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# Invasion during Extreme Weather: Success and Failure in a Temperate Perennial Grassland

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# Invasion during Extreme Weather

## *Success and Failure in a Temperate Perennial Grassland*

James C. Han and Stephen L. Young

**ABSTRACT**—Invasive and native plant species compete for resources in similar pools, with disturbances often favoring the invader. Yet, increased climate variability may be shifting the competitive edge back toward the natives. We conducted field studies in perennial grasslands to determine the effects of clipping and drought on resource availability (light and moisture) and subsequent establishment of *Carduus nutans*. We measured light penetration and soil moisture content in *C. nutans* monoculture, clipped and nonclipped grassland with *C. nutans*, and bare ground control plots. We also tracked phenology of the invader and grasses. Our studies revealed that light was a limiting resource in normal precipitation years; removing biomass (e.g., clipped grassland plots) allowed *C. nutans* to successfully establish, while not removing biomass (e.g., nonclipped grassland plots) resulted in premature death. Similarly, soil moisture was a limiting resource when light was abundant; a lack of precipitation in the second year reduced grass growth, which opened the canopy and allowed adequate light for *C. nutans* seedlings that also died prematurely under extremely low soil moisture levels. We found that *C. nutans* was unable to compensate for the low light and soil moisture in offsetting, yet consecutive seasons and failed to establish in a nonclipped grassland. The emergence of *C. nutans* in a temperate perennial grassland is not a sure sign of success. If left undisturbed, *C. nutans* seedlings may eventually die without having a significant impact on grasses.

**Key Words:** *Carduus nutans*, climate change, clipping, drought tolerance, extreme weather events, fitness, grazing, invasion resistance, musk thistle, plant plasticity, resource competition

### Introduction

Invasive plant species in grasslands of temperate regions have modified biotic communities and altered natural cycles with increasing frequency (Charles and Dukes 2007). In order to prevent negative impacts from invasive plant species, the focus of many restoration efforts has been on the creation of diverse grassland communities that provide a barrier against invasion (Berlinger and Knapp 1991; Bottoms and Whitson 1998). This approach provides a good base for understanding competition for resources by native and invasive plant species, including those in temperate regions (Pokorny et al. 2005). Access to available resources is important for invasive plant species (Thomas et al. 2002; Maron and Marler 2007). Moreover, spatiotemporal resource acquisition by native and invasive plant species is considered to be a key factor in invasion success (Zavaleta and Hulvey 2007).

Invasive plant establishment is often due to niches in plant communities that are created by variations in phenologies and traits (Godoy and Levine 2014; MacDougall et al. 2009). Wolkovich and Cleland (2010) argue that many invasive plants adapt quickly to changes in the environment through altered phenology (i.e., plasticity), thus making them better competitors for limited resources in niches (Hooper and Dukes 2010, Fargione and Tilman 2005). Over time, the change in phenology could be considered a fitness advantage that allows for invasive plants to become established and eventually dominate resident plant species (MacDougall et al. 2009; Chesson 2000).

In grasslands, a well-established perennial grass community can preempt belowground space by extending roots (Blank and Morgan 2012) and depleting resources to the detriment of the invader (Milbau et al. 2005). However, disturbance can reduce resistance by a perennial grassland community as openings in the canopy create niches that allow invasive plant species to establish (Feldman et al. 1968). Overgrazing is a disturbance that can lead to invasive plants establishing

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in openings, which fail to fill in with new vegetation (Leininger 1988; Beck 1999).

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). Yellow starthistle (*Centaurea solstitialis*), an invasive plant with similar characteristics as *Carduus nutans*, used water and light during phenological stages that functionally matched the target grassland plant community (Young et al. 2011). In this case, even an increase in available soil water during the vegetative stage of yellow starthistle was not enough to overcome the lack of light transmission through the dense canopy of the grasses. With overlapping resource use patterns and adequate biomass and cover, harsh conditions (e.g., drought) often will favor the established resident plant community over the invader (Cahill 2003).

Several resources have been studied as possible factors contributing to invasion, including moisture, light, and nutrients (e.g., Hovick et al. 2011; Throop et al. 2012; Novoa et al. 2014). Light availability, which is a function of leaf area, influences the success of invasive plant species (Reinhart et al. 2006; Thomsen and D'Antonio 2007; Young et al. 2011). The manipulation of light, through either blocking by the resident community or accessing by the invader, is largely a function of plant growth habit. Often, those species that grow taller or bushier and at a faster rate will be more successful in outcompeting neighboring plant species. In arid and temperate regions, soil moisture contributes to successful invasion, especially if the invader germinates earlier in the growing season (Davis and Pelsor 2001; Larson et al. 2001). Sheley et al. (1999) found *Centaurea diffusa* produces less seed when it is mowed compared with producing seed after mowing when soil moisture is adequate or replenished.

A short-lived biennial, *C. nutans* was introduced into the United States from Eurasia and now commonly occurs in the Midwest (Kok 2001). *Carduus nutans* begins as a rosette that develops extensive roots and then after bolting and flowering, senesces by flowering (~1,000 capitulum/plant) and dispersing seed prolifically (>20,000 seeds/plant) (Roeth et al. 2003). On range and pastureland, *C. nutans* competes with desirable forage and its sharp spines can deter livestock and wildlife from grazing (Hull and Evans 1973; Desrochers et al. 1988; Beck 1999). At low densities, *C. nutans* may reduce production of desirable plants (Reece and Wilson 1983; Sindel 1991). Perennial grass production in Nebraska increased about 212% following chemical control of *C. nutans* (Re-

ece and Wilson 1983). Dense infestations of the plant discourage animals from occupying infested areas (Rees 1991). Feldman et al. (1968) report greater *C. nutans* establishment in less vegetated habitats, which is in part due to a high level of irradiance (Wardle et al. 1992).

The Midwest is not immune to the effects of climate change, including extreme weather events and the threat of invasive species, like *C. nutans*. However, the concern with regard to increasing challenges for managing prairie grasslands could be unfounded in the future. Human efforts to actively control and contain invasive species have in the past been justified due to their seemingly rapid advancement, but as we enter into a new era of climate uncertainty, earlier springs, later falls, rising atmospheric CO<sub>2</sub>, and drought during years of normal annual precipitation will amplify what little we know about invasive species and the plasticity they exhibit that leads to life or in some cases death, as first described by Young (2015) and now here.

For two years, we studied *C. nutans* during normal (2011) and extremely low (2012) annual precipitation. Our goal was to determine the survivability of *C. nutans* in grasslands that had niches with resources that were available in offsetting, yet consecutive, seasons. We used (1) introduction or no introduction of *C. nutans* and (2) clipped or nonclipped perennial grasslands as factors with which we compared the spatiotemporal changes in light and soil moisture for *C. nutans* invasion during discreet phenological stages.

## Materials and Methods

### Experimental Design

Our study was conducted in the mixed-grass prairie region of central Nebraska, where average annual precipitation is 508 mm of which 80% occurs from late April to mid-October. 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. The dominant and uniformly distributed soil type was Cozad silt loam (fine-silty, mixed, mesic Fluventic haplustoll).

Our site was located in an area with a diversity of warm-season perennial grasses that included *Panicum virgatum*, *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Andropogon hallii* Hack., *Sorghastrum nutans* (L.) Nash, *Bouteloua curtipendula* (Michx.) Torr., *Desmanthus illinoensis* (Michx.) Mac-Mill. ex B. L. Rob. & Fernald, *Dalea purpurea* Vent., and

*Lupinus perennis* L. Due to the limited size of the area (300 m<sup>2</sup>) for our study and the need to uniformly apply clipping treatments and collect data with minimal disturbance, our experimental design followed a split-plot within a strip layout, according to Steel et al. (1997). We established three 18 × 5 m strips side by side, 0.3 m apart in an east–west direction. One strip was kept free of vegetation by cultivating and hand weeding (bare ground), while grasslands remained in the other two strips. For the two grassland strips, we clipped one and left the other one nonclipped. A total of 24 split-plots or plots (5 m × 2 m) were established in replicates of four on April 11, 2011. Within each strip, we randomly selected half the plots to be either planted (4) or not planted (4) with *C. nutans* seeds. We clipped, did not clip, or left bare any remaining area within respective strips.

