Research Article

Seed germination modeling of sterile oat biotypes susceptible and resistant to ACCase-inhibiting herbicides in response to temperature and drought stress

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Abstract: Temperature and water potential are the main determinants of the seed germination of plant species. Experiments were conducted to quantify the seed germination response of two sterile oat *Avena sterilis* subsp. *ludoviciana* (Durieu) Nyman biotypes susceptible and resistant to acetyl coenzyme A carboxylase inhibitor herbicides under six temperature regimes (5, 10, 15, 20, 25, and 30 °C), and five levels of drought stress (0.0,-0.3, -0.6, -0.9, and -1.2 MPa). The base temperature of seed germination in both biotypes was affected by drought stress. The base temperature changed from no stress to maximum stress in the susceptible biotype from 3.24 to 7.15 °C and in the resistant biotype from 3.12 to 7.43 °C. Thermal times required for 50% germination of the seed population at sub-optimal temperatures was increased from 26.2 to 87.8 °C day in the susceptible biotype and from 28.8 to 90.6 °C day in the resistant biotype. Increasing the temperature from 5 to 30 °C decreased the constant hydrotime from 10.92 to 1.66 MPa in the susceptible biotype and 11.52 to 1.98 MPa in the resistant biotype. The hydrothermal time constant for susceptible and resistant biotypes was 28.6 and 31.1 MPa. According to the hydrothermal time model, the herbicide-resistant biotype (-0.858 MPa) seeds require more water potential than the susceptible biotype (-0.905 MPa) to germinate at higher temperatures. Based on the parameters of the models, the germination response to temperature and water potential was similar in both susceptible and resistant biotypes. Consequently, maximum emergence of both biotypes is possible at 15 °C and without water stress conditions.

Keywords: Cardinal temperatures, Fitness cost, Hydrothermal time, Quantification, Water potential

Introduction

Sterile oat *Avena sterilis* subsp. *ludoviciana* (Durieu) Nyman is a significant problematic weed in winter crops in Iran. Like other weeds in the Poaceae family, winter sterile oat is considered a strong competitor for water, nutrients, and light due to its dense leaf cover, strong tillering ability, tall height, allelopathy, and ecological, biological, and botanical similarities to cereals such as wheat (Hasanfard *et al*., 2022). Armin and Asgharipour (2011)

reported that sterile oats with densities of 25, 50, and 75 plants m^{-2} reduced the economic yield of wheat by 10, 19, and 20%, respectively. These researchers found that increasing the density of sterile oats reduced wheat yield by reducing the number of fertile tillers per plant and spikes m^{-2}. It has also been reported that densities of 1 to 2 plants of sterile oat m^{-2} lead to a 5% reduction in wheat yield (Bussan and Maxwell, 2000).

Seed germination response of plant species to environmental factors such as temperature, light, drought, and salinity stresses affects their establishment (Toscano *et al.,* 2017; Wu *et al.,* 2015). Seed germination is considered one of the most important stages in the life cycle of plant species, especially in arid and semi-arid regions, which is influenced by two environmental regulators: temperature and water potential (Toscano *et al.,* 2017). Temperature and moisture can affect the percentage and rate of germination together or independently. Therefore, they are the most critical factors in the success or failure of a species (Nozarpour *et al.,* 2017; Kamkar *et al.,* 2012).

In general, the three temperatures of minimum (base temperatures), optimum, and maximum (ceiling) are known as cardinal temperatures in the germination process of seeds of any plant. In other words, the effect of temperature on germination is described as cardinal temperatures (Cave *et al.,* 2011).

Water potential is also considered a primary environmental factor in determining the seed germination of plants (Moral *et al.,* 2015). Seed embryo growth begins with water uptake, and therefore, the germination time pattern in the seed population is determined by soil water potential (Derakhshan and Gharineh 2015). Consequently, the success of natural propagation, especially in arid and semi-arid regions, depends on seed germination's response to several external factors, including water restriction (Krichen *et al.,* 2014).

The occurrence of resistant biotypes of weed has increased mainly because of the repetitive use of the same herbicide or herbicides with the same mechanism of action (Moss *et al.,* 2019). Herbicide resistance may or may not devolve

fitness penalties in the resistant populations (Tang *et al.,* 2019). Fitness is the ability of organisms to survive and reproduce in their habitat, which is considered an evolutionary success (Park and Mallory-Smith, 2005). Fitness surveys are important in developing evolutionary models for herbicide resistance (Maxwell *et al.,* 1990). Measuring and quantifying herbicide-resistance fitness cost is also essential for predicting the frequency of resistant (R) and susceptible (S) plants under various environmental conditions (Keshtkar *et al*., 2019). The anticipated detrimental effects of herbicide resistance mutations on plant fitness may arise as a direct impact on fitness-related traits (e.g., reduced pollen viability) and co-evolution of loci interactions (e.g., resistance and non-resistance alleles) contributing to changes in other plant traits (e.g., seed dormancy) that ultimately may, in particular ecological environments, lead to fitness costs (Lenormand *et al.,* 2018; Baucom, 2019). The rationale for measuring the cost of herbicide resistance (prediction of the impacts of management options on population dynamics) cannot be addressed using arbitrary components of fitness or a fixed value of relative fitness. Hence, measuring traits that include relevant processes and the primary causes of their variation is needed to inform management options (Cousens and Fournier-Level, 2018).

