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**A quantitative analysis of seed dormancy and germination in the winter
annual weed *Sinapis arvensis* (Brassicaceae)**

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Abstract

The aims of this study were to determine the effects of burial on germination and longevity and of water stress and temperature on germination and dormancy induction of the weed *Sinapis arvensis*. During exposure to the high temperatures of summer seeds buried in the field became nondormant, but low water potential and supra-optimal temperatures (constant not alternating) induced them into secondary dormancy. The threshold temperature for dormancy induction (TTDI) was about 19 °C when water was not limiting germination, and it decreased with a slope of 10°C per MPa as water potential decreased. Seeds had minimum dormancy (D_{min}) when $T < TTDI$, and D_{min} decreased 81.5 % per MPa increase in water potential. Dormancy induction increased linearly with a slope of 13.23 % for each additional centimetre of burial depth from 1 to 5.19 cm. Dormancy was induced to its highest level (96 %) in seeds buried at a depth of ≥ 5.19 cm; the remaining seeds were dead or were presumed to be dead *Sinapis arvensis* can form a persistent soil seed bank, and either water stress or conditions associated with increased burial depth can promote induction of secondary dormancy in the seeds.

Keywords: dormancy-nondormancy cycle; hydrothermal time; physiological dormancy; seed burial depth

Introduction

Seeds of many weed species can persist for years in the soil seed bank, which begins at seed dispersal and ends with germination or death of the seed (Walck et al. 2005). Weed seeds have different fates after becoming part of the soil seed bank, and they can be viable or nonviable. Viable seeds are dormant (different degrees of dormancy) or nondormant. Nondormant seeds can germinate, or they may not germinate due to environmental factors such as lack of water or light. Living seeds eventually lose viability if they do not germinate during burial, or they may germinate in situ and the seedlings die without being able to emerge above the soil surface (Baskin and Baskin 2014). However, in many species seeds are dormant, and thus they will not germinate until dormancy is broken and conditions are favourable for germination. Buried seeds can cycle between dormancy and nondormancy in response to seasonal temperature changes (Baskin and Baskin 2014). After seeds become nondormant, seedling emergence from the soil depends on burial depth, which can influence weed seedling emergence by affecting the availability of soil moisture, O₂ and light (Benvenuti 2007). Osmotic stress, hypoxia and other factors such as high or low temperatures may result in development of secondary seed dormancy (Gulden et al. 2004; Baskin and Baskin 2014). However, Gardarin et al. (2010) reported that germination of seeds of nine northwestern European agricultural weeds decreased with depth of seed burial, even if moisture, O₂ and light did not change.

An important aspect of improving weed control practices is learning how to best manipulate seed dormancy, which controls weed seedling emergence in arable soil (Soltani et al. 2013). The most accurate way to determine the viability and germination ability of seeds in the soil is to bury them, wait for various periods of

time, exhumed samples and checked for viability and germinability (Baskin and Baskin, 1985; 2006). This method allows one to determine if seeds exhibit dormancy/non-dormancy cycling (Baskin et al. 2003; Masin et al. 2006).

Dormancy and germination of seeds are mainly affected by temperature and water potential (Batlla and Benech-Arnold 2004; Alvarado and Bradford 2005). The relationship between speed of germination and temperature can be described with mathematical functions (Soltani et al. 2006). The advantage of these functions is that they include parameters such as cardinal temperatures and maximum rates of germination or emergence that are meaningful from a biological point of view (Soltani et al. 2013). Thermal time (TT) and hydrotime (HT) models also have been used to describe the effect of temperature and water potential on seed germination and dormancy (Bradford 2002). Gummerson (1986) developed the hydrothermal time model by combining thermal time and hydrotime models, and it was extended by Bradford (1990, 1997, 2002). This model has wide application in studies of seed dormancy and germination (Meyer et al. 2000; Batlla and Benech-Arnold 2004; Alvarado and Bradford 2005; Meyer and Allen 2009). There are few studies on the hydrothermal germination of winter annuals (Meyer et al., 2000; Meyer and Allen, 2009; Mesgaran et al., 2013), perhaps because the winter annual life cycle generally is not limited by soil moisture. However in warm and frequently dry environments, e.g. a Mediterranean climate, hydrothermal conditions could have a crucial role in the germination dynamics of winter annuals.

Using seeds of the facultative winter annual *Sinapis arvensis*, the aims of this study were to investigate the effects of (1) burial on germination and longevity, and (2) water stress and temperature on germination and dormancy induction. Specifically, we addressed the following questions. (1) What is the dormancy state

and longevity of buried seeds over time? (2) What controls the timing of germination of buried seeds? (3) What are the effects of temperature and water potential on dormancy and germination? (4) What is the effect of burial depth on seedling emergence and dormancy?

