

Heterosis and genetic parameters for grain quality in oat segregating populations

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Introduction

Oats (*Avena sativa* L.) is considered an important cereal crop in many regions worldwide.

Over 23.8 million metric tons of oat grains were produced worldwide in 2013 (FAO, 2015). Human consumption of oats is becoming a major trend due to its excellent nutritional profile (Ahmad et al., 2014; Butt et al., 2008). Oats has high protein quality, antioxidant components, high lipid contents (especially unsaturated fatty acid) and high fiber rates (Biel et al., 2014; Crestani et al., 2012; Daou and Zhang, 2012; Marshall et al., 2013; Rasane et al., 2013).

When oat grain is allocated to animal feeding, a high content of lipids, protein and carbohydrates, and lower fiber contents are required (Hizbai et al., 2012; Martinez et al., 2010). In contrast, for human consumption, grains with low lipid contents, rich in protein and fiber are preferred, especially β -glucans, which are related to reduced levels of cholesterol and sugar in the blood, weight loss as well as cancer prevention (Bae et al., 2009; Daou and Zhang, 2012; Hooda et al., 2010; Lazaridou and Biliaderis, 2007; Peterson et al., 2005).

The analysis of oat cultivars released in Brazil from 1982 to 1996 indicated that oat breeding programs reached a linear genetic gain for the traits cycle, grain yield, grain weight and hectoliter weight (Barbosa Neto et al., 2000). From the 1970's to 2013, the Brazilian average yield ranged from 940 to 2,290 kg ha⁻¹ (FAO, 2015). Nevertheless, oat breeders should also pay attention to the industrial and nutritional quality, due to an increasing demand for functional foods.

ABSTRACT: Improvement of quality-related traits of grains is a constant concern in white oat breeding programs, which challenges breeders to understand their dynamics. The performance of different genetic combinations must be thoroughly evaluated to make high nutritional quality cultivars available. This study aimed to estimate the heterosis on F₁ and F₂ generations, vigor loss, due to inbreeding, and correlation between the grain chemical components to understand the dynamics of these traits, considering two segregating oat progenies. The populations Albasul \times UPF 15 (population 1) and IAC 7 \times UFRGS 19 (population 2) were developed. Both populations showed transgressive segregant individuals. The combination Albasul \times UPF 15 provided significant heterosis for traits β -glucan total and soluble fiber contents, while the population obtained by crossing IAC 7 \times UFRGS 19 generated significant gain by heterosis for total fiber, insoluble fibers and non-structural carbohydrate contents. Considering the F₂ average for each population, one can observe that population 1 presents higher β -glucan and lipid contents than population 2. On the other hand, population 2 has higher protein content than population 1. In both populations, the non-structural carbohydrate content is strongly and negatively correlated with protein, total and insoluble fibers. Correlations between total fibers and lipids and between total fibers and insoluble fibers were both positive and high in both populations.

Keywords: *Avena sativa*, functional food, artificial hybridization, correlation

Artificial crosses allow recombination of different alleles, creating a wide range of recombinants (Pandini et al., 1997). Plant breeders must evaluate the performance of populations to predict the potential of different combinations. Crosses with variability and combinations that contain the most favorable alleles for target traits are desirable. In addition, the correlation analysis allows identifying traits that could be used for indirect selection (Falconer and Mackay, 1996).

This study aimed to estimate heterosis in F₁ and F₂ generations, vigor loss due to inbreeding and correlation among the grain chemical components in order to understand the dynamics of these traits, considering two segregating oat progenies.

