Woody plant proliferation in North American drylands: A synthesis of impacts on ecosystem carbon balance

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[1] Changes in the magnitude and direction of ecosystem carbon (C) balance accompanying woody plant encroachment are among the largest contributors to the uncertainty in the North American C budget. In this synthesis we identify the important species contributing to woody encroachment, summarize our current knowledge of aboveground and belowground C storage change with woody encroachment, and evaluate the range of human and natural disturbance factors that alter the course of C gains and losses within ecosystems experiencing woody encroachment. Available data indicate that relative to the historic vegetation, aboveground net primary production (ANPP) decreases with woody plant encroachment in arid regions (mean annual precipitation (MAP) < 336 mm), but increases in semiarid and subhumid regions (on the order of 0.7 g C m^{-2} yr^{-1} per mm of MAP over 336 mm). Soil organic carbon response to woody plant encroachment ranged from losses of 6200 g C m^{-2} to gains of 2700 g C m^{-2} with an average accumulation of 385 g C m^{-2} across all studies and did not appear to be closely coupled to ANPP. Taken together, in the absence of disturbance, woody encroachment appears to result in a net ecosystem C gain across most species and ecoregions. However, disturbance associated with wildfire, land management practices, and drought may quickly and significantly offset these gains and should be explicitly factored into regional-scale C balance estimates. Our findings may be used to better constrain future estimates of woody plant encroachment influences on the North American C budget.

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1. Introduction

[2] Woody plant encroachment (the increasing abundance and dominance of shrubs and trees) has been observed in numerous ecosystems over the past century [e.g., *Archer*, 1994; *Van Auken*, 2000]. This global phenomenon has resulted in a significant redistribution of carbon (C) between its major terrestrial reservoirs. Changes in ecosystem C storage accompanying the proliferation of trees and shrubs across a range of North American ecosystems constitute a potentially significant, but highly uncertain component of the North American C budget [*Houghton et al.*, 1999; *Houghton*, 2003; *Hurtt et al.*, 2002; *King et al.*, 2007; *Pacala et al.*, 2007]. Indeed, the effects of woody encroachment on ecosystem C pools may be positive, neutral or negative [*Asner and Martin*, 2004; *Jackson et al.*, 2002; *Knapp et al.*, 2008; *Wessman et al.*, 2004]. While substantial effort has gone into understanding the consequences of woody encroachment in specific ecosystems, comparisons of these processes across North America are few.

[3] The drivers of woody plant proliferation are complex and variable by ecoregion, reflecting interactions among climate (e.g., changes in amount and seasonality of precipitation), land use (e.g., grazing by domestic livestock, reductions in fire frequency/intensity), and atmospheric chemistry (e.g., increased CO_2 concentrations) [*Archer et al.*, 1995]. The effects of woody encroachment on ecosystem C budgets are thus uncertain, both because of the multiple, interacting drivers of change, and because the impact of woody encroachment on C distribution and storage varies substantially across ecoregions.

[4] Robust generalizations of woody encroachment impacts on ecosystem C balance are elusive owing to the diversity of bioclimatic zones across which it is occurring (e.g., temperate and subtropical; coastal and montane grass-

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lands; hot and cold deserts; savannas and shrub-steppe) and the diversity of plant functional types represented by encroaching woody plants (e.g., tree versus shrub; evergreen versus deciduous; N_2 fixing versus nonfixing, deep rooted versus shallow rooted, mesophytic versus xerophytic, broad-leaved versus needle-leaved). A lack of regional-scale historical data related to the timing, rate and extent of encroachment and a lack of quantitative information on how natural and human disturbances mediate the impact of encroaching woody plants on ecosystem C pools are additional sources of uncertainty in continental-scale C budgets.

[5] Although published continental-scale estimates of woody encroachment impacts on C budgets acknowledge that the magnitude and the sign of C balance is highly uncertain, all estimates have reported it as a potentially important C sink in the U.S. and North America. Past estimates of the upper limits of its contribution to the U.S. C sink range from 60 to 130 Tg C yr^{-1} or 25–46% of the U.S. C sink during the 1980s and 1990s [*Houghton et al.*, 1999; *Hurtt et al.*, 2002; *Houghton*, 2003]. *Houghton et al.* [1999] estimates assumed areas within the U.S. that were not forested or cultivated (nearly one-fourth of the U.S. land area) were undergoing woody plant encroachment and increasing C pools by 55 g C m^{-2} yr^{-2}. *Hurtt et al.* [2002] used a combined mechanistic demography model with an empirically based land use change model and derived an estimate of 130 Tg C yr^{-1} increase in C storage in nonforested and pasture ecosystems of the U.S. (one-third of the U.S. land area). In later work, *Houghton* [2003] reduced earlier estimates by half and gave what he felt was a more realistic estimate of 60 Tg C yr^{-1}. While these estimates point to the potential importance of woody encroachment in the continental C budget, results from several studies suggest such bookkeeping methods may be inflating its effect [*Hicke et al.*, 2004; *Jackson et al.*, 2002; *Strand et al.*, 2008].

[6] To clarify uncertainties associated with the consequences of woody encroachment in the North American C budget, we synthesize the current state of knowledge of the influence of this type of vegetation change on ecosystem C stocks at both the stand and regional scales; and its relationship to key environment variables. In doing so, we identify knowledge gaps; and when appropriate, suggest ways to better constrain estimates of the influence of woody encroachment on North America C budgets.

[7] This synthesis focuses on vegetation types and regions where woody plant encroachment is known to have been spatially extensive and is well-documented. Within North America such areas typically occur where the precipitation/evaporation (P/E) ratio is near or less than 1, which includes Great Plains grasslands of the U.S. and Canada and the arid and semiarid regions of Mexico and the western U.S. Although the strictest definition of the term "encroachment" suggests movement of populations into vegetation types where they did not previously exist, this term is often defined more broadly as an increase in the importance (abundance and eventual dominance) of trees and shrubs within grassland, savanna, shrub-steppe, and tundra ecosystems where they have historically occurred. We use this broader definition in our synthesis to include both movement of woody species into adjacent vegetation types and increases in the density and cover of existing populations of woody plants. The scope of our synthesis *excludes* afforestation, which is treated separately from woody plant encroachment in continental-scale North American C budgets [*Houghton*, 2003]. Although woody expansion has been occurring globally in arctic and alpine ecosystems [*Hallinger et al.*, 2010; *Stow et al.*, 2004; *Tape et al.*, 2006] and in urban and peri-urban landscapes, we have chosen to focus on drylands areas of the western U.S. (Figure 1) due to the paucity of data in these other systems.

[8] Within this scope, we first review the primary species contributing to woody plant encroachment across the U.S. and Canada and their rate of spread (although woody plant encroachment has been observed in Mexico, we found no quantitative accounts to draw from). We then synthesize what is known of aboveground and belowground C storage changes accompanying woody plant encroachment and ascertain the extent to which environmental variables mediate observed variation at the ecoregion scale. Finally, we examine how human and natural disturbance may alter the potential course of C accumulation or loss within ecosystems experiencing woody plant encroachment.

2. Species Contributing to Woody Encroachment and Rates of Spread

[9] Woody species known to proliferate within North American herbaceous plant communities encompass a broad range of taxonomic levels (monocots and dicots), leaf architectures (needle-leaved, broadleaf), leaf physiologies (evergreen, deciduous; long-lived, short-lived; mesophytic, xerophytic), rooting habits (shallow, deep), statures (suffrutescent, fruticose, and arboreal), and nitrogen metabolism capabilities (nitrogen fixers and nonfixers). Such diversity speaks to the potential competitive advantage woody life forms may have over herbaceous plants, even in arid and semiarid ecosystems where physiological traits (e.g., the C_4 photosynthetic pathway) and disturbance cycles (e.g., fire) are typically expected to favor grasses. For these reasons, forecasting the effect of woody encroachment on regional C dynamics is uniquely challenging.

[10] Although there are upwards of 20 documented woody species known to have proliferated in grassland, savanna and shrub-steppe ecosystems of North America over the last century, four groups, all present throughout the Holocene, stand out: (1) mesquite (*Prosopis* spp.) proliferation in Southern Great Plains (*Prosopis glandulosa*) and southwestern semidesert (*P. velutina, P. glandulosa*) grasslands and savannas, (2) juniper (*Juniperus* spp.) proliferation in Great Plains tall- and mixed-grass prairies (*J. virginiana*) and cold desert sagebrush steppe ecosystems of the Great Basin (*J. occidentalis*), (3) pine (largely *Pinus ponderosa*) proliferation in montane grasslands, savannas and meadows, and (4) creosote bush (*Larrea tridentata*)/tar bush (*Flourensia cernua)* proliferation in semidesert grasslands within the Sonoran and Chihuahuan deserts.

