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Mowing-Induced Changes in Soil Seed Banks and Populations of Plumeless Thistle (*Carduus acanthoides*) and Musk Thistle (*Carduus nutans*)

Philip W. Tipping*

Populations of plumeless thistle and musk thistle were mowed at various growth stages at two separate sites in Maryland during a 6-yr period to elucidate relationships among seed rain, soil seed banks, and population recruitment. The majority of seeds (96%) in the soil profile were distributed within 7.6 cm of the surface at both sites. Mowing plumeless thistle when most of the flower heads were at the full bud or postbloom stage did not reduce seed bank or plant densities, unlike mowing at full bloom, which significantly and quickly reduced both. Musk thistle responded differently, with plant density declining only with the postbloom mowing treatment, which occurred after the parent plant had dispersed seeds and died. Seed bank densities were unchanged by this treatment. This indicates that other factors may limit the recruitment and maintenance of musk thistle, such as allelochemical production by parents and interspecific plant competition. Density of musk thistle declined over an 11-yr period at one monitoring site, whereas plumeless thistle remained unchanged. The disproportionate seed-destroying activities of the weed biological control agent *Rhinocyllus conicus* on musk thistle may explain this difference.

Nomenclature: musk thistle, *Carduus nutans* Wienm. CRUNU; plumeless thistle, *Carduus acanthoides* L. CARAC.

Key words: Population dynamics, seed rain, seed bank dynamics.

Seeds dispersed from plants can contribute directly to the recruitment of the next generation or to future generations via storage in the soil seed bank. Seed storage in the soil maintains genetic inventories that permit species to exploit habitats that may be temporary or frequently disturbed (Auld and Denham 2006). It also serves as a hedge against local extinction in years of poor seed production or environmental stochasticity (Rogers and Hartnett 2001).

Consistent interceptions of the seed rain often do not result in concomitant reductions in subsequent plant populations because of physiological and environmental factors that may act in concert to prevent seed germination. Baskin and Baskin (2001) identified five general types of seed dormancy that extend the longevity of seed banks. Crawley (1990) suggested that plant recruitment is limited primarily by the lack of suitable germination sites (microsite limited) rather than by a lack of seeds (seed limited). Eriksson and Ehrlén (1992) suggested a more dynamic situation where both seed and microsite availability vary spatially and temporally, subject to factors such as dispersal, seed predation, or disturbance frequency.

Most studies on seed bank management have been conducted on arable land where, in the absence of seed inputs, the seed bank declines more rapidly with cultivation or herbicides than without them (Bridges and Walker 1985; Roberts and Neilson 1981; Schweizer and Zimdahl 1984; Warnes and Andersen 1984). In pastures, however, seed bank interactions with dormancy and spatial microsite variation remain poorly understood (Rice 1989).

I studied the response of musk thistle and plumeless thistle seed banks and plant populations to seed rain interruptions via mowing. These species are short-lived monocarpic perennials which can behave as annuals, winter annuals, or biennials

(Lacefield and Gray 1970; McCarty and Scifres 1969). They were introduced in North America in 1853 and 1878, respectively (Stuckey and Forsyth 1971), and they became serious weeds of pastures, rights-of-way, and natural areas in the United States and Canada (Desrochers et al. 1988; Dunn 1976). In Frederick County, Maryland, densities of musk thistle and plumeless thistle averaged 600 and 730 plants/ha respectively in pastures during 1989 (Tipping 1992).

The impetus for this study followed the collapse of a persistent (> 5-yr) monoculture of musk thistle after a mowing treatment in the fall of 1992. This was intended only to clear thistle debris from the 0.5-ha site where reproductive thistle densities often exceeded 10 plants/m² and bolting plants grew taller than 200 cm. Most bolted plants were dead when the site was mowed using a high-capacity rotary mower on September 30, 1992, and, unexpectedly, no thistles were found the next year despite extensive searching. Although a few plants were found in subsequent years during annual surveys conducted through 1999, the population never recovered.

The objective of this study was to evaluate the impact of phenologically based mowing regimes on thistle population dynamics in order to understand the population collapse at this site. However, the overall dearth of suitable musk thistle populations forced me to focus the experiment on the more common plumeless thistle. In addition to this research, I report thistle population trends at one long-term monitoring site.

