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Nine Cycles of Recurrent Selection for Increased Groat-Oil Content in Oat

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ABSTRACT

Increases in the groat (caryopsis)-oil content of oat (*Avena sativa* L.) raise the energy value of oat grain. Nine cycles of recurrent phenotypic selection for high groat-oil content were conducted in a genetically broad-based oat population that included germplasm from the wild relative *A. sterilis* L. Our objectives in this experiment were to determine if selection for high groat-oil content was effective and if selection reduced genetic variation for oil content; to identify agronomically acceptable lines with high groat-oil content; and to document the indirect effects of selection on grain yield, groat fraction, and oil yield. We evaluated 100 random lines from the base (C0) population and each of the nine selection cycle populations in three environments. Mean groat-oil content increased linearly during nine cycles of selection at a rate of 6.6 g kg^{-1} cycle^{-1} (equivalent to 6.7% of C0 population mean cycle^{-1}) from a mean of 98.2 g kg^{-1} in C0 to 158.5 g kg^{-1} in C9. The rate of gain from selection did not decrease in later cycles. Oil yield increased at a rate equivalent to 1.9% of C0 population mean cycle^{-1}, while mean groat fraction did not change and mean grain yield decreased at a rate equivalent to 3.2% of C0 population mean cycle^{-1}. For all traits, genetic variation did not decrease during selection cycles. Selected S_0-derived lines from the population with groat-oil contents >150 g kg^{-1} exhibited lower yield, greater lodging, and greater disease susceptibility compared with the best check cultivar.

Increases in the groat (caryopsis) oil content of oat would be useful for producing a higher energy feed grain (Price and Parsons, 1975). Oat oil also has excellent quality for human consumption, with relatively low linolenate (18:3) and high oleate (18:1) and linoleate (18:2) contents (Kalbasi-Ashtari and Hammond, 1977). Oat oil from genotypes with elevated levels of oil tends to be particularly favorable for human consumption, with higher levels of antioxidants (Peterson and Wood, 1997) and higher ratios of unsaturated to saturated fatty acids than normal genotypes (Schipper et al., 1991). If oat cultivars with higher groat-oil contents and acceptable agronomic performance could be developed, the use of oat as an oilseed crop could become economically feasible (Frey and Hammond, 1975).

Groat-oil content in oat is quantitatively inherited (Frey et al., 1975). Gene action for groat-oil content includes additive and nonadditive effects (Brown et al., 1974), although additive gene action predominates (Thro and Frey, 1985). Consistently high estimates of heritability of oil content in oats have been reported, and range from 0.50 to 0.93 (Baker and McKenzie, 1972; Branson and Frey, 1989b; Brown et al., 1974; Schipper and Frey, 1991b). Genotype × environment interaction for groat-oil content is not a major component of its phenotypic variance (Branson and Frey, 1989b; Gullord, 1986; Thro and Frey, 1985). Genotypic variation for groat-oil content has been observed among adapted cultivars (Brown and Craddock, 1972) and among wild relatives, including the progenitor species, *A. sterilis* (Frey and Hammond, 1975; Martens et al., 1979). Although the groat-oil content of wild *Avena* species does not exceed the levels found in domesticated oat (Rezai, 1977), Thro and Frey (1985) reported that alleles for higher oil content from *A. sativa* and *A. sterilis* are complementary. Thus, by combining alleles for higher oil content from the two species, development of oat genotypes with higher groat-oil contents than any previously reported in either species was facilitated (Thro and Frey, 1985).

