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By

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ABSTRACT

BETA-GLUCAN STUDIES IN OAT (AVENA SATIVA L.)

By

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β-glucan is a hypocholesterolemic water-soluble fiber component of oat (*Avena sativa* L.) grain. Despite beneficial physiological effects associated with β-glucan, few data are available on the effects of environment on β-glucan content and heritability has not been estimated.

One experiment was designed to examine the effect of N fertilizer on β-glucan concentration and other traits. Plantings were made at East Lansing and Caro, Michigan, in 1987, 1988, and 1989. The experimental design was a split plot with three replications. Whole plots consisted of three N levels (0, 37, and 74 kg ha^{-1}), and subplots consisted of five oat varieties (Heritage, Korwood, Ogle, Pacer, and Porter). Increased N levels tended to reduce test weight and hull percentage, while increasing grain yield, groat protein content, groat β-glucan content, and β-glucan yield. N application had no effect on groat weight. Differences between locations were observed for all traits except groat β-glucan concentration. Considerable climatic variability among years affected crop response. Test weight, hull percentage, groat weight, and grain yield were highest in 1987. In 1988, groat protein concentration was highest, however, lowest mean values were observed for

test weight, hull percentage, grain yield, groat weight, groat β-glucan concentration, and β-glucan yield. Grain yield, β-glucan concentration, and β-glucan yield were high in 1989, while test weight, hull percentage, and protein content were low. No significant differences in mean β-glucan concentration were found among cultivars. Pacer had the highest mean test weight, Porter the highest groat weight and protein content, and Ogle the highest grain yield and β-glucan yield, and lowest hull percentage. Correlations between β-glucan content and test weight, hull percentage, grain yield, or groat weight were mostly small or nonsignificant. Correlations between groat protein and groat β-glucan were significant, relatively large, and positive in 1987 and 1989, but were nonsignificant in 1988.

A second experiment was conducted to estimate heritability of oat β-glucan content. Two nested S_0-derived populations were developed from the crosses Garry × Hazel and Garry × Marion. Garry is a low β-glucan cultivar, while Hazel and Marion have high groat β-glucan contents. Broad sense heritabilities of 0.41 and 0.54 were observed for populations 1 and 2, respectively.

This dissertation is dedicated

to my Lord and Savior

Jesus Christ,

without whom

it would have never been possible;

and to my special wife,

Yarisa Montes-Brunner,

without whom

it would have never been accomplished.

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INTRODUCTION

β-glucan, a nonstarchy polysaccharide composed of mixed-linkage (1→3)- and (1→4)-β-D-glucopyranosyl units, was first isolated from oat in 1942 (Morris, 1942). This polysaccharide is also found in barley, and may adversely affect the malting, brewing, and feeding quality of this grain (Novacek and Peterson, 1967; Bourne et al., 1976). Primarily as a result of greater commercial interest in barley β-glucan than in oat, significantly more research has been done on the former.

There is currently new interest, however, in the use of oat β-glucan as an industrial hydrocolloid and as a nutritionally valuable dietary supplement. Oat gum, a crude extract of β-glucan containing small amounts of pentosan, ash, and protein, is highly viscous in aqueous solution, a characteristic which gives it potential application as a thickening agent in foods. As an industrial hydrocolloid, oat gum compares favorably with other commercial gums such as substituted celluloses, guar gum, and locust bean gum (Wood, 1986).

β-glucan is a water-soluble fiber which has been shown to produce beneficial physiological effects when incorporat-

ed in the human diet. Oat bran, which contains 70 to 80 g kg^{-1} β-glucan, was found to significantly reduce serum cholesterol levels of hypercholesterolemic patients (Anderson and Chen, 1986). Gould et al. (1980) reported improved glucose and insulin metabolism in nondiabetic and diabetic patients with oat bran diets. A third health benefit associated with oat bran is improved laxation due to fecal bulking (Meyer and Calloway, 1977; Anderson, 1980).

Differences in β-glucan content between oat cultivars have been documented, but few data are available on the genetic and environmental effects on β-glucan content. Moreover, the heritability of β-glucan content in oat has not been reported. The two chapters of this dissertation present the results of two studies designed to (1) determine the effect of soil N level, location, and year on β-glucan content in five oat cultivars, and (2) estimate the heritability of β-glucan in oat.

LITERATURE REVIEW

A substance similar to the nonstarchy polysaccharide lichenin from the lichen Iceland moss was first isolated from oat in 1942 (Morris, 1942). This unbranched polysaccharide, now known as β-glucan, is composed of mixed-linkage (1→3)- and (1→4)-β-D-glucopyranosyl units. The presence of β-(1→3)- and β(1→4)-glucosidic linkages was demonstrated by Acker et al. (1955b) by methylation analysis. Peat et al. (1957) found a ratio of β-(1→3)- to β-(1→4)- linkages of 1:3.2 by measurement of the consumption of periodate by oat "lichenin".

Evaluation of the oligosaccharides produced by enzymatic treatment of β-glucan showed that the molecule is mainly composed of two structural sequences: a tetrameric unit in which single (1→3)-β-linkages are alternated with two (1→4)-β-linkages, and a pentameric unit in which one (1→3)-β-linkage is alternated with three (1→4)-β-linkages (Parrish et al., 1960). Perlin and Suzuki (1962) demonstrated that lichenin and cereal β-glucan differ slightly in that a major proportion of the lichenin molecule consists of the tetrameric unit, while the cereal glucans are primarily composed of the pentameric unit. Evidence from enzyme stud-

ies suggests that oat β-glucan has a higher proportion of pentameric repeat units than barley β-glucan (Wood, 1986).

The presence of mixed-linkage (1→3),(1→4)-β-D-glucan has been reported in various lichens, cereals, grasses, bamboo, and mung bean in both endospermic and nonendospermic tissues (Table 1). With the exception of lichens and mung bean, mixed-linkage β-glucans are thought to be restricted to the Gramineae. Stinard and Nevins (1980) were unable to detect β-glucan in ten nongrass monocot species.

β-glucan is associated with the cell wall in both endospermic and nonendospermic plant tissues. At least a portion of the total β-glucan in barley endosperm is bound covalently to the cell wall, possibly by linkages to protein via serine, threonine, aspartic acid, or glutamic acid, or by ferulic acid cross-linking (Ballance and Manners, 1978).

Although the specific function of β-glucan in plant tissues is unknown, it has been suggested that it serves a storage function (Meier and Reid, 1982; Mares and Stone, 1973; Buchala and Wilkie, 1970), as physical reinforcement of the cell wall against cracking during dehydration and dormancy (Mares and Stone, 1973), as a structural component for binding together the microfibrillar phase of the wall (Labavitch and Ray, 1978), or may be involved in cell elongation (Masuda and Yamamoto, 1970; Huber and Nevins, 1979; Sakurai and Masuda, 1979). Much evidence has been presented to support the cell elongation hypothesis. Cell elongation

Table 1. Plant tissues in which (1→3),(1→4)-β-D-glucan has been identified.

Source	Tissue	Reference
Arundinaria japonica		
A. anceps	leaf and stem	Wilkie and Woo, 1976
Avena sativa	caryopsis	Preece and MacKenzie, 1952; Acker et al., 1955a; Peat et al., 1957; Parrish et al., 1960; Wood et al., 1977, 1978; Anderson et al., 1978; Prentice et al., 1980; Åman and Hesselman, 1985; McCleary and Glennie-Holmes, 1985; Åman, 1987; Åman and Graham, 1987; Henry, 1987
	coleoptile	Nevins et al., 1977; Yamamoto and Nevins, 1978
	hull and root	Buchala and Wilkie, 1971
	leaf	Fraser and Wilkie, 1971
	stem	Buchala and Wilkie, 1971
Cetraria islandica	thallus	Fukuoka et al., 1968
Evernia prunastri	thallus	Takeda et al., 1972
Hordeum vulgare	caryopsis	Fleming et al., 1974; Wood et al., 1977; Anderson et al., 1978; Prentice et al., 1980; Martin and Bamforth, 1981; Gill et al., 1982; Staudte et al., 1983; Ahluwalia and Ellis, 1984; Henry, 1984, 1987; Åman and Hesselman, 1985; McCleary and Glennie-Holmes, 1985; Åman, 1986; Åman and Graham, 1987
	coleoptile	Nevins et al., 1978
	leaf	Buchala and Wilkie, 1974
	stem	Buchala and Wilkie, 1970, 1974
Hydrochloa caroliniana	leaf and stem	Stinard and Nevins, 1980

Table 1 (cont'd).

Source	Tissue	Reference
Lithachne paucifolia	leaf and stem	Stinard and Nevins, 1980
Lolium multiflorum	endosperm	Smith and Stone, 1973; Burke et al., 1974; Anderson and Stone, 1978
L. perenne	endosperm	
Oryza sativa	caryopsis	Anderson et al., 1978; Shibuya and Misaki, 1978; McCleary and Glennie-Holmes, 1985
Panicum maximum	leaf and stem	Buchala, 1974
Phaseolus aureus	hypocotyl	Buchala and Franz, 1974
Phragmites australis	leaf and stem	Buchala, 1974
Saccharum officinarum	leaf and stem	Stinard and Nevins, 1980
Secale cereale	caryopsis	Anderson et al., 1978; Prentice et al., 1980; Åman and Hesselman, 1985; McCleary and Glennie-Holmes, 1985; Henry, 1987
	coleoptile	Nevins et al., 1978
	stem	Buchala and Wilkie, 1970
Sorghum bicolor	caryopsis	Woolard et al., 1976; Prentice et al., 1980
	mesocotyl	Nevins et al., 1978
Streptochaeta sodiroana	leaf and stem	Stinard and Nevins, 1980
Triticosecale	caryopsis	Anderson et al., 1978; Prentice et al., 1980; Åman and Hesselman, 1985; McCleary and Glennie-Holmes, 1985

Table 1 (cont'd).

Source	Tissue	Reference
Triticum aestivum	caryopsis	Anderson et al., 1978; Bacic and Stone, 1980; Prentice and Stone, 1980; Åman and Hesselman, 1985; McCleary and Glennie-Holmes, 1985; Henry, 1987
	coleoptile	Nevins et al., 1978
	leaf	Buchala and Wilkie, 1973
	stem	Buchala and Wilkie, 1970, 1973
Usnea rubescens	thallus	Nishikawa et al., 1974
Zea mays	caryopsis	McCleary and Glennie-Holmes, 1985
	coleoptile	Kivilaan et al., 1971; Nevins et al., 1978; Kato and Nevins, 1986
	stem	Buchala and Meier, 1973
Zoysia japonica	leaf and stem	Stinard and Nevins, 1980

in oat coleoptile segments is induced by an exo-(1→3)-β-D-glucanase isolated from *Sclerotinia libertiana* (Masuda and Wada, 1967; Masuda et al., 1970), while the glucanase inhibitor nojirimycin (5-amino-5-deoxy-D-glucopyranose) inhibits elongation (Nevins, 1975). Kivilaan et al. (1971) observed autolytic solubilization of β-glucan in isolated corn coleoptile cell walls, and concluded that cell wall glucan is hydrolyzed by glucanase during extension growth. A significant decrease in the β-glucan content of oat coleoptile cell walls is observed with auxin-induced cell elongation (Loescher and Nevins, 1972, 1973). Nevins (1977) suggests that auxin may alter β-glucan content by affecting those factors which regulate the synthesis or degradation of the polysaccharide.

Various techniques have been utilized for β-glucan analysis in cereal grains. Since a relationship exists between β-glucan content and viscosity of aqueous extracts, this method has been used in breeding programs for malting and feed barley (Greenberg and Whitmore, 1974; Bendelow, 1975; Aastrup, 1979). Quantitative methods of analysis include (1) acid hydrolysis followed by chromatography (Valent et al., 1980) or gel filtration on Biogel P-2 (Nevins et al., 1978; Yamamoto and Nevins, 1978; Stinard and Nevins, 1980), (2) periodate oxidation (Fleming and Manners, 1966; Smith and Stone, 1973b), (3) methylation analysis (Kato et al., 1981), (4) enzymatic hydrolysis (Prentice et al., 1980;

Martin and Bamforth, 1981), and (5) adsorption of Calcofluor to β-glucan followed by measurement of fluorescence intensity (Jensen and Aastrup, 1981; Jørgensen, 1983). Murphy (1987) also cites the use of image analysis, ELISA, and NIR in screening for β-glucan. Molecular and crystal structures of β-glucans have been examined by X-ray diffraction techniques (Marchessault and Deslandes, 1981) and ^{13}C-NMR spectroscopy (Dais and Perlin, 1982).

Estimates of β-glucan content in commercial cereals have been highly variable and may be affected by analytical method and other factors (Wood, 1986). Wood et al. (1978) observed that flour particle size, temperature, pH and ionic strength of the extraction media affected β-glucan yields in oat, and temperature was found to affect β-glucan extraction efficiency in barley (Prentice et al., 1980). β-glucan values reported for various cereals are shown in Table 2. It may be seen from the available literature that the relative order of magnitude of β-glucan content in the cereals is as follows: barley>oat>rye>sorghum>wheat>triticale>corn>rice. Barley and oat contain significantly greater levels of mixed-linkage β-glucans than do other commercial cereals.

β-glucans are responsible for various technical and nutritional properties that affect the utilization of barley and oat in the brewing, feed, and food industries. A barley β-glucan content of greater than 40 g kg^{-1} can decrease wort filtration rate, induce haze formation in beer, and possibly

Table 2. Reported β-glucan content of selected cereals.

Cereal	β-glucan content	Reference
	— g kg^{-1} —	
Barley	9.5-11.4	Fleming et al., 1974
	16-74	Bendelow, 1975
	16.6-17.1	Wood et al., 1978
	45-82	Prentice et al., 1980
	54.3-86.2	Martin and Bamforth, 1981
	27-52	Gill et al., 1982
	43-60	Ahluwalia and Ellis, 1984
	34.4-56.8	Henry, 1984, 1986, 1987
	37.5	Åman and Hesselman, 1985
	38.0-48.1	McCleary and Glennie-Holmes, 1985
	33-41	Åman, 1986
	30-135	Åman and Graham, 1987a, 1987b
Corn	1.2	McCleary and Glennie-Holmes, 1985
Oat	3.5-45.9	Wood et al., 1977, 1978
	25.0	Anderson et al., 1978
	48-66	Prentice et al., 1980
	30.0	Åman and Hesselman, 1985
	27-54	McCleary and Glennie-Holmes, 1985
	27-36	Åman, 1987
	22-42	Åman and Graham, 1987a, 1987b
	39.0	Henry, 1987
	31-55	McCleary et al., 1988
	32-63	Welch and Lloyd, 1989
	48.8-62.4	Peterson, 1991
	36-56	Welch et al., 1991
	39.1-68.2	Wood et al., 1991
Rice	1.3	Anderson et al., 1978
	0.4	McCleary and Glennie-Holmes, 1985
Rye	19.3	Anderson et al., 1978
	19-29	Prentice et al., 1980
	13.0	Åman and Hesselman, 1985
	14-21	McCleary and Glennie-Holmes, 1985
	25.0	Henry, 1987

Table 2 (cont'd).

Cereal	β-glucan content	Reference
	— g kg^{-1} —	
Sorghum	10.0	Prentice et al., 1980
Triticale	3.4	Anderson et al., 1978
	12.0	Prentice et al., 1980
	5.3	Åman and Hesselman, 1985
	4.2-5.8	McCleary and Glennie-Holmes, 1985
Wheat	3.4	Anderson et al., 1978
	14.0	Prentice et al., 1980
	5.4	Åman and Hesselman, 1985
	5.0-6.8	McCleary and Glennie-Holmes, 1985
	6.0	Henry, 1987

reduce extraction efficiency (McCleary and Glennie-Holmes, 1985). Barley and oat-based feeds may decrease food intake, growth rate, and feed conversion efficiency in chickens (Åman and Graham, 1987b). The addition of β-glucanase to these feeds has been shown to overcome the antinutritional effect of β-glucan (Broz and Frigg, 1986; Elwinger and Saterby, 1987).

Oat gum, composed primarily of β-glucan, exhibits high viscosity at low concentration, high pseudoplasticity at concentrations of 5 g kg^{-1} and greater, and stability to sugar and salt. These characteristics are desirable for industrial hydrocolloid applications, and in fact oat gum compares favorably with other high-viscosity neutral polysaccharides such as some substituted celluloses, guar gum,

and locust bean gum (Wood, 1986). Potential uses include ice cream, sauces, and salad dressings.

