REPORT
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Project:
Disturbance setting affects the establishment and reproductive output of yellow starthistle (*Centaurea solstitialis*)

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INTRODUCTION

Plants that are called ideal weeds by Baker (1965), ruderals by Grime (1977), and good colonizers by Bazzaz (1986), are generally annuals or short-lived perennials and possess a particular set of characteristics that allow rapid response to resources made newly available by disturbance (Davis et al. 2000). Yellow starthistle (YST; *Centaurea solstitialis*) is one such plant that we would expect to respond positively to disturbance. A native to the Mediterranean region, YST has many characteristics that allow rapid response to disturbance (Roché and Thill 2001), including a rapid growth rate (Sheley and Larson 1997), a high reproductive output (29,000 seeds/m^2; Callihan et al. 1993), a persistent seed bank and a lack of true dormancy (Joley et al. 1997, Joley et al. 2003), and the potential to disperse long distances (Maddox and Mayfield 1985).

Although invasion by YST is of great environmental and economic concern (DiTomaso 2000), with YST continuing to spread over large areas of the western United States (Pitcairn et al. 1997), surprisingly few experiments have investigated disturbance as a facilitator to the invasion of YST (but see Gerlach and Rice 2003, Gelbard and Harrison 2005, Hierro et al. 2006). Furthermore, context can greatly alter the role of disturbance in the plant invasion (i.e., disturbance size [e.g., Burke and Grime 1996, Gerlach and Rice 2003], timing and year-to-year variation [e.g., Crawley 2004, Gelbard and Harrison 2005], community composition and diversity [e.g., Hobbs 1989], native vs. non-native ranges [Hierro et al. 2006]).

In the present study, I examined the response of YST to disturbance of soil in two distinct settings. Specifically, I was interested in whether larger-scale soil disturbances, as might be caused by an anthropogenic disturbance (e.g., plowing), enhance the initial stage of invasion, while smaller-scale soil disturbances, as might be caused by more natural processes (e.g., animal burrowing, soil cracking from shrink-swell clays; Goldberg and Gross 1988), facilitate the continued spread of YST after initial invasion. I also examined the interaction between elevated nitrogen levels and disturbance on YST invasion and reproductive output. Elevated soil nutrients often accompany soil disturbance (Bazzaz 1983, Hobbs and Huenneke 1992), and may have a synergistic interaction with disturbance on the success of invasion by non-native species (Hobbs and Atkins 1988, Hobbs 1989, Huenneke et al. 1990, Burke and Grime 1996, Davis et al. 2000).

OVERVIEW OF EXPERIMENTS AND EXPECTATIONS

I conducted two separate experiments in two distinct settings: 1) larger-scale soil disturbances (2 m^2) subject to experimental seed addition at a site with low YST seed rain, minimal YST seed bank, and no neighboring YST patches; and 2) smaller-scale soil disturbances (0.05 m^2) without experimental seeding, but at a site with relatively high YST seed rain, an established YST seed bank, and potential influence from neighboring YST patches.

I expected YST to have an especially positive response to larger-scale soil disturbances, compared to smaller-scale soil disturbances, with that response enhanced by the addition of nitrogen. Still, I expected smaller-scale soil disturbances to positively influence YST establishment and reproductive output (e.g., Gerlach and Rice 2003, Gelbard and Harrison 2005). Thus, I anticipated that larger-scale disturbances would serve as the initial point of entry for the invasion of YST, while smaller-scale disturbances would act as secondary points of entry facilitating the spread of YST from initial sites of invasion.

METHODS

The study area was located on the grounds of the Lindquist Memorial Gardens of the Wasatch in South Ogden, Utah, in Weber County, U.S.A. Beyond the grounds actively being used by the memorial gardens are abandoned pastures dominated by the exotic, perennial forage grass (*Bromus inermis*) and a hillslope dominated by native perennial forbs (e.g., *Balsamorhiza sagittata*, *Hedysarum boreale*, *Wyethia amplexicaulis*; for details about plant community composition, see Rieder 2005). My work was conducted both within a pasture not yet invaded by YST (Experiment 1 in Site I; representing initial invasion of YST), and an immediately adjacent, invaded pasture and hillslope (Experiment 2 in Site II; representing continued spread of YST). Sites I and II were separated by approximately 50 m.

