Correlated Responses to Selection for Greater β-Glucan Content in Two Oat Populations

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ABSTRACT

Oat (*Avena sativa* L.) β-glucan lowers serum cholesterol in humans. Thus, enhancing its content in oat cultivars for human consumption is desirable. Phenotypic selection for greater β-glucan content was effective in two broad-based oat populations, BG1 and BG2. The initial and selected cycles of each of these populations were evaluated in 1996 and 1997 at two Iowa locations to determine the correlated responses of agronomic and grain quality traits to selection for greater β-glucan content. Correlated responses were generally unfavorable for agronomic performance, but favorable in terms of human nutritional value of oat grain. Mean protein content increased by 5% in one population while mean oil content and heading date did not change. Mean grain yield, biomass, and test weight were reduced by 25, 23, and 2%, respectively, in one population and not affected in the other. Plant height decreased by 5% in one population only. Genotypic variances were unchanged by selection, except the genetic variance for plant height in BG2 increased. Selection strengthened negative genotypic correlations between β-glucan content and grain yield, biomass, and oil content in both populations, and between β-glucan content and test weight, heading date, and height in one population. β-Glucan yield (the product of β-glucan content and grain yield) was positively genotypically correlated with both grain yield (r = 0.92 in both populations) and β-glucan content (r = 0.66 and r = 0.26 in the two populations). Selection for greater β-glucan yield could be used to improve β-glucan content and grain yield simultaneously.

High serum cholesterol level is a major risk factor of premature heart disease in humans (Phillips et al., 1978; Mayes, 1990). Oat soluble fiber lowers blood cholesterol levels when consumed in the daily diet, particularly in those individuals with initially high blood cholesterol level (Kurtzweil, 1994; Welch, 1995). Dietary control of serum cholesterol may, therefore, have a major impact on human health. The component responsible for lowering serum cholesterol is (1→3)(1→4)-β-D-glucan, or β-glucan, a cell wall polysaccharide found in the endosperm and subaleurone layers of cereal seeds (Davidson et al., 1991; Behall et al., 1997). Oat cultivars with greater β-glucan concentrations are desirable for human consumption.

Oat β-glucan content is a polygenic trait controlled by genes with mainly additive effects and no intergenic interaction, with heritability estimated on a single plot basis ranging from 0.45 to 0.58 (Holthaus et al., 1996; Kibite and Edney, 1998; Cervantes-Martinez et al., 2001). Cervantes-Martinez et al. (2001) conducted one cycle of phenotypic selection of individual S_0 plants for greater β-glucan content in two genetically broad-based oat populations. They found that mean β-glucan content increased 5.9 and 2.6 g kg^{-1}, and the genetic variance decreased by 9 and 22% in the two populations, respectively. Rankings of oat lines for β-glucan were generally consistent across environments. These findings indicate that phenotypic selection for greater β-glucan content will be effective to develop cultivars with elevated β-glucan content.

The potential association of oat β-glucan content with agronomic characteristics and other grain quality traits is important to consider because selection for greater β-glucan content might also change other traits as a correlated response. Correlated responses may cause changes in favorable or unfavorable directions in agronomically important traits when direct selection for a single trait is practiced. For example, Payne et al. (1986) reported that three cycles of recurrent selection for grain yield in spring oats increased grain yield, kernel number, kernel weight, and rate of grain filling, whereas heading date and maturity were delayed. Schipper and Frey (1992) found that five cycles of recurrent selection for greater groat oil content in oat did not affect groat protein content, but four cycles of recurrent selection for greater groat protein increased groat oil content.

Correlated responses to selection depend in part on the genotypic correlation between the selected trait and other traits. Genotypic correlations are caused by either pleiotropy, in which the same gene affects different traits, or linkage, when traits are controlled by different genes but the loci are genetically linked (Falconer and Mackay, 1996). Phenotypic correlations between traits can be due to genetic or environmental effects or both. β-Glucan content is not strongly correlated with grain yield (Holthaus et al., 1996; Kibite and Edney, 1998). However, Holthaus et al. (1996) reported a low positive phenotypic correlation, Kibite and Edney (1998) found a low negative phenotypic correlation, and Peterson et al. (1995) reported both low positive and negative correlations of β-glucan with grain yield. Phenotypic correlations of β-glucan with yield also can change from positive to negative depending on the environment (Brunner and Freed, 1994). β-Glucan content also has exhibited positive or nonsignificant correlations with test weight (Peterson et al., 1995), protein content (Brunner and Freed, 1994), and groat percentage (Holthaus et al., 1996). However, Saastamoinen et al. (1992)

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Abbreviations: BLUP, best linear unbiased predictor; h^2, heritability; NIRS, near-infrared reflectance spectroscopy; NMR, nuclear magnetic resonance; PI, plant introduction; REML, restricted maximum likelihood; SEC, standard error of calibration.

reported relatively high negative correlations of β-glucan concentration with protein content. β-Glucan concentration was correlated negatively with oil content (Welch and Lloyd, 1989; Kibite and Edney, 1998). Negative and nonsignificant correlations of β-glucan content and groat weight were found (Holthaus et al., 1996). Brunner and Freed (1994) attributed the negative correlation of β-glucan and groat weight to a greater ratio of cell wall to cell content in small groats. Groat β-glucan content tended to show no association with heading date and plant height (Welch and Lloyd, 1989; Holthaus et al., 1996), although some negative correlations were reported (Peterson et al., 1995).

Because selection for greater β-glucan content is designed to improve the effect of oat grain on human health, its effect on other components that affect the dietary quality of the grain, such as protein and oil, should be investigated. Oat grain protein has a well-balanced amino acid composition and greater digestibility than legume protein (Barnes, 1982). Increases in groat protein content of oats improve the nutritional value of the crop. On the other hand, increases in groat oil content would be unfavorable for human diets, because oat grain typically is used to contribute to a low fat and high soluble fiber diet (Holland, 1997).

