

ARTICLE

Pest management in future climates: Warming reduces physical weed management effectiveness

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Abstract

Climate change alters many aspects of weed performance and may also alter the effectiveness of management practices to control pests. Despite this concern, entire categories of widely used management practices, such as physical control, remain understudied in this context. We conducted a field experiment growing the invasive pest musk thistle (*Carduus nutans*) at ambient and experimentally elevated temperatures. We tested mowing management strategies that varied in the timing of a single mowing event relative to thistles' stem elongation phenology and compared these with an unmowed control. Results from this experiment informed demographic models to project population growth rates for different warming/mowing scenarios. Compared to plants grown under ambient conditions, warmed thistles were more likely to survive the same mowing treatment, flowered earlier in the season, grew to taller heights, and produced more flowering capitula. Proportional reductions in plant height and capitulum production caused by mowing were smaller under warming. Warming did not change the relative ranking of mowing treatments; mowing late in the growing season (2 weeks after individuals first reached a height of 40 cm) was most effective at ambient temperatures and under warming. Warming caused significant increases in projected local population growth rate for all mowing treatments. For invasive musk thistle, warmed individuals outperformed individuals grown at ambient temperatures across all the mowing treatments we considered. Our results suggest that to achieve outcomes comparable to those attainable at today's temperatures, farmers will need to apply supplemental management, possibly including additional mowing effort or alternative practices such as chemical control. We recommend that scientists test management practices under experimental warming, where possible, and that managers monitor ongoing management to identify changes in effectiveness. Information about changes in managed weeds' mortality, fecundity, and phenology can then be used to make informed decisions in future climates.

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KEYWORDS

Carduus nutans, climate change, integral projection model, invasive species, mechanical weed management, mowing

INTRODUCTION

Future food security depends on the continued productivity of crops and livestock in a changing climate (Godfray et al., 2010). Rising temperatures have the potential to affect the performance of crops and livestock, as well as their interactions with pests and pathogens (Howden et al., 2007), which are currently estimated to reduce annual yields of major crops by ~25%–40% (Flood 2010; Myers et al., 2017). Weeds, or undesirable plants that cause economic harm in croplands or rangelands, are projected to have increased impact under climate change in some cases, as weed ranges expand (Bradley et al., 2009) and competition between weeds and crops increases (Tungate et al., 2007). Weed impacts under climate change are largely uncertain, however, causing concern among managers (Beaury et al., 2020). Elevated temperatures can alter many aspects of weeds' biology, including their growth (Patterson et al., 1979), phenology (Zhang et al., 2012), demography (Keller & Shea, 2021), and dispersal (Zhang et al., 2011).

Climate change may also alter the effectiveness of management practices to control weeds. For example, researchers have found that increased CO₂ concentrations can reduce the effectiveness of herbicide (Ziska et al., 1999). Entire classes of weed management practices remain unstudied in the context of climate change (Ziska et al., 2011). In their most recent report, members of the Intergovernmental Panel on Climate Change (Porter et al., 2014) noted, "To date, studies on physical, cultural, or biological weed control are lacking." Lack of information about climate change impacts on management effectiveness can result in poor intervention choices and suboptimal outcomes.

Physical weed control techniques (also commonly called mechanical control techniques), including hand-pulling, hoeing, tilling, and mowing, are widely used methods for limiting the spread and local population growth of weeds (Ross & Lembi, 2009), but their continued effectiveness under climate change is uncertain (Birthisel et al., 2021). Physical damage can cause weed mortality (Bovey & Meyer, 1974), reduce weeds' carbohydrate reserves (Sturkie, 1930), and reduce or entirely prevent seed production (McCarty & Hatting, 1975). On organic farms, where chemical weed management is prohibited, physical weed control is an essential component of pest management plans (Bond & Grundy, 2001). On farms where herbicide

application is permitted, physical weed control is growing in importance due to the emergence and spread of herbicide resistant weeds (Norsworthy et al., 2012; Walsh & Powles, 2007) and increasing concern over the environmental impacts of ubiquitous herbicide application (Bourguet & Guillemaud, 2016; Geiger et al., 2010).

