Chapter 2
Woody Plant Encroachment: Causes and Consequences

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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

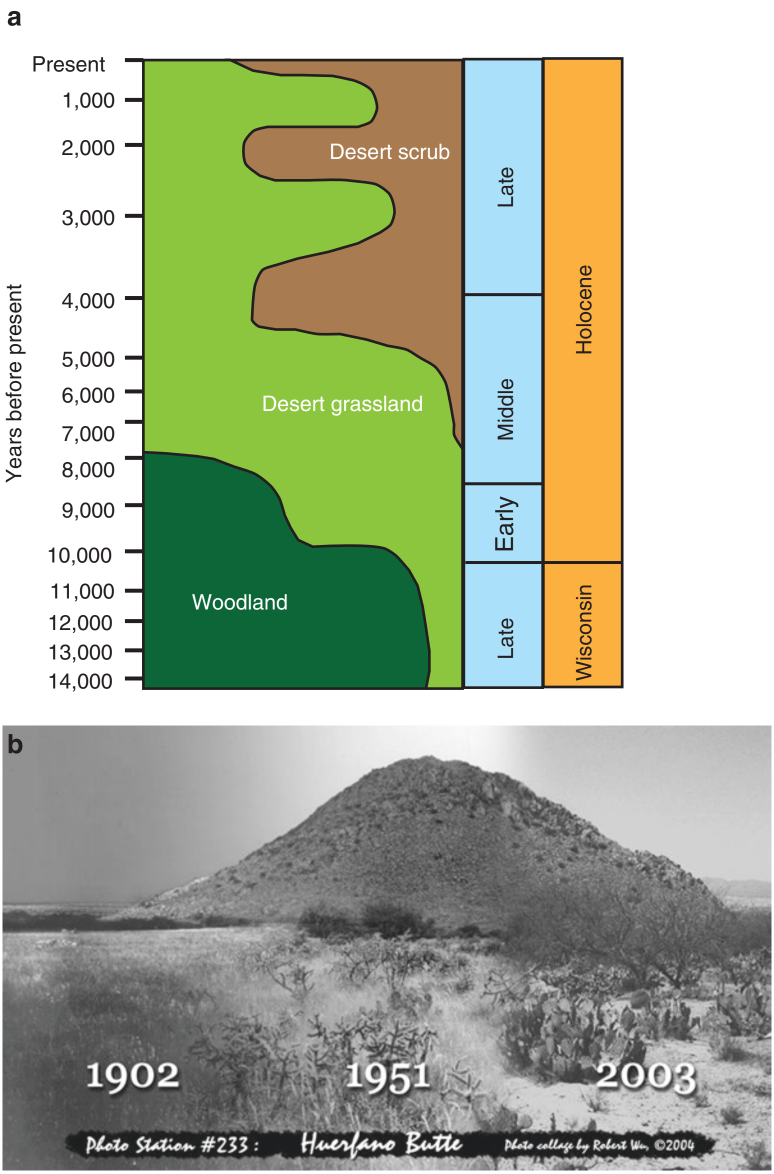

Fig. 2.1 (**a**) Holocene changes in woodland, desert scrub, and grassland in the southwestern USA (modified from Van Devender 1997) and (**b**) photographic record of increases in woody plant abundance at the Santa Rita Experimental Range, Arizona, USA, against the backdrop of Huerfano Butte (images 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}).

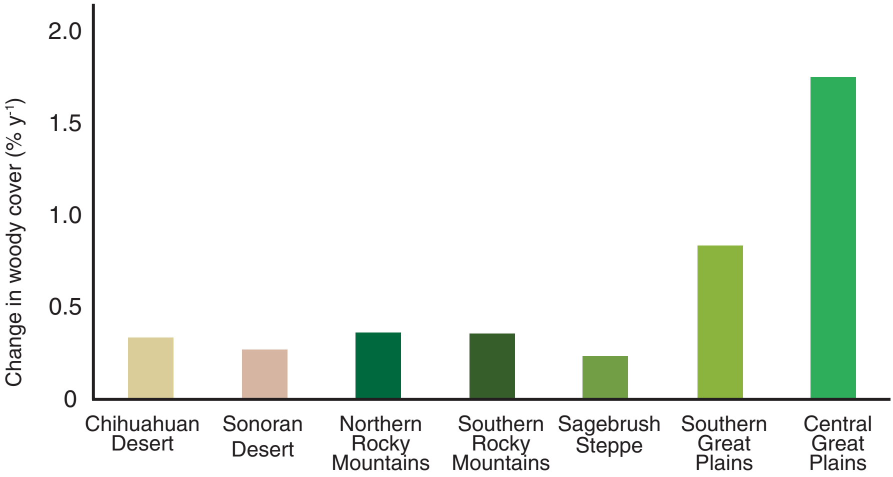

Fig. 2.2 Rates of woody encroachment in North American rangelands (modified from Barger et al. 2011)

