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A genetic model and molecular markers for wild oat (*Avena fatua* L.) seed dormancy

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Abstract Seed dormancy allows weed seeds to persist in agricultural soils. Wild oat (*Avena fatua* L.) is a major weed of cereal grains and expresses a range of seed dormancy phenotypes. Genetic analysis of wild oat dormancy has been complicated by the difficulty of phenotypic classification in segregating populations. Therefore, little is known about the nature of the genes that regulate dormancy in wild oat. The objectives of our studies were to develop methods to classify the germination responses of segregating wild oat populations and to find molecular markers linked to quantitative trait loci (QTL) that regulate seed dormancy in wild oat. RAPD markers OPX-06 and OPT-04 explained 12.6% and 6.8% respectively, of the F_2 phenotypic variance. OPF-17 was not significant in a simple regression model, but it was linked in repulsion to OPT-04. A three-locus model of seed dormancy in wild oat is presented based on the 41-day germination profiles of F_1, F_2, F_3, $BC_1P_1F_1$, $BC_1P_1F_2$, and $BC_1P_2F_1$ generations, and the 113 day germination profile of 126 F_7 recombinant inbred lines. Loci G_1 and G_2 promote early germination, and the *D* locus promotes late germination. If at least one copy of the dominant G_1 or G_2 alleles are present regardless of the genotype at *D* locus, then the individual will be nondormant. If the genotype is $g_1g_1g_2g_2D\_$, then the phenotype will be dormant.

Key words *Avena fatua* · Genetic model · Quantitative trait loci · RAPD analysis · Seed dormancy

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Introduction

Variable germination permits weeds to successfully infest agricultural fields despite weed management systems that minimize economic damage to the crop. Dormancy allows weeds to germinate over a long time period and increases the probability that some plants will escape control measures and reproduce. Seed dormancy is the inability of a viable embryo to germinate under favorable environmental conditions. The degree of seed dormancy within a population is variable and is determined by interactions among plant genotypes, maternal environments, harvest and postharvest conditions, and germination environment (Hareland and Madson 1989). There are two types of seed dormancy: coat-imposed dormancy is maintained by tissues that enclose the embryo, and embryo dormancy is controlled within the embryo itself (Bewley and Black 1982). Previous studies have found that some wild oat biotypes display embryo dormancy (Naylor and Simpson 1961; Foley 1992).

Wild oat seeds in natural populations express phenotypes that range from nondormant to highly dormant (Adkins et al. 1986). Afterripening, a physiological process that occurs during periods of warm dry conditions, converts dormant seeds to a nondormant state capable of germination (Foley 1994). The physiological basis for the maintenance and relief of the dormant state remains unknown. Several loci highly responsive to the environment regulate seed dormancy in wild oat (Naylor 1983). Germination response in wild oat is a heritable trait of

which about 50% of the phenotypic variance is due to genetic factors and the remaining 50% is due to environmental influence (Jana and Naylor 1980). Naylor and coworkers conducted genetic analyses of germination behavior in wild oat by intercrossing several wild oat biotypes having various dormancy phenotypes (Jana et al. 1979, 1988). In the genetic model proposed by Jana et al. (1979) locus *E* promotes early germination within the first 4 weeks; however, ungerminated seeds remain dormant due to slow afterripening imposed by loci L_1 and L_2. This model is based on relative germination rates at 20°C observed in several populations. Because this model has not been tested in advanced generations, it remains hypothetical.

Our hypothesis is that nuclear genes regulate seed dormancy in wild oat and that the nature of these genes can be understood by developing the necessary genetic populations and phenotypic classification methods. The objectives of the work presented here were: (1) to develop methods to classify segregating populations of wild oat, (2) to verify the validity or revise the previous genetic model of dormancy for wild oat, and (3) to find molecular markers linked to dormancy loci in selected F_2 bulks.

