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**ECOLOGY AND INVASIVE PROPERTIES OF MUSK
THISTLE (*CARDUUS NUTANS*) IN THE CENTRAL
PRAIRIES OF NEBRASKA**

by

Chengchou Han

A THESIS

Presented to the Faculty of
The Graduate College at the University of Nebraska
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Major: Agronomy

Under the Supervision of Professor Stephen L. Young

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ECOLOGY AND INVASIVE PROPERTIES OF MUSK THISTLE
(*CARDUUS NUTANS*) IN THE CENTRAL PRAIRIES OF
NEBRASKA

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University of Nebraska, 2012

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Musk thistle (*Carduus nutans*) is an herbaceous monocarpic herb introduced to the U. S. from Eurasia. The invasion of musk thistle can reduce forage area, soil stability, and reduce recreation and open areas for humans and wildlife.

Resistance of warm season and cool season perennial grass communities to musk thistle invasion is important for land managers to consider, especially where disturbance has made an area particularly susceptible. Our results show that disturbances, such as overgrazing can open up niches in canopies of warm season grass communities and facilitate invasion but not in cool season grass communities. The mechanism of invasion by musk thistle may depend on an overlap in the timing of resource use patterns by the invader and perennial grass communities. Our results showed that an undisturbed (e.g., non-grazed, normal precipitation) stand of warm season perennial grasses can suppress the establishment of musk thistle by restricting the amount of light that reaches the soil surface. A disturbance of extreme drought creates more niches in warm

season perennial grass communities (e.g., reduced growth), but newly germinating musk thistle plants cannot compete for the reduced amount of soil moisture. High disturbance (e. g., grazing) allowed extensive amounts of light to penetrate into overgrazed warm season perennial grass communities, which facilitated the successful invasion by musk thistle. In cool season perennial grass communities, light is less critical, regardless of soil moisture.

The unsuccessful invasion of musk thistle into cool season perennial grass communities is most likely due to grass root phenology and distribution (88 m m⁻²). Root growth and development and distribution patterns should be taken into account for effective perennial grass restoration in areas with high risk from invasive plant species.

The ecology of musk thistle seed suggests germination is strongly influenced by temperature, light, moisture, salinity, dormancy and habitat types and should be factored into an integrated invasive plant management plan that targets early growth of musk thistle seedlings.

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Resistance by warm and cool season perennial grasses to invasion of musk thistle (*Carduus nutans*)

ABSTRACT

Healthy perennial grass communities are often able to resist invasion by an alien plant species when functional similarities are shared between the invader and desirable species. Following disturbance (e.g., grazing) and drought conditions, a perennial grass community can be less likely to resist invasion, even with functionally similar characteristics as the invader. In previously established warm and cool season perennial grass communities, a study that included simulated grazing, was conducted to determine resistance from invasion by musk thistle (*Carduus nutans*). The warm season grass (WS) community (*Panicum virgatum* L., *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Andropogon hallii* Hack., *Sorghastrum nutans* (L.) Nash, *Bouteloua curtipendula* (Michx.) Torr., *Desmanthus illinoensis* (Michx.) MacMill. ex B.L. Rob. & Fernald, *Dalea purpurea* Vent. and *Lupinus perennis* L.) was separated from the cool season grass (CS) community (*Dactylis glomerata* L., *Bromus inermis* Leyss., *Bromus riparius* Rehmman and *Alopecurus arundinaceus* Poir.) by a distance of approximately 1.5 km. For each community, the following treatments were applied: simulated grazing (G), no grazing (NG), introduction of musk thistle (MT), and no musk thistle. A bare ground control (BG) was included next to each community to verify that no site factors were prohibiting

establishment of musk thistle. Established WS and CS communities resisted invasion of musk thistle for 2 years, except when grasses were grazed, primarily during the first year. In WS-G communities, musk thistle was the dominant plant by the second year (44% cover). Musk thistle emerged in WS-NG communities, but failed to establish due to the dense grass canopy in 2011 and drought conditions in 2012. In CS communities, musk thistle populations were very low (0.6% and 4.7% cover) in both years. Musk thistle in BG plots which next to WS and CS communities reached full maturity and the rosette stage in 2011 and 2012, respectively. The CS communities were better at resisting invasion by musk thistle, regardless of grazing, while only the WS-NG communities prevented establishment by the invader. We attribute this phenomenon to the different growth characteristics of the perennial grasses: largely sod-forming for cool season and bunching for warm season. Also, warm season grasses remain dormant longer into the spring than cool season species. The implications are that overgrazing can open up niches in a warm season grass community, while a mix of cool season grasses could help in preventing the establishment of an opportunistic invader, such as musk thistle.

Keywords: perennial grass, invasive, musk thistle, *Carduus nutans*, restoration

Introduction

Invasive plant species have established in the Central Prairie and across the Midwest during the past several decades (Mico and Shay 2002, Eddy and Moore 1998, Melinda and Knapp 2001). In prairie ecosystems, the effects of invasive plant species are significant in relation to ecosystem services (Young 2010) and changes in ecosystem properties (Gordon 1998). Invasive plant species can reduce native plant populations, reduce the viability of livestock production system, and degrade soil quality (Hejda et al. 2009, Eiswerth and Johnson 2002, D'Antonio and Meyerson 2002).

Pejchar and Mooney (2009) estimated that the cost to control invasive plants is in excess of \$120 billion per year in the United States. The economic cost to manage invasive plant species in rangelands is significant. Babbitt (1998) reported ranchers spend about \$5 billion each year to control invasive plant species in pastures and rangelands in United States.

The establishment of invasive plant species requires a niche or opening in the desired plant community (Beck 2001). In order to resist invasive plant species, the establishment or restoration of native perennial grass communities is one of the more desirable long-term strategies in prairies and rangelands (Berlinger and Knapp 1991, Bottoms and Whitson 1998, Laufenberg 2003). In these ecosystems, the goal of restoration efforts is to re-establish a functionally diverse plant species community to better compete with invasive plants for limited resources. Tilman et al. (1996, 1997) showed that higher diversity is beneficial for maintaining ecosystem function, while

preventing the establishment of new invasive plant species.

Much research reports that grass communities with high diversity can effectively resist invasion (Fargione and Tilman 2005, Wardle 2001). In particular, C4-dominant perennial grass communities, similar to those in the Central Prairies, can resist the establishment by invasive plant species that are functionally similar (Fargione et al. 2003). Moreover, Young et al. (2007 and 2009) and Brown et al. (1998) found that native or desirable plant communities with species functionally equivalent to the invader are better able to resist invasion compared to simple plant species diversity. In California, Young et al. (2009) reported that an established native perennial grass community consisting of *Elymus glaucus*, which is functionally similar to the non-native yellow starthistle (*Centaurea solstitialis*), was able to resist the invasive up to five years after planting. Similarly, Bugg et al. (1997) showed established native perennial grass communities suppressed non-native weeds. An established and healthy stand of perennial grasses usually has fewer weed problems compared to nearby areas that are devoid of native or desirable perennial grasses (Blumenthal et al. 2005, Rose et al. 2001).

Perennial grasses have an extensive root system that may include rhizomes that remain alive for years compared to annual species. Many annuals are shallow rooted with most roots distributed in upper soil profile. Although slower to develop, the root systems of perennial grasses can capture available resources over large spatiotemporal scales and facilitate a competitive advantage below-ground (Eggemeyer et al. 2008). Blank and Morgan (2012) found that mixed grasses including *Elymus wawawaiensis*

(Snake River wheatgrass), *Achnatherum hymenoides* (Indian ricegrass) and *Leymus triticoides* (creeping wild rye) were able to suppress *Bromus tectorum* L. (cheatgrass) by preempting biological soil space, where occupied by living microorganisms (Nannipieri et al. 2003), within the soil profile. Although it is speculative that physical space can influence plant growth, the presence of roots in soil space will restrict root development of competing plants in utility of that space if physical space is resource (Blank and Morgan 2012).

Musk thistle, a widely distributed invasive plant species found in the Central Prairies, continues to be problematic by creating large monocultures that reduce native plants and growth of forage for livestock and wild animals (Roeth et al. 2009). Musk thistle is a monocarpic herb which was first introduced into the United State from Europe, North Africa, and Asia in the late 1800's (Moore and Frankton, 1974). Musk thistle can reduce forage area, increase soil erosion, and reduce recreation and open areas for humans and wildlife (Roeth et al. 2003). A short-lived biennial, musk thistle develops a deep root over an 8-10 month period and then ends in prolific flowering and seed dispersal (Roeth et al. 2003).

Grazing has been used intentionally to manage prairies and rangelands, but ungulates were common in these areas long before settlement and the introduction of domesticated animals (Kinney 1996). Studies have varied in their conclusions regarding response by prairies and rangelands to grazing. Menke (1992) found that grazing helped to facilitate restoration of perennial grasses. However, a disturbance such as grazing can also create a niche in a plant community that allows for an

invasive plant, like musk thistle, to establish (Feldman et al. 1968, NDSU 2000).

Pastures and rangelands that are healthy and in good condition can be grazed with the correct techniques to prevent invasion from musk thistle (Beck 1999).

In this study we compared resistance of warm and cool season perennial grass communities to invasion by musk thistle using simulated grazing treatments. The objectives were to determine the resistance of warm season and cool season perennial grass communities by cover and biomass on effects of musk thistle introducing under grazing and non-grazing conditions. We hypothesized that non-grazed warm and cool season perennial grass communities would be the most successful in resisting invasion of musk thistle.

Materials and Methods

Site description

Field experiments were conducted in open rangelands at the West Central Research Extension Center (WCREC), North Platte, NE (41.090S, -100.769E) in 2011 and 2012. Average annual precipitation in North Platte is 508mm of which 80% occurs during the growing season, which last from late-April to mid-October (USDA, 1978). Warm and cool season perennial grass communities were established in 2007 at two separate locations, approximately 1.5 km apart. Bare ground control plots were established in 2011 and 2012 for warm season and cool season perennial grass

communities, respectively.

The soils in both perennial grass communities were Cozad silt loam (fine-silty, mixed, mesic Fluventic haplustoll) (Payero et al. 2008). Annual crops were grown at the two locations prior to the installation of the perennial grasses and no musk thistle occurred during these periods.

Experimental design

The perennial grass species established at the two locations are commonly occurring species in the Central Prairie (Boettcher et al. 1993). In 2008, *Panicum virgatum* L., *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Andropogon hallii* Hack., *Sorghastrum nutans* (L.) Nash, *Bouteloua curtipendula* (Michx.) Torr., *Desmanthus illinoensis* (Michx.) MacMill. ex B.L. Rob. & Fernald, *Dalea purpurea* Vent. and *Lupinus perennis* L. were planted in the warm season (WS) perennial grass community and by 2011, *P. virgatum* (switchgrass) had become the dominant grass species. In the cool season (CS) perennial grass community, *Dactylis glomerata* L., *Bromus inermis* Leyss., *Bromus riparius* Rehmann and *Alopecurus arundinaceus* Poir were planted and by 2011, *D. glomerata* (orchardgrass) and the two *Bromus* spp. were the dominant species (Table 1). All grasses were seeded at rates according to recommended guidelines (Anderson 2007). Following planting, grass communities established to full canopy cover each year.

For the WS and CS communities, the following treatments were applied:

simulated grazing (G), no grazing (NG), introduction of musk thistle (MT), and no musk thistle. Bare ground control (BG) which was established for warm season perennial grass communities and cool season perennial grass communities in 2012 was included next to each community to verify that no site factors were prohibiting establishment of musk thistle. The musk thistle treatments (added or not added) were randomly applied to grass plots that were grazed or non-grazed and the bare ground control plots. Perennial grass community and bare ground plots were 5 m x 2 m and replicated four times at each location. A narrow alley (0.3 m) separated adjacent plots.

Musk thistle seeds were collected in 2010 near the WCREC. Seeds were separated from the capitulum and cleaned using a seed blower. Germination test results indicated 30% of the seed was viable (data not shown). On April 18, 2011 in the WS and CS community plots, three musk thistle seeds were hand planted at points that were equidistant from neighboring points and the plot edges at 0.5 cm soil depth. Each plot was planted with 140 musk thistle seed. In 2011, musk thistle seedlings emerged approximately one month after planting. In 2012, musk thistle seed was planted in bare ground plots adjacent to the CS community using similar procedures to verify that musk thistle could establish in the same soil type and conditions of the CS community. WS communities also had seeds germinated in 2012. In all plots, mature musk thistle capitula were bagged and collected to prevent the addition of any new seeds to the soil seed bank.

The simulated grazing (referred to as grazing) treatments were conducted by a rotary mower and electrical hedge trimmers at 10 cm above the ground. Grass residue

was removed from the plots immediately following the grazing. Musk thistle seedlings were never damaged or killed by grazing. In 2011, plots in the WS communities were grazed approximately bi-weekly (5 times) beginning on June 1. A similar grazing interval was used for the CS community plots, except the last two treatments were not applied due to lack of growth. In 2012, a single grazing treatment was applied on April 21 and May 28 for CS and WS communities, respectively. No grazing was needed the remainder of the season due to severe drought conditions (Danckwerts and Stuart-Hill 1988). (Fig. 1).

The cover in WS, CS, and BG plots was estimated monthly from May to October in 2011, and May to August in 2012. Assessments were conducted within permanent 0.3 m² quadrats in four locations in the each plot. Cover was estimated visually to within 1% up to 10% cover and thereafter to the nearest 5% (10-100% cover). Plots were hand weeded before one week of cover estimating to accurately assess the target plant species. Low weed intensity affect little on perennial grass cover.

Biomass of perennial grasses was harvested once in all WS, CS plots on July 4, 2102 before the cessation of musk thistle plants. Three perennial grass samples were taken in each WS and CS plot by clipping all vegetation (not musk thistle) in a 0.3 m² area and placing in a drying oven at 70° C and weighing after three days. We also recorded the phenological stages of musk thistle and grass communities throughout the growing season in 2011 and 2012 (Fig. 2).

Statistical analysis

In order to compare the resistance of under grazing and non-grazing perennial grass communities to invasion by musk thistle, perennial grass cover was compared between seeded and non-seeded musk thistle conditions under grazing (G or NG) by analyzing with ANOVA implemented using the GLIMMIX procedure in SAS (Version 9.1.2, SAS Institute, Inc.). The Generalized Linear Mixed model (GLMM) analysis of variance included month, grazing and seeded musk thistle as fixed factors and block as random factor. Tukey's HSD test was used to compare mean cover of perennial grass from communities at the $p > 0.05$ level. Comparison of biomass was also analyzed by Fisher's Least Significant Difference to determine significant effects at the $p < 0.05$ level.

Results

Warm season perennial grass communities

In May 2011, plant cover in the WS communities was 15-30% (Fig. 3), indicating that the perennial grasses had not yet fully emerged from dormancy. For the treatments that included the introduction of musk thistle (Fig. 3B, 3D), this represents a niche for newly germinating musk thistle to establish with adequate time and resources. After a couple of months, cover of perennial grasses peaked in the WS communities and musk thistle had established in only the WS communities with

grazing and seeded musk thistle (Fig. 3B). In these grazed plots, musk thistle cover continued to increase through the end of 2011. In 2012, a gradual decline of musk thistle cover occurred from May through August.

In non-grazing WS communities, musk thistle was not able to establish, although a very small amount of cover (0.2%) was recorded in July 2011 and again in May and June 2012 (2%) (Fig. 3C, 3D). The rapid growth and sustained cover of the perennial grasses following emergence from dormancy in 2011 prevented invading musk thistle seedlings from normal growth and development. In 2012, cover of all WS perennial grasses declined due to either musk thistle establishment (Fig. 3B) or lack of precipitation (Fig. 3A, 3C, and 3D). Established musk thistle rosettes in the grazing WS communities were able to reach full maturity without restriction in growth and development.

Cool season perennial grass communities

Unlike the WS communities, the CS communities had none to very low cover of musk thistle (Fig. 4A-D). In 2012, cover in the CS communities was less than in 2011, yet in plots that had received musk thistle (CS-G-MT and CS-NG-MT), no or very little (5% cover) musk thistle was recorded (Figs. 4B, 4D). Cover of perennial grasses in all CS communities was greater than 50% in 2011 and increased from 20-30% to almost 40% in grazed plots in 2012. Non-grazed communities with seeded and non-seeded musk thistle had fairly uniform cover in 2011 and 2012, although lower in

the second year (Table 2).

Warm and cool season communities

The cover of perennial grasses in WS and CS communities was less in 2012 than 2011. In 2012, a lack of precipitation due to a severe drought impacted the growth of plants (Fig. 1). By May, cover in all WS communities that received musk thistle seed failed to increase. The growth response to the drought condition in the CS communities was less dramatic between the two years than for the WS communities.

Biomass

In 2012, musk thistle had reached maturity in plots where it had established during the previous year. In the WS and CS communities, grasses grew slowly from early to late summer, which included the period of biomass collection. In the WS communities, perennial grass biomass in plots that were seeded with musk thistle (WS-G-MT and WS-NG-MT) was significantly less than in plots that were not over seeded with musk thistle (Fig. 5A). There was also a difference (95 g m^{-2}) in biomass between grazing and non-grazing treatments. For CS communities, perennial grass biomass was less in grazed plots compared to non-grazed plots, regardless of whether or not musk thistle seed was added (Fig. 5B).

Discussion

Warm season perennial grass communities

Grazed warm season perennial grass communities failed to resist the invasion of musk thistle as evidenced by grass cover and biomass. As musk thistle cover increased in the second year (2012), perennial grass cover declined in WS-G-MT communities (Table 2). The repeated grazing disturbances created a niche for musk thistle to invade and subsequently establish. It is common for bunchgrass type plant communities to have bare ground areas around plants (Pendergrass et al. 2008). These openings or niches are sometimes filled with desirable forbs or the canopy from the grasses covers them. While all WS communities had these niches, only in the grazed treatments were they repeatedly exposed and lacked cover from desirable forb species. In WS communities where musk thistle seed had been added, the grasses were not able to recover fast enough from the grazing to prevent the establishment of the invader. This is consistent with another study that have reported the effects of disturbances similar to grazing (Gerlach and Rice 2003).

Musk thistle invaded the WS-G-MT communities in 2011 and had established and reached maturity by mid-summer in 2012. In contrast, the WS-NG-MT communities prevented musk thistle from establishing after the initial invasion in 2011. The few musk thistle seedlings that had emerged the first year were smaller (e.g., below the perennial grass canopy) and had just a single capitulum. In addition,

many other musk thistle plants never reached maturity and died by the end of 2011. Competition by non-grazed perennial grass communities was detrimental to most musk thistle seedlings.

In 2011, WS communities were dominated by switchgrass, which reached 120 cm and completely restricted light from reaching the soil surface by early July. In 2012, maximum perennial grass height in WS communities was 50 cm by mid-June, but lack of precipitation from the drought limited further grass development. Similarly, growth was severely limited for the few musk thistle seedlings that had survived from 2011 or germinated in early 2012. Again, musk thistle could not compete with the undisturbed perennial grasses and failed to establish.

Precipitation is a key factor that determines the rate and amount of growth and development by plants in grasslands, which can be indirectly related to plant diversity (Enloe et al. 2004, Young 2007). When water is readily available, all other things being equal, plant growth is limited only by time. In dry years, plant growth is limited and any newly established seedlings are usually the first to succumb to the high stress conditions. Many established plants (e.g., perennial grasses) have roots that can mine deep soil water stores and thus have an advantage, except in extreme drought conditions that last for several seasons. In WS communities, perennial grasses had been growing for 3 years prior to the introduction of musk thistle and therefore could withstand a year of below normal precipitation and above average heat. This is consistent with other studies on established native perennial grass communities which can resist invasion in the arid western North America where the invasive forb, yellow

starthistle (*Centaurea solstitialis*) is becoming a significant problem (Young et al. 2010).

Cool season perennial grass communities

The CS communities successfully resisted invasion by musk thistle even with repeated grazing for two years. The cool season grasses in these communities were less bunching and more sod-forming therefore, openings or niches were not readily available compared to openings or niche in the WS community. Similar to WS communities, grazing created a niche in CS communities, but because cool season grasses are active earlier in the season, unlike warm season grasses, the establishment by other plant species (invasive or desirable) is often not successful (Kok et al. 1986).

In the drought that occurred during 2012, grasses in the CS communities grew less rapidly and conducted only a single grazing treatment. Had grazing continued in 2012 at the same frequency as in 2011, a greater reduction in grass biomass may have allowed for additional musk thistle seedlings to establish, although this is doubtful since the musk thistle seed planted in 2011 was probably no longer viable or otherwise consumed by rodents or insects in the CS communities. There are numerous reports of feeding on seeds in the soil by animals and other biota can reduce total amount of seeds and this may have been the case in our study (Brown and Ojeda 1987, Vaughton 1998). Alternatively, the few seedlings of musk thistle that did emerge in 2012 most likely failed to establish because of competition with the grasses and any

existing musk thistle plants (McCarty and Scifres 1969).

Perennial grass cover in WS communities declined dramatically in 2012 compared to the change in cover for the CS communities during the same period. The reason could be warm season grasses (C4) weaken photosynthetic performance advantages (e.g. water-use and nitrogen-use efficiency) in drought conditions even warm season grasses favor drier habitats (Taylor 2011). C4 species typically have higher net leaf photosynthesis rates than their closest C3 relatives under high irradiation conditions (Taylor 2011). Ibrahim et al. (2008) reported the difference of rates of net leaf photosynthesis from C3 and C4 species was minimized under drought condition. This weaken photosynthetic performance advantages may severely influence the performance of WS communities in terms of cover. In drought conditions, C3 grasses may be able to resist potential invaders due to a high rate of belowground activity (Cahill 2003). Cool season perennial grasses have been found that they can suppress invasion by out competing with invasive plant when soil moisture decreased (Nernberg and Dale 1997).

All WS and CS communities and musk thistle exhibited early senescence in 2012 due to the drought (Fig. 2). While grass communities had less biomass, reduced leaf area, and truncated growing season, they were still capable of outcompeting musk thistle in all grass plots, except grazed warm season grasses that received musk thistle seed (WS-G-MT) (Fig. 3B). The reduced periods of vegetative growth by musk thistle compromised its ability to germinate or grow, except in BG and WS-G-MT plots in which it had established the previous year (2011).

The combination of plant physiology type (e.g., C3 and C4) and drought conditions can play an important role in perennial grass community resistance to invasion. C3 perennial grass communities that have developed prior to the initial establishment of an invasive plant, such as musk thistle, will be more able to resist invasion, even with repeat disturbances (e.g., grazing). In contrast, warm season C4 grasses are not as effective competitors once disturbance has occurred that repeatedly opens niches in the community. Our studies suggest disturbance has a larger impact than stress (e.g., drought) on the ability of perennial grass communities to resist invasion.

