

## Evidence of maternal effect on the inheritance of flax (*Linum usitatissimum* L.) seed coat color

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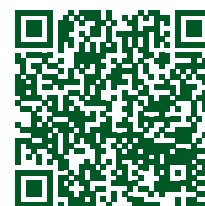
**Abstract:** This study aimed to investigate the presence of maternal effect on the inheritance of flax seed coat color. Direct and reciprocal crosses were performed between four yellow flax seed lines and two brown flax seed cultivars.  $F_1$  and  $F_2$  populations of direct and reciprocal crosses were evaluated for coat color. Four  $F_2$  populations were selected for analysis of coat color in the  $F_3$  generation. The phenotypic segregation pattern was assessed by the chi-square test. The nuclear genotype of the female parent influenced all  $F_1$ ,  $F_2$ , and  $F_3$  populations.  $F_1$  and  $F_2$  seeds were always equal to the phenotype of the female parent.  $F_3$  populations had a 3:1 ratio of plants producing yellow and brown seeds. The maternal effect resulted from the transfer of gene products from maternal cytoplasm to offspring, with evidence of the effect of a single gene with a dominant allele for the yellow phenotype.

**Keywords:** Chi-square test, genetic improvement, female parent, reciprocal cross.

### INTRODUCTION

Flax or linseed (*Linum usitatissimum* L.) is an autogamous, diploid ( $2n = 2x = 30$  chromosomes), annual winter plant (Allaby 2005). The plant can be used for the production of textile fibers, and its seeds can be used in human and animal nutrition and, mainly, for the extraction of flax seed oil, which is an important raw material in the chemical industry (Da'Coll Lúcio et al. 2021). Given its high content of linolenic acid, flax seed oil is susceptible to oxidation and polymerization, serving as an excellent drying agent for paints, varnishes, dyes, waxes, synthetic leather, and linoleum floors, among others (Dash et al. 2017, Parikh et al. 2019). Furthermore, the seed is rich in omega-3 and -6 fatty acids, protein, and digestible fiber. Raw flax seeds, flax seed flour, and flax seed meal constitute healthy additions to the human diet and may contribute to disease prevention. Flax seed oil and meal are also added to animal diets as energy sources (Singh et al. 2011, You et al. 2016).

Seed color is an important attribute influencing the market value of flax cultivars. This trait is mainly determined by the concentration, composition, and polymerization degree of tannins in outer coats (Bangar et al. 2021, Tomaszewska-Gras et al. 2021). Seed coat color in flax can range from yellow, olive, light brown, or dark brown (Diederichsen and Raney 2008) to variegated (Mitappali and Rowland 2003). Yellow flax seeds have thin and soft hulls. This coat color results from inhibition of the biosynthesis of proanthocyanidins,



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condensed tannins that impart a brown color to the seed coat (Kajla et al. 2015, Xu et al. 2015) and serve as a valuable source of antioxidants. It should be noted that, although yellow seeds do not contain tannins, their cotyledons are rich in carotenoids (Troshchynska et al. 2019).

Studies showed that yellow-seed genotypes had lower seed yield, attributed to the lower vigor, lower germination rate, and lack of flavonoids in yellow seeds (Saeidi and Rowland 1999, Zare et al. 2021, Abtahi et al. 2022). Abtahi et al. (2022) argued that red or brown seed colors may serve as effective markers for the indirect selection of oil- and protein-rich genotypes. Because of the importance of seed color in the export market, this trait is included in all flax breeding programs (Mittapalli and Rowland 2003, Sudarshan et al. 2017, Zare et al. 2021, Abtahi et al. 2022).

In flax, seed coat color is controlled by three (Tammes 1922, Barnes et al. 1960, Comstock et al. 1969) or four nuclear loci (Mittapalli and Rowland 2003). The Y1 allele confers a dominant yellow color to the seed coat, whereas alleles g, d, and b1 confer a recessive yellow color. In these cases, the alternative phenotype is always brown. There is also a recessive allele for the b1 locus, which is called b1<sup>ve</sup> because its expression produces a variegated seed coat (Saeidi and Rowland 1997). None of the previous studies reported the maternal effect on flax seed coat color.

