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Composted manure application promotes long-term invasion of semi-arid rangeland by *Bromus tectorum*

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Abstract. Nutrient-rich organic waste derived from sewage treatment facilities or livestock manure is often applied to rangelands of western North America to increase soil fertility, forage production, forage quality, and soil carbon storage. This practice can have a number of undesirable side effects, however, including plant invasion. While characteristics of both rangeland ecosystems and invasive plants suggest that organic waste application might often promote invasion, results to date are mixed, perhaps due in part to the paucity of long-term studies. Here, we describe the long-term (22 yr) effects of three types of organic waste—composted biosolids, composted cattle manure, and fresh cattle manure—on plant productivity and invasion in native mixed-grass prairie. Although composted manure and biosolids increased plant productivity and forage quality in the second year of the study, these effects did not persist. In contrast, *Bromus tectorum* (cheatgrass), which invaded the study site over the course of the experiment, was strongly facilitated by composted manure addition, with particularly large effects observed in years 17 and 22. These results show that nutrient-rich organic waste can favor invasive species even in the relatively invasion-resistant grasslands of the western Great Plains. They also demonstrate that effects of organic waste on invasion can become apparent quite gradually and persist for decades following the initial organic waste application. Together, results from experimental additions of organic and inorganic nutrients to native rangelands suggest that the risk of promoting invasive species is significant, and should be considered in programs that apply organic waste to rangelands of western North America.

Key words: biosolids; *Bromus tectorum;* invasion; manure; nitrogen; phosphorus; rangelands.

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Introduction

For several decades, nutrient-rich organic waste (henceforth organic waste) derived from urban wastewater treatment facilities (composted sewage, also known as biosolids) and agriculture (composted livestock manure or composted plant material) has been applied to rangelands to increase soil nutrient availability, plant productivity, and to provide an economical means of waste disposal (Larney and Angers 2012, Lu et al. 2012). Approximately 60% of biosolids produced by wastewater treatment facilities in the USA are recycled through land application (6–7 $\times$ 10^6 Mg per yr; Cogger et al. 2006). Benefits to society are well documented. Organic waste contains high levels of nitrogen (N), phosphorous (P), and potassium (K) as well as micronutrients (Larney and Angers 2012), and when applied to rangelands or tame pastures can increase forage productivity and quality (Pierce et al. 1998, Martinez et al. 2003, Meyer et al. 2004, Ippolito et al. 2010). Organic wastes also contain large amounts of organic matter, which can increase soil water-holding capacity and nutrient release from microbes (Barbarick et al.

2004, Ippolito et al. 2010). More recently, organic waste amendments have been proposed for increasing soil C storage, which is often limited by nutrient availability in natural ecosystems (Ryals et al. 2015).

Biosolids derived from wastewater treatment facilities that are applied to rangelands in western North America have N concentrations on the order of 2–5% (Table 1). Composted livestock manure can have N concentrations in the same range, and composted organic green wastes applied to California rangelands contain only slightly lower N concentration (1.9%; Table 1). Unfortunately, the same high nutrient content that makes organic waste useful for increasing plant growth can lead to plant invasion (Davis et al. 2000, Daehler 2003). Many invasive plants have traits such as rapid photosynthetic and growth rates that allow them to thrive under conditions of high resource availability (Pysek

Table 1. Summary of studies of the application of organic waste (biosolids [B], cattle manure [CM], or composted plant material [CMP]) to rangelands in western North America.