Materials and Methods

Effect of burial on germination and viability of seeds in the soil - experiment 1

Sinapsis arvensis seeds were collected from oilseed rape (*Brassica napus*) fields around Gorgan, Iran (36°51' N, 54°16' E and 13 m asl; Mediterranean climate), during May 2009. A germination test of fresh seeds was conducted in the dark at 20 °C, based on information for other species of *Sinapis* reported by the International Seed Testing Association (2009), and 100% of the seeds were viable and 98% dormant. Seeds were kept in the laboratory (20 ± 5 °C, 40 ± 10% RH, dark) until the beginning the experiment on 23 September 2009, and at this time another germination test was conducted at 20 °C in dark and in light. On this date, some of the seeds were buried in soil at the Gorgan University of Agriculture Science and Natural Resources (GUASNR) Research Farm, and the other seeds were kept in dry storage in the laboratory. For burial, 1000 *S. arvensis* seeds and 10 g of soil (dried silty clay loam) were placed in each of 54 4 × 8 cm nylon bags with a pore size of 10 µm. Each nylon bag was placed in a closed-top nylon basket to protect the seeds from predation, and the nylon baskets were buried at a soil depth of 30 cm. Farmers usually moldboard plough to a depth of 30 cm in autumn in the conventional cropping system in Gorgan, resulting in some seeds possibly being buried at this depth.

After burial, three bags (replicates) of seeds were exhumed monthly for the duration of the experiment. The exhumed samples (containing soil and seeds) were placed on a

mesh screen (holes 1 x 2 mm) and washed with tap water in room light. The isolated *S. arvensis* seeds were tested for viability by pinching 100 of them with fine-tipped forceps (crush test). The distinction between viable and nonviable seeds was based on seed firmness (firm vs. soft); soft seeds were considered to be dead and firm seeds viable (Borza et al., 2007; Taab and Andersson 2009). Decrease in seed viability was explained by a linear regression over time. Before regression analysis, data were transformed to a logarithmic scale. The regression model was back transformed to calculate the rates of seed loss.

Within 24 h after exhumation, viable seeds were used in germination tests conducted in dark and in light at 20 °C. Seeds stored in the lab also were tested for germination under the same conditions. For seeds stored in the lab and for those that were exhumed from burial, there were three replications of 50 seeds for each test condition. Seeds were placed on moist filter paper (Whatman No. 40) moistened with 10 ml of distilled water in 15-cm-diameter Petri dishes. Dark conditions were obtained by wrapping two layers of aluminum foil around each Petri dish. After 14 days, the germinated seeds were counted, and all remaining seeds were evaluated for dormancy and viability. For each month, nongerminated seeds were pinched with fine-tipped forceps (crush test) as described above. Germination percentage was based on number of viable seeds.

Minimum and maximum air temperatures during the experiment were obtained from a weather station with long-term reliable historical daily data in Gorgan. Soil temperatures were estimated using a regression model developed by Soltani et al. (2006) for Gorgan as follows:

$$y = 1.046x - 0.1616 \quad (1)$$

where x and y are air and soil temperatures, respectively.

Effect of water stress and temperature on germination and dormancy induction of nondormant seeds– experiment 2

Seeds were prepared as described in experiment 1. They were maintained in dry storage in the laboratory (as in experiment 1) until the beginning of experiment 2 (25 Oct 2009). Four replicates of 50 nondormant seeds, i.e. dormancy released by treating seeds with 2000 ppm GA3 (Edwards, 1969), were incubated in darkness at seven constant temperatures from 5 to 35 °C at 5 °C intervals and five water potentials, 0, -0.2, -0.4, -0.6 and -0.8 MPa at each temperature. Water potentials were maintained with solutions of polyethylene glycol 8000 (Michel 1983). Before seed placement, the filter paper was soaked for 24 h in Petri dishes containing an osmotic solution for the desired water potential. Seeds were monitored for germination twice a day (for 1 month), and they were considered to be germinated when the radicle was ≥ 2 mm long. After the germination test, the percentage of dormant viable seeds was determined by the crush test as explained in experiment 1.

Estimates of the time taken for cumulative germination to reach 50% of the maximum number of viable seeds in each replicate (D50) were interpolated from the germination progress curve versus time (Soltani et al., 2001). Visual basic editor of Excel was used to obtain D50 from cumulative germination versus time. Germination speed ($R_{50} \text{ h}^{-1}$) was calculated according to Soltani et al. (2001):

$$R_{50} = 1/D_{50} \quad (2)$$

To quantify the response of germination speed to temperature and to determine cardinal temperatures for germination, the following model was used for each water potential:

$$R_{50} = f(T)R_{max} \quad (3)$$

where $f(T)$ is a temperature ($^{\circ}\text{C}$) function and R_{max} the maximum rate of germination at the optimal temperature. Thus, $1/R_{max}$ indicates the minimum number of hours required for germination at the optimal temperature. The Dent-like function ($f(T)$), one of many functions that can be used to describe germination response to temperature, were used (Soltani et al. 2006):