Despite a sound theoretical background, related studies have concluded that there is no universality in the expression of fitness costs associated with herbicide resistance mutations (Cousens and Fournier-Level, 2018). Instead, these studies have determined that fitness cost expression in herbicide-resistant weeds depends on the particular herbicide resistance mutation, the dominance of the fitness cost, genetic background, and environmental conditions (Vila-Aiub *et al.,* 2009).

Although herbicide resistance may not increase or decrease the germination rate, its study is crucial in predicting possible population changes in future generations (Abdolahipour *et al*., 2013). The knowledge of the biological traits of herbicide-resistant and

herbicide-susceptible weed stands will be helpful in their management. Differences in the competence of herbicide-resistant and herbicide-susceptible weed biotypes make it possible to predict the evolution of herbicide resistance and design management strategies to exploit traits that reduce the ecological emergence of resistant weeds. The results of these experiments are valuable for developing model predictions and identifying the times when weed control is most effective (Valičková *et al.,* 2017; Vila-Aiub *et al.,* 2009).

Some mathematical models, known as hydrothermal time models (Onofri *et al.*, 2018), describe the relationship between germination properties, such as germination rate, and factors like temperature and water potential. The resulting parameters are used to predict the emergence of weeds in response to temperature and water potential, which are the two main factors affecting the germination of dormant seeds (Soltani *et al.,* 2013). In addition, the main advantage of these models is that their components have biological concepts; therefore, germination modeling is used to determine items such as cardinal temperatures for germination and emergence, to determine the base water potential for germination, and to determine the germination and emergence time (Sousa-Ortega *et al.,* 2021).

The primary objective of this study was to evaluate the effects of temperature and water stress on sterile oat seed germination and determine cardinal temperatures as basic information in biological studies of this weed species.

Materials and Methods

Plant materials and experimental factors

Seeds of resistant and susceptible sterile oat biotypes were prepared from a previous research project where the resistant biotype had shown cross-resistance to acetyl coenzyme A carboxylase (ACCase) inhibitors (e.g. clodinafop-propargyl), with target-site based resistance mechanism (Ile 1781 Leu) (Rastgoo *et al.,* 2009). Meanwhile, the seeds were stored in

paper bags at 5 °C. Homozygous resistant and susceptible plants in the F_1 generation were determined by ACCase genotyping, and each was grown in a pollen-proof enclosure to produce F_2 seeds. F_2 seeds were used for the main experiment (Rastgoo *et al.,* 2009).

The experiment was carried out in 2017 in the Faculty of Agriculture, Ferdowsi University of Mashhad's weed science research laboratory as factorial experiments in a completely randomized design with four replications. Experimental factors included temperature at six levels (5, 10, 15, 20, 25, and 30 °C) and drought stress using polyethylene glycol 6000 at five levels (0.0 -0.3, -0.6, -0.9, and -1.2 MPa). The Michel and Kaufmann method determined land levels (Michel and Kaufmann 1973).

Seed germination tests

After separating the lemma and palea from the seeds and removing the empty and damaged seeds, stratification treatment was performed to break the seed dormancy (Hasanfard *et al.,* 2021). Then, 25 seeds were counted and placed in Petri dishes with a 9 cm diameter covered with filter paper (Whatman Cat. No.1). Before placing the seeds in all experiments, 5% sodium hypochlorite was used to disinfect the seeds (3-5 minutes at room temperature), and then the seeds were washed with distilled water. 10 mL of the prepared solution was added to Petri dishes for each level of drought. One day before the start of each thermal cycle, the germinator was set at the desired temperature (in dark conditions). After ensuring the normal temperature fluctuation (±1 °C), the Petri dishes were placed in it.

In the early stages of the experiment, all germinated seeds were counted and removed at intervals of every 12 h. This operation was performed every 24 h because the germination rate had decreased. A seed was germinated when its radicle protruded through the seed coat by at least 2 mm. The solution was changed every two to three days to prevent water potential decline in the Petri dishes. The germinated seeds were counted for 21 days in all replications of the experimental treatments.

