Biol Invasions (2010) 12:3187–3194
DOI 10.1007/s10530-010-9710-2

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ORIGINAL PAPER

Non-native competitive perennial grass impedes the spread of an invasive annual grass

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Received: 8 May 2009 / Accepted: 27 January 2010 / Published online: 6 February 2010

Abstract Invasive plants are degrading wildlands around the globe by displacing native species, reducing biodiversity, and altering ecological functions. The current approach of applying herbicides to invasive plants in wildlands has not been effective at curtailing their expansion and, in certain circumstances, may do more harm than good. Preventing the spread of invasive species has been identified as an important strategy to protect wildlands. However, few prevention strategies have actually been tested. We hypothesized that establishing competitive vegetation next to infestations would increase the biotic resistance of the plant community to invasion and decrease the invasive species propagule pressure beyond the competitive vegetation. To evaluate this, we established twelve competitive vegetation barriers in front of invasive annual grass, *Taeniatherum caput-medusae* (L.) Nevski, infestations. The non-native perennial grass *Agropyron desertorum* (Fisch. ex Link) Schult. was seeded into plant communities adjacent to the infestations to create the competitive vegetation barriers. Soil nutrient concentrations and the spread of *T. caput-medusae* were compared between where *A. desertorum* was seeded and not seeded (control treatment) 3 years after treatment. Less *T. caput-medusae* and lower soil ammonium and potassium concentrations in the competitive vegetation barrier than control treatment ($P \leq 0.01$) suggest that establishing competitive vegetation increased the biotic resistance of the plant communities to invasion. *Taeniatherum caput-medusae* cover and density in the plant communities protected by the competitive vegetation barrier (locales across the barriers from the infestations) were ~42- and 47-fold less, respectively, than unprotected plant communities ($P < 0.01$). This suggests that invasive plant propagule pressure was decreased in the plant communities protected by competitive vegetation barriers. The establishment of competitive vegetation around infestations may be an effective strategy to prevent or at least reduce the spread of invasive plant species.

Keywords Biotic resistance · Invasibility · Medusahead · Prevention · Propagule pressure

Introduction

Invasive plants are decreasing biodiversity, reducing productivity, degrading wildlife habitat, and altering ecological functions of wildlands around the world

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(Randall 1996; DiTomaso 2000; Masters and Sheley 2001; Kolb et al. 2002; Davies and Svejcar 2008). Restoration of plant communities invaded by exotic plant species is expensive and rarely successful (Vitousek et al. 1997; D′Antonio and Meyerson 2002). Restoration is often impeded by a lack of native plant propagules (Davies and Svejcar 2008), persistent exotic plant seed bank (D′Antonio and Meyerson 2002), and/or invasive plant induced alterations to site characteristics (Cronk and Fuller 1995; D′Antonio and Meyerson 2002). Efforts to control invasive plants have in certain situations exacerbated the negative impacts of invader (Pearson and Callaway 2008). Thus, Davies and Johnson (2009) suggested that more efforts need to be directed at preventing exotic plant invasions.

To prevent continued invasion, efforts need to be developed, based on the ecology of invasion, to containing established invasive plant infestations and improving the biotic resistance of non-invaded plant communities to exotic plant invasion. However, information critical to accomplishing these tasks is limited. Davies and Sheley (2007) demonstrated that maintaining neighboring vegetation taller than the invasive plant species could potentially reduce invasive plant propagule pressure by limiting dispersal of invasive plant seeds. Applying herbicides or defoliating invasive plants at the edge of infestations has been suggested to potentially decrease propagule pressure in locations adjacent to infestations and reduce invasive plant spread (Sheley et al. 1999; Davies and Johnson 2009), but has not been tested. Establishing competitive vegetation around invasive plant infestations may be an effective strategy to limit the spread of invasive plants. Establishing competitive vegetation could increase the biotic resistance of the plant communities immediately adjacent to established infestations thereby increasing the distance between invasive plants and plant communities at risk of invasion. Most seeds disperse relatively close to their parent populations (Harper 1977; Fenner 1985; Davies 2008); therefore, increasing the distance between infestations and areas susceptible to invasion may decrease the rate of invasion by decreasing invasive plant propagule pressure. Furthermore, if the established vegetation increases the height and/or amount of horizontal obstruction, invasive plant propagule pressure could be reduced by interception of dispersing propagules. Physical interception of seeds by neighboring vegetation can reduce seed dispersal of invasive plant species (Davies and Sheley 2007).

