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Recurrent selection in oat for adaptation to diverse environments

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Summary

In order to test if selection can improve a population's adaptation to diverse environments simultaneously, three cycles of recurrent selection based on grain yield in Iowa, Idaho, and Norway were practiced in an oat (*Avena sativa* L.) population developed from North American, Scandinavian, and wild species (*A. sterilis* L.) germplasm sources. Specific objectives were to determine if selection: increased mean yields across environments and within all environments; changed the genetic correlation of yields in different environments; and changed genetic variation for yield within the population. We evaluated 100 to 210 randomly-chosen families from each cycle of selection at three Iowa locations, in Idaho, and in Norway for two years. Grain yield within each location and mean yields across locations increased significantly over cycles of selection. Mean yields across locations expressed as a percent of the original population mean increased at a rate of 2.6% per year. Several families from the third cycle population exhibited both high mean yields across locations and consistently high yields within all locations. Average genetic correlations of yield in different environments were higher in the second cycle than in the original population. A trend of reduced genetic variation and heritability was observed in Iowa only. These results suggest that we successfully improved mean population yield both within and across locations, and yield stability across environments, and in developing families with outstanding adaptation to diverse environments.

Abbreviations: FS – full-sib; HLS – percentage of hull-less seeds; REML – restricted maximum likelihood

The ability of crops to adapt to geographically diverse locations depends on plants' abilities to respond favorably to varying environmental conditions. Adaptive ranges of genotypes can best be assessed from evaluations conducted in diverse environments in terms of 'dynamic stability' *sensu* Becker & Leon (1988). Many stability parameters have been proposed to classify genotype adaptability, but almost none have been used as selection criteria (Becker & Leon, 1988; Lin & Binns, 1994; Lin et al., 1986; Simmonds, 1991). An important reason for this may be that selection on the basis of yield stability has been predicted to result in selection for genotypes with lower mean yield in many cases. Finlay & Wilkinson (1963) reported a negative relationship between mean yield and stability as measured by their regression parameter. Simmonds (1991) suggested that plant breeders have unconsciously selected for genotypes with lower stability (higher regression coefficients) by selecting almost exclusively for high yields in optimum environments. Helms (1993) found in his analysis of oat genotypes grown in numerous Iowa environments that selection for mean yield tended to select lines with low yield stability, while selection based solely on stability measures tended to select lines with low mean yield. He suggested that selection based on an index combining information about both mean yield and yield stability would identify stably high-yielding gen-

otypes, however actual response to such selection was not determined. It is not necessarily an easy task to select for genotypes that have both high and stable yields. Aastveit & Aastveit (1984), however, found no close relationship between mean yield and stability parameters in barley (*Hordeum vulgare* L.) genotypes grown in Norway.

An alternative approach to the study of adaptability to different environments is to consider the fitness trait measured in different environments as different traits with a genetic correlation (Falconer & Mackay, 1996). The magnitude of the genetic correlation between a trait measured in two different environments indicates the extent to which genetic effects on the trait in the different environments are similar. A high positive genetic correlation indicates that the population is well-adapted to both environments, while a negative correlation indicates that a population is adapted to only one of the two environments. This genetic correlation coefficient can be generalized to multiple environments and can be estimated from the univariate analysis of variance as an adjusted genotypic intraclass correlation coefficient (Cooper & DeLacy, 1994; Dickerson, 1962). Thus, the genetic correlation between yields measured in different environments refers to an entire population and is appropriate to compare the general adaptability of different populations measured in a common set of environments. Low or negative genetic correlations between yields in different environments would make it difficult to maintain a positive selection differential in multiple environments, and thus would hinder the potential for improving adaptation of a single population to all environments.

The objectives of this research were to develop a broad-based oat population incorporating North American, Scandinavian, and wild species (*A. sterilis* L.) germplasm and to determine if: (1) adaptation of this oat population to each of three diverse mega-environments (Idaho and Iowa, U.S.A., and Norway) and mean yield across environments could be improved simultaneously via recurrent selection, (2) the genetic correlation of yield in different environments changed due to selection, and (3) genetic variation for yield within and across environments changed due to selection.

Materials and methods

Population development

A practical objective of this research was to use locally-adapted genotypes from different continents to make a broadly-adapted, genetically diverse oat population available to oat breeders in both regions. A broad-based population was developed from crosses among 20 oat cultivars and experimental lines (Table 1). These original parents were chosen based on the results of yield trials conducted on a diverse set of genotypes tested simultaneously in Norway and Iowa in 1990–1992. The parental material included one Cultivar ('Sheldon') and nine experimental oat lines developed at Iowa State University. Five of these lines were developed from an *A. sterilis* introgression program and have 50% *A. sterilis* parentage. In addition, Sheldon and D921-643 have 12.5% *A. sterilis* parentage. Six different *A. sterilis* accessions are represented in the parentage of these lines (Table 1). Three other midwestern U.S. cultivars, 'Don', 'Ogle', and 'Premier', were used as parents. Two Canadian cultivars, 'AC Lotta', and 'Newman', were used, and contributed alleles for daylength insensitivity (Burrows, 1990, 1992). In addition, 'AC Lotta' contributed alleles for the hull-less trait. Four Scandinavian oat cultivars, 'Frigg', 'Lena', 'Martin', and 'Munin', and one experimental line were also used. The base population for selection, cycle 0 (C0), was developed directly from single crosses among the 20 parents, using a complete diallel mating design without reciprocals or selfs to produce 190 full-sib (FS) families.