Determination of cardinal temperatures and thermal time model

To determine the cardinal germination temperatures (base temperature, optimum temperature, and maximum temperature) for each level of water potential in the sterile oat population seeds, first, the cumulative germination percentage was plotted against time (in hours). From this curve, the time to 50% germination (t_{50}) was determined by fitting a Weibull equation to cumulative germination percentage (G) against time (t, in hours) according to Guillemin *et al*. (2012):

$$G = 0, if\ t < t_0\ , G = m\left[1 - e^{-\ln(2)\times(\frac{t-t_0}{t_{50}-t_0})^b}\right], if\ t > t_0 \qquad \text{(Eq. 1)}$$

Where m is the maximum germination percentage, t_0 is the time between the beginning of the incubation and the first germination, and b is the shape parameter. The reciprocal of the time taken for 50% of the seed population to germinate was considered to be the germination rate (GR). Then, the average germination rate against temperature was plotted separately for different levels of water potential. Equations 2 and 3 were then simultaneously fitted to the temperature range from base temperature to optimum temperature (Equation 2) and optimum temperature to maximum temperature (Equation 3), respectively, using a conditional equation.

$$GR = 1/t_g = (T-T_b)\ /\ TT_1 \qquad \text{(Eq. 2)}$$

$$GR = 1/t_g = (T_c-T)\ /\ TT_2 \qquad \text{(Eq. 3)}$$

Where TT_1 and TT_2 are the thermal time (Heat sum) to germination of fraction or percentage g (i.e., 50%), in the sub and supra-optimal temperatures, T is the germination temperature, and T_b is the base temperature. The optimum temperature, the peak point of the composite curve resulting from the two equations 2 and 3, is the point of intersection of the two fitted lines to the temperatures sub and supra the optimum temperature. In the next step, the data related to the water potential levels and the fit of the mentioned models, the values related to the base, optimum and maximum temperatures, and

thermal times (Degree Days) were determined for the seeds (Bradford 2002; Bradford 1990).

Determination of base water potential of germination and hydrotime model

For this purpose, values related to the average germination rate were used. First, the average seed germination rate curve was plotted by temperature relative to water potential. Then, by fitting the linear function (Equation 3), the physiological base water potential (Ψ_b) of seed germination as well as the hydro-time (HT) for each temperature were determined (Gummerson 1986; Bradford 2002; Bradford 1990) (Equation 4).

$$GR = 1/t_g = (\Psi\text{-}\Psi_{b(g)})\ /\ HT \qquad \text{(Eq. 4)}$$

Where the HT is hydrotime constant (MPa Days), Ψ is seed water potential (MPa), and $\Psi_{b(g)}$ is the base or threshold water potential for a specific germination fraction g (i.e., 50%) (MPa).

Determination of hydrothermal time requirement

To quantify the response of germination rate to temperature and water potential simultaneously, the hydrothermal time model was used (Equation 5):

$$GR = 1/t_g = (\Psi\text{-}\Psi_{b\ (g)})\ (T\text{-}T_b)\ /\ HTT \qquad \text{(Eq. 5)}$$

Where HTT is the hydrothermal time constant (MPa Degree Days) for sub-optimal temperatures, which combines cumulative thermal time at temperatures above base temperature and cumulative hydrotime at water potentials above base water potential, $\Psi_{b(g)}$ is the base or threshold water potential for a specific germination fraction g (i.e. 50%) (MPa), T is temperature and T_b is base temperature (Gummerson, 1986; Bradford, 2002; Bradford, 1990).

The experiments were conducted twice. As no significant differences were observed between the runs and treatments (p > 0.05), data was pooled over the experimental runs and averaged for analysis. Analysis and fitting related to seed germination modeling were performed by iterative optimization method with nonlinear model procedure (Proc Nlin) by SAS 9.4 statistical software (SAS Institute, Cary, NC, USA).

Results

Cardinal temperatures

Cardinal temperatures of the susceptible and resistant sterile oat biotypes in response to water potential were estimated by fitting the dent-like model. The dent-like model properly determined the relationship between germination rate and temperature at different water potentials. The coefficient of determination values (R^2) for the susceptible biotype ranged from 0.90 to 0.96, and for the resistant biotype, from 0.91 to 0.95 (Table 1). Also, the base temperature for germination in both biotypes was affected by water potential levels. Thus, base temperatures in susceptible biotypes changed from 3.24 to 7.15 °C, and in resistant biotypes, they changed from 3.12 to 7.43 °C for the lowest water potential (0 MPa) to the highest water potential (-0.9 MPa).

The optimum temperature range in the susceptible biotype under the lowest and highest water potentials was 6.20 and 2.18 °C, respectively. In contrast, in the resistant biotype, under the mentioned conditions, it was 5.84 and 1.70 °C, respectively. Maximum temperature for seed germination in the susceptible biotype under the lowest and highest water potential were 42.32 and 32.54 °C, respectively, and in the resistant biotype under the mentioned conditions were 41.65 and 32.34 °C, respectively (Table 1).

