

# Neighbor defoliation regulates Canada thistle (*Cirsium arvense*) in pasture by mediating interspecific competition

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## ABSTRACT

Little is known of the effect of selective plant defoliation at different intensities and frequencies in altering weed-forage dynamics in pasture. We conducted a field experiment to quantify *Cirsium arvense* responses to varying defoliation regimes of neighboring forage implemented for 2 years under high or low fertility conditions. Defoliation regimes were based on common grazing systems, and included: (1) high intensity–high frequency (HIHF) defoliation simulating continuous grazing, (2) high intensity–low frequency (HILF), (3) low intensity–high frequency (LIHF), and (4) deferred (DEF) defoliation to peak growth in late summer. All vegetation except *C. arvense* was defoliated during the growing season to examine weed responses to changes in neighboring forage abundance. Year-end *C. arvense* biomass at the end of the study was greatest in the HIHF treatment and lowest in the DEF, with the LIHF and HILF treatments intermediate in response. The HILF treatment also provided improved suppression of *C. arvense* biomass relative to the LIHF, although this response was inconsistent among sites. Trends in *C. arvense* shoot densities among defoliation treatments were similar to those for biomass. While weed abundance was lower in the absence of fertilization, rankings among defoliation treatments remained the same. Notably, trends in forage biomass among defoliation regimes followed a pattern opposite that of *C. arvense*, and are implicated in observed weed decreases. Our results indicate that defoliation regimes enhancing forage growth and biomass, particularly a DEF or HILF regime, reduce *C. arvense* the most. Grazing systems that employ these defoliation regimes are therefore likely to optimize the interspecific competitive suppression of *C. arvense*.

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## 1. Introduction

Traditional weed management has relied on intensive methods of weed control, including the use of herbicides and cultural practices (e.g. tillage, mowing). Within pastoral systems however, weed control using these methods may not be acceptable due to undesirable side effects such as the removal of beneficial broadleaf species (Hartley and Thomson, 1981). Additionally, affected areas are difficult to access and treat using these control methods, while other areas are restricted to low disturbance control measures (e.g. prohibition of herbicides near wetlands). As a result, a cumulative stress approach is suggested for achieving integrated weed control (Muller-Scharer and Schroeder, 1993). Given that the incidence and

abundance of pasture weeds depends in part on the presence of environmental conditions favoring weed invasion and spread (Suter et al., 2007), an increasing component of contemporary weed management strives for preventative weed suppression through interspecific competition from neighboring forage plants (Bourdôt, 1996). Decreased pasture vigor creates points of entry for weeds as light, water, space and nutrients become available (Edwards et al., 2000).

In many regions *Cirsium arvense* (L.) Scop. has been recognized as a problematic weed within both cultivated fields and permanent pastures (Edwards et al., 2000; Graglia et al., 2006), and is known to reduce forage biomass (Grekul and Bork, 2004). This plant is highly competitive due to an extensive root system and vigorous growth strategy (Donald, 1990), as well as its favorable response to fertilization (Nadeau and Vandenborn, 1990; Grekul and Bork, 2007).

The spread of *C. arvense* is likely to depend on the vigor and competitiveness of neighboring plants, which in turn, is affected by the presence of a defoliating herbivore and subsequent weed-forage dynamics (Edwards et al., 2000). By altering weed-forage

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interspecific relationships, controlled grazing by livestock may alter weed abundance. Grazing systems are intended to modify the intensity, timing or spatial distribution of use in order to balance defoliation stress with subsequent recovery of vegetation (Heitschmidt and Stuth, 1991). Continuous or high intensity–high frequency (HIHF) defoliation maximizes animal selectivity, leading to patchy use (Crawley, 1983), low plant vigor in repeatedly grazed areas, and increased weeds (Suter et al., 2007). Low palatability of *C. arvense* (Wood, 1987) results in selective avoidance by cattle allowing the weed to maintain high leaf area. Under increasing grazing pressure, neighboring palatable vegetation may decline, enhancing *C. arvense* competitiveness and growth via increased access to resources. This feedback cycle is ultimately enhanced by continuous, selective grazing (Edwards et al., 2000).