Materials and Methods

Seed Distribution within the Soil Profile. In order to gain insight into the soil seed bank characteristics, I first investigated the vertical stratification of plumeless thistle seeds in the soil at two sites in Maryland: Fort Detrick and Corcoran. The Fort Detrick site was a 0.5-ha heavily grazed horse pasture with persistent populations of plumeless thistle

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and also a few musk thistles. This site contained a mixture of pasture grasses including goosegrass (*Eleusine indica* L. Gaertn.), orchardgrass (*Dactylis glomerata* L.), barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.], and timothy (*Phleum pratense* L.). Two other thistle species, bull thistle [*Cirsium vulgare* (Savi) Tenore] and Canada thistle [*Cirsium arvense* (L.) Scop.], were also present in low densities. The Corcoran farm site was located in a 5-ha fallow field with about a 5% slope with persistent populations of plumeless thistle. Musk thistle had disappeared from the site several years prior to the study.

Sixteen 6 by 15-m plots were established at each site and sampled in June 1993 and June 1994 by taking a 2-cm-diam soil core every 1 m within a permanent 1 by 15-m transect that bisected the long axis of each plot. The soil cores were separated into three depths: (1) soil litter to 2.5 cm, (2) 2.5 cm to 7.6 cm, and (3) 7.6 cm to 12.7 cm. Samples were spread over a bed of potting soil in flats, kept moist, and held in a greenhouse under ambient light, temperature, and humidity. Seedlings were identified, recorded, and removed. The soil was gently stirred after no new emergence for 30 d, and stirring and 30-d observation periods were repeated three separate times before samples were discarded.

Mowing Experiments. Vegetation in the same plots described above was subjected to four mowing treatments based on the phenology of plumeless thistle, namely mowing when the majority of plants were at the full bud, full bloom, or postbloom stage (four replicates). Controls were not mowed. Mowing was done using a high-capacity rotary mower that cut ca. 5 cm above the soil surface and thoroughly ground up the cut portions. The full bud and full bloom stages were represented when the earliest developing flower heads were in the bud and bloom stages, respectively. Plants in the postbloom stage had already released seeds, although small axillary flower heads were often blooming. Mowing at full bud and full bloom loosely corresponded to the spring and summer seasons, respectively, whereas the postbloom mowing was done during the fall. The fall mowing was intended to mimic the treatment originally applied at the site mentioned in the introduction.

Some of the mowing treatments for earlier developing musk thistle were confounded by the focus of the research on the phenology of plumeless thistle. For example, when plumeless thistle was mowed at the bud and bloom stages, musk thistle was typically in the bloom stage and postbloom stage, respectively. As a consequence there was no bud-stage mowing treatment for musk thistle. Instead the treatments were no mowing (control) and mowing at an early bloom stage, a later bloom stage, and a postbloom stage. Plants in the postbloom stage were usually dead when mowing was done in the fall.

The soil seed bank was estimated each spring prior to the first mowing treatment by collecting samples from each site and processing them as described previously with the vertical distribution study. Plant densities were recorded on the same day by counting all thistles present within the plots.

Long-Term Populations. Six sites with permanent transects were established in 1988 at various sites in central and western Maryland and monitored each year for thistle densities.

However, all the sites except one were eventually destroyed or corrupted by weed control activities like mowing or spraying. The surviving site was at Four Locks, an abandoned 24-ha corn field in Allegany County. Six transects, each measuring 1 m by 20 m, were surveyed each spring and the numbers of all thistles were recorded. Generally, both thistle species were in the seedling and rosette stages.

Statistical Analysis. The effects of the mowing treatments on the seed bank and populations of thistles were examined using analysis of covariance with the first year's density as the covariate (SAS 1990). Parameters were estimated as linear functions that were algebraically derived from model constraints using ESTIMATE statements (SAS 1990). Linear contrasts were devised to test the hypothesis that levels of each treatment were equal to the control. The seed distribution within the soil profile was examined using ANOVA and differences between sites were examined using two sample *t* tests. Long-term thistle density trends and the relationship between seed banks and plant populations were examined using general linear regression (SAS 1990). Values were transformed using square root transformation when variances were heterogeneous.