[11] Estimating the effects of woody encroachment on regional C budgets begins with quantifying the rates and extent of woody species expansion. Variation in approaches to quantifying encroachment rates has resulted in a wide range of reported metrics. While not consistently related to either net primary production (NPP) or C stocks, the most widely used metric of encroachment is change in canopy cover over a specified time interval (Table 1). The spatial

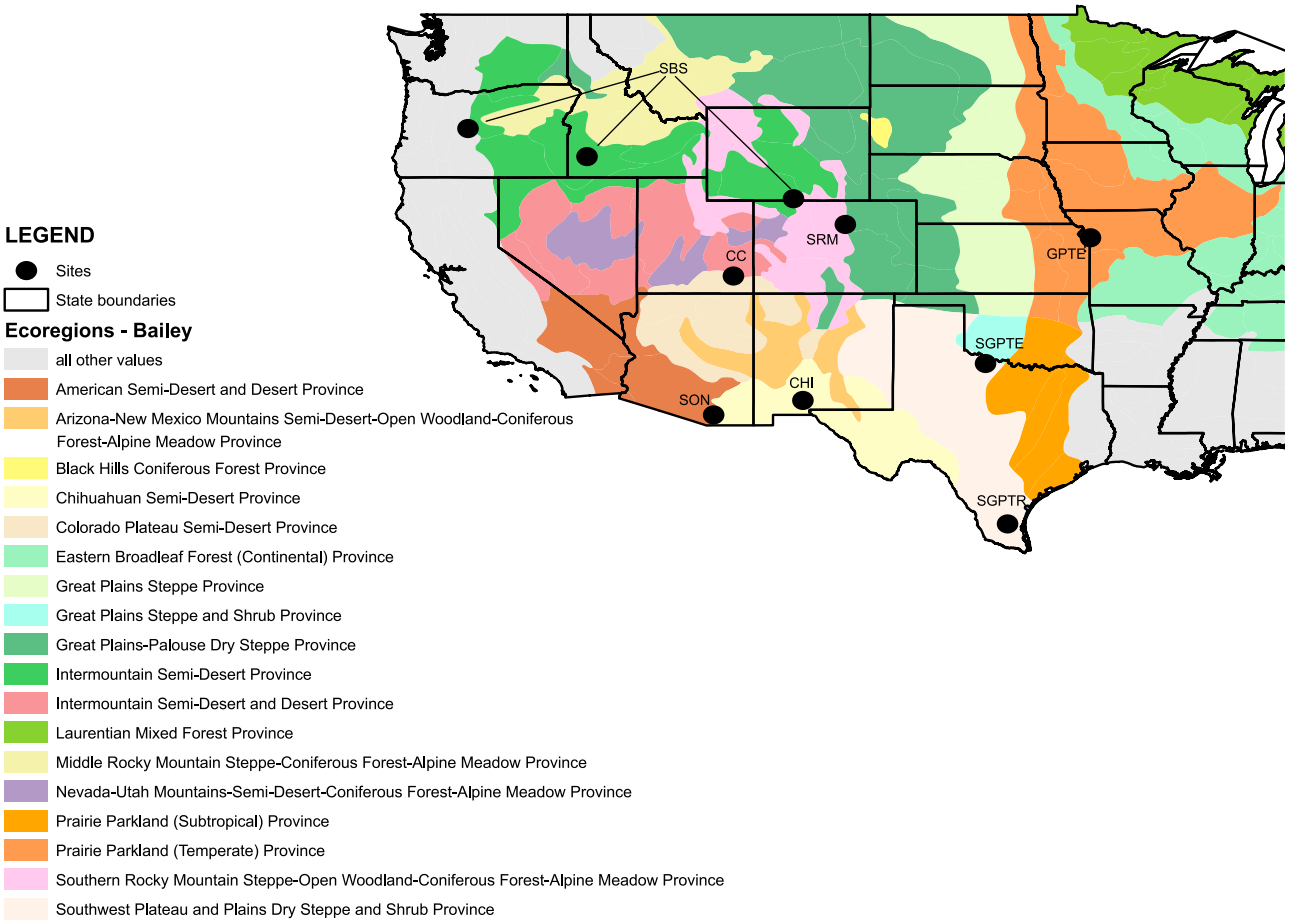


Figure 1. Map of major ecosystem provinces [*Bailey et al.*, 1994] evaluated for changes in carbon balance with woody encroachment. The circles with the following codes indicate the important study sites that contributed to our synthesis data: CC, Canyon Country, Northern Colorado Plateau; CHI, Chihuahuan Desert; GPTE, Great Plains Temperate; SBS, sagebrush steppe; SGPTE, Southern Great Plains Temperate; SGPTR, Southern Great Plains Subtropical; SRM, Southern Rocky Mountains.

and temporal intervals considered in these studies range from less than a decade to over a century and the populations sampled range from plots (0.04–0.4 ha) [*Miller and Rose*, 1995; *Soulé and Knapp*, 1998] to regions (~400–4000 km^2) [*Asner et al.*, 2003; *Strand et al.*, 2008]. Although the spatial and temporal scales of evaluation were highly variable across studies, some generalizations are possible: (1) Woody encroachment rates were 5–7 fold higher across the Central Great Plains ecoregion (1.7% cover change yr^{-1}) relative to ecoregions outside of the Great Plains (<0.4% cover change yr^{-1}) (Figure 2). (2) Trees (evergreen conifers and *Quercus* spp.) and shrubs exhibited similar encroachment rates across all ecoregions (Table 1; mean % cover change yr^{-1}; trees = 0.62% yr^{-1}, shrubs = 0.52% yr^{-1}). (3) Eastern red cedar (*J. virginiana*), an evergreen tree, and honey mesquite (*P. glandulosa*), an N_2 fixing deciduous arborescent, both of the Great Plains ecoregion, exhibited some of the highest rates of encroachment (Table 1; 2.3% yr^{-1}).

[12] Although our review of woody plant cover changes is important to identify those ecoregions and species that are undergoing change, there are important limits to our understanding of encroachment rates at a continental scale. First, plot-level population data are not likely to scale linearly to regional woody encroachment rates. Local plot studies of woody encroachment have typically targeted localities where encroachment is known to have occurred or to be occurring, and rates of increase derived from such studies may therefore overestimate regional rates. Because our understanding of why woody plants have proliferated in some areas and not others within an ecoregion is poor, scaling the rates observed at case-study sites to entire ecoregions can be misleading, even when rates are conservatively applied. For example, previous bookkeeping methods have assigned moderate ecosystem C increases to vast areas of land within the U.S. [*Houghton et al.*, 1999]. Although these moderate C accumulation rates may fall within a reasonable range, the spatial extent in which they are applied is likely far too broad (e.g., all U.S. pastureland).

[13] A second challenge to quantifying continental effects of woody encroachment on C dynamics involves the nonlinearities in rates of woody expansion and the ecosystem consequences of that expansion over time. Rates of woody plant encroachment are highly dependent on the amount of woody cover present at the beginning of the change interval, with rates of change typically decreasing with increasing

Table 1. Observed Rates of Woody Encroachment Across North America[a]

Location	Study	Method		Time Period (T_0–T_1)	Percent Woody Cover (T_0)	Percent Woody Cover (T_1)	Percent Δ Woody cover (yr^{-1})
	Mesquite (*Various Prosopis spp.*) *Encroachment Into Arid Grasslands* (*S*)						
Chihuahuan Desert	*Goslee et al.* [2003]	b		1936–1983	25.0	45.0	0.4
	Laliberte et al. [2004]	b,c		1937–2003	1.0	13.0	0.2
	Buffington and Herbel [1965]	d	(yes)	1855–1963	14.0	59.0	0.4
Sonoran Desert	*Browning et al.* [2008]	d		1936–1966	17.0	36.0	0.6
		d	(yes)	1966–1996	36.0	28.0	0.3
	King et al. [2008]	b,d	(yes)	1967–2005	15.0	14.0	<0.100
	Briggs et al. [2007]	b		1940–2001	6.0	14.0	0.1
	McClaran [2003]	d	(yes)	1960–2000	9.0	17.0	0.2
	Mesquite (*P. glandulosa*) *Encroachment Into Semiarid Grasslands* (*S*)						
Southern Great Plains	*Ansley et al.* [2001]	b		1976–1995	15.0	59.0	2.3
	Asner et al. [2003]	b,e,d,c	(yes)	1937–1999	32.6	42.3	0.2
	Archer et al. [1988]	b		1960–1983	8.0	36.0	1.2
	Juniper (*J. ashei and J. pinchotti*) *Encroachment Into Semiarid Grasslands* (*T*)						
	Smeins and Merrill [1988]	d		1949–1983	8.00	35.00	0.8
		d		1949–1983	10.00	30.00	0.6
		d	(yes)	1949–1983	14.00	10.00	−0.1
	Juniper (*Largely J. occidentalis*) *Encroachment Into Sagebrush Steppe* (*T*)						
Sagebrush Steppe	*Strand et al.* [2008]	e	(yes)	1946–1998	5.3	10.4	0.1
	Sankey and Germino [2008]	c		1985–2005	25.0	32.3	0.4
	Knapp et al. [2008]	d		1972–1995	21.7	34.5	0.6
	Miller and Rose [1995]	d		1881–1990	0.0	23.0	0.2
		d		1881–1990	0.0	12.0	0.1
		d		1881–1990	0.0	5.0	0.1
	Soulé and Knapp [1999]	b		1951–1994	11.0	19.0	0.2
		b		1951–1994	5.0	9.0	0.1
	Campbell et al. (submitted manuscript, 2011)	b	(yes)	1985–2005	10.0	14.0	0.2
	Eastern Red Cedar (*J. virginiana*) *and Various Shrub Encroachment Into Mixed-Grass Prairie* (*T*)						
Central Great Plains	*Briggs et al.* [2002]	b		1956–2000	0.0	100.0	2.3
	Walker and Hoback [2007]	NA		2005	NA	30.0	2.0
	Bragg and Hulbert [1976]	b		1937–1969	20.0	55.0	1.1
	Pine (*Largely Pinus ponderosa*) *Encroachment Into Arid Grasslands and Montane Meadows* (*T*)						
Southern Rocky Mountains	*Anderson and Baker* [2006]	b		NA	NA	NA	0.1
	Mast et al. [1997]	b	(yes)	1930–1995	14.6	50.9	0.7
	Coop and Givnish [2007]	b	(yes)	1935–1996	70.6	76.7	0.1
	Miller [1999]	b		1935–1991	50.0	80.0	0.5
Northern Rocky Mountains	*Bai et al.* [2004]	b	(yes)	1960–1990	52.9	63.7	0.4
	Oak (*Quercus spp.*) *and Pine* (*Pinus spp.*) *Encroachment Into Tall-Grass Prairie* (*T*)						
Central Great Plains	*Scharenbroch et al.* [2010]	b		1979–2002	20.0	60.0	1.7
	Robertson et al. [1996]	b		1940–1988	NA	NA	1.6

