Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs

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Abstract

Shrub encroachment into grass-dominated biomes is occurring globally due to a variety of anthropogenic activities, but the consequences for carbon (C) inputs, storage and cycling remain unclear. We studied eight North American graminoid-dominated ecosystems invaded by shrubs, from arctic tundra to Atlantic coastal dunes, to quantify patterns and controls of C inputs via aboveground net primary production (ANPP). Across a fourfold range in mean annual precipitation (MAP), a key regulator of ecosystem C input at the continental scale, shrub invasion decreased ANPP in xeric sites, but dramatically increased ANPP ($>1000 \, \text{g m}^{-2}$) at high MAP, where shrub patches maintained extraordinarily high leaf area. Concurrently, the relationship between MAP and ANPP shifted from being nonlinear in grasslands to linear in shrublands. Thus, relatively abrupt (<50 years) shifts in growth form dominance, without changes in resource quantity, can fundamentally alter continental-scale pattern of C inputs and their control by MAP in ways that exceed the direct effects of climate change alone.

Keywords: aboveground net primary production, carbon, climate change, grasslands, growth form, LAI, MAP, shrublands

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Introduction

A major challenge facing ecologists today is to predict how ecosystems will respond to forecast environmental changes and to evaluate the consequences of those responses. Woody plant encroachment into grasslands and the 'thickening' of woody plant density in rangelands and savannas are well documented and rapidly occurring global phenomena (Archer et al., 1988; Brown & Carter, 1988; Aguiar et al., 1996; Roques et al., 2001; House et al., 2002; Briggs et al., 2005). Putative causes of increased woody plant abundance vary, and include increased grazing intensity, reduced fire frequency, other alterations

in local land management practices and rising atmospheric CO_2 concentrations. But despite this site-specificity in mechanism, the widespread shift in growth form dominance has consistently been attributed to human activities (Schlesinger et al., 1990; Archer et al., 1995; Van Auken, 2000; Silva et al., 2001; Hoch et al., 2002; Geist & Lambin, 2004; Fensham et al., 2005; Havstad et al., 2006; Peters et al., 2006). Such a dramatic change in ecosystem structure and function differs fundamentally from successional changes occurring in postdisturbance forest lands; instead, this pervasive encroachment is more generally considered to be a manifestation of global environmental changes driving ecosystems to new states (Scheffer et al., 2001; Briggs et al., 2005; Smith et al., submitted).

Because grassland and savanna ecosystems account for 30–35% of global terrestrial net primary production

(Field *et al.*, 1998), any change in patterns or controls of carbon (C) inputs will have global implications. In the United States, nonforest lands undergoing shrub encroachment are estimated to cover 220–330 million ha, most in the xeric western states (Houghton *et al.*, 1999; Pacala *et al.*, 2001). Increased C storage due to shrub encroachment is purported to account for up to a third of the North American C sink (Houghton *et al.*, 1999), although more recent measurements of C pools above- and belowground have added uncertainty to these estimates (Jackson *et al.*, 2002). Here, we present results from a continental-scale assessment of the consequences of ecosystem conversion from graminoid to shrub dominance for aboveground net primary production (ANPP), a key component of C budgets that impacts most aspects of ecosystem structure and function. We show that this rapidly occurring phenomenon fundamentally alters both amounts and controls of C inputs into ecosystems independent of changes in climatic drivers or resource levels. Specifically, we (a) quantify patterns of responses in ANPP with shrub invasion across North America, (b) show that the relationship between mean annual precipitation (MAP) and ANPP is dramatically altered with shrub encroachment and (c) propose a biotic mechanism for these responses.