The abundance of genetic variation for oil content in cultivated oat and interfertile wild hexaploid oat and the higher heritability of the trait permit relatively rapid increases in groat-oil content from recurrent selection. Branson and Frey (1989b) developed a population from crosses among cultivated and wild oat germplasm with higher levels of groat-oil content. Three cycles of recurrent selection for increased groat-oil content in this population resulted in significantly elevated mean groat-oil content in the third cycle population (Branson and Frey, 1989b). Three further cycles of recurrent selection resulted in continued gains in groat-oil content, achieved at a reasonably constant, linear rate (Schipper and Frey, 1991b). Significant genetic variation for groat-oil content remained in the Cycle 6 population, suggesting that continued gains in groat-oil content could be achieved in this population. Also, long-term recurrent selection for increased seed oil content has been successful in maize (*Zea mays* L.) (Dudley, 1977; Misevic and Alexander, 1989). The biological upper limit for groat-oil content in oat is not known; oat lines developed from six cycles of recurrent selection contained the highest levels of groat-oil content ever reported in the genus *Avena*, 162.9 g kg^{-1} (Schipper and Frey, 1991b).

Our objectives in this study were to determine if three additional cycles of recurrent selection would result in continued increases in groat-oil content in this population; to evaluate the effects of nine cycles of recurrent selection for increased groat-oil content on grain yield, groat fraction, and oil yield; and to determine if genetic

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Abbreviations: BYDV, barley yellow dwarf virus; NMR, nuclear magnetic resonance.

variation for groat-oil content, grain yield, groat fraction, and oil yield have been exhausted after nine cycles of recurrent selection.

MATERIALS AND METHODS

Population Development

The development of the base population has been described in detail by Branson and Frey (1989b). Briefly, eight interspecific F_1s (from matings of eight high-oil *A. sterilis* accessions and eight high-oil *A. sativa* cultivars) were crossed to eight locally adapted cultivars. F_2 seed from each three-way mating was space-planted in the field and culled for cultivated type, adapted maturity, and plant height. Groat-oil contents of the remaining plants were assayed using the wide-line nuclear magnetic resonance (NMR) method described by Conway and Earle (1963). Selected F_2-derived lines were intermated, and the same criteria were used to select among F_2 progeny from these matings. Selected F_2-derived lines were mated at random to five unrelated locally adapted cultivars, the F_1 plants of these crosses were intermated, and the S_0 plants from these crosses formed the base (C0) population for selection.

The development of C0 through C6 populations was described by Schipper and Frey (1991b). The C4 through C6 populations used in this study were developed from “regime 1” of Schipper and Frey (1991b), which is identical to the individual plant selection method used for C0 through C3. For cycles C7 through C9, 30 parents were selected based on high oil content and intermated to form ≈1000 S_0 generation plants. S_0 plants were space-planted in the field and harvested individually. Phenotypic selection for acceptable levels of barley yellow dwarf virus (BYDV) symptoms, maturity, plant height, and cultivated seed type reduced the population to ≈500 S_0 plants harvested each cycle. The groat-oil content of seed from each harvested plant was estimated with NMR by Dr. D.E. Alexander at the University of Illinois. Remnant S_1 seed from 30 selected plants was grown in the greenhouse and intermated at random to develop 1000 S_0 plants of the next cycle population.

Population Evaluation Experiment

One hundred S_0-derived lines were randomly chosen from each cycle population (C0–C9) for the evaluation experiment. The generation of seeds within each line varied among cycles: $S_{0:4}$ lines represented populations C0 through C2, $S_{0:3}$ lines represented C3 through C5, $S_{0:2}$ lines represented C6 through C8, and $S_{0:1}$ lines represented C9. Five check cultivars (Dal, Hamilton, Ogle, Starter, and Webster) were included as repeated entries four times within each replication. The 1120 entries were planted in randomized complete block experiments with two replications at three Iowa locations in 1992: near Ames on a Nicollet silty loam soil (fine-loamy, mixed, superactive, mesic Aquic Hapludoll), near Kanawha on a Canisteo loam soil (fine-loamy, mixed, superactive, calcareous, mesic Typic Endoaquoll), and near Nashua on a Readlyn loam soil (fine-loamy, mixed, mesic, Aquic Hapludoll). Plots were hills of 30 seeds each, planted on a grid and spaced 0.3 m in perpendicular directions. Two rows of hills of a common cultivar were planted as border around each experiment to provide competition for peripheral plots. Experiments were treated with the systemic fungicide Bayleton [1-(4-chlorophenoxy)-3,3-dimethyl-1-(1H-1,2,4-triazol-1-yl)-2-butanone] to prevent crown rust disease (incited by *Puccinia coronata* Corda var. *avenae* W.P. Fraser & Ledingham). Grain yield was recorded on every hill plot. After threshing, seed of the same entry from the two hill plots at a location was combined to provide sufficient seed for grain quality testing. A sample of seed from each entry × location combination was dehulled to provide 3.5 to 5.0 g of oven-dried groats that were assayed for oil content by Dr. Alexander at the University of Illinois using NMR. Groat fraction, the proportion of whole grain mass that is due to groats, was measured on two subsamples of bulked samples of seed of each entry at each location. Groat fraction was estimated in each subsample by weighing ≈2 g of whole grain, dehulling the seeds manually with a roller, and weighing the resulting groats.