To investigate the potential for competitive vegetation to reduce the spread of invasive plants, we evaluated the ability of a competitive perennial bunchgrass to reduce the establishment and spread of *Taeniatherum caput-medusae* (L.) Nevski (medusahead). *Taeniatherum caput-medusae* is an exotic annual grass that reduces biodiversity, degrades wildlife habitat, and reduces forage production on native wildlands (Davies and Svejcar 2008). *Taeniatherum caput-medusae* can out-compete native vegetation because it initiates growth earlier and acquires more resources than many native plants (James et al. 2008; Young and Mangold 2008). Litter from *T. caput-medusae* has a slow decomposition rate allowing it to build up over time and stifle out desirable native plants (Bovey et al. 1961; Harris 1965).

A non-native perennial bunchgrass, *Agropyron desertorum* (Fisch. ex Link) Schult. (desert wheatgrass), was selected for the competitive vegetation barrier because perennial bunchgrasses are critical to preventing exotic annual grass invasions (Davies 2008; James et al. 2008) and bunchgrasses dominate the herbaceous understory in these native plant communities (Davies et al. 2006). *Agropyron desertorum* was also selected because it has broad ecological amplitude and subsequently it, combined with *A. cristatum* (L.) Gaertn. (crested wheatgrass), are grown on more than 6 million ha in the United States and Canada (Mayland et al. 1992). *Agropyron desertorum* also begins rapid growth early (Eissenstat and Caldwell 1987; Aguirre and Johnson 1991), is competitive for soil resources (Cook 1965; Berube and Myers 1982; Caldwell et al. 1985), establishes well (Hull 1974), and is less expensive to obtain seeds from than native perennial bunchgrasses.

The purpose of this study was to determine if establishing competitive vegetation, as a barrier, around exotic plant infestations could impede the spread of invasive plants by influencing biotic resistance to invasion and invasive species propagule pressure. We hypothesized that: (1) invasive plant establishment and soil nutrient concentrations would be less (increased biotic resistance) in plant communities where the competitive vegetation was established and (2) less invasive plants would establish (as an indicator of propagule pressure) beyond the competitive vegetation barrier compared to beyond the control.

Materials and methods

Study area

The study was conducted in the northwest foothills of Steens Mountain in southeast Oregon about 65 km southeast of Burns, OR. Elevations at the study sites are between 1,300 and 1,550 m above sea level. Topography is variable with different slopes and aspects. Soils are a complex of different series with 20–35% clay content and moderate to high shrink-swell potential (Natural Resource Conservation Service 2007). Long-term average annual precipitation at study sites was between 250 and 300 mm (Oregon Climatic Service 2007). Potential native plant communities would have been *Artemisia tridentata* ssp. *wyomingensis* (Beetle and A. Young) S.L. Welsh (Wyoming big sagebrush)—bunchgrass and *Artemisia arbuscula* Nutt. (low sagebrush)—bunchgrass communities. The most common perennial bunchgrasses at the study sites were *Elymus elymoides* (Raf.) Swezey (squirreltail) and *Poa secunda* J. Presl (Sandberg bluegrass). Other common perennial bunchgrasses were *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass) and *Achnatherum thurberianum* (Piper) Barkworth (Thurber needlegrass).

Experimental design

A randomized complete block design was used to evaluate the effectiveness of establishing a competitive vegetation barrier to reduce the spread of invasive plant species. Twelve sites were selected along the invading fronts of *T. caput-medusae* invasions across three >1,000 ha grazing allotments. Sites varied in topography, soils, elevation, and prior management. At each site a 50 × 10 m block was selected and divided into two 15 × 10 m plots with a 10 m buffer between treatments. The 15 m side of the plot paralleled the invasion front. Treatments were randomly assigned to one of the 15 × 10 m plots at each site. Treatments were either (1) established *A. desertorum* or (2) an undisturbed control. *Agropyron desertorum* was drill-seeded at 11 kg ha^{-1} in a 15 × 6 m band in front of the *T. caput-medusae* invasion in February of 2006. Prior to seeding *A. desertorum*, cover and density of large perennial bunchgrasses, *P. secunda*, *T. caput-medusae*, exotic annual grasses, perennial forbs, and annual forbs were similar between treatments and between the areas (unprotected and protected by an *A. desertorum* barrier) across the treatments from the infestations ($P > 0.05$). *Taeniatherum caput-medusae* spread was measured three growing seasons after seeding *A. desertorum*.