Selection for high yield in diverse environments

Frey et al. (1988) described a method to complete one cycle of recurrent selection per year in spring oats. This method was modified to produce enough seed for replicated yield testing using hill plots in five locations each year. Random crosses were made among selected parents from the previous cycle in a circular fashion in the greenhouse during the fall season to develop new cycle populations. Approximately five S_0 progeny were produced per cross to form a full-sib (FS) family. S_0 plants were grown in the greenhouse in the spring season and allowed to self-pollinate to form S_1 seeds. All S_1 seeds from the five plants constituting a FS family were bulked to form a full-sib family in the S_1 generation (FS-S1). At each of the five testing locations, three replications of the FS-S1 families plus check lines were grown in

Table 1. Parental cultivars and lines used to create the oat population used for selection

Line or cultivar	Origin	Comment or parentage
AC Lotta	Ottawa, Canada	Hull-less, daylength insensitive
Don	Illinois	
Frigg	Sweden	Sv0177/Sv56697//Condor
Lena	Norway	Sang/Unisignum
Martin	Norway	Gråkall/Tador
Munin	Norway	Mustang/Pol
Newman	Ottawa, Canada	Daylength insensitive
Ogle	Illinois	
Premier	Minnesota	
Sheldon	Iowa	*A. sterilis*, PI317989 (Israel)/Otter//Grundy/3/Noble
A80004-2	Norway	Mustang/PGR6848//Puthi
B605X	Iowa	Selection from an irradiated composite cross population
D921-643	Iowa	*A. sterilis*, PI317789 (Israel)/*3/Otter
H61-3-3	Iowa	B433/Garland//Holden/3/Clintford*6/B444/4/Ogle
H688-4	Iowa	Ogle/Lang//D209-13-3-1/Ogle
Z519-4	Iowa	Ogle/*A. sterilis*, PI309033 (Israel)
Z537-2	Iowa	Ogle/*A. sterilis*, PI411976 (Iraq)
Z562-3	Iowa	C19170/*A. sterilis*, PI324716 (Greece)
Z595-7	Iowa	*A. sterilis*, PI411560 (Eritrea)/Tippecanoe
Z615-4	Iowa	*A. sterilis*, PI411560 (Eritrea)/Ogle

randomized complete blocks in the summer season. Testing was conducted each year at three Iowa locations (Ames, Kanawha, and Nashua), Aberdeen, ID; and Kapp (for cycles C0-C1) or Ås, Norway (C2 and later cycle evaluations). For the yield evaluations, we sowed hill plots spaced on a grid 0.3 m apart in perpendicular directions with 20 (at Iowa locations) or 30 (other locations) seeds per hill. Two rows of hills of a common cultivar were planted as border around each experiment to provide competition for peripheral plots. Iowa experiments were treated with the systemic fungicide 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). Crown rust did not occur in Idaho or Norway. After harvest each summer, selections were made based on data from the yield evaluations at the five locations, and families were chosen for intermating to develop the next cycle in the greenhouse in the fall. S_2 plants from selected families were used for intermating.

The 190 C0 families were independently culled for plant height and heading date in 1992. Remaining families were selected based on mean yield over three environments, considering the mean over the three Iowa locations as a single environment mean. Because some of the families were segregating for the hull-less trait, which causes a reduction in grain yield simply due to the fact that the weight of hulls are not included, normal families and those segregating for the hullless trait were compared separately. Forty-six normal and four hull-less families were selected to be parents for C1. Selected families were intermated at random, with randomly-sampled S_2 plants from selected families used as parents. Each selected family was mated ten times, forming 250 parental pair combinations, and resulting in 250 C1 FS-S1 families.

No data were available from Norway in time to make selections in C1 in 1993. The seven highest-yielding families from Iowa and the seven highest-yielding families from Idaho were selected. The remaining parents were selected based on rank sums for yield across Idaho and Iowa. In total, two hull-less and 38 normal families were selected and mated at random to develop 192 C2 FS-S1 families as above.

Selections among C2 families were based on mean yield across the five locations in 1994, with 30 families chosen (including 2 hull-less families) and intermated as above, except that each family was mated 14 times, to develop 210 C3 families.

