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Sickleweed on the Fort Pierre National Grassland: An Emerging Threat

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ABSTRACT We report the first detailed field survey of sickleweed (*Falcaria vulgaris* L.) in the United States. Sickleweed is native to Europe, the Mediterranean, Asia Minor, and Iran and was first reported in the United States in 1922. It is listed by the Nebraska Invasive Species Council as a Category II invasive plant species. In recent years, abundance and distribution of sickleweed has increased dramatically in and around the Fort Pierre National Grassland (FPNG), South Dakota. Management of such a rapidly expanding population is hampered by a general lack of baseline information on the biology and ecology of sickleweed. We used an environmental gradient approach to describe the abundance and distribution of sickleweed on the FPNG and found that sickleweed colonization and expansion may be largely driven by small and large scale disturbances that create gaps in ground cover (bare soil and total vegetative cover plus litter), reduced diversity (H'), and altered competitive relationships with western wheatgrass. Minimizing disturbances that create gaps in litter and vegetative cover, decrease diversity, increase bare soil, and alter the dominance of western wheatgrass may reduce the colonization and expansion of sickleweed.

KEY WORDS Conditional inference trees, grassland invasibility, random forest, sickleweed, variable importance plots, western wheatgrass

As in most modern landscapes, exotic plants are a common feature of the Fort Pierre National Grassland (FPNG) with sickleweed (*Falcaria vulgaris* L.) serving as the most recent addition. Sickleweed is the sole member of its genus in the family Apiaceae (Umbelliferae) and is native to the central and southern parts of Western Europe, the European part of the former Soviet Union, the Caucasus, Western Siberia, Central Asia, the Mediterranean region, Asia Minor, and Iran where it is variously described as annual, biennial, or perennial (reviewed by Piya et al. 2013). Sickleweed was first recorded in the United States in 1922 on a farm in south-central Pennsylvania (Gress 1923) and is now described as an introduced perennial in 16 states of the U.S. (U.S. Department of Agriculture 2012*a*). It was first documented in South Dakota in 1961 in a grain field near Tyndall, Bon Homme County and was first collected on the FPNG in 1992 (Korman 2011). However, it is unknown how long sickleweed had been present in the area before being recorded. Because of the lag phase in population growth often associated with new introductions, many exotic species may not become abundant enough to be conspicuous for decades (Mack et al. 2000, Groves 2006, Theoharides and Dukes 2007, Ahern et al. 2010). The long-distance transport mechanism responsible for the introduction of sickleweed also is unknown; however, anecdotal evidence of its food and medicinal properties suggest that sickleweed may have been intentionally introduced as a garden herb but then spread as a contaminant in agricultural crop seed (Piya et al. 2013). Sickleweed produces a large number of seeds with potential germination rates > 80% (Royal Botanic Gardens Kew 2008, Korman 2011). High propagule pressure, coupled with a strong interest in the horticultural properties of the family, likely increased the probability of transport and establishment of sickleweed into new, climatically suitable habitats.

Like many exotic species considered benign in their native range, basic biological and ecological information on sickleweed that may provide insight on its invasibility and potential impact on grassland ecosystems in its introduced range is lacking. Ellenberg (1988) described sickleweed as a drought tolerant, common native weed of frequently disturbed sites in the grassland steppes of southeastern Europe. Common associates of sickleweed in its native range included summer pheasant's eye (*Adonis aestivalis* L.), golden chamomile (*Anthemis tinctoria* L.), carrot bur parsley (*Caucalis platycarpus* L.), hare's ear mustard (*Conringia orientalis* L.), field bindweed (*Convolvulus arvensis* L.), quackgrass (*Elymus repens* [L.] Gould), Kentucky bluegrass (*Poa pratensis* L.), Canada bluegrass (*P. compressa* L.), and intermediate wheatgrass (*Thinopyroum intermedium* [Host] Barkworth and D. R. Dewey; plant nomenclature follows U.S. Department of Agriculture 2012*a*). All of these associated species of sickleweed have successfully naturalized in North America and all except carrot bur parsley and summer pheasant's eye have been recorded in South Dakota (U.S. Department of Agriculture 2012*a*), suggesting that sickleweed may be pre-adapted to the environmental conditions of the Great Plains (Henery et al. 2010). The few published reports of sickleweed presence in the U.S. (Kansas and Louisiana) do not address its potential invasiveness (Gates 1939, Thomas and Raymond 1987), although Gress (1923) expressed considerable concern regarding the potential of sickleweed to become a noxious weed. Further, the Nebraska Invasive Species Council (http://snr.unl.edu/invasives.htm, accessed 9 Jan 2013) lists sickleweed as a Category 2 invasive plant species (a demon-

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strated invasive species whose eradication is still feasible).

In 2005, FPNG staff estimated that about 3,200 ha of the Grasslands were visually dominated by sickleweed, which generated considerable concern regarding how the aggressive spread and dense growth may be impacting native grassland species (C. Erickson, U.S. Forest Service, personal communication). The potential for exotic species, such as sickleweed, to enter into intact plant communities, become naturalized, and dominate the native constituents is a theme of much research and discussion (Lonsdale 1999, Davis et al. 2000, Mack et al. 2000, Richardson et al. 2000, Ahern et al. 2010). Seastedt and Pyšek (2011) provide a summary of the processes involved with plant invasions into grassland ecosystems and found increased resource availability generated by natural and anthropogenic disturbances to be the most common factor determining community level invasibility. Disturbance periodically and temporarily increases resource availability by creating gaps in plant cover that 1) decrease resource uptake by resident vegetation, 2) produce pulses of increased resource supply, or 3) alter levels of both reduced uptake and enhanced resource supply (Davis et al. 2000). Regardless of the mechanism, additional resources increase the vulnerability of a community to invasion. However, in species rich communities, intense competition from resident species may provide some level of resistance to invasion during periods of enhanced resource supply (Fargione and Tilman 2005), although the overall outcome may depend on the spatial scale of the study (Stohlgren et al. 2003).

