

ORIGIN, MAINTENANCE, AND ECOSYSTEM EFFECT OF VEGETATION PATCHES IN ARID LANDS¹

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ABSTRACT

A heterogeneous distribution of vegetation in patches or stripes is a common characteristic of arid and semiarid rangelands. Spatial heterogeneity occurs at different scales from 1 to 100 m². We present examples of mechanisms that originate and maintain patches at different scales. In the Patagonian steppe, there are two types of patches: shrubs encircled by a dense ring of grasses and scattered tussocks interspersed in a bare soil matrix. These two patch types are related in time because they represent phases of a cyclical succession. This phenomenon is driven by the changing balance of facilitation and competition. The cycle starts with the building of the ring of grasses around shrubs, followed by the destruction of the ring after shrub death with the consequent disintegration of the ring. Finally, the remaining tussocks form the scattered tussock patch type. In the Chilean Matorral, the mechanisms that account for the formation of patches also include the redistribution of seeds by birds. At a larger scale, stripes of woodland in Australia and Mexico are interspersed between larger areas with very low cover. In all cases, patches underneath individual plants, multispecies patches, or stripes concentrate water and/or nutrients. This heterogeneity in the distribution of resources may enhance production and ecosystem functioning in many cases and can be seen as a sign of rangelands in good condition.

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INTRODUCTION

Vegetation in arid and semiarid rangelands is scarce and spatially heterogeneous. Low water availability explains small primary production and plant cover (Lauenroth 1979, Sala, et al. 1988), but it does not explain the distribution of vegetation in dense clumps or patches interspersed in a bare soil matrix. Alternatively, the same low cover could have been distributed homogeneously in space. There is not a unique mechanism explaining the origin and maintenance of patches for all rangeland ecosystems, and there is not a complete understanding of the role of patches on the functioning of rangelands. The origin of patches in plant communities has been historically among the central themes of ecology (Watt 1947, Kershaw 1959, Greig-Smith 1965). In recent years, interest in the significance of patches for community functioning has been growing steadily (Wiens, et al. 1985). Along with the growing interest in incorporating patch heterogeneity into ecological theory and into novel methods for range management is the need to increase our understanding of patch dynamics. The objectives of this paper are: (1) to describe the processes which account for the origin and maintenance of patches in different rangelands and (2) to explore the meaning of spatial heterogeneity for their functioning. In order to satisfy these objectives, first we will present examples of the mechanisms that originate and maintain small scale patches in the Patagonian steppe and the Chilean Matorral and large scale patches in Australia and Mexico. Second, we will explore the consequences of patches for the functioning of rangelands based on theoretical considerations and empirical evidence.

THE ORIGIN AND MAINTENANCE OF PATCHES

In the Patagonian steppe, vegetation is composed of shrubs and tussock grasses. They are arranged in two patch types: shrubs encircled by a dense ring of tussock grasses and tussock grasses interspersed with bare ground (Soriano, et al. 1994). A model has been proposed for the origin and maintenance of this patchy structure in which spatial heterogeneity is viewed as reflecting phases of a cycli-

cal succession (Fig. 1). When a shrub seedling establishes and achieves a certain size, it generates favorable conditions for grass establishment. These favorable conditions result in the construction of a dense ring of grasses surrounding the shrub. The building of the ring represents the construction phase of the cycle. When the shrub dies and aerial protection disappears, the density of grasses becomes higher than the current carrying capacity of the ring which results in the death of some tussocks. The ring disappears as an entity, and grasses appear interspersed with bare soil patches forming the other patch type of the Patagonian steppe. This is the destruction phase of the cycle.

The model that represents a hypothesis of the dynamics of the Patagonian steppe cannot be tested with a single experiment, how-

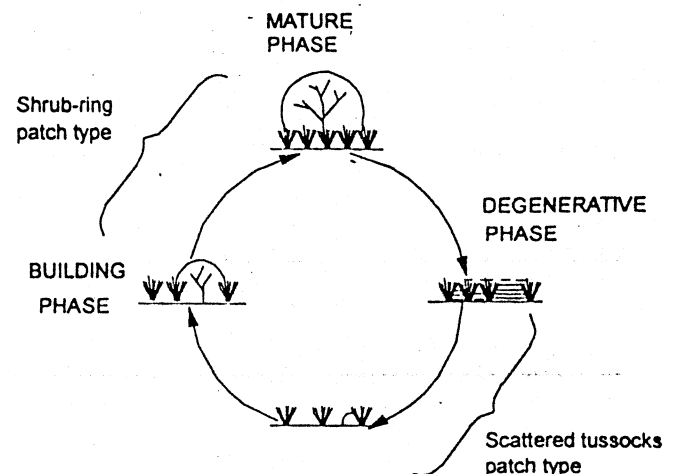


Fig. 1. The model proposed for the Patagonian steppe in which different structural patches represent phases of a cyclical succession. Shrubs germinate, establish, and, as they grow, modify the environmental conditions facilitating the establishment of grasses that form a dense ring around the shrub. After the shrub dies, the protection from desiccating winds disappears, the tussock grasses in excess of the carrying capacity die, the ring loses identity and the remaining tussock grasses form the scattered tussock patch type. Redrawn from Soriano, et al. 1994.

