Global Change Biology (2006) **12,** 1815–1822, doi: 10.1111/j.1365-2486.2006.01232.x

Invasive grass reduces aboveground carbon stocks in shrublands of the Western US

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Abstract

Understanding the terrestrial carbon budget, in particular the strength of the terrestrial carbon sink, is important in the context of global climate change. Considerable attention has been given to woody encroachment in the western US and the role it might play as a carbon sink; however, in many parts of the western US the reverse process is also occurring. The conversion of woody shrublands to annual grasslands involves the invasion of non-native cheatgrass (*Bromus tectorum*) which in turn leads to increased frequency and extent of fires. We compared carbon storage in adjacent plots of invasive grassland and native shrubland. We scaled-up the impact of this ecosystem shift using regional maps of the current invasion and of the risk of future invasion. The expansion of cheatgrass within the Great Basin has released an estimated 8 ± 3 Tg C to the atmosphere, and will likely release another 50 ± 20 Tg C in the coming decades. This ecosystem conversion has changed portions of the western US from a carbon sink to a source, making previous estimates of a western carbon sink almost certainly spurious. The growing importance of invasive species in driving land cover changes may substantially change future estimates of US terrestrial carbon storage.

Keywords: *Bromus tectorum*, carbon budget, cheatgrass, fire, Great Basin, invasive species, land cover change, woody encroachment

Received 23 December 2005 and accepted 1 March 2006

Introduction

Terrestrial carbon accounting is an important component of predicting long-term climate change. Large-scale changes in land cover affecting carbon storage should be included in estimates of current and future carbon flux. A prominent example of large-scale land cover change is conversion of shrubland to non-native cheatgrass (*Bromus tectorum*) grassland in the western US. Cheatgrass is a non-native annual grass prevalent in the states of Washington, Oregon, Idaho, and vast areas of Nevada and Utah (Mack, 1981). Cheatgrass tends to invade sagebrush (*Artemesia* spp.) communities, but is also present in pinyon-juniper (*Pinus* spp., *Juniperus* spp.) woodland and, more recently, has invaded lower elevation salt desert shrubland (*Atriplex* spp.) (Young & Tipton, 1989). Cheatgrass invasion has been linked to land use disturbance (Gelbard & Belnap, 2003; Bradley & Mustard, 2006), but the invasive species is likely to expand in area even without disturbance effects (Bradley & Mustard, 2006). Further, the growth of cheatgrass is enhanced by elevated levels of CO_2 relative to other native species (Smith *et al*., 1987, 2000), suggesting that the competitiveness of cheatgrass will continue for the foreseeable future.

The most compelling reason for including cheatgrass invasion in carbon accounting is close association with fire (D'Antonio & Vitousek, 1992). Whisenant (1990) showed that fire frequency increases 10-fold, to as often as every 5 years, following cheatgrass invasion. Fire frequency increases because cheatgrass creates dense vegetative cover, and thus, higher fuel load, on lands that formerly contained shrub and bunch grasses separated by open soil (Whisenant, 1990). Once this land burns the wind blown seeds of cheatgrass swiftly recolonize the area, creating a cheatgrass monoculture with a total loss of shrub biomass (Young & Evans, 1978). Even without repeated fires, cheatgrass dominates previously burned areas, preventing shrub regrowth (Billings, 1990).

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Although shrub loss, or 'woody elimination', is prominent in the western US, it has not been considered in the US terrestrial carbon budget (Houghton *et al*., 1999; Pacala *et al*., 2001). Instead, the opposite process of shrub gain, or 'woody encroachment', has received considerable attention. Several studies have described the spread of woody plants into grasslands and shrublands (Archer, 1994; Archer *et al*., 2001; Asner *et al*., 2003; Wessman *et al*., 2004), including sagebrush-dominated systems. In the US some of the difference between ground-based and atmospheric-based estimates of carbon flux (Prentice *et al*., 2001; Houghton, 2003) has been tentatively attributed to woody encroachment (Houghton *et al*., 1999; Pacala *et al*., 2001). An upper limit of carbon accumulation across all nonforested, noncultivated land in the western US is 122 Tg C yr^{-1} (Houghton *et al*., 1999), though this estimate does not include potentially offsetting decreases in soil carbon (Schlesinger & Pilmanis, 1998; Goodale & Davidson, 2002; Jackson *et al*., 2002). Because woody encroachment is the only land cover change currently considered in the western US, this region is thought to be a net carbon sink. However, consideration of the invasion of annuals in the carbon balance of the region may negate the carbon gains associated with woody encroachment while also reducing the potential land area available for encroachment.