Methods

We combined data from eight intensively studied North American sites (from Alaska to Virginia) in which shrubs (all native species) have invaded native graminoid-dominated communities (hereafter 'grasslands'; Table 1). Data were collected at the patch scale (grass vs. shrub-dominated patches), consistent with previous studies that have quantified changes in standing stocks of C due to shrub invasion of grasslands (Jackson *et al.*, 2002). Thus, each site provided paired shrub canopy and grassland intercanopy measurements of ANPP ($n = 2260$ plots sampled for all sites combined) as well as several other response variables. We initially evaluated a wide range of ecological responses to shrub encroachment, but we focused on responses in ANPP, and in particular its relationship with MAP, as a key continental scale driver of ecosystem function. Leaf area index (LAI) and leaf nitrogen (N) concentration were also evaluated in greater detail to infer potential mechanisms of responses.

Field methods

Aboveground net primary production (ANPP $g\,m^{-2}$ yr^{-1}) in graminoid-dominated plots was measured by direct harvest (clipping, sorting, drying and weighing, Knapp *et al.*, 2007), except at the two desert sites where nondestructive allometric measurements of plant volume were converted to biomass based on species-specific regression models (Huenneke *et al.*, 2001; Muldavin *et al.*, 2008). Within the shrub-dominated plots at each site, nondestructive allometric measurements of plant volume were converted to biomass (ANPP $g\,m^{-2}\,yr^{-1}$) at all sites based on species-specific regression models (e.g., Huenneke *et al.*, 2001; Shaver *et al.*, 2001; Lett *et al.*, 2004; Brantley & Young, 2007). Herbaceous species' richness (species number per m^2 at most sites) was assessed via fixed plot census techniques, LAI ($m^2\,m^{-2}$) was measured either directly or from allometric relationships for each site, leaf N content (%) was quantified from leaves of the dominant grass and shrub species collected near the time of peak biomass and levels of total soil N ($\mu g\,g^{-1}$) and soil organic C ($g\,m^{-2}$) were measured similarly across all sites (Robertson *et al.*, 1999); however, soils were sampled at different depths among sites. The depths of the soil cores sampled at each site varied because each site was sampled to the depth where root activity was the greatest. Thus, as described below, although the absolute values of soil N and C could not be directly compared, proportional differences between grassland and shrubland soils at each site can be compared across the sites. This is because soil depths sampled were identical within shrub- and grass-dominated patches at each site, permitting us to assess the consequences of shrub encroachment into grasslands on these soil properties. At the tussock tundra site (TUN), shrub encroachment was a consequence of N addition to plots [as a surrogate for the effects of warming (Shaver *et al.*, 2001)], thus we omitted data from this site for our analyses of patterns of response in leaf tissue chemistry and soils.

Additional data sources

Climatic parameters in Table 1 for Long-Term Ecological Research sites were obtained from site climatic summaries (http://intranet.lternet.edu/archives/documents/reports/Publications/climdes/). These included MAP, mean annual temperature (MAT), potential evapotranspiration (PET) and growing season length. PET data for the La Copita (THW) and Vernon, TX sites (SAV) are from Fipps & Flahive (2006), with general climate data for THW, SAV and Sagebrush steppe (SBS) from Department of Commerce, NOAA (1980), Scifres & Koerth (1987) and Marston (1990), respectively. General site descriptions and information, including purported mechanisms of shrub encroachment, can be found in Table 2.

Data analyses

We combined data from the two desert sites in New Mexico because of their similar climatic conditions and

Table 1 General site characteristics for the eight North American study sites from which data were compiled on the consequences of shrub encroachment into grassland

