Heritability of Lipase Activity of Oat Caryopses

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ABSTRACT

Oat (*Avena sativa* L.) is a potentially economically viable source of lipase, an enzyme used in foods, chemicals, and pharmaceuticals, which occurs on the surface of oat caryopses (groats). The objectives of this study were to: (i) estimate the broad-sense heritability of the lipase activity of oat caryopses, (ii) determine the genetic and phenotypic correlations between lipase activity and other important agronomic traits, and (iii) test whether five cycles of recurrent selection for test weight caused a correlated response in lipase activity. Entries included 10 check cultivars, 95 randomly chosen S_0-derived lines from the initial cycle (C0), and 19 S_0-derived lines from C5 of a population developed by randomly mating oat cultivars and lines adapted to the midwestern USA. Entries were grown at three Iowa locations in 1996 and 1997. Broad-sense heritability estimates for lipase activity were 0.22 on a sample basis in the population, and 0.63 on a line-mean basis. Lipase activity had positive genetic correlations with total biomass (r = 0.31), heading date (r = 0.53), and plant height (r = 0.58), positive phenotypic correlations with heading date (r = 0.18) and plant height (r = 0.26), and negative phenotypic correlations with biomass (r = −0.13), test weight (r = −0.30), weight of 50 seeds (r = −0.18), weight of 50 groats (r = −0.40), and groat percentage (r = −0.34). The C0 and C5 populations did not differ for mean lipase activity, indicating that selection for increased test weight did not affect lipase activity. We suggest that selection for cultivars with higher lipase activity and acceptable grain quality is possible.

Hydrolysis of fats and oils to free fatty acids is important in the production of detergents and a number of other industrial products (Vulfson, 1994). Currently, the energy- and capital-intensive Colgate-Emery process is employed to achieve commercial hydrolysis of fats and oils (Sonntag, 1982). The surfaces of oat caryopses (groats) are rich in lipase, an enzyme which hydrolyzes esters and lipids at a lipid-water interface. Oat has the potential to be an economical source of lipase for industrial hydrolysis under mild conditions and with relatively simple equipment (Shahani, 1975; Lee and Hammond, 1990; Parmar and Hammond, 1994). Oat lipase does not have obvious substrate specificity (O'Connor et al., 1992). Parmar and Hammond (1994) suggested that higher lipolytic activity of oat groats can be achieved by (i) using an impact-type dehuller instead of a wringer-type dehuller, (ii) using cultivars specifically selected for high lipase activity, (iii) exposing the fats to two to three lots of moist caryopses, and (iv) dilution of the substrate with hexane. Development of oat cultivars with increased lipase activity may attract new market uses for oat.

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Selection for oat cultivars with lower lipase activity may be important for other purposes. Lipase may have a role in the initiation of oxidative rancidity by some lipoxygenases that cause off-flavors in malt and beers and spoilage of wholemeal flour (O'Connor et al., 1992). Lipase activity is significantly higher in oat than in both barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.). Higher oil content increases feeding value of oat (Stothers, 1977), and selection for increased groat-oil percentage has been successful (Schipper and Frey, 1991). Low lipase activity may be particularly important for high-oil oat cultivars.

Parmar et al. (1994) detected significant differences for lipase activity among early and midseason oat cultivars. After a 5-d reaction period, the mean lipase activity for early oat lines ranged from 28.7 to 52.7% hydrolysis and that for midseason oat lines ranged from 32.3 to 61.3%. Both the groat percentage and the groat weight had significantly negative correlations with lipase activity. Groat weight and groat percentage, among other seed traits, affect test weight; therefore, selection for test weight may cause changes in groat weight and groat percentage, which may affect lipase activity. Test weight is the primary indicator of oat grain quality, so it is important to determine if test weight and lipase activity have a genetic correlation.

The objectives of this study were to: (i) estimate the broad-sense heritability of lipase activity of oat caryopses; (ii) determine the genetic and phenotypic correlations between lipase activity and other important agronomic traits; and (iii) test whether five cycles of recurrent selection for test weight caused a correlated response in lipase activity in a population developed by randomly mating oat cultivars and genotypes adapted to the midwestern USA. Results from this study will allow predictions of the effectiveness of direct and indirect selection for altered levels of lipase activity.