#### *Plant Phenology and Carduus nutans Populations*

The factors in our study were (1) *C. nutans* and (2) clipping during years of normal (2011) and extremely low (2012) annual precipitation. Treatments included introduced *C. nutans* (IC) or no introduction of *C. nutans* (NC) in the first year (2011) and clipped (CL) or nonclipped (NCL) perennial grass in both years (2011 and 2012). We carried out the study by measuring (1) survival (density), cover, aboveground biomass, plant basal diameter, number of branches and leaves, and height of *C. nutans*, (2) light transmission, and (3) soil moisture content at shallow and deep depths in *C. nutans* monoculture and both clipped and nonclipped grassland plots. For survival and cover of *C. nutans*, we applied the IC treatment to half of the clipped (CL-IC) and nonclipped (NCL-IC) grassland and bare ground (BG-IC) plots, which became *C. nutans* monocultures.

We administered clipping treatments at 10 cm above the ground using a rotary mower, electrical hedge trimmers, and minor amounts of hand weeding. We removed the grass residue from the strips immediately. In 2011 we clipped the grass strips approximately every two weeks (five times) beginning on June 1, which coincided with *C. nutans* rosette growth stage. In 2012 we applied a single clipping treatment to the grasses on May 28, with no further clipping for the remainder of the season due to little growth from the severe drought conditions. We avoided clipping *C. nutans* in order to more closely match natural conditions and also to maintain competitive ability.

On April 28, 2011, we planted 140 *C. nutans* seed into individual 5 m × 2 m plots in the strips of perennial grasses (clipped and nonclipped) and bare ground. A preliminary germination test indicated seed viability was near 30% for the collection (data not shown). In perennial grass and bare ground plots, three *C. nutans* seeds were hand planted at a point 0.5 cm below the soil surface. Points were equidistant from neighboring planting points. Seedlings emerged approximately one month after planting. We recorded the survival of *C. nutans* each month by counting plants in each plot and converting to plants per square meter. We placed small nylon bags on all flower heads in 2011 to prevent new seeds from being dispersed back into the plots. In the second year (2012), we recorded only newly emerged *C. nutans* plants, similar to 2011. No new seeds were planted in the second year. On a weekly basis, we recorded the phenology of the perennial grasses and *C. nutans*, along with detailed plant measurements for *C. nutans* (e.g., basal diameter, plant height, leaves per plant, and number of branches per plant) over the two seasons. We collected biomass of *C. nutans* in perennial grassland and BG-IC plots in the second year before the cessation of *C. nutans* growth.

We measured cover of *C. nutans* in BG-IC, CL-IC, and NCL-IC plots monthly from May to October in 2011 and May to August in 2012. Measurements were conducted within permanent 0.25 m<sup>2</sup> quadrats located randomly in each plot. We estimated cover visually to within 1% up to 10% and thereafter to the nearest 5% (10%–100% cover).

#### *Spatiotemporal Changes in Light*

We measured light transmission in grassland and BG-IC plots during the growing seasons of 2011 and 2012. Measurements were conducted during the noon hour when the sky was clear. One measurement was taken once above the canopy and four times below. Photosynthetically active radiation (PAR) was measured using a ceptometer (AccuPAR LP-80; Decagon Devices Inc., Pullman, WA, USA). The ceptometer sensor arm (80 cm long) was inserted on the soil surface below the canopy at four separate locations within each plot. The average of the readings was compared with PAR values of full sunlight above the canopy. Data was presented as the percentage of maximum light penetrating to the soil surface.

TABLE 1. Phenology of perennial grasses and *Carduus nutans* in the Midwest.

		<i>Carduus nutans</i>				Grasses	
		BG-IC		CL-IC	NCL-IC	CL-NC	NCL-NC
Year	Date	Majority	Minority	All	All	All	All
2011	May 25	Emergence	Emergence	Emergence	Emergence	Dormancy	Dormancy
2011	June 1	Rosette	Rosette	Rosette	Emergence	Vegetative	Vegetative
2011	Aug. 5	Rosette	Flower	Rosette	Died	Inflorescence	Inflorescence
2011	Sep. 24	Rosette	Senescence	Rosette		Dormancy	Rosette
2011	Oct. 1	Dormancy	Died	Dormancy		Dormancy	Dormancy
2012	Mar. 31	Rosette		Rosette		Dormancy	Dormancy
2012	Apr. 20	Bolt		Bolt	Emergence	Vegetative	Vegetative
2012	May 25	Flower		Flower	Emergence	Vegetative	Vegetative
2012	June 17	Flower		Flower	Emergence	Inflorescence	Inflorescence
2012	July 4	Senescence		Senescence	Died	Inflorescence	Inflorescence
2012	July 8	Senescence		Senescence		Dormancy	Dormancy

Notes: *Carduus nutans* growth stages are rosette, bolting, flowering, dormancy, and senescence. Perennial grass growth stages are vegetative, inflorescence, and dormancy. BG-IC = bare ground with *C. nutans* introduced, CL-IC = clipped grasslands with *C. nutans* introduced, NCL-IC = nonclipped grasslands with *C. nutans* introduced, CL-NC = clipped grasslands without *C. nutans* introduced, and NCL-NC = nonclipped grasslands without *C. nutans* introduced. Majority indicates 85% of established *C. nutans* in the BG-IC plots and minority is the remaining 15% of *C. nutans* in the same plots.

### Spatiotemporal Changes in Soil Moisture

We measured shallow soil water moisture in CL-NC, NCL-NC, BG-NC, and BG-IC throughout the growing season using a soil moisture sensor (EC-5; Decagon Devices, Inc., Pullman, WA, USA) that was vertically inserted 8 cm below the soil surface of each plot. Measurements were recorded hourly and averaged over a 24-hr period. We used a hydroprobe (503DR, CPN, Martinez, CA, USA) to take monthly measurements of deep soil water content at depths of 30, 60, 90, and 120 cm. We installed an access tube in the center of the same plots that were used for measuring shallow moisture. We calibrated the hydroprobe before taking measurements and converted the values to volumetric soil water content (Evetts and Steiner 1995).

### Statistical Analysis

We tested homogeneity and normality before the analysis of variance and data were log-transformed. We used a mixed-model repeated-measures analysis of variance to compare the effects of year and clipping on the number of *C. nutans* plants m<sup>-2</sup> (density) or *C. nutans* cover for BG-IC, CL-IC, and NCL-IC treatments. Fixed fac-

tors in the model included year (2011 and 2012), clipped (CL) or not (NCL), introduced *C. nutans* (IC) or not (NC), block effect, and all possible interactions. We used only block effect in the model for cover analysis and not for light transmission, which was an average ratio generated by multiple readings from the ceptometer in each plot, or density, which was based on plants per plot. Our previous studies on this experimental area show that block effect is not significant (Han and Young 2014a, 2014b). Subsequently, the model for analyzing cover also showed no significant effect from blocks.

We analyzed the light transmission ratio using the same approach as for comparing the effects of year and clipping on survival and cover, except CL-NC and NCL-NC treatments were included. Hurlbert (1984) suggested the use of data from repeated sampling is acceptable for statistical analyses only if successive dates are not considered independent replicates. We determined the differences among response of *C. nutans* to clipped (CL) and nonclipped (NCL) treatments by comparing the least-square means.

We compared biomass of sampled *C. nutans* plants across treatments ( $P < 0.05$ ). To assess the survivability of *C. nutans*, we used Tukey's HSD to test for dif-

