

Long-term population dynamics of seeded plants in invaded grasslands

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Abstract. In recent decades, dozens of studies have involved attempts to introduce native and desirable nonnative plant species into grasslands dominated by invasive weeds. The newly introduced plants have proved capable of establishing, but because they are rarely monitored for more than four years, it is unknown if they have a high likelihood of persisting and suppressing invaders for the long term. Beyond invaded grasslands, this lack of long-term monitoring is a general problem plaguing efforts to reintroduce a range of taxa into a range of ecosystems. We introduced species from seed and then periodically measured plant abundances for nine years at one site and 15 years at a second site. To our knowledge, our 15-year data are the longest to date from a seeding experiment in invaded, never-cultivated grassland. At one site, three seeded grasses maintained high densities for three or more years, but then all or nearly all individuals died. At the second site, one grass performed similarly, but two other grasses proliferated and at least one greatly suppressed the dominant invader (*Centaurea maculosa*). In one study, our point estimate suggests that the seeded grass *Thinopyrum intermedium* reduced *C. maculosa* biomass by 93% 15 years after seeding. In some cases, data from three and fewer years after seeding falsely suggested that seeded species were capable of persisting within the invaded grassland. In other cases, data from as late as nine years after seeding falsely suggested seeded populations would not become large enough to suppress the invader. These results show that seeded species sometimes persist and suppress invaders for long periods, but short-term data cannot predict if, when, or where this will occur. Because short-term data are not predictive of long-term seeded species performances, additional long-term data are needed to identify effective practices, traits, and species for revegetating invaded grasslands.

Key words: *Centaurea maculosa*; grassland; herbicide; invasive weed; rehabilitation; reintroduction; revegetation; seeding.

INTRODUCTION

Each year there are hundreds of attempts to establish species in areas where they do not currently exist. The bulk of these efforts aim to reintroduce native species where they have been extirpated (Griffith et al. 1989, Falk et al. 1996), although introductions of desirable nonnative species are not uncommon (e.g., Wilson and McCaffrey 1999, Fowler et al. 2008, Leprieur et al. 2009). Unfortunately, long-term monitoring of (re)introduced species has often been a low priority (Sarrazin and Barbault 1996, Hein et al. 1997). Consequently, little is known about the ability of (re)introduced taxa to persist in most ecosystems.

One system where long-term monitoring has been a particularly low priority is invasive weed-dominated grasslands. In recent decades, dozens of studies have

involved attempts to (re)introduce species into invaded grasslands. In some studies, the goal has been to replace the invaders with diverse native plant communities (e.g., Thompson et al. 2006, Hulet et al. 2010), but the more common goal is to introduce just one or two species capable of suppressing the invader while also providing wildlife cover, forage, and other ecosystem services (e.g., Lym and Tober 1997, Bottoms and Whitson 1998, Davies 2010). In either case, the species have rarely been monitored beyond four years after (re)introduction (e.g., Tyser et al. 1998, Mangold et al. 2007, Mazzola et al. 2008). Data from years five and six are rare (Bottoms and Whitson 1998, Enloe et al. 2005, Joshi 2008), and to our knowledge, only the study of Ferrell et al. (1998) monitored for as long as 10 years after introducing desirable species into an invaded, never-cultivated grassland. A few studies have measured for more than 10 years after seeding in abandoned croplands (Pakeman et al. 2002, Kiehl and Pfenhauer 2007) and disturbed, un-invaded grasslands (Hull 1971, Newman and Redente 2001), but population dynamics of

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(re)introduced species may differ greatly between these systems and never-cultivated grasslands dominated by highly aggressive exotic species.

A portion of sown seeds often germinate and survive the brief monitoring periods typical of (re)introduction studies in invaded grasslands (i.e., 1–3 years; e.g., Lym and Tober 1997, Mangold et al. 2007, Sheley 2007). But sizes of individual plants and plant populations (i.e., individuals per plot) often remain small over the brief monitoring periods (e.g., Masters et al. 2001, Mangold et al. 2007, Sheley et al. 2007, Davies 2010), and the small populations are sensitive to demographic stochasticity and disturbances such as herbivory and drought (Moles and Westoby 2004, Armstrong and Seddon 2008). To meet ecological and land use goals, the small, scattered plants must eventually form large populations capable of persisting without intensive, ongoing human intervention (Griffith et al. 1989). Unfortunately, with so few long-term data, it is unclear if the small, sparsely distributed plants have a reasonable likelihood of persisting and forming large, self-sustaining populations. Floral and faunal (re)introduction efforts are notoriously failure prone across a range of systems (Lyles and May 1987, Falk et al. 1996, Armstrong and Seddon 2008), suggesting these efforts may also be highly failure prone in invaded grasslands. Further suggesting failures may be common is a small number of (re)introduction studies showing seeded plants emerging then dying en masse over a few years in invaded grasslands (Seablom et al. 2003, Jessop and Anderson 2007, Fansler and Mangold 2011).

