Heredity **81** (1998) 674–682

Received 15 April 1998, accepted 20 May 1998

Temperature response in wild oat (*Avena fatua* L.) generations segregating for seed dormancy

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Crosses between parents with high and low levels of seed dormancy in wild oat were used to produce F_1, F_2 and backcross populations. Germination phenotypes were determined by imbibing all populations at 15 and 20°C. Rapid germination of genetically more dormant generations was favoured at the lower temperature, i.e. a generation by germination temperature interaction was observed. Evidence that dominance shifted from early germination at 15°C to late germination at 20°C is presented. Epistatic gene action may have been detected at 20°C but not at 15°C. Cumulative germination percentages of F_1 caryopses imbibed at 10, 15, 20 and 25°C revealed an inverse relationship between germination rate and temperature. The narrow-sense family heritability of the seed dormancy phenotype of F_7 recombinant inbred lines *per se* was $h^2_{f, F=1} = 0.75$ with exact confidence limits of 0.64 and 0.83. Six factors were estimated to be segregating between the dormant and nondormant parents. Genotype by germination temperature interactions may play an adaptive role that allows wild oat to persist in diverse ecosystems.

Keywords: *Avena fatua*, genotype–environment interaction, germination temperature, heritability, joint scaling, seed dormancy.

Introduction

Wild oat is a well developed system for the study of seed dormancy. Several well-characterized inbred lines have been isolated from weed populations, and these lines express a range of germination phenotypes (Adkins *et al*., 1986). Freshly harvested caryopses (hereafter referred to as seed) from line M73 will not germinate for at least 20 weeks at a germination temperature of 20°C, whereas fresh seed from line SH430 can complete germination within 14 days at the same temperature (Jana *et al*., 1988). Line M73 has true embryo dormancy because excised embryos do not germinate readily (Naylor & Simpson, 1961; Foley, 1992). Wild oat is an important economic weed that infests most major cereal producing regions of the world (Holm *et al*., 1977, pp. 105–113). Variable germination contributes to the success of wild oat as a widespread weed in cereal crops.

Germination behaviour in wild oat is a quantitative trait controlled by at least three genes (Jana *et al*., 1979, 1988). Estimates of the heritability (h^2) of seed dormancy in wild oat range from 0.23 to 0.56; therefore a large part of the total phenotypic value can be attributed to the environment (Naylor & Jana, 1976; Jana & Naylor, 1980). Temperature can affect wild oat seed dormancy four ways: (i) the level of dormancy is influenced by temperature during seed development; (ii) persistence of dormancy in the dry seed is determined by temperature; (iii) secondary dormancy, i.e. induced dormancy in a previously nondormant seed, can be influenced by temperature; and (iv) temperature can determine whether a seed germinates after it imbibes water (Simpson, 1990). Exposure of developing wild oat seed to low temperatures reduces germinability upon seed maturity, whereas high temperatures increase germinability (Sawhney & Naylor, 1979). Exposure of dry seed to high temperatures, e.g.

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40°C, results in rapid after-ripening (Foley, 1994). After-ripening is the interaction between a dormant seed and its environment that over time leads to the loss of dormancy (Simpson, 1990). Nondormant seeds germinated over a wide range of temperatures, 4–24°C, whereas the temperature optimum for germination of unafter-ripened dormant seeds was 4–12°C, with little germination occurring in the 20–24°C range (Naylor & Fedec, 1978). Apparently, wild oat has genetic and physiological mechanisms that respond to temperature and regulate seed germination. Understanding the response of wild oat to temperature may be the key to determine how dormancy is regulated in this species, and the first part of this process will be to characterize the genes that control wild oat seed dormancy.

The performance of genotypes that exhibit genotype by environment (GE) interaction may vary across environments. The influence of GE on seed germination has been observed in barley (Oberthur *et al*., 1995) and wheat (Paterson & Sorrells, 1990). However, these studies focused on the influence of the maternal plant environment on germination rather than the *germination* environment. Nothing is known about the genes that regulate germination response to temperature in wild oat.

Our hypothesis is that freshly harvested seed from F_1, F_2, BC_{P1} and BC_{P2} generations, produced by a cross between parents with high and low levels of dormancy, will vary in response to germination temperature. The objectives of our work were: (i) to determine if a genotype by germination temperature interaction occurs; (ii) to perform generation means analysis at two germination temperatures to characterize the activities of seed dormancy genes in wild oat; (iii) to estimate the heritability of seed dormancy on a family mean basis; and (iv) to estimate the number of genes segregating for dormancy in this species.