Conversion of woody plant communities to annual communities is an important ecological and biogeochemical process due to its broad spatial scale. Using remote sensing to map cheatgrass on a regional scale, Bradley & Mustard (2005) found that cheatgrass monocultures with dense understories covered a minimum of 20 000 km^2, or 5% of the Great Basin in the 1990s. Based on topography and soil properties 150 000 km^2 of the Great Basin have been estimated to be at high risk of cheatgrass invasion (Suring *et al*., 2005; Wisdom *et al*., 2005).

Woody plant community elimination as a result of invasion of annual grasses may affect carbon storage in several ways. First, carbon is lost through the volatilization of carbon stored in shrub biomass during fires. If burned, these woody communities are unlikely to regenerate (Billings, 1990). Second, net carbon exchange (NCE) is lower in invasive grass communities than in native shrubland, reducing carbon accumulation rates (Verburg *et al*., 2004; Prater *et al*., 2006). Third, conversion from a woody to annual life form will likely affect patterns of belowground carbon storage. Shallow soils may have increased carbon content as brome density increases (Ogle *et al*., 2004), while shrub-dominated systems have extensive rooting systems at 1–2 m depths and may store more carbon in deeper soils (Jobbagy & Jackson, 2000; Jackson *et al*., 2002). Additionally, decreased vegetative cover on burned landscapes may increase topsoil erosion, leading to losses of shallow soil carbon (D'Antonio & Vitousek, 1992).

In order to estimate the potential regional impact of cheatgrass invasion on carbon stocks, we compare aboveground carbon storage within plots in the sagebrush steppe and salt desert shrub communities with that of adjacent plots in cheatgrass-dominated grasslands. We also examine soil carbon in the adjacent plots to determine whether fire and associated cheatgrass invasion have led to a change in shallow soil carbon. Finally, we scale-up estimates of aboveground carbon stock changes resulting from the invasion of cheatgrass to the regional level using the current extent of cheatgrass (Bradley & Mustard, 2005) and extent of potential invasion (Suring *et al*., 2005; Wisdom *et al*., 2005).

Methods

Vegetation cover, aboveground biomass, and near-surface soil carbon of native shrublands and cheatgrass monocultures were measured at three sites in north central Nevada in May 2004. Plots representative of plant communities before and after conversion to cheatgrass grassland were sampled using a paired plot design: one plot in a burned grassland dominated by cheatgrass and another in unburned native shrubland. The paired plots were $30 \times 30\,m^2$, located within 500 m of each other, and at least 100 m from any burn edges or roads.

The three sites, representative of lands invaded by cheatgrass, were selected on Bureau of Land Management (BLM) lands subjected to grazing pressures typical of those experienced across the Great Basin. Native vegetation at these sites was representative of the range of communities cheatgrass typically invades, from a low-productivity salt desert shrub community to a high-productivity sagebrush community. Finally, the length of time since fire ranged from 3 to 18 years, with two fire events at one site. Fire frequency is high in cheatgrass-dominated areas (Whisenant, 1990), and multiple burns may become the norm for annual grasslands in the future.

The first site, located west of the Rye Patch reservoir (40.57°N, 118.34°W) at an elevation of 1280 m and a mean annual precipitation of approximately 190 mm (based on the Rye Patch Dam gage 13 km away), contained a dry desert shrub community, composed primarily of shadscale (*Atriplex confertifolia*) and saltbush (*Atriplex* spp.) with some cheatgrass under shrub canopies. Interspaces contained no native grasses. The annual grassland (burned in 2001) contained cheatgrass, as well as the non-native annuals *Halogeton glomeratus* and Russian thistle (*Salsola kali*).