However, plants do not always die, or even remain small, within a few years of being seeded into invaded grasslands. In fact, several studies report seeded plants rapidly growing large and suppressing grassland invaders (Klemp and Hull 1971, Lym and Tober 1997, Masters and Nissen 1998, Rose et al. 2001). Superficially, this rapid growth would seem to signify well-adapted species capable of persisting, remaining productive, and suppressing invaders for the long term. However, herbicides and/or tillage are routinely used to suppress invaders in the initial phases of these studies, so seeded populations have tended to grow large while experiencing atypically benign competitive environments. In plots that are not seeded, invaders generally recover from herbicides and/or tillage within one to five years (e.g., Lym and Messersmith 1985, Young et al. 1998, Benz et al. 1999). It may be that seeding merely lengthens this time period. Longer studies are needed to determine if seeded populations can continue suppressing invaders over the long term after effects of herbicides, tillage, and other seeding-related disturbances dissipate.

Our first objective was to determine if seeded species could persist at high levels and suppress grassland invaders for 15 years; a longer time period than has been measured to date. Our second objective was to determine if seeded species persistence and weed suppression depended on seeding rate and whether or

not various herbicides were used at the time of seeding. Our third objective was to quantify long-term effects of seeding on biomass of unseeded native species. Finally, our fourth objective was to see if short-term data are at all predictive of long-term (re)introduction outcomes. Because long-term data are lacking, it is unknown if seeded species persisting, or even growing rapidly, over the short term counts as evidence they will persist for the long term in invaded grasslands. If short-term responses to seeding prove to be very different from long-term responses to seeding, then short-term studies will be of limited value, and the need for long-term studies will be paramount. To accomplish our objectives, we remeasured plots of four published seeding studies 9–15 years after seeding.

METHODS

Study sites.—Three of the studies we remeasured (study 1, 2, and 3) began 1995 at a site northeast of Hamilton, Montana, USA (45°53' N, 113°59' W). The studies were separated by about 150 m. The invasive perennial forb *Centaurea maculosa*, along with smaller populations of other exotic species, had largely replaced the site's native bunchgrass-dominated (*Festuca scabrella*, *Pseudoroegneria spicata*) community (Sheley et al. 2001). Study 4 began in 2001 south of Ronan, Montana (47°29' N, 114°5' W) where two invasive perennial forbs (*C. maculosa*, *Potentilla recta*) and several exotic grasses (e.g., *Dactylis glomerata*, *Poa pratensis*) had all but completely replaced the native bunchgrass-dominated (*F. scabrella*, *P. spicata*) community (Sheley et al. 2006). Over the study period, neither site was burned nor grazed by livestock, although the site of studies 1–3 received some winter grazing by wild elk.

Study 1 procedures.—Sheley et al. (1999) factorially combined herbicide (with, without glyphosate), tillage (with, without), and nonnative grass (*Thinopyrum intermedium*) seeding rate (0, 500, 2500, and 12 500 seeds/m²) treatments. The authors measured seeded grass and *C. maculosa* biomass around peak standing crop two years after seeding, and Sheley et al. (2005) remeasured these variables six years after seeding. We remeasured biomass 15 years after seeding around peak standing crop (late July) by randomly placing a 0.44-m² circular frame in each plot, clipping all biomass to ground level, and sorting it into seeded grass, *C. maculosa*, other unseeded exotic (*Agropyron cristatum*, *Alyssum desertorum*, *Bromus inermis*, *Bromus tectorum*, *Poa bulbosa*, *Poa compressa*, *Thinopyrum ponticum*, *Tragopogon dubius*, *Vicia villosa*), and native plant (*Poa secunda*, *Festuca campestris*, *Chamerion angustifolium*) components. Biomass was dried for >48 h and weighed.

Study 2 procedures.—Jacobs et al. (2006) used a drill to apply 18 kg/ha of pure live seed of a nonnative (*T. intermedium*) and native (*P. spicata*) grass. Seeded grass and *C. maculosa* biomass data were gathered from randomly placed 1.0-m² frames five, six, eight, and nine

years after seeding, but Jacobs et al. (2006) do not report the grass data. These data are alongside data we gathered 15 years after seeding using methods described for study 1.

Study 3 procedures.—Sheley et al. (2001) factorially combined three seeded grasses with seven herbicide treatments and a no-herbicide control. A drill was used to apply 6 kg/ha of pure live seed of a native (*P. spicata*) and two nonnatives (*T. intermedium*, *Psathyrostachys juncea*). The authors measured *C. maculosa* and seeded grass biomass two years after seeding. We remeasured biomass 15 years after seeding using methods described for study 1.

Study 4 procedures.—Sheley et al. (2006) factorially combined four seeding rates (0, 977, 1322, 1557 seeds/m²) of a native grass seed mix (*Festuca campestris*, *Festuca idahoensis*, *P. spicata*) with three herbicide treatments (none, 2,4-D, picloram), two seeding treatments (broadcast, no-till drill), and two cover crop treatments (with/without *Triticum aestivum*). The authors measured seeded grass density one and three years after seeding. We remeasured the seeded grasses nine years after seeding using methods described for study 1, except 10 frames per plot were sampled instead of one. Also, we did not remeasure invasive weeds or other nonseeded species because seeded grasses were exceedingly rare and hence would not have detectably impacted the plant community. Of the original 144 plots, we sampled only the 33 plots that did not receive additional treatments (i.e., seeding, herbicides) between three and nine years after seeding.