Measurements

Herbaceous plant cover and density were measured by species is 0.2 m^2 frames in June of 2008. The 15 × 6 m barrier was measured by sampling twelve 0.2 m^2 frames at 1-m intervals on four 12-m transects. The 12-m transects were spaced at 2-m intervals and were parallel to the *T. caput-medusae* invasion front. The area beyond the 15 × 6 m barrier (in the non-invaded plant community) was measured using twelve 0.2 m^2 frames on one 12-m transect spaced four meters from the 15 × 6 m barrier. This transect was also parallel to the invasion front.

To estimate nutrient supply rates of potassium, phosphorus, and inorganic nitrogen (nitrate and ammonium) between treatments, four anion and cation PRS™-probes (Western Ag Innovations, Saskatoon, Saskatchewan, Canada) were randomly placed in each treatment plot. These PRS™-probe pairs were buried directly into the soil to estimate the availability of soil nutrients to plants in each treatment plot (Jowkin and Schoenau 1998). PRS™-probes attract and adsorb ions through electrostatic attraction on an ion-exchange membrane. The PRS™-probes were placed vertically in the upper 20 cm of the soil profile to estimate nutrient supply rates. The PRS™-probes were buried from the 1 May 2008 until 1 July 2008. PRS™-probes were returned to Western Ag Innovations for analysis. The probes were extracted with 0.5 N HCl and analyzed colourimetrically with an autoanalyzer.

Statistical analysis

Randomized complete block analyses of variance (ANOVA) were used to test for treatment differences between response variables (S-Plus v. 8.0). Differences between means were considered significant if P-values were <0.05 ($\alpha = 0.05$). Means are reported with standard errors (mean + SE). Data that did not meet ANOVA assumptions of normality and homogeneity of variance were log-transformed. For these analyses herbaceous vegetation was grouped into the following plant functional groups: large perennial bunchgrass (including *A. desertorum*), *P. secunda*, *A. desertorum*, *T. caput-medusae*, exotic annual grasses, perennial forbs, and annual forbs. *Poa secunda* was treated as a separate functional group from the other native perennial bunchgrasses because of its relatively short stature and more rapid phenology (Davies 2008; James et al. 2008). Exotic annual grasses functional group was composed largely of *T. caput-medusae*, but there was some *Bromus tectorum* L. (cheatgrass) in the research plots. *Bromus tectorum* is another exotic annual grass that is very problematic (Knapp 1996). Functional groups were used because they simplify analysis and can provide more meaningful results than analyzing species individually (Boyd and Bidwell 2002; Davies et al. 2007).