Materials and methods

Plant populations

Wild oat inbred lines M73 (dormant) and SH430 (nondormant) were used as parents to produce F_1 seed. Because Jana *et al*. (1979) found no statistical differences in the germination rates of F_1 or F_2 seed from reciprocal crosses between wild oat lines M73, CS40 and AN127, we used M73 as the seed parent and SH430 as the pollen parent in all crosses. Backcrosses were made to M73 ($BC_{1D}F_1$) and SH430 ($BC_{1ND}F_1$). All plant populations were grown in a greenhouse or growth chamber at 20°C ± 3°C with an 18:6 h light:dark photoperiod to keep the maternal environment as consistent as possible. Seeds were hand-harvested at maturity, dried at room temperature for 5 days, and stored at −20°C to prevent after-ripening.

A population of 126 F_2-derived recombinant inbred (RI) lines were produced by single-seed descent from the cross of M73 × SH430. RI lines were advanced from the F_3 to F_7 generations by randomly selecting one caryopsis from each line and inducing it to germinate in 10 mM gibberellic acid (GA) to avoid selection against dormant types.

Germination tests

F_1, F_2, $BC_{1ND}F_1$, $BC_{1D}F_1$, M73 and SH430 seeds were dehulled (lemma and palea removed), surface-sterilized in 95% by volume ethanol for 2 min and afterwards placed in a 2.6% sodium hypochlorite solution for 5 min. After rinsing the caryopses in sterile water to remove residual sodium hypochlorite, they were placed in sterile 24-well tissue culture plates lined with Whatman no. 1 filter paper and wetted with 120 μL of germination buffer containing 10 mM KH_2PO_4 and 0.2 mM $CaSO_4$ (pH 6.0). Germination phenotype classifications were conducted at 15 and 20°C. Classification experiments were conducted twice for both temperatures, and each classification included about 25 F_1, 480 F_2, 50 $BC_{1D}F_1$, 50 $BC_{1ND}F_1$, 480 M73 and 480 SH430 caryopses. The caryopses were placed in dark incubators at the appropriate temperatures, and treatments were arranged in a completely randomized design. The F_2 and both parents were replicated 10 times with 48 caryopses per tissue culture plate. Backcross populations were replicated twice with 25 caryopses per tissue culture plate, and the F_1 was replicated once with 25 caryopses per tissue culture plate. Germination was evaluated at regular intervals. At the end of all experiments the remaining ungerminated caryopses were induced to germinate with 10 mM GA to determine viability. Seeds that failed to germinate after 7 days in GA were considered dead and eliminated from the data.

The F_7 RI line phenotypes were determined at 15°C in separate classifications with both parents and F_1 populations included as controls. Surface sterilization was performed as described above. The F_7 RI lines were arranged in a completely randomized design with two replicates per RI line and six caryopses per replicate. The F_7 RI lines were classified twice at 15°C, but were not classified at 20°C because of insufficient numbers of remnant F_7 RI caryopses in many of the lines.

Additional experiments were conducted to classify the germination phenotypes of F_1 caryopses at 10 and 25°C. The F_1 classifications at these additional temperatures allowed the comparisons of F_1 germination at 10, 15, 20 and 25°C. These experiments included 50–100 each of F_1, M73 and SH430 caryopses, and the treatments were arranged in a completely randomized design with two replicates. The 10°C F_1 classifications were conducted twice, and the 25°C classification was conducted once.

Data analyses

Significance of differences between parents and populations was determined by 95% confidence intervals (Steel *et al.*, 1997). SAS PROC GLM (SAS Institute, 1990) was utilized for analyses of the GE interaction and the generation means. The effect of temperature within each generation was determined by Student's *t*-test. Generations were compared at the point in time when the differences between the corresponding parental lines accounted for a maximal portion of the total phenotypic variance as described by Paterson *et al.* (1989). Arc sine transformation was applied to germination percentage (decimal fraction) to achieve normality and obtain homogeneity of error variance.