Materials and Methods

In this study, two F₂ segregating oat populations were used. These populations originated from the cross Albasul (G1) \times UPF 15 (G2) (population 1) and IAC 7 (G3) \times UFRGS 19 (G4) (population 2). These genotypes are hulled oats. Parents were selected based on their contrasting β -glucan content in the grains to generate mapping populations. Here, we used a part of F₂ seeds derived from the crosses performed by Crestani et al. (2012). In the cold season of 2009, a field experiment was carried out sowing 133 and 138 F₂ seeds of populations 1 and 2, respectively. Next, ten seeds of each parent and F₁ population were sown in the adjacent rows. The experiment was conducted in Capão do Leão, Rio Grande do Sul State, Brazil (latitude 31°50' S, longitude 52°29' W, altitude 13 m). The experimental design used was completely randomized.

Soil preparation followed the same procedures used by Hawerorth et al. (2013). The soil chemical features at the time of the experiment were: organic matter 2 %, water pH 5.5, SMP index 6.5, P 19.7 mg dm⁻³, K 80.0 mg dm⁻³, Al 0.1 cmol_c dm⁻³, Ca 2.5 cmol_c dm⁻³ and Mg 0.8 cmol_c dm⁻³. Based on these analyses, the fertilization corrections with macronutrients (NPK) were performed to supply the demands for a grain yield ca. 2.0 t ha⁻¹.

At the end of the reproductive cycle, grains from each plant from the F₂ populations and from each row of parents and F₁ generations were harvested, treshed and stored individually in a cold chamber at 12 °C for the chemical analyses. The following traits corresponding to the chemical composition of white oat grains were evaluated: protein content (PROT), lipid (LIP), total fibers (TF), soluble fibers (SF), insoluble fibers (IF), β-glucans (BGLU) and non-structural carbohydrate (NSC). These traits were chosen according to different grain end-use requirements.

For the chemical quality analyses, the near-infrared reflectance spectrophotometry (NIRS) was used. According to the technique requirements, samples were manually dehulled until 7 g of crushed material was obtained for each plant of the segregating populations. Grains were crushed and sieved in an electric mill with a 0.5-mm mesh. The flour was analyzed in an NIRS instrument in Passo Fundo, Rio Grande do Sul State, Brazil.

Calibration curves were applied using the software ISI (Infrasoft International of NIR Systems, version 4.0, 1996) by performing the analyses on 100 white oat samples, according to the recommended methods (AOAC, 1997; AACC, 2010). The value of protein content was obtained by multiplying the correction factor 5.83 for N content identified in the sample. Non-structural carbohydrate was determined by difference. NIRS readings were performed as triplets and the results expressed as g 100 g⁻¹ on a dry basis.

The obtained results were analyzed by a distribution frequency and univariate statistical methods of position and dispersion measures: average, minimal and maximum, coefficient of variation (CV), skewness (S) and kurtosis (K). The reference values adopted for the skewness coefficient were: S = 0, normal distribution; S < 0, asymmetric distribution to the left; S > 0, asymmetric distribution to the right. Regarding kurtosis, the reference values were: K = 0, normal distribution (mesokurtic); K > 0, thinner than normal distribution (leptokurtic); K < 0, flatter than normal distribution (platykurtic) (O'Rourke et al., 2005).

Heterosis, heterosis significance and vigor loss were calculated, as reported before (Crestani et al., 2012). In addition, a Pearson Correlation (Steel and Torrie, 1960) was performed to estimate the association of traits.

The analyses were performed using the software SAS (Statistical Analysis System, version 9.3, 1999).

Results and Discussion

The largest contrast observed between parents was for the β-glucan content (Table 1). However, the coefficient

of variation was considered high for both populations (23.98 and 26.61, for populations 1 and 2, respectively). Population 1 (Albasul × UPF 15) presented a significant F₁ heterosis gain (19 %), vigor loss due to inbreeding (10 %) in the F₂. Individuals with β-glucan were observed with values ranging from 2.47 to 9.11 g 100 g⁻¹. There are reports on oat β-glucan values ranging from 2.85 to 8 g 100 g⁻¹ (Crestani et al., 2012; Redaelli et al., 2013; Skendi et al., 2003).