Despite the many efforts to investigate the potential determinates of invasibility, studies that focus specifically on recently introduced exotic plants in the early stages of establishment and not broadly considered invasive are limited (but see Zenni et al. 2009). During our initial reconnaissance we observed that wide variations in the abundance and distribution of sickleweed on the FPNG limited the stark contrasts of infested and non-infested that are common to most studies of established plant invasions (see Vilà et al. 2011). Consequently, we chose to use indirect gradient analysis to 1) describe the pattern of abundance and distribution of sickleweed on the FPNG, and 2) identify and evaluate the factors that may be useful in predicting the susceptibility of grassland communities to colonization by sickleweed. It is important to recognize that our indirect gradient approach is limited by a lack of critical information on propagule pressure. Newly introduced exotics, such as sickleweed, may be more constrained by propagule availability than by suitable habitats (Rouget and Richardson 2003). Despite this limitation, documenting the pattern of sickleweed invasion, before it becomes widespread, is an essential part of identifying the traits that may contribute to its success as an invader while increasing our understanding of the factors influencing community invasibility (Davis and Pelsor 2001, Eschtruth and Battles 2009). Such baseline information will help guide management decisions and direct future research.

STUDY AREA

The 46,977 ha of public land that constitutes the FPNG in central South Dakota (approx. N44° 16' to N43° 58' and W100° 03' to W100° 28') was originally homesteaded in the late 1800s shortly after Congress passed the Homestead Act of 1862. After the Great Depression and the Dust Bowl in the early 1930s, millions of hectares of land were abandoned much of which was subsequently purchased by the federal government for rehabilitation. In 1960, the Secretary of Agriculture designated about 1.5 million ha of these purchased lands as National Grasslands, including the FPNG, to be administered by the US Forest Service (Olson 1997).

The FPNG lies within the Bad River watershed that drains into the Missouri River and is characterized by gently rolling hills dominated by mixed grass prairie vegetation. The most recent 30-year average annual precipitation was 42 cm, 50 cm, and 51 cm for Fort Pierre, Midland, and Pierre, respectively, with about 80% occurring between April and September (South Dakota Office of Climatology 2012). In 2006 and 2007 precipitation was 50% less and 9% greater than the long-term average, respectively. Summers are generally warm with an average temperature of 23° C; however, daytime temperatures often exceed 38° C. Average temperature during the winter was 7° C with an average snowfall of 79 cm.

All of our study plots were located on deep, well drained, nearly level to moderately sloping clayey soils classified as a Clayey Ecological Site within Northern Rolling Pierre Shale Plains Major Land Resource Area (U.S. Department of Agriculture 2012*b*). Vegetation of the Historic Climax Plant Community within Clayey Ecological Sites was dominated by western wheatgrass (*Pascopyrum smithii* [Rydb.] Gould) and green needlegrass (*Nassella viridula* [Trin.] Barkworth) with smaller amounts of needle and thread (*Hesperostipa comata* [Trin. and Rupr.] Barkworth), and porcupine grass (*H. spartea* [Trin.] Barkworth). Shortgrass species such as buffalograss (*Bouteloua dactyloides* [Nutt.] J.T. Columbus) and blue grama (*B. gracilis* [Willd. *ex* Kunth] Lag. *ex* Griffiths) increased with continuous grazing by livestock. Big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* [Michx.] Nash), and sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.) were common associates of western wheatgrass and the shortgrasses on shallow hillsides (Thin Upland Ecological Sites; US Department of Agriculture 2012*b*). Exotic perennial grasses, likely introduced as forage species before the site was designated as a National Grassland, are common and include crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.), smooth brome (*Bromus inermis* Leyss.), and Kentucky bluegrass. All of the pastures containing our study plots were lightly to moderately grazed by cattle using Natural Resource Conservation Service guidelines (C. Erickson, U.S. Forest Service, personal communication). Prescribed fire was routinely used on the FPNG to reduce fire fuel loads, release nutrients, increase productivity, manage wildlife habitat, and manage non-native perennial grasses (U.S. Department of Agriculture 2009).

METHODS

We evaluated the cover and density of sickleweed and cover of associated vegetation within 36 randomly placed plots, each plot sampled once. Thirteen plots were established and evaluated in June 2006 while 23 were established and evaluated in June 2007. Plots were located in five pastures in the northeast and east central parts of the FPNG (distance between plots within pastures ≥200 m). Eighteen of the 36 plots were located in one, 453 ha pasture that received prescribed burns (unrelated to this study) in 2002 and 2005. The remaining 18 plots were randomly established into the other four pastures. While the prescribed fire was not a treatment in this study, it allowed us to sample the full continuum of potential variables that may influence the establishment of sickleweed in this grassland.

At each plot, we established two parallel 30-m transects, 20 m apart, then randomly placed 10, 20 × 50-cm (0.10 m^2) quadrats at least 1 m apart along each transect for a total of 20 quadrats. We estimated foliar cover of each species occurring in the quadrat and the amount of bare soil and litter using six cover classes (1 = ≤5%, 2 = 6–25%, 3 = 26–50%, 4 = 51–75%, 5 = 76–95%, and 6 = >95%; Daubenmire 1959). In grasslands, plant litter typically occupies a gradient from standing upright to lying directly upon the soil (Facelli and Pickett 1991). For the purpose of our study, we defined litter as horizontal dead vegetation with the bottom layer in direct contact with the soil surface. We used the mid-point of the cover classes to calculate mean cover for each species, bare soil, and litter for each plot, which was our experimental unit. We used mean cover values for each species to calculate the Shannon Diversity Index (H') for each plot. We estimated total cover by summing the cover values for all species occurring in a quadrat, but subtracted sickleweed for some analyses when indicated. Because of the potential interaction between total cover and litter (Suding and Goldberg 1999), we combined total cover and litter into a single value (total cover plus litter) following Gross (1984). We also summed cover values by origin (native and exotic plant species). We estimated the density of sickleweed using counts of individual stems occurring in each quadrat.

