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Improving grain yield in backcross populations from *Avena sativa* × *A. sterilis* matings by using independent culling for harvest index and vegetative growth index or unit straw weight*

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Summary. Grain yield was selected in *Avena sativa* × *A. sterilis* populations of segregates by applying independent culling for harvest index and either vegetative growth index or unit straw weight. Samples of lines intensively selected for harvest index had high harvest index but low grain yield because they had low vigor. Populations intensively selected for growth rate index or unit straw weight had high biological yield but low harvest index. Intensive selection for grain yield per se resulted in samples with high grain yield, but they were late and tall. Samples selected for harvest index at a 25% selection intensity first and subsequently selected for vegetative growth index or unit straw weight had grain yield as high as the samples selected for grain yield per se and vegetative growth index, and they had acceptable heading date and plant height. Backcrosses three and four were best, among the various BC generations, for selecting oat lines with high grain yield and suitable agronomic traits. CI 7463 was superior to CI 8044 as a recurrent parent, and B 445 was inferior to other *A. sterilis* accessions as a donor parent.

Key words: Oats – Selection – Growth rate – Biological yield – Independent culling – Harvest index

Introduction

Grain yield of oats can be expressed by the formula:

Grain yield =
growth rate × growth duration × harvest index.

That is, growth rate and growth duration determine biological yield, and harvest index measures the allocation of biological yield to grain yield. For oats grown in the midwestern USA, growth duration is limited to 100–110 days by climate and diseases, so only growth rate and harvest index are the variables that determine grain yield (Takeda and Frey 1976; Takeda et al. 1979). Growth rate and harvest index are genotypically independent among segregates from matings of *Avena sativa* × *A. sterilis* (Takeda and Frey 1977).

When two traits are genetically correlated, selection for one will cause an associated change in the second. Further, if two traits are inherited independently, intensive selection for one will cause the second trait to converge to the population mean in a population of finite size. Thus, when one trait is selected intensively, little genotypic variation may remain for the second trait within the selected sample.

Our primary objective was to evaluate several selection strategies for the independent culling method by using harvest index and either vegetative growth index or unit straw weight for improving grain yield of segregates from interspecific matings of oats. Also, we investigated the optimal number of backcrosses for obtaining maximum grain yield and whether donor parents had different prepotencies for producing high-yielding segregates.

Materials and methods

Materials

Materials for this study consisted of F_2-derived lines from all backcross generations, BC_0 through BC_5, of eight interspecific matings of oats. The eight matings were obtained by making all possible hybrids among two *A. sativa* lines, CI 8044 and CI 7463, and four *A. sterilis* accessions, B 442, B 443, B 444, and B 445. The *A. sativa* parent was used as the female and

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recurrent parent in all matings. After all backcrosses were completed, 80 F_2 seeds from each mating-backcross combination were space sown in the field. The bulk progeny from a plant was used to establish an F_2-derived line, that we evaluated in F_3.

Field experiment

The 4,000 oat lines (i.e., 80 lines from each of 48 mating-backcross combinations and 80 lines from each of two recurrent parents) were evaluated in a radomized complete-block experiment with two replicates sown on 8 April, 1972 at the Agronomy Field Research Center near Ames, Iowa, USA. The soil at that site is a silt loam of the Clarion-Webster-Nicollet series. The previous crop was soybeans (*Glycine max* L.), and the experimental site received a preplant broadcast application of 40 kg N and 25 kg of P_2O_5 and K_2O per ha. A plot was a hill sown with 30 seeds, and hills were spaced 30.5 cm apart in perpendicular directions. The experiment was surrounded by two rows of hills to provide competition for peripheral plots. It was hand-weeded, and a fungicide was sprayed onto the plants at weekly intervals from anthesis to maturity to control foliar diseases.

Eight traits were measured or calculated from each plot. Days to heading were recorded when 50% of the panicles had completely emerged. Plant height was the distance (cm) from ground level to the panicle tips. Biological and grain yields were the air-dry weights of the bundle of culms and grain from a plot. Straw yield was computed as biological yield minus grain yield, and harvest index was calculated as grain yield divided by biological yield and expressed as a percentage. Vegetative growth index was obtained by dividing straw yield by days to heading, and unit straw weight was determined by dividing straw weight by plant height.

