

ing. Most epidermal responses are activated by the secreted rhizobial signaling molecule Nod factor. This molecule activates a signaling pathway in root epidermal cells that leads to oscillations in the intracellular concentration of calcium. This calcium signal is perceived by a calcium- and calmodulin-dependent protein kinase (CCaMK), and it has recently been shown that, analogous to the cytokinin receptor, activation of CCaMK is sufficient to induce nodule formation in the absence of rhizobial bacteria (8, 9). Hence, the spontaneous formation of nodules can be induced by gain-of-function mutations in both the *CCaMK* and *LHK1* genes. Tirichine *et al.* show that a plant carrying the gain-of-function mutations in both of these genes generates more nodules than plants with either mutation alone, indicating an additive effect. Hence, it is likely that two separate signaling pathways function in nodulation.

It is therefore very surprising that the *LHK1* gain-of-function mutation depends on the gene *NSP2* to activate spontaneous nodules. *NSP2*, a transcriptional regulator, is a component of the Nod factor signaling pathway (10, 11) and is also necessary for CCaMK-induced spontaneous nodulation (9). It appears that even though these two path-

ways function independently, they converge at *NSP2*, suggesting that this regulator has dual functions in both Nod factor and cytokinin signal transduction during nodulation.

Perception of Nod factor by the plant is one of the first steps during the interaction between root cells and rhizobial bacteria. Because Nod factor accumulates in cell walls (12), it is highly unlikely that it can traverse the epidermis to induce responses in root cortical cells. It is possible that the localized production of cytokinins follows Nod factor perception, acting as a mechanism to coordinate epidermal and cortical responses during nodule formation. In this model, activation of Nod factor signaling at the epidermis leads to increased localized production of cytokinins. Cytokinins are then transported (most likely by active transport from cell to cell, but the mechanism remains unclear) to cortical cells where they are perceived by *LHK1* at the cell surface. This initiates cell division, leading to formation of the nodule primordium. This model predicts that rhizobial bacteria induce cytokinin production in legume roots or redirect cytokinin transport, and also predicts that CCaMK-induced spontaneous nodulation should require *LHK1*.

Cytokinins are also used by plants that do not form nodules in diverse developmental

pathways, including the regulation of root and shoot branching. A key question is whether plants that form nodules have evolved a unique response to cytokinins, or whether the appropriate activation of *LHK1* and its orthologs in other plant species is sufficient to induce nodule-like structures. Answering this question will provide insights into the ease of transfer of nodule organogenesis, a first step in transferring this symbiotic interaction into agriculturally important species.

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10.1126/science.1137588

ECOLOGY

Rangeland Ecology in a Changing World

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Millions of people in rangelands depend directly on livestock for their livelihoods, but the management of these regions is mired in controversy (see the figure). Early colonial efforts imposed economic management models based on equilibrium carrying capacities. In the 1990s, however, “the new ecology” took hold and challenged equilibrium models by exploring the variability and flux inherent in most ecological and social systems (1). Such models (2) described a disequilibrium rangeland system, in which animal numbers were limited by drought events, thereby preventing an impact on vegetation (3). Since then, a variety of rangeland responses have been described, in which environmental variation and density-

dependent effects on animal numbers are observed to a greater or lesser extent.

According to disequilibrium theory, herbivores have little impact on rangeland vegetation, because their numbers are regulated by environmental fluctuations (2). Droughts keep animal populations below levels where density-dependent competition for forage occurs (3). However, two problems have emerged from the disequilibrium literature. First, the process by which environmental variation regulates animal numbers is not clear. Second, if changes in vegetation are a normal part of variable, semiarid environments, then on what basis can variability be distinguished from potentially long-term degradation?

Recently, a new synthesis has addressed these challenges. It assumes that most rangeland systems respond to variability in rainfall. A fixed “carrying capacity,” in the strict sense

A synthesis of different models for assessing the balance between vegetation and livestock numbers in grazing lands may help policymakers integrate human and ecosystem needs.

of a stable equilibrium between primary production and grazing, is unlikely because rainfall and hence primary production covary over time, particularly in semiarid ecosystems. If primary productivity varies with rainfall, then it follows that “carrying capacity” will also vary over time. Instead of stability, a correlation between animal numbers and rainfall might be expected (4), and indeed has been observed over long time scales (5).