Biomass

The establishment of musk thistle in WS-G-MT communities reduced the biomass of perennial grasses, which indicates a disturbance such as repeated grazing can help in preempting WS communities and eventually facilitate musk thistle invasion. The difference in grass biomass within the non-grazing (NG) treatment, even when there were no musk thistle plants, can be attributed to the non-uniform stands of switchgrass in 2012. In 2011, switchgrass stands in NG treatments were uniform due to above average precipitation and full canopy. However, the conditions were quite different in 2012 and a lack of precipitation resulted in differences in canopy development in WS-NG-MT plots.

In the CS communities, biomass remained constant between grazed and

non-grazed treatments, indicating tolerance to disturbance and resulting in less chance for establishment by an invasive plant species (Kok et al. 1986). Further, as previously discussed, plant growth and resource acquisition timing that overlap with musk thistle are more important than disturbance in preventing the invader from establishing. Our results suggest that the conditions associated with overgrazing could be more of a problem in WS communities than CS communities (Hulbert 1986).

Conclusion and implications for management

Based on our results, WS communities that are continuously exposed to grazing disturbances create niches that reduce the competitive ability of perennial grasses and allow musk thistle to invade more easily. In WS-NG communities, failure of musk thistle to successfully establish is mainly due to competition and differences in timings of plant growth between an established perennial and newly germinated biennial.

In CS communities, the early season growth and lack of pronounced dormancy are possible growth characteristics that allow for the resistance to musk thistle invasion. In particular, the root systems of cool season grasses may be more active in shallow layers early in the season thereby restricting further development of musk thistle beyond germination.

Perennial grass communities that are functionally similar to the invader will often be better able to resist invasion. Largely, resource acquisition timing is the main

factor in a plant community being able to successfully resist invasion (Young 2009, 2010, and 2011). A fuller understanding of restoration of prairies and rangelands infested with invasive plant species is needed on the relationships between disturbance and stress, especially with increasing frequency of extreme events (Bradley et al., 2011).

Prairies and rangelands that are overgrazed are susceptible to establishment of musk thistle. In drought years, less frequent or no grazing could be key in preventing the initial invasion of musk thistle and avoiding establishment in later years with normal precipitation. The conditions of disturbance and stress (e.g., drought) highlight the importance of using proper grazing management strategies that match the conditions and plant types. By preventing the establishment of musk thistle, prairies and rangelands will be kept from being impaired and result in less costly management that is sustainable for longer periods.

Figures and Tables

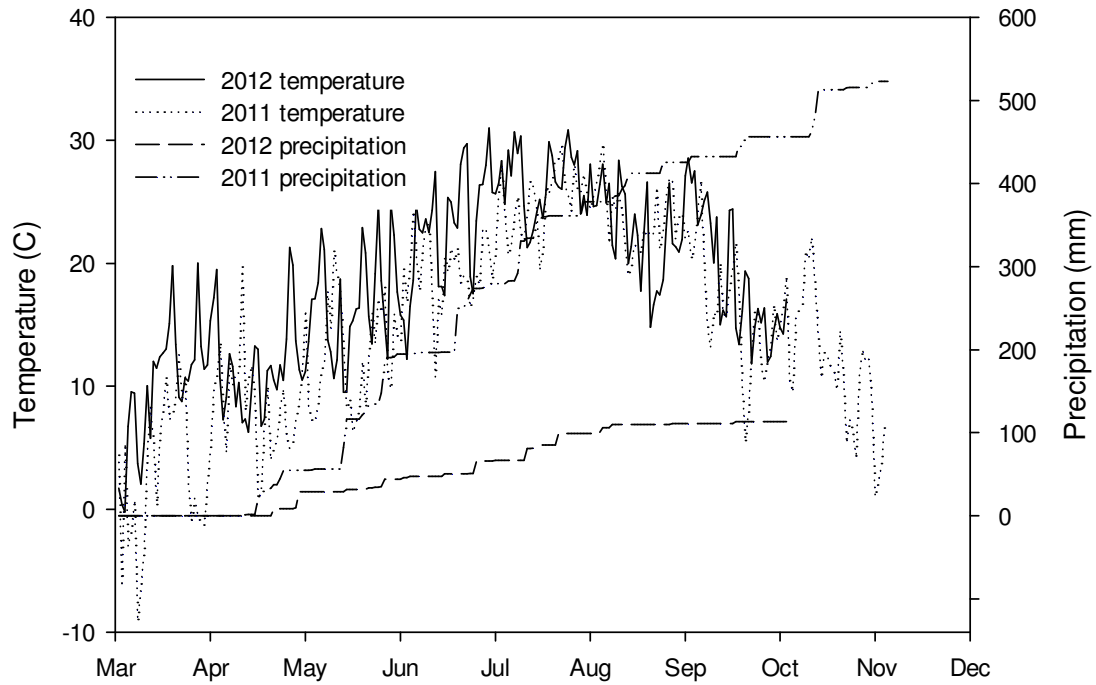


Figure 1. Average daily temperature and cumulative precipitation in 2011 and 2012 at the West Central Research & Extension Center in North Platte, NE (High Plains Regional Climate Center 2012)

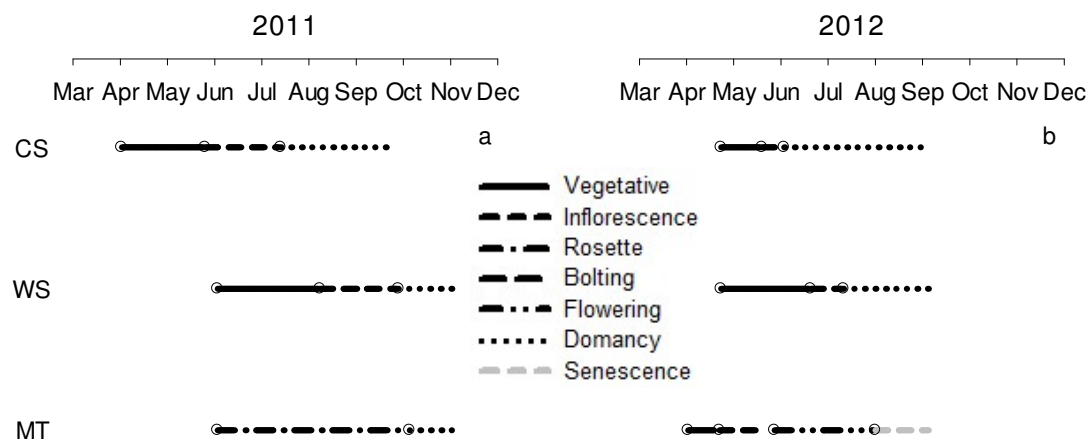


Figure 2. Phenology of musk thistle (MT), warm season perennial grasses (WS), and cool season perennial grasses (CS) in North Platte, NE, USA. The phenological stages for musk thistle are rosette, dormancy, bolting, flowering, and senescence, while the stages for grasses are vegetative, inflorescence, and dormancy.

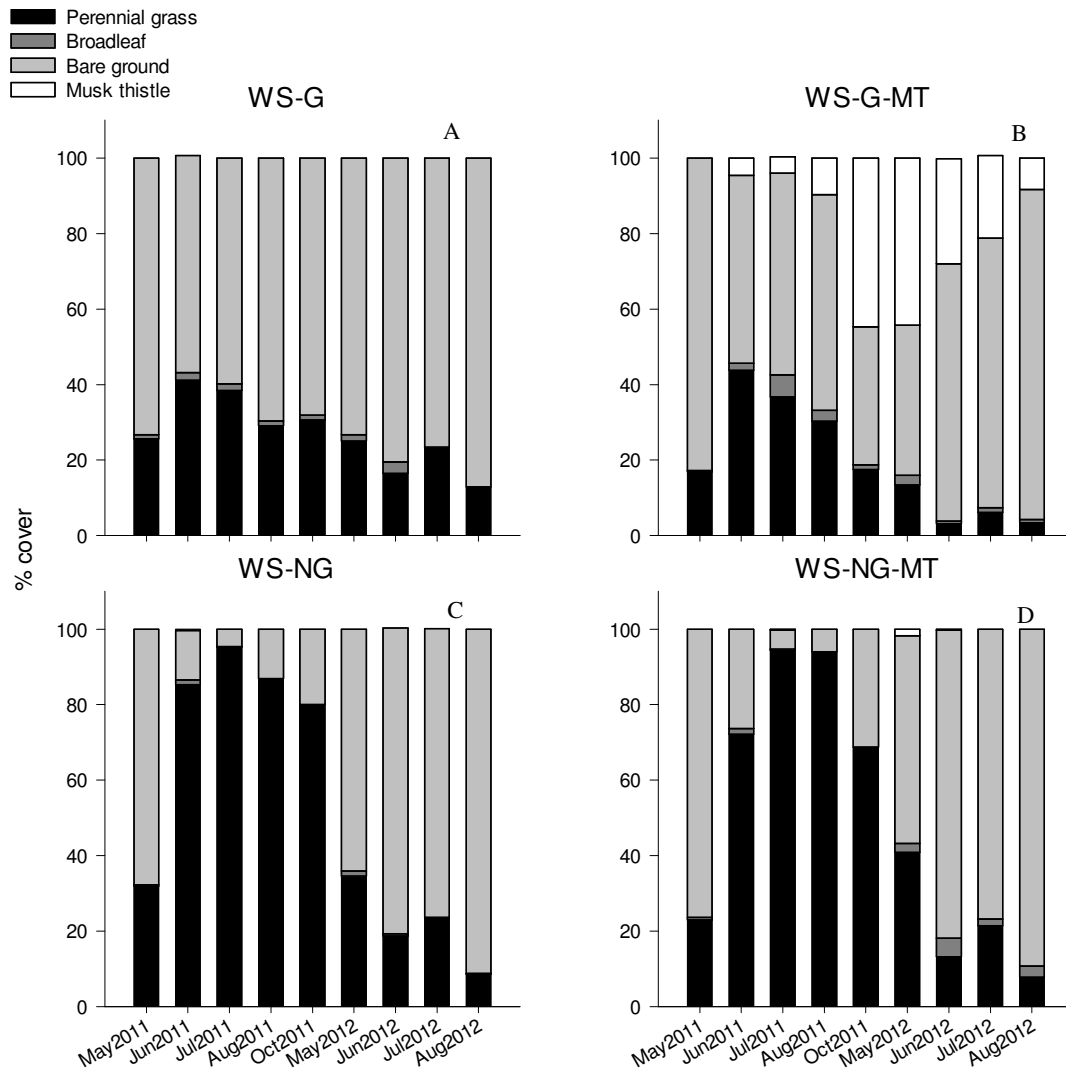


Figure 3. Plant cover in grazed warm season perennial grass communities without (A) and with (B) musk thistle seeded and non-grazed warm season perennial grass communities without (C) and with (D) musk thistle seeded for two years.

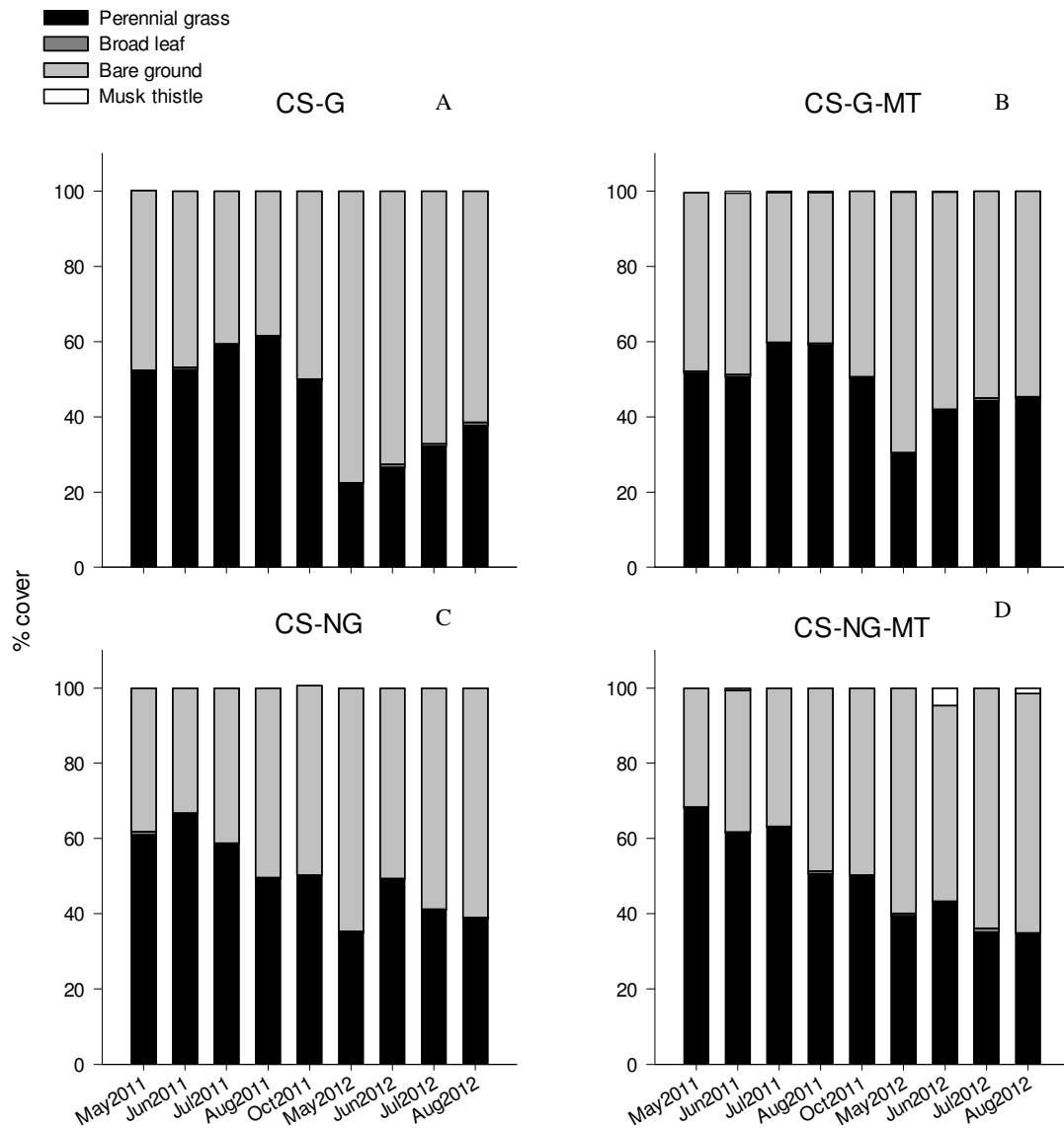


Figure 4. Plant cover in grazed cool season perennial grass communities without (A) and with (B) musk thistle seeded and non-grazed cool season perennial grass communities without (C) and with (D) musk thistle seeded for two years.

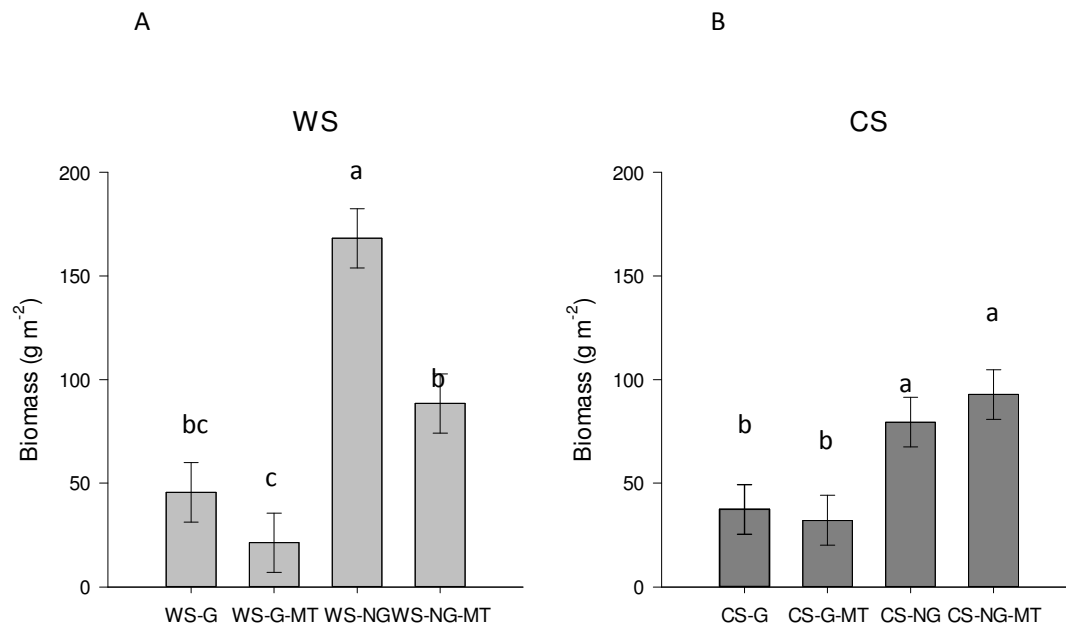


Figure 5. Mean perennial grass biomass in warm season (A) and cool season (B) perennial grass communities. Codes: warm season grasses grazed without (WS-G) and with (WS-G-MT) musk thistle seeded; warm season grasses non-grazed without (WS-NG) and with (WS-NG-MT) musk thistle seeded; cool season grasses grazed without (CS-G) and with (CS-G-MT) musk thistle seeded; cool season grasses non-grazed without (CS-NG) and with (CS-NG-MT) musk thistle seeded;. Significant differences denoted with letters ($p < 0.05$).

Table 1.

Species composition of warm season (WS) and cool season (CS) perennial grass communities in experimental plots established in 2007 the West Central Research & Extension Center, North Platte, NE.

Grass species	Common name	Rate kg ha ⁻¹
Warm Season Community		
<i>Panicum virgatum</i> L.	'Trailblazer' Switchgrass	8.96
<i>Andropogon gerardii</i> Vitman	Big bluestem	3.36
<i>Schizachyrium scoparium</i> (Michx.) Nash	Little bluestem	1.12
<i>Andropogon hallii</i> Hack.	Sand bluestem	1.68
<i>Sorghastrum nutans</i> (L.) Nash	Indiangrass	2.24
<i>Bouteloua curtipendula</i> (Michx.) Torr.	Sideoats grama	0.9
<i>Desmanthus illinoensis</i> (Michx.) MacMill. ex B.L. Rob. & Fernald	Illinois bundleflower	0.56
<i>Dalea purpurea</i> Vent.	Purple prairie clover	0.56
<i>Lupinus perennis</i> L.	Perennial lupine	0.56
Cool Season Community		
<i>Dactylis glomerata</i> L.	Orchardgrass	17.92
<i>Bromus inermis</i> Leyss.	Smooth brome	10.86
<i>Bromus riparius</i> Rehmman	Meadow brome	16.24
<i>Alopecurus arundinaceus</i> Poir.	Creeping foxtail	1.9

Table 2.

Tukey's HSD test (p values) was used to compare mean cover of perennial grass between grazed warm season perennial grass communities without (WS-G) and with (WS-G-MT) musk thistle seeded; non-grazed warm season perennial grass communities without (WS-NG) and with (WS-NG-MT) musk thistle seeded; grazed cool season perennial grass communities without (CS-G) and with (CS-G-MT) musk thistle seeded and non-grazed cool season perennial grass communities without (CS-NG) and with (CS-NG-MT) musk thistle seeded.

Treatment contrast	2011					2012			
	May	Jun	Jul	Aug	Oct	May	Jun	Jul	Aug
WS-G vs WS-G-MT	0.65	0.98	1.0	1.0	0.30	0.14	0.07	0.01	0.3
WS-NG vs WS-NG-MT	0.63	0.30	0.77	0.77	0.44	0.65	0.74	0.10	1.0
CS-G vs CS-G-MT	1.0	0.97	0.95	0.95	0.99	0.42	0.02	0.34	0.49
CS-NG vs CS-NG-MT	0.31	0.63	0.99	0.99	1	0.83	0.64	0.44	0.89

N/A indicates data not available. The GLMMIX procedure was used to determine significance (n=4). Bolded p values in each column indicate higher perennial grass cover in the first communities under treatment contrast and are significant at $p < 0.05$, except cover was higher in CS-G-MT plots.

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Mechanisms of musk thistle (*Carduus nutans*) invasion in disturbed perennial grasslands

Abstract

Successful invasion by an exotic species depends on the acquisition of resources across spatiotemporal scales. Although functionally similar species compete for the same resource pool, disturbances often shift the advantage in favor of the invasive species. Experiments were conducted in Central Nebraska, USA to determine musk thistle (*Carduus nutans*) invasion success into established warm and cool season perennial grass communities following disturbance (e.g., simulated grazing). Musk thistle was over seeded into plots of each grass type, which was cut (grazed) or left uncut (non-grazed) for two seasons. The non-grazed warm season perennial grass communities were most successful at suppressing musk thistle establishment through reduced light penetration (2% of maximum at the soil surface) in the first year (2011). During the second year (2012), lack of soil moisture prevented newly germinating musk thistle seedlings from establishing, even though light penetration was greater (40% of maximum at the soil surface). Although musk thistle biomass in grazed plots ($194.1 \pm 49 \text{ g plant}^{-1}$) was lower than in musk thistle monocultures ($679.7 \pm 53 \text{ g plant}^{-1}$), invasion was still successful in 2012. In the cool season grasses, musk thistle establishment was suppressed in both the grazed ($16.6 \text{ g plant}^{-1}$) and non-grazed (1.6 g plant^{-1}) treatments. In 2011, surface soil moisture (0-8cm) was adequate ($> 0.04 \text{ m}^3 \text{ m}^{-3}$) and in the second year, established musk thistle plants had adequate deep soil

moisture available ($> 0.09 \text{ m}^3 \text{ m}^{-3}$). In the absence of above-ground competition and low soil moisture, musk thistle can successfully establish in warm season perennial grass communities. The invasion of musk thistle into cool season perennial grass communities is inhibited by aboveground growth and belowground activity that overlaps with the invader. The ability of musk thistle to invade and establish in grazed warm season perennial grass communities and not in cool season perennial grass communities suggests important considerations of grasslands management for grazing, especially where musk thistle is common and drought conditions persist.

Keywords: cool season, drought, perennial grass, invasion, musk thistle, *Carduus nutans*, light, soil moisture, restoration, warm season

Introduction

Invasive plant species in the Central Prairie, U.S.A. have modified biotic communities and altered natural cycles with increasing frequency (Charles and Dukes 2007). In order to prevent further negative impacts from invasive plant species, the focus of many restoration efforts should be on the creation of diverse grass communities that create barriers against invasion (Berlinger and Knapp 1991; Bottoms and Whitson 1998, Laufenberg 2003). This approach is not only a good method for management but also furthers our understanding of the fundamental mechanisms of invasion, which are important in all plant communities, including those in the Central Prairie (Pokorny et al. 2005).