[a]In the methods to evaluate woody cover change, codes were used to indicate (1) the type of data that were used in evaluating woody cover change and (2) whether the survey incorporated disturbed sites. S, shrub; T, tree. The "tree" category includes both trees and aborescent conifer species. Under "methods," (yes) indicates that the survey included locations where woody cover was lost due to disturbance.
[b]Manual interpretation of aerial photography.
[c]Satellite imagery.
[d]Ground inventory.
[e]Automated interpretation of aerial photography.

woody cover [*Browning et al.*, 2008; *Fensham et al.*, 2005]. Work in Africa suggests the upper limit of woody plant cover in arid and semiarid systems is constrained by mean annual precipitation [*Sankaran et al.*, 2005]. However, below this upper limit, variation in woody cover may be substantial owing to local topoedaphic conditions or to land use practices. However, as most observations of woody expansion rates rely on only two time points, the shapes of these growth curves are largely undescribed for North America. Studies that have quantified woody cover over three or more time points suggest encroachment rates are nonlinear and stochastically punctuated by periods particularly favorable for woody plant establishment or growth [*Ansley et al.*, 2001; *Archer et al.*, 1988; *Bragg and Hulbert*, 1976; *Goslee et al.*, 2003; *Hoch et al.*, 2002]. In addition, even if encroachment is linear, as species turnover occurs, the C consequences of this increase may not be [e.g., *Lane et al.*, 1998]. Thus, the order-of-magnitude differences in encroachment rates in Table 1 and Figure 2 illustrate the risk of assuming simple, static cover change rates and point to

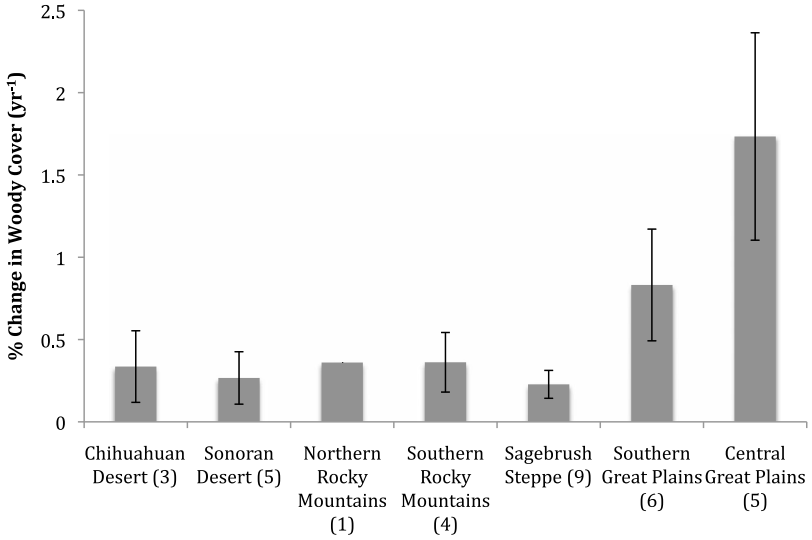


Figure 2. Summary of woody plant encroachment rates by ecoregion. Values are the mean (±1 SE) change in woody plant cover per year by ecoregion calculated from values reported in Table 1. Values following the ecoregion name on the *x* axis are the number of studies that contributed to the calculated mean within each ecoregion.

the need to develop cover change probability indices [*Browning and Archer*, 2011; *Fensham et al.*, 2005].

3. Potential for Aboveground and Belowground C Storage With Woody Encroachment

[14] Woody plant encroachment may alter ecosystem C balance via effects on aboveground and belowground pools and fluxes. Changes in NPP brought about by changes in species composition may alter ecosystem C uptake; and changes in carbon uptake must be balanced against C losses associated with changes in auto- and heterotrophic respiration, volatile organic carbon emissions, soil erosion and leaching losses associated with the loss of ground cover that often accompanies woody plant encroachment, volatile losses accompanying fire (both prescribed and wild), and biomass removals associated with land use and management activities. In this section we provide a synthesis of our current understanding of how climate and edaphic factors may mediate or constrain the net outcome of woody plant encroachment effects on C pools and fluxes. Subsequent sections then evaluate how major disturbance factors (i.e., land use and management activities, fire and drought) may further alter the course of ecosystem C changes occurring with woody plant encroachment.

3.1. Changes in Aboveground Relationships With Woody Plant Encroachment

[15] Changes in NPP represent changes in ecosystem C uptake and a key mechanism by which ecosystem C balance may be altered with woody plant encroachment. A recent analysis of field-based, plot-scale studies indicated that aboveground NPP (ANPP) decreases with shrub encroachment in arid systems and increases with increasing mean annual precipitation (MAP) in semiarid and subhumid systems [*Knapp et al.*, 2008]. The stimulation in ANPP in higher MAP sites appears to reflect the fact that shrubs have a canopy architecture that enables them to display greater leaf area than the grasses they replace. We expanded the *Knapp et al.* [2008] ANPP – MAP analysis to include additional sites encroached upon by coniferous trees and to include field and remote sensing studies conducted across a broader range of spatial scales and ecoregions. Results from this expanded synthesis confirm that the relationship found by *Knapp et al.* [2008] holds across a broader range of sites and growth forms (Figure 3a). Assuming that approximately half of ANPP is C, the slope of the regression suggests that for every mm increase in MAP above 336 mm, ANPP will increase by ca. 0.7 g C m^{-2} yr^{-1} relative to that of historic vegetation. Exploration of precipitation seasonality and precipitation-temperature interactions [*Neilson et al.*, 1992] might further clarify ANPP responses to woody plant encroachment.

[16] Ecosystem ANPP – MAP relationships were similar for tree (i.e., conifer trees and arborescents) and shrub encroachment, but the relationship between aboveground biomass (AGB) and MAP in shrub-encroached ecosystems versus tree-encroached systems differed dramatically. AGB in shrub-encroached ecosystems increased with MAP, whereas that of tree-encroached ecosystems declined (Figure 3b). There is some suggestion that the seasonality of precipitation may be an important factor in predicting tree AGB response across ecoregions. The greatest tree biomass response occurred in Great Basin sagebrush steppe sites encroached upon by western juniper *(J. occidentalis)*, sites strongly dominated by winter precipitation. All other tree-encroached sites exhibited more moderate increases in AGB regardless of species (*P. ponderosa, P. edulis, J. osteosperma, J. virginiana*) and occurred in regions with bimodal or significant summer precipitation. Due to the lack of tree biomass data points (Figure 3b, N = 6) we were not able to fully evaluate these patterns. AGB in tree-encroached systems

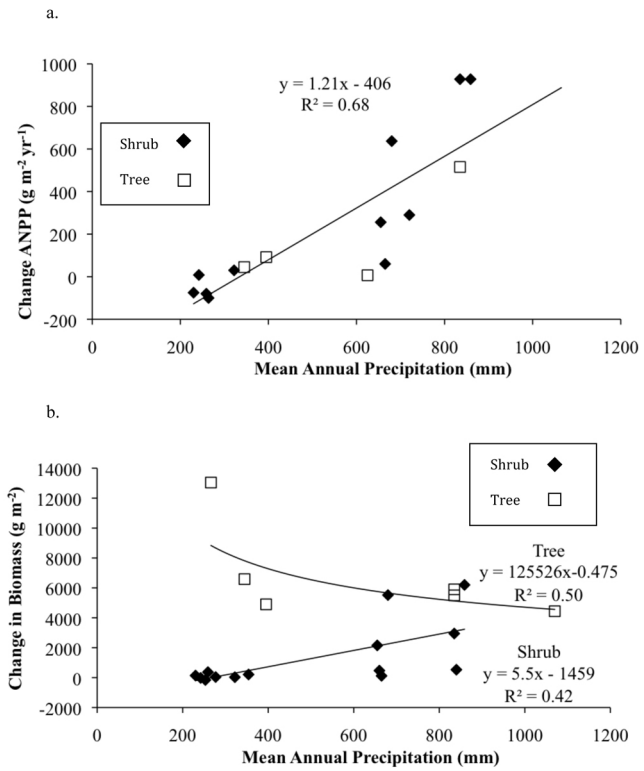


Figure 3. Changes in (a) aboveground net primary productivity (ANPP, g biomass m^{-2} yr^{-1}) and (b) aboveground biomass (AGB, g m^{-2}) with woody encroachment as a function of mean annual precipitation (MAP). Black diamonds, shrub species; open squares, tree species. The "tree" category includes both tree and aborescent conifer species. ANPP references: *Archer et al.* [2001], *Asner et al.* [2003], *Briggs et al.* [2005], *Lett et al.* [2004], D. P. Fernandez et al. (unpublished data, 2011), *Hicke et al.* [2004], *Huenneke et al.* [2002], *Hughes et al.* [2006], *Jackson et al.* [2002], *Knapp et al.* [2008], *Norris et al.* [2001], and *Strand et al.* [2008]. AGB references: *Asner et al.* [2003], *Bai et al.* [2009], *Browning and Archer* [2011], D. P. Fernandez et al. (unpublished data, 2011), *Jackson et al.* [2002], *Knapp et al.* [2008], *Lett et al.* [2004], *McKinley and Blair* [2008], *Norris et al.* [2001], and *Tiedemann and Klemmedson* [2000].

consistently exceeded that of shrub-encroached systems at the lower end of the MAP range. Thus, life form of the encroaching species appears to have a dramatic effect on aboveground C allocation, differences that were not evident in the ANPP data.