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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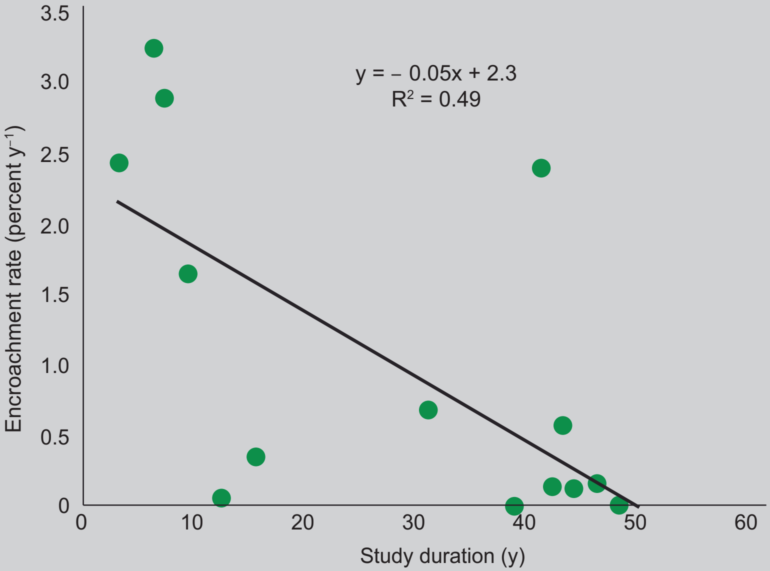
[1] A database of peer-reviewed research papers was compiled by searching for the terms “bush encroach*,” “brush encroach*,” “desertification,” “shrub grazing,” “shrub encroach,” “shrub invasion,” “shrub expansion,” “woody encroach*,” and “woody plant invasion” on the ISI Web of Knowledge. This search 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

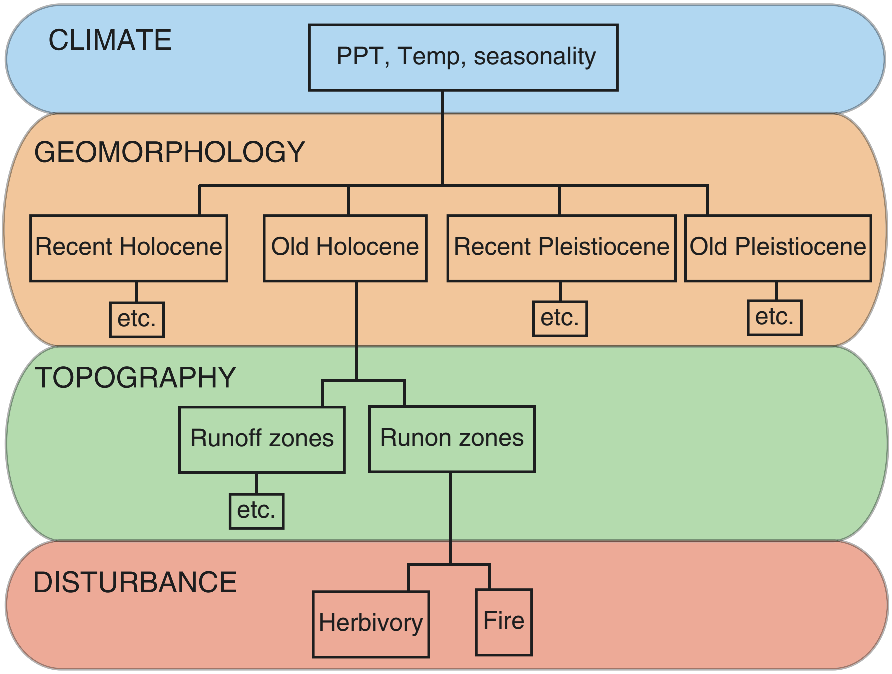


Fig. 2.3 The abundance of woody and herbaceous vegetation is determined by interactions across a hierarchy of drivers and constraints operating across a range of spatial and temporal scales. Changes in climate and atmospheric chemistry (e.g., increased CO_2 concentrations) determine grass-woody plant 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.

