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Environmental Triggers of Winter Annual Weed Emergence and Management to Reduce Soybean Cyst Nematode Reproduction on Winter Annual Weed Hosts

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ENVIRONMENTAL TRIGGERS OF WINTER ANNUAL WEED EMERGENCE
AND MANAGEMENT TO REDUCE SOYBEAN CYST NEMATODE
REPRODUCTION ON WINTER ANNUAL WEED HOSTS

by

Rodrigo Werle

A THESIS

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Winter annual weeds are becoming more common in many row crop fields in the midwestern USA. The impact of winter annual weeds in cropping systems is often overlooked because these weeds complete their lifecycle near the time of crop sowing. However, delayed soil warming, competition for nutrients during initial establishment of the main crop, difficult planting operations, and yield loss are some of the problems caused by dense mats of winter annual weeds. Moreover, some of these weeds have been reported as alternative hosts for pests such as the soybean cyst nematode (*Heterodera glycines*, SCN), considered the most important soybean pathogen in the USA. Research looking at the effect of time of herbicide application on SCN development on weed hosts has not been reported. Thus, our first objective was to evaluate how the development of SCN on henbit roots was affected by time of herbicide application and herbicide mode of action. The results of this research indicated that early management of henbit plants can significantly reduce SCN reproduction potential in the absence of its main host, soybean. In order to better manage weeds, it is important to know when they will emerge, since weeds are easily controlled during early stages of growth. The emergence pattern of
winter annual weeds common to the midwest region of the United States has not been reported. Therefore, our second objective was to understand and predict emergence of winter annual weed species using models based on the accumulation of modified thermal/hydrothermal time. The results of this research indicated that soil temperature was the main factor driving winter annual weed emergence. According to our findings, the majority of the winter annual weeds will emerge by late-fall in Nebraska, indicating that, as long as environmental conditions are adequate for herbicide application or mechanical cultivation, this would be the ideal time to manage these weeds. These results may help farmers to better manage winter annual weeds.
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Chapter 1

Literature Review

Soybeans

Soybean (*Glycine max* L.), a native species of eastern Asia, is believed to have emerged as a domesticated crop during the eleventh century B.C. in northeast China (Hymowitz 1990). Soybean was first introduced in the United States in 1765 (Hymowitz and Harlan 1983) and was grown primarily as forage until 1920, when the prominence of soybeans as a grain crop started. The first year grain soybean acreage exceeded soybean forage production in the United States was 1941 (Hymowitz 1990). Soybean is ranked as one of the most important crops worldwide and is primarily grown as an oil seed crop for livestock feed and biofuel feedstock (Masuda and Goldsmith 2009). The USA is the largest soybean producer in the world, representing more than 30% of the total soybean area harvested, followed by Brazil, Argentina, China, and India, respectively (Masuda and Goldsmith 2009). Soybean production in the USA is concentrated in 5 states in the upper midwest (Iowa, Illinois, Minnesota, Nebraska, and Indiana) (Anonymous 2011), where this crop acts as an attractive option for rotation with corn (*Zea mays* L.).

Winter Annual Weeds

Winter annual weeds typically emerge in the fall, overwinter as small seedlings, grow rapidly during the spring, and produce seeds and senesce by late spring or early summer (Radosevich et al. 1997; Creech et al. 2007a). These species have the ability to survive and grow during times of the year when environmental conditions, mainly temperature, are not favorable for the development of other plant species. Winter annual
weeds have become prolific in agricultural lands due to the increased adoption of conservation tillage practices (Swagata et al. 2009), widespread adoption of glyphosate-resistant crops and over-dependence on glyphosate (Owen and Zelaya 2005), and the subsequent reduced use of other herbicides (Shaner 2000). The impact of winter annual weeds in cropping systems is often overlooked because these weeds start to emerge at the time summer annual crops (e.g. corn and soybeans) are senescing and they complete their lifecycle about the time of crop sowing (Johnson et al. 2008). However, dense mats of winter annual weeds may result in delayed soil warming in spring (Bruce et al. 2000), competition for water and nutrients during initial establishment of the main crop, yield loss (Bernards and Sandell 2011), and difficult planting operations (Dahlke et al. 2001). Moreover, several winter annual weeds can act as alternative hosts for pests, including the soybean cyst nematode (*Heterodera glycines*, SCN) (Venkatesh et al. 2000).

Herbicide application during late fall or early spring is becoming a common practice among farmers due to the abundance of winter annual weeds. Research has shown that a fall herbicide application provides satisfactory weed control (Hasty et al. 2004) and may be beneficial when compared to an early spring application, especially during wet years, because farmers can better spread their workload over time (Krausz et al. 2003). Winter annual weeds are more susceptible to herbicide treatments in the fall when they are small, but herbicides should only be sprayed when environmental conditions are favorable for both operational application and foliar uptake (Hasty et al. 2004; Bernards et al. 2011). During late spring, herbicide application may not result in desired control because these weeds will be at an advanced growth stage (Johnson et al. 2008).
Thus, knowledge of the emergence pattern of winter annual weeds can be a useful tool to guide growers on weed control decisions.

**Soybean Cyst Nematode - SCN**

SCN is considered the most yield limiting disease of soybeans in the USA (Wrather and Koenning 2006). Although SCN was first described in 1952 in Japan, it is hypothesized that this endoparasitic plant nematode originated in China, where soybeans originated (Yu 2011). SCN was first detected in the USA in 1954 in North Carolina (Wrather et al. 1984) and currently it is found in most states where soybean is cultivated. It is speculated that SCN-cysts were first introduced in the United States into the Mississippi Delta on bagging from Japan (Riggs 1977). In Nebraska, the nematode was first detected in 1986 (Powers et al. 1989), and currently its presence has been confirmed in 52 of 93 counties (Giesler and Wilson 2011). SCN can damage host plants by removing essential plant nutrients from the root cells and disrupting the root vascular system, reducing water and nutrient uptake and transport from the roots to aboveground biomass (Hershman 1997; Asmus and Ferraz 2002). Additionally, SCN infection can indirectly damage soybeans by reducing rhizobium nodulation and facilitating the occurrence of some diseases caused by other soilborne pathogens (Wrather et al. 1984; Hershman 1997). The classic symptoms caused by SCN range from asymptomatic to stunting, yellowing and wilting (Niblack 2005; Asmus and Ferraz 2002). Soybean yield reduction up to 30% caused by SCN has been detected without showing any visual aboveground symptoms (Noel 1992). SCN symptoms are typically more pronounced for infected plants growing under stress conditions (Faghihi and Ferris 2006). The use of resistant varieties and rotation with nonhost crops (e.g., corn, sorghum, or wheat) are the
main strategies recommended for SCN management (Niblack 2005). Significant reductions in nematode populations have been observed after two years of rotation with nonhost crops (Wrather et al. 1984). These management practices may help to reduce SCN-infestations, but SCN eradication in infested fields is not a feasible practice due to the high longevity of cysts in soil and their resistance to control measures (Yang et al. 2002).

Soybean is the most important host for SCN, but a broad range of plant species have been reported as alternative hosts for this pathogen, including both crop and weed species (Yu 2011). Alternative hosts may allow the nematode to increase its population in the absence of its main host. Some examples of cultivated species that can act as alternative hosts for SCN are: common and hairy vetch, cowpea, clovers, edible beans, lespedeza, lupine, and pea (Niblack and Tylka 2008). Examples of alternative weed hosts are: common chickweed, common mullein, field pennycress, hemp sesbania, henbit, pokeweed, purple deadnettle, shepherd’s purse, and wild mustard (Niblack and Tylka 2008). Where SCN infestations are detected, crop species known as alternative hosts for SCN should not be included in the rotation scheme and alternative weed hosts must be managed in order to avoid potential increase in SCN population.

The SCN lifecycle starts when eggs retained inside the cyst hatch to juveniles at second stage (J2). Once hatched from the eggs, J2-infective juveniles need to encounter host roots and penetrate them. This process is aided by root exudates that attract juveniles. Failure in encountering the host results in juvenile starvation and consequent death (Hershman 1997). The J2-juveniles that successfully infect the susceptible host roots establish a feeding site known as “syncytium”, molt three times (J3, J4, and adult),
and eventually become either males or females (Wrather et al. 1984). The males leave the roots, move in the soil searching for females, mate, and die. The females remain attached to the roots, begin to swell and break through the root surface (a lemon-shaped structure white in color typically becomes visible without magnification). The majority of the eggs produced by the females are retained inside of their bodies. However, some of the eggs are deposited in a gelatinous matrix surrounding their body. As females age, die, and detach from the roots, they become a thick-walled protective structure for the eggs with dark coloration known as a “cyst” (Niblack et al. 2005; Wrather et al. 1984). Darkening of the body wall is an indicator that females have completed their lifecycle and no longer require nourishment from the host plant (Niblack et al. 2006). Niblack (2005) reported that an average female reproducing on soybean roots produces 200 eggs, but more than 600 eggs per cyst has been reported (Sipes et al. 1992). Wrather et al. (1984) reported that SCN completed its lifecycle within 24 days when developing at 23 C, and Niblack (2005) reported that under ideal conditions, SCN can go from J2 infective stage to viable egg within 22 days. Two to four SCN generations in susceptible soybean cultivars (Chen et al. 2001) and at least one SCN generation in winter annual weed hosts (Harrison et al. 2008) have been reported under field conditions, indicating that as long as temperature is favorable for SCN development (>5 C) (Alston and Schmitt 1988) and a susceptible host is present, this pathogen will continue its development.

SCN can only move a few centimeters on its own, but long distance dispersal can be promoted by farm equipment, drainage and flood water, wind, animals and even by infested soil that moves along with soybean grain (Wrather et al. 1984). Therefore, the use of SCN-resistant cultivars, crop rotation, adequate soil fertility and moisture
management, controlling weeds (especially alternative hosts of SCN), insects and
diseases, and soil sampling before planting soybeans (to detect the presence and level of
SCN infestations), along with sanitation practices such as washing equipment before
moving to another field (especially after leaving infested ones), may help growers to
minimize losses due to SCN (Niblack and Tylka 2008).

**Winter Annual Weeds Acting as Alternative Hosts for SCN**

Several winter annual weed species, including henbit (*Lamium amplexicaule*),
purple deadnettle (*Lamium purpureum*), field pennycress (*Thlaspi arvense*),
smallflowered bittercress (*Cardamine parviflora*), and common chickweed (*Stellaria
media*), have been reported as alternative hosts of soybean cyst nematode (*Heterodera
glycines*, SCN) (Venkatesh et al. 2000; Riggs 1992). SCN reproduction on henbit and
purple deadnettle roots in fields in the midwestern USA has been reported (Creech et al.
2007b). It is known that SCN development ceases when soil temperature drops below 5 C
(Alston and Schmitt 1988), thus the overlap of SCN activity and winter annual weed
growth under field conditions is limited to the period when soil temperatures are
favorable for both nematode development and weed growth (Johnson et al. 2008). When
winter annual weeds were first reported as alternative hosts, it was hypothesized that they
could act as “trap crops” for SCN because some of these weed species would stimulate
egg hatch and juvenile infection but then the cold weather would kill the individuals that
had not achieved maturity in the fall. However, Creech et al. (2007c) reported that after
infecting purple deadnettle roots, SCN juveniles survived during a period of cold
temperature inside the roots of this host and continued its development once temperatures
became favorable. This indicated that once SCN is inside the roots in the fall, if
temperature becomes unfavorable for development, juveniles can go dormant for a period of time and then resume development when conditions become favorable again (i.e., early spring). Nelson et al. (2006) reported that SCN population density increased between fall and spring when winter annual weeds were not controlled. However, when herbicides were fall applied and winter weeds controlled, the SCN population remained constant between fall and spring. On the other hand, Creech et al. (2008) found that in fields with low winter annual weed densities, weed control was not beneficial in managing SCN, because the presence of few weeds did not influence SCN population density. Creech et al. (2007b) found that the majority of SCN reproduction on winter annual weeds occurred during the fall, indicating that fall management of winter annual weeds can be the most effective way to minimize potential reproduction of SCN on these weed species. Thus, failure to manage winter annual weeds may provide an additional niche for SCN to develop and increase its population density in the absence of soybeans (Johnson et al. 2008).

**Emergence time of winter annual weeds**

Summer and winter annual weed species typically have consistent emergence patterns across years (Baskin and Baskin 1988). The germination requirements and emergence patterns of several summer annual weeds have been studied but little effort has been directed to winter annual weeds (Cici and Van Acker 2009). To date, there is limited information available on the biology and ecology of winter annual weeds, especially pertaining to the effects of temperature and water potential on seed germination, seedling emergence, and overwintering plant survival (Cici and Van Acker 2009).
Even though it is known that the majority of the winter annual weed species emerge in the fall, these species can be further classified as either obligate winter annual weeds or facultative winter annual weeds (Baskin and Baskin 1988, Cici and Van Acker 2009). Obligate winter annual weeds germinate only in the fall, when the soil temperatures are decreasing, and after becoming dormant during the winter, seeds will not germinate until next fall because exposure to high temperatures is required to overcome dormancy. Facultative winter annual weeds can germinate during both fall and spring (Baskin and Baskin 1988). Baskin and Baskin (1988) conducted an experiment with 75 species of winter annual weeds common to Kentucky and Tennessee and found that for 74 species the peak of emergence occurred during the first fall after planting the seeds, and that 34 of these 74 species also germinated in the spring. This indicates that 50% of the species included in this study were facultative winter annual weeds. Cici and Van Acker (2009) characterized some winter annual weed species according to their emergence time in Canada: only fall emergence represented obligate winter annual weeds, and mostly fall, mostly spring, or emergence in both fall and spring represented facultative winter annual weeds. According to the authors, the species emerging during both fall and spring represented the largest category, and none of the species were categorized as obligate winter annuals. When comparing the findings of Baskin and Baskin (1988) with Cici and Van Acker (2009) it is possible to hypothesize that mild winters from southern USA have allowed the development of obligate winter annual weed populations, whereas severe winters in Canada have selected for facultative winter annual weed populations. The ability to germinate in both fall and spring is advantageous for facultative winter annuals because the risk of a population being eliminated at one
period is reduced (i.e., late fall management or winter killing), thereby increasing the chances of offspring reaching the reproductive stage.

Typically, spring emerging facultative winter annuals will behave as short-lived annuals and produce less biomass and fewer seeds than fall emerged plants. The mortality rate of seedlings emerging in the fall is typically greater than that of seedlings emerging in the spring, but the greater reproduction potential of the first group justifies the risk of fall emergence (Regehr and Bazzaz 1979). In Canada, the majority of winter annual weed species emerge at two periods of time, April-May and September-October (Cici and Van Acker 2009), but emergence time of winter annual weeds in the midwestern region of the United States has not been reported.