Fig. 1 Sagebrush ecosystem with cheatgrass-dominated interspaces (left) adjacent to cheatgrass grassland (right) at the Jungo site.

The second site, located south of Button Point (41.00°N, 117.58°W) at an elevation of 1400 m and a mean annual precipitation of 210 mm (based on the Winnemucca Airport gage 20 km away), contained a mixed sagebrush (*Artmesia tridentata*) and Sandberg blue grass (*Poa secunda*) community with some cheatgrass under shrub canopies. The annual grassland portion of this site burned in 1986 and was dominated by cheatgrass.

The third site, located north of Jungo (40.99°N, 117.86°W) at an elevation of 1380 m and a mean annual precipitation of 210 mm (based on the Winnemucca Airport gage 13 km away), contained a sagebrush community with dense cheatgrass in shrub interspaces (Fig. 1). The cheatgrass grassland portion of this site burned twice, once in the mid-1980s and again in 2001.

The Rye Patch, Button Point, and Jungo locations represented the types of shrublands that cheatgrass typically displaces in the Great Basin and thus can be used to estimate aboveground carbon loss associated with the process. We measured aboveground biomass by destructively collecting plant material within ten $0.10\,m^2$ circular subplots within a grid in each plot. The collection was timed to coincide with peak aboveground biomass (mid-May). Litter (dead plant material not attached to a living plant) was minimal at all sites and was not included in the harvested biomass. Harvested plant material was dried at 60 °C for 48 h and weighed. Dry biomass was converted to aboveground carbon using a C/biomass conversion factor of 0.5.

Percent cover of native and invasive species was measured every meter along six randomly oriented 30 m line transects within each plot. Cover was classified as soil, native shrub woody vegetation, native shrub green foliage, native perennial grass, or cheatgrass.

The top 10 cm of soil was collected using a 2 cm diameter soil corer at 40 locations arrayed systematically in a grid within each plot. Although bulk density is likely to differ among sites, we assumed it to be the same between adjacent plots. Thus, differences in total carbon content correspond to carbon concentration at each site. Soils were dried at 100 °C for 48 h, sieved to remove rocks >2 mm diameter, ground using a mixer mill, and measured for carbon content using a modified Dumas C-N Analyzer. Soil carbon was dominantly organic; inorganic carbon measured within two samples from each plot using inorganic carbon coulometry, accounted for $<1\%$ of total carbon in all cases.

Average aboveground carbon ($g\,C\,m^{-2}$) was calculated for shrub system of the Great Basin by combining the results of this study with studies reported in the literature to determine average community aboveground carbon. Published studies of aboveground biomass in sagebrush, salt desert shrub, and cheatgrass communities have been collected across the Great Basin (Utah, Idaho, Oregon, and Nevada; Hull & Pechanec, 1947; Goodman, 1973; Young *et al*., 1989; Sapsis & Kauffman, 1991). The difference between average aboveground carbon stored in native shrubland and

Table 1 Mean percent land cover at three sites in the Great Basin

	Soil	Shrub (woody)*	Shrub (foliage)†	Native grass	Cheatgrass
Rye Patch					
Shrubland	60 (4)	24 (3)	11 (2)	–	4 (2)‡
Grassland	54 (4)	3 (1)§	–	–	18 (3)‡
Button Point					
Shrubland	50 (3)	18 (2)	19 (2)	11 (2)	2 (1)
Grassland	34 (4)	–	–	9 (2)	56 (4)
Jungo					
Shrubland	28 (4)	29 (4)	17 (3)	–	27 (4)
Grassland	61 (4)	–	–	1 (1)	37 (4)

Mean (±standard error).
*Shrub woody nonphotosynthetic vegetation.
†Shrub green foliage cover.
‡The invasive annuals *Halogeton glomeratus* and Russian thistle (*Salsola kali*) make up the remaining percent cover.
§Woody vegetation at this site consisted of burned stumps.

in cheatgrass monocultures determined the average carbon lost with cheatgrass invasion into salt desert shrub and sagebrush communities. We estimated the potential land cover (precheatgrass) in Great Basin shrublands using estimates of mean annual precipitation from PRISM (Daly *et al*., 2004) and an average precipitation threshold of 200 mm to differentiate between salt desert shrub and sagebrush communities (Houghton *et al*., 1975).

