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Chapter 2

Woody Plant Encroachment: Causes and Consequences

Steven R. Archer, Erik M. Andersen, Katharine I. Predick, Susanne Schwinning, Robert J. Steidl, and Steven R. Woods

Abstract Woody vegetation in grasslands and savannas has increased worldwide over the past 100–200 years. This phenomenon of "woody plant encroachment" (WPE) has been documented to occur at different times but at comparable rates in rangelands of the Americas, Australia, and southern Africa. The objectives of this chapter are to review (1) the process of WPE and its causes, (2) consequences for ecosystem function and the provision of services, and (3) the effectiveness of management interventions aimed at reducing woody cover. Explanations for WPE require consideration of multiple interacting drivers and constraints and their variation through time at a given site. Mean annual precipitation sets an upper limit to woody plant cover, but local patterns of disturbance (fire, browsing) and soil properties (texture, depth) prevent the realization of this potential. In the absence of these constraints, seasonality, interannual variation, and intensity of precipitation events determine the rate and extent of woody plant expansion. Although probably not a triggering factor, rising atmospheric CO_2 levels may have favored C_3 woody plant growth. WPE coincided with the global intensification of livestock grazing that by reducing fine fuels, hence fire frequency and intensity, facilitated WPE. From a conservation perspective, WPE threatens the maintenance of grassland and savanna

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ecosystems and its endemic biodiversity. Traditional management goals aimed at restoring forage and livestock production after WPE have broadened to support a more diverse portfolio of ecosystem services. Accordingly, we focus on how WPE and management actions aimed at reducing woody plant cover influence carbon sequestration, water yield, and biodiversity, and discuss the trade-offs involved when balancing competing management objectives.

Keywords Brush management • Mortality • Recruitment • Roots • Seedling establishment • Soil depth/texture

2.1 Introduction

The relative abundance or dominance of grasses and woody vegetation is highly dynamic at timescales ranging from decades to centuries to millennia (Fig. 2.1). Over the past 100 years or so, there has been a directional shift toward increased abundance of woody vegetation worldwide (Sala and Maestre 2014). The phenomenon of woody plant encroachment (WPE) in grasslands and savannas contrasts with deforestation and dieback occurring in many forested systems. The proliferating trees and shrubs can be non-native species that were introduced purposely or accidentally or native species that have either increased in abundance within their historic ranges or expanded their geographic range. Woody plants have been displacing grasses across bioclimatic zones. Trees proliferate in humid regions while unpalatable shrubs replace grasses in more arid regions, which is regarded as a type of desertification. In both cases, the proliferation of trees and shrubs threatens the maintenance of grassland and savanna ecosystems and the plants and animals that are endemic to these systems.

Proliferation of woody plants has long been of concern to range managers where grazing by cattle and sheep is the primary land use. Where funds and equipment were available, management was focused narrowly on reversing WPE with the goal of enhancing livestock production. Aggressively applied since the 1940s, “brush management” results have been mixed and their sustainability and cost-effectiveness questionable. As we gain a broader appreciation of how woody plants influence ecosystem processes and how changes in their abundance affect a broad portfolio ecosystem services, we are better positioned to evaluate trade-offs that must be considered as their abundance changes.

In this chapter we (1) review the rates, dynamics, causes, and consequences of woody plant proliferation over the past 100 years, (2) evaluate the extent to which interventions aimed at reducing woody vegetation have effectively restored lost or

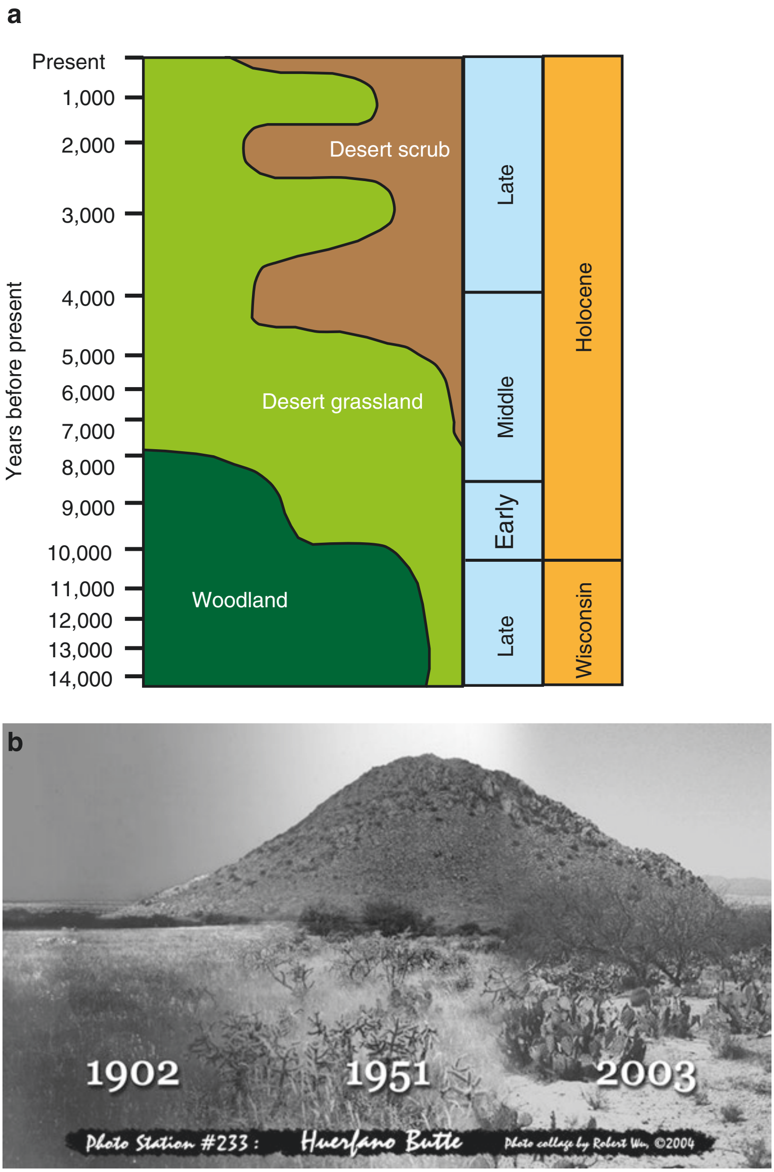

Fig. 2.1 (**a**) Holocene changes in woodland, desert scrub, and grassland in the southwestern USA (modified from Van Devender 1997) and (**b**) photographic record of increases in woody plant abundance at the Santa Rita Experimental Range, Arizona, USA, against the backdrop of Huerfano Butte (images are from public domain available from http://cals.arizona.edu/srer/photos.html; compiled by R. Wu)

altered key ecosystem services, and (3) assess trade-offs influencing ecological and socioeconomic decisions and priorities for managing woody plants in rangelands.

2.2 Rates of Change

Substantial increases in cover of woody plants can occur over decades. In North America, rates of encroachment vary by an order of magnitude among ecoregions (0.1–2.3 % cover year^{-1}, Barger et al. 2011) (Fig. 2.2). Their review indicated that rates of tree proliferation typically exceeded those of shrub proliferation, ostensibly reflecting the higher precipitation in areas where tree encroachment occurs. We might expect that differences in encroachment rates would differ among woody functional types, but the Barger et al. (2011) review found that rates were highest and comparable among scale-leaved evergreen (*Juniperus virginiana*) and N_2-fixing deciduous (*Prosopis glandulosa*) arborescents. Reported rates of change in woody cover across savannas and forest-savanna boundaries in Africa, Australia, and South America are comparable to those observed in North America (range = 0.1–1.1 % cover year^{-1}, Stevens et al. 2016), though maximum rates reported in their synthesis were much lower than those reported by Barger et al. (2011) for North America (1.1 vs. 2.3 % cover year^{-1}).

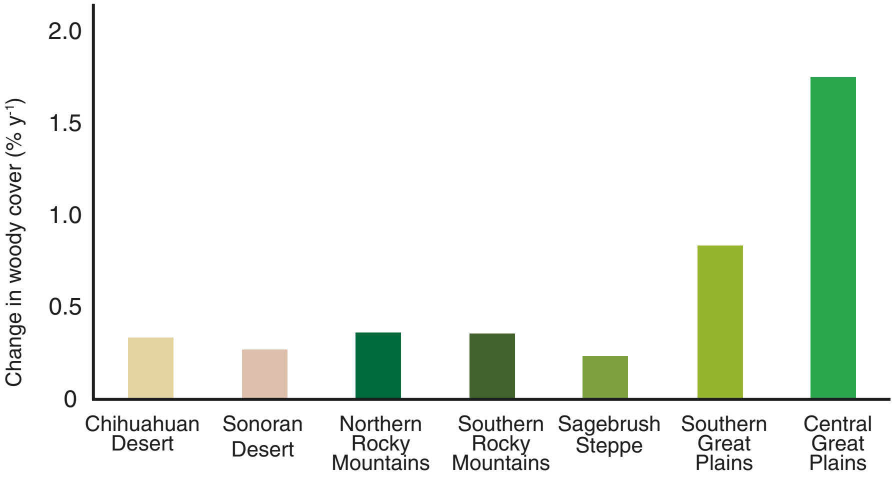

Fig. 2.2 Rates of woody encroachment in North American rangelands (modified from Barger et al. 2011)

Typically, research has targeted localities where encroachment is known to have occurred or is occurring. Estimates of encroachment rates, therefore, are likely biased. Furthermore, rates of encroachment tend to decline as woody proliferation progresses (Text Box 2.1). Variation in the rate and extent of encroachment is also mediated by local or regional differences in environmental factors, disturbance regimes, and land use as discussed in the following sections.

Text Box 2.1: Rates and Drivers of Woody Plant Encroachment

Absolute encroachment rates[1] range from nil to 3.3 % cover year^{-1} and average 0.85 % cover year^{-1}. Generally, rates of encroachment are highest in the early stages of encroachment, and then decline (e.g., Fensham et al. 2005) or fluctuate (Browning et al. 2008) as maximum cover thresholds are approached. Accordingly, studies based on long-term observations tend to report low rates of encroachment. Barger et al. (2011) found that rates of woody plant encroachment in North America were highest in Great Plains grasslands (1–2 % cover year^{-1}) and lowest in hot and cold deserts (<0.5 % cover year^{-1}). Trees and shrubs exhibited similar mean encroachment rates (0.62 and 0.52 %cover year^{-1}, respectively). Rates of increase for Great Plains species representing contrasting plant functional types (e.g., evergreen vs. deciduous; N_2 fixation potential) and dispersal mechanisms were comparable as well.

(continued)

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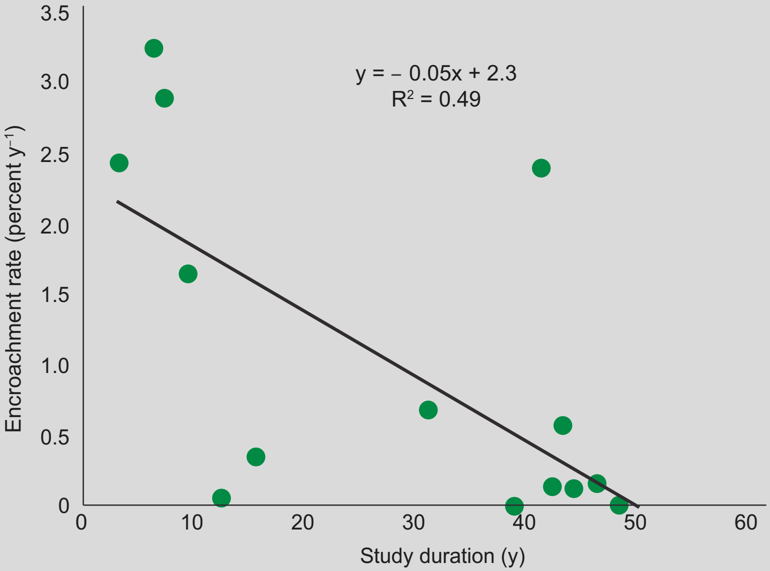
[1] A database of peer-reviewed research papers was compiled by searching for the terms "bush encroach*," "brush encroach*," "desertification," "shrub grazing," "shrub encroach," "shrub invasion," "shrub expansion," "woody encroach*," and "woody plant invasion" on the ISI Web of Knowledge. This search produced 865 unique references that were then subdivided into papers that quantified encroachment rates ($n = 289$) or relationships between shrub encroachment and grazing ($n = 149$).

Text Box 2.1: (continued)



Among papers reporting relationships between shrub encroachment and grazing, mean (±SE) shrub cover was statistically comparable on grazed sites (21 % ± 0.9) and sites protected from grazing (24 % ± 0.9). Overall, the presence or absence of grazing did not predict changes in shrub cover over time. Variation within many of these studies was high, indicating that the role of grazing is complex, even at the ranch level. Weighted regression analysis further indicated that precipitation, continent (North and South America, Australia, Africa), and grain size (i.e., plot/pixel size) were not significant predictors of grazing importance. Interestingly, there was a significant relationship between the data source (field sampling vs. remote sensing) and grazing importance. Assessments based on broad-scale remote sensing (aerial photos, satellite imagery) were more likely to conclude that grazing promotes shrub encroachment, whereas field-based studies were more likely to conclude that grazing has no effect on shrub encroachment. This may reflect the fact that studies of shrub encroachment and grazing based on field data focus on, and are restricted to, the outcomes of short-term grass-woody plant interactions at plant and patch scales, whereas remote sensing assessments reveal the longer term, landscape-scale outcomes of patch-scale dynamics (e.g., Milne et al. 1996). Photo credit: E. Andersen

2.3 Factors Influencing Abundance of Woody Plants

Given the global scale of the WPE phenomenon, deriving robust generalizations about the causes of woody encroachment has been challenging, as species adaptations, land-use history, and climate trends differ markedly among bioclimatic zones. Numerous factors (including climate, fire, and grazing/browsing regimes, concentrations of atmospheric CO_2, and levels of N deposition) co-occur and interact to promote or constrain increases in woody dynamics at local scales, with their relative importance and interaction strength differing markedly among locations (Archer 1994; Bond and Midgley 2000; D'Odorico et al. 2012). In any location, it may be difficult to distinguish between "necessary" and "sufficient" conditions. For example, it may be necessary for a given biotic or abiotic environmental condition to change for woody plants to gain an advantage over grasses (e.g., higher atmospheric CO_2 concentrations), but a change in that condition may not by itself be sufficient to trigger woody plant proliferation unless accompanied by other changes (e.g., reductions in fire and browser populations). Accordingly, assigning primacy to the potential drivers of woody plant encroachment remains a topic of active debate and research.

Because woody plant encroachment has occurred across a wide range of climates from tropical to arctic and arid to humid, drivers likely vary among climate zones. Grazing effects on fire regimes and competitive interactions among plants may predominate in humid regions, whereas grazing effects on levels of plant stress and erosional processes (reducing ground cover and increasing wind/water erosion) may predominate in more arid regions. Disturbance is superimposed against a backdrop of climate and soils to further modify the local abundance of shrubs or trees. Where climate and soils are capable of supporting an abundance of woody vegetation, the occurrence of periodic fire or an abundance of browsers utilizing woody vegetation can prevent them from attaining dominance. Conversely, preferential utilization of herbaceous vegetation by grazers may create opportunities for woody plants to establish (via reductions in competition) and persist (via reductions in fine fuel mass and continuity needed to carry fires). Woody plant cover at a given locale within a bioclimatic region is the net outcome of these interrelated and potentially interacting factors (Fig. 2.3). In the following sections, we review briefly some of the key drivers and their mediation by geomorphology, soils, and topography. Ultimately, the challenge for land managers will be to apply these perspectives appropriately and creatively to their local settings and situations.

2.3.1 Herbivory: Grazers and Browsers

Livestock grazing is a primary use of grasslands worldwide (Asner et al. 2004) and is often associated with WPE. The arrival of livestock with Anglo-European settlers in the Americas, Australia, and Southern Africa, although occurring at different times, coincided with dramatic and swift changes in woody abundance in grasslands

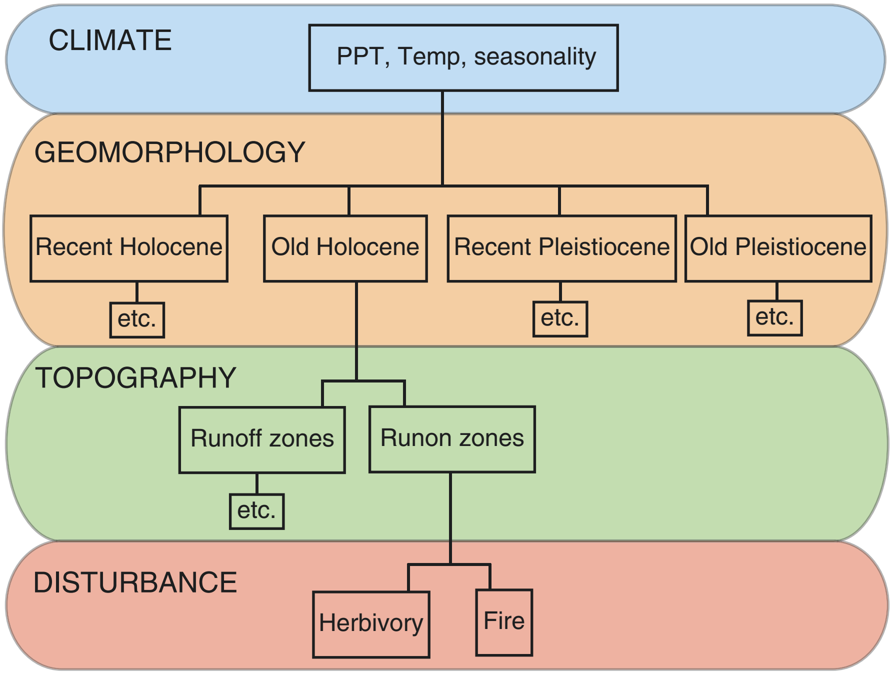


Fig. 2.3 The abundance of woody and herbaceous vegetation is determined by interactions across a hierarchy of drivers and constraints operating across a range of spatial and temporal scales. Changes in climate and atmospheric chemistry (e.g., increased CO_2 concentrations) determine grass-woody plant abundance at broad scales and over long time periods. Vegetation composition at local scales is mediated, and in some cases constrained, by geomorphology, soils, and topography via their effects on water and nutrient distribution. Soils and topography, in turn, mediate vegetation responses to disturbances associated with drought, fire, grazing or browsing pressure, and land use

and savannas (Archer 1994). Grazing by livestock removes fine fuels, which reduces fire frequency and intensity and also enhances woody plant recruitment (Madany and West 1983). The advantages for woody plants may be magnified where livestock are effective dispersers of their seeds. In addition, livestock introductions can be associated with displacement of native browsers and seed predators, releasing woody plants from top-down controls.

Reported effects of livestock on rates of woody plant encroachment have been variable due to differences in the inherent characteristics of study sites or the intensity, duration, or timing of grazing. Grazing has been associated with both substantial increases (Roques et al. 2001; Valone et al. 2002) and moderate or no increases in the cover of woody plants (Allen et al. 1995; Fensham et al. 2005). Further, grazing may even limit or retard shrub encroachment in some systems (Altesor et al. 2006; Batista et al. 2014). It is unclear to what extent these contrasting patterns might reflect differences in stocking rates and season(s) of use through time. Interpretation of grazing effects on shrub encroachment can vary with spatial and temporal scale. For example, conversion of grassland to shrub-dominated dune land in the Chihuahuan Desert occurred within large areas free of livestock, suggesting that factors other than livestock grazing were driving the change. However, closer inspection revealed that historically heavy livestock grazing had reduced ground cover and accelerated wind erosion in upwind areas. Aeolian deposition accelerated grass mortality via burial and promoted shrub recruitment to drive the conversion from grassland to shrubland in the downwind area excluded from livestock grazing (Peters et al. 2006). This example shows that grazing effects must be evaluated considering spatial context as well as land-use history.

Drivers of change must also be considered in the context of time. At a site in the Sonoran Desert, woody cover increased both within 74-year-old livestock exclosures *and* in the surrounding grazed landscapes, suggesting that factors other than grazing were responsible. However, heavy grazing in the late 1800s and early 1900s may have altered ecological processes in ways that predisposed the site to shrub encroachment prior to the time exclosures were established in 1932 (Browning and Archer 2011). In addition, cessation or relaxation of grazing subsequent to degradation may have promoted WPE by enabling a degree of grass recovery that then facilitated shrub recruitment (e.g., de Dios et al. 2014).

Preferential utilization of woody plants by wild browsers (e.g., Staver et al. 2009) or seed and seedling predators (Weltzin et al. 1997; Dulamsuren et al. 2008) may help maintain grassland and savanna communities. Activities of these herbivores can prevent shrubs and trees from establishing, prevent them from exerting dominance, and maintain them at a stature vulnerable to fire. Types and abundances of wildland herbivores can vary spatially and temporally and this can lead to highly variable effects on WPE. Understanding mechanisms that contribute to WPE can be especially difficult in areas where livestock grazing occurs in conjunction with native herbivores whose activities are also influencing plant composition and abundance (e.g., Heske et al. 1993). In some cases, native herbivores may be displaced by livestock or removed by managers if viewed as competing with livestock for forage (Weltzin et al. 1997). In those cases, the livestock grazing effects described earlier would be amplified by removal of native browsers. Maintaining populations of native herbivores in systems managed for livestock grazing may help maintain grass-woody populations in desired configurations while concurrently enhancing biodiversity and creating opportunities for lease hunting, game farming, and ecotourism revenue.

2.3.2 Climate

Grasslands of the world are situated between desert shrublands and woodlands/forests with respect to annual rainfall, annual temperature, and potential evapotranspiration. In the future, if climate becomes warmer and drier or if the frequency, magnitude, and duration of drought increase, present-day grasslands in some areas may become desert shrubland. In contrast, woodlands and forests could also shift to savanna or grassland (e.g., Allen et al. 2010; Anadón et al. 2014a) and increases in woody cover realized in recent decades may be reduced by a higher frequency of "hot droughts" (Bowers 2005; Breshears et al. 2005; Twidwell et al. 2014). Climate-change simulations under elevated atmospheric CO_2 predict pronounced shifts toward tree-dominated biomes (Scheiter and Higgins 2009). Changes in dry-season duration or precipitation seasonality will also influence the balance between grass and woody vegetation (Neilson et al. 1992; Bailey 2014).

Mean annual precipitation (MAP) determines the potential "carrying capacity" for woody plants and upper limit for woody plant cover (Sankaran et al. 2005). As MAP increases, the potential for landscapes to support woody cover increases linearly, becoming asymptotic at ca. 650 mm (Fig. 2.4). Shrub or tree savanna or open woodland communities may therefore characterize regions where MAP is below this threshold, whereas the tendency to develop woodland or forest communities to the general exclusion of grasses occurs above this threshold. Managers contemplating actions to regulate woody plant cover should first determine their sites' MAP in relation to this potential. Expensive interventions may not be warranted in areas where maximum cover potentials are relatively low.

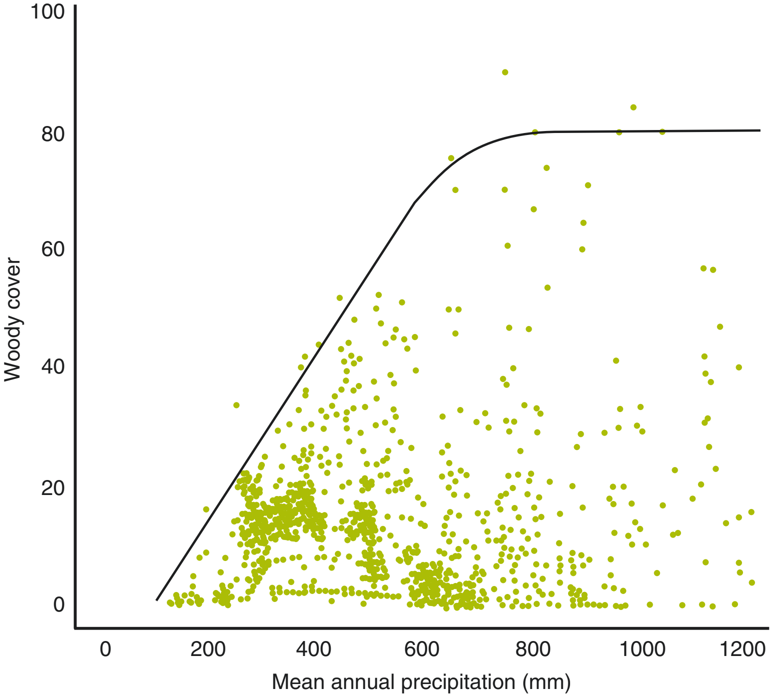


Fig. 2.4 Relationship between mean annual precipitation (MAP) and maximum woody plant cover in Africa. Maximum potential woody cover increases linearly with increases in MAP to ~650 mm, and then levels off at ~80 %. Note that many sites are well below their potential, ostensibly owing to constraints imposed by geomorphology, soils, topography, disturbance, and land use. Modified from Sankaran et al. (2005)

Depth of rainfall infiltration and seasonal timing of rainfall can interact with MAP to locally constrain the extent to which maximum potential woody cover might be realized at a given location. Rainfall that percolates deep into the soil is typically more assessable to deeper rooted woody plants than to shallow-rooted grasses. Accordingly, frequent low-intensity events (Good and Caylor 2011), large rainfall events (Kulmatiski and Beard 2013), and precipitation delivered during the period of grass dormancy (Walter 1979; Bond et al. 1994; Gao and Reynolds 2003) are more likely to recharge soil moisture at depths benefitting woody plants. Grasslands would therefore be favored in climates characterized by summer rainfall and small rainfall events that moisten only upper horizons (Neilson et al. 1992). At local scales, however, rainfall is redistributed by topography and the extent to which it infiltrates and percolates is influenced strongly by soil texture and depth (Sect. 2.3.3).

