

Henbit (*Lamium amplexicaule*), Common Chickweed (*Stellaria media*), Shepherd's-Purse (*Capsella bursa-pastoris*), and Field Pennycress (*Thlaspi arvense*): Fecundity, Seed Dispersal, Dormancy, and Emergence

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Winter annual weeds protect the soil from erosion and retain nutrients during the winter; however, they can also act as a host for crop pests and pathogens and impede planting. Increased knowledge of the reproductive biology and the seed fate of winter annuals would be useful to improve management and crop productivity. The objectives of this research were to determine the recruitment biology of shepherd's-purse, henbit, common chickweed, and field pennycress, including seed production, dispersal, dormancy, and seedling emergence, based on growing degree days (GDD). Henbit was the least prolific of the four weeds studied, producing 800 to 40,000 seeds m^{-2} at naturally occurring densities; shepherd's-purse was the most prolific, producing 11,000 to 400,000 seeds m^{-2} with 40 to 230 plants m^{-2} . Fifty percent seed rain occurred for henbit, common chickweed, shepherd's-purse, and field pennycress at 620, 790, 880, and 1300 GDD_{Base,0C}, respectively. Overall, seeds were dormant for all species at the time of dispersal. In 2 of 3 yr, dormancy of later-dispersed common chickweed decreased after 6 mo of storage at natural, fluctuating temperatures in the absence of water. The emergence patterns of the four species followed the Gompertz equation and were indicative of facultative winter annuals. The emergence patterns by rate were similar between henbit and common chickweed and between shepherd's-purse and field pennycress. Seed production, dispersal, dormancy, and seedling emergence were influenced by moisture; therefore, including a precipitation or soil moisture component into a GDD model (such as the use of hydrothermal time) would improve the accuracy of predicting winter annual reproduction, seed fate, and emergence.

Nomenclature: Common chickweed, *Stellaria media* (L.) Vill. STEME; field pennycress, *Thlaspi arvense* L. THLAR; henbit, *Lamium amplexicaule* L. LAMAM; Shepherd's-purse, *Capsella bursa-pastoris* (L.) Medik. CAPBP.

Key words: Dormancy, longevity, emergence, fecundity, recruitment, recruitment biology, seed rain.

The increase in winter annual weed growth over the past decade has been attributed to the adoption of conservation tillage practices (42% of the acreage in the United States lacks substantial soil disturbance [CTIC 2008]), a reduction in residual herbicide use in glyphosate-resistant crops, and milder winters (Cici and Van Acker 2009; Güeli and Smeda 2001; Krausz et al. 2003). Moderated temperatures through the winter months and in spring have influenced winter annual weed growth and development in the spring, resulting in greater weed biomass and seed development at the time of corn (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.] planting (Krausz et al. 2003). Winter annuals can serve as a cover, protecting the soil from erosion, and capturing nutrients that have not

been used by the crop. However, winter annuals can also be detrimental to crop production by impeding planting or serving as alternate hosts for pests and diseases (Crech et al. 2007; Mock et al. 2010; Nelson et al. 2006). For example, common chickweed is a host for black cutworm (*Agrotis ipsilon* Hufn.) (Sherrod et al. 1979), as well as an overwintering source of tomato spotted wilt virus and cucumber mosaic virus inoculum (Groves et al. 2001; Tomlinson and Carter 1970). In greenhouse experiments, henbit, field pennycress, and purple deadnettle (*Lamium purpureum* L.) were alternate hosts for a race 3 soybean cyst nematode (SCN) (*Heterodera glycines* Ichin.) accession from Ohio (Venkatesh et al. 2000). More recently, Crech et al. (2005) published the first report of SCN reproduction on purple deadnettle under field conditions, and Nelson et al. (2006) reported that winter annual weed hosts increased SCN population density from autumn to spring. SCN development does not occur at temperatures below 10 C (Hill and Schmidt 1989); therefore, warmer springs may

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increase the effect of the winter annual purple deadnettle and other winter annuals on SCN reproduction in the cropping system. Ultimately, winter annual weed management in the spring should be based on leaving the beneficial cover of winter annuals on the soil through the winter months and controlling them in the spring so as not to allow for the reproduction of pests, diseases, or viable seeds to contribute to the weed seed bank and increase future infestations.

A recent review of the recruitment biology of winter annual weeds in Canada found limited published information on seed dormancy, longevity, and recruitment characteristics for many winter annual weeds, including chickweed and stinkweed (field pennycress), two common weeds in eastern Canada and Michigan (Cici and Van Acker 2009). Seed fecundity and longevity were reported in only one refereed article for most winter annual species, and the base temperature for emergence and time to flowering and seed development was not reported for henbit, shepherd's-purse, or field pennycress. Because fluctuations in weed seed banks over time are governed by annual additions from seed rain and seed decay and germination rates (Baskin and Baskin 1989b, 2001; Benech-Arnold et al. 2000; Best and McIntyre 1975), understanding seed production, dispersal, dormancy, longevity, and emergence patterns will improve management of winter annual weed species.

Growing degree day (GDD) models are used successfully to predict the development of various crops, plant pests (Juskiw et al. 2001; Vinocur and Ritchie 2001), and weeds (Ball et al. 1995; Nord et al. 1999). Growers in Michigan have used GDD to time rotary hoeing in organic cropping systems (Taylor et al. 2012) and in microrate herbicide applications for weed control in sugar beet (*Beta vulgaris* L.) (Dale and Renner 2005). GDD-timed rotary hoeing in organic soybean and dry bean (*Phaseolus vulgaris* L.) resulted in weed control similar to calendar-day timings with fewer rotary-hoeing passes, and microrate herbicide applications improved weed control and reduced time and input costs for weed management in sugar beet. Flowering and seed production of most winter annual weeds occurs in the early spring when days are lengthening, yet little information exists on the GDD required to initiate seed formation nor the duration and extent of seed rain, all important biological attributes influencing the winter annual seed bank and future weed infestations. Tracking winter annual development by GDD could improve

timing of burndown herbicide applications or tillage before winter annual seed development, thereby reducing future infestations of winter annuals.