We first used t-tests (SAS Version 9.3; SAS Institute 2010) to discern differences between burned (18 plots) and unburned plots (18 plots) with respect to mean values of diversity (species richness and H'), sickleweed cover and density, total cover (including sickleweed), and cover of western wheatgrass, exotic species (minus sickleweed), native species (minus western wheatgrass), bare soil, and litter. We used PC-ORD (McCune and Mefford 2011) to calculate Shannon Diversity indices for each plot based on mean cover for each species.

We used non-metric multidimensional scaling (NMS) to analyze how the interrelationships among plant species may describe the landscape level distribution and abundance of sickleweed. The primary matrix contained mean cover values for all 63 species recorded on the 36 plots in the study. Because of the dominance of western wheatgrass and sickleweed in the majority of our plots, cover values were square-root transformed to allow less abundant species to influence the NMS analysis. We constructed a secondary matrix that contained mean plot values for total cover plus litter (minus sickleweed) and the variables included in Table 1, except sickleweed and western wheatgrass. To improve clarity, plots in the overlay were designated as burned and unburned and the ordination was rotated to align the horizontal axis with foliar cover of sickleweed. NMS was performed with PC-ORD for Windows, Version 6.09 (McCune and Mefford 2011), using the autopilot mode with Sørensen (Bray-Curtis) distance measure. We conducted 250 runs with real data and 250 runs with random data.

We generated variable importance plots, using Random Forest (RF) algorithms available in R-statistical software (R Core Team 2012), to help identify the relative strength between sickleweed density (response variable) and the vari-

Table 1. Mean values (±SD) for density and percent cover for sickleweed and percent cover for western wheatgrass, non-native species, native species, bare soil, and litter, and diversity [species richness and Shannon Diversity Index (H')] in burned and unburned plots on the Fort Pierre National Grasslands. Total cover is total cover for all species. Data were collected during the 2006 and 2007 field seasons. Mean values in burned plots followed by * are significantly different from unburned plots ($P < 0.05$).

	Sickleweed		Cover (%)						Diversity	
	Density (#/m^2)	Cover (%)	Western wheatgrass	Exotic	Native	Total	Bare soil	Litter	Richness	H'
Burned	86*	23*	30*	14	5*	71	43*	17*	9	1.2*
	(54.5)	(11.6)	(14.8)	(11.6)	(2.9)	(9.1)	(14.7)	(8.4)	(2.6)	(0.2)
Unburned	38	12	14	22	16	63	18	46	14	1.8
	(43.4)	(12.3)	(7.5)	(11.5)	(13.0)	(12.2)	(14.7)	(13.6)	(3.5)	(0.3)

ables in the secondary matrix plus mean cover values for the most common exotic perennial grass species (Kentucky bluegrass). Importance of each predictor variable was evaluated based on the percentage increase in the model's mean squared error as the values of each predictor variable were randomized across the samples (Pierce et al. 2012). Random Forest makes no distributional assumptions about the predictor or response variables. Although the approach is not suitable for hypothesis testing, it is a powerful tool for identifying and visualizing interactions among variables that are likely correlated (Cutler et al. 2007). We then evaluated the relationship between sickleweed density and the three most important variables using linear regression.

To fully explore the potential relationship between sickleweed invasion and grassland diversity, we used a Conditional Inference Tree model in RF (R Core Team 2012) to regress the distribution of H' in relation to percent bare soil, sickleweed cover, and western wheatgrass cover. Preliminary runs using all of the variables in the secondary matrix revealed that a model using only bare soil, western wheatgrass, and sickleweed yielded the most interpretable information. Conditional Inference Tree models are applicable to various types of regression problems (e.g., nominal, ordinal, numeric, etc.) and involve recursively partitioning data within a conditional inference framework in sequential steps (Hothorn et al. 2006). The first step tests the global null hypothesis of independence between the input variables and the response variable and the procedure stops if the hypothesis is not rejected using Monte Carlo procedures ($P \leq 0.10$). However, if the hypothesis is rejected, then the algorithm selects the input variable with strongest association with the response variable and calculates a corresponding P-value. The second step involves a binary split on the selected input variable. Step three involves repeating Step 1 and 2 until the model stops when $P > 0.10$ (Hothorn et al. 2006). We then calculated means (± 95% confidence intervals) for litter, bare soil, total cover (including sickleweed), native and exotic species richness and cover, and cover of sickleweed and western wheatgrass for each node.

RESULTS

We recorded a total of 51 native species with western wheatgrass as the clear dominant occurring in 100% of our plots (data not shown). American vetch (*Vicia americana* Muhl. ex Willd.) was a common native co-constituent with western wheatgrass occurring in 83% of our plots followed by green needlegrass (69%), blue grama (33%), and western yarrow (*Achillea millefolium* L.; 28%). The remaining native species occurred in fewer than 20% of the plots. Kentucky bluegrass was the most frequently occurring exotic species (94% of the plots) followed by sickleweed (89%), field brome (*B. arvensis* L.; 78%), dandelion (*Taraxacum officinale* F.H. Wigg,; 69%), western salsify (*Tragopogon dubius* Scop.; 61%), yellow sweetclover (*Melilotus officinalis* [L.] Lam.; 47%) and field bindweed (28%). The remaining five exotic species occurred in fewer than 20% of the plots.