Although parental β-glucan averages were higher in population 2 (IAC 7 × UFRGS 19), F₁ and F₂ averages were lower than those obtained for population 1. The average performance of F₁ was higher (19 %) and lower (-11 %) than the parental averages for populations 1 and 2, respectively. Considering vigor loss due to inbreeding depression in F₂, a higher loss (17 %) was observed for population 2 than for population 1 (10 %) suggesting the presence of non-additive interactions. According to previous reports, the β-glucan content in oat grains appears to be controlled by genes with predominant additive effects (Cervantes-Martinez et al., 2001). In barley, a diploid species, it was suggested that only the gene *HvCslF6* has high influence on the synthesis of β-glucans in the grains (Taketa et al., 2012).

One of the parents of population 2, IAC 7 has a superior industrial quality, with high β-glucan content (Crestani et al., 2012). The progeny originating from the cross between IAC 7 and UFRGS 19 showed individuals with average performance inferior to IAC 7 regarding the β-glucan content. Lack of complementarity was therefore observed between IAC 7 and UFRGS 19 for genes contributing to higher fiber content. There is possibility of epistatic interactions for this trait, as well as the specific gene combination in IAC 7, promotes high accumulation of BGLU.

In population 2, transgressive segregants were also observed for BGLU, with minimum and maximum values equal to 1.85 and 9.18 g 100 g⁻¹, respectively. Positive transgressive segregant individuals are desired by breeders aiming to obtain higher β-glucan contents, given their health benefits (Daou and Zhang, 2012; Hooda et al., 2010; Whitehead et al., 2014).

One experiment that evaluated 658 European oat genotypes reported the presence of individuals with the maximum of 6.77 g 100 g⁻¹ of BGLU content (Redaelli et al., 2013). Other studies on cultivars in the United States reported the BGLU content to around 5 g 100 g⁻¹ (Doehlert et al., 2013; Peterson et al., 2005). In genotypes in Brazil, individuals from both populations with even higher contents were observed (Table 1).

According to skewness coefficients shown on Table 1, both populations presented positive values (0.35 and 0.48). A graphical frequency distribution of populations 1 and 2 shows population 2 has higher probability to obtain individuals with a performance below the average (Figures 1A-B). A leptokurtic distribution (kurtosis = 0.38) for the β-glucan content was observed in population 2 (Table 1), indicating a less dispersive distribution, that is, a lower phenotypic variability between the individuals for the target trait.

Table 1 – Results from the descriptive statistical analysis of oat grain chemical components (g 100 g⁻¹) for both F₂ segregant populations, parental and F₁ average contents, heterosis (H_{F1}) and vigor loss due to inbreeding (LV).

Population	Character	G1	G2	F ₁	H _{F1}	Average (F ₂)	LV	σ (F ₂)	MiV (F ₂)	MaV (F ₂)	CV (F ₂)	S	K
				%		%				%			
POP1	BGLU	5.81	4.07	5.93	19.90*	5.31	10.42	1.27	2.47	9.11	23.98	0.35	-0.13
	PROT	17.19	19.09	18.70	3.08	18.62	0.41	1.07	15.97	21.68	5.75	0.33	0.38
Albasul ×	LIP	8.14	7.94	9.17	13.96	7.59	17.18	0.85	5.43	9.85	11.22	0.14	-0.22
	TF	9.49	9.47	10.00	5.82*	9.33	6.70	0.35	8.59	10.23	3.76	0.37	-0.18
UPF 15	IF	6.13	5.83	6.15	2.91	5.92	3.78	0.48	4.87	7.09	8.09	0.30	-0.43
	SF	3.36	3.67	3.86	9.81*	3.44	10.82	0.17	3.12	3.82	5.03	-0.10	-0.92
	NSC	65.16	63.53	65.28	1.21	62.5	4.25	1.59	57.86	66.97	2.55	-0.28	0.28
POP2	BGLU	7.60	5.54	5.80	-11.73*	4.81	17.03	1.30	1.85	9.18	26.61	0.48	0.38
	PROT	20.16	18.91	19.66	0.61	20.10	-2.26	1.56	15.83	24.95	7.75	0.60	0.93
IAC 7 ×	LIP	7.64	7.93	7.75	-0.48	6.46	16.61	0.68	4.66	8.35	0.68	-0.13	0.23
	TF	9.88	9.23	10.27	7.47*	9.37	8.76	0.40	8.62	11.10	4.30	1.10	2.82
UFRGS 19	IF	6.29	5.83	6.60	8.81*	5.91	10.39	0.52	4.97	8.02	8.86	0.94	1.98
	SF	3.72	3.43	3.68	3.04	3.53	4.14	0.20	3.07	3.90	5.66	-0.32	-0.87
	NSC	62.44	64.52	66.00	3.97*	62.08	5.94	2.02	54.39	66.27	3.26	-0.61	0.79