The timing of physical weed management within the season and relative to the phenology of targeted weeds can strongly affect its outcome (e.g., Brownsey et al., 2017; McCarty & Hatting, 1975; Milakovic et al., 2014). Understanding the importance of management timing on impact has the potential to save effort and costs. For example, a single well-timed mowing can equal the performance of repeated mowing (Zhang & Shea, 2012). As the seasonal timing of many plants' life cycle events shift in response to rising temperatures (Miller-Rushing & Primack, 2008), opportune times for applying weed control may also shift (Hatfield et al., 2011). Phenological shifts in response to climate change can alter the timing of life cycle events and also the duration of phenological stages (Post et al., 2008), thereby changing the timing and duration of life stages vulnerable to management and the timing and duration of periods during which weeds recover after being managed.

Musk thistle, *Carduus nutans* L., is among the most widely listed invasive weeds in the United States (Skinner et al., 2000), and it is known to have improved performance under warming (e.g., Keller & Shea, 2021), but the ability of management to mitigate these improvements remains unknown. This weed, also known as nodding thistle, is an herbaceous monocarpic perennial that grows as a low-lying rosette for one to several years before bolting and producing a flowering stem that can reach heights of over 2 m (Desrochers et al., 1988). Bolting begins in spring, and individuals typically flower in early summer (Desrochers et al., 1988). Individual musk thistle plants can produce over 10,000 pappus-bearing achenes that disperse on the wind (McCarty, 1982). Musk thistle is native to Eurasia, but it has established invasive populations in many areas around the globe, including in North America, South America, Australia, and New Zealand (GBIF, 2017). In its invaded range, musk thistle is common along roads, in waste areas, and in rangelands and pastures, where its spiny leaves deter herbivores and reduce livestock productivity (Desrochers et al., 1988).

Temperature affects many aspects of musk thistle performance. Prior work showed that plants grown under experimentally elevated temperature in the field had

higher survival, produced more capitula, and reached taller end-of-season heights than plants grown at ambient temperatures (Zhang et al., 2011). Capitula from experimentally warmed plants had a significantly higher probability of releasing seeds during wind-tunnel trials (Teller et al., 2016). Together, these changes are projected to increase local population growth rates and accelerate spread of musk thistle (Teller et al., 2016; Zhang et al., 2011). Elevated temperatures also advance the seasonal timing of stem elongation, flowering, and growth cessation (Zhang et al., 2012). Earlier flowering and seed release under warming can lead to earlier germination of new individuals, which in turn causes individuals to grow larger before their first winter and increases the proportion of individuals that flower as winter annuals rather than as biennials or perennials (Keller & Shea, 2021). The extent to which other weeds may show similar changes in growth patterns under climate warming remains largely unknown, as plants' responses to changing climate can be idiosyncratic, depending on individual species' traits and the structure of the ecosystem in which they are present (Peters et al., 2014; Ramesh et al., 2017; Stratonovitch et al., 2012).

Musk thistle is managed using a variety of methods including chemical control, classical biological control, and physical control (Trumble & Kok, 1982). As for many other rangeland weeds, mowing is widely recommended to reduce musk thistle seed production and plant height, which reduces dispersal distances of wind-dispersed seeds (DiTomaso, 2000; Trumble & Kok, 1982). Thistle height is an important contributor to the dispersal distances of their wind-dispersed seeds (Skarpaas & Shea, 2007) and reducing plant height is one common objective of mowing thistles (Trumble & Kok, 1982). Mowing can reduce population size when applied repeatedly or at specific, impactful points in the musk thistle life cycle (McCarty & Hatting, 1975; Tipping, 2008; Zhang & Shea, 2012, 2019). Recommendations vary for when mowing can be applied most effectively, ranging from prior to flowering to after flowering is complete (Tipping, 2008).

We measured the impact of elevated temperature on the effectiveness and optimal timing of physical weed control for musk thistle (*Carduus nutans*) in a split-plot field experiment applying mowing treatments to individuals grown in plots assigned to two temperature treatments: ambient and warmed. Specifically, we investigated how passive warming in fiberglass open top chambers (OTCs) affected mowing effectiveness at reducing four aspects of musk thistle performance: survival, timing of flowering (which affects offspring performance), end-of-season plant height (which affects seed dispersal), and flower head production. We used experimental results to inform demographic models to assess the population dynamics of

populations subjected to each mowing and temperature treatment combination. This research begins to fill the gap in vital knowledge concerning potential climate change impacts on widely used methods of weed management.

