded system as a whole in the long term (Wu, Thurow, and Whisenant 2000). Adequate monitoring of band integrity needs to be implemented with the explicit intention of providing early warning signs of

system degradation, together with clear guidelines as to appropriate ways to manage the landscape.

Summary

Noy-Meir (1979/80) discussed the biology of desert vegetation in terms of two competing hypotheses that he named *autecological* and *ecosystem*. The former hypothesis suggests that "the dynamics of each population are determined by its independent reaction to the environment," whereas the latter holds "that nature, in general, consists of integrated ecosystems, in which all populations and many environmental factors are (directly or indirectly) linked and regulated by biological interactions and feedbacks."

Clearly, the complex interrelationships between vegetation and various parts of the physical environment described in this review support the dominance of the ecosystem hypothesis. Explicit integration and cross-linking of knowledge about biota, resources, and physical conditions is essential to understand banded vegetation function (chapter 2, this volume). A range of abiotic processes (Shmida, Evenari, and Noy-Meir 1985) as well as biotic processes (Niering, Whittaker, and Lowe 1963; Noy-Meir 1985; Callaway 1995) contributes to the structure and functioning of banded landscapes. Also, spatial and temporal variability in the development of the successional process (Yarranton and Morrison 1974; Robinson et al. 1992), in turn, may arise from the variability in the outcome of biological interactions (Bronstein 1994).

Banded vegetation patterns can be considered as a nested organizational hierarchy (Urban, O'Neill and Shugart 1987; Mauchamp 1992). At the coarsest or landscape organization level, banded landscapes are a mosaic composed of vegetation bands and bare areas, linked by the dynamic redistribution of rainwater by sheetflow into an alternating runoff/runon pattern. At a second finer-scale level, as soil water availability increases from the upslope edge to somewhere within the vegetation band, the vegetation cover and biomass increases to a maximum (Galle, Ehrmann, and Peugeot 1999) and then decreases to the downslope bare zone. If the availability of light changes in concert with the gradient in water and biomass, zonation of vegetation species composition may occur, as it does in Niger. Without light restriction, only the plant population size distribution is affected, as in Mexico and Australia. Few of the models have explicitly incorporated the effects of biological interactions between vegetation elements at the within-band level (Mauchamp, Rambal, and Lepart 1994; Thiéry, d'Herbès, and Valentin 1995; Dunkerley 1997a,b; Lejeune, Couteron, and Lefever 1999).

A third and least-studied level considers the individual plants within the vegetation array. The elements linking them are demographic processes, biotic interactions (e.g., facilitation and inhibition/competition), and fine-scale abiotic factors, (e.g., microtopography, soil crusts). The present review reveals that vegetation dynamics are the outcome of complex interactions at this level. Models predicting

the behavior of individual system elements at this scale are inevitably complex, and none yet exist. The outcomes may be analyzed in terms of both succession models and of more process-based conceptual frameworks involving feedback loops (chapter 2, this volume). In the future, manipulative experiments in natural communities and careful analysis techniques (Gurevitch and Collins 1994) will be essential to verify those models.

Demographic processes such as dispersal and establishment need much more elucidation to build on the work of Mauchamp and co-workers (1993), López-Portillo, Montaña, and Ezcurra (1996), and López-Portillo and Montaña (1999). This becomes important as human-use patterns become threatening processes to the survival of the vegetation system. The differential survival of mature plants in the different zones of the pattern implies spatially linked physiological limitations for perennial species in relation to water availability and other factors. These relationships need further attention to shed light on the functional role of the observed vegetation structures in the provision of ecosystem services (Mauchamp et al. 1993; Montaña, Cavagnaro, and Briones 1995; Seghieri and Galle 1999).

References

Anderson, V.J., and Hodgkinson, K.C. 1997. Grass-mediated capture of resource flows and the maintenance of banded mulga in a semi-arid woodland. Aust. J. Bot. 45: 331–342.

Boaler, S.B., and Hodge, C.A.H. 1964. Observations on vegetation arcs in the northern region Somali Republic. J. Ecol. 52: 511–544.

Boudet, G. 1972. Desertification de l'Afrique tropicale seche. Adansonia Ser. 2 12 (4): 505–524

Boyd, S.R., and Brum, G.D. 1983. Postdispersal reproductive biology of a Mojave Desert population of *Larrea tridentata* (Zygophyllaceae). Am. Midl. Nat. 110: 25–36.

Bronstein, J. 1994. Conditional outcomes in mutualistic interactions. Trends Ecol. Evol. 9(6): 214–217.

Brown, J.R., and Archer, S. 1990. Water relations of a perennial grass and seedling vs adult woody plants in a subtropical savanna, Texas. Oikos 57: 366–374.

Bush, J.K., and van Auken, O.W. 1990. Growth and survival of *Prosopis glandulosa* seedlings associated with shade and herbaceous competition. Botan. Gaz. 151(2): 234–239.

Callaway, R.M. 1995. Positive interactions among plants. Botan. Rev. 61: 306–349.

Chambers, J.E., and MacMahon, J.A. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed ecosystems. Annu. Rev. Ecol. Syst. 25: 263–292.