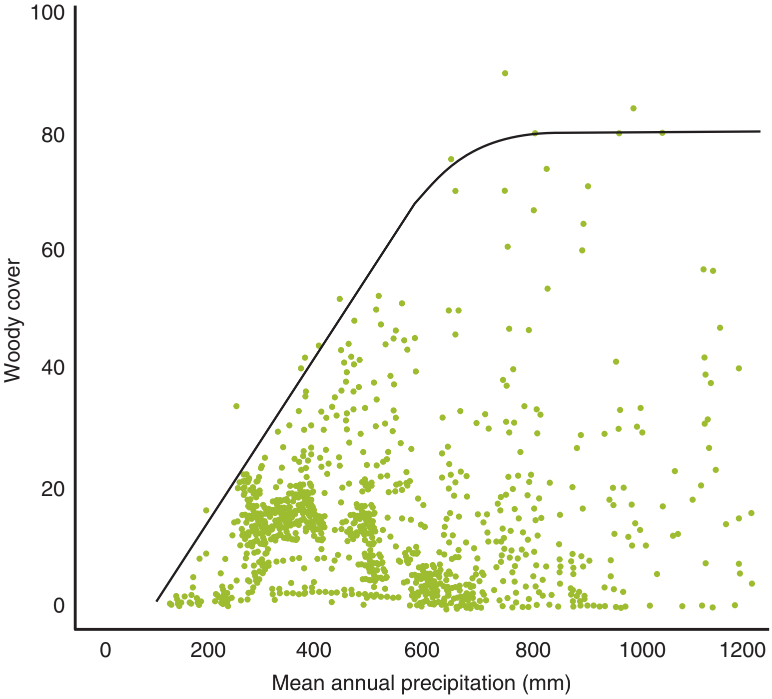


Fig. 2.4 Relationship between mean annual precipitation (MAP) and maximum woody plant cover in Africa. Maximum potential woody cover increases linearly with increases in MAP to ~650 mm, and then levels off at ~80 %. Note that many sites are well below their potential, ostensibly owing to constraints 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.

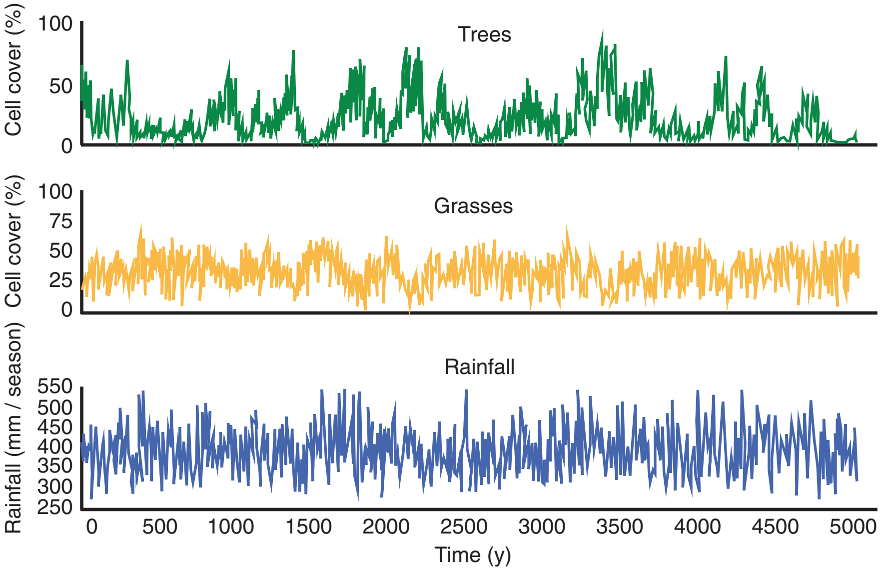


Fig. 2.5 Modeled fluctuations in grass and woody plant cover at decadal and longer time scales, assuming stationary stochastic rainfall distribution, in a savanna in Texas, USA (from van Wijk and Rodriguez-Iturbe 2002)

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.