Qualitatively, the dry conditions of 2006 appeared to have little effect on the cover and density of sickleweed. Sickleweed occurred in 8 of 13 plots sampled in 2006 (three burned and 10 unburned) where foliar cover averaged 15% (range = 0 to 50%) and density averaged 57 stems / m^2 (range = 0 to 222 stems / m^2; data not shown). In comparison, sickleweed occurred in 100% of the 23 plots sampled in 2007 (15 burned and 8 unburned) and foliar cover averaged 19% (range = 6 to 34%) while density averaged 65 stems / m^2 (range = 19 to 144 stems / m^2).

The prescribed fire greatly expanded the gradient of plant community composition and abundance, as well as bare soil and litter (Table 1). Density and foliar cover of sickleweed were 126% ($t_{34} = 2.98$, $P < 0.01$) and 92% ($t_{34} = 2.69$, $P = 0.01$) higher, respectively, in burned plots compared to unburned plots. Burned plots also had 114% more western wheatgrass ($t_{34} = 4.17$, $P < 0.01$), 139% more bare soil ($t_{34} = 5.02$, $P < 0.01$) and 13% more total vegetation cover ($t_{34} = 2.21$, $P = 0.03$), which included sickleweed, but 61% less litter ($t_{34} = 7.45$, $P < 0.01$), 69% less native species cover ($t_{34} = 3.57$, $P < 0.01$), and 36% less exotic species cover ($t_{34} = 2.03$, $P = 0.05$). The burned plots also had lower mean species richness ($t_{34} = 4.36$, $P < 0.01$) and H' ($t_{34} = 6.72$, $P < 0.01$). Within the exotic species functional group, two species emerged as co-dominants with sickleweed. Kentucky bluegrass cover was similar between burned and unburned plots ($t_{34} = 1.34$, $P = 0.19$), while cover for field brome averaged 0.6% in burned plots compared to 8% in unburned plots ($t_{34} = 3.19$, $P < 0.01$) (data not shown). Within the native species functional group, American vetch, although equally frequent across the plots (83% for burned and unburned plots), had three times as much cover in unburned plots compared to the burned plots (2.4% vs 0.6%, $t_{34} = 2.30$, $P = 0.03$). We recorded a similar but more pronounced pattern in cover of green needlegrass between unburned plots (mean cover = 4.7%) and burned plots (mean cover = 0.8%, $t_{34} = 3.29$, $P < 0.01$). Green needlegrass was also twice as frequent in unburned plots (94%) compared to burned plots (44%).

Differences in species composition and abundance among burned and unburned plots are reflected in the NMS ordination (Fig. 1). Results from the ordination produced a two-dimensional solution with a correlation coefficient for ordination distance and distance in the original dimensional space of 0.88 (r for Axis 1 = 0.71, Axis 2 = 0.17, final stress = 15.68 after 48 iterations, Monte Carlo P-value = 0.004). Percent bare soil, litter, native species foliar cover, total cover plus litter, and H' all had correlation coefficients with Axis 1 of greater than 0.60 ($P < 0.05$). Only exotic species cover, as a functional group, had a significant correlation coefficient with Axis 2 ($r = 0.59$, $P < 0.05$). The eight unburned plots located at the far left of Fig. 1 represented areas in our study

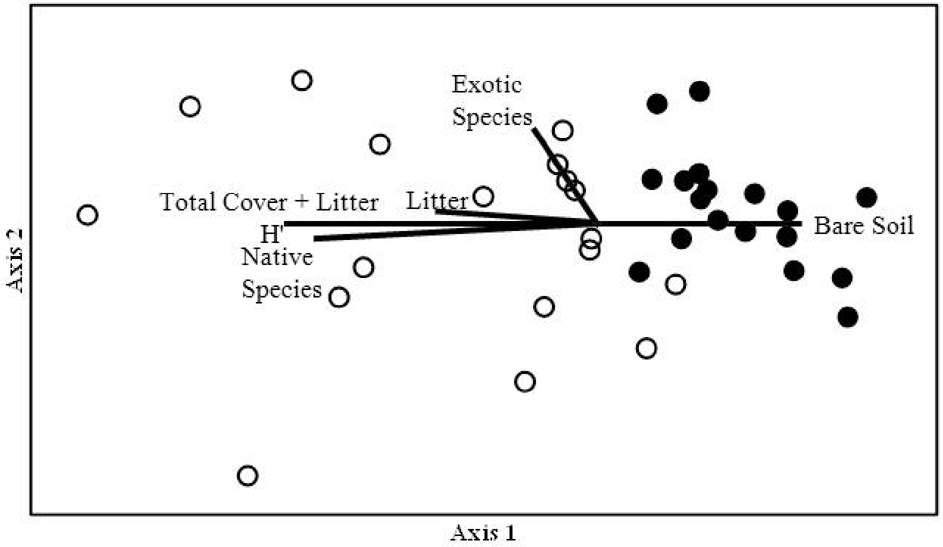

Figure 1. NMS Ordination of 36 plots sampled on the Fort Pierre National Grasslands during the 2006 and 2007 field season (solid symbols = burned plots, open symbols= unburned plots).

with the lowest cover values of sickleweed, western wheatgrass, and bare soil and the highest values of H'.

Based upon the results of the NMS ordination, we anticipated that bare soil, litter, native species cover, and H' could serve as important predictors of sickleweed abundance across the landscape. This expectation was partially confirmed with a variable importance plot that shows the ranked importance of the variables in the secondary matrix (Fig. 2a). Variable importance plots retain variables that may be ecologically important predictors even though they may be highly correlated with other predictor variables, such as between percent bare soil and total cover plus litter ($r = -0.90$, $P < 0.01$, data not shown). A significant amount of the variation in sickleweed density across the landscape was explained by variations in percent bare soil ($F_{1,34} = 34.1$, $P < 0.01$), total cover plus litter ($F_{1,34} = 63.9$, $P < 0.01$), and H' ($F_{1,34} = 19.6$, $P < 0.01$; Fig. 2b).