To obtain pooled estimates of within-location error variances for oil content, groat fraction, and oil yield, which were measured on a bulk of seed from each location, only the repeated check entries were analyzed as a completely randomized design replicated across locations. The means of each repeated check cultivar at each location were then included in the data set along with the experimental lines from the recurrent selection population. Combined analyses of variance across locations were conducted for each trait, including location, cycle of selection, cycle × location interaction, and line nested within cycle as effects in the model using SAS Proc GLM (SAS Institute, 1990). Checks were included in this analysis as a separate “cycle”. The residual mean square from this analysis represented genotype × environment interaction variance, which was then tested for significance using the pooled within-location error mean square. The error variances for oil content, groat fraction, and oil yield were adjusted because they were based on repeated entries within locations, while the overall analyses were based on a single observation or mean of each line from each location (Milliken and Johnson, 1992, p. 161). Cycle and check group means, standard errors of cycle and check group mean comparisons, individual line and check cultivar means, and standard errors of line and cultivar comparisons were estimated from this analysis. Checks were then deleted from the data set, and regression on number of cycles of selection was performed for each variable using SAS Proc Mixed (SAS Institute, 1997), considering cycles as the only fixed effects in the model. Finally, each cycle was analyzed separately to estimate genotype and genotype × environment interaction variance components and their standard errors using the restricted maximum likelihood procedure of SAS Proc Mixed (SAS Institute, 1997). The variance component estimates were used to estimate heritability of each trait within each cycle population. Covariance components for groat-oil content and grain yield were estimated from each cycle using multivariate analysis of variance in SAS Proc GLM (SAS Institute Inc., 1990). Genotypic correlations between groat-oil content and grain yield and their standard errors were estimated following Mode and Robinson (1959).

Advanced Line Evaluations

Lines from the recurrent selection population with groat-oil contents >150 g kg^{-1} were selected for further evaluation in large yield-trial plot experiments. Five $S_{0:3}$ lines from C9, five $S_{0:4}$ lines from C8, four $S_{0:3}$ lines from C7, one $S_{0:6}$ line from C5, and three check cultivars (Dal, Multiline E77, and Ogle) were included as entries in randomized complete block experiments with three replications grown in three Iowa locations: near Ames, near Nashua, and near Crawfordsville on a Mahaska silty clay loam soil (fine, smectitic, mesic Aquertic Argiudoll) in 1995. Plots were machine planted, four-row 3.72-m^2 plots, with 0.3 m between rows, 0.4 m between adjacent plots, and 2-m alleys between ranges of plots. These experiments were not treated with fungicide, and natural infestations of crown rust disease and barley yellow dwarf diseases occurred at all locations. Each plot at Ames and Nashua was rated visually for crown rust and BYDV reactions using a relative nine-point scale in which 1 is no disease and 9 is the greatest level of infection observed. Heading date and plant height were measured on every plot at Ames only. All plots were rated at maturity for lodging by estimating the percentage of plants in each plot lodged 30° or more past vertical. All plots were machine harvested, and grain yield and test weight were measured on every plot. Seeds from the three replications of each entry at each location were bulked, dehulled, and assayed for groat-oil content by NMR as above.