**Seedling emergence**

Weeds typically occur in multi-species complexes, with all species having unique survival characteristics. According to Davis et al. (2008), if all weed seeds were to emerge at the same time, weed management would be a simple task. Instead, weeds are an annual problem because after a single seed rain event they can infest agricultural lands and create soil seedbanks that may persist for several years (Conn et al. 2006). The period of weed emergence is a function of the species present in the seedbank and their interaction with the environment (Forcella et al. 1997, Stoller and Wax 1973). Knowledge of the weed species present in the soil seedbank and when these species are most likely to emerge is important in planning effective weed control programs (Buhler et al. 1997; Cici and Van Acker 2009; Forcella et al. 2000).

The success of any annual plant is directly correlated to its time of seedling emergence because it determines the ability of a plant to compete with its neighbors,
survive pests and rough environmental conditions, and to set seeds (Forcella et al. 2000). For some species, annual emergence occurs over a short period of time (i.e., few weeks), but for others it can occur over longer periods (i.e., months) (Ogg and Dawson, 1984). Seedling emergence is a complex process that can be divided in four different stages: i) dormancy; ii) germination; iii) pre-emergence elongation; and iv) emergence from soil (Forcella et al. 2000).

i) Dormancy. Seed dormancy is a common feature of weed species that protects seeds from germinating during periods of the year when environmental conditions are not favorable for plant development (Forcella et al. 2000). Normally, emergence of a weed species on arable land is observed when seed dormancy is at a minimum (Probert 1992). Environmental factors that affect dormancy can be divided in two categories (Benech-Arnold et al. 2000): i) those modifying dormancy level, or “dormancy-breaking factors” (i.e., temperature and soil moisture), and ii) those removing the ultimate constraint for germination, or “germination-stimulating factors” (i.e., light and air quality, temperature fluctuation).

ii) Germination. Germination is typically defined as “the first visual appearance of the radicle from the outermost structure enveloping the embryo” (Forcella et al. 2000). Once dormancy is overcome, germination becomes the key component of seedling emergence. In cultivated lands, the primary factors governing seed germination are soil temperature, moisture and gaseous conditions (Benech-Arnold et al. 2000). Water is an essential component and its absence prevents the germination from occurring. Germination commences with the uptake of water, or imbibition, by the dry seed, followed by embryo expansion. The uptake of water is triphasic with a rapid initial
uptake (phase I, imbibition) followed by a plateau phase (phase II). A further increase in water uptake (phase III) occurs as the embryo axis elongates and breaks through the covering layers to complete germination (Manz et al. 2005). Imbibed seeds will not germinate below a minimum or above a maximum temperature, and the minimum and maximum temperature requirements for seed germination vary among species (Zimdahl 2007). Steiner (1968) showed that seeds within a population, even with the same genotype, did not germinate all at the same time when exposed to the same environmental stimuli, indicating a survival mechanism to enhance the chances of species reproductive success.

iii) Pre-emergence elongation. In agricultural lands, weed seeds are distributed throughout the soil profile, being buried by tillage and planting implements, wheel and animal traffic, and natural soil shrinking and swelling. Seed burial can be either a negative or a positive consequence for the emergence process (Forcella et al. 2000). Sometimes germination can occur at deeper burial depths, but seed reserves may be exhausted before the seedling reaches the soil surface, resulting in seedling death (Li et al. 2006). Large-seeded species are more likely to emerge from deeper burial depths than small-seeded species (Grundy et al. 2003), and the same is true for larger seeds within the same species (Li et al. 2006).

iv) Emergence. Like germination, emergence itself is typically defined from a practical point of view. The process of emergence is defined as the “first appearance of a seedling at the soil surface” (Forcella et al., 2000), and ultimately is the process of interest, because this is the point when weeds are noticed in agricultural fields. Knowledge of when and for how long weed species are to emerge under field conditions
is useful to determine the best time for cultivation or other postemergence weed management tactics (Ogg and Dawson 1984).

**Predicting seedling emergence**

Although agriculture is increasingly relying on modern technology, knowledge of the biological systems in which these technologies are used is critical for reliable interpretation of data and for implementation of management strategies. Biological information for weeds is valuable and necessary for developing alternative management strategies. Scouting fields for pest problems is essential in any cropping system, whereas information on relative weed emergence time and sequence could increase the effectiveness of weed scouting trips. Producers with cropping systems that use little to no herbicides need information on weed emergence to plan cultural practices (i.e., tillage, planting time, and crop choice to effectively compete with weeds), and those who rely on chemical strategies need this information to plan the best time for herbicide application.

Seedling emergence has commonly been correlated to calendar date (Ogg and Dawson 1984; Baskin et al. 1986; Hatzler et al. 1999). This is one of the simplest and most practical approaches to describe weed emergence in years when temperature patterns are within the expected range and soil moisture is adequate, because accurate predictions of emergence can be expected. Because seasonal environmental patterns are site specific, emergence predictions are useful only to the region where experiments were conducted. However, more general emergence models can be developed by correlating emergence patterns to microclimatic conditions (Grundy and Mead 2000). Two different approaches that correlate emergence patterns to environmental conditions have been used: mechanistic and empirical emergence models (Forcella et al. 2000).
Mechanistic models are more complex because they simulate seed dormancy and germination, and seedling elongation and emergence as a function of environmental conditions (soil temperature, moisture, diurnal temperature fluctuation, air and light quality, and seed burial depth). Empirical models are simpler because they only correlate seedling emergence to microclimatic conditions (i.e., soil temperature, soil moisture). Even though mechanistic models might be biologically more accurate, they are more labor intensive and difficult to develop and use than empirical models. Therefore, the development and use of empirical models can provide useful predictions of seedling emergence (Forcella et al. 2000).

A number of different empirical approaches have been used to predict weed emergence, but the most commonly used empirical approaches are the thermal time (TT) and hydrothermal time (HTT) models. Because temperature is the main environmental factor regulating germination and emergence, TT models have been created to predict emergence of several weed species based on accumulation of heat units above a minimum base value ($T_{\text{base}}$) (e.g., growing degree days [GDD]). Because water is also an essential component for seed germination, Gummerson (1986) proposed the HTT concept, accounting for the effects of soil moisture on time of seedling emergence. HTT uses the TT concept but only allows accumulation of heat units when soil moisture is above some threshold soil water content required for seed germination ($\Psi_{\text{base}}$).

$T_{\text{base}}$ (C) and $\Psi_{\text{base}}$ (MPa) are critical parameters for TT and HTT accumulation, respectively. Researchers have used several approaches to obtain appropriate values to develop predictive models for weed emergence. Experiments under controlled conditions have been conducted to determine $T_{\text{base}}$ and $\Psi_{\text{base}}$ (Masin et al. 2005 and 2010).
Alternatively, $T_{\text{base}}$ and $\Psi_{\text{base}}$ have been estimated by iterating a set of temperatures or/and soil water potentials until the best statistical fit of a sigmoidal function to the relationship between cumulative TT/HTT and cumulative emergence is obtained (Izquierdo et al. 2009; Martinson et al. 2007). The same $T_{\text{base}}$ has been used for several species to compare emergence sequence across locations, even though $T_{\text{base}}$ differs among species (Myers et al. 2004). Accurate $T_{\text{base}}$ and $\Psi_{\text{base}}$ values for each species are necessary to improve the accuracy of predictive models of weed emergence.

Different kinds of weather data have been used to develop TT and/or HTT models, including: daily maximum and minimum air temperature obtained from the nearest weather station averaged on a daily basis (Leblanc et al. 2003); daily soil temperature and moisture measured *in situ* using buried temperature sensors connected to a data logger (Masin et al. 2010); daily maximum and minimum soil temperature measured *in situ* using buried sensors attached to a data logger averaged on a daily basis (Dorado et al. 2009); daily maximum and minimum air temperature and precipitation data obtained from the nearest weather station and daily average soil temperature and water potential estimated using the WeedCast software developed by Forcella (1998) (Leguizamón et al. 2005); daily maximum and minimum air temperature and precipitation data from the nearest weather station used to estimate daily average soil temperature and water potential using the STM$^2$ software developed by Spokas and Forcella (2009) (Schutte et al. 2008); or spatially interpolated daily average soil temperature data provided by the ZedX agricultural information systems provider (ZedX, Inc., Bellefonte, PA) (Myers et al. 2004). The quality of the input weather data input to build predictive models for weed emergence is critical for making predictions more
accurate and practical (Grundy 2003). Furthermore, scientists must be clear when describing the methods used to obtain weather data and to calculate TT and/or HTT, so others can correctly interpret and apply the reported models.

Leblanc et al. (2003), using maximum and minimum daily air temperature data to accumulate TT, predicted emergence of common lambsquarters (*Chenopodium album*) with satisfactory levels of accuracy, but this research was conducted in Quebec, Canada, where soil moisture is not a limiting factor during the time when common lambsquarters seedlings typically emerge. Therefore, where water is not a limiting factor during emergence, models based on air temperature could be easily used by farmers who typically don’t have an on farm weather station to collect soil temperature data to facilitate decisions on time of weed management. However, Roman et al. (2000), also predicting emergence of common lambsquarters in Canada, reported that the use of soil temperature to accumulate TT resulted in more accurate predictions than air temperature. Therefore, the use of soil temperature to calculate TT might be the most accurate approach because soil is the environment where germination takes place. In a situation where soil temperature data is not available, publicly available software that simulates soil temperature and moisture can be used (i.e., WeedCast, STM$^2$). WeedCast simulates soil temperature and moisture on a daily basis at 5 cm depth based on soil type, previous crop, and cultivation method, along with daily maximum and minimum air temperature, and precipitation data (Forcella 1998). STM$^2$ estimates soil temperature and moisture on a daily basis at several depths based on soil properties (sand, silt, clay, and organic matter), latitude and longitude, field elevation, average wind speed, daily maximum and minimum air temperature, and precipitation data (Spokas and Forcella 2009). These
models have been shown to be accurate when estimating soil temperature, but the accuracy of predicted soil moisture has been variable (Spokas and Forcella 2009; Leguizamon et al. 2005). However, in the absence of more accurate tools (e.g., *in situ* weather sensors), these software can provide rough estimations of microclimatic conditions to help growers predict weed emergence and make decisions regarding the time of weed management.

When comparing the accuracy of predictive models for weed emergence based on the accumulation of TT and HTT, Leguizamon et al. (2005) found that when water was not a limiting factor in the soil, a good relationship between TT and seedling emergence of *Avena sterilis ssp. ludoviciana* was obtained. However, when water was limiting, the use of HTT enabled the use of a single function to describe patterns of seedling emergence for this species in different sites. Masin et al. (2010) reported that a model based on HTT had the ability to predict pauses in weed emergence due to low soil water content, improving the accuracy of predictions. In general, HTT models have improved prediction, but monitoring soil water potential accurately can be difficult.

The starting time to accumulate TT or HTT is another important component when predicting seedling emergence and should have a biological meaning to support it. Myers et al. (2004) started to accumulate GDD on January 1 for predicting emergence of 8 summer annual species in the northeastern United States. Schutte et al. (2008), predicting emergence of giant ragweed (*Ambosia trifida*) in west central Ohio, started to accumulate hydrothermal time from March 1 because giant ragweed emergence typically begins mid- to late March in Ohio. Martinson et al. (2007), predicting emergence of wild oat (*Avena fatua*) in the northern United States, started to accumulate TT and HTT on April 1 of each
year. This date was chosen because it reflects the average time when soils in this area begin to thaw after freezing to depths of at least 50 cm each winter. Ekeleme et al. (2005), predicting seedling emergence of tropic ageratum (*Ageratum conyzoides*) in West Africa, started to accumulate hydrothermal time based on cultivation time for each year of the experiment (April 1, 1994 and 1998; March 1, 1997; May 1, 1999; and April 30, 2000). Masin et al. (2010), predicting emergence of velvetleaf (*Abutilon theophrasti*) and johnsongrass (*Sorghum halepense*) in north-central Italy, started to accumulate TT and HTT from March 1 in both years. Leguizamon et al. (2009), predicting emergence of six summer annual grasses in Argentina, started to accumulate thermal time on August 1 because it was expected that at this time the cold of winter (June-July) had released seed dormancy but germination had not started. Most of the studies cited above modeled emergence of summer annual weeds using accumulation of TT or HTT beginning right after periods of low temperatures. This can be supported by the fact that many summer annual weeds require a period of low temperatures to overcome dormancy (Forcella et al. 2000; Leguizamon et al. 2009). Even though no predictive models for winter annual weed emergence have been reported, the best time to start accumulating TT or HTT to predict emergence of these weed species may be when temperatures start to decrease after mid-summer, because many of these species require high temperatures to overcome dormancy (Forcella et al. 2000; Baskin and Baskin 1988).

**Research Summary and Objectives**

Winter annual weeds have become common in no-till agricultural lands in the midwestern USA. Delayed soil warming, competition for water and nutrients during
initial establishment of the main crop (i.e., soybean, corn), difficult planting operations, and yield loss are some of the problems caused by the presence of dense mats of winter annual weeds. Moreover, some of these weed species have been reported as alternative host for the soybean cyst nematode (*Heterodera glycines*, SCN).

Research looking at the window of herbicide application to provide better winter annual weed control has been conducted but the effect of time of herbicide application on SCN development on weed hosts has not been reported. Thus, our first objective was to evaluate how the development of SCN on henbit roots was affected by time of herbicide application and herbicide mode of action under controlled conditions. The results of this research may help farmers to understand the importance of early control of winter annual weeds, especially species that can act as alternative hosts of SCN.

The emergence pattern of summer annual weeds in the midwestern USA has been extensively studied, but little information is available for winter annual weeds. Thus, our second objective was to predict emergence of winter annual weed species common to the midwest region of the United States using novel models based on the accumulation of modified thermal/hydrothermal time. The results of this research may help farmers, crop consultants, extension educators, and scientists to understand when winter annual weed species are likely to emerge in the field, what the main environmental factors are that trigger winter annual weed seedling emergence (i.e., soil temperature, moisture), and to better answer the commonly asked question: “when is the best time to control winter annual weeds?"
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Chapter 2

Influence of Two Herbicides on Soybean Cyst Nematode (Heterodera glycines) Reproduction on Henbit (Lamium amplexicaule) Roots

Abstract

Soybean cyst nematode (SCN) is the most yield-limiting pathogen of soybean in the United States. Henbit is a prevalent winter annual weed species in no-till fields and is reported to be an alternative host of SCN. A greenhouse study was conducted to evaluate how the development of SCN on henbit roots was affected by herbicide mode of action and time of herbicide application. Henbit plants were grown in watertight pots placed in a water bath bench that kept soil temperature constant (27 ± 1 C) during the study. Ten d after transplanting, pots were inoculated with approximately 1,000 SCN eggs. At 7, 14, or 21 d after inoculation (DAI), henbit plants were sprayed with recommended dose of either glyphosate (870 g ae ha\(^{-1}\)) or 2,4-D (1,070 g ae ha\(^{-1}\)). The experiment was arranged in a randomized complete block design with five replications per treatment, and two experimental runs separated in time. At 28 DAI, the total number of SCN cysts and eggs, and plant shoot and root dry weight per pot were determined. Henbit root and shoot biomass increased as the time of herbicide application was delayed. Glyphosate reduced root biomass more than 2,4-D, but no differences in shoot biomass were detected. The number of SCN cysts per henbit plant and eggs per cyst increased as the herbicide application was delayed from 7 to 21 DAI. Glyphosate reduced the number of cysts found on henbit roots more than 2,4-D, especially at earlier application times. On plants treated with glyphosate, SCN-females produced only half the number of eggs of SCN-
females on henbit plants treated with 2,4-D, regardless of time of application. These results indicate that early control of henbit plants, especially with glyphosate, can reduce SCN reproduction potential in SCN infested fields.