Site, state	Latitude/ longitude	Biome type (site code)	MAP/MAT (mm °C^{-1})	PET (mm)	Growing season length (days)	Dominant grassland species (photosynthetic pathway)	Dominant shrub species E = evergreen, D = deciduous, N = putative N-fixer
Sevilleta National Wildlife Refuge, NM	34.1/−106.9	Chihuahuan desert (CHI)	242/13.3	747	210	*Bouteloua eriopoda* (C$_4$)	*Larrea tridentata* (E)
Sierra Madre, WY	41.20/−107.2	Sagebrush steppe (SBS)	259/6.2	483	100	*Poa secunda* (C$_3$), *Stipa comata* (C$_3$), *Elysium smithii* (C$_3$)	*Artemisia tridenta vaseyana* (E)
Jornada Experimental Range, NM	32.5/−106.8	CHI	264/14.4	794	255	*Bouteloua eriopoda* (C$_4$)	*Larrea tridentata* (E), *Prosopis glandulosa* (D, N)
University of Alaska's Toolik Field Station, AK	68.3/−149.43	Tussock tundra (TUN)	291/-12.5	114	55	*Eriophorum vaginatum* (C$_3$)	*Betula nana* (D), *Ledum palustre* (E)
Waggoner Ranch, TX	34.5/−99.2	Subtropical savanna (SAV)	655/17.0	1487	220	*Nasella leucotrica* (C$_3$), *Bouteloua curtipendula* (C$_4$)	Prosopis glandulosa (D, N)
La Copita, TX	27.4/−98.1	Subtropical thorn woodland (THW)	680/22.0	1448	289	*Chloris cuculatta* (C$_4$)	*Prosopis glandulosa* (D, N)
Konza Prairie Biological Field Station, KS	39.1/−94.6	Tallgrass prairie (TGP)	859/12.9	793	180	*Andropogon gerardii* (C$_4$)	*Cornus drummondii* (D)
Virginia Coast Reserve, VA	37.3/−75.9	Barrier island (ISL)	1065/14.2	786	245	*Spartina patens* (C$_4$)	*Myrica cerifera* (E, N)

Sites arranged from lowest to highest mean annual precipitation (MAP). MAT, mean annual temperature; PET, potential evapotranspiration.

ecological responses, and to reduce any bias that might occur from oversampling a particular ecosystem. Thus, with the exception of the information provided in Table 1, data reported for the Chihuahuan desert sites (CHI) represent an unweighted mean response of the Jornada and Sevilleta sites.

We conducted a preliminary assessment of 18 measurements of ecological responses to shrub encroachment, but as expected for such a diverse suite of sites, methods differed and the temporal and spatial intensity of data collection varied among sites. Thus, we restricted our analyses to comparable data collected from a majority of the sites. The combined data set allowed us to compare six response variables across the gradient of paired graminoid–shrubland sites, including four aboveground (ANPP, LAI, leaf tissue N and plant species richness) and two belowground variables [total soil N and organic C (Table 3)]. We could directly evaluate responses in ANPP, LAI and leaf N concentration for all the paired graminoid- and shrub-dominated

plots because of consistency in methodology. For these three variables, we assessed the consequences of conversion from graminoid to shrub dominance with paired *t*-tests (*t*-test procedure, SAS 9.1). For the other variables (species richness, soil organic C, total soil N) different methods or incomplete sampling among sites prevented a valid statistical analysis, thus in those cases we report only proportional changes between paired graminoid- and shrub-dominated plots (response ratios).

To assess the interactive effects of potentially important abiotic drivers, we conducted a principal components analysis (PCA) of the variables and responses in Table 4. We also compared the independent effects of all abiotic drivers on response variables with linear regressions (Table 3). The PCA identified those environmental parameters associated with ecosystem water relations as the most strongly related to ANPP, LAI and tissue leaf N. However, the PCA did not exceed MAP alone as a variable explaining continental scale patterns for any

Table 2 Characteristics of the eight sites with long-term data on the consequences of shrub encroachment into graminoid-dominated communities, including purported drivers of shrub invasion

Site	Biome type	Causes	Reference
Arctic, AK (TUN)	Tussock tundra	Warming/increase in N	Shaver *et al.* (2001)
Jornada, NM (CHI)	Chihuahuan desert	Overgrazing/drought	Havstad *et al.* (2006)
Konza, KS (TGP)	Tallgrass prairie	Fire frequency/intensity	Briggs *et al.* (2005)
La Copita, TX (THW)	Subtropical thorn woodland	Overgrazing/abiotic	Archer (1995)
Sevilleta, NM (CHI)	Chihuahuan desert	Overgrazing/drought	Kieft *et al.* (1998)
Vernon, TX (SAV)	Temperate savanna	Overgrazing/fire frequency/intensity	Hughes *et al.* (2006)
Virginia Coast Reserve, VA (ISL)	Temperate barrier island	Frequency of storms (hurricanes)	Hayden *et al.* (1991)
Sierra Madre, WY (SBS)	Sagebrush steppe	Fire frequency	Knight (1994)

References provide additional site information.