RESULTS AND DISCUSSION

Population Performance

Genotypic differences and genotype × environment interactions were highly significant for groat-oil content, grain yield, groat fraction, and oil yield. Significant differences among cycles were observed for groat-oil content, grain yield, and oil yield. Cycle × location interactions were not significant for these traits. No significant differences among cycles were observed for groat fraction.

All populations had higher groat-oil content than the checks (Table 1). Groat-oil content increased with each successive cycle of selection, and the linear regression coefficient was 6.64 ± 0.06 g kg^{-1} cycle^{-1} (Table 1), which is equivalent to 6.7% of the C0 population mean per cycle. The highest groat-oil content reported in *Avena* before this recurrent selection program was initiated was 116 g kg^{-1} from one of 4533 accessions sampled from the World Oat Collection (Brown and Craddock, 1972). The mean groat-oil content of the C9 population was 158 g kg^{-1}. Individual lines within the C9 population had groat-oil contents as high as 181 g kg^{-1} (Table 2). Recurrent selection has provided the means by which the groat-oil content in oat was increased above any value previously reported.

The regression coefficient for oil content for C0 through C3 in our experiment was 7.04 ± 0.22 g kg^{-1} cycle^{-1}, while Branson and Frey (1989b) reported a linear rate of increase for these same three cycles as 9.26 ± 1.12 g kg^{-1} cycle^{-1}. Therefore, the difference in the rate of gain reported for all nine cycles of selection compared with Branson and Frey's (1989b) previous report of 9.26 ± 1.12 g kg^{-1} cycle^{-1} for C0 through C3 was primarily due to environmental differences. Schipper and Frey (1991b) reported a mean rate of increase of 6.04 g kg^{-1} cycle^{-1} for C0 through C6, and the rate for the same cycles from our study was 6.16 ± 0.10 g kg^{-1} cycle^{-1}.

Table 1. Cycle and check means for oil content, grain yield, groat fraction, and oil yield for oat lines representing nine cycles of recurrent selection evaluated in hill plot experiments in three Iowa locations in 1992.

Cycle	Oil content	Grain yield	Groat fraction	Oil yield
	g kg^{-1}	g m^{-2}		g m^{-2}
0	98.2	364	0.718	25.7
1	106.5	366	0.724	28.1
2	113.1	354	0.720	28.8
3	119.5	343	0.718	29.4
4	124.9	333	0.720	30.0
5	127.8	324	0.726	30.0
6	137.5	319	0.717	31.6
7	149.7	246	0.716	27.1
8	151.2	284	0.722	31.1
9	158.4	286	0.720	32.8
Checks	74.7	356	0.734	19.3
LSD (0.05) cycle vs. check	10.2	46	NS	1.6
LSD (0.05) cycle vs. cycle	3.2	14	NS	4.3
Regression coefficient	6.6 ± 0.1	−11.6 ± 0.4	NS	0.50 ± 0.04

The increase in oil content in this population was accompanied by a decrease in grain yield, no change in groat fraction, and an increase in oil yield. The linear regression coefficient for grain yield on cycles of selection was −11.6 g m^{-2} cycle^{-1}, equivalent to a mean decrease of 3.2% of the base-population mean each cycle. Thus, grain yield exhibited a steady decrease during cycles of selection, but the decrease in grain yield between C6 and C7 was more than six times greater than the average per-cycle decrease. It is not clear why this decrease in productivity occurred in C7, but grain yield increased significantly after C7, in contrast to the general trend. Branson and Frey (1989a) reported no significant changes in grain yield for the first three cycles of selection, while Schipper and Frey (1992) reported a mean decrease equivalent to 0.8% of the base-population mean for the first six cycles of selection. Oil yield increased steadily with each successive cycle of selection, except that the C7 population mean was less than the C6 population mean (Table 1), due to the decrease in grain yield. The increase in oil yield resumed in C8, and the C9 population mean exhibited the highest oil yield among all cycles, at 32.8 g m^{-2} (Table 1), equivalent to 127.7% of the C0 mean. The linear regression coefficient of oil yield on cycle of selection was 0.50 ± 0.04 g m^{-2} cycle^{-1}, which is an average gain of 1.9% of the C0 population mean cycle^{-1}. Schipper and Frey (1992) reported significant linear increases in oil yield between C0 and C6 in this population, equivalent to 5.2% of the base-population mean per cycle. To maximize increases in oil yield in this population, selection for oil yield itself, or index selection for both groat-oil content and grain yield should be practiced.