Precipitation variability influences grass-woody dynamics via its effects on plant recruitment, growth, and mortality. Interannual and spatial variability in rainfall is high in the semiarid zone. Given the potential longevity of woody plants, exceptionally good recruitment years can set the stage for seed production and opportunities for recruitment decades into the future, whereas only exceptionally strong drought years can significantly reduce mature tree cover (Fensham and Holman 1999; Twidwell et al. 2014). Models incorporating these dynamics predict that decadal or longer deviations from mean tree density may result (Fig. 2.5). Few empirical data have been available to verify this nonstationary concept of savanna dynamics, due to the paucity of long-term data. However, where data are available, they support the notion that history matters and that the current state of the system does not necessarily reflect recent events or current ecological processes (Staver et al. 2011). These long stochastic return times make it difficult in practice to distinguish natural fluctuation from a regime shift, or a temporary upturn in woody plant abundance from directional, persistent woody encroachment.

The globally widespread proliferation of woody plants in arid and semiarid grasslands suggests the importance of broad-scale factors, such as climate change and increases in atmospheric CO_2, as do recent increases in shrub abundance in high-latitude systems where climate change effects on ecosystem processes have been pronounced (Myers-Smith et al. 2011). The grasslands encountered by the Anglo-European settlers of southwestern North America in the mid-1800s may have established and flourished under the conditions of the Little Ice Age. These grasslands were only marginally supported under the climate of the 1800s–early 1900s and were in the process of transitioning to desert scrub with the advent of warmer, drier conditions, with changes in vegetation lagging well behind the changes in climate driving them (Neilson 1986) (Fig. 2.1a). Broad-scale factors such as climate, however, cannot account for “fence-line contrasts” and local variation in rates and patterns of woody plant increases. These local dynamics ostensibly reflect changes in land use and spatial variation of disturbance regimes, such as livestock grazing and the abundance of browsers. In these cases, climate may not be the driver *per se*, but it will influence the rates and dynamics of woody cover change and may increase the susceptibility of the herbaceous vegetation to other agents of change.

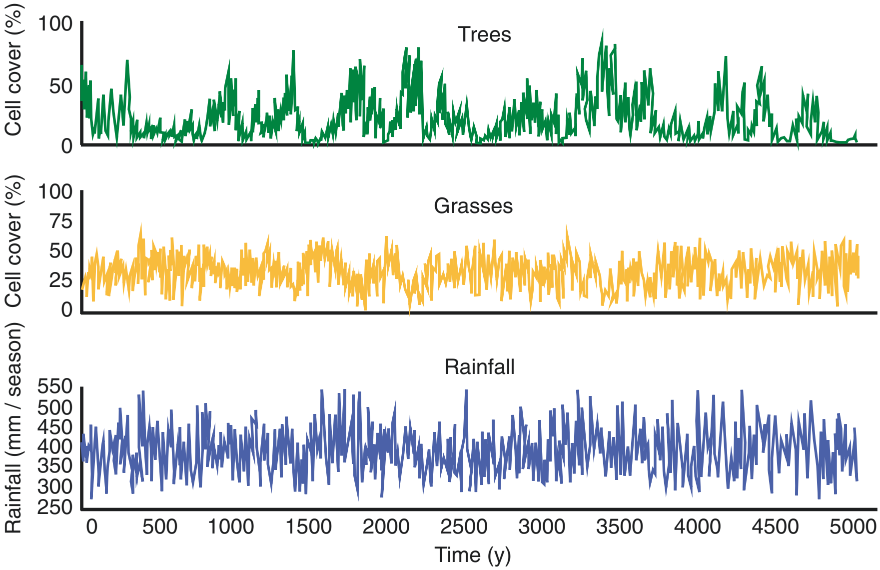


Fig. 2.5 Modeled fluctuations in grass and woody plant cover at decadal and longer time scales, assuming stationary stochastic rainfall distribution, in a savanna in Texas, USA (from van Wijk and Rodriguez-Iturbe 2002)

2.3.3 *Topography and Soils*

At the catena (hillslope) scale, edaphic properties—primarily soil depth and texture—mediate broad-scale climate and atmospheric chemistry effects. These effects, in turn, are mediated by topographic setting, which dictates radiant energy regimes (e.g., slope aspect effects), cold air drainage, and patterns of rainfall redistribution via runoff and runon (McAuliffe 2003). Grasses and woody plants possess different adaptations to exploit soil resources. Root mass decreases exponentially with depth in both life forms, but woody plants typically have a greater root mass at deeper depths and greater maximum rooting depths (Canadell et al. 1996; Jackson et al. 1996). Grasses, by contrast, have a dense, fibrous root system of limited depth, well suited to exploit soil resources in the upper 20–30 cm of the soil profile, where water and nutrients reach peak concentrations. Hence, grasses are generally favored by fine-textured surface soils and shallow soils that retain water and nutrients near the surface.

Woody plants are favored by deep, coarse soils that facilitate percolation and nutrient leaching. They are at a disadvantage on shallow soils where bedrock or claypan horizons restrict taproot extension. Many woody species have both a shallow, laterally extensive root system and deep taproots (Schenk and Jackson 2002). This reflects a generalist strategy for soil resource capture that allows them to use small rainfall events and the nutrients concentrated in the upper soil layers (Fravolini et al. 2005), but to also access water and nutrients (e.g., NO_3^-) percolated below the depths effectively exploited by grasses. Woody plants with this dimorphic root system can therefore exploit a wide range of growing season conditions (Scott et al. 2006; Priyadarshini et al. 2015).

The contrasting grass and woody plant rooting patterns are the basis for the "two-layer hypothesis," which characterizes the differential use of shallow and deeper soil resources by grasses and woody plants and grasses. The hypothesis appears to be widely applicable in a variety of dryland systems (Ward et al. 2013), but less so in mesic savannas with a shallow water table, where woody plants and grasses often have similar rooting depths and compete for moisture from the same soil horizons throughout the year (Rossatto et al. 2014). Interactions between topoedaphic properties and grass vs. woody plant rooting patterns help explain why some grassland sites are resistant to WPE and others are more susceptible (Knoop and Walker 1985). The two-layer hypothesis is a niche-based perspective, which helps explain how the amount of precipitation and its seasonality interact with soil properties (texture and depth) to influence the proportion of grasses and woody plants on a given site.

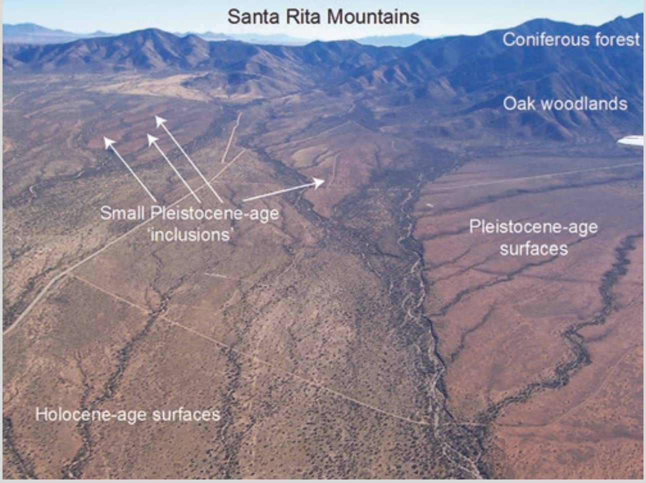
Grasses tend to dominate shallow soils, where lateritic or argillic horizons, bedrock, or limestone are near the surface; water and nutrient resources "perch" and concentrate above these impermeable layers (Molinar et al. 2002). However, if there are fissures or gaps in the impermeable layers that allow resources and woody plant roots to pass through, woody plants may thrive. Aboveground patterns in distribution, size, and mortality rates of woody plants that accompany drought may reflect variation in these edaphic heterogeneities (Bestelmeyer et al. 2011; Rossatto et al. 2014; Twidwell et al. 2014).

On playas and dry lake beds, where precipitation and runon accumulate in poorly drained, fine-textured topographic low points, conditions may become periodically anaerobic. These conditions tend to favor grasses to the exclusion of trees and shrubs regardless of grazing or fire regimes. Subtle, local variation in microtopography within such sites may, however, provide refuges for woody plants and influence local patterns of woody plant composition and abundance (e.g., Sklar and Valk 2003).

Distribution, size, and density of woody vegetation are also influenced by topography. In the Northern Hemisphere, south-facing slopes are warmer and drier than north-facing slopes and typically support less woody plant cover (Bailey 2014). Runoff from slopes concentrates water and nutrients in downslope areas and augments incoming precipitation, potentially enabling arroyos, washes, and intermittent drainages to support higher densities of larger-sized woody plants than upslope portions of the landscape (Coughenour and Ellis 1993). Runoff and runon relationships and their substantive influences on woody plant abundance are also evident on gently sloping landscapes (Tongway et al. 2001). Landscape-scale variation in rates and patterns of WPE in recent decades are therefore related to and constrained by topoedaphic variation (Wu and Archer 2005; Naito and Cairns 2011; Browning et al. 2012; Rossatto et al. 2014) (Text Box 2.2).

Text Box 2.2: Soils and Topography Influence Susceptibility to Woody Plant Encroachment

Woody plant encroachment on the Santa Rita Experimental Range in the North American Sonoran Desert dates back to the early 1900s and has been well documented (McClaran 2003). However, most of the shrub encroachment (primarily *Prosopis velutina*) has occurred on Holocene-age sandy soils. Within the Holocene-age portions of the landscape, shrub cover appears to have peaked at about 30–35 %, consistent with predictions of the model in Fig. 2.4, but sites on the landscape with a subsurface clay content of 17 % at 33 cm depth reached this cover asymptote about 30 years sooner than sites where the subsurface clay content was 25 % at 23 cm depth (Browning et al. 2008).



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Text Box 2.2 (continued)

Pleistocene-age surfaces, with their well-developed claypan horizons (39 % clay at 10 cm depth), have experienced similar climate and levels of atmospheric CO_2 enrichment and have experienced similar land-use (livestock grazing) and disturbance regimes (heavy grazing in the early to mid-1900s, and lack of fire) as the Holocene-age landscapes, and yet have persisted as C_4 grassland. Note that shrub abundance is also higher in runon areas (arroyos and intermittent drainages) in both geomorphic settings and that shrubs give way to trees as elevation increases.

In this bioclimatic zone, it appears that a clay content threshold for the occurrence and persistence of an "edaphic grassland" occurs somewhere between 25 % at 23 cm depth and 39 % at 10 cm depth. It remains to be seen whether the edaphic grasslands on the Santa Rita Experimental Range will persist under the predicted changes in climate. See McAuliffe (1997) for details on the geomorphology of this site. Photo credits: W. Cable, aerial image; J. Fehmi, ground-level photo.

2.3.4 Increased Atmospheric CO_2

Atmospheric CO_2 concentrations have increased over the time period that WPE has occurred, from ~290 ppm at the beginning of the twentieth century to ~380 at the end. In this range, photosynthesis in C_3 plants is CO_2 limited, so it is possible that rising atmospheric CO_2 has benefited C_3 woody plants more than C_4 grasses. The response of plants to elevated CO_2 has been reviewed extensively elsewhere, but as a rule of thumb, a doubling of atmospheric CO_2 from 350 to 700 ppm typically results in a 30–50 % increase in the carbon assimilation rate of C_3 plants under optimal conditions. In contrast, C_4 plants are not affected directly by atmospheric CO_2 because they concentrate CO_2 at the carboxylation sites to substrate saturation. Still, C_4 plants often receive a growth advantage through partial stomatal closure, which increases their water-use efficiency in water-limited environments. At the whole-plant level, elevated atmospheric CO_2 can elicit a wide range of growth responses depending on other co-limitations including other resource limitations (light, nitrogen, water), stress conditions (heat, frost), crowding, and species differences in growth and reproductive strategies (Körner 2006). As a result, a community may contain many species that show no response to elevated CO_2 at all. Projections of CO_2 enrichment effects should therefore be made cautiously and in the context of other drivers and constraints.

Woody encroachers are composed overwhelmingly of C_3 plants. By contrast, grasslands and savannas in tropical, subtropical, and warm-temperate biomes often are dominated by C_4 grasses. This pattern led to the hypothesis that woody encroachment might be a consequence of a CO_2-mediated correction in the competitive relationships between C_3 and C_4 plants (Idso 1992; Polley 1997). However, this cannot entirely explain WPE at the global scale, as woody plants also encroach into grasslands dominated by C_3 grasses. Woody plants have other structural and functional advantages over herbaceous vegetation, which increase their ecological opportunities under accelerated growth conditions (Poorter and Navas 2003). Whereas herbaceous plants lose most annual biomass accumulation to herbivory, combustion, or decomposition, woody plants build up woody biomass and carbohydrate storage over decades, thereby strengthening their ability to persist in the face of stress and disturbance. Woody plants are most vulnerable to injury, physiological stress, and competition when they are small, and faster growth would expedite their transition to more resilient and competitive life stages.

Global vegetation models have solidified support for the connection between atmospheric CO_2 and "woody thickening," both within woodlands and forests and through the expansion of woodlands into grasslands. Importantly, these models have set WPE into the context of a millennial-scale global transition that started during the last glacial maximum when atmospheric CO_2 was at a low point (Prentice et al. 2011). Examination of sediment records in the Chihuahuan Desert concluded that woody encroachment during the past 200 years is unprecedented in the context of the preceding 5500 years, that it was not related to droughts or changes in ENSO event frequency, and that it was contemporaneous with the rise in atmospheric CO_2 and known grazing impacts (Brunelle et al. 2014). However, it has been argued that WPE clearly outpaced the gradual increase in atmospheric CO_2 and the modestly elevated concentrations present in the early- to mid-1900s, by which time substantial encroachment had occurred (Archer et al. 1995). This suggests that while changes in atmospheric CO_2 might have been contributed to WPE in the early to mid-1900s, it was not a driver *per se*. Continuing increases in atmospheric CO_2, however, may increasingly favor woody plants. For example, dynamic global vegetation models suggest that with fire multiple stable biome states are possible across broad areas of Africa, but that the potential for multiple stable states will decline with further increases in atmospheric CO_2 as biomes will become deterministically tree dominated (Moncrieff et al. 2014).

Growth advantages realized by woody plants under high CO_2 conditions may enable them to minimize the time during which they are vulnerable to disturbance. For example, frequent fires are a major limitation to tree recruitment in subtropical savannas. These fires may kill saplings outright, necessitating recruitment from seed, or they may force saplings to regenerate from basal sprouts. In either case, the woody plants are kept in a fire-susceptible size class. In this scenario shrub or tree recruits are able to mature into tall savanna trees only during rare periods of infrequent fires when saplings can grow large to escape the flame zone. All else equal, an acceleration of sapling growth by CO_2 fertilization would increase the probability of escaping the flame zone and increase tree density (Bond and Midgley 2000).

2.4 Population Interactions Between Grasses and Woody Plants

In previous sections we focused on environmental drivers of woody plant encroachment. We now turn to mechanisms that govern the ecological interactions between grasses and trees or shrubs. There is a large body of ecological and range-management literature on the effects of woody plants on grasses (Scholes and Archer 1997; Blaser et al. 2013; Dohn et al. 2013). Here, we focus on factors that influence recruitment and abundance of woody plants into grass-dominated communities. Grass-woody plant interactions affecting the proliferation of woody plants are quite complex, involving multiple plant functional types with numerous contrasting traits and important differences in life history. Generally, population interactions are governed by nonlinear density effects (both intra- and interspecific) on species' vital rates and environment effects on those rates. In the context of WPE, three questions are especially relevant. First, how do populations of grasses resist invasion by woody plants and how do drivers of WPE lower resistance? This is the key question for explaining where and when WPE occurs. Second, beyond establishment, how do populations of grasses affect growth of woody plants and development from seedling to sapling to seed-producing mature tree? This question is relevant to explaining the rates of woody plant invasion, after having established a presence in grasslands. Third, what are the interactions that limit woody plant cover and establish an upper limit, or carrying in encroached ecosystems? In Sect. 2.4.4 we examine what, if anything, sets woody encroachers apart from the large number of woody species in a flora that have not proliferated in grasslands.

2.4.1 Establishment of Woody Plant Seedlings

The seedling and early establishment stage of the woody plant life cycle is typically the most vulnerable. Once past this stage, woody plants capable of vegetative regeneration (resprouting) may be highly persistent in the face of climatic events (drought, frost) or disturbances (browsing, fire) that top-kill them. Environment and neighbor interactions control population growth through effects on establishing seedlings, modifying their survivorship odds. This stage is therefore often described as a recruitment "bottleneck" constraining the proliferation of woody plants in grasslands (Bond 2008). The implication is that if individuals survive this stage, their odds of surviving to maturity are greatly improved.

Woody plant encroachment begins with deposition of seed within grassland communities. In instances where seed must be transported from distant seed sources, woody species dispersed by wind and birds would likely be the first colonizers. Species distributed by water are more likely to encroach from upstream or upslope to downstream or downslope locations than from lowland to upland locations. Some woody plants are dispersed readily by native ungulates and livestock. Examples include leguminous species whose hard seeds are encased in nutrient-rich pods (e.g., some acacia and mesquite species). The pods are eaten but the hard seeds may escape mastication, become scarified during passage through the digestive tract, and deposited in a moist, nutrient-rich media away from parent plants harboring seed predators. Furthermore, foraging ungulates would deposit seeds in areas where defoliated grasses have diminished capacity to suppress seedlings by fueling fire or preempting water and nutrients. Secondary dispersal agents, such as dung beetles, may disperse seeds further and bury them at depths conducive to germination and establishment. In North America for example, mesquite may have been “dispersal limited” during the Holocene, owing to extinctions of Pleistocene megafauna, but introduction of livestock by Anglo-European settlers facilitated dispersal of mesquites into upland grasslands (Brown and Archer 1987). Seed produced by woody plants that are already established in grasslands can additionally be dispersed locally by a variety of vectors, including ants and rodents. These processes, however, may involve trade-offs with seed predation (Nicolai et al. 2010). Though seldom considered, dispersal has important implications for the rate of WPE, for as the dispersal of viable, germinable seed increases, so too do opportunities for establishment (Groom et al. 2000).

When woody plant seedlings germinate in grasslands, they face intense competition for light, water, and soil nutrients. In lightly grazed, high-productivity grasslands, grasses will initially be taller than woody plant seedlings, reducing light availability (de Dios et al. 2014). Typically, grasses and woody seedlings in water-limited environments share the same shallow soil horizon (Kambatuku et al. 2013), so that grasses may furthermore monopolize soil resources to near exclusion of woody plant recruits, especially under environmental conditions that favor grasses: fine-texture or shallow soil sites with a summer rainy season characterized by small rainfall events that wet only the near-surface soils (Fravolini et al. 2005). However, grazing reduces grass leaf area, root density, and depth and therefore competitive effects on seedlings above and below ground. The intensity of grazing required to induce this response is likely to vary among sites, and may vary with soil condition according to their favorability for grasses. Thus, critical grazing levels may be relatively low on sandy, deep sites and higher on clayey or shallower sites (Knoop and Walker 1985).

Ground cover of many grasslands is characterized by a matrix of grass patches and bare ground. Grazing does not typically reduce grass biomass homogeneously and can contribute to increases in bare ground cover. These gaps in grass cover, which occur even in lightly grazed grasslands dominated by late seral, productive grasses, provide opportunities for woody seedlings to establish (Jurena and Archer 2003; Wakeling et al. 2015). In woody species that develop taproots, seedlings may establish during periods when soil water content is high and belowground competition is minimal. Under such conditions, which can occur in years of average rainfall, taproots grow quickly beyond the zone exploited by grasses thereby reducing below-ground competition with grasses (Brown and Archer 1990; Weltzin and McPherson 1997). Drought-induced reductions in grass density or cover, perhaps amplified by grazing, may create additional opportunities for establishment of woody plant seedlings when rains return. Once established, these seedlings may then persist through subsequent dry periods residual soil moisture is available below the grass root zone. This is a possible explanation for the "stair-step" or "ratchet" pattern of woody plant encroachment that has been observed in some areas. Collectively, these mechanisms help explain how some woody species can establish (1) under light grazing when grass competition should be highest (Brown and Archer 1989; Brown and Archer 1999, and references therein), and (2) under typical (non-episodic) climatic conditions (Watson and Westoby 1997), and (3) persist through periods of drought.

The relationship between grasses and woody plant recruits is not necessarily antagonistic. Grasses can in turn compete with and facilitate woody seedlings. A grass patch may increase water infiltration and reduce evaporation from the soil surface and subsequently deplete soil moisture by transpiration. The net effect on woody seedling survival depends on multiple factors including species, soil texture, rainfall amount/intensity, and temperature. Net effects of grasses on woody plant seedlings are more likely to be facilitative in arid or semiarid regions and competitive in more mesic grasslands and savannas (Good et al. 2014). In semiarid and arid grasslands, small-scale heterogeneity may be such that there are patches where woody seedling establishment is high and patches where it is low (Maestre et al. 2003a), as well as settings where facilitation by grasses more than offsets even strong belowground competition (Maestre et al. 2001; 2003b). Grasses can enhance microenvironmental conditions for woody seedlings by increasing root turnover and litter deposition, which function to improve soil organic matter, soil structure, fertility, and moisture retention. Grass stems can also capture surface-water runoff and sediment, increasing inputs of moisture and nutrients to the soil. In addition, grass shoots provide shade, reducing daytime temperature stress levels and evapotranspiration. In dry years, the radiative protection afforded by grass litter can significantly reduce woody seedling mortality (de Dios et al. 2014). Even in tropical and subtropical savannas, woody seedling growth and survival rates can be markedly higher in grass patches than in areas of bare soil. Consequently, levels of establishment can be higher on protected sites than on grazed sites (e.g., O'Connor 1995), especially if the protected sites are recovering from past brush management (e.g., Browning and Archer 2011).

2.4.2 Transitioning from Saplings to Adults

Once woody plants progress into the sapling stage, they have become far less vulnerable to competition, drought, and herbivory; they have passed through their most vulnerable stage. Saplings have better developed root systems, are taller, and have higher leaf area and carbohydrate reserves than seedlings. Unfavorable climate conditions and competition will affect their growth rates, but not necessarily their survival (Cardoso et al. 2016). Belowground competition grasses can slow sapling growth particularly during periods of higher than average rainfall (February et al.

2013) or if mineral availability is increased (Vadigi and Ward 2012) and can also be amplified by browsing (Vadigi and Ward 2014). Accordingly, competition, nutrient limitations, and herbivory can combine to slow sapling development and prolong the time they require to achieve a size that allows them to competitively dominate grasses and begin to influence microclimate and soil properties that will alter future patterns of community development.

Both browsing and fire constrain the progression from sapling to mature shrub or tree (Norton-Griffiths 1979; Augustine and McNaughton 2004; Vadigi and Ward 2014). The frequency and intensity of fire are coupled strongly to grassland productivity (Krawchuk and Moritz 2011) and to grazing (Anderies et al. 2002; Fuhlendorf et al. 2008). Grasslands that develop a high density of standing biomass generate litter capable of fueling hot fires that top-kill or kill saplings. Further, reliability of dry-season fire in more productive systems reduces the occurrence of temporal refuges or fire-free periods that would permit some tree cohorts to pass into a fire-tolerant life stage. Similarly, high spatial connectivity of grass cover would reduce the occurrence of spatial refuges or patches that escape fire during a burn event. Fire is therefore considered the main factor limiting tree cover in warm, semiarid to subhumid savannas that would, without fire, transition to a community dominated by woody plants (Bond 2008).

Saplings of many grassland and savanna species can regenerate vegetatively (resprout) after fire. However, even if saplings survive, repeated fires would prevent them from reaching maturity. Grasslands and savannas may therefore have “seedling banks” or “sapling banks” where woody plants persist in a diminutive state caused by fire or browsing events that occur with sufficient frequency to prevent them from growing past the flame or browse zone. These plants would be “waiting in the wings” for an opportunity to “escape”—an opportunity that may come when populations of browsers decline or when fires are suppressed or when grazers reduce the fine fuel density.

Herbivory and fire are linked so inextricably that some consider them a single disturbance regime: *pyric herbivory* (Archibald et al. 2005; Fuhlendorf et al. 2009; Fuhlendorf et al. 2012). In this view, when fire occurs randomly and herbivores roam freely, the two disturbances become spatially and temporally interdependent and the landscape is composed of a shifting mosaic of woody and herbaceous vegetation (Fuhlendorf and Engle 2001). In contrast, the traditional, independent management of fire and herbivory where livestock movements are regulated and relatively inflexible gives rise to a “fuel vs. forage paradox” (i.e., at a given time and place, grass biomass can be one but not both). Coupling the two, as pyric herbivory, averts this paradox because herbivores are attracted to, and concentrate their foraging on, recently burned areas, which allows other areas to accumulate the fuel mass needed to enable future fires that would keep woody plants in check. Subsequent prescribed burns conducted on these areas would then attract grazing animals and alleviate grazing pressure on the previously burned area to allow fuel to accumulate for a follow-up prescribed fire. The net result is a shifting mosaic of vegetation states that provides habitat for a variety of species with contrasting habitat requirements.

The prevalence of fire will determine which woody species in a local flora are more likely to pass from sapling to maturity. Among tree species of tropical Africa, seedlings that allocated resources preferentially to growth and resource-capture traits (e.g., height, leaf area, root-shoot ratios) survived better in ecotones between forests and savannas where fire frequency was low; species that allocated preferentially to carbohydrate storage in leaves and roots had better survivorship in fire-prone savannas (Cardoso et al. 2016). However, larger saplings survived better than smaller saplings, irrespective of allocation traits in either plant community. These results have implications for WPE and highlight a question we have not yet addressed: If environmental conditions change to favor "woody plant" proliferation, why have so few of the species comprising the woody plant flora in an area become encroachers? We return to the question of species selection in the context of WPE in Sect. 2.4.4.

2.4.3 Woody Plant Carrying Capacity

A population is at carrying capacity when strong negative density feedbacks on recruitment or positive density feedbacks on mortality (i.e., self-thinning) prevent further population increases. In general, these feedbacks are mediated by resource competition or simply by patch occupancy, in the sense that a tree or shrub seedling cannot mature in a patch already occupied by a mature tree, or, if it could, would not actually increase woody plant cover.

