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CROP HEREDITY AND NUTRITIONAL QUALITY

Inheritance and Heritability of Protein, Niacin, and Riboflavin in Oats

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In three segregating populations of oats it was found that the genes determining high protein percentage could be either recessive or dominant, depending upon the genetic background on which they operated. With one parent, the high protein percentage behaved as a dominant in one cross but recessive in the other; for another parent, low protein percentage behaved as the dominant in one cross but recessive in another. High niacin and riboflavin content in oats appeared to be dominant in each of the oat crosses. Heritability percentages for niacin and protein content ranged from 83 to 93, while those for riboflavin ranged from 0 to 52.

Largely as the result of research work in animal nutrition and plant breeding, there has recently developed an interest in the development of crop varieties which have improved nutritional qualities. The plant materials receiving the greatest attention with respect to nutritional quality are the grains of the cereal crops and the vegetative tissues of the forage crops. Prior to the effective selection of crop varieties with improved nutritional qualities, it will be necessary to establish the mode of inheritance of chemical components of the crops being investigated.

The chemical components of the cereal grains which have received the most attention are protein, several amino acids, and four of the B vitamins. Protein and oil content of corn was shown to be an inherited characteristic in the classic experiments on protein and oil selection conducted at Illinois (*6*). Several other investigations have shown that protein content in cereal grains is usually multigenically inherited with low protein percentage dominant (*3, 4*).

Burkholder, McVeigh, and Mayer (*1*), Ditzler, Hunt, and Bethke (*2*), and Richey and Dawson (*10*) found that the variability in the niacin content of corn grain was determined largely by heredity, a large number of genes being involved in the determination of this character. Richey and Dawson suggest that the genetic constitution of the corn endosperm determines in large part the niacin content of the grain, and that the genes for high niacin content are recessive. Frey and Watson (*5*) found large differences among oat varieties with respect to niacin and riboflavin content, with some strains containing twice the content of others. Frey and others (*4*), reporting on the inheritance of niacin, riboflavin, and protein in two oat crosses, found transgressive segregation for the first two components. The mean heritability values for niacin and riboflavin content of oat grain were 50 and 49%, respectively, while that for protein was only 15%.

The purpose of this paper is to give additional information on the inheritance and heritability of protein, niacin, and riboflavin in three oat crosses. It is a sequel to the earlier paper by Frey and others (*4*).

Materials and Methods

The grain from the oat varieties, Mindo, Colo, and C. I. 5298, and of randomly chosen F_3 progenies from the crosses Mindo × Colo, Colo × C. I. 5298, and C. I. 5298 × C. I. 3656, was grown at East Lansing, Mich., in 1952 and subsequently analyzed for niacin, riboflavin, and protein. (Seed of C. I. 3656 was not grown in the same experiment with the other varieties and selections, so the niacin, riboflavin, and protein contents given herein for this strain were collected in 1947, 1949, and 1950 and corrected according to the average of the other parent varieties to a 1952 basis.)

For this study, a number of single plants were randomly selected from the parent varieties and the F_2 population of the three crosses. As the amount of seed from single plants was not sufficient for the chemical determinations, it was necessary to grow F_3 progeny rows from which seed was harvested for analyses. Thus, the chemical contents were determined on the progenies from F_2 selections and supposedly should represent the average genotypes of the F_2 plants. The grain from each selection was prepared for chemical analysis by removing the empty hulls and grinding the sample through a 40-mesh screen.

Niacin content was determined by the method of Krehl, Strong, and Elvehjem (*7*) and the riboflavin content by the method of Snell and Strong (*9*). The nitrogen content of the oat grain was determined by the Kjeldahl procedure and protein percentage was derived by multiplying the nitrogen content by 6.25. The moisture content for the samples was rather uniform, so the analytical data were expressed on an air-dry basis, niacin and riboflavin as micrograms per gram, and protein as percentage of the total.

Experimental Results

Inheritance The frequency distributions for the protein percentages of the selections from the three

Table I. Frequency Tables of Protein Percentage of Selections in Three Oat Crosses and Their Parents

	Means of Protein Percentage Classes																
Parent or Cross	*13.7*	*14.2*	*14.7*	*15.2*	*15.7*	*16.2*	*16.7*	*17.2*	*17.7*	*18.2*	*18.7*	*19.2*	*19.7*	*20.2*	*20.7*	*21.2*	$\bar{x}$
Mindo	..	1	9	..	..	..	..	..	..	..	..	..	..	..	..	..	14.6
Mindo × Colo	..	1	7	8	26	20	8	5	2	..	..	..	..	..	..	..	15.9
Colo	..	..	..	..	..	8	2	..	..	..	..	..	..	..	..	..	16.3
Colo × C. I. 5298	3	13	38	22	23	8	1	..	1	..	..	..	..	..	..	..	15.1
C. I. 5298	..	..	8	2	..	..	..	..	..	..	..	..	..	..	..	..	14.8
C. I. 5298 × C. I. 3656	..	..	..	1	12	66	73	43	9	4	1	..	1	..	..	1	16.7
C. I. 3656	..	..	..	..	..	..	3	7	..	..	..	..	..	..	..	..	17.1

