PATCH DYNAMICS IN GRAZED ARID ECOSYSTEMS

by

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ABSTRACT

Spatially heterogeneous, or patchy, vegetation patterns are widely distributed in arid and semiarid ecosystems and their water-redistributing role is of great ecological interests. Studies have shown effects of rain and wind, vegetation interactions, and disturbances on patch pattern formation and dynamics. In the absence of a synthesis, I have undertaken a review to systematically understand effects of these interacting factors in patch pattern formation and dynamics for two types of spotted and banded patterns. These two patterns are widely distributed and have distinctive, yet complementary features that encompass most of the patch pattern characteristics. I found that: 1) wind is as important as rain in patch pattern formation; 2) shrubs have a facilitation effect on the surrounding vegetation via several mechanisms, and 3) grazing disturbances that include foraging, excretion, and trampling have different effects on vegetation dynamics depending on the patch type and amount of annual precipitation (e.g. wet or dry years).

1. INTRODUCTION

The natural world is heterogeneous and the term ‘patch’ is used to describe relatively discrete spatial units of it (Dale 1999). As a ‘patch’ will always be relative to the system under consideration (Pickett and White 1985), a precise definition of patch, especially one of ubiquitous applicability, does not exist (Du Toit et al. 2007). A general view of a patch is "a surface area differing from its surroundings in nature or appearance" (Wiens 1976). Here I use vegetation cover to distinguish vegetation patches that reside within a matrix of almost bare-ground. A recent review of the vegetation distribution in arid ecosystems supports the idea that plant distribution is patchy and it is commonly arranged in a two-phase mosaic of densely vegetated patches alternating with patches of (almost) bare soil (Aguiar and Sala 1999). Here I use the term ‘patch’ to indicate vegetation assemblage with a round (spotted) or strip-like (banded) shape, and the ‘interpatch’ to indicate bare-ground between ‘patches’.

The simplest way to distinguish arid and semi-arid areas is to use annual precipitation, where values of 0-300 mm and 300-600 mm refer to arid and semi-arid respectively (FAO 1987). Another way is by the aridity index, precipitation (P)/ potential evapotranspiration (PET), which range from 0.05-0.20 to 0.20-0.50 respectively (UNEP 1997). Globally, arid and semi-arid ecosystems account for about 30% of total land area by the second criterion (UNEP 1997). Understanding which moisture classification is used is important; for example, previous research on banded pattern vegetation have considered arid and semi-arid regions to have annual rainfall ranges from 50-750 mm (Valentin et al. 1999), a definition which exceeds the simplest FAO classification, but the

P/PET ratios of these regions fall into current UNEP classification standards of arid and semi-arid zones (Hiernaux and Gerard 1999, Couteron et al. 2000). Most patch pattern studies use the simpler precipitation level, instead of aridity index to identify arid and semiarid climates (Lejeune and Tlidi 1999, Meron et al. 2004, Giladi et al. 2007). Patch patterns do not show distinct differences between arid and semi-arid ecosystems; thus here I will use ‘arid’ to include both arid and semi-arid regions, where banded and spotted patterns occur.

Background

Important Roles of Patch Patterns

Arid ecosystems, where limited water availability governs most ecosystem processes, cover almost one third of the global land surface (UNEP 1997). In such ecosystems, vegetation has evolved several “strategies” for surviving in spite of less available precipitation, through organizing into a two-phase mosaic of vegetated and (almost) bare-ground patches (Noy-Meir 1973). This two-phase pattern appears to concentrate limited water through run-off from bare-ground patches (sources) on to vegetated patches (sinks) thus optimizing the plant productivity in arid ecosystems (Noy-Meir 1973, Ludwig and Tongway 1995).

Patch patterns are of great ecological interest because of their water-redistributing ecological roles and their widespread distribution in arid ecosystems. I divide roles of patch pattern studies into three categories to explain how important patch pattern are. First, vegetation patterns serve as a basis for generating hypotheses about processes that generate them. ‘Pattern and Process in the Plant Community’ by Watt (1947) profoundly influenced patch theory by presenting the view that a vegetation community is composed of different types of vegetation patches, often in different successional stages, such as establishment (initiation phase), growth (building phase) and senescence (degenerative phase). The pattern-process hypothesis has been further developed to recognize patches not only as manifestations of a stage of vegetation succession but to include factors including abiotic factors and disturbance (Wu and David 2002).

Second, patch patterns have an important role in water use. The two-phase patch pattern functions by concentrating the limited water resource through run-off from bare-ground patches (sources) to vegetated patches (sinks) (Noy-Meir 1973). This process support plant production which would be little or none if rain water were distributed evenly over the arid landscape. If climates become drier under ‘climate change’, the water-redistributing role will become more important. Arid ecosystems are characterized by low and sporadic rainfall, and consequently subject to frequent droughts. Under climate change, rainfall may become more variable and unpredictable so that arid ecosystems become more vulnerable (Le Houérou 1996).

Finally, bare-ground is identified as a basic structural and functional component of the system and co-equal with vegetation (Noy-Meir 1973). Bare-ground is not just void of vegetation, but is a component important to vegetation performance. In the source-sink theory, bare-ground is a source of water run-off to vegetation patches (Noy-Meir 1973). The consideration of bare-ground in the vegetation community broadens our perception beyond only considering vegetation in function and dynamics of a landscape.

Banded and Spotted Patterns

Two-phase vegetation patterns have many types. The most studied two-phase pattern is the banded pattern, in which plants (trees/shrub/grasses) aggregate into long narrow band, perpendicular to the slope in a matrix of bare-ground. Depending on the area of study as well as the shape and the transition state of the banded patterns, patterns have also been named dashed, stripe, strand, stipples, wave, arc, whorl, labyrinth, oval, gap or hole pattern (see in banded patterned vegetation summary in Bromley et al. 1997, the main reference table in Valentin et al. 1999, bands and spots patterns table in Aguiar and Sala 1999, three types of bands in Ludwig et al. 1999, other pattern types summary in Rietkerk et al. 2002). As shapes of some patterns are interchangeable, especially under different precipitation levels, the argument of whether all these patterns can be classified as one type of banded pattern, which would make it the most commonly occurring vegetation pattern all over the world, is still under discussion (Valentin et al. 1999, Aguiar and Sala 1999).

The only other two-phase pattern that is consistently distinguished from the banded pattern is the spotted pattern. It is characterized by single to several shrubs surrounded by bunch grasses (Aguiar and Sala. 1999). The main ecological difference between spotted and banded patterns is that spotted patterns occur on relatively flat areas less then slope gradient of 0.2%, while banded patterns occur on slope gradient between 0.2-2% (Valentin et al. 1999, d'Herbès et al. 2001), which are slopes of 1:50 to 1:500 (Bromley et al. 1997), with different drivers of wind and rain respectively (Figure 1) (Aguiar and Sala 1999, Ravi et al. 2011).

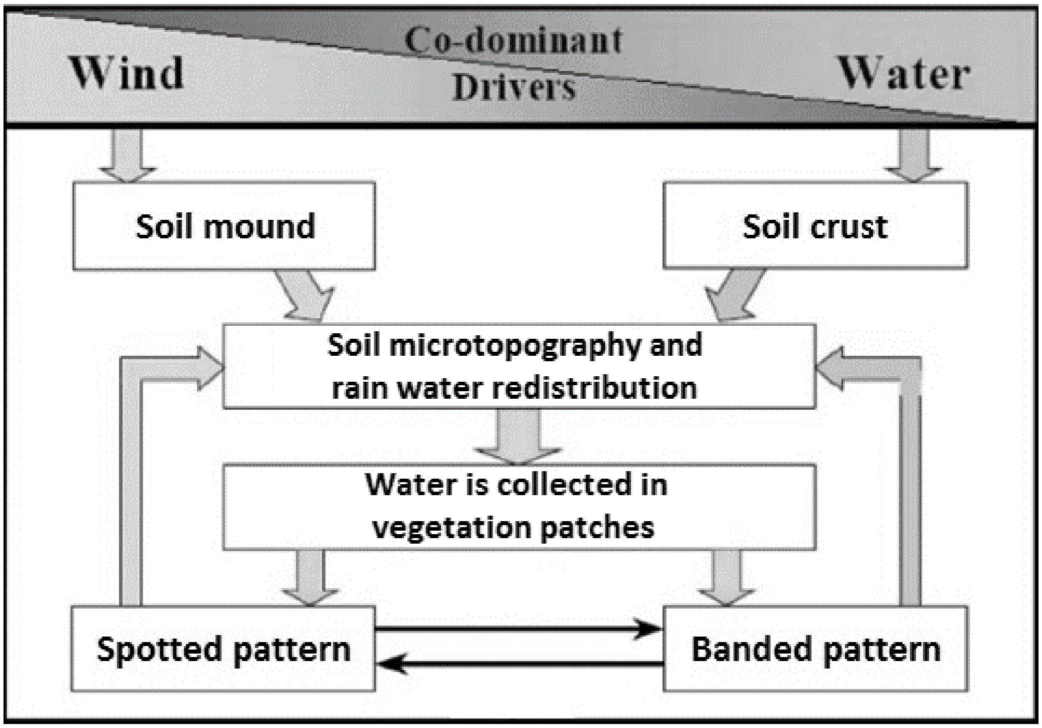

Figure 1. Banded and spotted patch patterns with different ecological drivers (edited from Ravi et al. 2011).

Objective

The goal of the literature review is to synthesize our understanding of abiotic and biotic processes that drive the formation and dynamics of arid land vegetation patch patterns, with special attention to the role of herbivores. The diversity of patch patterns and the ecological conditions underlying them both give us perspectives for understanding the phenomenon while potentially increasing the difficulty of developing a general explanations for cause and process in patch patterns formation and functioning. Based on this literature review, I will explain how the biotic and biotic drivers of arid land patch pattern vegetation dynamics interact with grazing disturbance.

Abiotic: Wind and Rain

Banded patch patterns are widely distributed, occurring on all continents (Galle et al. 2001). The typical banded pattern is called tiger bush in the northern part of Africa, where it occurs on gentle slopes, and reveals distinct vegetation stripes alternating with bare-ground and perpendicular to the slope (Clos-Arceduc 1956). Since then distinct patch patterns have been recorded and studied in many arid ecosystems of the world (Valentin et al. 1999) and lope as well as precipitation level have become the classification criteria for banded patterns (d'Herbès et al. 2001).

Another type of patch pattern, spotted pattern, has been reported for several regions of North and South America (Fuentes et al. 1984, Soriano et al. 1994). A well-known example is shrub patches in the Patagonian arid steppe (Auiar and Sala 1994). Spotted patterns occur on flat ground and are driven by wind, rather than water on a slope, which characterized banded patterns (Aguiar and Sala 1999). However, due to lack of understanding of the wind erosion process in forming the water-redistributing structure, spotted patterns are still regarded as one of the transitional stages of banded patterns (d'Herbès et al. 2001). In this review, I will consider spotted and banded patterns to be of equal ecological importance and analyze the ecological drivers of wind and water separately.

Biotic: Vegetation Interactions

A vegetation patch is an assemblage of more than one plant, and the vegetative interactions drive patch composition and dynamics. In the banded pattern, grass and tree species occur in spatially separate zones with increasing soil and root depth from the upper to lower slope (Ludwig et al. 2005). Species assemblages exist in separate zones, but the whole vegetation band is hypothesized to move upslope due to accumulation of soil, water, litter and seeds on the upslope edge of the vegetation band and degradation at the downslope portion (Aguiar and Sala 1999). However, such upslope movement is still under debate, as only band contraction and expansion are observed in alternating dry and wet years instead of upslope movement (Montana 2001).

In the spotted pattern, a shrub or a group of shrubs is circled by a ring of grass species (Soriano et al. 1994, Aguiar and Sala 1999). The shrub has a facilitation effect on the surrounding grasses, but when the grass grows bigger and denser the shrub is outcompeted. Thus, spotted pattern dynamics are driven by facilitation-competition interactions between shrubs and grasses, and go through cyclic succession (Soriano et al. 1994, Aguiar and Sala 1999). Because there has been no study of possible mechanisms of facilitation and competition in spotted patches over the last 15 years, study of both mechanisms are needed.

Grazing Disturbance

Arid ecosystems throughout the world are most used as grazing land for livestock (Neely et al. 2009) and wild herbivores (Olff et al. 2002). The main domestic grazers are sheep and cattle, and wild grazers include feral goats and kangaroos. My focus is on the general disturbance effects that grazing has on patch pattern formation and dynamics and does not separate the different types of grazers, although most research has been performed on cattle. Disturbance caused by grazing (hereafter termed grazing disturbance) is an important and long studied subject (White 1979, Sousa 1984, Briske et al. 2005), but addressing it in relation to patch pattern dynamics is rare. Moreover, the misleading concept of viewing grazing disturbance simply as overgrazing, which is equal to bare-ground initiation and maintenance, casts the herbivore as a culprit of the patch pattern landscape degradation (Freudenberger et al. 1997, Dunkerley 1997, HilleRisLambers et al. 2001) rather than including it as a component of the system. The ecological role of grazing in ecosystem functioning should be assessed because grazing is one of the most important economic activities of humans in arid land, and consequently potentially exerts great impact on vegetation patch pattern dynamics.

2. ABIOTIC FACTORS AND PATCH PATTERN FORMATION

Banded Pattern

The banded pattern of arid lands was first studied in British Somaliland (MacFadyen 1950a,b), and since then such vegetation patterns have been observed and studied in many regions of the Australian, African and American continents (White 1971). The banded pattern is often difficult to detect at the field level, but is visually apparent by aerial photographic and now they have been detected throughout twelve countries in five continents (Galle et al. 2001). The most representative is the tiger bush in Niger composed of the shrub species *Cambretum micranthum* (Figure 2).