The objective of this research was to determine the recruitment biology of four winter annual weeds, including seed production, dispersal, seed dormancy based on time of dispersal, and seedling emergence patterns, as related to growing degree days. Integrating winter annual weed biology information into cultural, biological, mechanical, and chemical control will improve management of winter annual weeds, reduce weed control costs, and mitigate crop yield and quality losses due to weeds (Buhler et al. 1997; Hall et al. 2000).

Materials and Methods

Fecundity and Seed Rain. In April of each year (2007–2010), plots measuring 2.3 m² were initiated at the Michigan State University Agronomy farm in native populations of shepherd's-purse, henbit, common chickweed, and field pennycress. Shepherd's-purse was studied only during 2009 and 2010, and common chickweed was studied at a second location in 2009. Plots were weeded by hand to create a monoculture of the weed of interest, and there were three replications of each weed species. Before flowering, nine seed collection cups (modified 473-ml drinking cups each with a 11-cm-diam opening [Solo Cup Company, Lake Forest, IL] with mesh-covered holes to allow for drainage, similar to Kegode et al. 1999) were placed on a grid set at 46-cm spacing in each plot. At that time, weed densities were recorded for henbit, field pennycress, and shepherd's-purse; common chickweed density was recorded as the percentage covering the plot. Because the seeds of shepherd's-purse and field pennycress are produced on racemes on elongated stems, cups were secured just above the soil surface using landscaping tacks taped to the exterior of the cups. Seed collection cups for henbit and common chickweed were buried flush with the soil surface. A triple cup system was placed in the ground (Figure 1) to exclude seed predators. A 946-ml cup with drilled drainage holes was placed in the ground using a golf cup cutter, a 473-ml seed-collection cup was placed inside, and a netted half-cup containing coarse gravel was placed on top. Seeds were collected weekly and cups replaced for the duration of seed rain. Collected cups were allowed to air dry in the laboratory. Once dry, seeds from the nine cups within each plot were combined, separated from debris, and counted.

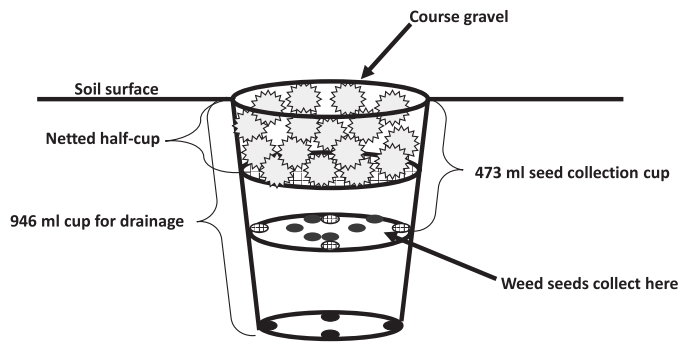


Figure 1. Triple-cup seed-collection system placed in the ground to exclude seed predators.

Seed Dormancy over Time, Based on Dispersal Time. Each week in April, May, and June, the collected and cleaned seed was divided into four groups of 50 seeds each. Seeds were placed in coin envelopes, which were then vacuum-sealed in plastic bags and stored outside in the field and exposed to natural summer temperature fluctuations until the time of laboratory-germination testing, thus enabling us to measure dormancy based on time of seed dispersal. Germination was measured at the time of collection and 2, 4, and 6 mo after dispersal and collection by placing seeds on 10-cm petri dishes lined with No. 1 Whatman filter paper (GE Healthcare Life Sciences, Piscataway, NJ) soaked in 2.5-ml distilled water. Dishes were sealed with laboratory film and placed in the dark at 25 C. Seeds were exposed to light for several minutes once each week when germinated seedlings were removed over the 3-wk germination period. Intact seeds that did not germinate were assumed viable and dormant because of the difficulty in tetrazolium testing such small seeds. Common chickweed, shepherd's-purse, and field pennycress have all demonstrated persistence in the seed bank for ≥ 5 yr (Thompson et al. 1993).

Emergence. To study emergence of these four weed species, metal frames were constructed measuring 1.0 m long, 1.0 wide, and 0.2 m tall and were buried 0.1 m in the soil. The sides of the frame and a hinged lid were covered with hardware cloth, and all hardware cloth on the sides was covered with No See-Um mesh fabric (Outdoor Wilderness Fabrics, Caldwell, ID) to prevent lateral seed movement out of the caged area. In early June of both 2009 and 2010, frames were placed at the Michigan State University Agronomy Farm in East Lansing, MI. Five hundred seeds of a single species were evenly distributed in the emergence area of each frame and lightly raked in. There were four replications of each weed species, each within its own frame. Henbit,

shepherd's-purse, and common chickweed seed was purchased from Herbiseed (Reading, Berkshire U.K.) for the emergence experiment only; field pennycress seed was collected from a field in East Lansing, MI, in 2008. Herbiseed dries collected seed to 8 to 12% moisture and then stores seed at 5 C. In this experiment, emergent plants were from the naturally occurring seed bank and the overseeding, similar to that used by Myers et al. 2004. The timing of overseeding was chosen to coincide with the time of winter annual seed rain. Emerged seedlings were recorded and removed biweekly from early June until mid-November and then again from April until June to follow emergence for 1 yr and to determine whether the overseeding and naturally occurring winter annual weed seed banks could be characterized as facultative winter annuals (Cici and Van Acker 2009). Following the final emergence counts in 2010, frames were removed, positioned elsewhere on the farm, and overseeded for the second year of emergence data.