**Nomenclature:** Glyphosate; 2,4-D; henbit, *Lamium amplexicaule* L. LAMAM; soybean, *Glycine max* (L.) Merr. ‘ASGROW 3005’; soybean cyst nematode, *Heterodera glycines* Ichinohe.

**Key words:** Nematode development, SCN alternative host, shikimate pathway, winter annual weed.
Introduction

Soybean cyst nematode is considered the most yield-limiting disease of soybean in the United States (Wrather and Koenning 2006). SCN is an endoparasitic plant nematode that was first detected in the United States in 1954 in North Carolina (Wrather et al. 1984) and is currently found in most states where soybean is cultivated. In Nebraska, the nematode was first detected in 1986 (Powers et al. 1989), and its presence has been confirmed in 52 of the 93 counties (Giesler and Wilson 2011). SCN can damage host plants by removing essential plant nutrients from the root cells and disrupting the root vascular system, reducing water and nutrient uptake and transport from the roots to aboveground biomass (Asmus and Ferraz 2002; Hershman 1997). Additionally, SCN infection can indirectly damage soybean by reducing rhizobium nodulation and facilitating the occurrence of some diseases caused by other soilborne pathogens (Hershman 1997; Wrather et al. 1984). The classic symptoms caused by SCN range from asymptomatic to stunting, yellowing, and wilting (Asmus and Ferraz 2002; Niblack 2005). Soybean yield reductions of up to 30% have been caused by SCN without visually detectable aboveground symptoms (Noel 1992). SCN symptoms are typically more pronounced for infected plants growing under stressful conditions (Faghihi and Ferris 2006). The use of resistant varieties and rotation with nonhost crops (e.g., corn, sorghum, or wheat) are the main strategies recommended for SCN management (Niblack 2005).

Winter annual weeds are species that typically emerge in the fall, overwinter as small seedlings, grow rapidly during the spring, and produce seeds and senesce by late spring or early summer (Creech et al. 2007a; Radosevish et al. 1997). These weed species have the ability to survive and grow during times of the year when environmental
conditions, mainly temperature, are not favorable for the development of other plant species. Winter annual weeds have become common in U.S. row crop production due to the increased adoption of conservation tillage practices (Swagata et al. 2009), widespread adoption of glyphosate-resistant crops and subsequent over-dependence on glyphosate (Owen and Zelaya 2005), and consequently the reduced use of other herbicides (Shaner 2000).

The impact of winter annual weeds in cropping systems often is overlooked because these weeds typically complete their lifecycle near to the time of sowing summer crops. However, dense mats of winter annual weeds can result in delayed soil warming during early spring (Bruce et al. 2000), competition for water and nutrients during initial establishment of the main crop (Bernards and Sandell 2011), and difficult planting operations (Dahlke et al. 2001). Moreover, several winter annual weeds, including henbit, purple deadnettle (*Lamium purpureum* L.), and field pennycress (*Thlaspi arvense* L.), have been reported as alternative hosts of SCN (Venkatesh et al. 2000). SCN reproduction on henbit and purple deadnettle roots in fields of the midwestern United States has been reported (Creech et al. 2007b). Henbit is one of the most prevalent winter annual weed species in no-till fields in Nebraska; thus, SCN reproduction could be elevated when this weed is not controlled.

Herbicide application during late fall or early spring is becoming a common practice due to the current problems associated with the presence of winter annual weeds. Research has shown that a fall herbicide application has provided satisfactory weed control (Hasty et al. 2004) and can be beneficial when compared to an early spring application, especially during wet years, because farmers can better spread their workload.
over time (Krausz et al. 2003). Winter annual weeds are more susceptible to herbicide treatments in the fall when they are small, but herbicides should only be sprayed when environmental conditions are favorable for both operational application and foliar uptake (Bernards et al. 2011; Hasty et al. 2004). During late spring, herbicide application might not result in desired control because these weeds are at an advanced growth stage (Johnson et al. 2008). Also, Creech et al. (2007b) found that the majority of SCN reproduction on winter annual weeds occurred during the fall. This suggests that fall management of winter annual weeds might be the most effective way to minimize potential reproduction of SCN on these weed species. Thus, failure to manage winter annual weeds could provide an additional niche for SCN to develop and increase its population density in the absence of soybean (Johnson et al. 2008).

Glyphosate and 2,4-D are two translocated herbicides recommended for the control of winter annual weeds (Bernards et al. 2011; Hasty et al. 2004). Glyphosate is a nonselective POST herbicide that inhibits 5-enolpyruvyl shikimate-3-phosphate (EPSP) synthase in plants. 2,4-D is a synthetic auxin POST herbicide that controls many broadleaf weeds (Senseman 2007). The interaction of herbicide application timing and SCN development on secondary weed hosts has not been reported. Thus, the objective of this research was to evaluate how the development of SCN on henbit roots was affected by time of herbicide application and herbicide mode of action. We hypothesized that earlier herbicide applications would result in better henbit control and reduced SCN reproduction in the henbit roots than later applications.
**Materials and Methods**

Henbit seeds were collected from the Agronomy Farm at the University of Nebraska in Lincoln, NE (40.85°N, 96.62°W) in April of 2010. A minimum of 40 plants were harvested in the field and allowed to dry in 30-L plastic containers in the greenhouse for 14 days. When dry, plant residues were discarded and mature seeds in the bottom of the containers were sieved and cleaned. Processed henbit seeds were kept in a dark room for 12 months to relieve their inherent dormancy (Baskin and Baskin 1984). Seeds of henbit and SCN-susceptible soybean (‘Asgrow 3005’) were planted in round, watertight plastic pots (10 cm diam and 12 cm high) filled with 750 ml sterilized soil (93% sand, 4% silt, 3% clay, and 0.4% organic matter). Pots were placed in a temperature-controlled water bath bench developed to keep root zone temperature constant (Figure 1). The temperature in the water bath bench was regulated by an Isotemp refrigerating heating circulator Model 3016D (Fisher Scientific Inc., Pittsburgh, PA) and was set at 27°C. Prior to planting, henbit seeds were placed in wet paper rolls and incubated in a sealed plastic container placed in the greenhouse (24 ± 2°C day and 19 ± 3°C night) for 4 days to allow radical emergence. One henbit seedling was transplanted per pot to a depth of 1 cm. Soybean seeds were planted directly in the soil at a depth of 3 cm (1 seed pot⁻¹) on the same day that henbit seedlings were transplanted. Ten days after planting, pots were inoculated with approximately 1,000 SCN eggs. SCN egg inoculum, further characterized as HG type 1.7, was obtained from mature cysts developed on susceptible soybean plants (‘Asgrow 3005’) in the water bath system described above. One thousand SCN eggs were delivered to each pot in two 1-ml aliquots of egg.
suspension (500 eggs ml\(^{-1}\)) in two 2-cm-deep holes made 0.5 cm from the main stem of the henbit or soybean plant. A set of noninoculated henbit plants was also maintained. The noninoculated plants were treated in a similar way, but instead of inoculation with the SCN egg suspension, only water was applied in the holes.

At 7, 14, and 21 DAI with SCN eggs, predetermined henbit plants were sprayed with the recommended dose of either glyphosate (870 g ae ha\(^{-1}\)) + ammonium sulfate (AMS) (2,860 g ha\(^{-1}\)) or 2,4-D (1,070 g ae ha\(^{-1}\)) + nonionic surfactant (350 ml ha\(^{-1}\)) + AMS (2,860 g ha\(^{-1}\)) (Bernards et al. 2011). Herbicide treatments were applied to henbit plants within a spray chamber (Research Track Sprayer; DeVries, Hollandale, MN) in 140 L ha\(^{-1}\) carrier volume using a TP8001E flat-fan nozzle tip (TeeJet Technologies, Spraying Systems Co., Wheaton, IL) at a pressure of 241 kPa (Figure 2). Plants were grown in a greenhouse at 20°C with 12-h supplemental lighting in addition to natural radiation. Plants were watered daily and special care was taken when watering to avoid cross-contamination of SCN eggs and vermiform infecting juveniles (J2). Soil temperature at 5 cm depth and air temperature at the plant canopy level were recorded on a daily basis using a WatchDog data logger Model 450 (Spectrum Technologies, Inc., Plainfield, IL).

Henbit and soybean plants were clipped at the soil surface at 28 DAI, oven-dried to constant mass at 60°C, and weighed. Pots were then saturated with water to facilitate soil removal. SCN cysts were collected by the sieving and decanting methodology described by Faghihi et al. (1986). Briefly, soil and roots from each pot were emptied into plastic buckets containing approximately 3 L of water. Roots were manually separated from the soil, placed over stacked sieves (840- over 250-μm pore), and gently sprayed
with pressurized water to dislodge cysts. The soil in the bucket was stirred vigorously to suspend soil and dislodge remaining cysts. The solution was poured over the stacked sieves (840- over 250-μm pore), and this procedure was repeated four times. Roots that remained in the soil were further captured by the 840-μm pore sieve. Cysts retained on the 250-μm pore sieves were rinsed with water from a squirt bottle, and the final extracts were refrigerated until cysts were counted. Roots were oven-dried to constant mass at 60 C and weighed. Cysts were counted by pouring all extracts into a plate count petri dish under a dissecting microscope. After counting, the solution containing SCN cysts was poured over stacked sieves (150- over 38-μm pore). Cysts retained by the 150-μm pore sieve were crushed using a rubber stopper and eggs were caught by the 38-μm pore sieve. SCN eggs retained on the 38-μm pore sieves were rinsed with water from a squirt bottle. The extract containing eggs was adjusted to 20 ml and 1 ml of acid fuchsin stain was added to the solution (Southey 1986). Beakers containing eggs and stain were microwaved until the suspension boiled (approximately 30 s per sample). Beakers were removed from the microwave and allowed to cool. Once cool, 1-ml aliquot of suspension was poured in a counting slide and eggs were counted. Egg counts were repeated three times and an average number of eggs per 1 ml of solution was taken to estimate the total number of eggs in the suspension. Number of eggs per cyst was calculated by dividing the estimated total number of eggs in the suspension by the total number of cysts per plant.

The experiment was conducted as a randomized complete block design with nine treatments. Treatments were comprised of SCN-inoculated henbit plants treated with two herbicides (glyphosate or 2,4-D) at three times of application (7, 14, or 21 DAI).
Additionally, SCN-inoculated soybean and henbit (control) plants and a set of noninoculated henbit plants not treated with herbicide were grown. SCN-inoculated soybean plants were grown in order to compare the development of the nematode in the main host (soybean) vs. its development on the alternative weed host (henbit), testing the additional hypothesis that soybean is a more suitable host for SCN than henbit. The noninoculated henbit plants were grown in order to test the additional hypothesis that the SCN infection on henbit roots would not impact the plant’s development. Each treatment was replicated five times and the experiment was repeated in time (first and second experimental runs were initiated on August 30 and September 13 of 2011, respectively). An ANOVA was performed using PROC GLIMMIX in SAS 9.2 (SAS Institute, Cary, NC). Experimental treatments were treated as fixed factors, whereas replication blocks nested within experimental runs were treated as random factors. Means were separated when the interaction or main effect was less than $P = 0.05$. Whenever necessary, data for the response variable was log transformed prior to analyses in order to satisfy Gaussian assumptions of normality and homogeneity of variance. All results presented were originated from the same mixed model analysis.
Results and Discussion

Air temperature in the greenhouse was greater in the second run (22.4 ± 0.3 C, mean ± standard error) than in the first run (20.9 ± 0.3 C). Consequently, soil temperature was also slightly greater during the second experimental run (27.3 ± 0.1 C) than in the first (26.8 ± 0.1 C). The small differences in air and soil temperature in this experiment did not alter soybean and henbit biomass, or SCN development (i.e., no statistical interactions with experimental run, data not shown).

SCN Development on Soybean and Henbit Roots

In preliminary studies under a similar controlled environment, cysts were detected at 21 d after SCN inoculation in both henbit and soybean roots (unpublished data). Wrather et al. (1984) reported that SCN completed its lifecycle within 24 d at 23 C, and Niblack (2005) reported that under ideal conditions, SCN can go from J2 infective stage to viable egg within 22 d. Therefore, 28 d was considered to be a sufficient amount of time to allow SCN to accomplish its primary lifecycle.

SCN-inoculated soybean root and shoot biomass was approximately three times greater than SCN-inoculated henbit at 28 DAI (Table 1). Soybean was a better host for SCN reproduction than henbit in terms of the number of cysts formed per plant (Table 1). These results corroborate those of Venkatesh et al. (2000) and Creech et al. (2007a), who also found more SCN cysts in soybean than in henbit roots. A likely explanation is the greater root mass in soybean compared to henbit, resulting in greater root soil exploration, consequently increasing the chances of a second-stage infective juvenile (J2) to find and penetrate the host root.
In contrast, the number of cysts produced per gram of root and the number of eggs per cyst did not differ between soybean and henbit (Table 1). Creech et al. (2007a) also found that the number of eggs per cyst was similar in soybean and henbit roots, but the number of SCN-cysts per gram of root was greater for henbit than soybean. Our results compare favorably with those of Niblack (2005), who reported an average of about 200 SCN eggs per cyst. However, Sipes et al. (1992) reported more than 600 eggs per cyst. Our results show that even though more SCN cysts were formed on soybean roots, henbit had the same potential to harbor this pathogen when compared on a unit root mass basis. Therefore, both species are suitable hosts for SCN.

**SCN Effect on Henbit Development**

SCN presence did not affect root or shoot growth of henbit (P = 0.45 and P = 0.86, respectively), and root and shoot biomass of the inoculated and noninoculated control treatments at 28 DAI did not differ (Table 1). These results are consistent with those of Creech et al. (2007a), who reported that SCN inoculation did not impact henbit plant growth or development.