Materials and Methods

Plant material

Well-characterized inbred wild oat (*Avena fatua* L.) lines M73 (dormant) and SH430 (nondormant) were used as parents to produce F_1 seeds (Fig. 1). Because Jana et al. (1979) found no statistical differences in the germination rates of F_1 or F_2 seed from reciprocal crosses among wild oat lines M73, CS40 and AN127, we used M73 as the seed parent and SH430 as the pollen parent to produce the F_1. Backcrosses were made to M73 ($BC_{1D}F_1$) and SH430 ($BC_{1ND}F_1$) using the F_1 as pollen parent in both cases. All plant populations were grown in a greenhouse or growth chamber at 20°C ±3°C with an 18:6-h light:dark photoperiod. Seeds were hand-harvested at maturity, dried at room temperature for 5 days, and stored at –20°C to prevent afterripening. A population of 127 F_2-derived recombinant inbred (RI) lines was produced by single-seed descent from the cross of M73 x SH430. RI lines were advanced from the F_3 to F_7 generations by randomly selecting one seed from each line and inducing it to germinate in 10 m*M* gibberellic acid (GA) to avoid selection against dormant types. One F_7 RI line produced seed of very low viability; therefore, germination results from this line were eliminated from the data set.

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 then placed in a 2.6% sodium hypochlorite solution for 5 min. Seeds were rinsed in sterile water to remove residual sodium hypochlorite, 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 m*M* KH_2PO_4 and 0.2 m*M* $CaSO_4$ (pH 6.0). Phenotype classification experiments were conducted twice, with each experiment including about 25 F_1, 480 F_2, 50 $BC_{1D}F_1$, 50 $BC_{1ND}F_1$, 480 M73, and 480 SH430 seeds. The seeds were placed in a dark incubator at 15°C for 44–52 days, and generations (treatments) were arranged in a completely randomized design. The F_2 and both parents were replicated ten times with about 48 seeds per tissue culture plate. The backcross populations were replicated twice with 25 seeds per tissue culture plate, and the F_1 was replicated once with 25 seeds per tissue culture plate. After 44–52 days of imbibition all ungerminated seeds were induced to germinate with 10 m*M* GA in the same manner as described by Paterson et al. (1989) except that they induced germination after 21 days. Seeds that failed to germinate after treatment with GA were considered nonviable, and their data were eliminated. Germination was evaluated daily for the first 14 days, and every 2–3 days thereafter. At regular intervals randomly selected F_2 seeds were planted as they germinated and grown to produce F_3 seeds. All $BC_{1D}F_1$ and $BC_{1ND}F_1$ seeds were planted and allowed to reproduce. Progeny testing was conducted by randomly selecting 10 seeds from each F_3 and $BC_{1D}F_2$ family tested. The phenotypes of the F_3 and $BC_{1D}F_2$ seeds were determined by the same methods as described above for several generations. In a modification of the method of Staub et al. (1989) seed from F_3 and $BC_{1D}F_2$ families were classified as nondormant / segregating if 0–8 progeny seed required GA to induce germination and as dormant if 9–10 seed required GA. Tissue samples were harvested from leaves of 3- to 6-week-old individual F_2 and $BC_{1D}F_1$ plants for DNA marker analysis.

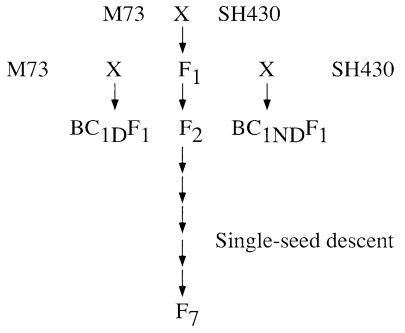

Fig. 1 The mating scheme used to produce all populations described herein. Dormant parent M73 was crossed with nondormant parent SH430 to produce the F_1. Subsequent self-pollination produced the F_2, and single-seed descent was used to produce the F_7. Backcrosses were produced by crossing the F_1 with the respective dormant and nondormant parents

The F_7 RI lines were classified at 15°C for 113 days in a separate experiment. All seeds were surface-sterilized as described above. Treatments were arranged in a completely randomized design with 6 seeds per replicate and two replications per F_7 RI line. Seeds from both parental lines and F_1s were included as controls. The experiment was conducted twice, therefore a total of 24 seeds were tested per F_7 RI line. Tissue samples were harvested from leaves of 3- to 6-week-old individual F_7 RI plants.