Source	Ecosystem and State/Province	Organic waste type	Precip. (mm)	Range of amounts applied: %N	Range of amounts applied: kg N/ha	Range of amounts applied: kg P/ha	Years of study	*Bromus tectorum* present/enhanced†	Other plant groups enhanced or suppressed
Wester et al. (1995, 2003)	Desert grassland, Texas	B	305	3.2–4.0	216–2897	197–2646	4	NR/no	None reported
Pierce et al. (1998)	Sagebrush steppe, Colorado	B	356	2.9	144–1153	100–800	4	NR/no	None reported
Newman et al. (2014)	C_3 grassland, British Columbia	B	401	4.5	900	NA	4	NP/no	+Native perennials; −Early seral forbs
Ryals et al. (2016)	Valley and coastal grassland, California	CMP	720–950	1.9	1309	NA	4	NP/no	−Annuals in coastal grassland
Fresquez et al. (1990), Loftin et al. (1995), White et al. (1997)	Desert grassland, New Mexico	B	212–320	4.9	1094–4376	36–144	8	NR/no	−Shrubs
Sullivan et al. (2006), Ippolito et al. (2010)	Shortgrass steppe, Colorado	B	380	4.7	118–1416	28–341	13	NR/no	+C_3 perennial grass; −C_4 shortgrass
Paschke et al. (2005)	Disturbed soil, Colorado (sagebrush steppe)	B	280	~4.0‡	~2240‡	NA	24	NR/no	−Perennial grass
Newman et al. (2014)	Invaded C_3 grassland, British Columbia	B	240–311	4.5	900	NA	5	PP/yes	+Exotic annual forbs
Borden and Black (2011)	Disturbed soil, Utah (sagebrush steppe)	B	400–800	2.8	962–1896	NA§	10	PS/yes	+Annuals; −Legumes
This study	Mixed-grass prairie, Wyoming	CM and B	384	2.0–2.1	454–473	248–360	23	PS/yes	None reported

Notes: Studies or treatments that mixed organic waste with other amendments (e.g., wood chips, water treatment residuals) are not included. For studies conducted on plots initially lacking vegetation, or being actively restored, the type of ecosystem that would occur in the study area is listed in parentheses.

† NR, not reported; NP, not present; PP, present in study plots prior to study; PS, present in study area prior to study.

‡ Nitrogen concentration in the biosolids used in this study not measured, but authors report it was likely within the range of 4–8% N. The N application rate listed here (kg/ha) assumes 4% N.

§ Phosphorus values reported in this study were an order of magnitude lower than all other organic waste studies and hence are not listed here due to uncertain validity.

and Richardson 2007, Blumenthal et al. 2009, van Kleunen et al. 2010, Penuelas et al. 2010). As a result, nutrient addition often favors invasive plants, particularly when they are competing with the slow-growing perennial species that dominate many semi-arid grasslands (Lauenroth et al. 1978, Blumenthal et al. 2008, Gonzalez et al. 2010, Seabloom et al. 2015).

Among previous studies of organic waste amendments in North American rangeland ecosystems, some report increased abundance and productivity of invasive plant species and reductions in native plant species diversity (Table 1). For example, across three rangeland sites in British Columbia, biosolid applications led to a sevenfold increase in exotic species cover (Newman et al. 2014). Furthermore, biosolids increased abundance of desirable, late-seral species only at the site with few invasive species, while suppressing desirable species at two sites with greater initial invasive species cover. Other studies found little effect of organic waste on plant invasion. Composted organic green waste applied to two California rangelands increased productivity of both native and introduced species without altering the relative abundance of two invasive species (Ryals et al. 2016). Understanding where and over what time frames organic waste amendments lead to invasion is important for predicting both the benefits and costs of this practice. Where organic waste amendments do promote invasion, they may not only reduce biological diversity but also counteract intended benefits such as increased forage production, forage quality, and C storage (Rice 2005, Bradley et al. 2006, Vila et al. 2011).

Bromus tectorum (cheatgrass) is a winter annual grass that has invaded tens of millions of hectares of North American rangeland (Di Tomaso 2000, Rice 2005, Bradley and Mustard 2006). In ecosystems west of the Rocky Mountains, where *B. tectorum* is most abundant, organic waste amendments have been found to facilitate its invasion in some cases (Borden and Black 2011, Newman et al. 2014). For example, biosolid application led to a ten-fold increase in *B. tectorum* cover at a reclaimed mine in Utah (Borden and Black 2011). Conversely, in a western Colorado restored sagebrush steppe, biosolid application favored perennial grasses over other life history types with no apparent invasion by *B. tectorum* (Paschke et al. 2005). Variation in *B. tectorum* response may be due to differences among studies in its presence/abundance, the types of other species present in the extant plant community, study duration, or the quantity of available nutrients applied (Table 1).