METHODS

Field experiment

We conducted a two-cohort field experiment at the Russell E. Larson Agricultural Research Center in Rock Springs, Pennsylvania (latitude 40.71° N, longitude 77.94° W) from 2014 to 2017. The site was prepared before planting each cohort by applying a Miller Offset Disk two times to kill aboveground vegetation and then applying a roller harrow to level the soil surface. This preparation mimicked the type of disturbance that promotes musk thistle establishment along roadsides and in pastures. We clipped all non-focal plants growing within plots to the soil surface weekly. This clipping avoided a possible interaction between temperature treatments and vegetative competition and also simulated grazed pasture, where musk thistle causes significant economic damage.

We marked blocks (10 in 2016, 16 in 2017), each containing two 2 × 2 m plots, one of which was randomly assigned to be warmed using a fiberglass cone open top chamber (OTC) and the other of which was left at ambient temperature. Open top chambers had basal diameter of 1.48 m and were constructed according to the International Tundra Experiment Manual (Molau & Mølgaard, 1996). Throughout the experiment, temperature was monitored hourly in warmed and ambient plots using HOBO pendant temperature loggers (Onset Computer Corporation Part# UA-002-08) installed at the soil surface. Open top chambers warmed plots by an average of 0.31°C, a relatively small amount compared to regional projections of increases of 2.9°C–5.3°C in annual surface air temperature by the end of this century (Hayhoe et al., 2007). Temperature differences between warmed and ambient control plots were greatest in January, when warmed plots averaged 0.71°C (95% CI [0.50°C, 0.91°C]) warmer than ambient plots, and the difference was least in September, when the average difference between warmed and unwarmed plots was not significant. Prior work at this field site showed no significant effect of OTCs on soil moisture or snow depth (Zhang et al., 2012).

Thistle seedlings were started in the greenhouse in August and transplanted in late September with ~13 g Osmocote slow release fertilizer to ensure plants bolted in the following summer. We planted four thistles separated by 50 cm in a square array at the center of each plot. Individual thistles within each plot were randomly assigned to four mowing treatments: early mow (mowed

at the first weekly census when the plant height exceeded 40 cm), middle mow (mowed 1 week after the plant grew over 40 cm tall), late mow (mowed 2 weeks after reaching a height of 40 cm) and a control that was not mowed, in a blocked split-plot design. Mowing was thus applied based on individual plants' stem elongation phenology, rather than on a fixed date for all individuals in a treatment to account for differences in phenology between plants grown at different temperatures, and followed prior recommendations for mowing timing, which are commonly related to thistle phenology (Trumble & Kok, 1982). Mowed plants were clipped to a height of 10 cm. Cut material was removed from the field, as is recommended to prevent mowed material from possibly continuing to mature seed (Zhang, 2011).

We recorded thistle height, and approximate percent leaf area lost to herbivores in weekly observations from spring through the summer. Flowering phenology observations were taken twice each week. The most-developed head on each plant was classified as non-flowering, early flowering (after first anthesis), full flowering (all florets on the capitula exerted), or senescing (brown, dry florets present on a post full-flowering capitula). We tied mesh bags over senescing flower heads before they began releasing seed at the site to prevent seed dispersal into other areas of the research facility and to retain seeds. Plants were harvested in late July and early August as they reached senescence. Harvested thistles were processed in the lab, where the final number of capitula they produced was recorded.

Data analysis

We analyzed the effects of warming and mowing by considering several plant responses to these treatments, including spring rosette size, date that plants reached the height threshold for mowing, date that plants first flowered, survival after mowing, and number of capitula produced. We analyzed treatment effects on rosette size, date of mowing, plant height, and date of flowering using linear mixed effects models fit using the function *lmer* from the package *lme4* (Bates et al., 2015) in the statistical computing program R version 3.4.1 (R Core Team, 2017). Data describing capitulum production were analyzed with a generalized linear mixed effects model with a Poisson error distribution and log-link function fit using the function *glmer*, also from the library *lme4*. In these models, we included mowing treatment, temperature treatment, the interaction between these two factors, and fall longest leaf length as predictors. We included nested random effects for plots within blocks in all models in order to account for our repeated split-plot experimental

design. We performed backward model selection based on AIC using the function *drop1*. To compare mean values across treatments, we used Tukey's Honestly Significant Differences post hoc tests (Tukey HSD) calculated with the function *lsmeans* from the library *lsmeans* (Lenth & Hervé, 2015).