The maternal effect is defined as the causal influence of the maternal genotype or phenotype on the offspring phenotype. Maternal genetic effects occur when genes present in the mother's genome affect the phenotype of her offspring (Wolf and Wade 2009). Many of the known maternal effect genes act via maternal mRNA or proteins (Berleth et al. 1988, Tong et al. 2000) that coordinate development, particularly prior to the maternal-to-zygotic transition, and often represent products from the majority of the genes in the genome (Baroux et al. 2008).

This study aimed to investigate the presence of maternal effect on the inheritance of flax seed coat color using direct and reciprocal crosses of yellow-seed lines and brown-seed cultivars.

## MATERIAL AND METHODS

F<sub>1</sub>, F<sub>2</sub>, and F<sub>3</sub> generations were produced by crossing contrasting genotypes for flax seed coat color. Two brown-seed cultivars and four yellow-seed lines of flax were used. The brown-seed cultivars were Caburé and Aguará, both from the National Institute of Agricultural Technology (INTA) of Argentina. The yellow-seed lines were LIN49, LIN57, LIN88, and LIN36, obtained from a Brazilian genetic improvement program. All genotypes have violet-blue flowers.

The study was carried out in 2020 and 2021 at the Center for Rural Sciences of the Federal University of Santa Catarina, Curitiba (lat 27° 16' 34" S, long 50° 30' 12" W, alt 1040 m asl, Cambisol, average annual precipitation of 1500 mm), Santa Catarina State, Brazil, and in 2022 at the Francisco Beltrão Campus of the Federal University of Technology - Paraná (lat 24° 05' 37" S, long 53° 05' 64" W, alt 553 m asl, Ferralsol, average annual precipitation of 1700 mm), Paraná State, Brazil.

In 2021, seeds from the four lines and two cultivars were sown in pots in a greenhouse. For synchronized flowering, cultivars were sown earlier than lines. Crosses were made with the plants in full bloom. Emasculation was performed in the late afternoon. Pollination was performed in the morning by placing an anther with pollen on the tip of the stigma of an emasculated flower. Sixteen F<sub>1</sub> populations were obtained, as described in Table 1.

The coat color of F<sub>1</sub> seeds from all crosses was evaluated individually and recorded. In 2021, 10 seeds of each F<sub>1</sub> population were sown under field conditions in Curitiba, Santa Catarina, Brazil. This procedure was used to obtain F<sub>1</sub> plants and F<sub>2</sub> seeds, the latter of which were produced by natural self-pollination. At maturity, all F<sub>1</sub> plants were harvested individually, and the coat color of F<sub>2</sub> seeds was evaluated and recorded. In 2022, F<sub>2</sub> seeds from four populations (LIN88 × Aguará, Aguará × LIN88, LIN88 × Caburé, and Caburé × LIN88) were sown under field conditions in Francisco Beltrão, Paraná, Brazil. At maturity, F<sub>2</sub> plants (100 plants per cross) were harvested individually, and the coat color of F<sub>3</sub> seeds was evaluated. Crop management was the same for both years. Seeds were sown at a spacing of 0.34 cm. Sowing, weeding, and harvesting were manual.

Observed values were compared with expected values within each F<sub>3</sub> population by a chi-square ( $\chi^2$ ) goodness-of-fit test at a significance level (alpha) of 0.05. Moreover, F<sub>1</sub>, F<sub>2</sub>, and F<sub>3</sub> populations were compared with their reciprocals. Statistical analyses were performed using GENES software (Cruz 1998).