[17] Although MAP may explain much of the variation in ANPP changes with woody plant abundance, edaphic properties (e.g., soil texture, depth, salinity) and topographic setting (e.g., slope aspect and inclination) exert strong local influences on aboveground responses. Increases in ANPP with *P. glandulosa* encroachment on coarser textured, deep clay loam sites has been shown to be higher than those on finer textured shallow clay sites in the Southern Great Plains [*Asner et al.*, 2003; *Hughes et al.*, 2006]; but where sites with fine-textured soils receive run-off from uplands, these relationships may be reversed [*Hibbard et al.*, 2003]. In a Sonoran Desert grassland, *P. velutina* AGB on clay soils was 1.4 times higher than that on sandy soils [*Browning et al.*, 2008]. However, as soil clay content approaches 30%, edaphically maintained grasslands resistant to shrub or tree encroachment may occur [*McAuliffe*, 1994]. Soil texture had no influence on AGB of western snowberry (*Symphoricarpos occidentalis)* encroaching into northern mixed-grass prairie communities [*Bai et al.*, 2009]. Uncertainty in regional estimates of C sequestration accompanying woody plant encroachment will thus depend, in part, on the extent to which we can spatially account for edaphic mediation of and constraints to woody plant ANPP and AGB.

3.2. Belowground Responses

[18] The soil organic matter reservoir often comprises nearly 90% of the C storage in terrestrial ecosystems [*Schlesinger*, 1997]. Thus, even small changes to this large reservoir may have dramatic implications for ecosystem C balance. Woody plant encroachment potentially changes the quantity, quality and spatial distribution of organic matter inputs into the soil reservoir and the degree to which such inputs are lost from this reservoir via soil respiration (root + microbial), leaching and erosion.

[19] Belowground NPP (BNPP) is difficult to quantify and this is particularly so for ecosystems containing woody plants with coarse, heterogeneous and deep root systems. Although generalizations regarding woody plant encroachment effects on ANPP and AGB are emerging (Figure 3) we know little of how these translate to BNPP and standing stocks of C in root biomass. Given the general differences in grass versus woody plant rooting depths we would predict reductions in root biomass in upper soil horizons and allocation to deeper soils with woody plant encroachment [*Canadell et al.*, 1996; *Jackson et al.*, 1996]. However, available data do not necessarily support this generalization [*Bai et al.*, 2009; *Hibbard et al.*, 2003]. *Hibbard et al.* [2001] found that fluctuations in monthly root biomass standing crop in shrub communities displacing grasslands in the Southern Great Plains far exceeded annual foliar litterfall inputs, suggesting that these belowground inputs of organic matter may drive soil C dynamics; and in this same system, *Boutton et al.* [2008] showed that roots account for 25–45% of the SOC accumulation. In both of these studies, root biomass in upper soil horizons was far lower in grassland communities than in shrubland communities that had replaced them. Similar responses in root biomass were observed in a northern mixed-grass prairie ecosystem whereby root biomass increased by more than 50 percent with encroachment of *S. occidentalis*, exceeding that of AGB [*Bai et al.*, 2009].

[20] Rooting depth in woodlands and shrublands averages 2 m greater than in grasslands [*Canadell et al.*, 1996; *Jackson et al.*, 1996] and roots of woody plants are typically more lignified than those of herbaceous vegetation. Following this, increases in rooting depth with woody encroachment [*Boutton et al.*, 1998] would be expected to promote C sequestration as a result of the greater allocation of low-quality organic matter to deeper soil layers where decomposition rates are low [*Biederman and Boutton*, 2009].

[21] Less clear is the role of changing root litter quality and turnover time with woody encroachment. The more lignified woody plant roots are generally thought to have slower turnover times as compared to herbaceous species. However, a comparison of root lignin concentrations (an

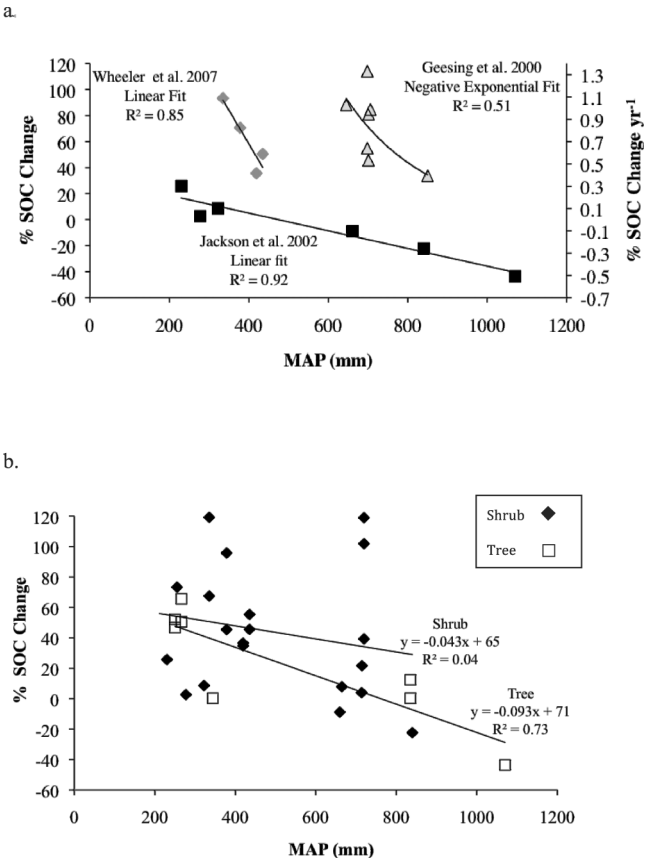


Figure 4. Changes in soil organic carbon (SOC) accompanying woody plant encroachment as a function of mean annual precipitation (MAP) (a) in three studies that used consistent sampling methodologies; and (b) in 36 sites spanning a range of species and ecoregions and encompassing a range of sample collection and processing methodologies. SOC references: *Bates et al.* [2002], *Boutton et al.* [2008], *Connin et al.* [1997], D. P. Fernandez et al. (manuscript in preparation, 2010), *Geesing et al.* [2000], *Gill and Burke* [1999], *Hibbard et al.* [2001], *Hughes et al.* [2006], *Jackson et al.* [2002], *Klemmedson and Tiedemann* [2000], *Knapp et al.* [2008], *Liao et al.* [2006], *McCulley et al.* [2004], *McKinley and Blair* [2008], *Scharenbroch et al.* [2010], *Smith and Johnson* [2003], *Springsteen et al.* [2010], *Throop and Archer* [2008], and *Wheeler et al.* [2007]. Black diamonds, shrub species; open squares, tree species. The "tree" category includes both trees and aborescent conifer species.

indicator of decomposability) between remnant and shrub-invaded grassland, found root lignin concentrations to be higher in the remnant grassland [*Boutton et al.*, 2008]. Root lignin concentrations in a desert subshrub were, however, comparable to perennial grasses resulting in similar decomposition rates in a Chihuahuan desert watershed [*Mun and Whitford*, 1997]. Given the heterogeneous distribution of woody plant lateral and tap roots, root biomass and litter quality studies are often biased toward relatively small diameter roots. This reflects the fact that sampling for roots is typically conducted by sparse, random coring. Such sampling has a low probability of encountering large, coarse, heavily lignified roots or is unable to sever and capture such roots when they are encountered.

[22] Soil organic carbon (SOC) reflects inputs from NPP excluding particulate (undecomposed) plant and animal products. The magnitude and direction of changes in the SOC pool with woody encroachment are highly uncertain and range from substantial increases, to substantial decreases to no net effects [*Asner and Archer*, 2010; *Hughes et al.*, 2006; *Jackson et al.*, 2000; *Wessman et al.*, 2004]. Changes in SOC pools accompanying woody plant encroachment may be inversely related to MAP, wherein substantial increases in SOC pools in arid systems gave way to substantial decreases in humid systems (Figure 4a) [*Jackson et al.*, 2002]. *Wheeler et al.* [2007] and *Geesing et al.* [2000] observed a similar inverse relationship within a narrower range of MAP in arid/semiarid systems. In an effort to assess the robustness of this pattern, we synthesized additional data from the literature. Changes in SOC with tree encroachment indicate an inverse relationship to MAP, consistent with the patterns in Figure 4a. However, SOC response to shrub encroachment is highly variable and unrelated to MAP (Figure 4b). Differences in patterns of SOC changes induced by life form may be partially explained by the similarity across the tree species evaluated in our synthesis; all trees are low to mid-elevation conifers. In contrast, shrub species in our data synthesis were much more broad in their functional types and include differences in such capabilities as N-fixation that may influence changes in SOC. Combining the tree and shrub SOC results, the overall response was highly variable ranging from losses of 6200 g C m^{-2} to gains of 2700 g C m^{-2} with an average accumulation of 385 g C m^{-2} (data not shown). Of the 13 studies that reported an estimated time since encroachment, rates of SOC change ranged from losses of 80 g C m^{-2} yr^{-1} to accumulations of 29 g C m^{-2} yr^{-1} with a mean of 2.2 g C m^{-2} yr^{-1} and showed no relationship to MAP.