**SCN-Infected Henbit Plant Response to Time of Herbicide Application and Mode of Action**

Results for the herbicide treated henbit plants are expressed as relative percentage of the nontreated SCN-inoculated henbit plants (Table 2).

**Henbit Response**

Herbicide application reduced henbit root and shoot biomass at 28 DAI. The 7 and 14 DAI application times resulted in 89 and 77% reduction in henbit root and shoot biomass, respectively. Even the 21 DAI application time resulted in at least a 30%
reduction in biomass (Table 2). Glyphosate reduced henbit root biomass more than 2,4-D (P = 0.03), especially at the earlier treatment date, but no differences in shoot biomass were detected (P = 0.36).

**SCN Response**

Herbicide application reduced the number of cysts per plant and eggs per cyst compared to the nontreated control. Lower reproduction ability of other cyst nematode species (i.e., rice cyst nematode, *Heterodera sacchari*) on stressed host plants has been reported (Audebert et al. 2000). Number of SCN cysts per plant and cysts per gram of root were influenced by the interaction of time of herbicide application and herbicide treatment (P = 0.0003 and P = 0.0019, respectively). Glyphosate reduced the number of cysts found on henbit roots more than 2,4-D did, especially at earlier application times (Table 2). No SCN cysts were detected on henbit plants treated with glyphosate at 7 DAI. In contrast, 2,4-D application at 7 DAI allowed cyst formation at very low numbers (only 3.3% of the nontreated control, Table 2). The number of cysts produced on henbit roots in the 2,4-D application at 14 DAI treatment was 43% of the control, whereas only 11% of the cysts were produced on glyphosate-treated plants (Table 2). The number of cysts produced on henbit roots was about 85% of the control when either herbicide was applied at 21 DAI (Table 2). Similarly, the number of cysts on a per gram of root basis in the 2,4-D application at 14 DAI was more than four times greater than on plants treated with glyphosate, but no difference in cysts per gram of root was detected when plants were treated at 21 DAI with either herbicide (data not shown). Glyphosate also reduced the number of eggs per cyst more than 2,4-D. On plants treated with glyphosate, SCN-
females produced only half the number of eggs of SCN-females on henbit plants treated with 2,4-D, regardless of time of herbicide application (Table 2).

We observed that cysts formed on nontreated soybean and henbit control plants were light yellow in color at 28 DAI. However, SCN cysts formed on plants treated with either herbicide at 7 or 14 DAI were consistently a darker brown color, and cysts formed on plants treated at 21 DAI showed initial darkening in parts of the cyst bodies (Figure 3). Darkening of the body wall is an indicator that females have accomplished their lifecycle and no longer require nourishment from the host plant (Niblack et al. 2006). The cysts formed on early-treated plants also were smaller in size. These results indicate that the early herbicide application forced the nematode to complete its lifecycle sooner, presumably due to SCN starvation resulting from plant death. Similarly, the sugarbeet cyst nematode (*Heterodera schachtii*) presented accelerated maturation when host foliage was removed (Gardner and Caswell-Chen 1997).

The greater impact of glyphosate on number of cysts per plant, cysts per gram of root, and eggs per cyst might be the result of a unique characteristic of nematode physiology. It was recently reported that phytoparasitic nematodes, including *H. glycines*, can modify basic plant metabolism and biochemical pathways (Niblack et al. 2006). Evidence for this is the recent discovery of chorismate mutase in SCN and other nematodes such as root-knot nematode (*Meloidogyne javanica*) (Bekal et al. 2003; Gao et al. 2003; Lambert et al. 1999). Chorismate mutases are enzymes present in the shikimate pathway, which occurs only in plants and microorganisms (e.g., fungi, bacteria). The shikimate pathway is not an active biochemical pathway in nematodes. In plants, the shikimate pathway is responsible for the biosynthesis of three aromatic amino acids
(phenylalanine, tyrosine, and tryptophan) and for a large number of secondary metabolites used for plant defense against biotic (e.g., insects) and abiotic factors (e.g., UV light) (Herrmann 1995; Niblack et al. 2006). Niblack et al. (2006) suggested that the nematode chorismate mutase might alter the shikimate pathway in plants in order to assist the nematodes in the parasitic process, although it is still unclear how plant metabolism is modified by this enzyme. The mode of action of glyphosate is the inhibition of EPSP synthase in plants, the penultimate step in the shikimate pathway (Herrmann 1995; Senseman 2007). Given the results of the present research and the findings reported in the literature, we hypothesize that modification of the shikimate pathway by glyphosate results in a reduced capacity for the soybean cyst nematode to maintain feeding sites (syncytium) in henbit roots.

**Practical Implications**

Nelson et al. (2006) reported that SCN population density increased between fall and spring when winter annual weed hosts of SCN were not controlled. However, when herbicides were fall-applied, SCN population remained constant between fall and spring. On the other hand, Creech et al. (2008) found that in fields with low winter annual weed densities, weed control had no impact on SCN populations because so few weeds were present to facilitate SCN population growth. To our knowledge, research to determine the critical density of winter annual weeds that can result in increased SCN populations has not been conducted. Our results indicate that under situations where density is high enough to result in increased SCN populations, henbit should be controlled shortly after emergence. Therefore, understanding emergence patterns of winter annual weeds under field conditions is essential to aid growers in timing fall weed control.
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Figure 1. Water bath bench developed to keep root zone temperature constant. The temperature in this system is regulated by an Isotemp refrigerating heating circulator Model 3016D (Fisher Scientific Inc., Pittsburgh, PA).
Figure 2. Spray chamber (Research Track Sprayer; DeVries, Hollandale, MN) used to deliver herbicide treatments.
Figure 3. Herbicide effect on SCN-cyst development on henbit roots. Cysts were harvested at 28 days after inoculation with 1,000 SCN eggs (DAI). A picture from a cyst developed on soybeans is included for comparison.
Table 1. Plant biomass and soybean cyst nematode (SCN) development on the nonherbicide treated control henbit plants (SCN-noninoculated and SCN-inoculated) and soybean plants (SCN-inoculated) at 28 days after inoculation with 1,000 SCN eggs \((n = 10)\).\(^a\)

<table>
<thead>
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<th>Species</th>
<th>Plant biomass</th>
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<tr>
<td></td>
<td>Root (g)</td>
<td>Shoot (g)</td>
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<tr>
<td>Soybean, SCN-inoculated</td>
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<td>1.25 a</td>
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<td>Henbit, SCN-inoculated</td>
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<td>0.40 b</td>
</tr>
<tr>
<td>Henbit, SCN-noninoculated</td>
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</tbody>
</table>

\(^a\)Root and shoot biomass, SCN cysts per plant and per gram of root, and SCN eggs per cyst data were log transformed prior to analysis to meet the ANOVA assumptions. Backtransformed means are presented for ease of interpretation. Means within a column followed by the same letter are not different at \(P \leq 0.05\).

\(^b\)No SCN cysts, and consequently no SCN eggs, were observed in any plant where SCN was not inoculated. Thus, these mean values had no variance.
Table 2. Relative (% of nontreated control plants\textsuperscript{a}) henbit root and shoot biomass and SCN development at 28 days after inoculation with 1,000 SCN eggs (DAI) as influenced by glyphosate or 2,4-D application at 7, 14, or 21 DAI (n = 10).\textsuperscript{b}

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Time (DAI)</th>
<th>Plant biomass</th>
<th>SCN development</th>
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<tr>
<td></td>
<td></td>
<td>Root (%)</td>
<td>Shoot (%)</td>
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<tr>
<td>Glyphosate</td>
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<td>21</td>
<td>52.1 a</td>
<td>58.2 a</td>
</tr>
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</table>

\textsuperscript{a} Mean values for the control treatment (henbit, SCN-inoculated) harvested at 28 DAI are shown in Table 1.

\textsuperscript{b} Root and shoot biomass, SCN cysts per plant, and SCN eggs per cyst data were log transformed prior to analysis to meet the ANOVA assumptions. Backtransformed means are presented for ease of interpretation. Means within a column followed by the same letter are not different at P≤0.05.

\textsuperscript{c} No cysts, and consequently no SCN eggs, were observed in any plant where glyphosate was applied at 7 DAI. Thus, these mean values had no variance.
References


Chapter 3

Environmental Triggers of Winter Annual Weed Emergence in the Midwestern United States

Abstract

Winter annual weeds are becoming more common in many row crop fields in the midwestern USA. These species typically emerge in the fall and complete their life cycle near the time of crop sowing in the spring. The objectives of this research were to understand the roles of soil temperature (daily average and fluctuation) and moisture on the emergence of nine winter annual weed species and dandelion, and also to develop predictive models for weed emergence based on the accumulation of modified thermal/hydrothermal time (mHTT). Research plots were established at Lincoln, Mead, and at two sites (irrigated and rainfed) near Clay Center, NE, in 2010 and 2011. In July of each year, 1,000 seeds of each species were planted in 15x20x6 cm mesh cages installed between soybean rows. Soil temperature and moisture were recorded at 2 cm depth in the soil. Emerged seedlings were counted and removed from the cages on a weekly basis until late-fall when emergence ceased and then started again when emergence resumed in late-winter until beginning of summer, when emergence stopped for all species. Emergence data were converted from weekly counts to cumulative emergence (%). Weather data was used to accumulate mHTT beginning on August 1. A Weibull function was selected to fit cumulative emergence (%) on cumulative mHTT (7 base temperature [T_{base}] x 6 base water potential [\Psi_{base}] x 3 base temperature fluctuation [F_{base}] candidate threshold values = 126 models) and also to days after August 1 (DAA1), for a total of
127 candidate models. The search for optimal thresholds ($T_{\text{base}}$, $\Psi_{\text{base}}$, and $F_{\text{base}}$) was based on the theoretic-model selection approach (AIC criterion), which indicated the importance of and the optimum base value for each component. A simple model including only $T_{\text{base}}$ provided the best fit to the data for most species included in this study (Carolina foxtail, shepherd’s purse, tansymustard, henbit, and field pansy). For field pennycress, a model based only on DAA1 resulted in the best fit. The best fit was achieved for downy brome and purslane speedwell by including $T_{\text{base}}$ and $\Psi_{\text{base}}$, and for dandelion by including $T_{\text{base}}$ and $F_{\text{base}}$. Including all three components improved model fit only for Virginia pepperweed. As expected, optimal base threshold values were species-specific. Soil temperature was the most important factor related to winter annual weed emergence and soil temperature fluctuation and moisture were not as critical as initially hypothesized in influencing time of emergence. According to our “basic” models (using $T_{\text{base}} = 0$ C across all species), downy brome, tansymustard, Carolina foxtail, henbit, and field pansy had the majority of the seedlings (>95%) emerging during the fall. Virginia pepperweed, purslane speedwell, dandelion, shepherd’s purse, and field pennycress were the species that had seedlings emerging during both fall and spring. Our predictive models can help growers make better management decisions regarding winter annual weeds.

dandelion, *Taraxacum officinale* G.H. Weber ex Wiggers TAROF; field pennycress, *Thlaspi arvense* L. THLAR; purslane speedwell, *Veronica peregrina* L. VERPG; field pansy, *Viola bicolor* Pursh VIORA.

**Key words:** modified hydro/thermal time, information-theoretic model comparison approach, AIC criterion, Weibull model, weather data.
**Introduction**

Winter annual weeds typically emerge in the fall, overwinter as small seedlings, grow during the spring, and produce seeds and senesce by late spring or early summer (Radosevich et al. 1997; Creech et al. 2007). These species have the ability to survive and grow during times of the year when environmental conditions, mainly temperature, are not favorable for the development of other plant species. Even though it is known that the majority of winter annual weed species emerge in the fall, these species can be further classified as either obligate or facultative winter annual weeds (Baskin and Baskin 1988). Obligate winter annual weeds germinate only in the fall when soil temperatures are decreasing. However, they become dormant during the winter and seeds will not germinate until next fall, because exposure to high temperatures is required to overcome dormancy. Facultative winter annual weeds can germinate during both fall and spring (Baskin and Baskin 1988). The ability to germinate during both seasons is advantageous, because the risk of an entire population being eliminated at one period is reduced (i.e., late fall management or winter killing), thereby increasing the chances of individuals reproducing. Cici and Van Acker (2009) have also characterized winter annual weed species according to their emergence time: “only fall emergers” representing obligate winter annual weeds, and “mostly fall”, “mostly spring”, or both “fall and spring emergers” representing facultative winter annual weeds.

Winter annual weeds have become abundant in row crop fields due to the increased adoption of conservation tillage practices (Swagata et al. 2009), widespread adoption of glyphosate-resistant crops and over-dependence on glyphosate for weed control (Owen and Zelaya 2005), and the subsequent reduced use of residual herbicides
(Shaner 2000). The impact of winter annual weeds in cropping systems is often overlooked because these weeds complete their lifecycle near to the time of crop sowing in the spring (Johnson et al. 2008). However, dense mats of winter annual weeds may result in delayed soil warming in spring (Bruce et al. 2000), competition for nutrients during initial establishment of the main crop, reduced yield of the subsequent crop when not controlled well in advance of plating (Bernards and Sandell 2011), and difficult planting operations (Dahlke et al. 2001). Moreover, several winter annual weeds can act as alternative hosts for pests, including the soybean cyst nematode (*Heterodera glycines*, SCN) (Venkatesh et al. 2000).

Herbicide application during late fall or early spring is becoming a common practice among farmers due to the abundance of winter annual weeds. Research has shown that a fall herbicide application provides satisfactory weed control (Hasty et al. 2004) and may be beneficial when compared to an early spring application, especially during wet years, because farmers can better spread their workload over time (Krausz et al. 2003). Winter annual weeds are more susceptible to herbicide treatments in the fall or early spring when they are small, but herbicides should only be sprayed when environmental conditions are favorable for both operational application and foliar uptake (Hasty et al. 2004; Bernards et al. 2011). During late spring, herbicide application may not result in desired control because these weeds will be at an advanced growth stage (Johnson et al. 2008). Even though fall herbicide application has been shown to be advantageous, the time of weed emergence has not necessarily been considered to decide the best time of application in the reports cited above. Thus, understating when and for
how long winter annual weed species will emerge in the field can help growers achieve even more satisfactory levels of control.

Weeds typically occur in multi-species complexes, with all species having unique survival characteristics. According to Davis et al. (2008), if all weed seeds were to emerge at the same time, weed management would be a simple task. Instead, weeds are an annual problem because after a single seed rain event they can infest agricultural lands and create soil seedbanks that may persist for several years (Conn et al. 2006). The period of weed emergence is a function of the species present in the seedbank and their interaction with the environment (Forcella et al. 1997; Stoller and Wax 1973). Knowledge of the weed species present in the soil seedbank and when these species are most likely to emerge is important in planning effective weed control programs (Buhler et al. 1997; Cici and Van Acker 2009; Forcella et al. 2000).