Statistical Analysis. For each portion of the experiment, time was converted into GDD (base, 0 C), similar to the method used by Bullied and Van Acker (2003). Seed rain and emergence data were then converted to a cumulative percentage of the total number of dispersed seeds and emerged seedlings (overseeded plus natural seed bank), respectively. Data were then fit to the Gompertz equation for cumulative, relative seed rain and cumulative emergence (Equation 1; Forcella et al. 2000) using SigmaPlot version 11.0 (Systat Software Inc., San Jose, CA):

$$Y = 100 \times \exp[-B \times \exp(-K \times X)] \quad [1]$$

where Y is the cumulative relative seed rain or emergence, B is the GDD lag time before seed rain or emergence begins, K is the dispersal or emergence rate, and X is the GDD accumulation. The ability to combine data across years was determined using the extra sum-of-squares principle for nonlinear regression analysis (Lindquist et al. 1996).

Seed dormancy data were subject to logarithmic transformations to normalize residuals before conducting the ANOVA and mean separation using Fisher's Protected LSD test ($P < 0.05$ using Proc Mixed in SAS version 9.2 (SAS Institute, Cary, NC).

Results and Discussion

Seed Fecundity and Rain. Fecundity (i.e., seed production per square meter) varied among the four

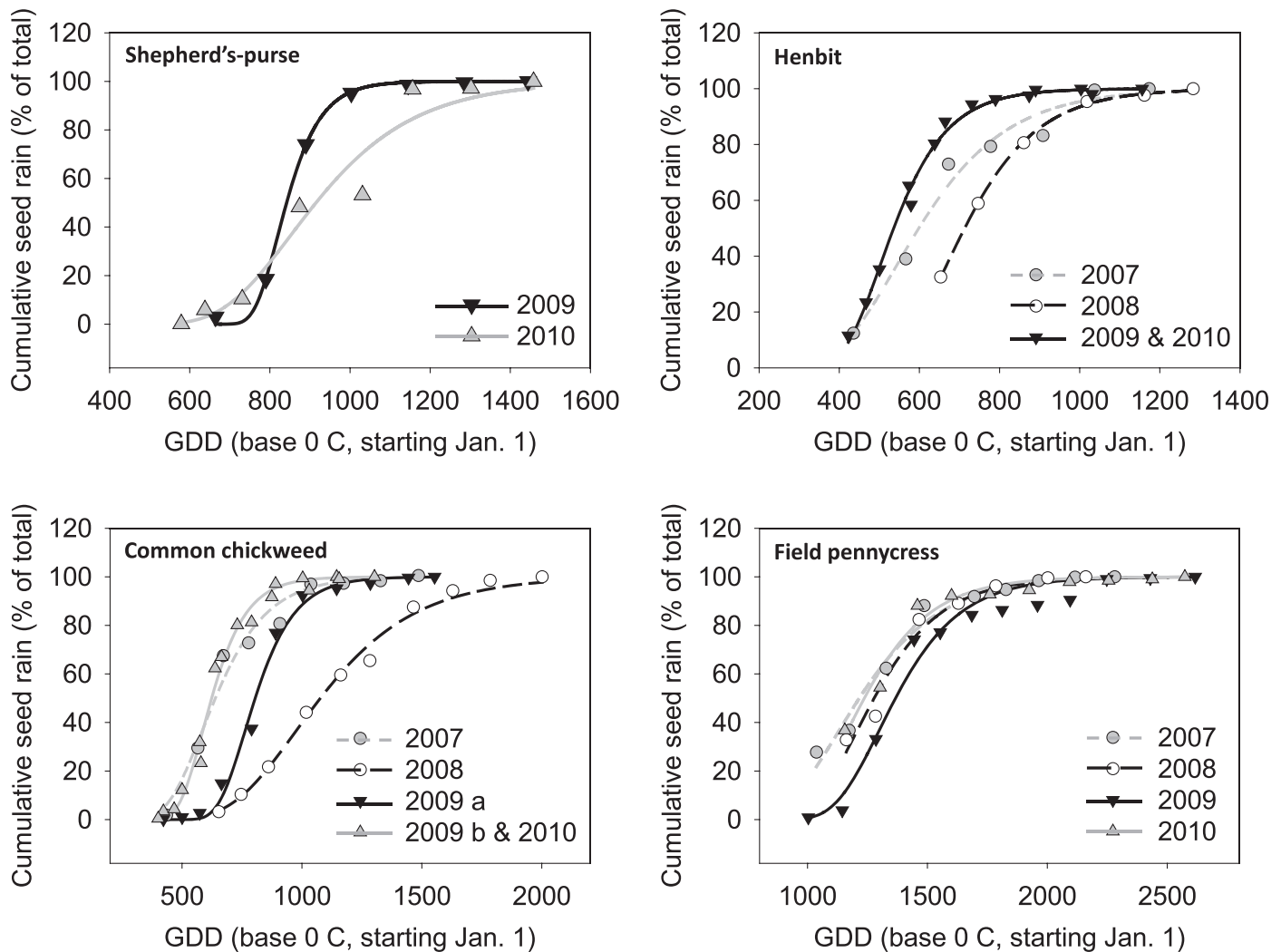


Figure 2. Cumulative seed rain of shepherd's-purse (top left), henbit (top right), common chickweed (bottom left), and field pennycress (bottom right). All data were fit to the Gompertz equation: $Y = 100 \times \exp[-B \times \exp(-K \times X)]$, where Y is cumulative seed rain, B is growing degree day (GDD) lag time before seed rain or emergence begins, K is dispersal or emergence rate, and X is GDD accumulation.