In the western Great Plains, *B. tectorum* is common, but less problematic than in the Intermountain Region. Disturbances that promote *B. tectorum* invasion west of the Rocky Mountains, including fire and grazing, have not led to widespread dominance by *B. tectorum* in the Great Plains (Mack and Thompson 1982, Milchunas et al. 1988, Ogle et al. 2003, Chambers et al. 2007, Reisner et al. 2013, Porensky and Blumenthal 2016, Pyke et al. 2016). A key question is whether organic waste additions, a distinct type of disturbance, will facilitate *B. tectorum* invasion in this invasion-resistant ecosystem. Organic waste addition to rangeland is a common practice in the Great Plains. For example, along the Colorado Front Range, where urban centers exist in close proximity to rangeland, an estimated 70 million kg of biosolids from many wastewater treatment plants is applied annually to nearby rangelands (Sullivan et al. 2006). To date, studies within the region have not documented invasion following these amendments (Fresquez et al. 1990, Wester et al. 2003, Sullivan et al. 2006). Addition of inorganic forms of N or P, however, has been found to promote invasive species, including *B. tectorum*, in shortgrass steppe and mixed-grass prairie (Milchunas and Lauenroth 1995, Blumenthal et al. 2008, Cherwin et al. 2009), suggesting the potential for invasion following organic waste application.

Given that both observations and theory suggest that organic waste amendments may facilitate invasion, a key question is why study results vary so widely (Table 1). If the absence of invasion reflects low propagule pressure, or the short-term nature of experiments, then it may not indicate low risk. Conversely, if particular types of organic waste do not promote invasion, or particular ecosystems are not made more susceptible to invasion through organic waste addition, then risks may indeed be low. This report describes the long-term influence of organic waste amendments on *B. tectorum* invasion of native mixed-grass prairie. We ask the following: (1) Do organic waste amendments increase productivity of native plants and/or *B. tectorum*? (2) Do effects of organic waste on native plants and *B. tectorum* depend on the type of waste applied? and (3) How do organic waste effects on native plants and *B. tectorum* change over time? To answer these questions, we measured biomass of *B. tectorum* and associated species 2, 4, 17, and 22 yr after a one-time application of composted biosolids, composted cattle manure, or fresh cattle manure to native mixed-grass prairie.

Materials and Methods

The initial purpose of this study was to investigate the potential of organic waste application for improving forage quantity and quality in mixed-grass rangeland. Plant productivity, species composition, and soil nutrient responses in treated vs. control plots were measured for five years (1993–1997). Many years later, we observed abundant *Bromus tectorum* in plots where it had previously been rare or absent. Plant productivity measurements were therefore repeated in 2010 and 2015 to investigate this response.

The study was conducted at the USDA-ARS High Plains Grasslands Research Station near Cheyenne, Wyoming, USA, on native mixed-grass prairie. A field site with a long-term history of light grazing by cattle and a slight (4%) southern slope was chosen (104°51′6.6″ W; 41°12′46.3″ N). Elevation was 1930 m, and soil was a sandy loam (Ascalon and Albinas) and sandy clay loam (Altvan). The site is semi-arid with 127 average annual frost-free days, mean annual precipitation of 384 mm, and mean temperature of 7.6°C. The vegetation is primarily perennial, with 55% cool-season grasses, 23% warm-season grasses, and a mix of forbs, sedges and small shrubs.

Bromus tectorum is a Eurasian winter annual grass that is now common in much of western North America (Mack 1981, Knapp 1996). It thrives in semi-arid grasslands and shrublands, particularly in areas where positive feedbacks develop between its abundance and fire frequency (Young and Evans 1978, Balch et al. 2013, Porensky and Blumenthal 2016). At the High Plains Grasslands Research station, *B. tectorum* is abundant in patches, but rarely a dominant species. Models and experiments, however, suggest that warming and changes in the seasonality of water availability are likely to increase its abundance both locally and regionally (Bradley 2009, Prevey and Seastedt 2014, Blumenthal et al. 2016). Note that we use "invasion" to refer to both the initial arrival of *B. tectorum* and subsequent increases in its abundance. Invasive species other than *B. tectorum* were rare at the study site.

The experiment contained 24 nine-by-nine m plots divided into six replicates of each of four treatments: (1) fresh feedlot cattle manure, (2) composted feedlot cattle manure, (3) composted biosolids, and (4) control (no treatment; analysis in Table 2). Treatments were randomized within three blocks, each containing two replicates of each treatment. Treatments were applied once, on 25–26 May 1993, as hand-spread surface applications of 22.4 metric tons/ha of each type of material. Cattle were excluded from the study area from 1993 through 1997; season-long grazing at a light stocking rate resumed in 1998. Previous work at this site has suggested that cattle grazing can inhibit invasive species, likely by favoring competitive grass species (Blumenthal et al. 2012). Grazing effects on *B. tectorum* could differ, however, due to its distinct early-season phenology, which limits exposure to grazing. Given these contrasting hypotheses, and the absence of a grazing treatment, it is difficult to evaluate how grazing exclusion or reintroduction might have interacted with the organic waste treatments in this study.