Potential (precheatgrass) land cover distribution in the Great Basin was compared with current cheatgrass extents based on a remote sensing derived map of cheatgrass presence (Bradley & Mustard, 2005). This map did not include Idaho or central Oregon and classifies 64% of cheatgrass with a commission error (pixels classified as cheatgrass that contain native vegetation) of 15% (Bradley & Mustard, 2005). Thus, regional estimates of current cheatgrass distribution underestimate the total invasion to date. Values of carbon loss per unit area for both salt desert shrub and sagebrush communities were multiplied by the total area currently containing cheatgrass to determine net aboveground carbon loss with current cheatgrass invasion. The same process was repeated using a map of land at high risk of future cheatgrass invasion (Suring *et al*., 2005; Wisdom *et al*., 2005) to determine potential future aboveground carbon losses if woody elimination continues.

Results

All woody cover was completely absent on the annual grassland plots (Table 1). Native grasses were found in only one grassland plot (Button Point, where native grasses were also abundant on the shrubland plot). At the Button Point and Rye Patch sites, shrubland areas contained very low densities of cheatgrass, suggesting that cheatgrass had invaded but was not abundant in the area before burning. At the Jungo site, where dense cheatgrass existed in shrub interspaces in the shrubland plot, shrubs were replaced primarily by bare soil after fire, with only a modest increase in cheatgrass cover.

Aboveground carbon was lower at grassland plots (22–94 $g\,C\,m^2$) than at shrubland plots (160–670 $g\,C\,m^2$) due to the loss of woody biomass (Table 2). The values of aboveground carbon for cheatgrass, salt desert ecosystems, and sagebrush systems obtained in these locations were similar to estimates reported from elsewhere in the Great Basin (Hull & Pechanec, 1947; Goodman, 1973; Young *et al*., 1989; Sapsis & Kauffman, 1991).

When our measured values for aboveground biomass in shrub and grassland plots were averaged with results from the literature with the same community types, we estimate that the loss of aboveground carbon averaged $440 \pm 180\,g\,C\,m^{-2}$ (SE) when sagebrush systems were lost and $110 \pm 50\,g\,C\,m^{-2}$ (SE) when salt desert shrub systems were lost (Table 2). Twenty thousand km^2 of the Great Basin are currently dominated by either cheatgrass monoculture or dense cheatgrass in a shrub matrix (Bradley & Mustard, 2005) (Fig. 2). Although some of these areas have not yet experienced loss of woody vegetation, they are at high risk of fire and future woody elimination. Of the total area, 18 000 km^2 were formerly sagebrush-dominated communities (average annual rainfall of >200 mm) and 2000 km^2 dry desert shrub (average annual rainfall of <200 mm). This pattern of ecosystem conversion has resulted in the loss, or imminent risk of loss once fire occurs, of 8 ± 3 Tg C. An additional 150 000 km^2 in the Great Basin are at high risk of cheatgrass invasion and future woody plant community elimination (Suring *et al*., 2005; Wisdom *et al*., 2005) (Fig. 2). Of that area,

Table 2 Mean aboveground carbon storage ($g\,C\,m^{-2}$) of invaded and native plant communities in the Great Basin

	Grassland	Shrubland	
	Cheatgrass	Desert shrub	Sagebrush
This study			
Rye Patch	48 (6)*	160 (49)*	
Button Point	94 (26)		340 (145)
Jungo	22 (2)*		670 (290)*
Other studies			
	70 (5)†	156 (32)‡	530 (56)§
		178 (32)‡	444 (169)¶
Average	59 (10)	165 (38)	497 (165)
Difference from cheatgrass		106 (48)	438 (175)

Mean (± standard error).
*Significant difference between invasive grassland and native shrubland plots ($P < 0.05$).
†Idaho – (Hull & Pechanec, 1947).
‡Utah – (Goodman, 1973).
§Oregon – (Sapsis & Kauffman, 1991).
¶Nevada – (Young *et al*., 1989).