Selection regime

Earlier, Takeda and Frey (1977) showed that, in this population of oat lines, variation in grain yield was nearly completely determined by vegetative growth index and harvest index, so we used independent culling to select grain yield via the latter two traits. Unit straw weight and vegetative growth index are closely correlated, and so we also used it and harvest index as a combination of selection traits. The expected genetic gains (ΔG) for this study were computed by using the formula of Young and Weiler (1960). Genetic gain (ΔG_D) from direct selection for a trait was predicted as

$$\Delta G_D = h^2 \cdot s \cdot k,$$

where h^2 and s are heritability and phenotypic standard deviation, respectively, for the trait, and k is the selection differential in standard units. Genetic gain from indirect selection (ΔG_I) through one trait was predicted as

$$\Delta G_I = h_1 \cdot h_2 \cdot r_g \cdot s_2 \cdot k,$$

where h_1 and h_2 are square roots of the heritabilities for the selected and responding traits, respectively, r_g is the genotypic correlation between the traits, s_2 is the phenotypic standard deviation of the responding trait, and k is the selection differential in standard units (Falconer 1960). Expected genetic gain in a responding trait from independent culling for two other traits (ΔG_{IC}) was predicted as

$$\Delta G_{IC} = k_1 (W_1 \alpha_1 s_1 + W_2 \beta_1 s_2) + k_2 (W_1 \alpha_2 s_1 + W_2 \beta_2 s_2),$$

where W_1 and W_2 are the genotypic regressions of responding trait on selected traits 1 and 2, respectively; s_1 and s_2 are the phenotypic standard deviations for traits 1 and 2, respectively; α and β measure the associations between heritabilities and genotypic correlations for traits 1 and 2 (Young and Weiler 1960); k_1 and k_2 are selection differentials in standard units for traits 1 and 2, respectively.

The data were subjected to analyses of variance and covariance, and genotypic variances and covariances were estimated by subtracting error mean squares from their counterpart mean squares for lines within mating-generation populations and dividing by two (number of replicates). Thus, the genotypic variances and covariances represent pooled estimates from within populations. Heritabilities were computed for each trait by using the formula

$$h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2}$$

where σ_g^2 and σ_e^2 are genotypic and error variances, respectively. Genotypic correlations were computed among pairs of traits by using the formula

$$r_g = \sigma_{gij} / (\sigma_{gi}^2 \times \sigma_{gj}^2)^{1/2},$$

where $\sigma_{g_{ij}}$ is the genotypic covariance between two traits and σ_{gi}^2 and σ_{gj}^2 are the genotypic variances of the two traits. To evaluate the actual gains from selection, oat lines were selected on the basis of line values in replicate 1, and the success from selection was evaluated on the basis of line values in replicate 2 and vice versa.

The ultimate selection intensity with each regime was 2%. Culling levels for selected and responding traits are shown in Table 1. In regimes 1, 5, 9, and 10, only a single trait was selected. In regimes 2–4, harvest index and vegetative growth index were selected with various intensities, and in regimes 6–8, harvest index and unit straw weight were selected with various intensities. In all regimes that involved selection for two traits, harvest index was selected first at a low intensity to assure that genotypic variation would remain for the trait selected second.

For purposes of selection, the F_2-derived lines from the 48 mating-backcross combinations were classified in three ways. (a) They were pooled by *A. sterilis* parent across generations and *A. sativa* parents. This gave 960 lines per male parent, and the number of selected lines per population was 19 (2% of 960). (b) They were pooled by *A. sativa* parent across generations and *A. sterilis* parents. This gave 1,920 lines per female parent, and the number of selected lines per population was

Table 1. Regimes and intensities of selection used to obtain actual grain yields from selection

Regime no.	Selection intensity for				
	Harvest index	Vegetative growth index	Unit straw weight	Grain yield	Total
1	0.02	–	–	–	0.02
2	0.25	0.08	–	–	0.02
3	0.50	0.04	–	–	0.02
4	0.75	0.03	–	–	0.02
5	–	0.02	–	–	0.02
6	0.25	–	0.08	–	0.02
7	0.50	–	0.04	–	0.02
8	0.75	–	0.03	–	0.02
9	–	–	0.02	–	0.02
10	–	–	–	0.02	0.02

39 (2% of 1,920). (c) They were pooled by backcross generation across matings. This gave 640 lines per backcross level, and the number of selected lines per population was 13 (2% of 640).