Thermal time requirement

Thermal time required for germination of 50% of the seed population at sub-optimal temperatures ($TT_{(50)}$) in the susceptible biotype ranged from 26.2 degree days (DD) in 0 MPa to 87.8 DD in -0.6 MPa, and in the resistant biotype ranged from 28.8 DD in 0 MPa to 90.6 DD in -0.6 MPa (Table 2).

Table 1 Estimating cardinal temperatures of seed germination in susceptible and herbicide-resistant biotypes of sterile oat to ACCase inhibitors in response to water potential caused by applying polyethylene glycol (PEG) and based on fitting the Dent-like model.

Water potential (MPa)	T_b (°C)		T_{o1} (°C)		T_{o2} (°C)		T_m (°C)		$(T_{O2}-T_{O1})$ (°C)		R^2		RMSE	
	S	R	S	R	S	R	S	R	S	R	S	R	S	R
0	3.24 (0.21)	3.12 (0.13)	12.01 (0.43)	12.73 (0.37)	18.21 (0.45)	18.57 (0.27)	42.32 (0.47)	41.65 (0.36)	6.20	5.84	0.96	0.95	0.047	0.050
-0.3	3.89 (0.34)	4.11 (0.27)	13.56 (0.21)	13.87 (0.45)	17.55 (0.37)	17.78 (0.52)	41.16 (0.44)	40.18 (0.27)	3.99	3.91	0.94	0.94	0.053	0.052
-0.6	5.78 (0.34)	5.43 (0.56)	14.78 (0.46)	14.64 (0.54)	18.42 (0.57)	18.78 (0.36)	39.33 (0.24)	39.56 (0.39)	3.64	4.14	0.93	0.93	0.058	0.057
-0.9	7.15 (0.48)	7.43 (0.36)	15.19 (0.23)	15.56 (0.54)	17.37 (0.28)	17.26 (0.36)	32.54 (0.43)	32.34 (0.14)	2.18	1.7	0.90	0.91	0.071	0.070

S: Susceptible, R Resistance, Tb: Base temperature, To1: first optimum temperature, To2: second optimum temperature, Tm: maximum temperature, To2-To1: optimum temperature range, R^2: coefficient of determination, RMSE: root mean square error. The values in parentheses are standard error.

Table 2 Estimated parameters of thermal time model fitting to seed germination of susceptible and herbicide-resistant to ACCase inhibitors biotypes of sterile oat in different water potentials caused by the application of polyethylene glycol (PEG).

Water potential (MPa)	Biotype	Tb (°C)	$TT_{(50)}$ (Degree Day)	$\sigma TT_{(50)}$ (Degree Day)	Final G (%)	R^2	RMSE
0	Susceptible	0.118(3.578)	1.62(26.205)	0.45 (0.02)	98.83 (1.89)	0.97	0.023
	Resistant	0.471(3.421)	2.45(28.836)	0.39 (0.01)	98.85 (2.14)	0.98	0.021
-0.3	Susceptible	0.566(3.918)	2.03(51.94)	0.51 (0.01)	82.85 (1.54)	0.98	0.032
	Resistant	0.981(3.879)	3.93(54.62)	0.50 (0.01)	83.12 (1.77)	0.98	0.025
-0.6	Susceptible	0.862(5.294)	2.40(87.79)	0.38 (0.01)	45.35 (1.17)	0.96	0.034
	Resistant	0.892(5.024)	3.69(90.63)	0.42 (0.02)	46.57 (1.38)	0.97	0.029

(Tb): Base temperature, (TT $_{(50)}$): thermal time at sub-optimal temperature, (Final G): Final germination and goodness of fit parameters including coefficient of determination (R^2), root mean square error (RMSE) resulting from fitting thermal time model for seed germination of sterile oat biotypes susceptible and resistant to ACCase inhibitor herbicide. The values in parentheses are standard error.

Hydrotime requirement

Figs. 1 and 2 of the fitted hydrotime model show the cumulative germination percentage of seeds of sterile oat biotypes susceptible and resistant to ACCase inhibitors for each temperature level. According to Table 3, the values of the coefficient of determination (R^2) based on the hydro time model for fitting cumulative germination percentage for the susceptible biotype ranged from 0.81 to 0.98, and for the resistant biotype, ranged from 0.83 to 0.99, Which indicates an appropriate description of the model for quantifying the relationship (Table 3). The hydrotime constant (HT) in both biotypes decreased with increasing temperature (Table 3). The lowest hydrotime constant of both biotypes was observed at 30 °C. Thus, with increasing temperature from 5 to 30 °C, the hydrotime constant in the susceptible biotype decreased from 10.92 to 1.66 MPa day and in the resistant biotype from 11.52 to 1.98 MPa day.