To analyze warming and mowing effects on thistle survival, we fit a binomial mixed effects model. Some combinations of warming and mowing treatments had 100% survival, making maximum likelihood estimation of regression model parameters impossible. We therefore employed Bayesian Markov chain Monte Carlo estimation to fit the binomial mixed-effects model using the function *MCMCglmm* from the library *MCMCglmm* (Hadfield, 2017). We used uninformative priors and ran the sampler for 130,000 iterations, discarding the first 30,000 and thinning by taking every 50th iteration. For this regression, we based our backward model selection on deviance information criterion (DIC) comparisons.

Demographic model

Data describing musk thistle demography under ambient temperatures and under warming in OTCs were collected in a separate field study (Keller & Shea, 2021), and used to develop a baseline demographic model. This co-located experiment used identical OTCs to those used in the experiment described here and was aimed at measuring the effect of shifting seed release phenology on musk thistle demography. In the prior experiment, seeds were planted at seven dates ranging from August through October (Keller & Shea, 2021) in each of 2 years (2012 and 2013) and individuals' performance was tracked through their entire lifespan. Details about this experiment can be found in Keller and Shea (2021). To add the effects of mowing that were observed in this study to the baseline model, we adjusted bolting individuals' probability of surviving and number of seeds produced by multiplying by constants, and we altered the date of first flowering to reflect the changes in these values documented here.

We constructed integral projection models (IPMs; Easterling et al., 2000; Merow et al., 2014; Ellner et al., 2016) in R to project the population growth rate of musk thistle populations at different temperatures managed under each of our four mowing treatments. IPMs use regression to model the relationship between organisms' states (in our case, their sizes, measured by log-transformed longest leaf length) and their vital rates including survival, growth, reproduction. We used log transformed fall longest leaf length as our state variable because in fall, all individuals are rosettes (except any ungerminated seeds in the seed bank, which are ignored

here due to extremely low second season germination observed in the field) because individuals that reproduced in the previous summer die after flowering. Longest leaf length has been shown in prior studies to be a good proxy for plant size (Kelly & Popay, 1985; Shea & Kelly, 1998). While we report plant height to inform managers of potential impacts of management on dispersal of musk thistle’s wind-dispersed seeds, this variable is not included in the demographic model. We built a kernel describing the probability of all possible annual size transitions, and we projected changes in the numbers and sizes of individuals $n(z, t)$ over time as follows:

$$n(z', t + 1) = \int_L^U [s(z, w) (1 - p_b(z)) G(z', z, w) + s(z, w) p_b(z) p_s(w, m) b(z) p_f(w, m) p_r c_0(z', d_f)] n(z, t) dz$$

where z indicates size at time t , z' indicates size at $t + 1$, w denotes temperature treatment, m denotes mowing treatment, and U and L denote the upper and lower size limits for individuals, respectively. Effects of temperature and mowing treatment were incorporated in model functions only where our regression analysis indicated they had significant impacts.

The first term in the integral describes annual transitions for individuals that do not reproduce. These individuals survive over winter based on a size- and temperature-dependent survival function $s(z, w)$. They do not reproduce, so this term includes $1 - p_b(z)$, where $p_b(z)$ represents the size-dependent probability of reproducing. Their size in the next year is projected by $G(z', z, w)$, the growth kernel, which gives the size and temperature-dependent frequency distribution of surviving individuals transitioning from size z to size z' . These non-reproductive individuals grow as flat rosettes and are not impacted by mowing in this model.

The second term in the integral describes annual transitions for individuals that do reproduce. Musk thistle is a monocarp, so reproducing individuals do not survive after reproducing, but rather contribute to the next year’s population by producing new individuals. To produce offspring, individuals must first survive over winter with probability $s(z, w)$ and reproduce with probability $p_b(z)$. Reproducing individuals extend flowering stems and are impacted by mowing, which causes temperature and mowing treatment-dependent mortality $p_s(w, m)$. Flowering individuals produce a size-dependent number of seeds, given by the function $b(z)$, which is modified by temperature and mowing treatments by multiplying by $p_f(w, m)$, the proportional change in fecundity relative to unmowed plants grown at ambient conditions. Seeds germinate and become established with probability p_r and grow to a size projected by $c_0(z', d_f)$, the frequency distribution of offspring sizes.

This distribution depends on the date of first flowering, d_f . In musk thistle, earlier flowering leads to earlier germination and larger offspring sizes (Keller & Shea, 2021).

