

Susan Schwinning · Osvaldo E. Sala · Michael E. Loik ·
James R. Ehleringer

Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems

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Changes in resource availability can alter the functioning of ecosystems, especially with regard to both population dynamics and the cycling of organic matter and nutrients. At perhaps one end of the spectrum, arid and semi-arid ecosystems represent an extreme in which essential resource availability (e.g., water) is discontinuously available and the availability of these resources impact the ecosystem as discrete pulse events interspersed among long periods of limited resource availability. The objective of the special section that follows is to contribute to our understanding of how pulsed events shape population dynamics, species interactions, and ecosystem processes in arid and semi-arid ecosystems.

There has been a renewed interest in recent years in the relationships between precipitation and ecosystem processes in arid and semi-arid lands. For many years, studies focused on the effects of mean precipitation, averaged at annual, seasonal, or monthly time scales. These studies suggested broad-scale relationships between precipitation amounts and seasonal distribution and the productivity of ecosystems (Le Houérou 1984; Le Houérou et al. 1988), or the plant functional type composition of water-limited systems (e.g., Neilson 1995; Smith et al. 1997). Though

some researchers asked questions about the effects of single rainfall events early on (e.g., Went and Westergaard 1949; Beatley 1974; Sala and Lauenroth 1982), this perspective received wider attention only in the last decade, in part through the development of stable isotope tracer methods in plant ecology (e.g., Caldwell et al. 1985; Ehleringer et al. 1991; Lin et al. 1996). More recently, studies also have begun to focus on intra-seasonal precipitation patterns, asking whether variability in rainfall event size, frequency, and timing alone affect the biological processes in water-limited ecosystems (e.g., Goldberg and Novoplansky 1997; Knapp et al. 2002; Schwinning et al. 2003).

With a view to addressing these questions, an international workshop was held at the University of Arizona in Tucson, USA (<http://ag.arizona.edu/research/schwinn/workshop.html>). This special issue contains both peer-reviewed synthesis papers that were generated through the collaboration of workshop participants, as well as original research contributions related to pulse dynamics in arid and semi-arid ecosystems.

A generation ago, two major paradigms for understanding rainfall effects in water-limited ecosystems were published: (1) the pulse-reserve paradigm of Noy-Meir (1974) and co-workers, and (2) Walter's (1971) two-layer soil water-partitioning model. Our understanding has advanced significantly since then, moving from the largely conceptual paradigms to an invariably more complex body of data and theory. Reynolds et al. (2004) critically review both paradigms, concluding that the accurate description of soil moisture dynamics is pivotal for addressing the dynamics of primary production and soil water partitioning.

While Walter (1971) envisioned water partitioning in vertical space to govern major patterns of plant functional type distribution, Ehleringer et al. (1991) and Lin et al. (1996) have provided strong evidence of this spatial partitioning. Evidence is mounting that partitioning over time may be at least as important (Reynolds et al. 2004; Schwinning et al. 2004a, b). However, the consequences of the hydraulic redistribution of water for species

S. Schwinning (✉)
School of Natural Resources, University of Arizona,
Biological Sciences East 325,
Tucson, AZ, 85721
e-mail: schwinn@Ag.arizona.edu

O. E. Sala
Facultad de Agronomía,
Av San Martín 4453,
Buenos Aires, 1417, Argentina

M. E. Loik
Department of Environmental Studies, University of California,
1156 High Street,
Santa Cruz, CA, 95064, USA

J. R. Ehleringer
Department of Biology, University of Utah,
257 South 1400 East,
Salt Lake City, UT, 84112-0840, USA

interactions and distributions have yet to be examined. Ryel et al. (2004) use a simulation model to illustrate that redistribution of shallow soil water to deeper layers may be an important component of the drought tolerance of deep-rooted plants, and may also remove water from the reach of more shallow-rooted competitors. Chesson et al. (2004) comprehensively review how pulsed resource supply can provide opportunities for coexistence.

The concept of response thresholds could be added to the library of major paradigms in the ecology of arid/semi-arid systems (Beatley 1974). Though contemporaneous with Noy-Meir's (1974) and Walter's (1971) conceptual contributions, the threshold idea has only recently gained momentum, as seen in several contributions in this special issue. Both Noy-Meir (1974) and Beatley (1974) recognized the importance of precipitation thresholds for triggering germination events, leading to the expectation that recruitment in long-lived perennial plants should be governed by rare but large recruitment episodes. Wiegand et al. (2004) revisited this paradigm and found through an analysis of *Acacia* population dynamics in the Negev Desert that both large, rare recruitment events and simultaneous low, continuous recruitment can be important for population maintenance. Not all organisms respond equally to pulse events. Huxman et al. (2004a, b) evaluate the consequences of variations in pulse size and frequency on the photosynthesis and respiratory activities of different biological components of an ecosystem and how these shape ecosystem-scale responses.