BGLU - β-glucan; PROT - Protein; LIP - Lipid; TF - Total fiber content; IF - insoluble fiber content; SF - Soluble fiber content; NSC - non-structural carbohydrates. σ (F₂) - standard deviation observed on F₂; MiV - minimum value; MaV - maximum value; CV% - coefficient of variation; S - skewness coefficient; K - kurtosis coefficient. *Significant heterosis at $p \leq 0.05$ by the t test.

The total fiber content ranges between 9.6 and 14.6 g 100 g⁻¹, depending on the genotype, environmental conditions, and the evaluation method adopted (Gutkoski and Trombetta, 1999; Manthey et al., 1999; Silva and Ciocca, 2005). Compared to these contents, the TF contents observed in the present work for parents and progenies are relatively low (Table 1). The gain obtained by heterosis was significant in both populations and both generated transgressive segregant individuals, however, in population 2, the individual with the highest TF content was obtained (11.10 g 100 g⁻¹) (Table 1). Positive segregant individuals represent potential elite genotypes for the development of high fiber containing cultivars. Diets with a high fiber content are a current trend in medical treatments, given the overwhelming incidence of obesity, diabetes and heart diseases (Sikora et al., 2013).

Even when low contrast parents were adopted, individuals with TF content higher than that of the best parent were obtained. This indicates the possibility to recover transgressive segregants from crosses involving parents with similar phenotype, probably because of complementary genes.

Population 2 displayed a highly positive skewness distribution (1.10) (Table 1), indicating that most individuals had a performance lower than the average of the population. The kurtosis coefficient (2.82) (Table 1) characterized a leptokurtic distribution and, consequently, a low phenotypic variability for the trait in F₂ generation (Figures 1C-D).

Insoluble fibers are composed by lignin, unsoluble pectins, cellulose and hemicellulose and integrate the total fiber portion (Butt et al., 2008).

In both populations, the average IF content was 5.9 g 100 g⁻¹ (Table 1). Previously, the IF content was observed at levels between 4.9 and 9.2 g 100 g⁻¹ (Doehlert et al., 2013; Gutkoski and Trombetta, 1999; Manthey et al., 1999; Silva and Ciocca, 2005). Only population 2 showed significant heterotic gain for the IF content (Table 1), which originat-

ed positive segregating individuals with higher IF content than parents did (8.02 g 100 g⁻¹). However, a larger number of individuals with performance below the parental average were also obtained (Figures 1E-F).

Soluble fibers comprise soluble pectins, gums, mucilage and some hemicellulose type molecules, and integrate the total fiber portion (Butt et al., 2008). In population 1, heterosis gains as well as vigor loss due to inbreeding were observed (Table 1). In general, either for populations or for their parents, SF contents around 3.5 g 100 g⁻¹ were observed. Other studies have found similar (Crestani et al., 2012; Silva and Ciocca, 2005) or higher (5.33 g 100 g⁻¹) values (Gutkoski and Trombetta, 1999). For many years, oat-breeding programs have focused on higher yields, resulting in increases in grain weight and size, reflecting on a higher non-structural carbohydrate accumulation.