Oat β-glucan has been shown to produce beneficial physiological effects when incorporated in the human diet. Hypocholesterolemic properties of oat products have been well documented. DeGroot et al. (1963) reported an average reduction of 11% in plasma total cholesterol levels with daily consumption of 140 g rolled oats over a three week period. More recent studies have shown average cholesterol reductions of 36% with a coarse oat fraction (Gould et al., 1980), 13% with oat bran (Kirby et al., 1981), 8% with rolled oats (Judd and Truswell, 1981), 10 to 17% with oat bran (Demark-Wahnefried et al., 1990), and 10.1 to 15.9% with different dosages of oatmeal and oat bran (Davidson et al., 1991). An additional benefit associated with oat products is that they appear to selectively decrease detrimental low density lipoprotein cholesterol while leaving unchanged or increasing levels of beneficial high density lipoprotein (Mathur et al., 1968; Anderson, 1980; Judd and Truswell, 1981; Kirby et al., 1981).

Fiber supplementation in the diet has been associated with decreased post-meal hyperglycemia (Jenkins et al., 1977) and proper regulation of bowel function (Kelsay, 1981). The water-soluble β-glucan of oat has been shown to affect the postprandial glucose response in humans (Hansen et al., 1987), and Gould et al. (1980) reported improved

glucose and insulin metabolism in nondiabetic and diabetic patients with oat bran diets. Oat fiber is associated with improved laxation due to fecal bulking, decrease in fecal transit time, and increase in fecal weight (Meyer and Calloway, 1977; Anderson, 1980; Judd and Truswell, 1981).

It should be noted that the (1→3),(1→4)-β-glucan of the lichens *Cetraria islandica*, *Evernia prunastri*, and *Usnea rubescens* has been shown to possess highly effective host-mediated antitumour activities against sarcoma 180 in mice (Fukuoka et al., 1968; Takeda et al., 1972; Nishikawa et al., 1974).

Genotypic differences for β-glucan content have been well documented in barley (Sparrow and Meredith, 1969; Bourne and Pierce, 1970; Bendelow, 1975; Wood et al., 1978; Aastrup, 1979b; Prentice et al., 1980; Martin and Bamforth, 1981; Morgan and Riggs, 1981; Gill et al., 1982; Ahluwalia and Ellis, 1984; Henry, 1984, 1986; McCleary and Glennie-Holmes, 1985; Åman, 1986; Åman and Graham, 1987a, 1987b) and in oat (Wood et al., 1977, 1978; Prentice et al., 1980; McCleary and Glennie-Holmes, 1985; Åman, 1987; Åman and Graham, 1987a, 1987b; McCleary et al., 1988; Peterson, 1991; Welch et al., 1991; Wood et al., 1991). Few data are available, however, concerning the effect of environment on β-glucan content in these cereals. Differences in β-glucan content due to location have been observed in barley (Bourne and Pierce, 1972; Bendelow, 1975; Smart, 1976; Molina-Cano

and Conde, 1982; Åman, 1986; Lehtonen and Aikasalo, 1987; Åman et al., 1989), and in oat (Peterson, 1991). Bendelow (1975) and Greenberg (1977) have reported significant genotype × location interactions for β-glucan content in barley; other workers have found this interaction to be nonsignificant (Bourne and Pierce, 1972; Gill et al., 1982; Henry, 1986). Peterson (1991) observed a significant genotype × location interaction for β-glucan content in oat.

Soil N level may have an influence on grain β-glucan concentration. Wood et al. (1977) reported a low β-glucan content of 3.5 g kg^{-1} in Hinoat grown with zero applied N compared with levels of 26.9 and 27.7 g kg^{-1} with normal fertilization. In a controlled greenhouse experiment with six oat cultivars, Welch et al. (1991) observed significant increases in β-glucan content for the high versus low N fertility treatment. Field studies to determine the effect of N fertilization on oat β-glucan concentration have not been reported.

It appears that β-glucan content in barley may be related to water availability during the growing season. Morgan and Riggs (1981) found increased viscosity of barley extracts as a result of drought stress. Bendelow (1975) observed β-glucan differences among three locations in Canada, and concluded that there appears to be an inverse relationship between β-glucan content and moisture level of the growth environment. In independent growth chamber ex-

periments, Aastrup (1979a) and Coles (1979) found a decrease in the total β-glucan content of barley grains with overhead watering as opposed to the same amount of water delivered to the roots. Aastrup also noted that barley samples with the lowest extract viscosities and presumably lower β-glucan levels come from areas in Denmark with the highest mean temperature, precipitation, and relative humidity. Possible mechanisms for the observed effect of decreased β-glucan as a result of rain include (1) degradation of β-glucans, (2) reduced synthesis of β-glucans, (3) modification of the β-glucans to yield polymers inaccessible to the β-glucanase used for the β-glucan determinations, and (4) leaching of the glucose, a precurser of β-glucans, from the flag leaf and awns (Aastrup, 1979a).

A diallel cross analysis of gum content in barley showed that gum content was controlled by two to three genes in a simple additive-dominance genetic system and that low gum content was strongly dominant (Greenberg, 1977). Gum content was found to be highly heritable in barley, suggesting that it should not be difficult to develop low gum cultivars. Lance (1984) reported that most of the variability for β-glucan content in segregating barley populations was due to additive effects, and estimated a narrow sense heritability value of 0.73 based on parent-offspring regression of F_4 means on parental F_3 means. Similar genetic studies have not been reported for oat.

LIST OF REFERENCES

Aastrup, S. 1979a. The effect of rain on β-glucan content in barley grains. Carlsberg Res. Commun. 44:381-393.

Aastrup, S. 1979b. The relationship between the viscosity of an acid flour extract of barley and its β-glucan content. Carlsberg Res. Commun. 44:289-304.

Acker, L., W. Diemair, and E. Samhammer. 1955a. The lichenin of oats. I. Properties, preparation and composition of the muciparous polysaccharides. Z. Lebensm. Unters. Forsch. 100:180-188.

Acker, L., W. Diemair, and E. Samhammer. 1955b. The lichenin of oats. II. Determination of molecular weight and further studies on constitution. Z. Lebensm. Unters. Forsch. 102:225-231.

Ahluwalia, B. and E.E. Ellis. 1984. A rapid and simple method for the determination of starch and β-glucan in barley and malt. J. Inst. Brew. 90:254-259.

Åman, P. 1986. A note on the content of mixed-linked β-glucans in Swedish barley. Swedish J. Agric. Res. 16:73-75.

Åman, P. 1987. The variation in chemical composition of Swedish oats. Acta Agric. Scand. 37:347-352.

Åman, P. and H. Graham. 1987a. Analysis of total and insoluble mixed-linked (1→3),(1→4)-β-D-glucans in barley and oats. J. Agric. Food Chem. 35:704-709.

Åman, P. and H. Graham. 1987b. Content and solubility of mixed-linked β-(1→3),(1→4)-D-glucans in Swedish barleys and oats. *In* I.D. Morton (ed.) Cereals in a European context. Ellis Horwood, Chichester, England.

Åman, P., H. Graham, and A.-C. Tilly. 1989. Content and solubility of mixed-linked (1→3),(1→4)-β-D-glucan in barley and oats during kernel development and storage. J. Cereal Sci. 10:45-50.

Åman, P. and K. Hesselman. 1985. An enzymic method for analysis of total mixed-linkage β-glucans in cereal grains. J. Cereal Sci. 3:231-237.

Anderson, J.W. 1980. Dietary fiber and diabetes. p. 193-221. *In* G.A. Spiller and R.M. Kay (ed.) Medical aspects of dietary fiber. Plenum Press, New York.

Anderson, J.W. and W.L. Chen. 1986. Cholesterol-lowering properties of oat products. p. 309-333. *In* F.H. Webster (ed.) Oats: Chemistry and technology. American Association of Cereal Chemists, Inc., St. Paul, Minnesota.

Anderson, M.A., J.A. Cook, and B.A. Stone. 1978. Enzymatic determination of 1,3:1,4 -β-glucans in barley grain and other cereals. J. Inst. Brew. 84:233-239.

Anderson, R.L. and B.A. Stone. 1978. Studies of *Lolium multiflorum* endosperm in tissue culture III. Structural studies on the cell walls. Aust. J. Biol. Sci. 31:573-586.

Bacic, A. and B. Stone. 1980. A (1→3)- and (1→4)-linked β-D-glucan in the endosperm cell-walls of wheat. Carbohydr. Res. 82:372-377.

Ballance, G.M. and D.J. Manners. 1978. Structural analysis and enzymic solubilization of barley endosperm cell-walls. Carbohydr. Res. 61:107-118.

Bendelow, V.M. 1975. Determination of non-starch polysaccharides in barley breeding programmes. J. Inst. Brew. 81:127-130.

Bourne, D.T., M. Jones, and J.S. Pierce. 1976. Beta glucan and beta glucanases in malting and brewing. Tech. Quart. Master Brew. Assoc. Amer. 13:3-7.

Bourne, D.T. and J.S. Pierce. 1970. β-glucan and β-glucanase in brewing. J. Inst. Brew. 76:328-335.

Bourne, D.T. and J.S. Pierce. 1972. β-glucan and β-glucanase: Review. Tech. Quart. Master Brew. Assoc. Amer. 9:151.

Broz, J. and M. Frigg. 1986. Effects of β-glucanase on the feeding value of broiler diets based on barley or oats. Arch. Gefluegelkd. 50:41-47.

Buchala, A.J. 1974. Xylans from the tropical grass *Panicum maximum*. Phytochem. 13:2185-2188.

Buchala, A.J. and G. Franz. 1974. A hemicellulosic β-glucan from the hypocotyls of *Phaseolus aureus*. Phytochem. 13:1887-1889.

Buchala, A.J. and H. Meier. 1973. A hemicellulosic β-D-glucan from maize stem. Carbohydr. Res. 26:421-425.

Buchala, A.J. and K.C.B. Wilkie. 1970. Non-endospermic hemicellulosic β-glucans from cereals. Naturwissenschaften 57:496.

Buchala, A.J. and K.C.B. Wilkie. 1971. The ratio of β-(1→3) to β(1→4) glucosidic linkages in non-endospermic hemicellulosic β-glucans from oat plant (*Avena sativa*) tissues at different stages of maturity. Phytochem. 10:2287-2291.

Buchala, A.J. and K.C.B. Wilkie. 1973. Total hemicelluloses from wheat at different stages of growth. Phytochem. 12:499-505.

Buchala, A.J. and K.C.B. Wilkie. 1974. Total hemicelluloses from *Hordeum vulgare* plants at different stages of maturity. Phytochem. 13:1347-1351.

Burke, D., P. Kaufman, M. McNeil, and P. Albersheim. 1974. The structure of plant cell walls. VI. A survey of the walls of suspension-cultured monocots. Plant Physiol. 34:109-115.

Coles, G. 1979. Relationship of mixed-link beta-glucan accumulation to accumulation of free sugars and other glucans in the developing barley endosperm. Carlsberg Res. Commun. 44:439-453.

Dais, P. and A.S. Perlin. 1982. High-field, ^{13}C-NMR spectroscopy of β-D-glucans, amylopectin, and glycogen. Carbohydr. Res. 100:103-116.

Davidson, M.H., L.D. Dugan, J.H. Burns, J. Bova, K. Story, and K.B. Drennan. 1991. The hypocholesterolemic effects of β-glucan in oatmeal and oat bran: A dose-controlled study. JAMA 265:1833-1839.

DeGroot, A.P., R. Luyken, and N.A. Pikaar. 1963. Cholesterol-lowering effect of rolled oats. Lancet 2:303-304.

Demark-Wahnefried, W., J. Bowering, and P.S. Cohen. 1990. Reduced serum cholesterol with dietary change using fat-modified and oat bran supplemented diets. J. Am. Diet. Assoc. 90:223-229.

Elwinger, K. and B. Saterby. 1987. The use of β-glucanase in practical broiler diets containing barley or oats: Effect of enzyme level, type and quality of grain. Swedish J. Agric. Res. 17:133-140.

Fleming, M. and D.J. Manners. 1966. A comparison of the fine-structure of lichenin and barley glucan. Biochem. J. 100:4P-5P.

Fleming, M., D.J. Manners, R.M. Jackson, and S.C. Cooke. 1974. The estimation of β-glucan in barley. J. Inst. Brew. 80:399-404.

Fraser, C.G. and K.C.B. Wilkie. 1971. β-glucans from oat leaf tissues at different stages of maturity. Phytochem. 10:1539-1542.

Fukuoka, F., M. Nakanishi, S. Shibata, Y. Nishikawa, T. Takeda, and M. Tanaka. 1968. Polysaccharides in lichens and fungi. II. Antitumour activities on sarcoma-180 of the polysaccharide preparations from *Gyrophora esculenta* Miyoshi, *Cetraria islandica* (L.) Ach. var. *orientalis* Asahina, and some other lichens. GANN 59:421-432.

Gill, A.A., A.G. Morgan, and D.B. Smith. 1982. Total β-glucan content of some barley cultivars. J. Inst. Brew. 88:317-319.

Gould, M.R., J.W. Anderson, and S. O'Mahony. 1980. Bio-functional properties of oats. p. 447-460. *In* G.G. Inglett and L. Munck (ed.) Cereals for food and beverages. Academic Press, NY.

Greenberg, D.C. 1977. A diallel cross analysis of gum content in barley (*Hordeum vulgare*). Theor. Appl. Genet. 50:41-46.

Greenberg, D.C. and E.T. Whitmore. 1974. A rapid method for estimating the viscosity of barley extracts. J. Inst. Brew. 80:31-33.

Hansen, I., B. Wiebe, F.M. Hansen, and K.E.B. Knudsen. 1987. Effect of wheat and oat fibre on postprandial glucose response in man. p. 512. *In* I.D. Morton (ed.) Cereals in a European context. Ellis Horwood, Chichester, England.

Henry, R.J. 1984. A simplified enzymic method for the determination of (1→3)(1→4)-β-glucans in barley. J. Inst. Brew. 90:178-180.

Henry, R.J. 1985. A comparative study of the total β-glucan contents of some Australian barleys. Aust. J. Exp. Agric. 25:424-427.

Henry, R.J. 1986. Genetic and environmental variation in the pentosan and β-glucan contents of barley, and their relation to malting quality. J. Cereal Sci. 4:269-277.

Henry, R.J. 1987. Pentosan and (1→3),(1→4)-β-glucan concentrations in endosperm and wholegrain of wheat, barley, oats and rye. J. Cereal Sci. 6:253-258.

Huber, D.J. and D.J. Nevins. 1979. Autolysis of the cell wall β-D-glucan in corn coleoptiles. Plant Cell Physiol. 20:201-212.

Jenkins, D., A. Leeds, M. Gassull, B. Cochet, and K. Alberti. 1977. Decrease in postprandial insulin and glucose concentrations by guar and pectin. Annals Internal Medicine 86:20.

Jensen, S.A. and S. Aastrup. 1981. A fluorimetric method for measuring 1,3:1,4-β-glucan in beer, wort, malt and barley by use of Calcofluor. Carlsberg Res. Comm. 46:87-95.

Jørgensen, K.G. 1983. An improved method for determining β-glucan in wort and beer by use of Calcofluor. Carlsberg Res. Comm. 48:505-516.

Judd, P.A. and A.S. Truswell. 1981. The effect of rolled oats on blood lipids and fecal steroid excretion in man. Am. J. Clin. Nutr. 34:2061-2067.

Kato, Y., K. Iki, and K. Matsuda. 1981. Cell-wall polysaccharides of immature barley plants. I. Isolation and characterization of a β-D-glucan. Agric. Biol. Chem. 45:2737-2744.

Kato, Y. and D.J. Nevins. 1986. Fine structure of (1→3), (1→4)-β-D-glucan from *Zea* shoot cell-walls. Carbohydr. Res. 147:69-85.

Kelsay, J.L. 1981. Effect of diet fiber level on bowel function and trace mineral balances of human subjects. Cereal Chem. 58:2-5.