Experiment 1: Larger-scale disturbance

In the uninvaded pasture (Site I), I identified a 20 × 30 m area and established 1 × 2 m plots at 20, randomly-selected locations in May of 2002. A complete factorial design analyzed the effect of two, randomly-assigned main treatments: 1) soil disturbance (disturbed vs. undisturbed); and 2) nitrogen addition (nitrogen vs. water only). I disturbed plots by clipping vegetation at the soil surface, removing the clipped vegetation, and rototilling the soil to a depth of 15 cm. The nitrogen treatment added approximately 40 g of N to each plot (equivalent to 200 kg of N/ha). Each treatment combination was replicated 5 times at the level of whole plots. Within each whole plot, seeded (100 seeds/sub-plot) and unseeded sub-plots (50 × 50 cm) were created and surrounded by a 25-cm buffer zone. Unseeded sub-plots were used to estimate the establishment of YST from the existing seed bank or ambient seed rain of YST. Approximately every two weeks after seeding, the number and developmental stage of YST plants (seedling, rosette, bolting, flowering) were recorded for each sub-plot. All flowers produced were counted (and subsequently removed from the plot to prevent colonization from unwanted seed rain in subsequent years). In the fall, a second germination event occurred, and the number of establishing seedlings on each sub-plot was recorded.

To investigate the impact of the main effects, disturbance and nitrogen, and their interaction on the establishment of YST, I used a two-way ANOVA (SAS Institute Incorporated 2002). I restricted the ANOVA to seeded sub-plots ($n = 20$), because of extremely low germination on unseeded sub-plots (i.e., a total of two spring seedlings and three fall seedlings emerged on all sub-plots combined). A simple chi-square test was used to determine if flowering plants were more commonly associated with disturbed plots.

Experiment 2: Smaller-scale disturbance

The abandoned pasture and native-forb covered hillslope (Site II), approximately 50 m from the site for the larger-scale disturbance experiment (Site I), have been invaded by YST. In Site II, I created relatively small soil disturbances approximately every 2.5 m along randomly placed transects. Plots were created during the mid-summer of 2000 to allow the accumulation of new seeds on freshly exposed soil during peak seed production, and were observed for two consecutive years (2001 and 2002). I used a paired-plot design (disturbed and undisturbed) with circular, paired plots (25 cm in diameter; 0.05 m^2) separated by 25 cm. Plots were disturbed in similar fashion to those in Experiment 1, except I used a small hand pick-axe to disturb soil rather than a rototiller.

On each plot, I monitored colonization (number of spring- and fall-establishing seedlings) and reproductive output of YST (number of flowering plants). Flowerhead production was recorded only in 2001. Response variables for YST within a given growing season were compared between disturbed and undisturbed plots using paired t-tests (SAS Institute Incorporated 2002).

RESULTS

Experiment 1: Larger-scale disturbance

Overall spring emergence and establishment for YST was very low (44 out of 2000 seeds yielded seedlings). Of those seedlings that established in the spring, 95% were on seeded plots, and of those, 74% were on disturbed plots. Within seeded sub-plots, only the main effect of disturbance showed a significant influence on YST spring seedling establishment (Fig. 1A; n = 20; ANOVA, $F_{3,16} = 5.76$, $P = 0.03$). Nitrogen addition (ANOVA, $F_{3,16} = 0.19$, $P = 0.67$) and the interaction between disturbance and nitrogen addition did not significantly influence spring establishment (ANOVA, $F_{3,16} = 1.19$, $P = 0.29$). Flowering plants were found only on disturbed plots (Fig. 1B; $n = 20$, $\chi^2 = 14.67$, $P = 0.002$).

In the fall, an additional 32 seedlings established from the initial experimental seeding, with 88% on seeded plots and of those, 97% on disturbed plots. As with spring seedling establishment, within seeded sub-plots, only the main effect of disturbance showed a significant influence on YST fall seedling establishment (Fig. 1C; $n = 20$; ANOVA, $F_{3,16} = 7.44$, $P = 0.01$).

Experiment 2: Smaller-scale disturbance

No significant difference in any measure of YST performance differed between disturbed and undisturbed smaller-scale plots in 2001 or 2002. There was no difference in the presence/absence of YST seedlings between disturbed and undisturbed plots in 2001 or 2002

(2001: $n = 51$, $\chi^2 = 1.46$, $P = 0.23$; 2002: $n = 50$, $\chi^2 = 2.10$, $P = 0.15$). In 2001, an analysis across all pairs of plots ($n = 51$) showed no significant difference between the disturbed and undisturbed plots in the number of spring seedlings (Fig. 2A; paired t-test; $t = 0.51$, $P = 0.61$), flowering YST (Fig. 2B; paired t-test; $t = 0.10$, $P = 0.18$), and flowerheads produced (Fig. 2C; paired t-test; $t = 1.40$, $P = 0.92$). Similar results for number of spring seedlings and flowering YST were found in 2002 (Fig. 2D and 2E). In addition, fall establishment in 2002 was observed on 10 of 50 pairs of plots, but did not differ between disturbed and undisturbed plots (Fig. 2F; paired t-test; $n = 51$ pairs of plots, $t = 0.00$, $P = 1.00$).