Selection differentials were computed for grain yield within and across locations as the difference between the mean of selected families and the overall population mean for the evaluation trials of each cycle. A weighted selection differential (Falconer & Mackay, 1996) was computed for C1 because not all selected families contributed equally to the next cycle population in that case. Although the specific selection criteria varied from cycle to cycle, we maintained a positive selection differential within each environment for each cycle.

Evaluation experiment

In 1995, the entire C3 population of 210 FS-S1 families was tested along with 100 randomly chosen FS-S2 families from each previous cycle population plus the 20 original parental lines. Entries from C0 to C3 were randomly assigned to four sets, such that each set contained all 20 original parents; 25 FS-S2 families from C0, C1, and C2; and 52 or 53 FS-S1 families from C3. Some parental lines were duplicated in sets to make 156 entries per set. A sets within replications design was used, and the entries within sets were arranged in 12 $\times$ 13 triple lattices of hill plots with 30 seeds per hill at each location (Ås, Aberdeen, Ames, Kanawha, and Nashua). In 1996, the same entries were used, except that only 100 randomly-chosen C3 families were included, and there were 132 entries per set. A sets within replications design was used, and the entries were arranged in 11 $\times$ 12 triple lattice at each of the same five locations. C0, C1, and C2 entries were FS-S3 families, and C3 entries were FS-S2 families.

Grain yields were measured on every plot in each environment. Heading dates and plant heights were measured on every plot at Ås, Aberdeen, and Ames. Above-ground biomass was measured on every plot at Ås (1995 only), Ames, Kanawha, and Nashua. Grain test weight was measured on samples of grain bulked over replications for each entry in each environment. The percentage of hull-less seeds from each line was estimated from samples of 200 seeds of grain bulked over replications for each entry in each environment. The percentage of hull-less seeds (HLS) was used to adjust the grain yield for any family or line that expressed more than 5% hull-less seeds in an environment. The adjusted yield was calculated as:

$$\text{Adjusted yield} = \frac{\text{Yield}}{(0.73 \times HLS) + (1 - HLS)}$$

We could not estimate groat percentage for each entry in each environment to make this adjustment precisely because of the prohibitively large number of entries and environments. Therefore, we chose 0.73 as a reasonable estimate of average groat percentage based on the average from 40 lines and cultivars and seven environments in the 1995 Iowa Oat Variety Trial.

Large-scale agronomic evaluations in Norway

Families with good performance in Norway in the 1995 experiment were re-evaluated in Norway in 1996. From this preliminary evaluation, 21 families were selected for large-scale agronomic evaluations in Norway in 1997. The selected families plus adapted check cultivars 'Olram', 'Biri', 'Frode', and Lena were planted in 5 $\times$ 5 lattice designs with two replications at each of four locations in southeastern Norway: Bjørke, Staur, Rød, and Ås. A 7.5-m^2 area was harvested from each 9 m^2 plot. Grain yield, date of grain maturity, and percent of stand lodged were measured at all four locations; heading date, plant height, 1000-grain weight, and percentage of stand uniform for plant height were measured at three locations; test weight and hull percentage were measured at two locations; percent of stand infected with powdery mildew (*Erysiphe graminis* D.C. ex Marat f. sp. *avenae*) from natural infestation was measured at one location.

Statistical analyses

For the purposes of comparing experimental families to check entries, we considered entries as fixed effects in these analyses. When check entries were not included in the analyses, as for estimating genetic components of variance, we considered all entries random effects sampled from larger populations. Environments, replications, and incomplete blocks were always considered random effects. Each set within each environment was analyzed separately, and entry means adjusted for lattice block effects were obtained using SAS Proc MIXED (SAS Institute Inc., 1997). Means over the three Iowa locations within each year were computed to estimate an Iowa mean for each entry within each set. All subsequent statistical analyses used the 'Iowa mean' averaged over the three Iowa locations as a single-environment mean value. Means over years were computed for entries within Ås, Aberdeen, and Iowa locations. Means over years and locations (considering the Iowa mean from each year as a single-location mean) were computed for each entry within each set. Finally, the cycle population means and the regression coefficient of population

mean yields on number of cycles of selection were estimated from a combined analysis over environments and sets.

Realized heritabilities for grain yield were estimated within each environment and across environments as the coefficient of regression of cumulative responses (estimated from the cycle means over years in the evaluation experiment) on cumulative selection differentials (estimated from the selection trials in different years, Falconer & Mackay, 1996). Estimated selection differentials did not account for differences in HLS because no data were available from the selection trials on this trait. Weighted least squares regression was used rather than standard least squares regression to account for variation due to genetic drift and for correlations between responses in different cycles. Following Walsh & Lynch (1999), the heritability estimate was:

$$h' = b = (S^T V^{-1} S)^{-1} S^T V^{-1} R$$

where S and R are 3×1 column vectors of cumulative selection differentials and responses for the environment concerned. V is the 3×3 variance-covariance matrix of the selection response. The elements of V are:

$$V_{i,i} = [2 f_i h^2 + (1/M_i + 1/M_0)]\sigma^2_{Ph}$$

and

$$Vij = [2 f_i h^2 \sigma^2_{Ph} + (1/M_0)]\sigma^2_{Ph}$$

where f_i is the inbreeding coefficient due to drift in the ith generation ($0 < i < j$), M_i is the number of families of generation i tested in the evaluation trial, and σ^2_{Ph} is the phenotypic variance of family means within the environment. The regression coefficient from standard least squares regression (without an intercept) was used as an initial estimate of h^2, and the equations were used iteratively until converging on a solution. The standard error of the estimate is the square root of the sampling variance: $V(b) = (S^T V^{-1} S)^{-1}$. The phenotypic variances of family means were estimated from the evaluation trial data by averaging over cycles within each environment. The inbreeding coefficient of each generation with respect to the initial population was estimated based on the number of families selected from each generation and the known variance of family size (Falconer & Mackay, 1996). This estimate should be considered an upper limit for the true inbreeding coefficient because the formulas used consider number of selected individuals intermated, whereas we actually selected full-sib families and then intermated ten S_2 individuals per family.

Variance components for families (σ^2_F), family-by-environment interactions (σ^2_{FE}), and residual error (σ^2_ε) were estimated for each cycle population using restricted maximum likelihood (REML) estimation procedures with SAS Proc MIXED (SAS Institute Inc., 1997). In most cases, estimates of the variance component parameters were first made using the method of moments based on SAS Proc GLM analysis, and these were used as initial estimates for the REML estimation procedure. Variance components for families and residual error were also estimated within each environment.

Heritabilities for yield across environments were estimated on a single-year family mean basis (the basis for selection in this program) as:

$$\hat{H} = \frac{\sigma^2_F}{\sigma^2_F + \sigma^2_{FY} + \frac{\sigma^2_{FL}}{3} + \frac{\sigma^2_{FYL}}{3} + \frac{\sigma^2_\varepsilon}{9}}$$

where σ^2_ε is the within-location error variance pooled over locations. The variance of family means across locations within Iowa contributes to σ^2_ε. Heritabilities for yield within locations were based on family means over three replications (or locations in the case of Iowa) from a single year:

$$\hat{H} = \frac{\sigma^2_F}{\sigma^2_F + \sigma^2_{FY} + \frac{\sigma^2_\varepsilon}{3}}$$

Approximate standard errors for heritability estimates were computed using the delta method (Lynch & Walsh, 1997).

The adaptability of each population was measured in terms of the average genotypic correlation of yields in different environments. The average genotypic correlation of yields in different environments was estimated as:

$$r_G = \frac{\sigma^2_F}{\sigma^2_F + \sigma^2_{FE'}}$$

where $\sigma^2_{FE'}$ is the family-by-environment interaction component of variance adjusted for heterogeneity of family variances among the different environments (Dickerson, 1962; Itoh & Yamada, 1990):

$$\sigma^2_{FE'} - \sigma^2_{FE} - V(\sigma_{F_i})$$

This corrected family-by-environment interaction component removes the contribution to the interaction due to differences among family variance components expressed in different environments, which leaves the component of genotype-by-environment interaction variance that complicates selection for broad

Table 2. Population means, phenotypic standard deviation of family means ($\sigma_{\overline{F}}$), selection differentials (S), and standardized selection differentials ($S/\sigma_{\overline{F}}$) of grain yield from selection trials within and across locations for each cycle of selection

Cycle (year)	Parameter	Idaho	Iowa	Norway	Mean over locations
C0	Mean (g m^{-2})	1133	391	299	603
(1992)	$\sigma_{\overline{F}}$ (g m^{-2})	216	50	58	106
	S (g m^{-2})	212	30	33	98
	$S/\sigma_{\overline{F}}$	0.99	0.61	0.58	0.92
C1	Mean (g m^{-2})	1166	231	488	628
(1993)	$\sigma_{\overline{F}}$ (g m^{-2})	221	53	149	109
	S* (g m^{-2})	166	46	46	87
	$S/\sigma_{\overline{F}}$	0.75	0.87	0.30	0.80
C2	Mean (g m^{-2})	1054	356	380	501
(1994)	$\sigma_{\overline{F}}$ (g m^{-2})	158	42	66	51
	S (g m^{-2})	202	44	30	74
	$S/\sigma_{\overline{F}}$	1.28	1.06	0.45	1.45
Overall	Cumulative S (g m^{-2})	580	120	109	259

* The selection differential for C1 was weighted to reflect unequal contribution of selected parents to next cycle.

adaptation (Cooper & DeLacy, 1994). Variance of the estimates of $V(\sigma_{F_i})$ were obtained using a jacknife procedure (Weir, 1990), and standard errors of the r_g estimates were estimated using the delta method (Lynch & Walsh, 1997).