Table 3 Summary of response variables showing the mean proportional change across all study areas when graminoid-dominated sites are converted to shrubland

Variable	N	Proportional change (%)	P-value
Leaf area index ($m^2 m^{-2}$)	7	52.93	0.05
Leaf nitrogen of dominant species (%N)	7	44.32	0.02
Soil inorganic nitrogen ($\mu g\, g^{-1}$)	6	17.34	NA
Soil organic carbon ($g\, m^{-2}$)	6	7.02	NA
Species richness (number of species area^{-1})	5	−79.95	NA

N, number of study areas included in the analysis. Proportional change is the ratio of the response variable (e.g., leaf area index) in the shrub-dominated area relative to that variable in the graminoid-dominated area averaged across all comparable sites. Production, leaf area index and leaf nitrogen values were analyzed using actual values (not proportional change) with paired *t*-tests (*t*-test procedure, SAS 9.1). NA, no statistical tests were possible due to different methodologies used [different soil depths for carbon and nitrogen (N), different sample areas for richness] among the sites.

of the ecological responses, and because a previous regional analysis of the consequences of shrub encroachment on soil C also identified MAP as a key driver (Jackson *et al.*, 2002), we focused our analyses on this abiotic environmental variable. All analyses were performed using SAS 9.1 at the $P < 0.05$ level of significance.

Results

We found that shrub encroachment led to a fourfold increase in ANPP ($P < 0.05$) when averaged across all sites (Fig. 1), with significant increases in LAI ($P < 0.05$) and leaf N ($P < 0.02$) also evident (Table 3). Across North America, ANPP varied strongly with MAP (Figs

Table 4 Principal components analysis of four abiotic factors [mean annual precipitation (MAP), mean annual temperature (MAT), potential evapotranspiration (PET) and growing season length (GSL)] and the correlations of each principal component with grassland and shrubland aboveground net primary production (ANPP) and leaf area index (LAI)

Eigen vectors	Eigen value	Proportion	Cumulative
Prin1	3.20	0.80	0.80
Prin2	0.64	0.16	0.96
Prin3	0.09	0.02	0.98
Prin4	0.06	0.02	1.00

Eigen vectors	Prin1	Prin2	Prin3	Prin4
MAP	0.38	0.92	0.09	0.02
MAT	0.54	−0.23	0.35	−0.74
PET	0.53	−0.27	0.43	0.68
GSL	0.54	−0.14	−0.83	0.05

	Pearson's correlation coefficient			
Response variable	Prin1	Prin2	Prin3	Prin4
Grassland ANPP	0.43	0.74*	0.20	0.25
Shrubland ANPP	0.61	0.66	0.14	0.24
Grassland LAI	0.52	0.48	0.28	0.01
Shrubland LAI	0.55	0.81**	0.13	−0.09

Although Prin2 was significantly related to shrubland LAI, and nearly so with grassland ANPP, simple linear regressions with MAP (Figs 2 and 3) explained more variance than correlations with these principal components.
*$P = 0.06$.
**$P = 0.03$.