Weighted least squares were used to estimate population parameters in joint scaling tests (Mather & Jinks, 1982, pp. 65–76) using the computational procedures described by Rowe & Alexander (1980) and Hayman (1958). Error terms for segregating and nonsegregating generations were determined in separate tests by SAS PROC GLM. Means of transformed germination percentages of six generations were fitted to models and tested by a chi-squared goodness-of-fit test following the procedure described by Mather & Jinks (1982, pp. 112–113). Models tested on the 15 and 20°C generation means were: a four-parameter model (mean, additive, dominance and temperature) that assumed no genotype by environment interaction; a three-parameter model (mean, additive and dominance) averaged across germination temperatures; three-parameter models fitted to generation means within each temperature; a six-parameter model that included genotype by environment interaction terms; and a nine-parameter model that included genotype by environment as well as epistatic terms. Data analyses treated generations and temperatures as fixed effects and blocks as random effects.

Family heritability and the 95% exact confidence limits of time to germination in days were obtained by an analysis of variance using the among-family variance component, σ_F^2, of 126 F_7 RI lines as described by Nyquist (1991, pp. 307 and 310). Additive gene action was assumed. The Castle–Wright formula (Spiess, 1989, p. 215) was used to estimate the number of effective factors, *k*, where $k = D^2/8\sigma_A^2$, $D = P_1 - P_2$, where P_1 and P_2 are the mean phenotypic values for each parent, and σ_A^2 is the additive variance in the random mating F_2 population. The latter was estimated as one-half of the variance component for among F_7 RI lines.

Cumulative germination percentages from an F_1 population incubated at 10, 15, 20 and 25°C were analysed by probit analysis (Finney, 1971, pp. 20–30) using the methods described by Schonbeck & Egley (1980). Germination percentages were transformed to probits that result in log-linear curves for seed populations that are normally distributed. The slope of the line is the reciprocal of the population standard deviation, and factors that affect the slope indicate an interaction with the germination rate. The probit of germination was derived in an EXCEL spreadsheet with the NORMSINV function (the inverse of the cumulative standard normal distribution or function NORMSDIST) and regressed on the common log of the days to germination. Differences between the cumulative germination percentages at each temperature were determined by least significant differences (LSD) at probability level 0.05.

Results

Generation by germination temperature interaction

Cumulative 10-day germination percentages of F_1, F_2, $BC_{1ND}F_1$ and $BC_{1D}F_1$ generations imbibed at 15 and 20°C, indicated that these generations germinated earlier at 15°C than at 20°C (Fig. 1a,b). An analysis of variance of the 10-day cumulative germination percentages of SH430, F_1, F_2, $BC_{1ND}F_1$, $BC_{1D}F_1$ and M73 generations germinated at 15 and 20°C revealed significant generation × temperature interactions (Table 1). Simple effects for temperature were significant for the F_1 and F_2 generations, but not for the SH430, $BC_{1ND}F_1$, $BC_{1D}F_1$ and M73 generations (Table 2).

Probit analysis indicated that F_1 caryopses would germinate rapidly at 10 and 15°C after early onsets of germination, whereas caryopses imbibed at 20 and 25°C germinated at lower rates after delayed onsets (Fig. 2). Comparisons of the slopes of the predicted probit functions over the 10–25°C temperature range indicated that there was an inverse relationship between germination rate and temperature.