Results and Discussion

Seed Distribution within the Soil Profile. Plumeless thistle seeds were differentially distributed by depth ($P < 0.0001$). A mean of 98 and 96% of all germinable seed were found within 7.6 cm depth in the soil at Corcoran and Fort Detrick, respectively, over the 2 yr of the study (Figure 1). Although there was no influence of year or site, there was a significant interaction of site and depth ($P = 0.0004$). A higher percentage of seeds were buried deeper at the Fort Detrick site as compared with the Corcoran site (23.6% vs. 11.2% buried at least 2.5 cm; $P = 0.01$).

Differences in the vertical distribution of plumeless thistle seeds between the two sites may be symptomatic of site usage. Despite a large disparity between the seed bank and populations of plumeless thistle, there was close correlation in the trends at the Corcoran site where seed bank densities exhibited a strong concurrence with plant densities (Figure 2). This was not the case at Fort Detrick (Figure 2). The reasons for this are unknown, but the Corcoran site was fallow and undisturbed, unlike Fort Detrick, which was routinely grazed and highly disturbed. Seed dispersed in disturbed sites probably had a greater chance of being buried or exposed by grazing disturbances, a factor that may have contributed to the greater yearly variability in recruitment. Neither plumeless nor musk thistle seeds exhibit innate dormancy and will readily germinate when exposed to light and moisture (McCarty et al. 1969). Jutila (1998) found less concurrence between the seed bank and the aboveground vegetation in grazed compared with ungrazed pastures. Buhler and Mester (1991) found a greater percentage of weed seeds in the upper 1 cm of soil when soil disturbance was minimized using no-tillage methods as compared to conventional tillage.

Seeds that are more deeply buried are perhaps more protected but less likely to germinate (McCarty et al. 1969)