Correlated response can be exploited to increase the expression of a primary trait if selection for a secondary trait produces greater genetic gain in the primary trait than direct selection (Hallauer and Miranda, 1988). Theoretically, this is possible when the product of the additive genetic correlation and the square root of the narrow sense heritability of the second trait is larger than the square root of the heritability of the main trait of interest (Falconer and Mackay, 1996). For example, Johnson et al. (1983) compared direct selection for increasing grain yield to indirect selection using vegetative growth rate on F_2-derived oat lines. They found that indirect selection via vegetative growth rate gave a greater increase in grain yield than direct selection for grain yield. Helsel (1985) also reported that indirect selection of biomass plus harvest index was more effective for improving oat grain yield than direct selection for grain yield.

The objectives of this study were to (i) estimate the correlated responses to selection of individual S_0 plants for high β-glucan in two oat populations, (ii) estimate changes in genetic variation and heritability of unselected traits in these populations, and (iii) estimate genotypic covariances and correlations between β-glucan content and grain quality and agronomic traits in these populations.

MATERIALS AND METHODS

Population Formation

The development of the oat populations was described in detail by Cervantes-Martinez et al. (2001). The original population was developed by intermating oat breeding lines and commercial cultivars chosen for their high β-glucan content or good agronomic characteristics. The S_0 seed of the base population for selection, BG1C0, was obtained from crosses involving primarily cultivars and experimental lines adapted to Iowa, Minnesota, or Ottawa, Canada, and chosen for their high β-glucan content. Selection for high β-glucan content was practiced among S_0 plants of BG1C0 grown in Aberdeen, ID, in 1992. The S_0 seed of the BG1C1 population was developed from random crosses among 40 parental $S_{0:1}$ lines selected from BG1C0.

A second base population (BG2C0) was developed by randomly mating the lines from BG1C1 with highest β-glucan content to lines from the BGPI population, which had from 12 to 37% plant introduction (PI) parentage. Selection for greater β-glucan content was practiced among S_0 plants from BG2C0 grown in Aberdeen, ID, in 1994. A single line with highest β-glucan content within each of the 50 families with highest mean β-glucan contents was selected. Fifty $S_{0:1}$ lines were selected from BG2C0 and intermated at random in the greenhouse to produce S_0 seed of the BG2C1 population. BG2C1 S_0 plants were grown without selection in Aberdeen, ID, in 1995 to develop $S_{0:1}$ lines.

Field Evaluation

The BG1C0, BG1C1, BG2C0, BG2C1, and BGPI populations were evaluated in a field experiment in 1996 and 1997. Fifty full-sib families from each of the BG1C0, BG2C0, BG2C1 populations, and 33 and 17 full-sib families from the BG1C1 and BGPI populations, respectively, were randomly chosen for evaluation. $S_{0:1}$ lines derived from the same cross represented a full-sib family. Two $S_{0:1}$ lines were randomly chosen from each full-sib family for evaluation, resulting in a total of 400 experimental $S_{0:1}$ lines in the experiment. The experimental design was a sets within replications design, in which each set received two $S_{0:1}$ lines from each of 10 full-sib families from each of the BG1C0, BG2C0, BG2C1 populations, two $S_{0:1}$ families from each of 4 to 10 full sib families of the BG1C1 population, and two $S_{0:1}$ families from each of zero to six full-sib families of the BGPI population to make a total of 40 full-sib families. Seven commercial oat cultivars were included in each set in duplicate. Each set also included five of the original parental lines, which were assigned to sets at random, and the high β-glucan experimental line, IAN979-5-2. Each set of 100 entries was arranged as a 10 by 10 square lattice with two replications at each environment. The experiment was grown at the Agronomy and Agricultural Engineering Field Research Center near Ames, IA, and the Northeast Research Center near Nashua, IA, in both years. The soil types were a Nicollet loam soil (fine-loamy, mixed, superactive, mesic Aquic Hapludolls) at Ames and a Readlyn loam soil (fine-loamy, mixed, superactive, mesic Aquic Hapludolls) at Nashua. Field plots were hills of 20 seeds spaced 0.3 m apart in perpendicular directions. Two rows of hills of a common check cultivar surrounded each set to provide competition to peripheral plots. Field experimental procedures were described by Cervantes-Martinez et al. (2001).

Heading date was recorded as the date when 50% of panicles in a plot were fully emerged. Plant height was measured as the distance from the ground surface to panicle tips. Heading date and plant height were measured in Ames in both years. Total aboveground biomass and grain yield were measured on each plot after drying straw and grain for at least 1 wk at ambient temperature. In order to have sufficient seed for spectrophotometry and chemical analysis, the grains from both replications of an entry within a location were bulked together and mixed thoroughly. Test weight was measured on each bulk of grain. Grain samples were then dehulled using an air pressure dehuller (Codema brand model LH 5095) to obtain ≈8 g of groats. The β-glucan, protein, and oil contents

of each groat sample on a dry matter basis were estimated with standard near-infrared reflectance spectroscopy (NIRS) equipment (Model 6250, Pacific Scientific Co., Silver Spring, MD). The β-glucan, protein, and oil values for each sample were the means of three measurements. β-Glucan contents of 92 samples from the 1996 evaluation and 95 samples from the 1997 evaluation, representing ≈10% of the total number of samples from each year's evaluation were measured with the automated flow injection analysis, as described by Lim et al. (1992), to calibrate the prediction equation for β-glucan content for each year evaluation. Protein contents of 52 samples (3% of the total number of samples) were measured using the Kjeldahl procedure (Bremner and Breitenbeck, 1983) to calibrate the prediction equation for protein content. Oil contents of 74 samples from the 1996 evaluation and 99 samples for the 1997 evaluation (representing 8 and 11% of the total number of samples from each year, respectively) were determined by nuclear magnetic resonance (NMR; Conway and Earle, 1963) performed at the University of Illinois to calibrate the prediction equation for oil content for each year evaluation. The calibration samples were selected on the basis of spectral features to represent the spectral variability of the whole set of samples. The prediction equations for each year of evaluation were developed using modified partial least squares (Benson, 1986; Cervantes-Martinez et al., 2001).