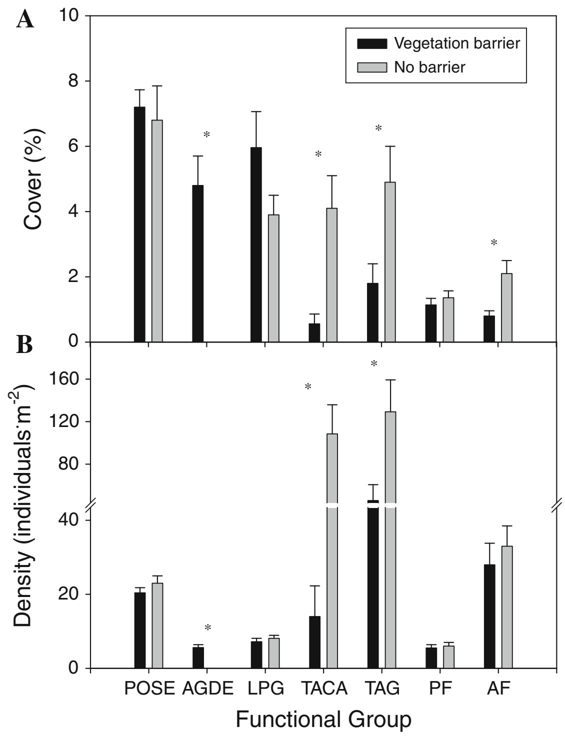

Fig. 1 Cover (**a**) and density (**b**) of plant functional groups in the competitive vegetation barrier (established *A. desertorum*) and no barrier treatments (mean + SE). POSE = *P. secunda*, AGDE = *A. desertorum*, LPG = large perennial bunchgrass, TACA = *T. caput-medusae*, TAG = total annual grass, PF = perennial forb, and AF = annual forb. *Asterisk* (*) indicates significant difference between treatments ($P < 0.05$)

Results

In the competitive vegetation barrier

Taeniatherum caput-medusae and total annual grass cover values were more than 7.1- and 2.7-fold greater in the control treatment than the *A. desertorum* treatment ($F_{1,11} = 10.06$, $P < 0.01$ and $F_{1,11} = 5.06$, $P = 0.04$, respectively; Fig. 1a). Annual forb cover was also greater in the control compared to *A. desertorum* treatment ($P = 0.01$). Cover of *A. desertorum* was greater in the *A. desertorum* than control treatment ($F_{1,11} = 26.89$, $P < 0.01$). *Agropyron desertorum* cover was 4.9 and 0.0 in the *A. desertorum* and control treatments, respectively. The cover of *P. secunda*, large perennial bunchgrasses, and perennial forbs did not vary between treatments ($F_{1,11} = 0.10$, $P = 0.75$, $F_{1,11} = 1.89$, $P = 0.19$, and $F_{1,11} = 0.34$, $P = 0.57$, respectively).

Taeniatherum caput-medusae and total annual grass densities were ~7.8- and 2.8-fold greater in the control compared to the *A. desertorum* treatment ($F_{1,11} = 9.92$, $P = 0.01$ and $F_{1,11} = 5.83$, $P = 0.04$, respectively; Fig. 1b). Density of *A. desertorum* was greater in the *A. desertorum* than the control treatment ($F_{1,11} = 31.99$, $P < 0.01$). Annual forb, perennial forb, large perennial bunchgrass, and *P. secunda* densities did not vary between treatments ($F_{1,11} = 0.39$, $P = 0.55$, $F_{1,11} = 0.74$, $P = 0.79$, $F_{1,11} = 0.98$, $P = 0.35$, and $F_{1,11} = 1.14$, $P = 0.31$, respectively).

Potassium and ammonium concentrations were reduced where *A. desertorum* was seeded ($F_{1,11} = 22.36$, $P < 0.01$ and $F_{1,11} = 25.61$, $P < 0.01$, respectively; Fig. 2). Potassium concentrations were approximately twofold greater in the control compared to the *A. desertorum* treatment. Ammonium concentrations were about 15-fold greater in the control than the *A. desertorum* treatment. Nitrate and phosphorus concentrations did not vary between treatments ($F_{1,11} = 4.05$, $P = 0.07$ and $F_{1,11} = 0.06$, $P = 0.81$, respectively).

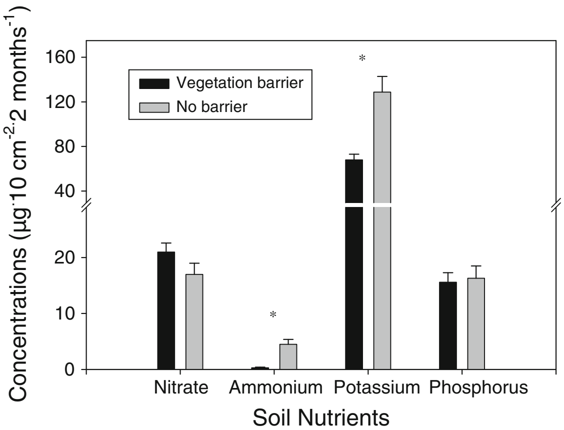

Fig. 2 Soil nutrient concentrations in the competitive vegetation barrier (established *A. desertorum*) and no barrier treatments (mean + SE). *Asterisk* (*) indicates significant difference between treatments ($P < 0.05$)

Beyond the competitive vegetation barrier

Cover and density of *T. caput-medusae* was less in plant communities protected by a barrier of established *A. desertorum* than unprotected plant communities ($F_{1,11} = 12.27$, $P < 0.01$ and $F_{1,11} = 12.27$, $P < 0.01$, respectively; Fig. 3). *Taeniatherum caput-medusae* cover was 42-fold greater in unprotected plant communities compared to plant communities protected by a barrier of established *A. desertorum*. *Taeniatherum caput-medusae* density was ~47-fold more in unprotected compared to protected plant communities.