Regulating grazing intensity and frequency can promote pasture vigor while continuing to make use of forage, although such approaches have rarely been tested for application in weed ecology. These techniques may be exploited in rotational grazing systems where an increase in grazing pressure (i.e. ratio of forage demand to supply) leads to a decrease in animal selectivity and greater uniformity of defoliation. High intensity–low frequency (HILF) grazing systems maintain high animal densities to intensely defoliate all vegetation over a short period of time, which is then followed by a long recovery period (Heitschmidt and Stuth, 1991). While the HILF system impacts weeds directly as it is designed to overcome animal avoidance of unpalatable plants, it may also reduce forage plant vigor. An alternate strategy is a short duration or low intensity–high frequency (LIHF) system, where forage is lightly defoliated during a brief grazing period, which is then followed by a short recovery period before regrowth occurs (Heitschmidt and Stuth, 1991). Despite little direct impact to avoided weeds, the latter practice theoretically maximizes forage vigor as it ensures rapid regrowth (Grignani et al., 1993; Bryan et al., 2000), and should therefore result in high sustained interspecific competitive pressure against weeds.

Previous studies examining weeds in pastures have examined primarily the impact of direct defoliation on weed abundance, either alone (e.g. Hoveland et al., 1996; De Bruijn and Bork, 2006) or in combination with other factors such as interspecific competition (e.g. Friedli and Bacher, 2001). Previous research on *C. arvense* indicates cattle grazing at high densities can be used as an effective tool for suppressing this weed in temperate pastures (De Bruijn and Bork, 2006). What remains unknown is the extent to which reductions in *C. arvense* arise specifically from varied forage defoliation regimes (i.e. variation in the intensity and frequency of neighbor defoliation) and the importance of this process in altering interspecific competition and associated weed-forage dynamics. Although previous studies have examined the impact of herbivore (rabbit or cattle) presence on *C. arvense* (Edwards et al., 2000; De Bruijn and Bork, 2006), these investigations have not examined variation in neighbor defoliation. Isolating the indirect affect of interspecific competition on weeds due to selective defoliation

**Table 2**

Growing season precipitation in relation to the long-term seasonal mean for each of the four study sites throughout the study period.

Site	Growing Season Precipitation (May–Aug; mm)			Long-term Precipitation
	1999	2000	2001	30-Yr Mean (mm)
1	235 (–4%) <sup>a</sup>	272 (+3%)	279 (+6%)	263
2	365 (–2%)	406 (+9%)	256 (–31%)	372
3	281 (–12%)	301 (–6%)	292 (–8%)	319
4	194 (–23%)	248 (–1%)	219 (–13%)	251
Mean	269 (–11%)	307 (–2%)	262 (–13%)	301

<sup>a</sup> Values in parentheses indicate deviation from the 30-yr mean.

requires controlled field studies where only neighboring forage plants are defoliated.

This study experimentally tested different forage defoliation regimes that simulate different grazing systems within temperate pastures. Specifically, we modified the intensity and frequency of defoliation of neighboring forage over two years, and assessed (1) *C. arvense* density and biomass responses, together with (2) patterns of season-long accumulated forage biomass.

## 2. Materials and methods

### 2.1. Study area

Replicated plots were located at each of four study sites across the Aspen Parkland region of central Alberta, Canada, from 1999 to 2001. Sites were selected for their suitability to evaluate the impact of defoliation and subsequent sward biomass growth on *C. arvense* under fertilized and unfertilized conditions. All sites had abundant, relatively uniform *C. arvense* (Table 1), with little variation in slope and aspect, and were free of chemical control for three years. Sites were representative of established pastures in the region with a history of summer grazing. Dominant grasses included smooth brome (*Bromus inermis* Leyess.), Kentucky bluegrass (*Poa pratensis* L.), and quackgrass [*Agropyron repens* (L.) Beauvois]. Common forbs other than *C. arvense* were dandelion (*Taraxacum officinale* Web.) and white clover (*Trifolium repens* L.), with sites 2 and 4 containing American vetch (*Vicia americana* Munlenb.).

All sites had soils that were loamy or silt loam in texture, with sites 1 and 2 on Black Chernozems (Typic Haplustoll) over glacial till parent material, site 4 on a Dark Gray Chernozem (Typic Haplustoll) over till, and site 3 on a river floodplain with a Humic Gleysol (Typic Endoaquoll). Selective soil properties are provided in Table 1, with organic matter particularly high on the floodplain (site 3). All sites were fenced to exclude large herbivores during summer and facilitate data collection, but were grazed during autumn (October) to prevent litter accumulation and maintain otherwise normal land use activities. Precipitation during the growing season (May to August) was recorded at each site and year (Table 2).

**Table 1**

Initial mean (SE) vegetation and soil characteristics of the 4 study sites, as sampled in 1999 prior to the implementation of treatments.