Kirby, R.W., J.W. Anderson, B. Sieling, E.D. Rees, W.L. Chen, R.E. Miller, and R.M. Kay. 1981. Oat-bran intake selectively lowers serum low-density lipoprotein cholesterol concentrations of hypercholesterolemic men. Am. J. Clin. Nutr. 34:824-829.

Kivilaan, A., R.S. Bandurski, and A. Schulze. 1971. A partial characterization of an autolytically solubilized cell wall glucan. Plant Physiol. 48:389-393.

Labavitch, J.M. and P.M. Ray. 1978. Structure of hemicellulosic polysaccharides of *Avena sativa* coleoptile cell walls. Phytochem. 17:933-937.

Lance, R.C.M. 1984. Genetic studies of the β-glucan content of barley (*Hordeum vulgare* L.). Diss. Abst. Int. 45: 742-B.

Lehtonen, M. and R. Aikasalo. 1987. β-glucan in two- and six-rowed barley. Cereal Chem. 64:191-192.

Loescher, W. and D.J. Nevins. 1972. Auxin-induced changes in *Avena* coleoptile cell wall composition. Plant Physiol. 50:556-563.

Loescher, W. and D.J. Nevins. 1973. Turgor-dependent changes in *Avena* coleoptile cell wall composition. Plant Physiol. 52:248-251.

Marchessault, R.H. and Y. Deslandes. 1981. Crystalline conformation of homo- and regular heteroglucan chains. Carbohydr. Polym. 1:31-38.

Mares, D.J. and B.A. Stone. 1973. Studies on wheat endosperm. I. Chemical composition and ultrastructure of the cell walls. Aust. J. Biol. Sci. 26:793-812.

Martin, H.L. and C.W. Bamforth. 1981. An enzymatic method for the measurement of total and water-soluble β-glucan in barley. J. Inst. Brew. 87:88-91.

Masuda, Y., S. Oi, and Y. Satomura. 1970. Further studies on the role of cell-wall-degrading enzymes in cell-wall loosening in oat coleoptiles. Plant Cell Physiol. 11:631-638.

Masuda, Y. and S. Wada. 1967. Effect of β-1,3-glucanase on the elongation growth of oat coleoptile. Bot. Mag. 80:100-102.

Masuda, Y. and R. Yamamoto. 1970. Effect of auxin on β-1,3-glucanase activity in *Avena* coleoptile. Dev. Growth Differ. 11:287-296.

Mathur, K.S., M.A. Khan, and R.D. Sharma. 1968. Hypocholesterolaemic effect of Bengal gram: A long-term study in man. Br. Med. J. 1:30-31.

McCleary, B.V. and M. Glennie-Holmes. 1985. Enzymic quantification of (1→3)(1→4)-β-D-glucan in barley and malt. J. Inst. Brew. 91:285-295.

McCleary, B.V., I. Shameer, and M. Glennie-Holmes. 1988. Measurement of (1→3),(1→4)-β-D-glucan. p. 545-551. *In* W.A. Wood and S.T. Kellogg (eds.) Methods of enzymology. Vol. 160. Academic Press, NY.

Meier, H. and J.S.G. Reid. 1982. Reserve polysaccharides other than starch in higher plants. p. 418-471. *In* F.A. Loewus and W. Tanner (eds.) Encyclopedia of plant physiology: New series. Vol. 13A, Springer-Verlag, NY.

Meyer, S. and D.H. Calloway. 1977. Gastrointestinal response to oat and wheat milling fractions in older women. Cereal Chem. 54:110-119.

Molina-Cano, J.L. and J. Conde. 1982. Genetic and environmental variation of gum content in barley. J. Inst. Brew. 88:30-33.

Morgan, A.G. and T.J. Riggs. 1981. Effects of drought on yield and on grain and malt characteristics in spring barley. J. Sci. Food Agric. 32:339-346.

Morris, D.L. 1942. Lichenin and araban in oats (*Avena sativa*). J. Biol. Chem. 142:881-891.

Murphy, C.F. 1987. Report of oat enhancement work session. Madison, WI. 16 Oct. 1987. USDA. Beltsville, MD.

Nevins, D.J. 1975. The effect of nojirimycin on plant growth and its implications concerning a role for exo-β-glucanases in auxin-induced cell expansion. Plant Cell Physiol. 16:347-356.

Nevins, D.J., D.J. Huber, R. Yamamoto, and W.H. Loescher. 1977. β-D-glucan of *Avena* coleoptile cell walls. Plant Physiol. 60:617-621.

Nevins, D.J., R. Yamamoto, and D.J. Huber. 1978. Cell wall β-D-glucans of five grass species. Phytochem. 17:1503-1505.

Nishikawa, Y., K. Ohki, K. Takahashi, G. Kurono, F. Fukuoka, and M. Emori. 1974. Studies on the water soluble constituents of lichens. II. Antitumor polysaccharides of *Lasallia*, *Usnea*, and *Cladonia* species. Chem. Pharm. Bull. 22:2692-2702.

Novacek, E.J. and C.F. Peterson. 1967. Metabolisable energy of the anatomical parts and other fractions of western barley and the effect of enzymes and water treatment. Poult. Sci. 46:1008.

Parrish, F.W., A.S. Perlin, and E.T. Reese. 1960. Selective enzymolysis of poly-β-D-glucans, and the structure of the polymers. Can. J. Chem. 38:2094-2104.

Peat, S., W.J. Whelan, and J.G. Roberts. 1957. The structure of lichenin. J. Chem. Soc. 3916-3924.

Perlin, A.S. and S. Suzuki. 1962. The structure of lichenin: Selective enzymolysis studies. Can. J. Chem. 40:50-56.

Peterson, D.M. 1991. Genotype and environment effects on oat beta-glucan concentration. Crop Sci. 31:1517-1520.

Preece, I.A. and K.G. MacKenzie. 1952. Non-starchy polysaccharides of cereal grains. II. Distribution of water-soluble gum-like materials in cereals. J. Inst. Brew. 58:457-464.

Prentice, N., S. Babler, and S. Faber. 1980. Enzymic analysis of β-D-glucans in cereal grains. Cereal Chem. 57:198-202.

Sakurai, N. and Y. Masuda. 1979. Effect of cycloheximide and cordycepin on auxin-induced elongation and β-glucan degradation of noncellulosic polysaccharides of *Avena* coleoptile cell wall. Plant Cell Physiol. 20:593-603.

Shibuya, N. and A. Misaki. 1978. Structure of hemicellulose isolated from rice endosperm cell wall: Mode of linkages and sequences in xyloglucan, β-glucan and arabinoxylan. Agric. Biol. Chem. 42:2267-2274.

Smart, J.G. 1976. The β-glucan content of New Zealand barley. Inst. Brew. Aust N.Z. Sec. Proc. 14th Conv. p. 161-168.

Smith, M.M. and B.A. Stone. 1973a. β-glucan synthesis by cell-free extracts from *Lolium multiflorum* endosperm. Biochim. Biophys. Acta 313:72-94.

Smith, M.M. and B.A. Stone. 1973b. Chemical composition of the cell walls of *Lolium multiflorum* endosperm. Phytochem. 12:1361-1367.

Sparrow, D.H.B. and W.O.S. Meredith. 1969. Malt cytolytic activity of barleys of diverse origins and its relation to maltability. J. Inst. Brew. 75:237-242.

Staudte, R.G., J.R. Woodward, G.B. Fincher, and B.A. Stone. 1983. Water-soluble (1→3),(1→4)-β-D-glucans from barley (*Hordeum vulgare*) endosperm. III. Distribution of cellotriosyl and cellotetraosyl residues. Carbohydr. Polymers 3:299-312.

Stinard, P.S. and D.J. Nevins. 1980. Distribution of noncellulosic β-D-glucans in grasses and other monocots. Phytochem. 19:1467-1468.

Takeda, T., M. Funatsu, S. Shibata, and F. Fukuoka. 1972. Polysaccharides of lichens and fungi. V. Antitumour active polysaccharides of lichens of *Evernia*, *Acroscyphus* and *Alectoria* spp. Chem. Pharm. Bull. 20:2445-2449.

Valent, B.S., A.G. Darvill, M. McNeil, B.K. Robertsen, and P. Albersheim. 1980. A general and sensitive chemical method for sequencing the glycosyl residues of complex carbohydrates. Carbohydr. Res. 79:165-192.

Welch, R.W., J.M. Leggett, and J.D. Lloyd. 1991. Variation in the kernel (1→3)(1→4)-β-D-glucan content of oat cultivars and wild *Avena* species and its relationship to other characteristics. J. Cereal Sci. 13:173-178.

Welch, R.W. and J.D. Lloyd. 1989. Kernel (1→3)(1→4)-β-D-glucan content of oat genotypes. J. Cereal Sci. 9:35-40.

Wilkie, K.C.B. and S. Woo. 1976. Non-cellulosic β-D-glucans from bamboo, and interpretative problems in the study of all hemicelluloses. Carbohydr. Res. 49:399-409.

Wood, P.J. 1986. Oat β-glucan: Structure, location, and properties. p. 121-152. *In* F.W. Webster (ed.) Oats: Chemistry and technology. American Association of Cereal Chemists, St. Paul, MN.

Wood, P.J., D. Paton, and I.R. Siddiqui. 1977. Determination of β-glucan in oats and barley. Cereal Chem. 54:524-533.

Wood, P.J., I.R. Siddiqui, and D. Paton. 1978. Extraction of high-viscosity gums from oats. Cereal Chem. 55:1038-1049.

Wood, P.J., J. Weisz, and P. Fedec. 1991. Potential for β-glucan enrichment in brans derived from oat (*Avena sativa* L.) cultivars of different (1→3),(1→4)-β-D-glucan concentrations. Cereal Chem. 68:48-51.

Woolard, G.R., E.B. Rathbone, and L. Novellie. 1976. A hemicellulosic β-D-glucan from the endosperm of sorghum grain. Carbohydr. Res. 51:249-252.

Yamamoto, R. and D.J. Nevins. 1978. Structural studies on the β-D-glucan of the *Avena* coleoptile cell-wall. Carbohydr. Res. 67:275-280.

CHAPTER ONE

OAT GRAIN β-GLUCAN CONTENT AND OTHER TRAITS AS AFFECTED BY NITROGEN LEVEL, LOCATION, AND YEAR.

ABSTRACT

β-glucan is a hypocholesterolemic water-soluble fiber component of oat (*Avena sativa* L.) grain. Despite beneficial physiological effects associated with β-glucan, few data are available on the effects of environment on β-glucan content. An experiment was designed to examine the effect of N fertilizer on oat β-glucan concentration and other traits. Plantings were made at East Lansing and Caro, Michigan, in 1987, 1988, and 1989. The experimental design was a split plot with three replications. Whole plots consisted of each of three N levels (0, 37, and 74 kg ha^{-1}), and subplots consisted of five oat varieties. Oat cultivars used were Heritage, Korwood, Ogle, Pacer, and Porter. Data were collected and analyses of variance conducted for test weight, hull percentage, grain yield, groat weight, groat protein content, groat β-glucan content, and β-glucan yield. Increased levels of applied N tended to reduce test weight and hull percentage, while increasing grain yield, groat

protein content, groat β-glucan content, and β-glucan yield. N application had no effect on groat weight. Differences between locations were observed for test weight, hull percentage, grain yield, groat weight, protein content, and β-glucan yield. Groat β-glucan concentration did not differ significantly between locations. Considerable climatic variability among years affected crop response. Test weight, hull percentage, groat weight, and grain yield were highest in 1987. In 1988, groat protein concentration was highest, however, lowest mean values were observed for test weight, hull percentage, grain yield, groat weight, groat β-glucan concentration, and β-glucan yield. Grain yield, β-glucan concentration, and β-glucan yield were high in 1989, while test weight, hull percentage, and protein content were low. No significant differences in mean β-glucan concentration were found among cultivars used in the study. Pacer had the highest mean test weight, Porter the highest groat weight and protein content, and Ogle the highest grain yield and β-glucan yield, and lowest hull percentage. Correlations between β-glucan content and test weight, hull percentage, grain yield, or groat weight were mostly small or nonsignificant. Correlations between groat protein and groat β-glucan were significant, relatively large and positive in 1987 and 1989, but were nonsignificant in 1988.

INTRODUCTION

Mixed-linkage (1→3),(1→4)-β-D-glucan (β-glucan) is a nonstarchy, water-soluble polysaccharide found in root, coleoptile, leaf, stem, and endosperm tissues of the Gramineae (Wilkie, 1979; Stinard and Nevins, 1980; Wood, 1986). Commercial cereals with particularly high β-glucan concentration (≈30 to 60 g kg^{-1}) include oat and barley (*Hordeum vulgare* L.). Numerous studies have documented the cholesterol-lowering effects of β-glucan and other water-soluble fibers in both experimental animals (Kahlon et al., 1990; Ranhotra et al., 1990; Shinnick et al., 1990) and in humans (DeGroot et al., 1963; Kirby et al., 1981; Anderson and Chen, 1986; Kestin et al., 1990; Davidson et al., 1991). Oat products are an especially good source of water-soluble dietary fiber due to their high β—glucan content, palatability and relatively low cost.

Genetic enhancement of β-glucan concentration has been identified as an important breeding objective to improve oat quality (Murphy, 1987). In order to effectively increase the β-glucan content of commercial oat cultivars, an understanding of the influence of genetic and environmental factors on grain β-glucan content is essential. Differences

in β-glucan content among oat varieties have been reported (Peterson, 1991; Welch et al., 1991; Wood et al., 1991). Åman and Graham (1987) found a range in β-glucan content of 22 to 42 g kg^{-1} in a survey of 42 oat cultivars, and Welch and Lloyd (1989) reported values of 32 to 63 g kg^{-1} β-glucan for 100 diverse oat genotypes.

Environmental effects and genotype × environment interaction on oat β-glucan content are less well understood. Numerous reports have documented differences in barley β-glucan content among locations (Bendelow, 1975; Molina-Cano and Conde, 1982; Henry, 1985; Åman, 1986; Lehtonen and Aikasalo, 1987; Åman et al., 1989) and years (Bourne and Pierce, 1970; Bourne and Wheeler, 1984). Peterson (1991) found significant differences for β-glucan content among twelve oat genotypes and nine locations. The genotype × location interaction was also significant. The effect of year to year variation on β-glucan concentration in oat is not known.

One environmental factor which may influence grain β-glucan content and other traits in oat is soil N. Elevated soil N levels have resulted in increased grain yield, plant height, straw yield, number of seeds per panicle, number of panicles per plant, lodging score, and groat protein content. Moreover, high soil N has led to decreases in kernel weight and harvest index (Frey, 1959; Portch et al., 1968; Ohm, 1976; Youngs and Gilchrist, 1976; Brinkman and

Rho, 1984). Wood et al. (1977) reported the extremely low β-glucan value of 3.5 g kg^{-1} for Hinoat grown with no applied N. In a controlled greenhouse experiment with six oat cultivars, Welch et al. (1991) observed significant increases in β-glucan content for the high versus low N fertility treatment. Field studies to determine the effect of N fertilization on oat β-glucan concentration have not been reported.

This study was designed to examine the effects of applied N fertilizer, location, and year on grain β-glucan content in five oat cultivars.

MATERIALS AND METHODS

The experiment was conducted at two Michigan locations in 1987, 1988, and 1989. The soil at East Lansing (42° N) is a Capac loam (fine-loamy, mixed, mesic Aeric Ochraqualfs), and the other site, near Caro (43° N), has a Tappan-Londo loam (Tappan: fine-loamy, mixed [calcareous], mesic Typic Haplaquolls; Londo: fine-loamy, mixed, mesic Aeric Glossaqualfs). Soil characteristics are presented in Table 1. There was considerable climatological variability between the two sites and among years the study was conducted (Tables 2 and 3).

The experimental design utilized was a split-plot with three replications. Whole plots consisted of each of three N levels (0, 37, and 74 kg ha^{-1} N) in a randomized block design, and five oat varieties were assigned to subplots. Oat cultivars used in the study were Heritage, Korwood, Ogle, Pacer, and Porter. Subplots consisted of five 4 m rows with 25 cm row spacing.

Maintenance fertilizer applications of 64 kg ha^{-1} N, 28 kg ha^{-1} P, and 53 kg ha^{-1} K were incorporated prior to planting at each site. Planting dates are listed in Table 4. Nitrogen treatments were applied to whole plots by

Table 1. Description of soil characteristics at East Lansing and Caro.