Results and discussion

Evaluation environments

Idaho was the optimum environment, with mean grain yields at least twice as great as either Iowa or Norway locations in each year (Table 2). Heterogeneity of error variances among the three mega-environments was not significant. The largest phenotypic standard deviation of family means and the largest absolute selection differentials occurred in Idaho each cycle, and the greatest standardized selection differential occurred in Idaho in two of three cycles. Norway had the lowest standardized selection differential among all locations in every cycle. Selection differentials were positive in each environment and across environments in every cycle, indicating that at least some selection pressure for increased grain yield occurred in each environment each cycle (Table 2). The selection differentials were generally smaller than one standard deviation of family means within each environment, however, indicating that higher selection intensities could have been achieved within any one location without altering the population size or testing resources within a location if specific adaptation had been the goal of selection.

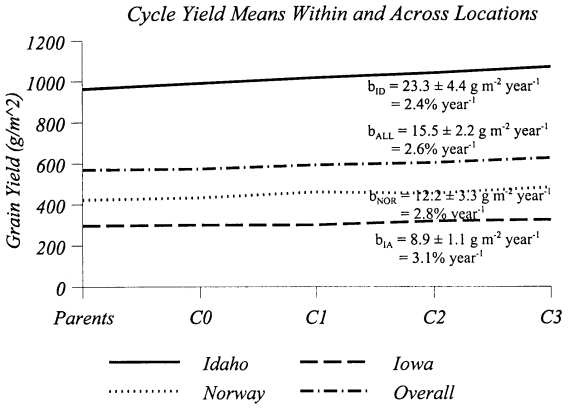

Figure 1. Mean grain yields of populations developed from different numbers of generations of recurrent selection averaged over two yr within and across locations of evaluation trials.

Population improvement

The regressions of population mean yields from the evaluation experiment on cycles of selection were significantly positive in all environments, and when expressed as a percent of the C0 population mean the regression coefficients ranged from 2.4% per year in Idaho to 3.1% per year in Iowa (Figure 1). In absolute units, yields increased most in Idaho (23.3 $\pm$ 4.4 g m^{-2} $year^{-1}$) and least in Iowa (8.9 $\pm$ 1.1 g m^{-2} $year^{-1}$). Yield gains averaged over locations were 2.6% per year of the C0 population mean. These yield gains from selection compared favorably to a gain of 2.6% per year reported by Pomeranke & Stuthman (1992) after five cycles of selection for yield in an adapted population based on selection and evaluation in Minnesota.

Individual family yields

The proportion of superior families for mean grain yields from the different cycles of selection provides another indication of the effectiveness of selection to produce more broadly adapted genotypes (Table 3). Seventeen of the 40 highest-yielding families were from C3, 14 were from C2, five from C1, and four from C0. Several families with extremely broad adaptation were identified. IA94366 (from C3) was the highest ranking entry across locations in set 2, and

Table 3. Grain yield means and ranks within and across locations and agronomic trait means across locations of best experimental and check entries from set 2 from 1995 and 1996 hill plot evaluations

Entry	Overall		Norway		Idaho		Iowa		Overall			
	Rank	Grain yield	Rank	Grain yield	Rank	Grain yield	Rank	Grain yield	Bio-mass	Test weight	Heading date	Height
		g m^{-2}		g m^{-2}		g m^{-2}		g m^{-2}	g m^{-2}	kg L^{-1}	dap[a]	m
IA94366 (C3)	1	782	4	621	2	1333	2	391	1118	0.471	60.9	1.14
IA94288 (C3)	2	771	1	689	6	1289	27	333	978	0.458	62.5	1.12
IA93282 (C2)	3	756	2	641	4	1300	38	323	1066	0.458	63.0	1.10
IA94358 (C3)	4	736	21	519	3	1319	6	368	969	0.464	58.3	1.06
Lena	5	733	3	624	8	1280	74	296	926	0.486	58.6	1.00
IA93320 (C2)	6	732	24	502	5	1292	1	402	921	0.474	56.0	1.03
IA94292 (C3)	7	723	22	509	1	1371	82	291	924	0.447	59.9	1.07
TA93290 (C2)	8	720	5	589	11	1248	38	323	946	0.456	60.9	1.02
IA94308 (C3)	8	720	11	551	7	1281	33	327	946	0.449	61.4	1.05
IA94270 (C3)	10	703	9	563	14	1219	35	326	924	0.460	58.4	1.07
IA93260 (C2)	11	696	8	564	21	1169	13	352	1012	0.439	59.4	1.04
Newman	19	660	14	544	35	1082	12	353	1070	0.509	56.9	1.03
Z615-4	27	644	79	389	9	1273	101	271	884	0.447	65.6	1.02
Frigg	30	632	29	488	28	1118	87	290	924	0.478	61.3	0.98
Martin	46	603	14	544	36	1076	121	189	750	0.453	61.3	1.01
Sheldon	56	587	39	462	80	938	9	361	949	0.518	56.7	1.02
Munin	75	559	63	423	63	1002	113	253	710	0.467	61.3	1.02
Ogle	77	558	87	367	79	943	7	363	977	0.473	59.2	0.97
AC Lotta	91	513	98	347	86	930	105	263	686	0.549	58.3	1.12
Don	112	473	115	284	103	853	91	282	714	0.498	55.8	0.92
Premier	115	469	119	263	107	841	66	302	747	0.526	57.5	0.94
LSD_1[b] (0.05)		101		131		181		52	161	0.116	1.4	0.05
LSD_2[c] (0.05)		88		113		157		44	140	0.100	1.2	0.04
LSD_3[d] (0.05)		71		93		128		37	114	0.082	1	0.03