**Table 1.** Direct and reciprocal crosses between yellow-seed lines and brown-seed cultivars of flax

Maternal progenitor ♀	Paternal progenitor ♂	Seed phenotype	No. crossed flowers	Seeds/capsule
LIN49	× Aguará	yellow × brown	4	6
Aguará	× LIN49	brown × yellow	14	9
LIN49	× Caburé	yellow × brown	11	7
Caburé	× LIN49	brown × yellow	8	5
LIN57	× Aguará	yellow × brown	10	7
Aguará	× LIN57	brown × yellow	15	6
LIN57	× Caburé	yellow × brown	11	7
Caburé	× LIN57	brown × yellow	9	7
LIN88	× Aguará	yellow × brown	11	7
Aguará	× LIN88	brown × yellow	10	8
LIN88	× Caburé	yellow × brown	16	8
Caburé	× LIN88	brown × yellow	9	7
LIN36	× Aguará	yellow × brown	16	5
Aguará	× LIN36	brown × yellow	15	8
LIN36	× Caburé	yellow × brown	15	5
Caburé	× LIN36	brown × yellow	7	4

## RESULTS AND DISCUSSION

F<sub>1</sub> seeds had the same coat color phenotype within each direct and reciprocal cross. F<sub>1</sub> seeds resulting from crosses with LIN88 (yellow seeds) as the female parent and Aguará or Caburé (brown seeds) as the male parent showed a yellow phenotype. F<sub>1</sub> seeds from crosses in which the female parent was a brown-seed cultivar exhibited a brown phenotype. Therefore, in comparing direct and reciprocal crosses, it was observed that the phenotype of F<sub>1</sub> seeds was always equal to the phenotype of the female parent (Table 2), suggesting the existence of maternal effect on the coat color of flax seed. After F<sub>1</sub> plants were harvested and thrashed and F<sub>2</sub> seeds analyzed, it was found that, for all direct and reciprocal crosses, there was no segregation of flax seed color. All seeds were yellow (Table 2).

**Table 2.** Number of yellow and brown seeds produced by F<sub>1</sub> and F<sub>2</sub> generations from direct and reciprocal crosses between yellow-seed lines and brown-seed cultivars of flax

Maternal progenitor ♀	Paternal progenitor ♂	F <sub>1</sub> seeds		F <sub>2</sub> seeds*	
		Yellow	Brown	Yellow	Brown
LIN49 (Y)	Aguará (B)	17	0	1000	0
Aguará (B)	LIN49 (Y)	0	96	1000	0
LIN49 (Y)	Caburé (B)	60	0	1000	0
Caburé (B)	LIN49 (Y)	0	44	1000	0
LIN57 (Y)	Aguará (B)	55	0	1000	0
Aguará (B)	LIN57 (Y)	0	62	1000	0
LIN57 (Y)	Caburé (B)	72	0	1000	0
Caburé (B)	LIN57 (Y)	0	51	1000	0
LIN88 (Y)	Aguará (B)	67	0	1000	0
Aguará (B)	LIN88 (Y)	0	84	1000	0
LIN88 (Y)	Caburé (B)	116	0	1000	0
Caburé (B)	LIN88 (Y)	0	51	1000	0
LIN36 (Y)	Aguará (B)	61	0	1000	0
Aguará (B)	LIN36 (Y)	0	97	1000	0
LIN36 (Y)	Caburé (B)	74	0	1000	0
Caburé (B)	LIN36 (Y)	0	17	1000	0

Y, yellow; B, brown.

\* All plants from the F<sub>2</sub> generation were evaluated.

**Table 3.** Chi-square tests for goodness-of-fit of seed color in pooled F<sub>2</sub> populations for all classes of crosses used to study the inheritance of flax seed coat color

