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Inheritance Pattern of β-glucan and Protein Contents in Hulless Barley

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ABSTRACT

Genetic analysis of β-glucan and protein content was conducted using an eight parent (ICNBF-582, ICB-102607, ICNBF93-328, SB91925, ICNBF8-613, BBSC congana, Petuina2 & ICNBF93-369) of hulless barley (*Hordeum vulgar*e L.) in diallel fashion. Generation mean analysis was carried out on P_1, P_2, F_1, F_2, BC_1 and BC_2 of crosses ICNBF93-369 × ICNBF-582 and SB91925 × ICB-102607, to complement the genetic information from the diallel analysis. Data showed that although additive and dominance variance were important, these traits was more influenced by additive effects. High values of narrow sense heritability for both traits also confirmed it. Generation mean and variance analysis indicated that additive effects were important for protein content in cross SB91925 × ICB-102607 and β-glucan content in both crosses. These analyses indicated over-dominance towards the better parent for protein content in cross ICNBF93-369 × ICNBF-582. To conclude, in order to improve β-glucan and protein content (except protein content in cross ICNBF93-369 × ICNBF-582), direct selection in early generation such as pedigree is possible. © 2010 Friends Science Publishers

Key Words: Hulless barley; Diallel; Generation means; β-glucan; Protein

INTRODUCTION

The β-Glucan has been known to scientists as a plant constituent for decades (Bhatty, 1999). For over twenty years, it has been studied for having favorable biological effects on mammals. It is known that β-Glucan is a powerful immune stimulant and a strong antagonist to both benign and malignant tumors. It lowers cholesterol and triglyceride level, normalizes blood sugar level, heals and rejuvenates the skin and has various other benefits (Tokunaka *et al.*, 2002; Akramiene *et al.*, 2007; Chan *et al.*, 2009). β-Glucan is a soluble fiber derived from the cell walls of algae, bacteria, fungi, yeast and seeds from the *Gramineae*.

Barley and oat are good sources of β-glucan than the found in wheat and rice. Mixed-linkage (1→3), (1→4)-β-glucans are major structural components of barley endosperm and aleurone cell walls, comprising 75% of endosperm (Delaney *et al.*, 2003). In 2006 the Food and Drug Administration (FDA) allowed the labels of food containing the soluble fiber β-glucan from barley products to claim that the consumption of these foods may reduce the risk of coronary heart disease (Shimizu *et al.*, 2008). Several authors have shown that hulless barley has more β-glucan content than hulled barley (Bhatty, 1999; Izydorczyk *et al.*, 2000; Yu *et al.*, 2002). In addition, hulless barleys, characterized by high protein content, (1.5-3.0% greater than the hulled genotypes), had great importance in breeding practice (Lasztity, 1996).

Barley β-glucan and protein content are polygenic traits (Siddquie & Alam, 2002; Islam *et al.*, 2006; Nasrallah *et al.*, 2007; Arabi *et al.*, 2008). Using double haploid (DH) lines derived from the cross Steptoe/Morex, Han *et al.* (1995) studied quantitative trait loci (QTL) of β-glucan content in barley grain and malt. They found that the QTL with the largest effects on barley and malt β-glucan were located on chromosomes 2H, 7H, 4H and 5H. Another study to determine the genetic factors influencing grain β-glucan content using 102 DH lines from the cross Beka × Logan were sown at two sites, Lleida (N.E. Spain) and Dundee (E. Scotland) Molina-Cano *et al.* (2007) reported three QTLs for β-glucan content. One QTL was located in the distal end of the long arm of chromosome 1H, in the same region as a gene for UDP-glucose-4-epimerase, an enzyme known to be involved in the synthesis of cell wall polysaccharides. Second QTL was mapped in the same area of chromosome 5H as a genetic factor shown previously, in the same cross, to influence grain protein content, while one in the centromeric region of chromosome 7H, close to the gene for naked (hulless) grain. Zale *et al.* (2000) investigated gene loci related to malting quality, in different populations of barley. They reported conservation in QTLs for grain protein on the short arm of chromosome 2 among five diverse mapping populations. Besides this, genetic factors,

controlling β-glucan and protein content are affected by environmental factors, including soil nitrogen level and precipitation (Lasztity, 1996; Fastnaught *et al.*, 1996; Zhang *et al*., 2001).