Analysis.—Our four response variables were biomass of (1) seeded grasses, (2) *C. maculosa*, (3) unseeded exotics (excluding *C. maculosa*), and (4) unseeded natives. The analysis focused on confidence intervals (CIs), which are well-suited for characterizing effect sizes and uncertainty (Hubbard and Lindsay 2008). In the text, mean $\pm x$ indicates the least squares parameter estimate (mean) and the upper (mean + x) and lower (mean - x) bound of the 95% confidence interval. Employing a Bayesian interpretation, if two 95% CIs do not overlap, the probability is >0.95 that the treatment with the larger-valued CI had the largest response (Gelman et al. 2004, Rinella and James 2010). However, the probability can still be >0.95 even where the CIs overlap, because the CIs summarize marginal distributions. When two CIs overlap in the figures and the probability is >0.95 that the treatment with the larger-valued CI had the largest response, we report the CI on the difference between the treatments in the text.

Seeded grass data from study 4 and unseeded exotic and unseeded native data from studies 1–3 contained several zeros and so could not be analyzed with standard parametric statistical models. Therefore, we calculated CIs for these responses using a nonparametric bootstrap algorithm (Dixon 2001). All other CIs were calculated from multiple linear regression models with natural-log-transformed biomass as the response. Where relevant,

the models had terms for years after seeding, replications, herbicides, seeded species, seeding rates, and interactions. Different random error variances were estimated for each seeded grass species in study 2 and 3, because predicted vs. observed graphs suggested more variation for *P. spicata* than for the nonnative grasses.

In study 1, tillage and herbicide terms were excluded from models because they had only minor effects (Sheley et al. 1999, 2005). In study 3, four of the eight herbicide treatments consisted of picloram either alone or combined with other herbicides. These four picloram-containing herbicide solutions were considered to be one treatment, because they produced similar responses (Sheley et al. 2001). Herbicides other than picloram were ineffective against the target invader, so these herbicide treatments were combined with the control for analysis (Sheley et al. 2001). Therefore, the model included picloram terms but excluded terms for the other herbicides and the different picloram rates. In study 4, herbicide and cover crop effects were excluded because they were minor (Sheley et al. 2006). For other exotic and other native responses, one CI was used to describe all three nonzero seeding rates of study 1 and one CI to describe all eight herbicide treatments of study 3, because the individual CIs were similar.

RESULTS

Precipitation.—Precipitation data for weather stations closest to the site of studies 1–3 (Hamilton, Montana) and the site of study 4 (Polson, Montana) suggest study-period averages plus or minus 1.0 study-period standard deviation usually bracketed the long-term average (Fig. 1). Exceptions where the study period appeared to be somewhat drier than the long-term average include September at the site of studies 1–3 and January–March and July at the site of study 2.

Study 1.—Two years after seeding, the seeded grass *T. intermedium* remained sparse, with point estimates suggesting natural log biomass values of about 1.2 regardless of seeding rate (Fig. 2; biomass was measured in g/m²). Exponentiating this point estimate suggests grass biomass was about $e^{1.2} = 3$ g/m². This same calculation for the highest seeding rate six years after seeding suggests seeded grass biomass production increased to $e^{4.2} = 67$ g/m² between two and six years after seeding, and there is strong evidence seeded grasses continued growing between six and 15 years after seeding (Fig. 2). Point estimates for 15 years after seeding suggest seeded plots produced about $e^{5.3} = 200$ g/m² regardless of seeding rate. Because of the small plot size (1.82 m²) and the lack of space between plots, the seeded grass spread from seeded to unseeded plots over the study period (Fig. 2).

Competitive effects of the seeded grass on *C. maculosa* were not evident two and six years after seeding (Fig. 2). Conversely, the seeded grass clearly suppressed *C. maculosa* 15 years after seeding: *C. maculosa* point estimates were 4.1 for the unseeded control compared

to 2.1 for the highest seeding rate (Fig. 2; values are ln-transformed, originally measured in g/m^2). Exponentiating the difference between these point estimates suggests the highest seeding rate reduced *C. maculosa* biomass by $100 - 100e^{(2.1-4.1)} = 86\%$. This is a conservative estimate because the seeded grass had colonized the unseeded controls by 15 years after seeding (Fig. 2). Had this not occurred, the controls would likely have supported more *C. maculosa* biomass.

In study 1, our data were inconclusive regarding effects of seeded grasses on native biomass (Fig. 3, CI overlaps zero), whereas seeded grasses clearly reduced unseeded exotics, with the point estimate suggesting a reduction of $2.5 \text{ g}/\text{m}^2$ (Fig. 3). Exotic biomass was $4.3 \pm 2.1 \text{ g}/\text{m}^2$ in unseeded plots. Point estimates suggest seeding reduced biomass of the exotic group by $100 - 100(4.3-2.5)/4.3 = 58\%$.

Study 2.—Due to large variation among measurement frames, biomass of the seeded bunch-forming *P. spicata* was not precisely estimated (Fig. 4). The large variation occurred because of the patchy distribution of the bunchgrass. Imprecision notwithstanding, CIs suggest *P. spicata* biomass production increased between five and 15 years after seeding (Fig. 4). The CI on the difference between these two years (-3.4 ± 2.8 ; measured as g/m^2 , values have been ln-transformed) confirms *P. spicata* biomass was greater in year 15, with the point estimate suggesting biomass in year five was only $100e^{-3.4} = 3\%$ of biomass in year 15.