We fit vital rate regressions with data from the concurrent, co-located, field experiment using identical OTCs. Full details describing this experiment are available in Keller and Shea (2021). We used log-transformed fall longest leaf length measured in centimeters as our state variable and set the upper size limit at 4.5 and lower size limit at -1 . These size boundaries were adequate to prevent problematic eviction, a common issue where IPMs project transitions beyond the bounds of considered sizes (Williams et al., 2012). Our model does not include a seed bank, as germination after the first growing season was minimal in our field study, though spring germination has been observed to occur in some populations (e.g., Lee & Hamrick, 1983), and seeds may potentially survive in a seedbank for several years (Burnside et al., 1996). The probability of germination was taken from Lee and Hamrick (1983). We evaluated the integral using numerical integration, discretizing the kernel into a large matrix with dimension 300×300 . The resulting matrix was then analyzed using the well-developed toolset for matrix population models, including analyses to calculate the per-capita population growth rate (λ) (Caswell, 2001). We used the R function *boot* from the library *car* (Fox et al., 2012) to perform 1000 bootstrapping iterations and estimate 95% confidence intervals for λ estimates.

RESULTS

We planted and monitored 208 thistles over the course of the experiment (Data S1). One individual assigned to the warming and early mowing treatment died during the winter and was excluded from our analyses. All surviving thistles grew as winter annuals, flowering in the summer following their first winter. By spring, warmed thistle rosettes had longest leaf lengths significantly larger than those of rosettes grown at ambient temperatures (as of mid-April, ambient mean = 17.3 cm, 95% CI [16.2, 18.3]; warmed mean = 21.2 cm, 95% CI [20.1, 22.2], t test $p < 0.001$; Appendix S1: Table S1). Across all mowing treatments, warmed thistles reached the 40 cm height threshold that determined mowing treatment time significantly earlier than did thistles grown at ambient temperatures. Warmed thistles were mowed 9.3 days earlier, on average (ambient mean = day of year 162.8, 95% CI [160.3, 165.2]; warmed mean = day of year 153.5, 95% CI [151.0, 155.9], t test $p < 0.001$; Appendix S1: Table S1).

Backward model selection did not retain interactions between warming treatments and mowing treatments in

any of the regressions for our responses (survival, day of first flowering, height, and fecundity). We therefore present field experimental results describing the impacts of temperature and the impacts of mowing separately, though the projection model includes both effects. Means presented in the following sections are least-squared means averaged across fall longest leaf lengths and across all levels of the other, non-focal treatment.

Thistle responses to mowing

Survival after mowing was not affected by early or middle mowing treatments, but was significantly reduced by late mowing (Figure 1a, Markov-Chain Monte Carlo p value (p -MCMC) = 0.01; Appendix S1: Table S2). All mowing treatments significantly delayed the timing of flowering (Figure 1b). Because we completely removed mowed material, we here consider flowering date to be the first

day on which anthesis was observed after mowing had occurred (if mowing was ever applied). Thus, the flowering date analyzed here corresponds to the date of flowering for capitula that could potentially produce seed under the focal management regime. Late mowing had the greatest effect on flowering date, pushing flowering back by 28.4 days on average (control mean = day of year 169.7, 95% CI [167.57, 171.8]; late mean = day of year 198.1, 95% CI [195.8, 200.3]; Tukey's HSD $p < 0.001$; Appendix S1: Table S3). End-of-season plant height was significantly reduced by all mowing treatments (Figure 1c). Late mowing was most effective, reducing plant height by 57.0 cm, on average (control mean = 123.5 cm, 95% CI [115.9, 131.2]; late mean = 66.5 cm, 95% CI [58.5, 74.6]; Tukey's HSD $p < 0.001$; Appendix S1: Table S3). Fecundity, here measured as the number of flowering capitula plants produced, was significantly reduced by all mowing treatments (Figure 1d). Late mowing had the largest effect on