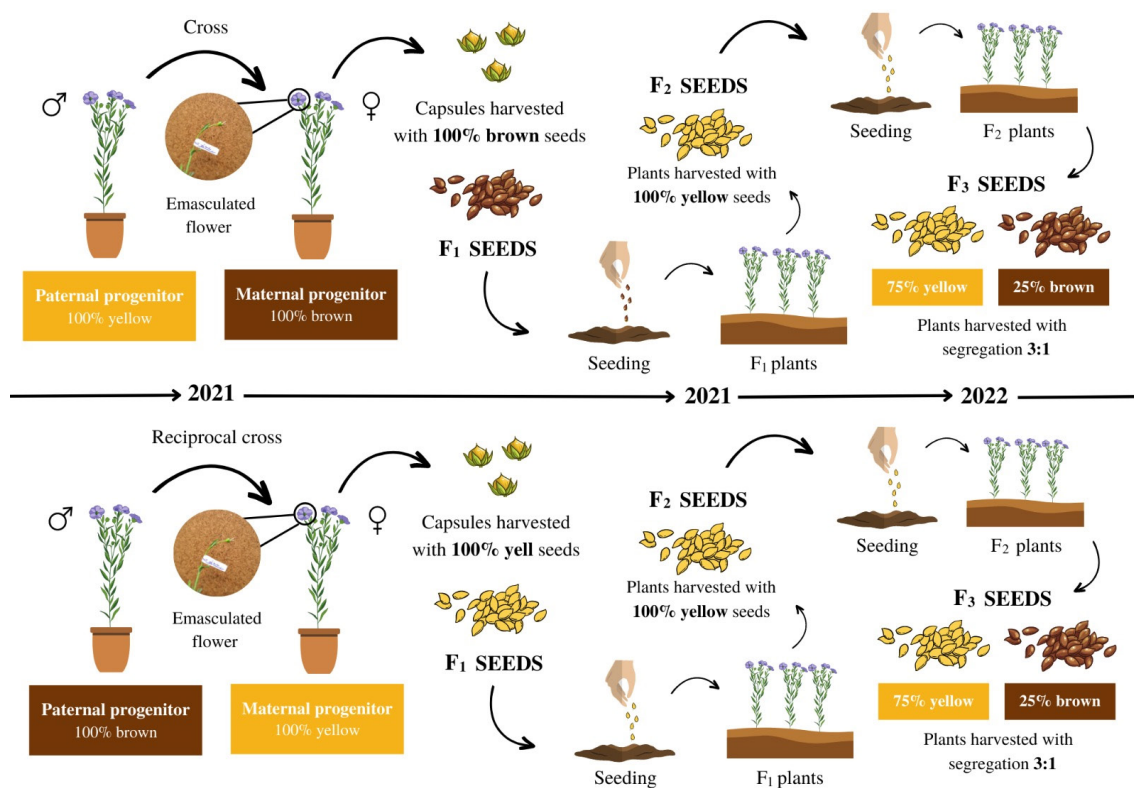
Maternal progenitor ♀	Paternal progenitor ♂	F <sub>2</sub> plants and F <sub>3</sub> seeds (number)		χ <sup>2</sup>	p-value
		Yellow	Brown		
LIN88 (Y)	Aguará (B)	72	28	0.48	0.48
Aguará (B)	LIN88 (Y)	70	30	1.33	0.25
LIN88 (Y)	Caburé (B)	75	25	0.0	1.00
Caburé (B)	LIN88 (Y)	73	27	0.21	0.64

Y, yellow; B, brown.

As shown in Table 3, F<sub>3</sub> seeds, originated from 100 F<sub>2</sub> plants from each cross, had the same 3:1 phenotypic segregation ratio of yellow to brown seeds, as confirmed by chi-square statistics. These findings indicate the presence of nuclear gene, containing two alleles under dominant allele interaction, with the dominant allele conferring the yellow and the recessive allele conferring the brown phenotype.

Analysis of F<sub>3</sub> seeds is important for confirming the results of previous generations. A summary of the steps and phenotypic results of the study of the inheritance of flax seed coat color is also presented in Figure 1.

The results for F<sub>2</sub> and F<sub>1</sub> seeds were compared with those previously reported in the literature (Tames 1922, Shaw et al. 1931, Barnes et al. 1960, Mitappali and Rowland 2003, Sodi et al. 2012). The literature states that three or four genes control flax seed color, with possible epistasis between genes. In the vast majority of cases, the dominant allele is brown, with the exception of the dominant allele Y1, which confers a dominant yellow phenotype (Green and



**Figure 1.** Schematic summary of the study of the inheritance of flax (*Linum usitatissimum* L.) seed coat color, with direct and reciprocal crosses, F<sub>1</sub> and F<sub>2</sub> populations (seeds and plants), and F<sub>3</sub> population (seeds).