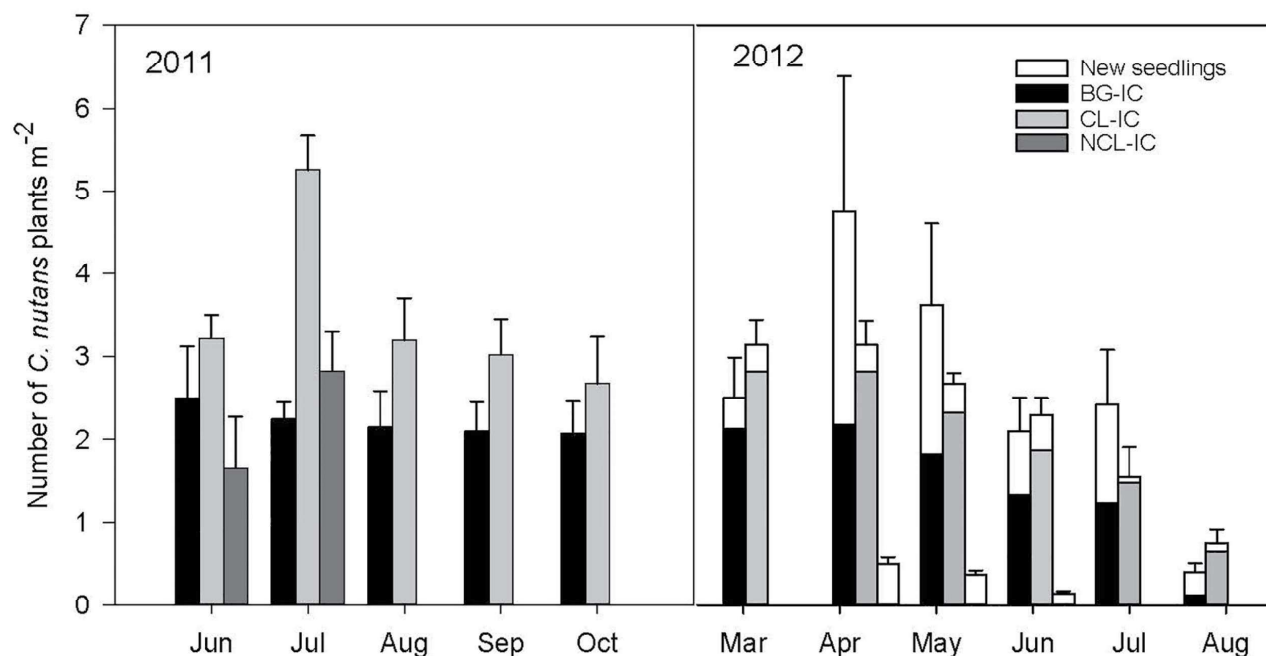


Figure 1. Number of *Carduus nutans* plants per m<sup>2</sup> in *C. nutans* monocultures (BG-IC = bare ground introduced *C. nutans*) and grasslands (CL-IC = clipped with the introduction of *C. nutans*; NCL-IC = nonclipped with the introduction of *C. nutans*) in 2011 and 2012. The error bars indicate standard errors of means.

ferences in mean values for *C. nutans* basal diameter, plant height, branches per plant, and leaves per plant in *C. nutans* monoculture (BG-IC), clipped (CL-IC), and nonclipped (NCL-IC) treatments. We used the monthly periods for analysis and the stages were early, mid-, and late rosette, bolting, and early and late flowering. All statistical analyses were conducted using SAS version 9.3 (SAS Institute, North Carolina).

## Results

### Plant Phenology and *Carduus nutans* Populations

In May 2011 the emergence of *C. nutans* from seed began, which was two months before the grasses came out of dormancy. Both plant types remained vegetative through midsummer, except for *C. nutans* in the NCL-IC plots, which grew slowly for one month and then died (Table 1). Seedlings of *C. nutans* in CL-IC and BG-IC developed into rosettes and from June to September remained vegetative before normal dormancy in late fall. Grasses were vegetative from June through mid-August with inflorescence in September and dormancy in late October. In the BG-IC plots, three out of 20 *C.*

*nutans* plants progressed to full maturity (bolting, flowering, seed dispersal) the first year.

By the end of April 2012, *C. nutans* rosettes had emerged from dormancy and were beginning to bolt (Table 1), while grasses were in the vegetative stage. Mature *C. nutans* plants flowered from May to August and were tallest in BG-IC (176 cm,  $P < 0.05$ ) and CL-IC (158 cm,  $P < 0.05$ ) plots. The grasses had started the inflorescence stage in late June, which was two months earlier than the previous year and likely the result of the extreme drought conditions.

Newly germinating *C. nutans* seedlings were observed in all IC plots in the second season (Fig. 1). A few *C. nutans* seedlings in the nonclipped grass plots (NG-IC) grew, but eventually died without producing capitula (Table 2) (see Young 2015).

In July 2011 precipitation was above normal and the maximum average number of *C. nutans* that established was greater than 5 plants m<sup>-2</sup> in the CL-IC plots (Fig. 1). In April 2012 the highest number of new *C. nutans* seedlings occurred in the BG-IC plots, but all seedling populations declined to zero by July (NCL-IC) or less than one by August (BG-IC, CL-IC). The decline in older *C. nutans* (nonseedlings) in year 2 was due to the drought conditions that caused one or two to mature sooner (Fig. 1).

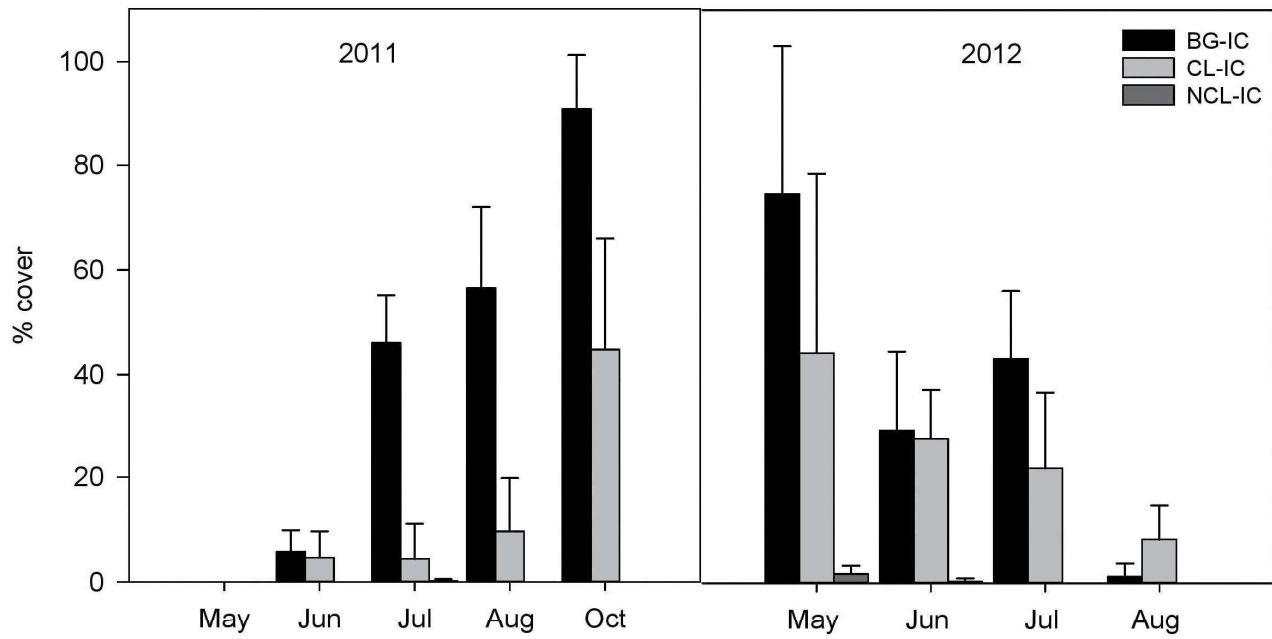


Figure 2. Mean percentage of cover of *Carduus nutans* in *C. nutans* monocultures (BG-IC = bare ground introduced *C. nutans*) and grasslands (CL-IC = clipped with the introduction of *C. nutans*; NCL-IC = nonclipped with the introduction of *C. nutans*) in 2011 and 2012. The error bars indicate standard errors of means.