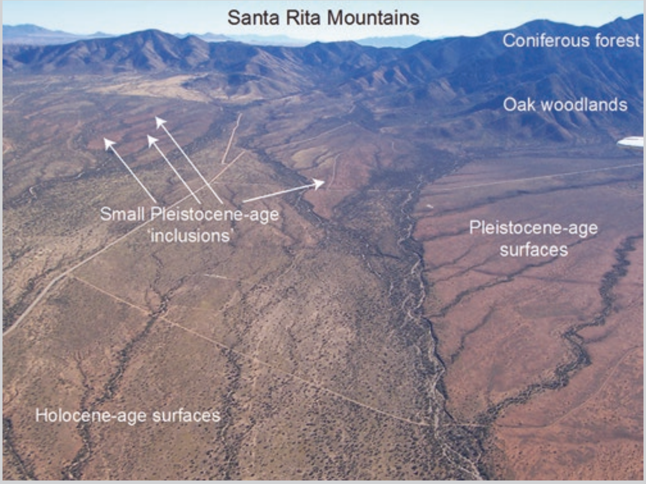
Grasses tend to dominate shallow soils, where lateritic or argillic horizons, bedrock, or limestone are near the surface; water and nutrient resources "perch" and concentrate above these impermeable layers (Molinar et al. 2002). However, if there are fissures or gaps in the impermeable layers that allow 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).

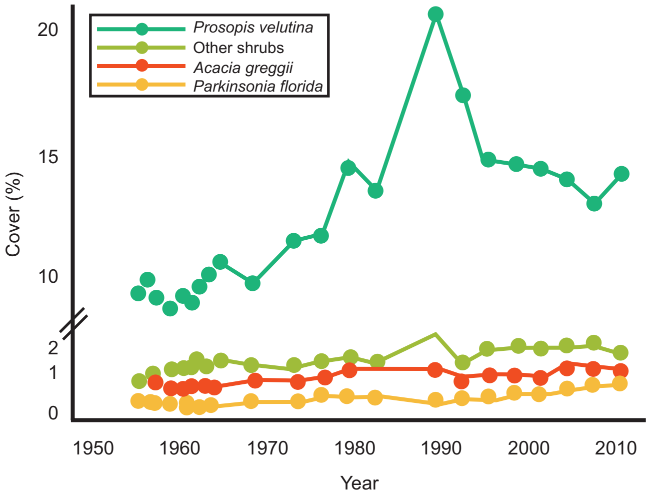

Fig. 2.6 Canopy cover of three shrub species and "all other shrubs" at a Sonoran Desert grassland (USA) where woody plant encroachment has been well documented. *Prosopis velutina* cover increased markedly from the 1950s to the 1990s, whereas that of *Acacia greggii* and *Parkinsonia florida* (both potentially 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-