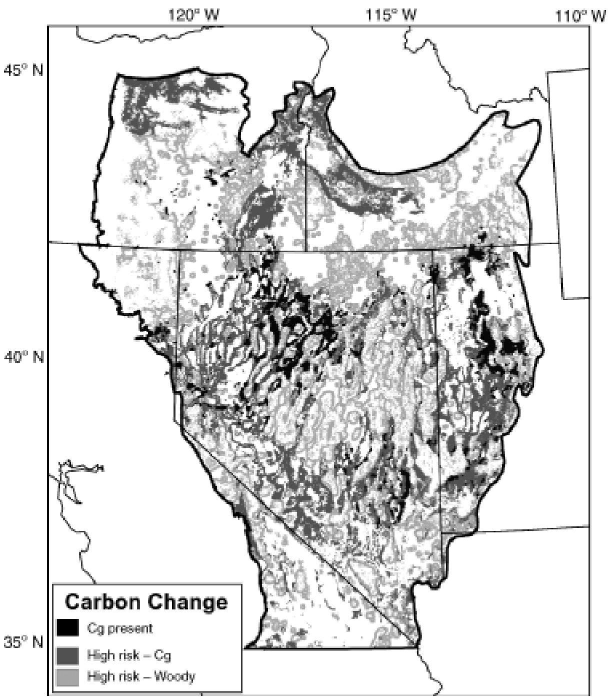

Fig. 2 Western lands contributing to carbon flux. Dark gray areas currently contain cheatgrass. Medium gray areas are at high risk of cheatgrass invasion and are a carbon source. Light gray areas are at high risk of woody encroachment and are a carbon sink.

Table 3 Carbon concentrations in the top 10 cm of soil on invasive grassland and native shrubland plots in the Great Basin

	Carbon concentration (%)		
	Invaded	Native	
	Cheatgrass	Desert shrub	Sagebrush
Rye Patch	0.48 (0.022)	0.44 (0.013)	
Button Point	1.37 (0.040)*		1.03 (0.037)*
Jungo	0.80 (0.034)		0.85 (0.034)

Mean (± standard error).
*Significant difference between invaded and native plots ($P < 0.05$).

100 000 km^2 are currently occupied by sagebrush and 50 000 km^2 by dry desert shrub. The potential carbon loss in areas at high risk of eventual conversion to annual grassland is 50 ± 20 Tg C.

Mean soil carbon concentration in the top 10 cm was higher in the sagebrush communities than in the desert shrubland, but conversion to cheatgrass had no significant effect on soil carbon concentrations except at Button Point, where the data show a higher carbon concentration within the grassland (Table 3). However, the lack of similar findings at the two other sites and in the literature suggests that this difference may be a result of pre-existing soil differences between the plots. Because the data on soils are inconsistent, we did not include shallow soil carbon values in our estimates of carbon stock change at the regional level.

Discussion

The difference in percent cover of paired grassland and shrubland plots illustrates the magnitude of the transition from native shrubland to cheatgrass-dominated ecosystems. Woody, nonphotosynthetic vegetation, a critical component of carbon storage in semiarid systems, is completely eliminated. The loss of woody vegetation in these areas is likely permanent, as cheatgrass dominates immediately following fires and competes effectively with native species for resources (Billings, 1990). Cheatgrass dominance in the western US has steadily increased since the early 1900s and is expected to continue its expansion unabated even if not more rapidly (Mack, 1981). Although the process of cheatgrass expansion has long been known, its implications on carbon cycling has been overlooked. This study suggests that the scale of this influence on US carbon budget is large.