Results

Heritability values were quite similar for the four traits (Table 2). These heritabilities may overestimate those that a breeder would realize in a cultivar development program because genotype × environment interaction was not eliminated in the estimation.

Selection in male parent population

Responses of grain yield, harvest index, and biological yield to selection within *A. sterilis* progeny groups via the various singletrait and independent culling regimes are shown in Figs. 1–3, respectively. The least significant difference (LSD) values were computed by using the pooled variance from within *A. sterilis* groups of progenies.

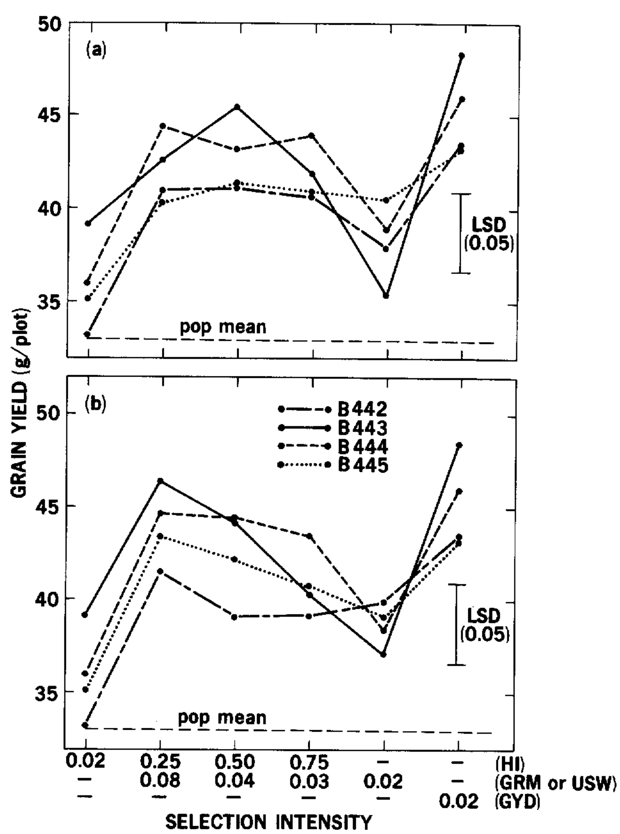

Fig. 1 a, b. Grain yield (*GYD*) means for samples of oat lines selected with *A. sterilis* parent groups via grain yield itself or independent culling for harvest index (*HI*) and (**a**) unit straw weight (*USW*) or (**b**) vegetative growth index (*GRM*)

Grain yield showed greatest response to selection in every *A. sterilis* parent group when it was the selection criterion (regime 10), and harvest index showed greatest response when it was the selection criterion (regime 1). This latter regime generally changed grain and biological yields minimally, but it did cause some gain in grain yield in all *A. sterilis* parent groups. Groups of lines selected for vegetative growth index (regime 5) or unit straw weight (regime 9) alone had high means for biological yield but low means for grain yield because they resulted in low means for harvest index. Response to selection for vegetative growth index and unit straw weight were very similar. For most selection regimes, except 5 and 9, samples of oat lines selected from B 443 and B 444 progeny groups had higher grain yield means that did those from B 442 and B 445 progeny groups.

Table 2. Heritability values for grain yield, harvest index, growth rate, and unit straw weight

Type of classification	Traits			
	Grain yield	Harvest index	Vegetative growth index	Unit straw weight
Male parent	0.39	0.31	0.43	0.37
Generation	0.40	0.27	0.31	0.30