Both studied populations presented positive skewness and platykurtic distribution (Figures 1G-H), indicative of a higher dispersion for the SF content.

The PROT content in oats is higher than in other cereals. It presents high digestibility and a balanced amino acid composition (Biel et al., 2014; Doehlert et al., 2013; Hawerth et al., 2013; Klose and Arendt, 2012). For the PROT content, an absence in heterosis gain in both populations was observed (Table 1), which can be an indicative of low combining ability between the parents, possibly due to the presence of similar loci that expresses reduced average performance for the trait, even after genetic recombination. An absence of hybrid vigor in F₁ does not mean that the populations had to be discarded, since distinct phenotypic classes can occur in F₂.

The average PROT content in population 1 was 17.2 g 100 g⁻¹, similar to the average PROT content reported by Hawerth et al. (2013) for Brazilian cultivars (18.71 g 100 g⁻¹) and also by Doehlert et al. (2013) that an-

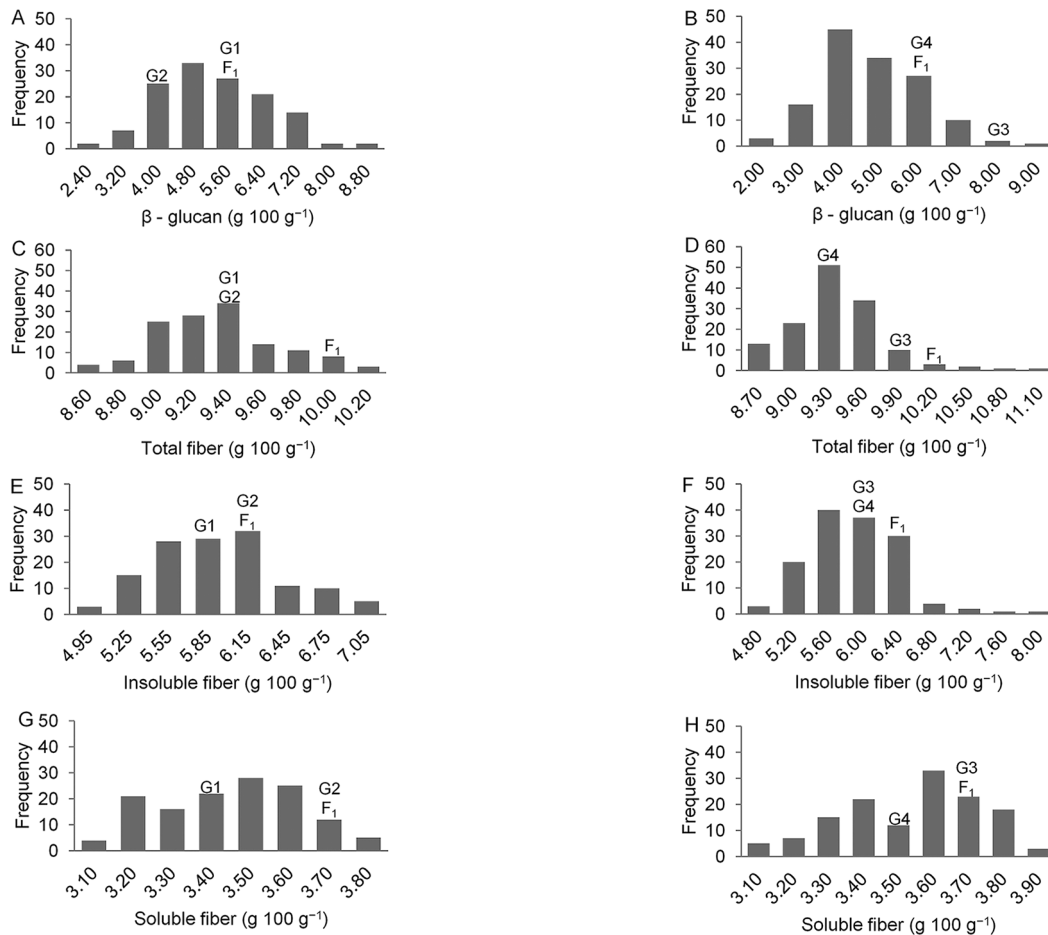


Figure 1 – Frequency distribution for individuals in F_2 generation, for the β -glucan content (A and B), total (C and D), insoluble (E and F) and soluble (G and H) fibers contents in oat grains, for population 1 (Albasul (G1) × UPF 15 (G2)) and 2 (IAC 7 (G3) × UFRGS 19 (G4)), respectively.

alyzed popular oat cultivars (18.11 g 100 g⁻¹) from North America. In a previous study on oat cultivars and lines from breeding programs in the United States, Canada and the Netherlands, an average equal to 16.5 g 100 g⁻¹ (Peterson et al., 2005) was found. A lower PROT content (13.7 g 100 g⁻¹) was observed for genotypes in Poland (Biel et al., 2014).

Population 2 presented higher PROT content average (20.10 g 100 g⁻¹) than population 1 in F_2 , and no vigor loss was observed for this trait. This population showed positive transgressive segregant individuals, displaying high PROT content. They are good candidates to generate elite lines for animal feeding and human consumption.

Earlier reports from our group (Crestani et al., 2012) have shown that IAC 7 had a great potential to generate progenies with high protein content. In our work, IAC 7 has high PROT and BGLU contents, and combined with genotype UFRGS 19, it has the ability to originate equally rich individuals regarding the PROT content, however, with low BGLU content.