Soil samples were collected in 1993 prior to treatment application, and in 1994, 1995, and

Table 2. Nutrient concentrations in added organic waste and total amounts of nutrients added per unit area for three organic waste amendments applied to native mixed-grass prairie in southeastern Wyoming.

	Concentrations				Added by waste	
Treatment	Total N (g/kg)	NH_4 (mg/kg)	NO_3 (mg/kg)	Total P (g/kg)	N (kg/ha)	P (kg/ha)
Biosolids	20.3	151	2730	16.1	454	360
Composted manure	21.1	206	2229	11.1	473	248
Fresh manure	6.7	10	61	1.9	151	43

1996 to assess the effects of treatments on soil. Five 0–7.5 cm deep cores per plot were collected and analyzed for total N and P. Total N concentrations were determined with a modified micro-Kjeldahl procedure (Schuman et al. 1973). Available P was assessed using the sodium bicarbonate method of Olsen and Sommers (1982). Samples were analyzed using a Technicon autoanalyzer (TRAACS 800; Technicon Industrial Systems, New York, New York, USA).

In 1993–1997, vegetation samples were harvested in early August to assess plant production and changes in species composition. Four 0.185-m^2 quadrats were clipped from each plot and separated into nine species groups. These species groups were then summed to yield total above-ground productivity. Sub-plot quadrats were averaged to obtain one biomass value per plot (kg/ha). Very little *B. tectorum* was found in the initial five years of sampling. For years in which no *B. tectorum* was recorded (1993, 1994 and 1996), we do not have records of whether it was not observed or whether it was included with biomass of other functional groups. Consequently, we treat these years as missing data with respect to *B. tectorum* biomass. In 2009, we observed a considerable amount of *B. tectorum* in some of the plots, and therefore decided to resume sampling. In late July 2010 and mid-July 2015, the plots were again sampled for production to investigate the long-term effects of the treatments. Five quadrats of 1.0 m^2 were clipped from each of the 24 plots, and *B. tectorum* was separated from the total above-ground biomass. Sub-plot quadrats were averaged to obtain one value per plot (treatment $n = 6$). Note that our late July and early August sampling dates approximated the time of peak standing crop for native species, but occurred after *B. tectorum* senescence, and therefore led to underestimates of both the absolute value of *B. tectorum* biomass, and the proportion of total plant biomass made up by *B. tectorum*.

Data were analyzed with repeated measures mixed models in JMP version 11 (SAS Institute, Cary, North Carolina, USA). Models included treatment, year, and their interaction as fixed effects, and block and replicate*treatment as random effects. Treatment-by-year interactions were significant for some variables; therefore, means and standard errors are shown for each year of the study in the figures.

Results

We found no pre-treatment differences in soil total P or N (1993; Fig. 1). In the first three years following treatment application, shallow soil (0–7.5 cm) P increased sevenfold with composted manure treatment, threefold with biosolids, and twofold with fresh manure relative to control plots (Table 3). This relates to the high initial P concentration in these amendments (Table 2). Treatments also significantly increased total soil N. Although pairwise differences (Tukey's HSD) were not significant, total soil N was 21% and 16% higher with biosolids and composted manure, respectively, relative to control plots. Application of fresh manure appeared to have little effect on soil N.

Among years in which above-ground biomass was harvested, 1994, 1996, and 1997 (and to a lesser degree 1993) had lower than normal growing season precipitation (embedded in Fig. 2). Years 1995 and 2010 were near the average precipitation, and 2015 was wetter than normal. Both total above-ground biomass and biomass of all species other than *Bromus tectorum* displayed year by treatment interactions: Treatment effects were significant only early in the study, in 1993 and 1995 (Table 3, Fig. 2).