The pattern of no difference in the performance of YST between disturbed and undisturbed plots was robust. Patterns remained the same when only those pairs of plots containing YST in at least one plot were analyzed, or when only plots from the abandoned pasture dominated by *B. inermis* ($n = 35$) or from the hillslope dominated by native perennial forbs ($n = 16$) were analyzed separately (data not shown).

DISCUSSION

The response of YST to disturbance is very different in the two settings investigated here. Larger-scale disturbed plots in the setting of Site I had a significant, positive influence on spring establishment, survival to flowering, and fall establishment of YST compared to undisturbed plots. This result is similar to the response of YST to 1 m^2 plots in the study by Hierro et al. (2006). In contrast, no difference was observed in any measure of YST performance (spring establishment, survival to flowering, flowerhead production, fall establishment) between the smaller-scale disturbed and undisturbed plots in Site II.

These two studies differ in several major features that may have impact on the response of YST to disturbance: 1) disturbance size; 2) matrix community composition; 3) presence of YST in aboveground vegetation; and 4) availability of YST seeds. First, and most obviously, plot size differed between these two experiments by a factor of 40 (0.05 m^2 to 2 m^2). Disturbance plot size has been investigated as an important factor influencing colonization by plants (e.g., Pickett and White 1985, Kotanen 1997) and the invasion of non-native species (Bergelson et al. 1993, Burke and Grime 1996, Gerlach and Rice 2003). Our results suggest that disturbance size was also important here, with much larger disturbances (2 m^2) more beneficial to YST establishment and reproductive output than smaller disturbances (0.5 m^2).

Second, in addition to disturbance size, the vegetation community that served as the matrix for experimental plots differed between the two experiments (*B. inermis*-dominated [Site I] vs. *B. inermis*-dominated pasture and native forb-dominated hillslope [Site II]), and may impact the response of YST to disturbance size. Given the consistent lack of difference in YST performance between disturbed and undisturbed plots in the smaller-scale experiment when analyzing plots in two drastically different plant communities (*B. inermis*-dominated pasture and native forb-dominated hillslope), I would suggest the different results in Experiments 1 and 2 are likely not due to differences in the matrix plant community in Site I and Site II.

Third, another potentially influential factor related to community composition that differs between these two studies is the presence of YST, with patches absent in Site I, but common in Site II (Rieder 2005). From a separate study, I show that YST seedlings survive better when near other YST or when surrounded by a high cover of YST (Rieder 2005), which may reflect that conspecific facilitation is at work in YST populations as may occur for other species of *Centaurea* (Callaway and Aschehoug 2000, Ridenour and Callaway 2001). Thus, in the absence of facilitative effects from YST neighbors, disturbance may more strongly influence the performance of YST, as suggested by the results from the larger-scale disturbance setting.

Finally, the two experiments differed in seeding methodology. The larger-scale plots were experimentally seeded, because the seed bank and yearly seed rain were expected to be low in Site I, while the smaller-scale plots relied on the existing seed bank and seed rain in Site II. Because the seed bank and seed rain were not quantified in Site II, I suspected propagule limitation might influence the results from the smaller-scale plots. While experimental seeding of larger-scale plots generated 16 seedlings/m^2, existing, ambient seeds on smaller-scale plots generated 49 seedlings/m^2 in 2001 and 83 seedlings/m^2 in 2002, suggesting adequate propagule pressure in Site II compared to the experimentally-imposed propagule pressure in Site I.

I caution that the effect of nitrogen in Experiment 1 may not be representative of the response of YST to nitrogen. The addition of nitrogen was expected to have a positive, if not a synergistic effect with disturbance, but appeared to have no effect on YST response. By mid-summer, perennial vegetation on undisturbed plots receiving nitrogen was noticeably darker green in color than vegetation on undisturbed plots receiving only water, indicating successful application of nitrogen at least to deep-rooted, well-established plants. Quickly drying soils following experimental seed addition, however, may have reduced the availability of nitrogen to establishing YST seedlings, thereby effectively removing the impact of nitrogen from the experiment.