Greater resource inputs into an ecosystem shift carrying capacities toward higher biomass densities. We have already noted that limits of woody plant cover increase with MAP up to a point when presumably other resources become more limiting (Fig. 2.4). However, in regions where annual precipitation is highly variable—a characteristic of many water-limited environments—it is challenging to pinpoint an absolute carrying capacity for woody plants, as mortality and recruitment in any given year are tied to that year's or the recent series of years' precipitation, not the long-term average. Precipitation deficits will decrease recruitment and increase adult mortality (Bowers 2005; Twidwell et al. 2014), but density-dependent mortality may also occur during more benign conditions (Meyer et al. 2008; Dwyer et al. 2010). Precipitation-induced fluctuations in recruitment and mortality rates (Fig. 2.5) may keep woody plants from reaching their MAP potential in some areas (Fig. 2.4).

Though the theory of density dependence or self-thinning is clear-cut, it has been difficult to find evidence of it in field studies. If density dependence is at play, it should leave an imprint on tree or shrub spatial distribution, such as a decrease in spatial aggregation with tree size or age (Meyer et al. 2008; Belay and Moe 2012). These patterns indicate that survivorship probabilities of woody plants decrease in the vicinity of woody plants. In savannas, the maintenance of long inter-canopy distance between mature trees is additionally mediated by grasses suppressing the seedling growth (Sea and Hanan 2012).

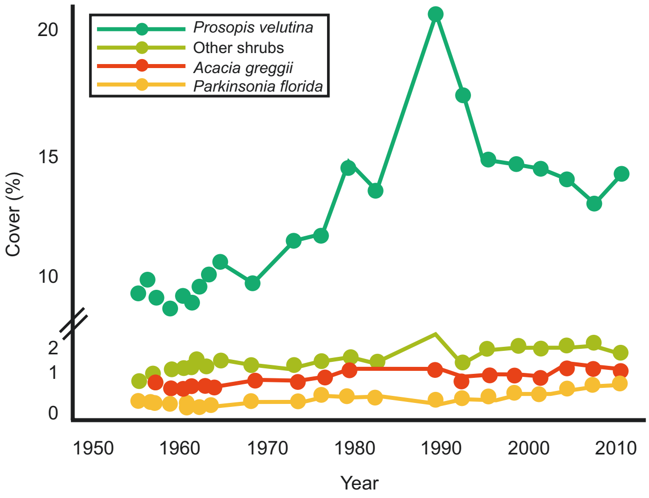

Fig. 2.6 Canopy cover of three shrub species and "all other shrubs" at a Sonoran Desert grassland (USA) where woody plant encroachment has been well documented. *Prosopis velutina* cover increased markedly from the 1950s to the 1990s, whereas that of *Acacia greggii* and *Parkinsonia florida* (both potentially N_2-fixing) and all other shrubs has remained low (note break in *y*-axis). Data are from the Santa Rita Experimental Range Digital Database, Pasture 8 (http://ag.arizona.edu/SRER/longterm/ltcover.xls)

Cover of velvet mesquite (*Prosopis velutina*) into grassland at a Sonoran Desert site is near the maximum level predicted by MAP in Fig. 2.4. The only woody encroacher at this site (Fig. 2.6), velvet mesquite has well-developed, shallow lateral roots extending well beyond their canopies. Intraspecific, shrub-shrub competition could therefore potentially explain why cover appears to have reached its maximum. However, an analysis of spatial patterns over a 74-year period failed to exhibit changes indicative of self-thinning (Browning et al. 2014). Are there explanations other than those related to plant spatial patterns that might set upper limits to shrub cover on a site? One hypothesis is related to hydraulic constraints on shrub size (e.g., Sperry and Hacke 2002; Hacke et al. 2006). As shrubs approach their upper size limit for a site with a given soil texture, depth, topographic setting, etc., their ability to maintain continuity in transport of xylem water may become increasingly jeopardized and lead to higher probabilities of branch or whole-canopy mortality. This loss of plant branch systems or canopies would reduce canopy cover that subsequently would be compensated by recruitment of new plants or growth of other, smaller plants if stand-level canopy cover were to be maintained. This more subtle form of density-dependent interaction manifests itself via canopy reductions rather than whole-plant mortality. Support for this proposition comes from observations of shrub height asymptotes and shifts in leaf-stem biomass allocation (Martinez and Lopez-Portillo 2003) and shrub size-abundance relationships (Allen et al. 2008).

Some woody encroachers can generate positive density dependence by facilitating the encroachment of other woody species. In these instances, the initial encroaching species, perhaps arriving via dispersal from wind, water, ungulates, rodents, or ants, adds vertical structure to the grassland community and modifies soils and microclimate subsequent to its establishment. Seeds of other woody species concentrated in other parts of the landscape may then arrive via birds attracted to this new vertical structure, and their germination, growth, and establishment would be enhanced through modifications of microclimate and soils from pioneer plants (Archer 1995; Stokes and Archer 2010). Facilitation, therefore, may have a combination of passive and active components: adding structure and altering local ecosystem processes. Active processes would include hydraulic lifting of soil moisture from deep to shallow layers (Zou et al. 2005) and modification of soil-nutrient pools and radiant-energy regimes (Barnes and Archer 1996; Barnes and Archer 1999). Where woody encroachment reduces grass biomass and cover, fire frequency and intensity can be reduced, enabling increased establishment of woody seedlings and clonal reproduction (Ratajczak et al. 2011a; Brandt et al. 2013). Accordingly, in fire-prone grasslands and savannas, encroachment by a relatively fire-tolerant or fast-growing woody species may facilitate the spread of fire-intolerant or slow-growing woody species. These processes have an important temporal component, as changes initiated by the initial encroaching species may occur gradually over decades (Throop and Archer 2008; Liu et al. 2013).

2.4.4 Why Do So Few Woody Species Proliferate in Grasslands?

The diverse mechanisms proposed to explain woody plant encroachment in Sect. 2.3 are united by being general enough to pertain to many woody plant species occurring in any biogeographic province. The treatment of “woody plants” as a *de facto* functional group befits investigation of woody plant encroachment as a global phenomenon, but ignores another important aspect of WPE: that very few woody species in a regional flora have actually become aggressive encroachers or have spearheaded the encroachment process (Stokes and Archer 2010; Barger et al. 2011). However, there are dozens of woody species with growth forms that should have benefited from the changes in drivers, yet have not proliferated (Fig. 2.6).

The apparent selectivity of woody encroachment suggests that it may be useful to examine the phenomenon under a different light: (1) which, if any, traits unify woody encroachers around the world and (2) what might this potentially tell us about the relative importance of various potential drivers? In addressing these questions we borrow from community theory the perspective of viewing the landscape distribution and abundance of species as the result of a regional species pool passing through a sequence of abiotic environmental and biotic community “filters”, such that species with mismatched trait combinations are excluded from a community (Keddy 1992). Applied to encroachment of tree and shrub species, we propose that there are a sequence of barriers for entering and proliferating in a grassland or savanna community (Fig. 2.7). One or more of these barriers may be made progres-

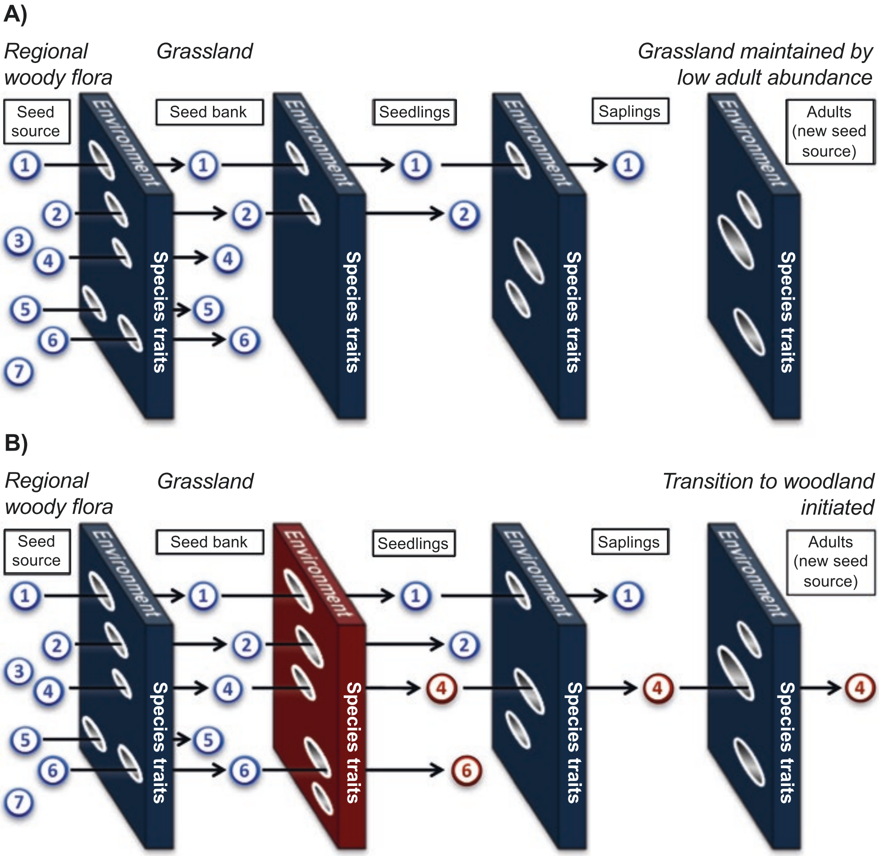

Fig. 2.7 Conceptual model of the species selection process in woody plant encroachment into grasslands. *Numbered circles* represent woody species and *blocks* represent barriers or trait filters constraining advancement to the next life stage. Each barrier may be comprised of several independent and interactive challenges to growth and survivorship (e.g., dispersal, predation, nutrient scarcity, disturbance). In this hypothetical example, (**a**) one or more barriers prevent any of the woody species in the flora from recruiting in the grassland. (**b**) Land-use change makes one barrier (in red) more surmountable, now permitting two additional species to get to the seedling stage (#4 and #6). However, one of these (#6) is constrained by the next life stage barrier, whereas the other (#4) is not. This framework explains how grazing, fire suppression, elevated CO_2, climate change, etc. could have nonselective positive effects on many woody plant species in a flora, and yet only a very narrow subset of those would be capable of developing a viable population in grassland. Research should seek to identify the combination of woody plant traits required for passage through all barriers. Doing so would help us explain past encroachment and predict encroachment under future environmental conditions

sively "leaky" or "porous" by changes in drivers of WPE. We furthermore integrate the concept with population biology to highlight the fact that the exclusion of species is most likely to occur during the more vulnerable and uncertain stages of population growth, specifically seed survivorship and dispersal, germination and seedling establishment. Each of these is necessary for grassland invasion and each is a potential bottleneck for WPE.

In this framework, encroaching woody species must have heightened responsiveness to at least one encroachment driver, but must also overcome all other barriers to surviving a precarious life stage. Non-encroachers either may not be responsive to drivers or remain limited by other barriers. Prior to woody plant encroachment, every woody species in the regional flora must have been limited by at least one environmental or community barrier in at least one life stage (Fig. 2.7a). For example, the high productivity and flammability of grasslands may have universally blocked recruitment of woody plants in grasslands, but individual species could have been excluded by any number of additional barriers, such as low-seed production or survivorship, shade intolerance, or slow growth.

The key effect of the historic drivers of WPE was to modify one or more of the filters in such a way that at least one species could pass through a former barrier. A *necessary* condition for a species in the regional pool to encroach would be the release from at least one recruitment bottleneck by a shift in environmental conditions. Nevertheless, many species meeting this requirement would have been prevented from encroaching through unyielding restrictions in other life-stage transitions. Environmental regime change would have been a *sufficient* condition to trigger woody encroachment only for species not constrained by additional recruitment bottlenecks (Fig. 2.7b). The relative paucity of species in the worldwide set of recognized "woody encroachers" suggests that most woody species remain excluded from grasslands through demographic barriers affecting recruitment, growth, or reproduction that have been essentially unchanged by regime shift.

What then are the traits that distinguish woody encroachers from non-encroachers? Table 2.1 lists a variety of functional attributes of woody encroachers on different continents. The list is not meant to be exhaustive, but only to provide examples. The list shows that woody encroachers are not consistently represented by, or restricted to, one or a few functional traits or groups. For example, it might be reasonable to expect that plants that fix N_2, are deciduous, and are livestock-dispersed would be aggressive encroachers—and they certainly can be. But so too can species that are evergreen, bird-dispersed, and lacking the capability of symbiotic N_2 fixation. Similarly, encroaching species can be subshrubs, shrubs, or treelike in stature and "woodiness," and may or may not be capable of vegetative regeneration following disturbance.

The conceptual framework in Fig. 2.7 paints the broader picture for organizing questions of woody encroachment based on species traits and provides a basis for developing and testing hypotheses regarding woody plant encroachment systematically. The main point is that not necessarily all traits, but certainly several

Table 2.1 Woody plants proliferating in grasslands and savannas encompass a wide variety of functional traits and taxonomic families

Functional traits	North America	South America	Africa	Australia
Stature				
Fruticose (shrubby)	x[1]	x[2]	x[3]	x[4]
Arboreal (treelike)	x[5,6]	x[9]	x[7]	x[8]
Leaf Habit				
Evergreen	x[1,5,6]	x[9]	x[10]	x[8]
Deciduous	x[11]	x[2]	x[12]	x[23]
Potential N_2 fixation				
Yes	x[11]	x[2]	x[7,10]	x[8]
No	x[1,5,6]	x[9]	x[12]	x[13]
Dispersal				
Livestock	x[11]	x[2]	x[7,20]	x[8]
Wind/water	x[1]	x[9]	x[14]	x[15]
Bird	x[5]	x[22]	x[12]	x[16]
Recruitment				
Readily generates from seed	x[11]	x[2]	x[7,10]	x[8]
Vegetative regeneration	x[11]	x[2]	x[7,14]	x[8]
Deep or dimorphic root system	x[11]	x[2]	x[17]	x[18]
Nativity				
Native species				
Exotic (non-native) species	x[19]	x[21]	x[20]	x[8,15,18]

An 'X' denotes that a functional trait is represented by a species on a given continent. Superscripts link a given trait to the species exhibiting that trait (bottom of table). Species list is not intended to be comprehensive

[1] Creosote bush, *Larrea tridentata*, Zygophyllaceae (Grover and Musick 1990)
[2] Mesquite, *Prosopis* spp., Fabaceae (Cabral et al. 2003)
[3] Blackthorn *Acacia mellifera,* Fabaceae (Kraaij and Ward 2006)
[4] Coastal wattle, *Acacia sophorae*, Fabaceae (Costello et al. 2000)
[5] Eastern red cedar, *Juniperus virginiana*, Cupressaceae (Barger et al. 2011)
[6] Ponderosa pine, *Pinus ponderosa*, Pinaceae (Barger et al. 2011)
[7] Karroo thorn, *Acacia karroo*, Fabaceae (O'Connor 1995)
[8] Prickly acacia, *Acacia nilotica*, Fabaceae (Kriticos et al. 2003)
[9] Quebracho blanco, *Aspidosperma quebracho-blanco*, Apocynaceae (Morello and Saravia-Toledo 1959)
[10] Paperbark thorn, *Acacia sieberiana*, Fabaceae (Mitchard and Flintrop 2013)
[11] Velvet mesquite, *Prosopis glandulosa*, Fabaceae (Bahre and Shelton 1993)
[12] African myrrh, *Commiphora Africana*, Burseraceae (Oba et al. 2000)
[13] Rubber vine, *Cryptostegia grandiflora*, Asclepiadaceae (Grice 1996)
[14] Sickle bush, *Dichrostachys cinerea*, Fabaceae
[15] Catclaw mimosa, *Mimosa pigra*, Fabaceae (Lonsdale 1993)
[16] Chinee apple, *Ziziphus mauritiana*, (Rhamnaceae) (Grice 1996)
[17] Blackthorn *Acacia mellifera*, Fabaceae (Kambatuku et al. 2013)
[18] Mesquite, *Prosopis* spp., Fabaceae (Robinson et al. 2008)
[19] Chinese tallow, *Sapium sebiferum* (Euphorbiaceae) (Bruce et al. 1995)
[20] Mesquite, *Prosopis* spp., Fabaceae (Shackleton et al. 2015)
[21] Paraiso, *Melia azedarach*, Meliaceae (Ruiz Selmo et al. 2007; Batista et al. 2014)
[22] Glossy privet, *Ligustrum lucidum*, Oleaceae (Tecco et al. 2006)
[23] Mulga, *Acacia aneura*, Fabaceae (Noble 1997)

key traits, could distinguish encroachers from non-encroachers in a given bioregion. Furthermore, common trait trade-offs could be influencing the selection of woody encroachers in interesting ways. Most species in a regional pool could be prevented from encroaching by a trade-off between seed dispersal and seedling survivorship such that some small-seeded species may readily disperse into grassland but not survive as seedlings, whereas large-seeded species could potentially establish but lack adequate dispersal. Seen in this light, it is clearer why there does not seem to be a universally applicable set of encroacher characteristics, but also why taxonomic groups that may be less constrained by dispersal-survivorship trade-offs do seem to contribute more species to the global set of woody encroachers. Knowledge of the trade-offs in trait combinations could to help to explain changes and patterns of WPE observed to date and also to predict future changes in woody species or functional group composition.

2.5 Ecosystem Services

Maintenance of a desirable mixture of herbaceous and woody vegetation is a key component of sustainable ecosystem management in grazed rangelands. Over the past century, this balance has been disrupted and shifted in favor of unpalatable shrubs in many areas of the world. Widespread conversion of grasslands and savannas to shrublands or woodlands has long been of concern to those whose livelihoods depend on livestock production; but the recent realization that this land cover change has significant implications for a myriad of other ecosystem services is now challenging us to adopt a broader perspective on this global phenomenon. Here, we review the effects of WPE on a subset of ecosystem services related to carbon sequestration, hydrology, and biodiversity. Management actions aimed at reducing woody cover also influence ecosystem service portfolios and these are reviewed in Sect. 2.6. The effects discussed here should be further considered in the context of the supply and demand perspectives presented in Chap. 14.

2.5.1 Carbon Sequestration: Plant and Soil Pools

The global phenomenon of WPE has resulted in a significant redistribution of carbon (C) among major terrestrial pools. Trees and shrub proliferation across a range of bioclimatic regions (Fig. 2.2) constitute a potentially significant, but highly uncertain component of the North American C budget (Barger et al. 2011). Presently we cannot confidently predict the magnitude, let alone the direction, of change (Eldridge et al. 2011). Robust generalizations about WPE impacts on ecosystem C balance are elusive because of insufficient quantification of woody plant productivity in encroached ecosystems. Definitive conclusions have been further constrained by confounding methodologies used to estimate soil organic carbon pools, and how those pools change with disturbance (e.g., drought, wildfire) and land management practices (e.g., prescribed burning, brush management). These knowledge gaps are amplified at regional scales where quantifying the net effects of WPE on regional carbon balance would require an accounting of the area undergoing WPE, the stages of encroachment, and the area recovering from past disturbances (Asner et al. 2003).

Studies quantifying herbaceous production in drylands in relation to climate, land use, and disturbance are numerous, but relatively few have simultaneously quantified woody plant production and even fewer have quantified plant *and* soil pools. Accordingly, we know very little about how ecosystem (plant + soil) carbon pools change with changes in grass-woody plant abundance. Scenarios where aboveground net primary production (ANPP) increases, decreases, or remains unchanged can be logically theorized following woody plant encroachment (House et al. 2003). At broad scales, if encroaching woody plants are *less* productive than the grass communities they replace net ANPP will *decrease*. Conversely, if encroaching woody plants are *more* productive than the replaced grass communities net ANPP will *increase*. Lastly, if grassland and woody plant communities are equally productive then no change in ANPP would be expected. So, which of these three scenarios is most likely to occur? As it turns out, the answer depends on rainfall.

Recent syntheses suggest that ANPP scales linearly with MAP in landscapes where woody plants have displaced grasses. At an MAP of ~340 mm the ANPP contribution to the C pool in woody plant-encroached landscapes switches from being a net C source to a net C sink (Fig. 2.8a). Whereas grassland ANPP stabilizes at MAP > 500 mm, woody plant ANPP continues to increase linearly with increases in MAP. This presumably reflects the ability of woody plants, with their more complex canopy architecture, to utilize greater leaf area than grasses (Knapp et al. 2008a). However, the belowground soil organic carbon (SOC) pool typically dwarfs the aboveground pool in drylands. Given its large size, even small changes in the SOC pool could have big impacts on ecosystem C balance, especially given the expansiveness of grasslands and savannas. So how and to what extent do these aboveground changes in plant production affect belowground C pools?

The SOC pool reflects long-term inputs from plant leaves, stems, and roots. This suggests that changes in the amount of SOC would vary with changes in the plant production. However, a survey of studies quantifying changes in SOC with WPE revealed no consistent patterns—it increased markedly in some cases, and remained unchanged, or decreased in others and had no correlation with MAP (Fig. 2.8b). This indicates that when grass communities are replaced by woody plant communities, there is a major difference between ANPP and belowground carbon pools: ANPP scales with MAP while SOC has no apparent relation to it. Reasons for this disconnect are unclear, but may (1) be an artifact of different soil sampling methodologies (see discussion in Barger et al. 2011; Throop et al. 2012), (2) reflect the nonequilibrium status of many landscapes experiencing WPE and the fact that changes in soils lag well behind the changes in the vegetation that drive them, and (3) plant species or functional group differences in allocation of carbon for aboveground vs. belowground growth.

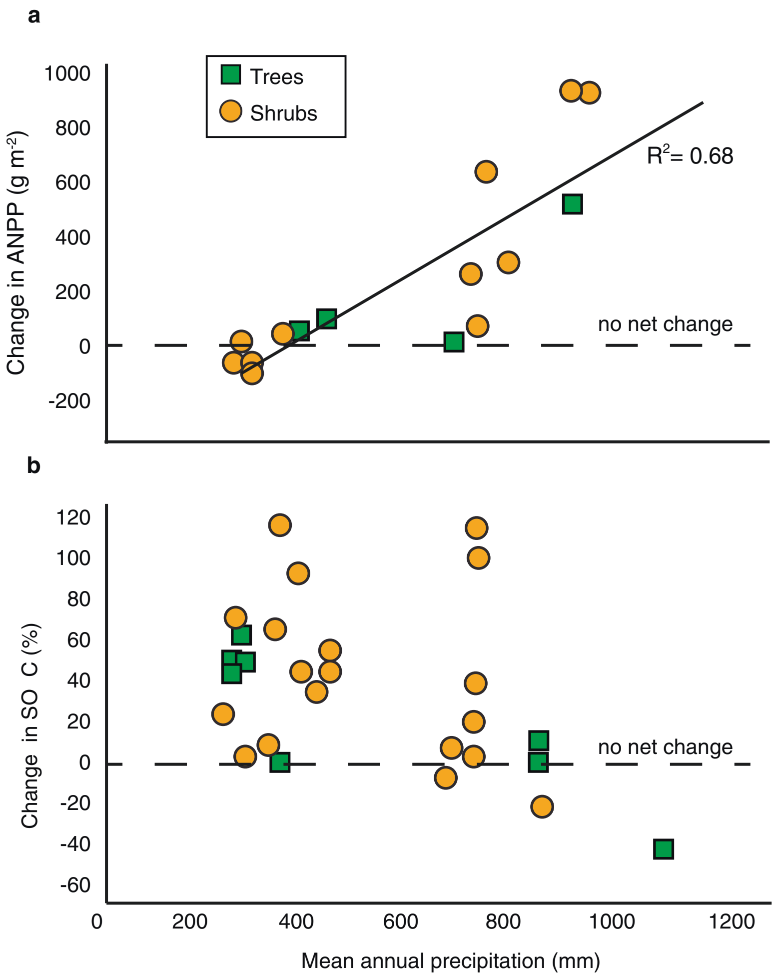

Fig. 2.8 Changes in (**a**) aboveground net primary productivity (g biomass m^{-2} year^{-1}) and (**b**) soil organic carbon with woody encroachment as a function of mean annual precipitation. Data span a range of species and ecoregions and encompass a range of sample collection and processing methodologies (from Barger et al. 2011)

Where landscape effects of both ANPP and SOC responses to have been taken into account in North America it appears that arid zones are likely to become net sources of carbon when WPE occurs, whereas higher rainfall areas will become net sinks (Fig. 2.9). Given that WPE has been occurring since the late 1800s in many of these regions, the sites depicted in Fig. 2.9 may have been at relatively advanced stages of woody plant stand development. Accordingly, the reported values may represent potential envelopes between the lower and upper limits of an ecological site. However, natural disturbances (e.g., drought, wildfire, pathogen outbreaks) and land management (Sect. 2.6) will alter the extent to which these potentials may be realized or maintained.

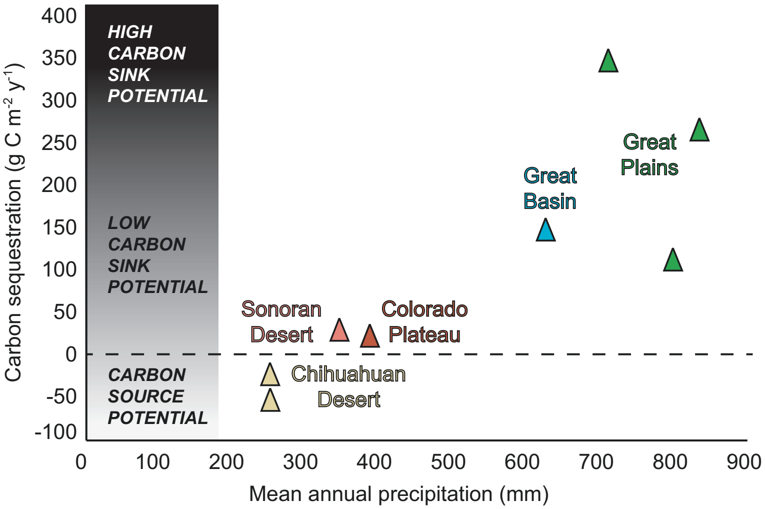

Fig. 2.9 Carbon source–sink potential with woody plant encroachment in North American ecoregions. Values are the mean of changes in aboveground net primary production plus soil organic carbon. Modified from Barger et al. (2011)

2.5.2 Hydrology

The hydrological impact of WPE has been of intense interest, as climate change and human demand for freshwater have increased, inciting global concerns about water security for communities (Vorosmarty et al. 2010). The question that generally concerns the public most is whether WPE decreases groundwater recharge and/or streamflow (Tennesen 2008). WPE has the potential to interfere with all components of the water budget equation: precipitation, evapotranspiration (ET), runoff (R), and deep drainage (D, recharge below the rhizosphere). Structural differences between woodlands and grasslands suggest that, in general, woodlands should have higher ET and lower R than grasslands (Bonan 2008). Four major mechanisms follow. First, woody plants can take up water stored in deeper soil layers (Sect. 2.3.3). Second, woodlands have lower albedo and greater air turbulence in the canopy boundary layer, which increases their potential ET (PET). Third, protracted periods of dormancy limit the number of days over which transpiration occurs in grasslands, whereas shrubs and trees, particularly if they are evergreen, have longer periods of transpiration (Donohue et al. 2007). Fourth, canopy interception of rainwater, a component of ET, is lower in grasslands especially when compared with needle- or scale-leaf conifers (e.g., *Pinus*, *Juniperus*) (Owens et al. 2006).

