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Inheritance and potential use of grain color in the identification of genotypes resistant to pre-harvest sprouting in wheat

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ABSTRACT - *The inheritance of grain color and pre-harvest sprouting in wheat was studied to identify genotypes with high resistance to pre-harvest sprouting and evaluate the possible use of grain color in indirect selection of resistant lines. The genotypes of most lines were characterized with regard to the loci that control grain color. No significant correlations between grain color and pre-harvest sprouting resistance were observed, but correlations were useful when the frequency of segregating genotypes with white grain was relatively high. Of the eight $F_{2:3}$ populations evaluated, only two differed significantly in grain sprouting between the white and red classes. Three genes for pre-harvest sprouting resistance seem to be present in the genotypes Frontana and Onix. Grain color should not be used as the only criterion for selecting wheat genotypes resistant to pre-harvest sprouting.*

Key words: *Triticum*, seeds, dormancy, pre-harvest sprouting.

INTRODUCTION

Pre-harvest sprouting or germination in the ear refers to the germination process of physiologically ripe seeds in the ear, ie, before harvest. This sprouting is a major problem in wheat production in many parts of the world (Cunha et al. 2004), for reducing the commercial value of the grain and restricting its use for animal consumption in some cases. In Brazil, the problem is most severe in the south, where temperatures during maturation and persistent rain at harvest time reduce grain dormancy, resulting in pre-harvest sprouting in most Brazilian cultivars. As a result, in critical years losses can amount up to $ 100 million (Bassoi and Flintham 2005).

The expression of pre-harvest sprouting depends on a series of factors such as climatic aspects, grain drying, caryopsis structure, morphology of the ear, genetic resistance to pre-harvest sprouting, maturation stage and possible expression of dormancy (Derera et al. 1977, Lush and Groves 1981, Bassoi 2004).

The existence of an association between color and grain pre-harvest sprouting is mentioned by several authors (Derera et al. 1977, Soper et al. 1989, McCaig and DePauw 1992, Flintham 2000, Kuraparthy et al. 2008). The red pigment of hexaploid wheat grain is determined by dominant R alleles of three genes located on homologous loci on the chromosomes 3A, 3B and 3D (Metzer and Silbough 1970, Bassoi 2004). While sprouting is controlled by many other genes that are unrelated to seed coat pigmentation, the association between grain color and the reduction in seed dormancy would make color particularly useful as morphological marker in the search for sprouting resistance in wheat breeding programs (Bassoi et al. 2006).

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This study aimed to contribute to information on the inheritance of grain color and pre-harvest sprouting, identify sprouting-resistant genotypes and to assess the potential of indirect selection based on grain color.

MATERIAL AND METHODS

Twenty-five segregating $F_{2:3}$ populations were evaluated, derived from diallel crosses among eight wheat genotypes differing in grain color and pre-harvest sprouting (1-CD 0545, 2-CD 0666, 3-CD 150, 4-OCEPAR 18, 5-IPR 85, 6-Ônix, 7-FRONTANA, and 8-PFAU*). PFAU* was derived from a cross of AMAD with the hybrid PFAU x SERI.1B. The study was conducted at the Cooperativa Central de Pesquisa Agrícola – COODETEC, in Cascavel and Palotina (Paraná, Brazil).

A rainfall simulator, a modified version of the model used by Okuyama et al. (2003), derived from the model of McMaster and Derera (1976) was used in a greenhouse. The simulator was programmed to promote ideal conditions for the occurrence of pre-harvest sprouting in wheat, allowing simultaneous monitoring of a large number of genotypes.

After irrigation, the ears were scored according to the 1-11 scale of McMaster and Derera (1976). Ears with grade 1 were considered resistant to pre-harvest sprouting, and the others susceptible. Samples of the seeds that did not germinate were subjected to a tetrazolium test to confirm the possibility of dormancy.

The ears of $F_{2:3}$ populations were threshed to determine grain color and texture, according to the criteria of the Brazilian Ministry of Agriculture, Livestock and Supply (MAPA 2008) for the identification of wheat descriptors.