Building upon the threshold concept, Ogle and Reynolds (2004) suggest that plant functional types may be distinguished by their phenological threshold responses to soil moisture and the lag times between pulse and response. Schwinning and Sala (2004) provide an evolutionary explanation for why thresholds and lag times may differ between species or geographical regions. An experiment by Cable and Huxman (2004) demonstrates that other ecosystem processes may also be governed by variable thresholds. They show that small rainfall events facilitate the respiration of biological crust-carbon, while large events promote the respiration primarily of root and microbial-carbon. Schwinning and Sala (2004) generalize the threshold paradigm to a wide range of ecosystem processes, in an attempt to organize the complex relationships between ecosystem process and precipitation across scales of biological organization and time.

A potentially important consequence of variable thresholds and tolerances for soil moisture regimes is a decoupling of the mechanisms of nutrient gain and losses (Austin et al. 2004; Schwinning and Sala 2004). For example, mineral and organic substrates tend to accumulate during dry periods, when there is little nutrient demand, leading to an excess of mineralization and denitrification during the early phases of the wet cycle. Thus, frequent wet-dry cycles may accentuate the loss of carbon and nitrogen from soil pools.

Since ecosystems have the capacity to store water, carbon, and nitrogen in various pools, and the sizes of some of these pools also influence system responses to new precipitation inputs, ecosystems clearly have a "memory" of past precipitation events. The memory for precipitation history can last at least several decades, for example, through the amount and composition of soil organic matter (Austin et al. 2004) or plant functional type composition (Reynolds et al. 2004). However, memory for recent rainfall events is the basis for ecosystem sensitivity to intra-seasonal precipitation patterns. For example, the length of a dry period before a rain event determines the size of a denitrification pulse (Austin et al. 2004), as well as the physiological and morphological readiness of higher plants for water use (Ogle and Reynolds 2004; Reynolds et al. 2004). Because of such memory effects, we cannot expect to understand the effects of precipitation either at the level of single rainfall events, or at the level of seasonal or annual precipitation totals. Sher et al. (2004) present data suggesting that within-season precipitation patterns are at least as important as precipitation totals in determining seedling growth and survivorship, and Lundholm and Larson (2004) illustrate that precipitation patterns can influence patterns of species diversity through effects on germination and seedling establishment.

There is mounting evidence that the seasonal timing of rain can fundamentally alter its role in ecosystem function. For example, Snyder et al. (2004) show that many woody plant species use only cold season rain for growth, but not summer rain. In North America, such species are predominantly found outside or peripheral to the North American Monsoon System's zone of influence. Constraints on summer water use also apply to biological soil crusts, which are more likely to lose rather than gain carbon during summer rainfall events (Belnap et al. 2004). Simulation results indicate that winter precipitation is a primary driver of plant productivity across North American warm deserts, despite substantial differences in seasonal rainfall distribution (Reynolds et al. 2004).

Soil texture modifies ecosystem responses to precipitation through controlling infiltration depths, water holding capacities and hydraulic conductivity for water. Noy-Meir (1974) postulated that sandy soils should support higher productivity than finer soils in low rainfall regimes and vice versa (the "inverse texture hypothesis"). Austin et al. (2004) add that finer textured soils should also have a higher mineralization rate across a wide range of precipitation regimes, but with soil texture effects maximal in the intermediate rainfall range. Huxman et al.'s (2004a) irrigation experiment demonstrates that ecosystem carbon dioxide exchange after rainfall is controlled by complex interactions between soil texture and the identity of two perennial grass species. The effects of geomorphology on species distributions is self-evident over much of the western American landscapes (McAuliffe 2003). Investigating the interactions of precipitation with soil surface and texture characteristics is an obvious way to progress in producing better mechanistic models for species distributions and biogeochemistry.

Why are questions about the effects of rainfall variability on ecosystem function raised now? Many studies are motivated by trying to infer the consequences of changing precipitation patterns in ecosystems where limited water availability governs most ecosystem processes. At least one-third of the earth's land area is occupied by water-limited ecosystems; human-induced desertification processes contribute to an expansion of this area and are likely to do so for the foreseeable future. As climate change research progresses in elucidating the drivers of El Niño and the Southern Oscillation and other climate "anomalies", we are also learning how global changes may affect climatic impacts on communities and ecosystems (Loik et al. 2004). Though the predictions of climate models still have large uncertainties, one result appears clear: future climate may be characterized by greater extremes and perhaps more erratic fluctuations, with potentially strong effects on inter-annual to intra-seasonal rainfall variability. The series of papers in this issue provide a good cross-section of the conceptual and experimental approaches which are underway to examine the implications of such changes for arid and semi-arid lands.

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