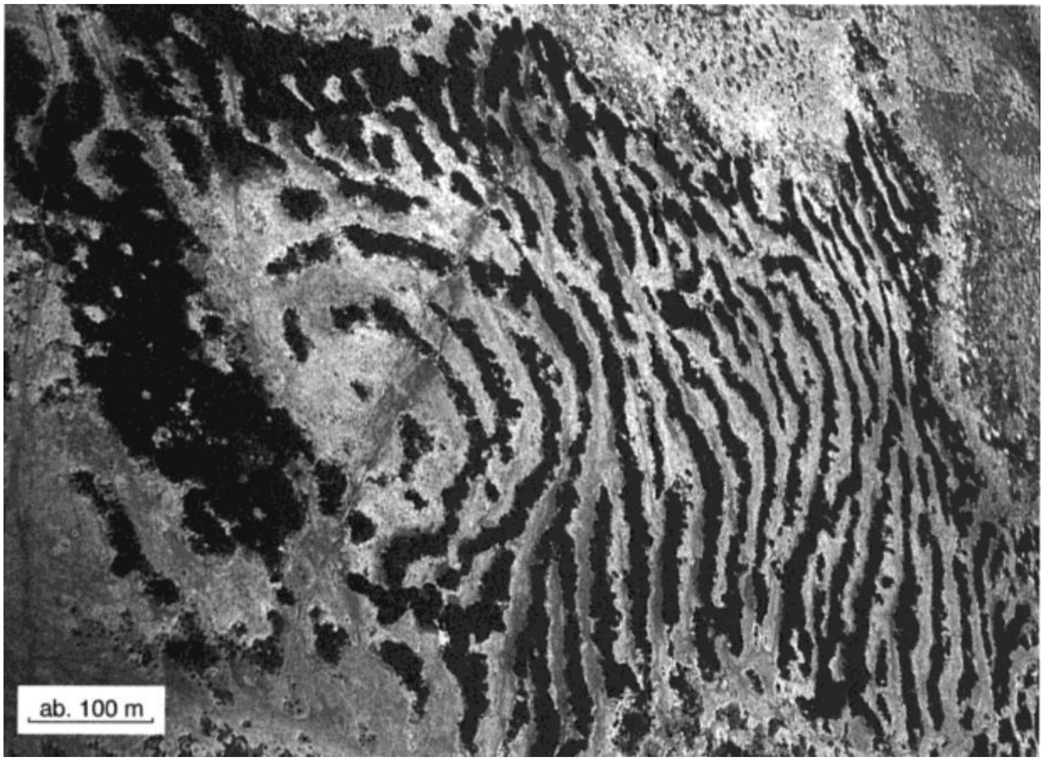

Figure 2. Banded pattern: tiger bush in Niger, 13º 40' N, 2º 20' E (from d'Herbès et al. 2001).

The minimum common conditions required for banded vegetation pattern occurrence are 1) arid climate, 2) high-intensity rainfall, and 3) a gentle slope (White 1971). In the arid land plant cover is patchy with loose soils within the interpatch. Soils in arid climates generally have loose sandy soils with low organic matter. When combined with low vegetation cover, sandy soils are subject to soil erosion (Valentin et al. 1999). Because of wind and rain erosion, soil materials are transferred to form a micro-topography (e.g., soil crust and soil mound) that regulates water redistribution. High-intensity rainfall (large quantity within a relatively short time) run-offs the gentle sloping bare-ground before fully infiltrating into the soil (White 1971). Run-off water is captured and transferred to vegetation bands and results in a pulse of vegetation growth (Ludwig and Tongway 1997).

The vegetation band and the bare-ground interband (band and interband hereafter) are two components of the banded pattern. Bands can range from 5-50 m in width and 20-400 m in length and represent about 20% of an entire area. The interband is typically three to five times as wide as the band (Aguiar and Sala 1999). While vegetation composition varies greatly from region to region, the band generally has a thin cover of grasses and forbs on the upslope margin, trees and shrubs in the middle and degrading vegetation in below (d’Herbès et al. 2001). The interband is characterized mainly by bare-ground, though annual herbs, sparse perennial grasses or woody plants can be present. The interband is the source of run-off water, sediments, and nutrients, while the band is the sink of these materials (Noy-Meir 1973).

The band and the interband can be further subdivided into five functional zones, characterized by infiltration rates and vegetation types (Figure 3). The two zones in the interband are run-off and sedimentation. Three zones in the vegetation band are pioneer, core and degraded in sequence from the upslope to the downslope (Valentin et al.1999, d'Herbès et al. 2001). The run-off and the sedimentation zones are dominated by bare-ground which is covered by soil crusts with low infiltration rates. The three zones in the band support distinctive plant communities: annual grasses and forbs in the pioneer zone; shrubs and/or trees in the core zone; and, low dying plant-cover in the degraded zone.

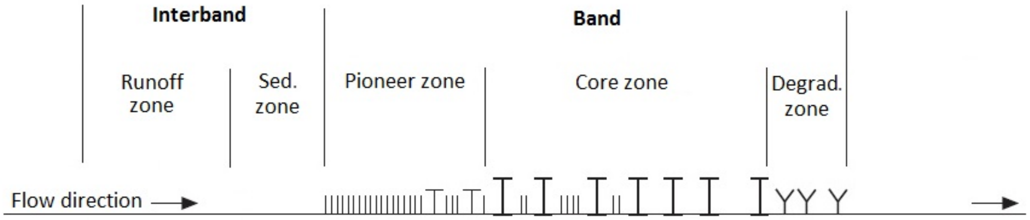

Figure 3. Components of the banded pattern. The very gentle slope of 0.2% is not visible in this scheme (edited from Seghieri et al. 1997, Valentin et al. 1999)

Interband

The interband is the source of run-off water. The low infiltration rate of bare-ground promotes run-off from the interband which is often due to the surface physical soil crusting. Soil crusts prevent infiltration and ensure that most precipitation of high intensity rainfalls have little chance to infiltrate, so run-off is generated and flowed down to the next vegetation band. Three types of soil crusts can occur within interbands: erosion and gravel crusts occur in the upslope run-off zone; and the sedimentation crust occurs in the downslope sediment zone (Valentin et al. 1999). In the following I explain crust forming processes and characteristics based on Valentin et al. (1999).

Erosion crusts develop on the upslope part of the interband when run-off removes soil from the tail of the degrading vegetation band upslope. Structural crusts have three layers: coarse sand in the upper layer; fine, densely packed grains in the middle; and fine particles of considerably reduced porosity in the lower layer. The lower layer is responsible for very low infiltration rate of the crust. Wind and water erosion remove two upper layers of structural crusts to leave only the lower layer with its fine grains of low permeability and from erosion crust. In some places, severe water erosion brings a layer of gravels above the erosion crust and generate a gravel crusts. In this case gravels armor the surface so that it tends to protrude above the surrounding level. The function of run-off in the interband is mostly generated by soil crusts of low infiltration rates, especially by erosion crusts. Erosion crusts have low infiltration rates, on average 85%, meaning that interband soils only absorb 15% of the rain water. In addition, erosion crusts cover more than half of the surface area of the interband.

The sedimentation zone is located at the lower part of interband, where ephemeral water ponds can occur. The sedimentation crust develops from fine grained silt eroded from erosion and gravel crusts above. The important characteristic of sedimentation crusts is that when dry, these crusts often break up into plates and curl up when shrinking. Cracks of sedimentation crusts are colonized by pioneer grassy vegetation. Once colonized, these sedimentation crusts often become more platy in structure, and with continued colonization, from the pioneer zone in the vegetated band. Thus sedimentation crusts can be interpreted as a transition zone between the interband and the band, enabling the vegetation to establish on it.

Band

As explained above run-off is the main function of the interband, and the remaining three zones occur within the water catching vegetation band. Even small obstructions to the run-off flow can trigger positive feedback mechanisms to cause sediment deposition and water infiltration and hence, vegetation development in the shape of a band. The band acts as a natural landscape sieve or filter, rather than a barrier, depositing sediment and water both within and through it. The water-capturing function of the band operates at different landscape scales, from bigger to smaller from bands, shrub mounds to grass clumps (Ludwig and Tongway 1995). For example, at the largest scale, distinct groves of mulga trees (*Acacia anuera*) that are separated by open intergroves (interband) in Australia act as an obstruction of water and nutrients from the upslope interband, have a scale ranging from 5-50 m in width to 20-400 m in length. At the smallest scale, individual shrub and grass clumps, even fallen logs act as obstructions, accumulating litter and soil particles. The high infiltration rate of soils in vegetated patches is due not only to the soil factors, but also due to the termite and ant activities (Tongway et al. 1989). Termites and ants are the dominant surface-active fauna in arid soils (Lal 1988) and their nest building activity increases the porosity of soil, thus increasing the infiltration rate. In the mulga grove in Australia, an infiltration rate 10 times higher in mulga groves than in the interbands was observed, partly due to the presence of termites and ant biopores (Greene 1992), demonstrating the biotic component in this water-redistributing system.

Spotted Pattern

Spotted patterns, characterized by well-spaced small groups of shrubs each surrounded by bunch grasses have been reported in several regions of North and South America (Aguiar and Sala 1999). A striking representative is the spotted pattern composed of the shrub species *Adesmia compestris* in the Patagonian steppe, where vegetation patches comprise 18% of the whole landscape (Figure 4) (Sala et al. 1989, Soriano et al. 1994). Black spots in the Figure 4 are shrub patches, while intervening light –color areas are bare-ground interpatches.

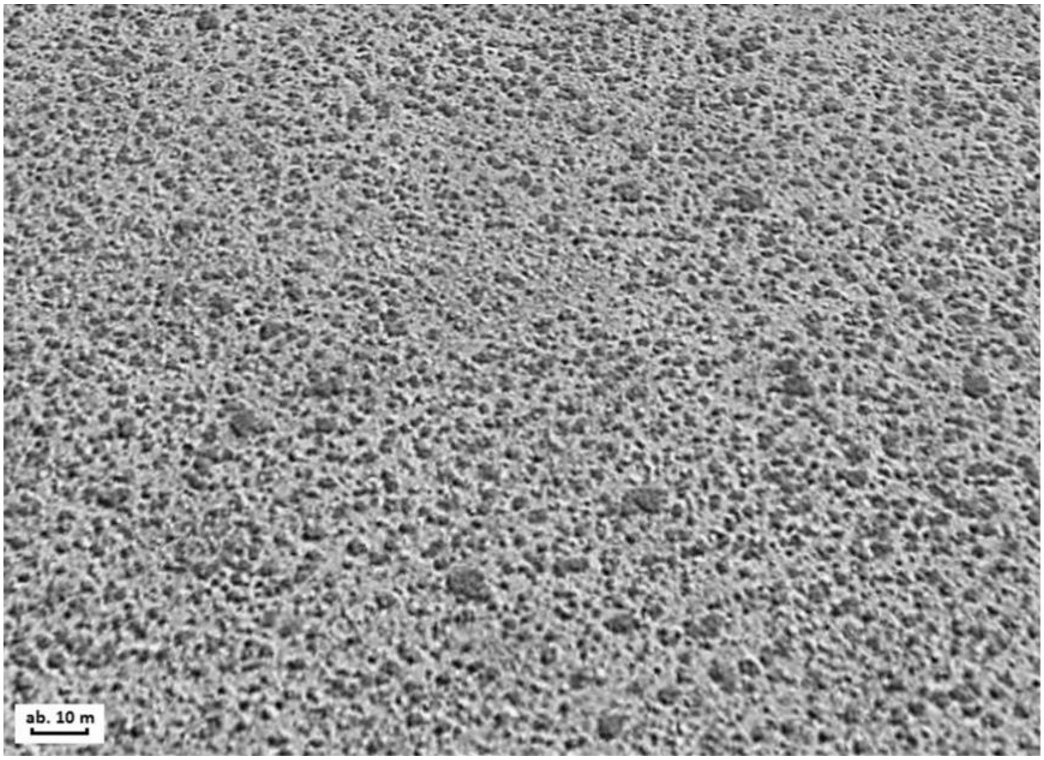

Figure 4. Spotted pattern in the Patagonia region of Argentina, 45^o 41' S, 70^o 16' W (from the Google Earth based on Sala et al. 1989).

Compared with wide range of banded pattern distributions and studies, spotted patterns have not been found in many places, and did not become a separate field of study until recently. In the past, the spotted pattern has been studied as shrub clumps (Fuentes 1984) or fertile islands (Garner and Steinberger 1989), but the intervening bare-ground was not included as a part of the system functioning. Aguiar and Sala (1999) were the first to consider the spotted pattern to be of the same ecological importance as the banded pattern. They refer to the spotted pattern as ‘leopard’ analogous to the ‘tiger’ of the banded pattern, however the wind process in forming the water-redistributing structure of spotted pattern is not clear, so that Aguiar and Sala’s synthesizing efforts have not rescinded the spotted pattern’s inferior status completely. In a recent review by d’Herbès et al. (2001) the spotted pattern was still regarded as one of the transitional states of banded patterns.

The uncertainty of whether banded patterns and spotted patterns are interchangeable is due to the fact that ecological drivers of wind and rain in arid ecosystems are interrelated and co-occurring processes (Ravi et al. 2011). The banded pattern dominates on slopes where rain run-off has a more prominent effect. In contrast in the spotted pattern, the aeolian process is more dominant. While the influence of wind and rain may vary with seasons, the fact that it is rare to observe both banded and spotted patterns on one landscape, or interchanging with each other distinguishes the phenomena. Indeed vegetation patterns are quite stable and exist in different ecological locations, in which the dominant driver is comparably stable.

Soil Mound

The soil mound formation is the critical process in forming the water-redistributing structure of the spotted pattern. In the formation of soil mound, two mechanisms are likely responsible: 1) biological accumulation of below- and above-ground litter below and around a shrub, and 2) physical transfer (erosion and deposition) of materials from the interpatch to the mound (Burke et al. 1998). Vertical soil texture and structure of the mound can demonstrate corresponding biological and physical processes, with two different soil layers distinguished by a crust between them (Figure 5, dashed line). This crust is the original soil surface where the shrub established and soil accumulation started to form the current elevated soil mound surface (solid line). The layer above has a darker color due to the presence of soil organic matter with loosely packed soils. In contrast, the lower layer is more densely packed, contains root materials and lacks of soil organic matters. On the other hand, the interpatch is lowered by erosion and so the ground surface in the interpatch (dotted line) is below the original soil surface (dashed line), which emphasized the elevation rise of the mound (Buis et al. 2010).

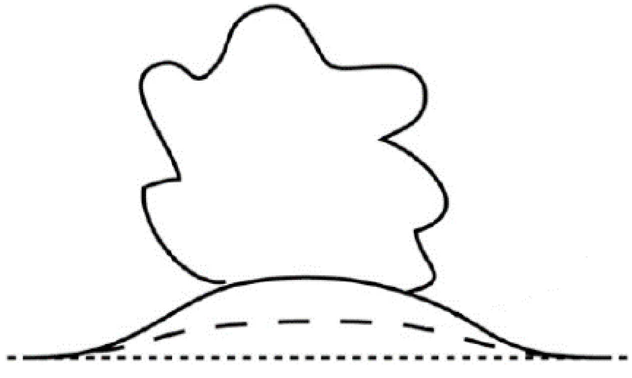

Figure 5. Structure of the soil mound. Solid line indicates actual mound surface, dashed line indicates the original crust surface in which the mound formation starts, and dotted line indicates actual interspace crust surface by erosion (from Buis et al. 2010).