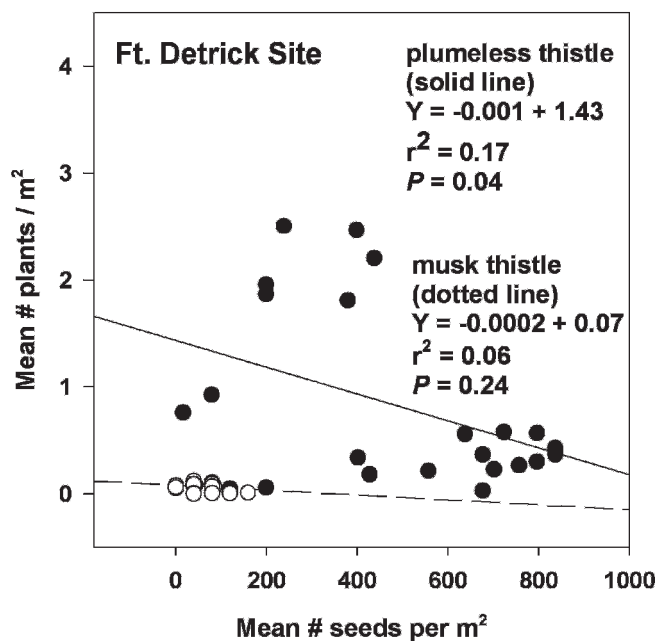
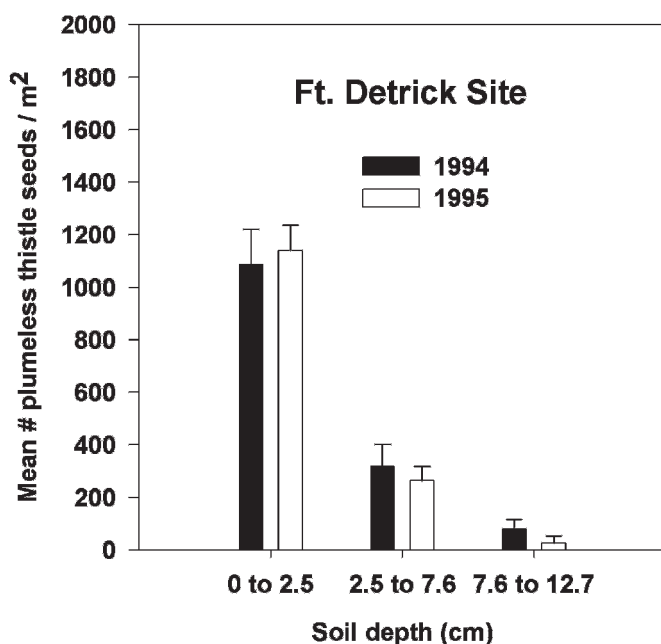
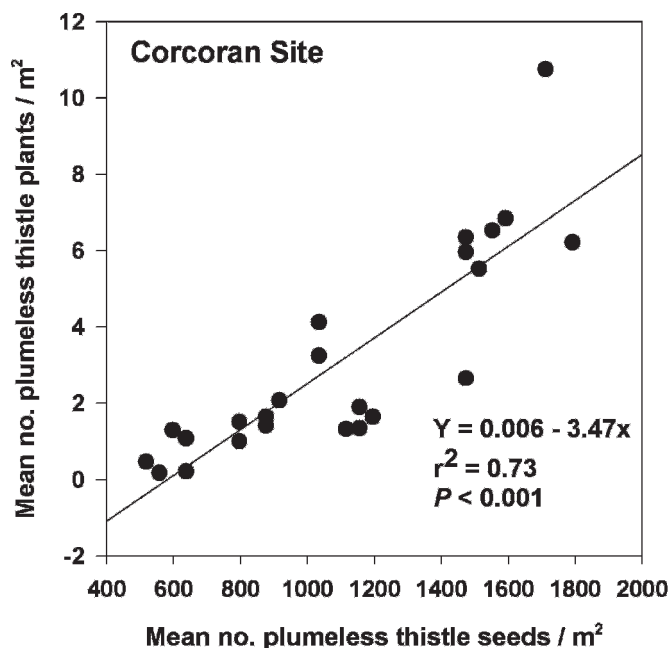
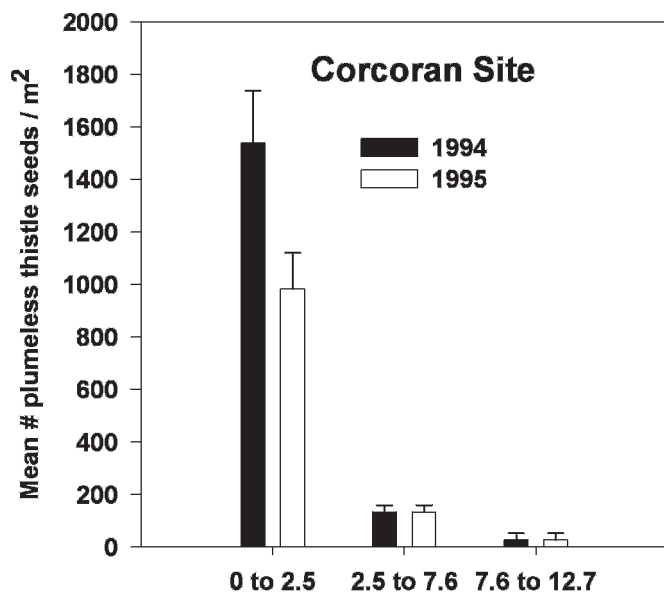


Figure 1. Mean (\pm SE) number of plumeless thistle seeds at various soil depths at two sites during 1994 and 1995.

and the deeper the burial, the longer the duration, probably as a result of enforced dormancy. McCarty et al. (1969) found no emergence for musk thistle seeds buried deeper than 5 cm and plumeless thistle seeds buried deeper than 4 cm. Burnside et al. (1996) found that 30% of musk thistle seed germinated after burial at 20 cm depth for 8 yr, indicating that enforced dormancy was present and acting to preserve a portion of the soil seed bank. Therefore, under the conditions found in this

Figure 2. Relationship between the soil seed bank and plant density of plumeless thistle at two sites subjected to phenologically based mowing regimes from 1994 to 1999.

study, a larger reservoir of deeply buried seeds would be expected at the more disturbed Fort Detrick site. This may also explain why musk thistle is now found closely associated only with very highly disturbed habitats such groundhog (*Marmota monax*) burrows (P. W. Tipping, personal observation).