MATERIALS AND METHODS

Plant Materials

We estimated the heritability of lipase activity in an oat population originally developed from crosses between adapted lines and cultivars. Klein et al. (1993) conducted recurrent selection for higher test weight in this population. We randomly selected 95 lines (K475-K557) from the initial population (C0) and 19 lines (P171-P270) from the fifth cycle of selection (C5) for higher test weight. The seeds of each line planted in 1996 represented progeny derived from two generations of self-fertilization (S_2 generation) from a non-inbred parent (S_0 generation). Therefore, we refer to the lines tested

Abbreviations: CR_x = correlated response of Trait X obtained by indirect selection for Trait Y; R_x = response of Trait X obtained by direct selection for Trait X; i_x, i_y = selection intensity for traits X and Trait Y, respectively; h_x, h_y = square root of narrow-sense heritability of traits X and Trait Y, respectively.

in 1996 as $S_{0:2}$ lines. Their selfed progeny, $S_{0:3}$ lines, were tested in 1997. Ten check lines chosen for their different levels of lipase activity and agronomic characteristics were included in the study: 'Ogle', 'Don', 'Starter', 'H811-3', 'Y907-5-5', 'Paul', 'Hytest', 'Brawn', 'Jerry', and 'Classic'.

Field Evaluations

Three repeated entries represented each check line in the experiment. The different entries of a common check were treated separately in the experiment, making a total of 144 entries. The experimental design was a 12-by-12 triple lattice design. The experiment was replicated at three Iowa locations in 1996 and 1997: Ames, on a Nicollet loam soil (fine-loamy, mixed, mesic Aquic Hapludoll); Nashua, on a Readlyn loam soil (fine-loamy, mixed, mesic Aquic Hapludoll); and Crawfordsville, on a Mahaska silty clay loam soil (fine, smectictic, mesic Aquic Argiudoll). We sowed hill plots spaced on a grid 0.3 m apart in perpendicular directions with 30 seeds per hill. Each experiment was surrounded by two rows of hills to provide competition to peripheral plots. All entries were sprayed with triadimefon, 1-(4-chlorophenoxy)-3,3-dimethyl-1-(*H*-1,2,4-triazol-1-yl)-2-butanone, a systemic fungicide, to control crown rust disease caused by *Puccinia coronata* Corda.

Heading date was recorded at Ames in both years when the first nodes of one-half of the plants in a plot had completely emerged above the flag leaf (White, 1995). Plant height, excluding awns, was measured at grain maturity at Ames in both years. All plants in a plot were bundled together at harvest and dried at ambient temperature for at least 1 wk after harvest, after which total above-ground biomass and grain yield of all plots were measured. Grain from the three replications of an entry at a location was bulked to provide sufficient seeds for estimating test weight and lipase activity. Approximately one-half of the seed from each entry was dehulled with an impact-type dehuller. Laboratory analysis of lipase activity was performed on the dehulled oat caryopses. In 1997 only, two samples of 50 seeds of each bulked grain sample were weighed to estimate 50-seed weight. Each sample was dehulled manually with a roller-type dehuller to produce 50 groats, from which 50-groat weight and groat percentage of each sample were estimated.

Lipase Activity Analysis

Lipase activity was estimated on the basis of the percentage of fatty acids hydrolyzed in a sample of soybean oil incubated with oat groats from an unstirred reaction as described by Parmar and Hammond (1994). Ten grams of oat caryopses randomly obtained from each bulk sample of one genotype grown in one environment were moistened with 2 mL of water in a 50-mL conical flask. After 2 h of moisture equilibrium at room temperature, 10 g of soybean oil were added, and the samples were incubated for 24 h at 37°C. An equal amount of soybean oil added to an empty 50-mL conical flask and incubated for 24 h at 37°C was used as a negative control. Next, 0.2 g of oil from each sample was dissolved in 15 mL of diethyl ether-methanol (2:1, v/v). A 5-mL aliquot was diluted to 50 mL with methanol and titrated to pH 9.0 with aqueous 0.01 *M* sodium hydroxide. The extent of hydrolysis was calculated as the ratio of free fatty acids to total fatty acids in the sample of soybean oil after incubation with oat groats by means of the following equation:

$$\%\ \text{hydrolysis} = 4.361 \times (\text{mL consumed by sample} - \text{mL consumed by control}).$$

