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INHERITANCE OF SOME MAJOR GENES AND THEIR ASSOCIATIONS WITH QUANTITATIVE TRAITS IN CULTIVATED OATS (Avena sativa L.)(*)

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ABSTRACT*: The objectives of this study were to determine the inheritance of segregation of isozyme loci and some major genes, and to detect the associations between isozyme variation and some major genes with quantitative traits in cultivated oats (**Avena sativa** L.). Four oat crosses involving N327-6, N313-2, Exeter, 78-34Cn5, and Pendragon cultivars were used in this experiment. Parents, F_1 and F_2 material for all crosses were sown in a completely randomized design.*

The inheritance of spring-habit and husked-naked traits were determined by single dominant genes. The isozyme Diaphorase (DIA) band-present allele behaved as a single dominant gene.

The traits, tiller number and kernel content in family 91-232-I and groat oil content in family 91-228-II had significant associations with DIA.

Winter types had the higher values for biological yield, grain yield, grains per panicle, longer ear emergence, and taller plant height, while spring genotypes possessed higher values for grain weight.

The husked genotypes had higher values for biological yield, grain yield, harvest index, groat oil content, and kernel weight, whereas naked genotypes possessed only higher kernel content.

Keywords*: Isozyme variation, quantitative trait, Diaphorase, oat, **Avena sativa,** spring genotypes, winter genotypes.*

INTRODUCTION

The efficiency of genetic improvement may be greatly increased, if a simple and accurate laboratory procedure can be developed for evaluating breeding population in

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early stages. If in a crop, a strong correlation was found between quantitative traits and marker loci, such as an isozyme or morphological markers, these associated markers could be very useful to utilize in the selection. If the plant breeder could select the outstanding individuals via isozyme markers, it saves time and cost.

Morphological markers are simply inherited genes that cause a visual change in a morphological trait such as kernel color, surface waxes, plant, chlorophyll deficiencies, altered leaf morphology, awnless or awned, flower color and pigmentation etc, (Horsley and Franckowiak, 1989).

Sax (1923) reported an association between a quantitative trait (seed size) and a monogenic one (seed coat pigmentation) in *Phaseolus vulgaris*. The pigmented F_2 segregation had a mean seed weight greater than that of the white segregates. Rasmusson (1935) found out an association between flowering time and flower colour in peas. Smith (1937) reported another association between coralla size and color in populations derived from the cross *Nicotiana langsdorffii x N. sanderae*.

Suneson *et al*. (1947) reported an association between semi- smooth awns and high yield in backross progeny involving the transfer of a small segment of chromosome V from Lion to Atlas barley. Similar association observed by Qualset *et al.* (1965) in barley (*Hordeum vulgare*).

Valentine *et al*. (1988) reported a linkage between grain size and fuoresrence/non-fuorescence in oats. The large grain size was associated with lemma non-fluorescence and medium with fluorescence.

Though these markers have served well in various types of basic and applied research, their use in many areas of plant breeding has been very limited . The developments in recent years of protein and DNA markers offer the possibility of developing new approaches to breeding procedures. These are isozymes, RFLP (Restriction Fragment Length Polymorphism) and RAPD (Random Amplified Polymorphic DNA).

Kjer *et al*. (1991) investigated associations between earliness (heading date) and marker loci in barley (*Hordeum vulgare* L.). Earliness was found to be controlled by two loci. Associations were also found between two absolutely linked C bands on chromosome 3 and QTL's for lodging, straw diameter, and length of top internode of the straw.

Yupsanis and Moustakas (1988) reported a relationship between colour of glume and the presence or absence of gliadin bands 42/45 in Durum wheat. Shenoy *et al*. (1990)

pointed out an association between Shikimate Dehydrogenase (SDH) and seed protein content in rice (*Oryza sativa* L.). Sdh-l^2 allele had an association with higher protein accumulation.

Hamrick and Allard (1975) used two enzyme genotypes differing genetically with respect to four of five quantitative characters measured to study the correlation between quantitative characters and isozymes genotypes in *Avena barbata*. They found variation between two genotypes for flowering time, seed maturation time, height and number of tillers.