Location	pH	OM†	CEC‡	P	K	Ca	Mg
		g kg^{-1}	cmol kg^{-1}	kg ha^{-1}			
East Lansing	6.2	26	9.8	164	273	1886	349
Caro	7.9	29	17.2	179	358	5197	747

† Organic matter.
‡ Cation exchange capacity.

Table 2. Temperature mean and range (in parenthesis) for the growing season at East Lansing and Caro, 1987 to 1989.

Year	Location	April	May	June	July
		°C			
1987	East Lansing	9(-7/28)	16(-1/32)	21(4/36)	23(6/36)
	Caro	10(-7/28)	17(-2/34)	22(2/36)	24(4/37)
1988	East Lansing	8(-3/27)	16(2/32)	20(2/37)	24(5/38)
	Caro	8(-5/26)	15(-1/33)	20(1/37)	24(5/38)
1989	East Lansing	6(-9/23)	13(-3/29)	19(6/33)	22(10/32)
	Caro	7(-8/22)	14(-1/30)	19(4/32)	22(6/34)

Table 3. Precipitation for the growing season at East Lansing and Caro, 1987 to 1989.

Year	Location	April	May	June	July	Total
		mm				
1987	East Lansing	42	30	63	62	197
	Caro	65	25	87	25	202
1988	East Lansing	102	16	4	61	183
	Caro	74	18	26	74	192
1989	East Lansing	49	125	85	46	305
	Caro	58	128	97	15	298

Table 4. Planting and harvest dates at East Lansing and Caro for 1987 to 1989.

	Planting date		Harvest date	
Year	East Lansing	Caro	East Lansing	Caro
1987	20 April	6 April	23 July	17 July
1988	12 April	22 April	22 July	27 July
1989	1 May	20 April	28 July	31 July

broadcasting urea approximately 3 wk after planting, or when plants were about 15 cm tall.

Grain was harvested at maturity (Table 4) with a plot combine. After air-drying in the greenhouse, samples were weighed, cleaned, and test weight was determined. Seed was dehulled in an impact type dehuller, and groat weight calculated as the mean of a random sample of 500 groats.

Groat samples were ground in a Cyclone Sample Mill (U.D. Corp., Boulder, CO) fitted with a 0.5 mm screen. Flour samples were stored in air-tight containers at -20°C until used. Groat protein content was calculated as Kjeldahl N × 62.5. β-glucan concentration was determined by the enzymatic method described by McCleary and Glennie-Holmes (1985), using the Biocon β-glucan kit (Quest-Biocon, Sarasota, FL). Total β-glucan yield was calculated as the product of groat β-glucan concentration and total groat yield. Groat flour moisture content was determined by oven

drying samples at 80°C for 24 hr. Results are reported on a dry weight basis.

Analyses of variance were conducted for individual sites, and combined across locations (Table 5) and years (Table 6). Locations and years were considered random, while N level and cultivar were considered fixed. Bartlett's test for homogeneity of variances (Steel and Torrie, 1980) indicated that error variances were heterogeneous in the analyses combined across years for hull percentage, test weight, groat β-glucan concentration, and β-glucan yield. Variance homogeneity was achieved for groat β-glucan concentration and β-glucan yield by log transformation of the data. Combined analyses of variance and separation of means for these variables were performed on transformed data. All reported means were converted back to the original scale after statistical analysis. Analyses of variance combined across years were not conducted for hull percentage and test weight due to error variance heterogeneity. Differences among means were evaluated using Duncan's new multiple range test. Simple correlations were calculated between groat β-glucan content and yield and other grain characteristics.

Table 5. Source, degrees of freedom, and expected mean squares for the analysis of variance combined across locations.

Source	DF	Expected mean squares
Locations (L)	l-1	$\delta^2_b + c\delta^2_a + nc\delta^2_{R(L)} + rnc\delta^2_L$
Rep(L)	l(r-1)	$\delta^2_b + c\delta^2_a + nc\delta^2_{R(L)}$
N levels	n-1	$\delta^2_b + c\delta^2_a + rc\delta^2_{NL} + rcl\theta^2_N$
N×L	(n-1)(l-1)	$\delta^2_b + c\delta^2_a + rc\delta^2_{NL}$
Error a	l(n-1)(r-1)	$\delta^2_b + c\delta^2_a$
Cultivars (C)	c-1	$\delta^2_b + rn\delta^2_{CL} + rnl\theta^2_C$
C×L	(c-1)(l-1)	$\delta^2_b + rn\delta^2_{CL}$
C×N	(c-1)(n-1)	$\delta^2_b + r\delta^2_{NCL} + rl\theta^2_{CN}$
N×C×L	(n-1)(c-1)(l-1)	$\delta^2_b + r\delta^2_{NCL}$
Error b	nl(r-1)(c-1)	δ^2_b

Table 6. Source, degrees of freedom, and expected mean squares for the analysis of variance combined across locations and years.

Source	DF	Expected mean squares
Years (Y)	y-1	$\delta^2_b + c\delta^2_a + nc\delta^2_{R(YL)} + rnc\delta^2_{YL} + rncl\delta^2_Y$
Locations (L)	l-1	$\delta^2_b + c\delta^2_a + nc\delta^2_{R(YL)} + rnc\delta^2_{YL} + rncy\delta^2_L$
Y×L	(y-1)(l-1)	$\delta^2_b + c\delta^2_a + nc\delta^2_{R(YL)} + rnc\delta^2_{YL}$
Rep(L×Y)	yl(r-1)	$\delta^2_b + c\delta^2_a + nc\delta^2_{R(YL)}$
N levels	n-1	$\delta^2_b + c\delta^2_a + rc\delta^2_{NYL} + rcy\delta^2_{NL} + rcl\delta^2_{NY} + rcyl\theta^2_N$
N×Y	(n-1)(y-1)	$\delta^2_b + c\delta^2_a + rc\delta^2_{NYL} + rcl\delta^2_{NY}$
N×L	(n-1)(l-1)	$\delta^2_b + c\delta^2_a + rc\delta^2_{NYL} + rcy\delta^2_{NL}$
N×Y×L	(n-1)(y-1)(l-1)	$\delta^2_b + c\delta^2_a + rc\delta^2_{NYL}$
Error a	yl(r-1)(n-1)	$\delta^2_b + c\delta^2_a$
Cultivars (C)	c-1	$\delta^2_b + rn\delta^2_{CYL} + rny\delta^2_{CL} + rnl\delta^2_{CY} + rnyl\theta^2_C$
C×Y	(c-1)(y-1)	$\delta^2_b + rn\delta^2_{CYL} + rnl\delta^2_{CY}$
C×L	(c-1)(l-1)	$\delta^2_b + rn\delta^2_{CYL} + rny\delta^2_{CL}$
C×Y×L	(c-1)(y-1)(l-1)	$\delta^2_b + rn\delta^2_{CYL}$
N×C	(n-1)(c-1)	$\delta^2_b + r\delta^2_{NCYL} + ry\delta^2_{NCL} + rl\delta^2_{NCY} + ryl\theta^2_{NC}$
N×C×Y	(n-1)(c-1)(y-1)	$\delta^2_b + r\delta^2_{NCYL} + rl\delta^2_{NCY}$
N×C×L	(n-1)(c-1)(l-1)	$\delta^2_b + r\delta^2_{NCYL} + ry\delta^2_{NCL}$
N×C×Y×L	(n-1)(c-1)(y-1)(l-1)	$\delta^2_b + r\delta^2_{NCYL}$
Error b	yln(r-1)(c-1)	δ^2_b

RESULTS AND DISCUSSION

Test Weight

According to the analyses of variance combined across locations, N level had a significant effect on test weight in 1987 and 1989, but not in 1988 (Table 7). Test weight means decreased with increasing N in 1989 (Figure 1), probably due to dry conditions at grain filling. Reductions in test weight at increased levels of soil N has been observed by other workers in oat (Ohm, 1976) and in wheat (Johnson et al., 1973). Test weights were high in 1987 (Table 8). Lower test weights observed in 1988 and 1989 may have been caused by drought in 1988, and possibly by increased late tillering resulting in poorly filled kernels at harvest in 1989.

Test weights tended to be higher at Caro than East Lansing for all three years (Table 8), however differences between the two locations were significant only in 1989 (Table 7). This finding may be due in part to the higher soil fertility at Caro. The cultivar × location interaction was significant for all three years (Table 7). Pacer tended to have the highest mean test weight across locations and years, followed by Porter, Korwood, Heritage, and Ogle (Table 8).

Table 7. Mean squares and significance in the analysis of variance for test weight and hull percentage combined across locations.

Source	DF	Test weight			Hull percentage		
		1987	1988	1989	1987	1988	1989
		Mean squares					
Locations (L)	1	41.52	6828.4	21468.9***	104.911***	36.131	7.151
Rep (L)	4	61.66	4904.5	149.5	1.308	24.474	6.016
N levels	2	264.12**	456.7	5621.5**	1.783	2.281	67.750*
N × L	2	0.13	1402.3	642.2	0.996	19.358	28.521
Error a	8	43.27	1013.2	351.0	1.906	5.456	11.976
Cultivars (C)	4	8875.84***	8957.3	8860.6†	33.088***	40.462	53.862
C × L	4	145.25**	2859.9†	1899.5***	1.263	23.241†	52.455***
C × N	8	75.43†	1095.4	291.7	3.503†	5.743	30.509**
N × C × L	8	55.10	638.7	317.7*	1.366	7.194	11.089
Error b	46‡	34.11	1269.4	143.1	1.798	9.655	8.398
CV (%)		1.2	8.4	2.8	5.2	14.7	14.3

†,*,**,*** Significant at P = 0.1, 0.05, 0.01, and 0.001, respectively.
‡ Error b degrees of freedom are 46 for test weight in 1987, 42 for hull percentage in 1987, and 48 for both traits in 1988 and 1989.

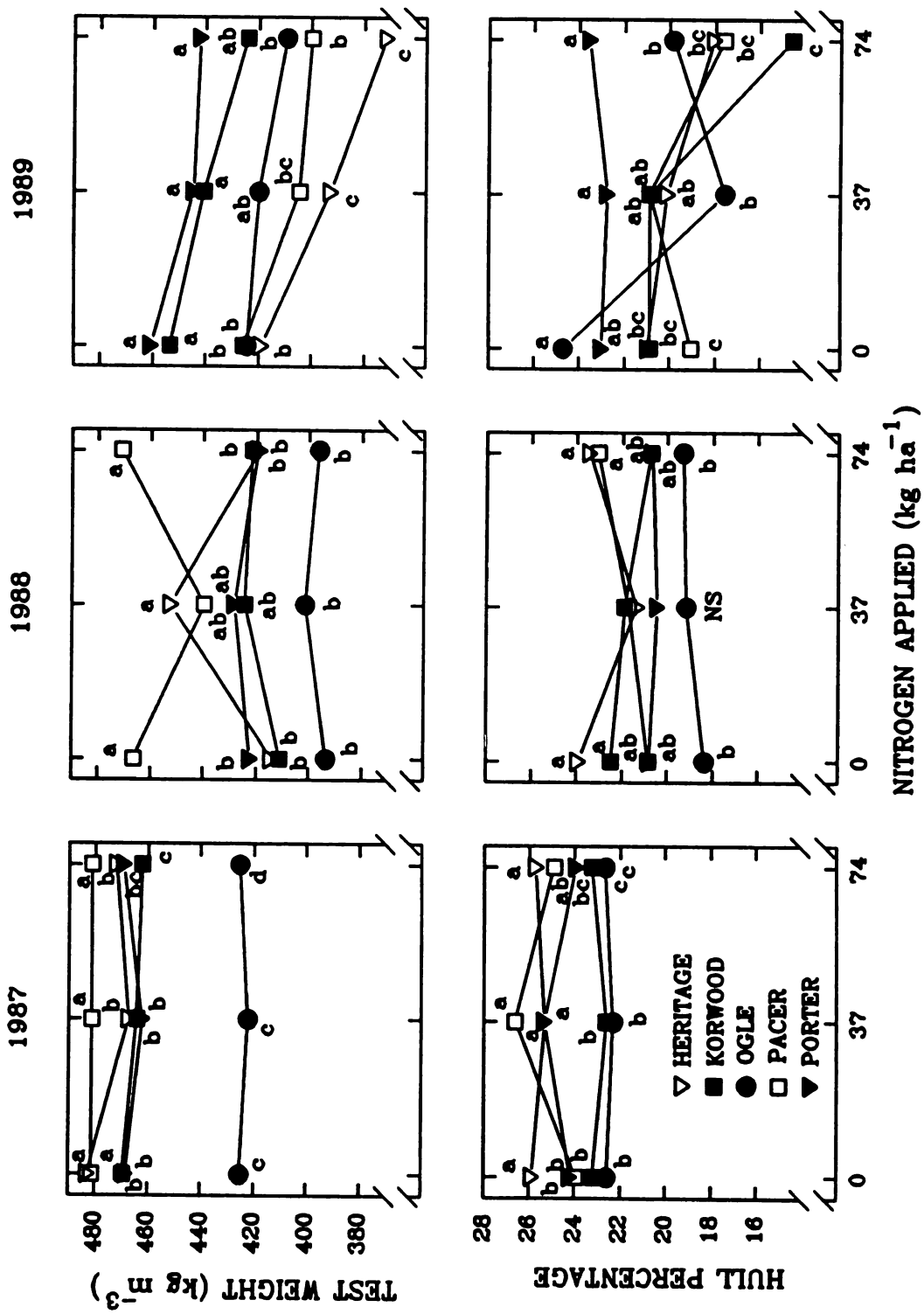

Figure 1. Responses of two traits to three levels of applied N in 1987, 1988, and 1989. Values represent means of two locations. At each level of N, Duncan's new multiple range test values characterize differences among varieties at P = 0.05.

Table 8. Test weight means for five oat cultivars grown at East Lansing (EL) and Caro, 1987 to 1989.

Cultivar	1987		1988		1989		Mean
	EL	Caro	EL	Caro	EL	Caro	
	kg m^{-3}						
Heritage	473.6b†	474.2ab	404.1b	452.9a	385.9c	402.7d	432.2
Korwood	464.8c	465.8c	402.3b	435.7a	407.5b	471.2a	441.2
Ogle	423.2d	425.2d	391.6b	402.5b	406.5b	429.1b	413.0
Pacer	484.5a	478.1a	467.8a	450.2a	403.1b	416.8c	450.1
Porter	461.7c	471.3b	417.6b	429.1ab	430.3a	468.0a	446.3
Mean	461.6	462.9	416.7	434.1	406.7	437.5	

† Within locations, means followed by the same letter are not significantly different at P = 0.05 according to Duncan's new multiple range test.

Hull Percentage

Hull percentage differences among N levels were significant only in 1989 (Table 7). A reduction in hull percentage at higher soil N levels (Figure 1) may have resulted from a decrease in synthesis of hull macromolecule components (i.e., cellulose and lignin) with a concomitant increase in groat components, especially protein, as N became more available. The reason for lack of response to soil N in 1987 is unknown, however, lack of response in 1988 is probably due to severe water deficits. The cultivar × N interaction was significant in 1987 and 1989 (Table 7). Differences in hull percentage among cultivars were highly significant in 1987, but not in 1988 or 1989 because of high significant cultivar × location interactions (Table 7). Ogle tended to have the lowest hull percentage followed by Korwood, Pacer, Heritage, and Porter (Table 9). Mean hull percentage was greater at Caro than at East Lansing for all years (Table 9), however, the difference was significant only in 1987 (Table 7).

Grain Yield

The effect of year on grain yield was highly significant in the analysis of variance combined across locations and years (Table 10). Yields were highest when rainfall was adequate, in 1987 and 1989, and were extremely low in the droughty 1988 growing season (Table 11). The year ×

Table 9. Hull percentage means for five oat cultivars grown at East Lansing (EL) and Caro, 1987 to 1989.