Soils of the mound are nutrient-rich. Due to shoots and stems close to the ground, bunch grasses and shrubs capture soils and litter blown by wind and sediments washed by water. The resulting soil mound formation is very prominent under shrubs. Soil mounds are known as ‘fertile islands’, ‘islands of fertility’ or ‘resource islands’ (Garner and Steinberger 1989, Schlesinger et al. 1996, Reynolds et al. 1999) due to nutrients, water and productivity relative to the adjacent interpatch area. ‘Fertile islands’ describe nutrient-rich sites which result both from accumulation of litter materials and soil biota activities that increase the mineralization and decomposition rate to increase nutrient availability. The soil biota includes termites and ants which are the dominant surface-active fauna in arid soils (Lal 1988) and they cut the woody material into pieces on the ground surface, which are later integrated into the soil and decomposed by other soil microbes, such as protozoa, nematodes and mites (Eldridge et al. 2001).

The litter input comes either from within the patch or is carried in from adjacent patches by wind. Shrub roots extend outward many times the canopy radius and penetrate more deeply into the soil than do grass roots. Because of the wide-spread root system, shrubs absorb nutrients from a larger sphere, drawing nutrients both from deep horizons and laterally from areas beyond the canopy. The nutrients thus accumulate in biomass and concentrate in soil beneath individual plants through litter fall, decomposition, root turnover and canopy leaching (Callaway 1995). The nutrient accumulation action of roots from the surrounding soil is termed “nutrient pumping” (vertical nutrient movement by deep roots) (Callaway 1995) and “nutrient mining” (horizontal nutrient movement by lateral roots from interspace) (Schlesinger and Pilmanis 1998).

Beside nutrients, three biotic processes enrich the mound with respect to water. First, water absorption by soil mounds. Since water is a scarce resource for plant growth in arid ecosystems, the water 'absorbing' function of the soil mound is critical in the spotted pattern formation. The soil mound 'absorbs' water because of the 'spongy' structure, which is due to improved soil aggregation and biopores (biologically derived soil pores > 0.75 mm) related to biological activity and vegetation roots (Ludwig et al. 2005). The nest building activity of termites and ants also increases the porosity of soil, thus increasing infiltration rate (Tongway et al. 1989).

Second, water may be concentrated and stored by shrubs. Tree and shrub canopies intercept rainfall and redistribute the water to the atmosphere by evaporation and to the ground by through-fall and stem-flow. Loss of intercepted water by evaporation may represent a significant loss in arid ecosystems (Pressland 1973). Stemflow accounts for only a small part of precipitation, approximately 5-10 % in low intensity rainfall (Zhang et al. 2013) but for several species stemflow can be up to 50% (Mauchamp and Janeau 1993). Since water is limited in arid lands, intercepted water, once partitioned as stemflow and through-fall, could be an important source of soil moisture (Tromble 1988), and plants may adapt to capture it as a mechanism to survive seasonal drought periods (Martinez-Meza and Whitford 1996). Stemflow can rapidly concentrate large volumes of water at the base of trees or shrubs along root channels and it can easily be available for plant roots and also be stored in deep soil layers to survive drought conditions (Martinese-Meza and Whitford 1996).

Third, water may be delivered to the dry surface soil by hydraulic lift. Hydraulic lift is a phenomenon of upward water movement from the moist deep soil horizon by roots of the transpiring plant to the upper part of the root system and into the dry soil of upper horizons (Gurevitch et al. 2002). Deeper roots appear to absorb and transport water both day and night. In the day-time, root water moves up to leaves by transpiration pull of plants from higher water potential to lower water potential, and when the stomata closes during the night, root water moves outward toward the dry soil in upper horizons. In this way, the fluctuation of soil water potential of daytime water depletion and night time resupply by hydraulic lift occur (Richards and Caldwell 1987). With hydraulic lift, additional moisture would be stored in upper soil layers where most root mass is present to support its maximum daytime transpiration as well as shallow-rooted plants surrounding. This phenomenon, hydraulic lift, may transfer water to neighboring plants with shallow roots and significantly benefit them during drought periods when deeply rooted neighbors increase the availability of soil moisture close to the surface (Gurevitch et al. 2002).

3. BIOTIC INTERACTIONS AND PATCH PATTERN SUCCESSION

Succession is a directional change in community composition and structure overtime (Allison 2003). The initial concept of succession, as promoted by Clements (1916), was a predictable process leading to a predictable 'static' climax vegetation. This idea was a major force in plant ecology for almost one century. The move away from the idea took several directions. One influential new perspective is patch cyclic succession by Watt (1947). The main difference between these two successional theories is that the Clements's theory assumes the plant community is a homogeneous entity that tends toward a final, determined end point. In contrast, Watt's theory stressed that a community is a dynamic mosaic of patches, in which each patch goes through cyclic rather than one-directional changes. Here I view succession as a long-term trend, which results from vegetation interactions without including the effect of disturbance regimes. Under disturbance regimes, I consider the change of plant communities as a dynamic process instead of a successional process.

Banded Pattern Succession

The notion of upslope migration or movement of vegetation bands has been a common thread in all studies of banded landscapes (White 1971, Greig-Smith 1979, Mabbutt and Fanning 1987, Montana et al. 1990, Tongway and Ludwig 1990, Montana 1992). It is based on the run-off/run-on theory that underpins the basic functioning of banded vegetation. The obstruction of overland flow by the band would favor soil deposition, water and nutrient concentration, and thus germination of pioneer plants on the upslope edge, which is called the building phase (Figure 6). Because of that seedlings are frequently observed to be concentrated on the upslope edge of the band (Montana et al.1990, Tongway and Ludwig 1990, Seghieri et al. 1997). In contrast, dead trees or shrubs are commonly reported near the downslope edge, which is called the degenerative phase to suggest that the downslope edge has difficulty maintaining itself (Valentin and Bresson 1992, Valentin and d'Herbès 1999). The migration "velocity" of bands has been assessed on a several sites: the fastest observed migration was 1.5 m/year for grass bands, 0.8 for shrubs, and 0.8 for trees (Valentin et al. 2001).

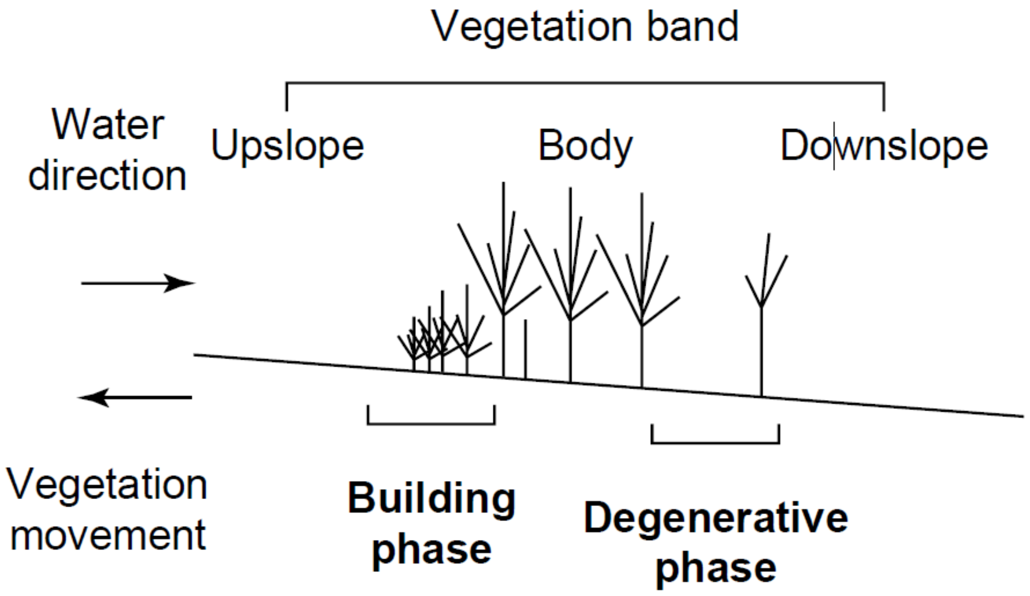

Figure 6. Banded pattern succession: upslope migration (from Aguiar and Sala 1999).

The hypothesis that vegetation bands slowly migrate upslope is in some cases questionable because some patterns remains stable for long periods (Valentin et al. 2001). Most supporting studies for upslope movement have been performed on herbaceous plants in the upslope pioneer fringe, where plants are likely to react more quickly to weather regime than trees/shrub (Montana et al. 2001). Plants in the core may also be slowly moving, but they have less consistent trend. For example, age and size class distribution of mesquite (*Prosopos glandulosa*) in Mexico did not systematically increase downslope within a band (Lopez-Portillo and Montana 1999) as would be expected in a moving band. If consistent, the missing age distribution implies that successful establishment of new plants is an infrequent event. Alternatively expansion/contraction of either on the upslope or downslope edge may be in response to alternating weather regimes; with the main body remaining stable. If so the seeming upslope movement of the band and its perimeter may be variable and intermittent, following the alternation of wet and dry years.

Skeptics also point to deep soils in some tree bands. For the upslope movement to occur with trees, a considerable build-up of soil material would have to occur in the grass/shrub zone and the process would be extremely slow. As soil beneath the band is often deeper than the soil in the interband area (Litchfield and Mabbutt 1962), long-rooted trees may have become self-stabilized due to the soil depth requirement (Wickens and Collier 1971). The spatial zonation of grass in shallow soil and trees in the deep soil may also be interpreted in terms of persistent zone separation of a previously established pattern with minor changes of extension/contractions resulting from rainfall fluctuation (Couteron et al. 2000). Thus the spatial variation of the vegetation in the band reflects water input and soil development, not necessarily upslope migration.

Spotted Pattern Succession

At the landscape scale, the ratio of different patch phases (initiation, building, and degenerative) is stable, giving the impression of a system at equilibrium (Aguiar and Sala 1998). This is consistent with Watt's (1947) patch dynamic equilibrium theory, in which he used seven plant communities to demonstrate his assertion that the overall landscape kept stable because of the stable ratio of different patch phases. That is, while each individual patch goes through cyclic succession, from bare-ground to vegetation establishment and degeneration, degenerating clumps are replaced by new establishing clumps so that the ratio of the different phases remains the same on the landscape as a whole (Figure 7) (Aguiar and Sala 1999).

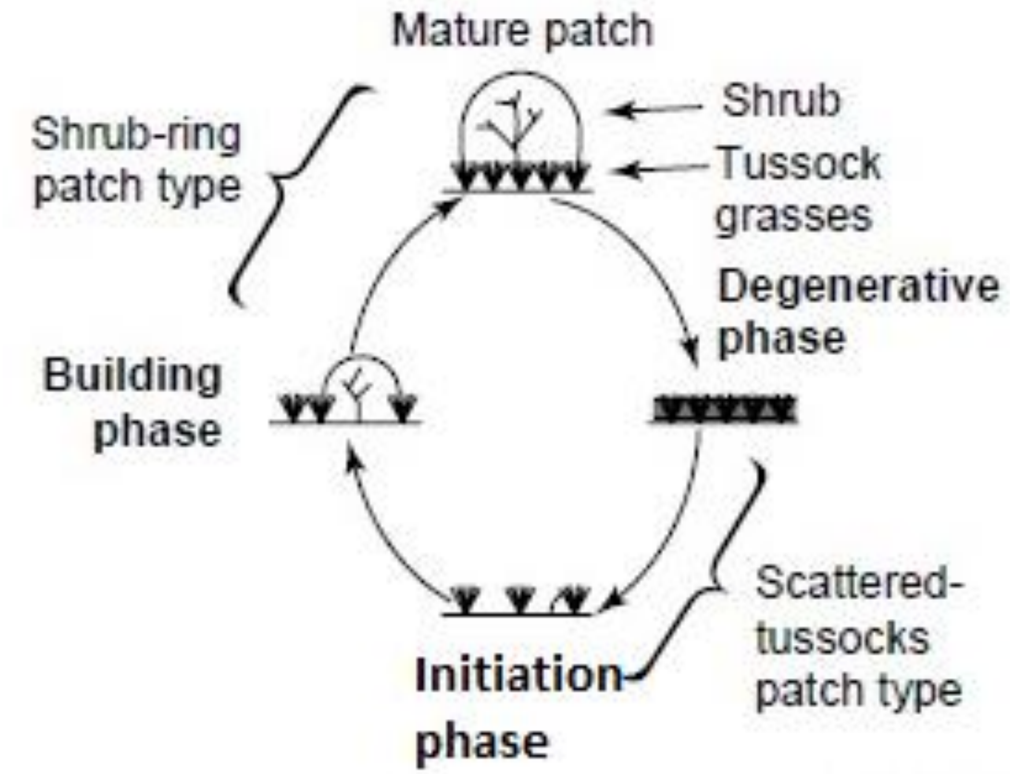

Figure 7. Spotted pattern dynamics: cyclic succession (from Aguiar and Sala 1999).

As the shrub grows (building phase) it creates a neighborhood with canopy facilitation that promotes both seed accumulation and seedling establishment, forming of a ring of grasses. As the ring of grasses matures, below-ground competition eventually excludes the shrub, and leads to the degenerative phase. When the shrub dies and collapses, the canopy facilitation disappears and grass zone becomes thinner. Grass mortality continues to yield bare-ground (initiation phase); then the open site provides a germination site for shrubs, and the shrub will capture grass seeds and facilitate their growth, initiating a new cycle of patch dynamics (Soriano et al. 1994, Aguiar and Sala 1994, 1999). Below I will examine mechanisms of facilitation and competition, namely interspecific interactions between the shrub and under-canopy grasses.

Facilitation

Shrubs are the dominant plant species in spotted patch patterns. Shrub characteristics of long life-span, deep-roots, tolerance of drought and erosion allow them to survive in water-limited conditions (Noy-Meir 1973). Shrub stems close to the ground and overhanging branches are especially effective at accumulating soil materials to make a soil mound; which is the main unit of the spotted pattern water-redistributing structure. Shrubs not only survive water-limited conditions by concentrating water and organic materials within the soil mound, their presence also facilitates the growth of other species under their canopy; thus, enhancing primary production and biodiversity in arid ecosystems (Shachak et al. 2008, Boeken and Orenstein 2001). Host shrubs have a significant role of facilitating the growth of other under-canopy plants via facilitation of seed capturing, microclimate amelioration and protection from herbivores.