The test results of pre-harvest sprouting and grain color data were subjected to chi-square tests to verify the hypotheses of segregation of genes controlling these traits in each of the 25 populations evaluated. A simple correlation study was also performed, using a Pearson test applied to the characteristics of pre-harvest sprouting, grain color and grain texture.

The means of pre-harvest sprouting of white and red grains in each population were compared using the t-test.

All statistical analyses were performed using software GENES (Cruz 2001).

RESULTS AND DISCUSSION

The test results of pre-harvest sprouting demonstrated the existence of genetic control in the trait expression, by the occurrence of different levels of sprouting among populations. Among the parents, Frontana, IPR 85 and Ônix performed particularly well, with very high pre-harvest sprouting resistance. Wheat cultivar Frontana, with the lowest number of sprouted grains, is considered a reference genotype for pre-harvest sprouting resistance, even under extremely favorable conditions for sprouting (Bassoi 2004).

The observed and expected proportions and the hypothesis test for inheritance of pre-harvest sprouting in seeds of $F_{2:3}$ wheat populations are presented in Table 1. In the evaluation of seed dormancy, only families with grade 1 were considered resistant to pre-harvest sprouting. The test results of these hypotheses allowed the estimation of the number of genes segregating for the expression of dormancy in each population. Despite the oligogenic inheritance pattern found in the assessment of dormancy inheritance in each individual population, the pattern was more complex in the joint assessment of the various populations.

When crossed with PFAU*, IPR 85, Ônix and CD 150, parent CD 0545 expressed segregation for three independent and complementary recessive genes, so that three genes in homozygosis were needed for seed dormancy (Table 1). However, when CD 0545 was crossed with CD 0666 and OCEPAR 18, two recessive, independent and complementary genes, segregated. The cross of CD 0545 with Frontana however revealed the action of three recessive genes, two of which were duplicate and one complementary. Therefore, the expression of dormancy required the presence of the duplicated genes plus a third gene, all homozygotic.

Different segregation patterns were associated with the crosses involving the parent CD 0666. The crosses of CD 0666 with CD 150 and PFAU* resulted in the segregation of three independent and complementary recessive genes (Table 1). When CD 0666 was crossed with Frontana, one recessive gene segregated and, in the cross with OCEPAR 18, segregation was observed for two complementary genes, a dominant and a recessive one. In the case of a cross with Ônix, the segregation observed indicated the action of three complementary recessive genes, two of them with duplicate effect.

Table 1. Observed and expected proportions, and test of hypothesis for inheritance of pre-harvest sprouting in seeds of F2:3 wheat populations