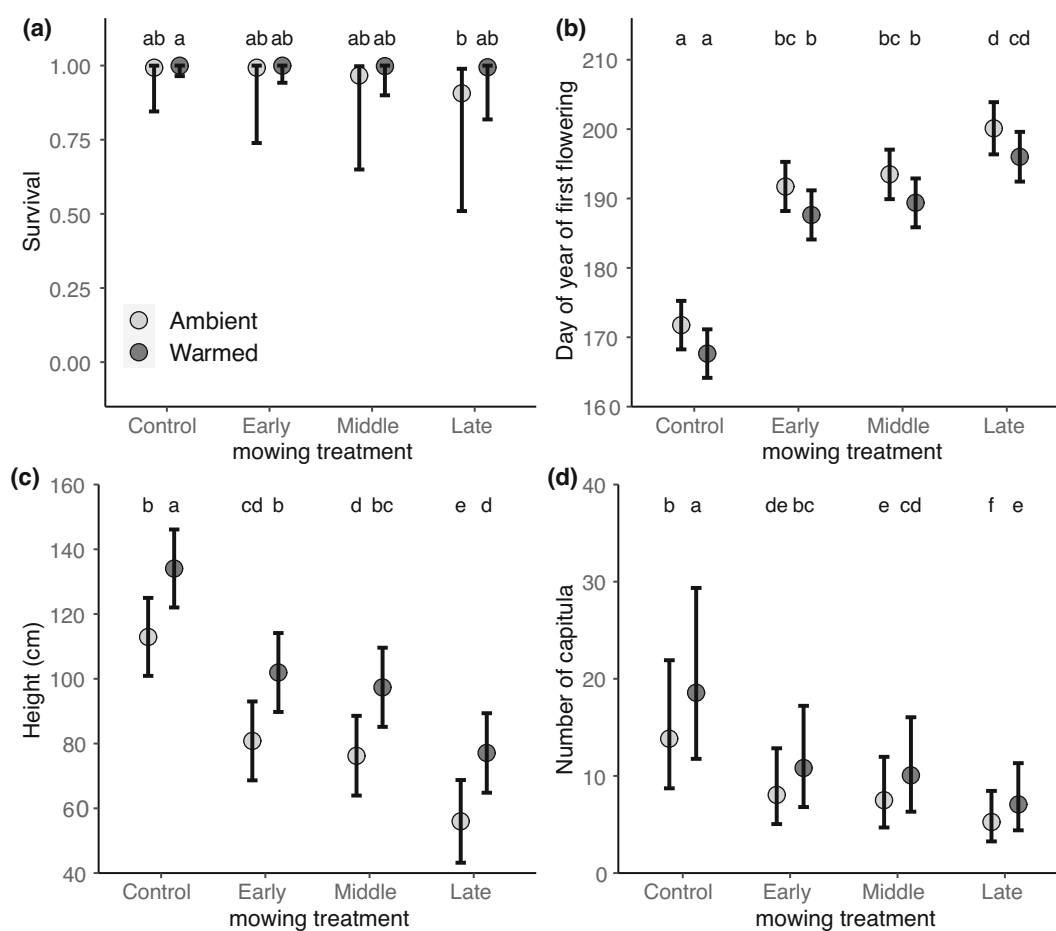


FIGURE 1 Responses of (a) post-mowing survival, (b) first flowering date, (c) end-of-season height, and (d) number of capitula to warming and mowing for musk thistles mowed at 0 (Early), 1 (Middle), and 2 weeks (Late) after individuals first reached 40 cm in height, plus an unmowed control. Points show estimated means and error bars show 95% confidence intervals. Results for warmed thistles are shown in dark gray, and results for thistles grown at ambient conditions are shown in light gray. Treatment combinations that do not share a letter label (across top of plot) are significantly different ($p < 0.05$), by Tukey's HSD test

fecundity, reducing capitula production by 9.9 capitula per plant, on average (control mean = 16.0 capitula per plant, 95% CI [11.6, 22.1]; late mean = 6.1 capitula per plant, 95% CI [4.4, 8.5]; Tukey’s HSD $p < 0.001$; Appendix S1: Table S3).

Thistle responses to warming

Thistles grown under experimental warming were significantly more likely to survive mowing (Figure 1a, p -MCMC = 0.012; Appendix S1: Table S2). Warming advanced flowering date by an average of 4.1 days across all mowing treatments (Figure 1b; ambient mean = day of year 189.3, 95% CI [187.3, 191.2]; warmed mean = day of year 185.2, 95% CI [183.3, 187.1]; t -test $p = 0.005$; S1: Table S3). Warming significantly increased plant height in all mowing treatments (Figure 1c). Experimentally warmed thistles were 21.1 cm taller, on average, than thistles grown at ambient temperatures (ambient mean = 81.5 cm, 95% CI [74.7, 88.3]; warmed mean = 102.6 cm, 95% CI [96.0, 109.3]; t test $p < 0.001$; Appendix S1: Table S3). Warming increased capitulum production by 2.8 capitula per plant, on average, across all mowing treatments (Figure 1d; ambient mean = 8.1 capitula per plant, 95% CI [5.9,11.3]; warmed mean = 10.9 capitula per plant, CI [7.9, 15.1]; t test $p = 0.0003$; Appendix S1: Table S3).