Why did grain yield decrease due to selection for oil content? There are two possible reasons for the yield decrease, genetic drift or a negative genetic correlation between grain yield and groat-oil content. Genetic drift due to intermating of finite numbers of parents causes inbreeding and random changes in allele frequencies. Misevic and Alexander (1989) reported that selection for higher oil content in maize resulted in decreased yield and suggested that inbreeding due to a small effective population size was the major cause. Miller et al. (1981), using a large effective population size, reported that grain yield did not decrease after seven generations of selection for higher oil in maize. Assuming that the effective population size each generation was equal to the numbers of S_0 plants selected (which is probably an underestimation of the effective population size, because the variance of family size was minimized), the inbreeding coefficient in C9 (relative to C0, assumed to be noninbred) is expected to be $F = 0.109$ (Falconer and Mackay, 1996). Inbreeding depression has not been

Table 2. Means of selected oat lines grown in three locations in hill plots in 1992 and in four-row, 3.72-m^2 plots in 1995.

	1995 Means								1992 Means			
							Disease reaction†					
Line	Groat oil content	Grain yield	Test weight	Lodging‡	Heading date§	Plant height§	BYDV¶	Crown rust	Groat oil content	Grain yield	Groat fraction	Oil yield
	g kg^{-1}	kg ha^{-1}	kg m^{-3}	%	dap#	m	score		g kg^{-1}	g m^{-2}		g m^{-2}
IA91001-2 (C8)	153.4	2391	331	61	78	0.85	6.9	7.5	168.0	263	0.715	37.9
IA91029-2 (C8)	147.4	2584	336	59	76	0.92	6.9	7.0	163.3	350	0.702	41.1
IA91042-2 (C8)	146.9	1742	305	55	78	0.97	7.0	8.0	168.7	248	ND††	ND
IA91055-1 (C8)	149.1	2634	347	63	76	0.81	7.2	7.7	158.7	361	0.702	38.4
IA91098-2 (C8)	148.8	2666	353	62	75	0.95	6.8	7.0	161.7	269	0.717	35.6
IA91313-1 (C9)	153.7	2100	299	58	79	0.91	7.2	7.7	171.3	231	ND	ND
IA91324-2 (C9)	151.7	1957	320	45	75	0.85	7.3	7.4	181.0	259	0.725	30.6
IA91331-1 (C9)	152.4	2050	327	41	77	0.83	6.9	7.2	165.7	280	0.683	38.4
IA91400-2 (C9)	154.9	2688	293	85	78	0.93	6.3	7.2	170.3	358	0.698	41.2
IA91422-2 (C9)	150.4	2534	341	60	77	0.90	6.7	7.2	170.0	300	0.663	33.0
N364-2 (C7)	150.1	2229	308	73	78	0.83	6.5	7.9	170.0	226	ND	ND
N900-7 (C7)	151.8	2082	360	70	73	0.82	8.0	6.0	162.3	248	ND	ND
N902-8 (C7)	148.5	2799	355	62	79	0.87	6.5	8.2	159.3	276	0.690	27.0
N944-1 (C7)	150.1	2441	349	69	78	0.91	6.9	7.0	160.3	270	0.723	35.2
Dal	79.1	2548	399	19	78	0.99	6.9	5.0	88.8	311	0.722	20.1
Multiline E77	56.8	2684	423	37	72	0.94	8.5	4.3	ND	ND	ND	ND
Ogle	57.5	4175	405	9	78	0.96	5.3	6.3	65.2	437	0.751	21.3
Mean	137.8	2497	344	56	77	0.90	6.9	7.0	128.4	322	0.721	29.2
LSD (0.05)	5.5	377	17	24	1	0.05	1.1	1.3	9.0	84	0.028	8.0

