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Effects of Seedling Emergence Timing on the Population Dynamics of Horseweed (*Conyza canadensis* var. *canadensis*)

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Horseweed is a surface-germinating ruderal facultative winter annual. The ruderal nature is a key adaptive characteristic that implicates emergence timing as an important recruitment factor. Experiments were established at three sites in southern Ontario, Canada, from 2009 to 2012 to determine the possible effect of emergence timing of horseweed on plant number, fecundity, and flowering timing. Emerged seedlings were tagged in 0.25-m^2 plots in five 2-wk cohorts in the fall and spring of each experimental season. Each plot was followed though until the plants contained within each plot completed their life cycle. Generally, spring-emerging plants were found to flower earlier than fall-emerging plants, but with fall emergence there were higher plant densities in August each season compared with spring emergence. Overall, there was no difference in fecundity between spring- or fall-emerging cohorts, but when cohorts were parsed beyond just spring or fall emergence, we found that plants emerging in early fall and early spring were more fecund and flowered earlier than plants emerging in late fall and late spring. Disturbance (tilled versus not-tilled) significantly affected emergence levels but not emergence timing. The differences in performance among emergence cohorts are likely due to spatial or temporal density-dependent growth advantages. These results show that spring-emerging cohorts of horseweed, especially early spring–emerging cohorts, should not be discounted when considering the weediness of this species, and this may hold true for other facultative winter annual weeds as well.

Nomenclature: Horseweed, *Conyza canadensis* (L.) Cronq. var. *canadensis*.

Key words: Canada fleabane, Facultative winter annuals, germination timing, recruitment.

Understanding the population dynamics of facultative winter annual weeds such as horseweed can provide insight into their recruitment nature and guide management approaches. Facultative winter annual weeds can emerge mostly in the fall, mostly in the spring, or equally in both seasons (Cici and Van Acker 2009). Horseweed is a surface-germinating ruderal facultative winter annual with recruitment that is highly susceptible to changes in microsite conditions (Buhler and Owen 1997; Grime 1977; Main et al. 2006; Nandula et al. 2006; Regehr and Bazzaz 1979).

Horseweed flowers and sets seed in late summer, with some seed germinating and forming an overwintering rosette, and other seed persisting and germinating in the spring of the following year (Regehr and Bazzaz 1979; Weaver 2001). The lack of dormancy within the seed suggests that microsite conditions play a significant role in the persistence and emergence timing of horseweed (Regehr and Bazzaz 1979; Weaver 2001). The ability to germinate in spring or fall highlights how important our understanding of microsite factors are to the relative success of this species, its competitiveness in certain farming systems (e.g., tilled vs. no-till systems), and the approaches and timing for management.

Horseweed plants may produce thousands of florets, with most florets containing 30 to 50 seeds each (Regehr and Bazzaz 1979; Weaver 2001). Each seed has a pappus, a fan-like structure that aids seed dispersal by wind. The seed morphology impacts the population dynamics of horseweed since wind dispersal mechanisms have promoted the recruitment of seeds both locally and globally (Dauer et al. 2007).

Observations on the emergence timing of horseweed have shown that it may emerge at any time in a season so long as recruitment conditions are suitable (Nandula et al. 2006). The continual emergence of horseweed is possible because of the lack of seed dormancy (Nandula et al. 2006).

Effects of emergence timing on individual plant performance affect density-dependent population growth given that intraspecific and interspecific interactions play a significant role in the population dynamics of all plant species including winter annuals (Donohue et al. 2005). Rees et al. (1996), for example, showed that for winter annual species, in the majority of scenarios, population size would increase by a factor of 1.5 if interactions between individuals were minimized. Van Acker and Cici

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(2012) found that in a comparison of spring- vs. fall-field pennycress (*Thlaspi arvense* L.) and shepherd's-purse [*Capsella bursa-pastoris* (L.) Medik.], spring-emerging cohorts produced earlier flowering plants. Donohue et al. (2005) found that germination timing can be a critical adaptation driving the adaptive evolution of genotypes in new locations and that the rate at which species expand their geographic range may be strongly influenced by the rate of evolution of emergence timing in winter annuals.