[a] Days after planting.
[b] LSD_1 (0.05) is appropriate for comparisons among experimental family means (including Z615-4).
[c] LSD_2 (0.05) is appropriate for comparing experimental family means to check line means.
[d] LSD_3 (0.05) is appropriate for comparisons among check line means.

it ranked fourth for yield in Norway, and second in both of Iowa and Idaho (Table 3). None of the check (parental) entries exhibited high yields so consistently across locations. For example, in set 2 the highest-yielding check line was Lena, which ranked fifth for overall yield, third in Norway (where it was developed), and eighth in Idaho, in each case not significantly different from IA94366. In Iowa, however, it ranked only 74 out of 132 entries (Table 3), significantly lower than IA94366. Similar observations can be made about other C3 families, such as IA94375 and IA94437 in set 4, that both ranked in the top 10 of 132 entries in each of the three locations.

The experimental entries represented full-sib families, and the genetic heterogeneity within these families may have provided populational buffering that enhanced their stability (Allard & Bradshaw, 1964). We hope to select inbred, pure-lines from these families and to test them along with parental lines and family bulks in the different target environments to determine if high yield and stability can be combined in a homozygous, homogeneous genotype.

The good performance of parental line ‘Z615-4’ was also interesting. This line ranked between second and fourth among the parental lines for mean yield across locations in the different sets (Table 3). This line is a selection from a cross between Ogle and an *A. sterilis* plant introduction from Eritrea, and it had higher mean yield across environments than its cultivated parent, Ogle, in all sets (Table 3). The performance of this line provides further indication of the

Table 4. Means of selected families and adapted check cultivars from large-plot yield trials in four Norwegian locations in 1997

Entry	Exotic parentage[a]	Grain yield	Test weight	1000-grain weight	Hull percentage	Heading date	Maturity date	Height	Lodging	Mildew reaction[b]	Visual uniformity
	%	kg ha^{-1}	kg L^{-1}	g	%	dap[c]		m	%	%	%
Biri (check)	0	6750	0.548	26.6	24.1	67	103	0.79	26	40	70
IA91266 (C0)	0	6720	0.548	32.8	23.8	65	107	0.84	24	41	45
Frode (check)	0	6710	0.562	33.2	22.9	68	107	0.84	38	49	67
IA92035 (C1)	50	6710	0.545	37.1	24.2	66	108	0.86	15	44	43
IA94287 (C3)	69	6620	0.538	36.2	23.8	71	110	0.91	66	21	43
IA91280 (C0)	25	6560	0.550	35.8	23.8	71	109	0.86	36	26	48
Lena (check)	0	6520	0.545	31.0	21.6	67	106	0.75	19	34	70
IA94406 (C3)	50	6400	0.542	33.2	26.0	66	109	0.90	44	28	48
IA94308 (C3)	69	6370	0.534	34.3	25.4	69	109	0.89	61	23	45
IA91275 (C0)	50	6350	0.551	30.4	22.5	68	105	0.87	25	32	50
IA92011 (C1)	50	6310	0.555	32.4	23.7	67	105	0.87	36	32	43
Olram (check)	0	6250	0.543	30.8	24.1	70	101	0.87	39	39	65
IA94430 (C3)	81	6250	0.557	39.0	24.8	69	109	0.93	65	33	45
IA93290 (C2)	75	6220	0.531	34.6	25.2	69	109	0.83	61	35	50
IA92042 (C1)	50	6170	0.542	32.0	24.0	71	110	0.90	40	30	50
IA94264 (C3)	75	6170	0.547	34.9	25.0	66	107	0.87	45	29	55
IA94421 (C3)	62	6149	0.550	38.3	24.0	67	110	0.92	47	25	43
IA92238 (C1)	100	6110	0.561	32.0	24.3	71	106	0.92	32	29	48
IA92041 (C1)	75	5990	0.552	39.4	24.5	67	109	0.88	41	25	38
IA94270 (C3)	75	5990	0.528	33.9	24.5	68	108	0.89	45	24	40
IA92114 (C1)	25	5950	0.552	34.6	23.3	63	106	0.80	8	34	33
IA94294 (C3)	75	5940	0.538	35.3	24.4	70	110	0.88	46	24	38
IA94309 (C3)	75	5920	0.513	35.3	26.0	66	109	0.82	40	34	35
IA92022 (C1)	50	5850	0.559	32.0	24.1	66	108	0.89	44	33	43
IA91136 (C0)	50	5420	0.563	35.1	22.2	65	105	0.87	40	36	50
LSD (0.05)		416	0.019	2.2	1.4	1.9	2.2	0.06	22	14	8
No. locations		4	2	3	2	3	4	3	4	1	3

[a] Percentage of parentage that does not include one of the original Scandinavian parents.
[b] Powdery mildew reaction scored as percentage of plants infected per plot.
[c] Days after planting.

utility of *A. sterilis* as a source of favorable alleles for improving cultivated oats (Holland, 1997).