Cultivar	1987		1988		1989		Mean
	EL	Caro	EL	Caro	EL	Caro	
	%						
Heritage	24.3a†	27.1a	23.5a	22.3ab	20.2b	19.2bc	22.6
Korwood	21.7b	24.3cd	19.5b	23.9a	15.7c	21.8ab	21.2
Ogle	21.7b	23.3d	18.4b	19.5b	20.4b	21.0ab	20.7
Pacer	24.1a	26.2ab	20.6b	23.1ab	20.7ab	17.6c	22.1
Porter	23.6a	25.4bc	20.9b	20.4ab	23.1a	23.1a	22.7
Mean	23.1	25.3	20.6	21.9	20.0	20.6	

† Within locations, means followed by the same letter are not significantly different at P = 0.05 according to Duncan's new multiple range test.

Table 10. Mean squares and significance in the analysis of variance for grain yield, groat weight, groat protein content, groat β-glucan content, and β-glucan yield combined across locations and years. Analyses for groat β-glucan and β-glucan yield were performed on log-transformed data.

Source	DF	Grain yield	Groat weight	Groat protein content	Groat β-glucan content	β-glucan yield
		Mean squares				
Years (Y)	2	121.587***	529.535***	6885.4***	0.575***	7.550***
Locations (L)	1	0.444	0.553	800.9	0.064	0.011
Y × L	2	4.992**	11.718***	678.3	0.018	0.227
Rep (L × Y)	12	0.402	0.940	435.1	0.044	0.096
N levels§	2	0.416	0.400	2961.1*	0.054	0.032
N × Y	4	0.941**	0.552	504.3	0.016**	0.049*
N × L	2	0.039	0.053	22.1	0.032**	0.021
N × Y × L	4	0.082	0.370	149.5	0.001	0.003
Error a	24	0.141	0.534	268.4	0.004	0.014
Cultivars (C)§	4	0.988	19.379	1179.8*	0.008	0.039
C × Y	8	0.456*	14.757**	206.3*	0.011*	0.013
C × L	4	0.566*	3.363	160.0†	0.022**	0.035
C × Y × L	8	0.124**	1.614***	88.6	0.008	0.016*
N × C§	8	0.063	0.072	99.0	0.004	0.009
N × C × Y	16	0.063	0.899**	110.3	0.003	0.007
N × C × L	8	0.069	0.369	124.7	0.003	0.003
N × C × Y × L	16	0.043	0.391	48.5	0.003	0.004
Error b	142‡	0.043	0.349	78.9	0.005	0.007
CV (%)		7.3	2.7	5.1	4.2	4.3

†,*,**,*** Significant at P = 0.1, 0.05, 0.01, and 0.001, respectively.
‡ Error b degrees of freedom are 142 for grain yield, and 138 for the other traits.
§ Significance determined according to McIntosh (1983).

Table 11. Grain yield means for five oat cultivars grown at East Lansing (EL) and Caro, 1987 to 1989.

Cultivar	1987		1988		1989		Mean‡
	EL	Caro	EL	Caro	EL	Caro	
	Mg ha^{-1}						
Heritage	4.039a†	3.476a	1.344b	1.644a	2.954c	3.511c	2.828b
Korwood	3.397d	3.312a	1.243b	1.601a	2.625d	3.635bc	2.635c
Ogle	3.786c	3.436a	1.585a	1.622a	3.711a	3.927a	3.011a
Pacer	3.816bc	3.216a	1.446ab	1.632a	3.273b	3.445c	2.805b
Porter	3.974ab	3.363a	1.310b	1.490a	3.346b	3.753ab	2.872b
Mean‡	3.802a	3.361b	1.385e	1.598d	3.182c	3.654a	

† Within locations, means followed by the same letter are not significantly different at P = 0.05 according to Duncan's new multiple range test.
‡ Means across cultivars or across locations and years followed by the same letter are not significantly different at P = 0.05 according to Duncan's new multiple range test.

location interaction was also significant.

The effect of N level on grain yield was not significant in the analysis of variance combined across locations and years due to the high N × year interaction (Table 10). The overall yield response to increased N is presented in Figure 2. Yields tended to increase from 0 to 37 kg ha^{-1} applied N, but decreased at the 74 kg ha^{-1} N treatment. This reduction was probably due mostly to increased lodging at the highest level of N, but reduced grain yields have been observed with high N levels even in the absence of lodging (Brinkman and Rho, 1984).

Yield differences among cultivars were not significant in the combined analysis of variance due to high cultivar × year and cultivar × location interactions (Table 10). Differences among cultivars in the individual analyses of variance were significant for all environments except Caro in 1987 and 1988 (Table 11). Ogle had the highest overall yield, followed by Porter, Heritage, Pacer, and Korwood (Table 11).

Groat Weight

There was a tendency for groat weight to decrease slightly as N level increased (Figure 2), but this reduction was not significant (Table 10). Frey (1959) and Ohm (1976) reported small but nonsignificant decreases in seed weight with increased soil N. Brinkman and Rho (1984) also

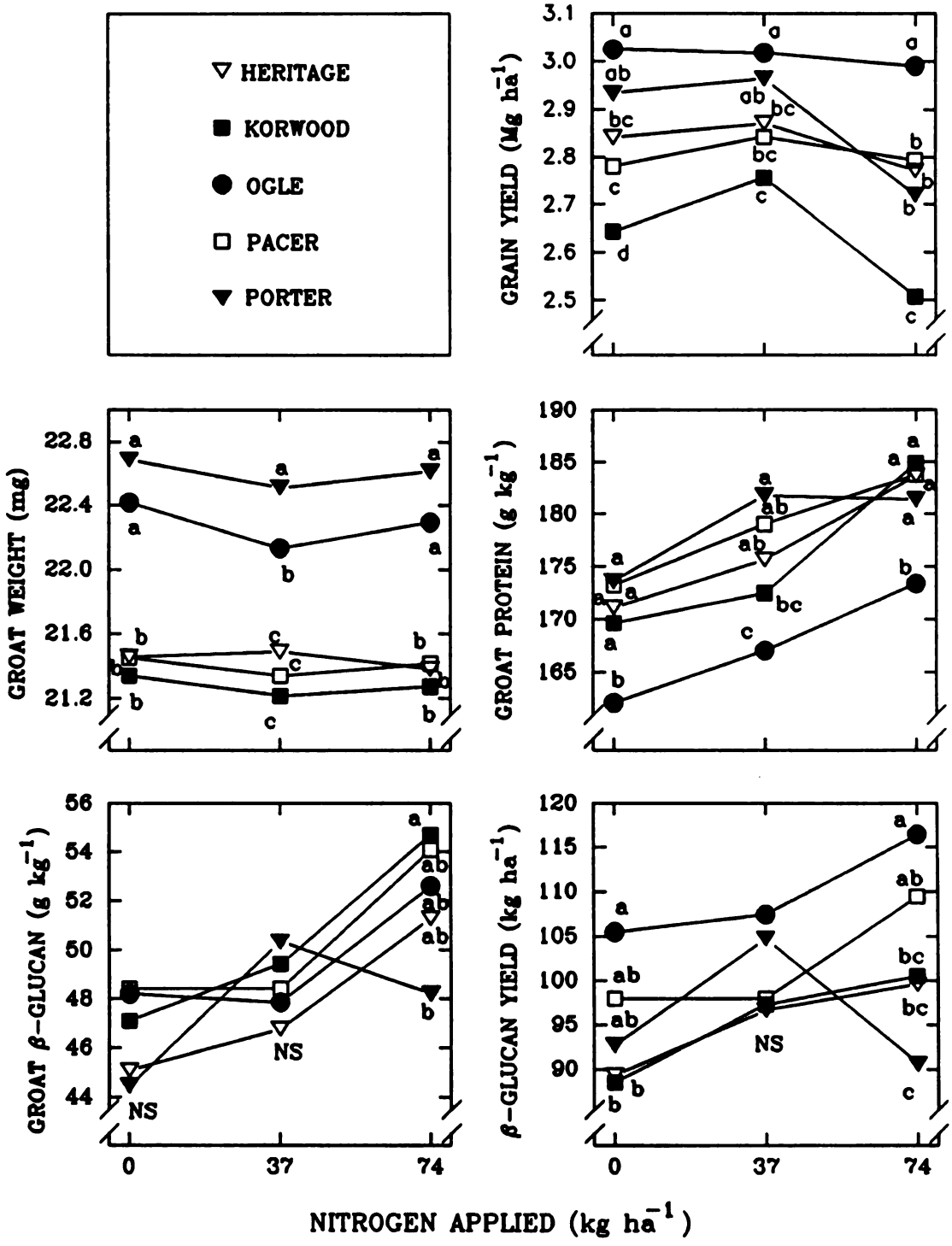

Figure 2. Responses of five traits to three levels of applied N. Values represent means of two locations and three years. At each level of N, Duncan's new multiple range test values characterize differences among varieties at P = 0.05.

observed small reductions in seed weight with increased soil N, but did not report statistical significance.

The effect of years on mean groat weight was highly significant (Table 10), with highest groat weights in 1987, when adequate moisture was available throughout the growing season (Table 12). Groat weights were lower in 1989 than in 1987, probably due to dry conditions at grain filling, and lowest in the droughty 1988 growing season. Differences between locations were significant in 1987 and 1988, and the year × location interaction was also significant. Mean groat weight was higher at East Lansing in 1987, and higher at Caro in 1988 (Table 12). Cultivar × year, cultivar × year × location, and N × cultivar × year interactions were all significant (Table 10). Porter had the highest mean groat weight, followed by Ogle, Heritage, Pacer, and Korwood (Table 12).

Groat Protein Content

The effect of years on groat protein content was highly significant (Table 10). Groat protein content appeared to be related to water availability. Protein levels were highest in 1988, the growing season in which severe water deficits occurred. Lowest protein contents were found in 1989, the year of greatest rainfall, and intermediate protein levels were observed in 1987, a growing season with moderate precipitation.

Table 12. Groat weight means for five oat cultivars grown at East Lansing (EL) and Caro, 1987 to 1989.

Cultivar	1987		1988		1989		Mean‡
	EL	Caro	EL	Caro	EL	Caro	
	mg						
Heritage	24.9ab†	24.1b	20.1a	20.6a	19.7c	19.4c	21.4c
Korwood	24.7ab	23.2c	18.3c	19.2b	20.8b	21.5b	21.3c
Ogle	24.1b	25.1a	19.1b	20.5a	22.4a	22.6a	22.3b
Pacer	25.2a	24.0b	19.8a	20.5a	19.8c	19.1c	21.4c
Porter	25.3a	24.9a	20.3a	20.9a	22.0a	22.3a	22.6a
Mean‡	24.8a	24.2b	19.5e	20.3d	20.9c	21.0c	

† Within locations, means followed by the same letter are not significantly different at P = 0.05 according to Duncan's new multiple range test.
‡ Means across cultivars or across locations and years followed by the same letter are not significantly different at P = 0.05 according to Duncan's new multiple range test.

Nitrogen level was significant in the analysis of variance combined across locations and years (Table 10). Groat protein concentration increased at higher soil N levels (Figure 2). Similar increases in grain protein content with applied N have been reported for oat (Ohm, 1976; Youngs and Gilchrist, 1976), wheat (Hucklesby et al., 1971; MacLeod and MacLeod, 1975) and barley (Atkins et al., 1955; Gately, 1968; Pomeranz et al., 1976). The effect of location was significant only in 1989, with higher groat protein levels at Caro (Table 13). Differences in protein content among cultivars were significant for all environments (Table 13). Porter had the highest protein concentration across locations and years, followed by Pacer, Heritage, Korwood, and Ogle. Cultivar × year and cultivar × location interactions were significant (Table 10).

Groat β-Glucan Content

The effect of year on groat β-glucan concentration was highly significant (Table 10). Mean β-glucan content in 1989 was 14% higher than in 1987, and 31% higher than in 1988 (Table 14). Low β-glucan values in 1988 may have been related to high precipitation during the grain filling and ripening periods. Severe water deficits occurred early in the 1988 growing season, limiting vegetative development and stimulating early heading. Subsequently, both East Lansing

Table 13. Groat protein content means for five oat cultivars grown at East Lansing (EL) and Caro, 1987 to 1989.

Cultivar	1987		1988		1989		Mean‡
	EL	Caro	EL	Caro	EL	Caro	
	g kg^{-1}						
Heritage	173.6a†	177.9ab	185.3b	189.3a	159.1ab	175.6a	176.8a
Korwood	177.7a	172.3bc	179.4b	181.5ab	168.6a	174.5a	175.7a
Ogle	162.1b	167.1c	181.6b	172.7b	156.9b	164.5b	167.5b
Pacer	175.7a	182.6a	187.8ab	190.0a	163.6ab	172.4ab	178.7a
Porter	171.7a	173.2bc	195.2a	188.4a	168.5a	176.6a	178.9a
Mean‡	172.2b	174.6b	185.9a	184.4a	163.3c	172.7b	

† Within locations, means followed by the same letter are not significantly different at P = 0.05 according to Duncan's new multiple range test.
‡ Means across cultivars or across locations and years followed by the same letter are not significantly different at P = 0.05 according to Duncan's new multiple range test.

Table 14. Groat β-glucan content means for five oat cultivars grown at East Lansing (EL) and Caro, 1987 to 1989.

Cultivar	1987		1988		1989		
	EL	Caro	EL	Caro	EL	Caro	Mean‡
	g kg^{-1}						
Heritage	53.4a†	47.8a	34.9b	41.9a	57.5a	62.5a	47.6a
Korwood	59.6a	48.4a	47.9a	37.7a	58.5a	59.0ab	50.4a
Ogle	54.8a	48.0a	48.6a	40.7a	56.9a	53.8b	49.6a
Pacer	55.3a	49.4a	38.4b	41.0a	66.5a	61.9a	50.2a
Porter	54.4a	43.7a	44.6a	37.3a	59.0a	54.6b	47.6a
Mean‡	53.8b	46.6c	41.5d	39.4d	58.8a	57.9a	

† Within locations, means followed by the same letter are not significantly different at P = 0.05 according to Duncan's new multiple range test.
‡ Means across cultivars or across locations and years followed by the same letter are not significantly different at P = 0.05 according to Duncan's new multiple range test.

and Caro received ≈46 mm rainfall in the 16 d period prior to harvest. Considerably less preharvest precipitation occurred in 1987 and 1989 (data not shown). Several workers have speculated that drought conditions may be related to increased β-glucan concentration in barley (Bendelow, 1975; Bourne and Wheeler, 1984; Åman and Graham, 1987) and oat (Welch et al., 1991). In separate reports, Aastrup (1979) and Coles (1979) both reported that overhead watering of barley plants resulted in lower grain β-glucan levels than if the same amount of water was delivered to the roots. Peterson (1991) observed a significantly higher mean β-glucan concentration for oat cultivars grown under dryland vs. irrigated conditions at two locations in Idaho.

In this study, drought occurred during vegetative and early reproductive growth periods in 1988, however, rainfall was high during grain ripening. Precipitation during the grain ripening period may have contributed to the low observed groat β-glucan contents in 1988. Several possible mechanisms by which β-glucan levels may be reduced as a result of rain were suggested by Aastrup (1979), and include (1) degradation of β-glucan, (2) reduced synthesis of β-glucan, (3) modification of the β-glucan to yield polymers inaccessible to the β-glucanase used for the β-glucan determinations, and (4) leaching of the glucose, a precurser of β-glucan, from the flag leaf and awns. More highly controlled studies need to be carried out to determine the

effect of amount and timing of precipitation on β-glucan content in oat grain. If preharvest rainfall proves to be a significant factor in reducing groat β-glucan concentration, then oat crops grown specifically for β-glucan content might be more successful in regions which experience consistently low preharvest precipitation. If the physiological basis for reduced β-glucan with rainfall can be determined, it may be possible to identify oat genotypes which are less affected by this factor.

Differences in groat β-glucan concentration between locations were not significant (Table 10).

