



Long-term dynamics in arid and semiarid ecosystems – synthesis of a workshop

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According to the United Nations (UNEP, Agenda 21), approximately one sixth of the world's population, 70% of all drylands with a total area of 3.6 billion hectares, and a quarter of the total land surface of the earth is endangered by desertification. The most obvious consequences are increasing poverty and the growing damage to 3.3 billion hectares of rangeland. These impressive figures illustrate the importance of developing mechanisms for combating desertification. However, there is an increasing number of scientists who doubt the accuracy of these figures and who speak of 'the myth of desertification' as a publicity tool (e.g., Thomas & Middleton 1994). Their criticism is based on the idea that dryland ecosystems might after all be well adapted to disturbances and may exhibit good recovery characteristics. Nevertheless, it has been increasingly recognized that arid and semiarid ecosystems often exhibit complex non-equilibrium dynamics involving complicated non-linear processes and stochastic event-driven behavior (Westoby et al. 1989; Walker 1993). Vegetation changes generally occur unpredictably in the short term (years) in response to rainfall, and episodically in the long term (several decades) in response to rare events, or due to grazing pressure, climatic change, altered disturbance regimes, or a combination of these factors. The complex dynamics of arid and semiarid ecosystems and especially the mismatch between observation times (years) and time scales of vegetation change (centuries) make it difficult to fully understand their long-term dynamics (Wiegand et al. 1995; Jeltsch et al. 1996). Hence, it is extremely difficult to establish whether an area is undergoing progressive, long-term decline in biodiversity and productivity (desertification), or whether it is merely suffering short-term drought, from which the land may recover if

human impact is reduced or eliminated. But for developing management strategies for sustained animal production and species conservation, it is necessary to know how resilient arid and semiarid ecosystems really are, and to assess their potential to recover from serious natural or human disturbances or stress. Long-term ecological monitoring and interdisciplinary approaches to interaction between rainfall, geology and ecology are required in order to gain a better understanding of long-term dynamics in arid and semiarid systems. These approaches include both field studies and modelling studies. The latter can help to extrapolate local information and knowledge gathered on shorter time scales to larger spatial and temporal scales. This knowledge originating from field and modeling studies forms an indispensable basis for identifying key factors and processes that shape the potential for both desertification and recovery therefrom. In the following we briefly summarize and link various papers (all this issue) on field and modeling studies that are based on contributions to the INTECOL symposium 'Long-term dynamics in arid and semi-arid ecosystems' in Florence, 1998, or that were inspired through discussions during and after the symposium

Field studies

A characteristic, immutable feature of arid or semi-arid rangelands is their changeability (Harrington et al. 1984), and because of their lack of 'persistence' they are often called 'fragile' or 'unstable'. But are they really unstable on the long-term, or do they persist within their changeable state as long as responses to events do not involve a fundamental alteration to the way the system functions? Are these systems

in a state of 'equilibrium', despite frequent disturbances and stochastic and highly variable rainfall, or do the driving forces cause non-equilibrium dynamics, including unpredictable changes and fluctuations of species' composition and abundance (Wiegand et al. 1995; Jeltsch et al. 1996, 1997, 1999)? Episodic events are driving factors of population dynamics especially for populations of long-lived plants in arid or semi-arid areas (Wiegand et al. 1995), but they are difficult to observe because rarity itself precludes detection within the limited time-frame of the typical field study. Therefore long-term research forms an indispensable basis for understanding population dynamics and management. In a 14-year study, Henschel & Seely (2000) investigated long-term growth patterns of *Welwitschia mirabilis*, a long-lived plant of the Namib Desert (Namibia), in relation to climatic data. Episodic rainfall events during three years were followed by quadruple growth rates, and one natural recruitment event was observed during the study period. Plant location affected growth rate; plants growing on the low banks, or ledges, of the main drainage channel grew at a higher rate, and responded better and longer to rainfall.