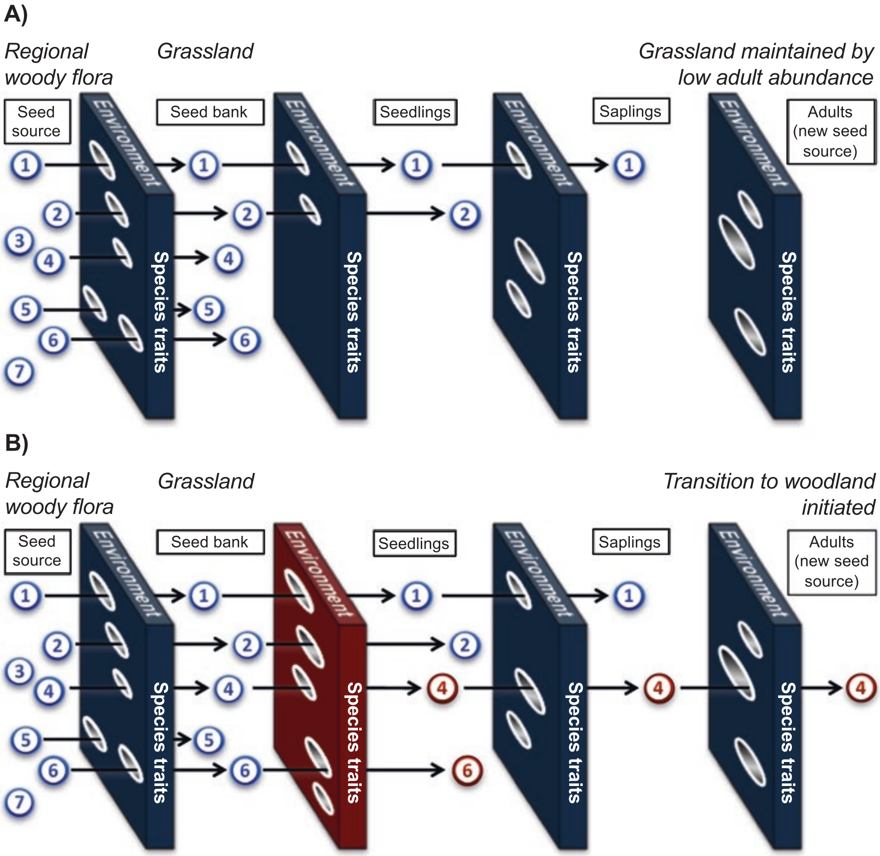

Fig. 2.7 Conceptual model of the species selection process in woody plant encroachment into grasslands. *Numbered circles* represent woody species and *blocks* represent barriers or trait filters constraining advancement to the next life stage. Each barrier may be comprised of several independent and 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 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 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.

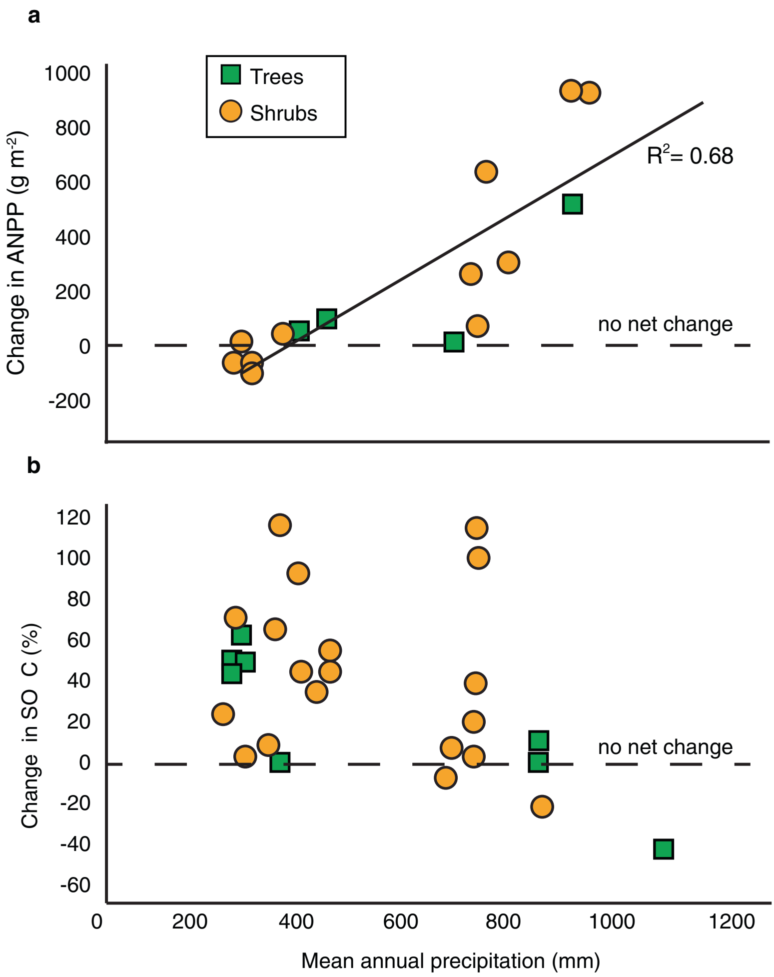

Fig. 2.8 Changes in (**a**) aboveground net primary productivity (g biomass m^{-2} year^{-1}) and (**b**) soil organic carbon with woody encroachment as a function of mean annual precipitation. Data span a range of species and ecoregions and encompass a range of sample collection and processing methodologies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