Dribnenki 1995, Popescu and Marinescu 1996). Previous studies showed that  $F_1$  seeds from direct and reciprocal crosses exhibited the same color: in crosses between brown (dominant) and yellow (recessive) seeds, the color of resulting seeds was brown, owing to the heterozygous genotype of the embryo, indicating single-gene nuclear inheritance. However, the results of the current study are contrasting and showed that the maternal effect was responsible for the coat color of flax seed.

Maternal inheritance is a conceptually related set phenomenon associated with uniparental inheritance of organelle genomes, cytoplasmic elements, symbionts, substances, and factors, as well as parent-of-origin gene expression effects, and maternally controlled genomic imprinting. Although conceptually similar, the types of maternal inheritance have widely differing mechanisms, evolutionary and genetic consequences, and evolutionary and genetic consequences (Badyaev 2013). Inheritance of cytoplasmic genes occurs via the transfer of mitochondria and chloroplasts from the female gamete to offspring. By contrast, the mechanism for the maternal effect is generally through the maternally provided 'environment', whether in the form of maternal messenger RNAs and proteins that are pre-loaded into the unfertilized egg or ovule, or in the form of post-zygotic influences via maternal traits such as nutritional provision. When the maternal effect is determining the inheritance of a trait, there is a causal influence of the maternal genotype or phenotype on the offspring phenotype (Wolf and Wade 2009).

Therefore, the maternal effect does not arise due to units of heredity, but due to products of the maternal supply. In line with the maternal effect hypothesis, a possible explanation for our findings is that the  $F_2$  seeds of the populations, despite having different genotypes, developed from genetically identical  $F_1$  plants. Therefore, the yellow color of the seeds was a result of gene products present in the mother's cytoplasm, which were transmitted to the offspring.

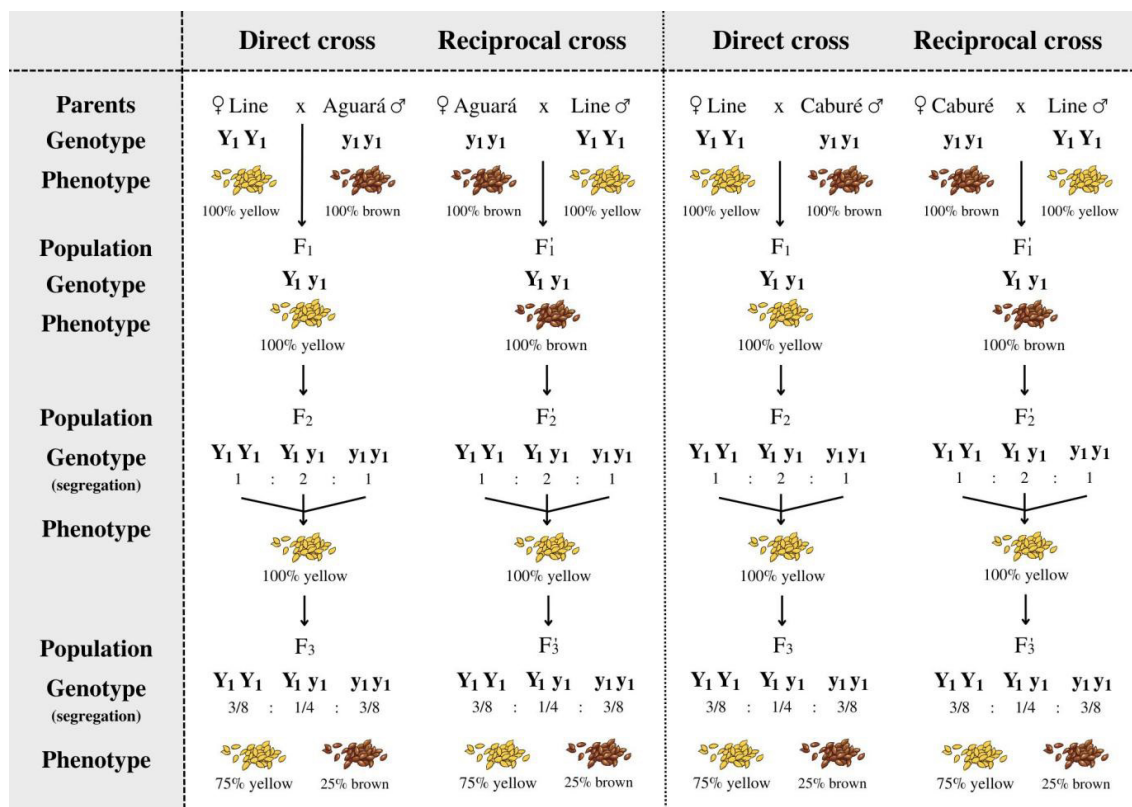
Flax seed consists of three major tissues: the diploid embryo and triploid endosperm as products of double fertilization and the maternal seed coat tissue (Venglat et al. 2011). According to Miart et al. (2021), the color of flax seed coat varies during seed development before the mature coat is established, suggesting the existence of modifications in some seed coat-specific components, including phenolic compounds such as proanthocyanidins. Soon after fertilization, the seed is translucent. The thick, clear, fragile coat of the fertilized ovule differentiates into a thin, dark, protective seed coat during seed development (Venglat et al. 2011). This explains why, in many crops, although the seed coat is of maternal origin, the final phenotype of the offspring seed is not always the same as that of the mother plant, being determined by the genotype of the embryo resulting from fertilization. The maternal effect has been related to seed color in other crops, such as sesame (Laurentin and Benitez 2014), rapeseed (Zhi-wen et al. 2005), and common bean (Possobom et al. 2015). Maternal effects have also been observed on the fatty acid composition of soybean (Gilsenger et al. 2010) and common bean seed size and morphology (Singh et al. 2017).