Groat β-glucan content increased at higher levels of applied N (Figure 2), however, N level was not significant in the analysis of variance across locations and years due to high N × year and N × location interactions (Table 10). Elevated groat β-glucan levels with increased N fertilizer could possibly be related to an increase in relative thickness of endosperm cell walls, or to a larger ratio of endosperm cell wall to cell content. In 1987 and 1988, groat β-glucan content increased significantly as applied N increased from 0 to 74 kg ha^{-1}, but differences were not significant in 1989 (Figure 3a). Figure 3b illustrates the N × location interaction. At East Lansing, groat β-glucan content at the 74 kg ha^{-1} N treatment was significantly higher than at the 0 and 37 kg ha^{-1} N levels, which were not significantly different. At Caro, on the other hand, the

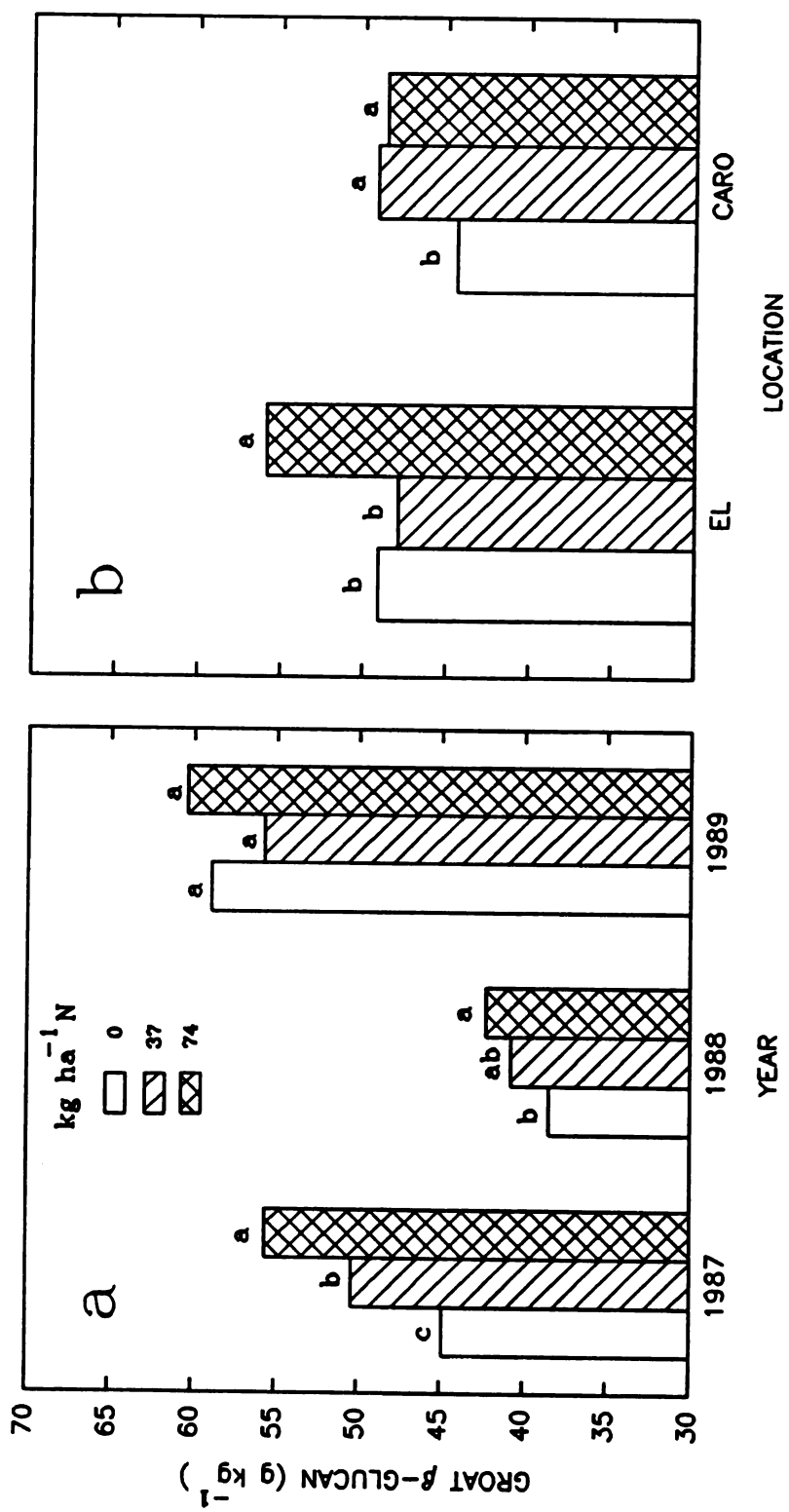

Figure 3. Effect of (a) N x year and (b) N x location interactions on groat β-glucan content. Means at each year and at each location are separated by Duncan's new multiple range test at P = 0.05.

groat β-glucan level at the 0 kg ha^{-1} N treatment was significantly lower than the other two N levels, which were not significantly different.

There were few differences in β-glucan content among the five cultivars used in this study (Table 14). Groat β-glucan levels were significantly lower for Pacer and Heritage in the 1988 East Lansing environment, and for Porter and Ogle in the 1989 Caro environment. Cultivar × year and cultivar × location interactions were significant (Table 10). Other workers have reported genotype × environment interactions for β-glucan content in oat (Peterson, 1991) and barley (Bendelow, 1975; Greenberg, 1977).

β-Glucan Yield

β-glucan yield is a function of total groat yield and groat β-glucan concentration. Since there was little variation for β-glucan content in the cultivars used in this study, β-glucan yield among cultivars was dependent primarily on groat yield. Takeda and Frey (1979) reported a similar relationship for groat protein. They found grain yield to be the primary determinant of protein yield. Protein percentage was negatively associated with grain yield and had little effect on total protein yield. Ogle had the highest mean β-glucan yield, followed by Pacer, Porter, Korwood, and Heritage (Table 15).

Table 15. β-glucan yield means for five oat cultivars grown at East Lansing (EL) and Caro, 1987 to 1989.

Cultivar	1987		1988		1989		Mean‡
	EL	Caro	EL	Caro	EL	Caro	
	kg ha^{-1}						
Heritage	161.1a†	121.9a	36.3c	53.1a	135.8b	177.8a	95.1b
Korwood	159.3a	121.4a	48.9b	46.9a	126.4b	167.4a	95.3b
Ogle	166.2a	127.1a	62.6a	52.9a	168.0a	166.9a	109.7a
Pacer	161.2a	117.6a	44.5bc	51.0a	172.2a	174.1a	101.6ab
Porter	165.4a	109.9a	47.2b	43.8a	151.8ab	157.5a	95.7b
Mean‡	156.7a	116.7b	44.4c	48.1c	147.2a	167.1a	

† Within locations, means followed by the same letter are not significantly different at P = 0.05 according to Duncan's new multiple range test.
‡ Means across cultivars or across locations and years followed by the same letter are not significantly different at P = 0.05 according to Duncan's new multiple range test.

Significant differences for β-glucan yield were observed among years (Table 10). Highest β-glucan yields were achieved in the cool, moist 1989 growing season (Table 15). Mean 1989 β-glucan yield was 13% greater than in 1987, and 71% greater than in 1988.

β-glucan yield tended to increase from 0 to 74 kg ha^{-1} applied N in all cultivars except Porter (Figure 2), however differences among N levels were significant only in 1987. Nitrogen level was not significant in the analysis of variance combined across locations and years (Table 10). The N × year and cultivar × year × location interactions were significant (Table 10). The N × year interaction is illustrated in Figure 4.

Correlations

Consistent and high correlations between traits is desirable in breeding because it may permit indirect selection for a characteristic for which quantification is difficult, time consuming, or costly, such as grain β-glucan content. Correlation coefficients between groat β-glucan concentration and other characteristics are presented in Table 16. Groat β-glucan content was not associated with test weight of hull percentage at any of the environments studied. Grain yield had a low positive correlation with β-glucan concentration at two environments, and a low negative correlation at another. Low negative correlations between

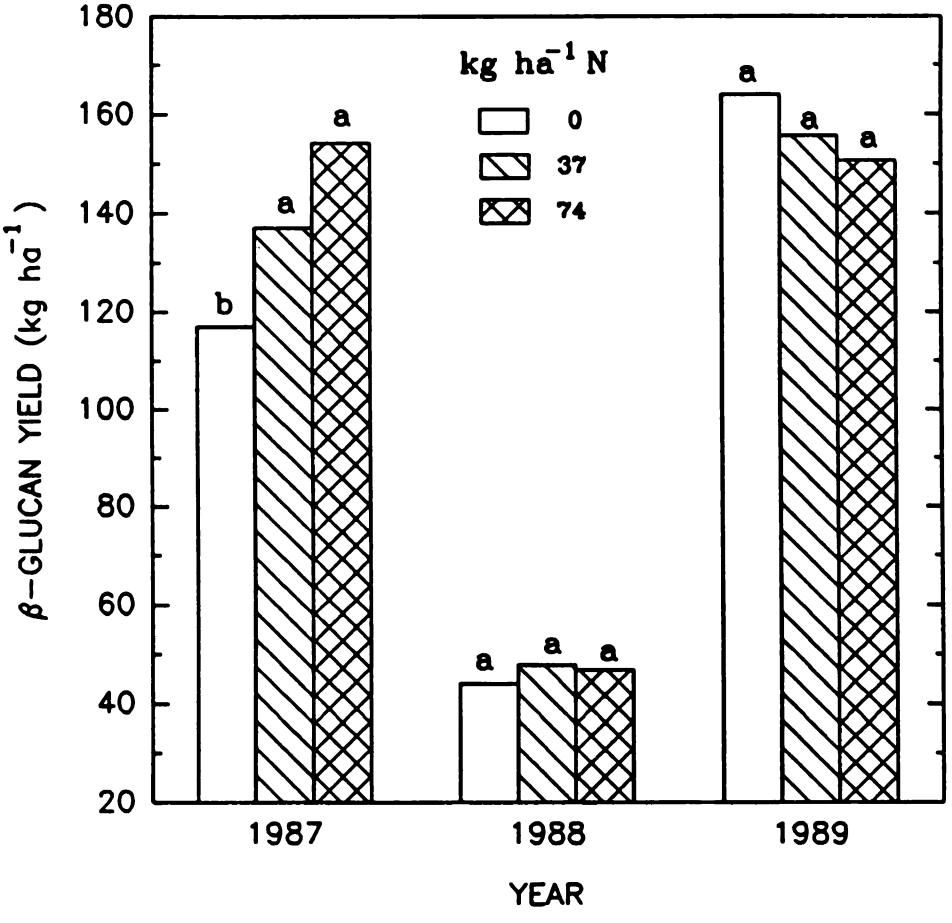

Figure 4. N × year interaction for β-glucan yield. Means at each year are separated by Duncan's new multiple range test at P = 0.05.

Table 16. Correlation coefficients (r) between groat β-glucan concentration and grain yield, test weight, hull percentage, mean groat weight, and groat protein content for East Lansing (EL) and Caro, 1987 to 1989.

	1987		1988		1989	
Variable	EL	Caro	EL	Caro	EL	Caro
Grain yield	0.08	0.29†	0.26†	-0.02	-0.08	-0.25†
Test weight	0.00	-0.10	-0.23	0.13	-0.13	-0.22
Hull percentage	-0.18	0.03	-0.07	0.13	-0.11	-0.17
Groat weight	0.02	-0.06	-0.25†	-0.09	-0.13	-0.43**
Protein content	0.72***	0.35*	-0.13	0.17	0.30*	0.57***

†,*,**,*** Significant at P = 0.1, 0.05, 0.01, and 0.001, respectively.

groat weight and β-glucan content were detected at East Lansing in 1988 and Caro in 1989. This may have occurred because small groats could have a higher ratio of cell wall to cell content than larger groats, and β-glucan is the primary component of endosperm cell walls. Higher correlations were found between β-glucan concentration and groat protein content than any other trait examined. Correlations of 0.72*** and 0.35* were observed for East Lansing and Caro, respectively, in 1987. In 1989, correlations between β-glucan and protein were 0.30* and 0.57*** for East Lansing and Caro, respectively. Correlations between groat protein and β-glucan concentration were not significant in 1988.

Åman (1987) found no significant correlations between β-glucan content and arabinoxylans, cellulose, Klason lignin, crude fiber, or thousand kernel weight in 121 oat samples. Welch and Lloyd (1989) reported nonsignificant correlations between β-glucan concentration and mean kernel weight or percent protein, and a significant but low negative correlation between β-glucan content and kernel oil in oat. Peterson (1991) observed no correlation between groat β-glucan content and 100 groat weight. In barley, Henry (1985,1986) found correlations between β-glucan and arabinose, xylose, or glucose to be nonsignificant, while significant but small positive correlations between β-glucan and grain N and grain hardness were observed.

Selection for high protein would be expected to be somewhat effective in selecting indirectly for high β-glucan concentration in oat, but not in every environment, e.g., in 1988 correlations between β-glucan and protein were small and nonsignificant (Table 16). High rainfall during grain ripening may reduce groat β-glucan content. A similar decrease in protein level would probably not occur since kernel dry matter, including protein, is largely deposited before the majority of β-glucan is synthesized in endosperm cell walls (Åman et al., 1989). Small or nonsignificant correlations between β-glucan content and grain yield, test weight, hull percentage, or groat weight suggest that none of these other traits would be useful for indirect selection of groat β-glucan. Indirect selection for high β-glucan concentration could be facilitated if morphological, isozyme, RFLP, or RAPD markers linked to genes controlling β-glucan content could be identified. On the other hand, lack of significant phenotypic correlations between groat β-glucan concentration and the other measured characteristics should allow selection for high β-glucan without affecting the other traits.

SUMMARY AND CONCLUSIONS

The effects of N level, location, and year on grain β-glucan content and other traits were examined in five oat cultivars. Considerable climatic variation occurred among years the study was conducted; this variability was an important factor affecting crop performance and grain quality.

Adequate moisture and moderate temperatures contributed to good crop performance in 1987. Test weight, hull percentage, groat weight, and grain yield were highest in 1987. Severe water deficits and warm temperatures occurred in the 1988 growing season, which limited vegetative growth and tillering and caused early heading. Drought was followed by high rainfall during grain filling and ripening. In 1988, groat protein concentration was highest, however lowest mean values for test weight, hull percentage, grain yield, groat weight, groat β-glucan concentration, and β-glucan yield were observed in this growing season. The 1989 growing season, generally cool and moist, was conducive to vegetative growth and tillering. Conditions were relatively dry during grain filling and ripening. Grain yield, β-glucan

concentration, and β-glucan yield were high in 1989, but test weight, hull percentage, and protein content were low.

Differences between locations were observed for test weight, hull percentage, grain yield, groat weight, protein content, and β-glucan yield. These differences were probably caused by climatic and edaphic variation between the East Lansing and Caro sites. Groat β-glucan concentrations were not significantly different between locations. Precipitation is probably the most important climatic variable affecting β-glucan content. Edaphic factors, with the exception of soil N, do not appear to significantly influence groat β-glucan concentration.

Increased levels of applied N tended to reduce test weight and hull percentage, while increasing grain yield, groat protein content, groat β-glucan content, and β-glucan yield. Nitrogen application had no significant effect on groat weight, although there was a tendency for groat weight to decrease slightly as N level increased. No significant differences in mean β-glucan concentration were found among the five oat cultivars used in the study. Pacer had the highest mean test weight, Porter the highest groat weight and protein content, and Ogle the highest grain yield and β-glucan yield, and lowest hull percentage.

Correlations between groat β-glucan content and grain yield were small and positive at two environments, and small and negative at another environment. No significant corre-

lations were found between β-glucan concentration and test weight or hull percentage. Groat weight had small negative correlations with groat β-glucan at two environments. Groat protein content had relatively large positive correlations with groat β-glucan concentration in 1987 and 1989, but correlations were nonsignificant in 1988. With the possible exception of groat protein content, none of the traits examined would be useful for indirect selection of high β-glucan content. On the other hand, selection for increased groat β-glucan should be possible without affecting the other characteristics.

Grain yield was more important than groat β-glucan concentration in determining β-glucan yield of the five oat cultivars examined. Based on the results of this study, it appears that the best strategy to increase total β-glucan yield of current commercial oat cultivars is to maximize total grain yield. Significant increases in total β-glucan yields via genetic enhancement of groat β-glucan concentration are likely to occur only if newly developed cultivars are also high-yielding. High groat β-glucan concentration is, however, an important quality component of oat grain that is produced for direct human consumption. Through breeding and the application of appropriate agronomic management practices, the desired goal of oat grain with increased β-glucan levels for food products should be attainable.

LIST OF REFERENCES

Aastrup, S. 1979. The effect of rain on β-glucan content in barley grains. Carlsberg Res. Commun. 44:381-393.

Åman, P. 1986. A note on the content of mixed-linked β–glucans in Swedish barley. Swedish J. Agric. Res. 16:73-75.

Åman, P. 1987. The variation in chemical composition of Swedish oats. Acta Agric. Scand. 37:347-352.