The constant value in this equation relates the volume of NaOH consumed to the proportion of fatty acids hydrolyzed in 10 g of soybean oil on the basis of the average molecular weight of soybean oil and the average molecular weight of the fatty acids in soybean oil (Lee, 1989).

Statistical Analysis

Analysis of variance was performed with the MIXED procedure of SAS (SAS Institute, Inc., 1997). For the purposes of estimating line means and comparing check entries with experimental lines, entries were considered fixed effects. Environments, replications, and incomplete blocks were considered random effects. Differences between the means of C0 and C5 populations for percentage of hydrolyzed oil and other agronomic traits were tested by a single-degree-of-freedom contrast.

To estimate genetic components of variance in the C0 population, C0 lines were considered random effects and variance components for lines and line × environment interaction were estimated with the SAS MIXED procedure. The genotypic correlations among traits were estimated from multivariate analysis of variance by the GLM procedure of SAS (SAS Institute, Inc., 1988). Phenotypic correlations among traits were estimated on the basis of line means across locations. Standard errors for genotypic correlations were estimated on the basis of formulas presented by Mode and Robinson (1959). Genetic correlations were considered not significantly different from zero if their standard errors were greater than the absolute values of the estimates.

The genotypic variance among $S_{0:2}$ families tested in 1996 includes $\sigma^2_A + (1/16)\ \sigma^2_D$, and the genotypic variance among $S_{0:3}$ families tested in 1997 includes $\sigma^2_A + (1/32)\ \sigma^2_D$ (Nyquist, 1991). Because the coefficients of the additive genetic variance were identical between years, and the coefficients of the dominance variance were small, genotypic variances were pooled across years.

The estimates of error variance for grain yield, biomass, heading date, and plant height were estimated directly from the analysis of the C0 lines. The error variances for other traits could not be estimated directly because seeds from the three replications of each entry in each environment were bulked to provide enough material for measurements. Therefore, the estimates of error variance for lipase activity, test weight, seed weight, groat weight, and groat percentage were obtained from the analysis of the check lines. Each check line was represented by three entries that were bulked separately over replications within each environment, so the error variance was estimated from the pooled variation among entries nested within check lines and environments. We used this error estimate to test the significance of genotype × environment interaction variance and to estimate phenotypic variance among samples bulked across replications within an environment.

The estimates of phenotypic variance of grain yield, biomass, heading date, and height on a plot basis are the sum of the estimates of genotypic variance, genotype × environment interaction variance, and among-plot error variance. The estimate of phenotypic variance of other traits on a bulked-sample basis is the sum of the estimates of among-sample error variance (estimated from the check lines), genotype × environment interaction variance, and genotypic variance. The estimate of phenotypic variance on a line-mean basis is $(\hat{\sigma}^2_e/re) + (\hat{\sigma}^2_{GE}/e) + \sigma^2_G$, where $\hat{\sigma}^2_G$ is the estimate of genotypic variance, $\hat{\sigma}^2_{GE}$ is the estimate of genotype × environment interaction variance, and $\hat{\sigma}^2_e$ the estimate of error variance. Heritability on a plot basis (for grain yield, biomass, heading date, and height) or on a bulked-sample basis (for other traits) was

Table 1. Means of all entries, C0 population, C5 population, and checks of oat evaluated at three locations for 2 yr.