WPE also can influence runoff by changing soil infiltration rates. In water-limited systems, runoff comes during intense rainfall events, when the precipitation input rates exceed the infiltration rate. Water begins to pond and run off, eventually flowing into streams (Dunne 1978). Woody cover may change the infiltration characteristics of soil through effects on soil quality and spatial heterogeneity of plant cover. A recent meta-analysis showed that these effects are highly context dependent (Eldridge et al. 2011). Shrub encroachment into grasslands is often classified as a "trigger" for soil degradation and "desertification" (Schlesinger et al. 1990). But a study conducted in a semiarid Mediterranean grassland in Spain showed that the effect can also be opposite (Maestre et al. 2009). In this example, shrubs establishing in degraded pastures created "islands of fertility" that enhanced vascular plant richness, microbial biomass, soil fertility, and nitrogen mineralization. In this sense, shrubs may be seen as reversing, rather than causing, desertification.

Regardless of changes in vegetation and soil structure, there are physical limits to the magnitude with which WPE can modify the hydrological budget. Potential effects are greatest where precipitation approximately equals PET (Zhang et al. 2001); above or below this threshold, ET is constrained either by precipitation or PET. Grassland and savanna biomes occur under both climate conditions. The Great Plains of North America, for example, straddle regions with precipitation surplus to the east and precipitation deficit to the west (Fig. 2.10). Therefore, WPE should have maximal hydrological consequences in central regions of the USA.

There are several caveats to these generalizations and we mention two: first, there are hydrological systems with large bypass-flow components. Bypass flow is

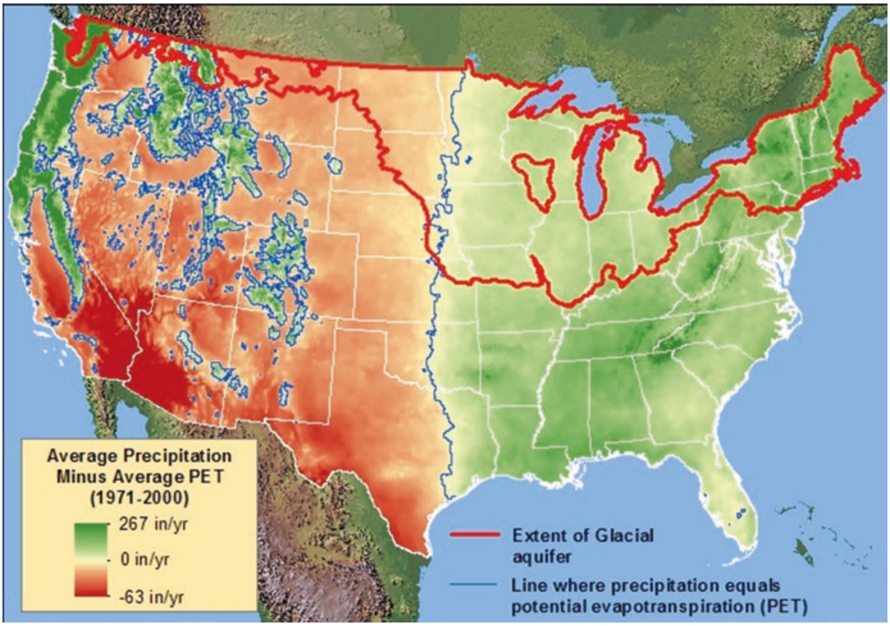

Fig. 2.10 A map of average precipitation (P) minus average potential evapotranspiration (PET) for the contiguous USA. P-PET decreases prominently from east to west and less so from north to south. Impacts of woody plant encroachment on ET are expected to be maximized near the 97th degree west longitude, where P approximately equals PET. Where P exceeds PET, ET is energy limited approaching PET; where PET > P, ET is water limited, approaching P, irrespective of woody cover

the rapid transport of water through the root zone by way of macropore conduits (e.g., channels left by large dead roots, cracks, and fissures in bedrock). Bypass flow expedites recharge of aquifers or spring-fed streams and the brief residence time for water in the rhizosphere means that vegetation has practically no influence on the volume of bypass flow. This minimizes the effect that WPE can have on the water budget. This was demonstrated in a series of rainfall simulation experiments in the karst region of Central Texas, a semiarid area where P is not far below PET. Shallow caves at the field site made it possible to capture drainage out of the root zone as cave drip. Juniper removal had no significant effect on the amount of water captured as cave drip (Bazan et al. 2013). Decades of controlled experiments in this region have generally returned the same result, that the effect of removing encroaching woody plants on ET and/or spring flow is small and short-lived (Wilcox et al. 2005) (Chapter 3, this volume).

A second important exception to the general pattern occurs in systems with shallow water tables, in which the incursion of deeply rooted trees can fundamentally alter the hydrological cycle, including precipitation. For example, a regional increase in the woody cover of the African Sahel zone has recently been linked to a precipitation feedback: as woody plant cover increased, more moisture (from groundwater) was cycled into the atmosphere, which increased cloud formation and rainfall. The positive-feedback loop closes when higher rainfall in turn increases woody cover (Scheffer et al. 2005). It has been suggested that this regional vegetation-precipitation feedback may be locally enhanced by a vegetation-infiltration feedback, in which infiltration is improved as a consequence of higher vegetation cover, enabled by WPE. Together, these two feedbacks are a powerful force of self-organization of the hydrological system, which can either be locked into an arid, low-productivity state or a mesic/high-productivity state (Dekker et al. 2007).

2.5.3 Biodiversity

Biodiversity, whether quantified as richness of species, plant functional groups, or animal guilds, is influenced strongly by WPE. From the perspective of vegetation structure, WPE is transformative: grasslands become shrub or tree savannas and shrub and tree savannas become shrublands or woodlands.

Grassland ecosystems are among the most endangered in North America, with most having been reduced to small remnants of their original distribution (Noss et al. 1995; Hoekstra et al. 2004). Initially, colonization of grasslands by woody plants involves new species that increase the biodiversity pool directly. Subsequently, modification of soil properties, vegetation structure, and microclimate may facilitate establishment by other novel plant and animal species. Maximum diversity in savanna-like configurations occurs often where woody and herbaceous plants are both well represented or where gains in new woody and herbaceous species outweigh losses of the initial grassland-obligate species (Fig. 2.11). As abundance of woody plants increases, grassland components eventually decrease and are

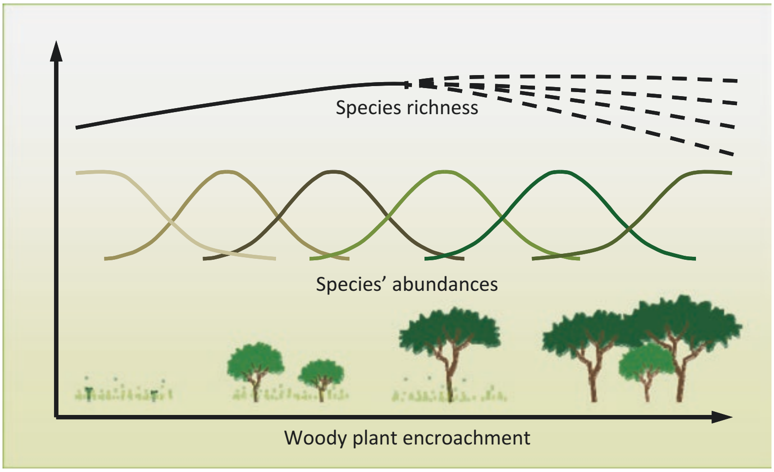

Fig. 2.11 Conceptual model of community changes in species abundances and richness with woody plant encroachment. Species richness is likely to be highest where both shrub-associated and grassland-associated species co-occur, with the endpoints varied, depending on the encroaching species

replaced by plants and animals adapted to shrublands or woodlands. In tropical and subtropical areas with large and diverse regional species pools, there may be a net increase in diversity along with concomitant changes in community structure. In other settings, there may be little or no net change in numerical diversity, but profound changes in community structure. In settings where the number of encroaching woody species is low, their proliferation may create virtual monocultures with little or no understory that will result in profound decreases in the diversity of plants and animals. Examples of the latter in North America include both native (juniper, ponderosa pine) and non-native (salt cedar, Chinese tallow) species. No matter the numerical changes in biodiversity, persistence of plants and animals endemic to grassland and open savanna ecosystems is jeopardized. Some grassland obligates are immediately lost at the initial stages of encroachment (e.g., Fuhlendorf et al. 2002; Lautenbach et al. 2016), whereas others may persist until woody plant cover reaches about 15 % (reviewed in Archer 2010).

2.5.3.1 Herbaceous Vegetation

Encroaching woody plants may have an immediate, adverse effect on herbaceous vegetation in some cases or a positive, facilitative effect in others. In the latter, woody plants may eventually suppress herbaceous plants as their density increases. These overstorey-understory relationships are influenced strongly by soil type, such that herbaceous plants may be suppressed on lowlands and facilitated on uplands (Hughes et al. 2006). Local- and landscape-scale diversity perspectives should therefore be kept in mind when generalizations are made.

A recent global analysis indicates that WPE generally has positive to neutral effects on plant diversity (Eldridge et al. 2011). However, evidence from North America indicates consistent declines in species richness (45 %, on average) (Ratajczak et al. 2011b). Variation in evolutionary history and Anglo-European land-use practices may account for these varied responses between North America and other continents. In addition, declines in North America plant diversity seem to vary with MAP. For example, long-term assessments of plant species richness in desert grasslands revealed linear declines with time since encroachment by an arid land shrub. Additionally, species-poor communities in areas invaded by the same shrub were less stable (more variable in time) than species-rich communities in nearby grassland-dominated areas (Baez and Collins 2008). In contrast, species richness declined exponentially with woody plant cover in humid grasslands invaded by an evergreen arborescent (Knapp et al. 2008b). These contrasts in arid and humid regimes (linear vs. exponential declines, respectively) suggest that the future magnitude and dynamics of vegetation diversity response to WPE will be mediated by climate change. Changes in species composition should not be lost in discussions of diversity. As we mentioned earlier, substantial changes in species, functional groups, or guilds, as well as changes in relative species abundances (evenness), can occur with small, or even no, net changes in species richness. Furthermore, these changes in species composition impact ecosystem processes related to primary production, nutrient cycling, and structure of tropic pyramids. Accordingly, measures of species richness alone provide a limited metric of changes in diversity.

As summarized in the next section, plant diversity changes have a multiplier effect on animal diversity by adding keystone structures and increasing vegetation heterogeneity (Tews et al. 2004).

2.5.3.2 Animals

Changes in the plant community associated with WPE have affected many grassland animals principally by reducing the quantity or quality of habitat and by altering a suite of fundamental ecological processes. Consequently, the abundance and distribution of many organisms that inhabit grassland ecosystems have decreased markedly (Samson 1994; Sauer and Link 2011). During the last 30 years, for example, grassland birds have declined more rapidly than any other group of birds in North America (Knopf 1994; Peterjohn and Sauer 1999; Vickery et al. 1999; Brennan and Kuvlesky 2005; Sauer and Link 2011).

Although long-term declines in the abundance and distribution of many grassland species have been relatively well documented, linkages between changes in grassland plant communities and their effects on animals are less clear. Vegetation structure is a key determinant of animal diversity, and because a principal consequence of WPE is a marked increase in vertical and horizontal structure, populations and communities of many resident animals shift markedly in response to woody encroachment (Skowno and Bond 2003; Coppedge 2004; Sirami and

Monadjem 2012). Although some species respond to changes in vegetation at broader scales, animals that function at smaller scales, such as small mammals and arthropods, are more likely to respond to changes in vegetation that alter local environmental characteristics (Wiens and Milne 1989). Consequently, some taxa, including birds, mammals, and reptiles, are more likely to respond to the structural changes in the plant community that accompany WPE, whereas other taxa, especially arthropods, are also likely to respond to changes in species composition that interfere with coevolved relationships with specific plant species (Litt and Steidl 2010). Relative to vertebrates, many arthropods are less mobile, depend on a narrower range of plants for food, cover, and sites for reproduction, and can have specialized relationships with specific plant species (Kremen et al. 1993). This makes them especially vulnerable to compositional changes in the plant community (Steidl et al. 2013). Changes in the arthropod community may feed back to influence multiple ecological processes, including pollination, decomposition, and nutrient cycling, as well as food resources for insectivores, including breeding grassland birds, small mammals, and reptiles.

Responses of animals to WPE vary broadly by taxa, plant community, and geographic region, but ultimately responses can vary by species (Ayers et al. 2001; Meik et al. 2002; Blaum et al. 2007a; Blaum et al. 2007b; Blaum et al. 2009). Species-specific responses are expressed frequently as sharp transitions in the probability of occupancy (i.e., changes in distribution) or as changes in demographic rates such as density, survival, or reproductive success at specific levels of woody plant cover (Grant et al. 2004; Sirami et al. 2009). For example, verdins (*Auriparus flaviceps*) and eastern meadowlarks (*Sturnella magna*), species common throughout grassland and shrublands of southern Arizona, respond strongly and oppositely to changes in the abundance of woody vegetation (Fig. 2.12). For verdins, as the amount of woody vegetation increases, the probability of them selecting an area for breeding increases; in contrast, the probability of eastern meadowlarks selecting an area for breeding decreases sharply as the amount of woody vegetation increases. Species-specific responses such as these explain why the effects of WPE on animal populations and communities vary with stage of encroachment (Fig. 2.11); composition of these communities shifts as density of woody plants changes. In early stages of encroachment when cover of woody plants is relatively low, vertical structure in the plant community increases. These structural changes increase the diversity of niche spaces available for exploitation by animals. Therefore, species capable of exploiting these niches are added to the initial animal community, increasing species richness and diversity. Overall richness and diversity of these areas increase as shrub-associated species join the existing community of grassland-associated species (Tews et al. 2004). In the southwestern USA, for example, increases in species richness of several taxa were associated with increased cover of woody plants (Arnold and Higgins 1986; Lloyd et al. 1998; Bestelmeyer 2005; Block and Morrison 2010).

As encroachment advances and shrub cover continues to increase, habitat for grassland-associated species declines, so their abundances decline. This pattern has been well documented for grassland birds (Coppedge et al. 2001; Cunningham and

Johnson 2006; Winter et al. 2006; Block and Morrison 2010), but has also been observed for mammals (Krogh et al. 2002; Blaum et al. 2007a) and reptiles (Mendelson and Jennings 1992; Pike et al. 2011). When woody cover exceeds species-specific thresholds, which as yet have been poorly established, populations of grassland-associated species are displaced (Grant et al. 2004; Sirami et al. 2009) and animal communities shift from being dominated by grassland-associated species to shrubland-associated species (Igl and Ballard 1999; Rosenstock and Van Riper 2001; Skowno and Bond 2003; Sirami and Monadjem 2012). Overall, richness of animal communities is likely maximized where cover of woody plants is below the threshold levels that displace grassland specialists but above levels where habitat becomes more exclusively suitable for shrub-associated species (Fig. 2.11); that is, where gains of new species outweigh losses of existing species (Archer 2010). This pattern of peak species richness at intermediate levels of woody cover has been documented for mammalian carnivores (Blaum et al. 2007a), arthropods (Blaum et al. 2009), and birds (Grant et al. 2004; Sirami and Monadjem 2012). Regardless of how encroachment affects animal diversity at local scales, animal diversity is ultimately reduced at broader scales if grassland-associated species are displaced.

Although systematic patterns in responses of animals to WPE are becoming clearer, the mechanisms governing them are not. Specifically, we do not understand clearly how WPE and other vegetation transitions influence demographic processes at the population scale or the behavior of individuals, particularly those related to habitat selection. In general, WPE influences populations and communities of animals directly by reducing both the quantity and the quality of habitat. Many animals rely on vegetation-based cues to indicate the presence of habitat—that is, to identify areas that provide the suite of resources necessary for survival and reproduction (Mannan and Steidl 2013). Therefore, as vegetation composition and structure change in response to WPE, areas that once provided habitat for a species may no longer provide that function. Specifically, as WPE proceeds, species will continue to persist in patches that provide habitat; as the vegetation transition continues, the same species could be displaced entirely.

WPE can lower habitat quality for animals that continue to inhabit encroached areas and reduce their survival or reproductive success. Changes in habitat quality may reflect changes in rates of predation or brood parasitism or changes in the types, abundance, or availability of food resources. WPE can alter predation risk by influencing the types, densities, and behaviors of predators in a community. For example, predation is often the primary cause of nest failure in grassland birds (Martin 1992) and is thought to be responsible for decreases in reproductive success of birds in areas encroached by woody plants (With 1994; Mason et al. 2005; Graves et al. 2010). Further, for songbirds nesting in grassland patches, the risk of nest predation increases with proximity to woody plants (Johnson and Temple 1990; Mason et al. 2005). WPE could affect food resources available to herbivores through changes in the composition or biomass of vegetation and subsequently to carnivores through changes in herbivore populations and communities (Maurer 1985). Among birds, declines in food availability can delay nest initiation or lead to nest failure (Ortega et al. 2006), and increase rates of nestling starvation (Maron and Lill 2005; Granbom et al. 2006) and predation (Dewey and Kennedy 2001; Zanette et al. 2003).

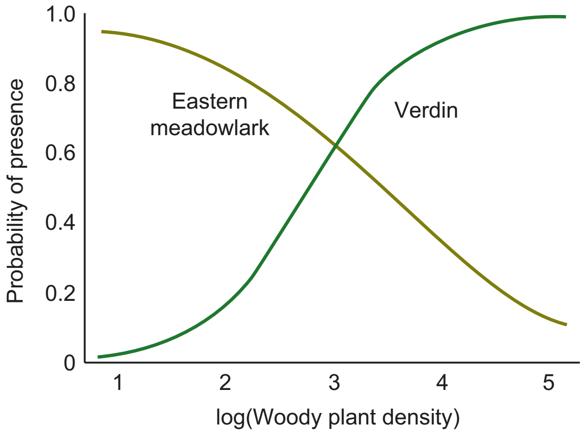

Fig. 2.12 Predicted probabilities of eastern meadowlark and verdin presence as a function of woody plant density in a Sonoran Desert grassland (R.J. Steidl, unpublished)

Additionally, food availability for nestlings could be affected by rates of brood parasitism by brown-headed cowbirds (*Molothrus ater*), which are correlated positively with woody plant cover (e.g., Johnson and Temple 1990; Shaffer et al. 2003).

Despite the global scale of the encroachment phenomenon and the tremendous number of grassland-associated animals that might be affected, only a modest amount of research has explored and quantified responses of animals to WPE. A variety of perspectives exist, but unifying, robust generalizations are still elusive. Some of the variation in results among studies might be attributable to artifacts of study design. For example, many studies simply contrast areas as “encroached” vs. “not encroached.” These coarse classifications likely occlude biologically meaningful variation in animal responses along complex gradients of vegetation structure, composition, and dominance, as well as their continuous changes throughout the encroachment process (e.g., Thompson et al. 2009). Many of the studies that have explored broader encroachment gradients use space-for-time substitutions as a way to compare areas with different amounts of woody cover. Although these approaches can be useful in understanding how animals respond to structural changes in habitat resources—especially when gradients span large areas—they are predicated on the assumption that animals respond to vegetation changes in space in the same way they respond to changes in time (Sirami and Monadjem 2012). In addition, areas that have been encroached by shrubs may differ inherently from areas that have not been encroached in ways that are not apparent to researchers, but that may be important to animals.

2.6 Management Perspectives

Proliferation of woody plants has long been of concern in areas where the primary land use is cattle and sheep grazing. WPE on these lands typically reduces production of valued forages, complicates animal handling, and improves habitat for ectoparasites. Furthermore, and despite limited supporting evidence, WPE is often presumed to adversely affect stream flow and groundwater recharge (Sect. 2.5.2). As a result, management of rangelands for production of cattle and sheep has focused historically on reducing the amount of woody vegetation using a variety of technologies (Bovey 2001; Hamilton et al. 2004). Known as “brush management” (North and South America), “woody weed management” (Australia), and “bush clearing” (Africa), these technologies may be applied singly, in combination, or sequentially. As a result, rangelands are complex mosaics of areas undergoing woody plant encroachment and areas subjected to, and transitioning from, past efforts to reduce woody cover (Asner et al. 2003; Browning and Archer 2011).

Cover and biomass of herbaceous vegetation that is valued as forage typically decline as woody plant abundance increases (Anadón et al. 2014b). This loss of forage production has traditionally been the impetus for brush management, with the expectation that reductions in tree or shrub cover would promote recovery of herbaceous production. More recently, interest in recovering grassland biodiversity has become a priority (Sect. 2.5.3.1). A synthesis of research on this topic indicates that responses of herbaceous vegetation to brush management are highly variable (Fig. 2.13). Although 64 % of investigations reported increases in forage production following brush management, those gains were, on average, short-lived, typically less than 5–7 years. Furthermore, herbaceous production and diversity remained unchanged, or even decreased—sometimes substantially—in 36 % of the studies. This range of herbaceous responses to brush control begs several questions. First, why is the response of herbaceous vegetation short-lived on some sites and longer lived on others? Second, why is herbaceous vegetation unresponsive to reductions in cover of woody plants at many sites? Third, what caused herbaceous vegetation at some sites to respond so negatively? Answers to such questions are needed if we are to identify where, when, how, and under what circumstances to intervene with a given brush management practice (Archer et al. 2011).

Integrated brush management systems (IBMS) (e.g. Noble and Walker 2006) are the hallmark of progressive, modern brush management. The IBMS approach advocates consideration of the type and timing of a given brush management technology and makes explicit allowances for the type and timing of follow-up treatments. This approach benefits from knowledge of how woody and herbaceous plants are likely to respond and how climate, soils, topography, and livestock and wildlife management might mediate plant responses. These considerations are crucial for long-term cost-benefit analysis of these treatments (e.g., Torell et al. 2005a). The conceptual model in Fig. 2.14 represents the kinds of ecological data that will be needed to evaluate the feasibility and sustainability of brush management practices from a forage production standpoint. Rangeland ecologists should develop families of curves for ecological sites in a given bioclimatic zone (e.g., McDaniel et al. 2005).

Historically, brush management treatments were often applied across entire landscapes and watersheds. However, it would be more effective to treat portions of a landscape and distribute treatments across landscapes in both time and space to create mosaics of vegetation structure, patch sizes, shapes, and age states (Scifres et al. 1988; Fulbright 1996) that would increase diverse habitats to potentially increase biodiversity (Jones et al. 2000) (Sect. 2.5.3.2). This would enable a

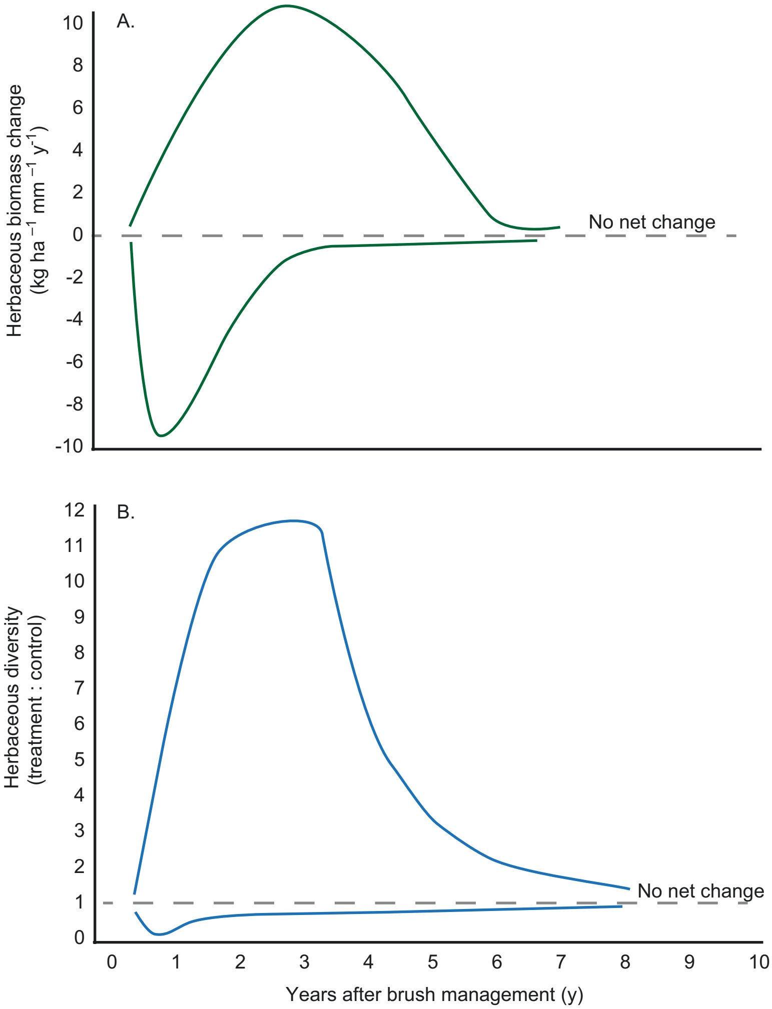

Fig. 2.13 Response envelope depicting the upper and lower limits of herbaceous (**a**) production and (**b**) diversity responses to brush management (based on data in Archer and Predick 2014)

low-diversity shrubland or woodland developing on a grassland site to be transformed into a patchwork of grassland-savanna-shrubland or woodland communities that promotes diversity at multiple scales (Chapter 5, this volume).