species studied. Henbit was the least prolific, producing 800 to 40,000 seeds m^{-2} at densities of 10 to 65 plants m^{-2} . Conversely, shepherd's-purse was the most prolific, producing 11,000 to 400,000 seeds m^{-2} at 40 to 230 plants m^{-2} . At lower densities, plants produced more seeds per individual (data not shown). Common chickweed produced 30,000 to 120,000 seeds per m^{-2} , similar to seed production reported by Lutman (2002). Field pennycress produced 3,000 to 30,000 seeds per m^{-2} at densities of 10 to 100 plants m^{-2} . Stevens (1932) reported 7,000 field pennycress seeds $plant^{-1}$; Warwick et al. (2002) and Holm et al. (1997) documented as high as 20,000 field pennycress seeds $plant^{-1}$. These studies appear to have examined seed production with little to no competition, unlike the present study where intraspecific competition was occurring.

The cumulative seed rain of each species fit the Gompertz equation, with R^2 values ranging from 0.90 to 0.99 (Figure 2; Table 1). Seed rain curves differed significantly among years, with the exception of the 2009 and 2010 henbit data, the 2009 site-*b* and 2010 common chickweed data, which were thus combined. By calculating the average GDD needed to reach 50% seed rain across years, henbit seed dispersal occurred first (50% seed rain by 620 GDD), followed by common chickweed and shepherd's-purse. Seed rain of field pennycress required more GDD (50% seed rain at 1,300 GDD) and occurred at a slower rate (i.e., lower K value; Table 1). In 2009, the time to 50% seed dispersal of henbit, common chickweed, and field pennycress was delayed compared with the GDD average of previous years. Precipitation during April 2009 (14.6 cm) was two to three times greater than

Table 1. Cumulative relative seed rain: Gompertz equation parameters,^a growing degree days, and calendar date to 50% dispersal.

	Year			
	2007	2008	2009 ^b	2010 ^c
Shepherd's-purse				
<i>B</i>	—	—	1.23 × 10 ⁶	153
<i>K</i>	—	—	0.017	0.006
<i>R</i> ²	—	—	0.97	0.95
50% GDD ^d	—	—	840	920
50% date	—	—	May 31	May 28
Henbit				
<i>B</i>	38	228	245	—
<i>K</i>	0.007	0.008	0.011	—
<i>R</i> ²	0.95	0.90	0.98	—
50% GDD ^d	600	710	540	—
50% date	May 13	May 25	May 11	—
Common chickweed				
<i>B</i>	54	37	868	374
<i>K</i>	0.007	0.004	0.009	0.010
<i>R</i> ²	0.96	0.99	0.99	0.97
50% GDD ^d	640	1,100	810	620
50% date	May 15	June 14	May 29	May 10
Field pennycress				
<i>B</i>	146	568	1,120	506
<i>K</i>	0.004	0.005	0.005	0.005
<i>R</i> ²	0.96	0.96	0.97	0.92
50% GDD ^d	1,200	1,300	1,400	1,200
50% date	June 16	June 25	June 30	June 12

^a Gompertz equation: $Y = 100 \times \exp[-B \times \exp(-K \times X)]$, where *Y* is cumulative seed rain, *B* is growing degree day (GDD) lag time before seed rain or emergence begins, *K* is dispersal or emergence rate, and *X* is GDD accumulation.

^b For henbit, this represents 2009 and 2010 combined, and for common chickweed, this represents site-a in 2009.

^c For common chickweed, this is for the equation that includes 2009 site-b and 2010.

^d Abbreviation: 50% GDD, growing degree days, base 0 C, to 50% seed rain.

in other years (average 5.5 cm). As a result, delayed seed abscission may have occurred in 2009 because of greater soil moisture at the time of seed maturation (Roberts et al. 2002; Senseman and Oliver 1993).

Seed Dormancy over Time, Based on Dispersal Time. Dormancy of shepherd's-purse and henbit seed collected from the plots was greater than 90% at the time of seed rain and 2, 4, and 6 mo after outdoor storage in the sealed bags (data not presented). Again, all seeds that did not germinate after 3 wk were presumed dormant. Future work could explore using an unimbibed seed crush test (Sawma and Mohler 2002). In previous research, 52 to 70% of henbit seed germinated under field conditions in the first 18 mo following seed rain (Roberts and Boddrell 1983). Other studies have indicated that high alternating day/night temperatures of 20/10 C and 25/15 C or a low temperature fluctuation of 5/6 C was important for after-ripening

of shepherd's-purse seed (Baskin and Baskin 1986, 1989a). Alternating temperatures were also required for after-ripening of henbit, ranging from 20/10 C to 35/20 C (Baskin and Baskin 1984). Baskin and Baskin (1988) indicated that temperature is the most influential environmental factor affecting dormancy and germination; soil moisture and light are secondary. The difference between those studies and the current study is that our seeds were not exposed to moisture, only seasonal temperature fluctuations at the soil surface during the storage periods (in Lansing, MI, average monthly temperatures reach highs of 28 C in July and lows of -9 C in January [Michigan State Climatologist's Office 2013]). This work suggests that imbibed conditions may be more important in dormancy release of seed of shepherd's-purse and henbit than previously thought. Examining the effects of combinations of storage temperatures and moisture levels on the seed dormancy of these species could provide valuable knowledge in the future (Forcella et al. 2000; Grundy 2003).

Table 2. Percentage of field pennycress dormancy after storage.

Storage period	Year ^a			
	2007	2008	2009	2010
mo.	%			
0	54 a	92 a	100 a	100 a
2	24 b	64 b	91 b	100 a
4	17 b	60 b	97 a	97 b
6	19 b	63 b	97 a	100 a

^a Means were separated using Fisher's Protected LSD test at $P \leq 0.05$.