SUMMARY

In summary, while these two studies were conducted as separate experiments, considering them together provides interesting insights. Given the ruderal traits of YST and evidence from previous work (e.g., Gerlach and Rice 2003, Gelbard and Harrison 2005, Hierro et al. 2006), I expected that disturbance, even if small (0.05 m^2), would strongly stimulate the establishment and reproductive output of YST. This was not the case. Only the larger-scale disturbance plots positively influenced YST performance. These two experiments differ strongly in their settings: smaller vs. larger disturbance, grass-dominated vs. forb-dominated plant communities, YST neighbors vs. no YST neighbors, naturally available seeds vs. experimental addition of seeds. Given our results, it is unlikely that differences in the matrix vegetation community or seed availability explain the difference in the response of YST to these two experiments. I suggest that disturbance size and the presence of YST neighbors may be important factors that interact to influence the response of YST to disturbance.

Importantly, this work suggests that the role of disturbance varies given the phase of invasion. Taken together, my results suggest that larger-scale disturbance encourages initial invasion of YST, and once invasion occurs, smaller-scale disturbances are not essential for continued invasion.

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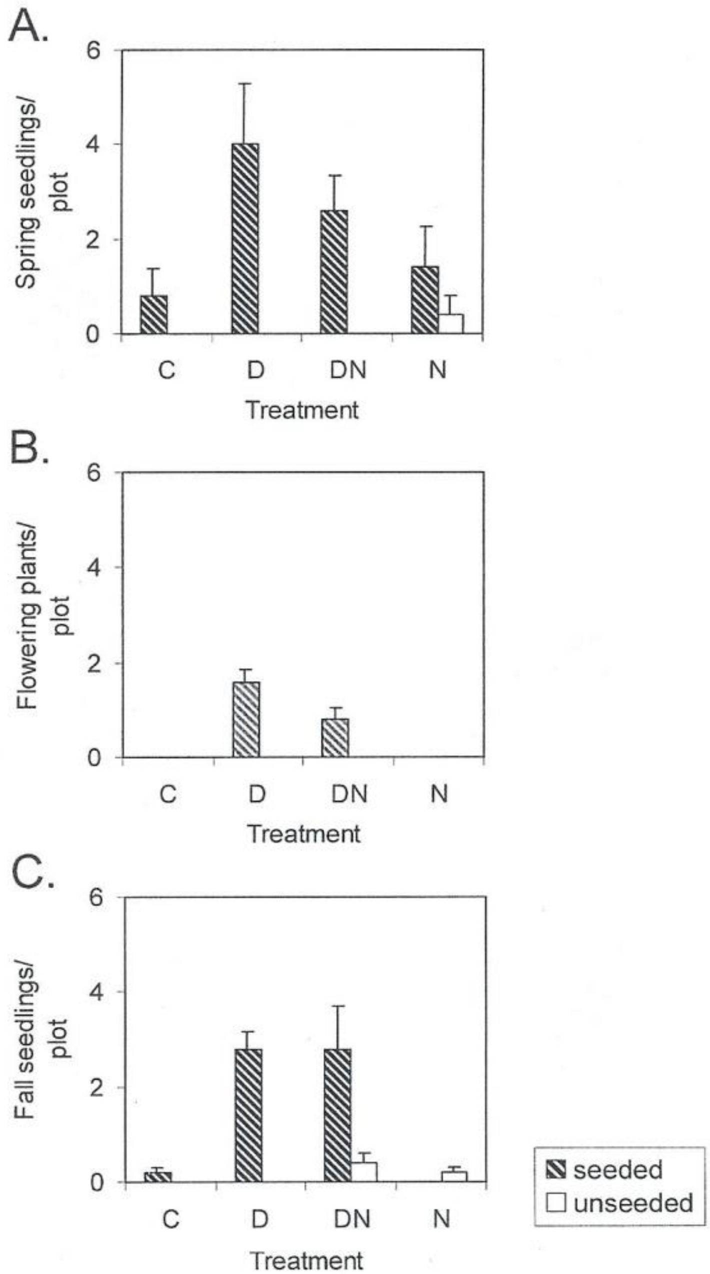

FIG. 1. Yellow starthistle (YST; *Centaurea solstitialis*) establishment and reproductive output on larger-scale disturbance plots in 2002. Average YST performance on seeded and unseeded sub-plots with four treatment combinations (C = control, D = disturbed, DN = disturbed with nitrogen addition, and N = nitrogen addition) are shown for: (A) number of spring-establishing seedlings; (B) number of flowering YST; and (C) number of fall-establishing seedlings. Data shown are means and standard errors.