ever several experiments were able to test portions of it. Experiments in which competition was reduced and grass seedling survival was monitored in different microsites yielded interesting and counterintuitive results (Aguilar, et al. 1992). Under natural conditions, seedling survival and seedling biomass were larger in the exposed microsites (bare soil areas) than in microsites protected by shrubs (leeward of shrubs). Under reduced competition, the pattern was reversed suggesting that there were two processes acting simultaneously, competition and facilitation. When competition was experimentally excluded the facilitation effect showed up, but it was overshadowed by competition under natural conditions. Competition, facilitation, and seed availability decrease with distance to a shrub with a ring of grasses resulting in maximum recruitment at intermediate distance (Aguilar, et al. 1994). Competition for soil water decreases with distance to the shrub with the ring of grasses as a result of grass root biomass also decreasing with distance. Facilitation is also mediated by water availability because potential evaporation increases with distance to the shrub (Soriano, et al. 1986, Aguilar and Sala 1994). Seed density also decreases with distance to shrubs because they create wind shadowed microsites which retain seeds (Aguilar, et al. 1996).

How do rings form if establishment is higher away from the shrub with the ring of grasses? Facilitation and competition depend on the size of the shrub (Fig. 2) (Aguilar and Sala 1994). Soriano, et al. (1994) showed that the cover of the ring of grasses was associated with the size of the shrub. This relationship was described by Richards' (1959) model. The magnitude of the competition effect is related to the completeness or cover of the ring of grasses. Competition exists between seedlings and adult grasses and not adult shrubs since they have deeper root systems which minimally compete with adult grasses (Sala, et al. 1989). Consequently, the intensity of competition will follow a similar pattern to that of the ring completeness, being zero at low completeness values when tussock grasses are far apart and then increasing exponentially as the size of the shrub and the completeness of the ring increase. On the contrary, facilitation is directly related to the size of the shrub because it depends on the physical protection from desiccating winds. This model (Fig. 2) suggests that facilitation should be more important than competition when shrubs are small which results in the formation of the ring of grasses. Beyond a shrub size threshold, competition overshadows facilitation marking the end of the construction phase and determining the maximum carrying capacity of the ring of grasses.

The Patagonian steppe is an example where patches originate as a result of the interactions among plants: competition between adult grasses and seedlings, and facilitation between adult shrubs and seedlings. The origin and maintenance of patches in the Chilean Matorral involves animals also which facilitate the dissemination of seeds (Fuentes, et al. 1984, Fuentes, et al. 1986). Birds disperse seeds and constrain the distribution of seeds and seedlings to bird perches. Nurse plants facilitate the establishment of new individuals by modulating the availability of seeds. Seedling survival is also higher near nurse plants as a result of amelioration of abiotic factors as well as protection from rabbit herbivory.

Vegetation patches in arid and semiarid rangelands occur at different scales. Whereas examples from the Patagonian steppe and the Chilean Matorral occur at the scale of 3 to 5 m², similar patterns have been reported at much larger scales (100 m²) in the woodlands of Australia and Mexico (Tongway, et al. 1990, Montaña, et al. 1990, Montaña 1990, Ludwig, et al. 1995). In one of the Australian cases, bands dominated by mulga trees (*Acacia aneura* F. Muell. ex Benth) alternate with bare soil areas with a few grass individuals. Similarly,