One of the big challenges of field studies is to find the underlying long-term ecological processes that determine vegetation dynamics (or plant condition) despite the strong short-term impact of unpredictable rainfall. This creates a problem in differentiating between changes in plant condition or vegetation composition due to variability in rainfall and those due to other factors such as plant location, disturbance, herbivory and competition. Three recent long-term studies in Makhtesh Ramon erosion cirque in the central Negev desert of Israel (Ward et al. 2000) have shown that rainfall is the major driving variable in this system, and that high spatial heterogeneity (including an altitudinal rainfall gradient) and high variation in rainfall cause great spatial and temporal variability in plant production, community composition, and plant species diversity in this study system. Using pairs of fenced and unfenced plots arranged along a rainfall gradient the authors were able to tease apart the effects of variance in rainfall and herbivory and found that some of the most significant factors for vegetation dynamics pertain to large mammalian herbivore impacts on the desert vegetation.

Mammal disturbances also played an important role in a seven-year study of Milton and Dean (2000) who investigated the impact of drought and disturbances on dynamics of a desert dune grassland in the

Northern Cape province of South Africa. The initial hypothesis was that establishment of ephemeral plants, and recruitment of perennial grasses was dependent upon small-scale disturbances, made by burrowing mammals or territorial antelopes, that reduced the density of living perennial grass tussocks. Initial results obtained in relatively wet years supported the initial hypothesis. However, a subsequent drought killed more than half of the established tufts of the perennial grass, and synchronous recruitment that followed the drought-induced mortality generated even-aged populations of the dominant perennial grass. Milton and Dean (2000) found that drought had little long-term effect on community composition, indicating a long-term equilibrium of the desert dune grassland.

However, the general question of equilibrium vs non-equilibrium dynamics in arid and semi-arid ecosystems is also complicated by the spatio-temporal heterogeneity of the abiotic factors, such as patchy rainfall, or heterogeneous landscape features and dynamics. For example, Thielbörger & Kadmon (2000) investigated environmental heterogeneity in a desert dune area at the Nizzana research site in the north-western Negev desert of Israel, where shrubs represent a favorable habitat for annual plants within a nutrient-poor matrix. They investigated if facilitation of desert shrubs increases the intensity of competition among the annual plants and found that such negative indirect effects were unimportant in determining the demographic response of understory annual plants. In addition to abiotic factors in arid and semiarid ecosystems it is important to consider biotic factors that modify soil roughness and resource availability, e.g., biological crusts. In their study of a crust on a desert sand dune area at the Nizzana research site in the north-western Negev desert (Israel), Prasse & Bornkamm (2000) found that well-timed, small-scale disturbances of the microbiotic crust increased vascular plant establishment probabilities because undisturbed crusts had lower seed trapping ability. This suggests a potential feedback process of long-term vegetation dynamics: disturbance of microbiotic crusts results in a higher number of emerging plants, which in turn represents a rough seed-trapping element leading to further increase in densities in consecutive years.

Modeling studies

Recent developments in computer techniques for simultaneously modeling the spatial and temporal responses of organisms to their environment (grid-based

and/or spatially explicit individual-based models) offer the possibility of quantitatively exploring the long-term vegetation dynamics of arid and semi-arid ecosystems. The main idea behind this approach is to combine the current knowledge about the processes that drive vegetation dynamics (in the short term) into the framework of a simulation model and to facilitate a systematic investigation of (the long-term) interactions between all relevant factors and their logical consequences (e.g., Wiegand et al. 1995; Jeltsch et al. 1996). Following this approach, Weber et al. (2000) modeled life histories and interactions of the major life forms in the Kalahari savanna (shrubs, perennial grasses, annuals) depending on grazing, fire, and various other types of disturbance in order to systematically investigate the long-term effects of small-scale grazing heterogeneity and alternative stocking strategies. Similarly, Wiegand K. et al. (2000) used an individual-based, spatially explicit simulation model to investigate the processes that shape the population dynamics of *Acacia raddiana* in the Negev desert (Israel). The two studies show that simulation modeling is a powerful tool for conducting controlled experimental manipulation for a large number of environmental conditions and over long time spans. Weber et al. (2000) conducted 50-year simulation experiments over a wide range of livestock utilization intensities for several scenarios of grazing heterogeneity and two alternative stocking strategies, experiments that would be hard to perform in the field. Their results show a threshold behavior of shrub cover increase: at low utilization intensities little change occurred; when utilization intensity exceeded a threshold, shrub cover increased drastically. For both stocking strategies, the thresholds were highly sensitive to grazing heterogeneity. Wiegand K. et al. (2000) performed various 200-year simulation experiments to systematically study the long-term effect of contrasting scenarios of recruitment, growth and mortality on simulated tree-frequency distributions.