Tilman (2001), Dukes (2002), and others have reported that exotic plant species are less likely to establish in species-rich habitats that have high functional diversity. Functional diversity refers to the range or value of species traits that influence ecosystem function (Tilman 2001). Plant communities with different functional groups are more likely to out compete invasive plant species that have similar resource use patterns (Hooper and Dukes 2010; Dukes 2002; Pokorny 2005). The overlap in time and space of resource acquisition by two plant species is considered to be a key factor in invasion success (Suding et al. 2003; Zavaleta and Hulvey 2007). Invasive plants that successfully establish, initially may avoid direct competition with residents by accessing excess or incompletely used resources (Elton 1958; Hierro et al. 2011). Young et al (2009, 2010) reported that when yellow starthistle (*Centaurea solstitialis*), an invasive plant in California, has functional similarities for acquisition

of resources with perennial grassland communities, the invader is less likely to establish because of direct competition with the grasses. Moreover, Young et al. (2011) found not only functional similarities between starthistle and perennial grass life histories, but an overlap in spatiotemporal resource use that contributed to invasion resistance by the native perennial grass species.

Access to resources is important for invasive plant species (Thomas et al. 2002; Maron and Marler 2007). Successful invasion is often due to spatiotemporal changes in available resources, which can be correlated with life histories of the invader and invaded plant community (Young et al. 2010; Seabloom et al. 2003). Young et al. (2011) found that yellow starthistle used water and light during phenological stages that functionally matched the target grassland plant community. In this case, even an increase in available soil water during the vegetative stage of starthistle was not enough to overcome the lack of light transmission through the dense canopy of the grasses. In other systems, soil water does contribute to successful invasion, especially if the invader germinates earlier in the growing season (Davis and Pelsor 2001; Larson et al. 2001). With overlapping resource use timings, harsh conditions (e.g., drought) often will favor the established resident plant community over the invader (Cahill 2003).

Light availability, which is a function of leaf area, also influences the success of invasion (Young et al. 2011; Reinhart et al. 2006; Thomsen and D'Antonio 2007). A decrease in the amount of light reaching the soil surface can suppress invasive plant species, as has been shown for *Crepis tectorum* (Naeem et al. 2000) and others

(Hamrick and Lee 1987; Roche et al 1994). In addition, McCarty et al. (1968) report musk thistle establishment in less vegetated habitats, which is in part due to a high level of irradiance (Wardle et al. 1992).

In rangelands, a well-established perennial grass community is able to resist invasion by synchronizing resources use patterns with the invader (Young et al. 2011), preempting belowground space through root growth and distribution (Blank and Morgan 2012), and depleting excess resources to the detriment of the invader (Milbau et al. 2005). Perennial grass communities are often more resistant to invasion than annual grasses (Young et al. 2011). However, a disturbance such as repeated grazing, can lower the resistance by a perennial grass community due to continuous and sometimes large openings in the plant canopy that create a niche for invasive plant species to establish (Feldman et al. 1968; NDSU 2000). Overgrazing can facilitate invasive plant survival, such as musk thistle and create sites for establishment of musk thistle in bare ground where failed to recover from overgrazing (Hulbert 1986; Leininger 1988; Rice and Randall 2001; Beck 1999).

Musk thistle is an introduced herbaceous monocarpic herb to the U. S. from Eurasia (Kok 2001). It is a state listed noxious weed that covers almost 6070 km² in Nebraska (NDA 2010). A short-lived biennial, musk thistle develops deep roots and then ends in prolific flowering and seed dispersal (Roeth et al. 2003). Here we studied changes in soil water and light and the response of musk thistle (*Carduus nutans*) with recording its life history monthly. We hypothesized that resource use patterns of musk thistle that are similar to perennial grass communities would prevent successful

establishment by the invader. In addition, disturbance such as grazing would facilitate successful musk thistle establishment and minimize the effect of functional similarities.

Materials and methods

Site description

The study was conducted at the West Central Research Extension Center (WCREC) in North Platte, NE (41.090S, -100.769E), where average annual precipitation is 508 mm of which 80% occurs from late-April to mid-October (USDA, 1978). The total seasonal precipitation was 513 mm in 2011 and 113 mm in 2012, which was 3% higher and 77% lower, respectively, than the historical average (Fig. 1). The cool season and warm season perennial grass communities were established in 2007 in neighboring fields separated by a distance of approximately 1.5 km. Bare ground control plots were established at each location.

The dominant soil type was Cozad silt loam (fine-silty, mixed, mesic Fluventic haplustoll) (Payero et al. 2008). Annual crops (e.g, corn, soybeans) were grown before the establishment of the perennial grass communities and no musk thistle occurred prior to the study period.

Experiment design

Two perennial grass communities, warm season (WS) and cool season (CS) with different phenologies were established as part of a previous study in 2007. The

grasses in these two communities use different photosynthetic pathways, which result in different growth habits over a single season. All perennial grass species are common to the Central Prairie region of the USA (Anderson 2007). The WS perennial grass community consisted of *Panicum virgatum* (switchgrass), which was the dominant species in 2011, *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Andropogon hallii* Hack., *Sorghastrum nutans* (L.) Nash, *Bouteloua curtipendula* (Michx.) Torr., *Desmanthus illinoensis* (Michx.) MacMill. ex B.L. Rob. & Fernald, *Dalea purpurea* Vent. and *Lupinus perennis* L. The cool season perennial grass community consisted of *Dactylis glomerata* L., *Bromus inermis* Leyss., *Bromus riparius* Rehmman, and *Alopecurus arundinaceus* Poir. By 2011, *D. glomerata* L. (orchardgrass) and the two *Bromus* spp. were the dominant species. All grasses were seeded at rates according to recommended guidelines (Anderson 2007). Following planting, grass communities established to full canopy cover each year.

The experiment was designed with the following three factors: 1) grass communities (WS, CS), 2) grazing disturbance (grazing, G; non-grazing, NG), and 3) musk thistle seeded (MT) or not. Each treatment, including a bare ground (BG) control had four replications. The musk thistle treatments (seed added (MT) or not added) were randomly applied to grass plots (G and NG) and an additional set of bare ground plots, not the BG control plots. The perennial grass community and bare ground plots were 5 m x 2 m with a narrow alley (0.3 m) separating adjacent plots.

Musk thistle seeds were collected in 2010 near the WCREC. Seeds were separated from the capitulum and cleaned by a seed blower. A preliminary

germination test indicated seed viability was near 30% for the collection (data not shown). In the WS and CS community plots, three musk thistle seeds were hand planted just below the soil surface at points equidistant from neighboring points and edges in each plot. The timing for planting the seeds might influence establishment of musk thistle. The planting date was chosen on April 28, 2011 when a rising daily temperature above 0 C was met. Each plot were planted 140 musk thistle seeds at 0.5 cm soil depth. Musk thistle seedlings emerged approximately one month after planting. In all plots, mature musk thistle capitula were bagged and collected in late summer and fall of 2011 to prevent any new seeds being added to the soil seed bank.

The simulated grazing (referred to as grazing) treatments were conducted at 10 cm above the ground using both a rotary mower and electrical hedge trimmers. Grass residue was removed from the plots immediately following the grazing. Musk thistle seedlings were never damaged or killed by the grazing treatments. In 2011, plots in the WS communities were grazed approximately bi-weekly (5 times) beginning on June 1. A similar grazing interval was used for the CS community plots, except the last two treatments were not applied due to lack of growth. In 2012, a single grazing treatment was applied on April 21 and May 28 to CS and WS communities, respectively. No grazing was needed for the remainder of the season due to severe drought conditions.

The light transmission of each treated grass community was measured during the growing seasons of 2011 and 2012. Photosynthetically active radiation (PAR) was measured using a recently calibrated ceptometer (AccuPAR LP-80; Decagon Devices

Inc., Pullman, WA, USA). The ceptometer sensor arm (80 cm long) was inserted into the canopy of each plot at the soil surface and four PAR readings were taken. The average of the readings was compared with PAR values of full sunlight above the canopy. The readings at the soil surface were taken right after the full sunlight reading was taken. Data are presented as percent of light transmission to the soil surface.

Shallow (0-8 cm) soil water content underneath plant communities was measured throughout the growing season using soil moisture sensors (EC-5; Decagon Devices, Inc., Pullman, WA, USA) that were vertically inserted down to 8cm below the soil surface. Measurements were recorded hourly and averaged over a 24-hr period. A hydroprobe (503DR, CPN, Martinez, CA, USA) was used to measure deep soil moisture at depths of 30, 60, 90 and 120 cm each month. One access tube was installed in the center of each plot and tubes were capped to keep moisture from entering. Hydroprobe was calibrated before measurements. Hydroprobe measurements were converted to volumetric soil water content (Evelt and Steiner 1995) and reported as a percentage. Soil moisture sensors and accesses tubes for neutron probe were installed only in perennial grass or musk thistle monocultures and the bare ground control plots.

The growth and development of musk thistle was recorded by counting the number of musk thistle plants in seeded plots each month. In the second year (2012), newly emerged musk thistle plants were recorded by a same method. The phenological growth stages of musk thistle and the perennial grasses were recorded throughout the growing season. Musk thistle biomass was collected in all WS, CS,

and BG plots in the second year before the senescence of musk thistle plants. Three plants were randomly chosen in each plot and cut at the soil surface. Plants were put in paper bags and placed in an oven (70°C), dried, and the weight was recorded.

Statistical analysis

The number of musk thistle plants in the perennial grass communities was log-transformed to improve normality and homogeneity of variance. The Generalized Linear Mixed model (GLMM) analysis of variance was used to compare the least square means of number of musk thistle plants within years. Fixed factors in the model included month, treatment, and all possible interactions of combinations. Block was treated as a random factor.

Soil moisture was combined for the deep (30 and 60 cm) and deepest (90 and 120 cm) depths by means and compared among treatments with the GLM model. Repeated measures analysis of variance in each year was conducted using fixed factors that included depth, treatment, and combinations of interactions. Tukey's HSD test was used to assess significant differences among musk thistle biomass within treatments at $p < 0.05$. All statistical analysis was conducted by SAS (SAS 2008).

Results

Phenological stages

In 2011, musk thistle germinated from seed that was planted in late April of the same year. Most of these plants developed into rosettes and from June to September

remained vegetative before becoming dormant in late fall (Fig. 2a). In MT monocultures, at least three plants in each plot flowered and set seed the first year.

In 2012, musk thistle that established in the previous year completed a two-year biennial life cycle, which is typical for the plant species (Roeth et al. 2003). Second year musk thistle rosettes broke dormancy and began to bolt at the end of April (Fig. 2b). Mature plants reached 180 cm in MT monocultures and warm season grass plots that had been grazed and received musk thistle (WS-G-MT). In these plots, plants flowered from June to August. In cool season grass communities, a total of six musk thistle plants flowered and reached a maximum height of 85 cm. The remaining plants (19 plants) did not advance past the rosette stage, even after two years.

Newly germinating musk thistle seedlings were observed in all WS plots in 2012 (Fig. 3b). Several of these plants eventually died, but a few in the non-grazed WS perennial grass plots that received musk thistle (WS-NG-MT) reached full maturity, although extremely stunted (20 cm) and only a single capitulum on each plant.

Musk thistle populations

The 2011 musk thistle plants in the WS grass communities completed their life cycle and senesced in August 2012. The number of musk thistle plants in WS grass communities increased early in the first two months of the 2011 and 2012 seasons and then either declined gradually (WS-G-MT) or dramatically to zero (WS-NG-MT) (Fig. 3). Even newly emerged musk thistle seedlings in the WS-NG-MT plots in 2012 died by mid-July. The number of musk thistle plants was greater in MT monocultures or

WS-G plots than plants in WS-NG plots across two years (Table 1).

In 2011, precipitation was above normal and musk thistle plant population peaked at 52 plants in the WS-G-MT plots (Fig. 3a). By the end of 2011, musk thistle rosette leaf cover had expanded across nearly the entire plots of MT monocultures and WS-G-MT (data not shown). In 2012, musk thistle cover declined due to early maturation and senescence as drought conditions intensified.

For the CS communities, low musk thistle populations were recorded after mid-2011 (Fig. 3a). Plots averaged less than four musk thistle plants and less than 1% cover (data not shown) and this trend was consistent in 2012, even though 1 or 2 new seedlings emerged. Although musk thistle populations were different in grazed and non-grazed treatments in 2012 (Table 1), the population was very low compared with that in WS-G communities (Fig. 3a, 3b). In April 2012, the highest musk thistle populations were recorded in all plots, partly due to germinating seedlings following precipitation events (Fig. 3b). For the remainder of the season, musk thistle populations declined to near or below 2011 counts.

Light

In all communities, light transmission to soil surface was greater by July and August of 2012 than for the same months in 2011 (Fig. 4c-d, g-h) due to the drought which was negatively impacting musk thistle and perennial grass growth. By mid-2011, WS-NG communities had complete canopy cover that resulted in less than 2% of full sunlight reaching the soil surface (Fig. 4c). During the same period, the

WS-G communities had 35% of full sunlight.

In 2012, light transmission was reduced to less than 16% in MT monocultures and WS-G-MT as musk thistle plants had increased in size and subsequently covered much of area of the plots (Fig. 4e). Later in 2012, light transmission increased as musk thistle plants bolted and began to flower and senesce. The fluctuation of light transmission influenced the increase in musk thistle numbers, growth, and maturity.

The CS communities had greater light penetration in the first two months of 2011, but by the end of the season there was no difference (Fig. 4c-d). In 2012, light transmission was consistently greater in grazed plots, but no difference occurred between CS communities that were over seeded with musk thistle (MT) or not (Fig. 4g-h). Fewer musk thistle plants emerged and grew in the CS communities observed.

Soil moisture

Moisture was above $0.08 \text{ m}^3 \text{ m}^{-3}$ for all of 2011 in surface (Fig. 5) and deeper (Fig. 6) soil depths except in WS communities with grazing ($0.04 \text{ m}^3 \text{ m}^{-3}$). In 2012, a severe drought resulted in 113 mm of precipitation, which was 396 mm below the 40-year average. The lack of soil moisture led to lower volumetric water contents at all depths within the soil profile (Figs. 5, 6).

In 2011, surface soil moisture was at or above $0.18 \text{ m}^3 \text{ m}^{-3}$ in bare ground (BG) and plant communities except WS-G plots, which declined below $0.04 \text{ m}^3 \text{ m}^{-3}$ by August (Fig. 5a). For combined deep soil moisture contents (30-120 cm), the CS grasses were consistently wetter than the MT (Fig. 6a, 6c), but the overall trend in

declining soil moisture was consistent in July and August for all treatments (Fig. 6). Soil moisture at 30-60 cm and 90-120 cm were lowest in WS-NG plots compared with moisture in other plots (Table 2), and was lower in August (Fig. 6).

The drought in 2012 caused surface soil moisture to decline from $0.31 \text{ m}^3 \text{ m}^{-3}$ in May to $0.12 \text{ m}^3 \text{ m}^{-3}$ (Fig. 5b). Similar to the deep soil moisture, the surface soil moisture was greater in the CS communities compared to the WS communities. In MT plots, surface soil moisture (Fig. 5b) was greater than soil moisture deeper in the profile (Fig. 6) during the latter months of 2012 when the plants were flowering (Fig. 2b). WS communities and musk thistle showed no difference in deeper soil moisture content for the months of May through August of 2012 (Table 2). For CS communities, deeper soil moisture content was similar across the two years (Fig. 6).

Biomass

Growth of musk thistle plants varied depending on location (WS, CS, or MT monoculture) and treatment (grazing (G) or non-grazing (NG)) (Fig. 7). In 2012, musk thistle plants in MT and WS-G-MT plots were larger in size than in the WS-NG-MT and the two CS treatments. Plants in the latter were extremely stunted with only a single flower head. Although musk thistle plants in the MT and WS-G-MT treatments were similar, biomass of MT plants was greater indicating bigger, not taller plants.

In the CS communities, six musk thistle plants were in the flowering stage (85 cm height), while all other plants were in the rosette stage. The growth of musk thistle in

the CS communities was affected by the perennial grasses and, therefore, biomass of musk thistle was lower than in the WS communities (Fig. 7).

Discussion

During this study, a dramatic change occurred in the weather pattern between the two years. In 2011, accumulated precipitation was above the 40-year average, while a severe drought resulted in less than a quarter of normal precipitation in 2012. The difference in precipitation between the two years had a large effect on the growth and establishment of musk thistle in the perennial grass communities. The wide variation in weather conditions allowed for the evaluation of musk thistle invasion and establishment in response to what could become more 'normal' conditions according to climate change models (Bradley et al., 2011).

Musk thistle successfully established in monocultures (MT) and grazed warm season perennial grass communities (WS-G-MT) following planting in the first year. While not a true invasion, the act of over seeding an invasive plant could be viewed as a type of simulation and thus corresponds with other studies that report greater musk thistle survival and development in open or overgrazed pastures and rangelands (Hamrick and Lee 1987, Beck 2001). Repeated grazing of WS communities (WS-G-MT) created an opening in the canopy which allowed more light to reach the soil surface in 2011. This benefitted initial musk thistle establishment and eventually allowed for plants to reach full maturity in the second year. In order to preempt available light and avoid shade by re-growth of perennial grasses, musk thistle

rosettes produced more leaf area quickly, which relates to leading invasion theories (e.g., superior competitor, niche resources) (see Craine 2005 and others). Moreover, we observed musk thistle plants in the WS-G-MT treatments projecting their leaves directly into vacant areas early in the season before perennial grass growth. Bazzaz (1996) has suggested greater plant plasticity and leaf acclimation during alternating intensities and exposures to light. Thus, our results reflect plasticity of musk thistle in response to variable light durations that occurred in the gaps of perennial grasses that were created by repeated grazing disturbances. These results suggest that musk thistle invasion success is highly dependent on access to light within a plant community.

After two years, musk thistle plants failed to survive in non-grazed warm season perennial grass communities (WS-NG-MT). In 2011, new musk thistle seedlings started to develop in these communities just prior to grass emergence and subsequent canopy closure. Musk thistle seedlings were forced to compete under rapidly changing light conditions by elongating stems, instead of normal rosette development and thus a trade-off occurred for normal tissue in exchange for stunted, misshapen seedlings that eventually produced a single capitulum. Those plants that failed to elongate, eventually died without producing flowers or seed. In areas where musk thistle is common or has the potential to invade, a dense and healthy pasture that is grazed minimally can prevent musk thistle establishment, primarily from the inability of the invader to tolerate shade (Hamrick and Janet 1987).

The failed and successful establishment of musk thistle in WS-NG-MT and WS-G-MT treatments, respectively, indicates an overlap in timing of resource (e.g.,

light) use when WS communities rapidly ascend canopy while musk thistle need sufficient light at the early rosette stage. Early growth of musk thistle in rosette form precludes the plant from access to light when growing among tall statured neighboring plants. The continued removal of biomass through grazing or other disturbance and subsequent opening in the canopy allowed musk thistle rosettes to become established. Without removal of the grass biomass, musk thistle responds by elongating early or remaining in rosette form. Therefore, it is important to consider grazing frequencies and durations for pastures or rangelands that are known to be infested with or threatened by musk thistle.

Surface soil moisture (0-8cm) less affect musk thistle plant populations in 2011, although it did influence successful musk thistle establishment during the drought year of 2012. The decline in surface soil moisture in WS-G plots in August of 2011 and 2012 could be due to the response of the grasses attempting to re-grow from the grazing treatment and thereby using more water. In non-grazed treatments (WS-NG and WS-NG-MT), grasses were flowering and producing seed during this period, which may require only minimal amounts of surface soil moisture. In contrast, roots of non-grazed WS communities may extend to deep soil depths and consume large amount of water when they are building aboveground biomass at vegetative stages (Fig. 2a). In addition to grass re-growth effects on soil moisture, the open niches in the WS-G treatments may have led to more moisture evaporating directly from the soil surface. We assumed surface soil moisture and intraspecific competition would reduce musk thistle populations dramatically in WS-G-MT treatments, but this was

not the case as more than half of the musk thistle plants survived over the two year period.

In 2012, surface soil moisture changes in treatments that had established and/or newly germinating musk thistle plants could have been a result of high amounts of shallow roots of musk thistle. As these plants developed early in the season, soil moisture declined, especially as musk thistle went from bolting (late June) to flowering (July) to senescence (August). The period of declining surface soil moisture for musk thistle was similar to that which occurred in WS-G plots during 2011 and 2012 when WS communities progressed from vegetative to flowering stages. This would indicate that WS communities and musk thistle have overlapping soil moisture use patterns during periods of early reproductive to late senescence growth stages. By disturbing the canopy (e.g., repeated grazing), the availability of light helped newly germinating musk thistle plants compensate their inability to compete for surface soil moisture that was being used by established perennial grasses.

Due to the growth habit of musk thistle, deep soil moisture (30-120cm) may not be a critical factor in competitive interactions between musk thistle and WS communities during years with normal precipitation. We found differences between deep soil moisture for musk thistle and WS communities in August 2011 before grasses moved to inflorescence stage (Fig. 2) (Table 2). Without adequate surface soil moisture, musk thistle will not germinate and, therefore, deep soil moisture has no effect on establishment. In drought years, musk thistle may germinate, but will probably fail to survive due to lack of soil moisture in the 0-30 cm layer of the soil. In

competitive conditions (e.g., MT monocultures, WS communities), newly germinated musk thistle plants may extend roots past this zone, only to encounter dry conditions created by established plants that grew during the same period. Invasive plants sometimes fail to compete with native plants under drought (Cahill 2003). Had 2011 been a drought year, we suspect soil moisture would have been a more significant factor in the success of musk thistle establishment in WS communities.

Cool season perennial grass communities were different from WS communities in terms of musk thistle establishment. For two years, the number of musk thistle plants in the CS communities was lower compared to MT monocultures and grazed WS communities (Fig. 3). Moreover, there was no difference in musk thistle population for CS-G or CS-NG treatments in 2011 (Table 1). Although a difference in musk thistle population between CS-G and CS-NG plots occurred in 2012, low musk thistle population (less than 3.75 ± 3.1 plants plot⁻¹) at the end of growing season indicates that disturbance, like repeated grazing may be less of an influence on the establishment of musk thistle in CS communities. Light transmission, which is directly related to grazing, may be not cause the increase of musk thistle populations in the CS communities. Kok et al. (1986) report a healthy tall fescue grass prairie can suppress the establishment of musk thistle and Blank and Morgan (2012) suggest cool season perennial grass communities can efficiently restrict the invasion of *Bromus tectorum* L. by occupying biological soil space. Our results suggest that even if light is sufficient in CS communities, musk thistle still is not able to compete and become dominant, like in WS communities.

Surface (0-8 cm) and deep (30-120 cm) soil moisture was above 0.13 and 0.24 $\text{m}^3 \text{m}^{-3}$ respectively CS communities, which was adequate for musk thistle germination and establishment. Regardless, the numbers of musk thistle plants remained low when compared to MT monocultures in nearby CS communities (19 ± 4.1 plants plot^{-1}) (data not shown) and at the other WS community location (21.5 ± 4.4 plants plot^{-1}) (Fig. 3).

