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Tolerance of two invasive thistles to repeated disturbance

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Abstract Many invasive species have short life cycles, high reproduction, and easily dispersed offspring that make them good ruderal species under disturbance. However, the tolerance of such ruderal species to disturbance is often overlooked. In a 2-year mowing study, we applied frequent intense disturbances to examine the tolerance of two congeneric invasive thistles, *Carduus acanthoides* and *Carduus nutans*, and potential differences in their responses. Our results show that both species can survive multiple mowing events, with *C. acanthoides* surviving repeated intense mowing through a whole season. Furthermore, *C. acanthoides* was found to adjust its growth form to the disturbance regime, and successfully overwintered and reproduced in the subsequent growing season if the disturbance was terminated. Our results support the idea that tolerance to disturbance should be considered when examining invasions by short-lived monocarpic species, since avoidance of disturbance via rapid life cycle completion and seed production, and tolerance of disturbance via regrowth can co-occur in these species. Consequently, management of short-lived invasives should take both life history strategies into account.

Keywords Disturbance · Tolerance · Invasive · *Carduus nutans* · *Carduus acanthoides*

Introduction

Ecosystems are continually exposed to a variety of disturbances. Natural disturbances, such as hurricanes and flooding, and human-mediated disturbances, such as land-use change and pollution, are becoming more common and severe in terms of frequency, intensity,

extent, and duration (Vitousek et al. 1997; Foley et al. 2005; Jentsch et al. 2007). These disturbances may cause partial or total destruction of biomass, significant changes in substrate properties, resource levels, species interactions, and thereby the structure and function of ecosystems (White 1979; Sousa 1984; Hobbs and Huenneke 1992; Grime 2001).

Plants may respond to disturbance using two different strategies (Bellingham and Sparrow 2000). Plants either avoid disturbance via defense or by escaping in space or time, or tolerate disturbance by regrowing after being damaged, thus reducing biomass loss (Belsky et al. 1993). For example, in severe disturbances that remove most aboveground biomass, plants either regenerate from seed and rapidly complete reproduction (avoidance), or are able to survive and resprout from stem or root fragments to recover lost biomass (tolerance) (Bell 2001). Although the trade-offs between disturbance avoidance and disturbance tolerance may lead to a perceived dichotomy in species responses (Bellingham and Sparrow 2000), these two distinct life histories can co-occur in many short-lived monocarpic species (Martínková et al. 2004; Klimešová et al. 2008; Latzel et al. 2009).

Invasive species are commonly believed to be disturbance adapted (Dukes and Mooney 1999). Many invasive species are classified as ruderals (Grime 2001), which are characterized by short lifespans, fast growth, large reproductive outputs, easily dispersed offspring, and persistent seed banks (Prinzing et al. 2002; Theoharides and Dukes 2007). These life history traits enable the invaders to avoid disturbance by regenerating rapidly from seed and completing their life cycles between disturbance events (Witkowski and Wilson 2001). Hence, numerous studies focus on seed germination, seedling emergence and survival, and seed bank dynamics of species under disturbance as these short-lived species are commonly believed to regenerate only via seeds (Fumanal et al. 2008; Tipping 2008; Meiman et al. 2009). However, the tolerance of these invasive species to disturbance is often overlooked. Failing to

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include tolerance as a possible additional tactic in the face of disturbance may lead to underestimates of the spread and persistence of invasive species in disturbed areas. Consequently, we should consider plant tolerance to disturbance when examining invasions by these short-lived species.

Here we present a study to examine the tolerance of two congeneric invasive thistle species, *Carduus acanthoides* and *Carduus nutans*, to a severe mowing regime. Both species are short-lived monocarps with rapid growth and massive production of wind-dispersed seeds (Desrochers et al. 1988), and colonize disturbed areas such as overgrazed pastures, roadsides, and railroad right-of-ways (Gassmann and Kok 2002; Kok and Gassmann 2002). The two species differ in their morphology and flowering phenology, with *C. acanthoides* having more stems, more but smaller capitula, a lower height at flowering, and a longer flowering period than *C. nutans* (Rhoads and Block 2000). The disturbance regime applied in this study was weekly clipping at 5 cm above ground after plant bolting. Mechanical management such as mowing is commonly applied to control thistle infestations (DiTomaso 2000). We used such a frequent and intense disturbance regime to mimic the commencement of weed eradication management, which often requires high levels of control activity (Panetta 2007). In addition, we used this severe mowing regime to magnify potential differences in the two species' tolerance to disturbance because a previous study (R.Z. and K.S., unpublished) shows that both species can survive and produce viable seeds after three mows at 5 cm above ground within a growing season. We hope to answer the following questions: (1) how does this repeated disturbance regime affect the fitness of the plants in terms of their survival, reproduction, and height (which affects seed dispersal distances for the two species; Skarpaas and Shea 2007)? And (2) do these two species differ in their tolerance to disturbance? The results from our study will improve our understanding of how short-lived invasive weeds tolerate disturbance, and the role that tolerance plays in invasions that occur in frequently disturbed habitats. Furthermore, such knowledge may also generate new insights to improve our use of disturbance to control invasions.