Large-scale agronomic evaluations in Norway

None of the selected experimental families had higher yields than the best adapted check, Biri, in the large-plot evaluations in Norway in 1997. Several of the families, however, had grain yields comparable to Biri combined with either superior grain weight (e.g., IA91266, IA92035, IA94287), lodging resistance (e.g., IA92035), or powdery mildew resistance (e.g., IA94287; Table 4). The highest-yielding experimental family in the Norwegian trial in 1997 was IA91266, which represents the progeny of the cross Lena × Frigg, and therefore does not represent a unique source of germplasm for Scandinavian breeding programs. Nevertheless, we found numerous other families with good yield potential and general agronomic performance in Norway with 50% or more 'exotic' (i.e., non-Scandinavian) parentage in their pedigrees (Table 4). Some high-yielding families were not only exotic with respect to Norway, but also contained significant percentages of wild species parentage. For example, IA91280 and IA94287 (Table 4) had 25% and 17% *A. sterilis* parentage, respectively. We suggest that these high-yielding families with exotic parentage represent a unique source of adapted germplasm for Scandinavian and other far-northern oat

Table 5. Variance component due to families (σ^2_F), broad-sense heritability (H), the average genotypic correlation of different environments (r_g), and realized heritability for grain yield estimated from the evaluation experiment

Cycle	Parameter	Location			
		Idaho	Iowa	Norway	Across locations
0	σ^2_F	8975 ± 2099	1395 ± 259	3148 ± 963	2000 ± 617
	H	0.48 ± 0.08	0.63 ± 0.06	0.35 ± 0.09	0.39 ± 0.09
	r_g	–	–	–	0.34 ± 0.04
1	σ^2_F	14099 ± 3086	840 ± 173	6259 ± 1160	2543 ± 765
	H	0.52 ± 0.07	0.54 ± 0.07	0.65 ± 0.06	0.42 ± 0.09
	r_g	–	–	–	0.42 ± 0.04
2	σ^2_F	15778 ± 3086	568 ± 148	5420 ± 1173	3654 ± 864
	H	0.60 ± 0.06	0.44 ± 0.08	0.53 ± 0.07	0.56 ± 0.07
	r_g	–	–	–	0.49 ± 0.05
3	σ^2_F	11593 ± 2901	148 ± 123	4630 ± 1160	2630 ± 815
	H	0.44 ± 0.08	0.12 ± 0.10	0.44 ± 0.08	0.39 ± 0.09
	r_g	–	–	–	0.39 ± 0.05
Overall	Realized H	0.14 ± 0.04	0.24 ± 0.06	0.38 ± 0.17	0.19 ± 0.06

breeding programs. The uniformity of these families is not acceptable for cultivars (Table 4), but that is because these are bulk families and not purelines. Selection within families may result in the identification of pure-lines from this population with higher yield potential than their family means. Pure-line selection has been practiced within these families in Iowa, and selected pure-lines (S_2-or later generation-derived) will be tested in multi-location trials in Iowa in 1999.

Estimated variance components and heritabilities for grain yield

We first checked if our random samples of 100 families from each population were large enough to provide robust estimates of variance components and heritabilities. We compared the variance component due to families and the heritability of family means across locations in 1995 estimated from the full set of 210 C3 families to the same parameter estimates from the subset of 100 C3 families that we randomly chose for the second year of testing. The parameter estimates from the full set were σ^2_F = 3123 ± 667 and H = 0.243 ± 0.045, while the estimates from the subset were σ^2_F = 3407 ± 1000 and H = 0.259 ± 0.065. The good agreement between our estimates from a random sample of 100 families and the full set of 210 families indicated that our sample sizes were adequate to estimate these genetic parameters.

Genetic variances and heritabilities within Idaho and Norway and across locations were almost all significantly higher in C2 than in C0, but not different between C3 and C0 (Table 5). We observed that genetic variance for yield did not decrease due to selection in Idaho and Norway and across locations. In contrast, the genetic variance and heritability for yield within Iowa decreased consistently over cycles of selection and were significantly lower in C3 than in C0 (Table 5). This perhaps occurred because adaptation to Iowa environments is strongly influenced by flowering time. Selection for adaptation in Iowa may have rapidly altered allele frequencies at loci affecting flowering time, resulting in improved mean yields with reduced genetic variation for yield. It is possible that further selection in the population may improve mean grain yield at a greater rate than grain yield within Iowa, i.e., that selection for broad adaptation may occur without corresponding improvement in specific adaptation to Iowa.