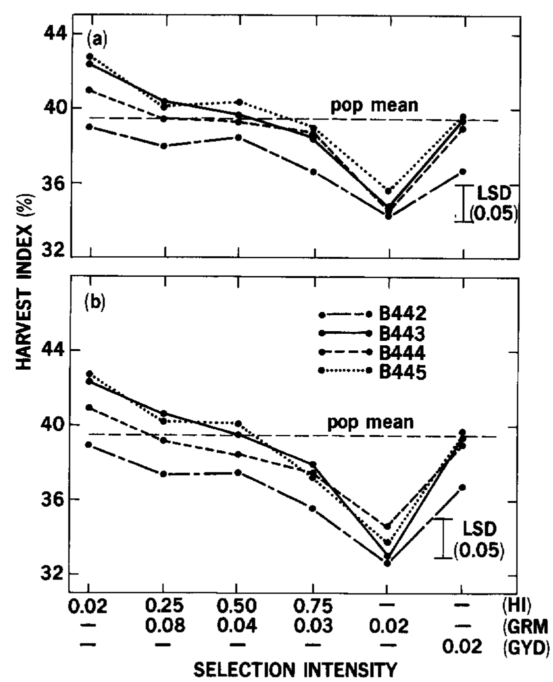

Fig. 2 a, b. Harvest index means for samples of oat lines selected within *A. sterilis* parent groups via grain yield (*GYD*) or independent culling for harvest index (*HI*) and (**a**) unit straw weight (*USW*) or (**b**) vegetative growth index (*GRM*)

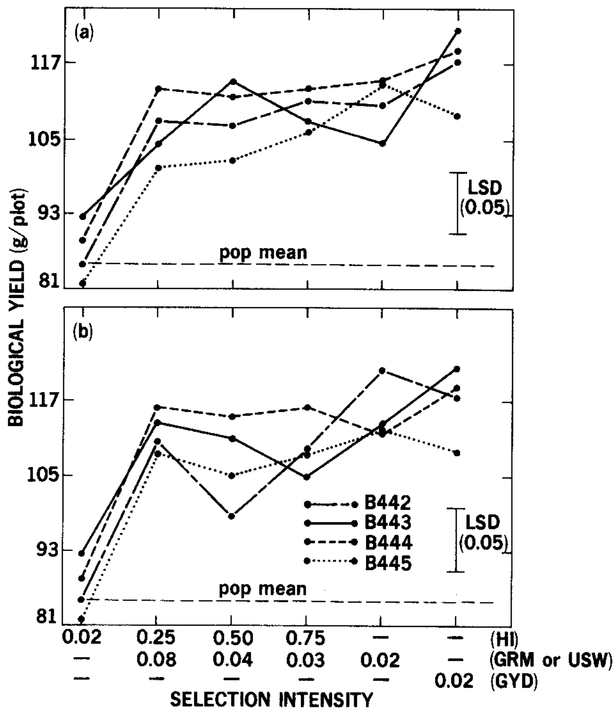

Fig. 3a, b. Biological yield means for samples of oat lines selected within *A. sterilis* parent groups via grain yield (*GYD*) or independent culling for harvest index (*HI*) and (**a**) unit straw weight (*USW*) or (**b**) vegetative growth index (*GRM*)

Also, selected samples from the B442 progeny group tended to have the lowest harvest index means, but differences between *A. sterilis* progeny groups were small.

Selection in female parent population

Means for eight traits for the samples of oat lines selected via various selection regimes with CI 7463 and CI 8044 progeny groups are given in Tables 3 and 4, respectively. Also shown are means of backcross generations for samples of lines selected by the various regimes. Lines selected for grain yield per se tended to be later and taller than either the recurrent parents or the populations of progenies. In contrast, for regimes 2 and 6 (selection intensities = 0.25 for harvest index and 0.08 for vegetative growth index or unit straw weight), grain yield means were high and heading date and plant height were moderate and acceptable. For samples selected for unit straw weight (regimes 6 to 9), plant heights were from 1 to 4 cm shorter than their counterparts selected for vegetative growth index (regimes 2 to 5). So unit straw weight may be a better selection criterion than vegetative growth index because, while effective for increasing vigor of oats, it keeps the plants shorter. However, if unit straw weight was selected

Table 3. Actual means for eight traits for samples of oat lines selected from the CI 7463 parent matings via various selection regimes and mean numbers of backcross generations for groups of selected lines