Soil temperature, water content, and light are the main environmental factors driving seed germination and emergence (Forcella et al. 2000). Blackshaw et al. (2002) showed that for henbit (*Lamium amplexicaule*), temperature had a greater impact on seed germination than water content. However, lack of soil moisture delayed germination of this species (Baskin et al 1986). Summer and winter annual weed species typically have consistent emergence patterns across years (Baskin and Baskin 1988). The germination requirements and emergence patterns of several summer annual weeds have been studied but little effort has been directed to understand the biology and ecology of winter annual weeds, and particularly the effects of temperature and water potential on seed germination, seedling emergence, and overwintering plant survival (Cici and Van Acker 2009).
Seedling emergence has commonly been correlated to calendar date (Ogg and Dawson 1984; Baskin et al. 1986; Hatzler et al. 1999). This is one of the simplest and most practical approaches to describe weed emergence in years when temperature patterns are within the expected range and adequate soil moisture is available, because accurate predictions of emergence can be expected. Because seasonal environmental patterns are site specific, these emergence predictions are useful only to the region where the experiments were conducted. More general emergence models may be developed by correlating emergence patterns to microclimatic conditions (Grundy and Mead 2000). Two different approaches that correlate emergence patterns to environmental conditions have been used to describe weed emergence: mechanistic and empirical models (Forcella et al. 2000). Mechanistic models are more complex because they simulate seed dormancy and germination, as well as seedling elongation and emergence as a function of environmental conditions (soil temperature, moisture, diurnal temperature fluctuation, air and light quality, and seed burial depth). Empirical models are simpler because they correlate seedling emergence only to microclimatic conditions (soil temperature and moisture). Even though mechanistic models have the potential to be more accurate, they are more labor intensive and difficult to develop and use than empirical models. Therefore, development and use of empirical models can provide useful predictions of seedling emergence until mechanistic models become available (Forcella et al. 2000).

A number of different empirical approaches have been used to predict weed emergence, but the most commonly used empirical approaches are thermal time (TT) and hydrothermal time (HTT) models. Because temperature is the main environmental factor regulating germination and emergence (Baskin and Baskin 1988), TT models have been
created to predict emergence of several weed species based on accumulation of heat units above a minimum base value ($T_{\text{base}}$) (e.g., growing degree days [GDD]). And because water is also an essential component for seed germination, Gummerson (1986) proposed the HTT concept, to account for the effects of soil moisture on seed germination and emergence. HTT only allows accumulation of heat units (TT) when soil moisture is above some threshold soil water content required for seed germination ($\Psi_{\text{base}}$).

Recent advances in statistical analysis (the information-theoretic model comparison approach [Anderson 2008; Stephens et al. 2005]) have allowed scientists in other areas to extract a tremendous amount of information from their datasets, knowledge that would be wasted in cabinets otherwise. Stephens et al. (2005) suggested that the information-theoretic model comparison (ITMC) is appropriate for use in observational studies that assess multivariate patterns of causality. Therefore, ITMC may be a powerful tool that could help many weed scientists select better models for emergence studies. Our main goal in this research was to use this new tool to improve the predictive accuracy of weed emergence models. This would include analyzing the roles of soil temperature and moisture on the emergence process of winter annual weeds, and also estimate base and maximum threshold values for daily average temperature, temperature fluctuation, and water potential that triggers emergence for each of the weed species included in our research.

It has been reported that the majority of the winter annual weed species emerge at two periods of time in Canada, April-May and September-October (Cici and Van Acker 2009), but the emergence pattern of the most prevalent winter annual weed species in the midwest region of the United States has not been reported. The objectives of this research
were: *i*) to understand the roles of soil temperature and moisture on the emergence process of nine winter annual weed species and dandelion, *ii*) to develop predictive models for weed emergence based on the accumulation of modified thermal/hydrothermal time models using the information-theoretic model comparison approach, and *iii*) to understand the emergence time of each species included in our research.
**Materials and Methods**

**Field experiments**

Field experiments were conducted to evaluate emergence patterns and develop models based on the accumulation of modified thermal/hydrothermal time (mHTT) to predict emergence of nine winter annual weed species and dandelion, a perennial weed species, in Nebraska (Table 1). Experiments were established at the Lincoln Agronomy Farm (LAF) and the University of Nebraska-Lincoln East Campus Farm (UNL), Lincoln, NE, the Agricultural Research and Development Center (ARDC), near Mead, NE, and the South Central Agricultural Laboratory (SCAL), near Clay Center, NE, during the summers of 2010 and 2011. At SCAL, two sites were established in each year, one under rainfed conditions (rainfed, SCALRF) and the second under irrigated conditions (irrigated land, SCALIL), for a total of 8 site-seasons (Table 2).

Individual lots of mature weed seeds for nine winter annual weed species and dandelion were collected from LAF, SCAL, or local farmer’s fields (Table 1) between late-April and early-June in 2010 and 2011. A minimum of 40 plants were harvested per species in the field and allowed to dry in 30 L plastic containers in the greenhouse for at least 14 days. When dry, plant residues were discarded and mature seeds in the bottom of the containers were sieved and cleaned. This procedure was used for all species but downy brome and Carolina foxtail. For these two species, seed-heads were collected from the field, allowed to dry in 30 L plastic containers, and seeds were harvested manually by pulling seeds from the seed-heads. To determine average seed mass, three sets of one hundred seeds of each species were weighed in 2010, and in 2011, ten sets of one hundred seeds of each species were weighed to determine average seed weight (Table 1).
One thousand seeds of each species were measured by weight and separated into individual packets to use for establishing experimental plots. The seeds collected in 2010 were used for the first experimental season (July 2010- July 2011), and the seeds collected in 2011 were used for the second experimental season (July 2011-July 2012). Therefore, fresh seeds of each species from the same source were used at the four sites in each season.

In all sites, a locally recommended soybean cultivar was planted in rows spaced 0.76 m apart in a no-till system and grown according to standard practices adopted for each farm (Table 2). In early July of each year, 15 by 20 cm wide by 6 cm deep mesh baskets were buried 5 cm deep in the plots. Baskets were filled with 3 cm of topsoil from the plot area and then 2 cm of sieved soil collected from the surrounding area was added over the top. A 1 cm lip of the basket was left above the soil surface to contain the seeds. In each block, 10 baskets were installed into the ground (1 basket species⁻¹) 1.2 m apart from each other centered between two soybean rows. Blocks were replicated six times at each site in each season.

At the end of July of each year (Table 2), one thousand seeds of each species were sown in each basket. The average optimal depth for winter annual weed recruitment has been reported to be 2 cm or less (Cici and Van Acker 2009); therefore, burial depth was further determined based on seed size. Seeds from downy brome (the largest seeded species included in this research) were thoroughly mixed with the soil from the top 2 cm layer of each basket. Carolina foxtail, dandelion, field pansy, field pennycress, henbit, shepherd’s-purse, tansy mustard, and Virginia pepperweed seeds were thoroughly mixed with the soil from the top 1 cm layer. Purslane speedwell seeds (the smallest seeded
species included in this research) were sprinkled at the soil surface and incorporated in the top 0.5 cm layer.

Starting a week after planting the weed seeds, seedling emergence was assessed on a weekly basis until December when emergence ceased and then started again when emergence resumed at the end of February (2011) or beginning of March (2012) on a biweekly basis (once every other week) until July, when emergence stopped for all species. Due to atypically high temperatures during the winter of 2011-2012 (Table 3), seedling emergence was assessed once in January of 2012. At each assessment, emerged seedlings were enumerated and pulled from the baskets with minimal soil disturbance.

**Weather data collection**

For the first season (2010-2011), soil temperature and moisture were measured at 2 cm depth in two locations within each site (approximately 4 m apart) using ECT soil temperature sensors and EC-5 moisture sensors (Decagon Devices, Pullman, WA). For the second season (2011-2012), soil temperature and moisture were measured at 2 cm depth in three locations (approximately 2 m apart) within each site using 5TE Moisture-Temperature-EC sensors (Decagon Devices, Pullman, WA). All sensors were connected to an Em50 ECH2O data logger (Decagon Devices, Pullman, WA) that recorded data at 30 minutes intervals.

**Validating moisture readings**

Validation tests were conducted to evaluate the accuracy of the soil moisture sensors (Figure 1). In the second season, three soil samples were taken from 1 to 3 cm depth within the area surrounding each sensor (within a 2 meter radius) at each site once a week during 8 consecutive weeks (the exact time that samples were collected was
recorded for further comparisons with the sensor’s instantaneous readings). In the laboratory, each soil sample was divided into 3 subsamples and immediately weighed. Soil was then dried at 105°C for at least 24 h and dry soil weight was recorded (Hillel 1998). Gravimetric soil water content ($\theta_g$, g water g soil$^{-1}$), also called mass wetness, was calculated as (Hillel 1998):

$$\theta_g = \frac{\text{weight loss in drying}}{\text{dry weight}} = \frac{(\text{wet weight} - \text{dry weight})}{\text{dry weight}} \quad [1]$$

where weight loss in drying represents the amount of water (g) present in the soil when samples were taken. Volumetric water content ($\theta_v$), the amount of water per volume of soil (cm$^3$ cm$^{-3}$), was calculated as (Hillel 1998):

$$\theta_v = \frac{\theta_g \times \rho_{\text{soil}}}{\rho_{\text{water}}} \quad [2]$$

where $\rho_{\text{soil}}$ is the soil bulk density (g soil cm$^{-3}$, the ratio of soil dry mass to sample volume) and $\rho_{\text{water}}$ is the water density (1 g water cm$^{-3}$). Soil bulk density for each site-season was determined by taking seven undisturbed soil samples from 0 to 4 cm depth around the sensors (these samples were further used to validate the modeled “soil-water characteristic curves” that will be described later). Because the sensors’ readings for the first season were not calibrated while the experiments were ongoing, the same sensors were reinstalled in June of 2012 at the UNL site at the soil depth of 2 cm and left for 18 consecutive days to record moisture data at 30 minute intervals. Four soil samples were taken every other day to validate the sensor’s readings during this 18 days period. In the soil laboratory, each sample was divided into 3 subsamples and volumetric water content estimated as described previously. Instantaneous readings by the sensors were regressed against the volumetric water content data obtained from the samples taken in the field. A similar approach has been used by others (Tarara and Ham 1997; Song et al. 1998). The
linear equations obtained from the regressions for each season were further used to calibrate the sensor’s readings (Figure 1).

The EC-5 and 5TE sensors read soil moisture data as volumetric water content (m$^3$ m$^{-3}$). In order to incorporate the hydrothermal time concept (Gummerson 1986) into predictive models for weed emergence, soil moisture data has to be expressed as soil matric potential ($\Psi$, kPa). Volumetric water content indicates the amount of water present in the soil, whereas matric potential indicates the availability of water, or the energy required to remove water from the soil by seeds or plant roots (Collis-George and Hector 1966). In order to convert volumetric water content to matric potential data, “soil-water characteristic curves” were developed for each site-season using the equations suggested by Saxton et al. (1986) (Table 4). These authors demonstrated that accurate soil-water curves can be developed based on soil texture, however, a single regression model is not adequate to completely describe the relationship between soil matric potential ($\Psi$, kPa) and volumetric water content ($\theta_v$, m$^3$ m$^{-3}$). This relationship is continuous and nonlinear from -10 to -1500 kPa (permanent wilting point), linear from -10 kPa to air entry potential, and constant below air entry potential (saturation) (Saxton et al. 1986). Therefore, to estimate $\theta_v$ at each of these $\Psi$ ranges, a different set of equations had to be used (Table 4).

To validate our empirical soil-moisture curves (Table 5) developed based on the Saxton et al. (1986) equations (Table 4), $\theta_v$ data was obtained using the pressure plate method described by Klute (1986) over the pressures of -10, -30, -60, -100, and -200 kPa (these were the pressures that the apparatus used to collect these data allowed us to exert). Briefly, seven undisturbed soil cores (using 5 cm diameter by 4 cm high rings) were
collected in each site-season from 0 to 4 cm depth (within 2 m radius from the sensors) using a core sampler. Undisturbed samples were brought to the laboratory, placed inside the pressure apparatus, saturated, exposed to the desired pressure, and when equilibrium was achieved (water was no longer being removed from the system) the samples were weighed. Then samples were saturated again and the next higher pressure exerted. Once samples were exposed to all target pressures, soil was removed from the rings and soil bulk density ($\rho_{\text{soil}}$, g soil cm$^{-3}$) determined. At each weighing time, gravimetric water content data was obtained and at the end converted to volumetric water content as described previously. Measured and estimated $\theta_v$ from samples across all site-seasons were regressed and a satisfactory correlation was detected ($R^2=0.91$), indicating acceptable accuracy of the soil-water curves (Figure 2).

**Calculating modified thermal/hydrothermal time ($m$HTT)**

Daily average $\theta_v$ data recorded by the sensors was calibrated and then converted to water matric potential ($\Psi$, kPa) using the parameters obtained from the soil-characteristic equations suggested by Saxton et al. (1986) (Table 4 and 5). Soil temperature data was averaged on a daily basis and daily temperature fluctuation was calculated as daily maximum - minimum soil temperature. In order to better understand the roles of soil temperature ($T$), soil moisture ($\Psi$), and daily temperature fluctuation ($F$) on the emergence process of winter annual weeds, the following modified thermal/hydrothermal time model ($m$HTT) was developed as an extension of the HTT model suggested by Gummerson (1986) and calculated as:

$$m\text{HTT} = \sum_{i=1}^{n} \{([T] \cdot [\Psi] \cdot [F]) \cdot (T_{\text{mean}} - T_{\text{base}})\} \quad [3]$$
where: $T$ is interpreted as $T_{\text{base}} < T_{\text{mean}} < T_{\text{max}} = 1$, otherwise $= 0$; $\Psi$ as $\Psi_{\text{base}} < \Psi < \Psi_{\text{max}} = 1$, otherwise $= 0$; and $F$ as $F_{\text{base}} < F < F_{\text{max}} = 1$, otherwise $= 0$. $T_{\text{base}}$ = base soil temperature for seedling emergence (C); $T_{\text{mean}}$ = daily mean soil temperature at 2 cm depth; $T_{\text{max}}$ = maximum soil temperature for seedling emergence; $\Psi_{\text{base}}$ = base matric potential for seedling emergence (kPa); $\Psi$ = daily mean matric potential at 2 cm depth, $\Psi_{\text{max}}$ = maximum matric potential for seedling emergence; $F_{\text{base}}$ = base daily soil temperature fluctuation for seedling emergence (C); $F$ = daily measured soil temperature fluctuation at 2 cm depth; $F_{\text{max}}$ = maximum daily soil temperature fluctuation for seedling emergence.