We speculate the main reason musk thistle plants failed to establish in CS communities was due to preemption and domination of growth by the CS communities. The perennial grasses in CS communities were less bunching and more sod-forming than grasses in the WS communities (Gilbert and Larson 1994; Beaty et al. 1978). Unlike the WS communities with niches that can allow musk thistle establishment, the carpet-like growth habit of CS communities prevented openings or niches of any great size in which musk thistle could germinate and develop. In addition, the development of musk thistle seedlings was greatly reduced due to their inability to compete with CS communities that began growth early in the season. These communities may also have an intense network of roots just below the soil surface that are preempting musk thistle seedlings. Even with repeated grazing, the temporary openings in CS communities were inadequate for most musk thistle plants to be successful in establishing, although this might change over longer periods.

Musk thistle biomass was greatest in the MT monocultures due, primarily to lack of interspecific competition. Although musk thistle biomass was lower in WS-G-MT plots compared to MT plots, musk thistle plants were well-established in the grazed

warm season plant community. Smith and Kok (1984) report high intraspecific mortality can occur in the early seedling stage of musk thistle, but this self-thinning characteristic may be less of a factor in overall establishment due to the biennial growth habit and long rosette stage. Nevertheless, grazing can facilitate the establishment of musk thistle in WS communities to a greater degree than non-grazed or CS communities during a two year period.

Conclusions

Our study shows that the establishment of musk thistle is strongly dependent on perennial grass community type (e.g., life history) and disturbance, such as grazing during key phenological growth stages. Musk thistle is most likely to establish in repeatedly disturbed (e.g., grazed) warm season perennial grass communities and less so in cool season perennial grass communities. With adequate soil moisture, the spatiotemporal change in light availability induces successful establishment of musk thistle in a WS, but not CS community. The structure and earlier growth of CS communities is most likely limiting musk thistle establishment over short periods (e.g., 2 years). During periods of drought, growth of most perennial grasses and invasive plant species is restricted and thus, invasion is less likely to occur, even in WS communities. The amount of annual precipitation will influence the phenological stages and development of both invasive and native species and, therefore, should be considered more carefully during prairie or rangeland management (Zhang et al. 2011). Over or repeated grazing of WS dominant grasslands should be avoided to

minimize the risk of musk thistle invasion. In drought years, complete elimination of grazing might be the best option in order to maintain the long-term function and health of semi-arid grasslands in North America and elsewhere.

Figures and Tables

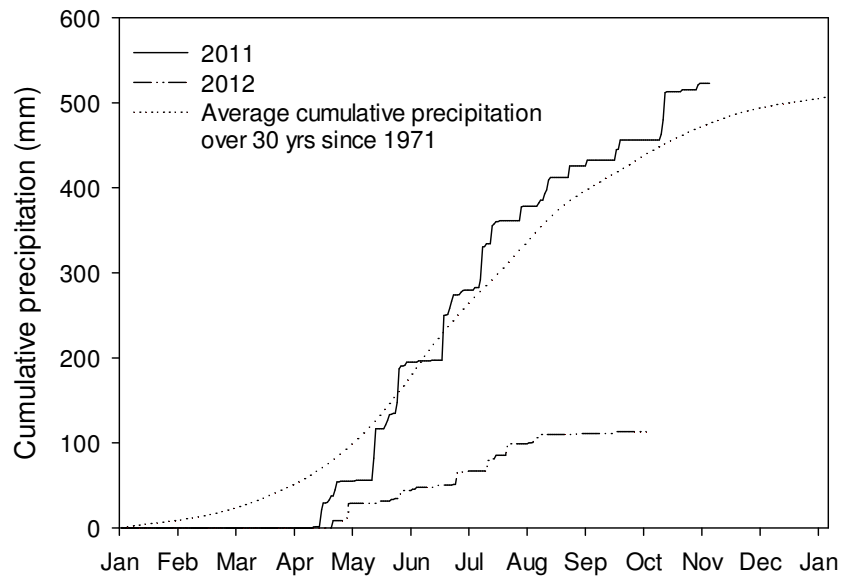


Figure 1. Average daily and cumulative precipitation in 2011 and 2012 at the West Central Research & Extension Center in North Platte, NE, USA.

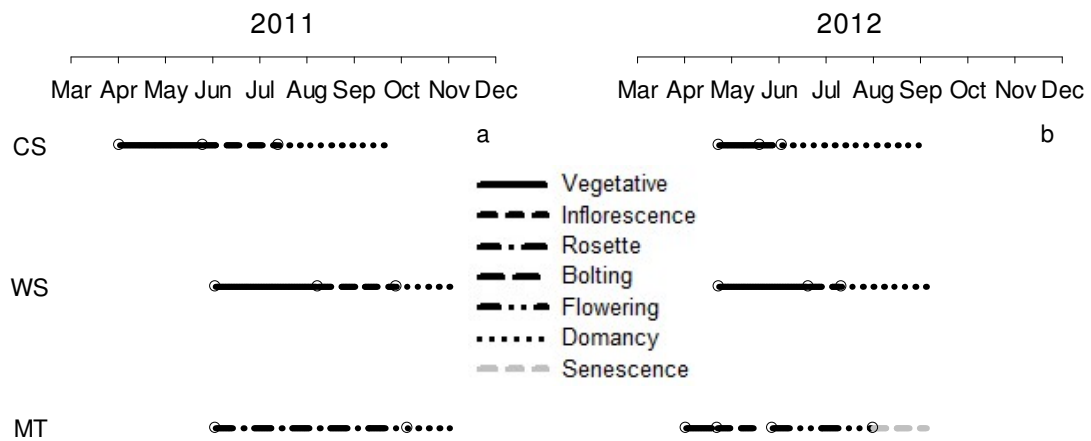


Figure 2. Phenology of musk thistle (MT), warm season perennial grasses (WS), and cool season perennial grasses (CS) in North Platte, NE, USA. The phenological stages for musk thistle are rosette, dormancy, bolting, flowering, and senescence, while the stages for grasses are vegetative, inflorescence, and dormancy.

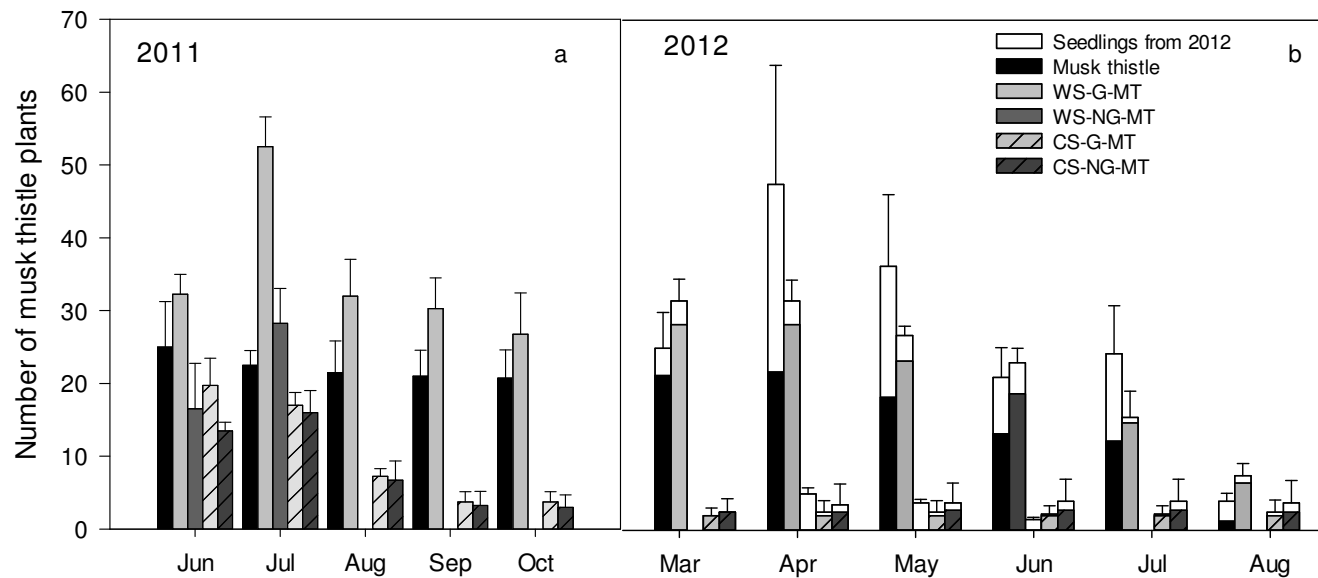


Figure 3. Number of musk thistle plants in all musk thistle seeded plots in 2011 and 2012. MT= musk thistle, WS-G-MT= grazed warm season perennial grass communities with musk thistle seeded, WS-NG-MT= non-grazed warm season perennial grass communities with musk thistle seeded, CS-G-MT= grazed cool season perennial grass communities with musk thistle seeded, CS-NG-MT= non-grazed cool season perennial grass communities with musk thistle seeded. The bars indicate standard errors of means. White stocked bars in 2012 represent new seedlings germinated in 2012.

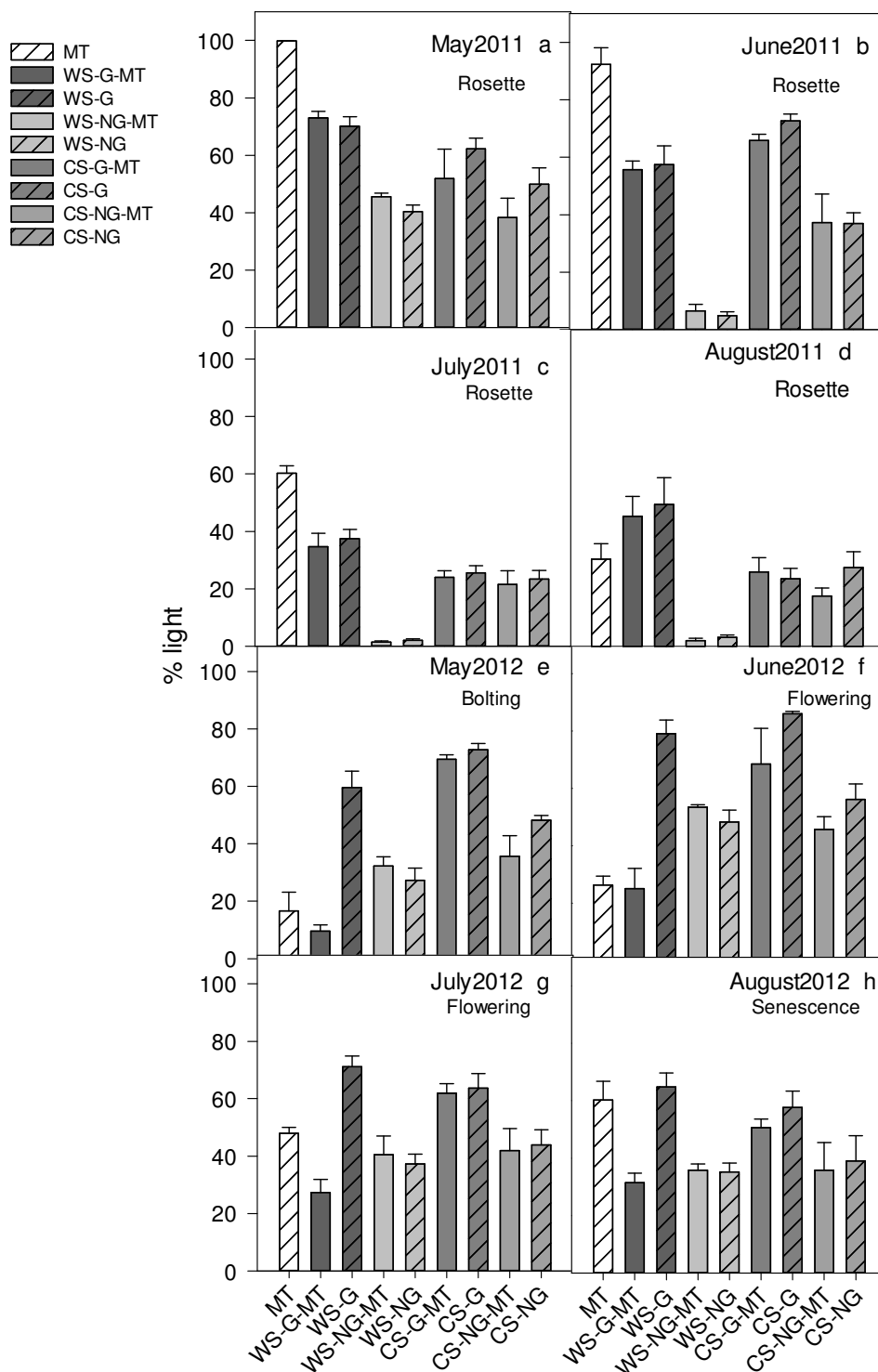


Figure 4. Percent of light transmission reaching the soil surface in musk thistle monocultures (MT), warm season (WS) and cool season (CS) perennial grass plots that were grazed (G) or non-grazed (NG). In WS or CS plots, musk thistle (MT) was added or not added. The bars indicate standard errors of means.

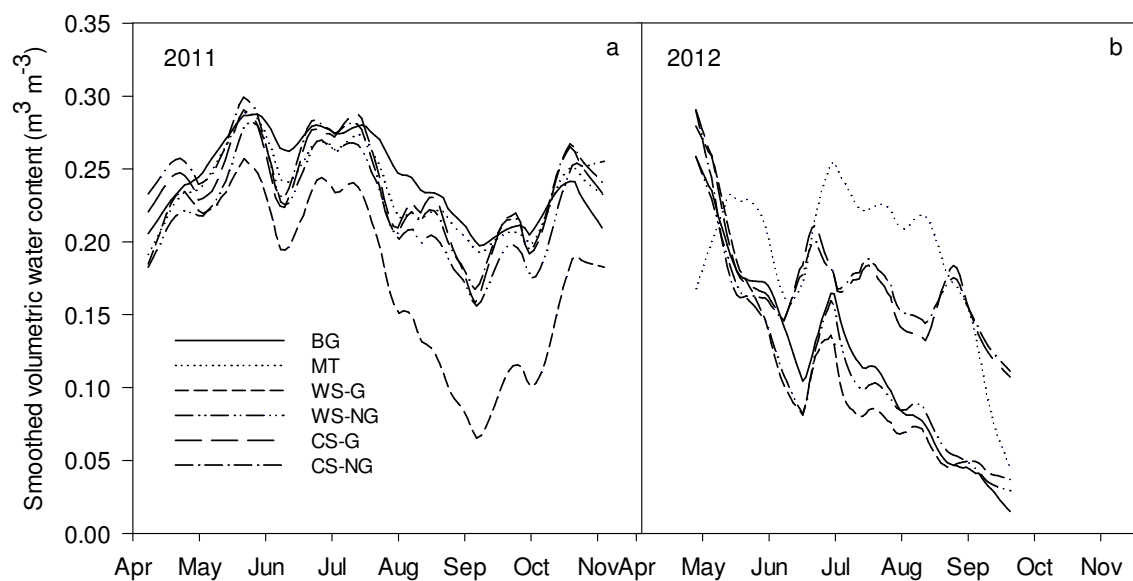


Figure 5. Daily surface (0-8 cm) soil moisture in plant communities for two years. The treatments were WS-G = grazed warm season perennial grass communities, WS-NG = non-grazed warm season perennial grass communities, CS-G = grazed cool season perennial grass communities, CS-NG = non-grazed cool season perennial grass communities, BG= bare ground and MT= musk thistle. Actual soil moisture data was negative exponential smoothed and plotted in order to facilitate patterns identification for each treatment.

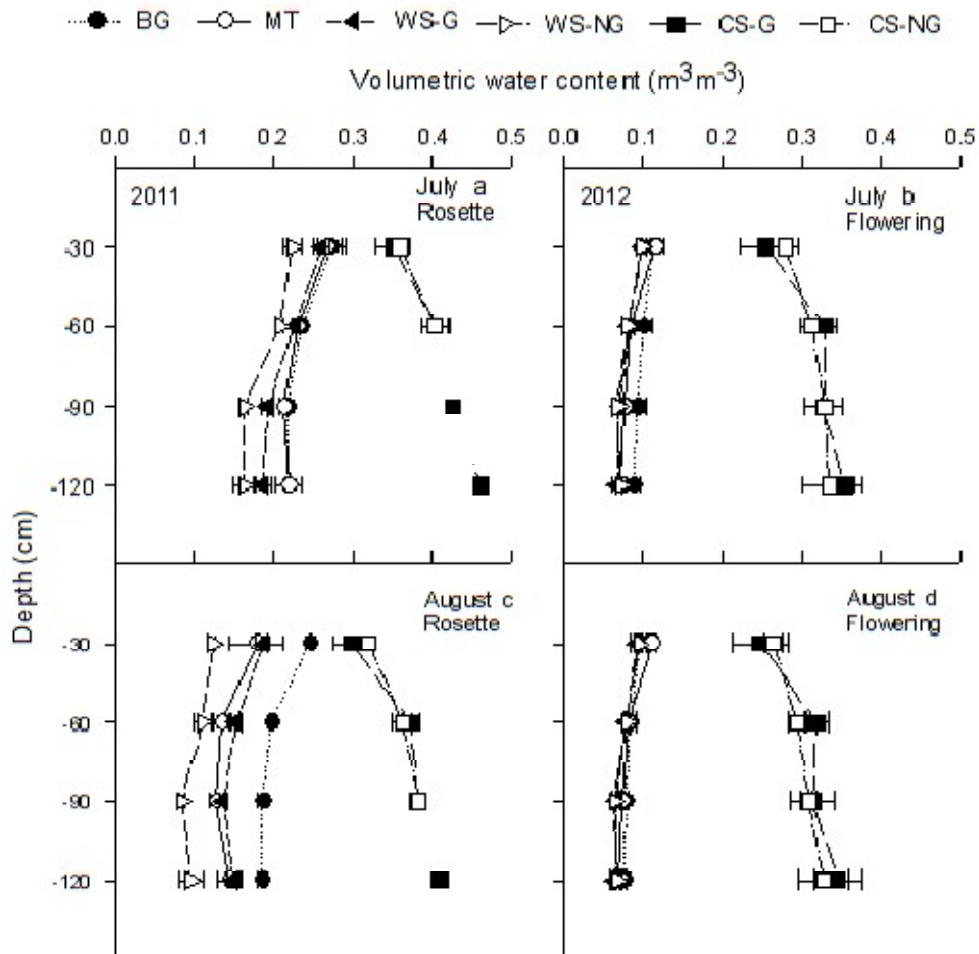


Figure 6. Soil moisture content combined across all depths (30-120 cm). WS-G = grazed warm season perennial grass communities, WS-NG = non-grazed warm season perennial grass communities, CS-G = grazed cool season perennial grass communities, CS-NG = non-grazed cool season perennial grass communities, BG= bare ground and MT= musk thistle. The bars indicate standard errors of means.

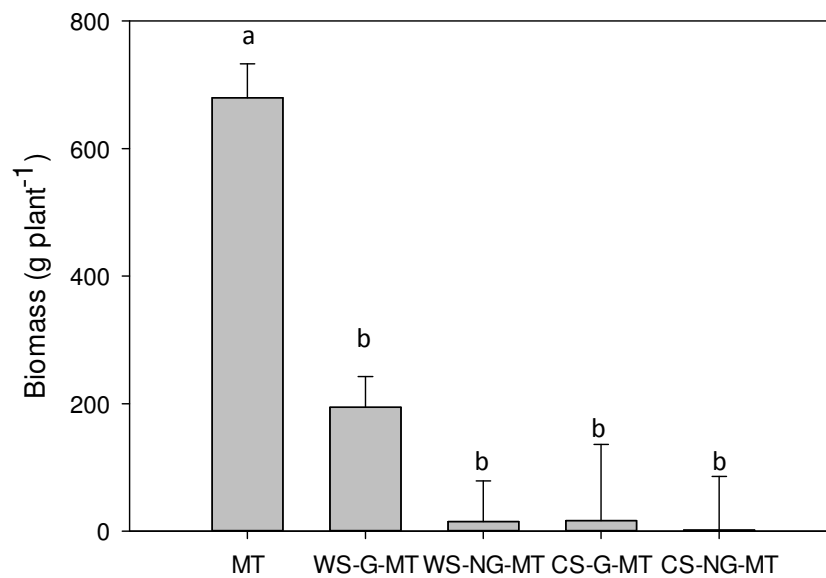


Figure 7. Above-ground biomass of musk thistle plants in monocultures and perennial grass communities after two years of growth. Treatments consisted of MT= musk thistle, WS-G-MT= grazed warm season perennial grass communities with musk thistle seeded, WS-NG-MT= non-grazed warm season perennial grass communities with musk thistle seeded, CS-G-MT= grazed cool season perennial grass communities with musk thistle seeded, CS-NG-MT= non-grazed cool season perennial grass communities with musk thistle seeded. The bars indicate standard errors of least square means. Letters denote significant different level at $p < 0.05$.

Table 1. Plant counts for musk thistle in monocultures (MT) and perennial grass communities that were grazed (e.g., WS-G-MT) or non-grazed (WS-NG-MT). The GLMMIX procedure was used to determine significance (n=4) of log-transformed plant counts. Bolded *p* values are significant at $p < 0.05$. Bolded *p* values and underlines bold *p* values indicate higher and lower musk thistle counts in the first communities under contrast communities, respectively. N/A indicates data are not available.

Contrast communities	----- 2011 -----					----- 2012 -----					
	Jun	Rosette		Senesce	Senesce	Rosette		Bolting	Flowering		Senesce
		Jul	Aug	Sep	Oct	Mar	Apr	May	Jun	Jul	Aug
MT vs WS-G-MT	0.28	<u>0.0006</u>	<u>0.035</u>	0.052	0.17	0.33	0.63	0.80	0.88	0.15	<u>0.031</u>
MT vs WS-NG-MT	0.052	0.51	N/A	N/A	N/A	N/A	<.0001	<.0001	<.0001	N/A	N/A
WS-G-MT vs WS-NG-MT	0.0023	0.0052	N/A	N/A	N/A	N/A	<.0001	<.0001	<.0001	N/A	N/A
CS-G-MT vs CS-NG-MT	0.34	0.79	0.43	0.34	0.30	0.12	0.067	0.065	0.060	0.06	0.046

Table 2. Soil moisture in musk thistle and perennial grass communities for two years. Treatments were musk thistle monocultures (MT), non-grazed and grazed warm season perennial grass communities (WS-NG and WS-G), and grazed and non-grazed cool season perennial grass communities (CS-NG and CS-G). Bare ground (BG) was used as a control. Bolded p values are significant at $p < 0.05$. Bolded p values indicate higher soil moisture in the first community under treatment contrasts. The underlines bold p values mean lower soil moisture in the first community under treatment contrasts. N/A indicates data are not available.