Given that the phenotype of  $F_2$  seeds is the result of the maternal nuclear genotype (heterozygous  $F_1$  plants), it is suggested that the yellow seed phenotype was dominant over the brown seed phenotype. The dominance of the yellow seed phenotype has been reported in previous studies suggesting that the Y1 gene, independent of the aforementioned G, D, and B1 genes, is responsible for such dominance (Green and Dribnenki 1995, Popescu and Marinescu 1996, Mittapalli and Rowland 2003). Mittapalli and Rowland (2003) reported the presence of the Y1 gene in the yellow-seed cultivar Bionda from Germany.

The results converge on the hypothesis of the expression of a dominant allele (Y1) conferring yellow seeds to lines (here represented by LIN88) and a recessive allele (y1) conferring brown seeds to cultivars Aguará and Caburé. To improve the understanding of the results, we adopted the following genotypic identification: LIN88 = Y1Y1, Aguará and Caburé = y1y1. It was considered that all yellow lines had the same genotype for the Y1 gene, given that they were from the same selection of plants that originated the LIN88 line. Likewise, both cultivars, originating from the same breeding program, were considered to have the same genotype, as supported by the results. Figure 2 presents a synthesis of our results, including seed phenotype and the genotypic composition of each population.

Direct and reciprocal crosses of yellow seed lines (Y1Y1) with brown seed cultivars (y1y1) resulted in  $F_1$  seeds with the phenotype of the female parent, which led to different phenotypes in direct and reciprocal crosses (Table 2 and Figure 2). Although  $F_1$  seeds from direct and reciprocal crosses showed the same nuclear genome (Y1y1), flax seed color resulted from the maternal genotype, as the cytoplasmic genome was different. Because flax is an autogamous plant (Hall et al. 2016) and  $F_1$  plants are self-pollinated, it would be expected that  $F_2$  seeds had the same genotypic segregation ratio





**Figure 2.** Model explaining maternal effect on flax seed coat color inheritance based on direct and reciprocal crosses and F<sub>1</sub>, F<sub>2</sub> and F<sub>3</sub> generations. Genotypes and phenotypes are presented, considering the Y<sub>1</sub> gene.

of a nuclear gene with two alleles (1:2:1). However, F<sub>2</sub> seeds also exhibited the phenotype resulting from the maternal nuclear genotype (F<sub>1</sub> plants, Y<sub>1</sub>y<sub>1</sub>), being 100% yellow (Table 2 and Figure 2).