Field pennycress has been classified as a facultative winter annual (Cici and Van Acker 2009). In 3 of 4 yr studied, field pennycress dormancy was greater than 90% upon dispersal (Table 2). However, in 2007, an average of 46% of the seed germinated immediately upon dispersal, and in 2007 and 2008, dormancy decreased by 30 and 28%, respectively, after 2 mo of storage (Table 2). Other studies on the dormancy of freshly matured field pennycress have reported conflicting results (NAPPO 2003). Field pennycress dormancy was broken by a period of cooling (12 C) followed by a transfer to a warmer temperature (22 C), or by a combination of temperature fluctuations, light, nitrate, and growth regulators (Saini et al. 1987). Canadian researchers reported no seed dormancy in plants grown in a glasshouse, whereas seed from field-grown plants were mostly dormant (Hume 1984). Roberts and Feast (1972) reported a notable amount of field pennycress seed that remained dormant until the second year of their study. In our research, biotype, precipitation, and relative humidity between the time of flowering and seed dispersal were similar among years. However, in 2007, when we observed less seed dormancy, more GDD were required for 100% of the plants to reach flowering (530 GDD, base 0 C from January 1) than in the other years (average 388 GDD), and there were fewer GDDs between 100% flowering and initial seed dispersal (507 GDD in 2007 vs. an average of 720 in the others). It appears that reduced time for seed formation may be linked to reduced levels of dormancy, supporting a similar finding reported by Baskin and Baskin (2001).

At the time of dispersal, nearly all common chickweed seed was dormant (Table 3), regardless of the time of seed abscission. In 2008, abscised seed from the early and intermediate dispersal periods was 67 to 85% dormant after 6 mo of burial; however, only 32% of the seeds were dormant after 6 mo of burial in the later seed dispersal group (Table 3). A similar trend occurred in 2010 where,

Table 3. Percentage of common chickweed dormancy after storage, based on the period of seed dispersal.

Year	Storage period	Seed dispersal period ^{a-d}		
		Early	Intermediate	Late
	mo.	%		
2008	0	99 a	95 a	96 a
	2	88 bA	75 abA	34 bB
	4	84 abA	60 bB	32 cC
	6	85 bA	67 bA	32 cB
2009	0	97 a	98 a	100 a
	2	89 abAB	94 aA	85 aB
	4	70 c	76 b	68 b
	6	79 bc	79 b	71 b
2010	0	100 a	99	100
	2	71 b	81	92
	4	100 a	91	94
	6	100 a	90	77

^a Seed dispersal categories were characterized by dividing the number of events for each year by three, creating overlapping ranges of the growing degree day (GDD, base 0 C) from January 1, and represented early (400–700 GDD), intermediate (600–1500 GDD), and late (900–2000 GDD). There was no overlap in GDD among the categories within a single year.

^b Means were separated using Fisher's Protected LSD test at $P \leq 0.05$.

^c Lowercase letters should be compared down the column, with different letters indicating significant differences among the means.

^d Uppercase letters should be compared across the row, with different letters indicating significant differences among the means.

after 6 mo of burial, the late-dispersed seed was less dormant (77%) than the earlier cohorts were (90 to 100%). In 2009, 71 and 76% of the seed remained dormant 4 and 6 mo after burial, respectively, when averaged across the time of seed abscission. Common chickweed after ripening has been shown to occur in both dry and moist storage conditions (Roberts and Lockett 1972), and other researchers have shown reduced dormancy when seeds were produced in the later stages of weed development (Baskin and Baskin 2001; Fenner 1991).

Emergence. In both years, the rate of emergence of henbit and common chickweed were similar to each other, as were shepherd's-purse and field pennycress (Figure 3). All emergence curves fit the Gompertz equation, with R^2 values ranging from 0.80 to 0.97, although equation parameters varied from year to year (Table 4). The emergence of henbit and common chickweed was delayed in 2010, compared with 2009. Based on the equations, henbit and common chickweed both required 1,600 GDDs (late August) to reach 50% emergence from the time of seeding in early June 2009, compared with

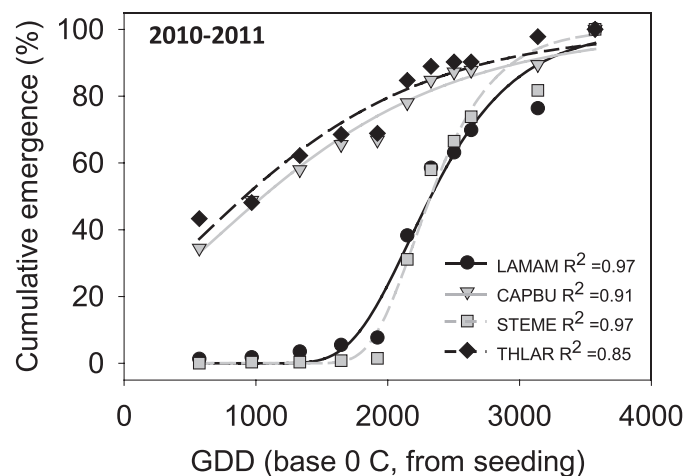
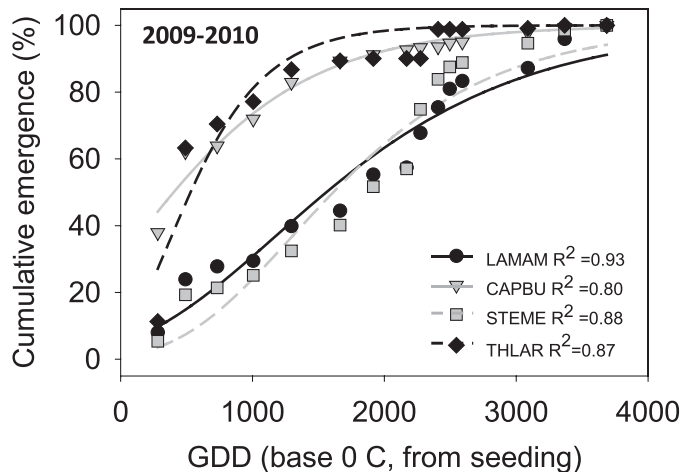