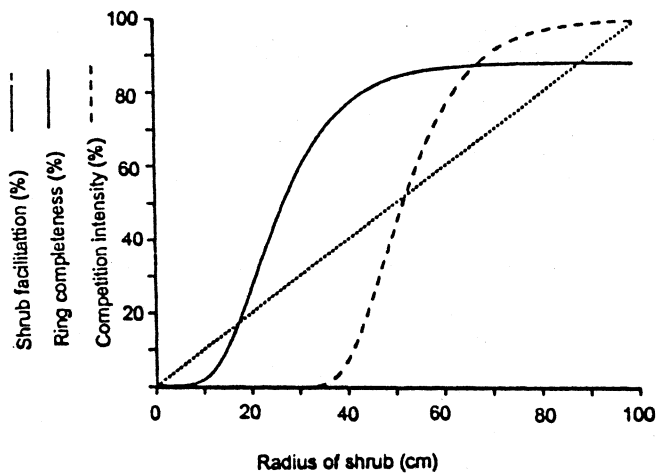


Fig. 2. The effect of shrub size on the completeness of the ring of grasses surrounding it and on the intensity of facilitation and competition. Completeness was estimated as the fraction of the ring covered by grasses. The relationship between shrub size and ring completeness was empirically determined (Soriano, et al. 1994). The magnitude of the facilitation is directly related to the size of the shrub, whereas the magnitude of competition is related to completeness of the ring. Redrawn from Aguilar and Sala 1994.

in the Chihuahuan Desert, vegetation stripes alternate with bare areas. These vegetated areas move upslope as has been demonstrated by the differential colonization of the upslope and downslope ecotones (Montaña, et al. 1990, Mauchamp, et al. 1993).

The patterns of dense vegetated patches, stripes, or bands interspersed with bare soil areas are similar at different scales. All the mechanisms that account for their origin and maintenance involve redistribution of resources or seeds by water, wind, or animals. However, the invoked mechanisms change at different scales. Plant-plant or plant-animal interactions such as competition and facilitation are crucial at small scales. At larger scales, the presence of source and sink areas accounts for the existence of the densely vegetated stripes (Ludwig and Tongway 1995).

THE ECOSYSTEM CONSEQUENCES OF PATCHES

A heterogeneous vegetation structure results in the concentration of resources underneath individual plants, patches, or stripes. Two decades ago, Charley and West (1975) introduced the term "islands of fertility" to describe the accumulation of nutrients underneath the canopy of shrubs in the semi-desert of Utah. Similarly, in the Chilean Matorral, the concentration of soil nitrogen, phosphorus, and soil organic matter were higher underneath than outside the canopies of shrubs (Gutierrez, et al. 1993). Smaller individuals such as those of the grass species *Bouteloua gracilis* were able to significantly modify the concentration of nitrogen and carbon underneath their canopies (Hook, et al. 1991). At a coarser scale, the upper soil layer of the mulga groves had higher available nitrogen than the intergroves (Ludwig and Tongway 1995). Phosphorus being an element less mobile in the soil showed similar trends but only in the uppermost layer.

What is the effect of this heterogeneous distribution of resources on the functioning of the entire ecosystem? Does it enhance or reduce production? Does it enhance or reduce ecosystem functioning in general? The answers to these questions have profound theoretical and applied implications. They can influence our understanding of the functioning of arid rangelands and our selection of management techniques which may try to either avoid or take advantage of heterogeneity. Schlesinger, et al. (1990) suggested that het-

erogeneity in the distribution of resources was a result of desertification while others indicate that it is necessary for the survival of many plants and animals in arid and semiarid rangelands (Stafford Smith and Pickup 1990).

We suggest that a conceptual model in conjunction with empirical information may clarify the issues of the ecosystem significance of spatial heterogeneity. Noy-Meir (1981) suggested that the model that relates production and precipitation is linear and has two thresholds (Fig. 3A). Below a minimum precipitation threshold production is zero; beyond a maximum precipitation threshold, further increases in precipitation do not result in increases in production. There is empirical support of the existence of the minimum and maximum thresholds. Analysis of the production patterns of 9498 grassland sites in the Central Grassland Region of North America indicated that primary production and precipitation are positively correlated and the linear model has a negative y-intercept (Sala, et al. 1988).

$$ANPP = -34 + 0.6 \cdot APPT$$

where ANPP is aboveground net primary production and APPT is annual precipitation. This equation can be rearranged as:

$$ANPP = 0.6 \cdot (APPT - 56)$$

where 0.6 represents the average water use efficiency and 56 is the ineffective precipitation or zero yield intercept (Noy-Meir 1973). The analysis of the production patterns of forests, grasslands, and deserts suggested the existence of an upper threshold in the response of production to precipitation (Webb, et al. 1978, Webb, et al. 1983).