The development of hulless barley cultivars with greater β-glucan and protein contents increase the nutritional and economic value of this crop (Bhatty, 1999). The choice of an efficient breeding procedure depends, to a large extent, on the knowledge of the genetic system controlling the character to be selected. The purpose of present investigations was to identify of inheritance and system of genetic control of grain β-glucan and protein content upon different crossing hulless barley varieties in Iran and Azerbaijan during 2005-2008.

MATERIALS AND METHODS

Chemical analysis: For β-glucan determinations, five g of seed was ground in a UDY Cyclone sample mill with a 0.5-mm mesh screen and concentrations were determined by using enzyme-specific mixed-linkage β-glucan detection assay kits from Megazyme (Megazyme International Ireland Ltd., Wicklow, Ireland). For protein measurement, 40 g of seed was ground with a 1 mm mesh screen and analyzed using a Perten 8611 near-infrared reflectance spectroscopy analyzer (Perten Instruments, Huddinge, Sweden, 2006) as described in American Association of Cereal Chemists (1983, Method 39-10).

Diallel analysis: The experimental material comprised eight genotypes of hulless barley provided by ICARDA, Aleppo, Syria: (1) ICNBF-582 (6-rowed), (2) ICB-102607 (2-rowed), (3) ICNBF93-328 (6-rowed), (4) SB91925 (2-rowed), (5) ICNBF8-613 (6-rowed), (6) BBSC congana (6-rowed), (7) Petuina2 (2-rowed) and (8) ICNBF93-369 (2-rowed). These genotypes were crossed in a diallel fashion including direct crosses (Griffing, 1956) and their reciprocals during crop season 2006-2007. Eight parents and their resulting 56 F_1's were grown on November 2007, in a randomized block design with three replicates in Iran. Ten healthy vigorous plants in the parents and F_1's progenies were selected randomly for analyzing β-glucan and protein contents. The differences among populations were tested by the analysis of variance for individual characters. To fulfill the assumption of absence of epistasis, no multiple allelism and independent gene distribution data were subjected to two tests: uniformity of Wr and Vr test (t^2) and the analysis of regression coefficient test (Singh & Chaudhary, 1985). After that, the data were subjected to graphical and component analyses according to Hayman (1954, 1957) and Jinks and Hayman (1953).

Generation mean and variance analysis: Generation mean analysis was carried out on six basic generation (the P_1 & P_2 parent cultivars, the F_1 & F_2 first & second filial generations & the BC_1 & BC_2) of two combinations of the parental cultivars, ICNBF93-369×ICNBF-582 (Cross I) and SB91925×ICB-102607 (Cross II) to complement the genetic information from the diallel analysis. We used the parents of the respective crosses as the male parent and the F_1 generation as the female parent and effected backcrosses to produce the BC_1 (F_1 back crossed to P_1) and BC_2 (F_1 back crossed to P_2) generations and the F_1 hybrids were selfed to obtain F_2 seeds. All these generations were produced during two cropping seasons and as such, all the six generations had to be grown together during the same cropping season (2007-2008) in a randomized block design with three replications. Sample size (i.e., number of plants analyzed) varied as follows: 10 plants for the P_1, P_2 and F_1 generations, 70-75 plants for the F_2 generations and 15 plants in the BC_1 and BC_2 generations. The genetic model that best fit the data was found by the mean of joint scaling test (Mather & Jinks, 1982) and the accuracy of the models was verified by χ^2-test. Components within each model were evaluated for significance by t-test (Kearsey & Pooni, 1996). The type of epistasis was determined only when dominance [h] and dominance×dominance [l] effects were significant. When these effects had the same sign, the effects were complementary, while different signs indicated duplicate epistasis (Kearsey & Pooni, 1996).