$$f(T) = \frac{T - T_b}{T_{o1} - T_b} \quad \text{if} \quad T_b < T < T_{o1} \quad (4)$$

$$f(T) = \frac{T_c - T}{T_c - T_{o2}} \quad \text{if} \quad T_{o2} < T < T_c$$

$$f(T) = 1 \quad \text{if} \quad T_{o1} < T < T_{o2}$$

$$f(T) = 0 \quad \text{if} \quad T \leq T_b \text{ or } T \geq T_c$$

where T is the temperature ($^{\circ}\text{C}$), T_b base temperature, T_{o1} lower optimum temperature, T_{o2} upper optimum temperature and T_c ceiling temperature. The parameters were estimated by the least squares method using the non-linear (NLIN) regression (R_{50} as y and T as x) procedure in SAS software.

A thermal time (TT $^{\circ}\text{C day}$) model was fitted using the following equation at sub- (5) and supra- (6) optimal temperatures (Bradford, 2002):

$$TT_{sub} = (T - T_b)t_g \quad (5)$$

$$TT_{supra} = (T_c - T)t_g \quad (6)$$

where T is the actual temperature, T_b base temperature, T_c ceiling temperature for germination and t_g time from addition of water to germination (g).

Quantification of seed germination was conducted in relation to water potential using the hydrotime model for each temperature (Gummerson 1986; Bradford 1990; Dahal and Bradford 1994):

$$\theta_H = (\varphi - \varphi_b(g))t_g \quad (7)$$

where θ_H is the hydrotime constant (MPa-hours), ψ actual seed water potential (MPa), $\psi_b(g)$ base water potential (MPa) defined for a specific germination fraction (g) and t_g time (hours) to radicle emergence of fraction g (%) of the seed population.

Assuming that the variation in ψ_b within a seed lot follows a normal distribution, hydrotime parameters were estimated by repeated probit analysis (equation 8) by varying θ_H until the best fit was reached for whole seed lots (Dahal and Bradford 1994):

$$probit(g) = [\psi - (\theta_H / t_g) - \psi_b(50)] / \sigma_{\psi_b} \quad (8)$$

where $\psi_b(50)$ is the median ψ_b and σ_{ψ_b} the standard deviation of ψ_b among seeds within the temperatures.

Dormancy induction was quantified with segmented functions on the response to temperature separately for each water potential as follows:

$$D = D_{min}, \quad \text{if } T > TTDI \quad (9)$$

$$D = D_{min} + b \times (T - TTDI), \quad \text{if } T \geq TTDI$$

where T and D are temperature ($^{\circ}\text{C}$) and percentage of dormant seeds, respectively, and D_{min} , $TTDI$ and b are the model parameters for minimum dormancy for each water potential, threshold temperature for dormancy induction and the slope of the increasing dormancy level, respectively. The parameters were estimated by the least squares method using the non-linear (NLIN) regression (D as y and T as x) procedure in SAS.

Effects of burial depth on seedling emergence and dormancy – experiment 3

The effect of burial depth on seedling emergence was studied in a roofless enclosure at GUASNR so that the buried seeds could be exposed to near-outdoor weather conditions. As described for experiments 1 and 2, 50 nondormant seeds (dormancy released by 2000 ppm GA₃) were sown at depths of 1, 2, 3, 4, 5, 6, 8, 10, 12, 15, 20 and 30 cm in plastic pots (15 cm diameter and 40 cm deep) filled with a silty clay loam soil (28% clay, 62% silt, 10% sand). The soil was excavated from a depth of > 0.5 m from farmland that not been plowed for at least for 50 years to avoid the presence of seeds of *S. arvensis*, which would invalidate the experimental data on seedling emergence. The pots were filled gravimetrically with the soil and packed to uniform strength to avoid differential resistance to seedling emergence. Holes in the bottom of the pots allowed drainage of excess water.

The experiment was a completely randomised design with four replicates for each seeding depth. It began on 1 Jan 2010, and the mean temperature during the experiment was 10.61 ± 6.53 °C (mean minimum air temperature 5.98 ± 3.24 and mean maximum air temperature 15.24 ± 4.37). Each pot was irrigated at 2- or 3-day intervals with 100 ml of water and observed daily for seedling emergence for 45 days; no seedling emerged after about 20 days. Emerged seedlings were counted and removed daily. After 45 days, the soil in the pots was examined for intact seeds by sieving it. Viable seeds were separated from dead seeds by the crush test as explained in experiment 1. Estimates of the time taken for cumulative emergence to reach 50% of the maximum number of emerged seedlings (D50) for each replicate were interpolated from the emergence progress curve as described in equation (2).