Table II. Frequency Tables of Niacin Content of Selections in Three Oat Crosses and Their Parents

	Means of Niacin Content Classes, γ/Gram																
Parent or Cross	*7.2*	*7.7*	*8.2*	*8.7*	*9.2*	*9.7*	*10.2*	*10.7*	*11.2*	*11.7*	*12.2*	*12.7*	*13.2*	*13.7*	*14.2*	*14.7*	*x*
Mindo	4	6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	7.5
Mindo × Colo	1	7	8	14	16	15	10	3	1	..	..	1	1	..	..	..	9.2
Colo	..	..	4	6	..	..	..	..	..	..	..	..	..	..	..	..	8.5
Colo × C. I. 5298	4	14	22	29	20	11	6	2	1	..	..	..	..	..	..	..	8.8
C. I. 5298	..	..	..	3	6	..	1	..	..	..	..	..	..	..	..	..	9.1
C. I. 5298 × C. I. 3656	..	..	..	..	1	26	53	73	39	21	5	..	..	1	1	..	10.7
C. I. 3656	..	..	..	..	..	..	7	3	..	..	..	..	..	..	..	..	10.3

oat crosses and their parents are given in Table I. Mindo and C. I. 5298 varieties contained the lowest protein percentages and Colo and C. I. 3656 the highest protein percentages. Each of the crosses contained selections which were higher and lower than the parents in protein percentage, which constitutes apparent transgressive inheritance. In the Mindo × Colo, and the C. I. 5298 × C. I. 3656 crosses, the transgression of protein percentage is only in the positive direction, while in the other cross, Colo × C. I. 5298, transgression occurs in both directions. The parental selections were very uniform, with no case in which the parents of a cross overlap. In the Colo × Mindo and C. I. 5298 × C. I. 3656 crosses, the mean protein percentage of the F_2-derived selections was closer to the highest than to the lowest protein parent, indicating a partial dominance for high protein percentage. In the Colo × C. I. 5298 cross the converse is apparent, the mean protein percentage more closely approximating that of the lowest parent, C. I. 5298.

These data present several interesting aspects: First, other studies reported on the inheritance of protein percentage in oats have shown that the low protein percentage is generally dominant (*4*), while in this study two of the crosses showed high protein percentage as being partially dominant. Secondly, the cross of Colo × C. I. 5298 showed a partial dominance for low protein percentage, with low protein being characteristic of C. I. 5298, while in the other cross involving this parent, C. I. 5298 × C. I. 3656, there was a partial dominance for high protein percentage. In other words, in the genetic background of the first cross, the genes determining protein percentage from C. I. 5298 exhibit dominance, while in the genetic background of the second cross they are expressed in a recessive manner. The genes determining protein percentage in Colo appeared to be partially dominant in the Mindo × Colo cross, but they appeared recessive in the Colo × C. I. 5298 cross, indicating the same reversal that occurred with the C. I. 5298 strain. The implications of the apparent dominance-recessive reversal of Colo and C. I. 5298 upon breeding for higher or lower protein content in oats are noteworthy. More data are needed to establish a mode of inheritance for genes of high or low protein percentage involved in oat crosses.

Data on niacin content for the three oat crosses and their parents are shown in Table II. The parental varieties varied considerably in niacin content, ranging from Mindo with a mean of 7.5 γ per gram to C. I. 3656 with 10.3 γ per gram. In the Mindo × Colo and C. I. 5298 × C. I. 3656 crosses the mean of the F_2 population is above the mean of the highest parent. This is similar to data reported by Frey and others (*4*), who found that the mean riboflavin contents of the F_2-derived strains in two oat crosses were greater than those of the highest riboflavin parents. In the Colo × C. I. 5298 cross the mean of the F_2-derived selections was midway between the means of the parents. However, the parents do not differ significantly in niacin content. In each cross there was transgressive segregation for niacin content; the transgression was for high niacin in the Mindo × Colo and C. I. 5298 × C. I. 3656 crosses, and in both directions in the Colo × C. I. 5298 cross.

The frequency distributions for riboflavin content in two oat crosses and their parents are given in Table III. In both crosses the mean riboflavin content of the F_2 selections approached the mean of the highest riboflavin parent, indicating dominance of the genes for high riboflavin content. Dominance for high riboflavin content was even more extreme in oat crosses reported previously (*4*). There was transgressive segregation for high riboflavin content in the Colo × C. I. 5298 cross, but all of the segregates in the Mindo × Colo cross fell within the parental range of riboflavin content.

