Available online at www.sciencedirect.com
ScienceDirect
Current Opinion in Environmental Sustainability

Emerging frameworks for understanding and mitigating woody plant encroachment in grassy biomes

Bradford P Wilcox[1], Andrew Birt[2], Samuel D Fuhlendorf[3] and Steven R Archer[4]

Grasslands and open savannas are transitioning to shrub-dominated or tree-dominated landscapes. This phenomenon, often referred to as *woody plant encroachment*, is occurring globally. The outcomes of interactions among the various drivers of this change differ biogeographically; in semi-arid and subhumid regions they are often related to grazing-induced changes in fire regimes. Two important theoretical and conceptual frameworks are emerging that help us understand the underlying mechanisms of these transformations and inform approaches for maintaining and restoring grasslands and open savannas: *alternative stable state theory* (ASST) and *pyric herbivory*. Alternative stable state theory is a way of explaining, understanding, and predicting ecosystem state transitions in dual-life-form systems, and pyric herbivory is built on the notion that reciprocal, spatially distributed interactions between grazing and fire are a key to maintaining grassland and open savanna landscapes. Considered in tandem, ASST provides insights into rates and dynamics of grass–woody vegetation transitions, with pyric herbivory providing a conceptual basis for designing sustainable, site-specific management strategies. Future progress will hinge on experimental evaluations of these linked frameworks and their subsequent refinement over longer time frames in an adaptive management context.

Addresses
[1] Department of Ecosystem Science and Management, Texas A&M University, College Station, TX, USA
[2] Texas Transportation Institute, Texas A&M University, College Station, TX, USA
[3] Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK, USA
[4] School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, USA

Corresponding author: Wilcox, Bradford P (bwilcox@tamu.edu)

Current Opinion in Environmental Sustainability 2018, **32**:46–52

This review comes from a themed issue on **Environmental change issues**

Edited by **Arun Agrawal**, **Chuan Liao**, **Cristy Watkins**, **Laura Vang Rasmussen** and **Reem Hajjar**

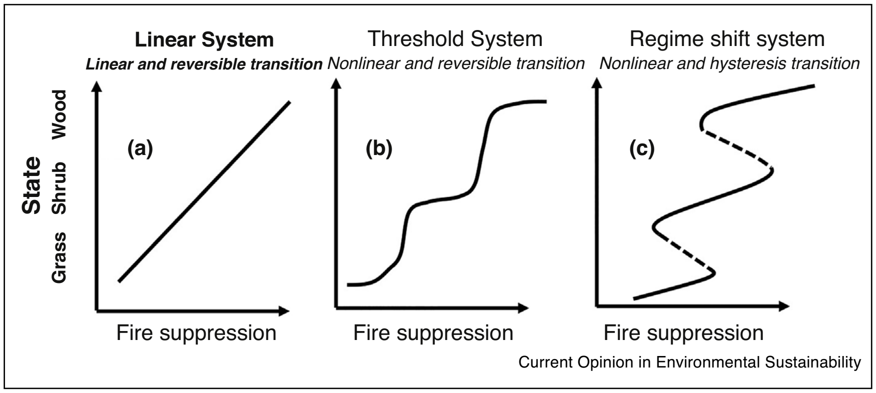
Received: 20-11-2017; Accepted: 12-4-2018

https://doi.org/10.1016/j.cosust.2018.04.005

Grasslands and savannas (ecosystems with woody plants scattered throughout a grassy matrix) are widespread in tropical, subtropical, and temperate regions. They cover some 20% of the global land surface, account for 30% of terrestrial net primary production, and make up by far the greatest proportion of burned areas worldwide [1]. These landscapes often function 'on the edge,' wherein moderate changes in climate/disturbance interactions may propel them to new functional configurations [2,3,4•,5•]. Definitions of savanna vary, depending on the floristics of the dominant graminoids and the stature, cover, and pattern of woody vegetation. However, adoption of static definitions based on these structural properties belies the highly dynamic nature of grass–woody ratios. While the upper limit of woody plant cover at regional and continental scales is set by mean annual precipitation [6,7], the realization of that potential is broadly constrained by geomorphology, soils, and disturbance [8••]. Herbivory and the frequency and intensity of fire are particularly important in shaping the functional character of savannas [9,10••,11–13]. Fire is especially important in bioclimatic regions where climate and soils are capable of supporting woodlands or forests [14••,15]. Herbivory, similarly, has a profound influence on the character of savannas and — depending on its form and intensity — may favor (via preferential utilization of grasses) or suppress (via browsing) tree growth and proliferation [16–19]. Grassland and savanna ecosystems and the plants and animals endemic to them are arguably endangered, owing to land-use practices fostering the proliferation of undesirable woody plants along with cropping and exurban development [20].