Random amplified polymorphic DNA (RAPD) analysis

DNA was extracted from frozen leaf tissue as described by Dellaporta et al. (1983). Based on the results of the F_3 progeny testing described above, DNA from eight true breeding nondormant F_2 individuals and eight true breeding dormant F_2 individuals was pooled to form nondormant and dormant bulks, respectively, for bulked segregant analysis (Michelmore et al. 1991). Polymerase chain reactions (PCR) were conducted according to Williams et al. (1990) with these modifications: each 20-µl reaction contained 25 ng of DNA template, 60 ng of primer, 125 µM of each deoxyribonucleotide triphosphate (dNTP), 2.5 m*M* $MgCl_2$, 10 m*M* TRIS-HCl pH 9.0, 50 m*M* KCl, 0.1% v/v Triton X-100, and 0.5 units of *Taq* polymerase. The reaction was cycled 40 times through 94°C for 45 s of denaturation, 37°C for 80 s of annealing, and 72°C for 2 min of extension in a thermal cycler. Samples were run on 1.2% agarose gels with 0.5× TRIS-borate EDTA (TBE) at 5 V/cm for 3 h, stained with ethidium bromide, and visualized on a UV trans-

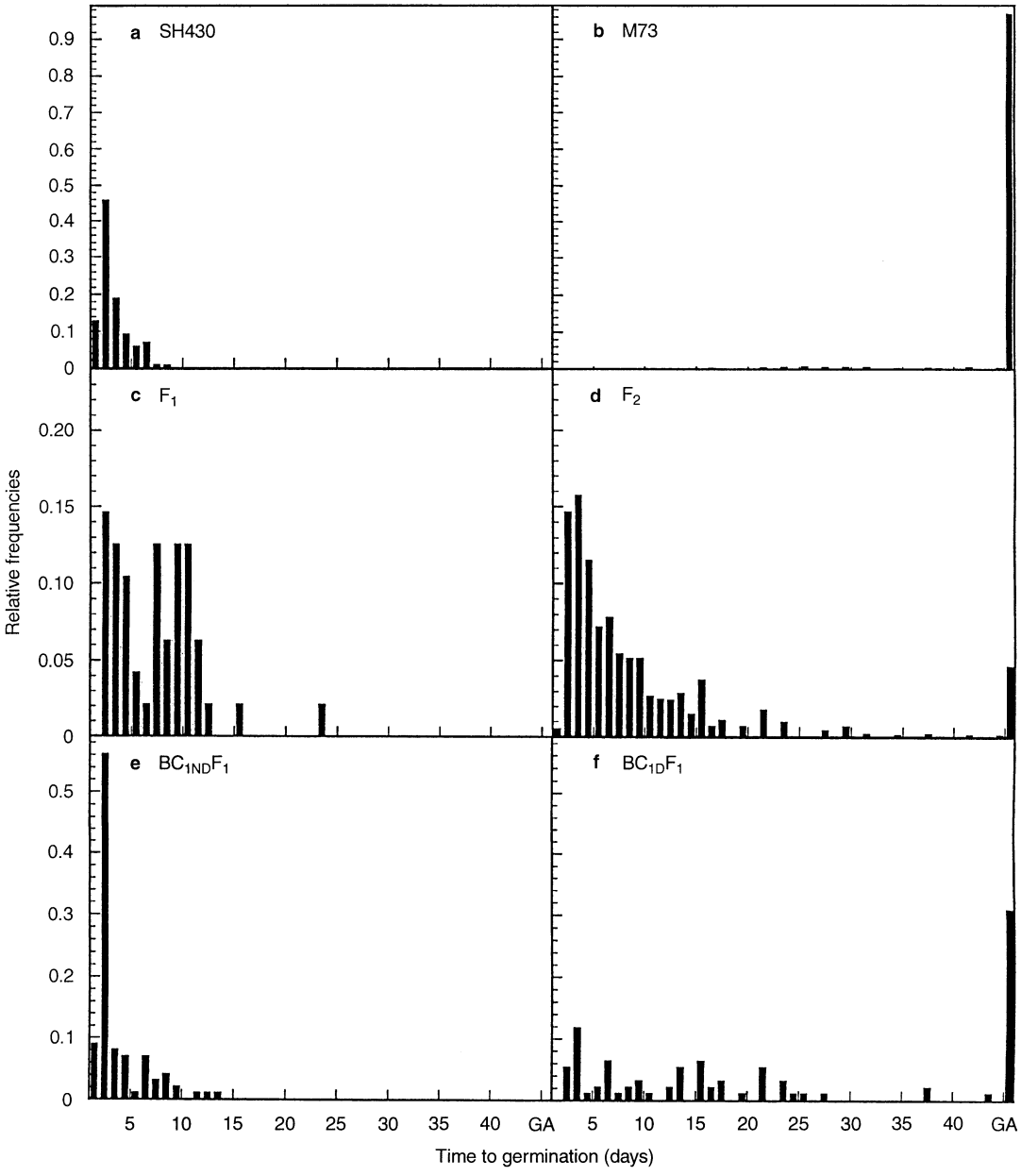

Fig. 2 a–f Frequencies of SH430 (**a**), M73 (**b**), F_1 (**c**), F_2 (**d**), $BC_{1ND}F_1$ (**e**), and $BC_{1D}F_1$ (**f**) seeds that germinated during 44 days of imbibition. On day 44 all remaining ungerminated seeds were induced to germinate with 10 m*M* GA

illuminator. The F_2 bulks were screened with 800 decamer random primers (Operon kits A through AN).

Data analyses