[23] Soil bulk density and clay content mediate the magnitude and direction of changes in SOC with woody encroachment. Soil C accumulation when woody plants encroach decreases as bulk density increases, with C losses being confined to soils with bulk densities above >1.6 g m^{-3} (Figure 5a). SOC appears likely to accumulate linearly with woody plant encroachment across clay contents ranging from 7 to 31% (Figure 5b), presumably reflecting greater occlusion and protection of organic matter afforded by clay micelles [*Franzluebbers and Arshad*, 1996, 1997; *Gill and Burke*, 1999; *Liao et al.*, 2006]. These relationships only emerged when SOC change was calculated in a way that accounted for the variable soil sampling depths across studies. The key role of clay content in mediating SOC response to woody plant encroachment has been exemplified in the Southern Great Plains, where SOC accumulation rates were over threefold higher in fine-textured soils as compared to adjoining coarse-textured soils [*Boutton et al.*, 2008].

[24] Lack of standardized soil sampling protocols hampered direct comparisons across studies. The labor and expense required to acquire and process soil samples makes it difficult to collect them at the intensity needed to represent the high degree of horizontal and vertical spatial variability in SOC distribution. In cases where SOC is promoted by woody plant encroachment the changes are typically greatest near the soil surface, decline with depth and may be

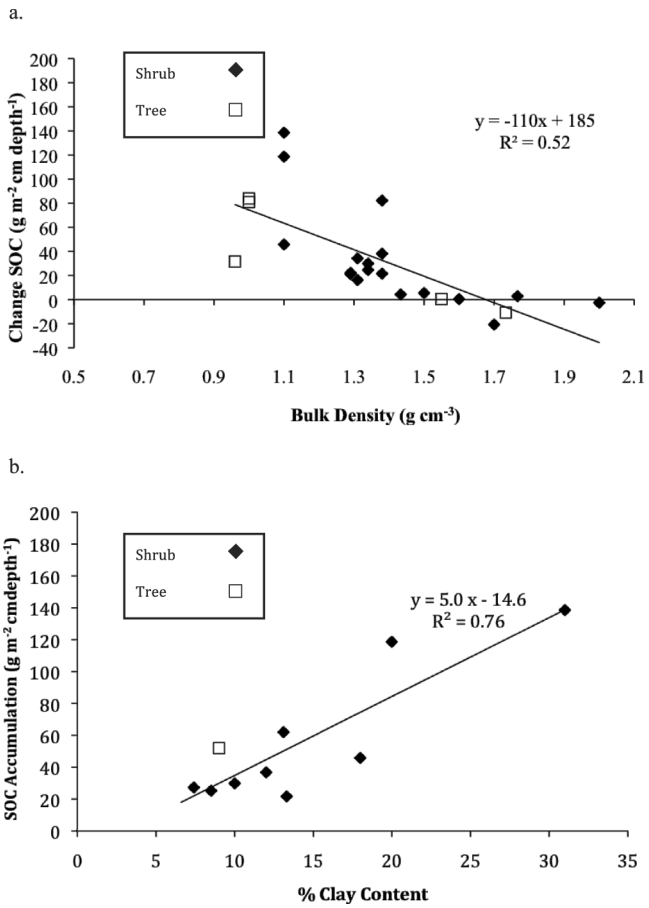


Figure 5. Relationship between changes in SOC with woody encroachment and two frequently reported soil properties: (a) bulk density and (b) texture as percent clay content. Soil samples in these studies were collected across a range of depths. As a result, we controlled for depth by calculating (SOC change (g m^{-2})/cm of soil sampled). Thus SOC units are expressed as g m^{-2} cm^{-1}. Black diamonds, shrub species; open squares, tree species. The "tree" category includes both trees and aborescent conifer species. Bulk density references (Figure 5a): *Bates et al.* [2002], D. P. Fernandez et al. (unpublished data, 2011), *Hibbard et al.* [2001], *Jackson et al.* [2002], *Klemmedson and Tiedemann* [2000], *McCulley et al.* [2004], *Scharenbroch et al.* [2010], *Throop and Archer* [2008], *Wheeler et al.* [2007]; and clay content references (Figure 5b): D. P. Fernandez et al. (unpublished data, 2011), *Hibbard et al.* [2001], *Liao et al.* [2006], *McCulley et al.* [2004], *Springsteen et al.* [2010], and *Wheeler et al.* [2007].

largely confined to the upper 20 or 30 cm of the soil profile [*Boutton et al.*, 2008; *McClaran et al.*, 2008]. Woody plant influences on SOC pools are also typically confined to soils in the subcanopy area and increase linearly with the size/age of the plant and decrease along bole-to-dripline gradients [*Huang et al.*, 2010; *Liao et al.*, 2006; *Throop and Archer*, 2008]. Much of the reported variation in SOC response to woody plant encroachment (Figure 4b) may thus be due to wide range of differences in: depths sampled, stand age, size/age of plants sampled within a stand, where samples were collected along bole-to-dripline gradients, species identity and growth habit and soil physical properties (e.g., texture, bulk density; Figure 5) at the sample location. Uncertainty in SOC response may also reflect the fact that woody plant encroachment often occurs in areas with a history of livestock grazing which itself has positive, neutral and negative effects on SOC pools [*Neff et al.*, 2009; *Derner et al.*, 2006; *Milchunas and Lauenroth*, 1993], an issue addressed in later sections of this paper.

[25] Despite consistent increases in ANPP with woody vegetation encroachment (Figure 3a) the trends in SOC are highly variable, ranging from substantial losses to large gains to no net change (Figure 4b). Changes in ANPP should change the magnitude of inputs into the soil C pool and thus influence SOC mass. However, our data synthesis suggests arid sites experiencing declines in ANPP with shrub encroachment can accrue substantial SOC, whereas sites experiencing substantial increases in ANPP may experience losses of SOC (Figures 3a and 4b). These opposing responses in ANPP and SOC changes may reflect species-specific differences due to: the quality of litter inputs, patterns of aboveground and belowground biomass allocation, soil physical and chemical properties (texture, pH, bulk density, etc.), modification of microclimate (soil temperature, stemflow, throughfall, evapotranspiration, etc.), and patterns of ground cover and erosion.

[26] In addition to improving our ability to predict the net outcome of complex interactions among plant species, topoedaphic setting, and climate on SOC responses to woody plant encroachment, we are also challenged with extrapolating the results obtained from plot-scale studies to landscape and region scales. Spatial sampling of SOC along a catena (hillslope) gradient in the Southern Great Plains, where woody cover has increased substantially over the past 100 years, revealed variation at two spatial scales [*Liu et al.*, 2010]. Smaller scale variation appeared to reflect the local influence of shrubs on SOC, whereas the larger scale variation appeared to reflect differences between plant communities. Furthermore, spatial uncertainty appears to increase with woody encroachment into grassland [*Liu et al.*, 2011]. These spatial scaling issues present significant challenges for designing appropriate SOC sampling protocols. Simulations of alternative sampling designs indicate that approaches combining stratified random sampling with transect sampling yield the best estimates of SOC pools; and that random sampling designs were less effective and required much higher sampling densities [*Liu et al.*, 2011].

[27] In some systems, the magnitude of SOC changes associated with woody plant encroachment can be predicted using algorithms that scale patterns of SOC distribution as a function of woody plant canopy area [*Throop and Archer*, 2008]. In these cases, remote-sensing tools could be used to estimate landscape SOC pools indirectly from measuring canopy area. However, this approach would require an ability to discern individual plant canopies on imagery, and assurances that land use history has not altered canopy area-SOC pool relationships [*Browning et al.*, 2009; *Huang et al.*, 2007].