The relationship between seedling emergence percentage and burial depth was described using an exponential model:

$$y = y_{max} \quad \text{if } x < x_o$$

$$y = y_{\max}(-b(x_o - x)) \quad \text{if } x \geq x_o \quad (10)$$

where x and y are burial depth and seedling emergence rate, respectively, and $y_{\max}$, b and x_o are model parameters showing the maximum rate of seedling emergence, slope and the turning point in a non-linear regression, respectively. The same model was used to describe dormancy induction as affected by the depth of burial:

$$\begin{aligned} y &= y_{\max}(b \times (x - x_o)) & \text{if } x < x_o \\ y &= y_{\max} & \text{if } x \geq x_o \end{aligned} \quad (11)$$

where x and y are burial depth and percentage of dormant seeds, respectively, and $y_{\max}$, b and x_o are model parameters showing the maximum dormancy induction, slope and the turning point in a non-linear regression, respectively. The parameters were estimated by the least squares method using the non-linear (NLIN) regression procedure in SAS.

Results

Effect of burial on germination and viability of seeds in the soil - experiment 1

Almost 100% of the seeds buried on 23 September 2009 were viable. Seed viability decreased at a constant rate of 1.9 % per 100 days [model based on back transformed data during the 570 days of the experiment (data not shown)]. Viability of seeds stored under laboratory conditions did not decrease during the experiment. Lab-stored seeds germinated to 0.7-4.8 % in dark and 0.4-7.6 % in light, and there were no significant differences over time (Fig 1).

Germination at the beginning of experiment was 2.7 and 5.4 % in dark and light, respectively (Fig. 1a). After 1 month of burial (23 October 2009), germination percentage was low, and it increased for seeds tested on 23 November and 23

December 2009, with another decrease until August 2010. There was no significant difference in germination for November 2009-exhumed seeds incubated in dark and light, but December 2009-exhumed seeds germinated to a significantly higher percentage in light than in dark. Maximum germination of buried seeds was 51 and 68 % on 23 September 2010 in dark and light, respectively. Germination percentage was maximum from 23 August 2010 (last month of summer) to 23 February 2011 (last month of winter), with a decrease in November 2010.

Effect of water stress and temperature on germination and dormancy induction of nondormant seeds– experiment 2

Estimates of cardinal temperatures were 0.30 to 1.94 °C for T_b , 17.2 to 21.4 °C for T_{o1} , 21.7 to 25.0 °C for T_{o2} and 30.0 to 36.6 °C for T_c , and estimates of R_{max} were 0.0102 to 0.0160 h⁻¹ (Table 1; Fig 2). The median thermal time to germination ($TT_{(50)}$) increased from 50.54 °C d (0 MPa) to 79.3 °C d ($\psi = -0.6$ MPa) at low ψ and sub-optimal temperatures (Table 1). Under supra-optimal temperatures, $TT_{(50)}$ ranged from 19.7 to 41.1 °C d. The R^2 values indicate a good fit of the thermal time model under both sub- and supra-optimal temperatures. The predicted germination time courses at the various water potentials (ψ) and temperatures generally fitted well with the observed germination data, with R^2 values of 0.92 to 0.98 (Fig 3; Table 2). The estimated values of $\psi_{b(50)}$, $\sigma_{\psi b}$ and $HT_{(50)}$ differed at different germination temperatures (Table 2). The highest $HT_{(50)}$ and lowest $\psi_{b(50)}$ were observed at 5°C and 15 °C, respectively.

The percentage of dormant seeds increased significantly with increasing temperature or decreasing water potential (Fig 4). R^2 values were 0.96, 0.96, 0.95 and

0.99 for -0.6, -0.4, -0.2 and 0 MPa, respectively. At 0 MPa, GA₃ overcame seed dormancy, but 15.8 % of seeds (*Dmin*) were dormant even at the optimum temperature and water potential. There was a linear relationship between *Dmin* and water potential, and *Dmin* was reduced by 81.5 % with each increase in water potential (Fig 5a). The threshold temperature for dormancy induction (TTDI) was 18.9 °C in 0 MPa, and higher temperatures increased dormancy induction by a slope of 5.3 % (Fig 4). For water stressed seeds, TTDI decreased significantly with a fixed slope (Fig 5b). TTDIs were 18.9, 20, 15.6 and 13.7 °C at 0, -0.2, -0.4 and -0.6 MPa, respectively. Minimum dormancy (*Dmin*) was 40.1, 54.2 and 65.5 % at -0.2, -0.4 and -0.6 MPa, respectively (Fig 4).