Phenological stage Treatment Contrasts	Rosette		Rosette		Flowering		Flowering	
	30-60		90-120		30-60		90-120	
	-----2011-----		-----2011-----		-----2012-----		-----2012-----	
	Jul	Aug	Jul	Aug	Jul	Aug	Jul	Aug
BG vs MT	1.0	0.0037	1.0	0.049	1.0	1.0	0.33	1.0
BG vs WS-G	1.0	0.037	0.68	0.14	0.67	1.0	0.70	0.97
BG vs WS-NG	0.25	<.0001	0.020	<.0001	0.0047	1.0	0.40	0.97
MT vs WS-G	1.0	<.0001	0.77	N/A	0.99	0.99	1.0	1.0
MT vs WS-NG	0.48	0.22	0.027	0.093	1.0	1.0	1.0	1.0
WS-G VS WS-NG	0.74	0.029	0.77	0.030	1.0	1.0	1.0	1.0
CS-G VS CS-NG	1.0	N/A	1.0	0.97	1.0	1.0	1.0	1.0

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Patterns of musk thistle (*Carduus nutans*) root growth in perennial grasslands of the Central Prairie

Abstract

The underground activity by an exotic species can be extensive at certain times of the season and result in significant impacts on neighboring plant communities. Root growth and development could be correlated with above-ground phenology that has a direct effect on competitive plant interactions. Studies were conducted in North Platte, NE to determine root growth patterns of musk thistle (*Carduus nutans*) and correlate below-ground activity with phenological development aboveground of perennial grasses. Monocultures of established warm season (WS) (*Panicum virgatum* L., *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Andropogon hallii* Hack., *Sorghastrum nutans* (L.) Nash, *Bouteloua curtipendula* (Michx.) Torr., *Desmanthus illinoensis* (Michx.) MacMill. ex B.L. Rob. & Fernald, *Dalea purpurea* Vent. and *Lupinus perennis* L.) and cool season (CS) (*Dactylis glomerata* L., *Bromus inermis* Leyss., *Bromus riparius* Rehmman and *Alopecurus arundinaceus* Poir.) perennial grass communities and newly planted musk thistle (MT) were monitored over a 2 year period. Simulated grazing was applied to half of the perennial grass plots (WS-G or CS-G) and musk thistle plots remained undisturbed. Weather patterns were different between the two years (e.g., normal and below normal precipitation in two years, respectively). Above-ground growth and development of plants was measured and *in situ* root images were taken monthly using a

minirhizotron camera to measure root length extension at shallow (0-28 cm), medium (28-56 cm), and deep (56-98 cm) soil depths. Musk thistle roots in the MT monocultures increased in the medium and deep depths from 6 to 16 m m⁻² over the two year period, primarily early in the growing season of above-ground growth and development. The grasses in the CS communities had the greatest amount of roots (88 m m⁻²) in the shallow depth and in the other depths. In WS communities, the amount of new roots (13 m m⁻²) in the normal precipitation year (2011) was greater than the amount (5 m m⁻²) in the second year during extreme drought conditions. Roots of grasses in the CS communities did not appear to be appreciably affected by the drought conditions in the second year. Grazing of the perennial grasses showed a negative correlation compared to the non-grazed grasses in the amount of roots deeper in the soil (24 m m⁻² vs. 31 m m⁻²). The new roots of musk thistle made up a larger proportion of total musk thistle roots (61%) than that of WS (43%) and CS (10%) perennial grasses and largely occurred during growing stage. The vigorous root growth of musk thistle may help facilitate its rapid invasion into perennial grasslands. These results provide insight on how musk thistle may be able to successfully establish in different perennial grass communities through spatiotemporal niches belowground. The effects of disturbance (e.g., drought, grazing) on WS communities further exacerbates conditions that would favor musk thistle establishment, suggesting a more diligent approach is needed to improve management of exotic species in Central Prairie grasslands.

Keywords: *Carduus nutan*, cool season, disturbance, distribution, drought, grazing, invasion, musk thistle, perennial grass, root minirhizotron, warm season

Introduction

In the Central Prairie, invasive plants are widely established in rangelands (Mico and Shay 2002, Eddy and Moore 1998, Melinda and Knapp 2001). The successful invasion of plant communities by nonindigenous plants and the resistance by native perennial grass communities to invasion depends on preempting resources aboveground (e.g., light) (DiTomaso et al. 2003) and belowground (e.g., soil moisture, nutrient, biological soil space) (Young et al. 2011; Daehler 2003; Blank and Morgan 2012). Root distribution patterns of native perennial grasses and invasive plants often occur in response to the dominant habitat type and variations in carbon and nutrient cycles (Aerts et al 1989; Jackson et al. 1997). However, few studies have addressed the significance of root growth and development for a season or the life cycle of a plant species (Larreguy et al. 2012; Young et al. 2010; Fernandez and Caldwell 1975). If a more thorough understanding of plant community resistance and plant invasion is expected, studies of belowground processes will be critical in the short- and long-term.

Native perennial grass communities are desirable for restoring degraded areas of the Central Prairies due to many factors, including root longevity, which confers greater potential for resistance to invasion by non-native species (Berlinger and Knapp 1991, Bottoms and Whitson 1998, Laufenberg 2003). Plant types that compose

these perennial grass communities include both warm season (C4) and cool season (C3) species. These two types of plants have differing physiology and phenology both above and belowground. The roots of many warm season perennial grasses can extend deeper into the soil profile compared to cool season perennial grasses, which prefer to extend more fine roots into shallow soils early in the spring (Fransen et al 2006; Steven et al 2002). Weaver (1954) reported roots of warm season perennial grasses, such as switchgrass (*Panicum virgatum* L.) to extend over 3 m into soil, while smooth brome grass (*Bromus inermis* Leyss.), a cool season perennial grass, has mainly fine roots in shallow (0-50 cm) soil depths (Gist and Smith 1948).

Musk thistle (*Carduus nutans*) is a C4 herbaceous monocarpic herb which was introduced to the United State from Eurasia (Kok 2001) and is commonly found in arid to semi-arid rangelands. As a biennial herb, musk thistle rosettes extend fine roots in shallow soil layers during the first year and develop large taproots deeper into the soil beginning in the spring of the second year (Ree et al. 1996). The variation in the growth and development of musk thistle roots may help contribute to its successful establishment in Central Prairie grasslands and rangelands, however research is lacking.

The successful resistance by perennial grass communities to invasive plant species is often due to the overlap in resource use patterns (Young et al 2010, 2011), which includes biological soil space (Blank and Morgan 2012.). This overlap occurs when the native and invasive plants use the same spatially and/or temporally available resources at specific phenological growth stages (Suding et al. 2003; Zavaleta and

Hulvey 2007). This is one reason for established native perennial grasses being able to resist invasion; they have an extensive root system in place for efficient uptake of resources. (Blank and Morgan 2012).

The growth and development of plant roots is affected by abiotic factors such as available soil moisture (Canham et al. 2012), adequate soil temperature (Steinaker et al 2010; Teskey and Hinckley 1981; Tierney et al 2003) soil nutrients (Drew and Saker 1975) and the biotic factor of interspecific competition (Harris 1977). DiTomaso et al. (2003) report that decreasing the availability of light to plant shoots and leaves corresponds to a reduction in root productivity for yellow starthistle (*Centaurea solstitialis*), an invasive plant species in California. Blank and Morgan (2012) indicate that early season root growth of cool season grasses results in a reduction of biological soil space for competitors, which increases resistance to invasion.

For many perennial grass communities, a disturbance such as repeated grazing may change root distribution and have an effect on resistance to invasion. Aboveground, the poorly timed grazing or overgrazing results in openings in the plant canopy that create a niche for an invasive plant species to establish (Feldman et al. 1968; NDSU 2000). Musk thistle is able to take advantage of niches in rangelands and pastures that fail to recover from overgrazing periods (Hulbert 1986; Leininger 1988; Rice and Randall 2001; Beck 1999). Belowground, the improper grazing can affect root production in the upper soil layers of perennial grasslands (Larreguy et al. 2012) and ultimately, result in altered carbon allocations that may lead to a reduction in root

biomass of native perennial grasses (Ludwig and Tongway 1995; Gill and Jackson 2000).

In this study, we compared root growth and development of musk thistle and warm and cool season perennial grass communities. We hypothesize that grazing would negatively affect root distribution and live root growth for grasses, thereby creating a niche for an invasive plant species. Further, musk thistle would potentially fill this niche based on our other research (Han and Young, *In Press*) and root growth measurements in separate monoculture plots. Our results will further the knowledge and understanding on root growth and development in relation to plant community stability in grasslands of the Central Prairies.

Materials and Methods

Site descriptions

The study was conducted at the West Central Research & Extension Center (WCREC) in North Platte, NE (41.090S, -100.769E), where average annual precipitation is 508 mm of which 80% occurs from late-April to mid-October (USDA, 1978). Warm season (WS) and cool season (CS) perennial grass communities were established in 2007 in two locations, which were approximately 1.5 km apart. Precipitation and soil temperature at 10 cm soil depth were recorded automatically at a nearby weather station operated by University of Nebraska. Soil temperature at 10 cm was used for correlating root activity at shallow depths.

The dominant soil type at the two locations was a Cozad silt loam (fine-silty,

mixed, mesic Fluventic haplustoll) (Payero et al. 2008). Annual crops were grown at the two locations before the establishment of the two grass communities and no musk thistle occurred during these periods.

Experiment design

The experiment included warm (WS) and cool (CS) season perennial grass communities. All perennial grass species chosen were common to the Central Prairie (Anderson 2007). The WS perennial grass communities were planted in 2009 with a mix of *Panicum virgatum* L., *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Andropogon hallii* Hack., *Sorghastrum nutans* (L.) Nash, *Bouteloua curtipendula* (Michx.) Torr., *Desmanthus illinoensis* (Michx.) MacMill. ex B.L. Rob. & Fernald, *Dalea purpurea* Vent. and *Lupinus perennis* L. and by 2011, *P. virgatum* was dominant. The cool season perennial grass community was planted in 2007 and included *Dactylis glomerata* L., *Bromus inermis* Leyss., *Bromus riparius* Rehmman and *Alopecurus arundinaceus* Poir. By 2011, *D. glomerata* L. (orchardgrass) and the two *Bromus* spp. were the dominant species (Table 1). All grasses were seeded according to recommended guidelines (Anderson 2007). Following planting, perennial grass communities established to full canopy cover each year.

For the WS and CS communities, a simulated grazing (G) treatment was applied to half of the plots and the remaining plots were not grazed (NG). Each treatment was replicated four times at each location. Musk thistle monocultures (MT) were established in bare ground plots using locally collected seed that was planted by hand

and allowed to grow naturally without disturbance. Shoot phenological stages of musk thistle and grass communities were recorded throughout the growing season for the two years (Fig. 2). Plots of perennial grasses and musk thistle monocultures were 5 m x 2 m and a narrow alley (0.3 m) separated adjacent plots. The simulated grazing (referred to as grazing) treatments were made at 10 cm above the ground using a rotary mower and electric hedge trimmers. Following grazing, grass residue was removed from the plots immediately. In 2011, plots in the WS communities were grazed approximately bi-weekly (5 times) beginning on June 1. A similar grazing interval was used for the CS community plots, except the last two treatments were not applied due to lack of growth. In 2012, a single grazing treatment was applied on April 21 and May 28 to CS and WS communities, respectively. No grazing was needed for the remainder of the season due to severe drought conditions.

In the fall of 2010, transparent butyrate minirhizotron tubes (180 cm) were installed in MT monoculture and WS and CS community plots. Root length measurements for fine roots (diameter < 0.2 mm) of perennial grass communities and musk thistle were recorded using an electronic scanner (CI-600 Root Scanner, CID, Inc., Washington, USA) attached to a laptop computer. The scanned areas of the soil, which included roots, were seven evenly spaced depths (0-14, 14-28, 28-42, 42-56, 56-70, 70-84 and 84-98 cm) starting at the soil surface of the perennial grass communities and musk thistle monocultures. The scanned images within each depth were 216 mm x 200 mm and used to calculate length of roots per square meter. The method for collecting images was similar to Johnson et al. (2001). To quantify total

(while and brown) roots and live (white) roots, digitized images were analyzed by outlining all visible roots on a computer touch screen using specialized root analysis software (Rootsnap!, FA. CID, Washington, USA). The mean root diameter was measured using a scale of 1:1 for images in each treatment. Root images were taken monthly starting in May 2011 and ending in September 2012 when musk thistle had senesced. No measurements were taken during winter when plants were dormant. Any weeds growing in plots were hand removed bi-weekly to prevent extraneous roots from appearing in images.

Statistical analysis

Data was averaged for three depths (0-28; 28-56; 56-98 cm). Total root length or live roots per unit area were compared at these three depths within a month for a treatment with the generalized linear mixed model and analysis of variance. Statistical analysis was applied within each year. Fixed factors in the model included depth, time, and grazing as well as possible combinations of interactions. Tukey's HSD test was used to separate means of total root length and live root length at $p < 0.05$. All analysis was in the GLIMMIX procedure of SAS (SAS 2008).

Results

Precipitation and Soil Temperature Patterns

For the two years of the study, precipitation was highly variable representing normal and extreme drought conditions. In 2011 and 2012, total seasonal precipitation

was 513 mm and 113 mm, respectively, which was 3% higher and 77% lower than the historical 30-year average. For an entire year, monthly precipitation amounts for 2012 were dramatically lower than 2011 (Fig. 1). In 2011, almost 30% of the yearly total precipitation amount occurred in May (140 mm) and almost 15% occurred in October (66 mm), with the later amount recharging the soil profile (Fig. 1a). However, extremely low amounts of precipitation for all of 2012 created extensive water deficits with a majority (89%) of the total precipitation occurring in late spring and early summer (Fig. 1b). Soil temperatures at 10 cm deep peaked at 30 C in August of both years (Fig. 1). In 2012, a greater number of warmer days occurred than in 2011.

Shoot Phenological Stages

In 2011, musk thistle germinated from seed that had been planted in plots earlier in April. Most of the plants developed into rosettes and from June to September remained vegetative before becoming dormant in late fall (Fig. 2a). Of the 84 musk thistle plants that established in all of the plots, a very small number (3.5%) flowered and set seed in the first year. In 2012, musk thistle that had established in the previous year completed a biennial life cycle, which is typical for the plant species (Roeth et al. 2003). Second year musk thistle rosettes emerged from dormancy and began to bolt at the end of April (Fig. 2b). Mature plants reached a maximum height of 180 cm in July and flowering spanned the months of June through August.

In 2011, grasses in the WS communities emerged from dormancy in June and by August, plants had reached full inflorescence. By the end of the season, the grasses in

the WS-NG treatments reached a maximum height of 150 cm, while grasses in the WS-G treatments grew back from repeated grazing to a maximum height of 30 cm. In 2012, maximum perennial grass height in WS-NG communities was 50 cm by mid-June, which remained unchanged for the remainder of the season.

Grasses in the CS communities failed to exhibit sizeable differences in height between grazed (CS-G) and non-grazed (CS-NG) communities for both study years. Average maximum grass height was 35 cm in both years. In 2012, grasses in the CS communities grew slowly and only a single grazing was applied to the CS-G treatment. The CS communities displayed dormant-like conditions (e.g., shorter, less robust) in 2012, due to the extreme drought conditions.

Root Distribution Patterns

Total root distribution for MT monocultures and each grass community (WS and CS) was different at three soil depths (0-28, 28-56, and 56-98 cm) (Fig. 3-6). In 2011 and 2012, the amount of live roots was similar for MT, WS, and CS at all depths (Fig. 4, 6), while total roots fluctuated, especially in grazed treatments and CS communities (Fig. 3, 5). Root diameter of plants in the MT monocultures and WS, CS communities ranged from 0.5 to 3.0 mm (data not shown).

Root length of plants (total roots and live roots, unless otherwise noted) in the MT monocultures was significantly lower compared to WS and CS communities (Fig. 3-6). There was no difference in root length found among soil depths (0-28, 28-56 and 56-98 cm), although an increase in total root length (16 m m^{-2}) at the 28-56 cm soil

depths occurred in both years (Fig. 3e, 5e). Distribution of live roots and total roots followed a similar pattern in 2011 (Fig. 3e, 4e), but live roots declined noticeably in June 2012 with plant flowering, while total roots remained high (Fig. 5e, 6e).

In 2011 and 2012, WS communities had the greatest amount of roots (white and brown) at the 56-98 cm depth late in the growing season regardless of grazing (Fig. 3a, 3c, 5a, 5c). In 2011, total root length of grasses in the WS-G communities increased from July to September, during inflorescence, while those in the WS-NG communities remained constant or declined. Live roots followed a similar pattern as total root length within the WS-G and WS-NG communities. In 2012, total root length declined at all three depths (Fig. 5a, 5c,) and was most likely a result of the extreme drought conditions. Total root length declined at shallow soil depths (0-28 cm) in WS-G communities in 2012 (Fig. 5a). Although deep roots increased or were high at the start of 2012, a gradual decline occurred after April or May (Fig. 5c). This coincided with the extreme drought conditions and lack of pre-season soil moisture recharge that occurred in the Central Prairie region. Similarly, the length of live roots declined after April to less than 1 m m^{-2} (Fig. 6a, 6c).

In 2011 and 2012, total root (white and brown) distribution patterns for grasses in the CS communities differed substantially among the three different soil depths (0-28, 28-56 and 56-98 cm) (Fig. 3b, 3d, 5b, 5d). Grasses in the CS-NG communities had greater root lengths than in CS-G communities for two years, especially at the medium depth (28-56 cm) in the second year (Fig. 3b, 3d, 5b, 5d). The greatest amount of roots for grasses in the CS communities always occurred in the shallow

depths (0-28cm), regardless of grazing or non-grazing treatments (Fig. 3b, 3d, 5b, 5d). Total root length in the shallow and medium depths decreased in June of the second year when drought conditions worsened. The amount of deep roots in the CS communities remained constant over the length of the study, even though at a lower number than those in the shallow and medium depths. Except for early in the growing season, live (white) root production was low during the two years (Fig. 4b, 4d, 6b, 6d).

Discussion

In theory, root distribution patterns of plant communities are largely related to the phenologies of plants distributed within a specified community (Steinaker et al. 2010). However, many abiotic factors influence root growth and development and include precipitation, soil temperature and disturbance in addition to obstructions, availability of nutrients, and allelopathic interactions. Here, we focus on the former in their effects on musk thistle roots and the potential for aiding in establishment in perennial grasslands of the Central Prairie.

Over two years, two distinct precipitation patterns occurred, which led to adequate soil moisture in the first year (2011) and below normal soil moisture in the second year (2012). This difference in soil moisture influenced the root distribution patterns for musk thistle and the two perennial grass communities. Aboveground phenology for all three plant communities was strongly influenced by the two different precipitation patterns. Life cycles of perennial grasses in the WS and CS

communities were shortened in 2012 due to severe drought and a lack of soil moisture. Both plant types avoided the drought by either completing vegetative growth during the year of normal precipitation (musk thistle) or accessing deeper soil moisture in the year of below normal precipitation (perennial grasses). Had the drought occurred in the first year, a different response from all plant types would be expected. Nevertheless, precipitation patterns constantly vary and measuring plant response during any two or more consecutive years when conditions change or remain the same can be helpful for identifying mechanisms that facilitate survival by one plant type over another.

Some perennial grass species are able to avoid drought by maturing more rapidly (Weaver and Clements 1938). However, we found no evidence that would suggest rapid aboveground phenological development related to a proliferation or dramatic reduction in belowground activity, only that roots appeared to decline because of lack in soil moisture. Had there been two consecutive years of normal precipitation, we might have been able to determine this. Nevertheless, during the two study years, a lack of soil moisture recharge at the end of 2011 and into early 2012 caused dry conditions in the soil which negatively affected root length in all grass communities and MT monocultures (Fig. 5).

Musk thistle had the lowest root production compared to the two perennial grass communities. This could be due to the short longevity of musk thistle roots (e.g., biennial) and the fact that it produces a main tap root that may not be easily captured in images taken in a stationary tube belowground. We addressed these two issues by

installing scanner tubes 1) well in advance of seeding musk thistle into plots and 2) at a 45° angle positioned directly underneath what would later become a dense population of musk thistle plants. Interestingly, new root production of musk thistle monocultures was similar to that in the WS and CS communities (Fig.4, 6), indicating that a greater proportion of the total amount of musk thistle roots was alive and active for the two year period (Fig. 3e, 4e, 5e, 6e). In addition, Rees et al. (1996) reported musk thistle can extend tap roots quickly into deep soil following emergence from dormancy in the spring of the second year, which supports our results (Fig. 6e). As a short lived herb, the root activities of musk thistle may facilitate its invasion into WS communities that have fewer roots distributed in the shallow soil profile. Also, the characteristic of rapid root expansion may facilitate the invasion of musk thistle into bare ground or overgrazed sites that have little competing vegetation.

Roots of warm season (WS) grass communities were more abundant at deeper soil depths (e.g., > 28cm). The highest proportion (70-80%) of root biomass for most warm season perennial grass species is in the upper 30 cm of soil (Weaver and Darland 1949; Kucera and Dahlman 1968; Kitchen et al. 2009). However, there are still many roots distributed deeper that are as important if not more, especially during drought in the upper soil layers. Tufekcioglu et al. (1999) reported roots of switchgrass were widely distributed in deep soil layers. The switchgrass ecotype in our studies was 'Trailblazer', which is an upland type that has a bunching growth habit and fewer spreading rhizomes. Root length of grasses in the WS-NG was associated with sufficient soil moisture and normal soil temperatures in first year (Fig

3a). In second year, total root length of grasses in the WS communities began higher or at a similar amount as the previous year, but decreased as the drought conditions worsened starting mid-season through to the end of the study. Live roots of grasses in the WS communities appeared to be more affected by soil moisture deficits than roots of musk thistle in the MT monocultures and grasses in the CS communities. In 2011, the pattern of live root length was similar to total root length, but in 2012 live roots decreased to near zero due to drought conditions. Some grasses are especially sensitive to soil moisture variation and tend not to produce new roots when soil moisture is limiting (Hild et al. 2001).

In cool season (CS) perennial grass communities, a large proportion of the roots were distributed in the shallow soil depth (0-28 cm). This is typical of sod-forming grasses, such as *Bromus inermis* Leyss., which was one of the dominant species in our field site. Live root production by grasses in shallow CS communities increased later in the season during cooler conditions (Fig. 4b, 4d), which indicate higher temperatures earlier in the season may have affected cool season grass root growth and development. High soil temperatures have been found to hinder the development of cool season grass roots (Liu and Huang 2005). Xu and Huang (2000) reported 49 days of high air/soil temperature (20/35C) reduced the number of creeping bentgrass (*Agrostis palustris* Huds. cv. Penncross) roots from 12 to 2 at shallow soil depths (5-7 cm). In addition, the genetics and physiology of cool season perennial grasses causes them to grow during the cooler parts of the year, including late fall and early spring. Nevertheless, live root lengths were similar for all three depths and very low (1 m m^{-2})

after starting out high in June 2011 and April 2012 (Fig. 4b, 4d, 6b, 6d), which may have been due a greater number of the 'brown' roots actually being alive. Grazing can reduce root growth of cool season grasses (Karl et al. 1993), but that was not the case here, as grasses in the CS-G and CS-NG treatments had similar increases and decreases in total and live roots throughout the growing season for both years.