3.3. Integrating Aboveground and Belowground C Responses to Woody Encroachment

[28] The combined aboveground and belowground response will determine whether C is stored or released from ecosystems undergoing woody plant encroachment. A summary of aboveground and belowground responses

Table 2. Summary of the Aboveground and Belowground C Responses With Woody Encroachment Across the Major Species and Ecoregions of the United States[a]

Ecoregion	MAP (mm)	Δ Aboveground Biomass (g C m^{-2})	Δ Belowground SOC (g C m^{-2})	Δ ANPP (g C m^{-2} yr^{-1})	Δ Belowground SOC (g C m^{-2} yr^{-1})	Δ ANPP + SOC (g C m^{-2} yr^{-1})	Reference[b]
			Mesquite (Prosopis spp.)				
Southern Great Plains, Temperate	798	1078	−760–155	110–122	−15–3	95–125	AN, AG (1) BS (2) BS, BA (3)
Southern Great Plains, Subtropical	709	2760	458–2700	319	3–54	322–373	BS (4, 6) AG, BS, BA (5) BA (7)
Sonoran Desert	388	210	110–597	10–17	1–12	11–29	BS (8, 10) BA (10) AG, AN (9)
Chihuahuan Desert	250	−64–20	−308	−48	−6 – −2	−54 – −50	AG (3) AG, AN, BS (1)
			Juniper spp.				
Great Basin *J. occidentalis*	625	6521	810–1306	130	5–26	135–156	AG, BS (11) BS (12, 13) AN (14)
Great Plains *J. virginiana*	835	2750–2951	26–428	258	0.17–9	258–267	AN (15) AG, AN (1) BS, BA (16) AG, BS, BA (17)
Colorado Plateau (Canyon Country) *J. osteosperma Pinus edulis*	345	3293	520	23	3–10	26–33	AN, AG BS, BA (18)
			Creosote Bush (Larrea tridentata)				
Chihuahuan Desert	250	−80–20	−183–225	−52–4	−4–13	−56–9	AN, AG, BS (1) BS, BA (3) AN (19) BS (1, 4, 20)

[a]Reported biomass values were converted to carbon units by multiplying by 0.5, which assumes that 50% of total biomass is carbon.
[b]The metrics and the papers reporting them are denoted as follows: AG, aboveground biomass; BS, belowground SOC; AN, ANPP; BA, belowground accumulation rate; and (1) *Knapp et al.* [2008]; (2) *Hughes et al.* [2006]; (3) *Jackson et al.* [2002]; (4) *Gill and Burke* [1999]; (5) *Hibbard et al.* [2001]; (6) *McCulley et al.* [2004]; (7) *Liao et al.* [2006]; (8) *Throop and Archer* [2008]; (9) *Browning and Archer* [2011] (10) *Wheeler et al.* [2007]; (11) *Tiedemann and Klemmedson* [1995]; (12) *Klemmedson and Tiedemann* [2000]; (13) *Bates et al.* [2002]; (14) *Strand et al.* [2008]; (15) *Norris et al.* [2001]; (16) *Smith and Johnson* [2003]; (17) *McKinley and Blair* [2008]; (18) D. P. Fernandez et al. (unpublished data, 2011); (19) *Huenneke et al.* [2002]; (20) *Connin et al.* [1997].

across the four general and most common encroachment groups outlined in section 2 suggests that, with the exception of the Chihuahuan Desert ecoregion, woody plant encroachment leads to a net accumulation of ecosystem C (Table 2). Moreover, ANPP change with woody encroachment across all species and ecoregions was greater than SOC changes, perhaps reflecting the nonequilibrium status of many landscapes experiencing this vegetation change and the fact that changes in soils lag well behind the changes in the vegetation that drive them.

[29] Changes in AGB pools were greatest in systems experiencing *Juniperus* and *Pinus* spp. encroachment (temperate grassland and Colorado Plateau), closely followed by *Prosopis glandulosa*-mixed shrub encroachment in subtropical Southern Great Plains grasslands (Table 2). It is interesting that these climatically diverse regions (subtropical versus temperate versus cold desert) occupied by highly contrasting woody plant functional groups (evergreen versus deciduous, N_2 fixing versus nonfixing) would have comparably high levels of aboveground biomass accrual. Subtropical and temperate grasslands of the Great Plains exhibited the highest historical rates of woody cover change (Figure 2) and these translated into the greatest aboveground and belowground C increases. Increases in belowground SOC mass were generally highest in the shrub-invaded subtropical grasslands; and as a result, this bioclimatic region had the highest overall increase in ANPP + SOC with woody plant encroachment. The region with one of the greatest increases in aboveground biomass (Colorado Plateau) also exhibited among the lowest increases in SOC, highlighting the disconnect between aboveground biomass and belowground SOC pools discussed earlier. Sonoran Desert sites experiencing woody plant encroachment exhibited marginal increases in ecosystem C mass with woody plant proliferation, whereas Chihuahuan Deserts sites exhibited declines in plant and soil C pools, regardless of whether encroachment was by the phreatophytic, N_2 fixing, deciduous shrub (*P. glandulosa)* or the xerophytic, shallow-rooted, evergreen nonfixing creosote bush (*Larrea tridentata*). Averaging data from Table 2 across ecoregion and MAP zones, our results suggest the Great Plains and Great Basin ecoregions have the highest C sink potential, whereas the drier ecoregions of the Colorado Plateau and Sonoran Desert have a low C sink potential. The Chihuahuan Desert ecoregion, has the potential to be a net C source with woody plant proliferation (Figure 6).

[30] The range of reported values across ecoregions in Table 2 and Figure 6 may represent the upper limits for changes in ANPP and biomass with woody encroachment. Woody plant encroachment has been occurring since the late 1800s in many areas. Thus, at the time these studies were conducted, many of these sites may have been at relatively advanced stages of encroachment. However, as discussed in the next section, disturbance will alter the extent to which these ecosystem potentials for C sequestration with woody encroachment may be realized or maintained.

4. Mediation of Woody Encroachment Effects on C Balance

[31] Our synthesis suggests that aboveground and belowground C responses to woody encroachment may be predicted from a combination of broad-scale environmental variables such as MAP and local soil physical characteristics

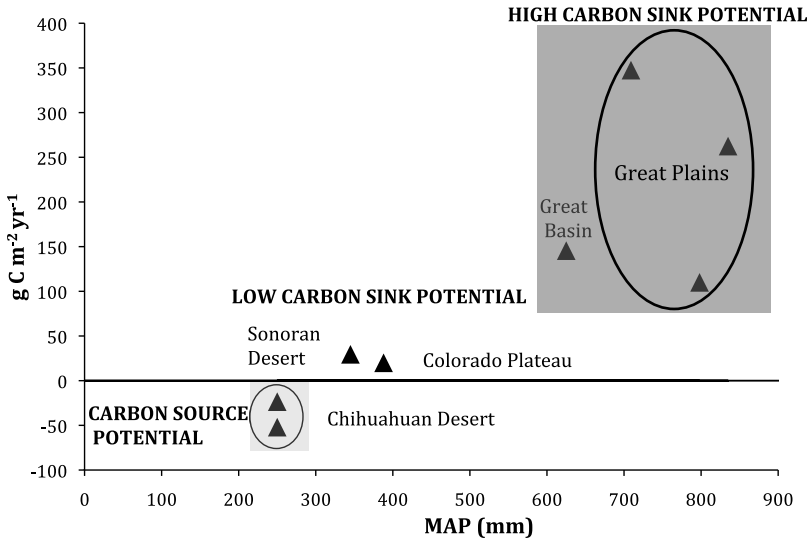


Figure 6. Carbon source-sink potential with woody plant encroachment in North American ecoregions. Values are the mean of Δ ANPP + SOC values reported in the literature (see Table 2 for species, data ranges and citations). Arid regions appear to be net sources (light gray box), whereas Sonoran Desert and Colorado Plateau sites appear to have weak sink potential. Great Basin and Great Plains sites have moderate to strong net sink potential (dark gray box). The black ovals designate multiple sites within the Chihuahuan Desert and Great Plains.

(Figures 3–5). In this section, we argue that knowledge of disturbance regimes and land use history will also be critical for improving estimates of ecosystem C responses to woody encroachment.

4.1. Historical Land Use

[32] Knowledge of land use history is paramount to interpreting and projecting ecosystem structure and function [*Foster et al.*, 2003; *Peters et al.*, 2006]. However, the paucity of spatially explicit historical records makes it difficult to account for legacy effects on present-day C stocks in areas experiencing woody plant encroachment. Livestock grazing is the most geographically extensive form of land use worldwide [*Asner et al.*, 2004] and heavy grazing by domestic herbivores in the late 1800s and early 1900s is a shared history for many of the world's arid and semiarid ecosystems [*Ash et al.*, 1997; *Holchek et al.*, 2003]. Grazing can directly or indirectly influence ecosystem C pools, the net effects ranging from positive to neutral to negative [*Conant and Paustian*, 2002; *Derner et al.*, 2006; *Milchunas and Lauenroth*, 1993; *Reeder and Schuman*, 2002]. Woody plant encroachment typically occurs against the backdrop of long-term but poorly documented livestock grazing [e.g., *Archer et al.*, 1995; *Fredrickson et al.*, 2006]; but even in cases where grazing histories are well-documented, its impacts on plant and soil carbon pools are uncertain [e.g., *Wheeler et al.*, 2007].

[33] Livestock grazing has been shown to have variable effects on woody plant abundance. In southeastern Oregon, western juniper (*J. occidentalis*) cover increased on both grazed and protected sites between the 1960s and 1990s), but more so on the grazed sites [*Soulé et al.*, 2003]. In contrast, a comparison of changes in shrub (*P. velutina*) abundance in a Sonoran desert grassland over a 40+ year period showed that shrub cover also increased on both grazed and protected sites between 1948 and 2006; but in this case, shrub biomass was 24% higher in protected areas [*Browning and Archer*, 2011]. Although MAP is a strong predictor of ANPP changes with woody plant encroachment, some of the high variability observed within MAP zones (e.g., Figure 3a, 600–700 mm MAP) might be explained if livestock grazing history could be accounted for.

[34] Variation in SOC response to woody plant encroachment (Figure 4b) may also reflect differences in land use history. In the few cases where historical grazing and woody plant encroachment effects on SOC have been explicitly taken into account, it appears that losses of SOC in grazed grasslands can be recovered subsequent to woody plant encroachment over decadal timescales; and that levels of SOC in the new shrub-dominated ecosystems can potentially exceed those that were in the original grassland ecosystem [*Archer et al.*, 2001; *Hibbard et al.*, 2003].