Seed Capturing. Seed bank density and richness are much higher inside patches than in bare-ground area (Pugnaire and Lazaro 2000, Marone et al. 2004, Giladi et al. 2007, Caballero et al. 2008). This spatial structure of the seed bank is due both to higher seed production within patches (seed source effect) and due to the capability of patches to trap wind-dispersed and ground-rolling seeds from surrounding areas (seed trapping effect) (Flores and Jurado 2003, Bullock and Moy 2004, Giladi et al. 2013). The seed source effect is due to short-distance dispersal characteristic, dispersing seeds mainly in the vicinity of parent plants and to a lesser extent (Caballero et al. 2008). Seed source and trapping effects of shrubs maintain the observed difference in seed bank abundance and vegetation composition inside and outside the patch, reinforcing the existence of patchy structures (Franco and Nobel 1989). To restate, the short-distance dispersal of herbaceous species and shrub source/trapping effects are regarded as important causes of two-phase patch pattern formation and maintenance in arid ecosystems (Giladi et al. 2007, 2013).

Microclimate Amelioration. Woody plant canopies affect the microclimate around them by altering solar radiation, wind speed, temperature (of air and soil), humidity, and soil evaporation (Davies-Colley et al. 2000). The main effects of canopies are reducing the amount of direct solar radiation (shading) and wind speed, leading to lower daytime temperatures and lower evaporation (Breshears et al. 1998). Savanna trees and shrubs may reduce the solar radiation by 45 to 60 % (Belsky et al. 1989, Georgiadis 1989) and reduce wind speed at the soil surface seven times as compared with the top of the shrub canopy (Leenders et al. 2007). The tree or shrub canopy keeps the under-canopy cooler during summer, and also reduces cold and frost exposure (Castro et al. 2002).

Temperature and humidity are among the most crucial factors governing germination of buried seeds (Forcella et al. 2000). The milder microclimate generated by shrub canopy, with relatively less extreme temperatures and higher humidity is important for seed germination of herbaceous (Breshears et al. 1998) and woody vegetation (Floyd 1983). For example, germination rates for the two needle pinyon (*Pinus edulis*) at a soil temperature of 30 °C are four times less than at 20 °C (Floyd 1983). The highest rate of germination of a perennial grass species *Piptochaetium napostaense* was found in seeds buried under shrub cover, due to the increased soil water-content (Mayor et al. 2007). Thus as a result of microclimate amelioration (temperature and humidity), the germination rate is higher in shrub patches than in open spaces, which further contributes to the vegetation production (Sanford et al. 1982, Vetaas 1992).

Protection from Herbivores. Palatable species may avoid predation through their association with nurse plants. The phenomenon is known as “defense guilds” in which some members of the plant community function as anti-herbivore beneficiaries for other species (Atstatt and Odowd 1976, Milchunas and Noy-Meir 2002). Some woody species can protect the growth of under-canopy species by means of 1) deterrents such as toxins, odors or thorns/spines which can repel against herbivory (Bakker et al. 2004, Smit et al. 2005, 2006); 2) unpalatable or less-digestible shrub patches will be less selected as herbivores generally avoid low quality patches of vegetation (Hjälten and Price 1997); and 3) the physical structure of the shrub with low-hanging branches and a dense canopy prevents or reduces access to plants living underneath their canopies (Facelli and Temby 2002).

Competition

As mentioned above, when grasses surrounding a shrub grow bigger and more dense, the interspecific competition between the plants increases and grasses eventually exclude the nurse plants by competition (the shrub) (Soriano et al. 1994). I outline the competitive process below. Because water is the main constraint of vegetation function in arid ecosystems, the interspecific competition is primarily for water (Aguiar and Sala 1998). The main water source in arid ecosystems is from precipitation (rain and snow) and while most is lost through evapotranspiration, only a small amount infiltrates into the soil where it is available to the plant (Paruelo and Sala 1995). From the plant water-use perspective, soil water can be divided into two different soil resources: upper soil water and deep soil water, primarily used by short-rooted grasses and deep-rooted shrubs respectively (Soriano and Sala 1983). Grasses will intercept the rain water in the upper soil layer, and prevent it infiltrating into deeper soil horizon to decrease the water availability to the shrub. When grasses grow bigger and denser, they can intercept significant amount of water in the upper soil layers, decreasing the amount of water moving to the deep soil layers, and consequently impeding shrub growth. In a grass exclusion experiment, shrub production was increased as a results of increased soil water infiltration in deep soil layers (Sala et al. 1989). Thus, grasses may directly consume the water or reduce the amount of water infiltrating to deep soil layers. As the grasses grow larger and denser, the interspecific competition becomes so strong that the host plant is excluded, thus causing the degeneration phase of the shrub patch.

4. GRAZING DISTURBANCES AND PATCH PATTERN DYNAMICS

Disturbance has long been recognized as an important factor affecting plant community dynamics (Pickett and White 1985). Originally many considered disturbance as a rare and unpredictable event, but in recent decades it has increasingly been treated as a natural process that occurs at different spatial and temporal scales in plant communities (Pickett et al. 1989). One of the most used definitions of disturbance "…is any relatively discrete event that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White 1985). A major effect of disturbance is the opening of space, and the opening of that space is usually associated with a change in resource availability: such as increased light, water or soil nutrients (Sousa 1984). As a result of human's impact on landscapes many types of disturbance including grazing, involve changes in intensity, frequency, or spatial extent.

Grazing is the principal practical method of exploiting natural vegetation in arid environments, and as the foundation for human livelihoods should be managed for environmental sustainability (Neely et al. 2009). Types of grazing regimes (intensity, animals, season, and husbandry) can directly and indirectly affect plant communities. Direct effects include removal of above-ground biomass; indirect effects include excretion and trampling (Bullock et al. 2000), all of which alter resource availability, and consequently composition and dynamics of the system. Here I synthesize studies of grazing disturbance in three ways: foraging, excretion and trampling, and examine the principle effect of each grazing disturbance on patch dynamics with the object of discovering principles useful in managing grazing disturbance on patch pattern dynamics.

Grazing Disturbance: Foraging—Patch Grazing

In range management, patch grazing refers to close and repeated grazing of small patches or individual plants while nearby vegetation is lightly grazed or ungrazed (Heady and Child 1994). It is also referred to as ‘spot overgrazing’ or ‘spot grazing’, and ungrazed or lightly grazed plants are termed “wolf” plants (Stoddart et al. 1975). When bunchgrasses remain ungrazed throughout a growing season, residual straw and stems accumulate which inhibit further livestock grazing, allowing those grasses to grow even larger than their neighbors and become palatable yet ungrazed wolf plants (Ganskopp et al 1992). The accumulation of persistent stems cause cattle to reject wolf plants, and their herbage may go unused for many years (Ganskopp and Bohnert 2004). Conversely, plants or individuals that are heavily grazed and consequently do not accumulate coarse culms are the preferred source of forage (Romo 1994). This selective grazing induces a pattern in which heavily grazed areas alternate with lightly grazed or ungrazed wolf plants (Bakker et al. 1984), in which heavily used patches are grazed repeatedly within the season and in following years (Ring et al. 1985). The differential use creates a micro-pattern mosaic of heavily grazed areas and lightly grazed patches (Bakker et al. 1984). Patch grazing may also produce short-term positive feedback, like increasing forage quality with increased nitrogen or crude protein in newly grown leaves (McNaughton 1984, du Toit et al. 1990, Jefferies et al. 1994) which may magnify the effect by inducing animals to continually re-graze a previously grazed patch. In the long term, however, repeated close grazing may eventually cause mortality and changes to the species composition, triggering a negative feedback (Pastor et al. 1997).

Reasons for Patch Grazing

Animal Behavior. Herding herbivores tend to split into subgroups. Livestock, such as cattle and sheep are gregarious animals that tend to form herds, which may be related to predation risk (McNaughton 1984). Herds provide individuals with collective benefits, such as spending less time detecting predators, and thus enabling them to spend more time foraging (Green 1992, Hirata et al. 2003). Herding can however, also have a negative impact on individuals since each member of the herd still requires its own space for physical and social requirements but may also need to avoid competition for feed while foraging (Hirata et al. 2003). The associations among individuals should evolve to optimize the trade-off between protection and feeding, thus yielding patterns of associations based on the status, experience and behavior of the individuals within the group (Keeling 1995). This leads to dynamic social subgroups within a herd, which are organized in fusion-fission societies (Lazo 1994). In ethology, a fusion-fission society is one in which size and composition of the social group change as time passes and animals move throughout the environment. For example, herding animals merge (fusion) to sleeping in one place or split (fission) to forage in small groups during the day (Aureli et al. 2008).

A herd can be split into several subgroups by fission. The subgroups are often matrilineal groups, which are derived from long-lasting associations among females and succeeding generations of their female offspring (Reinhardt and Reinhardt 1981, Lazo 1994). In contrast young males form groups of bachelors, which are less cohesive than female groups (Reinhardt and Reinhardt 1981). While fission tends to occur during uneventful times such as grazing, resting or ruminating in the pasture, group size and composition can be stable overall irrespective of activity. In contrast, fusion involves gathering into a compact flock or herd during critical situations. For example, fusion has been observed in sheep when they are anxious or when the flock was returning from the pasture to their shed (Kawai 1989). Fusion-fission is a behavioral tendency of herding ungulates, which results in patchy distribution when they are grazing.

Vegetation Response. Two types of positive feedbacks induce repeated grazing. Short-term repeated grazing has positive effects on grass growth, resulting in increased nitrogen concentration and increased biomass (McNaughton 1984, du Toit et al. 1990, Jefferies et al. 1994). Grazing stimulates regrowth and tillering in grass, and the nutrient content is enhanced by the greater proportion of young leaves which generally have a higher nitrogen or crude protein content and a relatively low percentage of cell wall components (Mattson 1980). Another possible mechanism for short-term increases of leaf nitrogen concentrations is from increased nitrogen availability in the soil, resulting from increased microbial activities due to root exudation after the short-term defoliation (Bardgett et al. 1998). Root exudation is exudation of photosynthetic carbon stored in roots to be used for root growth or released into the rhizosphere as root-derived exudates (Bardgett et al. 1998). Root exudation is a high-quality nutrient source for the growth and maintenance of rhizosphere microorganisms (Van Veen et al. 1989), especially decomposer bacteria, which have high decomposition rates (Bardgett et al. 1998). Thus, defoliation promotes bacterial growth through root exudation, increasing nitrogen mineralization and soil nitrogen availability to the plant.

Grazing also stimulates growth rates of grasses, thus increasing productivity by compensatory regrowth (Ferraro and Oesterheld 2002, Loeser et al. 2004). There are three types of compensatory growth: when defoliation increases growth rates, the response is known as overcompensation; when defoliated plants grow as fast as undefoliated plants the response is known as full compensation; whereas, when defoliation decreases growth rates the response may be either partial compensation or damage (Ferraro and Oesterheld 2002). While compensatory responses to defoliation are norm, the overcompensation is still under debate (Belsky et al. 1993). However, the debate no longer revolves around whether overcompensation exists, but rather, under what circumstances it occurs (Loeser et al. 2004). As plant response is determined by the growth stages and availability of resources that can be mobilized for post-damage regrowth, it is easier to observe overcompensation early in the growing seasons and/or in wet years (Lennartsson et al. 1998). Several mechanisms for compensatory responses have been identified (Ferraro and Oesterheld 2002); among them the most often mentioned is the activation of dormant meristems following apical meristem damage (Strauss and Agrawal 1999, Stowe et al. 2000, Tiffin 2000). Apical meristem damage decreases apical dominance and releases dormant meristems, thus allowing lateral branching, which leads to over compensatory responses and greater annual productivity (Stowe et al. 2000).

Long-term Effects of Patch Grazing

Repeated grazing may produce short-term positive feedback and induce herbivores to re-graze a previously grazed patch. Such repeated grazing will, in the long run, modify plant community composition and may eventually cause the negative feedback if there is insufficient recovery time between grazing events.

This grazing impact is the basis for the ‘increaser-decreaser’ classification of rangeland species (Dyksterhuis 1949, Foran et al. 1978) within heavily grazed and lightly grazed patches (Bakker et al. 1984, Senft et al. 1985). Short, decumbent grass species frequently characterize heavily grazed patches and taller, tufted species appear in lightly-grazed patches (McNaughton 1984, Hatch and Tainton 1990, O’Connor 1992), reflecting the increaser-decreaser model. While grazing pressure changes the plant community composition from decreaser to increaser types, some perennial grasses persist due to replacement of normal erect forms by decumbent forms through genotypic selection (Kemp 1937). Decumbent genotypes possess greater grazing avoidance because, in them, more meristematic and photosynthetic tissue is protected from removal by grazing, thus facilitating growth after defoliation (Briske and Anderson 1992). This type of the vegetation response can be called ‘stable’, as genotypes, rather than species are changed.

A compositional shift from decreaser towards increaser is usually due to a shift towards inaccessible or less palatable plant species (Jefferies et al. 1994, Paster et al. 1997). The shift is often characterized by replacement of taller perennial grasses by shorter perennial grasses, then annual grasses and finally bare-ground (Teague et al. 2004). The replacement may be patchy, rather than general, because herbivores will create patches of different grazing intensities. There is a threshold when patches are no longer grazed because of increasing bareness. The threshold occurs when the increases in nutrient concentration within the patch are directly offset by a reduction in grazing rate resulting from a diminished amount of food relative to the adjacent ungrazed condition (Hobbs and Swift 1988). Thus, in a system where regrowth of plants is slow or absent, there is a feedback between present and future grazing, and grazed patches are unlikely to be grazed again within a short time span. When regrowth is rapid, the feedback is positive and grazing enhances conditions for repeated grazing. Thus the spatial mosaic of grazed patches is expected to depend on duration, seasons and years, based on negative and positive feedback changes.

Grazing Disturbance: Excretion

Functions of Excretion

Nutrient Transfer. With each urination and defecation event, there is a transfer of nutrients from a single plant, at different scales, to the landscape. Such nutrient transfer occurs by (at least) three different mechanisms: nutrient partitioning, nutrient concentration and nutrient redistribution (Augustine and Frank 2001). Nutrient partitioning in urine and dung involves separation of nitrogen (N), phosphorous (P) and potassium (K). Most of N is excreted in urine, but almost all phosphorus P and K are deposited in dung (Whitehead 2000). All three nutrients are very important for plant growth and the relative percentage amounts in plants are: N 100%, K 25% and P 6% respectively (Motavalli and Marler 1998). Nitrogen rich urine patches and phosphorus rich dung patches provide different fertilization effects, and stimulate growth of different plant species, demonstrating that the spatial separation may generate patches of different composition and productivity.