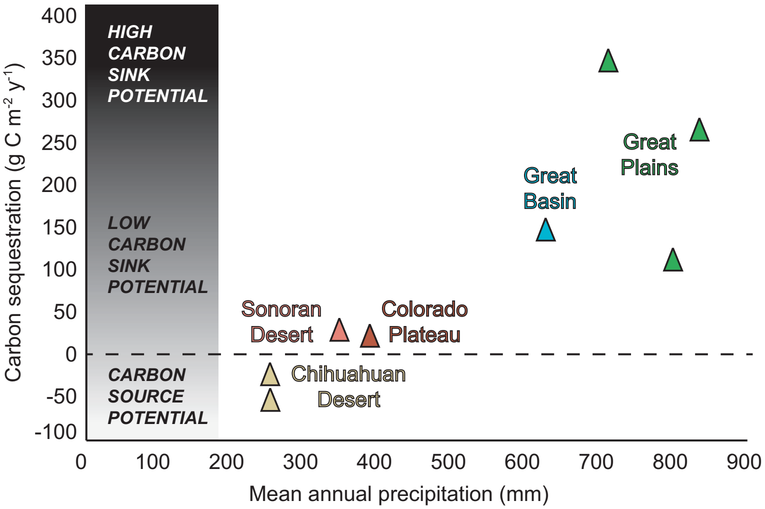

Fig. 2.9 Carbon source–sink potential with woody plant encroachment in North American ecoregions. Values are the mean of changes in aboveground net primary production plus soil organic carbon. Modified from Barger et al. (2011)

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

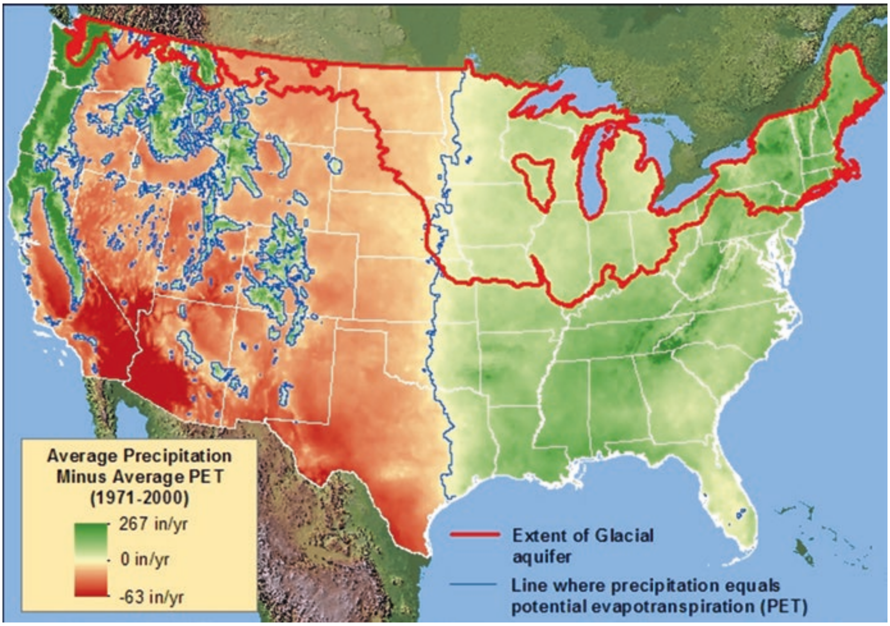

Fig. 2.10 A map of average precipitation (P) minus average potential evapotranspiration (PET) for the contiguous USA. P-PET decreases prominently from east to west and less so from north to south. Impacts of woody plant encroachment on ET are expected to be maximized near the 97th degree west longitude, 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