Entry	Lipase activity	Grain yield	Biomass	Test weight	Heading date	Plant height	Seed weight	Groat weight	Groat percentage
	% hydrolosis	g m^{-2}		kg m^{-3}	dap†	m	g		%
All Lines	11.6	360	934	511	76.0	0.99	1.57	1.16	74.2
C0	11.6	364	939	503	76.4	1.00	1.54	1.14	74.1
C5	11.6	342	918	541	72.9	0.97	1.66	1.22	73.5
Checks	10.9	350	920	530	77.7	1.00	1.66	1.25	75.9
C0 vs. C5‡	NS	**	**	**	**	**	**	**	**

** = significant at $P = 0.01$.
† dap = days after planting.

estimated as $H = \hat{\sigma}^2_G/(\hat{\sigma}^2_e + \hat{\sigma}^2_{GE} + \hat{\sigma}^2_G)$. Heritability on a line-mean basis was estimated as $H = \hat{\sigma}^2_G/(\hat{\sigma}^2_e/re + \hat{\sigma}^2_{GE}/e + \hat{\sigma}^2_G)$, where r is the number of replications per environment ($r = 1$ for traits measured on bulked samples) and e is the number of environments.

RESULTS AND DISCUSSION

Analysis of Variance

Differences among lines were significant ($P \leq 0.01$) for all traits within each environment and across all environments. The C0 and C5 population means were significantly different for all traits except lipase activity (Table 1). The C5 population had higher mean test weight and lower grain yield than the C0 population, and our results are consistent with those from three cycles of recurrent selection for higher test weight of oat by Klein et al. (1993). The C5 population also had lower mean biomass, earlier heading date, lower plant height, higher seed weight, higher groat weight, and lower groat percentage (Table 1). As hypothesized, selection for increased test weight caused correlated changes in groat weight and groat percentage. The phenotypic relationships among seed weight, groat weight,

Table 2. Mean lipase activity and agronomic characters of oat lines across two to six environments for 10 C0 lines with the highest lipase activity, 10 C0 lines with the lowest lipase activity, and the 10 checks.

Entry	Lipase activity	Grain yield	Biomass	Test weight	Heading date	Plant height	50–Seed weight	50–Groat weight	Groat percentage
	% hydrolysis	g m^{-2}		kg m^{-3}	dap†	m	g		%
Highest C0 lines									
K546-3	16.8	380	964	523	75.8	1.00	1.52	1.14	75.1
K514-2	15.8	374	1082	498	79.3	1.09	1.68	1.27	75.5
K536-1	15.8	402	1049	502	79.1	1.04	1.44	1.10	76.1
K567-1	15.7	316	1027	483	78.3	1.09	1.57	1.14	72.3
K531-4	15.3	326	880	499	79.5	0.97	1.78	1.29	72.4
K498-1	15.3	320	879	500	75.8	0.97	1.39	1.00	71.5
K499-2	15.2	420	992	509	78.7	0.97	1.46	1.08	73.8
K513-3	14.7	396	1056	502	80.0	1.04	1.55	1.15	73.9
K567-3	14.3	312	880	491	80.0	1.07	1.47	1.13	76.9
K491-3	14.2	370	961	495	78.2	0.98	1.43	1.04	72.7
Mean	15.3	361	977	500	78.5	1.02	1.53	1.13	74.0
Lowest C0 lines									
K498-2	8.6	317	842	510	71.5	0.95	1.50	1.12	74.9
K557-1	8.5	364	923	513	75.3	0.95	1.62	1.20	74.0
K468-2	8.5	297	866	514	75.5	0.98	1.62	1.20	74.5
K526-3	8.4	324	903	496	73.0	0.87	1.44	1.08	75.0
K525-2	8.3	381	1044	478	76.3	0.99	1.56	1.19	76.1
K524-2	8.2	352	869	490	73.1	0.93	1.61	1.21	74.8
K490-1	8.1	406	1011	500	74.0	0.98	1.45	1.06	73.2
K556-4	8.0	347	879	492	74.0	1.02	1.59	1.08	67.8
K555-1	7.8	351	898	503	73.2	0.98	1.46	1.07	73.0
K573-4	7.5	354	911	519	73.6	0.95	1.59	1.21	76.1
Mean	8.2	349	914	502	74.0	0.96	1.54	1.14	73.9
Check lines									
Ogle	8.5	369	900	547	77.9	0.96	1.55	1.17	75.7
Don	6.7	338	824	512	74.0	0.88	1.61	1.19	74.2
Starter	10.2	323	807	520	74.5	0.94	1.56	1.16	74.2
H811-3	14.5	373	970	495	79.8	1.07	1.64	1.16	70.7
Y907-5-5	15.2	320	912	489	78.7	1.08	1.70	1.22	71.6
Paul	12.8	219	851	618	82.1	1.08	1.30	1.30	100.0
Hytest	10.6	353	950	555	76.7	1.07	1.83	1.35	74.0
Brawn	9.7	417	1027	495	77.6	0.89	1.90	1.37	72.3
Jerry	8.1	398	1002	549	77.7	1.03	1.71	1.27	74.6
Classic	12.4	392	957	524	78.1	0.98	1.77	1.27	71.7
LSD (0.05) for comparisons between lines									
Experimental vs. experimental	5.3	68	140	22	3.0	0.06	0.24	0.19	7.9
Experimental vs. check	4.3	54	114	19	2.4	0.05	0.20	0.16	6.4
Check vs. check	3.0	39	81	16	1.7	0.03	0.14	0.11	4.6