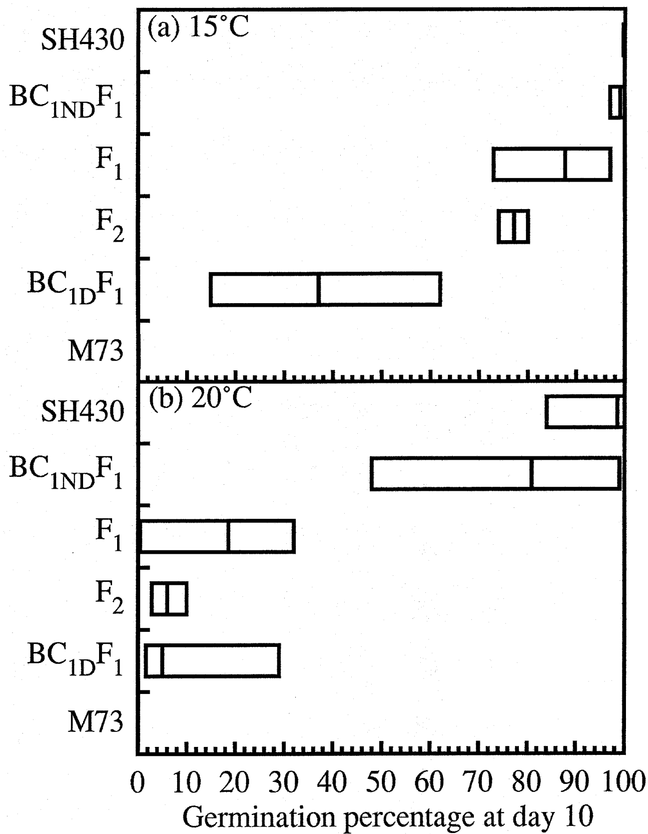

Fig. 1 Mean cumulative germination percentages after 10 days of imbibition at (a) 15°C and (b) 20°C, and 95% confidence intervals, of parents and early generations of wild oat.

Table 1 Effects of 15 and 20°C germination temperatures on the arc sine cumulative germination percentage of SH430, F_1, F_2, $BC_{1ND}F_1$, $BC_{1D}F_1$ and M73 generations of wild oat after 10 days of imbibition. The classifications were conducted twice

Source	d.f.	Mean squares[a] (Type III)
Time	1	0.0452
Temperature	1	1.9967
Error (a)	1	0.1211
Generation	5	10.2670**
Generation × temperature	5	0.9534**
Error (b)	10	0.0286**
Pure error (b)	113[b]	0.0058

[a]Arc sine of cumulative germination percentages.
[b]Three replicates missing in proportional subclass analysis.
$^{**}P<0.01$.

Table 2 Differences between 15 and 20°C imbibition temperatures on 10-day arc sine cumulative germination percentage means of SH430, $BC_{1ND}F_1$, F_1, F_2, $BC_{1D}F_1$ and M73 generations of wild oat

Generation	15°C means (radians)	20°C means (radians)	Differences (radians)
SH430	1.5708	1.5526	0.0182
$BC_{1ND}F_1$	1.4855	1.1164	0.3691
F_1	1.2153	0.4372	0.7781*
F_2	1.0711	0.2393	0.8318*
$BC_{1D}F_1$	0.6571	0.2201	0.4370
M73	0	0	0

$^{*}P<0.05$.

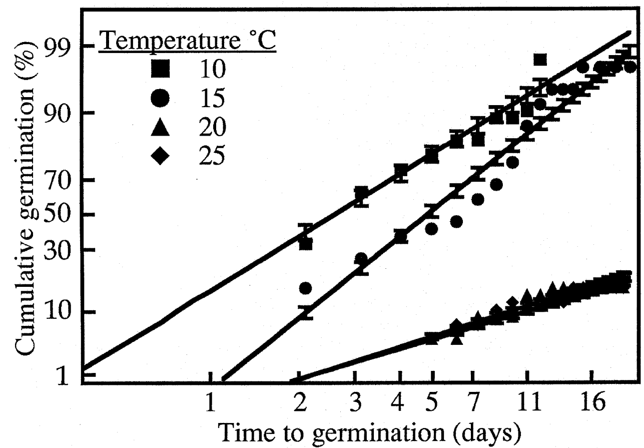

Fig. 2 Probit analysis of germination time courses of F_1 caryopses of wild oat imbibed at 10, 15, 20 and 25°C. The symbols represent the experimental observations and the lines represent cumulative normal distributions predicted at each temperature, on the basis of probit analysis of cumulative germination percentages plotted vs. log days. Error bars equal one-half of the LSD at probability level 0.05. Coefficients of determination, r^2, for the predicted germination time courses were: 10°C, 0.91; 15°C, 0.94; 20°C, 0.87; 25°C, 0.82.

Generation means analysis

The four-parameter model that assumed no generation by germination temperature interaction was unsatisfactory (Table 3). The three-parameter additive–dominance model that included generation means averaged across the 15 and 20°C germination temperatures was satisfactory (Table 4). This finding does not exclude epistatic interactions within some environments, though it suggests that epistatic effects balance out over all environments (Mather & Jinks, 1982, p. 112). The additive–dominance model

of gene action fitted the observed generation mean values at 15°C (Table 4). This means that the simple additive–dominance model was adequate to explain the inheritance of germination in the M73 × SH430 cross at 15°C. However, generation means observed at 20°C did not conform to predicted values of the three-parameter additive–dominance model. Failure of the additive–dominance model is evidence of epistatic interactions between the dormancy genes at 20°C (Mather & Jinks, 1982, p. 94). Generation means from the 15 and 20°C germination temperatures were fitted to the full six-parameter model; however, this model was unsatisfactory (Table 5). Our attempts to fit a nine-parameter model that included all environmental and epistatic terms (m, d, h, e, g_d, g_h, i, j, l) were also unsatisfactory (data not shown).