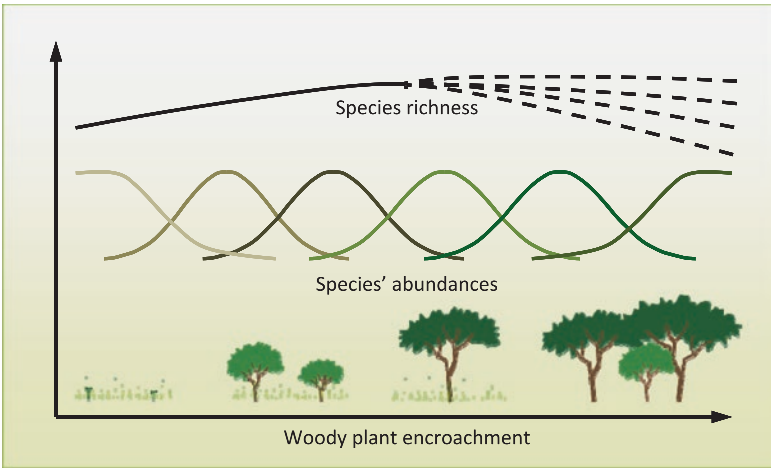

Fig. 2.11 Conceptual model of community changes in species abundances and richness with woody plant encroachment. Species richness is likely to be highest where both shrub-associated and grassland-associated species co-occur, with the endpoints varied, depending on the encroaching species

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).

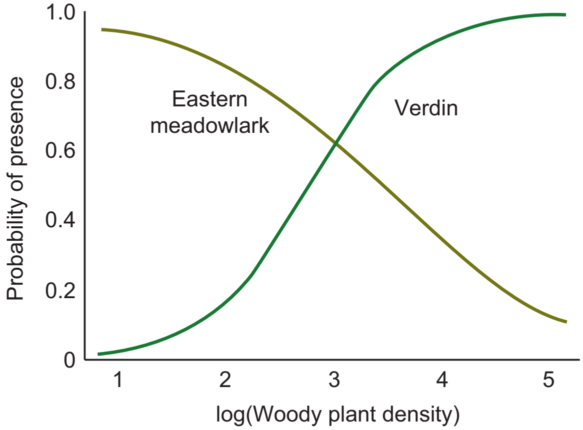

Fig. 2.12 Predicted probabilities of eastern meadowlark and verdin presence as a function of woody plant density in a Sonoran Desert grassland (R.J. Steidl, unpublished)

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

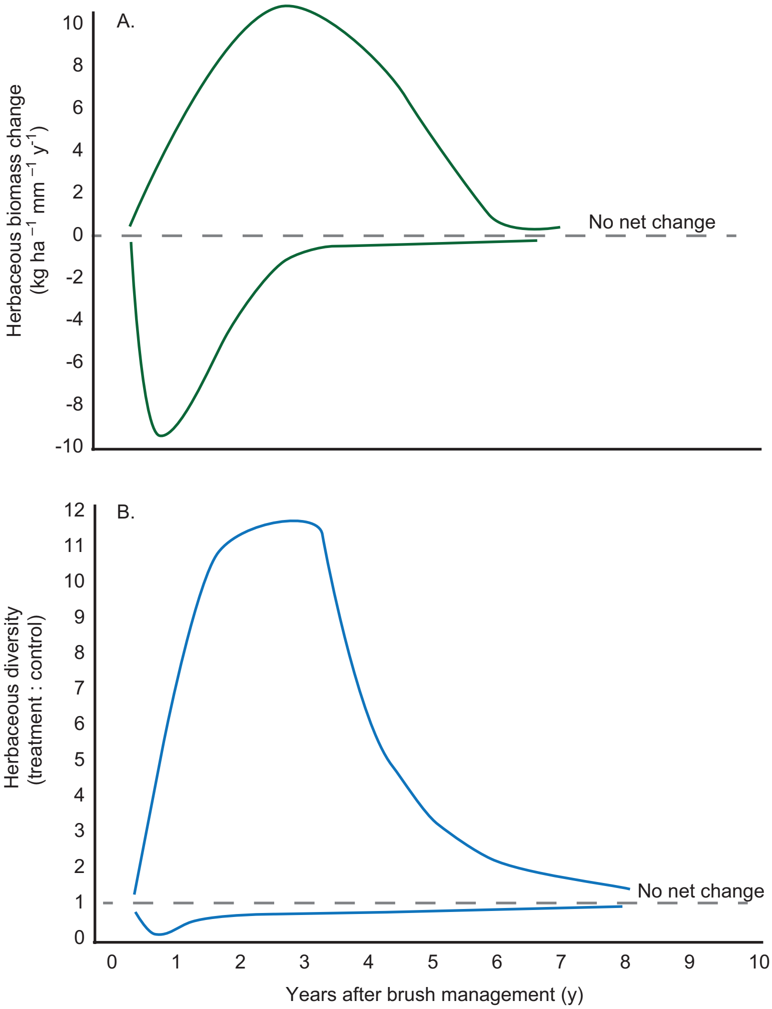

Fig. 2.13 Response envelope depicting the upper and lower limits of herbaceous (**a**) production and (**b**) diversity responses to brush management (based on data in Archer and Predick 2014)