Currently, semiarid lands in the western US are thought to be a net carbon sink as a result of woody encroachment (Houghton *et al*., 1999; Pacala *et al*., 2001). However, aboveground carbon losses resulting from the spread of cheatgrass may be of a magnitude sufficient to offset gains resulting from woody encroachment. One of the few studies to have considered woody encroachment over a large area and a long time period found that mesquite expansion over 400 km^2 of drylands in northern Texas between 1937 and 1999 accumulated an estimated 120 $g\,C\,m^{-2}$ in woody biomass (Asner *et al*., 2003). The magnitude of this gain is comparable to the loss associated with the conversion of dry desert shrub systems to cheatgrass (110 $g\,C\,m^{-2}$) and much less than the loss associated with the conversion of sagebrush systems (440 $g\,C\,m^{-2}$).

Cheatgrass invasion not only creates a carbon source, but also reduces the aerial extent of the potential woody sink. Many of the sagebrush systems that cheatgrass is replacing have previously been experiencing woody encroachment via sagebrush crown enclosure or pinyon-juniper expansion (Archer, 1994; Wessman *et al*., 2004). An upper estimate of all lands potentially susceptible to woody encroachment based on the criteria used by Houghton *et al*. (1999) (all nonforested, noncultivated land area) encompasses 450 000 km^2 in the Great Basin. However, pinyon-juniper encroachment is only likely to occur within 5 km of the sagebrush/woodland transition (Suring *et al*., 2005), a total area of only 200 000 km^2, of which 40 000 km^2 are highly susceptible to cheatgrass invasion. Thus, a more reasonable estimate for areas with a potential for long-term carbon storage due to woody encroachment could be reduced to 160 000 km^2, a third of the aerial extent initially considered susceptible to woody encroachment (Fig. 2). If the amount of carbon accumulated over 60 years in north Texas is applied to the maximum area available (160 000 km^2), the potential accumulation of carbon is 20 Tg C, less than half of the potential loss of 50 Tg C estimated here for the continued spread of cheatgrass. Cheatgrass invasion not only releases carbon, it also eliminates a carbon sink.

Carbon loss values associated with cheatgrass invasion are likely an underestimate. The map of current extents underestimates cheatgrass presence and does not include Idaho and central Oregon. Also, the area estimated to be at high risk of cheatgrass invasion does not include shrublands outside of the Great Basin in Oregon, Washington and eastern Utah (Mack, 1981). In addition to underestimating the extents of woody elimination, we also have not included changes in community NCE (Verburg *et al*., 2004; Prater *et al*., 2006).

Prater *et al*. (2006) compare daily integrated NCE between a sagebrush community and a postfire invasive annual community at several time periods in growing seasons between 18 July 2000 and 12 August 2003. Average postfire NCE (0.14 ± 0.08 SE $g\,C\,m^{-2}$ day) is significantly lower than average sagebrush NCE (0.50 ± 0.12 SE $g\,C\,m^{-2}$ day) for the period of measure. Assuming this difference is only present during the summer growing season (1 June–1 August), this difference amounts to a reduced uptake of 22 ± 12 $g\,C\,m^{-2}$ yr when sagebrush is replaced by invasive annuals. Scaling these values to a regional level would reduce uptake by 0.4 ± 0.2 $Tg\,C\,yr^{-1}$ in sagebrush communities where woody elimination is imminent and by 2.2 ± 1.2 $Tg\,C\,yr^{-1}$ in sagebrush communities at high risk of future conversion to annual grassland.

The effect of woody elimination on belowground carbon storage is highly uncertain. D'Antonio & Vitousek (1992) suggest that loss of vegetation on burned landscapes may increase soil erosion and lead to a loss of shallow soil carbon. However, our results for the top 10 cm of soil were inconsistent (Table 3). The higher concentration of soil carbon in cheatgrass communities at the Button Point site combined with the insignificant changes at the other two sites suggest that fire and cheatgrass invasion have not resulted in a loss of shallow soil carbon thus far. Elsewhere, shallow (30 cm) soil carbon appeared to increase with higher cheatgrass density, although the trend was not significant (Ogle *et al*., 2004).