Regression analysis was conducted to identify significant associations between single RAPD markers and days to germination (QGENE, single-point analysis, Nelson 1994). Regression models were tested that included significant RAPD markers (QGENE, single-point analysis, Nelson 1994). The coefficient of multiple determination (R^2) from the multiple regression model was employed to quantify the proportion of the total phenotypic variance explained by the markers in the F_2 population.

The SAS/CLUSTER (methods = WARD and AVERAGE) (SAS Institute 1989) procedure was used to classify the F_7 RI lines as progenies of nondormant, and dormant individuals by inputting the days to germination of every individual within every family into the CLUSTER procedure. The procedure began by considering the 12 observations for every family as the coordinates in a 12-dimensional space. The distances between all possible pairs of lines or clusters were calculated, and the two closest lines were merged to form a cluster that replaced the 2 old ones. Merging of the closest clusters was repeated until larger clusters were formed. For example, 2 lines consisting of individuals that all germinated early would have a small distance between them and would likely be clustered. In contrast, the distance would be great between 1 line of early-germinating individuals and another line of late germinating individuals, and a cluster would be unlikely. In this manner lines of nondormant, and dormant phenotypes were clustered into their respective categories.

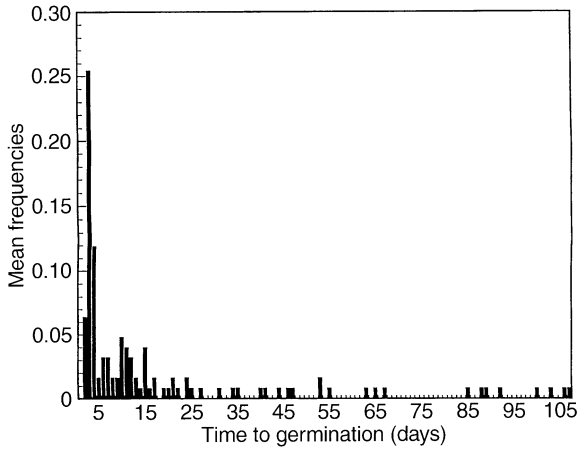

Fig. 3 Frequencies of F_7 RI line means that germinated during 113 days of imbibition. The means of each RI line are plotted. After 113 days all remaining ungerminated seeds were induced to germinate with 10 m*M* GA. Germination phenotypes of dormant seeds induced to germinate with GA were assigned to the actual day of germination between days 113 and 123