Effects of burial depth on seedling emergence and dormancy – experiment 3

The dormancy level depended on location of seeds in the soil profile, and it ranged from 28.5 % (at 1 cm depth) to > 90 % (≥ 6 cm) (Fig 6). The percentage of dead seeds did not change with increasing burial depth, and it ranged from 1.9 to 4.3 % (Fig 6). Maximum seedling emergence (68.4%) was at a burial depth of 1 cm, and seedling emergence percentage decreased from 1 cm to 8 cm soil depths (Fig 6). No seedlings emerged from seeds buried at a depth of 8 cm, and seedling emergence for seeds buried at 6 cm was only 5% (Fig 6). Seedling emergence percentage was described well by exponential regression (Fig 7a). R^2 and RMSE values for the model were 0.97 and 4.22, respectively. Seedling emergence rate was satisfactorily described by a segmented model ($R^2 = 0.99$) (Figure 7b). Thus, there was no change in rate of seedling emergence (around 0.08 day^{-1}) from a burial depth of 1 cm to 3.84 cm. However, burial in deeper layers of soil reduced seedling emergence rate by a fixed

slope of 0.02 (Fig. 7b). Percentage of dormant seeds increased with burial depth, and this response was described by a segmented function (Fig 8). Induction of dormancy increased linearly from 1 to 5.19 cm with a slope of 13.2 %. The non-linear regression model showed that dormancy induction was about 96 % at burial depths of 5.19 to 30 cm (Fig 8).

Discussion

Knowing the rate at which seeds buried in the soil lose viability can be helpful in the management of weeds in arable fields (Masin et al. 2006). Loss of viability in a cohort of *S. arvensis* seeds in the soil exhibited a Deevey Type II survivorship curve, i.e. a constant probability of death (Roberts and Dawkins 1967; Roberts and Feast 1973ab; Murdoch 2006). However, after longer periods of time the curve may be of another type. Seed viability decreased at a constant rate of 1.9 % per 100 days (6.9 % per year) during 570 days (experiment 1). Edwards (1980) reported that annual emergence of *S. arvensis* seedlings in field plots in the United Kingdom was c. 2.5% of the seed population and estimated that the annual death of seeds in the soil was c. 17.9%. At Wellesbourne in the United Kingdom, Roberts and Boddrell (1983) documented seedling emergence from *S. arvensis* seeds buried in nondisturbed soil in 1965, 1966 and 1967 for five consecutive years for each burial date, after which 9.1, 6.5 and 2.6 %, respectively, of the buried seeds were viable. Donald (1993) used several regression models to describe *S. arvensis* seed survival during 4 years and found that it decreased from 100 % to about 60 and 90 % after 1 year of burial in two different trials.

Seed longevity is influenced by several factors in the soil seed bank, and it may increase (Walker et al., 2010), decrease (Steckel et al., 2007) or not change (Egley and Chandler, 1983) with soil depth. Soil disturbance increases soil aeration and exposes seeds to light, thereby improving conditions for germination and reducing seed longevity (Cardina et al. 1998). Soil texture and structure, kind of plow, depth of disturbance, timing and amount of precipitation and irrigation, temperature and gas (CO_2/O_2) exchange potential of soil affect seed mortality, germination and dormancy in the soil seed bank (Baskin and Baskin 2014). In addition to the effects of environmental factors, including predation, natural ageing of seeds determines their maximum longevity in soil seed banks (Davis et al. 2008). Longevity of seeds in the soil is influenced by, moisture content, chemical composition and vigour of seeds, and it varies among species (Baskin and Baskin 2014). Garbutt and Witcombe (1986) reported that seeds of *S. arvensis* produce two "cohorts" of seedlings each year, one in spring and the other in autumn. Plants from seeds germinating in spring would behave as summer annuals, and those from seeds germinating in autumn would behave as winter annuals. Chepil (1946) and Roberts and Boddrell (1983) found that most seedlings of *S. arvensis* emerged in April-July in Canada and March-April in the United Kingdom, respectively, with sporadic emergence at other times during the growing season. Thus, most plants in Canada and England would be summer annuals. However, in Iran most plants are derived from seeds that germinate in autumn, and winter and consequently plants behave as winter annuals. In the second year of experiment 1 in our study, maximum germination was observed during the period of 23 August 2010 (last month of summer) to 23 February 2011 (last month of winter). Although there was a decline in germination of exhumed seeds in November 2011, there was no abrupt change in the temperature between October and December (Fig.

1b) that might help account for induction of secondary dormancy; soil moisture data were not collected, so possible effects of water stress are unknown.

Overall, our results are similar to those reported by Chepil (1946) and Roberts and Boddrell (1983) in that there was only one major period of germination during the study. However, unlike these two studies in which seeds were exposed to natural seasonal temperature changes, we incubated seeds at 20°C, which would approximate spring temperatures in Canada and the United Kingdom. Consequently, in our study seeds were capable of germinating for a longer period of time (late August to late February) than they were in the studies by Chepil (1946) and Roberts and Boddrell (1983). Our seeds were always incubated at 20°C, while those in the other two studies were germinating at natural field temperatures. Thus, it seems reasonable that as temperatures (and possibly water stress) increased in Canada (Chepil, 1946) and the United Kingdom (Roberts and Boddrell, 1983) with the beginning of summer there would be a decline in germination.