Theoretically, it is possible after disturbance for musk thistle to invade WS and CS perennial grass communities based solely on a lack of or decrease in root production by the grasses. For disturbances related to drought and grazing (Qian et al. 1997; Reeder and Schuman 2002), we found a clear difference in response between the two types for perennial grass communities. During drought conditions, live roots of grass communities decreased to near zero, except deep in the soil, and total root production decreased gradually over the growing season, especially at 0- 56 cm depths and in WS communities. Regardless of whether drought conditions lessen or remain unchanged in the years following, a niche has been opened in the upper soil profiles of WS and CS perennial grass communities that could potentially allow for musk thistle invasion and establishment. The use of perennial grasses by land managers for grassland restoration includes a consideration for the belowground occupancy that helps to prevent encroachment by invasive plant species. However, abiotic factors, like drought, and the differentiation in root growth patterns of WS and CS communities could result in differences in resistance to musk thistle invasion. Perennial grasses in the WS communities have bunch-forming roots and short rhizomes that may allow roots of musk thistle seedlings to establish in openings or

niches created by aboveground disturbances in the plant canopy (Chengchou and Young *In Press*). Contrastingly, the dense roots and rhizomes of the perennial grasses in the shallow and middle soil depths of the CS communities were sod-forming, which restricted most shallow root development and newly germinating musk thistle plants. Previously, we found musk thistle failed to establish in CS communities regardless of grazing duration, but successfully invaded WS communities that were grazed for similar periods (Han and Young, *In Press*).

Our study sheds light on how musk thistle invasion into two different perennial grass communities could be dependent on root distribution patterns of the invader and community and the importance of a particular disturbance (e.g., drought and grazing) that may lead to successful or failed establishment. Although not addressed in our theoretical approach, the variability in available resources (e.g., other than soil moisture), physical obstructions, and allelopathic effects from nearby vegetation are all associated with root distribution patterns and may further impact the successful establishment of an invasive plant species such as musk thistle. Young et al. (2011) reported perennial grass communities showed plasticity in water use patterns when the annual precipitation amounts changed between years. Alternatively, Eggemeyer et al. (2008) reported that eastern redcedar (*Juniperus virginiana*), a woody plant species, and warm season perennial grasses competed for water in the upper soil profile, but cedar showed plasticity in water uptake deep in the soil as seasons changed from early spring to mid-summer. In this case, the grasses failed to compensate. Considering the amount of published research on root growth and development of perennial grasslands

and invasive plant species is fairly limited (Jackson et al. 2001), it is important that research continue in this area to elucidate the importance of disturbance and avoid reduced long-term function and health by the establishment of invasive plant species.

Figures and Tables

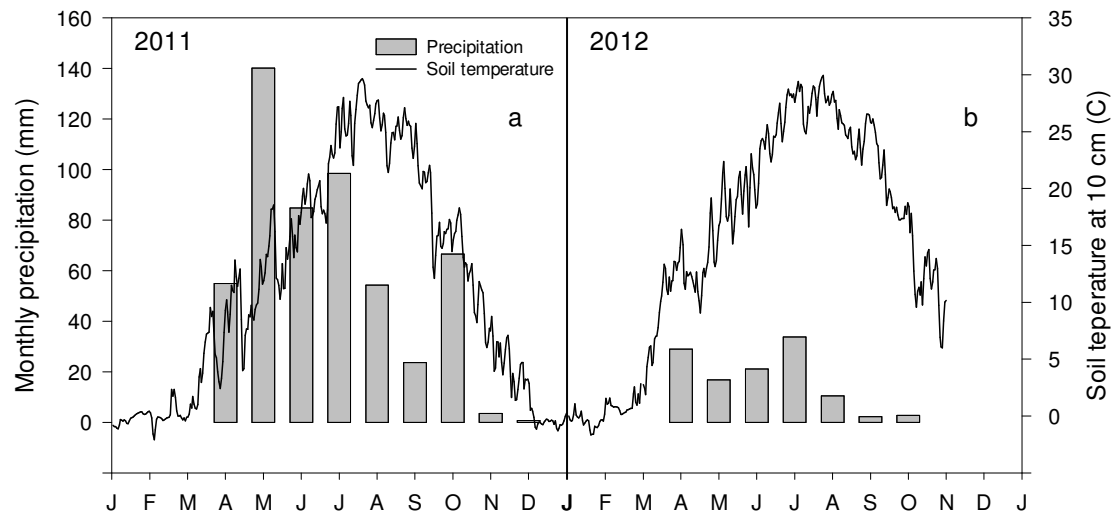


Figure 1. Monthly precipitation and soil temperature (10 cm) in 2011 and 2012 at the West Central Research & Extension Center in North Platte, NE, USA.

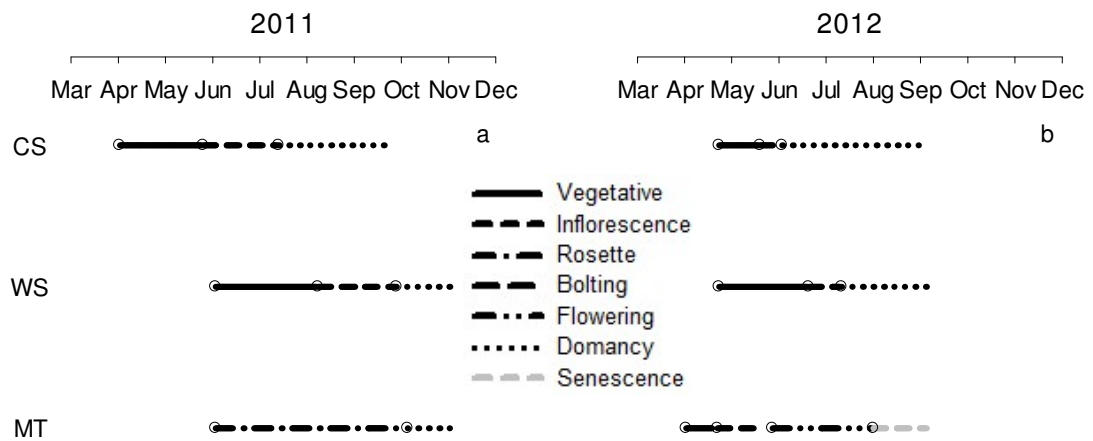


Figure 2. Phenology of musk thistle (MT), warm season perennial grasses (WS), and cool season perennial grasses (CS) in North Platte, NE, USA. The phenological stages for musk thistle are rosette, dormancy, bolting, flowering, and senescence, while the stages for grasses are vegetative, inflorescence, and dormancy.

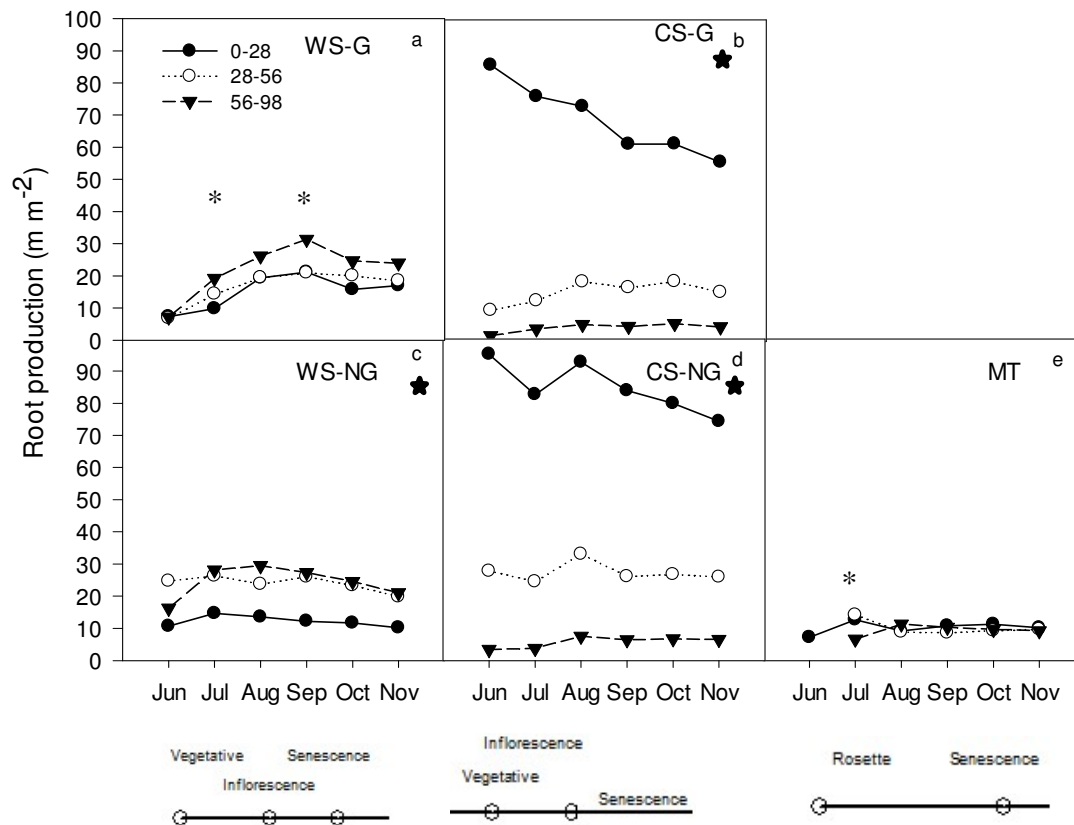


Figure 3. Total root (white and brown) length per image area (0.0423 m^{-2}) at three soil depths (cm) in 2011. WS-G = grazed warm season perennial grass communities, WS-NG = non-grazed warm season perennial grass communities, CS-G = grazed cool season perennial grass communities, CS-NG = non-grazed cool season perennial grass communities, and MT = musk thistle monocultures. Phenology of warm season perennial grasses (WS), cool season perennial grasses (CS) and musk thistle monocultures (MT) are listed. Unshaded circles on secondary x axis indicate the phenological periods for WS, CS, and MT. Asterisk indicate statistical differences at $P < 0.05$ for the three depths at each month within a treatment. Star indicates root production was different in this treatment at $P < 0.05$.

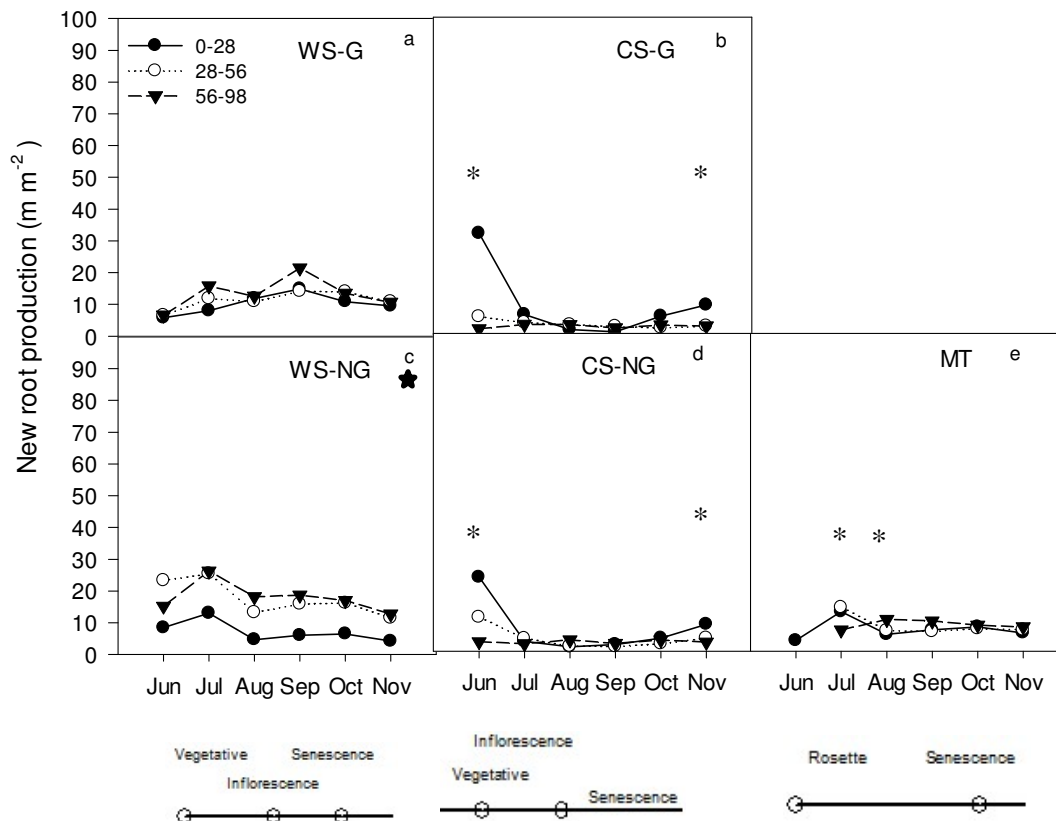


Figure 4. Live root (white and brown) length per image area (0.0423 m^{-2}) at three soil depths (cm) in 2011. WS-G = grazed warm season perennial grass communities, WS-NG = non-grazed warm season perennial grass communities, CS-G = grazed cool season perennial grass communities, CS-NG = non-grazed cool season perennial grass communities, and MT = musk thistle monocultures. Phenology of warm season perennial grasses (WS), cool season perennial grasses (CS) and musk thistle monocultures (MT) are listed. Unshaded circles on secondary x axis indicate the phenological periods for WS, CS, and MT. Asterisk indicate statistical differences at $P < 0.05$ for the three depths at each month within a treatment. Star indicates root production was different in this treatment at $P < 0.05$.

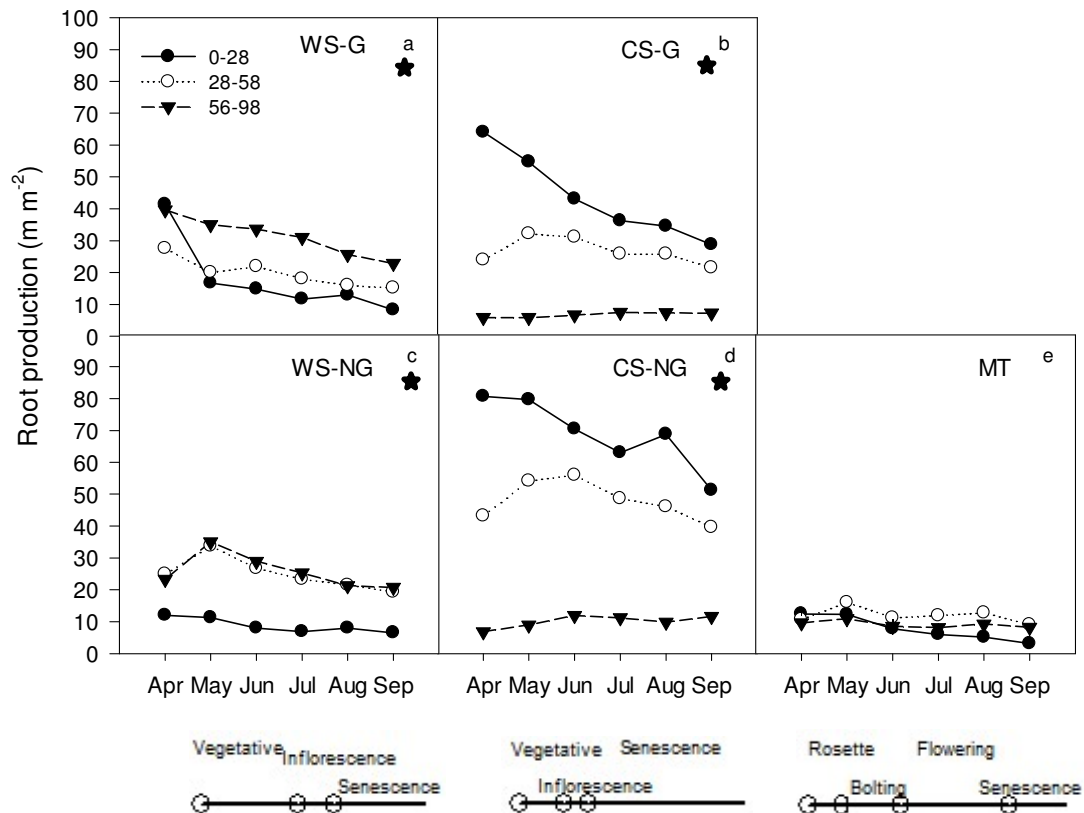


Figure 5. Total root (white and brown) length per image area (0.0423 m^2) at three soil depths (cm) in 2012. WS-G = grazed warm season perennial grass communities, WS-NG = non-grazed warm season perennial grass communities, CS-G = grazed cool season perennial grass communities, CS-NG = non-grazed cool season perennial grass communities, and MT = musk thistle monocultures. Phenology of warm season perennial grasses (WS), cool season perennial grasses (CS) and musk thistle monocultures (MT) are listed. Unshaded circles on secondary x axis indicate the phenological periods for WS, CS, and MT. Asterisk indicate statistical differences at $P < 0.05$ for the three depths at each month within a treatment. Star indicates root production was different in this treatment across months at $P < 0.05$.

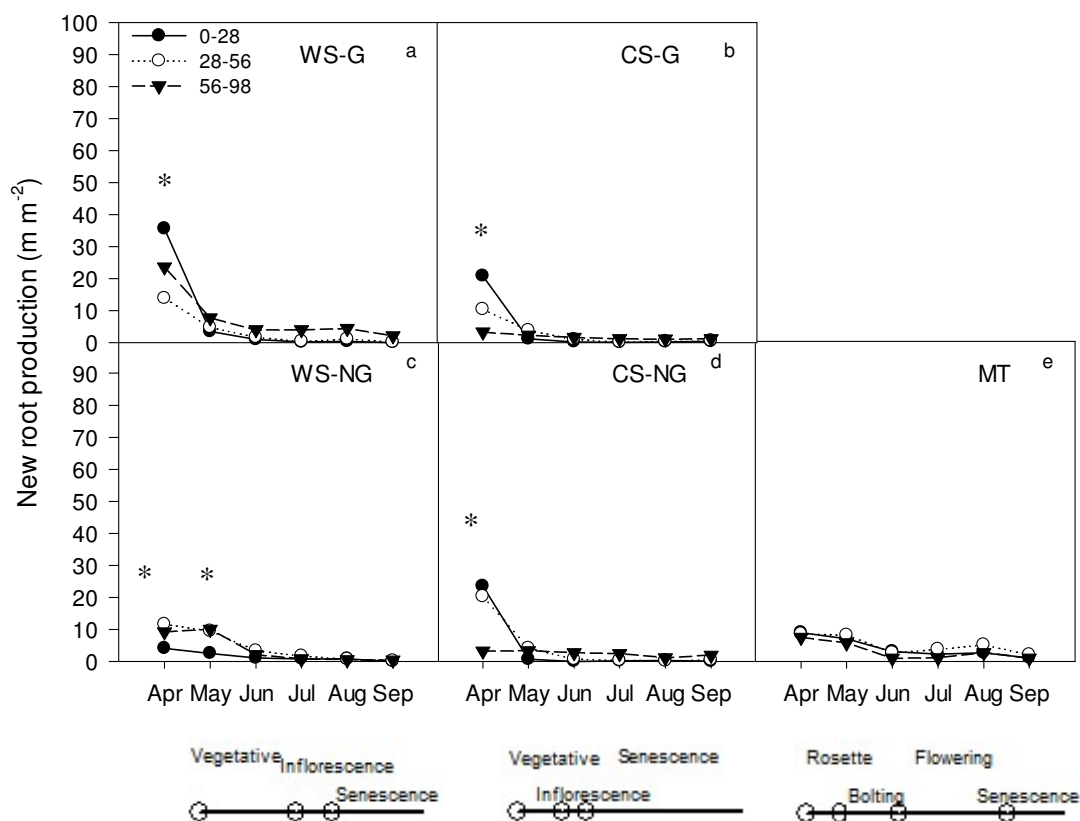


Figure 6. Live root (white and brown) length per image area (0.0423 m^{-2}) at three soil depths (cm) in 2012. WS-G = grazed warm season perennial grass communities, WS-NG = non-grazed warm season perennial grass communities, CS-G = grazed cool season perennial grass communities, CS-NG = non-grazed cool season perennial grass communities, and MT = musk thistle monocultures. Phenology of warm season perennial grasses (WS), cool season perennial grasses (CS) and musk thistle monocultures (MT) are listed. Unshaded circles on secondary x axis indicate the phenological periods for WS, CS, and MT. Asterisk indicate statistical differences at $P < 0.05$ for the three depths at each month within a treatment.

Table 1.

Species composition of warm season (WS) and cool season (CS) perennial grass communities in experimental plots established in 2007 the West Central Research & Extension Center, North Platte, NE.

Grass species	Common name	Rate kg ha ⁻¹
Warm Season Community		
<i>Panicum virgatum</i> L.	'Trailblazer' Switchgrass	8.96
<i>Andropogon gerardii</i> Vitman	Big bluestem	3.36
<i>Schizachyrium scoparium</i> (Michx.) Nash	Little bluestem	1.12
<i>Andropogon hallii</i> Hack.	Sand bluestem	1.68
<i>Sorghastrum nutans</i> (L.) Nash	Indiangrass	2.24
<i>Bouteloua curtipendula</i> (Michx.) Torr.	Sideoats grama	0.9
<i>Desmanthus illinoensis</i> (Michx.) MacMill. ex B.L. Rob. & Fernald	Illinois bundleflower	0.56
<i>Dalea purpurea</i> Vent.	Purple prairie clover	0.56
<i>Lupinus perennis</i> L.	Perennial lupine	0.56
Cool Season Community		
<i>Dactylis glomerata</i> L.	Orchardgrass	17.92
<i>Bromus inermis</i> Leyss.	Smooth brome	10.86
<i>Bromus riparius</i> Rehmman	Meadow brome	16.24
<i>Alopecurus arundinaceus</i> Poir.	Creeping foxtail	1.9

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Seed Germination Ecology of Musk Thistle (*Carduus nutans*) in the Central Prairie of Nebraska

Abstract

Musk thistle is an invasive weed that is widely distributed throughout much of Nebraska and the Central Prairies of the Midwestern USA. A series of laboratory and greenhouse experiments were conducted to determine the effect of various environmental factors on musk thistle seed germination. In the temperature and light fluctuation experiments, seeds had more than 58% germination in both alternating (30/20 C) and constant (20 and 25 C) temperature regimes, but low germination (34%) in 35/20 C. In the absence of light, musk thistle seed germination was greater in alternating temperature regimes less than 30/20 C. Alternating temperature regimes with 10 C and 15 C difference between light/dark conditions (25/15, 30/20C and 30/15 C) resulted in increasing germination. The response to temperature difference indicates day/night temperature difference can favor musk thistle germination in field conditions that fluctuate in a similar pattern. Both osmotic and salt stress can inhibit germination with high osmotic potentials (-0.385Mpa) having a greater impact. Habitat community impacted germination as seeds collected from an area dominated by warm season perennial grasses showed higher germination than seeds collected from the edge of a cool season perennial grass pasture. For the residence time on the parent plant, nine to twelve weeks duration of seeds in mature capitulum in a field condition accelerated germination comparing with seeds collected from three weeks duration after capitulum maturity. This indicates that seed exposed to alternating

temperature before dispersed may facilitate germination. In a greenhouse study, germination was highest under 80% shade, which may indicate that darker conditions (e.g., other plants or debris) are more favorable for the initial establishment of musk thistle seedlings. Results from this study will help in developing strategies for more precise management of musk thistle in regions of the Central Prairie similar to Nebraska.