Statistical Analysis

To compare population means, each trait was analyzed separately using PROC MIXED of SAS, with the overall mean and populations considered fixed effect factors and all other factors considered random (Littell et al., 1996). Heading date, plant height, grain yield, and biomass were measured on individual plots, so the random effects for these traits included environment, set, environment × set, replication within environment × set, block within replication × environment × set, family within set, environment × family within set, line within family within set, and environment × line within family within set, and experimental error. Test weight and groat β-glucan, protein, and oil contents were measured on bulks of grain bulked across replications within each environment; therefore, the statistical model for these traits did not include replication or lattice block terms. Significance of correlated responses to selection for greater β-glucan content were tested using contrasts between the BG1C0 and BG1C1 population means and between the BG2C0 and BG2C1 population means.

Genotypic best linear unbiased predictors (BLUPs) were obtained as linear functions of fixed and random effect estimates, such that the BLUP for genotype k within set i and population j was calculated as:

$$\text{BLUP}_{ijk} = \mu + S_i + \overline{ES}_{.i} + P_j + SP_{ij} + \overline{ESP}_{.ij} + G(SP)_{ijk}, \quad [1]$$

where μ is the overall mean, S_i is the effect of the ith set, $\overline{ES}_{.i}$ is the mean of the environment × set interaction effects involving the ith set averaged across all environments, P_j is the effect of the jth population, SP_{ij} is the effect of the interaction of the ith set and the jth population, $\overline{ESP}_{.ij}$ is the mean of the environment × set × population interaction effects involving the ith set and the jth population averaged across all environments, and $G(SP)_{ijk}$ is the effect of the kth genotype within the ith set and the jth population. The mean of population × environment interaction effects averaged across all environments was not included because the sum of the population × environment effects across all environments for each population is zero.

The components of variance were estimated for each population (BG1C0, BG1C1, BG2C0, and BG2C1) separately with the restricted maximum likelihood (REML) method (Searle, 1971) of SAS PROC MIXED (Littell et al., 1996), considering all effects except the overall random mean. Incomplete blocks were not included in this model because of severe unbalance resulting when each population was analyzed separately. Significance tests of the different components of variance were performed with a chi-square test of the difference between the −2 REML log-likelihood of the complete model and the model without the component of variance in question. The approximate P-value of the test was obtained by dividing the P-value of the chi-square statistic with one degree of freedom by two (Self and Liang, 1987; Littell et al., 1996). The significance of the residual variance was tested assuming asymptotic normality (Self and Liang, 1987; Littell et al., 1996).

Genotypic variance components were estimated as the sum of family and line within family variance components. The estimates of phenotypic variance on a plot basis for height, heading date, biomass, and grain yield were obtained as the sum of the variance components due to family, $S_{0:1}$ lines within families, family × environment interaction, environment × line within family interaction, and experimental error. Phenotypic variances on a plot basis were not estimable for test weight, β-glucan, protein, and oil content because these traits were not measured on individual plots.

The phenotypic variance on a line mean basis was estimated for height and heading date as

$$\hat{\sigma}^2_{\bar{P}} = \hat{\sigma}^2_{\text{family}} + \hat{\sigma}^2_{\text{line(family)}} + (\hat{\sigma}^2_{\text{env}\times\text{family}} + \hat{\sigma}^2_{\text{env}\times\text{line(family)}})/2 + (\hat{\sigma}^2_{\text{error}})/4, \quad [2]$$

for yield and biomass as

$$\hat{\sigma}^2_{\bar{P}} = \hat{\sigma}^2_{\text{family}} + \hat{\sigma}^2_{\text{line(family)}} + (\hat{\sigma}^2_{\text{env}\times\text{family}} + \hat{\sigma}^2_{\text{env}\times\text{line(family)}})/4 + (\hat{\sigma}^2_{\text{error}})/8, \quad [3]$$

and for test weight, and β-glucan, protein, and oil content as

$$\hat{\sigma}^2_{\bar{P}} = \hat{\sigma}^2_{\text{family}} + \hat{\sigma}^2_{\text{line(family)}} + (\hat{\sigma}^2_{\text{env}\times\text{family}} + \hat{\sigma}^2_{\text{env}\times\text{line(family)}})/4. \quad [4]$$

Heritabilities on a plot basis and on a line mean basis were estimated as

$$h^2 = (\hat{\sigma}^2_{\text{family}} + \hat{\sigma}^2_{\text{line(family)}})/\hat{\sigma}^2_{\text{P}}, \quad [5]$$

and

$$h^2 = (\hat{\sigma}^2_{\text{family}} + \hat{\sigma}^2_{\text{line(family)}})/\hat{\sigma}^2_{\bar{\text{P}}} \quad [6]$$

respectively.

Analysis of covariance was performed ignoring the family structure for simplicity. The analyses were performed on the basis of each entry's BLUP within each environment for heading date, plant height, grain yield, and biomass, and on the basis of each entry's bulk sample within each environment for test weight and groat β-glucan, protein, and oil contents. The mean products of environments, lines, and line × environment interaction were obtained separately for each population. The analyses were performed for each population with the multivariate analysis of variance (MANOVA) option of SAS Proc GLM (SAS Institute, 1989). The components of variance and covariance were estimated with the method of moments (Mode and Robinson, 1959). The genotypic covariance between traits W and Z was estimated as the covariance component due to lines. The phenotypic covariance was estimated on a sample-basis as

$$\hat{\sigma}_{\text{P}_{\text{WZ}}} = \hat{\sigma}_{\text{line}_{\text{WZ}}} + \hat{\sigma}_{\text{residual}_{\text{WZ}}} \quad [7]$$

where $\hat{\sigma}_{\text{line}_{\text{WZ}}}$ is the covariance due to lines and $\hat{\sigma}_{\text{residual}_{\text{WZ}}}$ is the

residual covariance due to environment × line interaction confounded with the experimental error covariance.