Nutrient concentration involves movement of nutrients from plants to excretion patches. Plant biomass or nutrients are removed from some parts of the pasture through grazing, but are returned to smaller areas in the form of feces and urine. In the grazing process, foraging involves intake of plant biomass, which may be excreted or converted to herbivore body biomass. About 60- 90% of ingested plant biomass returns back to the ground in the form of dung and urine patches of 80 cm and 20 cm in diameter respectively (Whitehead 2000, Afzal and Adams 1992). Urine and dung patches are therefore areas of the pasture where nutrients are recycled from excreta to soils and back to pasture plants. Although excretal patches may cover only 30-40% of the pasture surface annually, the high nutrient input stimulates herbage growth, which may represent up to 70% of the total annual pasture production (Saunders 1984).

At the landscape scale, topography (e.g., slope) and other site conditions (e.g., water source, shade) can exert differential effects on grazing and excretion behavior, leading to zonal heterogeneity in nutrient distribution (Jewell et al. 2007, Auerswald et al. 2010). Areas with preferred vegetation are used exclusively or mainly for grazing, and those near water, shade and shelters are used exclusively or mainly for resting and ruminating. Because animals spend more time in resting areas than in the grazing areas, nutrients gathered in feeding areas are transferred to resting area and a concentration of excreta and nutrients in the resting areas results (Auerswald et al. 2010, Hirata et al. 2011). For example, because domestic sheep prefer level areas for bedding, this preference results in 60% of dung being deposited on 15% of pasture area (Rowarth and Gillingham 1989).

Seed Transfer. It is commonplace to see seeds of herbaceous plants in dung of livestock (cattle, horses and sheep), and their seedling growing up from the dung. Studies show that endozoochory (seed-dispersal mechanism through animal intestine) may be an important ecological process in grazed ecosystems dominated by herbivores (Janzen 1984). The impact of herbivores on dispersal and recruitment may depend on herbivore size. Large herbivores are expected to have the strongest effect on plant seed dispersal. They consume large amounts of seeds (Malo and Suarez 1995) and, due to their larger home-ranges move over larger distance (Haskell et al. 2002). Survivorship is in the range of 1%-50% (Janzen 1984), which also depends on herbivore size: passage through the digestive tracts of larger herbivores than small may less influenced by physical forces, although chemical damage may be increased by longer retention time in the rumen of large herbivores (Ocumpaugh and Swakon 1993, Olson and Wallander 2002).

Effects of Excretion

Urine Effect. Forage of urine patches were preferred by cattle and sheep as they offer higher quantity and quality nutrients (Jaramillo and Detling 1992b). They are grazed almost immediately after deposition and heavy grazing continues for two to four months, and even into the next growing season (Legard et al. 1982). Urea-nitrogen, accounting for 75% of urine nitrogen (Ledgard et al. 1982) is rapidly transformed to plant available ammonia in the soil (Stillwell and Woodmansee 1981) and increases nitrogen concentrations and plant biomass (Thomas et al. 1986). Urine patches increase nitrogen concentrations in plants, and delay senescence thus lengthening the plant growing season (Jaramillo and Detling 1992b). With earlier growth, urine patches attract herbivores at the beginning of the season, thus initiating grazing, which is reinforced by repeated grazing. This repeated grazing creating the positive feedback of increasing nitrogen concentration and biomass production discussed in the Vegetation Response section (page 32). The delayed end-of-season leaf senescence seen on urine patches may be due both to increased nutrient concentrations and reduction in mean tissue age caused by repeated grazing (Day and Detling 1990).

As explained above, urine patches have higher nitrogen levels thus increasing the plant annual productivity (Day and Delting 1990, Jaramillo and Detling 1992a, Gough et al. 2000). For example, in a range site while urine patches covered only 2%, they provided 7% of the aboveground biomass and 14% of the nitrogen to herbivores from June through August (Day and Delting 1990). While the urine fertilization effect on plants can last up to two years (Blagden 1969), the effect is extended as the induced re-grazing continues. Even if the fertilization effect on plant productivity were not be significant, the increased re-grazing pressure on the urine patches might cause a shift in species composition (Bakker et al. 1984, Hatch and Tainton 1990, Fuls 1991).

Dung Effect. Dung patches are normally avoided because of the feces odor (Forbes and Hodgson 1985). Cattle's rejection of the area due to feces odor can continue for 0-35 days (Dohi et al. 1991). However, even after the odor has cleared, cattle continue to avoid the area until it disappears. Disappearance rates depend on humidity, temperature, and soil fauna activity (Dickinson and Craig 1990), and can be up to 6-8 years for complete decomposition in some arid land (Dai 2000). At the dung patch, buried plants die due to dung suppression, but after the dung is decomposed, the vegetation-free and nutrient rich gap will be recolonized by seeds from either the dung or nearby sources. Vegetation around dung patches is subjected to two opposite fertilizing and grazing gradients, which induce changes in vegetation texture and structure at fine scales (Gillet et al. 2010). Specifically, plants within 0-10 cm of the dung patch flourish both because of nutrient supplementation by the dung and grazing avoidance (Gillet et al. 2010). Since dung patches are dropped every year in different locations, they create a shifting mosaic of nutrient availability and grazing intensity; this induces seasonal scale micro-successions in plant communities.

As dung patches are rejected, animal's potential grazing area is reduced and the grazing pressure in urine patches may be increased even further. Urine and dung deposition may therefore be important factors in initiation of patch structure. At the end of the grazing season, urine and dung deposition may create a mosaic of heavily grazed urine patches and ungrazed dung patches and differences in plant height between urine and dung patches are likely to be carried over into the next grazing season (Mott 1985).

Grazing Disturbance: Trampling

Trampling has direct effects on soil and plants. Trampling smashes plants, destroy leave tissue, impact their growth or even kill them; Trampling can exert high pressure on soil and compact soil with heavy body mass and small hoof soil contact area, decrease water infiltration and soil oxygen, reducing soil microbial activity and release of nutrients. Thus, trampling include negative effects on established plants through break physical soil crusts and increase soil compaction; suppression of shoot and root development, but may have positive effects of knocking down litter and anchoring seeds.

Effects on Soil

Soil Crust Disruption. Trampling has various effects, some interpreted as positive, some as negative, depending on the landscape goal. Trampling adversely affects soil physical properties and it is most noticeable at the soil surface where soil crusts are broken up at high stocking rates (Belnap 1995). Biological and physical soil crusts are the principle types of soil surface in arid ecosystems, but not limited to arid ecosystems (Belnap 1995). Biological soil crust is mostly composed of cyanobacteria, lichens, and mosses: all are important for increased soil stability, water infiltration, and fertility of soils (Bowker 2007). Physical soil crusts are formed by wind and rain erosional forces (Graef and Stahr 2000). Disruption of both types by trampling can lead to increased erosion and desertification (Belnap 1995). Soil crust disruption effects, however, can also be positive. As physical soil crusts have a sealed and smooth surface with low infiltration rates, trampling can break them and allow for increased water capture. In addition crushing and compacting hoof prints can provide sites for seed deposition and seed germination, thus increasing seedling establishment (Oesterheld and Sala 1990, Boeken and Shachak, 1994, Savory and Butterfield 1998). Thus trampling of the physical soil crust may enhance annual net plant productivity at the risk of increasing soil erosion (Baddock et al. 2011).

Soil Compaction. Trampling compacts soil, decreasing soil water infiltration and increasing water run-off (Sheath and Carlson 1998). Increased run-off associated with decreased infiltration may lead to increased erosion, with associated loss of nutrients and decreased available plant water (Greenwood and McKenzie 2001). Soil compaction may also have negative effects on soil biota by increasing soil anoxia, thus decreasing nitrogen mineralization (Schrama et al. 2013). Furthermore, increased soil compaction will impede root growth by decreasing pore continuity, and restricting water and air movement (Soane et al. 1981). Soils are more susceptible to compaction under wet conditions (Warren et al. 1986), so grazing should be strictly prevented on wet soils (Hamza and Anderson 2005).

Hoof-induced soil compaction causes uneven soil surfaces; however, on uneven ground at and a coarser scale, trampling can beat down the cutting edges of gullies, (e.g., steep stream banks after flooding) creating a more gradual slope that could once again support vegetation (Savory and Butterfield 1998). On a landscape scale large herbivores can trample soil mounds under shrubs while they graze plants in the understory and browse on the shrubs. It was found that sheep trampling significantly decreased the mound size under shrub patches (Golodets and Boeken 2006). While decreased soil mound size may decrease plant-available resources (e. g. the fertile island effect), resource redistribution by trampling may reduce vegetation patches to bare interpatches, reverse the soil erosion and soil accumulation effect, and provide the possibility to initiate new vegetation patches in bare interpatches.

Effects on Plants

Trampling may mechanically affect plants by causing physical damage through detaching or killing plant material (Sun and Liddle 1993). Several mechanical traits, including leaf toughness, root strength, stem flexibility, and clonal growth have been suggested to play a role in plant tolerance to trampling (Dale and Weaver 1974, Kobayashi et al. 1999, Striker et al. 2011). Differences in tolerance to trampling can produce changes in the plant composition. The susceptible species decrease and are replaced by resistant species or new plants germinating from the seed bank. Trampling selects against woody plants and generally promotes species with rosettes, prostrate growth-forms, rhizomatous (Posse et al. 2000) or tussock growth-forms (Kobayashi et al. 1997) and thus reduces vegetation height (Bakker et al. 1984, Cole and Bayfield 1993) and herbage yield (Edmond 1964).

While trampling can have detrimental effects on live shoots, it may also have positive effects on detaching or breaking the dead leaves/stems to return to the ground or integrate them into soil surface (Savory and Butterfield 1998). This is especially the case for ungrazed plants, known as wolf plants with accumulated persistent stems, where trampling can physically break down stems to provide litter cover to the soil surface, increase the litter decomposition rate, or attract animals to further defoliate the stem free plants. Plant decomposition and resultant nutrient cycling is crucial to the health of the whole system. In arid ecosystems, in the absence of trampling herds, little of the vegetation production is able to decay through microbial decomposition. Thus most is left for very slow chemical oxidation: dead plant material turns gray and then black or physically breaks down from wind, rain, and hail (Savory and Butterfield 1998).

Effect of Grazing Disturbances on Patch Pattern Dynamics

Banded Pattern Dynamics

Three zones in banded pattern correspond to the three major grazing disturbance effects: the crusted interband, the upslope grass band, and the main body tree band by trampling, foraging and excretion. First I consider the interband under trampling effect for dry and wet years. The crusted interband is 3-5 times wider than the vegetation band, and it is the critical component of the water-redistributing structure of the banded pattern. In dry years, the vegetation band contracts due to reduced water collection. In this case, trampling will have a greater effect on the expanded crusted interband. Because of the drought, crusts in the interband become harder, and the trampling cannot increase soil compaction. The breaking of physical soil crusts by hooves is assumed to stimulate soil erosion (Baddock et al. 2011), but at the same time create micro sites. These hoof micro sites provide sites for seed deposition and vegetation establishment by intercepting the limited rain water. In dry years, it is impossible for run-off water to reach the vegetation band, or even it does, it does not benefit the vegetation band due to the small amount of the water that reaches it. In contrast, during wet years, soil crusts are soaked and soil particles become loose, making the soil subject to water erosion. In this situation, run-off water delivers both water and soil to the vegetation band; such water erosion may flatten the interband. Such flattening, on a longer time scale may impair the banded pattern’s water-redistributing structure and the band’s very existence. Thus, in wet years trampling may compact soils of the interband, reduce water erosion, and help preserve the band structure.

Second, I consider the pioneer grass and the mature woody zone of the band under foraging and excretion effects. The effect of herbivore foraging has higher impact in the grassy pioneer zone and excretion in the main body tree part in the banded pattern. First, under low intensity grazing, the grass and the herbaceous layer of vegetation slow water movement through the tree zone to enhance infiltration. Higher intensity grazing may destroy the grass and the herbaceous layer of vegetation that slows water movement through the tree zone and enhances infiltration. Thus heavy foraging is detrimental to banded pattern structure and function. However, the detrimental effect of heavy foraging is minor compared with wet and dry year conditions since vegetation responds mainly to the rain pulse rather than the effect of defoliation in the banded pattern (Hodgkinson and Freudenberger 1997, Vega and Montana 2011).

Second, excretion may influence the vegetation band by transferring nutrients from the grass zone to the tree zone, where animals spend time taking shelter from sun and wind, defecate, and urinate. However, the effect of excretion has not been studied. This might be because the grass zone and the tree zone have distinct habitat types due to the spatial zonation by soil depth and root depth, and so there is little chance to expand the population size or alter the grass/tree pattern regardless of nutrient transfer. However, nutrient transfer might benefit the tree zone and help off-set the upslope movement trend. It might be one of the reason why the banded pattern does not appear to move upslope but remain stabilized.

Spotted Pattern Dynamics

In spotted patterns, herbivores foraging on grasses and/or shrubs will affect the vegetation/bare patch balance and phase status. As understory grasses tend to intercept rain water before it infiltrates deep soil, reduction of grasses by heavy grazing (e.g., repeated grazing) will release shrub growth (Golluscio et al. 1998). On the contrary, under long periods of grazing, the shrub and grass ratio did not change significantly, such as 18% of the whole landscape in Patagonia in long periods (Soriano et al. 1994, Perelman et al. 1997). It is suggested the foraging do not decrease the quantity of grass, but changed the plant composition from decreaser to increaser types or the foraging defoliates both grass and shrub to keep the grass/shrub balance (Aguiar and Sala 1998).

Herbivory maintains the balance of vegetated and bare patches through resource transfer by excretion and trampling. Excretion (e. g., urine and dung) transfers nutrients and seeds from vegetation patches to the bare-ground and the trampling transfers soil and litter by trampling soil mounds and detaching coarse stems/litter. At the same time hoof disturbance in the interpatch integrates nutrients/seeds from the excretion and soil/litter from the trampling to stimulate vegetation establishment in the bare-ground, initiating a new vegetation patches.

Overall grazing disturbances (foraging, excretion, and trampling) seem to reverse the effect of permanent winds, which originally create the spotted pattern formation through one directional transfer of resources from the bare-ground to the shrub patch. In this way the balance of patch phases is maintained, thus ensuring the coexistence of patches to form a stable spotted landscape structure and dynamics.