† Disease reaction scored at Ames and Nashua only under natural infection using a nine-point relative scale of disease incidence, where 1 is no disease and 9 is highest level of infection observed.

‡ Lodging scored as percentage of stand lodged 30° or more.

§ Heading date and plant height recorded at Ames only.

¶ Barley yellow dwarf virus.

\# Days after planting.

†† No data.

widely reported in oat, but random shifts in allele frequency at loci affecting grain yield may have caused reductions in mean yield by chance. Because drift should not have been great and because the effects of any drift were not expected to cause significant yield changes, a negative genetic correlation between grain yield and groat-oil content may have been the primary factor in reducing yield. The bioenergy required for a plant to synthesize oil is greater than that required to synthesize an equal amount of either carbohydrate or protein (Penning de Vries et al., 1974). Increases in groat-oil content require either more photosynthate, reduced groat protein content, reduced grain yield, or increased translocation of photosynthate into groats (Schipper and Frey, 1991a). Thus, a negative genetic correlation between grain yield and groat-oil content is a possible result of these physiological relationships. However, the estimated genotypic correlation between groat-oil content and grain yield in the population was not consistently negative, ranging from −0.30 ± 0.11 in C9 to 0.43 ± 0.24 in C6 (Table 3). Furthermore, the genotypic correlation estimates from our experiment are not entirely consistent with those of previous experiments in the same population (Table 3). For example, Schipper and Frey (1992) reported a significantly negative estimate in C4, whereas the estimate was positive but not significantly different from zero in our study. Positive genetic correlations between grain yield and groat-oil content have been reported in previous experiments (Forsberg et al., 1974; Gullord, 1980; Thro and Frey, 1985). Because of the difficulty of precisely estimating genetic correlations, we are not certain of the cause of the decrease in grain yield resulting from selection for higher groat oil.

Line Performance

The results of the 1992 hill-plot evaluations and the 1995 four-row-plot evaluations both indicated that selected experimental lines from the recurrent selection population had consistently higher oil contents, but poorer agronomic performance, than the check cultivars.

The highest groat-oil content of any individual line was a C9 line (IA91324-2) with 181.0 g kg^{-1} groat oil in 1992 (Table 2). This level was more than twice the oil content of the highest oil check cultivar (Dal) and was almost twice as much as the mean oil content of the C0 population in 1992; however, none of the selected lines had yields similar to Ogle, the highest-yielding check cultivar. The 1995 experiments revealed other

Table 3. Genotypic correlations (r_g) from oat populations representing from zero to nine cycles of recurrent selection for high groat oil content estimated in three experiments each with different samples of genotypes and environments.

	r_g		
Cycle	This study	Schipper and Frey (1992)†	Branson and Frey (1989a)†
0	−0.23 ± 0.13	−0.19	−0.05
1	−0.18 ± 0.15	−0.06	−0.22
2	−0.26 ± 0.16	−0.21	−0.02
3	0.01 ± 0.15	0.12	−0.24
4	0.03 ± 0.17	−0.30*	
5	0.31 ± 0.15	0.08	
6	0.43 ± 0.24	0.12	
7	0.01 ± 0.12		
8	−0.13 ± 0.14		
9	−0.30 ± 0.11		

* Significant at the 0.05 probability level.