To account for the fact that selection differentials varied across locations each year, we estimated realized heritabilities for grain yield within each location and across locations. Realized heritabilities were estimated as 13.6 ± 4.2% in Idaho, 24.2 ± 5.5% in Iowa, and 38.3 ± 16.6% in Norway (Table 5). Realized heritability across environments was estimated to be 19.3 ± 4.9%. Thus, although selection intensity and absolute selection response were highest in Idaho, the

response measured as a proportion of cumulative selection differential was highest in Norway, where the absolute selection differential was lowest. The realized heritability in Norway was in good agreement with heritabilities estimated from variance components, while the realized heritability within Idaho was considerably lower than the heritabilities estimated from variance components in Idaho. This suggests that the genotype-by-year interaction component of variance is relatively more important in Idaho than in Norway.

Realized heritabilities estimated using the weighted least squares method were within four percentage points of the initial estimates obtained from standard least squares regression. The standard errors of the estimates obtained from weighted least squares, however, were an order of magnitude greater than standard errors of the usual least squares regression estimates. Experiments using replicated selection have shown that the standard error of the linear regression estimator seriously underestimates the true standard error of realized heritability (Falconer, 1977). The larger standard errors associated with the weighted least squares regression method we used are more realistic.

Genetic correlation of yields in different environments

We hypothesized that if selection for high yield in diverse environments acted to reduce the frequency of alleles that contribute to localized adaptation and to increase the frequency of alleles contributing to high yield in different environments (general adaptation), then the average genotypic correlation of yields in different environments should have increased in later cycle populations. The average genetic correlation of yield in different environments increased from a r_g = 0.34 $\pm$ 0.04 in C0 to r_g = 0.49 $\pm$ 0.05 in C2, then decreased to r_g = 0.39 $\pm$ 0.05 in C3 (Table 5). Only C2 had a significantly higher genetic correlation than C0. These results suggest that selection acted in part to enhance general adaptation to the different testing environments, providing evidence that yield stability and adaptation can be improved simultaneously with mean yield across environments. The decrease in the average genetic correlation of yield in different environments from C2 to C3 was accompanied by a decrease in genetic variance within and across environments. The two measures are related, because as the genotypic variance increases relative to the genotype-by-environment interaction variance, both the average genetic correlation in different environments and the heritability will increase, all other factors remaining constant. If the genetic correlations of yield in different environments were very low, then we would expect that selection for mean yield across environments would not be very effective because genotypes favorable in a specific environment would not necessarily be favorable across environments, and the result would be a low heritability for yield across environments. The genetic correlations between yields in target environments of this program were not high, but at least were positive, indicating that future improvements in mean performance from selection can be expected. In situations where the target environments are so different that the genetic correlations between yield in different environments are negative, the approach described here would likely not be useful. Instead, selection for specific adaptation to the different environments may be the only feasible approach (Ceccarelli, 1989; Simmonds, 1991).

Other studies have reported changes of stability associated with recurrent selection for high yield *per se*. Reysack et al. (1993) reported that an oat population resulting from four cycles of recurrent selection for high yield based on single-environment evaluations had a higher coefficient of regression of yield on mean environment yield as well as higher mean yields compared to the original population. They concluded that selection increased the responsiveness of the population to favorable growing conditions. Mareck & Gardner (1979) and Moll et al. (1978) reported similar results in maize. These results can be interpreted to indicate that selected populations had lower yield stability, following Simmonds (1991). In the cases cited, however, the selected populations generally yielded better than original populations even in the lower-yielding environments sampled, perhaps leading to the conclusion that the selected populations had broader adaptation, and therefore high stability. The definition of stability must be made in relation to a reference population of environments to be meaningful; in particular the degree of stress that occurs in the low-yield environments can substantially affect conclusions about genotypic stability (Ceccarelli, 1989).

The effects of locations on yield varied dramatically. Mean yields in Idaho were consistently on the order of three times greater than those in Iowa throughout both the evaluation and selection trials. Basing selections on mean yields across locations in this situation leads to greater emphasis on selecting genotypes that express high yield in the optimum en-

vironments at the expense of selection for genotypes that yield relatively well in less favorable conditions. Our comparison of the selection differentials that occurred in the different locations bears this out – the highest selection differentials always occurred in the optimum environment, Idaho (Table 2). The selection differential scaled to family mean standard deviations in 1993 was greater in Iowa than in Idaho, however, because in that year the selections were based primarily on rank sums from those two locations rather than means. To make better progress in improving stability of yields across environments in future cycles of selection, we will first standardize means from within each location before averaging across locations to obtain the overall mean for each family. This should eliminate the effect of differences in mean productivity across environments that affected the gain from selection in the first three cycles reported here.

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