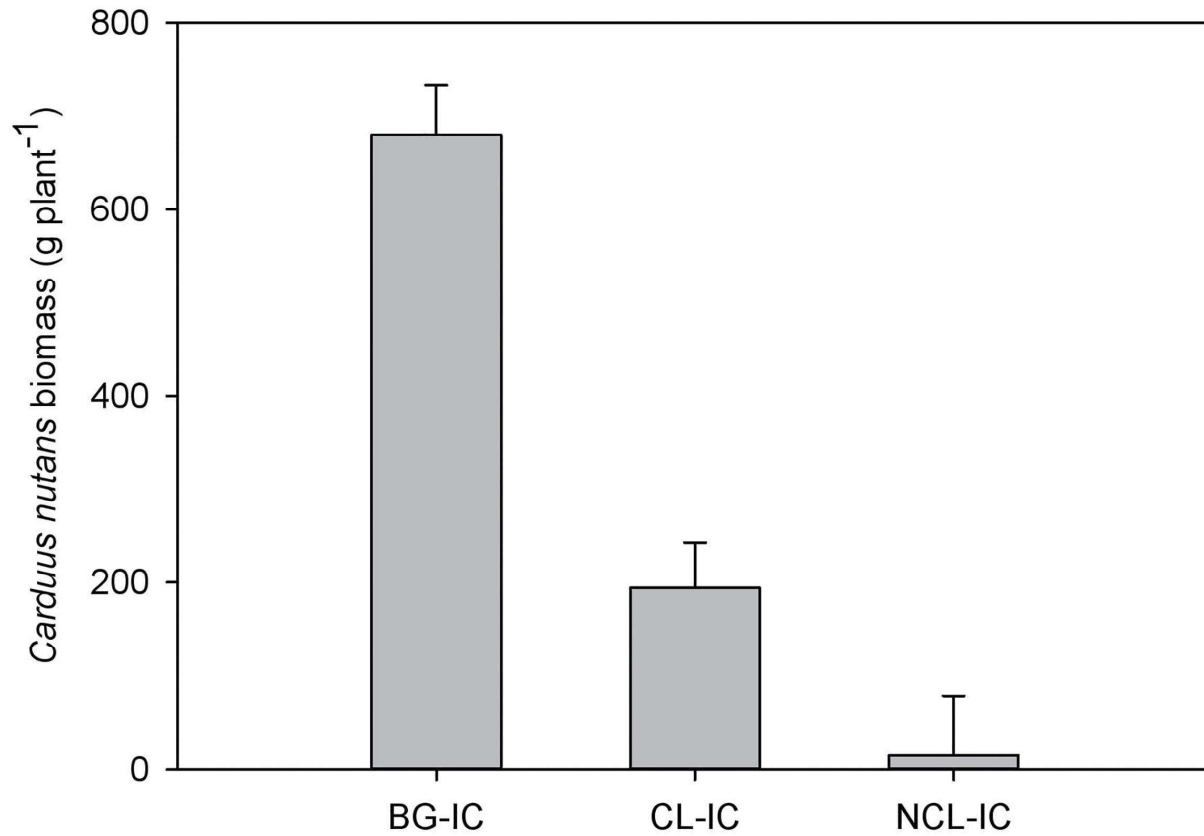


Figure 3. Aboveground biomass of *Carduus nutans* plants in *C. nutans* monocultures (BG-IC = bare ground introduction of *C. nutans*) and grasslands (CL-IC = clipped with the introduction of *C. nutans*; NCL-IC = nonclipped with the introduction of *C. nutans*). The error bars indicate standard errors of means.

TABLE 2. For each phenological stage and parameter, the statistical difference between treatments ( $n = 4$ ) denoted by a letter ( $p < 0.05$ ) using Tukey's HSD test.

Growth stage and timing	Date	BG-IC	CL-IC	NCL-IC
		Basal diameter (cm)		
Rosette, early	June 22, 2011	26a	11b	7b
	June 29, 2011	38a	15b	11b
Rosette, mid	June 11, 2011	65a	21b	14c
	Aug. 5, 2011	71a	19b	oc
Rosette, late	Sept. 24, 2011	98a	48b	oc
	Oct. 23, 2011	106a	59b	oc
Rosette, early	March 23, 2012	46a	34b	oc
Bolt	April 21, 2012	93a	71b	10c
Flower, early	May 22, 2012	81a	72a	36b
Flower, late	June 27, 2012	48a	24b	1c
		Height (cm)		
Bolt	April 21, 2012	57a	41b	oc
Flower, early	May 22, 2012	159a	143a	32b
Flower, late	June 27, 2012	176a	158b	28c
		Leaves plant <sup>-1</sup>		
Rosette, early	June 22, 2011	9a	6b	5b
	June 29, 2011	12a	7b	5c
Rosette, mid	July 11, 2011	25a	11a	6b
	Aug. 5, 2011	48a	13b	oc
Rosette, late	Sept. 24, 2011	88a	26b	oc
	Oct. 23, 2011	104a	32b	oc
		Branches plant <sup>-1</sup>		
Flower, early	May 22, 2012	7a	1b	oc
Flower, late	June 27, 2012	8a	3b	oc

Note: Phenological stages (rosette, bolt, flower) of *Carduus nutans* introduced into bare ground (BG-IC) and either clipped (CL-IC) or nonclipped (NCL-IC) perennial grasslands.

By the end of 2011, *C. nutans* rosette leaf cover had expanded across nearly the entire BG-IC plots and over 40% of the CL-IC plots (Fig. 2), which was also reflected in the basal diameters (59 cm,  $P < 0.05$  for CL-IC and 106 cm,  $P < 0.05$  for BG-IC) (Table 2). Early in 2012, *C. nutans* cover began to decline as plants matured under the increasingly intense drought conditions. The CL-IC plots had less than half the cover of *C. nutans* as BG-IC in May and July 2012. By August, *C. nutans* cover in the two treatments was near zero. During the two years, cover of *C. nutans* was never measured after July in NCL-IC because no plants remained.

The growth of *C. nutans* plants varied depending on the type of vegetation present (e.g., *C. nutans* or grasses) and whether the grasses were clipped (Fig. 3). The biomass of *C. nutans* in the bare ground plots (BG-IC) was greater than in the CL-IC and NCL-IC plots ( $P < 0.0001$ ). The difference in biomass was also reflected in height, with taller plants in the BG-IC when compared to NCL-IC plots (see Table 2), indicating that grass competition may have had an effect on the growth of *C. nutans*.

#### Spatiotemporal Changes in Light

In 2011 clipped grassland plots with *C. nutans* (CL-IC) had similar light transmission compared to clipped grassland plots with no *C. nutans* (CL-NC) ( $P = 0.088$ ), but by 2012 significantly less light was being transmitted in the CL-NC plots ( $P < 0.0001$ ) (Fig. 4). In all grassland plots, light transmission was greater by July and August of 2012 during the drought than for the same months in 2011 ( $P = 0.0024$ ) (Fig. 4). By June 2011, the nonclipped grassland plots (NCL-IC, NCL-NC) had almost complete canopy cover that lowered full sunlight reaching the soil surface to less than 2% (Fig. 4). During the same period, the clipped grassland (CL-IC, CL-NC) plots had 35% of full sunlight reaching the soil surface ( $P < 0.0001$ ).

In May 2012, light transmission was less than 16% in BG-IC ( $P = 0.02$ ) and CL-IC ( $P = 0.04$ ) plots, as *C. nutans* plants had increased in size and subsequently covered much of the area of each plot (see Fig. 2). Later in 2012, light transmission increased in these plots as *C. nutans* plants began to flower and senesce. The interaction among the factors of clipping and adding *C. nutans* and year on light transmission was significant ( $F_{1,168} = 20.91$ ;  $P < 0.0001$ ).