Population	Score	$F_{2:3}$ plants observed	Expected		χ^2	Prob (%)
			Segregation	$F_{2:3}$ plants		
CD 0545/PFAU*	> 1 (S)	197	63	195.89	0.402	52.6
	1 (R)	2	1	3.109		
CD 0545/IPR 85	> 1 (S)	197	63	196.87	0.005	94.31
	1 (R)	3	1	3.125		
CD 0545/Ônix	> 1 (S)	200	63	200.81	2103	64.64
	1 (R)	4	1	3.18		
CD 150/CD 0545	> 1 (S)	208	63	206.71	0.508	47.59
	1 (R)	2	1	3.28		
CD0545/CD0666	> 1 (S)	203	15	200.62	0.449	50.24
	1 (R)	11	1	13.37		
CD 0545/OC 18	> 1 (S)	191	15	187.5	1.045	30.65
	1 (R)	9	1	12.5		
CD0545/Frontana	> 1 (S)	176	57	180.79	1.163	28.07
	1 (R)	27	7	22.20		
CD 150/CD 0666	> 1 (S)	197	63	196.87	0.005	94.31
	1 (R)	3	1	3.125		
CD 0666/PFAU*	> 1 (S)	207	63	206.71	0.024	87.56
	1 (R)	3	1	3.28		
CD 0666/Frontana	> 1 (S)	112	3	108	0.592	44.14
	1 (R)	32	1	36		
CD 0666/OC 18	> 1 (S)	179	13	173.06	1.086	29.72
	1 (R)	34	3	39.93		
CD 0666/Ônix	> 1 (S)	191	57	190.59	0.007	92.90
	1 (R)	23	7	23.40		
CD 150/PFAU*	> 1 (S)	202	63	202.78	0.192	66.07
	1 (R)	4	1	3.21		
CD 150/Ônix	> 1 (S)	202	63	200.81	0.449	50.26
	1 (R)	2	1	3.18		
CD 150/OC 18	> 1 (S)	191	57	188.81	0.231	63.02
	1 (R)	21	7	23.18		
CD 150/IPR 85	> 1 (S)	193	15	194.06	0.093	76.03
	1 (R)	14	1	12.93		
CD 150/Frontana	> 1 (S)	207	61	204.92	0.449	50.25
	1 (R)	8	3	10.07		
IPR 85/OC 18	> 1 (S)	197	63	197.85	0.238	62.50
	1 (R)	4	1	3.14		
IPR 85/PFAU*	> 1 (S)	179	63	179.15	0.008	92.55
	1 (R)	3	1	2.84		
IPR 85/Ônix	> 1 (S)	199	15	196.87	0.366	54.46
	1 (R)	11	1	13.12		
Frontana/IPR 85	> 1 (S)	202	61	199.20	0.827	36.00
	1 (R)	7	3	9.76		
OC 18/Ônix	> 1 (S)	186	57	181.68	0.935	33.33
	1 (R)	18	7	22.31		
OC 18/PFAU*	> 1 (S)	202	15	200.625	0.150	69.77
	1 (R)	12	1	13.375		
Frontana/PFAU*	> 1 (S)	157	57	158.53	0.135	71.30
	1 (R)	21	7	19.46		
Ônix/PFAU*	> 1 (S)	187	57	183.46	0.621	43.05
	1 (R)	19	7	22.53		

In the cross of parent CD 150 with PFAU* and Ônix, segregation was observed for three independent and complementary recessive genes (Table 1). When crossed with IPR 85, segregation was observed for two complementary recessive genes, and in the cross with OCEPAR 18, for three recessive genes, two of which had duplicate and one complementary effect. Finally, in the cross with Frontana, three complementary genes segregated, two recessive and one dominant.

In the cross of parent IPR 85 with OCEPAR 18 and PFAU*, three independent and complementary recessive genes segregated (Table 1). When crossed with Frontana, segregation involved three complementary genes, two recessive and one dominant. In the cross of IPR 85 with Ônix, two independent and complementary genes segregated.

The parent OCEPAR 18, when crossed with Ônix (Table 1), segregated for three recessive genes, two of which had a duplicate and the other a complementary effect. In the cross with PFAU*, two recessive, independent and complementary genes segregated.

The same segregation of three recessive genes was observed when Frontana and Ônixn were crossed with PFAU* (Table 1), in which two of them had duplicate effect. The third gene had complementary effect to the first.

When the different populations were cross-evaluated, there was some inconsistency in the results. In the population derived from the cross of CD 0545 x PFAU*, for example, two $F_{2:3}$ plants were obtained resistant to sprouting and 197 susceptible families, a result consistent with the segregation of three complementary recessive genes. However, both in the cross CD 0545 x Frontana as in PFAU* x Frontana, the results are consistent with the segregation of three recessive genes, two duplicate and one complementary (ratio 57:7). This indicates that CD 0545 and PFAU* have the same genotype for the alleles of the dormancy genes present in Frontana.

Pre-harvest sprouting depends not only on the plant genotype, but also on the environmental conditions. It is therefore possible that the apparent resistance of the plants of the population derived from CD 0545 x PFAU* is a result of having escaped from pre-harvest sprouting due to the planting date. Assuming this possibility, the population does not segregate for dormancy, the descents are altogether susceptible and the two cultivars have no dormancy genes. In fact, the population size used was insufficient for full confirmation of the hypothesis of segregation of three complementary recessive genes (ratio 63:1). Thus, all segregation observed fitting the ratio of 63:1 should be evaluated with caution, because these populations do possibly not segregate genetically for dormancy.