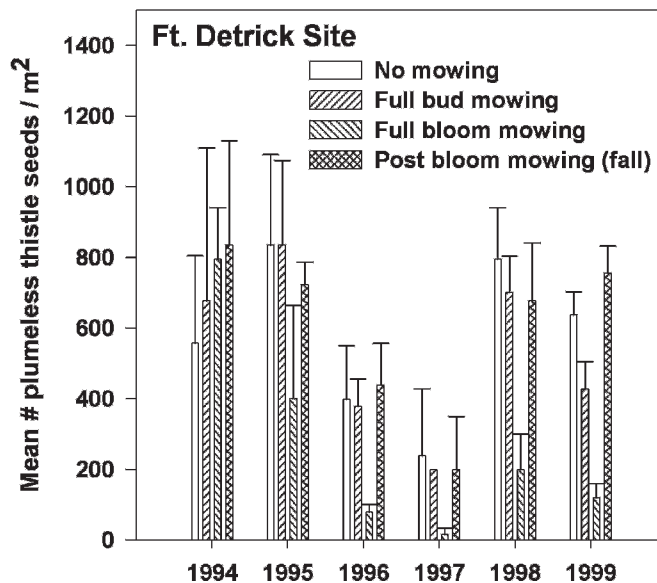
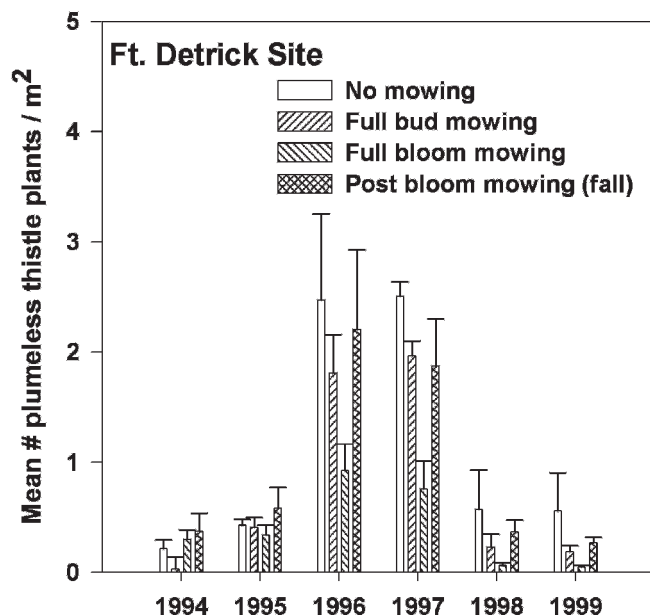
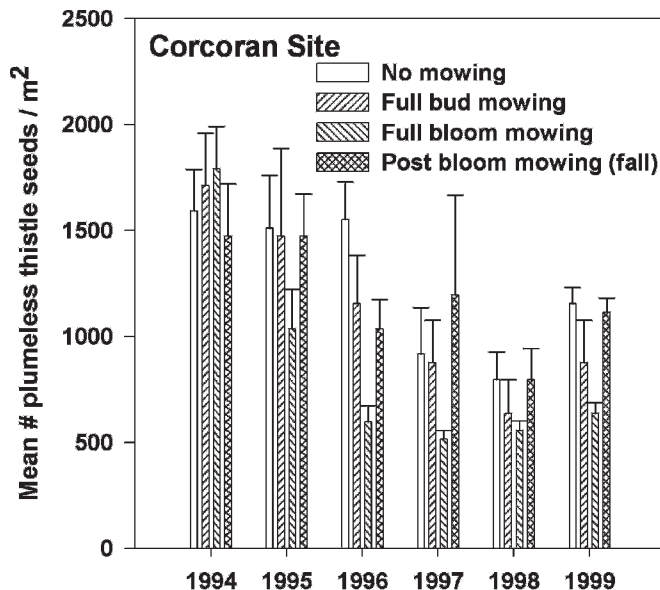
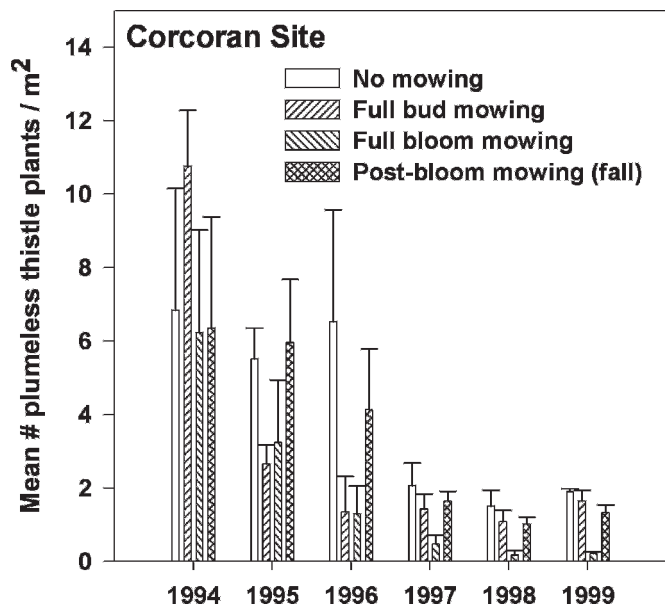