The frequency distribution for populations 1 and 2 is shown in Figures 2A-B. In both cases, a leptokurtic distribution was observed with a large concentration of individuals similar to the average.

For the LIP content, the F_1 generation of population 1 presented higher content than its parents did, however, a significant heterosis value was not observed (Table 1). Both populations presented vigor loss due to inbreeding, resulting in an F_2 generation with LIP content lower than that of the parental average, suggesting the presence of non-additive allelic interactions. The LIP content is a polygenic trait and high oil content is under a partial control of allelic dominance (Frey and Hammond, 1975). Moreover, the presence of pleiotropic effects in LIP synthesis was suggested (Hizbai et al., 2012). At the same time, QTLs (Quantitative Trait Loci) have been detected for the LIP content in oats (Tanhuanpää et al., 2010; Tanhuanpää et al., 2012).

The average LIP content for populations 1 and 2 were equal to 7.59 and 6.46 g 100 g⁻¹, respectively. Contents between 6 and 9.4 g 100 g⁻¹ have been reported previously (Crestani et al., 2012; Doehlert et al., 2013; Peterson et al., 2005).

Both parental combinations generated transgressive segregant individuals with either higher or lower grain LIP content. Oat grains with high LIP content are desirable in animal feed, due to the high caloric content (Hizbai et al., 2012; Martinez et al., 2010). On the other

hand, a low LIP content is desirable for human consumption (Peterson et al., 2005). The data distribution for this trait on both populations is shown. Skewness and kurtosis were similar to zero, suggesting normal data distribution (Figures 2C-D).

F₂ generations with higher LIP and lower PROT contents (Population 1), high PROT and low LIP contents (Population 2) were observed. In fact, QTLs affecting simultaneously PROT and LIP contents have been described in oats (Tanhuanpää et al., 2012).

Considering the NSC content, there was significant heterosis only for population 2, followed by a reduced vigor loss (Table 1). For both populations, the average of F₂ generation was lower than that of the parents showing poor performance. Considering the performance showed by population 2, a lower NSC content was observed, which was previously observed in IAC 7 progenies (Crestani et al., 2012).