1 and 2), and those sites with the highest grassland ANPP tended to show the largest relative and absolute increase in ANPP when converted to shrub dominance.
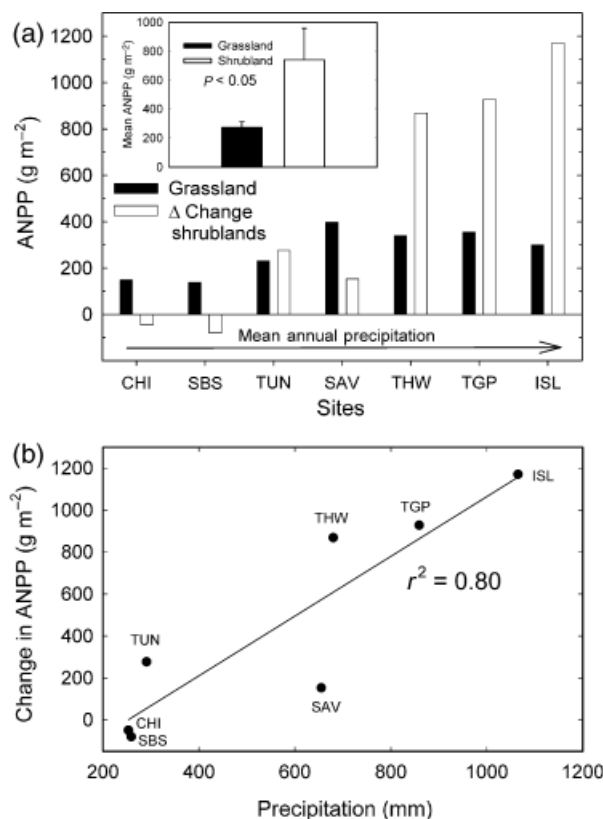
Fig. 1 (a) Patterns of aboveground net primary production (ANPP) in grasslands (black bars) and former grassland sites now dominated by shrubs (open bars) for each of the study sites (Table 1). Sites along the x-axis are ordered by increasing mean annual precipitation (MAP) and the largest responses in ANPP to shrub conversion occur in the most mesic sites. Inset: mean increase in ANPP over all sites with shrub encroachment into grasslands ($t = -2.42$, df = 6, $P = 0.05$). (b) The relationship between MAP and the change in ANPP for seven sites across North America where grassland has been converted to shrubland. Solid line indicates a significant positive relationship between MAP and the change in ANPP ($F = 20.5$, df = 6, $P = 0.006$). See Table 1 for three-letter site codes.
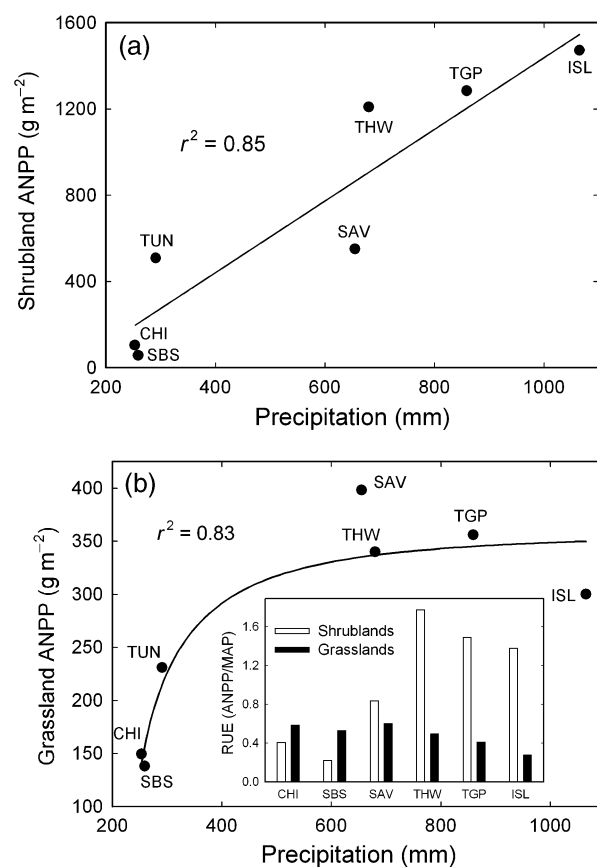

Fig. 2 Relationship between mean annual precipitation and (a) shrubland aboveground net primary production (ANPP) and (b) grassland ANPP for seven North American graminoid-dominated sites that have been converted to shrubland. Linear relationship for shrublands ($F = 28.70$, df = 6, $P = 0.003$). Relationship for grasslands was nonlinear ($y = a + b/x^2$): $F = 33.17$, df = 6, $P = 0.002$. Inset: Rain use efficiency [ratio of ANPP to mean annual precipitation (MAP); $g\,m^{-2}\,mm^{-1}$] for paired graminoid- and shrub-dominated sites across North America ordered from low to high MAP. See Table 1 for three-letter site codes.