5. CONCLUSION

Summary

In this paper I discussed the spatial distribution of plants in arid ecosystems, and integrated interacting effects of abiotic and biotic factors, and grazing disturbance to systematically describe mechanisms that drive the formation and dynamics of vegetation patch patterns. In arid ecosystems, two-phase patch patterns are of great ecological interest because their water-redistributing capacity increases plant production. From the abiotic perspective, water and wind are main ecological drivers for forming the water-redistributing structure by creating soil crusts and soil mounds in banded and spotted patterns respectively. Soil crusts and soil mounds function as 'delivering' and 'absorbing' water structures which deliver limited water resources from surrounding bare-ground to vegetation patches. This water transfer maximizes plant productivity in arid ecosystems.

From the biotic perspective, vegetation interactions are driving vegetation patch pattern succession. Here succession implies that the change of plant community from vegetation interactions only, rather than from disturbances. In banded patterns, vegetation succession appears as upslope movement. The upslope edge favors soil, water and litter deposition, thus stimulating vegetation growth; in contrast the downslope edge vegetation dies as a consequence of resource shortages, causing the overall vegetation bands to move upslope. The alternate scenario for banded pattern succession is self-stabilization. Deep-rooted trees are self-stabilizing due to soil depth requirements, and for the upslope movement to occur, a considerable build-up of soil material is necessary, but the process is extremely slow. In spotted patterns, vegetation goes through cyclic succession, from bare-ground through vegetation establishment, development, and degeneration to bare-ground, thus initiating a new cycle. This cycle can be regarded as being driven by interspecific interactions including above-ground facilitation and below-ground competition between the nurse shrub and under-canopy grasses.

Grazing is important to arid ecosystems economies. Grazing affects the vegetation through foraging, excretion, and trampling. In banded patterns, the foraging of grasses on the upslope edge of the vegetated band can reduce vegetation cover, which may decrease obstruction of water run-off and reduce infiltration. Excretion causes nutrient transfer from the grass zone to the tree zone because herbivores take shelter and resting in the tree zone. This may help off-set the upslope movement or reinforce the spatial zonation effect. Trampling effects differ between wet or dry years. In wet years, trampling can compact soil of interband bare-ground, preventing soil loss by rain erosion. In dry years, trampling breaks physical soil crusts, thus creating micro sites in which seeds anchor and promotes vegetation establishment by interception of the limited rain water.

In spotted patterns, foraging might not decrease the grass amount, but simply change plant species types or defoliate both grasses and shrubs to keep the grass/shrub balance. Excretion and trampling affect resource transfer from vegetation patches to bare-ground interpatches, and the trampling within interpatches integrates the nutrients/seeds from the excretion and litter to stimulate vegetation establishment in the bare-ground. The overall grazing disturbances (foraging, excretion, and trampling) counteract the permanent wind force, a one directional accumulation of resources in vegetation patches, to maintain the ratio of patch phases, thus ensuring a dynamic coexistence of patches.

Implications

The main purpose of this paper is to increase the understanding of patch pattern dynamics in arid landscapes. As spatial heterogeneity and plant community dynamics are two common features of all natural communities (Sousa 1984), the patch-based perspective has a potential to illuminate processes underlying patchiness. The term ‘patch’ is used to specify a particular spatial unit of vegetation. It can be linked to hierarchical interacting factors associated with different types of patches to understand underlying process and dynamics (Wu and David 2002). I relate patch processes to grazing. Grazing is a selective behavior that may result in overgrazing and/or over-resting, which causes mosaic landscapes with different intensities of grazing. And this patchy landscape formation and dynamics are related to patchy characteristics of plant and animal distribution These include molding on soil micro topography by rain and/or wind and facilitation and competition of plant species, where the vegetation tends to grow in a group or a patch within a certain distance to optimize the productivity. Herding herbivores also have a tendency to distribute patchily. Most of the large herbivores even in one herd, have the behavioral tendency of splitting (fission) and submerging (fusion) into small groups, and such groups have a patchy grazing effects on the vegetation. So in grazing management it is impossible to grasp the true nature of the patchy and dynamic landscape without integrating a patch perspective of abiotic, vegetation and herbivore grazing.

Taking a patch-perspective is also useful for understanding the water-redistribution function or source-sink dynamic of vegetation patch patterns. This knowledge can be applied in practice. A sink can be created by contour-trenching to prevent rain water erosion and divert it to irrigate adjacent sub-sites. This has been performed for afforestation and restoration purposes in arid ecosystems (Helman et al. 2014). Similar approaches to collect run-off water include, contour log/tree falling, contour stone/straw wattle, all of which have been shown to slow the run-off water flow, deposit sedimentation and increase infiltration (Oweis et al. 2001, Robinchaud et al. 2008). To make source-sink structures effective, the size of source areas must be considered. Regarding that in banded patterns, source areas (interband) are 3-5 times wider than sink areas (vegetation band), the width of source areas therefore, should be set at a certain distance based on the size of sink area, depending on site precipitation, slope gradient, and soil type etc.

The soil mound formation mechanism in spotted patterns also has significant implication for water movement and storage. Where branches of shrubs touch the ground they accumulate soil and litter and form soil mounds under the canopy. So, shrubs can be used for stabilizing moving sands and helping to establish vegetation cover. Because shrub stem structure is an important attribute for reducing wind speed and capturing soil particles, choice of shrubs with branches close to the ground is an important criterion for stabilizing depredated lands in arid areas (Leenders et al. 2007). In addition when using canopy facilitation effects, the spacing of the shrubs/trees is important. Planting them with appropriate spacing is a more economic and more effective restoration method, resulting in more productivity because of the optimum canopy than more compact spacing (Helman et al. 2014).

Suggestions

Spatial patterns repeat themselves in shapes, size, types, which means that using a patch-perspective is very effective for modeling the system (Turner et al. 2001). Such modeling can be used to analyze pattern as a basis for developing testable theories and predictive models (Weiner 1995). In fact, patch theory is not a new concept and there is a great development in theory, modeling and practice in landscape ecology (Turner et al. 2001). In banded and spotted patterns, as temporal scale is a major issue that may not be amenable to conventional studies over times-scales typical of scientific experiments: patch modeling is necessary to test the underlying theories and hypotheses, as well as predict the vegetation patch dynamics under climate change trends (Valentin et al. 2001).

For my personal concern and interest, Inner Mongolia in China is both my birth place and a likely region of banded and spotted vegetation (Valentin et al. 1999). Because there are no studies of patch patterns that occur there, it would be interesting to me and perhaps scientifically and socially beneficial for the community to investigate the distribution, maintenance and function of banded or spotted patterns in this region. The limited information available suggests that shrub patches have occurred but no information about the overall patterns. Shrub patches were found on slopes in this region, and the formation was explained by run-off rather than wind (Li et al. 2008). When it came to wind, shrub patches were treated as a special ecological phenomenon called nebkhas (coppice dune) (Zhang et al. 2011) rather than regarded as the common function of shrubs in arid ecosystems. In the intact landscape, these native shrub communities have a potential to be treated as a spotted pattern driven by wind.

REFERENCES CITED

Afzal, M. and Adams, W. A. 1992. Heterogeneity of soil mineral nitrogen in pasture grazed by cattle. Soil Science Society of America Journal, 56(4): 1160-1166.

Aguiar, M. R. and Sala, O. E. 1994. Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. Oikos, 70(1): 26-34.

Aguiar, M. R. and Sala, O. E. 1998. Interactions among grasses, shrubs, and herbivores in Patagonian grass-shrub steppes. Ecología Austral, 8(2).

Aguiar, M. R. and Sala. O. E. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends in Ecology and Evolution, 14: 273-277.

Allison, S. 2003. The virtual nature trail at Penn State New Kensington. Accessed on 12 October 2014. Available at: http://www.psu.edu/dept/nkbiology/naturetrail/ speciespages/spicebush.htm.

Atstatt, P. R. and Odowd, D. J. 1976. Plant defense guilds. Science, 193: 24-29.

Auerswald, K., Mayer, F., and Schnyder, H. 2010. Coupling of spatial and temporal pattern of cattle excreta patches on a low intensity pasture. Nutrient Cycling in Agroecosystems, 88(2): 275-288.

Augustine, D. J. and Frank, D. A. 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. Ecology, 82: 3149-3162.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., ... and Van Schaik, C. P. 2008. Fission-fusion dynamics. Current Anthropology, 49(4): 627-654.

Baddock, M. C., Zobeck, T. M., Van Pelt, R. S., and Fredrickson, E. L. 2011. Dust emissions from undisturbed and disturbed, crusted playa surfaces: cattle trampling effects. Aeolian Research, 3: 31-41.

Bakker, E. S., Olff, H., Vandenberghe, C., De Maeyer, K., Smit, R., Gleichman, J. M., and Vera, F. W. M. 2004. Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. Journal of Applied Ecology, 41(3): 571-582.

Bakker, J. P., De Leeuw, J., and Van Wieren, S. E. 1984. Micro-patterns in grassland vegetation created and sustained by sheep-grazing. Vegetation, 55(3): 153-161.

Bardgett, R. D., Wardle, D. A., and Yeates, G. W. 1998. Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. Soil Biology and Biochemistry, 30: 1867-1878.

Belnap, J. 1995. Surface disturbances: their role in accelerating desertification. In Desertification Developed Countries (pp. 39-57). Springer Netherlands.

Belsky, A. J., Amundson, R. G., Duxbury, J. M., Riha, S. J., Ali, A. R., and Mwonga, S. M. 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology, 1005-1024.

Belsky, A. J., Carson, W. P., Jensen, C. L., and Fox, G. A. 1993. Overcompensation by plants: herbivore optimization or red herring?. Evolutionary Ecology, 7(1): 109-121.

Blagden, P. A. 1969. The potassium cycle in grasslands. PhD thesis, University of Nottingham.

Boeken, B. and Orenstein, D. 2001. The effect of plant litter on ecosystem properties in a Mediterranean semi-arid shrubland. Journal of Vegetation Science, 12(6): 825-832.

Boeken, B. and Shachak, M. 1994. Desert plant communities in human-made patches: implications for management. Ecology Application, 4: 702-716.

Bowker, M. A. 2007. Biological soil crust rehabilitation in theory and practice: an underexploited opportunity. Restoration Ecology, 15(1): 13-23.

Breshears, D. D., Nyhan, J. W., Heil, C. E., and Wilcox, B. P. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. International Journal of Plant Sciences, 159(6): 1010-1017.

Briske, D. D. and Anderson, V. J. 1992. Competitive ability of the bunchgrass *Schizachyrium scoparium* as affected by grazing history and defoliation. Vegetatio, 103(1): 41-49.

Briske, D. D., Fuhlendorf, S. D., and Smeins, F. E. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. Rangeland Ecology and Management, 58: 1-10.

Bromley, J., Brouwer, J., Barker, A. P., Gaze, S. R., and Valentin. C. 1997. The role of surface water distribution in an area of patterned vegetation in a semi-arid environment, south-west Niger. Journal of Hydrology, 198:1-29.

Buis, E., Temme, A. J. A. M., Veldkamp, A., Boeken, B., Jongmans, A. G., van Breemen, N., and Schoorl, J. M. 2010. Shrub mound formation and stability on semi-arid slopes in the Northern Negev Desert of Israel: A field and simulation study. Geoderma, 156(3): 363-371.

Bullock, J. M., Marriott, C. A., Rook, A. J., and Penning, P. D. 2000. Plant responses to grazing, and opportunities for manipulation. In Grazing Management Proceedings of the British Grassland Society Conference (pp. 17-26). BBSRC Institute of Grassland and Environmental Research.

Bullock, J. M. and Moy, I. L. 2004. Plants as seed traps: inter-specific interference with dispersal. Acta Oecologica 25(1): 35-41.

Burke, I. C., Lauenroth, W. K., Vinton, M. A., Hook, P. B., Kelly, R. H., Epstein, H. E.,... and Gill, R. A. 1998. Plant-soil interactions in temperate grasslands. In Plant-induced Soil Changes: Processes and Feedbacks (pp. 121-143). Springer Netherlands.

Caballero, I., Olano, J. M., Escudero, A., and Loidi, J. 2008. Seed bank spatial structure in semi-arid environments: beyond the patch-bare area dichotomy. Plant Ecology, 195(2): 215-223.

Callaway, R. M. 1995. Positive interactions among plants. Botanical Review, 61: 306-349.

Castro, J., Zamora, R., Hódar, J. A., and Gómez, J. M. 2002. Use of shrubs as nurse plants: a new technique for reforestation in Mediterranean mountains. Restoration Ecology, 10(2): 297-305.

Clements, F. E. 1916. Plant Succession: An Analysis of the Development of Vegetation (No. 242). Carnegie Institution of Washington.

Clos-Arceduc, A. 1956. Etude sur photographies aériennes d'une formation végétale sahélienne: la brousse tigrée.

Cole, D. N. and Bayfield, N. G. 1993. Recreational trampling of vegetation: standard experimental procedures. Biological Conservation, 63(3): 209-215.

Couteron, P., Mahamane, A., Ouedraogo, P., and Seghieri, J. 2000. Differences between banded thickets (tiger bush) at two sites in West Africa. Journal of Vegetation Science, 11: 321-328.

d’Herbès, J. M., Valentin C, Tongway, D. J., and Leprun, J. C. 2001. Banded vegetation patterns and related structures. In Banded Vegetation Patterning in Arid and Semiarid Environments (pp. 1-19). Springer New York.

Dai, X. 2000. Impact of cattle dung deposition on the distribution pattern of plant species in an Alvar limestone grassland. Journal of Vegetation Science, 11: 715-724.

Dale, M. R. T. 1999. Spatial Pattern Analysis in Plant Ecology, (Cambridge studies in ecology). Cambridge University Press, Cambridge, U.K. New York.

Dale, D., and Weaver, T. 1974. Trampling effects on vegetation of the trail corridors of north Rocky Mountain forests. Journal of Applied Ecology, 767-772.

Davies-Colley, R. J., Payne, G. W., and Van Elswijk, M. 2000. Microclimate gradients across a forest edge. New Zealand Journal of Ecology, 24(2): 111-121.

Day, T. A. and Detling, J. K. 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology, 71:180-188.

Dickinson, C. H. and Craig, G. 1990. Effects of water on the decomposition and release of nutrients from cow pats. New Phytologist, 115(1): 139-147.

Dohi H., Yamada A., and Entsu S. 1991. Cattle feeding deterrents emitted from cattle feces. Journal of Chemical Ecology, 17: 1197-1203.