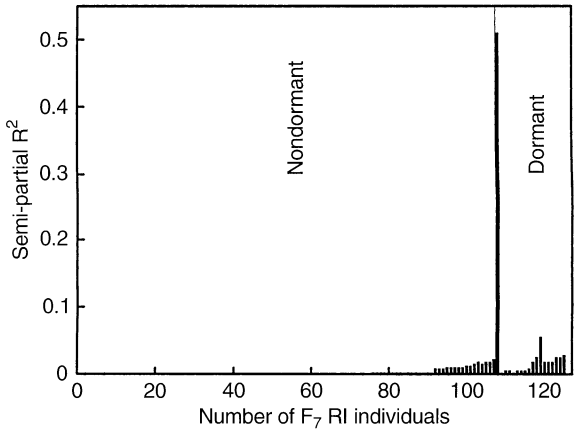

Fig. 4 Nondormant, and dormant F_7 RI clusters as classified by the SAS/CLUSTER procedure (method = WARD). The semi-partial R^2 distance indicates the distance between each cluster. At the beginning of the CLUSTER procedure all F_7 RI lines were considered separate clusters. The *bars* plotted indicate the semi-partial R^2 distances between adjoining F_7 RI clusters. Therefore, the number of bars is one less than the total number of families (126–1=125 bars shown). The *X-axis* depicts the number of F_7 lines in each cluster, i.e., the nondormant cluster consists of lines 1–109, and the dormant cluster consists of lines 110–126

Results

Germination tests

All SH430 caryopses germinated in less than 10 days, while 96% of the M73 caryopses remained ungerminated for 44 days and required GA to induce germination (Fig. 2 a, b). F_1 caryopses completed germination in less than 25 days and were classified as nondormant (Fig. 2 c). Most (84.6%) of the F_2 caryopses germinated within 14 days of imbibition (Fig. 2 d). During the period 15–44 days after imbibition the F_2 cumulative germination percentage advanced slowly from 84.6% to 95.4%, and the remaining 4.6% required GA to induce germination after day 44. Nearly all of the $BC_{1ND}F_1$ caryopses germinated within 10 days of imbibition and were classified as nondormant (Fig. 2 e). Of the $BC_{1D}F_1$ caryopses 69% germinated during 44 days of imbibition, and the remaining 31% were induced to germinate with GA (Fig. 2f). Most of the 126 F_7 RI lines germinated within 25 days of imbibition (Fig. 3).

A three-locus seed dormancy model

A model was developed by testing one- and two-locus models to describe the nondormant and dormant segregation, as determined by cluster analysis, in the F_7 RI lines as well as the other generations. However, the expected values from one- or two-locus models did not fit the observed segregation as indicated by chi-square analysis. The 126 F_7 RI line variances were partitioned by the SAS/CLUSTER procedure (method = WARD) into 109 nondormant and 17 dormant lines (Fig. 4). In a one-locus model one would expect 63 of F_7 RI lines to be dormant and 63 to be nondormant; therefore, this model is rejected based on the number of dormant and nondormant F_7 RI lines ($\chi 2 = 67.2$, $P = 2.2 \times 10^{-16}$). Results reported both here (Fig. 2c) and in Jana et al. (1988) indicate that nondormancy was dominant in the F_1. Therefore, in a two-locus model one would expect 94.5 of the F_7 RI lines to be nondormant and 31.5 to be dormant, but again this model does not fit the number of observed dormant and nondormant F_7 RI lines ($\chi 2 = 8.9$, $P = 0.0029$). The expected ratios from one three-locus model fit the observed ratios: the dominant alleles G_1 and G_2 at the G_1 and G_2 loci and the recessive allele *d* at *D* locus promote early germination (Table 1). The expression of *D* for late germination is dependent upon the alleles present at G_1 and G_2. According to the proposed model an embryo is nondormant if it has at least one copy of both dominant G_1 or G_2 alleles ($G_1\_G_2\_\_\_$) or at least one copy of either G_1 ($G_1\_g_2g_2\_\_$) or G_2 ($g_1g_1G_2\_\_\_$) alleles regardless of the genotype at the D locus. If the genotype is $g_1g_1g_2g_2D\_$, then the phenotype will be dormant. The proposed model for nondormancy

Table 1 A three-locus model of seed dormancy in wild oat: genotypes of nondormant and dormant wild oats and their genotypic frequencies [a]

Nondormant	Frequencies	Dormant	Frequencies
$G_1\_G_2\_\_\_$	9/16	$g_1g_1g_2g_2D\_$	3/64
$G_1\_g_2g_2\_\_$	3/16		
$g_1g_1G_2\_\_\_$	3/16		
$g_1g_1g_2g_2dd$	1/64		