Selection regime or progeny	Mean backcross generations[a]	Traits							
		Heading date (da)	Plant height (cm)	Biological yield (g/plot)	Grain yield (g/plot)	Harvest index (%)	Straw yield (g/plot)	Vegetative growth index (g/plot/da)	Unit straw weight (g/cm)
2	2.7	70	107	112	44	39	68	0.97	0.64
3	2.5	70	109	108	43	39	66	0.95	0.61
4	1.9	71	111	110	41	37	69	0.97	0.63
5	1.2	72	115	115	39	34	76	1.05	0.67
6	3.0	69	103	107	42	40	65	0.94	0.63
7	3.0	70	105	108	43	39	65	0.94	0.62
8	2.4	71	107	110	42	38	68	0.96	0.63
9	1.7	74	111	111	38	35	73	0.99	0.65
1	3.4	69	102	87	36	41	51	0.74	0.50
10	2.4	71	111	117	45	39	72	1.01	0.65
CI 7463	–	68	98	83	34	40	50	0.73	0.51
Original population mean	2.5	70	106	90	34	38	56	0.80	0.53
LSD (0.05)	0.3	0.8	2.0	4.7	2.0	1.0	3.1	0.04	0.03

[a] Number of backcrosses

Table 4. Actual means for eight traits for samples of oat lines selected from the CI 8044 parent matings via various selection regimes and mean numbers of backcross generations for groups of selected lines

Selection regime or progeny	Mean backcross generations[a]	Traits							
		Heading date (da)	Plant height (cm)	Biological yield (g/plot)	Grain yield (g/plot)	Harvest index (%)	Straw yield (g/plot)	Vegetative growth index (g/plot/da)	Unit straw weight (g/cm)
2	3.5	67	109	87	38	44	49	0.73	0.45
3	2.9	67	113	94	40	43	54	0.81	0.48
4	2.4	68	115	92	38	41	54	0.80	0.47
5	0.9	69	119	95	34	36	62	0.89	0.52
6	3.7	66	107	85	38	44	48	0.72	0.45
7	3.3	67	110	91	40	44	51	0.77	0.47
8	2.5	66	112	91	37	41	53	0.79	0.48
9	1.0	70	118	98	35	37	62	0.89	0.53
1	3.7	67	106	76	34	45	42	0.63	0.40
10	3.1	68	112	89	38	43	51	0.76	0.46
CI 8044	–	67	107	85	37	43	48	0.72	0.45
Original population mean	2.5	67	111	79	32	41	47	0.70	0.42
LSD (0.05)	0.3	0.6	1.8	3.6	1.6	1.0	2.4	0.03	0.02

[a] Number of backcrosses

Table 5. Frequencies of oat lines from different *Avena sterilis* parent groups in samples selected by ten selection regimes

Section regime	*A. sterilis* parent				χ^{2a}
	B442	B443	B444	B445	
1	41	38	37	40	0.26
2	27	54	48	27	15.23**
3	27	52	49	28	13.69**
4	38	41	41	36	0.46
5	24	52	38	42	10.36*
6	33	43	52	28	8.77*
7	35	47	49	25	9.64*
8	34	48	46	28	7.08
9	35	44	49	28	6.72
10	31	53	48	24	14.51**

[a] Chi-square value for independence; expected number of lines is 39
* $P<0.05$
** $P<0.01$

extremely, as in regime 9, plant height did not remain short.

The vigor traits, biological and straw yields, vegetative growth index, and unit straw weight responded similarly to selection. The poorest grain yield means were obtained with selection regimes 1, 5, and 9, i.e., regimes with only single components of grain yield. This shows the importance of both harvest index and a vigor trait in grain yield expression and emphasizes that any selection criterion (e.g., grain yield itself) or index must encompass both of these components to give maximum gains for grain yield.

There was a general tendency for regimes that put high selection intensity on harvest index (regimes 1, 2, and 6) to select samples of oat lines from advanced backcross generations (Tables 3 and 4). For example, the generation means when these regimes were used on CI 7463 progenies ranged from 2.7 to 3.4, and for CI 8044 progenies ranged from 3.5 to 3.7. In contrast, regimes that placed high selection intensity on vegetative growth rate or unit straw weight (regimes 5 and 9) had generation means that ranged from 0.9 to 1.7. When grain yield was the selection criterion (regime 10), the generation means were intermediate, and few lines were selected from the BC_0 and BC_5 because these generations had low harvest index and low vigor, respectively. High-grain yield lines from BC_0 and BC_2 tended to be late and tall.

The interaction of *A. sterilis* parent populations and selection regimes on numbers of lines retained is shown in Table 5. With regime 1 (harvest index), all *A. sterilis* parents contributed about equal numbers of lines. However, when vigor traits (i.e., vegetative growth index or unit straw weight), or grain yield were the criteria of selection, B443 and B444 contributed disproportionately high numbers of lines. Except with regimes 4 and 5, B445 was consistently deficient in contributing lines to the selected samples. Obviously, *A. sterilis* accessions have different potencies for improving vigor and grain yield of oat lines.