Demographic impacts of warming and mowing

None of our mowing treatments are projected to decrease musk thistle’s per capita population growth rate below one, indicating that under our favorable experimental conditions, with competition suppressed and adequate nutrients, a single mowing is insufficient to stop population growth for musk thistle populations (Figure 2). All mowing treatments significantly reduced population growth rate relative to unmowed controls grown at the same temperature (t tests, $p < 0.05$). Warming significantly increased population growth rate within each mowing treatment (t tests, $p < 0.05$).

DISCUSSION

Mowing was less effective in reducing musk thistle performance under experimental warming applied in the field. Compared to thistles growing at ambient conditions, warmed plants were more likely to survive mowing, flowered earlier, grew to taller heights, and produced more capitula. These changes contributed to more rapid

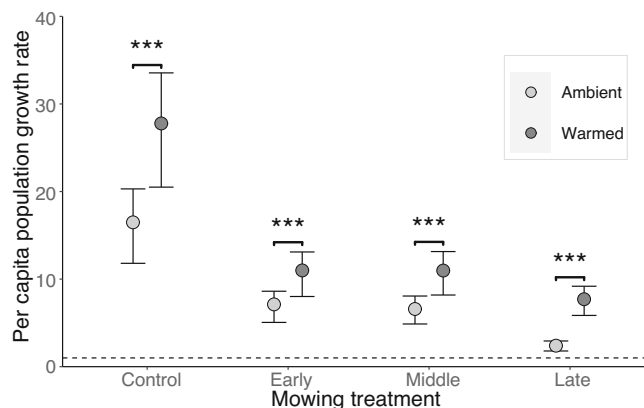


FIGURE 2 Projected local per-capita annual population growth rates for unmowed control thistles and for thistles mowed at 0 (Early), 1 (Middle), and 2 weeks (Late) after individuals first reached 40 cm in height at ambient temperatures (light gray) and under experimentally applied warming (dark gray). Error bars show a 95% confidence interval based on 1000 bootstrapping iterations. The horizontal dashed line at $y = 1$ indicates the population growth rate at which populations remain at equilibrium. Values above this line indicate projected population growth, while values below the line indicate projected decline. Within each mowing treatment, projected population growth rate for warmed and ambient plants was significantly different at $p < 0.001$, indicated by brackets with asterisks above

projected population growth rates for mowed thistles under warming, compared to thistles mowed at ambient temperatures. The most effective timing of mowing, relative to thistle’s growth, was not changed by warming. These results point to the potential for rising temperatures to alter the effectiveness of physical weed management in the future. Physical weed management plays a crucial role in integrated weed management plans as farmers work to ensure food security under climate change. Planning for successful weed management requires knowledge on weed biology and knowledge on the effectiveness of management practices, both of which, we show, are subject to alteration with changing climate.

Prior work has demonstrated that musk thistle biology is affected by elevated temperatures; experimentally warmed thistles had increased height, fecundity, and projected local population growth rate (Zhang et al., 2011). We show that these warming-induced changes in performance persist when plants are managed using mowing. Further, we show that estimates of management effectiveness based on current conditions are likely to overestimate mowing impacts under warmer conditions expected in the future. For example, at ambient temperatures, a single mowing 14 days after plants first reach a height of 40 cm is projected to reduce projected population growth rate by 85.3%, while the same management applied under moderate warming of 0.31°C reduced

population growth rate by only 72.4%. Therefore, in this case, information on changes in weed performance and on changes in management effectiveness are both required to accurately project outcomes. Even if farmers are aware that weed performance is expected to change under warming, their decisions may be hampered by inaccurate assumptions about continued management effectiveness, potentially leading to misguided management decisions.