[35] In arid regions, grazing-induced declines in grass cover are often accompanied by a loss and redistribution of soil resources [*Schlesinger and Pilmanis*, 1998]. Numerous studies have investigated this grass cover-erosion feedback, with the consensus that erosion by wind and water is capable of removing soil resources required for grass persistence and growth while creating fertile islands beneath shrub canopies [see *Okin et al.*, 2009]. The net result can be a dramatic increase in wind and water erosion resulting from increased bare areas in shrublands compared to the grasslands they replace. In mesquite-dominated shrublands in the Chihuahuan Desert, aeolian sediment flux was tenfold greater than that due to wind erosion from grasslands on similar soils [*Gillette and Pitchford*, 2004]. Flow and erosion plots in the Walnut Gulch Experimental Watershed in Arizona and the Jornada Long-term Ecological Research site in New Mexico have demonstrated significant differences in water erosion between grasslands and shrublands

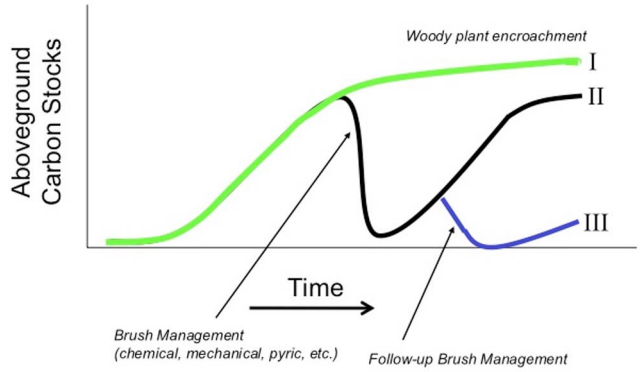


Figure 7. Regions undergoing woody plant encroachment are often mosaics of landscapes undergoing woody plant encroachment (I), landscapes recovering from some form of brush management imposed at a given stage of woody encroachment (II) and landscapes recovering from follow-up brush management treatments (III). Impacts of brush management on C pools and rates and patterns of recovery will be strongly influenced by the type of initial treatment (fire, herbicide or mechanical) and the timing and type(s) of follow up treatments.

developing on grasslands [*Wainwright et al.*, 2000]. Episodes of erosion are often associated with drought cycles, wherein depressed vegetation cover at the end of the drought makes the ecosystem vulnerable to erosion when rains return [*McAuliffe et al.*, 2006]. Thus, while grazing history and grazing effects are likely to strongly mediate plant and soil carbon pools, robust generalizations as how it mediates plant and soil C response to woody plant encroachment are not yet possible.

4.2. Brush Management

[36] Brush management, often conducted to promote herbaceous plant production for livestock grazing, is another land use that must be factored into C accounting schemes. In this synthesis we use the term "brush management" to collectively describe anthropogenic practices aimed at reducing shrub and tree abundance. It has been widely applied in arid, semiarid and montane rangelands since the 1940s using prescribed fire, mechanical treatments (e.g., shredding, chaining, roller-chopping, grubbing) and herbicides alone or in various combinations [*Bovey*, 2001; *Scifres*, 1980; *Valentine*, 1989]. As a result of past and ongoing brush management practices, regional landscapes in the central and western U.S. are complex mosaics of grasslands at various stages of shrub encroachment, and shrub-encroached grasslands at various stages of recovery from woody removal practices (Figure 7) [*Asner et al.*, 2003; *Browning and Archer*, 2011; *Hughes et al.*, 2006]. Accurate landscape- and regional-scale accounting of plant and soil C pools and projections of their future states would thus require knowledge of brush management histories. These management-induced reductions in woody plant C stocks over a relatively small area have the potential to offset and nullify accruals associated with encroachment over much larger areas.

[37] Despite the broad geographic extent of brush management, little is known of the impact of this land management practice on the C cycle. Brush management may temporarily reduce the aboveground woody biomass, but may increase ANPP by shifting the woody plant population to a younger more productive age-state [*Hughes et al.*, 2006]. Brush management reduces aboveground C pools in the short term by reducing vegetation cover, but may put C pools in fertile shrub islands at-risk for loss via wind and water erosion unless ground cover is quickly reestablished (Figure 8).

[38] For stands at advanced stages of development, removal of individual woody plants is known to cause a depletion of the SOC pool over the 10–15 years following treatment, the extent depending on whether or not shrubs are allowed to regenerate [*Klemmedson and Tiedemann*, 1986; *Tiedemann and Klemmedson*, 1986, 2004]. Along these lines, SOC losses, which had accumulated in response to shrub encroachment, were on the order of 67–78% in the top 10 cm of soil over a 40 year period following woody removal in a hot, semidesert rangeland [*McClaran et al.*, 2008]. These findings contrast those of *Teague et al.* [1999] who compared SOC on sites four and 22 years after root-plowing against untreated controls in the Southern Great Plains. They hypothesized that removal of the N_2 fixing shrub *P. glandulosa* would result in a decline in SOC owing to a loss of shrub cover thus reducing shading and increasing decomposition rates (higher soil temperatures and oxidation rates). No significant differences between treated and control sites were found.

[39] Virtually nothing is known of the fate of roots associated with woody plants subjected to brush management. When shoots of seedlings of shrubs capable of vegetative regeneration are removed, root biomass is substantially diminished relative to controls [*Weltzin et al.*, 1998]. Accordingly, woody plants experiencing brush management may be unable to fully support their root systems (section 3.2) and some or substantial root mortality may occur, even in cases when treatments only "top-kill" plants. This root mortality may compensate for losses of SOC that might otherwise be expected to accompany brush management [e.g., *Teague et al.*, 1999]. In cases where woody plants are actually killed by brush management treatments, substantial amounts of C may be sequestered in coarse, lignified roots, particularly those that occur at depths where rates of decomposition are exceedingly slow. The contrasting results of brush management practices on SOC and the paucity of data related to the fate of root systems highlights the complex nature of quantifying SOC change in response to management of woody plant communities. As with woody plant encroachment, there are currently no robust generalizations regarding brush management effects on SOC (Figure 4b).

4.3. Natural Disturbance Regimes: Fire and Drought

[40] Wildfires or prescribed burns occurring subsequent to woody plant encroachment will always reduce the standing aboveground C pools, the extent depending on their intensity, patchiness and return interval [*Bowman et al.*, 2009]. *Hoch et al.* [2002] reported almost 100% mortality of *J. virginiana* after fire in tallgrass prairie, but mortality was only ca. 30% where grazing had reduced fine fuel loads and fire severity. In a western juniper ecosystem, a regional-scale, low frequency, high intensity disturbance that included fire was estimated to offset region-wide juniper encroachment by 35% (J. L. Campbell et al., Assessing the carbon

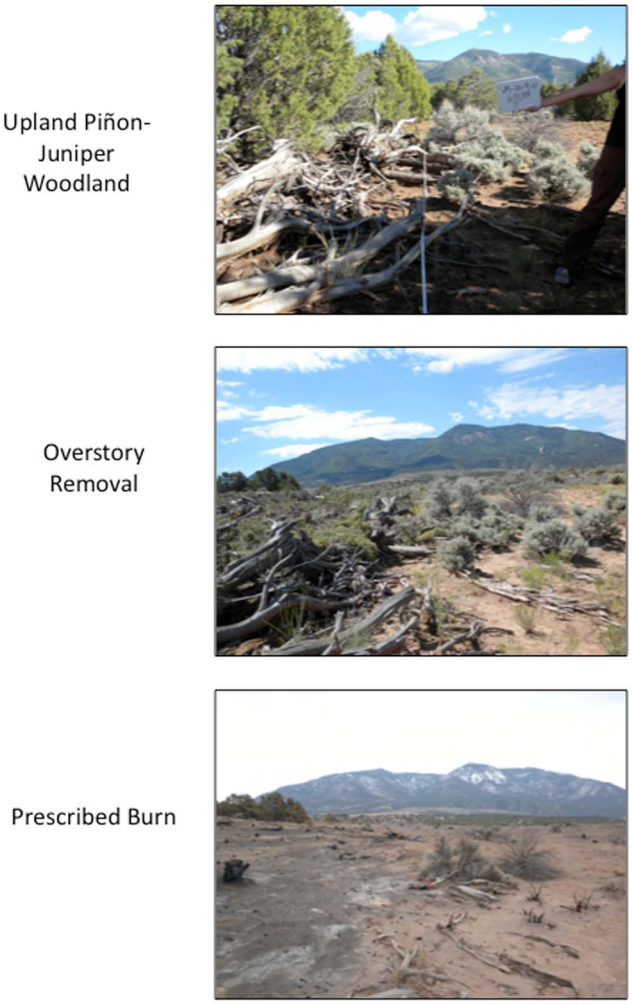


Figure 8. Woodland management in a piñon-juniper woodland, southeastern Utah. (top) Pretreatment density and cover of piñon-juniper trees in a site that was chained in the 1960s. (middle) Tree overstory removed in 2009. (bottom) Removal of the tree overstory was followed by prescribed fire in 2009. Brush management at these sites has resulted in significant redistribution of above and belowground C pools.

consequences of western juniper encroachment across Oregon, USA, submitted to *Rangeland Ecology in Management*, 2011). Thus, even infrequent fire may significantly offset aboveground C gains associated with woody encroachment. Although significant aboveground C may be lost in a fire event, under some conditions, shifts in the population structure of encroaching woody plants to younger, more productive age-classes will lead to significant C gains in a postfire environment [*Ansley and Castellano*, 2006; *Briggs et al.*, 2005].