[a] The blank spaces indicate that either the dominant or recessive form of the allele could be present and the phenotype would remain the same

Table 2 Mean cumulative percentage germination and chi-square analysis of the three-locus model of wild oat seed dormancy in six generations after 41 days of imbibition

Generation	Pedigree[a]	Mean[b]	Proposed parental genotype	Test ratio	χ^2	*P*-value
P_{ND}	SH430	100	$G_1G_1G_2G_2dd$			
P_D	M73	3.60	$g_1g_1g_2g_2DD$			
F_1	P_D x P_{ND}	100	$g_1g_1g_2g_2DD$ x $G_1G_1G_2G_2dd$	1:0	0	1
F_2	(P_D x P_{ND}) ⊗	94.96	$(G_1g_1G_2g_2Dd)^2$	61:3	0.10	0.7518
$BC_{1ND}F_1$	F_1 x P_{ND}	100	$G_1g_1G_2g_2Dd$ x $G_1G_1G_2G_2dd$	1:0	0	1
$BC_{1D}F_1$	F_1 x P_D	68.95	$G_1g_1G_2g_2Dd$ x $g_1g_1g_2g_2DD$	3:1	1.71	0.1909

[a] This generation was self pollinated (⊗)
[b] Mean cumulative percentage germination (total germinated seeds after 41 days of imbibition out of the total number of viable seeds)

Table 3 Chi-square analysis of the three-locus model of wild oat seed dormancy in F_3 and $BC_{1D}F_2$ families classified as nondormant (ND)/ segregating and dormant (D) after 44 days of imbibition

Generation	Pedigree[a]	Proposed parental genotype	ND / segregating families[b]	D families[c]	Test ratio	χ^2	P-value
F_3	[(P_D x P_{ND}) ⊗]⊗	$(G_1g_1G_2g_2Dd)^2$ ⊗	95	2	61:3	1.50	0.2211
$BC_{1D}F_2$	(F_1 x P_D) ⊗	($G_1g_1G_2g_2Dd$ x $g_1g_1g_2g_2DD$) ⊗	59	22	3:1	0.20	0.6531

[a] This generation was self pollinated (⊗)
[b] Nondormant / segregating families (0–8 progeny seeds out of 10 required GA treatment to germinate)
[c] Dormant families (9–10 progeny seeds out of 10 required GA treatment to germinate)

Table 4 RAPD polymorphisms among the dormant parent M73, nondormant parent SH430, dormant F_2 bulk, and nondormant F_2 bulk

Primer	Primer sequence 5' to 3'	Size bp[a]	M73	SH430	Dormant bulk	Nondormant bulk
OPF-17	AACCCGGGAA	1591	+	-	+	-
OPT-04	CACAGAGGGA	1373	-	+	-	+
OPX-06	ACGCCAGAGG	1545	-	+	-	+

[a] Approximate size of polymorphic band in base is pairs based on migration distance relative to DNA size markers

Table 5 Simple regression of RAPD marker scores on mean days to germination in 97 random F_2 individuals, and 82 random $BC_{1D}F_1$ individuals

Marker	Source of allele	Marker class means (days)			r^2	*P*-value[a]
		Present (*n*)	Absent (*n*)	Genotypic value		
F_2						
OPF-17	M73	10.7 (77)	7.9 (20)	1.4	0.0180	0.4265
OPT-04	SH430	8.6 (66)	13.3 (31)	–2.4	0.0682	0.0362
OPX-06	SH430	8.1 (69)	14.9 (28)	–3.4	0.1259	0.0018
$BC_{1D}F_1$						
OPT-04	SH430	20.1 (33)	26.5 (49)	–6.4	0.0276	0.1358
OPX-06	SH430	19.1 (34)	27.4 (48)	–8.4	0.0473	0.0497