The $i$ and $n$ represents the starting date for the accumulation of heat units (August 1) and the number of days after $n$, respectively. It has been reported that seeds of winter annual weeds are typically released from dormancy by high summer temperatures and will start to germinate when soil temperatures begin to decrease (i.e., mid-summer to early fall) (Forcella et al. 2000; Baskin and Baskin 1988); thus, August 1 was chosen as the starting date because at this time temperatures start to decrease in Nebraska (Table 3). Moreover, emerged winter annual weeds are not seen in Nebraska agricultural fields in July, probably due to excessive heat during this month. A set of initial base values for each soil threshold parameter with biological meaning was used to calculate $mHTT$ and are justified in the Results and Discussion section. A total of 126 possible combinations of threshold values were used. Emergence data were converted from weekly or biweekly counts to cumulative emergence (%) based on the total plant emergence per basket per season.

**Statistical analysis**
The cumulative emergence for each species was modeled with the Weibull function in which the independent variables were the 126 calculations of mHTT and days after August 1 as our “null model” (DAA1):

\[ y = Asym \times (1 - \exp(-\exp(lrc)\times(mHTT\ or\ DAA1)^{pwr})) \]  

[4]

where \( y \) is the cumulative emergence (%) at cumulative \( m \)HTT, \( Asym \) is the horizontal asymptote (theoretical maximum for \( y \) normalized to 100%), \( lrc \) is the natural logarithm for the rate of increase, and \( pwr \) is the power to which \( m \)HTT is raised (Crawley 2007). Weibull parameters (\( lrc \) and \( pwr \)) for each model were estimated using the NLME package of R version 2.15.1 (R Development Core Team 2012).

The information-theoretic model comparison approach (Akaike’s Information Criterion [AIC]), was used as the theoretical basis for model selection (Anderson 2008). Different from the traditional null-hypothesis testing, AIC is not considered a “test” because there is no statistical significance, asymptotic sampling distribution, or arbitrary P-values involved with it (Anderson 2008). This approach is highly recommend for observational studies and has been widely used in the ecological literature. The AIC relies on the maximum likelihood to estimate the expected distance between the predictive model and the “true generating mechanism” or reality (Anderson 2008). Moreover, model probability (Akaike weight or “AIC\( w_i \)”) indicates the weight of evidence in favor of model \( i \) being the actual best model in the pool of candidates, and can be further used to rank models. The AIC\( w \) for all models included in the pool of candidates must sum to 1. The AIC and model probability (AIC\( w \)) were computed for each model in the pool of candidates (total of 127 models for this study) using the AICcmodavg package of R version 2.15.1 (R Development Core Team 2012). The model
with the smallest value of AIC and highest probability (AIC\_w) was considered the model that closest described the full reality given the data (Anderson 2008), indicating the importance and the best threshold values for each environmental soil parameter on each species’ emergence.

Anderson (2008) recommends the inclusion of a “null” model in the pool of candidates to evaluate the worth of a particular assumption. In this case, the model based on DAA1 instead of mHTT was used as our “null” model, indicating that the accumulation of heat units would have no impact on weed emergence and a simple model based on day of the year would do a better job describing emergence.

**Model Goodness of Fit**

When using the AIC criterion, Anderson (2008) recommends reporting the goodness of fit for the top model. Therefore, the following goodness of fit tests were performed as indicators of top model quality for each species: RMSE, ME, \( d \), and bias.

Root mean square error (RMSE) was calculated according to Roman et al. (2000):

\[
\text{RMSE} = \left[ \frac{1}{n} \sum_{i=1}^{n} (P_i - O_i)^2 \right]^{1/2} \quad [5]
\]

where \( P_i \) is the predicted and \( O_i \) the observed value, and \( n \) is the total number of comparisons. The smaller the RMSE value, the closer the observed values are from the predicted ones. The modeling efficiency coefficient (ME), which differs to \( R^2 \) only by not having a lower bound, was calculated according to Mayer and Butler (1993):

\[
\text{ME} = 1 - \left[ \frac{\sum_{i=1}^{n} (O_i - P_i)^2}{\sum_{i=1}^{n} (O_i - \bar{O})^2} \right] \quad [6]
\]
where $\hat{O}i$ is the mean observed value. ME values can range from $-\infty$ to 1, with values closer to 1 indicating more accurate predictions. The index of agreement ($d$) was calculated as (Willmott 1981):

$$d = 1 - \left[ \frac{\sum_{i=1}^{n} (Oi - Pi)^2}{\sum_{i=1}^{n} (Oi - \bar{O}i)^2 + \sum_{i=1}^{n} (Pi - \bar{O}i)^2} \right]$$  \[7\]

where $d$ varies between 0 and 1, with a value closer to 1 indicating better prediction of the model (Willmott 1981). Bias was calculated according the formula suggested by Daly et al. (1994):

$$bias = \frac{1}{n} \sum_{i=1}^{n} (Pi - Oi)$$  \[8\]

where the closer the $bias$ to 0, the more accurate the prediction. Bias can be used as an indicator of systematic overprediction ($bias > 0$) or underprediction ($bias < 0$) by the model (Willmott and Matsuura, 2005). These indices (RMSE, ME, $d$, and $bias$) have been commonly used in the literature and seem to be relevant methods to measure model performance (Spokas and Forcella 2009; Spokas and Forcella 2006; McGiffen et al. 2008).
Results and Discussion

According to our preliminary analysis, placing a restriction on $\Psi_{\text{max}}$, $T_{\text{max}}$, and $R_{\text{max}}$ did not improve model performance for any species in this study (data not shown). Therefore, these parameters were withdrawn from subsequent mHTT models that were then interpreted as $\Psi_{\text{base}} < \Psi = 1$, otherwise $= 0$; $F_{\text{base}} < F = 1$, otherwise $= 0$; $T_{\text{base}} < T = 1$, otherwise $= 0$. The search for optimal $\Psi_{\text{base}}$, $T_{\text{base}}$, and $F_{\text{base}}$ based on the AIC criterion indicated the importance of and the optimum base value for each of these soil components. All three components were only important for one species tested, and a simple model including only $T_{\text{base}}$ performed the best for most species (Table 6).

Justifying the Selected Base Values

Grundy et al. (2000) reported 1.4 C and -1330 kPa as the base temperature and base matric potential, respectively, for common chickweed, a common winter annual weed species in North America and Europe. Similarly, Bond et al. (2007) described that at 5 C with matric potential of -1400 kPa, no germination of common chickweed was observed. Fernandez-Quintanilla et al. (1990) reported 0.8 C and 1500 kPa as the base temperature and base matric potential, respectively, for *Avena sterilis*, a common winter annual weed in winter cereal crops in Europe. Blackshaw et al. (2002) reported that henbit emergence declined as soil matric potential and temperature decreased from field capacity (-33 kPa) to permanent wilting point (-1500kPa) and from 20 to 5 C, respectively. Base temperature of 0 C has been commonly used for winter annual weeds (Bullied et al. 2003; Ball et al. 2004). Temperature fluctuation has been reported to increase germination rates of winter annual weeds (Bond et al. 2007). Moreover, emergence under field conditions has been reported to be restricted to the period when
the soil temperature and temperature range permissive for germination overlap (Benech-Arnold et al. 2000). Therefore, including daily temperature fluctuation in predictive models for weed emergence may improve the accuracy of predictions. Thus, we decided to include 7, 6, and 3 candidate threshold values for $T_{base}$, $\Psi_{base}$, and $F_{base}$, respectively. For $T_{base}$, the following values were used: 0, 1, 2, 3, 4, 5, and 6°C. $T_{base} = 0$°C has been commonly used for winter annual crops and weeds, but we wanted to further understand and estimate the “close to ideal” base temperature to best describe the emergence pattern of each species. For $\Psi_{base}$, the candidate values were: -1000, -1500 (permanent wilting point), -2000, -2500, and -3000 kPa, plus a $-\infty$ kPa. $\Psi_{base} = -\infty$ kPa simulated a situation where adding soil matric potential to $mHTT$ calculation would not improve model prediction. This represents the traditional thermal time (TT) calculation used by many authors where: $TT = \sum_{i=1}^{n} (T_{mean} - T_{base})$. This range of $\Psi_{base}$ values allowed us to identify species that were more sensitive to soil moisture. For $F_{base}$, 0, 5, and 10°C were used. $F_{base} = 0$°C simulated a situation where including temperature fluctuation on $mHTT$ calculation would not improve model prediction. This represents either the traditional TT calculation mentioned previously (when $\Psi_{base} = -\infty$ kPa) or the traditional hydrothermal time (HTT) calculation suggested by Gummerson (1986) where: $HTT = \sum_{i=1}^{n} (\Psi \times [T_{mean} - T_{base}])$. The combination of all threshold values (7 $T_{base} \times 6$ $\Psi_{base} \times 3$ $F_{base}$ candidate values = 126 possible combinations) plus adding a model using day of the year (DAA1) resulted in 127 candidate models that were compared using the AIC criterion.

**Estimation of $T_{base}$, $\Psi_{base}$, and $F_{base}$ and their importance for each species**
The search for optimal base temperature, matric potential, and temperature fluctuation for the \( m \)HTT model for seedling emergence of each weed species included in this study identified clear optima for each property threshold. The estimated \( T_{\text{base}}, \Psi_{\text{base}}, \) and \( F_{\text{base}} \) reported in this manuscript are expected to be biologically relevant since they were obtained from an analysis that utilized the progression of cumulative emergence over time under field conditions.

Based on the AIC criterion, for Carolina foxtail, shepherd’s purse, tansymustard, henbit, and field pansy the best fit of the model to the data occurred when \( m \)HTT was calculated including only \( T_{\text{base}} \) with values of 0, 0, 5, 2, and 1 C, respectively (Table 6, Figure 3). For downy brome and purslane speedwell, the best fit occurred when \( m \)HTT was calculated including \( T_{\text{base}} \) and \( \Psi_{\text{base}} \) with threshold values of 5 C and -3000 kPa, and 6 C and -3000 kPa, respectively (Table 6). For Virginia pepperweed, the best fit occurred when \( m \)HTT was calculated including all three parameters, \( T_{\text{base}}, \Psi_{\text{base}}, \) and \( F_{\text{base}} \), with threshold values of 0 C, -3000 kPa, and 5 C, respectively (Table 6, Figure 3). For dandelion, the best fit occurred when \( m \)HTT was calculated including \( T_{\text{base}} \) and \( F_{\text{base}} \), with threshold values of 5 C and 5 C, respectively (Table 6, Figure 3). For field pennycress, a simple model including only DAA1 performed the best (Table 6, Figure 3). This indicates that for this species there might be some factors driving germination and emergence other than temperature and moisture.

Daws et al. (2008) showed that large seeded species were able to germinate under drier conditions when compared to small seeded species, suggesting that base matric water potential would be smaller (more negative) for large seeded species. This is an indicator that small seeded species are more “conservative”, germinating at less-negative
water matric potential, reducing the likelihood of seedling mortality due lack of soil moisture. Therefore, we hypothesized that large seeded species in this study would be less sensitive to soil matric potential than small seeded species. According to AIC criterion, purslane speedwell, Virginia pepperweed, and downy brome were the only species that responded to $\Psi_{\text{base}}$ (−3000 kPa for these three species; Table 6). Purslane speedwell was the smallest-seeded species included in this study and Virginia pepperweed was also one of the smallest seeded species in this study (Table 1), supporting Daws et al. (2008) findings. Conversely, downy brome was the largest-seeded species included in this study (Table 1). Downy brome sensitivity to $\Psi_{\text{base}}$ is likely due to the fact that it was the first winter annual weed to emerge under field conditions (Figure 4). It germinates at times when the crops are still actively growing and therefore sensitivity to water protects this species from unfavorable conditions forcing it to respond to minimum matric potential in order to germinate. The -3000 kPa was the minimum $\Psi_{\text{base}}$ included in our analysis, and perhaps the inclusion of more-negative matric potential values would have allowed us to further compare our findings with those of Daws et al. (2008).

Based on the AIC criterion, the $T_{\text{base}}$ for Carolina foxtail, shepherd’s purse, and Virginia pepperweed emergence is 0 C; field pansy = 1 C; henbit = 2 C; downy brome, tansymustard, and dandelion = 5 C; and purslane speedwell = 6 C; indicating that the initial set of $T_{\text{base}}$ values included on our analysis ranging from 0 to 6 C were adequate for these species. Including temperature fluctuation into the $mHTT$ calculation was only important for Virginia pepperweed and dandelion, which responded to 5 C as the threshold. Ability to sense temperature fluctuation may be interpreted as a burial depth
sensing mechanism (Kegode et al. 1998). Virginia pepperweed was the only species that responded to all three soil threshold parameters evaluated in this study (Table 6).

In general, our results are similar to those of Blackshaw et al. (2002) and Baskin and Baskin (1988), who reported soil temperature as the main factor driving winter annual weed emergence. Adding a critical value for soil moisture into our mHTT was only important for three species. Scattered rainfall events were common from mid-summer to late-fall in the region where this study was conducted (Figure 5), probably providing enough water to trigger germination for these weed species, leading us to conclude that matric water potential was adequate for germination during most of the study not allowing our models to detect threshold values. This likely explains why winter annual weeds were not as sensitive to $\Psi_{\text{base}}$ as expected. Temperature fluctuation was the least important soil threshold component in this study.

Comparing “top” to “basic” models across species

RMSE has been used as an indicator to compare model efficiency, and the smallest RMSE indicates the most accurate model (Roman et al. 2000; Martinson et al. 2007). In this research a similar analysis was performed, where the “top” model selected according to the AIC criterion was compared to the mHTT model using only $T_{\text{base}} = 0$ C (or “basic” model). This comparison was possible for all species but Carolina foxtail and shepherd’s purse in which the top model contained only $T_{\text{base}} = 0$ C.

The “top” model performed better, or had a smaller RMSE, than the “basic” model. This was true for all species (Table 6 and 7). This finding reinforces the importance of using adequate base values when accumulating heat units to predict weed emergence and leads us to conclude that more “accurate” base values result in better
performance of predictive models. It is also possible to conclude that for most of the species that further responded to $\Psi_{\text{base}}$, $F_{\text{base}}$, of higher $T_{\text{base}}$ (i.e., dandelion, Virginia pepperweed, purslane speedwell, and tansymustard), leaving these parameters out of the model or using a non-adequate threshold decreased prediction accuracy because larger RMSE differences ($\Delta$ RMSE) were observed between top and basic models (Table 7). Similar findings have been reported by Roman et al. (2000), where calculation of thermal time using air temperature resulted in greater RMSE than when soil temperature was used. This finding is supported by the fact that soil is the environment where seeds germinate.