Levings *et al*. (1971) investigated the inheritance of an auxin inducible peroxidase (PER) in *Avene sativa*. F_2 segregation produced a 3:1 (monohybrid) ratio with presence the enzyme dominant to the null condition. Souza and Sorells (1989) observed the same results for the Diaphorase enzyme.

The objectives of this study were to determine the inheritance or segregation of isozyme loci and some major genes and to dedect the association between isozyme variation and some major genes with quantitative traits in cultivated oats (*Avena sativa* L.).

MATERIALS AND METHODS

Five oat cultivars N327-6, N313-2, Exeter, 78-34Cn5, and Pandragon were used as parent (Table 1). The parents N327-6, N313-2, Pendragon, and Exeter had different band pattern from 78-34Cn5 for Diaphorase (DIA). Also the other characteristics were taken into consideration. In particular, oil content was the most important criteration in the determination of parental line.

Four oat crosses were used in this experiment. Twenty seeds from each parent, 4, 5,1 and 5 F_1 seeds for crosses 91-228 (N327-6 x 78-34 Cn5), 91-229 (N313-2 x Pendragon, 91-231 (N313-2 x Exeter), and 91-232 (N313-2 x 78-34Cn5) respectively and 100 seeds from each F_2 (200 for one cross) were sown. Each F_2 population derived from a single F_1 plant The total 615 seeds from different generations were sown in 30 cm pots containing J No. 3 compost in a non-replicated completely randomized design in the glasshouse as a pot experiment at Welsh Plant Breeding Station on 25 th March 1992. The plants were harvested in the last week of July.

Observations were recorded on days to heading, panicle per plant, plant height and panicle length, grain yield per plant, total biomass, harvest index, grains per panicle,

grain weight, kernel weight, kernel percentage, groat oil percentage, naked/husked grain percentage, and winter/spring habit segregation.

Table 1. The characteristics of parental oat cultivars

Cultivars	Pedigree	Origin	Spring/ winter	Husked/ Naked	Notes
Pendragon	06765CnI10/Bulwark	UK	W	N	Naked, medium oil
N327-6	Unknown	USA	S	H	High oil line
N313-2	Unknown	USA	S	H	High oil line
78-34Cn5	Pioneer x Oyster	USA, UK	W	H	Medium oil line
Exeter	Victory x Rusota	USA	S	H	Low oil line

Starch Gel Electrophoresis: In order to determine isozyme segregation in F_2 populations, starch gel electrophoresis analysis was carried out. Gel was stained for Diaphorase (DIA) isozyme system.

Analyses of Variance: In order to determine whether there is significant difference between isozyme, spring-winter, and naked-husked classes, the data was analyzed by means of a one-way analysis of variance, computed using statistical program GENTS version 5. Two isoyme classes were identified in three families (91-281-I, 91-228-II, and 91-232-I) in two crosses, spring-winter classes in four families (91-228-I, 91-228-II, 91-229-I, and 91-232-I) in three spring x winter crosses, and a naked-husked class in a naked x husked cross (91-229). Families refer to groups of F_2 plants from single F_1 plants.

The segregation for a major gene trait was tested against the expected ratio 3:1 using the Chi Square test to determine whether the observed ratio deviated from expected.

RESULTS AND DISCUSSION

Isozyme assay

Isozyme locus segregation was examined for DIA alleles in the two crosses (N327-6x 78-34Cn5 and N313-2 x 78-34Cn5). Isozyme locus segregation was observed between present and null alleles in the three families of these crosses (91-228-I, 91-228-II, and 91-232-I). Present allele behaved dominant against null allele. There was distinct isozyme variation among parental lines for DIA, 78-34Cn5 had one none active (null) band, while the other parents possessed 6 active bands. Although isozymes generally show

codominance, these alleles gave a dominant-recessive type of segregation with two different types of phenotypes or genotypes in the F_2 (Figure.1).