Figure 3. Mean (\pm SE) number of plumeless thistle plants in plots at two sites subjected to phenologically based mowing regimes from 1994 to 1999.

Figure 4. Mean (\pm SE) number of plumeless thistle seeds in the soil bank at two sites subjected to phenologically based mowing regimes from 1994 to 1999.

Overall, plant densities were relatively low given the belowground estimates of germinable seed. Generally, the relationship between the soil seed bank and plant populations is weak and unpredictable (Cardina and Sparrow 1996). Roberts and Ricketts (1979) found that total seedling numbers represented 3 to 6% of the numbers of seeds in a cultivated soil. In this study the percentage was 0.3% for

plumeless thistle and 0.05% for musk thistle (data not shown) despite the preponderance of seeds in shallow locations, which would potentially make them available for germination. However, this shallow placement also makes them vulnerable to increased aging and predation (Ballaré et al. 1988; Sheppard et al. 1989; van Esso et al. 1986). Crawley (1992) pointed out that many studies on postdispersal seed herbivory have recorded losses approaching 100%. McCallum and Kelly

Table 1. Parameter estimates (regression coefficients) of the differences between phenological mowing treatments and the control treatment for the soil seed bank and plant densities of plumeless thistle and musk thistle at two sites.^a

Contrast with control	Corcoran site		Fort Detrick site	
	Seeds/m ²	Plants/m ²	Seeds/m ²	Plants/m ²
Plumeless thistle				
Full bud	-131.11 (127.55)	-1.44 (0.79)	-183.12 (117.56)	-0.20 (0.17)
Full bloom	-392.71 (127.00)**	-1.94 (0.79)**	-219.86 (102.15)*	-0.71 (0.15)**
Postbloom	-74.80 (121.07)	-0.57 (0.75)	-1.11 (118.34)	-0.11 (0.18)
Musk thistle				
Early bloom	n/a	n/a	-18.00 (30.11)	0.006 (0.01)
Late bloom	n/a	n/a	-10.48 (26.16)	-0.007 (0.01)
Postbloom	n/a	n/a	42.80 (30.31)	-0.04 (0.01)**

^a Values in parenthesis are the standard error of the mean.

* Denotes 0.05 significance levels for specified contrasts to the control treatment.

** Denotes 0.01 significance levels for specified contrasts to the control treatment.

(1990) estimated that postdispersal seed predation resulted in the destruction of 85% of the musk thistle seed that reached the ground. However, seed predation, although undoubtedly contributing to the general depletion of the seed bank, does not explain the disparity between above- and belowground populations because both were recorded on the same day.

Therefore, other localized factors may constrain germination, including the availability of germination microsites (Eriksson and Ehrlén 1992), soil type, environmental influences (DeJong and Klinkhamer 1998), and interspecific competition (Fenner 1978).

Impact of Mowing on Plumeless Thistle. Plant density differed at each site so sites were analyzed separately. The effect of year was the most important influence at both sites on the number of plants/m² ($P < 0.0001$ for both Corcoran and Fort Detrick). This was followed by the effect of the mowing treatment ($P = 0.0037$ and $P < 0.0001$ for Corcoran and Fort Detrick, respectively) (Figure 3). The same outcomes were present for the number of seeds/m² in the seed bank (Figure 4).

Mowing plumeless thistle at full bud did not reduce seed bank or plant densities (Table 1) because plants often regrew before the hotter, dryer conditions of full summer and produced and dispersed seeds. However, there was a full bloom-stage mowing effect on plumeless thistle at both sites for seed and plant densities (Table 1). Although plants mowed at full bloom also regrew, environmental conditions were less favorable resulting in shorter plants with only a few flower heads. Mowing at the postbloom stage had no effect on either above- or belowground components of the plumeless thistle populations (Table 1).