Reduced mowing effectiveness under experimental warming may necessitate increased effort and/or use of alternative management. Our results indicate that later mowing is most effective. If mowing is delayed too long, however, thistles will set seed before being mowed. Repeated mowing has the potential to make up for lost effectiveness of single mowing strategies (Zhang & Shea, 2012) but is more costly. Alternatively, chemical control can supplement or replace physical control. Musk thistle has been a repeated target for classical biological control, and several biocontrol agents from musk thistle's native range including *Rhinocyllus conicus*, *Trichosirocallus horridus*, and *Cassida rubiginosa* have been released in countries around the world (Kok, 2001). Phenological synchrony between musk thistle and biological control agents contributes to control outcomes (Surles & Kok, 1977), and synchrony is also subject to change with changing climate. Mowing can interfere with biological control if plants are mowed while immature insects are developing within capitula (Tipping, 1991). Integrating physical and biological control under future climates will therefore likely require reconsideration of how multiple management practices interact.

Our approach, in which we tested management effectiveness under experimentally altered climatic conditions to anticipate and possibly preempt changes in management effectiveness, has wide applicability to managed systems. Plants' responses to climate change can vary substantially from species to species (Miller-Rushing & Primack, 2008), and the effectiveness of management applied to plants under climate change is also likely to change in idiosyncratic and species-specific ways. Unfortunately, systematic, proactive testing of the impacts of the diverse aspects of climate change, including elevated atmospheric CO₂ concentration and altered precipitation regimes, along with rising temperatures, on the diverse array of problematic weed species is a huge challenge. Where the preemptive, experimental approach we applied here is not feasible, our findings reinforce suggestions that managers should monitor management outcomes to detect changes in management effectiveness as they arise. Recording changes in weed population sizes or densities, together with changes in investment in managing weed populations, may help to identify scenarios

where management effectiveness is being reduced by changing climate. Declines in management outcomes for a given amount of effort would indicate a growing problem, as would increased effort to achieve consistent results. The U.S. National Fish, Wildlife and Plants Climate Adaptation Joint Implementation Working Group (2014) explicitly calls for adaptive management to track changing management effectiveness and implement updated management plans. Adaptive management has the potential to help managers track changes in the systems they monitor and refine management selections to account for changes (Williams & Brown, 2012).

The degree to which physical weed management's effectiveness will diminish in other systems under changing climate remains unknown. In many cropping systems, weeds grow in competition with crops, and the relative responsiveness of species to changing climate will influence outcomes (Ramesh et al., 2017). Further, plant species' responses to warming can be unique (e.g., Bradley et al., 2009) and may be difficult to predict without carrying out experiments or analyses targeted at specific problematic species. Our study focused on a species that reproduces only once, and a management practice that targets only reproducing individuals. Hoeing or hand pulling, however, which are widely applied around the world, can target all individuals of weedy species, with potentially very different demographic effects (Birthisel et al., 2021). These differences highlight the importance of representative case studies, where management effects are investigated as they are realistically employed on farms. Additionally, climate warming is just one component of climate change. Atmospheric carbon dioxide concentrations continue to rise, precipitation patterns are changing, and variability in a number of climatic variables is increasing (IPCC, 2014). Temperature increases are also likely to progress beyond the level of warming we tested here (IPCC, 2014), with potentially nonlinear effects on weed growth. The combined effects of these various changes may produce different outcomes than those reported here. Future work examining the interactive effects of these other expected changes would certainly enhance predictions regarding weed responses to management under changing climate.

A deeper understanding of the mechanisms driving differences in musk thistle's vulnerability to mowing under warming would also be valuable to better understand how generalizable the changes we observed here may be. For example, the rapid acceleration of the life cycle under warming seen in *C. nutans* (Keller & Shea, 2021) may not eventuate in all species, or if such shifts occur, may have different underlying mechanisms. Also, warming-induced changes in plants' resource allocation may critically affect their vulnerability to physical

weed management. In the related weed *Cirsium arvense*, for example, differences in allocation of resources above and below ground in response to elevated atmospheric CO₂ concentrations drive changes in susceptibility to herbicide (Ziska et al., 2004). Detailed reports describing changes in other economically costly weeds' growth patterns under climate conditions projected to occur in the future may illuminate the range of possible outcomes and identify vulnerable periods for management.

Our results show that business-as-usual application of weed management practices will not continue to produce the same outcomes as temperatures rise over the coming decades. Warming increased the performance of musk thistle and also decreased the effectiveness of mowing in delaying flowering and reducing plant survival, height, and fecundity. While mowing is projected to remain a useful tool to reduce musk thistle local population growth rates, its ability to help managers reach management objectives will be reduced under warming. These results highlight the potential for rising temperatures to alter not only the performance of pest species, but also the effectiveness of management tools used to limit their impact.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

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