Table 3 Estimates of the genetic parameters and their standard errors in the additive–dominance model, including temperature, of the arc sine cumulative germination percentages of M73, SH430, F_1, F_2, $BC_{1ND}F_1$ and $BC_{1D}F_1$ generations of wild oat imbibed at 15 and 20°C for 10 days. This model assumes no genotype-by-environment interaction

Parameter	15 and 20°C
Mean	0.62 ± 0.08
Additive	0.79 ± 0.07
Dominance	0.32 ± 0.13
Temperature (e)	0.22 ± 0.06
χ^2	50.20
P	0.0000
d.f.	8

Inheritance and an estimate of the number of segregating factors

An analysis of variance for time to germination in 126 F_7 RI lines classified twice in time was used to estimate the family variance component, σ^2_F, family by time interaction, σ^2_{FT}, and experimental error, σ^2 (Table 6). Family heritability, $h^2_{f,F=1}$, was estimated by $h^2_{f,F=1} = \sigma^2_F/[\sigma^2_F + (\sigma^2_{FT}/T) + (\sigma^2/RT)] = 0.75$, where T (number of times) = 2, and R (number of replicates) = 2 (see Nyquist, 1991, eqn 97). The analysis of variance indicated that the two classifications in time were not homogeneous (the time × line term was significant). Even though environmental conditions were controlled from time 1 to time 2, we believe that it is extremely difficult to remove most of the random error that contributes to this heterogeneity because of the extreme sensitivity of the wild oat germination phenotype to the germination environment. This error contributed to a lower estimate of heritability. The 95% exact confidence limits of the family heritability were 0.64 and 0.83. Based on mean days to germination of SH430 = 2.4, and M73 = 100.7, the number of segregating factors was estimated to be $98.3^2/8(188.81) = 6.4$.

Discussion

Epistatic interactions

Results presented in Table 4 suggests that epistatic interactions between dormancy genes may have been detected at 20°C but not at 15°C. However, our attempts to fit these data to models that include epistatic terms, or both genotype-by-environment interaction and epistatic terms, have not been satisfactory (analyses not shown). We have detected a genotype-by-environment interaction between the

Table 4 Estimates of the genetic parameters and their standard errors in the additive–dominance model, of the arc sine cumulative germination percentages of M73, SH430, F_1, F_2, $BC_{1ND}F_1$ and $BC_{1D}F_1$ generations of wild oat imbibed at 15 and 20°C for 10 days

Parameter	15 and 20°C[a] averages	15°C[b]	20°C[b]
Mean	0.78 ± 0.08	0.80 ± 0.02	0.71 ± 0.18
Additive	0.79 ± 0.08	0.79 ± 0.02	0.80 ± 0.18
Dominance	−0.04 ± 0.14	0.44 ± 0.04	−0.40 ± 0.34
χ^2	7.22	4.38	21.98
P	0.07	0.36	0.0002
d.f.	3	3	3

[a]Based on generation means averaged across temperatures.
[b]Based on generation means within each temperature.

Table 5 Estimates of the genetic parameters and their standard errors in the additive–dominance model with temperature interaction terms, of the arc sine cumulative germination percentages of M73, SH430, F_1, F_2, $BC_{1ND}F_1$ and $BC_{1D}F_1$ generations of wild oat imbibed at 15 and 20°C for 10 days