Methods

Study species

Carduus nutans L. (musk thistle: Asteraceae) and *C. acanthoides* L. (plumeless thistle), usually occur in disturbed habitats in their native Eurasia, and commonly invade pastures, rangelands, roadsides, and disturbed areas in North America (Allen and Shea 2006). The stems and foliage of both species are prickly, and likely to deter herbivory (Desrochers et al. 1988). Both species can grow up to 2 m in height under favorable conditions, and have single fleshy taproots (Desrochers

et al. 1988; Feldman and Lewis 1990). Both species are monocarpic perennials, which can behave as summer annuals, winter annuals, biennials, or short-lived perennials (Tipping 2008). Their germination occurs in spring and fall, followed by a rosette stage for one or more years (Allen and Shea 2006). Flowering of the two species requires vernalization. Plants bolt during late spring, flower in summer, and die after producing a large number of wind-dispersed seeds (approximately 3,000–7,000 seeds per plant for *C. nutans* and 1,000–10,000 seeds per plant for *C. acanthoides*) (McCarty 1982; Feldman and Lewis 1990). However, the two species have contrasting morphology and flowering phenology: *C. acanthoides* has a lower branching pattern than *C. nutans*; *C. acanthoides* has a longer flowering period from June to October, compared to *C. nutans* which flowers from May to August (Rhoads and Block 2000). *C. acanthoides* produces more, smaller capitula (1.2–1.6 cm), which are sometimes clustered, while *C. nutans* produces fewer, larger capitula (1.5–4.5 cm in head diameter), which are solitary (Rhoads and Block 2000).

Experimental site

The experimental site was a pasture at the Russell E. Larson Agricultural Research Farm, Rock Springs, Pennsylvania (latitude 40.711°, longitude -77.942°). The pasture was dominated by *Arrhenatherum elatius*, *Dactylis glomerata*, *Elytrigia repens*, *Phleum pratense*, *Taraxacum* spp., *Plantago lanceolata*, *Linaria vulgaris*, *Trifolium* spp., and *Galium* spp.

The site was prepared prior to transplanting the thistle rosettes, to mimic the disturbed areas in which these thistles are commonly observed. A Miller Offset Disk was applied twice to kill all aboveground vegetation, and then a Roller Harrow was applied to level the surface when the soil was fairly dry.

Experimental design

In the summer of 2007, seeds of the two species were collected from two naturally occurring populations in Pennsylvania. These seeds were sown and germinated in a greenhouse. In October 2007, we transplanted 3-week-old seedlings of both species into the field, where they overwintered as rosettes. In early April 2008, we applied approximately 13 g slow-release fertilizer (Osmocote Flower/Vegetable Food, N–P–K: 14–14–14) per plant to ensure that most of the rosettes would bolt in the summer and therefore behave as winter annuals. At the end of May 2008, 50 bolting plants (with obvious elongated stems) of each species were chosen randomly from those available to be included in the experiment.

We used hand clipping to mimic mowing in farming practice. Clipping was initiated in May 2008 after thistles bolted—this was when thistles exceeded surrounding

pasture species and would be likely to be noticed by managers. Forty plants of each species were assigned randomly to be weekly hand-clipped to 5 cm above ground together with surrounding vegetation in a 50 cm × 50 cm area (a maximum of 25 cuts were given by the end of the growing season in mid-November). The other ten plants remained uncut as controls. All *C. nutans* individuals, and the *C. acanthoides* controls, died before November 2008. However, 29 out of the 40 cut *C. acanthoides* were still alive in mid-November 2009, when we paused the experiment because of snow cover. Of these 29 *C. acanthoides* plant, 21 survived the winter, and were included when the experimental treatments resumed in April 2009. Ten of these remaining *C. acanthoides* were assigned randomly to receive the same cutting treatment (weekly clipping to 5 cm above-ground) as in 2008, while the other 11 plants were left uncut for the second growing season. The purpose of having uncut plants in 2009 was to examine the recovery of *C. acanthoides* that had been intensely cut only in the previous growing season.