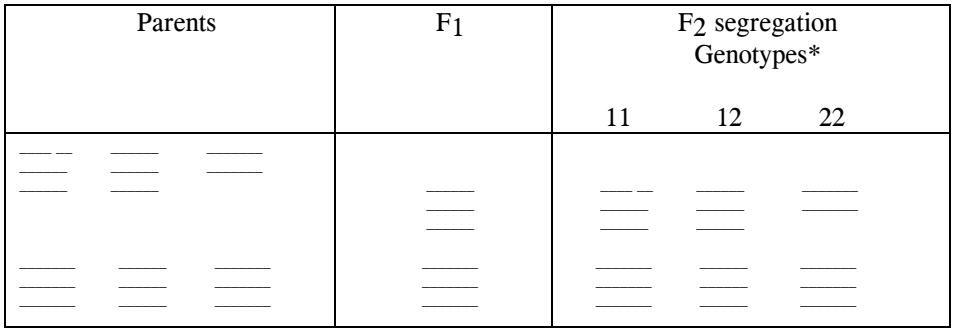

Figure 1 F_2 Segregation of DIA locus.

*:11 and 12 refer to the dominant homozygous and heterozygous genotype respectively. 22 represents the homozygous recessive genotype. Dia3, while the Dia1 and Dia3 loci showed a 1:2:1 segregation with two active alleles, Dia2 was in agreement with a 3:1 ratio with an active and a null allele.

The heterozygous genotype could not be distinguished from dominant present allele homozygous genotype.Therefore,family segregation in F_2 generation was tested against a 3:1 ratio. No significant deviation was determined for any family and all were in agreement with the expected 3:1 ratio. The number of plants in each family, their segregation frequencies and X^2 values is shown in Table 2. Souza and Sorells (1989) reported similar segregation for same alleles in North American oat cultivars. DIA loci segregation observed by Wehling (1991) in *Secale cereale L.* for Dia1, Dia2, and

Table 2. Segregation of a null allele for diaphorase isozyme in two oat crosses. The plants in F_2 population were scored for the presence or absence of a null allele.

Cross	Family	Cross Phenotype	Total	Frequency Present/Null		DF	Goodness Fit X^2
N327-6x 78-34Cn5	91-228-I	Present/Null	97	70	27	1	0.4158 NS
	91-228-II	Present/Null	99	71	28	1	0.5690 NS
	Total					2	0.9848 NS
	Pooled		196	141	55	1	0.9795 NS
	Heterogenity					1	0.0053 NS
N313-2 x 78-34Cn5	91-232-I	Present/Null	95	76	19	1	0.2666 NS

The Inheritance of Growth Habit

The spring and winter growth habit were observed in three spring x winter crosses and segregation recorded . The record was done according to the growing habit in early vegetative stage. The plants that had errect habit were recorded as completely spring type, prostrate plants were considered completely winter type, and the plants that had the growing habit between these defined types, were assumed intermediate. It was very difficult to distinguish clearly the complete spring type from intermediate. Thus, the completely spring and intermediate types were combined and 3 :1 ratio used to calculate X^2 values in all families.

As seen from Table 3, spring and winter habit segregations, except one family were in agreement with 3 : 1 ratio. According to these results, spring and winter segregations seem to be monogenic. Although segregation in a family deviated significantly from the expected 3 : 1 ratio, it was only significant at the level of $P< 0.05$. It could be due to sampling error. Similar results were obtained by Thomas and Naqvi (1991). On the contrary, Pugsley (1971) reported that the spring habit of growth in wheat was governed by three dominant genes, any one of which was able to inhibit the expression of the winter habit.

Table 3. Frequency of spring and winter type progenies in F_2 populations.