Genotypic and phenotypic correlations between the traits W and Z were obtained as

$$r_G = \hat{\sigma}_{line_{WZ}} / \sqrt{\hat{\sigma}^2_{line_W}\ \hat{\sigma}^2_{line_Z}}, \text{ and}$$

$$r_P = \hat{\sigma}_{P_{WZ}} / \sqrt{\hat{\sigma}^2_{P_W}\ \hat{\sigma}^2_{P_Z}}, \text{ respectively,} \quad [8]$$

where $\hat{\sigma}^2_{line_W}$ and $\hat{\sigma}^2_{line_Z}$ and $\hat{\sigma}^2_{P_W}$ and $\hat{\sigma}^2_{P_Z}$ are the variance components due to lines, and are the phenotypic variances estimated on a sample-basis for the traits W and Z, respectively. Approximate standard errors of the correlation estimates were obtained with the formulas given by Mode and Robinson (1959).

RESULTS AND DISCUSSION

Evaluation Environments

The range of mean β-glucan content across environments was 47.6 to 66.5 g kg^{-1}. The mean β-glucan content in 1996 was 21% greater than in 1997. To determine if specific climatic variables explained the differences in mean β-glucan content, we computed the mean minimum and maximum daily air temperature and mean daily precipitation across days within four equal periods of the growing season in each environment. None of the climatic variables were significantly related to mean β-glucan content, but inferences from this result are restricted by the limited sample of environments. We attempted to minimize the influence of other agroecological factors on the evaluation experiment by harvesting hill plots before significant lodging was observed, and by treating the plots with a systemic fungicide to prevent crown rust disease (*Puccinia coronata* Corda. var. *avenae* W.P. Fraser & Ledingham; Cervantes-Martinez et al., 2001).

Validation of Prediction Equations

The prediction equations for β-glucan content had an R^2 of 0.76 for the 1996 evaluation and 0.80 for 1997, with standard errors of calibration (SECs) of 4.7 and 3.8 g kg^{-1}, respectively (Cervantes-Martinez et al., 2001). A single prediction equation, with R^2 equal to 0.95 and with a SEC of 5.3 g kg^{-1}, was developed for protein content in both years. The R^2 of the prediction equation for oil content was 0.92 for the 1996 evaluation and 0.90 for 1997. The SEC was 2.1 g kg^{-1} for 1996 and 2.7 g kg^{-1} for 1997. Even with larger sample sizes used for calibration, our prediction equations for β-glucan content were less precise than those for protein or oil content. These results indicate that oat β-glucan content is more difficult to measure precisely than protein and oil content via NIRS. Increasing sample sizes (to >10% of all grain samples) for the calibration equation for β-glucan content may be required to improve its reliability.

Correlated Responses to Selection

The original base population for selection, BG1C0, had mean agronomic and grain quality traits similar to the commercial cultivars used as checks (Don, Marion, Hazel, Premier, Ogle, Starter, and Noble), except that mean plant height of BG1C0 was greater than the checks (Table 1). This suggests that the original population BG1C0 had good agronomic characteristics before selection was initiated. The BG2C0 population had lower mean grain yield, biomass, test weight and oil content, and greater protein content than the checks, indicating that the original BG2C0 population had good grain quality characteristics, but lower agronomic performance before selection was initiated.

One cycle of selection for greater β-glucan content increased mean β-glucan content in both populations (Table 1). Selection did not change the mean grain yield, biomass, or test weight in BG1; however in BG2, it resulted in significant decreases in mean grain yield of 85 g m^{-2}, in biomass of 212 g m^{-2}, and in test weight of 10 kg m^{-3} (Table 1). Mean protein content increased by 9 g kg^{-1} and mean plant height decreased by 5 cm after one cycle of selection in BG1, but these components did not change in BG2. Mean oil content and heading date remained unchanged in both populations.

Lines with greatest β-glucan content across environments had a tendency toward lower grain yield and biomass and greater protein content compared with the checks (Table 2). However, some individual lines with greater β-glucan content and agronomic and grain quality trait values comparable with the commercial cultivars used as checks were observed in each set. For example, IA94190-10 had greater β-glucan content and similar grain yield compared with most of the check cultivars, and had good general performance for other traits (Table 2). Similar results were observed in the other sets, suggesting that it may be possible to identify lines with superior β-glucan content, grain quality, and agronomic performance from these populations to develop cultivars.

Table 1. Population means of five experimental oat populations, check cultivars, and parental lines for agronomic and grain quality traits evaluated in four Iowa environments.

Population or group	β-Glucan content	Grain yield	Biomass	Test weight	Protein content	Oil content	Heading date	Height
	g kg^{-1}	g m^{-2}		kg m^{-3}	g kg^{-1}		dap†	cm
Check cultivars	55.3a‡	398a	1019a	501a	180c	68ab	83ab	95b
Parental lines	54.7a	328a	923bc	501a	190b	67cd	85a	96b
BG1C0	53.9a	374a	1056a	493ab	184c	67bc	85a	100a
BG1C1	59.9c	398a	1056a	493ab	193ab	66cd	83ab	95b
BG2C0	63.5d	335b	920c	487b	196a	64d	83b	92c
BG2C1	66.0e	250d	708d	477c	196a	65cd	84ab	92c
BGPI	56.9b	354ab	966abc	467c	191ab	72a	83ab	98ab

† dap = days after planting.
‡ Means for the same trait followed by the same letter were not significantly different at $P = 0.05$ based on orthogonal contrasts.