Bromus tectorum invaded the experiment progressively, being observed in 7, 5, 21, and 24 plots in 1995, 1997, 2010, and 2015, respectively. Patterns of invasion, with the northern block containing more plots occupied by *B. tectorum* (four, three, eight, and eight plots in the same years, respectively), and greater *B. tectorum* biomass in all years (60%, 85%, 55%, and 46% of total *B. tectorum* biomass, respectively), suggest that the seed source may have been a population on the hill to the north of the experiment. It is also possible that *B. tectorum* seeds could have been introduced in the organic waste amendments. However, there was no evidence that *B. tectorum* presence was initially associated with one or more organic waste treatments. Rather, the few plots containing *B. tectorum* early in the study included all treatments. *Bromus tectorum* was most abundant in 2015, likely due to both progressive invasion and a very wet winter and spring (415 mm). In that year, it made up an average of 14% of the total plant biomass.

Organic waste application significantly increased *B. tectorum* biomass production across years (Table 3, Fig. 2). Although trends toward

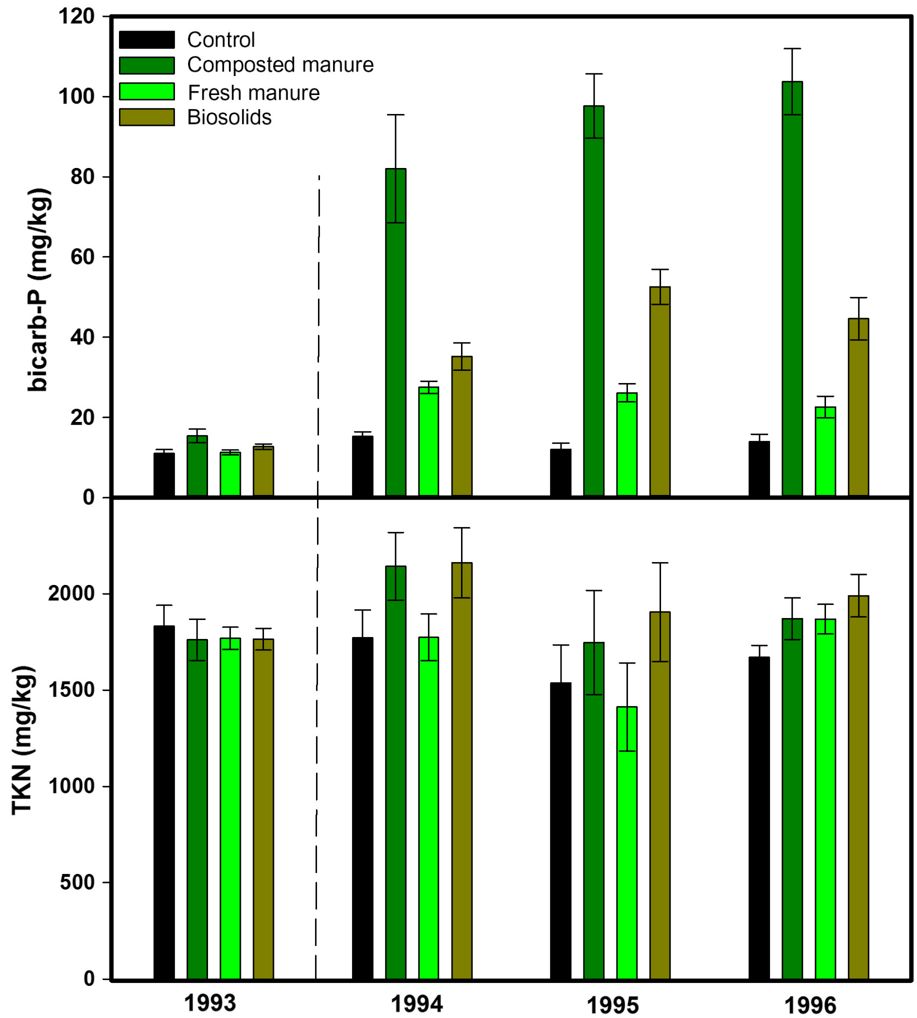

Fig. 1. Mean and standard error of soil N (total Kjeldahl nitrogen, TKN) and P (bicarbonate-extracted P) in the 0–7.5 cm depth prior to organic waste application (1993), and in three subsequent years. Treatment effects in the three post-treatment years were significant for both soil P and soil N. Soil N varied significantly among years, and treatment-by-year interactions were not significant for either soil P or soil N (Table 3). Tukey's HSD tests ($P < 0.05$) were conducted among treatments across all years, due to the lack of treatment-by-year interactions (for P, composted manure > biosolids > fresh manure > control; for N, pairwise differences were not significant).