Compared to the bunchgrass *P. spicata*, the more evenly distributed rhizomatous *T. intermedium* was more precisely estimated (Fig. 4). *T. intermedium* showed a steady increase in biomass production between five and 15 years after seeding (Fig. 4). The CI on the difference between the year five and year 15 biomass means (-2.6 ± 0.4 ; ln-transformed values) suggests *T. intermedium* biomass in year five was only $100e^{-2.6} = 7\%$ of that in year 15.

The data do not provide strong evidence *P. spicata* reduced the invader *C. maculosa* in any year, whereas *T. intermedium* clearly reduced the invader 15 years after seeding (Fig. 5). *T. intermedium* reduced the invader eight and nine years after seeding as well: CIs on the biomass difference between *T. intermedium*-seeded and unseeded treatments for eight (-0.9 ± 0.7 ; ln-transformed) and nine (-0.8 ± 0.7) years after seeding do not overlap zero. Point estimates suggest *T. intermedium* reduced invader biomass by 59%, 55%, and 92%.

In study 2, both seeded grasses reduced unseeded native biomass, with point estimates suggesting reductions of $15\text{--}20 \text{ g}/\text{m}^2$ (Fig. 3). The data were inconclusive regarding effects of seeded grasses on unseeded exotics.

Study 3.—Two years after seeding, the seeded grass *P. juncea* was detected only where picloram had been applied, and here it yielded 1.0 ± 1.0 (ln-transformed biomass). Fifteen years after seeding, *P. juncea* was not detected in any plots.

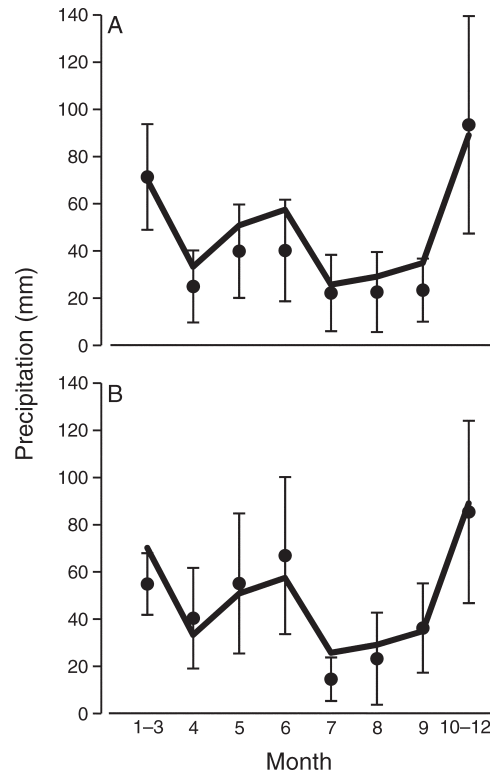


FIG. 1. Western Montana precipitation data from the site of (A) studies 1–3 and (B) the site of study 4. Presented are 94-year averages (solid lines) and the averages (dots) and standard deviations (vertical bars) over the study periods. The study periods were (A) 2001–2010 and (B) 1995–2010. The horizontal axis gives months of the year with January–March (1–3) and October–December (10–12) grouped together.

As with *P. juncea*, *P. spicata*, and *T. intermedium* were detected two years after seeding only where picloram had been applied (Fig. 6). Conversely, *P. spicata* and *T. intermedium* were present in all plots 15 years after seeding. As was the case in study 2, *P. spicata* abundances were more variable than *T. intermedium* abundances in study 3. Fig. 6 CIs suggest seeded grasses biomass production was greater where picloram had been applied 15 years earlier, compared to where it had not been applied. In the case of *T. intermedium*, the CI on the biomass difference between untreated and picloram-treated plots (-0.5 ± 0.4 ; ln-transformed) confirms this grass produced more biomass where the herbicide had been applied. The point estimate suggests *T. intermedium* biomass was $100e^{-0.5} = 40\%$ lower where picloram had not been applied.

P. spicata did not demonstrably suppress *C. maculosa* during either sampling year (Fig. 7). Two years after seeding, *T. intermedium* did not conclusively suppress *C. maculosa*, but 15 years after seeding, this grass greatly suppressed the invader where picloram had been applied (Fig. 7).

Both seeded grasses caused small reductions in unseeded native biomass in study 3, with point estimates