Table 2. Best linear unbiased predictors (and ranks among 95 entries) of agronomic and grain quality traits of experimental oat lines with highest mean β-glucan content and check cultivars across four environments from set one.

Line	β-Glucan content	Grain yield	Biomass	Test weight	Protein content	Oil content	Heading date	Height
	g kg^{-1}	g m^{-2}		kg m^{-3}	g kg^{-1}		dap†	cm
IA94031-7‡	71 (1)§	270 (76)	822 (72)	483 (51)	204 (17)	60 (82)	83 (65)	93 (64)
IA95172-1¶	68 (2)	338 (52)	853 (66)	492 (31)	197 (28)	74 (18)	80 (84)	95 (51)
IA94031-6‡	68 (3)	266 (70)	805 (73)	483 (50)	206 (12)	59 (89)	84 (45)	89 (79)
IA95181-6¶	68 (4)	172 (92)	430 (93)	467 (85)	213 (2)	60 (85)	84 (36)	89 (78)
IA95109-2¶	68 (5)	294 (67)	723 (83)	479 (60)	195 (34)	65 (62)	86 (8)	82 (88)
IA95029-3¶	68 (6)	290 (69)	730 (82)	472 (77)	218 (1)	59 (88)	83 (61)	91 (72)
IA95148-3‡	68 (7)	261 (79)	702 (85)	484 (46)	190 (50)	64 (65)	84 (52)	85 (85)
IA95109-3#	67 (8)	250 (84)	689 (86)	483 (49)	200 (24)	60 (84)	88 (2)	82 (87)
IA94190-10††	67 (9)	390 (30)	976 (44)	499 (15)	189 (53)	67 (49)	79 (88)	92 (71)
IA95148-1¶	67 (10)	228 (88)	652 (90)	473 (75)	192 (44)	62 (74)	85 (16)	90 (76)
Mean	68	276	738	481	200	63	84	89
Range	67–71	172–390	430–976	467–499	189–218	59–74	79–88	82–95
IAN979-5-2‡‡	63 (11)	362 (42)	998 (38)	471 (78)	190 (52)	78 (5)	88 (1)	90 (77)
Premier§§	61 (36)	449 (5)	1065 (19)	521 (1)	178 (84)	64 (64)	84 (39)	96 (43)
Marion§§	58 (49)	517 (2)	1270 (2)	498 (20)	173 (86)	75 (15)	85 (20)	109 (3)
Starter§§	56 (54)	387 (31)	958 (48)	515 (3)	188 (60)	66 (53)	81 (80)	92 (67)
Hazel§§	51 (72)	449 (6)	1072 (17)	496 (23)	186 (66)	80 (2)	83 (66)	91 (73)
Noble§§	50 (76)	336 (54)	947 (50)	509 (6)	196 (32)	62 (76)	84 (38)	95 (45)
Don§§	49 (78)	381 (33)	887 (60)	487 (41)	170 (90)	75 (16)	81 (79)	87 (83)
Ogle§§	48 (79)	442 (8)	1183 (8)	476 (66)	181 (75)	64 (69)	84 (50)	96 (42)
Mean	54	415	1047	497	183	70	84	94
Range	48–63	336–517	887–1270	471–521	170–196	62–80	81–88	87–109
Mean of all entries	58	343	937	485	192	68	84	95
$LSD_{L\ vs\ L}$¶¶	4	71	139	30	9	4	3	8
$LSD_{L\ vs\ C}$##	3	61	120	26	8	3	3	7
$LSD_{C\ vs\ C}$†††	1	50	98	21	7	3	2	5

† dap = days after planting.
‡ Line from BG2C0.
§ Rank of genotypes within parenthesis.
¶ Line from BG2C1.
# Line from BG1C1.
†† Line from BG1C0.
‡‡ Check line considered as a line for pairwise comparisons.
§§ Check cultivar.
¶¶ Least significant difference at the 0.05 probability level for pairwise comparisons of line vs. line.
Least significant difference at the 0.05 probability level for pairwise comparisons of line vs. check.
††† Least significant difference at the 0.05 probability level for pairwise comparisons of check vs. check.

Genetic Variances and Heritabilities

The full-sib family and $S_{0:1}$ line within full-sib family variances were significant for all traits and all populations, except for the family variance in BG1C0 and the line within family variance in BG1C1 for test weight. The environment × family interaction variance was not significant for grain yield, biomass, test weight, heading date, or height in the four populations, except for biomass in BG1C0 and BG2C0, test weight in BG2C0, and heading date in BG1C1. The environment × family interaction variance was not significant for protein and oil content only in BG1C0 and BG2C1, respectively. The family variance was larger than the environment × family interaction variance for all traits in BG1 and BG2, except for biomass, test weight, protein content, and heading date in BG1C0.

The changes in genetic variance from BG1C0 to BG1C1 and from BG2C0 to BG2C1 were estimated to determine the effect of selection for greater β-glucan content on the genetic variability of other traits. The phenotypic and the genotypic variances for grain yield, biomass, test weight, and protein and oil content did not significantly change in BG1 and BG2 following selection, except for grain yield and biomass in BG2 (Table 3). The phenotypic variance decreased for plant height in BG1, and increased for heading date in BG1, and biomass and plant height in BG2. The genotypic variance significantly increased only for plant height in BG2 (Table 3).

Introduction of unadapted PI parents contributed to an increase of the genetic variance of β-glucan content when intermated with the parents of BG1C1 to form BG2C0 (Cervantes-Martinez et al., 2001). The BGPI population crosses also resulted in a significant increase in the genetic variance of plant height, as observed in the comparison of BG2C0 with BG1C1 (Table 3). Mean test weight was reduced by 5%, but mean oil content increased by 9% (Table 1). No change was observed in the means of grain yield, biomass, protein content, heading date, or plant height (Table 1).