Thus, the magnitude and direction of ANPP alteration with shrubs replacing graminoids appeared to be strongly driven by MAP (Fig. 1). With the exception of LAI, none of the other ecological variables (Table 3) were related to any of the environmental gradients encompassed by these sites (Table 1). Further, there was no evidence to suggest that differences in local grazing history or time since conversion from graminoid to shrub dominance were related to large-scale patterns across these eight sites.

The continental pattern of responses in ANPP as shrubs replaced grassland was best understood by examining differences between the two growth forms in their relationship between MAP and ANPP (Fig. 2).

The relationship between ANPP and MAP for shrub patches was linear up to 1100 mm MAP, but in grassland sites this relationship was linear only at low MAP, reaching a plateau above 600 mm (Fig. 2). As a consequence, rain use efficiency (RUE; ANPP/MAP, Le Houerou et al., 1998), a fundamental measure of the ecosystem-level conversion of precipitation to productivity, decreased for grass-dominated sites as MAP increased (Fig. 2 inset). In contrast, RUE increased substantially with shrub encroachment in the most mesic sites.

This alteration in the relationship between a key environmental driver (MAP) and ecosystem function (ANPP) corresponded to progressively larger differ-
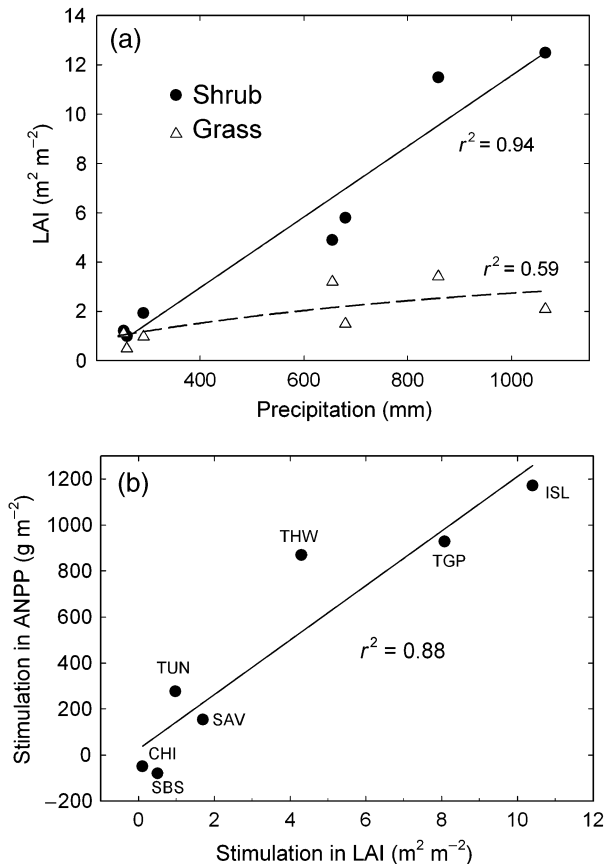
Fig. 3 (a) The relationship between mean annual precipitation and shrub leaf area index (LAI, solid line) and grassland LAI (dashed line) for seven North American sites. Relationship for shrubland: $F = 74.62$, df $= 6$, $P = 0.003$. Relationship for grassland: $F = 6.62$, df $= 6$, $P = 0.05$. (b) Relationship between mean stimulation in LAI with shrub encroachment and responses in aboveground net primary production ($F = 38.4$, df $= 6$, $P = 0.002$). See Table 1 for three-letter site codes.

ences in LAI in shrubs vs. grasses along the MAP gradient (Fig. 3a). The relationship between MAP and LAI differed dramatically between the paired grassland–shrubland plots, with extraordinarily high LAI (11.7–12.5) in shrub patches at the more mesic end of the gradient, resulting in as much as a sixfold increase in LAI with shrub encroachment. The stimulation in LAI after conversion to shrub dominance corresponded strongly with the pattern of increased ANPP across the United States (Fig. 3b).