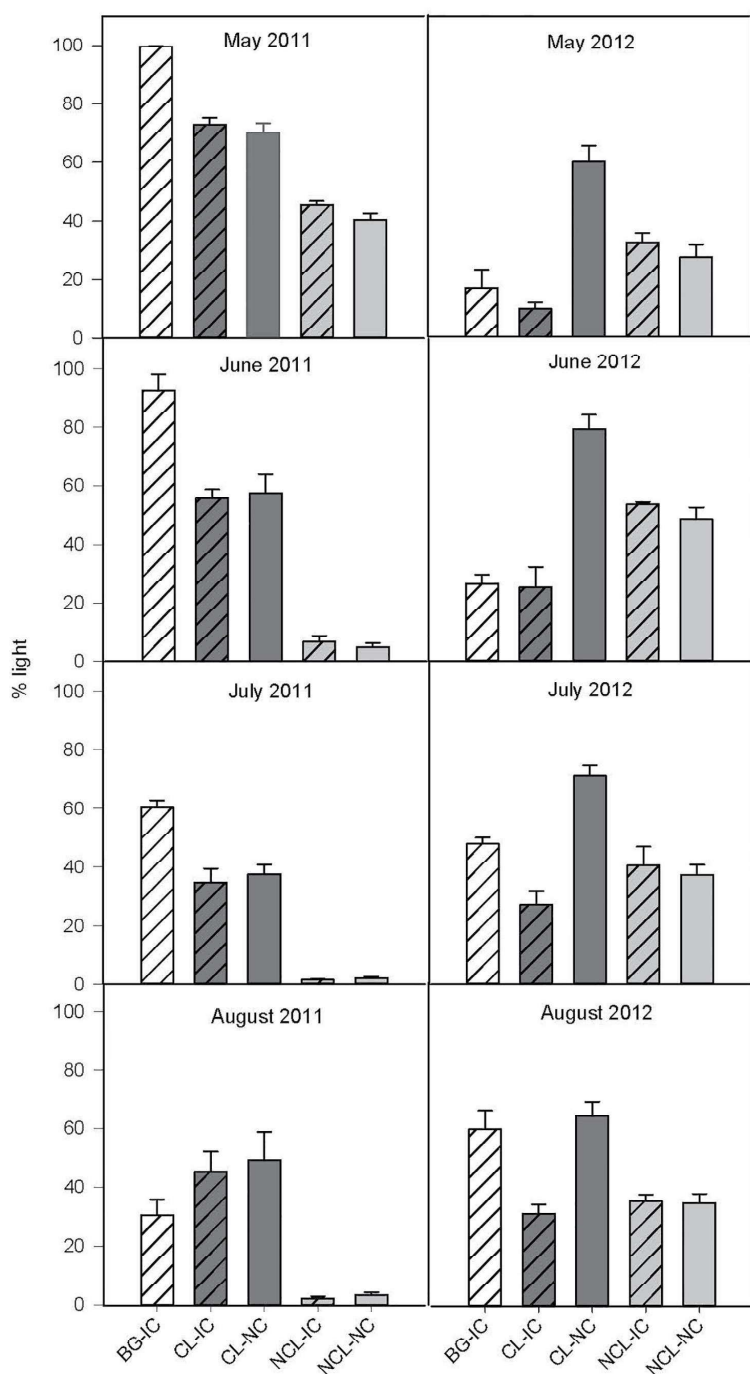


Figure 4. Percentage of light transmitted to the soil surface in *Carduus nutans* monocultures (BG-IC = bare ground introduced *C. nutans*) and grasslands (CL-IC = clipped with the introduction of *C. nutans*, CL-NC = clipped without the introduction of *C. nutans*, NCL-IC = nonclipped with the introduction of *C. nutans*, and NCL-NC = nonclipped without the introduction of *C. nutans*) in 2011 and 2012. The error bars indicate standard errors of means.

### Spatiotemporal Changes in Soil Moisture

In April 2011 surface soil moisture was  $\geq 0.18 \text{ m}^3 \text{ m}^{-3}$  in bare ground without (BG-NC) and with (BG-IC) *C. nutans*. Surface soil moisture in clipped and nonclipped grassland plots (CL-NC, NCL-NC) declined rapidly from  $0.26 \text{ m}^3 \text{ m}^{-3}$  in July to  $0.13 \text{ m}^3 \text{ m}^{-3}$  in September (Fig. 5). The severe drought in 2012 caused surface soil moisture to decline from greater than  $0.26 \text{ m}^3 \text{ m}^{-3}$  in April to  $0.12 \text{ m}^3 \text{ m}^{-3}$  in June and near  $0.07 \text{ m}^3 \text{ m}^{-3}$  by late September (Fig. 5). In BG-IC plots, surface soil moisture was less than for the other treatments during the months when the plants were bolting, flowering, and beginning to set seed. Short rain events in late June and July briefly increased surface soil moisture.

In July 2011, deep ( $>30 \text{ cm}$ ) soil water content was similar for BG-IC, BG-NC, CL-NC, and NCL-NC (Fig. 6). A month later, the nonclipped grassland (NCL-NC) plots had the least soil water content at depths deeper than  $30 \text{ cm}$  ( $0.085 \text{ m}^3 \text{ m}^{-3}$ ), while clipped grasses (CL-NC) and *C. nutans* (BG-IC) had similar deep soil water content. In June 2012, BG-IC plots had the least deep soil water content ( $0.08 \text{ m}^3 \text{ m}^{-3}$ ), but for July and August, deep soil water content was similar for all treatments (Fig. 6).

### Discussion

Following planting in the first year, *C. nutans* successfully established in bare ground (BG-IC) and warm-season perennial grasslands that had been disturbed by clipping (CL-IC). The act of overseeding an invasive plant species could be viewed as a type of invasion and thus corresponds with other studies that report greater *C. nutans* survival and development in open or overgrazed pastures and rangelands (Hamrick and Janet 1987; Beck 2001). Similar to actual grazing, the clipping that we administered in

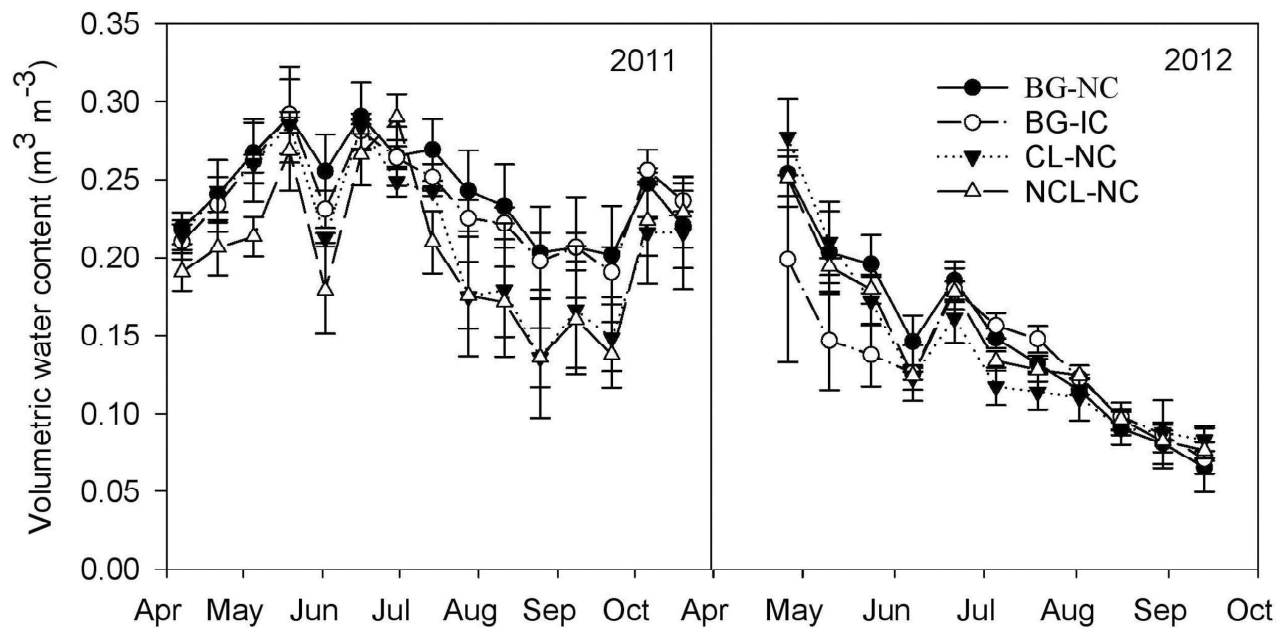


Figure 5. Average daily surface (0–8 cm) soil moisture reported biweekly in 2011 and 2012. BG-NC = bare ground without introduced *Carduus nutans*, BG-IC = bare ground with introduced *Carduus nutans*, CL-NC = clipped grasslands without the introduction of *C. nutans*, and NCL-NC = nonclipped grasslands without the introduction of *C. nutans*. The error bars indicate standard errors of means.

our study created openings or niches in the perennial grass canopy, which allowed more light to reach the soil surface based on the cover data shown in Figure 2. This benefited initial *C. nutans* establishment and eventually allowed for plants to reach full maturity in the second year.

Biomass of *C. nutans* was greatest in the *C. nutans* monoculture (BG-IC) plots, which we suspect was due to fewer plants and lack of interspecific competition. Although *C. nutans* biomass was lower in clipped grasslands (CL-IC) compared to BG-IC plots, the plants were well established among the grasses. Kok et al. (1986) report high intraspecific mortality can occur in the early seedling stage of *C. nutans*, but this self-thinning characteristic may be less of a factor in the overall establishment due to rapid and large growth habit that includes a long rosette stage, thus eliminating the need for excessive seedlings to emerge at one time. In addition, Smith and Shea (2010) and Zhang and Shea (2012) related increasing levels of disturbance (e.g., tillage, mowing, or hand weeding) to the successful establishment of *C. nutans*, which supports our findings that clipping can facilitate the establishment of *C. nutans* in warm-season perennial grasses.