Impact of Mowing on Musk Thistle. Unlike plumeless thistle, mowing in the fall when the plants were dead caused significant declines in musk thistle densities at Fort Detrick (Table 1). This occurred despite a predictable lack of a corresponding decline in soil bank seed density (Table 1). Mowing this species at any other time had no effect on soil seed bank and seedling numbers (Figure 5).

Factors other than seed rain seem to play a larger role in the regulation of musk thistle, which showed no response to

mowing except after the parent plant had produced and dispersed seed and died. Seedlings are poor competitors (Allard 1965) and may benefit from some protection provided by parents when they are recruited in close association. When the fall mowing treatment removed these decaying parents, any physical and allelopathic protection they may have provided was eliminated, thereby allowing cool-season grasses to outcompete seedlings. Wardle et al. (1993) proposed that musk thistle was allelopathic while mature plants were dying and the decaying thistle tissue stimulated seedlings.

Plant litter can influence the colonization of the next generation of plant species at a site although the mechanisms are not always clear (Bergelson 1991; Facelli and Pickett 1991). Sauer (1978) suggested that the standing dead culms and leaves of *Agropyron spicatum* (Pursch) Scribn. & J. G. Sm. provided a physical shelter for new growth. Musk thistle is recruited primarily in the fall in the Mid-Atlantic region of the United States when parental litter is relatively intact, whereas plumeless thistle is recruited primarily in the spring when parental litter has largely degraded. Therefore, if the presence of parental litter is linked to increased seedling survival in musk thistle, then fall mowing should influence recruitment in musk but not plumeless thistle. In this study, interspecific competition, perhaps mediated by allelochemic or physical factors, may explain why musk thistle densities declined under this treatment, but more research is needed on this question.

Long-Term Population Trends. Musk thistle density declined over 11 yr at the Four Locks site to very low levels, while plumeless thistle density remained unchanged (Figure 6). Thistle population trends at this site were representative of landscape-level trends throughout central and western Maryland during the same period (P. W. Tipping, personal observation). During this time period, there were no significant changes in land use patterns, no introductions of novel herbicides, and no expansions of county weed control programs. One possible explanation for the decline of musk thistle but not plumeless thistle was herbivory by *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae), a classical weed biological-control agent that routinely destroyed a portion of the seed crop of musk thistle every year. Plumeless thistle

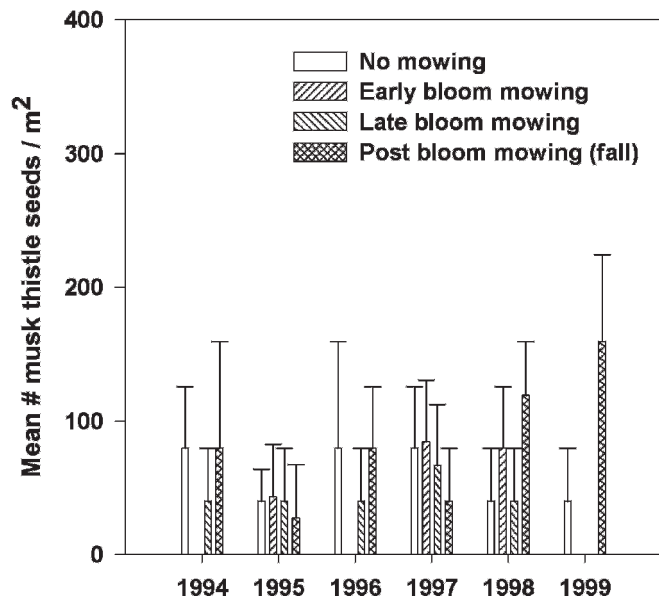
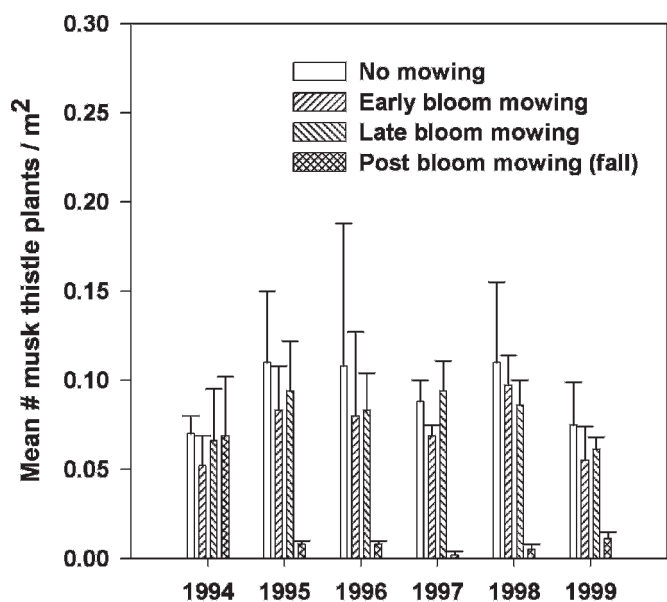