Site	Location	<i>Cirsium arvense</i>		Herbage Biomass (g m <sup>–2</sup> )	Soil OM (%)	Soil Nutrients <sup>a</sup>			
		Density (shoots m <sup>–2</sup> )	Biomass (g m <sup>–2</sup> )			N	P	K	S
						(g m <sup>–2</sup> )			
1	53°42'24" N 112°33'10" W	32 (3)	39 (5)	206 (9)	10.1	4.7	0.7	43	3.3
2	52°18'55" N 114°31'48" W	13 (1)	48 (11)	228 (19)	11.0	1.1	0.7	80	1.6
3	54°00'57" N 114°22'44" W	49 (5)	312 (42)	391 (22)	33.5	13	1.1	101	329
4	53°47'5" N 111°27'24" W	32 (3)	48 (7)	195 (10)	<5	–	–	–	–

<sup>a</sup> Soil chemistry was available for sites 1 through 3 only. Soil OM at site 4 was an estimate based on soil survey information.

## 2.2. Experimental design and defoliation treatments

At each site, a split-block design was used to assess the influence of four combinations of neighboring (forage) defoliation intensity and frequency, with and without fertilization, on *C. arvense* abundance, as well as associated season-long forage growth. Fertilizer regimes were assigned to main plots and defoliation regimes to subplots, with 5 replicate subplots of each fertilization by defoliation combination. Within each site, two whole plots measuring 10 by 10 m were established, one of which was randomly selected for annual fertilization. Based on initial soil samples collected in 1999, fertilizer was applied at 100–45–10–15 kg ha<sup>-1</sup> of N–P–K–S in each year (1999–2001) between 15 May and 31 May. Fertilization was intended to ensure macronutrient limitations did not restrict forage growth and subsequent interspecific competition with *C. arvense*.

Within each of the four sites, 20, 1 by 1 m permanent subplots were systematically established in each of the fertilized and unfertilized whole plots. Four defoliation regimes were applied to five randomly selected subplots, with each regime simulating a unique grazing system. Defoliation included high intensity–high frequency (HIHF), a high intensity–low frequency (HILF) regime, a low intensity–high frequency (LIHF) regime, and finally deferred (DEF) defoliation until the end of the growing season in mid-August. Defoliation (i.e. clipping) regimes were applied throughout 2000 and 2001 following an initial year of baseline sampling at peak growth in 1999, and included the following treatments administered from 15 May to 31 August:

- 1] HIHF – subplot forage (i.e. all vegetation excluding *C. arvense*) clipped to a stubble height of 2 cm every 2 weeks,
- 2] LIHF – subplot forage clipped to a height of 10 cm every 2 weeks,
- 3] HILF – subplot forage clipped to a height of 2 cm every 6 weeks,
- 4] DEF – subplot forage clipped once at the end of the growing season (mid-August) following unimpeded growth throughout the summer.

Vegetation growth after 31 August was negligible as this corresponds to the late growing season in the region, with the first killing frost typically in early September.

## 2.3. Vegetation measurements

All measurements were made within a central 0.25 m<sup>2</sup> (50 by 50 cm) quadrat within the 40, 1 m<sup>2</sup> subplots at each site. This procedure maintained a 25 cm treated buffer and ensured treatment responses were not influenced by adjacent vegetation. Subplots at three sites were sampled in late August of 1999 prior to the implementation of treatments to establish initial *C. arvense* abundance (shoot density and biomass). Year-end herbage biomass in 1999 was assessed by harvesting *C. arvense* and neighboring forage at the end of the growing season to ground level.

In 2000 and 2001, the scheduled defoliation treatments were applied to each subplot, with defoliation prior to 15 August occurring only on the non-*C. arvense* component. All biomass removed during the application of treatments within each subplot was retained, leading to accumulated forage values throughout the growing season. After 15 August, remaining forage was harvested to ground level and added to the material previously removed. Final biomass samples were dried at 50 °C to constant mass and weighed, with all data presented as dry matter values.

Unlike the forage component, *C. arvense* plants in each nested subplot were not harvested until 15 August after growing unimpeded throughout the growing season, thereby simulating animal

avoidance of the plant during summer. *C. arvense* shoot densities were measured within each subplot prior to harvest. Harvesting of *C. arvense* was uniform across treatments within a site, and followed flowering and the onset of dormancy to minimize sampling effects on future *C. arvense* growth.

## 2.4. Data analyses

Following the assessment of data for normality, forage and *C. arvense* abundance (shoot density and biomass) data from 2000 to 2001 were analyzed using an ANOVA with Proc Mixed (SAS Institute Inc., 1988) for a split-block design. Fixed factors included fertilization (whole plot), defoliation (subplot), and sites, which exhibited substantial variation in initial conditions (Table 1). Although fertilization treatments were unreplicated within sites, emphasis during analysis was on defoliation and any interactions of the latter with fertilization or site. Thus, fertilization and site effects are discussed only in the context of significant ( $P < 0.05$ ) interactions with defoliation. No transformations were necessary. Baseline data from 1999 were initially included as a covariate to assess the importance of starting *C. arvense* and neighboring forage abundance in each subplot on subsequent measures, but were removed in the final model due to the absence of covariate effects ( $P > 0.10$ ; Table 3).