Table 3. Mixed-model results for soil and plant responses to organic waste applied to native mixed-grass prairie in southeastern Wyoming.

	Total biomass		*Bromus tectorum* biomass		Non-*B. tectorum* biomass		Soil P		Soil N	
	F_{df}	*P*	F_{df}	*P*	F_{df}	*P*	F_{df}	*P*	F_{df}	*P*
Treatment	$4.9_{3,18}$	**0.012**	$5.1_{3,18}$	**0.01**	$4.5_{3,18}$	**0.016**	$163_{3/18}$	**0.0001**	$3.4_{3,18}$	**0.040**
Year	$105_{6,120}$	**<0.0001**	$103_{6,120}$	**<0.0001**	$60_{6,120}$	**<0.0001**	$0.33_{2/40}$	0 .73	$3.8_{2,40}$	**0.030**
Trt. × year	$3.6_{18,120}$	**<0.0001**	$1.3_{18,120}$	0.18	$4.0_{18,120}$	**<0.0001**	$0.62_{6,40}$	0 .72	$0.38_{6,40}$	0.89

Note: Significant *P*-values (<0.05) are listed in bold.

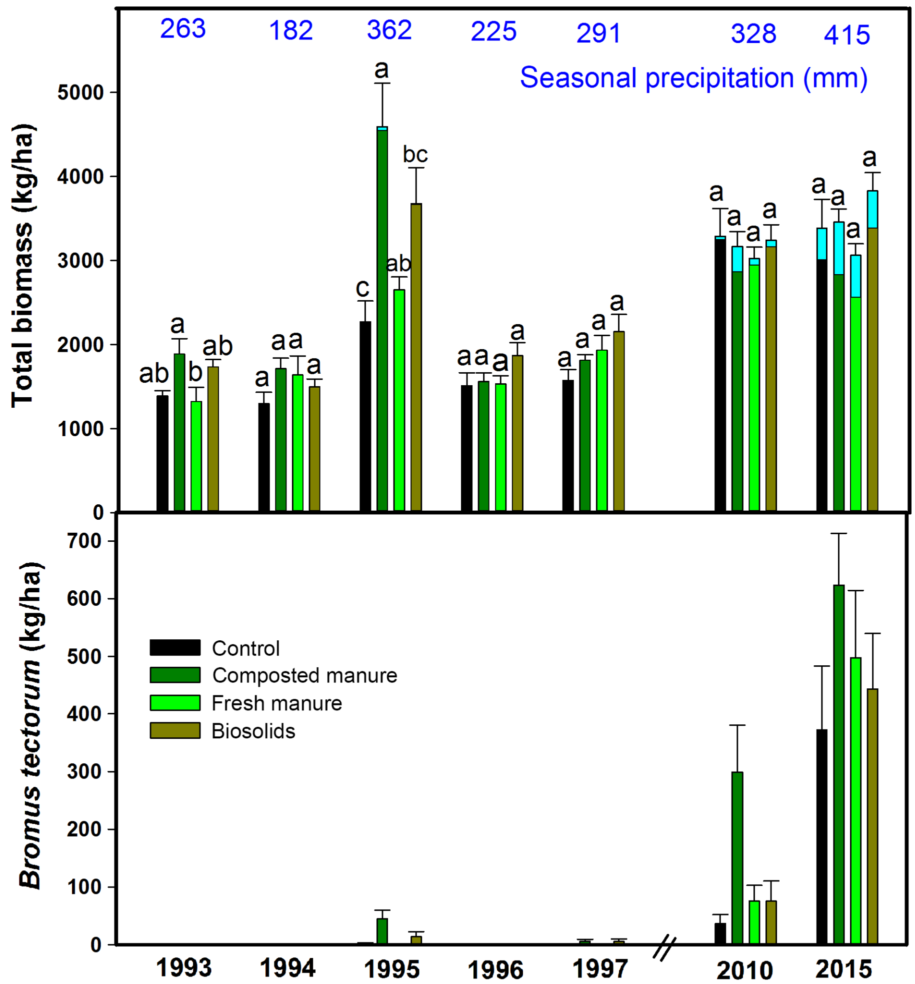

Fig. 2. Total above-ground biomass (with the proportion made up by *Bromus tectorum* shaded blue) and *B. tectorum* above-ground biomass as a function of organic waste treatment. Treatment and year effects were significant for both total biomass, and *B. tectorum* biomass, while treatment-by-year interactions were significant for total biomass (Table 3; Tukey's HSD tests conducted by year, with different letters indicating significant differences among means) but not *B. tectorum* biomass (Tukey's HSD tests conducted among treatments across all years: composted manure > control). Seasonal precipitation, listed in the top panel above each year, includes records from 1 January to 31 July. Note that *B. tectorum* was harvested after senescence and its absolute biomass and proportional biomass are therefore underestimated here. *B. tectorum* biomass was not recorded separately from other biomass categories in 1993, 1994, or 1996, and these years should be viewed as containing missing data rather than zero biomass production.