Cross	Family	Spring	Winter	Total	Ratio	D F	X^2	Probability
N327-6 x 78-34Cn5	91-228-1	80	20	100	3:1	1	1.3333	NS
	91-228-II	82	18	100	3:1	1	2.6133	NS
	Total					2	3.9466	NS
	Pooled	162	38	200	3:1	1	3.8400	< 0.05
	Heterogenity					1	0.1066	NS
N313-2 x Pendragon	91-229-I	83	17	100	3:1	1	3.4133	NS
N313-2 x 78-34Cn5	91-232-I	84	16	100	3:1	1	4.3200	< 0.05

Inheritance of the Naked Grain Character

Segregation for the naked grain character in the F_2 was in agreement with either a 3:1 or 1:2:1 ratio. The result showed that nakedness was governed by a major dominant gene (see Table 4). This agrees with the result of Boland and Lawes (1973). Jenkins and Hanson 76) also proposed three modifying genes that effect the dominance.

Table 4. Husked and Naked segregation of F_2 population (N313-2 x Pendragon)

Cross	Naked	Husked	Total	Ratio	DF	X^2	Probability
N313-2 x Pendragon	76	23	99	3:1	1	0.1640	NS
			OR				
	Complete Naked	Intermediate	Complete Husked				
	27	49	23	1:2:1	2	0.3344	NS

Association Between Quantitative Traits and Isozyme Genotypes

For the DIA locus, 3 out of 42 variance analyses showed of evidence significant effect of isozyme genotypes (at $P < 0.05$ level). The significant associations were found for the tiller number and kernel content for 91-232-I, and groat oil content for 91-228-II. The means of quantitative traits in terms of isozyme genotypes of DIA present and null loci were given in Table 5.

The traits, the tiller number and kernel content in family 91-232-I and groat oil content in family 91-228-II had significant association with DIA. Similarly, statistically significant associations between the enzyme/morphological character and herbicide response in population of *Avena barbata* and *A. fatua* were reported by Price *et al*., (1985). On the other hand, Stuber et al., (1987) pointed out that there were significant associations between Dia1 and ear number, kernel number, and second ear grain weight in maize. A significant association was observed between the segregation of markers and oil content in soybean by Diers *at al*., (1992).

Associations Between Quantitative Traits and Growth Habit Genotypes

As seen in Table 6, according to the variance analysis results, 28 out 57 analysis had significant association in four families (91-288-I, 91-288-II, 91-229-I, and 91-232-I). Seven of the analyses were significant at $P < 0.05$ level, one at the $P < 0.01$ level and twenty at the 0.001 level, respectively.

The winter and spring segregation makes a large contribution to the plant height in three families. Similar associations were obtained by Powell *et al*., (1985b) in barley for the *denso* dwarfing gene and daylength response loci. On the other hand , Worland and Law (1986) observed that the day length insensitivity (Ppdl) effected on height in wheat.ns were observed between growth habit locus and biological yield, grain yield, grain weight and grain per panicle in one family (91-228-II). Winter types had higher values for biological yield, grain yield and grain per panicle, while spring genotypes possessed higher values for grain weight. Similar results were reported by Powell *et al*., (1985a) in barley between an erect group which possessed dwarfing allele and *nutants* group which

possessed the corresponding *nutants* for the characters, such as grain weight, main stem weight and single plant weight.

Table 5. The maen of quantitative traits of the families in two crosses in terms of isozyme genotypes of DIA present and null loci.

	N327-6 x 78-34Cn5				N313-2 x 78-34Cn5	
	91-228-I		91-228-II		91-232-I	
Traits	Present	Null	Present	Null	Present	Null
Ear Emergence	36.74	37.22	32.93	34.11	31.17	30.79
Maturity	76.17	75.70	72.39	73.43	69.17	68.16
Grain Filling Period	39.43	38.48	39.46	39.32	37.93	37.37
Habit	1.94	2.04	1.76	2.04	1.75	1.63
Plant Height	144.00	146.70	149.20	51.80	41.60	141.70
Panicle Length	23.12	23.53	25.73	27.01	26.74	26.73
Tiller Number	6.13	6.53	6.08	6.32	6.26	7.05*
Biological Yield	30.00	34.10	37.50	40.60	41.07	44.56
Grain Yield	11.27	12.36	17.11	18.55	19.94	22.03
Grain Weight	29.13	29.87	34.60	34.79	33.24	33.74
Harvest Index	34.83	34.68	44.90	45.38	48.26	48.80
Grain per Panicle	58.40	61.40	82.20	83.90	97.90	97.30
Oil Content	-	-	10.43	9.66*	11.87	12.80
Kernel Weight	-	-	28.11	28.47	28.38	26.10
Kernel Content	-	-	81.29	81.73	79.31	77.76*

* P < 0.05

Table 6. The mean of quantitative traits of the families in three crosses in terms of spring and winter genotypes.