*C. arvense* and forage biomass, together with *C. arvense* shoot density from each year (2000 and 2001), were analyzed separately to evaluate the temporal pattern of vegetation responses. In 2001, only three sites were examined because trespass cattle at site 2 precluded sampling that year. Overall year effects were also examined to assess the impact of growing conditions on response variables. Post-hoc mean comparisons using Tukey's method were conducted for all significant F-test main effects and any interactions that included defoliation. Comparisons were made using a significance of  $P < 0.05$ , except for the assessment of 3-way interactions, which were done with  $P < 0.10$  to account for limited sample sizes ( $n = 5$ ). All analyses were conducted using LSmeans.

**Table 3**

Summary of ANOVA  $F$ -value<sup>a</sup> results for the analysis of *C. arvense* shoot density and biomass, as well as neighboring forage biomass, showing effects of defoliation regime and fertilization across multiple sites in each of 2 years.

	df	<i>Cirsium arvense</i>		Forage
		Density (shoot m <sup>-2</sup> )	Biomass (g m <sup>-2</sup> )	Biomass (g m <sup>-2</sup> )
<b>2000</b>				
1999 Covariate <sup>b</sup>	—	0.04	4.56	5.15
Site <sup>c</sup>	3	37.93***	37.79***	22.81***
Fertilizer (Fert)	1	1.36	3.28	270.53***
Site × Fert	3	8.68***	2.37	0.72
Defoliation (Def)	3	12.25***	0.76	42.47***
Def × Site	9	2.50*	1.07	2.67**
Def × Fert	3	2.16	1.19	8.34***
Def × Site × Fert	9	1.71	1.02	1.10
<b>2001</b>				
1999 Covariate <sup>b</sup>	—	0.00	0.00	0.00
Site <sup>c</sup>	2	20.52***	25.60***	142.08***
Fert	1	0.24	8.22**	153.30***
Site × Fert	2	12.04***	7.74***	1.55
Def	3	12.96***	11.82***	53.28***
Def × Site	6	3.47**	5.98***	3.93**
Def × Fert	3	1.89	1.01	4.98**
Def × Site × Fert	6	2.43*	4.22***	1.14

<sup>a</sup> \*, \*\*, \*\*\* Indicate significance at  $P < 0.05$ ,  $P < 0.01$ , and  $P < 0.001$ , respectively.

<sup>b</sup> Covariate results shown were run in the initial model and subsequently removed due to lack of significance.

<sup>c</sup> Number of sites sampled in 2000 and 2001 was 4 and 3, respectively.

### 3. Results

#### 3.1. *Cirsium arvense* abundance

In 2000, *C. arvense* density exhibited defoliation and defoliation by site effects (Table 3). In contrast, there were no defoliation effects on year-end *C. arvense* biomass. One year later during 2001, there were more complex interactions evident, with significant defoliation, defoliation by site, and defoliation by site by fertilization effects for both *C. arvense* shoot density and biomass (Table 3).

*C. arvense* shoot density and biomass exhibited similar trends with the greatest weed abundance in HIHF subplots, which then generally declined through the LIHF and HILF, reaching a minimum in the DEF (Table 4). While all four defoliation regimes differed in biomass of *C. arvense*, the LIHF and HILF defoliation regimes remained similar ( $P > 0.05$ ) in final *C. arvense* shoot density (Table 4).

Responses in *C. arvense* shoot density appeared as early as 2000 through a defoliation by site effect. Sites first showing differences among defoliation treatments included sites 1 and 3, where the HIHF treatment was greater ( $P > 0.05$ ) than each of the HILF and DEF regimes (Table 4). Unlike shoot density, *C. arvense* biomass did not respond to defoliation in 2000.

By 2001, differences became more evident in both *C. arvense* shoot biomass and density among defoliation treatments (Table 4). Fertilization also resulted in greater differences in *C. arvense* abundance (shoot density and biomass) among defoliation treatments, specifically the LIHF compared to the HIHF and HILF treatments, but only at site 1 (Table 4). At site 3, the DEF treatment had lower *C. arvense* shoot density than the HIHF treatment under both fertilized and unfertilized conditions. Similarly, both the DEF and HILF treatments reduced *C. arvense* biomass relative to the HIHF and LIHF treatments at site 3, but only in the absence of fertilization. In contrast to the other sites, no differences were apparent in *C. arvense* (density or biomass) at site 4.