A conditional inference tree was created to test the hypothesis of independence between bare soil, sickleweed and western wheatgrass cover, as the predictor variables, and H' as the response variable (Fig. 3a). We found that low percent bare soil (≤9%) had the strongest association to H' where 8 unburned plots were classified into Node 2 of the tree ($P < 0.001$; median H' = 1.88, range = 1.68 to 2.58, $n = 8$). When percent bare soil was greater than 9%, plots were grouped into Node 3 then separated based on western wheatgrass dominance ($P = 0.02$). When western wheatgrass cover was ≤31% and when sickleweed cover was ≤20%, plots were classified into Node 5 (Median H' = 1.50, range 1.30 to 1.99, $n = 13$), and when sickleweed cover was >20% (Median H' = 1.22, range 1.09 to 2.07, $n = 6$) plots were classified into Node 6. Plots with the lowest H' values were classified into Node 7 (Median H' = 1.01, range 0.82 to 1.25, $n = 7$), which was characterized by western wheatgrass cover values greater than 31%.

Mean values of percent bare soil and percent litter varied among the 4 nodes while total cover, which included sickleweed, was fairly constant (Fig. 3b). Fig. 3b also shows that differences among median values of H' in the regression tree were largely a reflection of differences in native species richness among the nodes in addition to differences in cover values for exotic and native species, sickleweed and western wheatgrass. Species richness and H' were highest in plots with the lowest values of both sickleweed and western wheatgrass and decreased concomitantly with increased cover of either sickleweed or western wheatgrass. Based on the results of the classification tree, we calculated Pearson correlation coefficients between sickleweed and western wheatgrass using plots classified into Nodes 6 and 7 (Fig. 4a), and between H' and combined cover values of sickleweed and western wheatgrass (Fig. 4b). We found a strong negative relationship between sickleweed and western wheatgrass in plots where the two species were major constituents (Fig. 4a). When foliar cover of sickleweed and western wheatgrass were combined at the plot level into a single value, it explained 66% of the variation in H' and depicted a gradient of decreasing diversity values with increasing combined cover (Fig. 4b).

DISCUSSION

Evaluating the colonization of a recently introduced exotic plant species is a complex task that involves simultaneously evaluating the characteristics of the colonizing invader and the invaded community (Rejmanek and Richardson 1996,Theoharides and Dukes 2007, Catford et al. 2012). Sickleweed was the third most frequently occurring spe-

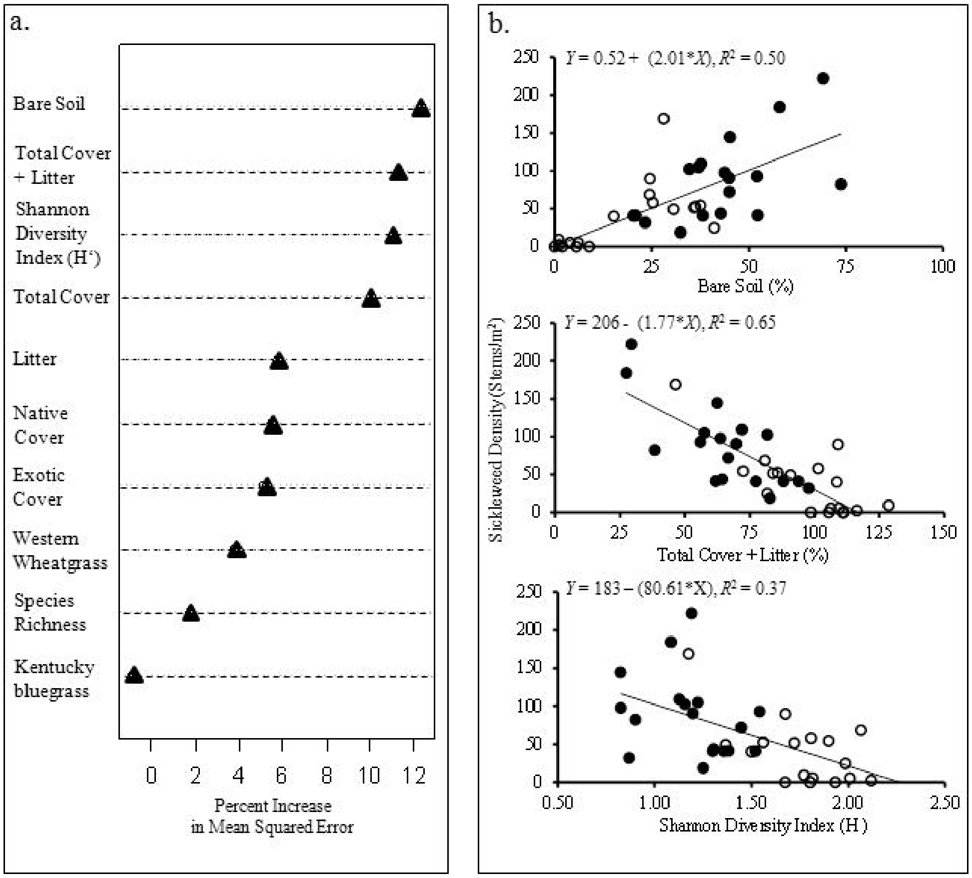

Figure 2. Variable importance plot using sickleweed (*Falcaria vulgaris* L.) density as the response variable (a). Variables are ranked from highest (top) to lowest (bottom). Results of the linear regression of the top three variables from the importance plot (b). Burned plots are represented by open symbols, unburned plots are represented by filled symbols.

cies in our study, behind western wheatgrass and Kentucky bluegrass, and its abundance and distribution varied along a gradient of factors that interacted to influence the colonization and expansion of sickleweed on the FPNG, some of which can be attributed to disturbance. All of the sampled pastures were grazed by cattle at least sometime during the study period and half the plots were located in a pasture that was burned twice by a prescribed fire. Incomplete consumption of standing vegetation and litter by fire (Stronach and McNaughton 1989), patch grazing by livestock (Archibald 2008), and soil disturbances by small mammals (Collins and Barber 1985) probably interacted to influence variations in ground cover (bare soil and total vegetative cover plus litter) and H' that emerged as the best predictors of sickleweed abundance in this grassland (Fig. 2).