However, shallow soils are certainly not the only soil carbon pools affected by woody elimination. Sagebrush rooting depth can reach 2 m (Taber, 1964), much deeper than annual grasses. Accordingly, studies in other semiarid sites have shown that shrub systems store the same or significantly more soil organic carbon than grasslands (Jackson *et al*., 2002), particularly between 1 and 2 m depths (Jobbagy & Jackson, 2000). The soil carbon dynamics of woody elimination for both shallow and deep soils need further investigation.

The observation that western rangelands may be gaining carbon in some regions and losing it in others lends support to the argument for more complete carbon accounting in computing national annual carbon fluxes (i.e. all areas, all potentially changing components of the ecosystem). Aboveground carbon changes reported here are large relative to total carbon storage in semiarid systems. If large-scale changes have been overlooked in this region, they may have been overlooked in other regions as well.

Including the process of woody elimination in an accounting of carbon stocks in arid and semiarid regions raises a number of questions. Will the increasing importance of non-native grasses reverse the long-term carbon sink associated with woody encroachment? Has it already gone from positive to negative? Is the trend limited to the western US or will it affect arid and semiarid carbon stocks at a global scale? Will the rate of grass invasion and associated carbon loss increase in the future? Whatever the answers, it is clear that invasive species in semiarid systems are changing the dynamics of long-term carbon storage. A closer look in other regions seems warranted.

Acknowledgements

This work was supported by the NASA Land Use Land Cover Change Program, the Global Carbon Cycle Program at NOAA's Climate Program Office, and the American Society for Engineering Education. We thank S. Bradley and L. Schneider for contributions to data collection. O. Sala, W. Schlesinger, and G. Woodwell provided constructive feedback.

References

Archer S (1994) Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: *Ecological Implications of Livestock Herbivory in the West* (eds Vavra M, Laycock W, Pieper R). pp. 13–68. Society of range management, Denver.

Archer S, Boutton TW, Hibbard KA (2001) Trees in grasslands: biogeochemical consequences of woody plant expansion. In: *Global Biogeochemical Cycles in the Climate System* (eds Schulze D, Heimann M, Harrison S, Holland E, Lloyd J, Prentice I, Schimel D), pp. 115–138. Academic Press, San Diego.

Asner GP, Archer S, Hughes RF *et al*. (2003) Net changes in regional woody vegetation cover and carbon storage in Texas Drylands, 1937–1999. *Global Change Biology*, **9**, 316–335.

Billings WD (1990) Bromus tectorum, a biotic cause of ecosystem impoverishment in the Great Basin. In: *Patterns and Processes of Biotic Impoverishment* (ed. Woodwell GM), pp. 301–322. Cambridge University Press, New York.

Bradley BA, Mustard JF (2005) Identifying land cover variability distinct from land cover change: cheatgrass in the Great Basin. *Remote Sensing of Environment*, **94**, 204–213.

Bradley BA, Mustard JF (2006) Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecological Applications*, **16**, 1132–1147.

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.

Daly C, Gibson WP, Doggett M, *et al*. (2004) Up-to-date monthly climate maps for the conterminous United States. In: *14th AMS Conference on Applied Climatology*. Paper P5.1, CD-ROM, Seattle, WA.

Gelbard JL, Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology*, **17**, 420–432.

Goodale CL, Davidson EA (2002) Carbon cycle: uncertain sinks in the shrubs. *Nature*, **418**, 593–594.

Goodman P (1973) Physiological and ecotypic adaptations of plants to salt desert conditions in Utah. *Journal of Ecology*, **61**, 473–494.

Houghton RA (2003) Why are estimates of the terrestrial carbon balance so different? *Global Change Biology*, **9**, 500–509.

Houghton RA, Hackler JL, Lawrence KT (1999) The US carbon budget: contributions from land-use change. *Science*, **285**, 574–578.

Houghton JG, Sakamoto CM, Gifford RO (1975) *Nevada's Weather and Climate*. Nevada Bureau of Mines and Geology, Reno, NV.

Hull ACJ, Pechanec JF (1947) Cheatgrass – a challenge to range research. *Journal of Forestry*, **45**, 555–564.