Significant year effects were evident for both *C. arvense* biomass ( $F_{1,192} = 12.9$ ,  $P < 0.01$ ) and density ( $F_{1,192} = 12.4$ ,  $P < 0.01$ ). In 2000

and 2001, mean *C. arvense* density was 13.1 and 10.3 shoots  $m^{-2}$ , while *C. arvense* biomass averaged 128 and 85  $g m^{-2}$ , respectively, across all sites sampled. Examined in detail, the difference between years was associated primarily with site 3, where *C. arvense* biomass and shoot density ( $P < 0.0001$ ) decreased in 2001. At all other sites *C. arvense* density remained unchanged, while *C. arvense* biomass at site 1 increased ( $P < 0.05$ ) into the second year.

#### 3.2. Neighboring forage responses

Accumulated forage yields in 2000 and 2001 exhibited significant defoliation, defoliation by site, and defoliation by fertilization effects (Table 3). Comparison between years revealed significant year ( $F_{1,192} = 19.6$ ,  $P < 0.0001$ ) effects on forage biomass, with 308 and 363  $g m^{-2}$  in 2000 and 2001, respectively. Forage biomass in the HIHF treatment was less than the other three defoliation treatments in 2000 at all sites except site 3 (Table 5). Additionally, forage biomass in the DEF was greater than in all other treatments at sites 1 and 3. Finally, forage was greater in the HILF relative to the LIHF treatment at site 1 during 2000, and sites 1 and 3 during 2001 (Table 5). No differences in forage biomass were apparent at site 4 between the DEF, HILF and LIHF defoliation regimes (Table 5).

Defoliation effects on forage biomass were similar regardless of fertilization, although the addition of fertilizer resulted in greater differences among defoliation treatments (Table 5). More specifically, fertilization led to forage biomass values in the HILF treatment that were more likely to be greater than those in the LIHF.

### 4. Discussion

#### 4.1. *Cirsium arvense* response to neighbor defoliation

In the present study, *C. arvense* density and biomass in the HIHF treatment were similar to or greater than those in the other treatments. Conversely, *C. arvense* density and biomass in the DEF and HILF treatment were similar to or lower than those in the other treatments. Given that defoliation during the growing season was applied only to non-*C. arvense* herbage, the differences among treatments are attributed to variable interspecific competition between the weed and neighboring forage, as influenced by the timing and intensity of defoliation. This finding is important given that previous studies have examined the role of the animal in direct weed control (e.g. Popay and Field, 1996; De Bruijn and Bork, 2006) rather than weed responses induced by competition (Edwards et al., 2000; Ferrero-Serrano et al., 2008). Edwards et al. (2000)

**Table 4**  
Mean *C. arvense* shoot density and biomass for the various defoliation regimes and fertilization treatments at each site in either 2000 or 2001.

Year	Site	Fert <sup>a</sup>	Defoliation Regime				SE
			HIHF	LIHF	HILF	DEF	
<i>C. arvense</i> Density (shoots m <sup>-2</sup> )							
2000	1	—	80 a <sup>b</sup>	65 ab	54 bc	39 c	7.1
	2	—	36 a	24 a	20 a	20 a	
	3	—	98 a	79 b	50 c	48 c	
	4	—	34 a	21 a	38 a	24 a	
	All	—	62 a	47 b	41 bc	33 c	
2001	1	F	147 a	77 b	48 c	38 c	11.7
		NF	54 a	58 a	35 ab	19 b	
	3	F	53 a	30 ab	32 ab	24 b	
		NF	69 a	65 a	49 a	11 b	
	4	F	17 a	12 a	21 a	9 a	
		NF	34 a	25 a	34 a	25 a	
	All	—	62 a	44 b	36 b	21 c	
<i>C. arvense</i> Biomass (g m <sup>-2</sup> )							
2001	1	F	452 a	269 b	54c	48 c	36.6
		NF	134 a	105 a	69 ab	11 b	
	3	F	107 a	96 a	106 a	87 a	
		NF	164 a	126 ab	77 bc	17 c	
	4	F	8 a	6 a	37 a	3 a	
		NF	19 a	12 a	17 a	8 a	
	All	—	147 a	102 b	60 c	29 c	

<sup>a</sup> F and NF indicate fertilized and unfertilized treatments, respectively.

<sup>b</sup> Within a row, means of data from 2000 with different letters differ at  $P < 0.05$ , while means of data from 2001 with different letters differ at  $P < 0.10$ .

**Table 5**  
Mean accumulation of forage biomass obtained under the different defoliation treatments at each site during 2000 and 2001.