higher *B. tectorum* biomass with organic waste were observed for all treatments, in pairwise comparisons only composted manure differed significantly from the control. The absolute size of the *B. tectorum* biomass response to composted manure was much larger in the final two years of the study (Fig. 2), but large proportional responses were present in every year in which *B tectorum* was observed, leading to a non-significant treatment-by-year interaction (Table 3).

Discussion

The western Great Plains contain the largest tracts of intact grassland in North America (Samson et al. 2004), and nutrient-rich organic waste is commonly applied within the region (Sullivan et al. 2006). This experiment was designed to test the efficacy of organic waste amendments for increasing forage production. Production was indeed increased by the composted manure and biosolid amendments in 1995, two years after treatment application. This early increase in productivity of native rangeland plants, however, gave way to persistent increases in *Bromus tectorum*. Composted manure increased *B. tectorum* biomass in all years in which the species was recorded (2, 4, 17, and 22 yr after treatment). In 2010 and 2015, *B. tectorum* biomass was 800% and 67% greater with composted manure, respectively, while total plant productivity in plots treated with composted manure was similar to that in control plots. Effects of biosolids and fresh manure on *B. tectorum* were less clear. Although trends toward higher *B. tectorum* biomass with these amendments suggested the potential for them to promote *B. tectorum* invasion, the differences were not significant. Note that such negative results should be treated with caution given the high spatial variability, and therefore statistical uncertainty, resulting from the naturally occurring spread of *B. tectorum*. Further study would be helpful to understand why different types of organic waste can have different effects on *B. tectorum*.

These results demonstrate that composted manure addition can facilitate *B. tectorum* invasion even in relatively invasion-resistant grassland in the western Great Plains. Notably, invasion increased with nutrient addition rates that were low (for N) or similar (for P) to previous studies (Table 1), including a study in a shortgrass steppe ecosystem similar to the mixed-grass prairie studied here (Sullivan et al. 2006). Thus, organic waste application rates previously considered to be safe for increasing forage production and quality in the western Great Plains may increase susceptibility of these ecosystems to invasion.

To our knowledge, this is only the second organic waste amendment study more than 20 yr long (Paschke et al. 2005). While proportional effects of composted manure on *B. tectorum* were similar across years, absolute *B. tectorum* cover increased over time, leading to much larger absolute effects of the composted manure addition later in the study. It is also important to note that sampling was conducted after *B. tectorum* senescence in all years, leading to an underestimate of *B. tectorum* biomass production, greater than 40% of which can be seed mass (Blumenthal et al. 2016). Temporal trends in treatment effects were likely due to a combination of progressive invasion of the site and higher precipitation in 2010 and 2015. Progressive invasion of the site may have occurred naturally, or may have been accelerated by seed rain from more heavily invaded composted manure plots. Both progressive invasion of the site and treatment effects could also have been influenced by other processes, such as grazing management or changing climate, both of which can affect plant invasion in this ecosystem (Harmoney 2007, Blumenthal et al. 2012, 2016, Prevey and Seastedt 2014). These temporal patterns demonstrate that invasion can take considerable time to become apparent following composted manure addition to otherwise undisturbed perennial grasslands. They also demonstrate that the influence of composted manure on invasion is not ephemeral, but rather can become more pronounced over decadal time scales.

Studies to date suggest that where *B. tectorum* is present (three out of three cases), it is likely to respond positively to organic waste amendments (Table 1). Over short time frames, low propagule pressure may limit invasion following waste application. The fact that we observed the largest treatment effects decades into this study, however, suggests that lack of initial propagule pressure does not equate to lack of invasion risk. Given the difficulty of excluding invasive species propagules, the best method for limiting invasion risk in the context of organic waste application may be to limit the nutrient concentrations of the wastes applied. For example, nutrient-rich organic waste can be mixed with high C:N organic waste, such as wood chips, leading to nutrient immobilization (Borden and Black 2011). Addition of high C:N organic matter alone can often inhibit invasive species (Perry et al. 2010), suggesting that such mixtures could potentially increase soil organic matter while having smaller effects on nutrient availability and therefore invasion (Borden and Black 2011, Ryals et al. 2016).