We conducted weekly censuses from May 2008 to November 2008, and from April 2009 to October 2009, which included plant stem number, plant height, and developmental status (e.g., flowering, setting seed, and dead). Flowering was defined as appearance of visible florets. Death was defined as total senescence of aboveground biomass with no green tissue left. Pollen bags were put onto capitula when florets turned brown in order to prevent seed dispersal. Plants were destructively sampled following their death. The capitula were separated and counted either as viable (contained developed seeds) or aborted (no seed set).

Data analysis

We conducted statistical analyses on survival to reproduction, capitulum production, and plant height at flowering of the two species in R (R Development Core Team 2008). A parametric regression model with Weibull distribution (survreg function in the package of “survival”) was used for the survival analysis of both species in 2008. A Kolmogorov–Smirnov test (Zar 1999) was used to test the difference in the survival of *C. acanthoides* in 2009 because of the non-proportional hazard of plant death. Number of capitula and plant height were analyzed using generalized linear models (GLMs; Crawley 2007). We specified the error distribution as Gaussian in the analyses for plant height, and we used a Quasi-Poisson distribution for number of capitula to account for overdispersion in the data. The ratio of aborted versus viable capitula was analyzed using a logistic regression model by specifying a binomial error distribution in the GLM.

To test how a plant’s recovery capability changed over time, we analyzed plant height before each clipping for the experimental groups using generalized linear mixed models (GLMMs, Crawley 2007) with time as the

fixed effect and time nested in plant as the random effect. For the 2009 data, because treatment started only when plants exceeded the height of 5 cm, plants of height 5 cm or lower in the early season were excluded from the analysis.

Results

Survival to reproduction

In 2008, all controls flowered and then died by the end of the growing season. Twenty-four cuts were needed to kill all *C. nutans* (Figs. 1a, 2a). However, 72.5% of the cut *C. acanthoides* were still alive at the end of the growing season (after 25 cuts) (Figs. 1a, 2d), with 72.4% of these plants surviving the winter and resuming growth in the following spring.

In 2009, all *C. acanthoides* that were not cut in the 2nd year flowered and died (Fig. 2d). All *C. acanthoides* that continued to receive the repeated cutting died without flowering except one plant, which survived until the termination of the experiment in August (a total of 21 cuts in 2009, Fig. 1b).

The survival analyses show that the frequent intense cuts delayed plant death for both species in 2008 ($P < 0.01$). The Kolmogorov–Smirnov test shows that the two survival curves follow different trajectories in 2009 ($D = 0.78$, $n_1 = 9$, $n_2 = 11$, $P < 0.01$, Fig. 1b).

Reproduction

For both species, all of the controls produced viable capitula; 30.0% of cut *C. acanthoides* and 57.7% of cut *C. nutans* had produced buds on their short stems between successive cuts in the 1st year. These buds were removed in the following cutting events. However, we believe they would have developed into viable capitula if cutting had ceased.

For *C. nutans*, all cut plants died without reproducing. For *C. acanthoides*, all plants that were cut in both years died without reproducing. The *C. acanthoides* controls produced significantly more capitula than those that were cut in the 1st year and uncut in the 2nd year (123.3 ± 23.1 vs 26.0 ± 5.8 , $df = 20$, $P < 0.001$, Fig. 2e). Furthermore, controls had a significantly lower proportion of aborted capitula (10.1 ± 2.5 vs $39.1 \pm 3.9\%$, $df = 20$, $P < 0.001$, Fig. 2e).

Plant height

Plant height at the beginning of the experiment did not differ between cut plants and controls ($P > 0.1$) for either species. The heights of living *C. acanthoides* as the experiment was resumed in the 2nd year were not different between treatments ($P > 0.1$).