Variance components (additive, dominance & environment) were estimated as described by Kearsey and Pooni (1996) and Farshadfar (1998), using the following equations:

For additive variance: $V_{[d]} = (2VF_2 - VBC_1 - VBC_2)$, for dominance variance:

$V_{[h]} = 4\ (VF_2 - 1/2V_{[d]} - E)$, for environment variance: $V_E = 1/4\ (VP_1 + VP_2 + 2VF_1)$, for average degree of dominance:

$(H/D)^{1/2} = (V_{[h]}/V_{[d]})^{1/2}$.

In addition, broad-sense (h_b^2) and narrow-sense (h_n^2) heritabilities were estimated using the variance component method (Wright, 1968) and variance of F_2 and back cross generations (Warner, 1952), respectively as:

$$h_b^2 = \{VF_2 - [(VP_1 + VP_2 + 2VF_1)/4]\} / VF_2$$

$$h_n^2 = [VF_2 - (VBC_1 + VBC_2)/2] / VF_2$$

Response to selection was estimated (Farshadfar, 1998) with 5% selection intensity (i) (selection differential, K= 2.06) as:

$$R = i \times h_n^2 \times \sqrt{VF_2}$$

RESULTS AND DISCUSSION

Diallel analysis: Analysis of variance showed highly significant differences among parents and F_1's for β-glucan and protein content (data not shown). The estimates of genetic parameters obtained from diallel cross for both of traits under study are given in Table I. Although additive

(D) and dominance (H_1) components were positive and signification for β-glucan and protein content, the relative magnitude of D was higher than the dominance components (H_1 & H_2) indicating the preponderance of additive (fixable) effects in controlling the inheritance of the characters studied. Also, the average degree of dominance lesser than unity indicated partial dominance occurring in the inheritance of both traits. The estimate of narrow sense heritability was 0.527 and 0.582 for β-glucan and protein content, respectively.

The difference H_1-H_2 indicated the unequal distribution of genes for both crosses. This claim was strengthened by the ratio of $H_2/4H_1$, which was lesser than 0.25 (Table I). Ratio of $[(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F]$ more than unity for these traits indicated that dominant genes were more frequent. Correlation analysis of the genotypes and Wr+Vr values showed dominant gene control for β-glucan content. However this analysis showed recessive gene control for protein content (Table I).

Generation mean and variance analysis: Analysis of variance for both traits in two crosses showed significant difference among generations (data not shown). Different 3 to 5 parameter models showed the best fit to generation means of both traits and cross combination (Table II). As is shown in Table III, additive effects for both traits were negative in both the crosses. The negative and positive signs for additive effects depended on which parent was chosen as P_1 (Edwards *et al.,* 1975; Cukadar-Olmedo & Miller, 1997). While dominance component only were positive and signification for β-glucan in cross SB91925 × ICB-102607 and protein content in cross ICNBF93-369 × ICNBF-582. Generation variance analysis (Table III) indicated additive variance was larger than dominance for protein content in cross SB91925 × ICB-102607 and β-glucan content in both crosses. At the same time, the average degree of dominance was lesser than unity, showing a partial dominance gene action for both traits except for protein content in cross ICNBF93-369 × ICNBF-582. The $(H/D)^{1/2}$ ratio as indicated over dominance towards the better parent for protein content in cross ICNBF93-369 × ICNBF-582.

Data showed different types of epistasis interaction effects were found for traits and cross combinations (Table II). Additive×dominance [j] epistasis was positive and significant for β-glucan content in both crosses and protein content in cross SB91925 × ICB-102607. Dominance×dominance non-allelic interaction [l] was significant and negative for β-glucan content in cross SB91925 × ICB-102607 and protein content in both crosses. No additive×additive [i] type of interaction was present in the genetic control of the studied traits.