Differences in performance between spring- and fall-emerging cohorts of horseweed have been studied to a very limited extent. Studies to date suggest that spring emergence occurs for less than one-third of shed seeds and that the spring cohort of seedlings do not form rosettes (Buhler and Owen 1997, Michigan). Regehr and Bazzaz (1979) are alone in having published research on this. They suggested that spring-emerging horseweed may not form a rosette, and they reported that for horseweed populations from the U.S. Midwest, spring-emerging plants produce less seed and seed with lower longevity, while seed from fall-emerging plants experiences higher mortality, but individual fall-emerging plants produce more seed per plant.

Time of emergence may play a significant role in the population dynamics of horseweed, yet the influence of emergence timing on the performance of horseweed has been investigated to a very limited extent. The objective of this study is to explore the effect of emergence timing of horseweed on fecundity, plant density, and flowering timing. This study will allow us to gain a deeper understanding of the population dynamics, recruitment nature, and biology of winter annuals in general, and horseweed specifically. The results of this work will also provide information to help us to better manage this important weed species.

Materials and Methods

Experiments were conducted at three locations and followed for three winter annual (late summer through to following summer) growing seasons (2009 to 2010, 2010 to 2011, 2011 to 2012) in a northern region of North America; south-central Ontario, Canada (Woodstock, Simcoe, and Guelph). The Woodstock site was a Guelph Loam series soil (Gray Brown Luvisol) containing 35% sand, 52% silt, 13% clay, and 3.6% organic matter, with a pH of 6.4. The Simcoe site was situated on a Berrien sandy-loam soil containing 55% sand, 30% silt, and 15% clay, 1.93% organic matter, with a pH of 6.8. The Guelph site was situated on a very fine sandy loam soil containing 55 to 60% sand, 28 to 34% silt, and 10 to 11% clay with a neutral pH. The horseweed infestations at each of these existed previously and were not augmented for this study.

Emergence Timing. At each site, ten 0.25-m^2 quadrats were marked as observational plots. Plot locations were randomly selected by placing a grid over the observational area and using a random number generator to select the location of each plot on the grid. To characterize emergence timing we counted seedlings at each site once per week from Julian week 34 (August 26 to September 8) to Julian week 47 (November 19 to 25) in the fall and from Julian week 15 (April 9 to 16) to Julian week 24 (June 4 to 17) in the spring. No seedlings were removed once counted. The same plots were followed through all three seasons in order to monitor changes in the populations over time.

To investigate the role of soil disturbance in emergence, half (five) of the plots at each site were disturbed by hand tillage and the other half were left undisturbed. Disturbance treatments occurred once each season in Julian week 33 (August 13 to 19) just as new horseweed seed for the given year was starting to be shed and just before emergence counts started for a given season. For the disturbance treatments we used a hand rake to till each plot (three to four rakings in each of two directions in each plot) to a depth of 3 to 4 cm. Disturbance treatments were aggressive enough to eliminate existing vegetation in each plot each season.

Cohorts. To facilitate data analysis and interpretation, the emergence data were classified into emergence timing cohorts. A total of 10 cohorts per winter annual season were classified, and each emergence cohort covered a 2-wk emergence period. The five fall cohorts ran from August 26 to September 8, September 9 to 22, September 23 to October 6, October 7 to 20, and October 21 to November 3 each year. The five spring cohorts ran from April 9 to 22, April 23 to May 6, May 7 to 20, May 21 to June 3, and June 4 to 17 each year. The key performance measures we included in the study were survival of emerged seedlings, flowering timing, and fecundity. Survival (plant number/plot) was the number of horseweed plants at any stage of development (rosettes, seedlings, bolting, etc.) present in each plot in August of the following year. Given the indeterminate nature of horseweed, flowering timing was recorded as Julian week of first seed shed for five plants at each site for each

Table 1. The effect of emergence timing on flowering timing (Julian calendar week when first seed shed occurred) of horseweed. Results represent pooled data for either tilled or not-tilled plots and for three sites in southern Ontario, Canada collected within three individual seasons (2009 to 2010, 2010 to 2011, 2011 to 2012).