† Standard errors of correlations not reported. Correlations were tested for significance using *t*-tests.

agronomic deficiencies of the high oil lines that were not easily observed in the hill-plot experiments. The test weights of all high oil lines were significantly lower than the lowest test weight among the checks (Table 2). Lodging at maturity is extremely difficult to score accurately in hill-plot experiments because of 0.3-m distances between plots, and no previous evaluations of lodging resistance of these high-oil lines had been made. The high-oil lines lodged significantly more than Ogle, the most lodging-resistant check, in the large-plot evaluations. All high-oil lines exhibited significantly more BYDV disease symptoms than Ogle, which is relatively resistant to the disease. All high oil lines were also more susceptible to crown rust disease than the partially resistant check multiline E77. These results indicate that high-oil lines from advanced cycles of this population lack sufficient agronomic adaptation and disease resistance to be competitive with current high-yielding cultivars. However, we expect that these lines will be useful donors of high-oil alleles in matings with agronomically elite cultivars to develop new breeding populations. Furthermore, all experimental lines tested were S_0-derived, and therefore, genetically heterogeneous. We are conducting within-line selection in an attempt to identify superior pure lines.

The absolute values of groat-oil contents from the 1995 experiments were lower than those of the 1992 hill-plot experiments (Table 2). Although genotype × environment interaction is of relatively limited importance for groat-oil content in this population, environmental effects do cause differences in oil content. Growth-chamber and field experiments have indicated that higher temperatures, particularly during the postanthesis growth stage, cause decreased oat oil contents (Bjornstad et al., 1994; Saastamoinen et al., 1990). The mean daily temperatures across testing locations for the growing season were 15.8°C in 1992 and 17.1°C in 1995. The mean daily temperature for the month of July, which was the primary grain filling month in both years, was 19.7°C in 1992 and 23.5°C in 1995. Higher temperatures and crown rust infection in the 1995 experiment were probably causes of the reduced oil contents observed in that year.

Frey and Hammond (1975) suggested that oat cultivars with a groat-oil content of 170 g kg^{-1} and with current levels of protein content and agronomic performance could be grown economically as an oilseed crop. Our results indicate that, while some of the high-oil lines developed in this population have the potential to produce oil contents sufficient to satisfy the requirements of Frey and Hammond (1975), oil content varies enough across environments to suggest that lines with even higher oil content potential may be required. Furthermore, lines selected directly from this population do not have sufficient agronomic potential to make an economically viable oilseed crop. However, our results are encouraging for several reasons: First, we have developed oat genotypes with significantly higher groat-oil content. Second, further increases in oil content seem possible. Finally, the genetic correlation between oil content and grain yield does not exclude the possibility of developing lines with very high-oil content and good yield potential. High oil lines from the latest cycles of selection from this population also have enhanced levels of antioxidants (Peterson and Wood, 1997) and higher ratios of unsaturated to saturated fatty acids (Schipper et al., 1991), which make oil from high-oil oat lines more favorable for human consumption.

Table 4. Genotypic variance component (σ^2_G) and heritability estimates (h^2) from oat populations representing each of zero through nine cycles of selection for increased groat oil content.

	Oil content		Grain yield		Groat fraction		Oil yield	
Cycle	σ^2_G	h^2	$\sigma^2_G \times 10^2$†	h^2	$\sigma^2_G \times 10^4$	h^2	σ^2_G	h^2
0	71 ± 11	0.71	17.0 ± 4.2	0.33	1.42 ± 0.38	0.30	9.5 ± 2.5	0.32
1	53 ± 8	0.75	9.9 ± 3.1	0.24	1.24 ± 0.32	0.32	7.5 ± 2.3	0.25
2	41 ± 7	0.69	9.8 ± 3.2	0.22	1.81 ± 0.52	0.27	5.9 ± 2.2	0.19
3	51 ± 8	0.73	10.0 ± 2.8	0.28	1.59 ± 0.35	0.39	10.7 ± 2.7	0.33
4	48 ± 8	0.59	8.4 ± 2.6	0.25	2.14 ± 0.46	0.43	8.0 ± 2.5	0.25
5	54 ± 10	0.52	10.1 ± 2.7	0.22	1.79 ± 0.37	0.45	14.4 ± 3.3	0.36
6	32 ± 6	0.48	2.8 ± 1.6	0.12	2.69 ± 0.57	0.43	5.7 ± 2.2	0.19
7	56 ± 9	0.68	27.9 ± 5.4	0.50	2.19 ± 0.54	0.40	15.8 ± 6.4	0.30
8	67 ± 13	0.53	22.0 ± 4.7	0.42	2.34 ± 0.50	0.51	17.5 ± 5.7	0.35
9	54 ± 9	0.65	47.3 ± 7.8	0.68	2.25 ± 0.59	0.56	35.4 ± 10.9	0.55