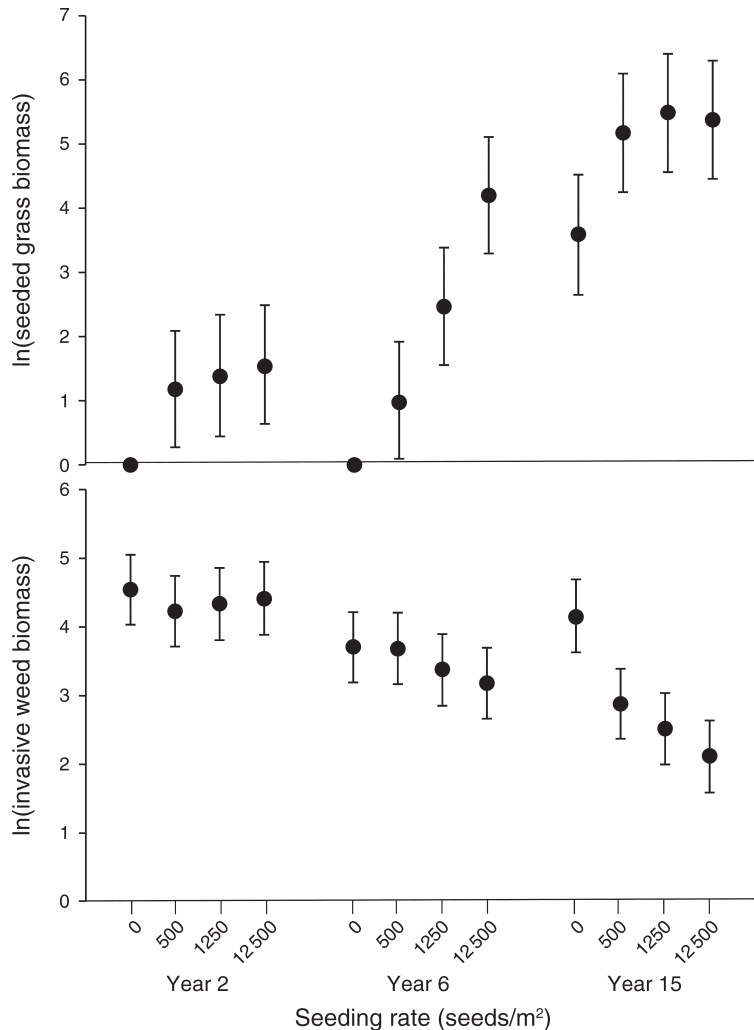


FIG. 2. Seeded grass biomass (measured as g/m^2) and effects of the seeded grass on *C. maculosa* biomass (measured as g/m^2) in study 1. Point estimates (dots) and 95% CIs (bars) estimate invasive weed (*Centaurea maculosa*) and seeded grass (*Thinopyrum intermedium*) biomass 2, 6, and 15 years after seeding the nonnative grass. The horizontal axis shows seeding rates (seeds/m^2).

suggesting reductions of about 6 g/m^2 (Fig. 3). Native grass biomass was low ($9 \pm 4.2 \text{ g/m}^2$) in unseeded plots. The point estimates suggest seeded grasses reduced unseeded native biomass by $100 - 100(9-6)/9 = 67\%$. The data were inconclusive regarding effects of seeded grasses on unseeded exotics (Fig. 3).

Study 4.—Native grass densities one year after no-till drill seeding at low, medium, and high rates were 32 ± 14 , 63 ± 14 , and $132 \pm 42 \text{ plants/m}^2$, respectively. Corresponding densities for broadcast seeding were 23 ± 14 , 28 ± 10 , and $30 \pm 10 \text{ plants/m}^2$. Seeded grass densities remained high, and in some treatments became higher, by three years after seeding (Sheley et al. 2006).

Nine years after seeding, no seeded grasses were observed in 20 of 31 seeded plots that were sampled, and only trace quantities were observed in the other 11 plots. Fig. 8 suggests mean seeded grass biomass was less than 3 g/m^2 regardless of treatment. This quantity is clearly

trivial given that biomass production can exceed 1000 g/m^2 at the site (Sheley et al. 2006). The CIs for unseeded and seeded plots overlap, suggesting the sampled seeded species occurred naturally, not in response to seeding (Fig. 8).

DISCUSSION

Two of our study's seeded grasses (*T. intermedium* and *P. spicata*) proved capable of persisting at high levels 15 years after seeding (Figs. 2, 4, 6), and at least one of these grasses (*T. intermedium*) greatly suppressed the invader (Fig. 2, 5, 7). Moreover, we observed prolonged upward trends in grass production that lead us to believe these (re)introduced grasses may continue proliferating and displacing the invader well beyond 15 years (Figs. 2, 4). Bolstering this belief is the finding that *T. intermedium* spread ($\sim 2 \text{ m}$) to plots where it was not sown in study 1 (Fig. 2). We interpret the ability of this

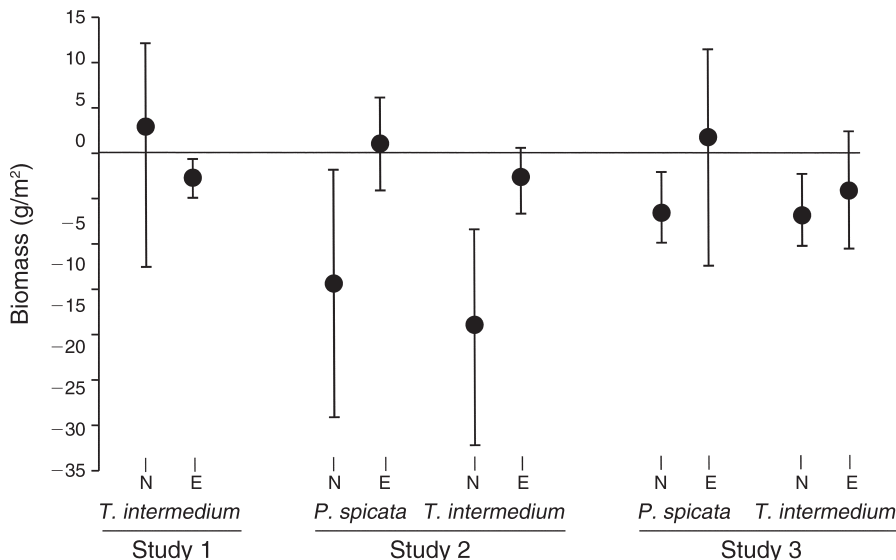


FIG. 3. Effects of seeded grasses on unseeded natives and exotics in studies 1–3. Point estimates (dots) and 95% CIs (bars) estimate effects of the seeded grasses *Thinopyrum intermedium*, *Pseudoroegneria spicata*, and *Thinopyrum intermedium* on biomass of unseeded natives (N) and unseeded exotics excluding *Centaurea maculosa* (E). Data were gathered 15 years after seeding. CIs estimate the difference between seeded and unseeded treatments (seeded minus unseeded), so, for example, a point estimate of -14 for the N group suggests seeding reduced native biomass by 14 g/m^2 .