The increase in germination percentage between the time seeds were buried in September and exhumed in November indicates that some dormancy break occurred during this time (Fig. 1a). Roberts and Boddrell (1983) reported that some seeds of *S. arvensis* germinated immediately after they were sown in autumn. They also found some variation in the degree of dormancy in seeds collected in different years and thus different germination percentages of autumn-sown seeds. Although exhumed seeds germinated to 48 and 22 % at 20°C in our study in November and December 2009, respectively, they did not reach 20% germination again until July 2010. During the period January to June-July 2010, dormancy break occurred in the buried seeds, and from August 2010 to February 2011 germination of exhumed seeds at 20°C ranged from 35 to 70 %. The lab-stored seeds did not afterripen and maximum

germination was c. 10%. Thus, the summer environmental conditions (probably the long period at high summer temperatures) promoted dormancy-break, but those in the lab did not.

Between February and April 2011, buried seeds of *S. arvensis* lost the ability to germinate at 20°C. According to the literature review conducted by Gardarin and Colbach (2015), dormancy induction occurs in buried seeds of *S. arvensis* between March and June. However, a limitation of experiment 1 in our study is that exhumed seeds were tested for germination only at 20°C. Thus, we cannot determine if the low germination percentage in April 2011 represents an induction into dormancy (loss of ability to germinate over the full range of temperatures at which nondormant seeds can germinate) or into conditional dormancy (loss of ability to germinate at some portion of the range of temperatures at which nondormant seeds can germinate). The loss of ability of buried *S. arvensis* seeds to germinate at 20°C as temperatures increase in spring is similar to the responses of buried seeds of the weedy winter annual *Capsella bursa-pastoris*. Whereas buried seeds of winter annuals typically enter secondary dormancy in autumn and early winter (as temperatures decrease), those of *C. bursa-pastoris* do not enter secondary conditional dormancy until spring (as temperatures increase) (Baskin and Baskin 1989). Buried seeds of *C. bursa-pastoris* exhibit an annual nondormancy (ND)/conditional dormancy (CD) cycle, and based on the similarity of germination response of *S. arvensis* and *C. bursa-pastoris* seeds, it is assumed that buried seeds of *S. arvensis* also have an annual ND/CD cycle.

Much is known about the dormancy breaking and germination requirements of seeds of winter annuals, especially with regard to responses to temperature (Baskin and Baskin 2014). However, there are only a few reports of using hydrothermal time

models to investigate seed dormancy and germination in winter annual weeds:

Bromus tectorum (Bauer et al. 1998, Bair et al. 2006; Meyer et al., 2000; Meyer and Allen, 2009), *Hordeum spontaneum*, *Phalaris minor*, *Raphanus raphanistrum* (Mesgaran et al. 2013) and volunteer oil seed rape (Soltani et al. 2013). Our study quantified the germination responses of *S. arvensis* seeds to temperature and water potential by hydrotime and thermal time models for the first time. The lowest $\psi_b(50)$ was observed at 15 °C (Table 2), and dormancy induction also was low at 15 °C (Fig 5). The mean percentage of dormant seeds was 49.1, 43.1, 43.1, 49.7, 67.3, 90.7 and 99.7 at 5, 10, 15, 20, 25, 30 and 35 °C, respectively, across the range of water potentials. Thus, low soil water potential and supra-optimal temperatures that occur with the beginning of summer can induce seeds of *S. arvensis* into secondary dormancy. Seeds that germinate at lower $\psi_b(50)$ have lower degrees of dormancy, and increasing temperature leads to increase in $\psi_b(50)$ (Meyer et al. 2000; Meyer and Allen 2009). The threshold temperature for dormancy induction (TTDI) in *S. arvensis* was about 19 °C when water was not limiting germination, and TTDI decreased as water potential decreased, with a slope of 10 °C per MPa (Fig 5, 6b).