Jackson RB, Banner JL, Jobbagy EG *et al*. (2002) Ecosystem carbon loss with woody plant invasion of grasslands. *Nature*, **418**, 623–626.

Jobbagy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications*, **10**, 423–436.

Mack RN (1981) Invasions of *Bromus tectorum* L. into Western North America: an ecological chronicle. *Agro-Ecosystems*, **7**, 145–165.

Ogle SM, Ojima D, Reiners WA (2004) Modeling the impact of exotic annual brome grasses on soil organic carbon storage in a northern mixed-grass prairie. *Biological Invasions*, **6**, 365–377.

Pacala SW, Hurtt GC, Baker D *et al*. (2001) Consistent land- and atmosphere-based US carbon sink estimates. *Science*, **292**, 2316–2320.

Prater MR, Obrist D, Arnone JA *et al*. (2006) Net carbon exchange and evapotranspiration in postfire and intact sagebrush communities in the Great Basin. *Oecologia*, **146**, 595–607.

Prentice IC, Farquhar GD, Fasham MJR *et al*. (2001) The carbon cycle and atmospheric carbon dioxide. In: *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (eds Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA), pp. 183–237. Cambridge University Press, Cambridge, UK and New York, NY.

Sapsis DB, Kauffman JB (1991) Fuel consumption and fire behavior associated with prescribed fires in sagebrush ecosystems. *Northwest Science*, **65**, 173–179.

Schlesinger WH, Pilmanis AM (1998) Plant-soil interactions in deserts. *Biogeochemistry*, **42**, 169–187.

Smith SD, Huxman TE, Zitzer SF *et al*. (2000) Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. *Nature*, **408**, 79–82.

Smith SD, Strain BR, Sharkey TD (1987) Effects of CO_2 enrichment on four great basin grasses. *Functional Ecology*, **1**, 139–143.

Suring LH, Wisdom MJ, Tausch RJ *et al*. (2005) Modeling threats to sagebrush and other shrubland communities. In: *Habitat Threats in the Sagebrush Ecosystem: Methods of Regional Assessment and Applications in the Great Basin* (eds Wisdom MJ, Rowland MM, Suring LH), pp. 114–119. Alliance Communications Group, Allen Press, Lawrence, KS.

Taber RD (1964) The root system of Artemesia tridentata at 9500 feet in Wyoming. *Ecology*, **45**, 633–636.

Verburg PSJ, Arnone JA, Obrist D *et al*. (2004) Net ecosystem carbon exchange in two experimental grassland ecosystems. *Global Change Biology*, **10**, 498–508.

Wessman CA, Archer S, Johnson LC *et al*. (2004) Woodland expansion in US Grasslands. In: *Land Change Science* (ed.

Gutman G), pp. 185–208 Kluwer Academic Publishers, the Netherlands.

Whisenant SG (1990) Changing fire frequencies on Idaho's snake river plains: ecological and management implications. In: *Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, Las Vegas* (eds McArthur ED, Romney EM, Smith SD, Tueller PT), pp. 4–10. Intermountain Research Station, Forest Service, US Department of Agriculture, Ogden, UT.

Wisdom MJ, Rowland MM, Suring LH *et al*. (2005) Evaluating species of conservation concern at regional scales. In: *Habitat Threats in the Sagebrush Ecosystem: Methods of Regional Assessment and Applications in the Great Basin* (eds Wisdom MJ, Rowland MM, Suring LH), pp. 5–74. Alliance Communications Group, Allen Press, Lawrence, KS.

Young JA, Evans RA (1978) Population dynamics after wildfires in Sagebrush Grasslands. *Journal of Range Management*, **31**, 283–289.

Young JA, Evans RA, Palmquist DE (1989) Big sagebrush (*Artemesia tridentata*) seed production. *Weed Science*, **37**, 47–53.

Young JA, Tipton F (1989) Invasion of cheatgrass into arid environments of the lahontan basin. In: *Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, Las Vegas* (eds McArthur ED, Romney EM, Smith SD, Tueller PT), pp. 37–40. Intermountain Research Station, Forest Service, US Department of Agriculture Ogden, UT.