Fig. 3 can be used to summarize the separate and interacting effects of ground cover and diversity on the abundance and spatial distribution of sickleweed. Plots classified into Node 2 had the lowest cover values for sickleweed (sickleweed was absent in five of the eight plots), little bare soil, and high amounts of litter. Ellenberg (1988) describes sickleweed as a frequent constituent of disturbed sites in southeastern Europe, which suggests that a certain amount of bare soil may be required for sickleweed to establish successfully. Disturbances (drought, fire, livestock grazing, small mammals) that simultaneously increase bare soil and decrease litter and vegetative cover create gaps that can enhance seed germination and seedling survival ("safe sites" *sensu* Harper 1977). Foster et al. (2002) reported that small-scale disturbances (animal activity) and light penetration were the best predictors of invasibility of successional grassland in northeast Kansas. Similarly, Gross et al. (2005) found that the occurrence of non-resident species in a Michigan grassland was significantly higher in plots where cover had been experimentally reduced compared to undisturbed plots.

Safe sites created by gaps in ground cover may be especially important for species with relatively small seeds such as sickleweed (0.9 mg) that have little stored energy (Royal Botanic Gardens Kew 2008). In a study involving 35 grassland species of various seed sizes, Jensen and Gutekunst (2003) reported that seedling establishment in litter was significantly and positively correlated with seed size to the

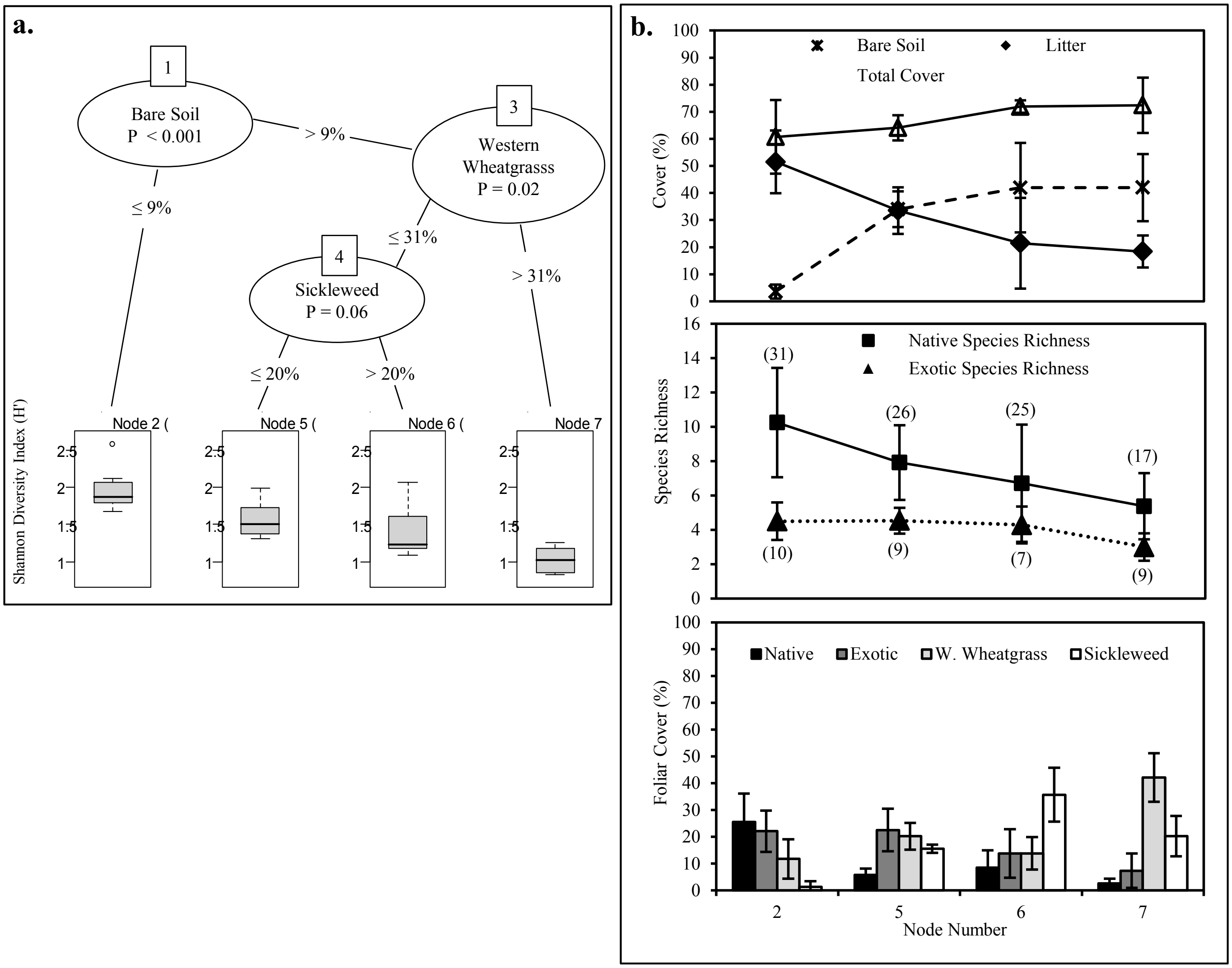

Figure 3. Conditional inference tree with H' as the response variable and cover values for bare soil, sickleweed (*Falcaria vulgaris* L.), and western wheatgrass (*Pascopyrum smithii* [Rydb.] Gould) as the predictor variables (a). Mean values (± 95% confidence limits) per node for total foliar cover, bare soil, litter, native and exotic species richness and foliar cover (total richness / node in parenthesis), and cover for western wheatgrass (W. Wheatgrass) and sickleweed (b).