	Families							
	91-228-I		91-228-II		91-229-I		91-232-I	
Traits	Spring	Winter	Spring	Winter	Spring	Winter	Spring	Winter
Ear Emergence	35.75	41.70***	31.50	41.17***	32.69	41.29***	29.87	38.56***
Maturity	75.35	79.25***	71.00	80.11***	72.76	81.24***	67.80	76.13***
Grain Filling	39.50*	37.55	39.50	38.94	40.07	39.94	37.93	37.56
Habit	1.73	3.00***	1.58	3.00***	1.61	3.00***	1.52.	3.00***
Plant Height	144.10	148.30	146.00	168.10***	130.30	142.60***	139.80	154.90***
Panicle Length	23.48	22.65	25.76	27.75*	24.22**	22.19	26.90	26.12
Tiller Number	6.18	6.65	6.07	6.61	6.13	6.59	6.30	6.50
Biological Yield	31.10	32.70	36.00	49.50***	39.30	45.50*	41.04	45.13
Grain Yield per Plant	11.63	12.11	16.52	22.19***	17.53	18.90	20.04	20.87
Grain Weight	29.65	28.11	35.18***	32.47	31.28	28.66	33.60*	31.81
Harvest Index (%)	35.27	33.75	45.11	44.81	43.31	40.90	48.50	45.92
Grains per Panicle	60.20	58.80	77.70	104.40***	91.00	103.30*	97.10	101.60
Oil Content	-	-	10.25	9.98	9.42	9.28	12.24*	10.99
Kernel Weight	-	-	28.91***	25.35	28.22	26.27	26.43	25.54
Kernel Content	-		81.58	80.64	92.25	90.07	79.00	78.77

* P < 0.05 ** P < 0.01 *** P < 0.001

Surprisingly, groat oil content was higher in all spring genotypes. This was in contrast to the result of Schipper and Frey (1991), because they noted that the increases in photosynthetic capacity provide the extra bioenergy required for synthesis of more groat oil. Since winter gonotypes had higher biological yield, therefore it was expected that the winter genotypes should have had greater groat oil content.

Association Between Quantitative Traits and Naked-husked Genotypes

For the naked-husked genotypes, 9 out of 15 variance analyses showed of evidence significant effects of naked-husked genotyps (See Table 7).

Naked-husked locus made a large contribotion to the variation for grain filling period, tiller number, biological yield, grain yield per plant, grain weight, harvest index, oil content, kernel weight and kernel content. It was expected, kernel content was higher in naked genotypes, but other traits which were in favour of husked genotypes.

Table 7. The mean values of the quantitative traits for the naked and husked genotypes in the N313-2 x Pendragon F_2 population.

Traits	**Naked Genotype**	**Husked Genotype**	
Ear Emergence	34.29	33.70	
Maturity	73.39	75.39	
Grain Filling	39.61	41.70	*
Habit	1.89	1.69	
Plant Height	132.6	132.1	
Panicle Length	23.65	24.57	
Tiller Number	6.05	6.83	*
Biological Yield	39.40	44.70	*
Grain Yield per Plant	16.18	22.01	***
Grain Weight	28.93	37.13	***
Harvest Index (%)	40.94	49.39	***
Grains per Panicle	94.20	89.70	
Oil Content	9.12	10.26	***
Kernel Weight	26.97	30.72	
Kernel Content	95.48***	80.37	

* $P < 0.05$ *** $P < 0.001$

REFERENCES

Boland, P., and D.A. Lawes, 1973. The inheritance of the naked grain character in oat studied in a cross between the naked variety Caesar and the husked variety BO1/11. Euphytica, 22: 582-591.