grass to spread as a sign its populations can be self-sustaining in *C. maculosa*-infested grasslands. As with the nonnative *T. intermedium*, our study also suggests the native *P. spicata* may be capable of spreading, and thus forming self-sustaining populations, in *C. maculosa*-infested grasslands. In study 3, *P. spicata* quickly established from sown seed in plots sprayed with picloram, but this grass appeared to fail to establish from sown seed in unsprayed plots (Fig. 6). This suggests the *P. spicata* we observed in unsprayed plots

late in the study was a consequence of spread from sprayed plots. However, we cannot completely rule out the possibility that *P. spicata* gradually established from seeds that were sown in the unsprayed plots, not spread from sprayed plots, over the study period.

Similar to our study, Ferrell et al. (1998) also tracked *T. intermedium* introductions for an extended period in grassland infested by an invasive perennial forb (i.e., *Euphorbia esula*). From six to 10 years after seeding, *T. intermedium* cover estimates changed from 62% to 72%

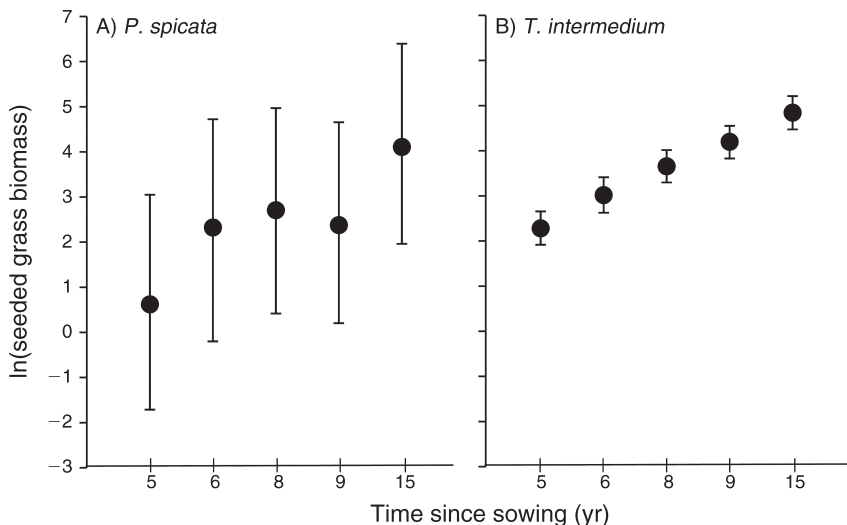


FIG. 4. Seeded grass biomass (measured as g/m^2) in study 2. Point estimates (dots) and 95% CIs (bars) estimate nonnative (*Thinopyrum intermedium*) and native (*Pseudoroegneria spicata*) grass biomass 5, 6, 8, 9, and 15 years after the grasses were sown into *Centaurea maculosa*-infested grasslands.

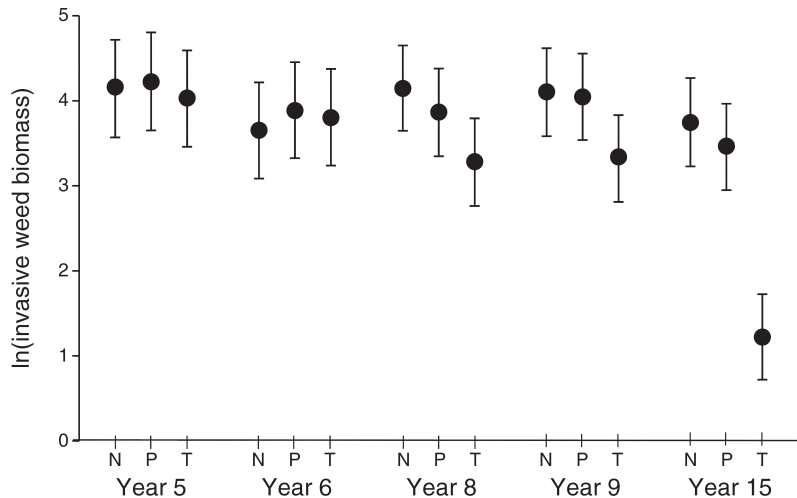


FIG. 5. Effects of seeded grasses on *Centaurea maculosa* biomass (measured as g/m^2) in study 2. Point estimates (dots) and 95% CIs (bars) estimate biomass of the invasive *Centaurea maculosa* 5, 6, 8, 9, and 15 years after sowing no grass (N), a native grass (*Pseudoroegneria spicata*; P), or a nonnative grass (*Thinopyrum intermedium*; T).

in tilled plots and from 52% to 49% in untilled plots (Ferrell et al. 1998). Combined with our study, these values show *T. intermedium* can persist at high levels alongside *E. esula* and *C. maculosa*, two of the most aggressive invaders of North American grasslands. Additionally, *T. intermedium* can competitively suppress both these invaders. In the Ferrell et al. (1998) study, point estimates for 10 years after seeding suggest *T. intermedium* reduced *E. esula* cover by 51% in tilled plots

and by 29% in untilled plots. In our study, point estimates suggested *T. intermedium* can reduce *C. maculosa* biomass by more than 90% (Figs. 5, 7).