Our results are in accord with what is known about N and P effects on both *B. tectorum* and semi-arid grasslands. Field and greenhouse studies suggest that increases in N and P can facilitate

B. tectorum growth, reproduction, and competitive ability (Dakheel et al. 1993, Lowe et al. 2003, Chambers et al. 2007, Adair et al. 2008, Cherwin et al. 2009, James et al. 2011, Concilio et al. 2013, Belnap et al. 2016). Because *B. tectorum* is an annual, shallow soil resources such as those resulting from surface application of organic waste can be particularly important to its success (Belnap et al. 2016). Addition of non-organic forms of N and P has also been found to increase the susceptibility of semi-arid Great Plains grasslands to invasion (Lauenroth et al. 1978, Milchunas and Lauenroth 1995, Paschke et al. 2000, Blumenthal et al. 2008, Blumenthal 2009, Cherwin et al. 2009).

The relative importance of N vs. P in this study was not clear. While N is the primary limiting nutrient at the site, soil P in the control plots was relatively low for rangeland soils (13 mg/kg) and could also have limited plant productivity, including that of *B. tectorum* (Whalen et al. 2003, Cherwin et al. 2009, Dijkstra et al. 2012, Concilio et al. 2013). Furthermore, the composted manure had proportionally larger effects on soil P than on soil N (721% vs. 16% increases, respectively). The composted manure treatment also had larger effects on soil P than did the other two treatments, which may explain its stronger effects on *B. tectorum*. Finally, P is quite immobile in soil and likely remained in the upper layer where it would be available to shallow-rooted *B. tectorum*. We speculate that the combination of N enrichment and P enrichment that comes with organic waste amendment may be particularly advantageous to *B. tectorum* competing against slower-growing native species.

More broadly, these results contribute to a growing body of work showing that nutrient enrichment of native grasslands, including organic waste addition, can increase competitiveness of invasive relative to native species (Lauenroth et al. 1978, Seabloom et al. 2003, Borden and Black 2011, Newman et al. 2014). Many invasive species thrive under conditions of high nutrient availability (Davis et al. 2000, Gonzalez et al. 2010, Perry et al. 2010), due to traits that enable rapid resource acquisition and growth (Pysek and Richardson 2007, Blumenthal et al. 2009, Leishman et al. 2010, Penuelas et al. 2010, van Kleunen et al. 2010). In contrast, relatively slow-growing native species that dominate many nutrient- and water-limited grasslands are often less able to take advantage of increases in resource supply (Lauenroth et al. 1978, Chapin 1980, Tilman 1990). For example, in 37 widely distributed grasslands of the Nutrient Network experiment, both N and P addition increased the cover of exotic relative to native species (Seabloom et al. 2015). Consequently, the addition of nutrient-rich organic waste to nutrient-poor grasslands should be expected to promote invasion when invasive plant propagules are present.

The long-term ecological impacts of *B. tectorum* invasion following organic waste addition could be substantial. As a forage, *B. tectorum* is available only in the early spring and is unreliable among years due to its variable productivity (Haferkamp et al. 2001, Rice 2005). *Bromus tectorum* can also negatively influence plant diversity, wildlife, and carbon storage (Melgoza et al. 1990, Rice 2005, Bradley et al. 2006, Germino et al. 2016).

Notably, some likely impacts of *B. tectorum* invasion would directly counteract common goals of organic waste addition. For example, the treatment-by-year interaction we observed for biomass of species other than *B. tectorum* indicated a shift from positive to negative effects on biomass over time (Fig. 2). Thus, *B. tectorum* invasion may ultimately lead to reduced productivity of desirable forage species in areas treated with composted manure relative to untreated rangeland. Similarly, the combination of biosolid addition and invasion led to substantial reductions in productivity of desirable species in both restored sagebrush steppe in Utah, and established grassland in British Columbia (Borden and Black 2011, Newman et al. 2014). Over time, therefore, invasion has the potential to increase the costs relative to the benefits of nutrient-rich organic waste amendments in native rangelands.

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