Cohort[a]	Flowering timing[b]
	week
5 (June 4–17)	38.6 e
5 (October 20–November 3)	38.4 e
4 (May 21–June 3)	37.6 d
4 (October 6–20)	37.5 d
3 (May 7–20)	35.4 c
3 (September 22–October 6)	35.5 c
2 (April 23–May 6)	35.1 bc
1 (April 9–22)	35.0 abc
2 (September 8–22)	34.6 ab
1 (August 26–September 8)	34.5 a

[a] Numbers represent numbered cohort order for each season.
[b] Means within columns followed by different letters denote significant differences at $P < 0.05$ according to Tukey's HSD.

Table 2. The effect of emergence timing (cohort) on the fecundity of horseweed. Results represent pooled data for either tilled or not-tilled plots and three sites in southern Ontario, Canada collected within three individual seasons (2009 to 2010, 2010 to 2011, 2011 to 2012).

Cohort[a]	Fecundity[b]
	capitula/plant
5 (October 20–November 3)	635.8 a
5 (June 4–17)	644.9 a
4 (October 6–20)	754.4 b
4 (May 21–June 3)	771.2 b
3 (May 7–20)	888.06 c
3 (September 22–October 6)	906.42 cd
2 (April 23–May 6)	982.5 cde
2 (September 8–22)	995.6 de
1 (April 9–22)	996.0 de
1 (August 26–September 8)	1008.8 e

[a] Numbers represent numbered cohort order for each season.
[b] Means within columns followed by different letters denote significant differences at $P < 0.05$ according to Tukey's HSD.

cohort (plants were chosen randomly from among the plots at each site and tagged using colored paper clips with a specific color designating a particular cohort). Fecundity was measured by multiplying the average number of seeds per flower by the number of flower heads on each tagged plant (these counts were done just prior to tillage treatments). Average number of seeds per flower was determined by counting the number of seeds per capitula in 50 capitula from 10 surviving plants chosen at random at each site each year. For this study the average number of seeds per flower was 46.

Statistical Analysis. Statistical analysis of data was conducted using JMP 10.0.2 software (SAS Institute 2010, SAS Campus Drive, Cary, NC 27513, SAS Institute, Inc.). All data were subjected to an ANOVA using a repeated measures linear mixed effects model with year (random), site (random), season (fall vs. spring) (random), cohort (random), and till/no-till (fixed) as factors, and with replication nested in site for fecundity (capitula/plant), plant number (in each 0.25-m^2 plot), and flowering date (Julian week of first seed shed). On the basis of an examination of residual plots, data were deemed to meet the assumptions of ANOVA including homogeneity of variance. In all cases, means were considered to be significantly different on the basis of $P < 0.05$.

Results and Discussion

In a comparison of spring vs. fall emergence cohorts, spring-emerging horseweed plants flowered significantly earlier than fall-emerging plants (ANOVA, F ratio $= 5.39$, $P < 0.0203$, df $= 1$, $n =$ 1,699) (Table 1). Spring-emerging plants rarely pass through a rosette phase like their fall-emerging counterparts, resulting in less time and energy spent in the seedling stage (Buhler and Owen 1997). This ability enables a shorter time to bolting and flowering while not affecting fecundity per plant and, in fact, fecundity per plant was not significantly different between spring- and fall-emerging plants (ANOVA, F ratio $= 0.099$, $P < 0.7529$, df $= 1$, $n = 1{,}699$, Table 2).

When emergence timing was parsed beyond spring or fall we found that horseweed plants emerging in early fall and early spring were more fecund and flowered earlier than plants emerging in late fall and late spring. This effect was consistent in all three seasons, at all sites, and under both tilled and not-tilled conditions (Tables 1 and 2). Early-emerging plants, either fall or spring emerging, were visibly larger and taller than plants that emerged later (either in fall or spring) (personal observation). Previous studies have shown that plant height may be exponentially related to fecundity in horseweed (Dauer et al. 2008; Regehr and Bazzaz 1979). Due to the single stalk morphology and ruderal nature of horseweed, adaptations for optimizations of high dispersal and high fecundity in a relatively short lifespan directly correlate plant height with biomass (Dauer et al. 2008). These results show that horseweed plants that have an early start, either in spring or fall, are more likely to produce more seed. For fall-emerging plants, late fall emergence may

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Table 3. The effect of emergence timing on the survival (%) of horseweed plants in August. Results represent data pooled for tilled and not-tilled plots and for three sites in southern Ontario, Canada.