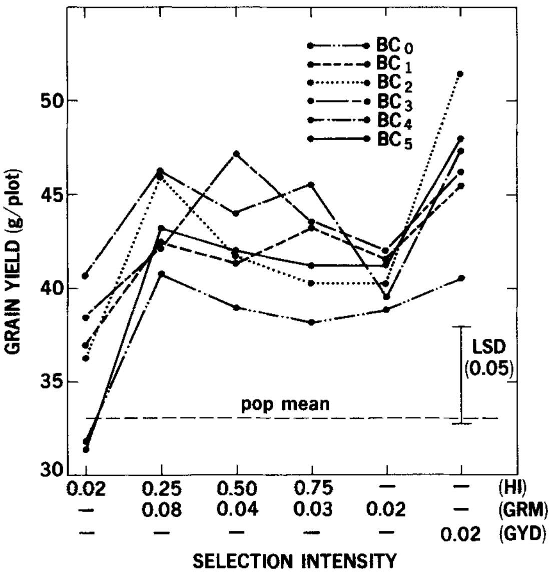

Fig. 4. Grain yield means for samples of oat lines selected within backcross generations via grain yield (*GYD*) itself or independent culling for harvest index (*HI*) and vegetative growth rate (*GRM*)

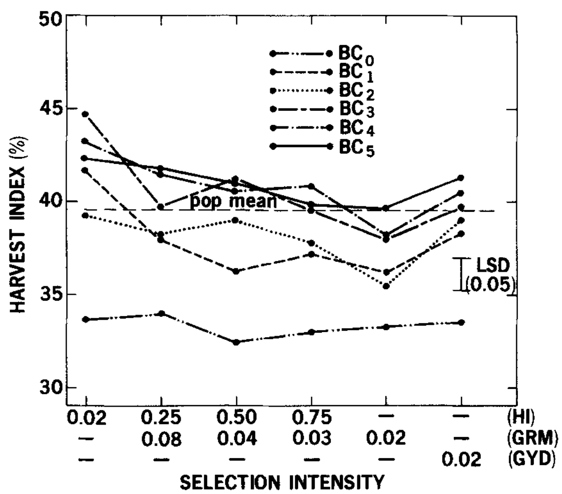

Fig. 5. Harvest index means for samples of oat lines selected within backcross generations via grain yield (*GYD*) or independent culling for harvest index (*HI*) and vegetative growth rate (*GRM*)

Selection in backcross generations

Response of grain yield, harvest index, and biological yield to selection within backcross generations of oats via various single-trait and independent culling regimes are shown graphically in Figs. 4–6, respectively. Note that the responses in these figures are only for regimes 1 to 6 and 10; the responses to selection via vegetative growth rate and unit straw weight were so similar that only those that utilize vegetative growth index are presented.

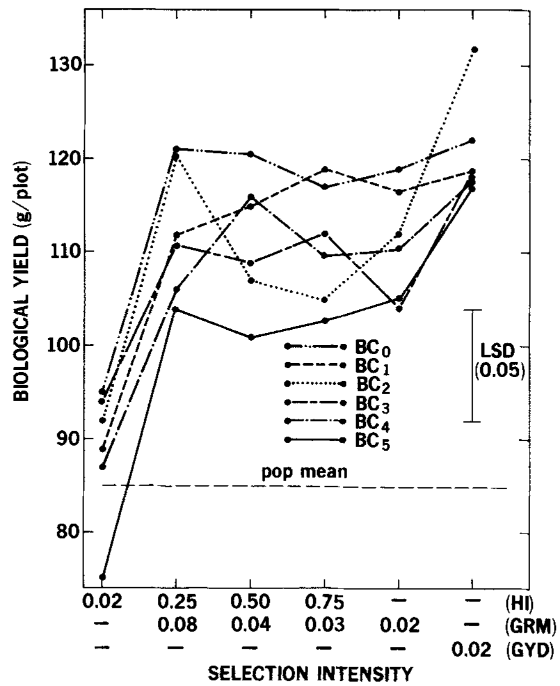

Fig. 6. Biological yield means for samples of oat lines selected within backcross generations via grain yield (*GYD*) or independent culling for harvest index (*HI*) and vegetative growth index (*GRM*)