Similarly, higher model efficiency (ME) and agreement ($d$) were observed when the top model was compared to the basic model for all species. Moreover, smaller biases were observed when top models were used instead of basic models for all species but field pennycress, which had a greater bias when the top model was used. Overall, these results support the use of AIC model selection criterion to determine the importance and search for best values for each soil parameter.

**Emergence sequence according to our “basic” models**

Using a constant base temperature ($T_{\text{base}} = 0$ C) across all species to accumulate heat units enabled us to understand winter annual weed emergence sequence under field conditions (Figure 4). A similar approach has been taken by others (Myers et al. 2004). Even though base temperature differs among species, this approach allowed us to generate results that may easily be used to guide weed control activities. Moreover, $T_{\text{base}} = 0$ C has been commonly used for winter annual weeds and crops (Bullied et al. 2003;
Ball et al. 2004; McMaster and Wilhelm 1997) and the models obtained from this analysis still resulted in reasonable fit (Table 7).

According to our results, downy brome was the first winter annual weed species to emerge, with the majority of the seedlings (>70%) emerging during late summer (Figure 4). Tansymustard, Carolina foxtail, henbit, and field pansy started to emerge during late summer but had the majority of the seedlings emerging during the fall (Figure 4). These 5 winter annual species had the majority of the seedlings emerged by the end of the fall (>95%); therefore, they can be classified as “fall emergers” or obligate winter annual weeds (Cici and Van Acker 2009; Baskin and Baskin 1988). Approximately 70% of the Virginia pepperweed and purslane speedwell seedlings emerged in the fall and the remaining 30% emerged in the spring (Figure 4). These two species can then be classified as “mostly fall emergers” according to Cici and Van Acker (2009). Dandelion emerged in equal proportion during fall and spring, and fits into the “fall and spring emitter” category (Figure 4) (Cici and Van Acker 2009). Dandelion was the only perennial species included in this study and had the highest RMSE and lowest ME, indicating a lower model quality (for both top and basic model) when compared to the other species (Table 6 and 7). This emergence behavior was expected since perennial species tend not to have a “predictable” emergence pattern (Baskin and Baskin 1988). Finally, shepherd’s purse and field pennycress were the species that had some seedlings emerging in the fall (approximately 30%) but the majority emerged during late winter and spring (Figure 4); thus, these two species can be classified as “mostly spring emergers” (Cici and Van Acker 2009). Because Virginia pepperweed, purslane speedwell, shepherd’s purse and
field pennycress emerged during both fall and spring, these species can be further classified as facultative winter annual weeds (Baskin and Baskin 1988). Baskin and Baskin (1988) conducted an experiment with 75 species of winter annual weeds common to Kentucky and Tennessee and found that 50% of the species were facultative winter annual weeds. For the present study, half of the species were classified as obligate and half as facultative winter annual weeds corroborating with the Baskin and Baskin (1988) findings, suggesting that the winters in the midwestern region of the USA are still mild enough for establishment and development of obligate winter annual species. According to Cici and Van Acker (2009), the majority of the winter annual weed species in Canada behave as facultative winter annuals, indicating that severe winters in this region have selected for species or genotypes that are able to germinate during both fall and spring. Facultative winter annual species are able to minimize the risk of a population being eliminated by a hard freeze, thereby increasing the chances of at least some individuals reproducing.

In a study by Baskin and Baskin (1988), downy brome was considered an obligate winter annual, whereas field pennycress and shepherd’s purse were considered facultative winter annual weeds, corroborating to our findings. Conversely, Baskin and Baskin (1988) found henbit to be a facultative winter annual weed, whereas we found it to be an obligate winter annual. Typically, fall emerged plants of winter annual weeds produce more biomass and seeds than spring emerged plants. Perhaps the relatively mild winters in recent years (Krauz et al. 2003) have allowed fall emerged plants to dominate henbit populations, thereby suppressing the spring-germinated ones, selecting for fall emerging genotypes. Similar findings have been reported by Raynal and Bazzaz (1975), which
found fall emergers suppressing development of early spring emergers. According to these authors, the fall emergers invest in root growth during late fall and winter, and close canopy in early spring, thereby shading and suppressing early-spring emergers.

**Final considerations**

In general, winter annual weeds presented a consistent emergence pattern across sites and years allowing us to develop predictive models with satisfactory accuracy. The AIC criterion allowed us to select models with the best fit to the data. Therefore, the information-theoretic model comparison approach can be a powerful tool for weed scientists seeking to select adequate base threshold values and models to predict emergence of different weed species based on observational field studies. The emergence pattern of five out of the ten species included in this study were adequately represented by simple thermal time models; indicating that temperature is likely the main factor driving winter annual weed emergence. Soil moisture was not as critical as expected. This may be due to the fact that crops are senescing and scattered precipitation events during the fall are common in the region where this study was conducted. The most complex $m$HTT model including $T_{\text{base}}$, $F_{\text{base}}$, and $\Psi_{\text{base}}$ best described emergence for only one species. However, we believe that the $m$HTT has the potential to improve predictions for summer annual weeds. The results of this research also provide knowledge on the emergence pattern of winter annual weeds under field conditions. According to our findings the majority of winter annual weeds emerge by late fall in Nebraska, indicating that, as long as environmental conditions are adequate for herbicide application and uptake or mechanical cultivation, this would be the ideal time to manage these weeds.
Acknowledgements

The authors would like to thank Gustavo Mastria, Bruno Vieira, Irving Schleufer, Lia Marchi, and Thomas Miorini for technical assistance and also Dr. Anita Wingeier for the help in the soil laboratory. Drs. Drew Tyre and Adam Davis provided essential knowledge for the statistical analysis. This research was funded by the Nebraska Soybean Board.
Figure 1. Calibration chart and equations for volumetric soil water content as measured by the sensors EC-5 (2010-2011) and 5TM (2011-2012).
Figure 2. Estimated volumetric water content (θv, m³ m⁻³) according to Saxton et al. (1986) method compared to measured θv according to Klute (1986) method.
Figure 3. The emergence pattern of nine winter annual weeds and dandelion as predicted by mHTT at LAF = Lincoln Agronomy Farm, Lincoln, NE; UNL = East Campus Farm, Lincoln, NE; ARDC = Agricultural Research and Development Center, Mead, NE; SCAL = South Central Agricultural Laboratory (RF = Rainfed, IL = Irrigated Land), Clay Center, NE. The data for all replications (n=6) in each site-season is shown. The solid line represents the “top model” selected according to AIC criterion and the base threshold values (T_{base}, Ψ_{base}, and/or F_{base}) for each species are listed at the bottom of each figure. For THLAR a model based on DAA1 (days after August 1) performed the best.
Figure 4. Winter annual weed emergence sequence in Nebraska. Accumulation of thermal time started on August 1 of each year. Base temperature of 0 C was used across all species. Fall, winter, and spring vertical lines represent the soil thermal time accumulated at the beginning of each season, respectively, averaged across the two experimental seasons and the four sites.
Figure 5. Precipitation data from August 1 until November 15 in each experimental site during both seasons 2010 and 2011. LAF = Lincoln Agronomy Farm, Lincoln, NE; UNL = East Campus Farm, Lincoln, NE; ARDC = Agricultural Research and Development Center, Mead, NE; SCAL = South Central Agricultural Laboratory (RF = Rainfed, IL = Irrigated Land), Clay Center, NE. Data obtained from the High Plains Regional Climate Center (HPRCC, http://www.hprcc.unl.edu). Amount of irrigation applied during each season at SCALIL was added to HPRCC precipitation data.
Table 1. Weed species included in this study, their respective collection site, and 100 seeds weight ± standard error (g).

<table>
<thead>
<tr>
<th>Common name</th>
<th>Latin name</th>
<th>Family</th>
<th>Bayer code</th>
<th>Site</th>
<th>2010</th>
<th>Site</th>
<th>2011</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carolina foxtail</td>
<td><em>Alopecurus carolinianus</em></td>
<td>Poaceae</td>
<td>ALOCA</td>
<td>LAF&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.0247±0.0005</td>
<td>LAF</td>
<td>0.0176±0.0002</td>
</tr>
<tr>
<td></td>
<td>Walt.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Downy brome</td>
<td><em>Bromus tectorum</em> L.</td>
<td>Poaceae</td>
<td>BROTE</td>
<td>SCAL&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.3695±0.0030</td>
<td>SCAL</td>
<td>0.2929±0.0045</td>
</tr>
<tr>
<td>Shepherd’s-purse</td>
<td><em>Capsella bursa-pastoris</em> (L.) Medik.</td>
<td>Brassicaceae</td>
<td>CAPBP</td>
<td>LAF</td>
<td>0.0110±0.0001</td>
<td>LAF</td>
<td>0.0108±0.0002</td>
</tr>
<tr>
<td>Tansymustard</td>
<td><em>Descurainia pinnata</em> (Walt.) Britt.</td>
<td>Brassicaceae</td>
<td>DESPI</td>
<td>LAF</td>
<td>0.0139±0.0005</td>
<td>LAF</td>
<td>0.0141±0.0002</td>
</tr>
<tr>
<td>Henbit</td>
<td><em>Lamium amplexicaule</em> L.</td>
<td>Lamiaceae</td>
<td>LAMAM</td>
<td>LAF</td>
<td>0.0545±0.0006</td>
<td>LAF</td>
<td>0.0557±0.0006</td>
</tr>
<tr>
<td>Virginia pepperweed</td>
<td><em>Lepidium virginicum</em> L.</td>
<td>Brassicaceae</td>
<td>LEPVI</td>
<td>SCAL</td>
<td>0.0205±0.0002</td>
<td>SCAL</td>
<td>0.0241±0.0002</td>
</tr>
<tr>
<td>Dandelion&lt;sup&gt;c&lt;/sup&gt;</td>
<td><em>Taraxacum officinale</em> G.H. Weber ex Wiggers</td>
<td>Asteraceae</td>
<td>TAROF</td>
<td>SCAL</td>
<td>0.0390±0.0008</td>
<td>SCAL</td>
<td>0.0468±0.0004</td>
</tr>
<tr>
<td>Field pennycress</td>
<td><em>Thlaspi arvense</em> L.</td>
<td>Brassicaceae</td>
<td>THLAR</td>
<td>SCAL</td>
<td>0.1120±0.0022</td>
<td>SCAL</td>
<td>0.0988±0.0007</td>
</tr>
<tr>
<td>Purslane speedwell</td>
<td><em>Veronica peregrina</em> L.</td>
<td>Scrophulariaceae</td>
<td>VERPG</td>
<td>SCAL</td>
<td>0.0030±0.0001</td>
<td>SCAL</td>
<td>0.0026±0.0001</td>
</tr>
<tr>
<td>Field pansy</td>
<td><em>Viola bicolor</em> Pursh</td>
<td>Violaceae</td>
<td>VIORA</td>
<td>Verdon NE</td>
<td>0.0362±0.0004</td>
<td>Omaha NE</td>
<td>0.0241±0.0003</td>
</tr>
</tbody>
</table>

<sup>a</sup>LAF: Lincoln Agronomy Farm, Lincoln, NE.
<sup>b</sup>SCAL: South Central Agricultural Laboratory, Clay Center, NE.
<sup>c</sup>Dandelion was the only perennial species included in this study.
Table 2. Summary of location, soil description, soybean planting and harvest dates, soybean yield, and weed seed planting date for each experimental site.

<table>
<thead>
<tr>
<th>Site&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Season&lt;sup&gt;b&lt;/sup&gt;</th>
<th>GPS</th>
<th>Soil type&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Clay (%)</th>
<th>Silt (%)</th>
<th>Sand (%)</th>
<th>OM (%)</th>
<th>SPD&lt;sup&gt;d&lt;/sup&gt;</th>
<th>SHD&lt;sup&gt;e&lt;/sup&gt;</th>
<th>Soybean yield (kg ha&lt;sup&gt;-1&lt;/sup&gt;)</th>
<th>WPD&lt;sup&gt;f&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAF</td>
<td>1</td>
<td>40.8532 N 96.6168 W</td>
<td>SCL</td>
<td>27</td>
<td>54</td>
<td>19</td>
<td>3</td>
<td>05/28/2010</td>
<td>10/20/2010</td>
<td>3,629</td>
<td>07/23/2010</td>
</tr>
<tr>
<td>ARDC</td>
<td>1</td>
<td>41.1554 N 96.4183 W</td>
<td>SCL</td>
<td>28</td>
<td>53</td>
<td>19</td>
<td>2.8</td>
<td>05/28/2010</td>
<td>10/20/2010</td>
<td>3,898</td>
<td>07/24/2010</td>
</tr>
<tr>
<td>ARDC</td>
<td>2</td>
<td>41.1611 N 96.4239 W</td>
<td>SCL</td>
<td>33</td>
<td>54</td>
<td>13</td>
<td>2.3</td>
<td>05/17/2011</td>
<td>10/21/2011</td>
<td>4,160</td>
<td>07/21/2011</td>
</tr>
<tr>
<td>SCALRF</td>
<td>1</td>
<td>40.5793 N 98.1385 W</td>
<td>SL</td>
<td>20</td>
<td>57</td>
<td>23</td>
<td>2.3</td>
<td>06/04/2010</td>
<td>09/30/2010</td>
<td>2,486</td>
<td>07/23/2010</td>
</tr>
<tr>
<td>SCALIL</td>
<td>1</td>
<td>40.5744 N 98.1331 W</td>
<td>SL</td>
<td>15</td>
<td>64</td>
<td>21</td>
<td>2.7</td>
<td>05/29/2010</td>
<td>11/11/2010</td>
<td>4,166</td>
<td>07/23/2010</td>
</tr>
<tr>
<td>SCALIL</td>
<td>2</td>
<td>40.5683 N 98.1347 W</td>
<td>SL</td>
<td>27</td>
<td>56</td>
<td>17</td>
<td>2.6</td>
<td>05/24/2011</td>
<td>10/26/2011</td>
<td>4,469</td>
<td>07/22/2011</td>
</tr>
</tbody>
</table>

<sup>a</sup> Site: LAF = Lincoln Agronomy Farm, Lincoln, NE; UNL = East Campus Farm, Lincoln, NE; ARDC = Agricultural Research and Development Center, Mead, NE; SCAL = South Central Agricultural Laboratory (RF = Rainfed, IL = Irrigated Land), Clay Center, NE.

<sup>b</sup> Season: 1 = 1<sup>st</sup> experimental season (July 2010-July 2011); 2 = 2<sup>nd</sup> experimental season (July 2011-July 2012).