This model has important implications for the effect of spatial heterogeneity on total ecosystem production based on the condition of a patchy environment, where in some areas concentrate resources (sinks), and other areas provide resources (sources). In the case of water, those are run-on and run-off areas. The amount of water redistributed depends on the proportion of sources and sinks, and on the fraction of precipitation that runs off which, in turn, depends on the magnitude of the precipitation event; soil water content at the time of the event, topography, plant cover, stocking rate, etc. (Branson, et al. 1981). If average precipitation falls below the lower threshold and it is homogeneously distributed, available water is (P_a) and production should be zero (Fig. 3B). If there is redistribution, the source areas will give up some water, resulting in less available water (P_o), and production will continue to be zero. However, the sink areas will receive precipitation plus run-on, resulting in a higher water availability (P_i), which now is higher than the threshold. Consequently, there will be production in the sink areas. This analysis suggests that in arid regions heterogeneous systems may have higher production than homogeneous systems. On the contrary, in mesic grasslands in which average precipitation is close to the upper threshold, heterogeneous systems should have lower production than homogeneous systems. This analysis was performed for water redistribution, and it can be similarly performed for other resources that limit production at different times. Nitrogen and phosphorus can be redistributed in the same manner as water. In the case of nutrients, biological mechanisms can be invoked in addition to abiotic mechanisms to account for the redistribution of nutrients. Roots forage for nutrients beyond canopy projection and most of the aboveground litter is deposited underneath the canopy. Finally, animals can contribute to the redistribution of nutrients and concentration in patches.

We recognize that in many cases there is a nested hierarchy of patches, where fine scale patches form part of patches at a coarser scale. Our analysis suggests that there is not a simple answer to the question of whether patchiness has a positive or negative effect on ecosystem functioning. It suggests the answer is scale dependent;

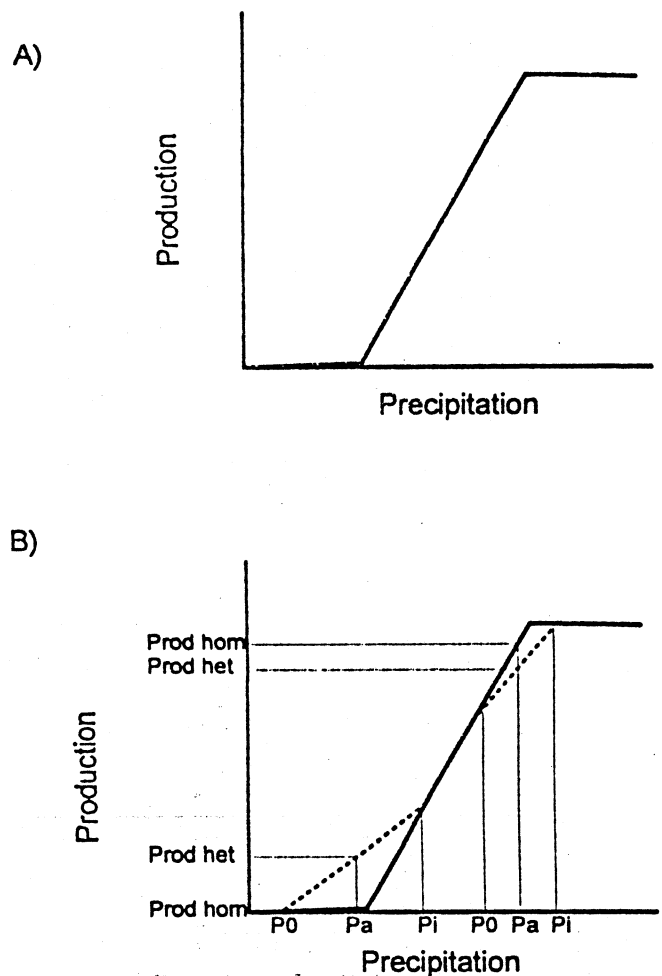


Fig. 3. A) Conceptual model of the relationship between primary production and annual precipitation. The model suggests that there is a linear relationship between primary production and precipitation in between lower and upper thresholds. B) The effect of homogeneous or heterogeneous distribution of resources on production. P_a is the available water if vegetation was uniformly distributed, and Prod hom, the resulting production. P_o is the available water in source areas, P_i is the available water in sink areas and Prod het is the resulting production in systems with a heterogeneous distribution of precipitation. Redrawn from Noy-Meir 1981.

patchiness at one scale may enhance production and indicate "healthy rangelands," while at other scales, such as in the Chihuahuan Desert, patchiness may decrease ecosystem functioning and indicate degradation. We suggest that overgrazing may reduce spatial heterogeneity and the redistribution of resources at a fine scale but, at the same time, may create heterogeneity at coarser scales (Sala 1988).

CONCLUSIONS

The heterogeneous distribution of vegetation in patches or stripes is a common feature of arid and semiarid grasslands. This spatial heterogeneity is generally created by the action of vegetation and animals mainly through the redistribution of resources and seeds. This redistribution of resources may result in an increase in production in particular, and ecosystem functioning in general, at the level of whole ecosystems.

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