Figure 3. Cumulative emergence of shepherd's-purse, henbit, common chickweed, and field pennycress during 2009 to 2010 (left) and 2010 to 2011 (right). All data were fit to the Gompertz equation: $Y = 100 \times \exp[-B \times \exp(-K \times X)]$, where Y is cumulative seed rain, B is growing degree day (GDD) lag time before seed rain or emergence begins, K is dispersal or emergence rate, and X is GDD accumulation.

Table 4. Cumulative relative emergence: Gompertz^a equation parameters and growing degree days to 50% seed emergence.

	Year	
	2009	2010
Shepherd's-purse		
B	1	2
K	0.001	0.001
R^2	0.80	0.91
50% GDD ^b	400	1,100
50% date	June 27	August 1
Henbit		
B	3	131
K	0.001	0.002
R^2	0.93	0.97
50% GDD ^b	1,600	2,300
50% date	August 27	October 3
Common chickweed		
B	4	777
K	0.001	0.003
R^2	0.88	0.97
50% GDD ^b	1,600	2,300
50% date	August 27	October 3
Field pennycress		
B	3	2
K	0.003	0.001
R^2	0.87	0.85
50% GDD ^b	530	920
50% date	July 4	July 24

^a Gompertz equation: $Y = 100 \times \exp[-B \times \exp(-K \times X)]$, where Y is cumulative seed rain, B is growing degree day (GDD) lag time before seed rain or emergence begins, K is dispersal or emergence rate, and X is GDD accumulation from the time of planting in early June.

^b Abbreviation: GDD, growing degree days, base 0 C, to 50% emergence.

2,300 GDD (early October) in 2010. These large differences from one year to the next may be attributed to reduced moisture availability but not maternal effects because the studies were in the same field (natural seed bank and same seed lot/collection for overseeding), and 30 cm of rain fell during summer 2009, compared with 18 cm in 2010) (Figure 4). Henbit and common chickweed emergence occurred in summer, fall, and winter/spring in both years (Table 5). In contrast, 90% or more of shepherd's-purse and field pennycress emergence took place during the summer in 2009, 78% or more in 2010 (Table 5).

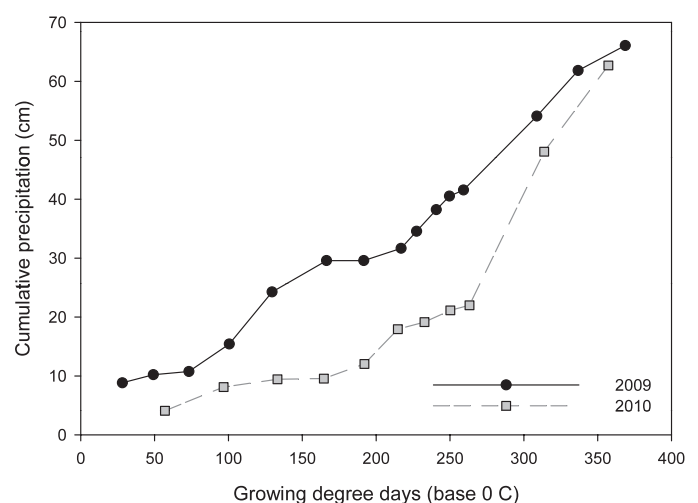


Figure 4. Precipitation during the course of the weed emergence trial. Data were collected from the East Lansing, MI, Enviroweather station located at the Hancock Turfgrass Research Center (available at: <http://www.agweather.geo.msu.edu/mawn/station.asp?id=htc>).

Table 5. Percentage of winter annual emergence by season.

Season ^a	Precipitation		GDD ^b		Shepherd's-purse		Henbit		Common chickweed		Field pennycress	
	2009	2010	2009	2010	2009	2010	2009	2010	2009	2010	2009	2010
	cm		base 0 C		%							
Summer	30	18	2,050	2,148	91 a ^d	78 a	55 a	38	52 a	31	90 a	85a
Fall	14	9	585	619	3 b	10 b	28 b	32	37 a	43	9 a	6b
Winter/spring ^c	21	36	1,052	840	5 b	12 b	17 c	30	11 b	26	1 b	10b

^a Summer, June 8 (2009)/June 14 (2010)–September 22; fall, September 23–December 22; winter/spring, December 23–June 3 of the subsequent year.

^b Abbreviation: GDD, growing degree days.

^c Winter/spring, December 23–June 3 of the subsequent year.

^d Different letters are used to indicate significant differences among seasons within a given year. Means were separated using Fisher's Protected LSD test at $P \leq 0.05$.

Field pennycress seed was collected from the Michigan State University Agronomy Research farm and used each year in the emergence study. This population of field pennycress, as well as the other weeds included in this study, appears to be facultative winter annuals. Because seed for the emergence study was purchased for the other three weed species, it is uncertain whether the conditions under which the seed was produced or stored (maternal environment and after-ripening conditions) influenced the emergence pattern of these three weed species; however, the difference between years is attributed to a difference in soil moisture in the field. Because these plants were removed upon dispersal, it is uncertain what percentage, if any, of the summer-emerging plants would produce seed before winter. Further understanding of these summer-emerging plants could affect weed control timing efforts aimed at reducing seed bank inputs.