Nomenclature: Musk thistle, *Carduus nutans*

Key words: germination, invasive plant, prairie, temperature regime, light, osmotic potential, NaCl.

Introduction

Musk thistle is an herbaceous monocarpic herb which was introduced to the United State from Eurasia (Kok 2001). It continuously evades control efforts and infests most regions of North American (Roeth et al. 2009). Musk thistle has been found in all states except Vermont, Maine, Florida and Hawaii and the provinces of Canada at northern border of US from British Columbia to Nova Scotia (USDA, NRCS 2012). In Nebraska, musk thistle has been reported in all but five counties (Roeth et al. 2009) and is a state listed noxious weed that covers almost 6070 km² (NDA, 2010). Musk thistle can inhabit many regions that include rangelands, pastures, rights-of-way, and wastelands (Allen and Shea 2006). In grassland regions with low diversity and richness, musk thistle may establish more easily (Beck 2001). Musk thistle phenology depends largely on climate and habitat characteristics (McCarty and Scifres 1969; Sindel 1991; Edmonds and Popay 1983). Musk thistle can behave as a summer annual, winter annual and short-lived perennial in Canada (Desrochers et al. 1988). In Nebraska, musk thistle has been classified as a biennial and observed as summer annual and biennial in many areas (Roeth et al. 2003).

Losses associated with musk thistle include reduced forage area, increased soil erosion, and a reduction in recreation area and habitat for wildlife (Roeth et al. 2003). The dynamic phenology of musk thistle results in seeds being dispersed and exposed to various environmental conditions in different times of the year. Musk thistle seed germinates easily under 15 to 30 C with moisture conditions and this contributes to its highly prolific nature in spring and fall (McCarty and Scifres 1969; Popay and Medd

1990; Lee and Hamrick 1983). Musk thistle flowers can contribute large amounts of seed to the seed bank, which can remain viable for more than 10 years and facilitate continued invasion (Burnside et al. 1981; Desrochers et al. 1988). Roeth et al. (2003) found that an individual musk thistle plant can produce up to 20,000 seeds within 100 or more capitula.

A comprehensive report on the ecology of musk thistle seed germination is lacking. Germination of musk thistle seed in a range of environmental conditions could potentially help in further understanding of the invasion properties. Successful germination of musk thistle seed and emergence of seedlings depends on the conditions of the surrounding environment (Hamrick and Lee 1987; Medd and Lovett 1978; Popay and Medd 1990; Popay and Kelly 1986).

A well-established pasture or rangeland in good condition can suppress germination, growth and development of musk thistle (Popay and Kelly 1986). The occurrence of musk thistle in the Central Prairies may be an indicator of suitable conditions that favor the invasive plant. In this context, it is important to understand seed ecology of musk thistle in terms of the effects of temperature, light, moisture, salinity, dormancy, and habitats.

One of the most important factors in seed germination is the range of temperatures that seeds are exposed to (Baskin and Baskin 1998). Musk thistle seed from multiple years in different weather conditions may behave differently under various temperature regimes and light conditions. Medd and Lovett (1978) reported 75% musk thistle seed germination under 30/20 C day/night alternating temperature

and 25% germination when temperature was held constant at 30 C. The fluctuation in day/night temperatures may be critical for increasing germination of musk thistle seed.

Moisture and light, not day/night fluctuation, can affect seed viability (Hamrick et al. 1987; Sindel 1991). Beck (2001) reported greater musk thistle seed germinated on bare soil in open pasture and areas poorly vegetated due to light availability. Although germination of musk thistle seed can occur in dryer soil conditions, research has shown that it favors moist soil (Beck 1999; Hamrick and Lee 1987). Still, research on musk thistle tolerance to a range of water stress conditions has not been studied extensively.

Research by Granstrom (1987) has shown that seed viability is affected by duration of storage and although some studies indicate musk thistle seed lacks dormancy (Desrochers et al. 1988), others have indicated that it has a period of “innate” dormancy (Medd and Lovett 1978; Popay and Medd 1990). Lacefield and Gray (1970) report 2% germination of fresh musk thistle seed, while 50% germination after 8 weeks.

The length of time that musk thistle seed stays in the capitulum may affect germination. In addition, musk thistle seed in capitulum that remains attached to a dehisced plant (dead) carcass and out of contact with the soil through the fall and winter may benefit from the relatively dryer and less damp conditions encountered by seed dispersed on the soil. Further, the seeds that remain on upright plant carcasses may benefit from trapped winter snow later in the spring as seeds are finally released

to the ground and begin germination (Desrochers et al. 1988). Musk thistle seed from erect plant carcasses could be adding additional seed to the soil seed bank. Martin and Rahman (1987) report variation in germination among musk thistle seed collected from immature to early maturing capitulum. However, germination of musk thistle seed under increasing maturities or amounts of time spent on the parent plant has not yet been reported. It is important to understand variation in germination of mature seed that remains on the plant to better apply control treatments during the later growth stages of the plant.

Precondition effect such as competition can influence germination responses in the subsequent germination (Baskin and Baskin 1998). The ecotypic difference of seed in a species could vary significantly due to exposure to environment with and without competition (Jordon et al. 1982). As musk thistle can grow in a wide range of habitats (Roeth et al. 2009), the difference of how habitat communities influence the germination responses has not been fully studied yet.

In order to better understand the early growth and development of musk thistle, different conditions representing potential environments of the Central Prairie were applied to seed in laboratory and greenhouse experiments. The results from these experiments will lead to a better understanding of how plants may be responding to changes in the environment and better assess the invasion potential. This information could help to maximize various approaches to weed management. Our objective was to determine the effect of temperature regimes, light availability, moisture, salinity, residence time, and habitat community conditions on musk thistle seed germination

and growth.

Materials and Methods

Seed collection

Seeds were collected from musk thistle plants growing in three locations that all had similar climate conditions as the West Central Research & Extension Center (WCREC) in North Platte, NE (41.090S, -100.769E). At North Platte, the average annual precipitation is 508 mm of which 80% occurs during the growing season during late-April to mid-October (USDA 1978). The first site (1) was in experimental plots at the WCREC that included bare ground and a mix of warm season perennial grasses dominated by *Panicum virgatum* L. (switchgrass). The second site (2) was located in a field 32 kilometers east from WCREC (41.010S, -100.586E). The dominant species at this location were *Agropyron smithii* (western wheatgrass), *Bouteloua gracilis* (blue grama) and *Bouteloua curtipendula* (sideoats grama). The third site (3) for collecting musk thistle seeds was on the edge of a grass pasture dominated by *Bromus inermis* (smooth brome) and sloped to a drainage ditch at the WCREC.

At sites 1-3, musk thistle plants produced seed that was collected and used in experiments during 2010, 2011, and 2012 to test response to a range of environmental conditions. For collecting, musk thistle seeds were considered mature when the white pappus of capitulum had fully expanded and seeds were detaching from receptacle

(Martin and Rahman 1987). Depending on the set of experiments, seeds were separated from the capitulum and stored at room temperature or processed immediately. The average weight of 50 seeds collected from site 1, 2, and 3 was 0.145 ± 0.006 g, 0.159 ± 0.008 g and 0.118 ± 0.008 g, respectively.

For site 1, seeds collected in 2011 were subjected to **temperature regimes** and **salinity** experiments and seeds collected in 2012 were used in the **light availability** and **residence time** experiments. Seeds collected from site 2 in 2010 and 2011 were subjected to **moisture stress** and **temperature-light fluctuation** experiments. At site 3, seeds were collected in 2010 and used for the **habitat community** experiment that also involved site 1. Additional information for the seed sources for experiments is listed in Table 1.

Germination tests for musk thistle seed in all experiments were conducted according to the following procedure. Fifty musk thistle seeds were placed on moist blotter paper in petri dishes that were sealed with Parafilm and inserted into germination chambers. Each chamber was set to be illuminated for 8 hrs light during a 24-hr period. The photosynthetic photon flux density in the germination chambers was 75-125 lux. For treatments requiring total darkness, petri dishes were wrapped in aluminum foil. Accumulated germination was recorded for each petri dish following the initiation of the experiment. The criterion used to determine whether a seed had germinated was whether the radicle had extended to 2mm. Germinated seeds were removed after counting.

Temperature and Light Fluctuation Experiments

Musk thistle seeds were placed in petri dishes and incubated in germination chambers for 16 days. The treatments were combinations of alternating light/dark and total dark with two fluctuating temperature regimes (35 C day/20 C night and 30 C day/20 C night) and two constant temperature settings (25 C day/night and 20 C day/night) during a 24-hr period. Half of the petri dishes were wrapped in aluminum foil for treatments requiring total darkness. Seed counts were determined as described previously.

Temperature Regimes Experiments

Musk thistle seeds were exposed to alternating temperature regimes with 15 C and 10 C light/dark differences (e.g., 35 day/20 night, 30 day/15 night, 30 day/20 night and 25 day/15 night C). Seeds were incubated in the germination chamber for 28 days. Seed counts were determined as described previously.

Moisture Stress Experiments

The effect of osmotic potential (ψ) on musk thistle seed germination was measured using 10 PEG (50% w/v polyethylene glycol 6000, Hampton research, Aliso Viejo, CA) solutions. An isopiestic thermocouple psychrometer (SC-10, Decagon Devices, Pullman, WA) and a Vapro® vapor pressure osmometer (WESCOR, Logan, UT) were used to measure the osmotic potential values of solutions in which seeds were exposed. Seeds were put into the following 12 solutions

(-0.0275, -0.0633, -0.0733, -0.0739, -0.0895, -0.178, -0.192, -0.2806, -0.385, -0.554, -0.717, and -1.320 Mpa) that were mixed with distilled water and PEG in volumes of 370:10, 63: 1, 31: 1, 15:1, 7:1, 250:30, 3:1, 175:60, 165:60, 1:1, 135:75 and 100:100 ml.

Osmotic potential of the solutions was measured with either the vapor pressure osmometer or the isopiestic thermocouple psychrometer. Distilled water was used as the control. Four replicates of 50 seeds each were placed in petri dishes and inserted into the germination chamber. Each petri dish was wrapped with aluminum foil to prevent desiccation. The chambers were set the same as the second temperature fluctuation treatment (30 C day/20 C night) for 21 days. Seed counts were determined as described previously.

Salinity Experiments

Salt stress was determined by adding 5ml solutions containing 10, 40, 80, 160 and 320 mM sodium chloride (NaCl) to petri dishes with musk thistle seed collected from site 1 (Stanton et al. 2012). Distilled water was used as control. The range of concentrations used in this experiment was similar to those that may occur in Central Prairie grasslands of Nebraska (Hoffman 1997). Petri dishes containing 50 seeds were placed in a germination chamber set at 30 C day/15 C night temperature regime with 8 hrs day over a 24-hr period. Seed counts were determined as described previously over a 30 day period.

Habitat Community Experiments

Germination of seeds from musk thistle plants growing in two different habitats was compared. Seeds were collected in sites 1 and 3, where the dominant plant species were *Panicum virgatum* (site 1) and *Bromus inermis* L. (site 3). At each site, musk thistle seeds were collected in September (2011) and July (2012), which was three weeks after plants had completed the seed set stage. In 2012, extremely dry conditions caused plants to mature earlier than normal. Seeds were placed in petri dishes in germination chambers set at 30 C day/15 C night temperature regime with 8 hrs day over a 24-hr period. Seed counts were determined as described previously over a 30 day period.

Residence Time Experiments

At site 1, seeds were collected from musk thistle plants at set periods from June to September, 2012. Mesh cloth bags (7 x 10 cm) were placed over mature musk thistle terminal capitulum when flowers first started to turn brown after pollen receptivity had finished. For 3 days, plants were checked visually and inflorescences that had reached full maturation of seed (e.g., color of the corolla) were bagged and left on the plants. A total of 40 bags were placed on inflorescences on up to 40 different musk thistle plants.

The first inflorescences were bagged on June 2, 2012 and three days later all 40 inflorescences were bagged. Bags with inflorescences were collected from standing musk thistle plants at 3-week intervals beginning with the first one on June 23, 2012

and ending with the last one on August 26, 2012. For each collection, ten bags were removed from plants and immediately assessed for head diameter, number of seeds, and seed weight. Also, it was noted whether adult weevils (*Rhinocyllus conicus*), a natural enemy of musk thistle, were present and the number. Following assessments, 50 seeds were placed in 8 petri dishes (400 seeds total) and placed in the germination chamber set at 30 C day/15 C night temperature regime with 8 hrs day over a 24-hr period. Seed counts were determined as described previously over a 30 day period. This same procedure was used for each of the four collections.

Light Availability Experiments

In this experiment, shading treatments were used to simulate light condition at the soil surface in grasslands of the Central Prairie. Musk thistle seeds collected from site 1 were placed on the surface of soil in plastic pots (22 cm in diameter, 16 cm in height) in the greenhouse. The soil in pots was Cozad silt loam collected from WCREC.

The treatments included various shade cloth fabrics (e.g., 40%, 60% and 80%) and a non-shaded control. The treatments were replicated four times and pots were arranged randomly on a greenhouse bench. Pots were watered every other day to prevent surface crusting and desiccation of musk thistle seed. Fifty seed were sown on the surface of soil (not mixed in) of each pot. Shade was constant during experiments. For 60 days, germinated seed were measured weekly in each treatment and following germination were discarded from the pot.

Statistical Analysis

Musk thistle seed germination in all experiments was presented as percentage of germinated seeds of the total number of seeds in the petri dishes. The number of experiments for germinating musk thistle seeds under each environmental factor was two (experiments 1 and 2), except the residence time experiments (Table 1). Due to interactions between experiments 1 and 2, data was presented separately and not combined.

Variance in the data was tested for normality by plotting residuals and determining whether transformation would improve homogeneity. It was concluded that no transformation was needed and thus, ANOVA was applied to non-transformed percentage values. Fisher's Least Significant Difference was used to test the significance of means at the $p > 0.05$ level. Model parameter estimations were conducted using PROC NLIN and NLMIXED (SAS Institute 2009).

An exponential decay model was fitted to germination values from moisture stress experiments using Sigmaplot 12.0 (Systat Software Inc. 1735 Technology Drive, Suite 430, San Jose, CA 95110, USA). The model fitted was

$$G = G_{\max} * \exp(-G_{\text{rate}} * x) \quad [1]$$

where G represents the total germination (%) at moisture stress x , G_{\max} is the maximum germination, and G_{rate} indicates the slope of the curve. For the temperature

and light fluctuation, temperature regimes, salinity, habitat community, residence time, and light availability experiments, a three-parameter sigmoid model,

$$G = G_{\max} / \{1 + \exp [-(x - x_{50}) / G_{\text{rate}}]\} \quad [2]$$

was fitted to germination, where G is total germinated seeds at day x or concentration x , G_{\max} is the maximum germination, x_{50} is time required for 50% of the maximum germination and G_{rate} is the slope of the curve.

Parameter estimates for germination in the moisture, habitat community, residence time, and light availability experiments are listed in Table 2.

Results and Discussion

Temperature and light fluctuations

Under constant temperatures (e.g., 25 and 20 C), the effect of fluctuating light/dark resulted in greater germination of musk thistle seed compared to constant dark conditions (Figure 1). When temperature fluctuated (e.g., 30/20 or 35/20), germination in light/dark or dark conditions was not statistically different, except for the dark conditions in 2010 and 2011. In general, fluctuations in light/dark have a greater effect on germination than temperature and this is consistent with studies by Medd and Lovett (1978). In the dark, musk thistle seed has poor germination, regardless of fluctuating temperatures. This is typically the condition in healthy,

vigorous grasslands in the Central Prairies that prevent light from penetrating the canopy and creating light/dark fluctuations at the soil surface where musk thistle seed is usually located.

Temperature regimes

In the four temperature regimes (35/25, 30/20, 30/15, and 25/15C), germination of musk thistle seed was greatest at the lowest regime (25/15 C) (Figure 2). This is often the condition in late fall or spring in the Central Prairies and represents periods of greatest musk thistle germination (High Plains Regional Climate Center 2011; Medd and Lovett 1978; Lee and Hamrick 1983; Popay and Medd 1990). Interestingly, the highest temperature regime had poor germination and required the longest time to reach 50% maximum germination (Figure 2). In drought stress years, higher temperatures could create this type of response.

By alternating temperature regimes 10 C (e.g., 25/15 C and 30/20 C) or 15 C (e.g., 30/15 C), maximum germination and time to reach 50% of maximum germination was higher and faster, respectively, for musk thistle seed. Our results are consistent with other studies that showed musk thistle seed germinates better under temperature regimes that have a low of 15C (Roeth et al. 2009; Hull and Evans 1973; Medd and Lovett 1978; Popay and Medd 1990). These low temperatures are typical for the Central Prairies in the spring and fall when musk thistle seed can germinate (Blake, 1935). During this time, the weather, including precipitation, in the Central Prairies is ideal for germination of musk thistle and facilitates potential invasion

opportunities.

Moisture Stress (osmotic potential)

As moisture for germinating musk thistle seed was decreased, germination also declined. Germination decreased with the increases in osmotic potential from -0.0275 to -1.32Mpa. In 2010 and 2011, a similar pattern of decreasing germination occurred for both years (Figure 3).

Musk thistle seed germination declined rapidly when the osmotic potential increase above -0.2806Mpa. Although there was still 2% germination observed under -0.7175Mpa, inactive seeds were noted and it was suggested that even during dry periods between precipitation, musk thistle seed rarely germinates (Beck 1999). High osmotic potential inhibits germination of musk thistle seeds, which indicates establishment of musk thistle is difficult, in what might appear to be favorable conditions.

Salinity

A sigmoid model was fitted to the germination of musk thistle seeds under increasing salinity. High salinity concentrations above 160 mM resulted in lower germination (Figure 4) and musk thistle seeds failed to germinate at salinity concentrations of 320 mM.

In our studies, germination variation was recorded for different concentrations of salinity across experiments. Also, Germinations were stimulated by low

concentrations which were similar to Kaya et al. (2009), suggesting maximum germination of musk thistle did not vary much under salinity concentrations below 5 ds m⁻² (about 45 mM salinity). Our results showed a general lower germination (48 to 73%) compared to Kaya (92%) at low concentrations which may be related to germination variability in seeds from different populations (Baskin and Baskin 1998). High salinity can inhibit seed germination (Gulzar and Khan 2002), although musk thistle has been found in saline soils (Beck 1999). Our results show a concentration of 80 mM NaCl will suppress germination of musk thistle. Although salinity conditions are not frequently reported in the Central Prairies of Nebraska, a high water stress effect created by salinity may hinder germination of musk thistle.

Habitat Community

Germination of seeds collected from site 1 (experimental plots) was faster and at a greater total amount (94%) after 30 days than seeds from site 3 (edge of grass pasture) (Figure 5). The difference in germination between the two sites was probably due to various environmental factors, which preconditioned the seed for germination (Baskin and Baskin 1998).

One of most common precondition factors that effects germination is competition. For example, seeds of *Nemophila menziesii* (baby blue eyes) exhibited a decrease in germination when maternal plants were grown in competition with *Bromus diandrus* (ripgut brome)(Platenkamp and Shaw 1993). The competitive conditions may cause *N. menziesii* to transport more nutrients to develop vegetative

structures than to reproduction, which could result in lower viability of seeds.

Musk thistle plants growing on bare ground may benefit from a less competitive environment and thereby, produce more viable seeds. Kok et al. (1986) showed that habitat dominated by *Festuca arundinacea* Schreb.(tall fescue) reduced germination of musk thistle and seed that did germinate failed to reach the reproductive stage. The allocation of resources by plants to produce more vegetation in a competitive environment compared to a non-competitive environment is a fitness advantage that is common in the 'superior competitor' theory of invasion (Clark and Knox 2009). Musk thistle may be diverting resources to growth, instead of reproduction in highly competitive growing conditions. Site 3 had significant shading from neighboring plants, which may have resulted in less robust plants that were preconditioned for lower growth and viability of seed.

Residence Time

Residence time had a significant effect on germination of seeds in capitulum (Figure 6). Germination increased with an increasing amount of time that seeds in capitulum spent on the mature plant. Seeds collected 9 and 12 weeks after maturation germinated faster than seeds collected only 3 weeks after maturation.

These results suggested musk thistle seeds that remain attached to the parent plant longer in capitulum have higher germination due to exposure to fluctuating temperatures and light/dark conditions that help in breaking dormancy. The longer into the summer and early fall that a seed remains in capitulum on the plant, the more

chance there is for exposure to lower temperatures and higher day temperatures, which favor germination and is consistent with our temperature-light fluctuation experiments. This phenomenon has been seen in other invasive plant species, including leafy spurge (Chao et al. 2011). Moreover, musk thistle may have an after-ripening period (DiTomaso and Healy 2007), which indicates a period of time needed for seeds in capitulum to break dormancy.

All four collection periods showed similar total germination after 32 days. This highlights the fact that seeds which stay in capitulum longer have a similar germination rates as seeds that are dispersed to soil earlier, yet are not viable. Musk thistle is able to provide a constant supply of seeds that are viable at the end of the season, either on the mature plant or the soil surface. The ability of plants to supply seed is another reason to control plants before flowering and if that period is missed, applying chemicals beyond this stage is of little to no value in managing musk thistle.

Light Availability

Germination of musk thistle seedlings was greater (67%) under 80% shade than any of the other treatments, including no shade (Figure 7). The darker conditions also resulted in more seed germinating faster than the conditions that had more light penetration, which is depicted by the three-parameter sigmoidal model (Table 2). The treatment with no shade had the lowest germination (1%-2%), which suggest that although light can be beneficial in the germination of musk thistle seeds, some fluctuation is preferred, even at low levels. This is consistent with the

temperature-light fluctuation experiments that had poor germination in completely dark conditions, but germination improved when light/dark fluctuated.