Parameter	15 and 20°C
Mean	0.76 ± 0.07
Additive	0.80 ± 0.07
Dominance	0.02 ± 0.13
Temperature (*e*)	0.04 ± 0.07
Temperature × additive (g_d)	-0.01 ± 0.07
Temperature × dominance (g_h)	0.42 ± 0.13
χ^2	24.05
P	0.0005
d.f.	6

generations and germination temperatures; however, the generation means observed cannot be explained simply by genotype-by-environment interaction (Table 5). It appears likely that epistatic interactions among three or more dormancy genes occur in the M73 × SH430 cross at 20°C. However, we do not presently have sufficient generations available to test the hypothesis that three or more genes are interacting to produce the observed phenotypes. Jana *et al.* (1979, 1988) described a genetic model of seed dormancy for wild oat. In their model the *E* gene promotes rapid after-ripening, and genes L_1 and L_2 promote slow after-ripening. Their proposed genotype of dormant M73 was $eel_1l_1L_2L_2$, and that of nondormant SH430, $EEl_1l_1l_2l_2$, i.e. a two-gene model was proposed for the cross studied herein. L_1 and L_2 are both epistatic to *E*. Thus $EEL_1L_1L_2L_2$ is dormant. The fact that Jana *et al.* (1988) performed phenotype classifications at 20°C but not 15°C may explain how they detected epistatic interactions between *E* and L_2. Furthermore, Jana *et al.* (1988) tested in only one environment, and this may explain why they detected only two genes segregating for seed dormancy in the M73 × SH430 cross. Epistasis suggested by the generation means analysis at 20°C (Table 4) may be caused by the epistatic interactions between *E* and L_2 as well as one or more other genes. Interactions among the genes segregating between M73 and SH430 at 20°C may slow the rate of germination in some generations. The number of effective factors estimated by the Castle–Wright (Spiess, 1989) procedure was more than six in F_7 RI lines germinated at 15°C. This suggests that more germination-related genes are expressed at 15°C than at 20°C. It may be that higher expression in dormancy genes at 20°C down-regulates the expression of germination-related genes; therefore, more genes are silent at 20°C than at 15°C. Traditionally, seed dormancy has been thought of as a biochemical block to germination (Bewley & Black, 1994). Could it be that the genotype-by-environment interaction and epistasis reported here is part of the block that results in seed dormancy?

In the context of the model of Jana *et al.* (1979, 1988) the lower germination rate at 20°C may indicate that the expression of the L_2 locus is greater at high temperatures. Epistasis detected at 20°C but not at 15°C may mean that the L_2 gene masks the expression of *E* more at higher temperatures than at lower temperatures. Inverse relationships between temperature and germination rate have been observed previously in five dormant wild oat biotypes (Naylor & Fedec, 1978). Dormant M73 germinated most rapidly at 4–8°C but did not germinate at 20–24°C. In contrast, nondormant wild oat line CS40 germinated rapidly over the entire 4–24°C temperature range (Naylor & Fedec, 1978). Roberts (1961) found an inverse relationship between germination rate and temperature in dormant rice lines. Nondormant rice germinated readily over the 27°C to 42°C range. The temperature optimum for germination of dormant rice was 27°C, but at 42°C no germination occurred, i.e. the same trend observed in wild oat. Schonbeck & Egley (1980) found that the germination rate of dormant redroot pigweed seeds (*Amaranthus retroflexus* L.) was more rapid at

Table 6 Analysis of variance for 126 F_7 RI lines of wild oat and expected mean squares

Source	d.f.	Expected mean square	Mean square
Line	125	$\sigma^2 + r\sigma^2_{FT} + tr\sigma^2_F$	2002.91**
Time × line	125	$\sigma^2 + r\sigma^2_{FT}$	500.46**
Error	248	σ^2	163.03

$^{**}P < 0.01$.

25°C than at 40°C. Mares & Ellison (1989) found that freshly harvested dormant wheat grains did not germinate when imbibed at temperatures of 20°C or higher. However, dormant wheat grains imbibed at 4°C for 48 h, then returned to 20°C, germinated like fully after-ripened grains.

Significance of the genotype-by-germination temperature interaction

The ecological role for the interaction between wild oat seed genotype and germination temperature is not known. Results shown here and elsewhere have demonstrated that higher temperatures inhibit the germination of dormant wild oats (Naylor & Fedec, 1978). However, high temperatures also enhance the rate of after-ripening of dry dormant wild oat seed, thus increasing the potential for the seed to germinate (Foley, 1994). Some have suggested that the genotype-by-germination temperature interaction has an adaptive ecological role that allows wild oats to infest diverse ecosystems (Naylor & Fedec, 1978). Soil temperature may provide the environmental cues so that wild oat can germinate at the appropriate season (Fenner, 1985). The relationship between rate of after-ripening and germination temperature may be the environmental sensing mechanism that decreases the probability of encountering unacceptable growing conditions after germination. A thorough understanding of the role of temperature in the germination of wild oat awaits further study.