The heritability estimated on a plot-basis ranged from 0.33 to 0.45 for grain yield, from 0.21 to 0.36 for biomass, from 0.55 to 0.62 for heading date, and from 0.38 to 0.67 for plant height (Table 4). These estimates are lower than the plot-basis heritability estimates reported for grain yield, biomass, heading date, and plant height by Hoi et al. (1999), but comparable with the line mean basis heritability estimates reported for yield by Klein et al. (1993). Changes in heritabilities for grain yield, biomass, test weight, and protein and oil contents after one cycle of selection for greater β-glucan were generally small in both populations because no significant

Table 3. Phenotypic and genotypic variance component estimates (and their standard errors) of four experimental oat populations.

Trait	Variance component	BG1 Population			BG2 Population		
		BG1C0	BG1C1	Change	BG2C0	BG2C1	Change
		$g^2\ m^{-4}$		%	$g^2\ m^{-4}$		%
Grain yield	Phenotypic†	13 739 (626)‡	14 800 (832)	8	13 190 (602)	10 894 (511)	−17**
	Genotypic§	4 884 (882)	4 933 (1115)	1	6 076 (1011)	4 748 (810)	−22
Biomass	Phenotypic	66 142 (3075)	65 880 (3782)	0	50 609 (2356)	95 355 (4559)	88**
	Genotypic	17 089 (3469)	20 018 (4680)	17	18 132 (3203)	19 052 (4332)	5
		$kg^2\ m^{-6}$		%	$kg^2\ m^{-6}$		%
Test weight	Phenotypic	673 (50)	637 (59)	−5	884 (65)	854 (67)	−3
	Genotypic	203 (48)	253 (65)	25	406 (81)	333 (72)	−18
		$g^2\ kg^{-2}$		%	$g^2\ kg^{-2}$		%
Protein content	Phenotypic	142 (11)	155 (14)	9	140 (11)	118 (9)	−16
	Genotypic	95 (16)	129 (24)	36	103 (17)	77 (14)	−25
Oil content	Phenotypic	31 (2)	26 (2)	−16	50 (4)	44 (3)	−12
	Genotypic	24 (4)	22 (4)	−8	46 (7)	35 (6)	−24
		dap^2		%	dap^2		%
Heading date	Phenotypic	7.9 (0.5)	10.8 (0.9)	37**	11.0 (0.7)	11.0 (0.8)	0
	Genotypic	4.4 (0.8)	6.6 (1.5)	50	6.3 (1.1)	6.1 (1.2)	−3
		cm^2		%	cm^2		%
Height	Phenotypic	55 (4)	27 (2)	−51**	42 (3)	68 (5)	62**
	Genotypic	21 (4)	15 (3)	−29	24 (4)	41 (7)	71*

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability.
† Phenotypic variance estimated as $\hat{\sigma}^2_P = \hat{\sigma}^2_{family} + \hat{\sigma}^2_{line(family)} + \hat{\sigma}^2_{env\times family} + \hat{\sigma}^2_{env\times line(family)} + \hat{\sigma}^2_{error}$.
‡ Sampling standard deviations of variance estimates within parenthesis.
§ Genotypic variance estimated as $\hat{\sigma}^2_G = \hat{\sigma}^2_{family} + \hat{\sigma}^2_{line(family)}$.

changes in phenotypic and genotypic variances were observed for these traits (Table 3).

Heritabilities estimated on a line mean basis were considerably larger than the corresponding plot-basis heritabilities for those traits estimated on individual plots (Table 4). For example, heritability of line means for grain yield ranged from 0.79 to 0.86 (Table 4). Heritability of test weight on a line mean basis was lowest among all traits and ranged from 0.46 to 0.62. Line mean basis heritabilities of groat oil and protein contents were very high, ranging from 0.87 to 0.97 (Table 4). The heritabilities of groat oil and protein contents may be greater than that for β-glucan content (estimated to be 0.80 to 0.85 from this same experiment by Cervantes-Martinez et al., 2001), in part, because of the greater precision of NIRS prediction equations for those traits.

Genotypic and Phenotypic Correlations

In general, β-glucan content exhibited low negative genotypic correlations with grain yield, biomass, test weight, and oil content in BG1 and BG2, except in BG1C0, in which its genotypic correlations with grain yield and biomass were positive (Table 5). β-Glucan content genotypically was correlated positively with protein content in BG1 and BG2. Heading and height exhibited low negative genotypic correlations with β-glucan content in BG1 and low positive correlations in BG2. In all but one case, the sign of the genotypic correlation estimate in the base population (BG1C0 or BG2C0) agreed with the sign of the correlated response to selection in that population. The only exception was groat oil content, which had a negative genotypic correlation with β-glucan content in BG2C0 ($r = -0.24$,

Table 4. Heritabilities (and their standard errors) of agronomic and grain quality traits for four experimental oat populations evaluated in four Iowa environments.

Population	Grain yield	Biomass	Test weight	Protein content	Oil content	Heading date	Height
	h^2 on a plot basis†						
BG1C0	0.35 (0.04)	0.27 (0.04)	NA‡	NA	NA	0.55 (0.05)	0.38 (0.05)
BG1C1	0.33 (0.05)	0.31 (0.05)	NA	NA	NA	0.62 (0.05)	0.58 (0.06)
BG2C0	0.45 (0.04)	0.36 (0.04)	NA	NA	NA	0.56 (0.05)	0.59 (0.05)
BG2C1	0.43 (0.04)	0.21 (0.03)	NA	NA	NA	0.56 (0.05)	0.67 (0.04)
	h^2 on a line mean basis§						
BG1C0	0.80 (0.03)	0.71 (0.05)	0.46 (0.06)	0.89 (0.03)	0.94 (0.03)	0.83 (0.03)	0.71 (0.05)
BG1C1	0.79 (0.04)	0.76 (0.05)	0.57 (0.06)	0.95 (0.04)	0.96 (0.04)	0.83 (0.04)	0.83 (0.04)
BG2C0	0.86 (0.02)	0.81 (0.03)	0.62 (0.05)	0.90 (0.03)	0.97 (0.04)	0.83 (0.03)	0.85 (0.03)
BG2C1	0.85 (0.02)	0.64 (0.06)	0.56 (0.05)	0.87 (0.04)	0.95 (0.04)	0.82 (0.04)	0.85 (0.03)