Disequilibrium theory cannot explain this correlation because a central tenet is that animal numbers are below the level at which density-dependent competition for forage occurs (2, 3). In low-rainfall years, however, density-dependent competition is possible even at quite low animal densities, because primary productivity is limited by lack of water, and animals will compete for the little forage that is available. Over time, no stable equilibrium between animal numbers and primary produc-

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tion will be reached because the position of central tendency changes according to rainfall, and the system can be described as non-equilibrium. At other times or scales, however, other environmental factors like drought, fire, nutrient limitation, forage quality, or rainfall frequency might dominate (4, 6, 7), and the coupling between rainfall and animal numbers will be weak.

Thus, a synthesis of disequilibrium and equilibrium theory describes a system that is not at equilibrium, but in which animal numbers fluctuate in response to a variable environment. At certain times, for example, during a series of low- to medium-rainfall years, or at key resource areas like dry-season grazing, these fluctuations may be mediated by density-dependent effects (8). At others, for example, during extreme environmental events like droughts, or outbreaks of disease, the system will be stochastically driven, and the correlation between animal numbers and rainfall will be weak. It is likely that disequilibrium, in its strict sense of a system dominated by environmental variation, can occur only in extremely dry environments and/or in exceptionally prolonged drought periods, when there is literally no primary productivity for which animals can compete (9). It therefore seems critical to distinguish disequilibrium systems (3) as a restricted subset of non-equilibrium systems, the latter being defined more broadly in terms of all systems that are not at equilibrium.

Given this broader definition of nonequilibrium, research into systems not at equilibrium can be reframed in terms of how factors like density dependence, environmental stochasticity, drought, disease, and nutrients interact; the thresholds at which different factors become dominant; and how these interactions are expressed in terms of plant-herbivore dynamics. Research has shown that consistently high stock levels can transform the vegetation composition of semiarid rangelands. For example, in Namaqualand, South Africa, a mixture of palatable woody plants and perennial herbaceous species was replaced through heavy grazing by a system dominated by unpalatable woody species and annuals (10). In the Rio Grande Plain, United States, and New South Wales, Australia, grass-dominated rangelands were replaced by a more wooded landscape when grazing levels were high and fire was suppressed (11, 12), whereas in Kimberley, South Africa, rainfall frequency and nutrient availability were found to be more important factors than animal abundance in woody-plant encroachment (13). Rather than a continuum of variation in vegetation, then, rapid transitions in vegetation



Sensitive to environmental conditions. Millions of people in drylands depend directly on livestock for their livelihoods.

types have been observed when the interactions among livestock density, rainfall, grazing history, fire, and nutrients reach critical thresholds (14, 15).

Systems theory can help us understand rangeland complexity. The concept of carrying capacity—long associated with assumptions of stability and equilibrium—can be usefully replaced by the idea from chaos theory of a “moving attractor” (11, 16). In rangelands, this would be a point that varies depending on rainfall and toward which animal numbers tend. Similarly, the state-and-transition understanding of rangelands (14) can be reinterpreted in terms of the moving attractor concept, where alternative persistent states may be considered as regions of higher-probability space, known in systems theory as a domain of attraction.

Conceptual frameworks like stable states and moving attractors may also provide a useful underpinning for addressing the second major research challenge, that of how to define degradation in a variable system. Annual-dominated systems might maintain a long-term average in animal numbers and therefore not be degraded in terms of animal productivity, but might still be considered degraded in terms of the loss of plant diversity and cover that can accompany heavy grazing, or because of effects on soil erosion or nutrient cycling. Moreover, a grazing system dependent on annuals is likely to become disequilibriumal, that is, driven by environmental stochasticity, because of the increased likelihood of a complete failure of primary productivity in drought years.

Analysis of vegetation dynamics (4), clarity in the definition of degradation (17), and a refinement of disequilibrium theory to incorporate density dependence at different scales, as well as environmental sto-

chasticity and variability in forage quality (7), have opened new opportunities for dialogue between the natural and social sciences, particularly with regard to the interplay between ecological, social, and economic systems (4, 18). However, this still leaves policy-makers with the challenge of how to integrate the views of multiple stakeholders, with different value systems, in order to reconcile biodiversity conservation and livelihood concerns across contested rangeland landscapes.

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19. We thank N. Allsopp, D. Brockington, P. Carrick, R. Rohde, and S. Vetter for helpful comments on the text.

10.1126/science.1136577