In contrast to *T. intermedium* and *P. spicata*, *P. juncea* in study 3 and all seeded grasses in study 4 illustrate that seeded species can establish but then fail to persist in invasive weed-dominated grasslands. Several other studies also demonstrate failures of seeded species to persist (Lym and Tober 1997, Ferrell et al. 1998,

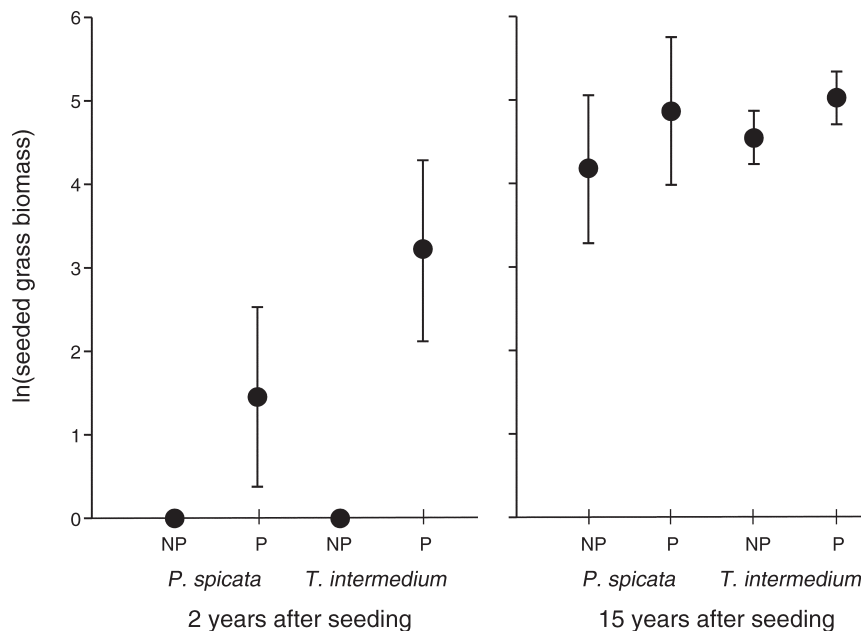


FIG. 6. Seeded grass biomass (measured as g/m^2) in study 3. Point estimates (dots) and 95% CIs (bars) estimate biomass of a native (*Pseudoroegneria spicata*) and nonnative (*Thinopyrum intermedium*) grass 2 and 15 years after they were sown into plots treated (P) and not treated (NP) with the herbicide picloram.

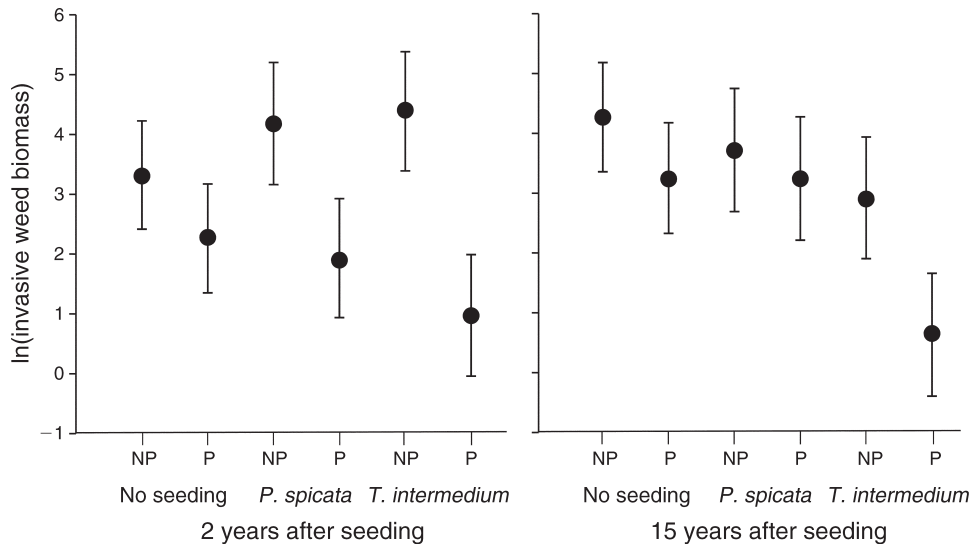


FIG. 7. Effects of seeded grasses on *Centaurea maculosa* biomass (measured as g/m^2) in study 3. Point estimates (dots) and 95% CIs (bars) estimate biomass of the invasive *Centaurea maculosa* 2 and 15 years after applying (P) or not applying (NP) the herbicide picloram and sowing of a native grass (*Pseudoroegneria spicata*), a nonnative grass (*Thinopyrum intermedium*), or no grass.