The dominance [h] and dominance×dominance [l] gene effects showed opposite signs for protein content in cross ICNBF93-369 × ICNBF-582 and β-glucan content cross SB91925 × ICB-102607, indicating the presence of duplicate dominant epistasis in the expression of these traits, which limit the range of variability. This kind of epistasis generally hinders the improvement through selection and hence a higher magnitude of dominance and Dominance×dominance type of interaction effects would not be expected. It also indicated that selection should be delayed after several generations of selection until a high level of gene fixation is attained (Farshadfar, 1998). Greater estimates of narrow sense heritability and consequently greater gain from selection were found in β-glucan content in both crosses and protein content in cross SB91925 × ICB-102607 (Table III).

Table I: Components of diallel variance and their estimates of β-glucan and protein content

Components	β-glucan	Protein
$\hat{D}$	0.969 ± 0.067**	1.532 ± 0.106**
$\hat{H}_1$	0.422 ± 0.154**	0.501±0.244*
$\hat{H}_2$	0.275 ± 0.134*	0.295 ± 0.212$^{n.s}$
$\hat{F}$	0.693 ± 0.158**	1.065±0.25**
$\hat{h}^2$	0.691 ± 0.089**	- 0.022 ± 0.142$^{n.s}$
$\hat{E}$	0.12 ± 0.022**	0.17±0.03**
Proportion of components of variance		
$(H_1/D)^{1/2}$	0.659	0.571
$H_2/4H_1$	0.162	0.147
$[(4DH_1)^{1/2} + F / (4DH_1)^{1/2} - F]$	3.36	4.104
R ($W_r + V_r$, Y_r)	-0.853**	0.739**
h_b^2	0.7	0.71
h_n^2	0.527	0.582

ns, * and ** : non significant, significant at 5% and 1% of probability levels, respectively.
D: additive variance, H_1 and H_2: dominance genetic variance and corrected dominance genetic variance, F: product of additive by dominance, h^2: square of difference P vs All, E: environmental variance, whole, $(H_1/D)^{1/2}$: average of degree dominance, $H_2/4H_1$: Proportion of genes with positive and negative effects in parents, $[(4DH_1)^{1/2} + F / (4DH_1)^{1/2} - F]$: Proportion of dominant and recessive genes in parents, R ($W_r + V_r$, Y_r): correlation between parental measurement (Yr) and Wr+Vr values, h_b^2 : heritability for diallel in a broad sense, h_n^2 : heritability for diallel in a narrow sense.

Table II: Estimate of genetic components of means for β-glucan and protein content in two crosses

	β-glucan		Protein	
Generation	Cross I	Cross II	Cross I	Cross II
M	6.05 ± 2.22**	6.15 ± 0.41**	7.91 ± 2.27**	9.42 ±2.54**
[d]	-0.92 ± 0.17**	-1.25 ± 0.51*	-0.95 ± 0.2**	-0.89 ± 0.16**
[h]	-	12.3 ± 4.82*	13.34 ± 5.8*	-
[i]	-	-	-	-
[j]	2.4 ± 0.72**	3.19 ± 0.95**	-	3.4 ± 0.71**
[l]	-	-11.23 ± 2.59**	-11.35 ± 3.57**	-6.6 ± 2.21**
χ^2	1.65$^{n.s}$	0.55$^{n.s}$	0.34$^{n.s}$	1.11$^{n.s}$

ns,* and ** : non significant, significant at 5% and 1% level of probability, respectively.
M = the mean of all generation, [d] = the sum of additive effects, [h] = the sum of dominance effects, [i] = the sum of additive × additive interaction, [j] = the sum of additive × dominance, [l] = the sum of dominance × dominance interaction, χ^2: Chi-square

Table III: Estimate of variance components, average degree of dominance and heritabilities for β-glucan and protein content in two crosses