Fig. 1 Survival curves for *Carduus acanthoides* (black lines) and *Carduus nutans* (grey lines) in both growing seasons. **a** Solid lines Cut plants, dotted lines controls. **b** Solid line *C. acanthoides* that received cutting in both years, dotted line plants cut only in 2008. Plus symbol Censored data

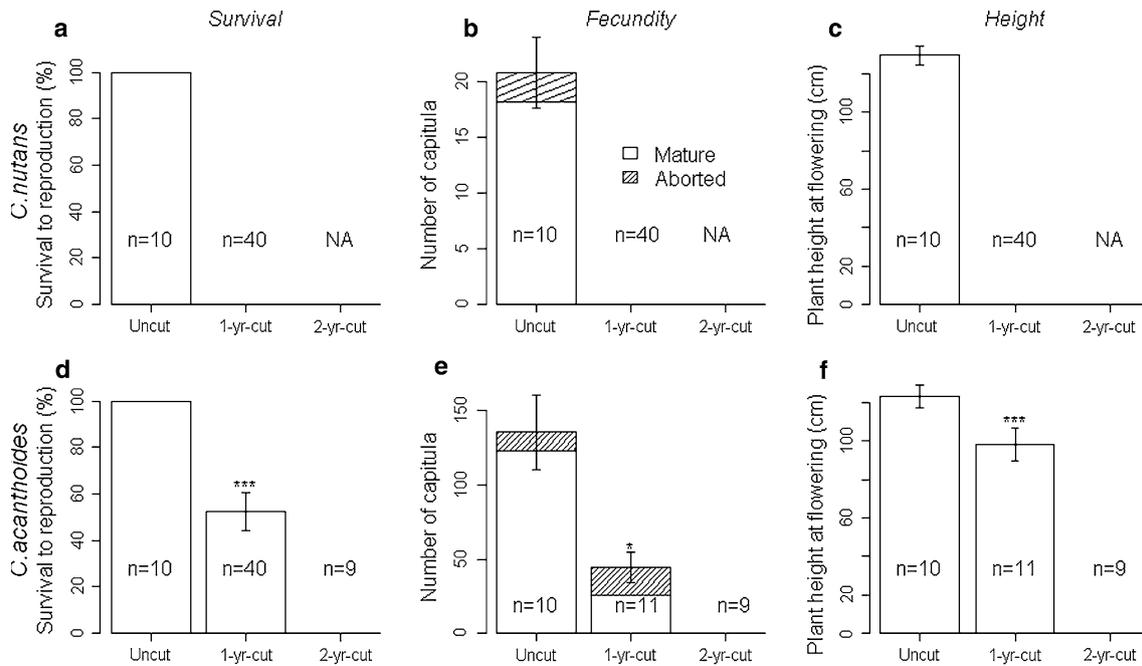
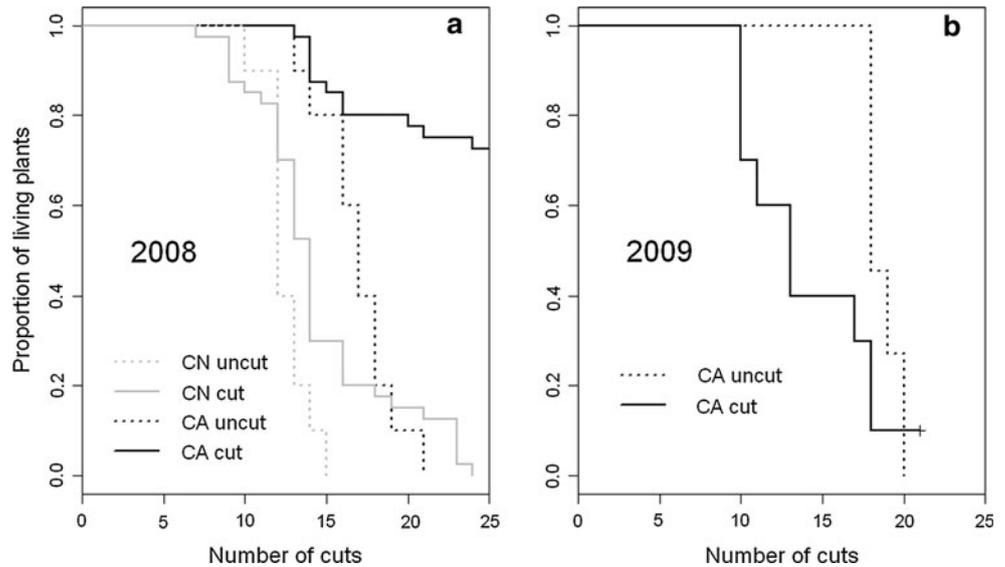