Economic analyses of brush management suggest that assessments based solely on increased forage and livestock performance may not be economically justified, especially when external subsidies are not available (Torell et al. 2005b; Tanaka et al. 2011). Full and explicit consideration of other ecosystem services may, however, change the cost-benefit assessment. Knowledge gaps remain, but a large and growing body of work on woody plant encroachment impacts on ecosystem ser-

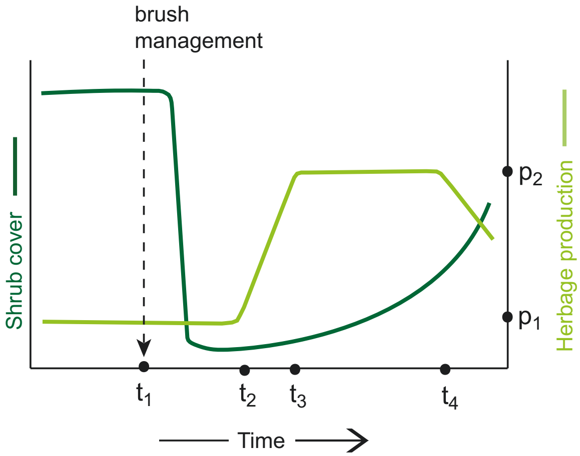

Fig. 2.14 Generalized conceptual model of herbaceous response to brush management. The lag time in response (t_1 to t_2), the magnitude of (p_1 to p_2) and time to peak herbaceous response (t_1 to t_3), the duration of peak elevated production response (t_3 to t_4), and the time frame over which herbaceous productions decline as shrubs reestablish (t_4 onward) vary with numerous factors. Knowledge of the relationships depicted in this conceptual model for a given ecological site will help determine the type, timing, and appropriate sequencing of brush management practices in an integrated brush management system (IBMS) approach (from Archer and Predick 2014)

vices is developing (Archer 2010; Barger et al. 2011; Eldridge et al. 2011). Much less is known about how post-encroachment management of woody vegetation influences those services. The scientific community is challenged with quantifying and monitoring the concomitant impacts of woody plant encroachment and brush management so that trade-offs (e.g. Nelson et al. 2009) can be objectively evaluated at spatial and temporal scales relevant to land management and policy (Fig. 2.15).

Rangelands prone to woody plant encroachment present a novel series of dilemmas, challenges, and opportunities for mitigation. For example, proliferation of woody plants can promote primary production and carbon sequestration under some circumstances, and may trigger new land-use drivers for biofuel production (Park et al. 2012) or as industries seek opportunities to offset CO_2 emissions. Woody plant proliferation in grasslands and savannas managed traditionally for grazing may therefore shift from being an economic liability to a source of income and economic diversification. However, under this scenario, grasslands and savannas and the plants and animals endemic to them would be at risk and their influences on hydrology, tropospheric chemistry (such as non-methane hydrocarbons, Guenther et al. 1999), and mesoscale meteorology altered. At present, our ability to evaluate and weigh these trade-offs, and their potentially synergistic interactions, is limited owing to variable, and often conflicting, results, and by limited scientific information (Archer and Predick 2014). These ecosystem-science challenges are magnified when placed in the human dimension context of cultural traditions, stakeholder preferences and priorities, market externalities, and climate change (Chapter 14, this volume). Given the cost and short longevity of brush management treatments, the adage “an ounce of prevention is worth a pound of cure” is applicable. In areas where WPE is at advanced stages, grassland restoration may not be economically feasible or sustainable and alternative land uses should be considered.

Grasslands and savannas are integral to the global carbon, water, and nitrogen cycles, and to human well-being (Campbell and Stafford Smith 2000; Reynolds et al. 2007; Peters et al. 2015). Their extensive airsheds and watersheds provide habitat for wildlife and a variety of ecosystem goods and services important to both local and distant settlements and cities. As such, they have considerable multipurpose value. A key component of dryland ecosystem management is maintaining the proportions of herbaceous and woody plants within a range that satisfies a given set of objectives and values, some of which may be conflicting (e.g., wildlife vs. livestock, Du Toit et al. 2010; Augustine et al. 2011). Perspectives on woody plants in rangelands vary widely depending on cultural traditions and land-use goals and objectives. In many regions of the world, woody plants are a valued source of food (e.g., honey, fruits, seeds), fuel, charcoal, and construction materials and an important source of fodder for browsing livestock (e.g., goats, camels), and wildlife. Additionally, there is growing recognition that woody plants on rangelands can provide products with potential commercial (e.g., gums, resins) or medicinal value.

Policy and management issues related to rangeland conservation have evolved to extend well beyond the traditional concerns of livestock production and game management (wildlife valued for sport hunting) to include potential effects on hydrology, carbon sequestration, biological diversity, atmospheric chemistry, and climate system (Archer 2010; Eldridge et al. 2011). The research community is challenged with quantifying and monitoring these varied impacts so that trade-offs (Fig. 2.15) can be assessed objectively and used as the foundation for science-based decision making. The management community is challenged with devising approaches for creating or maintaining woody-herbaceous mixtures in spatial arrangements that negotiate and balance competing land use and conservation objectives.

2.7 Future Perspectives

The woody plant encroachment phenomenon highlights the challenges of integrating stochastic and deterministic drivers of environmental change and plant trait representations to predict vegetation change. Vegetation models that account for the complexity of these interactions will be better suited to predict how changes in climate and atmospheric conditions will influence the future structure, function, and distribution of grasslands, savannas, woodlands, and forests (e.g., Scheiter and Higgins 2009). Among the philosophical differences that remain are the long-standing controversies regarding the influence of equilibrial dynamics, based upon the persistent properties of mature plants, and the influence of random environmental events and externalities on recruitment, mortality, and mutable competitive hierarchies of species during establishment.

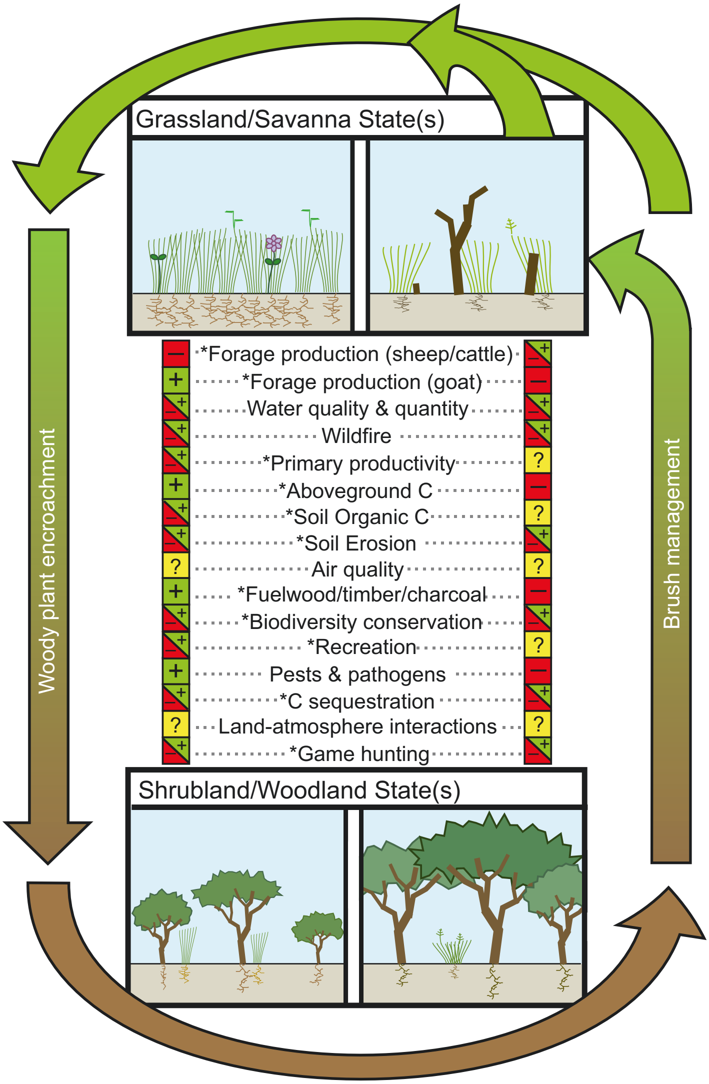

Fig. 2.15 Potential outcomes of woody plant encroachment and associated “brush management” activities. Symbols in boxes denote potential decreases (−), increases or improvements (+), mixed, context-dependent results (−\+), or insufficient information (?). From Archer and Predick (2014)

Research on WPE should draw from and contribute to the area of trait-based ecology. Discussions framed in terms of “woody plants” and their proliferation in “grasslands” do not help explain why only a few of the many woody species in a flora have become encroachers. What specific traits allowed these species to proliferate in grasslands after livestock introduction, while most other woody species could not? How do those traits determine the varied ecosystem effects of WPE on carbon stocks, soil fertility, and water budget? What traits may explain the idiosyncratic responses of herbaceous vegetation to brush management? Such questions are germane to those being asked in modern evolutionary ecology. Their answers have real-world implications for human welfare, rural economies, and climate change readiness.

There is broad consensus in the Earth sciences that the regulation of global water and carbon cycles by terrestrial vegetation is a critical aspect upon which the climate future of our planet depends. There remain significant knowledge gaps not the least of which center on vegetation change in the world's herbaceous communities. The influence of WPE on local water budgets, we are now learning, can influence the hydrological cycle at regional scales.

A better understanding of the controls over woody plant "carrying capacity" is needed to position us to predict how community dynamics and ecological processes will respond to changing environmental conditions. The upper limits of woody cover in rangelands seem to be dictated by mean annual precipitation, but mechanisms contributing to the MAP constraint are not clear. Density-dependent mechanisms would be a logical expectation, but studies quantifying interactions among woody plants in rangelands are uncommon and should receive more emphasis. The limited evidence available for density-dependent control over woody plant density or cover is equivocal. Our understanding of the extent to which the upper limits of woody plant cover are governed by the traits of seedlings influencing recruitment patterns and the traits of adult plants that influence ecosystem processes is limited. Alternative conceptual models highlight stochastic spatial processes, in which the equivalent of a carrying capacity is an emergent property of recruitment and disturbance probabilities.

Woody plant proliferation in grasslands and savannas has been ongoing for decades and is approaching or exceeding 100 years in some areas. Our focus has been on understanding the encroachment process, its rates, causes, and consequences. But "encroachment" is not the end of the story. We know relatively little of the dynamics of the shrubland or woodland communities that have developed on former grassland and how they might change through time. Understanding post-encroachment dynamics is important if we are to predict how ecosystem structure and function might continue to unfold over time. With accelerating rates of climate change and other anthropogenic disturbances, the potentially novel and dynamic communities of plants and animals created in the wake of Anglo-European settlement may be a natural laboratory for studying vegetation dynamics in the Anthropocene.

Responses of herbaceous vegetation to brush management are highly variable. Herbaceous production and diversity increase on some sites, but decrease on others, and positive responses, when they occur, vary greatly in their longevity. Improvements in our ability to explain these varied responses will enable us to identify (1) where and when brush management intervention might be most likely to achieve the outcomes desired for a given set of management or policy goals, and (2) the combination and time series of intervention methods that are most likely to effect desired changes within socioeconomic constraints.

Uncertainties and knowledge gaps regarding the impact of WPE and subsequent brush management activities on carbon sequestration are substantial. Studies quantifying the herbaceous production responses to WPE and brush management are abundant, but robust predictions are elusive, particularly with brush management. Data quantifying woody plant productivity is a major data gap, as are estimates of belowground production. Flux-tower networks targeting WPE-brush management areas will enable us to better determine source-sink relationships. Recent advances in tools for gathering remote-sensing data (e.g., LIDAR; unmanned aerial vehicles; multispectral, hyperspectral, and thermal satellite-based sensor arrays) have given us new capabilities for quantifying aboveground vegetation structure and biomass over expansive and remote areas. Furthermore, these technologies have the potential to quantify cacti, an important and sometimes very abundant, plant functional type on rangelands. The contributions of cacti have been virtually ignored in biomass and ANPP estimates of the aboveground carbon pool. These synoptic perspectives will position us to inventory carbon stocks more accurately at regional scales, where landscapes are mosaics of areas in various stages of WPE and recovery from extreme events or management interventions. Studies quantifying changes in the soil organic carbon pool with WPE have been accumulating over the past 10–15 years, but there is an urgent need to balance these with data documenting brush management impacts. In both cases, there is a need for standardization of methodologies if we hope to develop robust, meaningful generalizations.

From a conservation perspective, WPE represents a major threat to grassland and savanna ecosystems and their endemic plants and animals. This perspective needs to be considered explicitly when evaluating ecosystem service portfolios that have focused traditionally on forage and livestock production, water quality/quantity, etc. Biodiversity perspectives should be broadened similarly to include organisms valued for their functional and charismatic roles, as well as animals valued for hunting and plants valued for forage.

Concerns over WPE will be complicated by the invasion and proliferation of non-native grasses. Acting as "transformer species," these exotic grasses can change the character, condition, function, and form of native ecosystems. Once established, non-native annual and perennial grasses can generate massive, high-continuity fine fuel loads that predispose grasslands to fires that can be more frequent and intense than those with which they evolved. The result is the potential for shrublands and woodlands developing on former grasslands to be quickly and radically transformed into exotic grass monocultures over large areas. This is well under way in the North American cold desert region (e.g., cheatgrass, *Bromus tectorum*) and is in its early stages in hot deserts. These transformations have profound effects on ecosystem processes (Betancourt 2015) and biodiversity (Steidl et al. 2013) and present unique management challenges. More research is needed to develop an understanding of how WPE and non-native grasses could be comanaged to conserve biodiversity and ensure the sustained provision of core ecosystem services.

Assessments of woody plan encroachment and actions taken to halt or reverse it must be broadly considered and evaluated in the context of plant and animal community dynamics, biodiversity, and ecosystem function. The near-term context will be largely determined by land-use priorities and socioeconomic externalities. Over the longer term, climate change will determine the context within which land-use and socioeconomic decisions are made. Management therefore needs to address ongoing and near-term challenges associated with WPE while positioning us to anticipate and adapt to changes on the horizon.

2.8 Summary

Woody plant encroachment (WPE) is an umbrella phrase describing increases in abundance and distribution of woody plants in grassland and savanna plant communities worldwide. WPE has been documented in arid, semiarid, and subhumid climate zones and in tropical, subtropical, temperate, and arctic regions. WPE has been traditionally associated with ecosystems degraded due to intensive grazing by cattle and sheep. We now appreciate, however, that woody plants play important roles in maintaining ecosystem processes on these degraded landscapes. Consequently, their proliferation is now viewed more appropriately as a symptom, rather than cause, of degradation.

2.8.1 Causes

Although numerous efforts have sought to elucidate the proximate causes of woody encroachment, robust generalizations remain elusive. The WPE process is highly context dependent and influenced by numerous, interacting location-specific factors related to climate, fire frequency and intensity, grazing/browsing regimes, soil properties, and functional traits of the encroaching species and native browsers.

MAP sets an upper limit to woody plant cover, which tends to plateau to a maximum above 650 mm. However, local patterns of disturbance (fire, browsing) and soil properties (texture, depth) may prevent this potential from being realized. In the absence of these constraints, interactions among the seasonality, interannual variation, and intensity of precipitation events will determine the rate and extent of woody plant recruitment. Precipitation in arid grasslands varies markedly in both space and time. This can cause cover of woody plants to wax and wane at decadal or longer time scales, which helps to explain the high variation observed in rates of WPE. Climate zones with higher precipitation have the capacity for rapid conversion from grassland to woodland, but decadal-scale variation in precipitation can make it difficult to distinguish natural fluctuations from directional changes in vegetation communities.

Paleoecological studies indicate that the balance between grass- and woody-plant-dominated communities has fluctuated over the last 10,000 years, suggesting climate as a long-term determinant. However, WPE in the "Anthropocene" is more complicated. Concentrations of atmospheric CO_2 have been increasing exponentially since the advent of the industrial revolution. Although probably not a triggering factor *per se*, rising CO_2 levels may well have been a supporting factor in that woody plants, which are characterized by the C_3 photosynthetic pathway, would have benefited more from CO_2 "fertilization" than the C_4 grasses that dominate tropical, subtropical, and warm-temperate regions. Further, woody plants can use higher assimilation rates to expedite the accumulation of woody biomass and carbohydrate storage. This would lower their mortality risks during the critical establishment phase while also enabling more rapid growth to sizes where they could escape constraints imposed by fire and browsers.

Woody plant encroachment has also coincided with the global intensification of livestock grazing. Prior to the introduction of domestic grazers, an abundance of fine fuels produced by grasses stimulated periodic fires that regularly suppressed woody plant recruitment and controlled the density of mature shrubs and trees. The introduction of large numbers and high concentrations of livestock reduced both the density and continuity of fine fuels, which reduced fire frequency and intensity, and facilitated development of woody plant communities. Locally, woody plants benefited from secondary factors, such as livestock dispersing seeds or by displacing native browsers and seed predators.

When woody plant seedlings germinate in the immediate proximity of mature grasses, they face potentially intense competition for light, water, and soil nutrients. Grazing reduces grass biomass both above- and belowground and therefore the ability of grasses to competitively suppress shrub seedlings. However, this does not explain why woody plants are also encroaching into areas protected from grazing livestock. In many grasslands, ground cover consists of bare and vegetated patches, and thus spatially variable levels of competition. In addition, where annual rainfall is monsoonal or bimodal, woody seedlings may germinate and establish during those periods when competition for soil moisture is low. Having survived the most vulnerable period immediately after germination, woody plants rapidly develop deep taproots below the primary root zone of grasses. This increases their access to water that has infiltrated more deeply and alleviates competition for water with grasses. As woody seedlings grow taller, they incrementally gain competitive dominance over their grass neighbors and may begin to displace grasses through resource competition. At some stage, grasses can substantially influence the dominance of woody saplings only through their influence on the fire cycle. However, woody encroachers capable of regenerating vegetatively (resprouting) often survive fire. Then if grazing reduces fire frequency, plants in these "seedling" or "sapling banks" are poised to grow quickly and escape the flame zone of future fires. Eventually, these plants will produce seed and intensify propagule pressure in grasslands. Long-term maintenance of grassland and savanna ecosystems is therefore contingent on maintaining a balance woody plants and grasses based on climate, disturbance, and species traits.

2.8.2 Consequences for Ecosystem Services

Traditional concerns related to the loss of forage production accompanying WPE have been broadened to include consequences for provision of services related to primary production and carbon sequestration. Because of the global extent and magnitude of the impact of WPE, these changes can potentially significantly affect the global carbon budget and energy balance. If encroaching woody plants are less productive than the grasses they replace, then ecosystem ANPP would decline; if they are more productive than the grasses they displace, then ANPP would increase; and if ANPP of encroaching woody plants is comparable to that of the grasses they are replacing, then there would be no net change. Evidence indicates that all three scenarios are at play, with changes in ANPP scaling linearly with MAP. Below an MAP of ~340 mm, ANPP will decline with WPE and above this level ANPP will increase. Our understanding of WPE effects on the soil organic C pool, which typically dwarfs the aboveground pool in grasslands, is poor. Some studies show large increases in soil organic C with WPE, whereas others show no change or large decreases. Reasons for this range of responses have yet to be explained. This is a major knowledge gap that needs to be filled if we are to understand fully the effects of WPE on the carbon cycle.

WPE has the potential to reduce streamflow and/or groundwater recharge by reducing deep recharge and runoff through increases in evapotranspiration (ET). However, evidence for the relationship between WPE and water yield has been equivocal and may depend on climate, edaphic factors, and traits of the encroaching woody species. WPE may impact the water budget only where MAP approximately equals PET. Where deep-rooted trees have encroached in grasslands on sites with shallow water tables, ET has increased, but where recharge and runoff are controlled strongly by physical properties of the soil, WPE has had little additional effect on the hydrological budget.

WPE markedly affects biodiversity and threatens the very existence of grassland and savanna ecosystems and their endemic plants and animals. In North America, diversity of herbaceous plants declines ~45 % when woody plants encroach. Changes in vegetation structure and species composition accompanying WPE contribute to the loss of grassland-adapted animals by reducing both the quantity and quality of their required habitat. Because a principal result of WPE is a marked increase in vertical and horizontal vegetation structure, composition of animal communities shifts to favor species that prefer woody vegetation. WPE can affect habitat quality for grassland-associated species that persist within encroached areas through changes in rates of predation or changes in the types, abundance, or availability of food resources. Ultimately, when woody cover exceeds species-specific thresholds, populations of grassland-associated species are displaced by shrubland- or woodland-associated species.

2.8.3 Management

Proliferation of woody plants has long been of concern in areas managed primarily for grazing cattle and sheep, where WPE typically reduces production of forage, complicates animal handling, and improves habitat for ectoparasites. As a result, multiple strategies have been developed to reduce cover of woody vegetation. Collectively known as "brush management," these approaches include prescribed burning, mechanical clearing, and herbicide application. Responses of herbaceous vegetation to brush management practices have been highly variable and typically short-lived. Early goals for brush management centered on eradicating shrubs to improve production of livestock, which gave way to efforts aimed at shrub "control," which gave way to integrated brush management systems (IBMS). IBMS is ecologically based and predicated on using location-specific knowledge of vegetation characteristics, climate, soils, and topography to determine the type, sequencing, and timing of initial and follow-up treatments. In the IBMS model, landscapes are comanaged for livestock and wildlife, and with consideration for the diverse portfolio of ecosystem services that rangelands provide.

Unless subsidized, brush management is rarely economically feasible based solely on increases in forage production and livestock performance. However, consideration of "intangibles" related to enhancements of other ecosystem services will influence the conclusions taken from traditional, narrowly focused cost-benefit calculations. For example, brush management contributions to the conservation of grassland ecosystems and the plants and animals unique to them constitute an important benefit that is largely unaccounted for. Conversely, increased potential for carbon sequestration may be a positive outcome of WPE that would have to be weighed against potential reductions in biodiversity, water yield, or changes in vegetation structure that affect key wildlife species adversely. The scientific community is challenged to quantify and monitor the concomitant impacts of WPE and brush management on the diverse components comprising an ecosystem service portfolio so that trade-offs can be evaluated objectively in the context of a clear set of goals and priorities.

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Chapter 3
Ecohydrology: Processes and Implications for Rangelands

Bradford P. Wilcox, David Le Maitre, Esteban Jobbagy, Lixin Wang, and David D. Breshears

Abstract This chapter is organized around the concept of ecohydrological processes that are explicitly tied to *ecosystem services*. Ecosystem services are benefits that people receive from ecosystems. We focus on (1) the regulating services of water distribution, water purification, and climate regulation; (2) the supporting services of water and nutrient cycling and soil protection and restoration; and (3) the provisioning services of water supply and biomass production. Regulating services are determined at the first critical juncture of the water cycle—on the soil surface, where water either infiltrates or becomes overland flow. Soil infiltrability is influenced by vegetation, grazing intensity, brush management, fire patterns, condition of biological soil crusts, and activity by fauna. At larger scales, water-regulating services are influenced by other factors, such as the nature and structure of riparian zones and the presence of shallow groundwater aquifers. Provisioning services are those goods or products that are directly produced from ecosystems, such as water, food, and fiber. Work over the last several decades has largely overturned the notion

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that water supply can be substantially increased by removal of shrubs. In riparian areas, surprisingly, removal of invasive, non-native woody plants appears to hold little potential for increasing water supply. Here, the primary factor appears to be that non-native plants use no more water than the native vegetation they displace. Clearly there is a close coupling between biota (both fauna and flora) and water on rangelands—which is why water-related ecosystem services are so strongly dependent on land management strategies.

Keywords Ecosystem Services • Infiltration • Rangeland Hydrology • Riparian • Groundwater • Overland Flow • Soil Water • Climate • Water Supply • Climate Regulation • Erosion • Spatial Variability • Scale • Thresholds • Connectivity

3.1 Introduction

The distribution, quality, and provisioning of water are intimately related to how rangeland landscapes function and are managed, particularly with respect to land-use change. Understanding the linkages between vegetation and the water cycle is a major focus of ecohydrology, an emerging discipline that melds the sciences of hydrology and ecology as a means of addressing complex environmental issues. Its scientific heritage also embraces many other disciplines, including watershed management, plant physiology, soil science, geomorphology (Newman et al. 2006), and of course rangeland hydrology (Branson et al. 1981). In addition, the importance of interactions between fauna and the water cycle is increasingly being recognized.

Ecohydrology is very much an applied science with a focus on problem solving (Nuttle 2002; Jackson et al. 2009b; Wilcox et al. 2011), but at the same time it has a firm theoretical foundation (D'Odorico et al. 2012, 2013a; Turnbull et al. 2012; Saco and Moreno de las Heras 2013). Because of its strong intellectual roots in research conducted on drylands—including semiarid and subhumid rangelands (Rodriguez-Iturbe and Porporato 2004; D'Odorico and Porporato 2006; Newman et al. 2006)—and its "transdisciplinary" nature, ecohydrology has advanced our knowledge of rangelands (Wilcox and Newman 2005; Wilcox et al. 2012a). But much more needs to be done to take full advantage of the scientific strengths of ecology and hydrology (King and Caylor 2011).

In this chapter, we present some of the major ecohydrological advances that have occurred in rangelands in the last quarter century and discuss their importance for management. There has been extraordinary scientific progress on so many fronts that it will be impossible to adequately address all of them; but we aim to provide a comprehensive overview of those most relevant to rangeland systems. We rely extensively on the recent publication of several review papers and books dealing with the ecohydrology of rangelands (D'Odorico and Porporato 2006; Newman et al. 2006; D'Odorico et al. 2010; Asbjornsen et al. 2011; Wang et al. 2012a).

We have organized our chapter around the concept of *ecosystem services*—as elaborated in the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment

2005). Ecosystem services are benefits that people receive from ecosystems. They can be categorized as *regulating services*, *supporting services*, *provisioning services*, and *cultural services*. We focus on (1) the regulating services of water distribution, water purification, and climate regulation; (2) the supporting services of water and nutrient cycling and soil protection and restoration; and (3) the provisioning services of water supply and biomass production. In addition, we review current conceptual, theoretical, and technical developments that will provide a foundation for future advances in rangeland ecohydrology—advances critical to informed management decisions and actions needed to meet the growing environmental challenges of rangeland systems.