	β-glucan		Protein	
Generation	**Cross I**	**Cross II**	**Cross I**	**Cross II**
V [d]	0.52	0.29	0.22	0.66
V [h]	0.08	0.13	0.32	0.073
V_E	0.05	0.06	0.12	0.052
$(H/D)^{1/2}$	0.39	0.66	1.21	0.33
h_b^2	0.84	0.75	0.61	0.87
h_n^2	0.79	0.61	0.35	0.82
R	12.04	8.29	3.46	9.12

$V_{[d]}$: Additive variance $V_{[h]}$: Dominance variance V_E: Environmental variance $(H/D)^{1/2}$: Average degree of dominance $h^2_{b:}$ Broad sense heritability $h^2_{n:}$ Narrow sense heritability R: Genetic advance.

Genetic studies of β-glucan in populations derived from doubled haploid (DH) and single seed descent lines from various crosses (Powell *et al.*, 1985) found that β-glucan in barley is controlled by a simple additive genetic system. In other studies, Islam *et al.* (2006) and Siddquie and Alam (2002) showed that β-glucan content in hulless barley is under the influence of additive effects. Also heritability estimates for β-glucan content have ranged from 0.55 to 0.88 (Humphreys & Mather, 1996; Holthaus *et al.*, 1996; Siddquie & Alam, 2002; Islam *et al*., 2006). Cervantes-Martinez *et al.* (2001) investigated the heritability of β-glucan content in various populations and showed that direct selection was the most suitable method to improvement of this trait. Taking into consideration other studies on the considerable contribution of the additive effects in controlling β-glucan content (Powell *et al.*, 1985; Siddquie & Alam, 2002; Islam *et al.*, 2006), it can be concluded that in order to improve this trait, methods based on direct selection in early generation such as pedigree can be applied.

Although generation means analysis in the cross ICNBF93-369 × ICNBF-582 showed that dominance effects had a greater contribution than additive effects in determining the protein content, this analysis for the cross SB91925 × ICB-102607 as well as the diallel cross showed that additive effects had a greater share in controlling this trait. In addition narrow sense heritability of this trait was low in the cross ICNBF93-369 × ICNBF-582, while high in the cross SB91925 × ICB-102607 as well as in the diallel cross. Anis'kov *et al.* (2008) reported that over dominance gene effects and complementary type of non-allellic interaction for protein content in barley. They suggested that hybridization method be applied in order to improve this trait in their samples. Arabi *et al.* (2008) reported genetic components of variance for various traits, including protein content in the parental and F_1 generations of a 9×9 diallel cross in hulless barley. Both genetic components (additive & dominance) were deemed to be involved in the inheritance of protein content. Nasrallah *et al*. (2007) also reported that both additive and non-additive genetic variances played important role in the inheritance of this trait, although, epistatic effects were not pronounced. Fregeau-Reid *et al*. (2001) showed the involvement of additive×additive type of epistasis in the inheritance of the protein percentage and suggested direct selection method for improving barley varieties with high protein content. In another research, El-Shawaf *et al.* (1994) reported that non-additive gene action is mainly responsible for the inheritance of this trait. Moreover, that low values of heritability for protein content indicated that this trait was greatly influenced by the environmental factors.

CONCLUSION

If the additive variance had a great share and the narrow sense heritability was high (such as β-glucan content in both experiments & protein content in diallel analysis & SB91925 × ICB-102607 cross in this research), direct selection can be applied. On the other hand, if the dominance variance had the greater share and there is over dominance (such as protein content in cross ICNBF93-369 × ICNBF-582), then using heterosis and hybridization-based methods such as bi-parental mating and/or diallel selective mating would yield better results. In this case, both variances contributed in controlling these traits, but their share varied amongst populations. Therefore before any improvement, appropriate crossings should be carried out so that sufficient information about controlling the trait in the given population is obtained and the share of additive, dominance and epistatic effects are determined, followed by selection of an appropriate improving method.

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