Based on the results of the smallest number of sprouted grains, greatest number of non-germinated grains

and the lowest sprouting scores, the cultivars Frontana, IPR 85 and Ônix were identified as the most resistant to pre-harvest sprouting. Considering the average sprouting of the parents, it was inferred that dormancy occurs only in the parents Frontana, IPR 85 and Ônix. In crosses that exclude these parents, segregation for dormancy would only occur if there were complementary genes. One can also observe from Table 1 that the most sensitive parent is PFAU*, probably devoid of dormancy genes. In the populations derived from crosses Frontana, IPR 85 and Ônix with PFAU*, it was observed that both populations, the one derived from Frontana and the one derived from Ônix, segregate at a ratio of 57:7, indicating the presence of three recessive and two duplicate genes, the third being complementary to the first. The population derived from IPR 85 x PFAU* however segregated at a ratio of 63:1, indicating the segregation of three complementary recessive genes. Although this segregation of 63:1 should be evaluated with caution for this population size, segregation is to be expected in this population, since one parent is dormant and the other not.

The segregation observed in families derived from crosses between parents with dormancy indicates that IPR 85 has other genes of dormancy than Frontana and Ônix, because both populations segregated for the trait. The population derived from Ônix x IPR 85 segregated at a ratio of 15:1, indicating the existence of two different complementary recessive genes in IPR 85 and Ônix. The population derived from Frontana x IPR 85 segregated at a ratio of 61:3, indicating the presence of three genes differing between the two parents, of which two are dominant and one recessive, and all epistatic (complementary).

The segregation in populations derived from crosses between resistant and susceptible parents indicates a differentiated genetic control of dormancy in each of the three dormant parents. For instance, the segregation observed in crosses between Frontana and CD 0666 was 3:1, and 57:7 of the segregation observed in the cross between Ônix and CD 0666. It is possible that different genes control dormancy in each resistance source, or that there is an allelic series in the dormancy genes, in which the relation of dominance is variable depending on each genetic combination. These relationships must be better explored in future studies of genetic mapping of loci involved.

Andreoli et al. (2006) found that, in the F_2 population derived from the cross between Frontana x OR1 and its reciprocal OR1 x Frontana, dormancy in wheat seeds appeared to be associated with two genes, A|a and B|b; only seeds under double recessive homozygosis (aabb) are dormant.

Based on the results of this study, it was hypothesized that Frontana and Ônix have three genes for the determination of resistance to pre-harvest sprouting, and that this resistance is expressed only when all alleles are homozygous recessive (aa bb cc), and that two of these genes are duplicated. However, it is not possible to determine whether the two dormancy sources have the same genes or the same dormancy alleles.

Due to the hexaploid constitution of wheat, part of the genes present in the genome are repeated in the genomes B and D, making the segregation patterns complex and complicating the genetic analyses (Breiman and Graur 1995). In the case of grain color, control is exercised by three independent and homologous genes located on the chromosomes 3A, 3B and 3D. The alleles that confer the red grain color are called *R-A1b*,*R-B1b*, and *R-D1b*, and alleles that confer white grains are called *R-A1a*, *R-B1a*, and *R-D1a* (Sherman et al. 2008).

The red color of a wheat grain may be associated with dormancy. Seven of the eight parents used in this allele study have red and only PFAU* has white seeds. The results of segregation observed in the populations that expressed variability for wheat grain color are shown in Table 2. To facilitate the discussion of the data, the genes of red grain will be referred to as A, B and C.

The populations derived from crosses between PFAU* with OC 18, CD 150, IPR 85 and Ônix segregated at a ratio of 15:1 (red : white) (Table 2), indicating that each of these lines with red grain has two dominant genes that control the grain color. The population derived from cross PFAU* x CD 0666 segregated for one dominant gene, while in the population derived from PFAU* x CD 0545 no plant had white seeds. Since the parents differ in relation to grain color, it is possible that CD 0545 has three dominant genes for red and that no plants with white seeds were obtained due to the population size. To illustrate this possibility, it is worth remembering that if there are 200 plants in an F_2 population derived from crosses between parents differing in three genes for a particular characteristic, the probability of not obtaining any recessive homozygous plants for the three genes in question is 4.3%.