† dap = days after planting.

Table 3. Estimates of genotypic (σ^2_G), genotype-environment interaction (σ^2_{GE}), and error (σ^2_e) variance components (with SE) and broad-sense heritabilities on a plot- or sample-basis and on a line-mean-basis for a random-mated (C0) oat population containing 95 S_0-derived lines.

Parameter estimates	Lipase activity	Grain yield	Biomass	Test weight	Heading date	Plant height	50–Seed weight	50–Groat weight	Groat percentage
	(% hydrolosis)^2	(g m^{-2})^2		(kg m^{-3})^2	(dap)^2	(m)^2	(g)$^2 \times 10^{-3}$	(g)$^2 \times 10^{-3}$	(%)^2
σ^2_G	2.8 (0.7)	790 (198)	2 988 (778)	83 (21)	4.0 (0.7)	12.2 (2.3)	9.5 (1.8)	6.5 (1.2)	1.5 (0.6)
σ^2_{GE}	5.2 (0.7)	235 (222)	840 (1025)	100 (23)	1.1 (0.3)	0.9 (1.1)	1.1 (0.8)	1.1 (0.5)	0.2 (0.7)
σ^2_e	4.7 (0.6)	7173 (333)	36 025 (1556)	233 (26)	2.7 (0.2)	16.9 (1.3)	6.1 (0.5)	3.4 (0.4)	6.5 (0.9)
Sample-or plot-basis heritability†	0.22	0.10	0.07	0.20	0.51	0.41	0.57	0.59	0.18
Line-mean-basis heritability‡	0.63	0.60	0.58	0.60	0.80	0.79	0.80	0.81	0.40

† Sample-basis or plot-basis heritability calculated as $H = \sigma^2_G/(\sigma^2_E + \sigma^2_{GE} + \sigma^2_G)$.
‡ Line-mean-basis heritability calculated as $H = \sigma^2_G/(\sigma^2_E/re + \sigma^2_{GE}/e + \sigma^2_G)$; r = number or replications, e = number of environments.

groat percentage, and test weight are complex, but it seems that test weight and lipase activity can be modified independently of one another. Individual C0 lines with highest lipase activity tended to have higher biomass, later heading date, and greater plant height than lines with lowest lipase activity, but they had very similar grain yield, test weight, seed weight, groat weight, and groat percentage (Table 2).