3.2 Ecosystem Services

The provisioning of water to ensure that humans obtain the quantity and quality of water needed is the most fundamental service provided by ecosystems (Falkenmark and Rockstrom 2004; Brauman et al. 2007). Paradoxically, this is especially true of rangelands, even though most are considered "drylands," which by definition convert a relatively small percentage of precipitation into streamflow or groundwater (Wilcox et al. 2003b). Water produced on rangelands, whether drawn from aquifers or from surface sources, is vitally important to support the people, livestock, and wildlife that inhabit these regions (Le Maitre et al. 2007; Reynolds et al. 2007). Many dryland population centers are growing at alarming rates, and this growth brings with it numerous environmental stresses (D'Odorico et al. 2013a). The degradation of rangelands diminishes their ability to regulate and provide water (MEA).

Figure 3.1 illustrates an important conceptual advance in understanding water dynamics in rangelands: the explicit partitioning of water resources into "blue water" (liquid water) and "green water" (vapor- or water-produced evapotranspiration [ET]) (Falkenmark and Rockstrom 2004, 2006; Gordon et al. 2005; Falkenmark et al. 2009; Rockstrom et al. 2009; Hoff et al. 2010). To date, the water management community has focused almost exclusively on blue water resources and has failed to recognize the opportunity to effectively allocate green water. Maximizing the amount of green water used for plant production or transpiration and minimizing the amount lost as soil evaporation is an imperative. How rangelands are managed—especially their surface cover—has a tremendous effect on both the relative proportion of blue water to green water and the partitioning of green water between E and T. The ability of rangelands to regulate and provide water is strongly dependent on conditions at three critical junctures in the terrestrial water cycle (Falkenmark and Rockstrom 2004). The first and most critical is whether water infiltrates into the soil or becomes *overland flow*—which is mainly a function of rainfall intensity, slope, and soil infiltrability. The importance of soil infiltrability has long been recognized (Smith and Leopold 1941) and has been the focus of considerable research in the last half century or more. It is influenced by many factors, including management practices; for example, overgrazing that results in a loss of vegetation cover and an increased exposure of bare soil can dramatically reduce soil infiltrability (Blackburn et al. 1982; Snyman and du Preez 2005).

Water that does not infiltrate becomes overland flow on slopes, but the final outcome in terms of net water losses is highly scale dependent. At the hillslope scale, runoff–runon dynamics become important and are strongly influenced by the spatial variability of infiltration. For example, overland flow may be generated from some areas on the hillslope only to infiltrate the soil somewhere downslope (Bergkamp 1998a; Wilcox et al. 2003a), and can contribute to surface and groundwater recharge.

The second critical juncture is at the root zone: soil water may drain out of the root zone, and eventually be stored as groundwater or discharged into a stream as baseflow, or may stay in the root zone and eventually be transpired or evaporated from the soil surface. Although largely a function of climate, soil, and geological characteristics, this process can also be affected by management strategies, especially if the functional type of vegetation—and particularly its rooting depth—is changed. The linkage between vegetation and groundwater is very much influenced by the depth to groundwater. Recent work has highlighted the importance of rangelands where groundwater tables are shallow and strongly influenced by vegetation that are termed *groundwater-coupled rangelands* (Jobbágy and Jackson 2004a).

The third critical juncture is the fate of soil water: whether it is absorbed by plants and transpired or lost through evaporation from the soil surface, which is often described as the partitioning of E and T (Fig. 3.1). This juncture is critical because it dictates the amount of biologically available water on rangelands (Falkenmark and Rockstrom 2004; Newman et al. 2006). The portioning of E and T is central to water cycling and is discussed in more detail in the section *Supporting Services*, below.

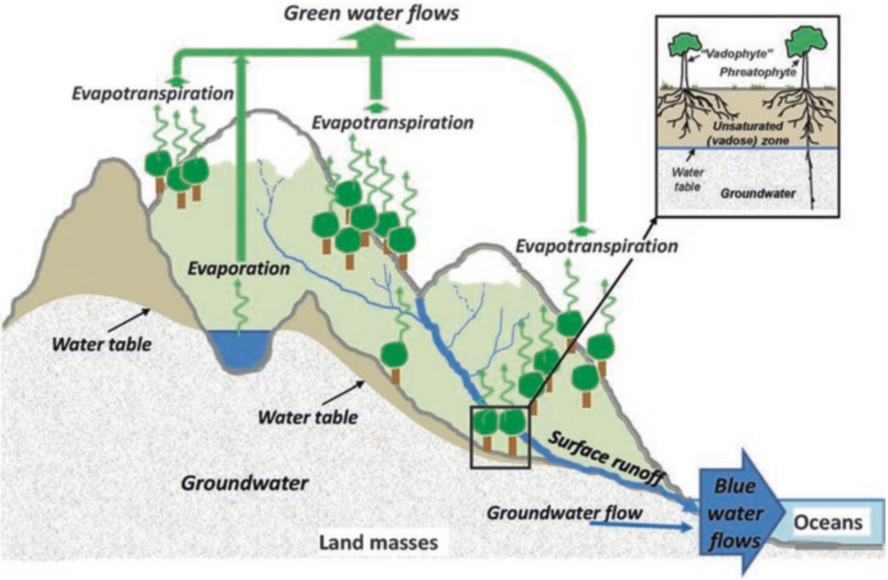


Fig. 3.1 Conceptual diagram of the water cycle, highlighting blue (liquid) and green (vapor) flows. Source: Figure 1 in D'Odorico et al. (2010)

3.2.1 Regulating Services: Water Distribution and Purification

Ecosystem services regulating water on rangelands include those that affect the amount, timing, and quality of blue water flows. These are to a large extent determined at the first critical juncture of the water cycle—on the soil surface, where water either infiltrates or becomes overland flow. For this reason, a great deal of research, most of it conducted at the point or plot scale, has focused on understanding the infiltration process and how it is affected by different management strategies (Pyke et al. 2002; Stavi et al. 2009).

3.2.1.1 Infiltration: Water Regulation at the Soil Surface

Infiltration of water into the soil is enhanced and maintained by the presence of vegetation, both by direct influences (soil protection, root action, etc.) and by modification of the soil through the addition of organic matter. This tight coupling between vegetation and soil infiltrability on rangelands was recognized many years ago (Smith and Leopold 1941; Woodward 1943; Dyksterhuis and Schmutz 1947; Dortignac and Love 1961); but recent research is adding greatly to our understanding by providing specifics concerning how management practices and disturbances (grazing, shrub management, fire) and vegetation cover types (shrubs vs. grasses, biological soil crusts) affect soil infiltrability, but also the contributions of spatial variability and scale. In addition, we now recognize that fauna—large and small—can significantly affect soil infiltrability.

Influence of Grazing. There is an extensive body of work examining the ecohydrological influence of grazing, and specifically its influence on soil infiltration. Much of this work was conducted in the USA in the 1970s and 1980s and has been summarized in several review papers (Gifford 1978; Wood et al. 1978; Wood and Blackburn 1981; Blackburn et al. 1982; Trimble and Mendel 1995). The findings consistently show that, irrespective of grazing systems, light-to-moderate grazing generally has little adverse effect on the ecohydrology of rangelands and may even have a positive effect, whereas heavy grazing generally significantly decreases soil infiltrability. These conclusions have been verified by more recent investigations conducted on rangeland throughout the globe (Hiernaux et al. 1999; Ludwig et al. 1999; Savadogo et al. 2007).

Influence of Shrubs. Over the past several decades, grasslands and savannas worldwide have been undergoing a process of woodland conversion, often described as woody plant encroachment (Archer 1994; Archer et al. 2011). For many rangelands, attempts to reverse this process or even to control it have met with minimal success (Archer et al. 2011). During the past quarter century, considerable research has been focused on understanding the ecohydrological implications of this conversion (Huxman et al. 2005; Wilcox et al. 2006). It has generally been found (though not always—see Moran et al. (2010)) that infiltration rates are higher beneath shrub canopies than in intercanopy areas (Lyford and Qashu 1969; Seyfried 1991;

Bergkamp 1998b; Schlesinger et al. 1999; Wilcox 2002; D'Odorico et al. 2007; Wilcox et al. 2008; Pierson et al. 2010; Daryanto et al. 2013; Eldridge et al. 2013), primarily owing to the accumulation of organic matter under shrubs, root activity (Joffre and Rambal 1993; Martinez-Meza and Whitford 1996; Jackson et al. 2000), and soil disturbance by fauna (see "Influence of Fauna" section). In some situations the chemical composition of the litter may cause water repellency (hydrophobicity), which reduces the infiltration capacity of soils beneath the canopy, at least in the short term (Doerr et al. 2000). In addition, burning can cause or aggravate hydrophobicity (Hester et al. 1997; Cammeraat and Imeson 1999).

Influence of Biological Soil Crusts. Biological soil crusts are the community of living organisms, including fungi, lichens, cyanobacteria, and algae, at the soil surface. The integrity of biological soil crusts, which are common in many drylands, is extremely sensitive to disturbance such as heavy grazing or off-road vehicle traffic (Belnap and Lange 2001). The relationship between biological soil crusts and processes of soil infiltrability is complex: their presence can increase, decrease, or have no effect on this process (Eldridge 2003; Warren 2003; Belnap 2006b). One factor that appears to determine local hydrological response is the successional stage, or status of crust development. As crusts mature, the biomass of cyanobacteria, mosses, and lichens increases—which in turn increases aggregate stability, shear strength, and roughness of the soil surface (Belnap 2003, 2006a). A six-level classification of level of crust development (LOD) was recently developed for biological soil crusts, based on (1) color (light to dark, visual assessment); (2) presence of mosses/lichens; and (3) soil surface roughness (Belnap et al. 2008). Soil crust classification was found to be strongly related to infiltration rates, with infiltration being highest where crusts were the most developed (Belnap et al. 2013).

Influence of Fauna. A recent review of ecohydrological studies revealed a strong emphasis on plant–hydrology interactions, with few studies of fauna–hydrology interactions (Westbrook et al. 2013). Only 17 % of the 339 papers reviewed considered fauna–hydrology interactions, and more than half of those focused on how hydrology affects fauna rather than how fauna function to influence ecohydrology. Fauna are usually seen as passive beneficiaries of ecohydrological changes rather than as playing a key role in the formation of vegetation patterns.

Fauna have both direct and indirect effects on ecohydrology, ranging from micro-perturbations to the macro-perturbation commonly described as ecosystem engineering (Whitford and Kay 1999; Jones et al. 2006; Butler 2007; Hastings et al. 2007; Jones 2012; Raynaud et al. 2013). These processes are critical for producing the organic matter that binds with mineral soil particles to form aggregates (peds), which facilitate the movement of water through soils and thereby increase infiltration and percolation rates and capacities (Weaver 1926; Coleman et al. 1992; Lavelle 1997; Angers and Caron 1998; Roth 2004; Jones et al. 2006). Soil fauna, particularly the mammals and macro-invertebrates (such as earthworms, termites, or cicadas), engineer ecosystems by creating openings at the soil surface and tunnels, also known as macropores, beneath the soil surface (Beven and Germann 1982; Lavelle 1997; Leonard et al. 2004; Roth 2004). These openings increase infiltration and percolation of water through the soil profile (Dean 1992; Angers and Caron 1998;

Whitford and Kay 1999; O'Farrell et al. 2010), in the same way as do the channels left by decayed plant roots (Beven and Germann 1982). Clearly, one cannot separate the roles played by animals from those played by plants; but, in combination, they significantly affect how water moves through the soil (Shafer et al. 2007)—including processes such as groundwater recharge, which in turn affect plant productivity and other ecosystem services.

Influence of Fire. The frequency and intensity of wildfires are increasing on rangelands as a result of several factors, including rising temperatures and the invasion of non-native grasses (Running 2006; Wilcox et al. 2012b). In addition, prescribed fire is now more commonly applied as a management tool for many rangelands (Twidwell et al. 2013). A number of recent reviews summarize the extensive literature on the hydrological consequences of fire on rangelands; in general, study results indicate that the infiltration capacity of soils is significantly reduced immediately following fires, but the extent of this reduction depends on fire severity, degree of hydrophobicity, antecedent soil moisture, and topographic position (Baker and Shinneman 2004; Shakesby and Doerr 2006; Pierson et al. 2011).

3.2.2 Overland Flow: Regulation at the Hillslope Scale

Water that does not infiltrate, of course, becomes overland flow or surface runoff. It is at the hillslope scale that important interactions take place between vegetation patches and runoff. Surface runoff may be captured and stored by vegetation patches or other surface obstructions, a process known as runoff–runon (Ludwig et al. 2005).

An important conceptual advance in describing and clarifying the linkages between surface runoff and vegetation patches is the trigger-transfer-reserve-pulse (TTRP) framework (Fig. 3.2) (Ludwig et al. 1997, 2005). This framework was originally proposed as a way of describing runoff–runon processes observed in areas of banded vegetation (Anderson and Hodgkinson 1997; Dunkerley and Brown 1999; Valentin and d'Herbes 1999; Tongway and Ludwig 2001); it was subsequently verified for other vegetation patch types in semiarid settings (Reid et al. 1999; Wilcox et al. 2003a; Ludwig et al. 2005). The framework assumes that the redistribution of resources from source areas (bare patches) to sink areas is a fundamental process within drylands, and that this process may be disrupted if vegetation patch structure is altered by disturbances such as overgrazing or multiyear drought. These dynamics govern how runoff and runon vary with scale in semiarid settings. In regions where runoff is efficiently captured down slope by vegetation patches, unit-area runoff and erosion diminish rapidly with increasing scale. But where vegetation patch structure has been disturbed and runoff is not efficiently captured, declines in runoff with increasing scale are much smaller (Fig. 3.3). Erosion may even increase as runoff increases with increasing scale, leading to rilling and gully formation (Wilcox et al. 2003a; Moreno de las Heras et al. 2010).

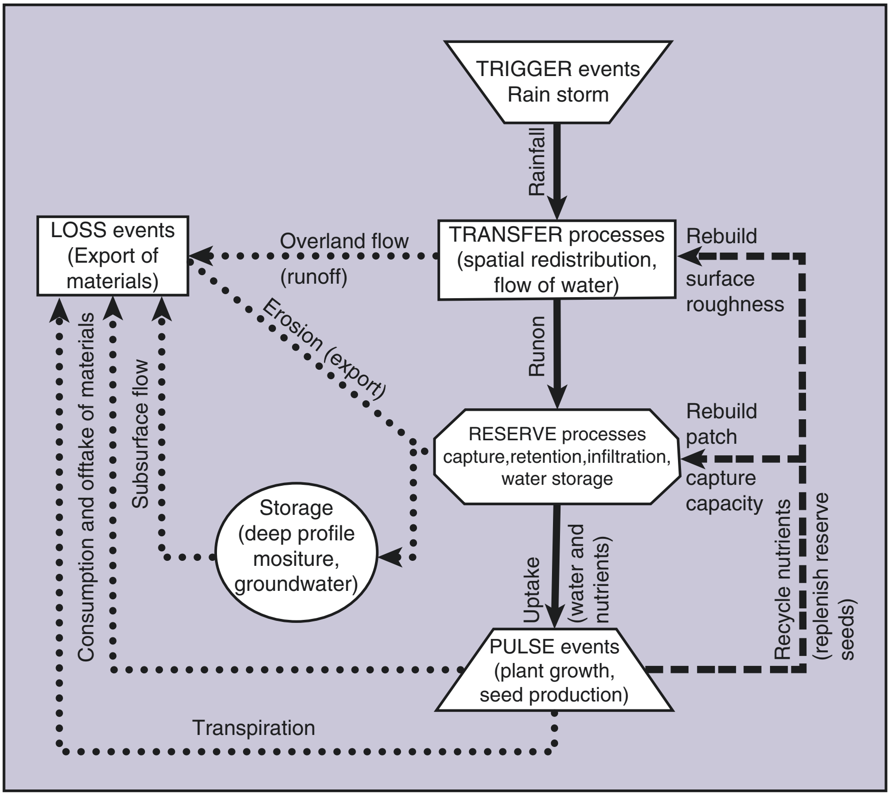
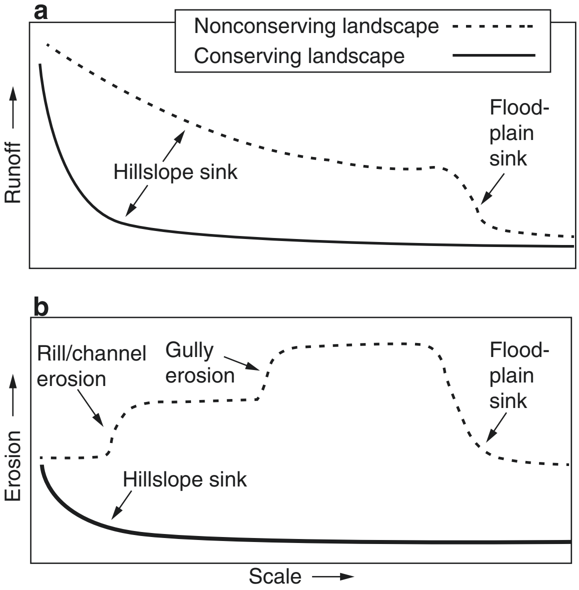


Fig. 3.2 The Trigger-Transfer-Reserve-Pulse framework illustrates how temporal events (e.g., water input from rainfall) initiate a number of other events. Solid arrows indicate direct action of flows of water, dashed arrows indicate feedbacks, and dotted arrows indicate losses (including transpiration, lateral subsurface flow, and groundwater recharge). Source: Figure 4 in Le Maitre et al. (2007)

Fig. 3.3 Hypothetical relationships demonstrating the relative changes in runoff and erosion with changes in scale and how these relationships are altered by disturbance. Source: Figure 9 in Wilcox et al. (2003)



3.2.3 Drainage: Water Regulation Within the Soil

Water that enters the soil may either evaporate, be transpired by plants, or drain out of the root zone and ultimately contribute to groundwater and streamflow. On rangelands, drainage is generally (but not always) a small percentage (<5 %) of the water budget (Wilcox et al. 2003b). Vegetation management that alters the amount of woody plants may affect drainage because woody plants are deeper rooted than grasses or forbs and tend to transpire more water. Therefore, woodlands and forests generally use more water than grasslands (Zhang et al. 2001). The relationship is complex, however, especially for drylands, as it is modified by other factors—including climate, soils, and topographic position (Huxman et al. 2005).

The shrub–streamflow framework (Fig. 3.4) was developed to aid in determining which landscapes are most "hydrologically sensitive" to changes in woody plant cover. A hydrologically sensitive landscape is one in which a shift in functional vegetation type (woody to nonwoody or vice versa) causes an important shift in the water balance. Hydrological sensitivity is dictated or strongly influenced by how vegetation change affects drainage; and it is also influenced by factors such as depth to water table, soil and geological characteristics, and topographic position. The shrub–streamflow framework uses these concepts to predict where hydrologically sensitive shrublands might exist (Wilcox et al. 2006).

The first criterion for hydrologic sensitivity—the presence of shallow groundwater—is likely to be stronger where the groundwater table is within a few meters of the surface, as in riparian zones or groundwater-coupled rangelands. Obviously, this condition affords more opportunity for interaction between deep-rooted vegetation and groundwater.

Seasonality of precipitation is a second criterion in determining hydrologic sensitivity. Those rangelands having the greatest potential for water to move deeply into the soil—beneath the rooting zone of herbaceous plants—will be the most hydrologically sensitive. Such deep drainage occurs in regions where winter precipitation is high. It is no coincidence that the strongest linkage between woody plants and streamflow has been observed in Mediterranean climates where precipitation is often "out of phase" with potential ET. For example, in South Africa (van Wilgen et al. 1998), Spain (Puigdefabregas and Mendizabal 1998), Australia (Walker et al. 1993), and California (Hibbert 1983), dramatic changes in drainage have been observed following vegetation changes in native shrublands. Similarly, shrublands in which soil recharge comes mainly from snowmelt may be hydrologically sensitive; a large pulse of melting snow often produces enough water to saturate or exceed the water storage capacity of the upper soil (Baker 1984; Seyfried and Wilcox 2006).

Finally, soil or geological conditions also determine hydrologic sensitivity, by affecting the potential for deep drainage. We would expect higher hydrologic sensitivity where soils are sandy (Moore et al. 2012; Dzikiti et al. 2013), are deeply cracked (Richardson et al. 1979), or are shallow and overlie fractured bedrock (Huang et al. 2006).

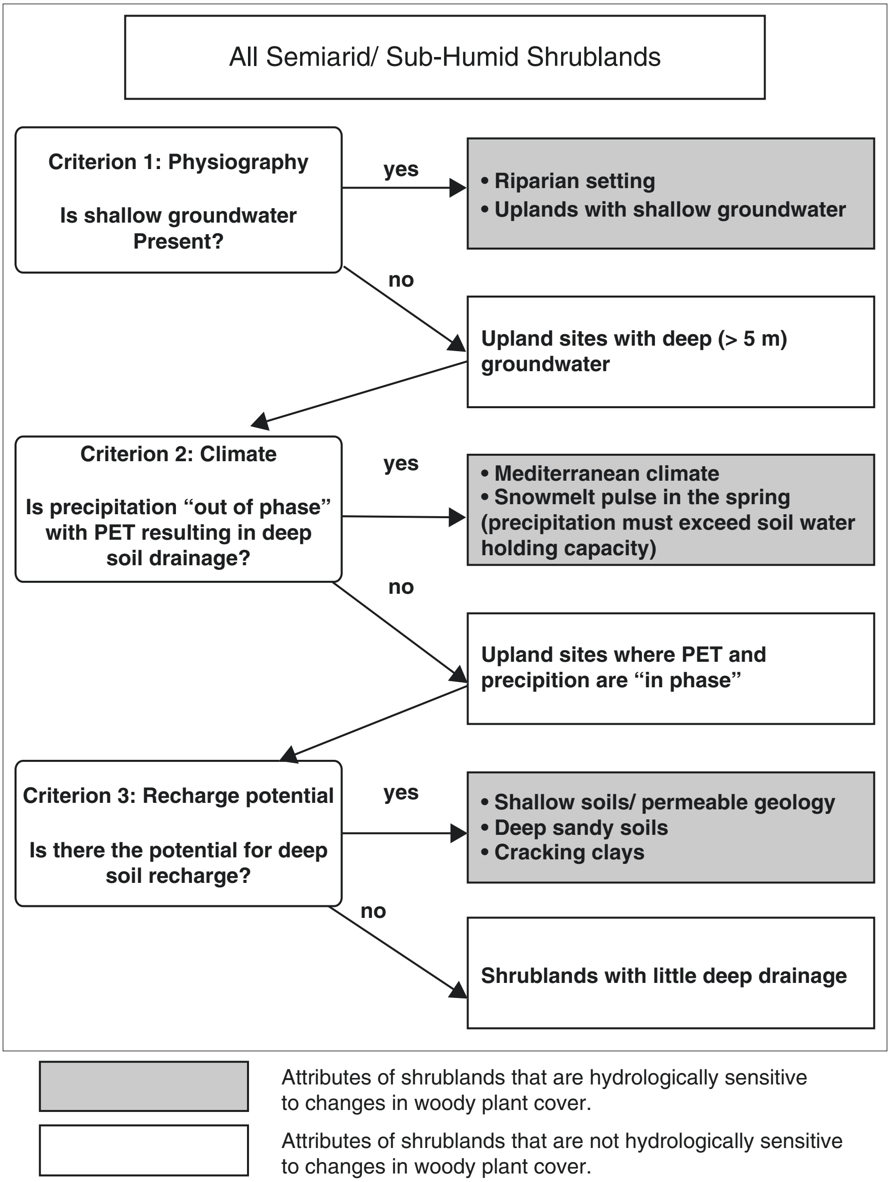


Fig. 3.4 The shrub–streamflow framework: Classification of the potential for increasing streamflow in various shrublands. Source: Figure 1 in Wilcox et al. (2006)

For many rangelands, the opportunities for deep drainage are quite limited, because of either climate or soils. In these landscapes, shifting from a grassland to a shrubland will have little effect on the overall water balance, but may nevertheless affect drainage in important ways. For example, in areas where even small amounts of drainage can be significant (such as sites where hazardous wastes are buried), the presence of deep-rooted shrubs may ensure that drainage below the root zone seldom occurs (Scanlon et al. 2005b, c; Seyfried et al. 2005).

3.2.4 Riparian Systems: Regulation at the Watershed Scale

The common perception is that rangelands are exclusively dryland environments. Even when the presence of riparian environments is recognized, these are generally seen as a minor component of the entire landscape system. However, there is a growing body of research showing that riparian environments are not only key habitats for rangeland fauna and flora, but also critical providers of ecosystem services to rangeland inhabitants (Milton 1990; Dean et al. 1999, 2002; Naiman et al. 2002; Sabo et al. 2005; Le Maitre et al. 2007; Soykan and Sabo 2009; Jones et al. 2010; Merritt and Bateman 2012).

Many of the features and key processes in groundwater-coupled systems are likewise found in riparian environments. The principal differences are that (1) riparian zones receive inputs of surface water, often from areas far upstream, that play a major role in their ecology (Boulton and Hancock 2006; Bunn et al. 2006; Nagler et al. 2008) and (2) the dynamics of riparian zones are strongly influenced by flow regimes and fluvial processes (Ward 1998), particularly sediment movement (Naiman et al. 1999; Tabacchi et al. 2000).