Seeds of these four weed species were dormant at the time of seed dispersal in May and June; however, later-dispersing common chickweed seed cohorts exhibited less dormancy in 2 of the 3 yr of our study. Winter annual seeds that disperse before implementation of weed management practices will remain dormant throughout the summer months in the northern United States. The pattern of emergence of these four weed species and the time of seed rain was similar each year, although the time to 50% emergence or cumulative seed rain was delayed when soil moisture was limited. Use of GDD to predict seed rain is limited unless a second parameter of soil moisture or precipitation is added to create a prediction model using hydrothermal time. As climate moderates and tillage systems and crop rotations change, niches available for winter annual weed species will also change. Will weeds considered facultative winter annuals continue to germinate in both the fall and the spring, or will

emergence patterns change to be more competitive with spring-planted crops? As glyphosate-resistant weed infestations increase, will the use of residual herbicides and tillage reduce the winter annual weed populations over time? Our research adds to the body of knowledge on recruitment biology of these four weed species, in particular field-based patterns of seed rain and the emergence of these four species using GDD, as well as seed dormancy, at the time of, and following, dispersal. Our conclusions are based on a single population of each weed species, and maternal effects may influence seed characteristics, including dispersal and dormancy in time, as well as field-emergence patterns (Grundy et al. 2003). It would be interesting to compare multiple populations of individual weed species to determine differences in seed dispersal, dormancy, and emergence across populations collected from differing environments. By developing predictive population models on winter annual weed emergence, including GDD and hydrothermal time, across a range of winter annual populations, we may be able to better predict the species of winter annual weed that is best-adapted to a cropping system and develop effective weed management strategies for the future.

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Literature Cited

Ball DA, Klepper B, Rydrych DJ (1995) Comparative above-ground development rates for several annual grass weeds and cereal grains. *Weed Sci* 43:410–416

- Baskin CC, Baskin JM (1988) Germination ecophysiology of herbaceous plant species in a temperate region. *Am J Bot* 75:286–305
- Baskin CC, Baskin JM (2001) Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. San Diego: Academic. 666 p
- Baskin JM, Baskin CC (1989a) Germination responses of buried seeds of *Capsella bursa-pastoris* exposed to seasonal temperatures changes. *Weed Res* 29:205–212
- Baskin JM, Baskin CC (1989b) Role of temperature in regulating timing of germination in soil seed reserves on *Thlaspi arvense* L. *Weed Res* 29:317–326
- Baskin JM, Baskin CC (1984) Effects of temperature during burial on dormant and non-dormant seeds of *Lamium amplexicaule* L. and ecological implications. *Weed Res* 24:333–339
- Baskin JM, Baskin CC, Parr JC (1986) Field emergence of *Lamium amplexicaule* L. and *L. purpureum* L. in relation to the annual seed dormancy cycle. *Weed Res* 26:185–190
- Benech-Arnold RL, Sanchez RA, Forcella F, Kruck BC, Ghersa CM (2000) Environmental control of dormancy in weed seed banks in soil. *Field Crops Res* 67:105–122
- Best KF, McIntyre GI (1975) The biology of Canadian weeds, 9: *Thlaspi arvense* L. *Can J Plant Sci* 55:279–292
- Buhler DD, Hartzler RG, Forcella F (1997) Implications of weed seedbank dynamics to weed management. *Weed Sci* 45:329–336
- Bullied WJ, Van Acker RC (2003) Conventional- and conservation-tillage systems influence emergence periodicity of annual weed species in canola. *Weed Sci* 52:886–897
- Cici SZ, Van Acker RC (2009) A review of the recruitment biology of winter annual weeds in Canada. *Can. J Plant Sci* 89:575–589
- Creech JE, Johnson WG, Faghihi J, Ferris VR (2007) Survey of Indiana producers and crop advisors: a perspective on winter annual weeds and soybean cyst nematode (*Heterodera glycines*). *Weed Technol* 21:532–536
- Creech JE, Johnson WG, Faghihi J, Ferris VR, Westphal A (2005) First report of soybean cyst nematode reproduction on purple deadnettle under field conditions. *Crop Manag.* doi: 10.1094/CM-2005-0715-01-BR
- [CTIC] Conservation Technology Information Center (2008) Amendment to the National Crop Residue Management Survey Summary. <http://www.ctic.purdue.edu/media/pdf/National%20Summary%202008%20%28Amendment%29.pdf>. Accessed: June 7, 2012
- Dale TM, Renner KA (2005) Timing of postemergence micro-rate applications based on growing degree days in sugarbeet. *J Sugar Beet Res* 42:87–101
- Fenner M (1991) The effects of the parent environment on seed germinability. *Seed Sci Res* 1:75–84
- Forcella F, Benech-Arnold RL, Sanchez R, Ghersa CM (2000) Modeling seedling emergence. *Field Crops Res* 67:123–139
- Groves RL, Walgenbach JF, Moyer JW, Kennedy GG (2001) Overwintering of *Frankliniella fusca* (Thysanoptera: Thripidae) on winter annual weeds infected with Tomato spotted wilt virus and patterns of virus movement between susceptible weed hosts. *Phytopathology* 91:891–899
- Grundy AC (2003) Predicting weed emergence: a review of approaches and future challenges. *Weed Res* 43:1–11
- Grundy AC, Peters NCB, Rasmussen TA, Hartmann KM, Sattin M, Anderson L, Mead A, Murdoch AJ, Forcella F (2003) Emergence of *Chenopodium album* and *Stellaria media* of different origins under different climatic conditions. *Weed Res* 43:163–176
- Güeli R, Smeda RJ (2001) Soybean weed management with fall applied herbicides. Page 98 in Proceedings of the North Central Weed Science Society. Milwaukee, WI: North Central Weed Science Society
- Hall JC, Van Eerd LL, Miller SD, Owen MDK, Prather TS, Shaner DL, Singh M, Vaughn KC, Weller SC (2000) Future research directions for weed science. *Weed Technol* 14: 647–658
- Hill NS, Schmitt DP (1989) Influence of temperature and soybean phenology on dormancy induction of *Heterodera glycines*. *J. Nematol* 21:361–369
- Holm LG, Doll J, Holm E, Pancho JV, Herberger JP (1997) *World Weeds: Natural Histories and Distribution*. New York: J. Wiley. Pp 843–853
- Hume L (1984) The effect of seed maturity, storage on the soil surface, and burial on seeds of *Thlaspi arvense* L. *Can J Plant Sci* 64:961–969
- Juskiw PE, Jame YW, Kryzanowski L (2001) Phonological development of spring barley in a short-season growing area. *Agron J* 93:370–379
- Kegode GO, Forcella F, Clay S (1999) Influence of crop rotation, tillage, and management inputs on weed seed production. *Weed Sci* 47:175–183
- Krausz RF, Young BG, Matthews JL (2003) Winter annual weed control with fall-applied corn (*Zea mays*) herbicides. *Weed Technol* 17:516–520
- Lindquist JL, Mortensen DA, Clay SA, Schmenk R, Kells JJ, Howatt K, Westra P (1996) Stability of Corn (*Zea mays*)–velvetleaf (*Abutilon theophrasti*) interference relationships. *Weed Sci* 44:309–313
- Lutman PJ (2002) Estimation of seed production by *Stellaria media*, *Sinapis arvensis*, and *Tripleurospermum inodorum* in arable crops. *Weed Res* 42:359–369
- Michigan State Climatologist's Office (2013) 30 Year Summary of Monthly Values for Lansing: Climate Normals and Extremes by Month—1981–2010 time period. <http://climate.geo.msu.edu/stations/4641/>. Accessed May 1, 2013
- Mock VA, Creech E, Ferris VR, Hallett SG, Johnson WG (2010) Influence of winter annual weed removal timings on soybean cyst nematode population density and plant biomass. *Weed Sci* 58:381–386
- Myers MW, Curran WS, VanGessel MJ, Calvin DD, Mortensen DA, Majek CA, Karsten HD, Roth GW (2004) Predicting weed emergence for eight annual species in the northeastern United States. *Weed Sci* 52:913–919
- Nelson K, Johnson WG, Wait JD, Smoot RL (2006) Winter-annual weed management in corn (*Zea mays*) and soybean (*Glycine max*) and the impact on soybean cyst nematode (*Heterodera glycines*) egg population densities. *Weed Technol* 20:965–970
- [NAPPO-PRA] North American Plant Protection Organization–Pest Risk Assessment (2003) Pest Fact Sheet: *Thlaspi arvense* L. <http://www.napso.org/PRA-sheets/Thlaspiarvense.pdf>. Accessed November 16, 2006
- Nord CA, Messersmith CG, Nalewaja JD (1999) Growth of *Kochia scoparia*, *Salsola iberica*, and *Triticum aestivum* varies with temperature. *Weed Sci* 47:435–439
- Roberts HA, Boddrell JE (1983) Seed survival and periodicity of seedling emergence in ten species of annual weeds. *Ann Appl Biol* 102:523–532