Fig. 2 Effects of weekly clipping on the fitness of *C. nutans* (a–c) and *C. acanthoides* (d–f). **a, d** Survival to reproduction. In **d**, survival to reproduction (represented by the second bar) was calculated as the product of survival until the following spring from the 1st year (21/40), and flowering probability of surviving plants that were not cut in the 2nd year (11/11). **b, e** Lifetime fecundity; *stripe pattern* aborted capitula, *plain pattern* mature capitula containing viable seeds. **c, f** Plant height at flowering. The three treatments are on the x-axis: controls (uncut), plants that were cut only in the 1st year (1-year-cut), and plants that were cut in both

years (2-year-cut). Note that the third treatment did not apply to *C. nutans* as all *C. nutans* died in the 1st year (NA); control *C. acanthoides* flowered and died in 2008 while *C. acanthoides* that were cut only in the 1st year flowered and died in 2009. The *n* values denote number of replicates for each treatment. Note that *n* = 9 for the third bars in **d, e**, and **f**, because one plant survived 2 years of cutting treatments to remain alive at the end of the experiment. Stars denote statistical significance (* *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001) for differences between controls and *C. acanthoides* that had been cut in the 1st year

Repeated removal of the shoot apex disrupted apical dominance, resulting in short plants with more than one induced stem. All continuously cut plants were below 5 cm when they died. The *C. acanthoides*

controls were significantly taller than plants that were cut in the 1st year but not in the 2nd year (123.0 ± 5.8 vs 98.3 ± 8.4 cm, *df* = 20, *P* = 0.028, Fig. 2f).

Changes in heights of living plants before each week's clipping (pre-cut height) are shown in Fig. 3. Height of controls increased until mid-July, when it reached an asymptote. Recovered height of cut plants was greater early in the season, and then diminished towards the end of each growing season. A significant declining trend was found for recovered height of both species in both years ($P < 0.001$).

The two species differed in their tolerance to the repeated disturbance regime. While no *C. nutans* survived the cutting to reproduce in the first growing season (Fig. 2b), cut *C. acanthoides* individuals (even those that had developed buds between cuts) were found to stop stem elongation and instead grew new leaves to form rosettes near the plant base, thus escaping successive cuts. Out of 40 cut *C. acanthoides*, 21 survived the 1st year's disturbance and successfully overwintered as rosettes. These *C. acanthoides* also had a 100% flowering probability if cutting ceased in the second growing season.

Discussion

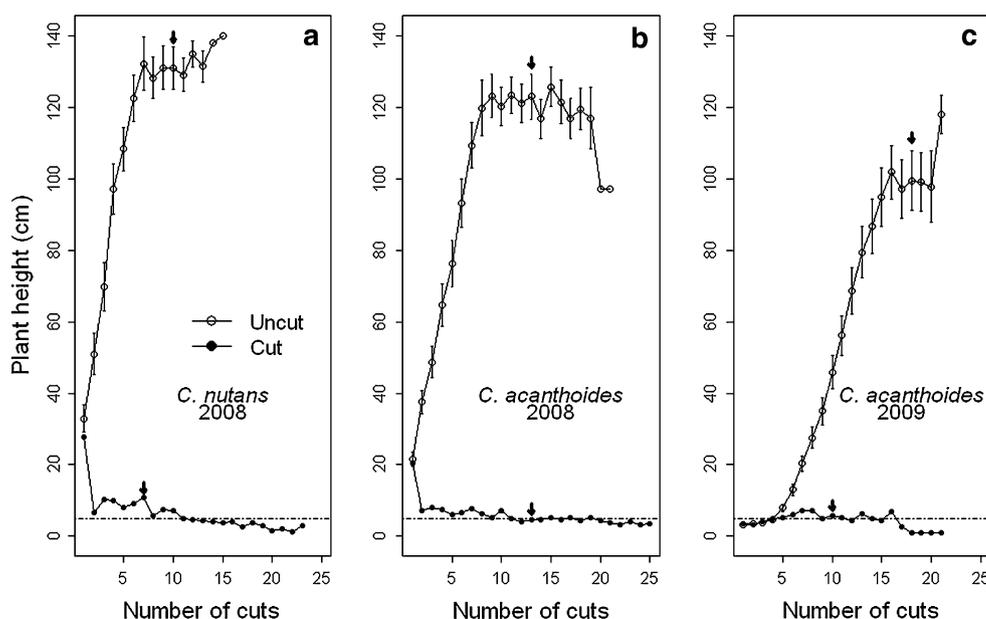
Our study shows that two common invasive weeds in North America, *C. nutans* and *C. acanthoides*, have considerable tolerance to repeated severe disturbance. Although repeated mowing eventually caused large reductions in the survival, reproduction, and height of both species, these species were found to retain high recovery ability and survive numerous cuts (> 10 cuts). Moreover, even though climatic differences between the 2 years may have affected the magnitude of plant recovery, our results in the second growing season nevertheless show that *C. acanthoides* individuals, after being repeatedly cut in the previous growing season,

still had the potential to regrow and reproduce once cutting stopped.