Discussion

This assessment of the ecological consequences of the shift in growth form dominance from graminoids to shrubs across North America is notable for its geographic extent (eight sites spanning 5550 km), the wide

climatic gradients (200–1100 mm MAP; −12.5 to 22.0 °C MAT) encompassed by these sites, and its control of local climatic and edaphic factors through the use of paired plots at each site. Our ability to assess the breadth of response variables quantified across these sites was, unfortunately, constrained by differences in methodologies, which limited the statistical assessment of the effects of woody plant encroachment on soil N and P pools or species richness. Nonetheless, our results suggest that only slight alterations in soil organic C could be attributed to shrub encroachment at the continental scale, which contrasts with results from previous studies (Jackson *et al.*, 2002; Wessman *et al.*, 2004; Briggs *et al.*, 2005). Conversely, we do have supportive evidence that plant species richness declined steeply with shrub encroachment, as reported previously (Table 3; Wessman *et al.*, 2004; Briggs *et al.*, 2005). Further, we did detect consistent increases in leaf N in shrub- vs. grass-dominated patches, which would be expected to have a host of ecosystem consequences, including higher rates of photosynthesis, litter decomposition and N cycling (Meentemeyer, 1978; Hobbie, 1992; Reich *et al.*, 1997). This response in leaf N can, in part, be related to the replacement of C_4 grasses by C_3 shrubs, several of which were also putative N-fixers (Table 1).

The primary, continental-scale impact of shrub encroachment into these previously graminoid-dominated ecosystems was the altered pattern and control of ANPP. The magnitude of alteration in ANPP due to shrub encroachment was clearly related to the productivity of grasslands and consequently to MAP. Although ANPP in shrub patches was reduced relative to adjacent grasslands in more xeric sites (Fig. 1; Huenneke *et al.*, 2002; Wessman *et al.*, 2004), conversion to shrub dominance increased ANPP in mesic regions and thus, the capacity of high-resource ecosystems to utilize MAP. Increased leaf N in shrubs relative to grasses may have contributed to an overall increase in ANPP (Reich *et al.*, 1997), but a positive relationship between leaf N and ANPP (not shown) was driven by a single site and was insufficient to explain the continental-scale pattern, because not all shrubs were N-fixers and N-fixing shrubs in xeric sites did not lead to increased ANPP. Instead, we posit that the primary mechanism for this pattern is the potential for shrubs in mesic regions to support much higher leaf area than grasses under similar climatic and resource constraints. Indeed, LAI measured in shrub patches in TGP and ISL (as well as from a site in Texas not included in Fig. 3, S. Archer, unpublished data) consistently exceeded values for most forests (Marshall & Waring, 1986; Pierce & Running, 1988; Vose *et al.*, 1995; Norby *et al.*, 2003; Brantley & Young, 2007). Similarly, ANPP in patches dominated by shrubs also exceeded values for most temperate

forests (Knapp & Smith, 2001; Huxman et al., 2004). Such hotspots in LAI and ANPP associated with the shrub growth form are due in part to its unique architecture, which permits the dense and homogeneous display of leaves vertically through the canopy and minimizes self-shading as they invade open grasslands (Horn, 1971; Rundel, 1991). This can explain an increase in RUE without any change in MAP. Indeed, RUE for the grasslands represented by our sites was well within the range of values reported previously for other biomes, whereas RUE for shrubs in more mesic sites far exceeded that measured previously (Huxman et al., 2004).