Heritability The heritability percentages for protein, niacin, and riboflavin contents in three oat crosses given in Table IV were calculated in the broad sense (*8*). This method of

Table IV. Heritability Percentages of Protein, Niacin, and Riboflavin in Three Oat Crosses

	Chemical Constituent		
Cross	*Protein*	*Niacin*	*Riboflavin*
Mindo × Colo	90	93	0
Colo × C. I. 5298	88	86	52
C. I. 5298 × C. I. 3656	89	86	..

Table III. Frequency Table of Riboflavin Content in Oat Grain of Selections from Two Crosses and Their Parents

	Means of Riboflavin Content Classes, γ/Gram										
Parent or Cross	*1.1*	*1.2*	*1.3*	*1.4*	*1.5*	*1.6*	*1.7*	*1.8*	*1.9*	*2.0*	$\bar{x}$
Mindo	3	1	3	3	..	..	..	..	..	..	1.26
Mindo × Colo	6	22	40	8	1	..	..	..	..	..	1.27
Colo	..	..	4	2	3	1	..	..	..	..	1.41
Colo × C. I. 5298	7	14	34	27	12	9	3	1	1	1	1.37
C. I. 5298	2	5	3	..	..	..	..	..	..	..	1.21

calculating heritability percentages gives an estimate of the proportion of the variance in a segregating population which is genetic. There are errors associated with this method, as no distinction is made between dominance and epistasis effects which are not very heritable and additive genetic effects which are highly heritable. The heritability values for protein and niacin were high, being much greater than those reported earlier for these chemical components. The fact that the parenteral values for protein and niacin content were very homogeneous may be responsible for the high heritability percentages. The heritability percentages for riboflavin were 0 and 52%, respectively, for the Mindo × Colo and Colo × C. I. 5298 crosses. The second value corresponds very closely with those previously reported (*4*).

Table V. Correlation Coefficients of Protein, Niacin, and Riboflavin in Three Oat Crosses

	Cross		
Correlation of	Mindo × Colo	Colo × C. I. 5298	C. I. 5298 × C. I. 3656
Niacin and protein	0.50[a]	0.38[a]	0.42[a]
Riboflavin and protein	0.10	0.21	..

[a] Significance at 1% level.

Association of Characters The correlation coefficients between protein and niacin and riboflavin in the three oat crosses are given in Table V. As in previous reports by Frey and Watson (*5*) and Frey and others (*4*), the correlation coefficients between niacin and protein were significant in each cross, while those between riboflavin and protein were significant in neither cross. To plant breeders this would mean that selection for higher protein content in oat strains would be accompanied by increases in niacin content. Nevertheless the correlation coefficients of niacin and protein are of a low enough magnitude to make it possible, if desired, to obtain with diligent selection a low protein–high niacin strain of oats.

Discussion

One of the most interesting and practical aspects of the data reported herein and those reported previously is the dominance of high riboflavin and high niacin content demonstrated in oat crosses. It seems possible that oat varieties can be selected with a much higher niacin or riboflavin content than those now being grown. The procedure to be followed in breeding for improved niacin and riboflavin content is open to question. Probably the most effective system would be recurrent selection in which the high niacin strains would be selected and intercrossed. Later the grain of the progeny of the intercrosses would be analyzed, again high niacin strains would be selected, and the cycle repeated until the desired niacin content was obtained. The heritability values for niacin are encouraging, as they indicate that selection for this characteristic should be rather effective.

The dominance for high or low protein percentage seems to depend upon the genetic background of the particular oat cross. In two of the crosses the high protein percentage appears to be dominant; in the other cross low protein percentage seems to be dominant. This could present a problem, as it could not be predicted from these data whether high protein percentage would be recessive or dominant in an oat cross until the cross had been tried; further data are needed.

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RUMEN CHEMISTRY

In Vitro Studies with Rumen Microorganisms Using Carbon-14–Labeled Casein, Glutamic Acid, Leucine, and Carbonate

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The microorganisms of the rumen have a profound effect on the carbohydrate of the diet. The cellulose of the herbivorous ration is attacked in the rumen, releasing large quantities of readily fermentable substances which, together with similar products in the food, are largely converted to volatile fatty acids. It has been estimated that these short-chain fatty acids provide about 70% of the cow's daily caloric intake (*6*).

Previous studies have indicated that the metabolic activity of microorganisms in the rumen is not restricted to cellulose and fermentable carbohydrates like glucose but also involves amino acids and protein of the ration. Degradation of protein in the feed was indicated by appearance of ammonia following the addition of casein to in vitro rumen preparations (*2, 13, 19*). This ammonia might have come from amide nitrogen which could be released without destruction of amino acids. However, El-Shazly found (*7*) that the increase of ammonia was correlated with the increase of branched-chain fatty acids, indicating that essential amino acids had been metabolized.

The present study was undertaken to trace the fate of protein and amino acids in the rumen of sheep, using carbon-

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