Woody plant encroachment (WPE) — the dramatic increases in woody plant cover and density observed in many regions of the world over the past 100 years — is affecting primary production, hydrology, nutrient cycling, and biodiversity at local to continental scales [8••,21,22] and has socioeconomic implications for pastoral societies and commercial ranching enterprises that depend on livestock production [23]. These herbaceous-to-woody transformations will likely continue under future climate regimes [24–27]. Although considerable research has been directed toward WPE, the drivers (including direct, indirect, and interacting effects associated with changes in climate, fire and grazing regimes, atmospheric CO_2 enrichment, N-deposition) and mechanisms associated with this global ecological phenomenon remain the topic of active debate [8••,28]. Land managers are being

Figure 1



Potential responses of savanna landscapes to changes in fire regimes in the North American Central Great Plains. Solid lines indicate stable equilibria; the dotted lines in **(c)** delineate unstable equilibria, at the border between basins of attraction for alternative stable states. Redrawn from Ratajczak *et al.* [36].

challenged to develop robust conservation plans for savanna ecosystems and to effectively restore and maintain sites that have undergone WPE. To date, however, such plans have proven to be incomplete and only marginally effective [20]. Because WPE has occurred across a wide range of ecoregions and climates (from tropical to arctic and arid to humid), the strength and relative importance of drivers and the nature of their interactions likely varies among bioclimatic zones. For example, in arid regions grazing may primarily affect plant stress and erosional processes (reducing ground cover and increasing wind/water erosion), whereas in more humid regions it may primarily affect fire regimes and competitive interactions among plants [8••]. Here, we draw from studies in semiarid to humid systems to explore two interrelated frameworks for understanding and mitigating WPE in grasslands and savannas.

These two emerging theoretical frameworks are proving valuable for understanding vegetation dynamics on grasslands and savannas in semiarid to humid bioclimactic zones. *Alternative stable state theory* (ASST) is a way of explaining and understanding major shifts in vegetation; *pyric herbivory* recognizes that intrinsic and reciprocal interactions between grazing and fire are critical for maintaining grass-dominated, open savanna landscapes. Both should be elements of sustainable conservation plans to bring about broad-scale maintenance and restoration of mixed grass–woody plant systems. Pyric herbivory reestablishes the notion of fire and grazing as endogenous processes — creating anew the fine-fuel/fire feedback that is critical for maintaining grasslands and open savannas. These two theories are linked in that fire-driven alternative states require stabilizing feedbacks, one of which is pyric herbivory (a critical one — disruptions of fire–herbivory interactions can cause rapid shifts between ecosystem states) [29].

Alternative stable state theory

Alternative stable state theory [14••,30] is based on resilience and adaptive cycles. It has been used in both managed and wildland systems to explain differences in rates of and susceptibility to change in ecosystem structure and function [31••]. The ASST framework has proven effective for explaining why savanna landscapes can abruptly change in response to exogenous perturbations *outside their historical range* [14••,32,33] and is increasingly employed to understand transitions in savanna landscapes on regional as well as global scales [5•,11,34].

Key concepts of the ASST framework are first, that alternative states governed by strong stabilizing feedbacks may exist under the same exogenous environmental conditions; second, that abrupt state shifts can occur if these stabilizing feedbacks are weakened [11]; and third, that a change in state represents a catastrophic shift or critical transition, such that reversing the environmental conditions to pre-transition levels will not result in restoration of the previous state because of hysteresis [30,35]. For example, Ratajczak *et al.* [33,36•] concluded, on the basis of almost 30 years of data, that the transition from grasslands to shrublands in the North American Central Great Plains represents a transition between alternative attractors that is nonlinear and prone to hysteresis (Figure 1c), rather than a linear and reversible process (Figure 1a) or a nonlinear and reversible threshold process (Figure 1b). In these and other grassland and savanna systems, fire behavior (frequency and intensity) and/or fire suppression represent negative or positive feedbacks associated with the maintenance of a grassland state. Fire suppression is a positive feedback that, by removing a key constraint, enables the establishment of woody plants and the transition from grassland to woodland. Frequent fires, on the other hand, are negative