Several things are obvious about selection in the various backcrosses. As might be expected, grain yield and harvest index were inferior in the BC_0. Biological yield was high in BC_0, but the low harvest index caused inferior grain yield. Regimes 2 (selection intensities of 0.25 for harvest index and 0.08 for vegetative growth index) and 10 (grain yield per se) gave very high responses in biological and grain yields. Responses in harvest index means were high in BC_5 for all selection regimes, but biological yields were low, so generally grain yield responses were only moderate in this generation. Generally, the lowest grain yield responses occurred with regimes 1 (harvest index only) and 5 (vegetative growth index only) in all backcross generations. This shows the importance of a balance between vegetative vigor and harvest index.

The optimum backcross generation for selecting for grain yield via regime 10 was BC_2. In this generation, plant vigor due to introgression of *A. sterilis* genes is retained, and harvest index due to genes from *A. sativa* has been recovered; the result is high grain yield.

Discussion

In this study, intensive selection for harvest index resulted in a sample of oat lines, all of which were early, short, and high in harvest index, but they had low vigor and grain yield. Thus, high harvest index does not necessarily give high yield. For a crop with high biological yield, such as tropical rice (*oryza sativa* L.) (Tanaka et al. 1966; Kawano and Tanaka 1969), improving harvest index will increase grain yield. For oats, however, harvest index is optimal at 45% (Takeda et al. 1987), and improved varieties are already at this level, so the only effective way to improve the grain yielding ability of this crop is to increase its vegetative growth rate while holding harvest index and growth duration at present levels.

Independent culling was an effective selection strategy for increasing grain yield of oats. Selecting via independent culling for harvest index and either vegetative growth rate or unit straw weight was no more effective for improving grain yield than selecting for grain yield per se. However, samples of lines selected via the best independent culling strategy were shorter and earlier than those selected via grain yield per se. Rosielle and Frey (1975) reported that harvest index was an effective selection criterion for increasing grain yield of oats if heading date and plant height were restricted. Our results suggest using a mild selection intensity for harvest index (i.e., 25%) in the first stage of independent culling, and a high selection intensity (i.e., 8%) for a vigor trait in the second stage will give the best improvement in grain yield. More intense selection for harvest index restricts the genetic variability for vigor traits so much that little or no improvement can be made in the second stage. Similar results were found by Takeda and Frey (1985 b) for *A. sativa.*

Vegetative growth rate is a good indicator of oat plant vigor, but unit straw weight also may be a good criterion for the second stage of independent culling. Samples of oat lines using the latter trait were noticably shorter than those using vegetative growth rate, and the grain yields were equally good.

Response of grain yield to selection varied among matings. Greater gains were made in matings with CI 7463 than in those with CI 8044. This supports the results of Takeda and Frey (1977), that transgressive segregation for vegetative growth rate was much greater in CI 7463 matings. In general, among the *A. sterilis* parents, B 443 and B 444 were superior to B 445 for producing oat lines with high vegetative growth rates and grain yields. Cox and Frey (1984) also found that *A. sterilis* accessions varied in their general combining ability for vegetative growth rate and that specific combining ability also occurred for this trait among interspecific matings.

Lawrence (1974), from computations of the probability of obtaining high-yielding oat lines with suitable agronomic traits, concluded that the BC_2, BC_3, and BC_4 were the optimal generations of *A. sativa* × *A. sterilis* matings for selection. We found that BC_0 and BC_5 contained few high-yielding lines because the former had low harvest index and the latter has low vegetative growth rate. Further, lines selected for high grain yield in BC_0 to BC_2 were too tall. Therefore, BC_3 and BC_4 would be the best generations for selection. Takeda and Frey (1985 a) found that at least three backcrosses were needed to give a high proportion of oat lines that had high grain yield, high protein percentage, and good agronomic traits.

In summary, independent culling for both assimilate productivity (i.e., vegetative growth index or unit straw weight) and assimilate partitioning (harvest index) was an effective strategy for selecting high-yielding oat lines with desirable agronomic traits. It should be most useful for populations of lines in which both assimilate productivity and partitioning traits have significant genetic variability, e.g., intermediate backcross generations of interspecific matings.

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