Cumulative seed germination of susceptible and herbicide-resistant to ACCase inhibitor biotypes was fitted to the water potential and temperature data using a three-parameter sigmoidal model (Figs. 1 and 2). The results showed that the germination percentage decreased significantly in both biotypes at all temperatures with increasing water potential, and the time to reach 50% germination increased significantly.

The base water potential [$\psi b_{(50)}$] indicates the level of water potential at which the seed germination reaches less than 50% of the maximum germination at lower water potentials (Sousa-Ortega *et al.,* 2021). The highest water potential required for germinating 50% of the seeds [$\psi b(50)$] for the susceptible and resistant biotypes was -0.553 and -0.516 MPa at 30 °C. Also, the lowest $\psi b(50)$ in susceptible and resistant biotypes was -0.844 and -0.848 MPa, respectively, at 15 °C.
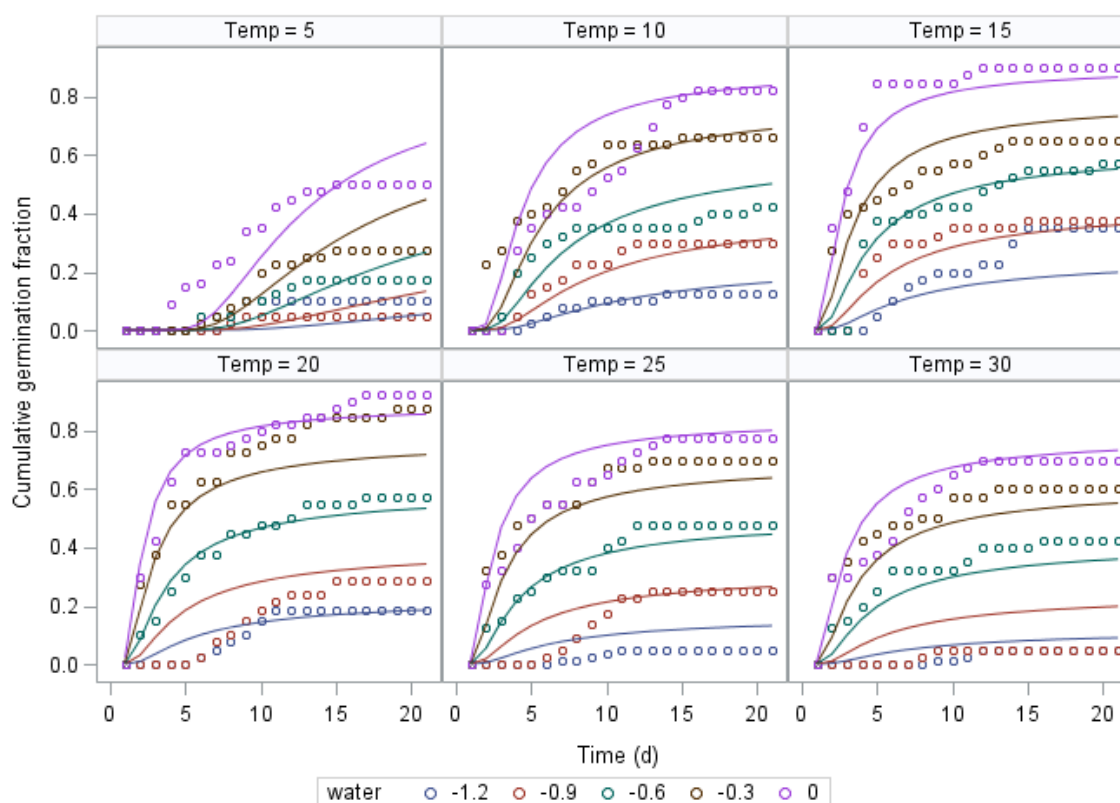