The NSC content in populations 1 and 2 were 65.16 and 62.44 g 100 g⁻¹, respectively. This value was a bit lower than the average (67.56 g 100 g⁻¹) found in previous reports for oat cultivars in Brazil (Hawerth et al., 2013). For genotypes in Poland, the average NSC content was equal to 13.7 g 100 g⁻¹ (Biel et al., 2014).

Transgressive segregants with NSC higher than the average plus a standard deviation were obtained in both populations. These genotypes can be promising not only because they represent a higher accumulation of energy in the caryopsis, but also because they normally have higher grain size. Both populations showed negative kurtosis distributions, increasing the possibility of selecting individuals with above average NSC content (Figures 2E-F).

Correlation values are meaningful depending on their sign (positive or negative) and magnitude, and estimated values below -0.50 and above 0.50 are usually accepted (Lopes et al., 2002). Many significant correlations were found, however, within the interval 0.50 and -0.50 (Table 2). This could be a reflection of the large number of individuals measured, resulting in a greater number of freedom degrees used by the *t* test. With a few exceptions, the significance and magnitude of the correlations remained similar between the two populations.

The NSC content presented negative correlations with all other traits for both populations. Negative and high magnitude (below -0.50) correlations were observed between contents of NSC and those of PROT, TF and IF. These negative correlations have been previously reported (Biel et al., 2014; Crestani et al., 2012; Peterson et al., 2005). In addition, the amylose content, a starch component, presented negative correlation with the PROT content (Hang et al., 2007). NSC was also negatively correlated with LIP, but only for population 1 with high magnitude (-0.62).

Negative correlations between the NSC content and the other chemical components suggest that the increase in the starch content is not accompanied by an increase in contents of PROT, IF and TF. TFs are composed of IF and SF. TF contents were positively correlated (above 0.50) with the IF content in both populations, however, with SF only in population 1. A positive correlation between LIP and TF was also observed (above 0.50). Although no biological explanation was found for this correlation, some pleiotropic or linkage effect may be the cause for these associations.