[a] Indicates the significance of the regression coefficient

is duplicate dominant at two loci (G_1 and G_2) and recessive at a third (*dd*). We hypothesize the genotype of SH430 to be $G_1G_1G_2G_2dd$ and that of M73 to be $g_1g_1g_2g_2DD$ (Table 2). The segregation ratios of the F_1, F_2, $BC_{1ND}F_1$ and $BC_{1D}F_1$ generations were consistent with the expectations of the model (Table 2). Chi-square analysis of the number of nondormant / segregating and dormant F_3 and $BC_{1D}F_2$ families was consistent with the expectations of the three-locus model (Table 3). The partitioning of the 126 F_7 RI lines reported above into 109 nondormant and 17 dormant lines by the WARD method suggests a segregation ratio of 7:1 (nondormant:dormant) and that three loci segregated in the M73 x SH430 cross ($\chi2$ = 0.11, *P* = 0.7365). The SAS/CLUSTER (method = AVERAGE) was employed to verify the partitioning of the F_7 RI lines. This procedure partitioned the lines into 114 nondormant and 12 dormant lines, also in agreement with the expected 7:1 segregation of the three-locus model ($\chi2$ = 1.0, *P* = 0.3125). The hypothetical genotype of the dormant F_7 RI lines is $g_1g_1g_2g_2DD$.

RAPD analysis

A total of 800 random primers were screened to identify polymorphisms between dormant and nondormant DNA bulks. On average each primer amplified about 10 frag-

Table 6 Segregation ratios of RAPD marker pairs in 127 F_7 recombinant inbred lines

Marker pairs	Expected ratio	No. observed[a]	χ^2	*P*-value
OPF-17 / OPT-04	1:1:1:1	7:57:57:6	80.33	0
OPT-04 / OPX-06	1:1:1:1	39:29:26:33	2.98	0.3947
OPF-17 / OPX-06	1:1:1:1	33:35:32:27	1.09	0.7795

[a]The phenotype order is: (1) both markers present; (2) first marker present, second absent; (3) first marker absent, second present, 4) both markers absent

ments. Three random primers - - OPF-17, OPT-04, and OPX-06 - - were found to produce polymorphic bands between the dormant and nondormant bulks (Table 4). Simple regression of the phenotype, days to germination of individuals in a random F_2 population, on scores for markers OPT-04 and OPX-06 revealed a significant association of those markers with early germination, but no such relationship was observed for marker OPF-17 (Table 5). Similarly, a simple regression of days to germination in the $BC_{1D}F_1$ population on OPT-04 and OPX-06 scores indicated a significant relationship between OPX-06 and early germination but not OPT-04. OPF-17 was present in 80 out of 82 $BC_{1D}F_1$ individuals, therefore simple regression analysis could not be performed in this generation. Chi-square analysis of marker segregation in 127 F_7 RI lines revealed that markers OPF-17 / OPT-04 were linked in repulsion with 10.2% recombination, while marker pairs OPT-04 / OPX-06 and OPF-17 / OPX-06 segregated independently (Table 6).

Discussion

Application of the model to previous work

The model of Jana et al. (1979, 1988) predicts a different outcome in the number of nondormant and dormant F_7 RI lines than we observed. They performed genetic analysis on eight wild oat lines and developed a genetic model that explained the differences in germination rates among F_1, F_2, and backcross generations derived from crosses between these populations. They presented a genetic model and hypothesized that the genotype of M73 was $eel_1l_1L_2L_2$, and that of SH430 was $EEl_1l_1l_2l_2$. Therefore, *E* and L_2 segregate in the cross of M73 (eeL_2L_2) x SH430 (EEl_2l_2). Consequently, if two genes were segregating in this cross, one would expect 31.5 (25%) of 126 F_7 RI lines to be dormant. However, only 17 (13.5%) of these lines were found to be dormant, significantly less than expected ($\chi 2 = 8.9$, $P = 0.0029$). Genetic analysis of dormancy may differ because different genetic lines were used to develop segregating populations and germination temperatures were different. Jana et al. (1979) used nondormant line CS40 and classified the germination of their populations at 20°C, whereas we used line SH430 and classified our populations at 15°C. Our previous investigations revealed a genotype-by-environment (GxE) interaction for germination temperature in our F_1 and F_2 populations (Fennimore et al. 1998). Mean germination after 10 days of imbibition was greater at 15°C than at 20°C. In the same paper we described evidence for the presence of epistatic interactions between wild oat dormancy loci (Fennimore et al. 1998). Therefore, epistatic interactions between loci G_1, G_2, and *D* from the model presented here are consistent with data from generation means analysis. Clearly, more research needs to be done to understand the GxE and epistatic interactions among dormancy loci and to further refine our model.