The segregation in cross Frontana x PFAU* was 7:9 (red : white) (Table 2), indicating the presence of two duplicate recessive genes controlling the red color. In this

Table 2. Observed and expected proportions, and test of the hypothesis for inheritance of grain color in $F_{2:3}$ wheat populations

Population	Color	Plants $F_{2:3}$ observed	Expected		χ^2	Prob (%)
			Segregation	Plants $F_{2:3}$		
CD 150/PFAU*	Red	199	15	195.00	1.31	25.19
	White	9	1	13.00		
IPR 85/PFAU*	Red	172	15	169.68	0.50	47.76
	White	9	1	11.31		
Ônix/PFAU*	Red	184	15	188.43	1.67	19.59
	White	17	1	12.56		
OC18/ PFAU*	Red	193	15	199.68	3,58	5,83
	White	20	1	13.31		
CD 0666/OC 18	Red	201	15	199.68	0.13	71.02
	White	12	1	13.31		
CD0545/PFAU*	Red	200	63	196.87	3.17	7.47
	White	0	1	3.12		
CD 0666/Ônix	Red	212	63	211.64	0.03	84.33
	White	3	1	3.35		
CD 0666/PFAU*	Red	155	3	153.00	0.10	74.64
	White	49	1	51.00		
Frontana/PFAU*	Red	77	7	76.56	0.00	94.68
	White	98	9	98.43		

case, the expression of red seems to require the presence of one of the two homozygous genes.

In the populations derived from crosses between parents with red seeds, the population derived from CD 0666 x OC 18 segregated in a ratio of 15:1 (two dominant genes), and the population derived from CD 0666 x Ônix segregated in a ratio of 63:1 (three dominant genes) (Table 2). Thus, in CD 0666 the red grain color is controlled by one dominant gene and in Ônix by two dominant genes. As the population segregates for three genes, the gene present in CD 0666 is different from the genes present in Ônix. The population derived from OC 18 x CD 0666 however segregated at a ratio of 15:1, indicating that these two parents differ in two genes related to grain color. As both have red beans, it is to be expected that each of them has a dominant gene for red color. However, in the cross of OC 18 x PFAU*, the population also segregated for two genes, indicating that OC 18 would have two dominant genes. Future work with molecular markers may clarify this issue.

The results obtained in the allele test for wheat grain color indicate that the tested lines have the genotypes listed in Table 3. An analysis with molecular markers can identify each one of the genes A, B and C as gene R.

Inadequate seed dormancy is associated with pre-harvest sprouting. To suppress the sprouting, it is necessary to increase the traits that restrict germination. According to Flintham (2000) the grain dormancy and color are characteristics inherited as pleiotropic effects of

Table 3. Definition of the genotypes of wheat varieties/lines used as parents for the genes of red grain color

Parent	Grain color	Genotype
PFAU*	White	aa bb cc
CD 0545	Red	AA BB CC
Ônix	Red	AA BB cc
CD 0666	Red	aa bb CC
CD 150	Red	AA bb CC or aa BB CC
IPR 85	Red	AA bb CC or aa BB CC
Frontana	Red	2 recessive genes for red color
OC 18	Red	-

dominant R alleles and represent a series of genes that work similarly, located in the homologous loci in the chromosomes 3A, 3B and 3D of hexaploid wheat. The red grain is a traditional marker for sprouting resistance in wheat breeding programs. White seeds have been considered as on average more susceptible to sprouting than red seeds, although both vary somewhat in this respect (Bassoi et al. 2006).