Dormancy in *S. arvensis* seeds also can be described with *Dmin*. This parameter shows the minimum depth (intensity) of dormancy when $T < \text{TTDI}$ for each water potential and therefore the portion of dormancy induction due to water potential. Luzuriaga et al. (2006) found that small plants of *S. arvensis* mainly produced black seeds and large plants produced red seeds, Further, black seeds had stronger dormancy than red seeds. We used a mixed seed lot, and this may help to explain why a portion of the seeds remained dormant (*Dmin*) even after treatment with GA_3 and incubation at optimum water potential and temperature. *Dmin* decreased 81.5 % with each increase in water potential (Fig 5a). It seems, then, that *Dmin* also can be used to

show depth (intensity) of nondeep PD at the non-limiting water potential. Dormancy induction did not change significantly between low and high temperatures (when $T < TTDI$), but there was a slightly greater increase in dormancy induction at 5 °C than at 10 or 15 °C, especially at lower water potentials (Fig 4). It is well known that low temperatures such as 5°C can induce seeds of winter annuals into secondary dormancy (Baskin and Baskin, 2014). Thus, induction of dormancy in buried seeds of *S. arvensis* between February and April 2011 may be related more to increase in water stress than to increase in temperature.

Seeds of *S. arvensis* are very sensitive to water stress, and a decrease in water potential to -0.6 MPa can induce secondary dormancy (at least 65 % at $T < TTDI$). This response to water stress has the potential to be of use in management of this winter annual weed because crop species such as oil seed rape (Soltani et al. 2013) and sugarbeet (Farzane & Soltani, 2011) can germinate at $\psi_b(50)$ lower than -0.6 MPa. Thus, we suggest that water stress could be used to induce seeds of *S. arvensis* into secondary dormancy, but the stress would not prevent germination of the crop species. However, although *S. arvensis* would not be competing with crop plants, its seeds would remain in the soil seed bank and be a problem in future years. There are other reports of dormancy induction by water stress in weedy species such as *Chenopodium bonus-henricus* L. (Khan and Karssen 1980), *Rumex crispus* (Samimy and Khan 1983) and volunteer oil seed rape (Momoh et al. 2002; Gulden et al. 2004). Gulden et al. (2004) showed that a decrease in water potential increased the rate of dormancy induction in oil seed rape, and Momoh et al. (2002) found that osmotic stress was more effective than low oxygen concentration in inducing dormancy in seeds of this species.

In experiment 3, the rate and percentage of seedling emergence of *S. arvensis* decreased with an increase in burial depth, and the percentage of seeds induced into dormancy increased. In general, failure of seedlings to emerge could result from (1) unfavourable conditions for germination, (2) induction of seed dormancy or (3) pre-emergence mortality (fatal germination). Dormancy induction in *S. arvensis* increased linearly with a slope of 13.23 % with each additional centimetre of burial depth from 1 to 5.19 cm, and it was highest (96 %) in seeds at depths ≥ 5.19 cm (Fig 8). The reason for increased dormancy with increased depth of seed burial was not determined. However, given that seeds were in pots in the same location in the greenhouse and that the soil was watered regularly, it does not seem likely that either temperature or water stress is related to the linear increase in dormancy induction with depth. The decrease in germination with an increase in depth of burial may be due to the re-induction of dormancy.

Re-induction of dormancy in buried seeds may be linked to interactions between seed metabolism and the soil gas environment, rather than the depletion of seed energy reserves (Benvenuti et al., 2001). Decreased metabolic activity of buried seeds, confirmed by a slower seedling emergence, would prevent the toxic fermentation metabolites from reaching the threshold that can block seed germination and re-induce dormancy (Holm, 1972). However, high soil moisture, soil compaction, high microbial activity and/or poor soil structure may decrease soil oxygen concentration or inhibit movement of gases within the soil, leading to accumulation of volatile fermentation products that inhibit germination (Chantre et al. 2009). Edwards (1969) found that a decrease in oxygen concentration, such as might be expected with an increase in soil depth, did not induce seeds of *S. arvensis* into dormancy *per se*.

However, at oxygen levels below 0.1 atm the rate of production of germination-inhibiting substances increased with a decreased in oxygen supply.

In summary, freshly-matured seeds of *S. arvensis* were dormant when collected in May 2009 (spring) and did not after-ripening during 23 months of dry storage under ambient laboratory conditions. However, seeds buried in the soil in October 2009 germinated to high percentages when exhumed monthly from August 2010 to February 2011 and tested at 20°C but did not germinate when exhumed in April 2011. Our studies on germination responses of *S. arvensis* seeds to temperature and water potential using hydrotime and thermal time models reveal that low water potential is an important factor in inducing seeds into secondary dormancy, which helps to explain why dormancy induction in seeds of this weedy winter annual is delayed until spring when temperatures and thus water stress are increasing. We also found that an increase in burial depth increased the percentage of seeds induced into secondary dormancy. However, mean temperature and water content did not explain the relationship between depth of seed burial and dormancy induction. Thus, depth of burial *per se* also can promote induction of secondary dormancy and thereby potentially increase the size of the soil seed bank.