Cisse, S. 1981. Sedentarizations of nomadic pastoralists and "pastorization" of cultivators in Mali. In The future of pastoral people, ed. D. Aronson, pp. 318–324. Ottawa, Ontario, Canada. CDRI

Cornet, A., Montaña, C., Delhoume, J.P., and López-Portillo, J. 1992. Water flows and the dynamics of desert vegetation stripes. In Landscape boundaries: consequences for biotic diversity and ecological flows, eds. A. Hansen and F. Di Castri, pp. 327–345. Ecological studies 92. New York: Springer-Verlag.

Couteron, P., Mahamane, A., and Ouedraogo, P. 1996. Analyse de la structure de peuplements ligneux dans un fourré tigré au Nord-Yatenga (Burkina Faso): état actuel et conséquences évolutives. Ann. Sci. Forest. 53: 867–884.

Couteron, P., Mahamane, A., Ouedraogo, P., and Seghieri, J 2000. Differences between banded thickets (tiger bush) at two sites in West Africa. J. Veg. Sci. 11: 321–328.

Crisp, Michael D. 1978. Demography and survival under grazing of three Australian semi-desert shrubs. Oikos 30: 520–528.

Dunkerley, D.L. 1997a. Banded vegetation: development under uniform rainfall from a simple cellular automation model Plant Ecol. 129: 103–111.

Dunkerley, D.L. 1997b. Banded vegetation: survival under drought and grazing pressure based on a simple cellular automaton model. J. Arid Environ. 35: 419–428.

Dunkerley, S.L., and Brown, K.J. 1995. Runoff and runon areas in a patterned chenopod shrubland, arid western New South Wales, Australia: characteristics and origin. J. Arid Environ. 3· 41–55.

Ellner, S., and Shmida. A. 1981. Why are adaptations for long-range dispersal rare in desert plants? Oecologica 51: 133–144.

Galle, S., Seghieri, J., and Mounkaïla, H. 1997. Fonctionnement hydrologique et biologique à l'échelle locale. Cas d'une brousse tigrée au Niger. In Fonctionnement et gestion des écosystèmes contractés sahéliens, eds. J.M. d'Herbès, J.M.K. Ambouta, and R. Peltier, pp. 105–118. Paris: John Libbey Eurotext.

Galle, S., Ehrmann, M., and Peugeot, C. 1999. Water balance in a banded vegetation pattern. The case study of tiger bush in western Niger. Catena 37: 197–216.

Green, D.S. 1983. The efficacy or dispersal in relation to safe site density. Oecologia 56: 356–358.

Greig-Smith, P. 1979. Pattern in vegetation. J. Ecol. 67: 755–779.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52: 107–145.

Gurevitch, J., and Collins, S.L. 1994. Experimental manipulation of natural plant communities. Trends Ecol. Evol. 9(3): 94–98.

Harper, J.L. 1977. Population biology of plants. London: Academic Press.

Harper, J.L., Clatworthy, J.N., McNaughton, I.H., and Sagar, G.R. 1961. The evolution and ecology of closely related species living in the same area. Evolution 15: 209–227.

Harper, J.L., Williams, J.T., and Sagar, G.R. 1965. The behaviour of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. J. Ecol. 53· 273–286.

Howe, H.F., and Smallwood, J. 1982. Ecology of seed dispersal. Annu. Rev. Ecol. Syst 13: 201–228.

Kemp, P.R. 1989. Seed banks and vegetation processes in deserts. In Ecology of soil seed banks, eds. M.A. Leck, V.T. Parker, and R.L. Simpson pp. 257–282. New York: Academic.

Lejeune, O., Couteron, P., and Lefever, R. 1999. Short range co-operativity competing with long range inhibition explains vegetation patterns. Acta Oecol. 20: 171–184.

López-Portillo, J., and Montaña, C. 1999. Spatial distribution of *Prosopis glandulosa* var. *torreyana* in vegetation stripes of the southern Chihuahuan Desert. Acta Oecol. 20: 197–208.

López-Portillo, J., Montaña, C., and Ezcurra, E. 1996. Stem demography of *Prosopis glandulosa* var. *torreyana* in vegetation arcs and associated bare areas. J. Veg. Sci. 7: 901–910.

Ludwig, J.A., Tongway, D.J., and Marsden, S.G. 1994. A flow-filter model for simulating the conservation of limited resources in spatially heterogeneous, semi-arid landscapes. Pac. Conserv. Biol. 1: 209–213.

Ludwig, J., Tongway, D., Freudenberger, D., Noble, J., and Hodgkinson, K., eds. 1997. Landscape ecology, function and management: principles from Australia's rangelands. Melbourne: CSIRO Publishing.

Mabbutt, J.A., and Fanning, P.C. 1987. Vegetation banding in arid Western Australia. J. Arid Environ. 12: 41–59.

Macdonald, B.C.T., Melville, M.D., and White, I. 1999. The distribution of soluble cations within chenopod-patterned ground, arid western New South Wales, Australia. Catena 37: 89–105.