Masters and Nissen 1998, Wilson et al. 2004). Compared to *T. intermedium* and *P. spicata*, *P. juncea* appears to be a generally less effective species for revegetating invaded grasslands. In the Ferrell et al. (1998) study, *P. juncea* cover estimates decreased from 59% to 19% in tilled plots and from 49% to 0% in untilled plots between six and 10 years after seeding. In both our study and the Ferrell et al. (1998) study, it appears that herbicidal control of the invader promoted *P. juncea* establishment, but this grass could not maintain productive stands or prevent reinvasion after herbicide ceased suppressing the target invader. Collectively, data from these two long-term studies suggest some revegetation species may consistently outperform others in invaded grasslands.

Data from our study provide a rare glimpse into long-term effects of seeding on naturally occurring native species (Fig. 3). There is concern that seeding practices and competition from seeded species may greatly reduce biomass of naturally occurring native populations (Cox and Anderson 2004). However, seeding cannot greatly reduce resident native biomass when it is already very low, as was the case in our study and similar studies (Masters et al. 2001, Rose et al. 2001). Yet, native biomass reductions of even the small magnitudes we observed could be concerning in cases where the natives are rare, threatened, or endangered (Fig. 3).

Disturbances associated with seeding (i.e., herbicides, tillage) can reduce invader populations to a small fraction of carrying capacity (Rice et al. 1997, Lym 2000), and seeded populations are also often far from carrying capacity for a period of years after seeding. According to competition models (Lotka 1925, Huston and Smith 1987), which have been successfully used to

describe plant population dynamics (e.g., Freckleton and Watkinson 2001, Rinella and Sheley 2005), population sizes change rapidly until they equilibrate at carrying capacity. This implies the less transient, longer-lasting effects of seeding on relative plant abundances cannot be assessed until the species reach carrying capacity. And it can take a long time to reach carrying capacity: Point estimates of Ferrell et al. (1998) suggest large changes in relative species abundances were still occurring later than six years after seeding, and our data provide strong evidence for large changes later than two, five, six, eight, and nine years after seeding (Figs. 2, 4–

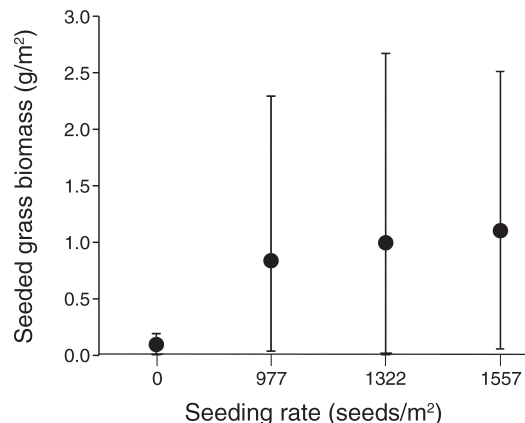


FIG. 8. Seeded grass biomass (measured as g/m^2) in study 4. Point estimates (dots) and 95% CIs (bars) estimate biomass of the native grasses *Festuca campestris*, *Festuca idahoensis*, and *Pseudoroegneria spicata* nine years after a mix of these species was sown into invasive weed-infested grasslands. The horizontal axis shows native grass seeding rates.

7). Our data do, however, suggest abundances may have stabilized at carrying capacity by 15 years after seeding in some cases. In particular, although different seeding rates resulted in a range of seeded grass biomass levels in year six, the different seeding rates appeared to converge at the same seeded grass carrying capacity by year 15 (Fig. 2). Also, although plots treated with different herbicides had much different seeded grass biomass levels in year two, they appeared to be converging at the same carrying capacity by year 15 (Fig. 6). It appears more than a decade is sometimes required to characterize the relatively stable, lasting effects of seeding on invaded grasslands.

Short-term studies can identify effective methods for (re)establishing species in ecosystems (Colas et al. 2008, James and Svejcar 2010). However, our data and those of Ferrell et al. (1998) illustrate that data from short-term studies do not reliably predict the long-term outcomes of (re)introduction efforts in invaded grasslands. While Ferrell et al. (1998) observed two seeded grasses persisting at high abundances in the short term, in the long term, one of these grasses became rare in tilled plots and likely extinct in untilled plots. Similarly, although early results were promising for three species at one site (Sheley et al. 2006) and for *P. juncea* at another site (Sheley et al. 2001), our remeasurement showed these species nearly or completely failed to persist. While some species failed to persist, others gradually flourished. For example, point estimates suggest *T. intermedium* and *P. spicata* made up only 4% and 6% of total biomass, respectively, two years after they were seeded. Corresponding estimates for 15 years after seeding were 90% and 73%. In summary, newly established species can go on to express the entire gamut of outcomes, from extinction to dominance, and short-term data have no clear value for predicting which of these outcomes will occur.

Our results show (re)introductions can sometimes shift invaded grasslands toward more desirable states over the long term, at least in terms of native biomass production and wildlife and livestock forage production (Thompson 1996). However, because there are so few long-term data, it is not at all clear if applying a given seeding practice to a given site is likely to result in highly abundant seeded species capable of persisting and suppressing invaders over the long term. Factors determining if, when, and where seeded species will flourish over the long term include environmental conditions and seeding techniques as well as traits of both the invader(s) and the seeded species. It will be necessary to manipulate these factors and then measure plant responses over long time spans in order to identify consistently effective seeding practice. Our data suggest species (re)introductions can sometimes be an effective tool for managing invasive weeds in grasslands, but more long-term data will be needed to develop consistently effective (re)introduction programs.

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