Year	Site	Fert <sup>a</sup>	Defoliation Regime					
			HIHF	LIHF	HILF	DEF	SE	
<i>Forage Biomass</i> (g m <sup>-2</sup> )								
2000	1	—	172 d <sup>b</sup>	252 c	318 b	417 a	25.6	
	2	—	184 c	302 b	345 ab	406 a		
	3	—	354 b	399 b	343 b	527 a		
	4	—	182 b	309 a	269 a	333 a		
	All	F	276 c	413 b	444 b	554 a		18.6
	NF	169 b	218 b	194 b	288 a			
2001	1	—	88 d	203 c	283 b	421 a	31.0	
	3	—	370 d	513 c	661 b	794 a		
	4	—	178 b	296 a	317 a	345 a		
	All	F	271 d	438 c	559 b	665 a		25.3
		NF	153 c	237 b	281 b	375 a		

<sup>a</sup> F and NF indicate fertilized and unfertilized treatments, respectively.

<sup>b</sup> Within a row, means with different letters differ ( $P < 0.05$ ).



documented increases in *C. arvensis* following competitive release from grasses reduced by rabbit grazing, although variation in defoliation intensity and frequency were not examined. Ferrero-Serrano et al. (2008) described synergistic effects of grass competition and weevil foraging on the biological suppression of *C. arvensis* but under greenhouse conditions.

In the current study, delaying forage defoliation until late summer resulted in the lowest *C. arvensis* and often coincided with greater accumulated forage biomass. Uninterrupted forage growth therefore appears to have minimized *C. arvensis*, likely by maximizing reductions in available light, moisture and nutrients. The few *C. arvensis* shoots observed in the understory of DEF subplots were generally short-statured (data not shown), weak-stemmed and chlorotic, symptomatic of exposure to low light.

In contrast, forage plants with poor vigor from frequent defoliation appeared to result in a competitive advantage in favor of *C. arvensis* in HIHF subplots. Repeated intense defoliation would render resident grasses susceptible to root mass reductions (Biswell and Weaver, 1933; Evans, 1973; Richards, 1984), decreasing their competitive fitness below ground. Undeveloped *C. arvensis* were likely to exploit available resources in this situation, including available light and soil nutrients, in turn contributing to the marked reduction in forage biomass in this treatment. Evidence for this was evident at site 1 where *C. arvensis* increased within HIHF subplots when fertilized. Preferential uptake of available nutrients by undeveloped *C. arvensis* would be consistent with previous studies documenting *C. arvensis* biomass increases under fertilization (Lowe et al., 2002; Grekul and Bork, 2007).

The two-year delay in producing differences in *C. arvensis* biomass suggested that the defoliation regimes required more than one year for effects to become measurable. Reductions in *C. arvensis* within the HILF and LIHF treatments relative to the HIHF may be partially attributed to either a longer recovery period between defoliation events (HILF) or reduced defoliation intensity (LIHF). As both practices led to increases in forage biomass, this could also have led to more intense competition against neighboring weeds, and may account for why rotational grazing reduces seedling recruitment of weeds (Edwards et al., 2005).

Relative to the LIHF treatment, the HILF regime occasionally had greater *C. arvensis* reductions, presumably because forage was kept in a more rapid stage of growth under infrequent defoliation. These results parallel those of Hoveland et al. (1996), where more frequent cutting of alfalfa (*Medicago sativa* L.) was a factor increasing the invasion of weedy grasses. Maintaining rapid forage growth would cause more intense competition between herbage (primarily grasses) and neighboring *C. arvensis*. Seeding of competitive perennial grasses has been shown elsewhere to reduce *C. arvensis* (Wilson and Kachman, 1999).

Among the sites examined, *C. arvensis* responded to modified defoliation only at sites 1 and 3, with results immediately evident in 2000. In contrast, *C. arvensis* failed to change in abundance at sites 2 and 4 (although data for site 2 in 2001 were not available). Examination of the environmental data from the four sites does not shed any clear insight into differentiating between responsive and non-responsive sites. For example, while excessive weed populations may have constrained the ability of neighboring vegetation to respond to altered defoliation, we found the greatest forage responses at site 3, which also had the most abundant *C. arvensis* at the start of the study (Table 1), discounting this possibility. Similarly, marked weed reductions were observed at site 1 where both weed abundance and initial forage conditions were initially low to moderate (Table 1).

Observed soil characteristics among the study sites (Table 1) also failed to shed insight on why some sites exhibited limited weed responses to our defoliation treatments. Sites with favorable weed

reductions had both high soil organic matter and associated fertility (site 3) and low fertility (site 1) (Table 1), although the addition of fertilizer at site 1 did enhance the reduction in *C. arvensis* abundance under modified defoliation. Finally, growing conditions (i.e. precipitation) across the study sites were also relatively consistent with long-term normals throughout the study (Table 2), and therefore should not have constrained forage recovery in our investigation.