These data highlight the unappreciated role that alterations in biotic constraints to ANPP can play in determining the impacts of this and perhaps other global change phenomena on ecosystem C inputs. In this case, higher LAI in shrubs vs. grasses alleviated biotic constraints on productivity associated with the grass growth form. Traditionally, precipitation, temperature and nitrogen have been invoked as the most important limitations to ANPP at both the site and biome scales (Webb et al., 1983; Hooper & Johnson, 1999; Knapp & Smith, 2001). However, biotic constraints, such as meristem limitation (Knapp & Smith, 2001) or those resulting from particular plant species assemblages can reduce ANPP well below the climatic/edaphic site potential (Harcombe et al., 1993; McCarthy et al., 2006; Tilman et al., 2006). In the case of shrubs replacing grasses, ANPP in more productive grasslands is subject to extreme light limitation because graminoid meristems are only found at or below the soil surface (Knapp & Seastedt, 1986). In contrast, the complex branching architecture in shrubs permits more options for the deployment of meristems and leaves, allowing woody species to support very high LAI. Removal of this biotic limitation to ANPP fundamentally alters the relationship between precipitation and C inputs and does so in a time frame that is much shorter, and at a magnitude that is much greater, than that by which climate change alone is likely to impact ecosystem C inputs. This pattern is not uniform across North America, however. Increased ANPP with shrub encroachment was not evident in xeric grasslands, where ANPP is generally limited by water rather than light or leaf area (Knapp & Smith, 2001). Thus, production advantages of the shrub growth form are absent here, and increased shrub abundance may reduce RUE if increased bare ground between shrubs reduces soil water infiltration and increases evaporation (Huenneke et al., 2002; Bhark & Small, 2003; Kurc & Small, 2004).

The nonlinear relationship between ANPP and MAP in these graminoid-dominated sites (Fig. 2) contrasts with the linear relationship reported by Sala et al. (1988) for Great Plains grasslands. This may reflect the broader geographic distribution of sites in our study, and the restriction of graminoid-dominated communities to edaphically poor sites in the eastern regions of North America vs. the more productive soils of the central Great Plains. However, even in the most productive southeastern Great Plains region analyzed by Sala et al. (1988), grassland ANPP averaged only $600 \, g \, m^{-2}$ in years with average MAP. This represents less than half of the ANPP measured in the most mesic sites converted to shrub dominance in our study (Fig. 1).

Although shrub encroachment can lead to high LAI, ANPP and RUE in mesic regions, it is uncertain if these attributes are sustainable in the long term. Alternatively, they may represent a transient response, characteristic of nonequilibrium ecosystems subject to shifting resource limitations (Seastedt & Knapp, 1993; Smith et al., submitted). Eventually, biotic constraints on ANPP (decreased LAI as shrubs increase in density, canopies close and self-shading occurs) or other resource limitations may moderate these responses. Nonetheless, there are two important consequences of the replacement of grasses by shrubs with respect to future climates. First, shifting precipitation control of ANPP from a form that is nonlinear and plateaus at moderate MAP to a relationship characterized by a stronger linear increase with MAP (Fig. 2) suggests that interannual variation in ANPP will increase regionally in response to variability in rainfall, a pattern not seen historically in the more mesic regions of the United States (Knapp & Smith, 2001). Second, increased cover of woody plants with high LAI will increase evapotranspiration at the ecosystem scale (Farley et al., 2005) placing these systems at greater risk than grasslands if extreme weather patterns occur, particularly droughts. Recent drought-induced mortality of woody plants in the southwestern United States (Breshears et al., 2005) and historic records of tree mortality during the major droughts of the last century (Weaver, 1968) are sobering reminders that shifts to dominance by woody species, particularly in sites historically dominated by more drought tolerant grasses, may exacerbate ecosystem instability in the face of future more extreme climate regimes (IPCC, 2007).

Acknowledgements

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