† Actual values equal reported values times the indicated factor.

Genotypic Variances and Heritabilities

Genotypic variance components and heritabilities for groat-oil content and for grain yield fluctuated from cycle to cycle with no obvious trends (Table 4). There is no evidence that nine cycles of recurrent selection caused significant decreases in heritabilities for groat-oil content, grain yield, or oil yield. This argues against the importance of genetic drift as a cause of the reduction in grain yield during cycles of selection. More importantly, continued gain from selection for groat-oil content and oil yield can be expected in this population, and the biological upper limit to groat-oil content is still not evident.

Genotypic variance components and heritabilities for groat fraction tended to increase slightly with increasing cycles of selection (Table 4). The increase in genotypic variance and heritability for groat fraction occurred without changes in the mean value for that trait across cycles of selection, and groat fraction appears to be genetically unrelated to groat-oil content. If alleles conferring increased groat fraction were originally in repulsion phase linkage disequilibrium in the base population, then decreased linkage disequilibrium because of continued recombination during cycles of selection may have permitted increased expression of genetic variance.

Our results clearly indicate the power of recurrent selection to improve the population mean performance for a quantitative trait, while maintaining genetic variation for continued improvement in the population. Also, recurrent selection has proven to be an excellent method to introgress favorable alleles from a wild species into the gene pool of the cultivated species. Repeated recombination allows for linkages between favorable and unfavorable alleles in linkage blocks derived from the wild species to be broken and provides for new linkages among favorable alleles from different sources to be formed. Selection in relatively large population sizes allows for rare favorable recombination events to be recovered in selected genotypes, and maintenance of relatively large parental population sizes prevents loss of favorable alleles originally at low frequencies. Some disadvantages of recurrent selection also became clear in this study. Continued selection for a single trait may result in unfavorable responses in other traits, whether due to negative genetic correlations or genetic drift. Lines from advanced cycles of selection may not be agronomically competitive with elite cultivars.

Our results indicating that genetic variation and heritability for groat-oil content have not been significantly reduced after nine cycles of selection are similar to those of Dudley (1977), who showed that 76 generations of selection for higher oil in maize changed the mean population value from <50 g kg^{-1} to almost 190 g kg^{-1} without eliminating genetic variation for oil content in the population. Miller et al. (1981) reported no change in additive genetic variance for oil content in maize after five cycles of recurrent selection for higher oil content. Misevic and Alexander (1989) reported that progress from selection for oil content in maize continued through 24 cycles of recurrent selection without exhibiting a plateau in response. These results are similar to those of some longer-term phenotypic recurrent selection studies on traits of relatively lower heritability in plants. For example, 14 cycles of recurrent mass selection for grain yield did not change genetic variation for yield in a maize population (Mulamba et al., 1983), while 16 cycles of recurrent phenotypic selection for forage yield in bahiagrass (*Paspalum notatum* var. *saurae* Parodi) reduced population variation, but not by enough to prevent additional progress (Burton, 1992). Our results, together with those of other studies, indicate that long-term selection in a closed gene pool for a trait even of higher heritability can cause significant changes in mean phenotype without reducing genetic variation for the trait.

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