In order to preempt available light and avoid shade by regrowth of perennial grasses, *C. nutans* rosettes pro-

duced leaf area more quickly in BG-IC and CL-IC plots, which relates to current invasion theories (e.g., superior competitor, niche resources) to make the resources less available (see Craine 2005 and others). Moreover, we observed *C. nutans* plants in the CL-IC plots projecting their leaves directly into vacant areas early in the season before perennial grass growth (Han, personal observation). Bazzaz (1996) has suggested greater plant plasticity and leaf acclimation can occur during alternating intensities and exposures to light. From our results and those of others (e.g., Wardle et al. 1992; Renz and Schmidt 2012; Sanderson et al. 2012), it is evident that *C. nutans* invasion success is highly dependent on access to light within a stand of perennial grasses. It could be that the plasticity in *C. nutans* growth is accentuated when gap size within perennial grasses varies widely from clipping disturbances.

For two years, *C. nutans* plants failed to survive in the nonclipped warm-season perennial grasses (NCL-IC). In the first year (2011), most of the *C. nutans* germinated and the seedlings began to grow among the established plants just prior to grass emergence from dormancy and subsequent canopy closure. Once aboveground competition intensified, *C. nutans* seedlings were forced to adjust to rapidly declining light conditions by elongating stems a short distance. Within the first season, even the appear-

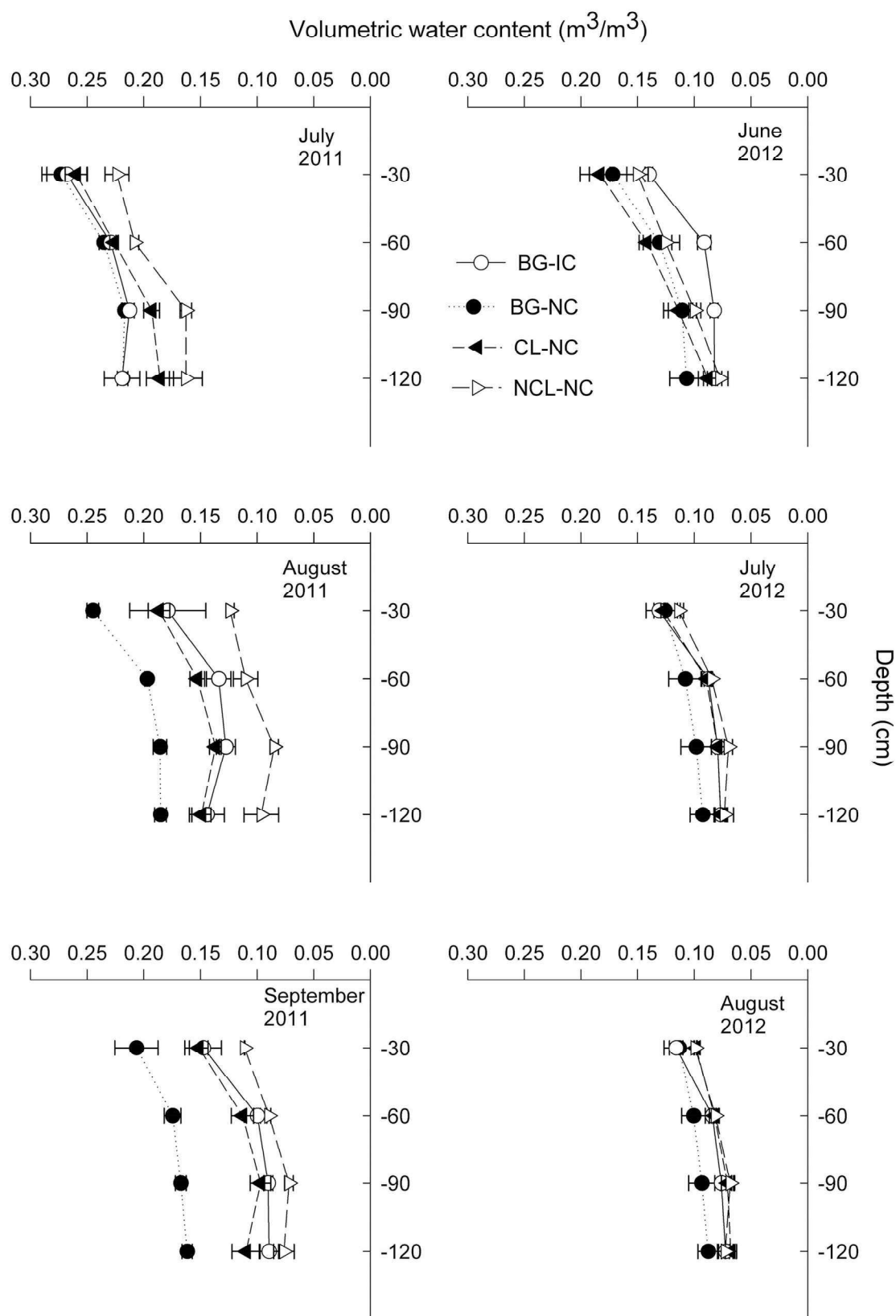


Figure 6. Volumetric soil water content at 30, 60, 90, and 120 cm in 2011 and 2012. BG-NC = bare ground without introduced *Carduus nutans*, BG-IC = bare ground with introduced *Carduus nutans*, CL-NC = clipped grasslands without the introduction of *C. nutans*, and NCL-NC = nonclipped grasslands without the introduction of *C. nutans*. The error bars indicate standard errors of means.

ance of bolting is atypical of growth that usually occurs by *C. nutans* (Wardle et al. 1992; Han and Young 2013). The plasticity in growth that allowed *C. nutans* to survive in the CL-IC plots was inadequate for survival in the NCL-IC plots. Thus, a trade-off may be occurring in *C. nutans* during long periods of low light or darkness whereby normal rosette development is substituted for stunted, misshapen seedlings that progress through a modified bolting stage and result in a single terminal flower bud that fails to become mature or set seed; a similar phenomenon identified in other invasive plant species (Chun et al. 2007; Gandiaga et al. 2009; Molina-Montenegro et al. 2013). In areas where *C. nutans* is common or has the potential to invade, a dense and healthy pasture that is grazed minimally can prevent *C. nutans* establishment, primarily from the inability of the invader to tolerate long periods of shade (Hamrick and Janet 1987).

Plasticity is a change in a plant in response to the environment, while resource use timing relates to plant life history; both contribute to successful invasion by *C. nutans*, but we believe the latter could be a more important factor. Wardle et al. (1992) studied the response of *C. nutans* seedlings to pasture canopy and found that preflowering thistle mortality was strongly related to vegetation type (bare, legume, or grass). In our study, shade from tall statured perennial grasses contributed to the lack of early growth of *C. nutans* (see Han and Young 2014a). The continuous removal of biomass through clipping and subsequent opening in the canopy allowed *C. nutans* rosettes to become established, similar to Smith and Shea (2010). Surface soil moisture resources, which were adequate for *C. nutans* plants to germinate early in 2011 and 2012, were reduced in the perennial grass plots as the season progressed, most dramatically in the second year when drought conditions intensified. Weaver (1958) and Young et al. (2010) showed perennial grass roots extend deep in the soil and can access available water during important aboveground biomass growth stages. Alternatively, a reduction in perennial grass root vigor and subsequent lack of development in deep soil profiles have been correlated to high grazing intensity in the prairies of Nebraska (Weaver 1950).

The decline in surface soil moisture of the *C. nutans* bare ground (BG-IC) plots in 2012 was most likely due to roots at these shallow soil layers and not soil evaporation, as cover was near 75%. As plants developed early in the season, shallow and deep soil moisture content rapidly declined, beginning in September of the previous year (deep soil moisture) and then as *C. nutans* growth in

2012 proceeded from rosette (March and May) to bolting (June) and then more gradually as plants senesced over the remainder of the summer. This same pattern of rapid soil moisture decline during a short but intensive change in growth stage (e.g., rosette to bolting) has been documented for yellow starthistle in California (Young et al. 2011). The period of declining surface and deep soil moisture content in *C. nutans* plots was similar to CL-NC plots during 2012 when grasses progressed from vegetative to flowering stages. The overlap in declining soil moisture content of the grass and *C. nutans* plots during periods of relatively quick and intense growth indicates that a narrow but important period of competition may exist between two functionally different species. Without disturbance (e.g., repeated clipping) and enough soil moisture, newly germinating *C. nutans* plants are at a competitive disadvantage and will likely fail to establish in healthy perennial grass stands.