Dunkerley, D. L. 1997. Banded vegetation: development under uniform rainfall from a simple cellular automaton model. Plant Ecology, 129(2): 103-111.

Du Toit, J. C., Danckwerts, J. E., and Zacharias, P. J. 2007. Method for discriminating objectively between patches and non-patches in a semiarid environment. Grassland Science, 53(2): 61-67.

Du Toit, J. T., Bryant, J. P., and Frisby, K. 1990. Regrowth and palatability of Acacia shoots following pruning by African savanna browsers. Ecology, 71(1): 149-154.

Dyksterhuis, E. J. 1949. Condition and management of range land based on quantitative ecology. Journal of Range Management, 2: 104-115.

Edmond, D. B. 1964. Some effects of sheep treading on the growth of 10 pasture species. New Zealand Journal of Agricultural Research, 7(1): 1-16.

Eldridge, D. J., Lepage, M., Bryannah, M. A., and Ouedraogo, P. 2001. Soil biota in banded landscapes. In Banded Vegetation Patterning in Arid and Semiarid Environments (pp. 105-131). Springer New York.

Facelli, J. M. and Temby, A. M. 2002. Multiple effects of shrubs on annual plant communities in arid lands of South Australia. Austral Ecology, 27(4): 422-432.

FAO. 1987. Improving Productivity of Dryland Areas. Committee on Agriculture (Ninth session). FAO, Rome.

Ferraro, D. O. and Oesterheld, M. 2002. Effect of defoliation on grass growth: a quantitative review. Oikos, 98(1): 125-133.

Flores, J. and Jurado, E. 2003. Are nurse-protégé interactions more common among plants from arid environments?. Journal of Vegetation Science, 14(6): 911-916.

Floyd, M. E. 1983. Dioecy in five *Pinus edulis* populations in the southwestern United States. American Midland Naturalist, 405-411.

Foran, B. D., Tainton, N. M., and Booysen, P. D. V. 1978. The development of a method for assessing veld condition in three grassveld types in Natal. Proceedings of the Annual Congresses of the Grassland Society of Southern Africa, 13(1): 27-33.

Forbes, T. D. A. and Hodgson, J. 1985. The reaction of grazing sheep and cattle to the presence of dung from the same or the other species. Grass and Forage Science, 40: 177-182.

Forcella, F., Benech Arnold, R. L., Sanchez, R., and Ghersa, C. M. 2000. Modeling seedling emergence. Field Crops Research, 67(2): 123-139.

Franco, A. C. and Nobel. P. S. 1989. Effect of nurse plants on the microhabitat growth of cacti. Journal of Ecology, 77: 870-886.

Freudenberger, D., Hodgkinson, K., and Noble, J. 1997. Causes and consequences of landscape dysfunction in rangelands. Landscape Ecology Function and Management: Principles from Australia's Rangelands (pp. 63-77). CSIRO Publishing, Collingwood, Australia.

Fuentes, E. R., Otaiza, R. D., Alliende, M. C., Hoffmann, A., and Poiani, A. 1984. Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. Oecologia, 62(3): 405-411.

Fuls, E. R. 1991. The effect of nutrient rich sediment deposits on the vegetational traits of a patch-grazed semi-arid grassland. Vegetatio, 96:177-183.

Galle, S., Brouwer, J., and Delhoume, J. P. 2001. Soil water balance. In Banded Vegetation Patterning in Arid and Semiarid Environments (pp. 77-104). Springer New York.

Ganskopp, D., Angell, R., and Rose, J. 1992. Response of cattle to cured reproductive stems in a caespitose grass. Journal of Range Management, 401-404.

Ganskopp, D. and Bohnert, D. 2004. Wolfy forage: Its effect on cattle distribution and diet quality. Eastern Oregon agricultural research center. Range Field Day Report, 4-9.

Garcia, D. and Ramón Obeso, J. 2003. Facilitation by herbivore-mediated nurse plants in a threatened tree, *Taxus baccata*: local effects and landscape level consistency. Ecography, 26(6): 739-750.

Garner, W. and Steinberger, Y. 1989. A proposed mechanism for the formation of fertile islands in the desert ecosystem. Journal of arid Environments, 16(3): 257-262.

Georgiadis, N. J. 1989. Microhabitat variation in an African savanna: effect of woody cover and herbivores in Kenya. Journal of Tropical Ecology, 5: 93-108.

Giladi, I., Segoli, M. and Ungar, E. D. 2007. The effect of shrubs on the seed rain of annuals in a semiarid landscape. Israel Journal of Plant Sciences, 55(1): 83-92.

Giladi, I., Segoli, M., and Ungar, E. D. 2013. Shrubs and herbaceous seed flow in a semi-arid landscape: dual functioning of shrubs as trap and barrier. Journal of Ecology, 101: 97-106.

Gillet, F., Kohler, F., Vandenberghe, C., and Buttler, A. 2010. Effect of dung deposition on small-scale patch structure and seasonal vegetation dynamics in mountain pastures. Agriculture, Ecosystems and Environment, 135(1): 34-41.

Golluscio, R. A., Sala, O. E., and Lauenroth, W. K. 1998. Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. Oecologia, 115(1-2): 17-25.

Golodets, C. and Boeken, B. 2006. Moderate sheep grazing in semiarid shrubland alters small-scale soil surface structure and patch properties. Catena, 65: 285-291.

Gough, L., Osenberg, C. W., Gross, K. L., and Collins, S. L. 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. Oikos, 89(3): 428-439.

Graef, F. and Stahr, K. 2000. Incidence of soil surface crust types in semi-arid Niger.

Soil and Tillage Research, 55(3): 213-218.

Green, W. C. 1992. Social influences on contact maintenance interactions of bison mothers and calves: group size and nearest-neighbour distance. Animal behaviour, 43(5): 775-785.

Greene, R. 1992. Soil physical properties of three geomorphic zones in a semiarid mulga woodland. Soil Research, 30: 55-69.

Greenwood, K. L. and McKenzie, B. M. 2001. Grazing effects on soil physical properties and the consequences for pastures: a review. Australian Journal of Experimental Agriculture, 41: 1231-1250.

Greig-Smith, P. 1979. Patterns in vegetation. Journal of Ecology, 67: 755-779.

Gurevitch, J., Scheiner, S. M., and Fox, G. A. 2002. Soil, Mineral nutrition, and belowground interactions. In the Ecology of Plants. Sinauer Associates Incorporated.

Hamza, M. A. and Anderson. W. K. 2005. Soil compaction in cropping systems: a review of the nature, causes and possible solutions. Soil and Tillage Research, 82: 121-145.

Haskell, J. P., Ritchie, M. E., and Olff, H. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature, 418: 527-530.

Hatch, G. P. and Tainton, N. M. 1990. A preliminary investigation of area-selective grazing in the Southern Tall Grassveld of Natal. Journal of the Grassland Society of Southern Africa, 7(4): 238-242.

Heady, H. F. and Child, R. D. 1994. Rangeland Ecology and Management. Westview Press, Inc.

Helman, D., Lensky, I. M., Mussery, A., and Leu, S. 2014. Rehabilitating degraded drylands by creating woodland islets: Assessing long-term effects on aboveground productivity and soil fertility. Agricultural and Forest Meteorology, 195: 52-60.

Hiernaux, P. and Gerard, B. 1999. The influence of vegetation pattern on the productivity, diversity and stability of vegetation: The case ofbrousse tigrée'in the Sahel. Acta Oecologica, 20(3): 147-158.

HilleRisLambers, R., Rietkerk, M., Bosch, F. van den, Prins, H. H. T., and Kroon, H. de.

2001. Vegetation pattern formation in semi-arid grazing systems. Ecology, 82: 50-61.

Hirata, M., Higashiyama, M., and Hasegawa, N. 2011. Diurnal pattern of excretion in grazing cattle. Livestock Science, 142: 23-32.

Hirata, M., Nakagawa, M., Funakoshi, H., Iwamoto, T., Otozu, W., Kiyota, D., Kuroki, S., and Fukuyama, K. 2003. Mother-young distance in Japanese Black cattle at pasture. Journal of Ethology, 21: 161-168.

Hjältén, J. and Price, P. W. 1997. Can plants gain protection from herbivory by association with unpalatable neighbours?: a field experiment in a willow-sawfly system. Oikos, 317-322.

Hobbs, N. T. and Swift, D. M. 1988. Grazing in herds: when are nutritional benefits realized?. American Naturalist, 760-764.

Hodgkinson, K. C. and Freudenberger. D. O. 1997. Production pulses and flow-ons in rangeland landscapes. Landscape Ecology Function and Management: Principles from Australia's Rangelands (pp. 23-34). CSIRO Publishing, Collingwood, Australia.

Janzen, D. H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. American Naturalist, 338-353.

Jaramillo, V. J. and Detling, J. K. 1992a. Small-scale heterogeneity in a semi-arid North American grassland. II. Cattle grazing of simulated urine patches. Journal of Applied Ecology, 29: 9-13.

Jaramillo, V. J. and Detling, J. K. 1992b. Small-scale heterogeneity in a semi-arid North American grassland. I. Tillering, N uptake and retranslocation in simulated urine patches. Journal of Applied Ecology, 29: 1-8.

Jefferies, R. L., Klein, D. R., and Shaver, G. R. 1994. Vertebrate herbivores and northern plant communities: reciprocal influences and responses. Oikos, 193-206.

Jewell, P. L., Käuferle, D., Güsewell, S., Berry, N. R., Kreuzer, M., and Edwards, P. J. 2007. Redistribution of phosphorus by cattle on a traditional mountain pasture in the Alps. Agriculture, Ecosystems and Environment, 122(3): 377-386.

Kawai, K. 1989. The flexible grouping and behavioral character of a flock of Suffolk ewes (*Ovis aries*). Journal of Ethology, 7: 41-51.

Keeling, L. 1995. Spacing behaviour and an ethological approach to assessing optimum space allocations for groups of laying hens. Applied Animal Behaviour Science, 44(2): 171-186.

Kemp, W. B. 1937. Natural selection within plant species as exemplified in a permanent pasture. Journal of Heredity, 28(10): 329-333.

Kobayashi, T., Hori, Y., and Nomoto, N. 1997. Effects of trampling and vegetation removal on species diversity and micro-environment under different shade conditions. Journal of Vegetation Science, 8(6): 873-880.

Kobayashi, T., Ikeda, H., and Hon, Y. 1999. Growth analysis and reproductive allocation of Japanese forbs and grasses in relation to organ toughness under trampling. Plant Biology, 1: 445-452.

Lal, R. 1988. Effects of macrofauna on soil properties in tropical ecosystems. Agriculture, Ecosystems and Environment, 24(1): 101-116.

Lazo, A. 1994. Social segregation and the maintenance of social stability in a feral cattle population. Animal Behaviour, 48: 1133-1141.

Ledgard, S. E., Steele, K. W., and Saunders. W. H. M. 1982. Effects of cow urine and its major constituents on pasture properties. New Zealand Journal of Agricultural Research, 25: 61-68.

Leenders, J. K., Van Boxel, J. H., and Sterk, G. 2007. The effect of single vegetation elements on wind speed and sediment transport in the Sahelian zone of Burkina Faso. Earth Surface Processes and Landforms, 32(10): 1454-1474.

Legard, S. E, Steele, K. W., and Saunders W. H. M. 1982. Effect of cow urine and its major constituents on pasture properties. New Zealand Journal of Agricultural Research, 25: 61-68.

Le Houérou, H. N. 1996. Climate change, drought and desertification. Journal of Arid Environments, 34: 133-185.

Lejeune, O. and Tlidi, M. 1999. A model for the explanation of vegetation stripes (tiger bush). Journal of. Vegetation. Science, 10: 201-208.

Lennartsson, T., Nilsson, P., and Tuomi, J. 1998. Introduction of overcompensation in the field gentian, *Gentianella campesteris*. Ecology, 79: 1061-1072.

Li, X. J., Li, X. R., Song, W. M., Gao, Y. P., Zheng, J. G., and Jia, R. L. 2008. Effects of crust and shrub patches on runoff, sedimentation, and related nutrient (C, N) redistribution in the desertified steppe zone of the Tengger Desert, Northern China. Geomorphology, 96(1): 221-232.

Litchfield, W. D. and Mabbutt, J. A. 1962. Hardpan soil of semiarid southwestern Australia. Journal of Soil Science, 13: 148-159.

Loeser, M. R., Crews, T. E., and Sisk, T. D. 2004. Defoliation increased above-ground productivity in a semi-arid grassland. Rangeland Ecology and Management, 57: 442-447.

Lopez-Portillo, J. and Montana, C. 1999. Spatial distribution of *Prosopis glandulosa var. torreyana* in vegetation stripes of the southern Chihuahuan Desert. Acta Oecologica, 20(3): 197-208.

Ludwig, J. A. and Tongway, D. J. 1995. Spatial organization of landscapes and its function in semi-arid woodlands, Australia. Landscape Ecology, 10: 51–63.

Ludwig, J. A. and Tongway, D. J. 1997. A landscape approach to rangeland ecology. Landscape Ecology Function and Management: Principles from Australia's Rangelands (pp. 1-12). CSIRO Publishing, Collingwood, Australia.

Ludwig, J. A., Tongway, D. J., and Marsden, S. G. 1999. Stripes, strands or stipples: modelling the influence of three landscape banding patterns on resource capture and productivity in semi-arid woodlands, Australia. Catena, 37(1): 257-273.

Ludwig, J. A., Wilcox, B. P., Breshears, D. D., Tongway, D. J., and Imeson, A. C. 2005. Vegetation patches and run-off-erosion as interacting ecohydrological processes in semiarid landscapes. Ecology, 86: 288-297.

Mabbut, J. A. and Fanning, P. C. 1987. Vegetation banding in arid Western Australia. Journal of Arid Environments, 12: 41-59.

Macfadyen, W. A. 1950a. Soil and vegetation in British Somaliland. Nature, 165:121.

Macfadyen, W. A. 1950b. Vegetation patterns in the semi-desert plains of British Somaliland. Journal of Geography, 116: 199-211.

Malo, J. E. and Suarez, F. 1995. Herbivorous mammals as seed dispersers in a Mediterranean dehesa. Oecologia, 104: 246-255.

Marone, L., Cueto, V. R., Milesi, F. A., and Casenave, J. L. D. 2004. Soil seed bank composition over desert microhabitats: patterns and plausible mechanisms. Canadian Journal of Botany, 82(12): 1809-1816.