Åman, P. and H. Graham. 1987. Analysis of total and insoluble mixed-linked (1→3),(1→4)-β-D-glucans in barley and oats. J. Agric. Food Chem. 35:704-709.

Åman, P., H. Graham, and A.-C. Tilly. 1989. Content and solubility of mixed-linked (1→3),(1→4)-β-D-glucan in barley and oats during kernel development and storage. J. Cereal Sci. 10:45-50.

Anderson, J.W. and W.L. Chen. 1986. Cholesterol-lowering properties of oat products. p. 309-333. *In* F.H. Webster (ed.) Oats: Chemistry and technology. American Association of Cereal Chemists, Inc., St. Paul, MN.

Atkins, R.E., G. Stanford, and L. Dumenil. 1955. Effects of nitrogen and phosphorus fertilizer on yield and malting quality of barley. Agric. Food Chem. 3:609-615.

Bendelow, V.M. 1975. Determination of non-starch polysaccharides in barley breeding programmes. J. Inst. Brew. 81:127-130.

Bourne, D.T. and J.S. Pierce. 1970. β-glucan and β-glucanase in brewing. J. Inst. Brew. 76:328-335.

Bourne, D.T. and R.E. Wheeler. 1984. Environmental and varietal differences in total β-glucan contents of barley and the effectiveness of its breakdown under different malting conditions. J. Inst. Brew. 90:306-310.

Brinkman, M.A. and Y.D. Rho. 1984. Response of three oat cultivars to N fertilizer. Crop Sci. 24:973-977.

Coles, G. 1979. Relationship of mixed-link beta-glucan accumulation to accumulation of free sugars and other glucans in the developing barley endosperm. Carlsberg Res. Commun. 44:439-453.

Davidson, M.H., L.D. Dugan, J.H. Burns, J. Bova, K. Story, and K.B. Drennan. 1991. The hypocholesterolemic effects of β-glucan in oatmeal and oat bran: A dose-controlled study. JAMA 265:1833-1839.

DeGroot, A.P., R. Luyken, and N.A. Pikaar. 1963. Cholesterol-lowering effect of rolled oats. Lancet 2:303-304.

Frey, K.J. 1959. Yield components in oats. II. The effect of nitrogen fertilization. Agron. J. 51:605-608.

Gately, T.F. 1968. The effects of different levels of N, P and K on the yields, nitrogen content and kernel weights of malting barley (var. Proctor). J. Agric. Sci., Camb. 70:361-367.

Greenberg, D.C. 1977. A diallel cross analysis of gum content in barley (*Hordeum vulgare*). Theor. Appl. Genet. 50:41-46.

Henry, R.J. 1985. A comparative study of the total β-glucan contents of some Australian barleys. Aust. J. Exp. Agric. 25:424-427.

Henry, R.J. 1986. Genetic and environmental variation in the pentosan and β-glucan contents of barley, and their relation to malting quality. J. Cereal Sci. 4:269-277.

Hucklesby, D.P., C.M. Brown, S.E. Howell, and R.H. Hageman. 1971. Late spring applications of nitrogen for efficient utilization and enhanced production of grain and grain protein of wheat. Agron. J. 63:274-276.

Johnson, V.A., A.F. Dreier, and P.H. Grabouski. 1973. Yield and protein responses to nitrogen fertilizer of two winter wheat varieties differing in inherent protein content of their grain. Agron. J. 65:259-263.

Kahlon, T.S, R.M. Saunders, F.I. Chow, M.M. Chiu, and A.A. Betschart. 1990. Influence of rice bran, oat bran, and wheat bran on cholesterol and triglycerides in hamsters. Cereal Chem. 67:439-443.

Kestin, M., R. Moss, P.M. Clifton, and P.J. Nestel. 1990. Comparative effects of three cereal brans on plasma lipids, blood pressure, and glucose metabolism in mildly hypercholesterolemic men. Am. J. Clin. Nutr. 52:661-666.

Kirby, R.W., J.W. Anderson, B. Sieling, E.D. Rees, W.L. Chen, R.E. Miller, and R.M. Kay. 1981. Oat-bran intake selectively lowers serum low-density lipoprotein cholesterol concentrations of hypercholesterolemic men. Am. J. Clin. Nutr. 34:824-829.

Lehtonen, M. and R. Aikasalo. 1987. β-glucan in two- and six-rowed barley. Cereal Chem. 64:191-192.

MacLeod, J.A., and L.B. MacLeod. 1975. Effects of spring N application on yield and N content of four winter wheat cultivars. Can. J. Plant Sci. 55:359-362.

McCleary, B.V. and M. Glennie-Holmes. 1985. Enzymic quantification of (1→3)(1→4)-β-D-glucan in barley and malt. J. Inst. Brew. 91:285-295.

McIntosh, M.S. 1983. Analysis of combined experiments. Agron. J. 75:153-155.

Molina-Cano, J.L. and J. Conde. 1982. Genetic and environmental variation of gum content in barley. J. Inst. Brew. 88:30-33.

Murphy, C.F. 1987. Report of oat enhancement work session. Madison, WI. 16 Oct. 1987. USDA, Beltsville, MD.

Ohm, H.W. 1976. Response of 21 oat cultivars to nitrogen fertilization. Agron. J. 68:773-775.

Peterson, D.M. 1991. Genotype and environment effects on oat beta-glucan concentration. Crop Sci. 31:1517-1520.

Pomeranz, Y., N.N. Standridge, E.A. Hockett, D.M. Wesenberg, and G.D. Booth. 1976. Effects of nitrogen fertilizer on malting quality of widely varying barley cultivars. Cereal Chem. 53:574-585.

Portch, S., A.F. McKenzie, and H.A. Steppler. 1968. Effect of fertilizers, soil drainage class and year upon protein yield and content of oats. Agron. J. 60:672-674.

Ranhotra, G.S., J.A. Gelroth, K. Astroth, and C.S. Rao. 1990. Relative lipidemic responses in rats fed oat bran or oat bran concentrate. Cereal Chem. 67:509-511.

Shinnick, F.L., S.L. Ink, and J.A. Marlett. 1990. Dose response to a dietary oat bran fraction in cholesterol-fed rats. J. Nutr. 120:561-568.

Steel, R.G.D. and J.H. Torrie. 1980. Principles and procedures of statistics. McGraw-Hill, NY.

Stinard, P.S. and D.J. Nevins. 1980. Distribution of noncellulosic β-D-glucans in grasses and other monocots. Phytochem. 19:1467-1468.

Takeda, K. and K.J. Frey. 1979. Protein yield and its relationship to other traits in backcross populations from an *Avena sativa* × *A. sterilis* cross. Crop Sci. 19:623-628.

Welch, R.W., J.M. Leggett, and J.D. Lloyd. 1991. Variation in the kernel (1→3)(1→4)-β-D-glucan content of oat cultivars and wild *Avena* species and its relationship to other characteristics. J. Cereal Sci. 13:173-178.

Welch, R.W. and J.D. Lloyd. 1989. Kernel (1→3)(1→4)-β-D-glucan content of oat genotypes. J. Cereal Sci. 9:35-40.

Wilkie, K.C.B. 1979. The hemicelluloses of grasses and cereals. p. 215-264. *In* R. Tipson and D. Horton (eds.) Advances in carbohydrate chemistry and biochemistry. Vol. 36. Academic Press, NY.

Wood, P.J. 1986. Oat β-glucan: Structure, location, and properties. p. 121-152. *In* F.W. Webster (ed.) Oats: Chemistry and technology. American Association of Cereal Chemists, St. Paul, MN.

Wood, P.J., D. Paton, and I.R. Siddiqui. 1977. Determination of β-glucan in oats and barley. Cereal Chem. 54:524-533.

Wood, P.J., J. Weisz, and P. Fedec. 1991. Potential for β-glucan enrichment in brans derived from oat (*Avena sativa* L.) cultivars of different (1→3),(1→4)-β-D-glucan concentrations. Cereal Chem. 68:48-51.

Youngs, V.L. and K.D. Gilchrist. 1976. Note on protein distribution within oat kernels of single cultivars that differ in protein concentration. Cereal Chem. 53:947-949.

CHAPTER TWO

HERITABILITY OF β-GLUCAN CONTENT IN OAT

ABSTRACT

β-glucan is a water-soluble fiber component of oat (*Avena sativa* L.) grain which has hypocholesterolemic properties. Despite beneficial physiological effects associated with oat β-glucan, heritability of this trait has not been investigated. An experiment was conducted to estimate broad sense heritability of β-glucan content in oat. Two different S_0-derived populations with nested family structure were developed from crosses between low and high β-glucan oat cultivars. Each population was planted separately in the field using a randomized complete block design with two replications. Population 1 resulted from the cross Garry × Hazel, and population 2 from the cross Garry × Marion. Garry is a low β-glucan cultivar, while Hazel and Marion have high groat β-glucan contents. A single plant was harvested from each plot at maturity and β-glucan content was determined. Variance components and heritabilities were calculated for each cross. Absence of discrete classes and normal frequency distributions of S_0-derived lines suggest

polygenic inheritance of groat β-glucan content. Population 2 had a high proportion of positive transgressive segregants, indicating that Marion appears to be a good source of genes for high β-glucan content. Broad sense heritabilities of 0.41 and 0.54 were observed for populations 1 and 2, respectively. Heritabilities of this magnitude are sufficient to expect genetic gain from selection.

INTRODUCTION

Heritability estimates are an important source of information for the plant breeder. An understanding of the magnitude of heritability of a trait facilitates determination of appropriate breeding and selection procedures, and helps predict the relative ease or difficulty of genetic improvement for that character (Hanson, 1963).

Mixed-linkage (1→3),(1→4)-β-D-glucan (β-glucan), a non-starchy, water-soluble polysaccharide, is an important quality component of oat grain. Numerous workers have demonstrated a hypocholesterolemic response when β-glucan or other water-soluble fibers are consumed by experimental animals (Kahlon et al., 1990; Ranhotra et al., 1990; Shinnick et al., 1990) or humans (DeGroot et al., 1963; Kirby et al., 1981; Anderson and Chen, 1986; Kestin et al., 1990; Davidson et al., 1991). Murphy (1987) cites the genetic enhancement of β-glucan content in oat as an important breeding objective to improve quality. Despite the significance of this trait, information concerning the heritability of β-glucan concentration in oat has not been reported.

Published heritability values for other biochemical quality traits in oat have exhibited a wide range of values

(Table 1). Groat oil content has the highest overall mean heritability (0.77), followed by niacin (0.70), fatty acids (0.54), protein (0.49), and riboflavin (0.38). In general, heritabilities for these characters are sufficiently high to permit genetic gain from selection.

Heritability estimates for β-glucan content in barley (*Hordeum vulgare* L.) have been intermediate to high. In the F_2 of a diallel cross using six spring barley cultivars, Greenberg (1977) found narrow and broad sense heritabilities of 0.37 and 0.74, respectively, for extract viscosity, a trait highly correlated with β-glucan content. Lance (1984) reported that most of the variability for β-glucan content in segregating barley populations was due to additive effects, and estimated a narrow sense heritability value of 0.73 based on parent-offspring regression of F_4 means on parental F_3 means. These results suggest that early generation selection for β-glucan content is possible in barley.

The objective of this study was to estimate genetic variances and broad sense heritabilities of groat β-glucan concentration in two segregating S_0-derived oat populations.

Table 1. Reported heritability estimates for various biochemical quality traits in oat.

Trait	Heritability		Method of calculation	Population	References
	Range	Mean			
Protein		0.15	VC_B†	F_2 plants	Frey et al., 1954
	0.88-0.90	0.89	VC_B	F_3 lines	Frey et al., 1955
	0.09-0.52	0.30	R‡	F_3-F_4	Campbell and Frey, 1972
	0.27-0.81	0.49	VC_B	F_2-derived lines	Campbell and Frey, 1972
	0.27-0.74	0.54	R	F_1-F_2	Ohm and Patterson, 1973a
		0.76	R	F_1-F_2	Ohm and Patterson, 1973b
	0.35-0.49	0.43	R	F_2-F_3, F_3-F_4, F_6-F_7	Frey, 1975
		0.41	VC_B	F_3 lines	Sraon et al., 1975
	0.27-0.53	0.39	VC_B	F_2-derived F_3 lines	Takeda and Frey, 1979
Oil	0.18-0.93	0.79	VC_B	F_4 lines	Baker and McKenzie, 1972
	0.59-0.79	0.74	VC_B	F_2 lines	Brown et al., 1974
Fatty acids	0.00-0.99	0.69	VC_B	15 cultivars	Youngs and Püskülcü, 1976
	0.30-0.72	0.59	VC_B	F_2-derived F_4 lines	Thro et al., 1985
	0.06-0.56	0.33	R	F_3-F_4	Thro et al., 1985
Niacin	0.42-0.58	0.50	VC_B	F_2 plants	Frey et al., 1954
	0.86-0.93	0.90	VC_B	F_3 lines	Frey et al., 1955
Riboflavin	0.39-0.58	0.49	VC_B	F_2 plants	Frey et al., 1954
	0.00-0.52	0.26	VC_B	F_3 lines	Frey et al., 1955

† Variance components, broad sense.
‡ Parent-offspring regression.

MATERIALS AND METHODS

Two S_0-derived populations with nested family structure were developed from crosses made in the greenhouse during March 1990 between oat genotypes with different groat β-glucan contents. Population 1 resulted from the cross Garry × Hazel, and population 2 from the cross Garry × Marion. Garry is a low β-glucan cultivar, while Hazel and Marion have high β-glucan contents (D.M. Peterson, 1989, personal communication). Thirty five F_1 seeds per cross were planted in 10 cm pots on 10 July 1990, and grown to maturity in the greenhouse. Twenty five F_1 plants were randomly selected and seed from individual plants was sown in the greenhouse on 4 Oct. 1990 to form 25 F_2 (S_0) lines. Single S_1 seeds from two randomly selected plants per S_0 line were harvested at maturity and planted individually in 10 cm pots in the greenhouse on 28 Dec. 1990. S_2 seed harvested from 50 individual S_1 plants per population comprised the lines used for heritability estimation.

Fifty random S_0-derived lines, the two parental cultivars, and a check variety were planted in the field at East Lansing on 3 May 1991. The experimental design utilized was a randomized complete block with two replications. Separate

experiments were planted for each population. Individual plots consisted of a 1 m row with 30 cm row spacing. Approximately 50 seeds were planted per plot. Plots were surrounded by a check cultivar to minimize border effects.

The soil at East Lansing is a Capac loam (fine-loamy, mixed, mesic Aeric Ochraqualfs). Fertilizer was incorporated prior to planting at a rate of 64 kg ha^{-1} N, 28 kg ha^{-1} P, and 53 kg ha^{-1} K. Plots were kept weed free by manual cultivation. Late planting due to early wet conditions was followed by warm, dry weather early in the growing season, which reduced tillering and caused early heading. Total precipitation during the growing season was 171 mm.

A single plant per plot was harvested at maturity, which corresponded to 19 July for population 2 and 26 July for population 1. Panicles were threshed, and seed dehulled in an impact type dehuller. Groat samples were ground in a Cyclone Sample Mill (U.D. Corp., Boulder, CO) fitted with a 0.5 mm screen. Flour samples were stored in air-tight containers at -20°C until used. β-glucan concentration was determined by the enzymatic method described by McCleary and Glennie-Holmes (1985) and modifified by McCleary and Codd (1991), using the Biocon β-glucan kit (Quest-Biocon, Sarasota, FL). Groat flour moisture was determined by oven drying samples at 80°C for 24 hr. Results are reported on a dry weight basis.

β-glucan data for S_0-derived lines of populations 1 and 2 were subjected to individual analyses of variance. The form of analysis of variance and expected mean squares are presented in Table 2. Variance components in the mean square expectations were equated to genetic variance components which were then estimated using weighted least squares. Broad sense heritability was calculated on a progeny mean basis, using the formula:

$$h^2 = \frac{\delta^2_G}{\delta^2/r + \delta^2_G}$$

where δ^2_G = genetic variance, δ^2 = error variance, and r = number of replications. Standard errors for heritability estimates were calculated according to Hallauer and Miranda (1988). A chi-square test and skewness and kurtosis values were used to assess normality of the frequency distributions of S_0-derived populations (Snedecor and Cochran, 1967). Comparisons were made between midparental values and population means using a *t* test appropriate for samples of unequal size (Snedecor and Cochran, 1967). Differences between parental and transgressive segregant means were evaluated using the Mann-Whitney test.