extent that establishment of small-seeded, early successional species was substantially reduced by litter. Gross and Werner (1982) reported that two species with very small seeds (≤0.20 mg) established and survived only in patches of bare soil while larger-seeded species (1.0 to 6.8 mg) established and survived in a broad range of ground cover types that included bare soil, litter, mosses, lichens, grasses, and herbaceous dicots. Furthermore, Gross (1984) later found that the relative growth rates of these same two small-seeded species in bare soil and litter were twice that of the larger-seeded species used in that study.

The effects of litter are complex and produce a range of positive and negative effects on germination and seedling establishment of individual plant species to the extent that community structure can be altered by the abundance of litter (Facelli and Pickett 1991, Xiong and Nilsson 1999, and references therein). Litter and vegetative cover influence light availability, soil moisture and temperature, temperature fluctuations, and soil fertility. Litter can also serve as a mechanical barrier preventing seeds from establishing contact with soil (Hamrick and Lee 1987), especially large seeds (Jensen and Gutekunst 2003). While smaller seeds, such as sickleweed seeds, may percolate through the litter layer to the soil (Rotundo and Aguiar 2005, Donath and Eckstein 2010), any small seeds trapped on top or within a litter layer either do not germinate or if they do germinate soon die because they fail to establish contact with the soil (Fowler 1988). Seedlings, regardless of seed size, emerging from beneath the litter

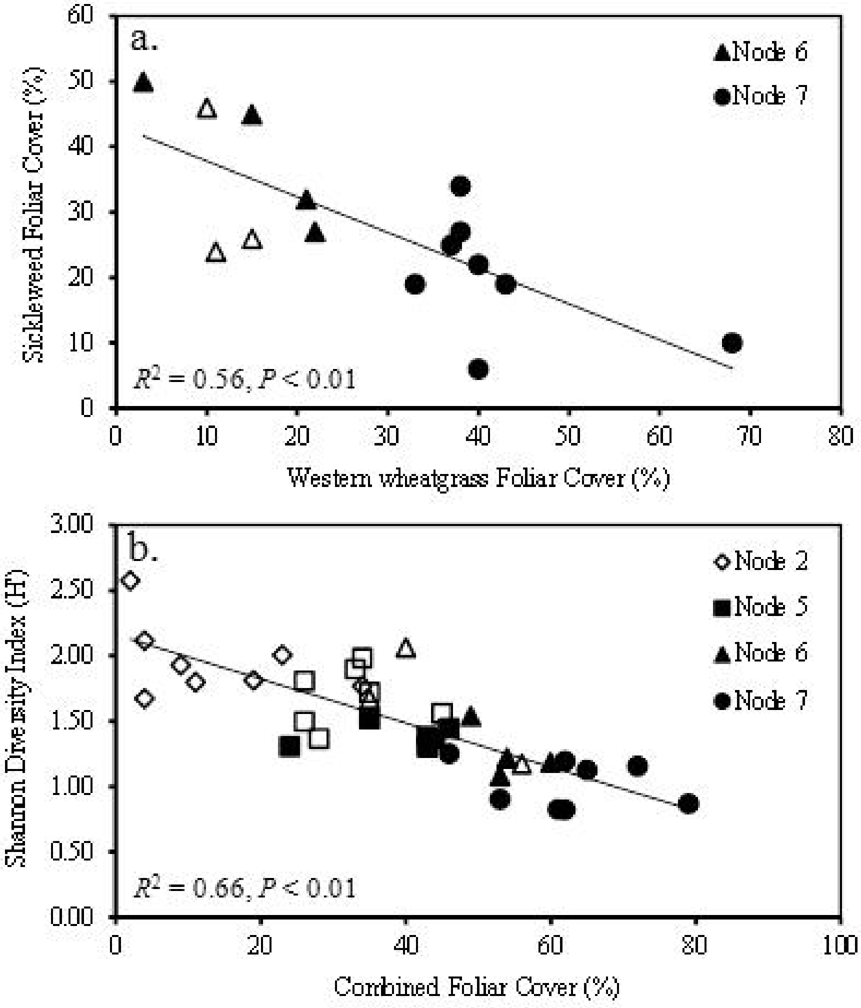

Figure 4. Relationship (scatterplot with coefficients of determination and significance level of linear regression) of sickleweed (*Falcaria vulgaris* L.) and western wheatgrass (*Pascopyrum smithii* [Rydb.] Gould) cover (a) and Shannon Diversity Index and combined cover of western wheatgrass and sickleweed (b). Burned plots are represented by open symbols, unburned plots are represented by filled symbols.

layer must penetrate through to reach sunlight (Fowler 1988, Hamrick and Lee 1987, Rotundo and Aguiar 2005), however, large-seed species definitely have the advantage on sites with abundant litter (Donath and Eckstein 2010). At the same time, moderate amounts of litter that allow seeds to percolate through to the soil, lower soil temperatures, reduce evaporative water loss, and do not restrict seedling emergence, can enhance germination and survival of both small- and large-seeded species (Wellstein 2012).