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Table 1 - Parameter estimates of the thermal time model describing nondormant seed germination of *S. arvensis* at a range of water potentials. Prior to the test, seeds were treated with GA₃ to release primary dormancy. At each water potential, seeds were incubated at 5, 10, 15, 20, 25, 30 and 35 °C. T_b, T_{o1}, T_{o2} and T_c, base, lower optimum, upper optimum and ceiling temperatures (°C), respectively; R_{max}, maximum rate of germination (h⁻¹); Final (%), mean germination percentage at each water potential; R² coefficient of determination of the regression thermal time model; and TT₍₅₀₎, °C day thermal time for 50% of maximum germination at sub- and supra-optimal temperatures. Numbers in parentheses represent the standard errors.

WP (MPa)	T _b	T _{o1}	T _{o2}	T _c	R _{max}	Sub-optimal			Supra-optimal		
						Final (%)	TT ₍₅₀₎	R ²	Final (%)	TT ₍₅₀₎	R ²
0	1.94 (0.456)	21.35 (3.022)	22.55 (2.776)	36.46 (2.500)	0.0160 (0.0002)	83.1 (1.28)	50.54 (1.768)	0.98	24.7 (3.05)	35.82 (3.816)	0.93
-0.2	1.87 (0.376)	21.18 (2.904)	21.66 (3.187)	36.57 (2.655)	0.0149 (0.0002)	60.0 (1.86)	54.04 (1.868)	0.98	16.7 (3.89)	41.07 (4.567)	0.92
-0.4	0.67 (0.345)	17.24 (0.787)	24.75 (0.235)	30.00 (0.162)	0.0106 (0.0003)	43.3 (1.88)	70.64 (1.667)	0.99	9.3 (2.11)	20.65 (4.406)	0.95
-0.6	0.30 (0.554)	18.57 (1.127)	25.00 (4.199)	29.99 (2.159)	0.0102 (0.0003)	28.6 (1.69)	79.30 (2.213)	0.99	7.3 (2.75)	19.66 (1.599)	0.95

Table 2 - Parameter estimates of the hydrotime model for seven temperatures describing nondormant seed germination of *S. arvensis* at a range of water potentials. Prior to the test, seeds were treated with GA₃ to release primary dormancy. $\psi_{b(50)}$, median base water potential; $\sigma_{\psi b}$ standard deviation of base water potential; $HT_{(50)}$, hydrotime constant (MPa-hours); R^2 , coefficient of determination of the regression hydrotime model; and Final (%), mean germination percentage (numbers in parentheses represent the standard errors) at each temperature.

Temperature (°C)	$\psi_{b(50)}$	$\sigma_{\psi b}$	$HT_{(50)}$	R^2	Final (%)
5	-0.544	0.337	159.05	0.92	50.88 (3.54)
10	-0.681	0.596	131.53	0.98	56.88 (2.62)
15	-0.737	0.607	90.22	0.97	56.53 (2.87)
20	-0.463	0.334	31.87	0.92	50.28 (3.45)
25	-0.096	0.622	39.19	0.96	32.63 (2.16)
30	0.064	0.366	34.59	0.94	9.00 (1.42)

Figure captions:

Fig 1. Changes in (a) germinability of *Sinapis arvensis* seeds buried on 23 Sept. 2009, and (b) maximum and minimum soil temperatures. Air temperatures obtained from a weather station in Gorgan were converted to soil temperatures using equation 1. Error bars are ± 1 SE. MF, maintained in field; ML, maintained in lab.

Fig 2. Effect of temperature and water potential on germination rate (hour^{-1}) of *Sinapis arvensis* seeds. The lines show dent-like functions used to describe the response of germination rate to temperature at each of the four water potentials. Error bars are ± 1 SE.

Fig 3. Germination time courses for seeds of *Sinapis arvensis* incubated at each of four water potentials at 5, 10, 15, 20, 25 and 30 °C. Symbols indicate interpolations of observed germination data and lines germination time courses predicted by the hydrotime model based on parameter estimates in Table 2. Error bars are ± 1 SE.

Fig 4. Effects of temperature and water potential on dormancy induction in *Sinapis arvensis* seeds. The lines show segmented functions used to describe the response of dormancy induction to temperature for each water potential. Error bars are ± 1 SE.

Fig 5. Changes in the parameters of the model used to explain dormancy induction. (a) Minimum dormancy, D_{min} , and (b) threshold temperature for dormancy induction (TTDI). Lines are fitted linear regressions that describe changes in parameters in response to water potential. Error bars are ± 1 SE.

Fig 6. Fates of *Sinapis arvensis* seeds at the different soil depths in a pot experiment.

Fig 7. Relationship between seedling emergence percentage (a) and emergence rate (b) with burial depth in *Sinapis arvensis* seeds. Error bars are ± 1 SE.

Fig 8. Relationship between dormant seeds (%) and burial depth in *Sinapis arvensis*.

The line shows segmented function used to describe the response of dormancy induction to burial depth.

Error bars are ± 1 SE.

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Figure1. xxx

Figure2. xxx

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