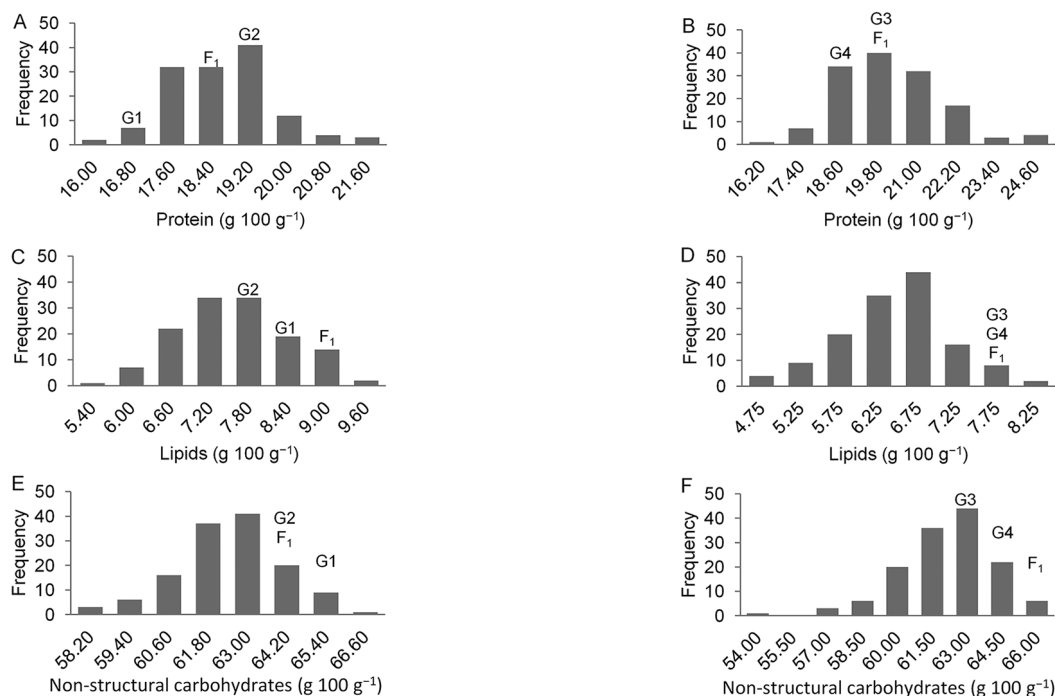


Figure 2 – Distribution of frequency for individuals in F₂ generation, for contents of protein (A and B), lipid (C and D), and non-structural carbohydrate (E and F) in oat grains, for population 1 (Albasul (G1) × UPF 15 (G2)) and 2 (IAC 7 (G3) × UFRGS 19 (G4)), respectively.

Table 2 – Values of Pearson correlation coefficients between protein (PROT), lipid (LIP), total fiber (TF), insoluble fiber (IF), soluble fiber (SF), β -glucan (BGLU) and non-structural carbohydrate (NSC), measured in two segregant population F₂ - POP1 (Albasul \times UPF 15) and POP2 (IAC 7 \times UFRGS 19).

Characters	Pearson correlation coefficients					
	LIP	TF	IF	SF	BGLU	NSC
PROT (POP 1)	-0.0858 ^{ns}	0.3036**	0.2871**	0.0060 ^{ns}	0.2939**	-0.7082**
PROT (POP 2)	-0.0663 ^{ns}	0.5382**	0.4971**	0.1354 ^{ns}	0.2218**	-0.8754**
LIP (POP 1)		0.6191**	0.5143**	0.2126*	-0.1433 ^{ns}	-0.6205**
LIP (POP 2)		0.5746**	0.4499**	0.4042**	-0.1122 ^{ns}	-0.4059**
TF (POP 1)			0.9454**	0.0723 ^{ns}	0.2912**	-0.7801**
TF (POP 2)			0.9415**	0.2387**	0.4289**	-0.8317**
IF (POP 1)				-0.2543**	0.4318**	-0.7043**
IF (POP 2)				-0.1015 ^{ns}	0.5376**	-0.7495**
SF (POP 1)					-0.4694**	-0.1220 ^{ns}
SF (POP 2)					-0.2721**	-0.2810**
BGLU (POP 1)						-0.1985*
BGLU (POP 2)						-0.2348**

**, * Significant at $p \leq 0.01$ and $p \leq 0.05$, by the t test, respectively; ns = non-significant.

PROT and BGLU were significant and positively correlated, although with low magnitude. In barley, the β -glucan content remained positively correlated with the protein content throughout selection (Hang et al., 2007). For both populations, there were no significant associations between PROT and LIP, PROT and SF, or LIP and BGLU traits. The lack of association between PROT and LIP could be a result of interference of the NSC content, masking potential associations. These populations have been improved to form RILs (Recombinant Inbred Lines) and associations will be tested within pools of large and small grains to isolate NSC effects.

Understanding the dynamics of traits related to grain chemical composition in oats is essential for genetic gains related to grain chemical components. The associations between LIP, PROT and fiber contents display a complexity that is dependent not only on the grain chemical composition of superior genotypes, but also on their ability of transmitting their properties to the progeny, as observed for the cultivar IAC 7.

The reported populations have different performances for the evaluated traits, however, both present transgressive segregant individuals for these traits. The combination Albasul \times UPF 15 generated heterosis for contents of BGLU, TF and SF, while the population obtained from the cross IAC 7 \times UFRGS 19 generated heterosis for contents of TF, IF and NSC. Considering the average of F₂ generation for each population, we observed that population 1 presented higher BGLU and LIP contents than population 2 did. On the other hand, the PROT content was higher in population 2 than in population 1. In both populations, the NSC content is strongly and negatively correlated (below -0.50) with PROT, TF and IF. The correlations were positive and high (above 0.50) between TF and LIP, and between TF and IF, for both populations.

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