The power of models is especially enhanced when observed patterns or long-term sets of data can be used to calibrate parameters or assess the importance of different hypothesized processes (Jeltsch et al. 1999). Paruelo et al. (2000) calibrated their non-spatial model of ecosystem functions in the Patagonian steppe with seasonal curves of the NDVI index derived from satellite images, and Wiegand K. et al. (2000) systematically compared snapshot information in the form of observed size frequency distributions of *A. raddiana* trees with simulated tree-frequency distributions and

could confirm the hypothesis that recruitment events are a major factor shaping long-term population dynamics, and that that paucity of recruitment has been a normal feature of *A. raddiana* in the Negev over many years. Similarly, Wiegand T. et al. (2000) used two sets of shrub size data that were collected with an 8-year difference in the same area of the Tierberg study site in semiarid Karoo (South Africa) to assess formerly unknown size-age relations for different shrub species.

High variability in precipitation is characteristic for arid or semiarid areas, and because of the inherent short-term availability of soil water as a resource, water dynamics are a key-factor of long-term vegetation dynamics. Especially the question of how (or whether) the ecosystem would be able to buffer, on the long-term, the great year-to-year variability in rainfall is difficult to study in the field. Reynolds and Kemp (2000), and Paruelo et al. (2000) tackled this problem by using simple mechanistic ecosystem models to explore long-term patterns of evapotranspiration in communities with different functional groups, using long-term rainfall data sets. In their study for a warm desert site in the Jornada Basin, southern New Mexico (USA) Reynolds and Kemp (2000) found that variation in transpiration was 3 times greater than variation in rainfall (CV of rainfall = 35%), but variation of evaporation was smaller than variation in rainfall. Similarly, Paruelo et al. (2000) found in their study on soil water dynamics across a rainfall gradient in Northwestern Patagonia (Argentina) that the coefficients of transpiration, evaporation and annual net primary production were, in general, lower than the CV of annual precipitation. This pattern suggests a buffering capacity of the ecosystems, being able to dampen at the functional level, inter-annual changes in the availability of resources. Ecological buffer mechanisms also play a crucial role in the general savanna theory proposed by Jeltsch et al. (2000). In their article, the authors suggest an alternative viewpoint on the classical 'savanna question', which focuses on the unusual long-term coexistence of trees and grasses in this biome. Instead of discussing the question whether savannas are equilibrium or non-equilibrium systems, they focus on the boundary of the system and search for mechanisms (i.e., the buffer mechanisms) that prevent a savanna from transition to other biomes. These mechanisms are identified as general key factors for savanna existence in different parts of the world.

Discussion

The contributions to the special issue highlight the necessity of combined, interdisciplinary approaches to tackle the increasing problems of arid and semi-arid ecosystems. These problems include ethical, cultural, and socioeconomic, as well as ecological, aspects and are inevitably linked to the long-term dynamics of the ecosystem itself. It has become clear that long-term monitoring, the indispensable basis of understanding and management, needs to be accompanied by other approaches such as experiments and modeling studies. In particular, the combined approach of long-term field research and carefully constructed, spatially-explicit simulation models has the potential to gain the most understanding about natural long-term dynamics and the possible consequences of anthropogenic impact. A large number of studies have shown that spatial heterogeneity and spatial processes on different scales play an important role in the dynamics of these systems. This aspect should be considered in future research, e.g., by focussing on climatic or geomorphological gradients, comparative studies and spatially-explicit models.

However, our current understanding of the functioning of dryland ecosystems and their ability to absorb impacts is inadequate to predict future effects with certainty. Society will have to decide on the levels of uncertainty that are still acceptable and we will have to find a balance between economic input into ecosystem research and conservation and ecological risk of degradation. To minimize this risk, both basic and applied ecological research is necessary. Without a better understanding of natural processes and their long-term consequences, and without comparative studies between different arid and semi-arid ecosystems, any attempt to manage these systems will increase the risk of long-term damage. As there is not yet any technology available that can reverse the more extreme effects of degradation in arid and semiarid ecosystems, we will have to maximize efforts to avoid degradation to retain options for future generations.

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