The most likely explanation for the observed variation in weed responses to defoliation among sites was the extent of neighboring vegetation response to changes in defoliation intensity and frequency. Reductions in weed abundance at sites 1 and 3 coincided directly with large increases in accumulated forage. Although forage biomass responded favorably at site 2, the loss of this site in 2001 did not allow for the examination of subsequent weed responses during the second year. In contrast, the lack of response in *C. arvensis* at site 4 correlated directly with very limited changes in forage growth across defoliation treatments at this location, which in turn, may reflect a history of heavy grazing and associated poor forage vigor. At site 4, only the HIHF treatment differed from the others in forage, and not until the final year, which may have been insufficient time to produce detectable changes in weed abundance arising from altered interspecific competition.

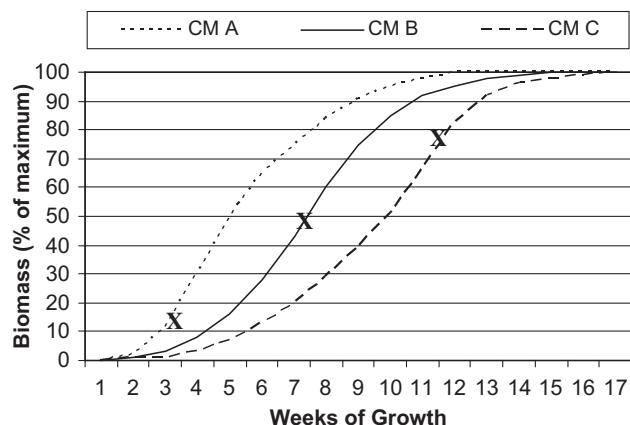
Poor initial pasture sward vigor would inhibit (or at least delay) the ability of a sward to respond to a favorable change in defoliation. Moreover, *C. arvensis* has been found to comprise more than 21% of propagules in the seed bank of prairie soils (Travnicek et al., 2005), potentially increasing the resistance of weed populations to change. Finally, *Cirsium arvensis* has been noted to have high genetic diversity (Slotta et al., 2006), and our study sites could have contained different ecotypes of the weed that differ in competitive ability.

#### 4.2. Forage responses to varied defoliation

Accumulated forage yields responded to defoliation, fertilization and site, often in combination with one another. The greatest forage biomass generally occurred within the DEF, followed by the HILF and LIHF regimes, and then the HIHF treatment. Moreover, differences among treatments were consistent regardless of fertilization. Although evident during the first year, differences between treatments, particularly the HILF and LIHF regimes, became more pronounced in the second year, suggesting a cumulative effect of treatments to ongoing changes in forage vigor; positive in the HILF and DEF treatment, but negative in the HIHF.

Among treatments, DEF defoliation allowed for the longest uninterrupted rest period before initial defoliation and led to maximum forage accumulation. This result indicates that any defoliation during the growing season decreases total biomass, in turn accounting for the greater *C. arvensis* in plots defoliated at any point during the growing season. In contrast to the DEF, HIHF defoliation produced the lowest forage biomass during both years, particularly under fertilization. Intense, frequent defoliation apparently did not allow for pasture recovery adequate to sustain rapid growth. Associated increases in *C. arvensis* may have further stressed forage plants through high interspecific competition, enhancing the reduction of grass biomass previously documented due to the weed in the region (Grekul and Bork, 2004).

HILF defoliation generally led to greater forage biomass than the HIHF treatment. Although forage plants in both these treatments were cut to a 2-cm height at harvest, the extended rest period apparently enhanced plant regrowth. These results are consistent with other trials performed in similar vegetation in the region (Donkor et al., 2002), and suggest intermittent heavy defoliation may be sustainable when accompanied by long rest (Hormay and



**Fig. 1.** Hypothetical forage biomass growth curves (as % accumulated current annual standing biomass over time) for three contrasting forage community (CM) types that respond differently to utilization level as a result of varying rates of growth. The inflection point on each curve, denoted by an 'X', is the theoretical point at which the biomass remaining after defoliation is expected to result in the most rapid rate of regrowth for swards with rapid (CM A), moderate (CM B), and slow (CM C) initial growth rates.

Talbot, 1961). Notably, our data contradict recent suggestions that there is little benefit to plant production from the use of rotational grazing (i.e. intermittent defoliation) systems relative to continuous (i.e. HIHF) grazing (see Briske et al., 2008), and highlights the need for more research to elucidate the morpho-physiological mechanisms regulating forage growth.