Genetic mechanisms in other species

There is a diversity of genetic mechanisms for dormancy in cereals and other plants. In studies of grain dormancy in white-kerneled wheat cultivars Paterson and Sorrells (1990) found multiple genes dominant for late germination. In contrast, Bhatt et al. (1983) found that two genes recessive for late germination controlled seed dormancy in their wheat populations. Oberthur et al. (1995) detected evidence for epistasis between three seed dormancy genes in barley where the allelic state of restriction fragment length polymorphism (RFLP) marker *PSR128* appeared to regulate the expression of quantitative trait loci (QTL) linked to RFLP markers *BCD402B* and *Amy2*. These results suggest that the dormancy allele linked to *PSR128* has an effect on the physiological pathway leading to the imposition, maintenance, and/or release of dormancy and is at least partly epistatic to other dormancy loci (Han et al. 1996).

In noncereal species Garbutt and Witcombe (1986) found that maternal genetic factors in *Sinapis arvensis* controlled coat-imposed dormancy, and they detected another locus that influenced embryo dormancy. Ecker et al. (1994) found that seed dormancy in *Eustoma grandiflorum* was controlled by several nuclear genes that respond to chilling. Seed dormancy in cucumber (*Cucumis sativa*) was found to be controlled by three to seven recessive nuclear genes (Staub et al. 1989).

Molecular markers

Dominant alleles at RAPD markers OPT-04 and OPX-06 are associated with nondormancy, i.e., are linked in coupling to dormancy QTL (Table 4). OPT-04 and OPX-06 may mark the G_1 and G_2 alleles, respectively, and OPF-17 may mark the g_1 allele. A reasonable explana-

tion for the lack of significance of OPF-17 in the simple regression analysis can be attributed to the difficulty of detecting the influence of the g_1 allele alone in the F_2, since g_1 is recessive to G_1, and G_2 and D are epistatic to g_1. In other words, the fact that OPF-17 does not mark an allele with a major effect on the phenotype is consistent with the model presented here. Markers OPF-17 and OPT-04 may be linked to a QTL that affects seed dormancy, and OPX-06 may be linked to a second QTL for dormancy.

Weed emergence models

Interest in alternative weed management systems have been driven in part by regulatory efforts such as the Food Quality Protection Act of 1996 (Goldman 1997), a process that may result in severe limitations in herbicide options available to farmers. Weed management systems based on predictive weed emergence models are one such alternative system that may allow growers to increase the efficiency of weed management inputs. Variability in the dormancy state of soil seedbanks, within and between fields, makes the development of weed emergence models a formidable task (Forcella et al. 1992). Recent emergence models have focused on the influence of the environment on germination (Forcella et al. 1992, 1997). Approximately 50% of the wild oat germination phenotype is due to the influence of the environment, while the other 50% is due to genetic factors (Jana and Naylor 1980). An emergence model based on weather data alone would only address 50% of the factors that influence germination in wild oat. The characterization of major dormancy genes would allow weed scientists to estimate the effects of genotype-by-environment interaction on germination. The cloning of major dormancy genes would provide information on the stability of weed populations, gene flow, and mutation rates. For an inbreeding species like wild oat a seedling emergence model would include a genetic index based on the proportion of nondormant and dormant alleles such as G_1, G_2 and D in a wild oat population. The model would combine environmental and genetic information to make emergence predictions.

Conclusions

At least three loci regulate dormancy in wild oat. In the model supported by these data G_1 and G_2 promote early germination, while the third locus, D, promotes late germination. If at least one copy of the dominant G_1 or G_2 alleles are present regardless of the genotype at the D locus, i.e., one at the G_1 locus or one at the G_2 locus, then the individual will be nondormant. If the genotype is $g_1g_1g_2g_2D\_$ then the phenotype will be dormant. RAPD marker OPT-04 and OPX-06 may be linked to dormancy loci. RAPD markers OPF-17 and OPT-04 may mark different alleles at the same locus, i.e., g_1 and G_1, respectively.

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