Diers, B.W., P. Keim, W.R. Fehr, and R.C. Shoemaker, 1992. RFLP analysis of soybean seed protein and oil content. Theor. Appl. Genet 83: 608-612.

Hamrick, J.L., and R.W. Allard, 1975. Correlations between quantitative characters and enzyme gonotypes in Avena barbata. Evolution 29: 428-442.

Horsley, R.D., and J.D. Franckowiak, 1989. A proposal on identification of major genes in spring barley using morphological markers. Barley Genetics Newsletter 19: 68-72.

Jenkings, G., and P.R. Hanson, 1976. The genetics of naked oats (*Avena nuda L.*) Euphytica, 25: 167-174.

Kjer, B., V. Huan and J. Jensen, 1991. Associations between 23 quantitative traits and 10 genetic markers in a barley cross. Plant Breeding 106: 261-274.

Levings, C.S., C.W. Stuber, and C.F. Murphy, 1971. Inheritance of an auxin inducible peroxidase in oats (*Avena sativa L.*). Crop Sci. 11: 271-272.

Powell, W., W.T.B. Thomas, P.D.S. Caligari, and J.L. Jinks. 1985a. The effects of major genes on quantitatively varying characters in barley. Heredity 54: 343-348.

Powell, W., P.D.S. Caligari, W.T.B. Thomas, and J.L. Jinks. 1985b. The effects of major genes on quantitatively varying characters in barley 2. The denso and daylength response loci. Heredity 54: 349-352.

Price, S.T., R.W. Allard , J.E. Hill, and J. Naylor, 1985. Associations between discrete genetic loci and genetic variability for herbicide reaction in plant populations. Weed Sci. 33: 650-653.

Pugsley, A.T. 1971. A genetic analysis of the spring winter habit of growth in wheat. Aust. J. Agric. Res. 22: 21-31.

Qualset, C.O., C.W. Schaller, and J.C. Williams, 1965. Performence of isogenic lines of barley as influenced by awn length, linkage blocks, and environment. Crop Sci. 5:489-494

Rasmusson, J., 1935. Studies on the inheritance of quantitative characters in Pisum. I. preliminary note on the genetics of time of flowering. Heritidas 20:161-180.

Sax, K., 1923. The association of size differences with seed-coat pattern and pigmentation in *Phaseolus vulgaris.* Genetics 8:552-560.

Schipper, H., and K.J. Frey, 1991. Growth analysis of oat lines with low and high groat oil content. Euphytica 54 :221-229.

Shenoy, V.V., D.V. Seshu, and J.K.S. Sachan, 1990. Shikimate Dehydrogenase-I^2 allozyme as a marker for high seed protein content in rice. Crop Sci. 30.937-940.

Smith, H.H., 1937. The relation between genes affecting size and color in certain species of Nicotiana. Genetics 22:361-375.

Souza, E., and M.E. Sorellls, 1989. Inheritance and frequency of a null allele for diaphorase activity in North American oat cultivars. J. Hered. 80:501-503.

Stuber, C.W., M.A. Edwards, and J.F. Wendal. 1987. Molecular marker-facilitated investigation of quantitative trait loci in maize. II. Factors influencing yield and its component traits. Crop. Sci. 27:639-648.

Valentine, J., D.M. Jones, and B.T. Middleton, 1988. Exploiting new germplasm in winter oat breeding at Aberystwyth. p 66-75. Third International Oat Conference. July, 4-8, 1988. Lund, Sweden.

Thomas, H., and Z.H. Naqvi, 1991. Monosomic analysis of response to vernalisation in winter oat. Euphytica 57: 151-155.

Worland, A.J., and C.N. Law, 1986. Genetic analysis of chromosome 2D of wheat. I. The location of genes affecting height, daylength insensitivity, hybrid dwarfism, and yellow rust resistance. Z. Pflanzenzüchtg 96: 331-345.

Yupsanis, T., and M. Moustakas, 1988. Relationship between quality, colour of glume and gliadin electrophoregrams in durum wheat. Plant Breeding 101: 30-35.