Mauchamp, A. 1992. L'hétérogénéité spatiale, sa dynamique et ses implications dans une mosaique de végétation en zone aride. Doctoral thesis. Montpellier: USTL-Montpellier II University.

Mauchamp, A., Montaña, C., Lepart, J., and Rambal, S. 1993. Ecotone dependent recruitment of a desert shrub, *Flourensia cernua*, in vegetation stripes. Oikos 68: 107–116.

Mauchamp, A., Rambal, S., and Lepart, J. 1994. Simulating the dynamics of a vegetation mosaic: a spatialized functional model. Ecol. Model. 71: 107–130.

May, R.M (1981) Patterns in multi-species communities. In Theoretical ecology, ed. R.M. May, pp. 197–227. Oxford: Blackwell Scientific Publications.

Montaña, C 1992. The colonization of bare areas in two-phase mosaics of an arid ecosystem. J. Ecol 80: 315–327.

Montaña, C., López-Portillo, J., and Mauchamp, A. 1990. The response of two woody species to the conditions created by a shifting ecotone in an arid environment J Ecol. 78: 789–798.

Montaña, C., Cavagnaro, B., and Briones, O. 1995. Soil water use by coexisting shrubs and grasses in the southern Chihuahuan Desert. J. Arid Environ. 31. 1–13.

Nelson, J.F., and Chew, R M. 1977. Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. Am. Mid. Natur. 97: 300–320

Niering, W.A., Whittaker, R.H., and Lowe, C.H. 1963. The saguaro: a population in relation to environment. Science 142: 15–23.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers Ann Rev Ecol Syst 4: 25–51

Noy-Meir, I. 1979/1980. Structure and function of desert ecosystems. Israel J. Bot. 28: 1–19.

Noy-Meir, I. 1985. Desert ecosystems structure and function. In Hot deserts and arid shrublands. Ecosystems of the world 12A. eds. M. Evenari, I. Noy-Meir, and D.W Goodall, pp. 93–102. Amsterdam: Elsevier.

Pulliam, H.R 1988. Sources, sinks, and population regulation. Am. Natur. 132: 652–661.

Reichman, O.J. 1984. Spatial and temporal variation of seed distributions in Sonoran Desert soils. J. Biogeogr 11: 1–11.

Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M L , Fitch, H.S., and Martinko, E.A. 1992. Diverse and contrasting effects of habitat fragmentation. Science 257: 524–526.

Schaal, B.A. 1980. Measurement of gene flow in *Lupinus texensis*. Nature 284: 450–451

Seghieri, J., and Galle, S. 1999. Run-on contribution to a Sahelian two-phase mosaic system: soil water regime and vegetation life cycles. Acta Oecol. 20: 209–217.

Seghieri, J., Galle, S., Rajot, J.L., and Ehrmann, M. 1997. Relationships between the soil moisture regime and the growth of the herbaceous plants in a natural vegetation mosaic in Niger. J. Arid Environ. 36: 87–102.

Shmida, A, Evenari, M., and Noy-Meir, I. 1985. Hot desert ecosystems: an integrated view. In Hot deserts and arid shrublands, vol. 12B, eds. M. Evenari, I. Noy-Meir, and D.W. Goodall, pp. 379–387. Amsterdam: Elsevier.

Slatyer, R.O. 1961. Methodology of a water balance study conducted on a desert woodland (*Acacia anuera* F. Muell.) community in central Australia. UNESCO Arid Zone Res 16: 15–26

Thiéry, J., d'Herbès, J.M , and Valentin, C. 1995. A model simulating the genesis of banding patterns in Niger. J. Ecol. 83: 497–507.

Tongway, D.J., and Ludwig, J A. 1990 Vegetation and soil patterning in semi-arid mulga lands of eastern Australia. Aust. J. Ecol. 15: 23–34.

Urban, D L , O'Neill, R V, and Shugart, H.H., Jr. 1987. Landscape ecology BioScience 37. 119–127

van der Meulen, F., and Morris, J W. 1979. Striped vegetation patterns in a Transvaal savanna (South Africa). Geo-Eco-Trop. 3: 253–266.

White, L P. 1970 *Brousse tigrée* patterns in southern Niger. J. Ecol 55: 549–553.

White, L.P. 1971. Vegetation stripes on sheet wash surfaces. J. Ecol. 59. 615–622.

Wickens, G E., and Collier, F W. 1971. Some vegetation patterns in the Republic of Sudan. Geoderma 6: 43–59.

Worrall, G.A. 1959. The Butana grass patterns. J. Soil Sci. 10: 34–53

Worrall, G.A 1960. Patchiness in vegetation in the northern Sudan J Ecol. 48: 107–115.

Wu, X.B., Thurow, T.L., and Whisenant, S.G 2000. Fragmentation and functional change of tiger bush landscapes in Niger. J. Ecol. 88: 790–800.

Yarranton, G.A., and Morrison, R.G. 1974. Spatial dynamics of a primary succession: nucleation, J. Ecol. 62: 417–428.

Montana C., Seghieri Josiane, Cornet Antoine.

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