Although we strongly suspect that the availability of safe sites, as influenced by the amount of litter, bare soil, and total vegetative cover, was the primary environmental barrier to sickleweed colonization on the FPNG, the effect of reduced safe sites may have been enhanced in some plots by competition from a diverse assemblage of native and exotic species. Stohlgren et al. (1999) reported that at small spatial scales (≈ 1 m^2) exotic plant richness in several central Great Plains grassland communities decreased with increasing plant species richness and cover. Similarly, Dukes (2002) showed that the invasion success of a specific invader (yellow star thistle [*Centaura solstitialis* L.]) at the neighborhood scale decreased with increasing species richness. In contrast, Foster et al. (2002) found that susceptibility of Kansas grassland to invasion was greatest in high diversity microsites. Foster et al. (2002) concluded that the positive relationship between diversity and invasibility observed in their study was largely attributable to the extrinsic factors (light and small-scale disturbances) that promoted colonization and establishment of both native and exotic species. In our study, about 37% of the variation in sickleweed density at a relatively broad spatial scale was explained by the variation in H' (Fig. 2). Groups of plots with low sickleweed abundance were among the most diverse (Fig. 3a, Node 2) and sickleweed abundance tended to increase with decreasing diversity (Nodes 5 and 6), while total cover remained relatively constant (Fig. 3). However, diversity may have simply co-varied with the disturbance factors that influenced availability of safe sites in a manner similar to that described by Foster et al. (2002; also see Stohlgren et al. 1999, 2003).

The relationship between diversity and sickleweed abundance is further complicated by the potential role of western wheatgrass in limiting sickleweed growth (Fig. 4a). Western wheatgrass is a perennial, sod-forming cool season grass long recognized as a strong native competitor (Weaver 1942), and the negative relationship between cover of sickleweed and western wheatgrass we found suggests that competition between the two species could restrict sickleweed expansion on some sites. In greenhouse germination trials conducted by sowing sickleweed seed into separate pots containing bare soil or western wheatgrass sod (plants and soil), Korman (2011) reported that germination of sickleweed seeds was significantly higher in bare soil pots (54%) compared to pots containing unclipped western wheatgrass sod (24%). Clipping western wheatgrass plants significantly increased germination of sickleweed seeds compared to unclipped pots (34% vs. 24%). In addition, the average height of sickleweed seedlings five weeks after germination in unclipped western wheatgrass pots was 29% less than sickleweed seedlings in bare soil pots, although the differences were not statistically significant (Korman 2011).

We also found that when sickleweed cover was added to western wheatgrass cover the combined values explained a larger portion of the variation in H' across this grassland (Fig. 4b) than sickleweed alone. Changes in H' across the combined cover gradient coincided with reductions in native species richness and cover and exotic species cover while total cover remained relatively constant (Fig. 3b). Overall, only 5 of 50 native species we recorded (excluding western wheatgrass) were found in all four nodes of the classification tree compared to 6 of 11 exotic species (excluding sickleweed) (data not shown). Thirteen of the native species recorded during the study were found only in plots classified into Node 2. In comparison, Nodes 5, 6, and 7 had four, four, and three native species, respectively, restricted to those nodes. This suggests the majority of the differences in native species richness can be attributed to the loss of infrequent species.

Although empirical evidence is sparse, low species diversity, especially forbs, is commonly associated with western wheatgrass dominated grasslands (Weaver 1942). We could find no published accounts regarding the competitive ability of sickleweed; however, a wide variety of observational studies that compared heavily invaded sites with non-invaded sites document significant reductions in native species diversity following exotic plant invasions, with competition as the most frequently described mechanism (see syntheses by Levine et al. 2003 and Vilà et al. 2011). In their meta-analysis of invasive plant impacts, Vilà et al. (2011) generally found increased plant production, indicating higher resource use, and reduced richness in invaded communities and they noted that this relationship was often driven by the addition of a single, highly competitive species (sampling effect). Plots classified into Node 6 may represent an example of such a sampling effect by sickleweed (Fig. 3b). At the same time, the negative effect that western wheatgrass typically has on forb diversity (Weaver 1942) and sickleweed (our study) provides evidence for a strong sampling effect by western wheatgrass, which may contribute resistance to sickleweed invasion on sites dominated by western wheatgrass (Fig. 3b, Node 7, Fig. 5a). However, higher resource use could also be due to complementary resource use among two or more species either through variations in resource use efficiency, colonization and competitive ability, or success under different environmental conditions (Fargione and Tilman 2005). Total foliar cover remained fairly consistent among sampled plots despite substantial changes in native species richness, cover of native and exotic species, and changes in cover for sickleweed and western wheatgrass. Collectively, the evidence suggests that sickleweed colonization on the FPNG may be influenced by complementarity at low levels of disturbance (high diversity under low bare soil/high litter conditions) and by a sampling effect from western wheatgrass at higher levels of disturbance (low diversity under high bare soil/low litter conditions).

MANAGEMENT IMPLICATIONS

Although not widely recognized as invasive, it is clear that sickleweed can easily become a dominant in intact native grasslands. Sickleweed colonization and expansion in this grassland appeared to be largely driven by environmental conditions that simultaneously impacted safe site availability, patterns of diversity, and productivity of western wheatgrass. Combinations of natural and anthropogenic disturbances that create gaps in litter and vegetative cover, increase bare soil, decrease diversity, and alter the competitive ability of western wheatgrass may increase opportunities for sickleweed to colonize and spread. One of the more difficult aspects of detecting and documenting the early invasion process involves identifying the subtle ecological impacts of sickleweed dominance, which is an important component of establishing management priorities. However, treating infestations as soon as possible is the most economical approach to avoiding the long-term residual effects of large contributions to the seed bank, native species loss, and ecosystem modification.

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