<sup>c</sup> Soil type: SCL = Silty Clay Loam; SL = Silt Loam.

<sup>d</sup> SPD = soybean planting date.

<sup>e</sup> SHD = soybean harvesting date.

<sup>f</sup> WPD = weed planting date.
<table>
<thead>
<tr>
<th>Month</th>
<th>LAF</th>
<th>UNL</th>
<th>ARDC</th>
<th>SCAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>August</td>
<td>30.2</td>
<td>32.8</td>
<td>30.0</td>
<td>29.5</td>
</tr>
<tr>
<td>September</td>
<td>25.7</td>
<td>26.0</td>
<td>23.8</td>
<td>25.4</td>
</tr>
<tr>
<td>October</td>
<td>18.7</td>
<td>22.1</td>
<td>21.2</td>
<td>18.6</td>
</tr>
<tr>
<td>November</td>
<td>8.8</td>
<td>10.7</td>
<td>11.5</td>
<td>8.4</td>
</tr>
<tr>
<td>December</td>
<td>2.4</td>
<td>2.2</td>
<td>5.0</td>
<td>2.1</td>
</tr>
<tr>
<td>January</td>
<td>0.9</td>
<td>-1.5</td>
<td>6.5</td>
<td>0.1</td>
</tr>
<tr>
<td>February</td>
<td>4.7</td>
<td>4.0</td>
<td>5.5</td>
<td>3.6</td>
</tr>
<tr>
<td>March</td>
<td>11.1</td>
<td>10.4</td>
<td>20.9</td>
<td>10.1</td>
</tr>
<tr>
<td>April</td>
<td>17.7</td>
<td>17.7</td>
<td>20.8</td>
<td>17.1</td>
</tr>
<tr>
<td>May</td>
<td>23.4</td>
<td>23.1</td>
<td>26.7</td>
<td>23.1</td>
</tr>
<tr>
<td>June</td>
<td>29.0</td>
<td>28.7</td>
<td>30.7</td>
<td>28.6</td>
</tr>
<tr>
<td>July</td>
<td>31.6</td>
<td>33.1</td>
<td>35.8</td>
<td>30.8</td>
</tr>
</tbody>
</table>

LAF = Lincoln Agronomy Farm, Lincoln, NE; UNL = East Campus Farm, Lincoln, NE; ARDC = Agricultural Research and Development Center, Mead, NE; SCAL = South Central Agricultural Laboratory, Clay Center, NE.
Table 4. Derived soil-water characteristic equations obtained from Saxton et al. (1986) used to estimate soil matric potential ($\Psi$, kPa) from volumetric water content ($\theta_v$, m$^3$m$^{-3}$).

<table>
<thead>
<tr>
<th>Applied tension range, kPa</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt;1500 to 10</td>
<td>( \Psi = A \theta_v^B )</td>
</tr>
<tr>
<td></td>
<td>( A = \exp[a + b , (%C) + c , (%S)^2 + d(%S)^2(%C)] \times 100 )</td>
</tr>
<tr>
<td></td>
<td>( B = e + f , (%C)^2 + g , (%S)^2 + g , (%S)^2(%C) )</td>
</tr>
<tr>
<td>10 to ( \Psi_e )</td>
<td>( \Psi = 10 - (\theta - \theta_{v10})(10 - \Psi_e)/(\theta_{vs} - \theta_{v10}) )</td>
</tr>
<tr>
<td></td>
<td>( \theta_{v10} = \exp[(2.302 - \ln A)/B] )</td>
</tr>
<tr>
<td></td>
<td>( \Psi_e = 100 , [m + n , (\theta_{vs})] )</td>
</tr>
<tr>
<td></td>
<td>( \theta_{vs} = h + j , (%S) + k \log_{10} (%C) )</td>
</tr>
<tr>
<td>( \Psi_e ) to 0</td>
<td>( \theta_{vs} = \theta )</td>
</tr>
</tbody>
</table>

**Coefficients:** \( a = -4.396; \, b = -0.0715; \, c = -4.880 \times 10^{-3}; \, d = -4.285 \times 10^{-5}; \, e = -3.140; \, f = -2.22 \times 10^{-3}; \, g = -3.484 \times 10^{-5}; \, h = 0.332; \, j = -7.251 \times 10^{-4}; \, k = 0.1276; \, m = -0.108; \, n = 0.341; \, p = 12.012; \, q = -7.55 \times 10^{-2}; \, r = -3.8950; \, t = 3.671 \times 10^{-2}; \, u = -0.1103; \, v = 8.7546 \times 10^{-4}. \)

**Definitions:** \( \Psi \) = water potential (kPa); \( \Psi_e \) = water potential at air entry (kPa); \( \theta_v \) = volumetric water content (m$^3$m$^{-3}$); \( \theta_{vs} \) = volumetric water content at saturation (m$^3$m$^{-3}$); \( \theta_{v10} \) = volumetric water content at 10 kPa (m$^3$m$^{-3}$); \( (\%S) \) = percent sand; \( (\%C) \) = percent clay.
Table 5. Summary of estimated coefficients using Saxton et al. (1986) equations to develop the soil-water characteristic curves for each site-season.

<table>
<thead>
<tr>
<th>Location</th>
<th>Season</th>
<th>A</th>
<th>B</th>
<th>$\Psi_e$ (kPa)</th>
<th>$\theta_{v10}$ (m$^3$ m$^-3$)</th>
<th>$\theta_{vs}$ (m$^3$ m$^-3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAF</td>
<td>2010-2011</td>
<td>0.095</td>
<td>-5.171</td>
<td>6.326</td>
<td>0.406</td>
<td>0.502</td>
</tr>
<tr>
<td></td>
<td>2011-2012</td>
<td>0.070</td>
<td>-5.663</td>
<td>6.541</td>
<td>0.416</td>
<td>0.509</td>
</tr>
<tr>
<td>UNL</td>
<td>2010-2011</td>
<td>0.095</td>
<td>-5.171</td>
<td>6.326</td>
<td>0.406</td>
<td>0.502</td>
</tr>
<tr>
<td></td>
<td>2011-2012</td>
<td>0.084</td>
<td>-5.752</td>
<td>6.807</td>
<td>0.436</td>
<td>0.516</td>
</tr>
<tr>
<td>ARDC</td>
<td>2010-2011</td>
<td>0.152</td>
<td>-4.348</td>
<td>5.580</td>
<td>0.382</td>
<td>0.480</td>
</tr>
<tr>
<td></td>
<td>2011-2012</td>
<td>0.131</td>
<td>-4.779</td>
<td>6.184</td>
<td>0.404</td>
<td>0.498</td>
</tr>
<tr>
<td>SCALRF</td>
<td>2010-2011</td>
<td>0.245</td>
<td>-3.915</td>
<td>5.198</td>
<td>0.388</td>
<td>0.469</td>
</tr>
<tr>
<td></td>
<td>2011-2012</td>
<td>0.111</td>
<td>-5.030</td>
<td>6.329</td>
<td>0.409</td>
<td>0.502</td>
</tr>
</tbody>
</table>

A and B = equation coefficients; $\Psi_e$ = water potential at air entry (kPa); $\theta_{v10}$ = volumetric water content at 10 kPa (m$^3$ m$^-3$); $\theta_{vs}$ = volumetric water content at saturation (m$^3$ m$^-3$). LAF = Lincoln Agronomy Farm, Lincoln, NE; UNL = East Campus Farm, Lincoln, NE; ARDC = Agricultural Research and Development Center, Mead, NE; SCAL = South Central Agricultural Laboratory (RF = Rainfed, IL = Irrigated Land), Clay Center, NE. The Saxton et al. (1986) equations are summarized in Table 4.
Table 6. Optima $T_{\text{base}}$, $\Psi_{\text{base}}$, and $F_{\text{base}}$ values, Weibull model parameters ($lrc$ and $pwr$), and AIC weights (AIC$w$)\(^a\) for the top predictive model according to AIC criterions, and the models’ Goodness of fit (RMSE, ME, $d$, and bias) for each species.

<table>
<thead>
<tr>
<th>species</th>
<th>$T_{\text{base}}$</th>
<th>$\Psi_{\text{base}}$</th>
<th>$F_{\text{base}}$</th>
<th>$lrc$</th>
<th>$pwr$</th>
<th>AIC$w$</th>
<th>RMSE</th>
<th>ME</th>
<th>$d$</th>
<th>bias</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALOCA</td>
<td>0</td>
<td>- $\infty$ (ni)(^b)</td>
<td>0 (ni)</td>
<td>-37.9336</td>
<td>5.1994</td>
<td>0.83</td>
<td>17.9</td>
<td>0.81</td>
<td>0.95</td>
<td>+ 0.41</td>
</tr>
<tr>
<td>BROTE</td>
<td>5</td>
<td>-3000</td>
<td>0 (ni)</td>
<td>-15.1998</td>
<td>2.3213</td>
<td>0.25</td>
<td>13.4</td>
<td>0.82</td>
<td>0.96</td>
<td>+ 0.40</td>
</tr>
<tr>
<td>CAPBP</td>
<td>0</td>
<td>- $\infty$ (ni)</td>
<td>0 (ni)</td>
<td>-39.1470</td>
<td>5.0970</td>
<td>1.00</td>
<td>21.4</td>
<td>0.67</td>
<td>0.92</td>
<td>- 0.52</td>
</tr>
<tr>
<td>DESPI</td>
<td>5</td>
<td>- $\infty$ (ni)</td>
<td>0 (ni)</td>
<td>-36.0000</td>
<td>5.1781</td>
<td>0.72</td>
<td>15.1</td>
<td>0.85</td>
<td>0.96</td>
<td>+ 0.38</td>
</tr>
<tr>
<td>LAMAM</td>
<td>2</td>
<td>- $\infty$ (ni)</td>
<td>0 (ni)</td>
<td>-39.6805</td>
<td>5.5415</td>
<td>0.58</td>
<td>17.0</td>
<td>0.82</td>
<td>0.96</td>
<td>+ 0.19</td>
</tr>
<tr>
<td>LEPVI</td>
<td>0</td>
<td>-3000</td>
<td>5</td>
<td>-16.4955</td>
<td>2.3535</td>
<td>0.82</td>
<td>18.9</td>
<td>0.72</td>
<td>0.93</td>
<td>- 0.28</td>
</tr>
<tr>
<td>TAROF</td>
<td>5</td>
<td>- $\infty$ (ni)</td>
<td>5</td>
<td>-19.5807</td>
<td>2.8282</td>
<td>0.49</td>
<td>24.0</td>
<td>0.54</td>
<td>0.89</td>
<td>- 0.30</td>
</tr>
<tr>
<td>THLAR(^c)</td>
<td>ni</td>
<td>ni</td>
<td>ni</td>
<td>-18.1129</td>
<td>3.3803</td>
<td>1.00</td>
<td>21.2</td>
<td>0.74</td>
<td>0.94</td>
<td>- 2.20</td>
</tr>
<tr>
<td>VERPG</td>
<td>6</td>
<td>-3000</td>
<td>0 (ni)</td>
<td>-36.4044</td>
<td>5.2621</td>
<td>1.00</td>
<td>23.1</td>
<td>0.63</td>
<td>0.91</td>
<td>+ 0.64</td>
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<tr>
<td>VIORA</td>
<td>1</td>
<td>- $\infty$ (ni)</td>
<td>0 (ni)</td>
<td>-47.7200</td>
<td>6.5660</td>
<td>0.58</td>
<td>17.7</td>
<td>0.82</td>
<td>0.96</td>
<td>+ 0.04</td>
</tr>
</tbody>
</table>

\(^a\)Only the AIC$w$ for the top model for each species is shown in this table.

\(^b\)ni indicates that the specific environmental soil parameter was not important on improving model accuracy according to the AIC criterions.

\(^c\)For THLAR a model based on DAA1 (days after August 1) performed the best.
Table 7. Weibull function parameters ($lrc$ and $pwr$) for the predictive basic models using $T_{base} = 0$ C across all species, basic models’ Goodness of fit (RMSE, ME, $d$, and $bias$), and RMSE difference between basic and top\textsuperscript{a} model according to AIC criterions ($\Delta$ RMSE).

<table>
<thead>
<tr>
<th>species</th>
<th>$lrc$</th>
<th>$pwr$</th>
<th>RMSE</th>
<th>ME</th>
<th>$d$</th>
<th>$bias$</th>
<th>$\Delta$ RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALOCA</td>
<td>-37.9336</td>
<td>5.1994</td>
<td>17.9</td>
<td>0.81</td>
<td>0.95</td>
<td>+0.41</td>
<td>0.0</td>
</tr>
<tr>
<td>BROTE</td>
<td>-14.2493</td>
<td>2.0710</td>
<td>13.6</td>
<td>0.81</td>
<td>0.95</td>
<td>+0.60</td>
<td>0.2</td>
</tr>
<tr>
<td>CAPBP</td>
<td>-39.1470</td>
<td>5.0970</td>
<td>21.4</td>
<td>0.67</td>
<td>0.92</td>
<td>-0.52</td>
<td>0.0</td>
</tr>
<tr>
<td>DESPI</td>
<td>-29.4958</td>
<td>4.0620</td>
<td>16.1</td>
<td>0.83</td>
<td>0.96</td>
<td>+0.68</td>
<td>1.0</td>
</tr>
<tr>
<td>LAMAM</td>
<td>-36.7810</td>
<td>5.0569</td>
<td>17.3</td>
<td>0.82</td>
<td>0.96</td>
<td>+0.31</td>
<td>0.3</td>
</tr>
<tr>
<td>LEPVI</td>
<td>-18.4166</td>
<td>2.4815</td>
<td>22.1</td>
<td>0.56</td>
<td>0.90</td>
<td>-0.47</td>
<td>3.2</td>
</tr>
<tr>
<td>TAROF</td>
<td>-20.2745</td>
<td>2.6645</td>
<td>30.6</td>
<td>0.15</td>
<td>0.80</td>
<td>-0.73</td>
<td>6.6</td>
</tr>
<tr>
<td>THLAR</td>
<td>-85.4195</td>
<td>11.2153</td>
<td>22.4</td>
<td>0.72</td>
<td>0.93</td>
<td>-0.77</td>
<td>1.2</td>
</tr>
<tr>
<td>VERPG</td>
<td>-25.3617</td>
<td>3.4168</td>
<td>26.2</td>
<td>0.49</td>
<td>0.88</td>
<td>+0.27</td>
<td>3.1</td>
</tr>
<tr>
<td>VIORA</td>
<td>-45.5454</td>
<td>6.2188</td>
<td>17.8</td>
<td>0.82</td>
<td>0.96</td>
<td>+0.13</td>
<td>0.1</td>
</tr>
</tbody>
</table>

\textsuperscript{a}RMSE for the top model for each species is presented in Table 6.
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