Table 2. Source, degrees of freedom, and expected mean squares for the nested analysis of variance.

Source	DF†	Expected mean squares
Replications	$r-1$	
S_0-derived	n_0-1	$\delta^2_\epsilon + r\delta^2_{S1(S0)} + rn_1\delta^2_{S0}$
S_1 in S_0	$n_0(n_1-1)$	$\delta^2_\epsilon + r\delta^2_{S1(S0)}$
Error	$(r-1)(n_0n_1-1)$	δ^2_ϵ

† r = number of replications, n_0 = number of S_0 families, n_1 = number of S_1 families per S_0 family.

RESULTS AND DISCUSSION

Mean groat β-glucan values for populations 1 and 2 and their respective parental cultivars are presented in Table 3. Discrete classes are not apparent in frequency distributions for groat β-glucan content of S_0-derived lines, suggesting polygenic inheritance of this trait (Figure 1). In barley, Greenberg (1977) reported β-glucan content to be controlled by two or three genes, and Lance (1984) estimated control by four additive genes and a few but undetermined number of dominant genes. Powell et al. (1985) determined the number of effective factors for β-glucan content in spring barley crosses to be three to five. Chi-square, skewness, and kurtosis values were not significant ($P = 0.05$) for either population, indicating normality of the frequency distributions. As pointed out by Rosielle and Frey (1977), symmetrical and normal frequency distributions are compatible with additive gene action. Additive gene effects for β-glucan content have been shown to be important in barley (Greenberg, 1977; Lance, 1984; Powell et al., 1985).

In the absence of linkage, agreement of cross means with midparental means suggests additive gene action is

Table 3. Mean groat β-glucan content and standard errors for the crosses Garry × Hazel and Garry × Marion and their respective parental cultivars grown at East Lansing in 1991.

Population	β-glucan content	n
	—— g kg^{-1} ——	
Garry × Hazel	48.1 ± 4.4	50
Garry × Marion	56.9 ± 4.3	50
Garry	44.7 ± 1.1	6
Hazel	71.8 ± 0.9	4
Marion	59.0 ± 2.2	4

present (Mather and Jinks, 1971). A positive but nonsignificant (P = 0.05) deviation of 8.8% was observed for the mean of population 2 from its midparental value (Figure 1). The mean of population 1, however, had a large, significant (P = 0.001) deviation of -17.5% from the midparental mean. This deviation could be due to dominance with or without epistatic gene action, or to linkage of unfavorable alleles determining β-glucan content. Pixley and Frey (1991) observed significant negative deviations of population means from midparental means for test weight and grain yield, and cited several reports of dominance and additive × additive epistasis for other quantitative traits in oat.

The proportion of transgressive segregants with significantly lower or higher groat β-glucan content than the respective low or high parent varied with the cross. In population 1, 16% of the lines had significantly lower groat β-glucan concentrations than the low parent (Garry), and no positive transgressive segregants were observed (Figure 1).

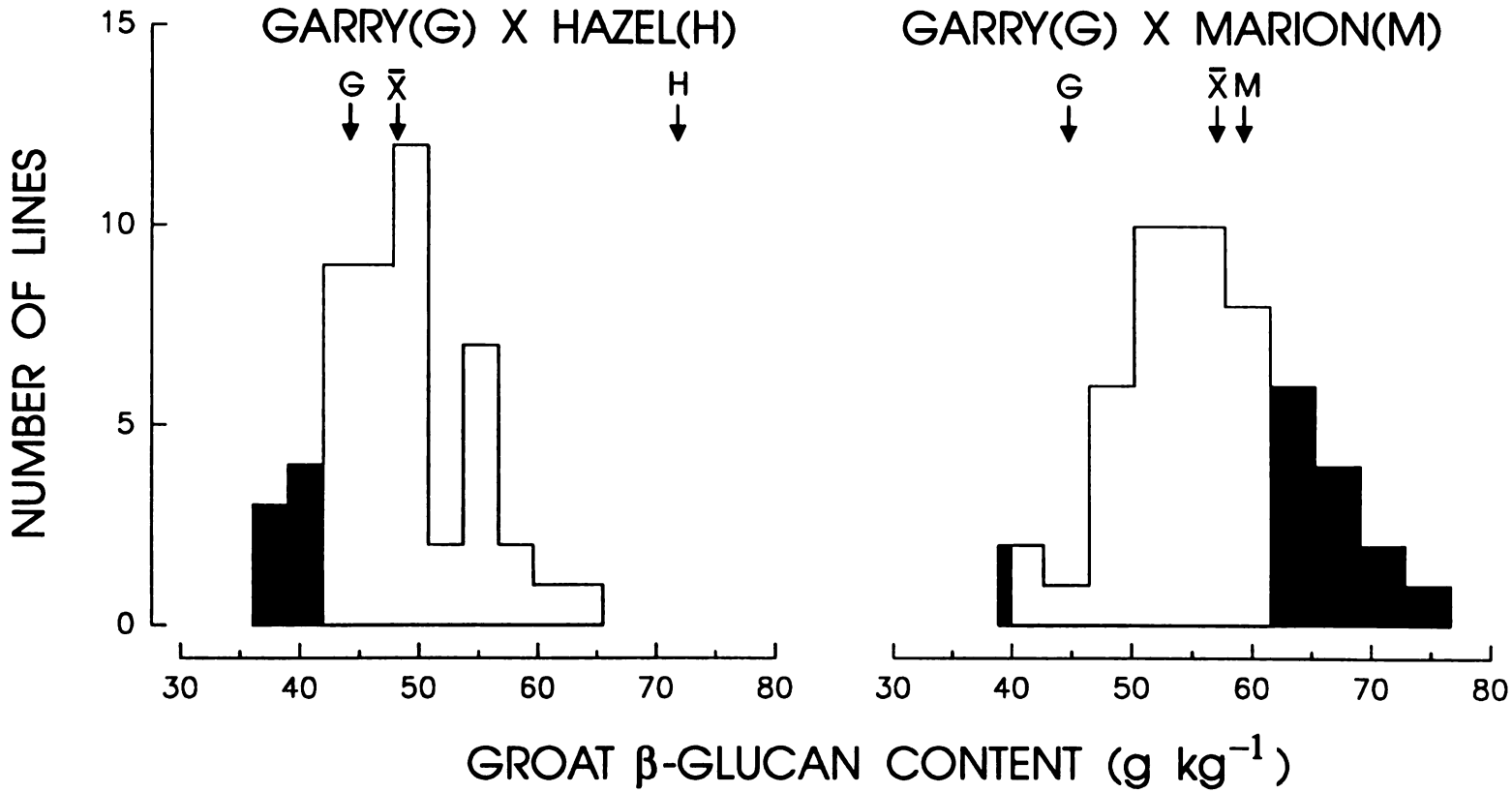

Figure 1. Frequency distributions for groat β-glucan content of S_0-derived lines from crosses Garry x Hazel and Garry x Marion. Black areas represent transgressive segregants with significantly lower or higher mean β-glucan values than the respective low or high parental means.

Negative transgressive segregation was observed in only 2% of the lines in population 2, whereas 26% of the lines had higher β-glucan levels than the high parent (Marion). The most extreme positive transgressive segregant in population 2 had 23% higher β-glucan concentration than Marion. The high proportion of positive transgressive segregants in population 2 suggests that lines with high β-glucan content could be obtained from crosses utilizing Marion as a parent.

Variance components and broad sense heritabilities are presented in Table 4. Heritabilities of β-glucan concentration reported in this study are lower than heritability estimates of β-glucan in barley (Greenberg, 1977; Lance, 1984), and are of similar magnitude to those reported for protein content in oat (Table 1). Since evaluation of β-glucan concentration was carried out in advanced (F_4) lines, dominance variance is expected to be small, and most genetic variance should be additive. Therefore, observed heritabilities may approximate narrow sense values.

Heritability values reported in this study may be biased upward because the estimate of genetic variance was obtained in one year at one location. Thus, the estimate of genetic variance includes δ^2_{GYL}, δ^2_{GL}, and δ^2_{GY} in addition to δ^2_G (Dudley and Moll, 1969). Genotype × environment interaction for groat β-glucan content appears to be important in oat. Peterson (1991) reported a significant genotype × location interaction for β-glucan content in oat, and

Table 4. Genetic (δ^2_G) and error (δ^2) variance components and broad sense heritabilities (h^2) for groat β-glucan content in two oat crosses.

Population	δ^2_G	δ^2	$h^2 \pm SE$
Garry × Hazel	13.51	39.38	0.41 ± 0.01
Garry × Marion	22.80	38.34	0.54 ± 0.24

Brunner (1992) observed significant genotype × location and genotype × year interactions for groat β-glucan.

Heritabilities estimated in this study are of sufficient magnitude to expect genetic gain from selection. Because heritability values are intermediate, and genotype interactions with environment are probably important, selection for β-glucan content in oat should be based on replicated trials in advanced generations.

SUMMARY AND CONCLUSIONS

Genetic variances and broad sense heritabilities were estimated in two segregating S_0-derived oat populations developed from crosses between cultivars with different groat β-glucan concentrations. Population 1 resulted from the cross Garry (low) × Hazel (high), and population 2 from the cross Garry (low) × Marion (high).

Normal frequency distributions of S_0-derived lines and absence of discrete classes suggest polygenic inheritance of groat β-glucan content. Population 2 had a high proportion of positive transgressive segregants, indicating that Marion appears to be a good source of genes for high β-glucan content.

Broad sense heritabilities of 0.41 and 0.54 were observed for populations 1 and 2, respectively. These values may be biased upward because the estimate of genetic variance was obtained in one year at one location, and evidence suggests genotype × environment interactions are important.

Heritabilities estimated in this study are of sufficient magnitude to expect genetic advance from selection. Since heritabilities were intermediate, and genotype × environment interactions appear to be important, selection

for β-glucan content in oat should be based on replicated trials in advanced generations.

LIST OF REFERENCES

Anderson, J.W. and W.L. Chen. 1986. Cholesterol-lowering properties of oat products. p. 309-333. *In* F.H. Webster (ed.) Oats: Chemistry and technology. American Association of Cereal Chemists, Inc., St. Paul, MN.

Baker, R.J. and R.I.H. McKenzie. 1972. Heritability of oil content in oats, *Avena sativa* L. Crop Sci. 12:201-202.

Brown, C.M., A.N. Aryeetey, and S.N. Dubey. 1974. Inheritance and combining ability for oil content in oats (*Avena sativa* L.). Crop Sci. 14:67-69.

Brunner, B.R. 1992. Oat grain β-glucan content and other traits as affected by nitrogen level, location, and year. Ph.D. Dissertation, Chapter 1.

Campbell, A.R. and K.J. Frey. 1972. Inheritance of groat protein in interspecific oat crosses. Can. J. Plant Sci. 52:735-742.

Davidson, M.H., L.D. Dugan, J.H. Burns, J. Bova, K. Story, and K.B. Drennan. 1991. The hypocholesterolemic effects of β-glucan in oatmeal and oat bran: A dose-controlled study. JAMA 265:1833-1839.

DeGroot, A.P., R. Luyken, and N.A. Pikaar. 1963. Cholesterol-lowering effect of rolled oats. Lancet 2:303-304.

Dudley, J.W. and R.H. Moll. 1969. Interpretation and use of estimates of heritability and genetic variances in plant breeding. Crop Sci. 9:257-262.

Frey, K.J. 1975. Heritability of groat-protein percentage of hexaploid oats. Crop Sci. 15:277-279.

Frey, K.J., H.H. Hall, and M.C. Shekleton. 1955. Inheritance and heritability of protein, niacin, and riboflavin in oats. J. Agric. Food Chem. 3:946-948.

Frey, K.J., M.C. Shekleton, H.H. Hall, and E.J. Benne. 1954. Inheritance of niacin, riboflavin and protein in two oat crosses. Agron. J. 46:137-139.

Greenberg, D.C. 1977. A diallel cross analysis of gum content in barley (*Hordeum vulgare*). Theor. Appl. Genet. 50:41-46.

Hallauer, A.R. and J.B. Miranda. 1988. Quantitative genetics in maize breeding. 2nd ed. Iowa State Univ. Press, Ames, IA.

Hanson, W.D. 1963. Heritability. p. 125-140. *In* W.D. Hanson and H.F. Robinson (eds.) Statistical genetics and plant breeding. National Academy of Sciences, Washington.

Kahlon, T.S, R.M. Saunders, F.I. Chow, M.M. Chiu, and A.A. Betschart. 1990. Influence of rice bran, oat bran, and wheat bran on cholesterol and triglycerides in hamsters. Cereal Chem. 67:439-443.

Kestin, M., R. Moss, P.M. Clifton, and P.J. Nestel. 1990. Comparative effects of three cereal brans on plasma lipids, blood pressure, and glucose metabolism in mildly hypercholesterolemic men. Am. J. Clin. Nutr. 52:661-666.

Kirby, R.W., J.W. Anderson, B. Sieling, E.D. Rees, W.L. Chen, R.E. Miller, and R.M. Kay. 1981. Oat-bran intake selectively lowers serum low-density lipoprotein cholesterol concentrations of hypercholesterolemic men. Am. J. Clin. Nutr. 34:824-829.

Lance, R.C.M. 1984. Genetic studies of the β-glucan content of barley (*Hordeum vulgare* L.). Diss. Abst. Int. 45: 742-B.

Mather, K. and J.L. Jinks. 1971. Biometrical genetics. Cornell Univ. Press, Ithaca, NY.

McCleary, B.V. and M. Glennie-Holmes. 1985. Enzymic quantification of (1→3)(1→4)-β-D-glucan in barley and malt. J. Inst. Brew. 91:285-295.

McCleary, B.V. and R. Codd. 1991. Measurement of (1→3), (1→4)-β-D-glucan in barley and oats: A streamlined enzymic procedure. J. Sci. Food Agric. 55:303-312.

Murphy, C.F. 1987. Report of oat enhancement work session. Madison, WI. 16 Oct. 1987. USDA, Beltsville, MD.

Ohm, H.W. and F.L. Patterson. 1973a. A six-parent diallel cross analysis for protein in *Avena sterilis* L. Crop Sci. 13:27-30.

Ohm, H.W. and F.L. Patterson. 1973b. Estimation of combining ability, hybrid vigor, and gene action for protein in *Avena* spp. L. Crop Sci. 13:55-58.

Peterson, D.M. 1991. Genotype and environment effects on oat beta-glucan concentration. Crop Sci. 31:1517-1520.

Pixley, K.V. and K.J. Frey. 1991. Inheritance of test weight and its relationship with grain yield of oat. Crop Sci. 31:36-40.

Powell, W., P.D.S. Caligari, J.S. Swanston, and J.L. Jinks. 1985. Genetical investigations into β-glucan content in barley. Theor. Appl. Genet. 71:461-466.

Ranhotra, G.S., J.A. Gelroth, K. Astroth, and C.S. Rao. 1990. Relative lipidemic responses in rats fed oat bran or oat bran concentrate. Cereal Chem. 67:509-511.

Rosielle, A.A. and K.J. Frey. 1977. Inheritance of harvest index and related traits in oats. Crop Sci. 17:23-28.

Shinnick, F.L., S.L. Ink, and J.A. Marlett. 1990. Dose response to a dietary oat bran fraction in cholesterol-fed rats. J. Nutr. 120:561-568.

Snedecor, G.W. and W.G. Cochran. 1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, IA.

Sraon, H.S., D.L. Reeves, and M.D. Rumbaugh. 1975. Quantitative gene action for protein content in oats. Crop Sci. 15:668-670.

Takeda, K. and K.J. Frey. 1979. Protein yield and its relationship to other traits in backcross populations from and *Avena sativa* × *A. sterilis* cross. Crop Sci. 19:623-628.

Thro, A.M., K.J. Frey, and E.G. Hammond. 1985. Inheritance of palmitic, oleic, linoleic, and linolenic fatty acids in groat oil of oats. Crop Sci. 25:40-44.

Youngs, V.L. and H. Püskülcü. 1976. Variation in fatty acid composition of oat groats from different cultivars. Crop Sci. 16:881-883.