† Heritability on a plot-basis estimated as $(\hat{\sigma}^2_{family} + \hat{\sigma}^2_{line(family)})/(\hat{\sigma}^2_{family} + \hat{\sigma}^2_{line(family)} + \hat{\sigma}^2_{env\times family} + \hat{\sigma}^2_{env\times line(family)} + \hat{\sigma}^2_{experimental\ error})$ for grain yield, biomass, heading date, and height.
‡ NA = not applicable.
§ Heritability on line mean-basis estimated as $(\hat{\sigma}^2_{family} + \hat{\sigma}^2_{line(family)})/[\hat{\sigma}^2_{family} + \hat{\sigma}^2_{line(family)} + (\hat{\sigma}^2_{env\times family} + \hat{\sigma}^2_{env\times line(family)})/4 + \hat{\sigma}^2_{experimenetal\ error}/8]$ for grain yield and biomass; as $(\hat{\sigma}^2_{family} + \hat{\sigma}^2_{line(family)})/[\hat{\sigma}^2_{family} + \hat{\sigma}^2_{line(family)} + (\hat{\sigma}^2_{env\times family})/4]$ for test weight, protein and oil; and as $(\hat{\sigma}^2_{family} + \hat{\sigma}^2_{line(family)})/[\hat{\sigma}^2_{family} + \hat{\sigma}^2_{line(family)} + (\hat{\sigma}^2_{env\times family} + \hat{\sigma}^2_{env\times line(family)})/2 + \sigma^2_{experimental\ error}/4]$ for heading date and height.

Table 5. Estimates (and standard errors) of genotypic and phenotypic correlations between β-glucan content and agronomic and grain quality traits for four experimental oat populations evaluated in four Iowa environments.

Population or group	Grain yield	Biomass	Test weight	Protein content	Oil content	Heading date	Height
				Genotypic correlation†			
BG1C0	0.31 (0.12)	0.15 (0.14)	−0.21 (0.14)	0.32 (0.11)	−0.12 (0.12)	−0.10 (0.13)	−0.11 (0.13)
BG1C1	−0.25 (0.15)	−0.16 (0.16)	−0.01 (0.17)	0.15 (0.14)	−0.13 (0.14)	−0.39 (0.15)	−0.21 (0.15)
BG2C0	−0.15 (0.12)	−0.28 (0.12)	−0.13 (0.13)	0.08 (0.12)	−0.24 (0.11)	0.18 (0.14)	0.29 (0.13)
BG2C1	−0.49 (0.11)	−0.49 (0.11)	−0.14 (0.15)	0.30 (0.12)	−0.28 (0.11)	0.27 (0.17)	0.19 (0.16)
				Phenotypic correlation‡			
BG1C0	0.16 (0.07)	0.05 (0.07)	−0.11 (0.07)	0.26 (0.07)	−0.10 (0.08)	−0.03 (0.09)	−0.11 (0.09)
BG1C1	−0.05 (0.09)	0.04 (0.09)	−0.02 (0.09)	0.14 (0.10)	−0.14 (0.10)	−0.19 (0.11)	−0.17 (0.11)
BG2C0	−0.09 (0.08)	−0.15 (0.07)	−0.06 (0.07)	0.05 (0.08)	−0.17 (0.08)	0.09 (0.10)	0.15 (0.10)
BG2C1	−0.21 (0.07)	−0.21 (0.07)	−0.01 (0.08)	0.20 (0.07)	−0.20 (0.08)	0.13 (0.10)	0.06 (0.10)
BGPI	0.10 (0.14)	0.08 (0.13)	0.05 (0.11)	0.07 (0.14)	−0.15 (0.14)	0.29 (0.15)	0.09 (0.17)

† Genotypic correlation estimated as: $\hat{\sigma}_{line_{w,z}}/(\hat{\sigma}^2_{line_w}\,\hat{\sigma}^2_{line_z})^{1/2}$.
‡ Phenotypic correlation estimated on a sample-basis as $(\hat{\sigma}_{line_{w,z}} + \hat{\sigma}_{residual_{w,z}})/[(\hat{\sigma}^2_{line_w} + \hat{\sigma}^2_{residual_w})(\hat{\sigma}^2_{line_z} + \hat{\sigma}^2_{residual_z})]^{1/2}$.

Table 5), but which exhibited a nonsignificant increase of 1 g kg^{-1} following selection (Table 1).

Selection for greater β-glucan content resulted in unfavorable changes in genotypic correlations between β-glucan content and grain yield and biomass. Yield and biomass were correlated positively with β-glucan content in the initial base population BG1C0, but were correlated negatively with β-glucan content in BG1C1. Their strongest negative correlations were observed in BG2C1, the population with greatest β-glucan content. Although most previous reports suggested that β-glucan content and grain yield were not strongly genotypically correlated (Peterson et al., 1995; Holthaus et al., 1996; Kibite and Edney, 1998), these correlation estimates were based on populations with typical β-glucan contents. Our results suggest that β-glucan content and grain yield will tend to become negatively correlated as selection produces populations with β-glucan contents greater than current typical population levels. This will hinder attempts to develop cultivars with both greater grain yields and greater β-glucan contents. For example, based on the significant heritabilities (h^2) of β-glucan content ($h^2 = 0.85$, Cervantes-Martinez et al., 2001) and grain yield ($h^2 = 0.79$, Table 4) observed in BG1C1, their negative genotypic correlation in this population ($r = -0.49$, Table 5), and the consistency observed between the sign of genotypic correlations within selection populations and the sign of correlated responses to selection, we predict that a second generation of selection for greater β-glucan content in the BG2 population would result in a further increase in β-glucan content and a continued decrease in grain yield. Additional random mating and introduction of new germplasm into these populations could ameliorate the strengthening effects of selection on unfavorable genotypic correlations. Introduction of germplasm from the PI parents may have reduced the negative effect of selection on the genotypic correlation of β-glucan content with grain yield, biomass, test weight, and height when intermated with the selected parents of BG1 to form BG2C0 (Table 5).