In the Central Prairies, taller warm season grasses that are in good condition may create a shade environment which is similar to 80% shade treatment. The shady conditions may favor the initial establishment of musk thistle seedlings, but the lack of light penetration due to rapid growth of the grasses will eventually lead to low survival of musk thistle plants. Hamrick and Lee (1987) reported musk thistle suppression under low light conditions in dense pastures.

For the few musk thistle seeds that germinate successfully in no shade, there is potential for them to reach full maturity and set seed. Yet, there is a trade-off for musk thistle seeds and seedlings in response to light resources. On the one hand, fluctuating light and low light conditions are conducive to germination, but they are only created in competitive environments with taller, denser plants (e.g., native perennial grasses in the Central Prairies). On the other hand, constant light is not highly desirable for musk thistle seed to germinate, yet the environment is less competitive and benefits one or more seedlings that successfully germinate and establish in those conditions. The relative success of musk thistle in these two different conditions is an example of the range of plasticity found in the species.

One of the most important factors in the successful (e.g., high amount) germination of musk thistle seed was a cool temperature regime and secondarily, fluctuating light/dark conditions, which are common in the Central Prairies of Nebraska. Moisture stress inhibits germination of musk thistle seed, which is not

surprising and is the case in drought conditions. Similarly, salinity inhibits germination of musk thistle seed, especially at higher levels. Thus, both moisture and salt stress can prevent germination of musk thistle, although saline environments might be slightly more tolerable.

Germination of musk thistle seeds collected from experimental plots with bare ground had higher germination than seeds from the edge of a grass pasture. This environmental or habitat difference could have preconditioned the seed to be less viable in highly competitive environments (Baskin and Baskin 1998). Musk thistle seed germination can vary significantly based on location and the effects from neighboring plants. Musk thistle seeds stored in capitulum for 9 to 12 weeks after maturity in the field germinated faster than seed collected after only 3 weeks of maturity. Before seeds disperse to soil, a period of stratification by cold night temperatures may facilitate the occurrence of after-ripening.

These results indicate in the Central Prairies of Nebraska, the germination of musk thistle seed is influenced by many conditions. The competition for not only light and moisture, but the effects of other environmental factors play a role in germination and establishment of musk thistle seed and seedlings, respectively. The series of experiments reported here indicate several factors that allow musk thistle seed to be resilient in the Central Prairies of Nebraska and allow for the development of more effective and efficient weed management strategies.

Figures and Tables

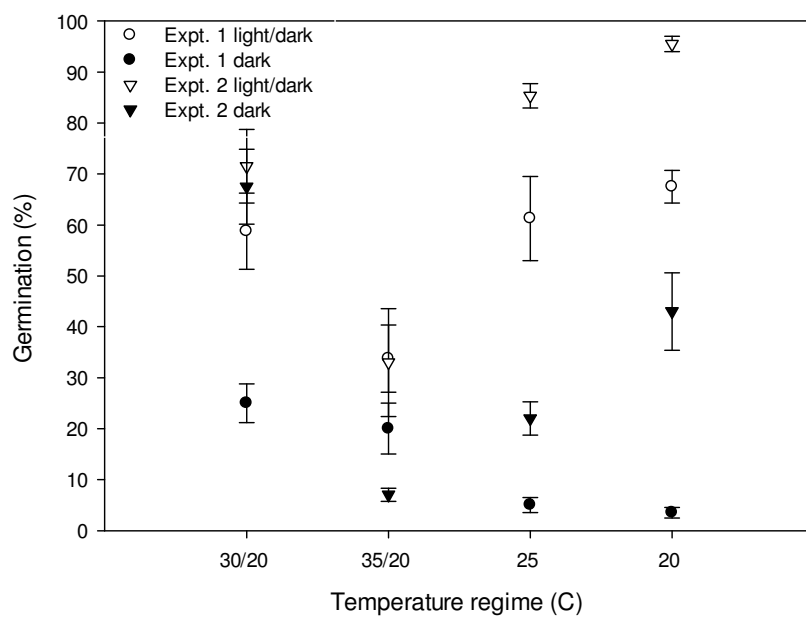


Figure 1. Effect of alternating light/dark temperature regimes (30/20, 35/20, 20 and 25 C) with light (light/dark and dark) conditions in a 8-h photoperiod after 16 d incubation of growth chamber on germination (%) of musk thistle seeds collected from 2010 and 2011 years in site 2. Vertical bars are standard error of mean. Circle and inverted triangle stand for experiment 1 and 2, respectively. Also shaded and unshaded symbols mean light/dark and total dark, respectively.

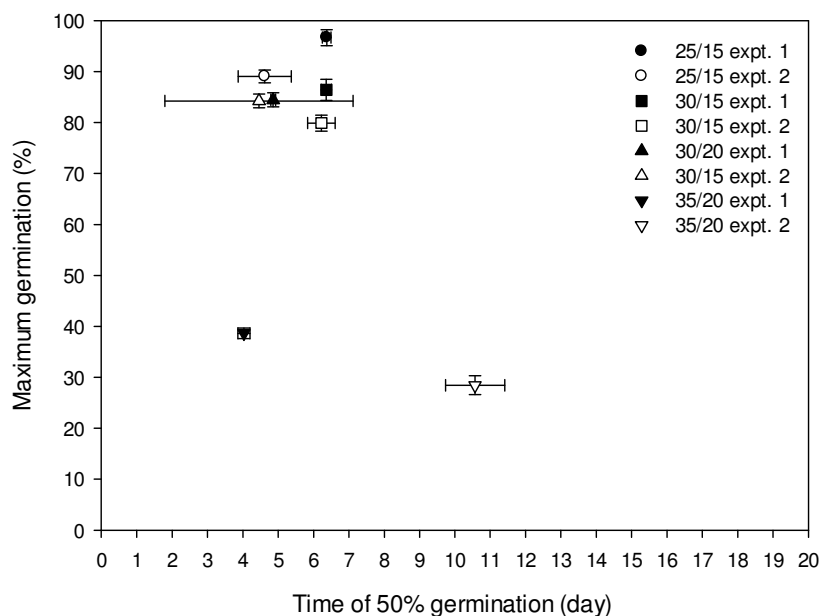


Figure 2. Effect of alternating light/dark temperature regimes (25/15, 30/15, 30/20 and 35/20 C) on germination (%) of musk thistle seeds collected from site 1 in 2011. Vertical and horizontal bars are standard error of coefficient of 50% maximum germination days (X_{50}) and maximum germination (G_{max}) from the fitted three-parameters sigmoid models $G = G_{max}/\{1 + \exp[-(x - x_{50})/G_{rate}]\}$, respectively. Shaded and unshaded symbols separately stand for experiment 1 and 2.

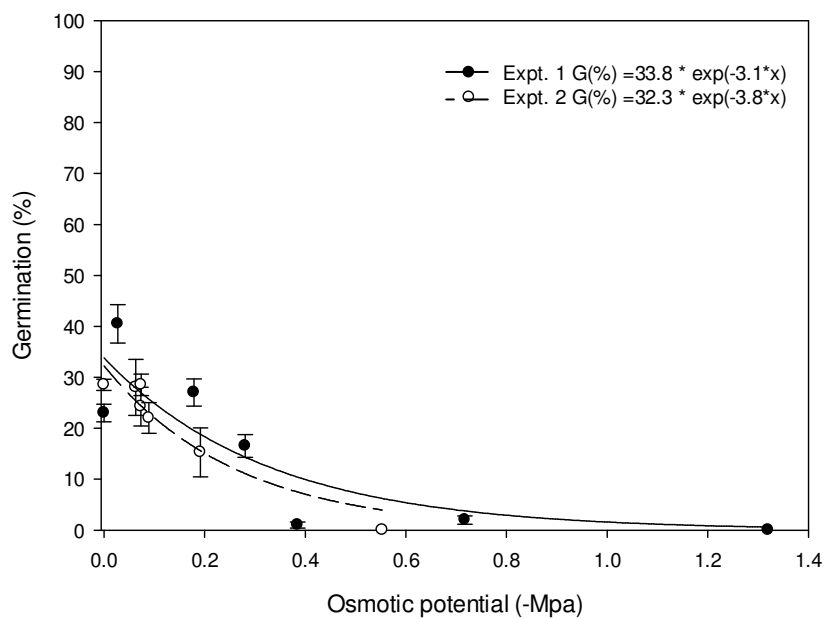


Figure 3. Effect of osmotic potential on germination (%) of musk thistle seeds incubate at 30/20 C growth chamber in a dark condition after 21 d incubation. Seeds were collected from 2010 and 2011 years in site 2. Vertical bars are standard error of mean. Lines represent the exponential decay curve models $G(\%) = G_{\max} * \exp(-G_{\text{rate}} * x)$ fitted to the data. Shaded and unshaded symbols stand for experiment 1 and 2, respectively.

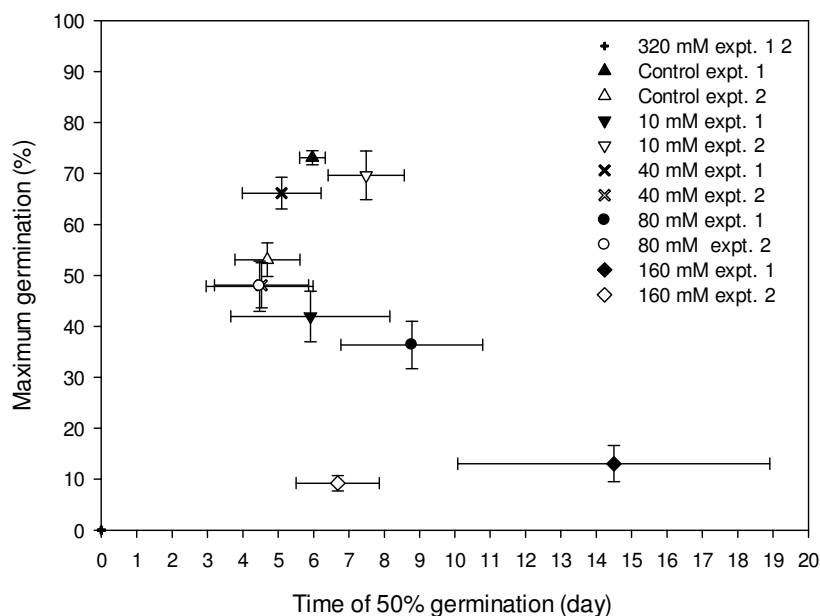


Figure 4. Effect of sodium chloride (NaCl) concentration on germination (%) of musk thistle seeds at 30/15 C growth chamber. Seeds were collected from site 1 in 2011. Vertical and horizontal bars are standard error of coefficient of 50% maximum germination days (X_{50}) and maximum germination (G_{max}) from the fitted three-parameters sigmoid models $G (%) = G_{max}/\{1 + \exp [-(x - x_{50})/ G_{rate}]\}$, respectively. Shaded and unshaded symbols separately stand for experiment 1 and 2.

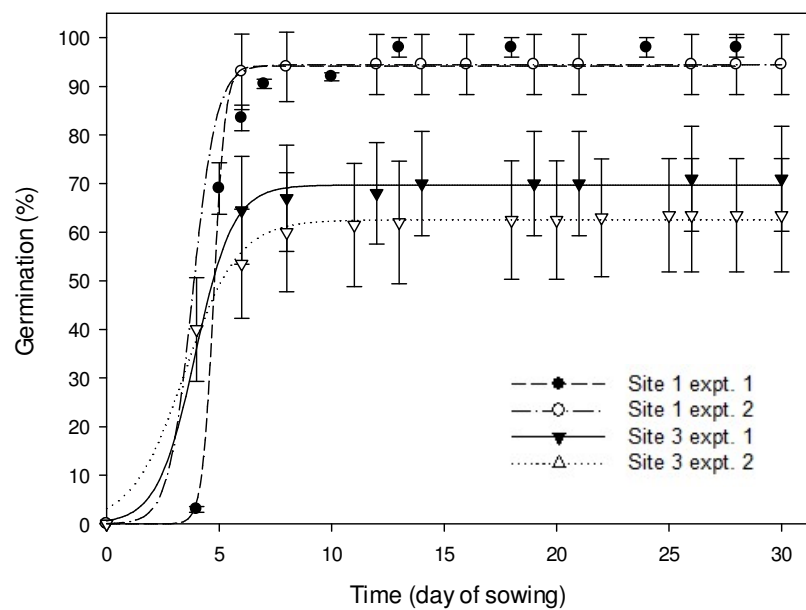


Figure 5. Effect of sites difference (1 and 3) on germination (%) of musk thistle seeds.

Vertical bars are standard error of mean. Lines represent the three-parameters sigmoid curve models $G (\%) = G_{\max} / \{1 + \exp [-(x - x_{50}) / G_{\text{rate}}]\}$ fitted to the data. Shaded and unshaded symbols stand for experiment 1 and 2, respectively.

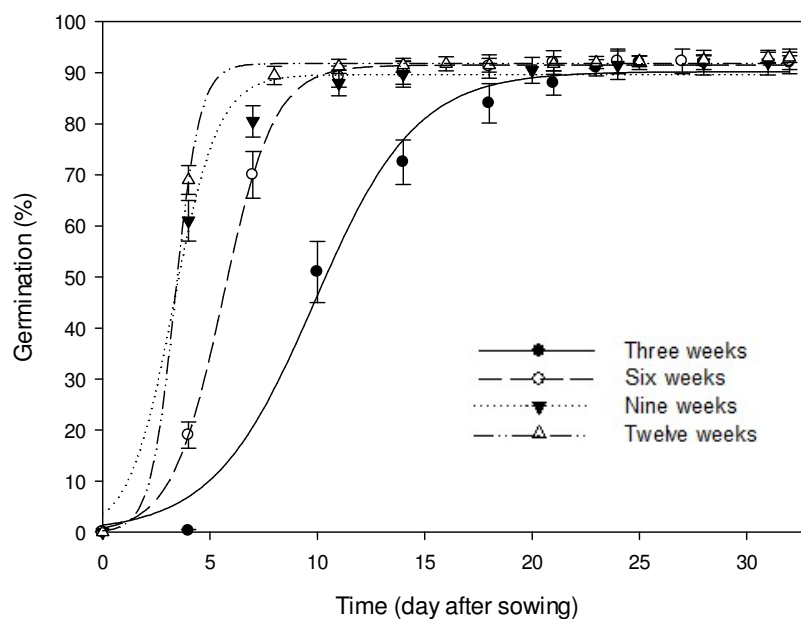


Figure 6. Effect of different residence time on germination (%) of seeds collected from capitulum in site 1, 2012. Vertical bars are standard error of mean. Lines represent the three-parameters sigmoid curve models $G (\%) = G_{\max}/\{1 + \exp [-(x - x_{50})/G_{\text{rate}}]\}$ fitted to the data. Shaded and unshaded symbols stand for experiment 1 and 2, respectively.

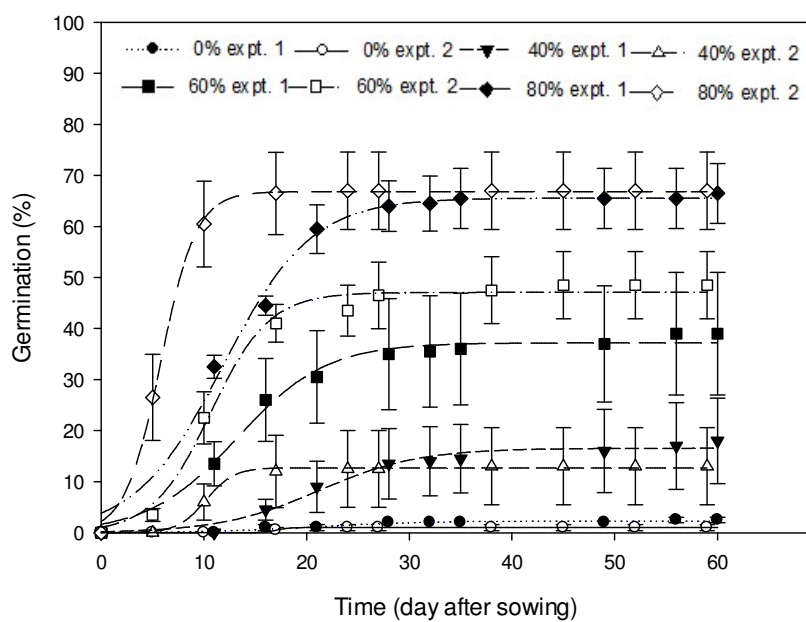


Figure 7. Effect of different shade levels on germination (%) of musk thistle seeds in greenhouse. Seeds were collected from site 1 in 2012. Vertical bars are standard error of mean. Lines represent the three-parameters sigmoid curve models $G (\%) = G_{\max}/\{1 + \exp [- (x - x_{50})/ G_{\text{rate}}]\}$ fitted to the data. Shaded and unshaded symbols stand for experiment 1 and 2, respectively.

Table 1. Information of musk thistle seeds germination experiments which includes seed source location, collection years, number of replicate, amount of seeds per replicate, and repeated times.

Experiment	Seed source – year & location			Replicate	Amount of seeds per replicate	Repeated times
	2010	2011	2012			
Residence time			Site 1	8	50	1
Habitat		Site 1 and 3 ^a		4	50	2
Community						
Moisture stress	Site 2	Site 2		2010 4 2011 8	50 50	Conducted by 2 different equipment
Salinity		Site 1		4	50	
Temperature and light fluctuation	Site 2	Site 2		2010 dark 10, light 4; 2011 4	2010 dark, light 20; 2011 50	2
Light availability			Site 1	4	50	2
Temperature regimes		Site 1		4	50	2

^a Site 1 was in experimental plots at the West Central Research Extension Center (WCREC) that included bare ground and a mix of warm season perennial grasses which dominated by *Panicum virgatum*. Site 2 was located in a field 32 kilometers east from WCREC (41.010S, -100.586E). The dominant species at this location were *Agropyron smithii*, *Bouteloua gracilis* and *Bouteloua curtipendula*. Site 3 was on the edge of a grass pasture which dominated by *Bromus inermis* and sloped to a drainage ditch at the WCREC.

Table 2. Parameter estimates of the exponential decay model and the three-parameter sigmoid model fitted to germination of musk thistle seeds in Figure 3, 5, 6 and 7.

Experiment	Treatment	Parameter estimates (\pm standard error) ^a			
		experiment	X ₅₀	G _{max}	G _{rate}
Moisture stress	Measured by vapor pressure osmometer	1	-	33.9 \pm 3.2	3.2 \pm 0.7
	Measured by isopiestic thermocouple psychrometer	2	-	32.3 \pm 2.6	3.8 \pm 0.9
Habitat community	Slope	1	3.9 \pm 4.0	69.8 \pm 3.1	0.9 \pm 1.6
		2	3.4 \pm 0.8	62.4 \pm 3.5	1.2 \pm 0.9
Residence time	Bare ground	1	4.8 \pm 0.05	94.2 \pm 1.2	0.3 \pm 0.05
		2	3.8 \pm 7.7	94.4 \pm 0.05	0.5 \pm 1.8
		1	9.9 \pm 0.3	90.2 \pm 1.3	2.4 \pm 0.3
		1	5.6 \pm 0.1	91.5 \pm 0.9	1.2 \pm 0.1
Light availability	0%	1	3.3 \pm 0.2	89.7 \pm 1.1	1.0 \pm 0.2
		1	3.4 \pm 0.5	91.8 \pm 0.4	0.6 \pm 0.4
		1	20.8 \pm 2.3	2.3 \pm 0.2	5.3 \pm 1.9
		2	17 \pm 1.0	1.0 \pm 0.2	0.6 \pm 2727.2
Light availability	40%	1	21.2 \pm 5.1	16.5 \pm 3.1	4.8 \pm 4.2
		2	10.2 \pm 2.8	12.7 \pm 2.2	1.4 \pm 7.3
		1	13.2 \pm 3.2	35.2 \pm 3.9	4.3 \pm 3.4
		2	10.7 \pm 1.1	47.1 \pm 2.0	2.8 \pm 1.0
Light availability	60%	1	11.9 \pm 0.9	65.6 \pm 1.9	4.3 \pm 1.0
		2	5.8 \pm 0.7	66.8 \pm 2.5	1.7 \pm 0.8

^a X₅₀, days requiring for 50% maximum germination; G_{max}, Maximum germination (%); G_{rate}, slope. The exponential decay model was fitted to the germination under moisture stress, and the three-parameter sigmoid model was fitted to habitat communities, residence time and light availability experiments. A dash (-) indicates the parameters were not available.

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Conclusions

Prairies and rangelands that are overgrazed are susceptible to establishment of musk thistle. In drought years, less frequent or no grazing could be key in preventing the initial invasion of musk thistle and avoiding establishment in later years with normal precipitation. The conditions of disturbance and stress (e.g., drought) highlight the importance of using proper grazing management strategies that match the conditions and plant types. By preventing the establishment of musk thistle, prairies and rangelands will be kept from being impaired and result in less costly management that is more sustainable over longer periods.

Our study shows that the establishment of musk thistle is strongly dependent on perennial grass community type (e.g., life history) and disturbance, such as grazing during key phenological growth stages. Musk thistle is most likely to establish in repeatedly disturbed (e.g., grazed) warm season perennial grass communities and less so in cool season perennial grass communities. With adequate soil moisture, the spatiotemporal change in light availability induces successful establishment of musk thistle in a WS, but not CS community. The structure and earlier growth of CS communities is most likely limiting musk thistle establishment over short periods (e.g., 2 years). During periods of drought, growth of most perennial grasses and invasive plant species is restricted and thus, invasion is less likely to occur, even in WS communities. The amount of annual precipitation will influence the phenological stages and development of both invasive and native species and therefore, should be considered more carefully during prairie or rangeland management. Over or repeated

grazing of WS dominant grasslands should be avoided to minimize the risk of musk thistle invasion. In drought years, complete elimination of grazing might be the best option in order to maintain the long-term function and health of semi-arid grasslands in North America and elsewhere.

A key factor that influences the success of musk thistle invasion into different perennial grass communities is the root distribution patterns of the invader and community in combination with a particular disturbance event (e.g., drought and grazing). Although not addressed in our theoretical approach, the variability in available resources (e.g., other than soil moisture), physical obstructions, and allelopathic effects from nearby vegetation are all associated with root distribution patterns and may further impact the successful establishment of an invasive plant species, such as musk thistle.

For the ecology of seed germination, our results indicate that in the Central Prairies of Nebraska, the germination of musk thistle seed is influenced by many conditions. The competition not only for light and moisture, but the effects of other environmental factors play a key role in the germination and establishment of musk thistle seed and seedlings, respectively. The series of experiments that were conducted indicate several factors that allow musk thistle seed to be resilient in the Central Prairies of Nebraska and the need for developing more effective and efficient weed management strategies.

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