Lower forage in the LIHF treatment relative to the HILF indicates that cumulative growth was affected by the combined intensity and frequency of defoliation. Moreover, because forage biomass in the HILF regime was greater at 2 of 3 sites by 2001, neighboring forage appeared more heavily dependent on (or sensitive to) defoliation frequency rather than intensity (i.e. clipping height). This finding contrasts the common notion that strict maximum use levels (e.g. 50–60%) are needed for pasture swards to maintain forage vigor and production (Bryan et al., 2000; Saul and Chapman, 2002), which in our study would have been met through the more conservative LIHF defoliation regime.

Although the mechanism responsible for the greater forage biomass in the HILF relative to the HIHF is unknown, one possible explanation is that HILF defoliation may maintain more rapid rates of vegetative growth. Dominant grasses in our study included smooth brome grass, quackgrass and Kentucky bluegrass, all of which have extensive underground rhizomes (Looman, 1983), characteristics that promote rapid regrowth and render these species tolerant of defoliation. Graber (1933) found increased harvest intensities of Kentucky bluegrass increased total season-long biomass removal, although that study did not examine the tradeoff between changes in defoliation frequency and intensity.

Infrequent defoliation within the HILF treatment, even at levels as high as 70% or more, may have resulted in the primary forage grasses maintaining a more rapid rate of growth (i.e. biomass gains near the inflection point of curve A in Fig. 1) throughout the growing season. We hypothesize that more favorable and sustained regrowth accounts for the greater herbage accumulated in HILF plots. In contrast, the more conservative but frequent defoliation within the LIHF regime may have been less effective at maintaining grasses in rapid stages of growth (Parsons et al., 1988) (e.g. at the middle rather than bottom of curve A in Fig. 1), in turn leading to less season-long herbage biomass accumulation. Despite the positive effect of HILF defoliation on herbage biomass documented here, similar results may not occur for plant communities less adapted to withstand or recover from infrequent but intense

defoliation (see alternative curves B and C in Fig. 1). For example, frequent and intense defoliation are known to reduce biomass in arid grasslands (e.g. Jacobs and Sheley, 1999), which may account for the observed variation in herbage responses among our study sites.

Differences in forage biomass among defoliation treatments may also have resulted from feedback associated with the improved decline in *C. arvensis* populations observed in the HILF treatment. Reduced *C. arvensis* would allow more resources to be utilized by neighboring forage plants. Moreover, increased forage production under HILF defoliation is supportive of grazing systems employing this regime, as short but intense periods of grazing are known to overcome animal selectivity (Popay and Field, 1996), and therefore lead to reductions in the abundance of weeds such as *C. arvensis* through direct grazing impacts (De Bruijn and Bork, 2006). Based on the results of the current study and previous work (De Bruijn and Bork, 2006), HILF grazing may therefore confer two benefits contributing to weed reduction, including direct weed control as well as competitive shifts in favor of forage plants, in turn maximizing weed suppression. Operating together, HILF grazing systems are more likely to result in greater overall weed control.

Trends in forage production among defoliation treatments remained similar regardless of fertility, although fertilization increased differences among defoliation treatments. These results suggest the utilization of added nutrients by forage is maximized within intermittently defoliated systems (e.g. the HILF). In contrast, slow growing plants in the HIHF system appear less able to make efficient use of those nutrients (Biswell and Weaver, 1933; Jameson, 1963; Evans, 1973), and instead are further subject to competition from neighboring weeds positively impacted by nutrient addition.

## 5. Conclusions

Our results indicate that the type of defoliation regime of neighboring vegetation is capable of altering the abundance of *C. arvensis* in cool-season temperate pastures, although the effectiveness of these impacts varied among study sites. These results were further supported by observed patterns of cumulative forage growth, which were opposite those of *C. arvensis* abundance, suggesting a role by the former in regulating the weed through interspecific competition. Among all treatments, delaying defoliation until late summer was most successful in suppressing *C. arvensis*, although this system requires rest from grazing for the entire summer and is therefore not feasible in areas managed for ongoing livestock production. Among systems employing summer grazing, HIHF defoliation consistently resulted in the lowest forage biomass and greatest *C. arvensis* abundance. Despite some inconsistencies among study sites, the temperate pastures examined here were well-adapted to tolerate intense defoliation provided a long recovery period was provided to facilitate rapid forage regrowth and maintain plant vigor, which in turn suppressed *C. arvensis* through interspecific competition. Thus, when DEF (deferred) grazing is not possible, the use of a HILF (high intensity – low frequency) defoliation regime may provide an alternative method to suppress *C. arvensis*, thereby reducing the need for more intensive weed control strategies.

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