[41] The impact of fire on belowground C storage and cycling in areas experiencing shrub and tree encroachment is poorly known. In a mesic grassland undergoing shrub (*Cornus drummondii*) encroachment, past fire (~1 year) had no effect on SOC stocks [*Lett et al.*, 2004]. Fire following woody plant proliferation may also influence long-term storage of soil C via deposition of partially combusted biomass or black carbon. Black carbon is highly resistant to decomposition relative to the plant material from which it was derived, and thus represents a long-term soil C storage pool. In fire-adapted temperate savanna ecosystems, black carbon comprises 5–17% of the total SOC pool [*Ansley et al.*, 2006; *Dai et al.*, 2005]. Declines in fire return intervals with woody proliferation may reduce black carbon inputs to the SOC pool relative to grassland or shrubland sites that burn more frequently. When fire does occur in the woody plant communities, however, the greater AGB may elevate black carbon inputs to the soil system.

[42] Perhaps the greatest potential for wildfire to influence ecosystem C dynamics is via its role in converting some of the shrublands and woodlands that have developed over the past 100 years to grasslands dominated by monocultures of nonnative grasses. Aboveground C losses with conversions to annual grassland may be as high as 8 Tg C, with projected releases to the atmosphere of 50 Tg C over the next several decades [*Bradley et al.*, 2006]. In cold desert sagebrush steppe ecosystems of the western U.S., this level of C release with annual grass invasion could completely offset any increases in C with woody encroachment that has occurred over the last century. However, the story may be quite different in southwestern U.S. hot deserts where highly productive, deeply rooted, fire-prone perennial grasses introduced from Africa [*Franklin et al.*, 2006; *Williams and Baruch*, 2000] are proliferating in shrublands derived from grasslands [e.g., *Kupfer and Miller*, 2005].

[43] Drought has potentially important, but poorly documented impacts on C stocks in ecosystems undergoing woody plant encroachment. The drought of the 1950s and the early 2000s provide interesting and contrasting insights into the dynamics of woody plants with implications for carbon accounting. While the 1950s drought caused only modest declines in the major shrubs in Sonoran Desert scrub communities, the 2000s drought caused substantial mortality in numerous species, including the long-lived, xerophytic creosote bush [*Bowers*, 2005].

[44] The 2000s drought also had dramatically more impacts than the 1950s drought on piñon-juniper woodlands of the western U.S. [*Shaw et al.*, 2005] where trees have proliferated since the late 1800s [*Blackburn and Tueller*, 1970; *Miller and Wigand*, 1994; *Tausch and Nowak*, 1999; *Barger et al.*, 2009]. Across southwestern Colorado, a region where tree mortality was particularly high, approximately 11% of the woody vegetation was damaged in the 2000s drought, with stand-level losses of aboveground C associated with the transformation of live trees to woody snags averaging 1000 g m^{-2} yr^{-1}, nearly fortyfold higher than C losses associated with brush management and wildfire [*Huang et al.*, 2010]. In southeastern Utah, estimates of aboveground C accumulation with piñon-juniper encroachment in a black sagebrush site was on the order of 3300 g C m^{-2} over a 60 year period (D. P. Fernandez et al., unpublished data, 2011). However, tree mortality following the 2000s drought at these same sites resulted in a 40% decline in aboveground C. Thus, regional drought-induced mortality events have the potential to offset C accumulation that had occurred over previous decades with woody plant encroachment. Effects of these aboveground disturbances on belowground C storage are unknown and no clear generalizations emerged from this synthesis.

[45] It is interesting to note that while the 2000s drought had major impacts on piñon-juniper systems, widespread reductions in woody plant abundance in Chihuahuan and Sonoran Desert sites encroached upon by *Prosopis* spp. and *L. tridentata* have not yet been reported; and there is no evidence in long-term plot or aerial photography records at the Santa Rita Experimental Range in southern Arizona of major reductions in cover of encroaching *P. velutina* induced by the 1950s drought [*Browning et al.*, 2008; *Browning and Archer*, 2011]. However, flux tower data from this site indicate net C losses on the order of 14–95 g C m^{-2} yr^{-1} during the 2000s drought period, the magnitude being inversely proportional to precipitation [*Scott et al.*, 2009]. Thus, the substantial gains in soil [*Wheeler et al.*, 2007] and aboveground C accompanying 100+ years of shrub encroachment in this system may be at risk if the future frequency, intensity and duration of drought conditions increase as predicted; particularly so if these new conditions induce widespread shrub mortality.

[46] In the Southern Great Plains, the drought of the 1950s is reported to have reduced the abundance of encroaching *P. glandulosa* and associated shrubs 40–75% depending on soil type; however, recovery via vegetative regeneration was rapid [*Carter*, 1964]. Aerial photos from the region indicted that total woody cover declined from 13% to 8% during this drought period; then increased from 8% to 36% in the 23 years following the drought [*Archer et al.*, 1988]. It thus appears that the drought of the 1950s induced nonlinear dynamics and primed the system for rapid rates of shrub encroachment in the postdrought period [*Archer*, 1989; *Scanlan and Archer*, 1991] with minimal negative consequences for ecosystem C stocks [*Hibbard et al.*, 2003].

[47] Although climate change was not directly addressed in our synthesis, the future trajectory of woody plant encroachment dynamics will be mediated by future climate. Drylands of the western U.S. are predicted to experience more arid conditions over the next century [*Seager et al.*, 2007]. Thus, we anticipate that decreases in precipitation and the occurrence of more frequent and extended droughts may cause mesophytic grasses in present-day grasslands to give way to xerophytic shrubs. However, our data suggest the C sink strength of these new shrub communities would be reduced relative to present-day conditions and ecoregions that are currently carbon neutral with respect to woody plant encroachment may become significant C sources (Figure 6).

5. Summary

[48] 1. Woody encroachment rates vary widely across ecoregions. Woody cover change ranged from <0.1 to 2.3% yr^{-1} across ecoregions. Proliferation rates were typically highest in the temperate Great Plains, and lowest in hot and cold deserts (Figure 2).

[49] 2. ANPP changes with woody plant encroachment scale positively and linearly with MAP across North American drylands. We can, with some confidence, predict changes in ANPP with woody plant encroachment at the stand level from MAP. Results suggest that ANPP declines with woody encroachment in MAP zones <336 mm yr^{-1}, and increases 0.7 g m^2 yr^{-1} for each for each mm increase in precipitation across MAP zones >336 mm.

[50] 3. Changes in belowground C with woody plant encroachment are not consistently predicted from ANPP or environmental variables. The greatest challenge in evaluating woody encroachment effects on ecosystem C stocks is adequately characterizing the large and spatially heterogeneous belowground organic C reservoir. There was evidence that climate and edaphic characteristics interact to explain a significant fraction of the variance in SOC response to woody encroachment when assessments are not confounded by differences in sampling protocol or land use histories.

[51] 4. The magnitude and sign of C change with woody encroachment differs by ecoregion. In the absence of disturbance, woody encroachment results in net C gains in most ecosystems. The notable exception was in more arid regions, where ecosystem C response to woody encroachment was neutral to negative (Table 2 and Figure 6).

[52] 5. Disturbance may significantly offset decades of C gain associated with woody plant encroachment. Numerous factors interact to mediate the impact of woody plant encroachment on the ecosystem C pools and fluxes. Disturbances such as brush management, drought, and wildfire are of particular significance owing to their ability to rapidly reduce aboveground C in biomass accumulating during the course of woody plant encroachment. However, the magnitude of aboveground C loss is highly variable and dependent on the type, intensity and spatial extent of disturbance. Limited available data suggest SOC in woody-encroached ecosystems will decline or remain unchanged in a postdisturbance environment.

6. Reducing Uncertainties

[53] In the most recent North American C balance assessment [*King et al.*, 2007] woody plant encroachment in drylands is a significant sink. However, uncertainties associated with this estimate are >100%. Thus, it is not clear whether this land cover change represents a net source of C at the continental scale; or a sink whose strength is on par with that of forests. Reducing these uncertainties is thus crucial and would include:

[54] 1. Acquiring quantitative information on the spatial extent of woody encroachment across bioclimatic regions. Although there is a solid basis for predicting changes in ecosystem C from a combination of climate and edaphic variables, a lack of quantitative information on the spatial extent of woody encroachment prevents us from integrating across bioclimatic regions. This is especially so in Arctic tundra and the arid and semiarid regions of Mexico. Further exploration of these patterns through the integration of multiples technologies, such as comparing historical and modern aerial photography and fusing remotely sensed data of different scales, will make it possible to derive better estimates of woody encroachment rates across a range of ecoregions. Where historical reconstructions are not possible, baseline maps of regional woody cover should be developed so that future changes can be accurately evaluated.

[55] 2. Using simple, linear regression models (Figures 3–5) in conjunction with precipitation and soils maps to constrain estimates of site-level C balance within ecoregions. This simplistic approach could be upgraded as process-based models become available.

[56] 3. Explicitly consider disturbance history when generating estimates of C change with woody plant encroachment. Land use maps for drylands should explicitly account for livestock grazing and brush management and should be used in conjunction with soil, precipitation and drought maps to evaluate woody cover extent and change. Recent advances in quantifying and evaluating disturbance impacts at regional and continental scales in forests (see *Amiro et al.* [2010] and other papers in this special section) should be adapted for use in drylands.

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