Figure 1 Fitting of the hydrotime model to the cumulative seed germination of susceptible sterile oat biotype to ACCase inhibitors in different water potentials caused by PEG application at different temperatures. The points are the observed values, and the lines are the predicted values.
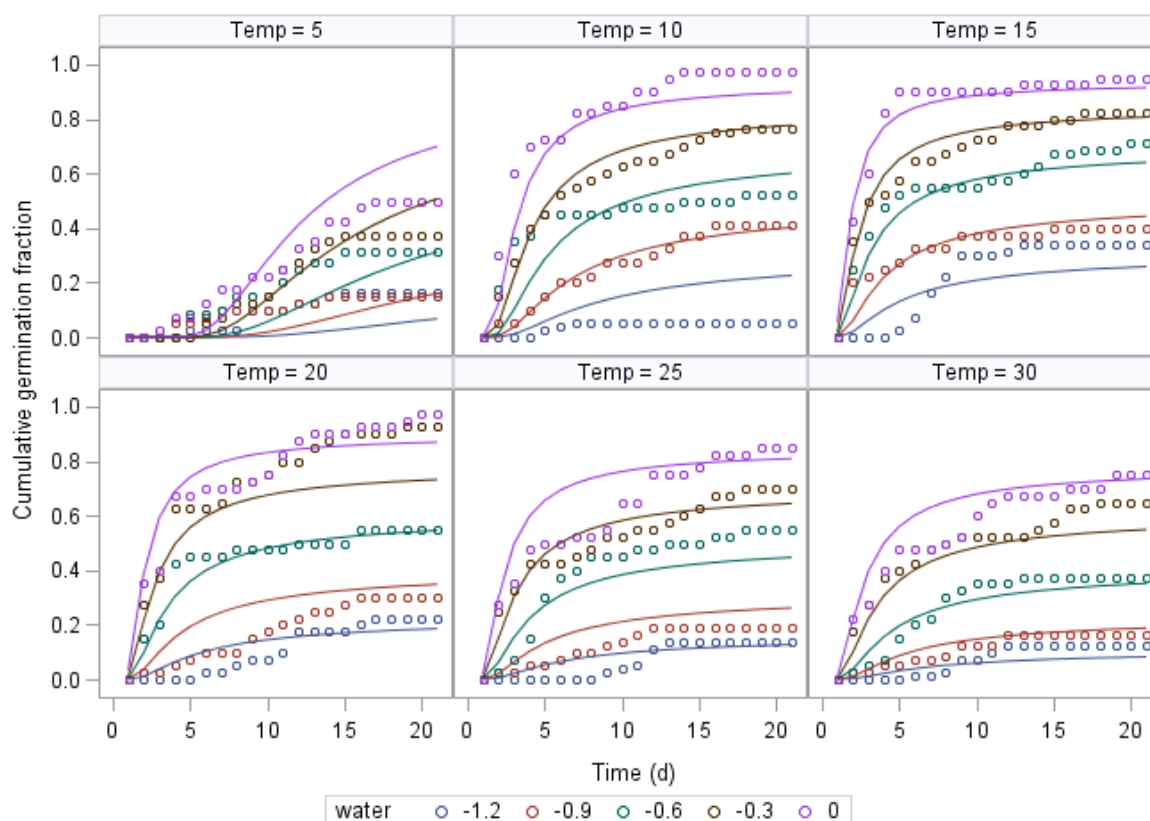
Figure 2 Fitting of the hydrotime model to the cumulative seed germination of resistance sterile oat biotype to ACCase inhibitors in different water potentials caused by PEG application at different temperatures. The points are the observed values, and the lines are the predicted values.

Table 3 Parameters obtained from the fit of the hydrotime model to the seed germination of sterile oat biotypes susceptible and resistant to ACCase inhibitor herbicides.

Temperature (°C)	Biotype	HT (MPa day)	ψb (50) (MPa)	$\sigma\psi b$ (MPa)	R^2	RMSE
5	Susceptible	10.92(0.237)	-0.684(0.029)	0.663(0.027)	0.81	0.044
	Resistant	11.52(0.821)	-0.594(0.050)	0.778(0.057)	0.83	0.043
10	Susceptible	4.125(0.328)	0.772(0.034)	0.535(0.034)	0.92	0.029
	Resistant	4.671(0.118)	-0.757(0.017)	0.607(0.017)	0.93	0.031
15	Susceptible	1.829(0.171)	-0.844(0.024)	0.610(0.027)	0.95	0.033
	Resistant	2.181(0.099)	-0.848(0.016)	0.629(0.018)	0.96	0.019
20	Susceptible	2.074(0.118)	-0.802(0.016)	0.481(0.015)	0.97	0.025
	Resistant	2.230(0.136)	-0.796(0.020)	0.480(0.019)	0.97	0.021
25	Susceptible	2.147(0.165)	-0.659(0.022)	0.575(0.022)	0.98	0.025
	Resistant	2.503(0.196)	-0.620(0.024)	0.619(0.025)	0.98	0.028
30	Susceptible	1.658(0.181)	-0.553(0.024)	0.562(0.027)	0.95	0.033
	Resistant	1.977(0.155)	-0.516(0.018)	0.647(0.020)	0.99	0.021

HT: Hydrotime constant, ψb (50): the water potential required for germination of 50% of seeds, and $\sigma\psi b$: deviation of water potential for seed germination or uniformity index of seed germination and goodness of fit parameters including Coefficient of determination (R^2) and root mean square error (RMSE) resulting from the hydrotime model for seed germination of susceptible and herbicide-resistant biotypes to ACCase inhibitors of sterile oat. The values in parentheses are standard error.

The lowest deviation of the base water potential (σ) in both biotypes, with an average of 0.48 belonged to a temperature of 20 °C. Therefore, seed germination uniformity was higher at 20 °C in both biotypes than at other temperatures.