No till						Till					
2009–2010		2010–2011		2011–2012		2009–2010		2010–2011		2011–2012	
Cohort[a]	Survival[b] (mean %)	Cohort	Survival (mean %)	Cohort	Survival (mean %)	Cohort	Survival (mean %)	Cohort	Survival (mean %)	Cohort	Survival (mean %)
1 (August 26–September 8)	94 a	1 (August 26–September 8)	90 a	1 (August 26–September 8)	90 a	1 (August 26–September 8)	94.6 a	1 (August 26–September 8)	87.2 a	2 (September 8–22)	92.6 a
2 (April 23–May 6)	90.6 a	2 (September 8–22)	82 ab	2 (September 8–22)	88 ab	5 (October 20–November 3)	90.6 ab	5 (October 20–November 3)	86.6 a	1 (August 26–September 8)	90 a
2 (September 8–22)	90.6 a	3 (September 22–October 6)	78.6 ab	3 (September 22–October 6)	71.2 bc	2 (September 8–22)	89.2 abc	2 (September 8–22)	84.6 a	1 (April 9–22)	84.6 ab
3 (September 22–October 6)	86.6 a	2 (April 23–May 6)	77.2 ab	2 (April 23–May 6)	70 c	1 (April 9–22)	88.6 abc	2 (April 23–May 6)	83.2 a	2 (April 23–May 6)	82 ab
1 (April 9–22)	84.6 a	1 (April 9–22)	70.6 b	1 (April 9–22)	69.2 c	2 (April 23–May 6)	87.2 abc	3 (May 7–20)	78 ab	5 (October 20–November 3)	76.6 abc
3 (May 7–20)	82.6 a	3 (May 7–20)	68.6 b	3 (May 7–20)	54.6 cd	3 (September 22–October 6)	86.6 abc	1 (April 9–22)	77.2 ab	3 (September 22–October 6)	71.2 bc
4 (May 21–June 3)	56.6 b	4 (October 6–20)	47.2 c	4 (October 6–20)	48.6 d	3 (May 7–20)	78 bc	3 (September 22–October 6)	75.2 abc	5 (June 4–17)	68.6 bc
4 (October 6–20)	56.6 b	4 (May 21–June 3)	44 c	4 (May 21–June 3)	41.2 d	4 (October 6–20)	75.2 cd	5 (June 4–17)	71.2 abc	3 (May 7–20)	59.2 c
5 (June 4–17)	14.6 c	5 (October 20–November 3)	13.2 d	5 (June 4–17)	17.2 e	4 (May 21–June 3)	64 d	4 (October 6–20)	64.6 bc	4 (October 6–20)	32.6 d
5 (October 20–November 3)	9.6 c	5 (June 4–17)	12 d	5 (October 20–November 3)	16.6 e	5 (June 4–17)	50 e	4 (May 21–June 3)	59.2 c	4 (May 21–June 3)	30.6 d

[a] Numbers represent numbered cohort order for each season.
[b] Means within columns followed by different letters denote significant differences at $P < 0.05$ according to Tukey's HSD.

not allow for the formation of robust rosettes. The formation of a rosette helps reduce overwintering mortality in horseweed in spring (Main et al. 2006; Regehr and Bazzaz 1979). Plants emerging in the late fall and spring are also subjected to more competition, including intraspecific competition, which can lead to reduced fecundity and greater mortality (Grime 1977; Main et al. 2006). In this study we also found that earlier emerging cohorts of horseweed had significantly higher survival (Table 3). This effect may be related to density-dependent competition as well as accumulated biomass.