Discussion

Establishing competitive plants around infestations can reduce the spread of invasive plants. Competitive plant barriers probably reduce the spread of invasive plants by decreasing the availability of resources to exotics, reducing the spatial dispersal of propagules by physically intercepting them, and increasing the distance invasive plants have to disperse to find suitable conditions for establishment. Increasing biotic resistance to invasion and reducing the spatial dispersal of invasive plant propagules are key components to preventing and containing exotic plant invasions (Davies and Johnson 2009). However, additional research investigating seed dispersal and

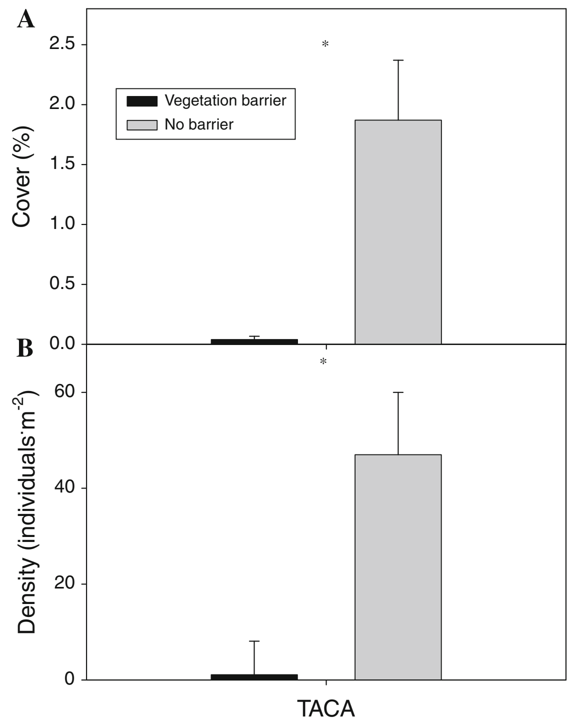

Fig. 3 *Taeniatherum caput-medusae* (TACA) cover (**a**) and density (**b**) in the plant communities beyond the competitive vegetation barrier (established *A. desertorum*) and plant communities without a barrier between them and a *T. caput-medusae* infestation (mean + SE). *Asterisk* (*) indicates significant difference between treatments ($P < 0.05$)

evaluating competition between potential competitive plants selected for barriers and invasive plants will be required to determine if these mechanisms are slowing the spread of invasive plants.

Less *T. caput-medusae* cover and density in the areas where *A. desertorum* was established suggest that competitive vegetation can increase the biotic resistance of plant communities adjacent to exotic plant infestations. A reduction in soil nutrient concentrations where *A. desertorum* was established also suggests that establishing competitive vegetation can increase the biotic resistance of plant communities to invasion. However, without direct evidence we can only speculate that this may be a mechanism contributing to the decreased invasion where *A. desertorum* was established based on previous research correlating invasion risk with excess resources (Huenneke et al. 1990; Burke and Grime 1996; Davis et al. 2000; Dukes 2001). For example, exotic annual grasses competitiveness with native plants increases as soil resource concentrations increase (Young and Allen 1997; Vasquez et al. 2008).