Figure 5. Mean (\pm SE) number of musk thistle seeds in the soil seed bank and plants in plots at the Fort Detrick site subjected to phenologically based mowing regimes from 1994 to 1999.

largely escapes attack by this species because of phenology. This weevil was first introduced into the Maryland area in 1975 and by 1988 had achieved densities of 15.2 and 15.5 larvae per primary seed head in Frederick and Washington counties, respectively (Tipping and Hight 1989). Consistent landscape-level reductions in annual seed rain, coupled with a short-lived soil seed bank, should logically reduce populations except in more disturbed areas with reduced interspecific

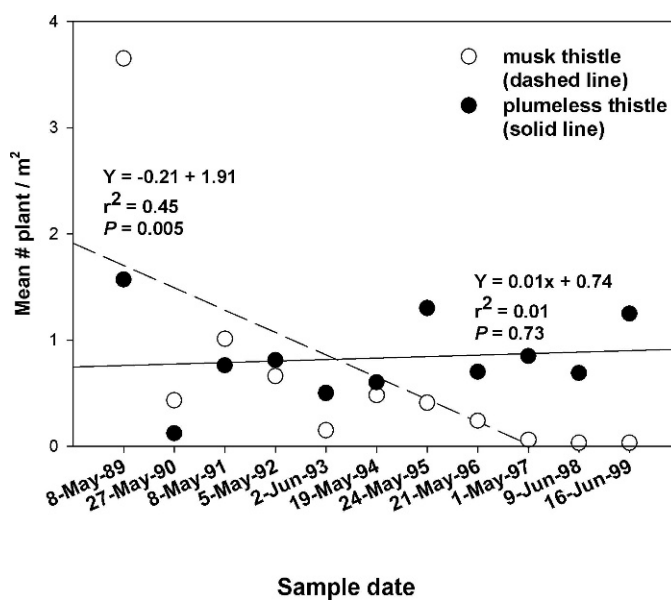


Figure 6. Population density trends for plumeless and musk thistle at the Four Locks site from 1989 to 1999.

competition. Jongejans et al. (2006) found that seed production is a key factor in the population dynamics of musk thistle in its native range.

As mentioned in the introduction, there was no recovery of musk thistle populations at the site that stimulated this research. One explanation is that the annual reproductive population of thistles was recruited predominately by the seed crop produced in the same year which, despite reductions from *R. conicus*, was sufficient to maintain the population as long as interspecific plant competition was suppressed. This suppression may have been provided by the parents that attained some critical mass of size and density thereby providing crucial advantages to the next generation through enhanced seedling survival. However, once this parental biomass was removed via mowing, interspecific plant competition overwhelmed the less-competitive seedlings. The end result was a sudden and dramatic reduction in musk thistle populations to a point where recovery seems unlikely without the agency of disturbance. The events that took place at this site may describe a process whereby a normally fugitive species such as musk thistle gains tenure at a site through mechanisms that confer significant and localized survival advantages to the next generation of their progeny. A 7-yr study with plumeless thistle also showed a higher proportion of recruitment in close association with parents (Jongejans et al. 2007).

Therefore, although direct reduction of seed rain can immediately reduce the seed banks of both species, additional factors such as plant competition and allelopathy may play important roles in the regulation of aboveground thistle populations, especially with musk thistle. The elucidation of these factors and their interaction may expand control options, as well as provide insight into the mechanisms of establishment and spread of invasive plant species.

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