Genetic and molecular components of dormancy

Our hypothesis is that genetic factors regulate the shift between nondormancy at 15°C and dormancy at 20°C (Fig. 1). Observations to support this hypothesis are: (i) the mean 10-day germination percentages of F_1 and F_2 caryopses were lower at 20°C than at 15°C (Fig. 1); (ii) there was a significant interaction between the germination temperature and 10-day cumulative germination of F_1 and F_2 generations (Table 2); (iii) there was an inverse relationship between temperature and the germination rate of F_1 caryopses (Fig. 2); (iv) an analysis of 10-day germination percentages for six generations, i.e. generation means analysis, suggests the presence of significant epistatic effects at 20°C, but not at 15°C (Table 4); and (v) germination phenotype is a heritable trait. The fact that the 10-day cumulative germination of SH430 did not decrease at 20°C suggests that slow germination was not caused by physiological stress at that temperature; rather that the lower cumulative germination of the F_1 and F_2 generations was principally the result of genetic effects.

The potential for a wild oat seed to germinate is determined by its after-ripening status and the alleles present at the dormancy loci. Previous work has demonstrated that the degree of dormancy in an individual wild oat seed is in part dictated by the state of after-ripening in the seed (Foley, 1994; Fennimore & Foley, 1998). Evidence presented here indicates that the alleles present at the dormancy loci also contribute to the degree of dormancy in an individual seed. Differences in the cumulative germination percentages of F_1 and F_2 populations (Fig. 1) imply that the status of alleles at the E and L_2 loci establishes the initial level of dormancy in those seeds. The idea of dormancy allele status is compatible with the threshold model of seed dormancy. In this hypothetical model membrane-bound autophosphorylating protein kinases exist in two forms: an active unphosphorylated Ca^{2+}-dependent form in nondormant embryos, and an inactive phosphorylated form in dormant embryos (Trewavas, 1988). For example, the $BC_{1ND}F_1$ seeds may have germinated more rapidly than the $BC_{1D}F_1$ seeds because of a greater proportion of membrane-bound protein kinases in the active unphosphorylated Ca^{2+}-dependent form (Fig. 1). The relative dosage of E and L_2 alleles in the seeds of the $BC_{1ND}F_1$ and $BC_{1D}F_1$ generations may control the relative proportion of protein kinases in either the germination or dormancy conformation, i.e. they have different dormancy thresholds.

The expression of seed dormancy genes can be modified by their environment. Vegis (1964) considered that changes in the state of seed dormancy involve changes in the temperature requirements for germination. As the depth of dormancy increases, the range of temperature over which germination is possible narrows to the point at which germination is no longer possible at any temperature and the seed is fully dormant. This implies that dormancy is a relative state in seeds that are less than fully dormant, and that the expression of dormancy is dependent upon external conditions like temperature (Vleeshouwers *et al.*, 1995). The differences in germination response between the six generations germinated at 15 and 20°C (Fig. 1) and F_1 caryopses germinated at 10–15°C, and those germinated at 20–25°C (Fig. 2), are consistent with Vegis's (1964) concept of relative dormancy. For example, F_1 caryopses are relatively nondormant when imbibed at 10–15°C, but are relatively dormant when imbibed at 20–25°C. Dormancy genes

or gene products interact with the environment by relaxing or increasing the stringency of conditions necessary for germination to occur. This is consistent with the view that dormancy is an adaptive trait (Simpson, 1990).

The germination of a single seed in a test does not indicate its dormancy state, but for a population of seeds germination at a range of temperatures can provide more complete information about the relative state of dormancy in the population (Vleeshouwers *et al*., 1995). This implies that the classification of populations segregating for seed dormancy or preharvest sprouting at only one temperature could provide misleading information about the activity of dormancy genes, because the relative germination across a small range of temperatures can vary greatly.

Acknowledgements

We thank Ms Judy Santini for her assistance in statistically analysing the data, and Dr Sally Mackenzie for her helpful suggestions. This work was supported by a grant from the National Science Foundation (IBN-938055). This is journal paper series no. 15463 of the Purdue Agricultural Research Program.

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