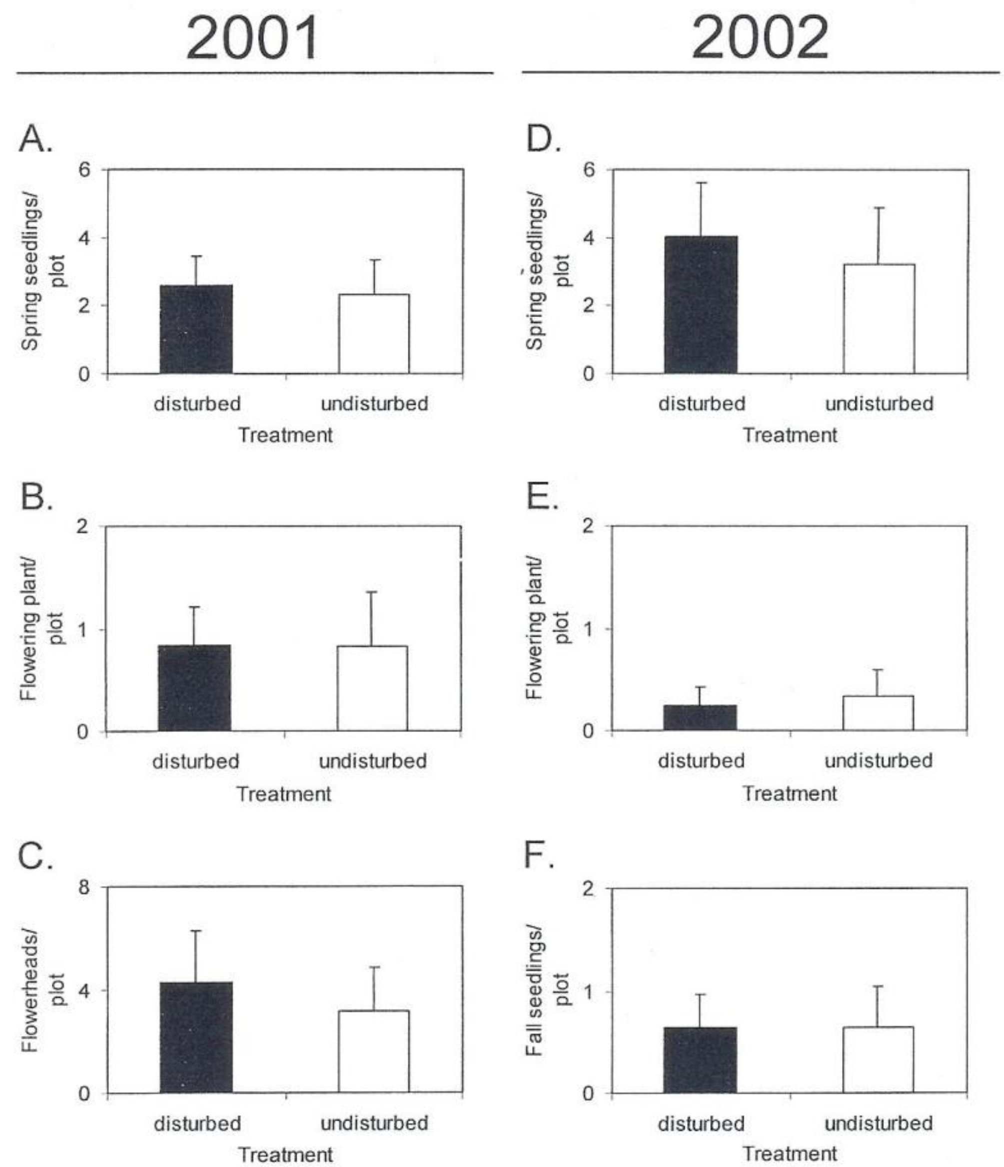

FIG. 2. Yellow starthistle (YST; *Centaurea solstitialis*) establishment and reproductive output on small-scale disturbed and undisturbed plots in 2001 and 2002. Mean YST performance on disturbed and undisturbed plots for 2001 is shown for: (A) number of spring-establishing seedlings; (B) number of flowering YST; and (C) number of flowerheads. Mean YST performance on disturbed and undisturbed plots for 2002 is shown for: (D) number of spring-establishing seedlings; (E) number of flowering YST; and (F) number of fall-establishing seedlings. Fall-germinating seedlings were absent in 2001. Flowerhead production was not measured in 2002. There were no significant differences for any measure of YST performance in either year based on paired t-tests. Data shown are means and standard errors.