Less *T. caput-medusae* establishment in the *A. desertorum* barrier and possibly the physical interception of *T. caput-medusae* seeds dispersing from the infestation probably resulted in few *T. caput-medusae* in plant communities protected by a barrier of established *A. desertorum*. With >40-fold more *T. caput-medusae* in plant communities not protected than those protected by a *A. desertorum* barrier, these results demonstrate that establishing a competitive vegetation barrier around infestations can significantly reduce the spread of invasive plant species into surrounding non-invaded plant communities. Decreasing *T. caput-medusae* establishment in non-invaded areas adjacent to infestations may have resulted in less propagule pressure in plant communities protected by the barrier because most *T. caput-medusae* seeds disperse relatively short distances (Davies 2008). Thus, by decreasing *T. caput-medusae* establishment in the *A. desertorum* barrier, less *T. caput-medusae* plants may have been close enough to disperse seeds into plant communities protected by the barriers. Interception of invasive plant propagules by neighboring vegetation can also reduce the spatial seed dispersal of invasive species (Davies and Sheley 2007).

Some *T. caput-medusae* established beyond the *A. desertorum* barrier. This suggests that the effectiveness of competitive vegetation barriers could be improved by making them wider and incorporating an early detection and eradication program for satellite populations that establish beyond competitive vegetation barriers. Integrating other actions may improve the effectiveness of invasive plant management. The competitive vegetation barrier may have also been more effective if it had been implemented farther from the infestation edge. This would have allowed the competitive vegetation to become better established prior to experiencing competition from the invader. Better established vegetation is often more competitive with invasive plants (Clausnitzer et al. 1999; Reever-Morghan and Rice 2005).

Establishing non-native competitive vegetation around invasive plant infestations has some potential risks. Non-native competitive vegetation may outcompete native plants and ultimately cause the same problems as the invader targeted for containment. Native perennial bunchgrasses appear to be reduced by the establishment of *A. desertorum*, either through competition and/or by the impacts of the disturbance created by drill-seeding. However, *A. desertorum* establishment does not appear to negatively impact perennial forbs and *P. secunda*, but recruitment in the future may be limited because of the competitive nature of *A. desertorum*. *Agropyron desertorum* has been demonstrated to be more competitive than native perennial bunchgrasses (Caldwell et al. 1985; Eissenstat and Caldwell 1987). Thus, all the impacts, both positive and negative, from establishing non-native competitive vegetation on the areas adjacent to invasive plant infestations have not been fully realized. However, considering the negative impacts of *T. caput-medusae* on biodiversity, wildlife habitat, and livestock forage production (Davies and Svejcar 2008), it may be an acceptable risk to use *A. desertorum* to help impeded the spread of *T. caput-medusae*. Furthermore, *Agropyron desertorum* also provides similar wildlife habitat, nutrient cycling, and ecosystem functions as native bunchgrasses in these ecosystems (Eiswerth et al. 2009). Because of the potential for non-native to cause similar problems as exotic invaders, careful consideration of the impacts of non-native plant species that could potentially be used to contain invasive plant infestations is imperative to prevent unintended negative consequences. However, this concern can be alleviated in some situations by using native vegetation.

Conclusions

Establishing competitive vegetation adjacent to infestations may reduce the spread of invasive plants. In this study, *A. desertorum* reduced the establishment of exotic annual grass where it was established and in adjacent non-invaded areas. However, some invasive plants may establish beyond the competitive vegetation barrier; thus, integrating competitive vegetation barriers with other management actions may be needed to effectively limit the spread and subsequently negative impacts of invasive plants. However, additional research needs to determine if competitive vegetations barriers could impede the spread of other invasive plants and what mechanisms are operating to reduce the establishment of the invasive plants. Caution must be exercised when selecting non-native plant species to be used as a competitive barrier to invasive plant spread to minimize unintended negative consequences. Thus, future research should evaluate the potential for native vegetation to impede the spread of invasive plants.

Acknowledgments We thank Brett Bingham, Stacy McKnight, Elaine Cramer, Tate Walters, Julie Garner, Shawna Lang, Josh Monson, Matt Coffman, Eric Hough, and Rachel Svejcar for assisting with data collection. The authors also are grateful to the Burns-District Bureau of Land Management (BLM) for providing the land for this research project. Specifically, the authors thank Lesley Richman, BLM Weed Ecologist, for assisting with locating and securing the study area. The authors also appreciate thoughtful reviews of the manuscript by Ed Vasquez and Dustin Johnson. The Eastern Oregon Agricultural Research Center is jointly funded by the USDA-Agricultural Research Service and Oregon State University. This experiment complies with the current laws of the country it which it was performed.

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