- Roberts JA, Elliott KA, Gonzalez-Carranza ZH (2002) Abscission, dehiscence, and other cell separation processes. *Annu Rev Plant Biol* 53:131–158
- Roberts HA, Feast PM (1972) Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. *Weed Res* 12:316–324
- Roberts HA, Lockett PM (1975) Germination of buried and dry-stored seeds of *Stellaria media*. *Weed Res* 15:199–204
- Saini HS, Bassi PK, Goudey JS, Spencer MS (1987) Breakage of seed dormancy of field pennycress (*Thlaspi arvense*) by growth regulators, nitrate, and environmental factors. *Weed Sci* 35:802–806
- Sawma JT, Mohler CL (2002) Evaluating seed viability by an unimbibed seed crush test in comparison with the tetrazolium test. *Weed Technol* 16:781–786
- Senseman SA, Oliver LR (1993) Flowering patterns, seed production, and somatic polymorphism of three weed species. *Weed Sci* 41:418–425
- Sherrod DW, Shaw JT, Luckmann WH (1979) Concepts of black cutworm field biology in Illinois. *Environ Entomol* 8:191–195
- Stevens OA (1932) The number and weight of seeds produced by weeds. *Am J Bot* 19:784–794
- Taylor EC, Renner KA, Sprague CL (2012) Organic weed management in field crops with a propane flamer and rotary hoe. *Weed Technol* 26:793–799
- Thompson K, Band SR, Hodgson JG (1993) Seed size and shape predict persistence in soil. *Funct Ecol* 7:236–241
- Tomlinson JA, Carter AL (1970) Studies on the seed transmission of cucumber mosaic virus in chickweed (*Stellaria media*) in relation to the ecology of the virus. *Ann Appl Bio* 66:381–386
- Venkatesh R, Harrison SK, Riedel RM (2000) Weed hosts of soybean cyst nematode (*Heterodera glycines*) in Ohio. *Weed Technol* 14:156–160
- Vinocur MG, Ritchie JT (2001) Maize leaf development biases caused by air-apex temperature differences. *Agron J* 93:767–772
- Warwick SI, Francis A, Susko DJ (2002) The biology of Canadian weeds, 9: *Thlaspi arvense* L. (updated). *Can J Plant Sci* 82:803–823

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