In contrast, genotypic correlations between protein and oil contents and β-glucan content were generally favorable and more consistent across populations. Protein and β-glucan contents were positively genotypically correlated in both BG1C0 and BG2C1, the populations with least and greatest β-glucan contents, respectively (Table 5). Oil and β-glucan contents were negatively genotypically correlated, with the greatest negative correlation exhibited by BG2C1 (Table 5). Oat cultivars designed for milling for food uses would optimally possess greater β-glucan and protein contents and lower oil contents, in order to contribute to a high fiber, low fat diet. Therefore, the strengthened negative correlation between oil and β-glucan contents following selection for greater β-glucan content was desirable.

Phenotypic correlations of β-glucan content with agronomic and grain quality traits were generally lower than the corresponding genotypic correlations (Table 5). The estimates of the phenotypic correlation of β-glucan content with yield, protein and oil content, heading, and plant height obtained in this study were lower than the values reported by other authors (Brunner and Freed, 1994; Peterson et al., 1995; Holthaus et al., 1996; Kibite and Edney, 1998), probably because we estimated the phenotypic correlation directly from the components of variance and covariance, rather than from total variances and covariance. Phenotypic correlations estimated by the latter method are biased.

In summary, protein content consistently exhibited the most favorable correlated responses to selection for greater β-glucan content. Mean protein content increased following selection in BG1 and remained unchanged in BG2, while its heritability tended to increase in both populations. The increase in heritability will permit enhanced response to direct selection for greater protein content in these selected populations. Similarly, oil content exhibited a trend of decreasing mean and a greater negative correlation with β-glucan content as selection increased β-glucan content. Thus, selection for greater β-glucan content tended to improve other nutritional characteristics of oat grain by increasing protein content and decreasing oil content.

In contrast, unfavorable responses were observed for grain yield, biomass, and test weight, the means of which were reduced following selection in BG2. Further, genotypic correlations between grain yield or biomass and β-glucan content changed from positive in the initial base population to negative, following selection. The correlated decrease of 25% of the population mean grain yield in BG2 (Table 1) was particularly troubling, because it resulted in a 22% reduction in the yield of

β-glucan per unit land area, assuming that the groat percentage did not change. Therefore, selection methods designed to improve both β-glucan content and grain yield simultaneously must be implemented if agronomically acceptable cultivars with elevated β-glucan contents are to be developed.

An optimal selection index could be developed for the populations used in this experiment, based on the genotypic and phenotypic variance and covariance components estimated in this study. The optimal index will require assignment of relative economic weights to grain yield and β-glucan content, which will be difficult. Alternatively, selection for greater β-glucan yield (the product of groat yield and groat β-glucan content) may be a simple and effective method to simultaneously improve both grain yield and β-glucan content across a broader range of oat breeding populations. Previous research on protein content and grain yield in oat suggests that selection for yield of chemical components of grain should be effective. For example, Kuenzel and Frey (1985) reported that protein content and grain yield in oat F_2–derived lines from 27 matings had a phenotypic correlation of −0.33, whereas protein yield, obtained as the product of protein content and grain yield, had a phenotypic correlation of −0.09 with protein content and 0.98 with grain yield. Moser and Frey (1994) demonstrated that recurrent selection in oat for greater protein yield was effective at increasing protein yield per se, as well as both grain yield and protein content.

β-Glucan yield was estimated assuming a constant groat percentage for all genotypes. This assumption is supported by the lack of correlation between β-glucan content and groat percentage (Holthaus et al., 1996) The genotypic correlations of β-glucan yield with grain yield and β-glucan content were 0.92 and 0.66, respectively, in BG1C0 and 0.92 and 0.26, respectively, in BG2C0. These values suggest that selection for β-glucan yield would allow the simultaneous improvement of β-glucan content and grain yield.

Although Cervantes-Martinez et al. (2001) demonstrated that single-plant selections for increased β-glucan content were effective, the same is not likely to be true for grain yield. Thus, breeding strategies for integrating improvement in both β-glucan content and grain yield will require development and testing of breeding lines that can be replicated and grown under population densities mimicking oat production practices. This would require more time to complete a cycle of selection, and would reduce the gains from selection for β-glucan content per unit time, however. Alternatively, culling for minimal β-glucan contents based on single-plant evaluations could be combined with selection for both β-glucan content and grain yield (or β-glucan yield) among lines developed by self-fertilizing selected S_0 plants.

CONCLUSION

Phenotypic selection of individual S_0 plants for greater groat β-glucan content increased the expression of this trait by 11% in BG1 and 4% in BG2 (Cervantes-Martinez et al., 2001). The effects of this selection regime on other grain quality traits were favorable: protein content tended to increase and oil content tended to decrease as correlated responses. However, selection for greater β-glucan content reduced the mean grain yield, biomass, and test weight by 25, 23, and 2%, respectively, in BG2. The genetic variances of grain quality and agronomic traits were generally not affected. Unfavorable increases in the magnitude of the negative genotypic correlations between β-glucan content and grain yield, biomass, and test weight were observed following selection for greater β-glucan content, and this likely contributed to the unfavorable correlated changes in the BG2 population mean. Strategies for selecting agronomic traits simultaneously with β-glucan content should be implemented. For example, selection for greater β-glucan yield should improve β-glucan content without decreasing grain yield.

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