Riparian environments are typically located in the lowest parts of a landscape, where surface water (overland flow) and groundwater (subsurface flow) collect; thus they integrate outputs from all watershed-scale processes (Naiman et al. 2002). Their structure is long and narrow with a very large perimeter-to-area ratio—which makes them highly connected to, and thereby highly influenced by, events originating in the adjacent drylands. The headwaters section of a river typically has steep gradients, and the river bed contains rocks or boulders with little accumulation of fine sediments, whereas the middle and lower reaches are characterized by extensive alluvial deposits and wide floodplains (e.g., Nile, Platte, Euphrates, Ganges) (Vannote et al. 1980; Wiens 2002). These deposits are typically heterogeneous, with coarse sediments that can capture, store, and transmit large volumes of water interspersed vertically and horizontally with fine sediments that have a lower storage capacity and low transmissivity (Blasch et al. 2006; Morin et al. 2009). In humid-to-semiarid landscapes, rainfall is sufficient to generate runoff and groundwater that sustain river systems, and the rivers are gaining water, albeit seasonally. But in arid landscapes the rivers are often hydrologically disconnected from the adjacent dryland areas—except for losing water to the floodplain, and gaining water during rainy seasons or after very high rainfall events.

Water use by riparian communities has been intensively studied in the southwestern USA, mainly to estimate transmission losses, but also to quantify the effects of woody species such as the invasive or saltcedar (*Tamarix* spp.) on these losses. Evapotranspiration rates can exceed annual rainfall in these arid environments (Doody et al. 2011). Early research on saltcedar suggested that its water use was very high: up to 200 m^3 ha^{-1} day^{-1} (Sala et al. 1996); but subsequent research has found that it is much lower and close to that of the native poplars and willows that grow in riparian systems of the southwest. Therefore, removal of these plants would have little effect on water loss if native riparian shrubs remain (Nagler et al. 2009; Shafroth et al. 2010b; Doody et al. 2011). Similar work in Australia found that although invasive *Salix* species in the river channel can use large quantities of water (±2000 mm year^{-1} vs. 1500 mm year^{-1} for open water), overall ET for this invasive species is very similar to that found for native riparian *Eucalyptus* forest (Doody and Benyon 2011; Doody et al. 2011).

In the floodplain of the perennial San Pedro River in Arizona, *Prosopis* woodlands have replaced native grasslands, increasing ET from 407 to 639 mm year^{-1} (Scott et al. 2006). Evapotranspiration from *Prosopis* woodlands in floodplains linked to perennial rivers ranges from about 350 to 750 mm year^{-1} (Scott et al. 2004, 2008), which suggests that other perennial river systems (such as those in South Africa where native tree species such as *Acacia karroo* are sparse or absent) could be similarly affected by invasion of non-native species.

The Working for Water program in South Africa, a national initiative for removal of invasive plants, emphasizes clearing to increase river flows (van Wilgen et al. 1998). Extensive invasions by *Acacia mearnsii*, Eucalyptus species, willows, and poplars have taken place along perennial rivers in the arid grasslands and savannas of the interior, where the native riparian species are mainly shrubs or small trees. If the difference between the annual ET from stands of these species and that from native species is as much as indicated by some studies (Dye and Jarmain 2004), or by data for willows and eucalypts from Doody and Benyon (2011) and Doody et al. (2011), removal could lead to an increase in river flows that would be substantial and very important for downstream water users and ecosystems. However, there may be other cases in which streamflows could be significantly reduced, such as invasions of species that are high water users along ephemeral streams (Doody et al. 2011; Hultine and Bush 2011).

The distinct species composition, structure, and dynamics of riparian environments generate a suite of ecosystem services very different from that of dryland environments. This makes them a key resource area, particularly in developing countries where they are less likely to have undergone extensive transformation by agriculture and other activities (Tockner and Stanford 2002; Kgathi et al. 2005; Brauman et al. 2007).

Recent work has also documented the extent to which large fauna can alter riparian processes. For example, in riparian ecosystems, large-scale earthworks are created mainly by the activities of fauna, particularly large mammals, which shape floodplains at a range of scales, from the microtopographical to that of river channels (Naiman and Rogers 1997; Moore 2006). Ecosystem modifications brought about by beavers, through the construction of dams, have been well studied; but much less is known about the ecological roles played by large mammals. In wetlands like the Okavango, large mammals (elephant, buffalo, hippopotamus) open up flow paths for water through reeds, changing water circulation patterns. Similarly, warthogs carve out feeding patches that form temporary pools during the wet season, creating habitats for many other species to complete their life cycles.

Riparian vegetation provides important feedbacks to the river system: it captures and stabilizes sediments, shapes river channels, and determines and regulates biotic processes (and, thus, water quality) (Tabacchi et al. 2000; Naiman et al. 2002). By these means, the vegetation creates its own habitat as well as that for animal species, and ensures its replacement through succession. Further, riparian vegetation serves as a buffer, shielding the aquatic ecosystems from the effects of land-use practices in adjacent environments—by filtering sediments, nutrients, and other pollutants (Naiman et al. 1999; Tabacchi et al. 2000; Brauman et al. 2007; Corenblit et al. 2009).

3.2.5 Regulation in Groundwater-Coupled Rangelands

In all rangelands the recharge, transport, and quality of groundwater depend on the nature of deep drainage and solute leaching. Where groundwater tables are shallow, reciprocal interactions between vegetation and groundwater are often observed (Le Maitre et al. 1999). This two-way exchange of water and solutes increases primary and secondary production, particularly under dry climatic conditions; at the same time; however, it renders water, soil, and vegetation resources more vulnerable to land management.

Groundwater-coupled rangelands—those in which shallow water tables are found, and the potential for a strong coupling between vegetation and groundwater exists—are increasingly recognized as important, and yet are poorly understood. These ecosystems have been categorized as "groundwater dependent"; yet the degree to which they are dependent varies greatly in time and space (Boulton and Hancock 2006; Eamus and Froend 2006). For this reason, we prefer the term "groundwater coupled" to describe the broad array of rangelands characterized by shallow water tables. We do know that vegetation has a major role in regulating groundwater resources in these systems, and significant strides have been made recently in understanding these ecohydrological interactions.

Many rangeland landscapes host, at their lowest topographic points, shallow groundwater zones that are sustained by local or distant recharge sources (Tóth 1999). In dry rangelands, where evapotranspiration recycles essentially all precipitation inputs back to the atmosphere, local recharge is negligible (Scanlon et al. 2006) and such shallow aquifers are rare. Regions where they do occur are characterized by sandy or rocky soils (such as sand dunes, fractured rock outcrops), highly seasonal and intense precipitation regimes, and zones of extensive lateral flow and intense runon. In such regions, at least some deep drainage into the saturated zone will eventually take place (Scanlon and Goldsmith 1997; Athavale et al. 1998; Seyfried et al. 2005; Small 2005; Gates et al. 2008). Recharge from more distant sources is particularly significant in arid regions located downstream of water-yielding mountains. For example, shallow water tables, wetlands, and lakes fed by mountain snowmelt are found at topographic lows within sand-dune rangelands such as the Great Sand Dunes of Colorado (Wurster et al. 2003), the Bahrain Jaram and Taklamakan deserts in China (Thomas et al. 2000; Chen et al. 2004; Gates et al. 2008), and the Monte desert in Argentina (Jobbágy et al. 2011).

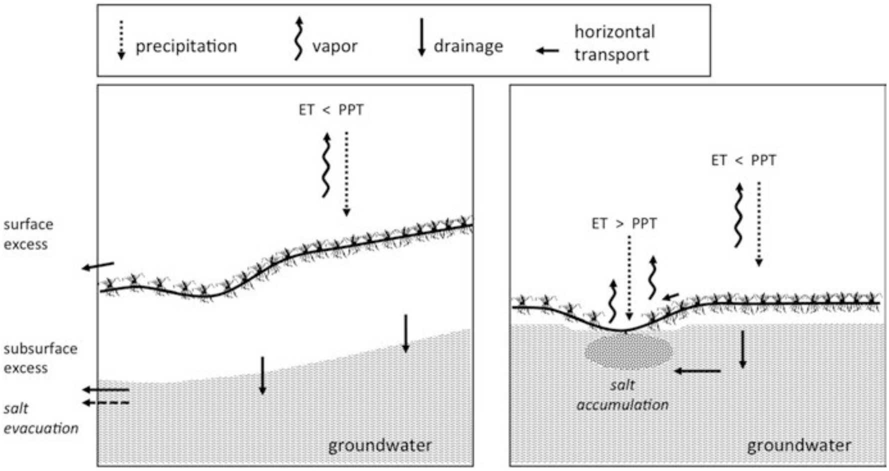


Fig. 3.5 Schematic of water balance for two landscape types in a subhumid climate. In sloped landscapes, vegetation regulates the rate of groundwater recharge. Groundwater gains that are eventually balanced by liquid discharge to streams (taking with it salts and dissolved nutrients). In flat landscapes, groundwater gains can be balanced only through higher evaporative discharge. When water leaves the landscape as vapor, its solute load is left behind. Transpiration results in salt build-up in the root zone, and direct evaporation results in salt build-up on the surface

In more humid rangelands, local groundwater recharge is more widespread and frequent, and shallow water tables are commonly found at topographic lows and along riparian corridors (Jobbágy and Jackson 2007). Finally, shallow water tables are a widespread feature in very flat, sedimentary rangelands (Fan et al. 2013) (Fig. 3.5); some conspicuous examples are the steppes of Western Siberia, the Northern Caspian plains in Asia, the grasslands of the Llanos and Pampas in South America, and the Miombo systems of sub-Saharan Africa (von der Heyden 2004).

3.2.5.1 Vegetation Dynamics Affect Groundwater Consumption

Groundwater consumption by rangeland plants is dictated by the interplay of water demand and accessibility. Most plants use groundwater in a dynamic and facultative manner, according to rainfall variability, preferring surface/shallow soil moisture when available (Engel et al. 2005). When soil moisture is low, the ability of plants to access groundwater depends, first, on the depth to the water table. Most rangeland plants access groundwater from the capillary fringe, where upflowing water and air coexist in the pore spaces of soils. Special adaptations include root aerenchyma tissue that enables species to survive and grow in saturated soils by providing air spaces to supply oxygen and facilitate groundwater consumption where water tables are very close to the surface (Visser et al. 2000). The optimum condition for plants is one in which the water table is deep enough to prevent waterlogging, but still high enough for easy access to groundwater (Jackson et al. 2009a). Groundwater use declines as water table levels drop, both in space—along topographic gradients

(Zencich et al. 2002; Gries et al. 2003; Nosetto et al. 2009)—and through time, e.g., as depth shifts seasonally (Stromberg et al. 1992; Naumburg et al. 2005; Cooper et al. 2006). Certain shrub and tree species can have maximum rooting depths of many meters (Schenk and Jackson 2002), and some observations suggest groundwater uptake from as deep as 20 m below the surface (Haase et al. 1996; Gries et al. 2003); but in dry ecosystems where water tables exceed depths of 10 m, it is rare to find significant groundwater use by plants (Zencich et al. 2002).

Other variables governing groundwater consumption by plants include water salinity and the fluid transport properties of soils and sediments. As the salinity of groundwater increases, the number of plant species able to tolerate the salinity declines, as does the rate at which the water is used. In groundwater-coupled rangelands, this relationship is commonly reflected by a series of drops in the diversity and productivity of vegetation along gradients of increasing salinity (Perelman et al. 2001). With regard to fluid transport properties, coarse-textured materials with high hydraulic conductivity favor groundwater recharge, whereas clay-dominated materials limit it to negligible rates (Jobbágy and Jackson 2004b).

3.2.5.2 Land Use/Management Affects Groundwater Consumption

The way in which the vegetation and soils of groundwater-coupled rangelands are managed can have a strong influence on the exchange of water and solutes, and thereby the availability and quality of groundwater for human and livestock consumption, among other uses. Reciprocally, intense extraction of groundwater can significantly alter the structure and functioning of groundwater-coupled rangelands. Groundwater consumption often rises when deep-rooted woody species become abundant (Huxman et al. 2005) or when salt-tolerant species proliferate in areas where high salinity levels previously limited consumption of groundwater (Pataki et al. 2005). Conversely, where rangeland use contributes to a reduction in the density of deep-rooted species the overall reduction in leaf area and transpiration decrease groundwater consumption (Meglioli et al. 2013).

This trade-off can lead to actions having different potential outcomes in different situations. In the very dry, sand-dune landscapes of central Argentina, groundwater-coupled woodlands occupy less than 15 % of the land area, but represent the major source of forage for local herders. At the same time, these woodlands may consume up to 17 % of the mountain-source recharge that sustains the aquifer—which is the only local source of water for humans and livestock (Jobbágy et al. 2011). If groundwater consumption by these woodlands were to be reduced, for example through clearing of the vegetation, the actual effect on groundwater availability would be very localized and minor, but the negative effect on forage availability and the herding economy would be huge.

A contrasting example comes from groundwater-coupled rangelands along river banks in the southwestern USA; here, mesquite encroachment has resulted in a doubling of groundwater consumption—producing more biomass, but with little benefit to livestock production (Scott et al. 2006). Finally, there are situations in which groundwater consumption can be a desirable factor in hydrological regulation. In many rangelands in Australia, the removal of native vegetation for cultivation led to massive waterlogging and salinization of the soils (Turner and Ward 2002). The only means of reversing this process has been reforestation of large areas of the watershed (Barrett-Lennard 2002; Asseng et al. 2010)—the biomass gains and consequent water losses to lower the water table in this case both bringing benefits.

Rangeland use can affect not only the amount of available groundwater, but also its quality. When plants consume groundwater, they typically filter out salts at the root surface, which then accumulate in the absorption zone (Heuperman 1999), raising groundwater salinity (Jobbágy and Jackson 2007). Salinity levels tend to stabilize once the maximum tolerance of the consuming species is reached (Nosetto et al. 2008). It should be noted that where water tables are shallow enough to connect the capillary fringe with the surface, substantial amounts of groundwater can be lost through direct evaporation. If salinity is high, evaporation can seriously damage surface soils (Lavado and Taboada 1987). To reduce direct evaporation and restore transpiration, management methods such as halting grazing and creating means for retaining surface runoff appear to be effective (Alconada et al. 1993; Chaneton and Lavado 1996).

Groundwater availability and quality can also be compromised by rangeland uses involving animals, such as livestock. For example, continual livestock trampling has worn channels in groundwater-fed meadows. If the overall slope of the ground is somewhat steep, such channeling can rapidly lower the water table, leading to shifts in rangeland composition and productivity (Loheide and Booth 2011). The quality of groundwater is often affected as well, as has been documented in corrals and homestead areas in the groundwater-coupled woodlands of central Argentina. The combined effects of denudation from overgrazing and nutrient concentration from feces and urine have switched the net groundwater flux from discharge (losing water) to recharge (gaining water), at the same time placing soluble nitrogen contaminants into the groundwater (Meglioli et al. 2013).

Groundwater-coupled rangelands in many regions have been severely affected by direct human interventions—such as intensive pumping of groundwater—greatly drawing down the water table. Some of the most dramatic examples have been documented in the Owens Lake basin in California (Elmore et al. 2006; Pritchett and Manning 2012).

3.3 Regulating Services: Climate Regulation

The water cycle in rangelands is strongly influenced by vegetation dynamics, owing in part to the tight coupling between the water, energy, and biogeochemical cycles in these systems (Noy-Meir 1973; Austin et al. 2004; Wang et al. 2009b). In rangelands where water availability is typically low, the dominant factor controlling vegetation cover and interannual variability in vegetation productivity is mean annual precipitation. The effects of rainfall on vegetation productivity have been investigated in many parts of the world, such as the western USA (Nippert et al. 2006) and northern Africa (Le Houérou and Hoste 1977). For example, shrub encroachment has been shown to change the spatial patterns of water infiltration into soils (Daryanto et al. 2013), thus affecting local water balance. In the Mojave desert in the southwestern USA, paired lysimeter data showed that when vegetation productivity increased significantly following elevated winter precipitation, soil water storage was reduced by half, precluding drainage below the root zone (Scanlon et al. 2005a). Such vegetation-controlled soil water flow has been occurring for 10,000–15,000 years in this region (Scanlon et al. 2005a), as it most likely has in many other rangeland ecosystems across the globe. A contrasting example comes from southwestern Australia, where replacement of perennial vegetation with annual crops led to much higher groundwater recharge, which resulted in soil salinity problems (Turner and Ward 2002).

Vegetation dynamics not only influence local hydrological conditions, but they also affect local and regional climate. Recent studies have shown that invasive shrubs in rangelands modify surface energy fluxes, causing greater nighttime air temperatures near the soil surface—particularly during the winter—thus producing a positive feedback for further shrub encroachment (D'Odorico et al. 2013b). At the regional scale, the effect of vegetation changes on climate has been observed in the Sahel (West Africa); although rainfall variability in this region is mainly influenced by variations in the surface temperature of the oceans, it is also accompanied by variations in vegetation, as seen during the multi-decadal drying trend from the 1950s to the 1980s (Zeng et al. 1999; Hein and de Ridder 2006; Prince et al. 2007). Another modeling exercise showed, in addition, that vegetation dynamics in the late 1960s in the Sahel played a critical role in maintaining the drought through the following decades. The course of the drought has been marked by a forced shift from a self-sustaining wet climate equilibrium to a similarly self-sustaining, but dry climate equilibrium (Wang and Eltahir 2000). Other research has indicated the role vegetation plays in the dynamics of the West African monsoon (Zheng and Eltahir 1998; McAlpine et al. 2009).

3.4 Supporting Services: Water Cycling and Protection Against Erosion

Supporting services are those required for the production of other ecosystem services. Their effects on people are either indirect or manifest over a very long time. Examples of supporting services include soil formation, nutrient cycling, water cycling, and protection against erosion. Of these, water cycling and protection against erosion are most germane to ecohydrology.

3.4.1 Water Cycling: With a Focus on E vs. T

The cycling of water on rangelands is obviously driven by many factors, some of which have been discussed in the previous section. A fundamental factor is the process of evapotranspiration (ET), which on most rangelands accounts for more than

95 % of the water budget (Wilcox et al. 2003b). Evapotranspiration is the sum total of interception—water captured by vegetation or litter and subsequently evaporated, transpiration, and evaporation from the soil or surface of water bodies. Recently, ecohydrologists have recognized the importance of better understanding the dynamics of ET, and in particular have placed more emphasis on accurately partitioning ET into soil evaporation and transpiration (Newman et al. 2006). Soil evaporation, from an ecohydrological perspective, is not a productive use of water because it does not contribute to plant productivity and carbon sequestration, food, fiber, or fuel production (D'Odorico et al. 2013a). This insight indicates that the main focus of ecohydrology should be to develop methods for better partitioning of the green water resources (i.e., decrease soil evaporation and increase transpiration) in semiarid and subhumid landscapes (Falkenmark and Rockstrom 2004). The same insight is motivating ecohydrologists to better understand and quantify ET.

Evapotranspiration can be partitioned into three components: (1) water that is intercepted by foliage and then evaporates back to the air; (2) water that is intercepted by litter on the soil surface, infiltrates into that litter and into the soil, and then evaporates; and (3) water that infiltrates into soil, is absorbed by plants, and later transpired back to the atmosphere. An additional process, previously not taken into account, is the potential for plants to absorb foliar-intercepted rainfall (Breshears et al. 2008); this process can be important during protracted periods of water stress, allowing plants to take advantage of rainfall events that are just large enough to be intercepted, but not large enough to infiltrate soil (Loik et al. 2004; Owens et al. 2006). This process has not been fully investigated, and the degree to which it may affect multiple species of plants is not yet known.

The rate at which soil evaporation takes place depends on several variables, including soil texture, soil temperature, and near-surface wind; these in turn are affected by basic properties of rangeland structure, such as the amount and type of woody-plant canopy cover. Recently, considerable work has focused on ways to identify the linkages between vegetation characteristics, soil evaporation, and microclimates for a diverse set of rangeland vegetation types—including mesquite, piñon-juniper, ponderosa pine, eucalypt, and saguaro cactus (Breshears and Ludwig 2010; Royer et al. 2010; Villegas et al. 2010a, b; Zou et al. 2010; Royer et al. 2012). Other recent work has focused on understanding how changes in woody plant cover may affect the ratio of transpiration to ET (Wang et al. 2010b, 2012a).

3.4.2 Protection of Soils Against Erosion and Degradation

3.4.2.1 Understanding the Importance of Vegetation Patch Structure

Another important supporting service of healthy rangelands is that of soil protection from erosion—in other words, on healthy rangelands, soils are not eroding. The obvious reason for this is that vegetation cover is adequate. But what is adequate cover? Many rangelands, particularly in drier climates, have significant areas of bare ground and yet are not eroding. According to Ludwig et al. (1997), Vegetation patch structure is the key: vegetation patches must be numerous enough and large enough to be able to recapture soil eroded from bare areas. In fact, the transfer of water, soil, and nutrients from bare areas (sources) to vegetated areas (sinks) is a fundamental process within drylands that may be disrupted if the vegetation patch structure is disturbed. "Resource-conserving" drylands are organized such that runoff is quickly captured by, and concentrated in, vegetation patches—minimizing the loss of resources from the landscape. Resource concentration of resources increases the efficiency of their use, which translates to higher net primary productivity and the maintenance of rangeland functionality (Stavi et al. 2009).

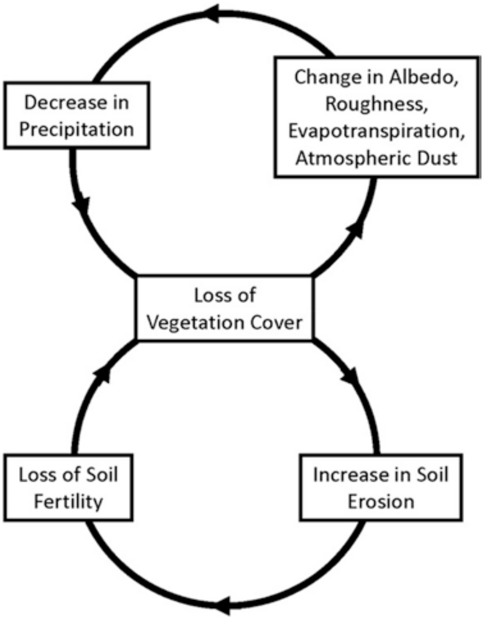
If a disturbance, such as overgrazing, reduces the density and size of vegetation patches, the system will become "leaky" or "nonconserving"—less efficient at trapping runoff, leading to a loss of valuable water and nutrient resources (Ludwig and Tongway 2000). A positive-feedback loop may then reinforce the degradation process: the higher runoff rates will mean less water available to plants and higher erosion rates (Davenport et al. 1998; D'Odorico et al. 2013a). This degradation cycle may proceed to the point that overland-flow runoff increases in both amount and energy, erosion increases, and plant density and production declines, and the microclimate becomes more extreme (Fig. 3.6). Recognition of these processes is important not only for understanding how rangelands retain function, but also for how to devise more effective remediation strategies (Tongway and Ludwig 1997).

3.4.2.2 Wind and Water Erosion

Erosion research on rangelands has traditionally focused on water erosion and associated fluvial processes. One key advance in recent decades is recognition of the importance of wind-driven transport (aeolian) and its linkage with water erosion (Breshears et al. 2003; Belnap et al. 2011). Aeolian processes are much better understood now, thanks to improvements in measurement methods (Zobeck et al. 2003)—including relative humidity near the soil surface (Ravi et al. 2007a), the effects of vegetation patterns, and predictions of how vegetation structure influences horizontal sediment transport (Okin and Gillette 2001). Like water erosion, aeolian sediment transport is strongly influenced by the structure and arrangement of vegetation patches (Field et al. 2012). But when a grass patch is denuded (as can be caused by overgrazing) and the soil is exposed to wind action, there is a "double-whammy" effect: not only is the potential for recapturing the sediment lost, but also the wind causes the bare patch to generate additional sediment (Field et al. 2012). In the absence of disturbance, shrublands may inherently generate more wind-derived sediment than grasslands, as they have greater surface roughness as well as less intercanopy ground cover (Breshears et al. 2009). Aeolian erosional processes may also be interrelated with fire dynamics (Ravi et al. 2007b, 2009; Field et al. 2011a).

Under future climatic conditions, in regions where precipitation may become more intense while simultaneously drought frequency and intensity increase,

Fig. 3.6 Feedback loops in the degradation process. Positive feedbacks are depicted between loss of vegetation cover and (top loop) decreased precipitation and changes in atmospheric conditions; and (bottom loop) soil erosion and loss of fertility. Source: Figure 4 in D'Odorico et al. (2013)



fluvial and aeolian erosion processes will be affected in different ways. A simple but important point is that fluvial erosion occurs in rangelands only during the infrequent precipitation events that have sufficient magnitude and intensity to generate runoff, whereas small wind gusts occurring frequently can result in regular, ongoing aeolian sediment transport even during less windy periods of the year. Consequently, aeolian transport is a relatively constant and ongoing process (Field et al. 2011b) and may even be highly interactive with fluvial processes (Belnap et al. 2011).

3.5 Provisioning Services: Water Supply

Provisioning services are considered as those goods or products—food, fiber, and water—that are directly produced from ecosystems. Water supply, including its magnitude, timing, and quality, is a fundamental service provided by rangelands, even those having relatively dry climates. Given that most rangelands are in semiarid settings, the amount of "blue water" is generally quite low—often less than 5 % (Wilcox et al. 2003b). Nevertheless, given the extent of rangelands, even a relatively small fraction of blue water can translate to a considerable amount of freshwater, which is of particularly high value in regions where the quantity is very limited. In rangelands having more humid climates, cold and snowy climates, or rocky or very sandy soils, "blue water" outputs can be much higher (Wilcox et al. 2006).

Water supply as a provisioning service is essentially a product of the array of regulating services discussed above. The amount of "blue water" supplied by a given landscape, i.e., water flow to streams and aquifers, is fundamentally a function of climate, vegetation, soils, and geology. Of these factors, vegetation and—to a lesser extent—soils are the most affected by rangeland management. The concept of managing vegetation for the purpose of augmenting water supply has a long, complicated, and rich history. In fact, one could argue that it is a fundamental tenet of the science and art of watershed management (Wilcox 2010). The last decade in particular has seen a considerable refinement of our understanding of the linkage between vegetation and water supply on rangelands—especially concerning the effects of removing woody plants and invasive riparian species (Huxman et al. 2005; Edwards and Roberts 2006; Shafroth et al. 2010a; Doody et al. 2011; Hultine and Bush 2011; van Wilgen et al. 2012). With respect to the USA, the issue has been reviewed in detail in Archer et al. (2011). In general, large-scale woody plant removal has not resulted in measurable increases in streamflows or groundwater recharge, although increases would have been anticipated given (1) the long experience of similar manipulations (various levels of clear-cutting) carried out in forest watersheds (Bosch and Hewlett 1982) and (2) experience with the reductions in water yield brought about by the reverse type of intervention, i.e., the establishment of tree plantations in areas that were originally treeless (Farley et al. 2005; Jobbagy et al. 2013). The only areas in which there may be a true potential for enhancing water supply through woody plant removal appears to be those having annual precipitation above 500 mm (Zhang et al. 2001) along with at least one of the following conditions: (1) predominantly winter precipitation or significant snow accumulation; (2) permeable (sandy) and deep soils; and (3) karst geology (Huxman et al. 2005).