Martinez-Meza, E. and Whitford, W. G. 1996. Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan Desert shrubs. Journal of Arid Environments, 32: 271-287.

Mattson, W. J., Jr. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics, 11: 119-161.

Mauchamp, A. and Janeau, J. L. 1993. Water funneling by the crown of *Flourensia cernua*, a Chihuahuan Desert shrub. Journal of Arid Environments, 25(3): 299-306.

Mayor, M. D., Boo, R. M., Pelaez, D. V., Elia, O. R., and Tomas, M. A. 2007. Influence of shrub cover on germination, dormancy and viability of buried and unburied seeds of *Piptochaetium napostaense* (Speg.) Hackel. Journal of Arid Environments, 68(4): 509-521.

McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. The American Naturalist, 124(6): 863-886.

Meissner, R. A. and Facelli, J. M. 1999. Effects of sheep exclusion on the soil seed bank and annual vegetation in chenopod shrublands of South Australia. Journal of Arid Environments, 42(2): 117-128.

Meron, E., Gilad, E., von Hardenberg, J., Shachak, M., and Zarmi, Y. 2004. Vegetation patterns along a rainfall gradient. Chaos Solitons Fractals, 19: 367-376.

Milchunas, D. G. and Noy-Meir, I. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. Oikos, 99: 113-130.

Montana, C. 1992. The colonization of bare areas in two-phase mosaics of an Arid Ecosystem. Journal of Ecology, 80: 315-327.

Montana, C., Lopez-Portillo, J., and Mauchamp. A. 1990. The response of two woody species to the conditions created by a shifting ecotone in an Arid ecosystem. Journal of Ecology, 78: 789-798.

Montana, C., Seghieri, J., and Cornet, A. 2001. Vegetation dynamics: recruitment and regeneration in two-phase mosaics. In Banded Vegetation Patterning in Arid and Semiarid Environments (pp. 132-145). Springer New York.

Motavalli, P. and Marler, T. 1998. Fertilizer facts: Number 1. Essential plant nutrients. College of agriculture and life sciences at University of Guam.

Mott, J. J. 1985. Mosaic grazing - animal selectivity in tropical savannas of northern Australia. Proceedings of the XVth International Grassland Congress.1129-1130.

Neely, C., Bunning, S., and Wilkes, A. 2009. Review of evidence on drylands pastoral systems and climate change. Rome: FAO.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics, 4: 25-51.

O'Connor, T. G. 1992. Patterns of plant selection by grazing cattle in two savanna grasslands: a plant's eye view. Journal of the Grassland Society of Southern Africa, 9(3): 97-104.

Ocumpaugh, W. R. and Swakon, D. H. D. 1993. Simulating grass seed passage through the digestive system of cattle: a laboratory technique. Crop Science, 33: 1084-1090.

Oesterheld, M. and Sala, O. E. 1990. Effects of grazing on seedling establishment: the role of seed and safe-site availability. Journal of Vegetation Science, 1(3): 353-358.

Olff, H., Ritchie, M. E., and Prins, H. H. 2002. Global environmental controls of diversity in large herbivores. Nature, 415(6874): 901-904.

Olson, B. E. and Wallander, R. T. 2002. Does ruminal retention time affect leafy spurge seed of varying maturity? Journal of Range Management, 55: 65-69.

Oweis, T., Prinz, D., and Hachum, A. 2001. Water harvesting. Indigenous knowledge for the future of the drier environments. International Centre for Agricultural Research in the Dry Areas (ICARDA) (pp. 40). Aleppo, Syria.

Paruelo, J. M. and Sala, O. E. 1995. Water losses in the Patagonian steppe: a modelling approach. Ecology, 510-520.

Pastor, J., Moen, R., and Cohen, Y. 1997. Spatial heterogeneities, carrying capacity, and feedbacks in animal-landscape interactions. Journal of Mammal, 78:1040-1052.

Perelman, S. B., León, R. J., and Bussacca, J. P. 1997. Floristic changes related to grazing intensity in a Patagonian shrub steppe. Ecography, 20(4): 400-406.

Picket, S. T. and White P. S. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic press.

Pickett, S. T. A., Kolasa, J., Armesto, J. J., and Collins, S. L. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos, 129-136.

Posse, G., Anchorena, J., and Collantes, M. B. 2000. Spatial micro-patterns in the steppe of Tierra del Fuego induced by sheep grazing. Journal of Vegetation Science, 11: 43-50.

Pressland, A. J. 1973. Rainfall partitioning by an arid woodland *Acacia aneura F. Muell.* In southwestern Queensland. Australian Journal of Botany, 21: 235-245.

Pugnaire, F. I. and Lazaro, R. 2000. Seed bank and understory species composition in a semi-arid environment: The effect of shrub age and rainfall. Annals of Botany, 86: 807-813.

Ravi, S., D'Odorico, P., Breshears, D. D., Field, J. P., Goudie, A. S., Huxman, T. E., ... and Zobeck, T. M. 2011. Aeolian processes and the biosphere. Reviews of Geophysics, 49(3).

Reinhardt, V. and Reinhardt, A. 1981. Cohesive relationships in a cattle herd (Bos indicus). Behaviour, 77: 121-151.

Reynolds, J. F., Virginia, R. A., Kemp, P. R., de Soyza, A. G., and Tremmel, D. C. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecological Monographs, 69(1): 69-106.

Richards, J. H. and Caldwell, M. M. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia, 73(4): 486-489.

Rietkerk, M., Boerlijst, M. C., van Langevelde, F., HilleRisLambers, R., van de Koppel, J., Kumar, L., ... and de Roos, A. M. 2002. Self-organization of vegetation in arid ecosystems. The American Naturalist, 160(4): 524-530.

Ring, C. B., Nicholson, R. A., and Launchbaugh, J. L. 1985. Vegetational traits of patch grazed rangelands in west central Kansas. Journal of Range Management, 38: 51-55.

Robichaud, P. R., Pierson, F. B., Brown, R. E., and Wagenbrenner, J. W. 2008. Measuring effectiveness of three postfire hillslope erosion barrier treatments, western Montana, USA. Hydrological Processes, 22(2): 159-170.

Romo, J. T. 1994. Wolf plant effects on water relations, growth and productivity in crested wheatgrass. Canadian Journal of Plant Science, 74: 767-771.

Rowarth. J. S. and A. G. Gillingham. 1989. Effects of withholding fertilizer on pasture production and phosphate cycling in hill country pasture. Proceedings of the New Zealand Grassland Association, 51: 17-20.

Sala, O. E., Golluscio, R. A., Lauenroth, W. K., and Soriano. A. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia, 81: 501-505.

Sanford, W. W., Usman, S., Obot, E. O., Isichei, A. O., and Wari, M. 1982. Relationship of woody plants to herbaceous production in Nigerian savanna. Tropical Agriculture, 59: 315-318.

Saunders, W. M. H. 1984. Mineral composition of soil and pasture from areas of grazed paddocks, affected and unaffected by dung and urine. New Zealand Journal of Agricultural Research, 27(3): 405-412.

Savory, A. and Butterfield, J. 1998. Holistic Management: A New Framework for Decision Making. Island Press.

Schlesinger, W. H. and Pilmanis, A. M. 1998. Plant-soil interactions in deserts. In Plant-induced Soil Changes: Processes and feedbacks (pp. 169-187). Springer Netherlands.

Schlesinger, W. H., Raikes, J. A., Hartley, A. E., and Cross, A. F. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology, 77: 364-374.

Schrama, M., Heijning, P., Bakker, J. P., van Wijnen, H. J., Berg, M. P., and Olff, H. 2013. Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. Oecologia, 172: 231-243.

Seghieri, J., Galle, S., Rajot, J. L., and Ehrmann, M. 1997. Relationships between soil moisture and growth of herbaceous plants in a natural vegetation mosaic in Niger. Journal of Arid Environments, 36(1): 87-102.

Senft, R. L., Rittenhouse, L. R., and Woodmansee, R. G. 1985. Factors influencing patterns of cattle grazing behavior on shortgrass steppe. Journal of Range Management, 82-87.

Shachak, M., Boeken, B., Groner, E., Kadmon, R., Lubin, Y., Meron, E., …and Ungar, E.D. 2008. Woody species as landscape modulators and their effects on biodiversity patterns. BioScience, 58: 209-221.

Sheath, G. W. and W. T. Carlson. 1998. Impact of cattle treading on hill land: 1. Soil damage patterns and pasture status. New Zealand Journal of Agricultural Research, 41: 271-278.

Smit C, Béguin D, Buttler A, and Mueller-Schaerer H. 2005. Safe sites for tree regeneration in wooded pastures: a case of associational resistance? Journal of Vegetation Science, 16: 209-214.

Smit C, den Ouden J, and Mueller-Schaerer H. 2006. Unpalatable plants facilitate tree sapling survival in wooded pastures. Journal of Applied Ecology, 43: 305-312.

Soane, B. D., Blackwell, P. S., Dickson, J. W., and Painter, D. J. 1981. Compaction by agricultural vehicles: a review I. soil and wheel characteristics. Soil and Tillage Research, 1: 207-237.

Soriano, A. and Sala, O. E. 1983. Ecological strategies in a Patagonian arid steppe. Vegetation, 56: 9-15.

Soriano, A., Sala, O. E., and Perelman, S. B. 1994. Patch structure and dynamics in a Patagonian arid steppe. Vegetatio, 111(2): 127-135.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics, 353-391.

Stillwell, M. A. and Woodmansee, R. G. 1981. Chemical transformations of urea-nitrogen and movement of nitrogen in a shortgrass prairie soil. Soil Science Society of America Journal, 45(5): 893-898.

Stoddart, L. A., Smith, A. D. and Box, T. W. 1975. Range Management. New York: McGraw Hill.

Stowe, K. A., Marquis, R. J., Hochwender, C. G., and Simms, E. L. 2000. The evolutionary ecology of tolerance to consumer damage. Annual Review of Ecology and Systematics, 565-595.

Strauss, S. Y. and Agrawal, A. A. 1999. The ecology and evolution of plant tolerance to herbivory. Trends in Ecology and Evolution, 14(5): 179-185.

Striker, G. G., Mollard, F. P. O., Grimoldi, A. A., León, R. J. C., and Insausti, P. 2011. Trampling enhances the dominance of graminoids over forbs in flooded grassland mesocosms. Applied Vegetation Science, 14: 95-106.

Sun, D. and Liddle, M. J. 1993. The morphological responses of some Australian tussock grasses and the importance of tiller number in their resistance to trampling. Biological conservation, 65(1): 43-49.

Teague, W. R., Dowhower, S. L., and Waggoner, J. A. 2004. Drought and grazing patch dynamics under different grazing management. Journal of Arid Environments. 58(1): 97-117.

Thomas, R. J., Logan, K. A. B, Ironside, A. D., and Milne, J. A. 1986. Fate of urine-N applied to an upland grass sward. Plant and Soil, 91: 425-427.

Tiffin, P. 2000. Mechanisms of tolerance to herbivore damage: what do we know? Evolutionary Ecology, 14(4-6): 523-536.

Tongway, D. J., Ludwig, J. A., and Whitford, W. G. 1989. Mulga log mounds: Fertile patches in the semi-arid woodlands of eastern Australia. Australian Journal of Ecology, 14(3): 263-268.

Tongway, D. J. and Ludwig, J. A. 1990. Vegetation and soil patterning in semi-arid mulga lands of eastern Australia. Australian Journal of Ecology, 15: 23-24.

Tromble, J. M. 1988. Water interception by two arid land shrubs. Journal of Arid Environments, 15: 65-70.

Turner, M. G., Gardner, R. H, and O’Neill, R. V. 2001. Landscape Ecology in Theory and Practice: Pattern and Process. Springer.

UNEP.1997. World Atlas of Desertification, United Nations Environment Program Edward Arnold, London.

Valentin, C. and Bresson, L. M. 1992. Morphology, genesis and classification of surface crusts in loamy and sandy soils. Geoderma, 55: 225-245.

Valentin, C. and d’ Herbès. J. M. 1999. Niger tiger bush as a natural water harvesting system. Catena, 37: 231-256.

Valentin, C., d’Herbès, J. M and Poesen, J. 1999. Soil and water components of banded vegetation patterns. Cantena, 37: 1-24.

Valentin, C., Tongway, D. J. and Seghieri, J. 2001. Banded landscapes: ecological developments and management consequences. In Banded Vegetation Patterning in Arid and Semiarid Environments (pp. 228-243). Springer New York.

Van Veen, J. A., Merckx, R., and Van de Geijn, S. C. 1989. Plant-and soil related controls of the flow of carbon from roots through the soil microbial biomass. Plant and Soil, 115(2): 179-188.

Vega, E. and Montana, C. 2011. Effects of overgrazing and rainfall variability on the dynamics of semiarid banded vegetation patterns: a simulation study with cellular automata. Journal of Arid Environments, 75(1): 70-77.

Vetaas, O. R. 1992. Micro-site effects of trees and shrubs in dry savannas. Journal of Vegetation Science, 3(3): 337-344.

Wahl, M. and Hay, M. E. 1995. Associational resistance and shared doom: effects of epibiosis on herbivory. Oecologia, 102(3): 329-340.

Warren, S. D., Thurow, T. L., Blackburn, W. H., and Garza, N. E. 1986. The influence of livestock trampling under intensive rotation grazing on soil hydrologic characteristics. Journal of Range Management, 39: 491-495.

Watt, A. S. 1947. Pattern and Process in the Plant Community. Journal of Ecology, 35: 1-22.

Weiner, J. 1995. On the practice of ecology. Journal of Ecology, 153-158.

White, L. P. 1971. Vegetation stripes on sheet wash surface. Journal of Ecology, 59: 615-622.

White, P. S. 1979. Pattern, process and natural disturbance in vegetation. Botanical. Review, 42: 229-299.

Whitehead, D. C. 2000. Nutrient Elements in Grassland. CABI Publishing, Wallingford.

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

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics, 81-120.

Wu, J. and David. J. L. 2002. A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. Ecological Modelling, 153: 7-26.

Zhang, P., Yang, J., Zhao, L., Bao, S., and Song, B. 2011. Effect of *Caragana tibetica* nebkhas on sand entrapment and fertile islands in steppe–desert ecotones on the Inner Mongolia Plateau, China. Plant and soil, 347(1-2): 79-90.

Zhang, Y., Wang, X., Hu, R., Pan, Y., and Zhang, H. 2013. Stemflow in two xerophytic shrubs and its significance to soil water and nutrient enrichment. Ecological Research, 28: 567-579.