To evaluate the association between wheat grain color and dormancy/ sprouting resistance, the correlation between characteristics of grain color, texture and grain sprouting was evaluated for each of the populations that segregated for the traits (Table 4). The results showed a negative correlation between grain color and pre-harvest

Table 4. Correlation between the traits grain color, pre-harvest sprouting and grain texture of $F_{2:3}$ wheat populations

Population	Color/Sprouting	Color/Texture	Sprouting/Texture
CD 150/PFAU*	-0.1316	-0.0269	-0.0138
CD 0666/PFAU*	-0.0966	0	0
CD 0666/OCEPAR 18	-0.0593	-0.0168	-0.0082
CD 0666/Ônix	-0.0292	0	0
Frontana x PFAU*	-0.5784**	-0.1947**	0.0355
OCEPAR 18/PFAU*	-0.0975	-0.1139	0.0533
IPR 85/PFAU*	0.1132	0	0
Ônix/PFAU*	-0.0915	-0.0217	0.1035

** Significant at 1% probability by the t-test.

sprouting (-0.5784), and also between grain color and texture (-0.1947), but only for cross Frontana x PFAU*. The lack of correlation between the traits in most populations can be explained by the low number of plants with white grains (Table 2). The population of the cross Frontana x PFAU* was the only in which the number of plants with white seeds was similar to that of plants with red seeds (98 white and 77 red).

In order to verify the existence of significant differences between the means of sprouting observed in white and red classes each segregating population, the

means were compared in a t-test. Of the eight segregating populations studied, the difference for mean sprouting between the white and red classes was significant in only two (crosses CD 150 x PFAU* and Frontana x PFAU*) (Table 5). It should be noted that a single dominant R allele is sufficient to determine the expression of red wheat grains, but two or three homozygous genes are needed to determine dormancy. Consequently, increasing the dose of dominant R alleles tends to raise the level of pre-harvest sprouting resistance (Bassoi and Flintham 2005).

Table 5. Results of the t-test comparing the means of pre-harvest sprouting in white and red seeds of $F_{2:3}$ wheat populations

Population	Mean of sprouting		t	Probability (%)
	White	Red		
CD 150/PFAU*	6.777	5.778	2.396	3.777*
CD 0666/PFAU*	6.265	5.974	1.264	20.713
CD 0666/OCEPAR 18	4.250	3.726	0.963	64.423
CD 0666/Ônix	5.666	5.137	0.394	72.507
Frontana x PFAU*	6.857	4.000	8.761	0*
OCEPAR 18/PFAU*	6.650	5.942	1.878	6.780
IPR 85/PFAU*	5.777	6.584	0.983	64.470
Ônix/PFAU*	6.058	5.311	1.658	10.767

* Significant value at 5% probability by the t-test.

CONCLUSIONS

In seven of the eight wheat lines used as parents, the genotypes containing loci responsible for the grain color inheritance were fully or partially characterized. Among the genotypes evaluated, Frontana and Ônix have three genes for the determination of pre-harvest sprouting resistance, and this expression only occurs when all alleles are recessive homozygous.

The red seed color is not considered solely as a full guarantee of greater pre-harvest sprouting resistance.

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Herança e uso potencial da cor de grãos para a identificação de genótipos resistentes à germinação pré-colheita em trigo

RESUMO - *Foi realizado um estudo de herança da cor de grãos e da germinação pré-colheita em trigo. Foram identificados os materiais com maior resistência à germinação pré-colheita, e avaliada a possibilidade de utilização da cor de grãos na seleção indireta de linhagens resistentes. Foram caracterizados os genótipos da maioria das linhagens, nos locos que controlam a cor dos grãos. As correlações foram ineficientes para identificar uma possível associação entre a cor dos grãos e a resistência à germinação, mas foram úteis quando a frequência de segregantes com grãos brancos mostrou-se relativamente alta. Das oito populações $F_{2:3}$ avaliadas, apenas duas apresentaram diferenças significativas quanto à germinação de grãos entre as classes branco e vermelho. Três genes para resistência à germinação da espiga parecem estar presentes nos genótipos Frontana e Onix. A cor dos grãos não deve ser utilizada como critério único para a seleção de trigos resistentes à germinação na espiga.*

Palavras-chave: *Triticum*, sementes, dormência, germinação na espiga.

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