Hydrothermal time requirement

The hydrothermal time model described the seed germination response to temperature (T) and water potential (Ψ). In the present study, the coefficient of determination (R^2) for susceptible and herbicide-resistant biotypes was 0.94 and 0.93, respectively, indicating a suitable prediction of the hydrothermal time model for the seed germination of sterile oat seeds in response to the temperature and water potential (Table 4).

Discussion

The increase in germination base temperature with the decrease in water potential in sterile oat biotypes indicates that both biotypes can adapt to the effects of climate change. In this way, water stress will increase the base temperature for germination, thereby increasing the likelihood of germination and ultimately expanding its geographical distribution due to global temperature rise. By decreasing the water potential from 0 to -0.8 MPa, the base temperature in soybean *Glycine max* L. and velvetleaf *Abutilon theophrasti* Medik increased (Bakhshandeh *et al.,* 2011). The study results by Jenabbiyan *et al*. (2013) were also similar to the mentioned experiments.

With decreasing water potential, the base temperature for seed germination increased

while the optimum and maximum temperatures decreased (Table 1). Therefore, the results showed that the changes in cardinal temperatures for the two sterile oat biotypes (susceptible and resistant to ACCase inhibitors) are similar in response to water potential. Likely, the two studied biotypes do not have a genetic difference in their response to water potential. However, as the water potential decreases, the base temperature of germination increases, which probably reduces the number of days that germination is possible in these two biotypes. Loddo *et al*. (2019) also reported that the high density of *Chloris barbata* Sw. in the Sumbe region of Angola is related to higher temperatures than the base temperature of this species.

In both biotypes, the thermal time required for sub-optimal temperatures for seed germination was increased with decreasing water potential. In other words, it is estimated that the necessary thermal time to germinate half of the seed population of both sterile oat biotypes at sub-optimal temperatures increased with increasing drought stress levels. The high coefficient of determination for sub-optimal temperatures ($R^2 = 0.96$) also shows the high accuracy of the estimated thermal time model (Table 2). In a similar experiment, the thermal time required for 50% germination of purple nutsedge (*Cyperus rotundus*) tubers was estimated to be 123.8 DD based on the Gamble model (Mijani *et al.,* 2021). It has also been reported that broomrape's average thermal time (*Orobanche* sp.) increased with decreasing water potential (Kebreab and Murdoch, 1999).

Table 4 Estimated parameters of fit of hydrothermal time model to seeds germination of sterile oat biotypes susceptible and resistant to ACCase inhibitors.

Biotype	HTT (MPa DD)	ψb (50) (MPa)	σψb (MPa)	T_b (°C)	T_o (°C)	k	R^2	RMSE
Susceptible	28.616 (0.970)	-0.905 (0.014)	0.595 (0.010)	3.167 (0.288)	15.521 (0.328)	0.029 (0.001)	0.94	0.045
Resistant	31.068 (1.386)	-0.858 (0.013)	0.611 (0.011)	3.340 (0.129)	16.102 (0.416)	0.027 (0.002)	0.93	0.049

HTT: Hhydrothermal time constant (MPa), ψb (50): water potential required for germination of 50% of seeds (MPa), σψb (deviation for ψb, MPa), Tb (base temperature, °C), To (optimum temperature, °C), K (constant coefficient)), and goodness of fit parameters including Coefficient of determination (R^2) and root mean square error (RMSE) resulting from the hydrothermal time model. The values in parentheses are standard error.

The results of the hydrotime model also show a slight difference between the two susceptible and herbicide-resistant biotypes in their germination response to temperature. A similar study reported that the hydrotime constant of velvetleaf (*Abutilon theophrasti*) and soybeans decreased with increasing temperature from 7 to 25 °C (Bakhshandeh *et al.*, 2011).

The more negative base water potential at 15 °C in both biotypes indicates that they are more tolerant to drought stress at this temperature than at other temperatures. In a similar experiment, it was reported that the base water potential of *Lesquerella fendleri* decreased with increasing temperature from 10 to 30 °C (Windauer *et al.*, 2007).

The hydrothermal time constant (HTT) for susceptible and resistant biotypes was 28.6 and 31.1 MPa DD, respectively. The base water potential [$\psi b_{(50)}$] for susceptible and resistant biotypes was estimated at -0.905 and -0.858 MPa. The higher base water potential in resistant biotypes indicates that the seeds of this biotype need more moisture to germinate at higher temperatures. Also, in this model, the base temperature for susceptible and resistant biotypes was 3.167 and 3.340 °C, and the optimum temperature for germination was estimated at 15.5 and 16.1 °C, respectively. The hydrothermal time constant for *Pinus radiata* and *Buddleja davidii* was reported to be around 165 and 105 MPa DD (Watt *et al.*, 2010), respectively. In another experiment, the hydrothermal time constant for *Phalaris minor* seed germination was estimated at 1000 MPa D hour (Derakhshan and Gherekhloo 2015). Yasari *et al.* (2018) also accurately quantified the germination response of *Abutilon theophrasti* Med. at different temperature and moisture conditions using the hydrothermal time model. If resistance reduces the germination rate of sterile oats, the faster emergence of susceptible biotypes allows growers to control these biotypes using ACCase-inhibiting herbicides. On the other hand, with the simultaneous emergence of susceptible and resistant seedlings, it is impossible to distinguish between them. The herbicides will increase the resistant alleles in the sterile oat population.