The strong tolerance of *Carduus* spp. to repeated mowing is in contrast to expectations based on the trade-off between reproductive effort and regrowth capability (Bellingham and Sparrow 2000), and between plant defense and regrowth capability (van der Meijden et al. 1988). Both species are typical representatives of the ruderal strategy: they produce a large number of easily dispersed seeds and have short life cycles and persistent seed banks. They also invest significantly in physical defense (i.e., prickles on stems and leaves). Their high tolerance is probably based on resources stored in their fleshy taproots. Previous studies show that root carbon storage plays an important role in resprouting ability of monocarpics (Klimešová and Klimeš 2003; Sosnová and Klimešová 2009). Although no study has examined the root systems of these two species in particular, studies of other nonclonal thistles suggest that their deep taproots may be good at resource acquisition and storage (DiTomaso et al. 2003; White and Holt 2005; Eckersten et al. 2010). Additionally, disturbance timing also affects tolerance (Martinková et al. 2008). Since our cutting treatments started after bolting but before flower emergence, plants' investment in reproduction (both resource reallocation and meristem differentiation) was not complete. Therefore, plants were possibly able to utilize remaining resources for regrowth.

The two species, though similar in their life cycles, differ in their tolerance to repeated disturbance. *C. acanthoides* was more tolerant than *C. nutans* as it maintained a higher survival and higher recovery ability after being damaged. Moreover, flowering in cut *C. acanthoides* was found to delay to the second growing season while all cut *C. nutans* died in the first

Fig. 3 Dynamics of plant height for *C. nutans* (a) and *C. acanthoides* in 2008 (b) and in 2009 (c). Error bars Standard errors for controls (open symbols). Standard errors for pre-cut height of cut plants (filled symbols) are too small to be represented in the graph. Dashed horizontal line Height of 5 cm to which plants were cut weekly, arrows point at which the first death occurred in each group. Note that the last few data points of each curve are potentially biased because of limited sample size of living plants toward the end of the experiment



growing season. This large phenological delay, although not expected for strict monocarpic species (Huhta et al. 2009, Piippo et al. 2009), has also been observed in other monocarpic species under severe disturbance (Klimešová et al. 2007). This strategy enables *C. acanthoides* to adjust its life history to disturbance and increases its chances of survival and reproduction in the future. The greater tolerance of *C. acanthoides* may be due to its lower branching pattern, later flowering phenology and longer flowering period. The lower branching pattern, and hence a lower shoot apical meristem position, minimized loss of meristems and preserved the meristem pool, which is crucial for later regrowth (Rosenthal and Kotanen 1994; Huhta et al. 2000; Rautio et al. 2005). This result agrees with a previous finding in *Centaurea solstitialis*, where a low-branching phenotype was less affected by mowing than a high-branching phenotype (Benefield et al. 1999). Furthermore, a longer flowering period ensures a slower increase in reproductive investment in *C. acanthoides*, which reduces biomass loss in the cutting treatment.

Our results provide new insights for management. More attention should be paid to the strong tolerance of *Carduus* spp. when managing these invasive weeds. These species have a great potential for recovery after being damaged, and may cause further infestations if not completely eradicated, especially given their large reproductive outputs and significant dispersal ability (Desrochers et al. 1988; Skarpaas and Shea 2007). Furthermore, as suggested by this study and also noted in other studies (R.Z. and K.S., unpublished; Gao et al. 2009), purely increasing management frequency without attention to appropriate timing may not effectively reduce plant fitness. This notion is especially important for management of *C. acanthoides*, given the findings of the present study.

In conclusion, some short-lived invasive species have considerable tolerance to repeated disturbance. This tolerance of disturbance may be especially important for their establishment at invasion fronts, where propagule pressure is low and Allee effects are likely (Wilson et al. 2009). Therefore tolerance to disturbance, in addition to rapid growth rate and large seed production, should be taken into account when studying invasions of ruderal species, as potential synergistic effects between disturbance tolerance and avoidance may accelerate invasion processes. Furthermore, management should be adjusted to acknowledge the tolerance of these species, especially when native counterparts are not as adapted to disturbance.

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