Surprisingly, the conventional wisdom has even been overturned in the case of riparian areas invaded by alien shrubs. Until recently it was widely accepted that removal or control of invasive riparian shrubs such as Russian olive (*Elaeagnus angustifolia)* and saltcedar (*Tamarix ramosissima)* would result in substantial water savings. A recent comprehensive review on the subject, however, concluded that there is in fact little evidence for large-scale water supply augmentation through these interventions (Shafroth et al. 2010a). The primary finding was that the invasive species do not appear to use more water than the native vegetation they displace (Doody et al. 2011; Hultine and Bush 2011).

Finally, studies of groundwater recharge in the sandy deserts of Central Argentina have yielded some paradoxical results. Certain regions that are highly degraded from constant wind erosion and dune formation, with severe loss of both forage and sediment, have nevertheless seen an improvement in freshwater supply as recharge gives rise to high-quality groundwater lenses (Jobbágy et al. 2011). Except for this peculiar example of vegetation denudation proceeding in concert with gains in groundwater, the region is characterized by low-quality groundwater. In undisturbed areas it exhibits high total salt and/or arsenic content, while in disturbed areas with high animal concentrations it is less salty but polluted with nitrogen (Aranibar et al. 2011; Meglioli et al. 2014).

3.6 Observational and Conceptual Advances

As noted in previous sections, the availability and distribution of water in the landscape are of paramount importance for rangelands. Over the last few decades, a number of exciting developments have taken shape, both observational and conceptual. The former category includes *in situ* and remote-sensing monitoring tools—such as field-deployable, laser-based spectroscopy instruments that determine the ratios of hydrogen and oxygen isotopes (Lee et al. 2005; Wang et al. 2009a); portable 3D LIDAR systems for plant canopy analysis; electromagnetic imaging (EMI) devices for *in situ* soil water moisture monitoring; and distributed temperature-sensing (DTS) and remote-sensing tools, including drones and radio-controlled helicopters with lightweight digital cameras, that gather data for estimating key hydrological variables (Alsdorf et al. 2000). These and other recent developments are revolutionizing data gathering, in terms of both the scale and the precision of information used to inform ecohydrological measurement and investigation. It would be impractical to try to cover all the advances here; we have therefore selected a few that are closely related to topics already discussed in this chapter: the observational technologies of remote sensing and stable isotopes, and the conceptual advances in understanding nonlinear ecosystem behavior, scale and spatial variability, and hydrological connectivity. Discussions of other geophysical advances (e.g., EMI) can be found in the following sources (e.g., Robinson et al. 2008; Zreda et al. 2012).

3.6.1 Observational Advances

3.6.1.1 Remote Sensing for Investigating Components of the Water Budget

Remote-sensing technology has a long history in rangeland management (e.g., Prince and Tucker 1986). One of its key advantages is that it enables extrapolation not just in space, but also temporally, offering insight into change of vegetation pattern and development through time. Rapid developments in remote-sensing-based hydrological monitoring are providing unprecedented temporal and spatial coverage in estimates of hydrological variables such as rainfall, soil moisture, ET (Kustas et al. 1994; Garcia et al. 2008), surface water level (Alsdorf et al. 2000), and groundwater storage (Yeh et al. 2006).

In rangelands, the irregular spatial and temporal distribution of rainfall imposes key constraints on ecosystem function and development. Remote measurement of precipitation has an extensive history, with numerous hydrological investigations being informed by the two-decade-long Tropical Rainfall Measuring Mission (TRMM) satellite system (Kummerow et al. 2000) and related sensors. Over the coming years, the next generation of satellite rainfall-measuring systems, referred to as the Global Precipitation Measurement (GPM) mission, will provide a much-needed update to the space-based rainfall monitoring capacity. The GPM Core Observatory is in the final stages of testing at the NASA Goddard Space Flight

Center; launch is scheduled for early 2014. The resolution of spatial and temporal rainfall data derived with CPM will exceed that possible with previous designs and it will enable a much greater range of ecohydrological investigations in rangelands.

Like other water-limited systems, rangelands are characterized by a strong coupling between the dynamics of soil moisture and vegetation productivity. Soil moisture can be estimated remotely, through either active or passive microwave-based systems—each of which involves a compromise between spatial and temporal resolution. Although passive microwave sensing can be used for routine, daily global-scale estimates of soil moisture (Njoku and Entekhabi 1996), which makes it an ideal technique for large-scale studies, it also has a clear limitation: the spatial resolution of retrievals is quite coarse (approximately 25 km) (McCabe et al. 2005). Active microwave sensing provides a higher spatial resolution (up to a few kilometers), but the repeat time is generally on the order of a few days. It is possible that improved data sets for large-scale ecohydrological investigations can be obtained by merging the best features from multiple systems and sensors (e.g., Liu et al. 2011).

3.6.1.2 In Situ Methods for Measuring Components of the Water Budget

Partitioning of Evapotranspiration

Evapotranspiration is a major component of the water budget and accounts for up to 95 % of the total water input (e.g., precipitation) in rangelands (Huxman et al. 2005). It has two distinct constituents (E and T), which are controlled by different mechanisms. Partitioning of ET is important not only for better understanding the water budget but also for predicting the biogeochemical fluxes driven by hydrological variations (Wang et al. 2010a). Efficient use of the limited water resources in rangelands requires maximizing the productive water loss (T) and minimizing the unproductive water loss (E) (Wang and D'Odorico 2008). Separating E from T, however, has always been a difficult task—especially from the observational point of view at larger scales.

A useful tool for separating E from T is stable isotopes of water, because E and T carry distinct isotopic signatures. Traditionally, the stable isotopic compositions of water samples are measured by isotope ratio mass spectrometry (IRMS), while the vapor-phase measurements are based on cryogenic water vapor collection coupled with IRMS. Such methods are labor intensive and time consuming. Over the past decade, a revolutionary change has taken place in water isotope measurement: the appearance of spectroscopy-based instruments capable of continuously measuring water vapor isotopic compositions (Fig. 3.7) (Lee et al. 2005; Wen et al. 2008; Wang et al. 2009a; Griffis et al. 2010).

Monitoring of Soil Moisture

Perhaps the most important recent innovation for measuring soil moisture *in situ* is the COSMOS monitoring system (Zreda et al. 2012). Based on both the release of fast and slow neutrons from interactions between water in the soil column and a

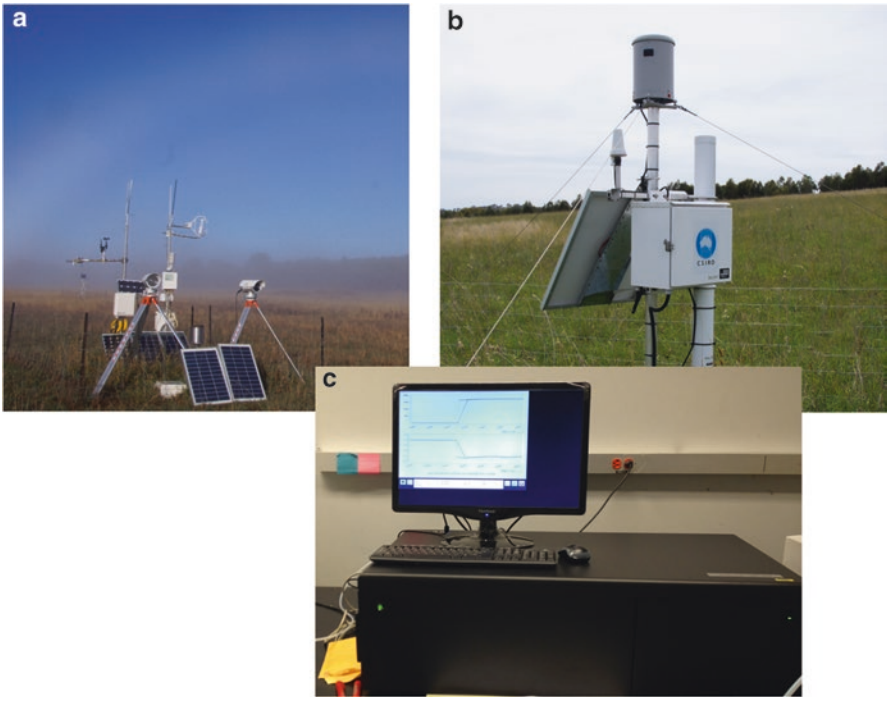


Fig. 3.7 Examples of recent advances in hydrological monitoring technology. (A) Eddy covariance system and scintillometer for ecosystem-scale measurements of sensible heat flux (evapotranspiration); (B) COSMOS system for monitoring ecosystem-scale soil moisture; (C) spectroscopy-based instrument for measuring the isotopic composition of water vapor in situ, which can be used in applications such as partitioning of evapotranspiration

regular flux of cosmic rays from space, the COSMOS system provides, for the first time, a reliable estimate of the soil wetness in a system. In addition, because the hydrogen in the top layer will have more sensitivity to the neutron counts, COSMOS, combined with modeling to separate the various hydrogen pools in the average measurement, has the potential to discriminate between moisture in the topsoil and that in the subsoil. The COSMOS installations are revolutionary in terms of bridging the spatial divide that often exists between remote-sensing and *in situ* measurement approaches. If a network of these systems can be distributed globally, our ability to monitor ecosystem change and development will be markedly improved.

3.7 Conceptual Advances

The last quarter century has seen considerable advances in our conceptual understanding of ecohydrological processes and interactions, particularly in regard to (1) spatial variability and scale, (2) ecosystem thresholds and feedbacks, and (3) hydrological connectivity of landscapes.

3.7.1 Spatial Variability and Scale

Understanding spatial dynamics and scale relationships has been a formidable challenge in both ecology and hydrology and, by extension, ecohydrology (Wood et al. 1990; Sivapalan and Kalma 1995; Sposito 1998; Grayson and Bloschl 2000; Western et al. 2001). Nevertheless, important advances have been made (Newman et al. 2006; Asbjornsen et al. 2011). For example, comparative studies across spatial scales have revealed the nonlinear nature of runoff and erosion with changing scales and how disturbance alters these relationships (Fig. 3.3) (Bergkamp 1998a; Puigdefabregas et al. 1999; Wilcox et al. 2003a; Favreau et al. 2009; Moreno de las Heras et al. 2010). Nonlinear responses in runoff and erosion are the result of redistribution across the landscape as well as alterations in runoff generation mechanisms with changing scale (Seyfried and Wilcox 1995).

Similarly significant strides have been made in quantifying the spatial variability of infiltration at the hillslope scale (Berndtsson and Larson 1987; Seyfried 1991; Pierson et al. 1994, 2001; Bhark and Small 2003; Daryanto et al. 2013). Infiltration capacities are generally higher under shrub canopies than in intercanopy areas, and these differences markedly influence patterns of soil moisture (Breshears and Barnes 1994, 1999). In addition, runon from intercanopy patches often contributes additional water to the shrub patches (Ludwig et al. 2005). Correspondingly, a number of conceptual advances have enhanced our understanding of the spatial variability of vegetation patterns on rangelands and how these are regulated by rainfall and runoff (HilleRisLambers et al. 2001; Rietkerk et al. 2002, 2004; Thompson et al. 2011).

Faunal activities also play an important role in structuring dryland landscapes as well. One feature of many arid landscapes is the formation of mounds, generally regularly dispersed, that range in diameter from a few meters to tens of meters. Known as *mima mounds* in the western USA, they are called *heuweltjies* in South Africa, where they cover from 14 to 25 % of the landscape (Lovegrove and Siegfried 1986, 1989; Whitford and Kay 1999). Their regular distribution is probably the result of competition among fauna for resources (Lovegrove and Siegfried 1986; Laurie 2002). Most authors agree that these enigmatic features are initiated by animals, whether mammals or invertebrates. One theory regarding the heuweltjies is that they developed over buried termite nests (Milton and Dean 1990; Moore and Picker 1991), but a recent paper argues that they are relicts of shrub-clump-controlled erosion processes (Cramer et al. 2012). Whatever their origin, the accumulation of transported organic matter, softer soil, and food remains they contain increases their fertility (Midgley and Musil 1990) and infiltration rates (Dean 1992), supports a distinctive suite of plant species (Knight et al. 1989), and attracts faunal activity—digging by termite-eating mammals, burrowing by rodents and/or nesting ostrich (Lovegrove and Siegfried 1986, 1989; Milton and Dean 1990), and foraging by game and domestic livestock (Armstrong and Siegfried 1990; Kunz et al. 2012). The movement of water across and between the vegetation mosaic and the heuweltjies has not been studied to determine whether these mounds contribute to groundwater recharge; but their higher infiltration rates (Dean 1992) suggest that their ecohydrological function may be analogous to that of the vegetation patches; that is, they may capture and filter runoff and act as foci for deep infiltration and recharge of groundwater.

The origins of the mima mounds in North America are no less controversial, but in this case small mammals (gophers) appear to be the primary drivers for the accumulation of materials (Whitford and Kay 1999; Jackson et al. 2003; Horwath and Johnson 2006; Johnson and Horwath-Burnham 2012). Whether or not that proves to be the sole explanation, these features also accumulate materials and alter the ecohydrology of the landscape. These important soil modifications justify the need for further research into the ecohydrological consequences of soil (Westbrook et al. 2013).

As noted by Vivoni (2012), our understanding of the role of scale and spatial variability in ecohydrological processes on rangelands will certainly increase in the future as remote-sensing and computational capabilities continue to progress.

3.7.2 Ecological Threshold and Feedback Mechanisms

Ecological thresholds and feedback loops are intimately related (Runyan et al. 2012; D'Odorico et al. 2013a). Threshold behavior occurs when a relatively small change in external drivers causes a disproportionally large response. A classic example of an ecological threshold is the transition between two stable states—such as the transition from a grassland or savanna to woodland or highly eroded state (D'Odorico et al. 2013a). The shift or change in state is induced and maintained by positive feedbacks that destabilize the system (Chapter 6, this volume). Examples of positive feedbacks are those between vegetation cover and (1) erosion, (2) soil moisture, and (3) climate (Runyan et al. 2012; D'Odorico et al. 2013a). The desertification feedback loop presented in D'Odorico et al. (2013a) (Fig. 3.6) illustrates these: A decrease in vegetation cover triggers the loss of water, nutrients, and soil that may as changes in albedo and evapotranspiration. All of these changes in turn create an environment that is less conducive to vegetation growth. In the last decade in particular, a considerable amount of work has been done that helps us better understand feedback loops and their important role in ecohydrological interactions (D'Odorico et al. 2007, 2012, 2013a, b; Stavi et al. 2009; Runyan et al. 2012; Turnbull et al. 2012).

3.7.3 Hydrological Connectivity

Hydrological connectivity refers to the water-mediated transfer of matter, energy, and organisms within or between elements of the hydrologic cycle (Pringle 2001). We now recognize that hydrological connectivity is essential for ecological integrity—and, more important, that activities by humans that disrupt this connectivity (dams, interbasin water transfers, etc.) can have dramatic negative consequences (Pringle 2003). "Connectivity" can be more broadly understood as the transfer of energy, matter, and organisms by not only water but also other vectors—such as wind and animals (Peters et al. 2006; Okin et al. 2009). One of the major benefits of studying connectivity in physical processes is that it identifies cross-scale interactions. For example, how do various different stomata in individual grass leaves, when under stress (e.g., from grazing or drought), function to modify water fluxes at the landscape scale? Answering such questions, on the basis of information from smaller scales, will significantly improve our ability to make predictions at larger scales (Peters et al. 2004). Hydrological connectivity has proved useful in explaining ecohydrological patterns on at the landscape scale as previously indicated (Wainwright et al. 2011). However, quantifying connectivity among different scales is still a major challenge, owing largely to a lack of a conceptual framework and modeling approaches applicable at multiple scales (Miller et al. 2012). Analogical models, which simulate the behaviors of complex physical systems using laws and theorems known to control components of those systems, may be able to fill some of these gaps. Recently, Wang et al. (2012b) developed a conceptual framework that uses electrical circuit analogies and Thévenin's theorem to upscale ecohydrological and biogeochemical processes from point scales to watershed scales. This conceptual work, by providing a means of representing concomitant processes at both small and large spatial scales, may prove useful for multi-scale rangeland management efforts.

A number of important conceptual advances have improved our understanding of hydrological connectivity and flows—longitudinal, lateral, and vertical—within river systems as well as between river systems and landscapes, and the importance of this connectivity for river ecosystem structure, functioning, and maintenance of ecosystem services (Naiman et al. 1999; Ward et al. 2001; Wiens 2002; Caylor et al. 2004; Boulton and Hancock 2006). Combined with hydrogeomorphology, connectivity processes play a vital role in the structuring of river systems and the ecosystem services they provide (Thorp et al. 2006, 2010) (Fig. 3.8). The implication, for those involved in land management and in water resource management—two traditionally separate policy and legislative domains—is important: the two are actually inseparable (Postel and Thompson 2005). In fact, rivers are complex social–ecological systems, and if we are to ensure continued delivery of the numerous essential ecosystem services they provide, including their traditional use as water conduits, we must advance our knowledge of not only the scientific but also the social and economic aspects of managing them (Chapter 8, this volume).

3.8 Future Perspectives

The past quarter century has seen impressive advances in our understanding of ecohydrological processes on rangelands, and new research is providing a much clearer picture of water dynamics (amounts and timing of both green and blue water and how these fluxes are affected by biota). These advances are attributable not only to the sheer number of new studies but also to the development of new observational methodologies, such as remote sensing and the use of stable isotopes. We anticipate that these advances will continue.

In addition, new conceptual and theoretical approaches, coupled with increases in computational power, have significantly improved our ability to predict and model ecohydrological processes. These approaches have and will continue to prove particularly useful for elucidating (1) spatial variability and scale, (2) ecosystem thresholds and feedbacks, and (3) hydrological connectivity of landscapes. We expect that the near future will bring further developments in all these areas, paving the way for more new and exciting insights into the ecohydrology of rangelands.

3.9 Summary

Our discussion of recent advances in the ecohydrology of rangelands has been organized around the concept of ecosystem services, especially those related to water. The fate of water in rangeland environments and, by extension, that of the flora and fauna that depend on this water are determined by conditions at three critical junctures: (1) The soil surface—will water infiltrate or run off? (2) The vadose zone—will water remain in the root zone or move beyond it? (3) The root zone—will water be transpired or evaporate?

Rangeland ecosystem services are categorized as regulating, supporting, and provisioning. Water-regulating services include those that affect the amount, timing, and quality of blue water flows. These are to a large extent determined at the first critical juncture of the water cycle—on the soil surface, where water either infiltrates or becomes overland flow, depending on the infiltrability of the soil. Soil infiltrability in turn depends on myriad factors, including vegetation, grazing intensity, brush management, fire patterns, condition of biological soil crusts, and activity by fauna. At larger scales, water-regulating services are influenced by other factors, such as the nature and structure of riparian zones and the presence of shallow groundwater aquifers. Finally, an important ecohydrological interaction that occurs at large scales is that between the land surface and the atmosphere. Climate regulation may result from feedbacks between rangeland vegetation and rainfall patterns.

Supporting services are those required for the production of other ecosystem services. Examples include the process of ET, which supports water cycling, and the

Fig. 3.8 (Continued) Thoms and Parsons 2003); and (2) the ecological measures of food chain length (FCL), nutrient spiraling (NS), and species diversity (SpD), the first two scaled from long to short and the third from low to high. The light bar within each box is the expected median, with the shading estimating the range of conditions. The size of each arrow reflects the magnitude of lateral, longitudinal, and vertical connectivity. Source: Figure 1.1 and color plate 1 (revised) in Thorp et al. (2008)

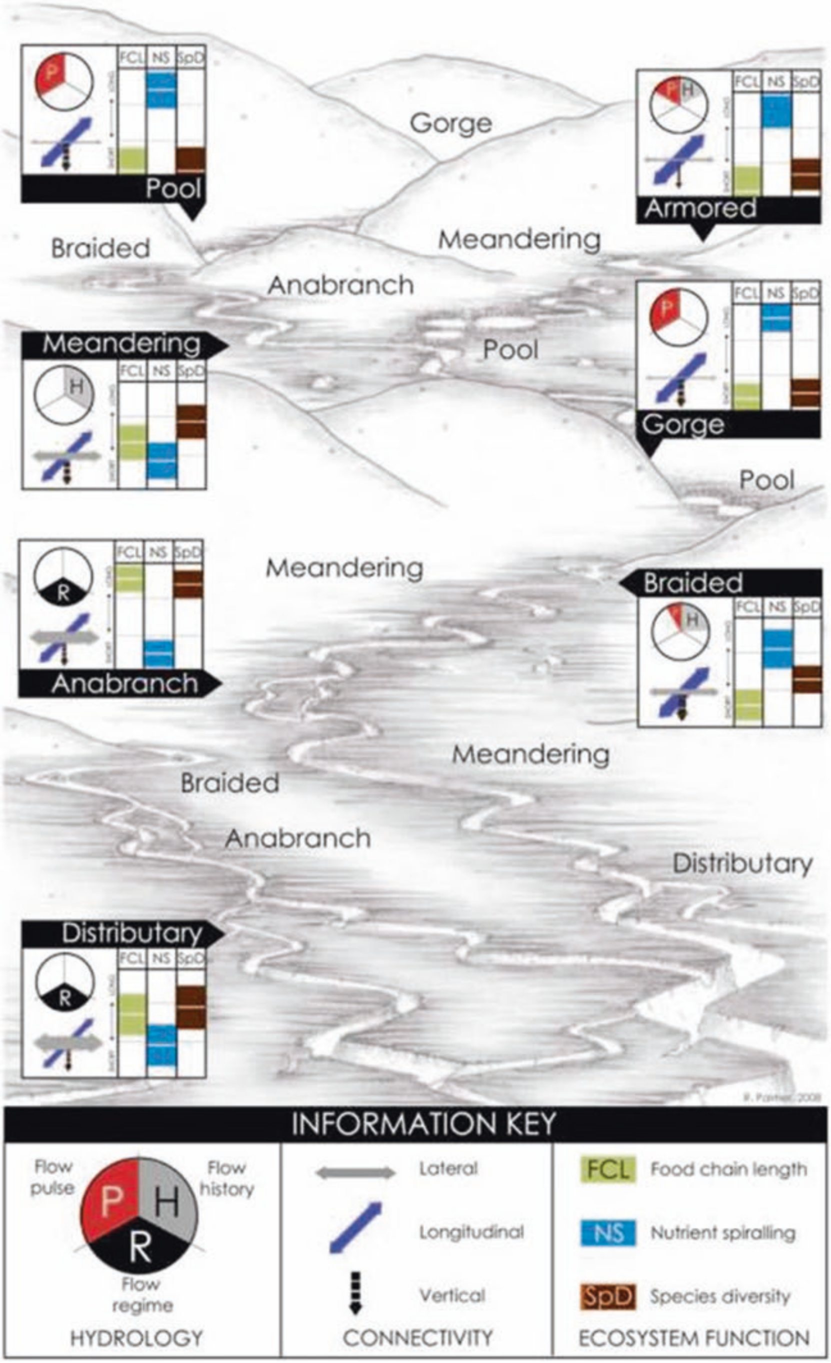


Fig. 3.8 A conceptual riverine landscape, depicting various functional process zones (FPZs) and their possible arrangement in the longitudinal dimension. Information contained in the boxes show the hydrological and ecological conditions predicted for that FPZ, including (1) the hydrological scale of greatest importance (scales being flow pulse, flow history, and flow regime, as defined by

processes by which soils are protected against erosion or degradation. The process of ET has become a subject of active inquiry in ecohydrological research—in particular, the partitioning of ET into soil evaporation and transpiration. From an ecohydrological perspective, soil evaporation is not a productive use of water because it does not contribute to plant productivity. An improved understanding of ET partitioning may lead to new management insights concerning methods for shifting more green water to productive uses. The processes that act to protect soils from erosion and/or degradation are also important ecohydrological support services. We now recognize that vegetation patch structure has a very large influence on soil erosion. Fundamentally, vegetation patches must be numerous enough and large enough to effectively capture water and sediment coming off of the bare patches. If such a patch structure is lost, rangelands begin eroding at rates that render the ecohydrological balance of the land unsustainable. Another factor affecting soil erosion, and which has been the focus of much recent research, is wind—and how it is related to water erosion. New measurement methods are yielding fresh insights into aeolian processes.

Provisioning services are those goods or products that are directly produced from ecosystems, such as water, food, and fiber. With respect to ecohydrology, the production of water from rangelands and how that production is affected by different management strategies are issues of paramount importance—but concerning which there has also been considerable misunderstanding. Work over the last several decades has largely overturned the notion that water supply can be substantially increased by removal of shrubs. Evidence of a true potential for enhancing water supply through woody plant removal has so far been found only in upland regions, and appears to be limited to those having annual precipitation above 500 mm, along with at least one of the following conditions: (1) predominantly winter precipitation or significant snow accumulation and (2) deep and permeable (sandy) soils (Huxman et al. 2005). But even where these conditions are met, in many cases the additional amount of water gained through manipulation of vegetation may be marginal. In riparian areas, surprisingly, removal of invasive, non-native woody plants appears to hold little potential for increasing water supply. Here, the primary factor appears to be that non-native plants use no more water than the native vegetation they displace.

We hope that by making an explicit linkage between ecohydrological processes and the ecosystem services concept, we have made it easier to grasp the multifaceted and complex nature of these processes on rangelands. Clearly there is a close coupling between biota (both fauna and flora) and water on rangelands—which is why water-related ecosystem services are so strongly dependent on land management strategies.

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