Conclusion

Based on the results of this experiment, the temperature and water potential significantly affected the seed germination indices of both sterile oat biotypes. The base temperature, optimum temperature range, and maximum germination temperature of both biotypes increased, decreased, and decreased, respectively, as the water potential decreased from high (0 MPa) to low (-0.9 MPa). While seed germination percentage decreased with increasing drought stress, most germination occurred at 15 °C and 0 MPa water potential. As in the mentioned conditions, less time was needed to reach the average of 50% of seed germination. The models provided fairly reasonable estimates of the seed germination behavior of sterile oat biotypes susceptible and resistant to ACCase inhibitors herbicides in response to temperature and water potential. According to the hydrothermal time model, seeds of herbicide-resistant biotypes require more moisture than susceptible biotypes for germination at higher temperatures. The parameters obtained from this experiment (base temperature, optimum temperature, and maximum temperature) can be used for models for predicting the seed bank dynamics of sterile oat biotypes susceptible and resistant to ACCase inhibitors (e.g., clodinafop-propargyl) and the management of fields infected with resistant biotypes.

Competing interests
The authors declare that there are no interests to declare.

Acknowledgments

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مدلسازی جوانه‌زنی بذر بیوتیپ‌های یولاف وحشی زمستانه حساس و مقاوم به علفکش‌های بازدارنده ACCase در پاسخ به دما و تنش خشکی

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چکیده: دما و پتانسیل آب از مهم‌ترین عوامل تعیین‌کننده جوانه‌زنی بذر گونه‌های گیاهی هستند. پژوهش حاضر به‌منظور کمّی‌سازی پاسخ جوانه‌زنی بذر دو بیوتیپ یولاف وحشی *Avena sterilis* subsp. *ludoviciana* (Durieu) Nyman حساس و مقاوم به علفکش‌های بازدارنده استیل کوانزیم آ کربوکسیلاز در پاسخ به شش سطح دمایی (۵، ۱۰، ۱۵، ۲۰، ۲۵ و ۳۰ درجه سلسیوس) و پنج سطح تنش خشکی (۰، ۰/۳- ، ۰/۶- ، ۰/۹- و ۱/۲- مگاپاسکال) انجام شد. براساس نتایج، دمای پایه جوانه‌زنی در هر دو گونه تحت‌تأثیر تنش خشکی قرار گرفت. از شرایط عدم تنش به حداکثر تنش در بیوتیپ حساس دمای پایه از ۳/۲۴ به ۷/۱۵ درجه سلسیوس و در بیوتیپ مقاوم از ۳/۱۲ به ۷/۴۳ درجه سلسیوس تغییر کرد. ترمال‌تایم مورد نیاز برای جوانه‌زنی ۵۰ درصد جمعیت بذری در دماهای زیر بهینه، در بیوتیپ حساس از ۲۶/۲ تا ۸۷/۸ درجه سلسیوس در روز و در توده مقاوم از ۲۸/۸ تا ۹۰/۶ درجه سلسیوس در روز افزایش یافت. با افزایش دما از ۵ به ۳۰ درجه سلسیوس ثابت هیدروتایم در بیوتیپ حساس از ۱۰/۹۲ به ۱/۶۶ مگاپاسکال روز و در بیوتیپ مقاوم از ۱۱/۵۲ به ۱/۹۸ مگاپاسکال روز کاهش یافت. ثابت هیدروترمال تایم برای بیوتیپ‌های حساس و مقاوم به‌ترتیب ۲۸/۶ و ۳۱/۱ مگاپاسکال درجه سلسیوس روز بود. براساس مدل هیدروترمال تایم بذرهای بیوتیپ مقاوم (۰/۸۵۸- مگاپاسکال) به علفکش در مقایسه با بیوتیپ حساس (۰/۹۰۵- مگاپاسکال) برای جوانه‌زنی در دماهای بالاتر به پتانسیل آب بیشتری نیازمند هستند. به‌طورکلی براساس مدل‌های برآورد شده، پاسخ جوانه‌زنی به دما و پتانسیل آب در هر دو بیوتیپ حساس و مقاوم مشابه بود. براساس نتایج این آزمایش، رویش حداکثری هر دو بیوتیپ در دمای ۱۵ درجه سلسیوس و شرایط بدون تنش رطوبتی محتمل است.

واژگان کلیدی: پتانسیل آب، دمای کاردینال، کمّی‌سازی، هزینه شایستگی، هیدروترمال تایم