The shortened time to flowering for late-emerging plants (either fall or spring) may indicate a set time in each season for flowering if growth requirements are met ad libitum. A 4- to 6-month period after the beginning of bolting has been observed as the time it takes to reach full reproductive maturity for horseweed (Regehr and Bazazz 1979), but maximum flowering timing, in general, for horseweed in southern Ontario is early August (personal observation). Other potential factors influencing the relationship between emergence timing and flowering timing may be lack of nutrients required to maximize growth or reproduction. In this case, most plants have physiological mechanisms designed to cut their losses and promote flowering to maximize fitness. Some horseweed plants, for instance, have been observed to flower at a height of only 10 cm, reinforcing the notion of resource-limiting induction of reproduction (personal observation). Day length and light intensity may also play a factor in time to flowering although no studies have been conducted on the effect of daylength or light quantity on the flowering timing of horseweed. Cohorts of horseweed emerging in the late fall and late spring may be experiencing either the set time to flowering or resource limitations because both cohorts reach bolting stage at later dates than their earlier emerging counterparts. Some studies suggest bolting in this species is not directly related to daylength (e.g., Nandula et al. 2006). If this was the case, most plants would bolt around the same period each year. Instead, we observed that plants bolted after ~6 wk of growth, regardless of rosette or seedling size. Our results suggests that horseweed plants that emerge earlier have a greater chance of bolting earlier, leading to possibly significant competitive advantages.

In the sites we used for this study, more horseweed seedlings emerged in the fall vs. the spring (Figure 1). Over all factors, peak plant emergence occurred between August 27 and September 9 (112.1 plants/

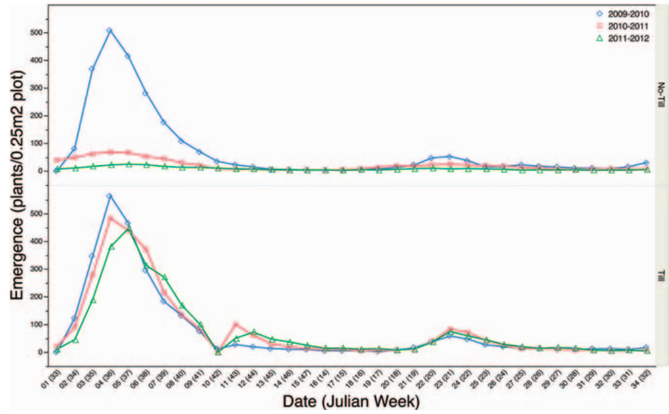

Figure 1. Observed emerging timing for horseweed seedlings in tilled or no-tilled plots over three winter annual seasons in southern Ontario, Canada.

0.25 m^2) and May 14 and May 27 (10.44 plants/ 0.25 m^2) of each season (Figure 1). This result represents a significant (order of magnitude) difference in the proportionality of horseweed emergence when comparing spring vs. fall emergence levels and compares to previous findings of 5 to 32% spring emergence (Buhler and Owen 1997).

Disturbance. Disturbance (tilled vs. not-tilled) significantly affected emergence levels but not emergence timing (Figure 1; Table 3). In the tilled plots emergence levels were very similar (almost identical) among the three seasons, while in the plots that were not tilled the total emergence density dropped significantly in seasons 2 and 3 (2010 to 2011 and 2011 to 2012) versus season 1 (2009 to 2010). This result may be due to the early effects of succession and competition. Without tillage, other competitive plants (including mature horseweed plants) likely reduced the recruitment opportunities for horseweed. Horseweed is a ruderal species and therefore is inherently a first colonizer to new available microsites favorable to germination (Weaver 2001). Over time, horseweed can lose favorable recruitment microsites to other weeds including hardier winter annuals and perennials such as common chickweed [*Stellaria media* (L.) Vill.] and Canada thistle (*Cirsium arvense* L.), respectively (personal observation). Even with the formation of a rosette in the winter, to create a competitive advantage in the spring, horseweed is eventually subjected to high density-dependent competition factors, and recruitment is subsequently reduced. In the tilled plots the tillage removed other competing plants each season, reducing barriers to recruitment. In addition, tillage creates favorable recruitment microsites for ruderal species (Brown and Whitwell 1988).

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The lack of a significant differences overall in fecundity between fall- and spring-emerging plants, but the significant differences between early- and late-emerging plants within spring or fall cohorts, is a unique and important result not only for horseweed but perhaps for other facultative winter annual weeds. It confirms that emergence timing is an important factor affecting the performance of horseweed, but it also shows that fall-emerging plants do not necessarily outperform spring-emerging plants. This may have broader implications in studies that have chosen to compare only fall- vs. spring-emerging cohorts of facultative winter annual weeds (Buhler and Owen 1997; Dauer et al. 2007; Regehr and Bazzaz 1979). It also has implications for the characterization, modeling, and prediction of population performance for horseweed and perhaps other facultative winter annuals.

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