At the beginning of a drought period, *C. nutans* may germinate but ultimately fail to survive, most likely due to lack of soil moisture in the 0–30 cm depths of the soil. In competitive conditions, whether interspecific (grasses) or intraspecific (*C. nutans*), newly germinated *C. nutans* plants may extend roots past the surface layer, only to encounter dry conditions created by established plants (perennial grasses, second-year *C. nutans*) that grew during the same period. Not surprisingly, the rapidly changing conditions that occur with drought causing a decrease of soil moisture are a significant factor that contributes to the lack of success of some invasive plants being able to establish in native plant communities (Cahill 2003). Had 2011 been a drought year, we suspect soil moisture would have been a more significant factor limiting the success of *C. nutans* establishment in the CL-IC plots in 2012.

## Conclusion

In this study, we set up a midwestern perennial grassland for invasion by *C. nutans* and then captured the process, which was influenced by extreme drought and eventually ended in survival or death of the invader. While extensive research has been published on terrestrial plant invasion success relating to plant traits (Kempel et al. 2013), disturbance or stress (Alpert et al. 2000), functional or species diversity (Shea and Chesson 2002), and biotic interactions (Mitchell et al. 2006), our study has placed an equal emphasis on *C. nutans* failure and success in attempting to establish in

perennial grassland niches. Kolar and Lodge (2001) and Theoharides and Dukes (2007) describe the transitions that nonindigenous plant species must overcome for the invasion process to continue, including transport, colonization, establishment, and landscape spread. Our study demonstrates *C. nutans* was unable to colonize in the nonclipped grasslands due to the abiotic filters of low light and soil moisture, while in the clipped grasslands the invader had successfully established and with additional years and favorable conditions (e.g., continued disturbance) would probably spread throughout the landscape.

Drought and shading are effective for preventing *C. nutans* from colonizing perennial grasslands of temperate regions. Less well known is the degree to which *C. nutans* invading perennial grasslands uses available resources during critical periods, such as the flowering stage, and/or alters growth to better access limited resources. Similar is the dichotomy between resource acquisition and conservation by invasive and native plants described in a review by Funk (2013). While the identification of a “switch” has yet to be identified that allows *C. nutans* to shift between uptake of and growth to resources, our study shows that plasticity and the availability of resources contribute to both the success and failure of *C. nutans* invading perennial grasslands of the midwestern United States.

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## References

- Alpert, P., E. Bone, and C. Holzapfel. 2000. “Invasiveness, Invasibility and the Role of Environmental Stress in the Spread of Non-Native Plants.” *Perspectives in Plant Ecology, Evolution and Systematics* 3:52–66.
- Bazzaz, F. A. 1996. *Plants in Changing Environments: Linking Physiological, Population, and Community Ecology*. Cambridge: Cambridge University Press.
- Beck, K. G. 1999. “Biennial Thistles.” In *Biology and Management of Noxious Rangeland Weeds*, ed. R. L. Sheley and J. K. Petroff, 145–61. Corvallis: Oregon State University Press.
- Beck, K. G. 2001. *Musk Thistle*. Fact Sheet 3.102. Fort Collins: Colorado State University.
- Berlinger, B., and J. A. Knapp. 1991. “Impacts of the Conservation Reserve Program in the Central Great Plains.” In *The Conservation Reserve—Yesterday, Today and Tomorrow*, ed. L. Joyce, J. Mitchell, and M. Skold, 46–49. General Technical Report RM-203. Washington, DC: USDA–Forest Service.
- Blank, R. R., and T. Morgan. 2012. “Suppression of *Bromus tectorum* L. by Established Perennial Grasses: Potential Mechanisms.” *Applied and Environmental Soil Science* 2012:1–9.
- Bottoms, R. M., and T. D. Whitson. 1998. “A Systems Approach for the Management of Russian Knapweed (*Centaurea repens*).” *Weed Technology* 12:363–66.
- Cahill, J. F. 2003. “Neighbourhood-Scale Diversity, Composition and Root Crowding Do Not Alter Competition during Drought in a Native Grassland.” *Ecology Letters* 6:599–603.
- Charles, H., and J. S. Dukes. 2007. “Impacts of Invasive Species on Ecosystem Services.” In *Biological Invasions*, ed. W. Nentwig, 217–37. Berlin: Springer.
- Chesson, P. L. 2000. “Mechanisms of Maintenance of Species Diversity.” *Annual Review of Ecology, Evolution, and Systematics* 31:343–66.
- Chun, Y. J., M. L. Collyer, K. A. Moloney, and J. D. Nason. 2007. “Phenotypic Plasticity of Native vs. Invasive Purple Loosestrife: A Two-State Multivariate Approach.” *Ecology* 88:1499–1512.
- Craine, J. M. 2005. “Reconciling Plant Strategy Theories of Grime and Tilman.” *Journal of Ecology* 93:1041–52.
- Davis, M. A., and M. Pelsor. 2001. “Experimental Support for a Resource-Based Mechanistic Model of Invasibility.” *Ecology Letters* 4:421–28.
- Desrochers, A. M., J. F. Bain, and S. I. Warwick. 1988. “The Biology of Canadian Weeds, 89. *Carduus nutans* L. and *Carduus acanthoides* L.” *Canadian Journal of Plant Science* 68:1053–68.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. London: Methuen.
- Evelt, S. R., and J. L. Steiner. 1995. “Precision of Neutron Scattering and Capacitance Type Soil Water Content Gauges from Field Calibration.” *Soil Science Society of America Journal* 59:961–68.
- Fargione, J., and D. Tilman. 2005. “Niche Differences in Phenology and Rooting Depth Promote Coexistence with a Dominant C4 Bunchgrass.” *Oecologia* 143:598–606.
- Feldman, I., M. K. McCarty, and C. J. Scifres. 1968. “Ecological and Control Studies of Musk Thistle.” *Weed Science* 16:1–4.
- Funk, J. L. 2013. “The Physiology of Invasive Plants in Low-Resource Environments.” *Conservation Physiology* 1:doi:10.1093/conphys/coto26.