Heritability of Traits

Genotypic and genotype × environment interaction variances of the C0 population were significant for all traits. The broad-sense heritability of lipase activity on a bulked-sample basis in the C0 population was estimated to be 0.22, and the broad-sense heritability on a line-mean basis was 0.63 (Table 3). Their comparison indicates that genotypes should be evaluated over a number of environments to obtain accurate estimates of lipase activity. Because σ^2_D contributes relatively little to the estimate of genotypic variance among $S_{0:2}$ and $S_{0:3}$ families, the broad-sense heritability estimates were considered approximately equal to narrow-sense heritability. Lipase activity had lower heritability than heading date, plant height, seed weight, and groat weight, but higher heritability than grain yield, biomass, test weight, and groat percentage (Table 3).

Correlations among Traits

Among C0 lines, lipase activity had significantly positive genetic correlations with biomass, heading date, and plant height (Table 4). The C0 population had been random-mated for only two generations (Klein et al., 1993), and was likely not in linkage equilibrium. These genetic correlations, therefore, may be due to either pleiotropy or linkage. Because heading date and height had plot-basis heritability estimates of 0.51 and 0.41, respectively, which are greater than the sample-basis heritability estimate of lipase activity, the relative efficiency of indirect selection for lipase activity based on those two traits was explored.

According to Falconer and Mackay (1996, p. 319), the relative efficiency (RE) of indirect selection is:

$$RE = \frac{CR_X}{R_X} = \frac{i_Y h_Y r_{AXY}}{i_X h_X}$$

where CR_X is the correlated response in Trait X (in this case, lipase) due to selection for Trait Y (heading date or height); R_X is the direct response in Trait X due to selection for Trait X; i_Y and i_X are selection intensities; h_Y and h_X are square roots of the heritabilities; and r_{AXY} is the additive genetic correlation coefficient for Traits X and Y (estimated by the genetic correlation coefficient, Table 4).

Given the same intensity of selection for all traits and selection practiced on individual plot values, the relative efficiency of indirect selection for lipase activity based on heading date would be

$$(0.51^{1/2} \times 0.531)/\ 0.22^{1/2} = 0.808.$$

The relative efficiency of selection based on plant height would be

$$(0.41^{1/2} \times 0.582)/\ 0.22^{1/2} = 0.791.$$

Because the relative efficiencies are <1, direct selection for lipase activity is predicted to be more effective than indirect selection for this trait. Screening for lines with desired heading date and plant height is, however, much less labor intensive and time consuming than direct screening for lines with the desired level of lipase activity, thus making indirect selection simpler than direct selection. Heading date strongly influences adaptation, and selection for heading date outside of the adaptive range is not desirable. Heading date and plant height,

Table 4. Genotypic and phenotypic correlations between lipase activity and other traits of C0 oat lines.

Trait	Grain yield	Biomass	Heading date	Plant height	Test weight	Seed weight	Groat weight	Groat percentage
				Genotypic correlations				
Lipase activity	NS	0.32 ± 0.16	0.53 ± 0.26	0.58 ± 0.29	NS	NS	NS	NS
				Phenotypic correlations				
Lipase activity	NS	−0.130**	0.180**	0.264**	−0.301**	−0.176**	−0.395**	−0.344**

** Significant at $P = 0.01$.

therefore, may be helpful for preliminary selection to eliminate lines that are predicted to be beyond the desired range of lipase activity based on genetic correlations.

Lipase activity in the C0 population had negative phenotypic correlations with biomass, test weight, seed weight, groat weight, and groat percentage (Table 4). The negative correlations between lipase activity and groat weight and between lipase activity and groat percentage agree with findings by Parmar et al. (1994). Lipase activity had positive phenotypic correlations with heading date and plant height. Since phenotypic correlation is composed of both genetic and environmental correlations, the phenotypic correlation and the genetic correlation between two traits may not be of the same sign if the environmental correlation is significant and acting against the genetic correlation. For example, biomass and lipase activity had a positive genetic correlation and a negative phenotypic correlation.

Lipase had significant heritability in a population representative of elite Midwestern U.S. oat germplasm. Selection for either increased or decreased lipase activity is predicted to be effective. Multiple-environment evaluations of lipase activity are recommended because of the existence of genotype × environment interactions. Lipase activity was genetically independent of test weight, indicating that lipase activity can be increased or decreased via selection without necessarily reducing grain quality.

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