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-

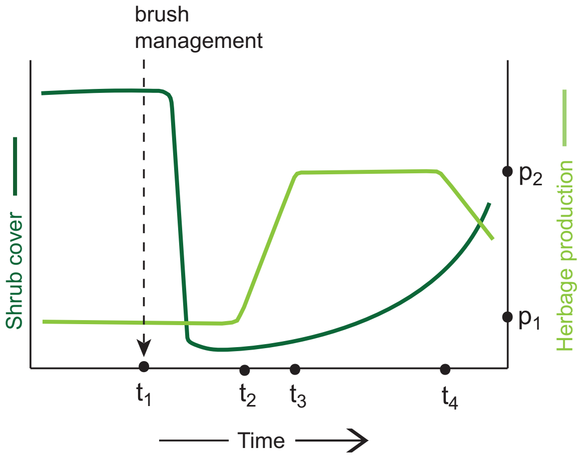

Fig. 2.14 Generalized conceptual model of herbaceous response to brush management. The lag time in response (t_1 to t_2), the magnitude of (p_1 to p_2) and time to peak herbaceous response (t_1 to t_3), the duration of peak elevated production response (t_3 to t_4), and the time frame over which herbaceous 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.

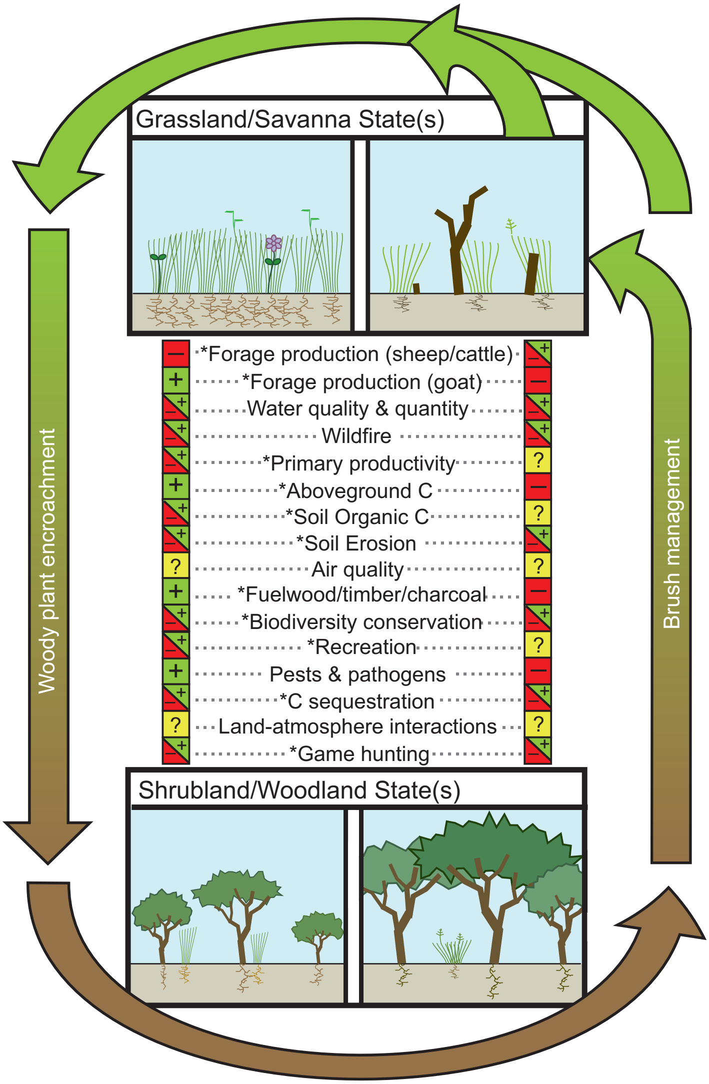

Fig. 2.15 Potential outcomes of woody plant encroachment and associated "brush management" activities. Symbols in boxes denote potential decreases (−), increases or improvements (+), mixed, context-dependent results (−\+), or insufficient information (?). From Archer and Predick (2014)

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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