- Gandiaga, S., J. C. Volin, E. L. Kruger, and K. Kitajima. 2009. "Effects of Hydrology on the Growth and Physiology of an Invasive Exotic, *Lygodium microphyllum* (Old World Climbing Fern)." *Weed Research* 49:283–90.
- Godoy, O., and J. M. Levine. 2014. "Phenology Effects on Invasion Success: Insights from Coupling Field Experiments to Coexistence Theory." *Ecology* 95:726–36.
- Hamrick, J. L., and M. L. Janet. 1987. "Effect of Soil Surface Topography and Litter Cover on the Germination, Survival, and Growth of Musk Thistle (*Carduus nutans*)." *American Journal of Botany* 74:451–57.
- Han, C., and S. L. Young. 2013. "Ecology of Musk Thistle (*Carduus nutans*) Seed Germination for Grasslands of Temperate Climates." *Weed Science* 61:549–56.
- Han, C., and S. L. Young. 2014a. "Drought and Grazing Disturbances and Resistance to Invasion by Warm- and Cool-Season Perennial Grassland Communities." *Ecological Restoration* 32:28–36.
- Han, C., and S. L. Young. 2014b. "Root Growth of Two Perennial Grass Types and Musk Thistle (*Carduus nutans*) in Temperate Grasslands of North America." *Invasive Plant Science and Management* 7:387–97.
- Hierro, J. L., C. J. Lortie, D. Villarreal, M. E. Estanga-Mollica, and R. M. Callaway. 2011. "Resistance to *Centaurea solstitialis* Invasion from Annual and Perennial Grasses in California and Argentina." *Biological Invasions* 13:2249–59.
- Hooper, D. U., and J. S. Dukes. 2010. "Functional Composition Controls Invasion Success in a California Serpentine Grassland." *Journal of Ecology* 98:764–77.
- Hovick, S. M., D. E. Bunker, C. J. Peterson, and W. P. Carson. 2011. "Purple Loosestrife Suppresses Plant Species Colonization Far More than Broad-Leaved Cattail: Experimental Evidence with Plant Community Implications." *Journal of Ecology* 99:225–34.
- Hull, A. C., and J. O. Evans. 1973. "Musk Thistle (*Carduus nutans*): An Undesirable Range Plant." *Journal of Range Management* 26:383–85.
- Hurlbert, S. H. 1984. "Pseudoreplication and the Design of Ecological Field Experiments." *Ecological Monographs* 54:187–211.
- Kempel, A., T. Chrobock, M. Fischer, R. P. Rohr, and M. van Kleunen. 2013. "Determinants of Plant Establishment Success in a Multispecies Introduction Experiment with Native and Alien Species." *Proceedings of the National Academy of Science* 110:12727–32.
- Kok, L. T. 2001. "Classical Biological Control of Nodding and Plumeless Thistles." *Biological Control* 21:206–13.
- Kok, L. T., T. J. McAvoy, and W. T. Mays. 1986. "Impact of Tall Fescue Grass and *Carduus* Thistle Weevils on the Growth and Development of Musk Thistle (*Carduus nutans*)." *Weed Science* 34:966–71.
- Kolar, C. S., and D. M. Lodge. 2001. "Progress in Invasion Biology: Predicting Invaders." *Trends in Ecology and Evolution* 16:199–204.
- Larson, D. L., P. J. Anderson, and W. Newton. 2001. "Alien Plant Invasion in Mixed-Grass Prairie: Effects of Vegetation Type and Anthropogenic Disturbance." *Ecological Applications* 11:128–41.
- Leininger, W. C. 1988. *Non-Chemical Alternatives for Managing Selected Plant Species in the Western United States*. Cooperative Extension XCM-118. Fort Collins: Colorado State University.
- MacDougall, A. S., B. Gilbert, and J. M. Levine. 2009. "Plant Invasions and the Niche." *Journal of Ecology* 97:609–15.
- Maron, J., and M. Marler. 2007. "Native Plant Diversity Resists Invasion at Both Low and High Resource Levels." *Ecology* 88:2651–61.
- Milbau, A., I. Nijs, F. Raedemaeker, D. Reheul, and B. D. Cauwer. 2005. "Invasion in Grassland Gaps: The Role of Neighbourhood Richness, Light Availability and Species Complementarity during Two Successive Years." *Functional Ecology* 19:27–37.
- Mitchell, C. E., A. A. Agrawal, J. D. Bever, G. S. Gilbert, R. A. Hufbauer, J. N. Klironomos, J. L. Maron, W. F. Morris, I. M. Parker, A. G. Power, E. W. Seabloom, M. E. Torchin, and D. P. Vázquez. 2006. "Biotic Interactions and Plant Invasions." *Ecology Letters* 9:726–40.
- Molina-Montenegro, M. A., C. Palma-Rojas, Y. Alcayaga-Olivares, R. Oses, L. J. Corcuera, and L. A. Cavieres. 2013. "Ecophysiological Plasticity and Local Differentiation Help Explain the Invasion Success of *Taraxacum officinale* (dandelion) in South America." *Ecography* 36:718–30.
- Novoa, A., R. Rodriguez, D. Richardson, and L. Gonzalez. 2014. "Soil Quality: A Key Factor in Understanding Plant Invasion? The Case of *Carpobrotus edulis* (L.) N.E.Br." *Biological Invasions* 16:429–43.
- Pokorny, M. L., R. L. Sheley, C. A. Zabinski, R. E. Engel, T. J. Svejcar, and J. J. Borkowski. 2005. "Plant Functional Group Diversity as a Mechanism for Invasion Resistance." *Restoration Ecology* 13:448–59.
- Reece, P. E., and R. G. Wilson. 1983. "Effect of Canada Thistle (*Cirsium arvense*) and Musk Thistle (*Carduus nutans*) Control on Grass Herbage." *Weed Science* 31:488–92.
- Rees, N. E. 1991. "Biological Control of Thistles." In *Noxious Range Weeds*, ed. L. F. James, J. O. Evans, M. H. Ralphs, and R. D. Child, 264–73. Boulder, CO: Westview Press.
- Reinhart, K. O., J. Gurner, R. Tirado, and R. M. Callaway. 2006. "Invasion through Quantitative Effects: Intense Shading Drives Native Decline and Invasive Success." *Ecological Applications* 16:1821–31.
- Renz, M. J., and M. L. Schmidt. 2012. "The Effects of Increasing Grazing Height on Establishment of Pasture Weeds in Management-Intensive Rotationally Grazed Pastures." *Weed Science* 60:92–96.
- Roeth, F., S. Melvin, and I. Schleufer. 2003. *Noxious Weeds of Nebraska: Musk Thistle*. Extension Circular 176. Lincoln: University of Nebraska.
- Sanderson, M. A., G. Brink, L. Ruth, and R. Stout. 2012. "Grass-Legume Mixtures Suppress Weeds during Establishment Better than Monocultures." *Agronomy Journal* 104:36–42.

- Shea, K., and P. Chesson. 2002. "Community Ecology Theory as a Framework for Biological Invasions." *Trends in Ecology and Evolution* 17:170–76.
- Sheley, R. L., S. Kedzie-Webb, and B. D. Maxwell. 1999. "Integrated Weed Management on Rangeland." In *Biology and Management of Noxious Rangeland Weeds*, ed. R. L. Sheley and J. K. Petroff, 57–68. Corvallis: Oregon State University Press.
- Sindel, B. M. 1991. "A Review of the Ecology and Control of Thistle in Australia." *Weed Research* 31:189–201.
- Smith, J. P., and K. Shea. 2010. "Seedling Emergence and Early Survival of *Carduus* spp. in Three Habitats with Press and Pulse Disturbances." *Journal of the Torrey Botanical Society* 137:287–96.
- Steel, R. G. D., J. H. Torrie, and D. A. Dickey. 1997. *Principles and Procedures of Statistics*, 3rd ed. New York: McGraw-Hill.
- Theoharides, K. A., and J. S. Dukes. 2007. "Plant Invasions across Space and Time: Factors Affecting Nonindigenous Species Success during Four Stages of Invasion." *New Phytologist* 176:256–73.
- Thomas, E. M., M. Jamie, and H. B. Jean. 2002. "Effect of Community Structure on Invasion Success and Rate." *Ecology* 83:898–905.
- Thomsen, M. A., and C. M. D'Antonio. 2007. "Mechanisms of Resistance to Invasion in a California Grassland: The Roles of Competitor Identity, Resource Availability and Environmental Gradients." *Oikos* 116:17–30.
- Throop, H. L., L. G. Reichmann, O. E. Sala, and S. R. Archer. 2012. "Response of Dominant Grass and Shrub Species to Water Manipulation: An Ecophysiological Basis for Shrub Invasion in a Chihuahuan Desert Grassland." *Oecologia* 169:373–83.
- Wardle, D. A., K. S. Nicholson, and A. Rahman. 1992. "Influence of Pasture Grass and Legume Swards on Seedling Emergence and Growth of *Carduus nutans* L. and *Cirsium vulgare*." *Weed Research* 32:119–28.
- Weaver, J. E. 1950. "Effects of Different Intensities of Grazing on Depth and Quantity of Roots of Grasses." *Journal of Range Management* 3:100–113.
- Weaver, J. E. 1958. "Summary and Interpretation of Underground Development in Grassland Communities." *Ecological Monographs* 28:55–78.
- Wolkovich, E. M., and E. E. Cleland. 2010. "The Phenology of Plant Invasions: A Community Ecology Perspective." *Frontiers in Ecology and the Environment* 9:287–94.
- Young, S. L. 2015. "When an Invasive Plant Fails to Invade." *Frontiers in Ecology and the Environment* 13:450–51.
- Young, S. L., G. B. Kyser, J. N. Barney, V. P. Claassen, and J. M. DiTomaso. 2010. "Spatio-Temporal Relationship between Water Depletion and Root Distribution Patterns of *Centaurea solstitialis* and Two Native Perennials." *Restoration Ecology* 18:323–33.
- Young, S. L., G. B. Kyser, J. N. Barney, V. P. Claassen, and J. M. DiTomaso. 2011. "The Role of Light and Soil Moisture in Resistance to Invasion by Yellow Starthistle (*Centaurea solstitialis*)." *Restoration Ecology* 19:599–606.
- Zavaleta, E. S., and K. B. Hulvey. 2007. "Realistic Variation in Species Composition Affects Grassland Production, Resource Use and Invasion Resistance." *Plant Ecology* 188:39–51.
- Zhang, R., and K. Shea. 2012. "Integrating Multiple Disturbance Aspects: Management of an Invasive Thistle, *Carduus nutans*." *Annals of Botany* 110:1395–1401.