Natural self-pollination of F<sub>2</sub> plants generated F<sub>3</sub> seeds, had a 3:1 phenotypic segregation of yellow to brown seeds, respectively (Table 3 and Figure 2). In segregating populations such as those of F<sub>2</sub> plants, which gave origin to F<sub>3</sub> seeds, 50% of plants are expected to be homozygous (1/4 dominant and 1/4 recessive) and 1/2 heterozygous. Each homozygous F<sub>2</sub> plant was expected to produce a homogeneous offspring regarding the color (F<sub>3</sub> seeds), without segregation for color. Dominant homozygous plants generated yellow seeds and recessive homozygous plants generated brown seeds. Heterozygous F<sub>2</sub> plants, on the other hand, were expected to produce segregating F<sub>3</sub> seeds: 1/2 homozygous (1/4 dominant and 1/4 recessive) and 1/2 heterozygous. Therefore, after two generations of self-fertilization, the F<sub>3</sub> population was expected to be composed of 3/8 homozygous dominant yellow seeds, 1/4 heterozygous yellow seeds, and 3/8 homozygous recessive brown seeds. However, we observed a 3:1 phenotypic segregation (75% yellow and 25% brown), because F<sub>3</sub> seeds expressed the phenotype of the F<sub>2</sub> maternal genotype. F<sub>3</sub> seeds from heterozygous F<sub>2</sub> plants did not show segregation; all seeds were yellow, which was the dominant phenotype. In fact, none of these plants produced seeds with phenotypic segregation (Figure 2). A phenotypic segregation of 5/8 yellow seeds to 3/8 brown seeds is expected to be expressed in F<sub>4</sub> seeds.

The proposed model explains the maternal genotype effect on the inheritance of flax seed coat color, suggesting the presence of the Y<sub>1</sub> gene (Green and Dribnenki 1995, Popescu and Marinescu 1996, Mittapalli and Rowland 2003) in the germplasm of yellow lines. These lines are likely similar for the color genotype to the cultivar Bionda from Germany and the introduction CPI84495 from Australia, which exhibit dominance of yellow coat (Green and Dribnenki 1995, Popescu and Marinescu 1996).

Our results differ from those of previous studies with flaxseed. Mitappali and Rowland (2003) carried out an extensive study of flaxseed seed coat color, with genotypes from different germplasms, showing brown, yellow and even variegated (yellow parts and brown parts) seed phenotypes. However, even with a wide variety of genotypes, the authors do not report on the inheritance of maternal effect on flax seed coat color. Therefore, the absence of genetic studies with germplasm of flax cultivated in South American countries such as Brazil and Argentina was the motivation of this research.

The results reported here add a new facet to our understanding of the inheritance of flax seed color, describing for the first time the effect of the maternal genotype. These findings complement previous studies by providing evidence that the genetic background of parents is relevant to the inheritance of flax seed color, suggesting that this trait has more than one mode of inheritance. The results of studies on the inheritance of flax seed coat color should be considered in genetic breeding programs, as seed color influences the market value of flax seed. Additionally, flax seed color is related to several yield parameters and the physical and nutritional quality of seeds (Sudarshan et al. 2017, Zare et al. 2021, Abtahi et al. 2022)

## CONCLUSION

The nuclear genotype of the female parent was responsible for flax seed coat color in crosses of Brazilian lines with Argentine cultivars. The maternal effect resulted from the transfer of gene products from maternal cytoplasm to offspring. The germplasm showed a single dominant gene with the yellow phenotype dominant and the brown phenotype recessive.

## REFERENCES

- Abtahi M, Mirlohi A, Sharif-Moghaddam N and Ataii E (2022) Revealing seed color variation and their possible association with yield and quality traits in a diversity panel of flax (*Linum usitatissimum* L.). **Front Plant Science** **13**: 1038079.
- Allaby RG, Peterson GW, Merriwether DA and Fu Y (2005) Evidence of the domestication history of flax (*Linum usitatissimum* L.) from genetic of the sad2 locus. **Theoretical and Applied Genetics** **112**: 58-65.
- Bangar SP, Singh A, Trif M, Kumar M, Kumar P, Kaur R and Kaur N (2021) Process parameter optimization and characterization for an edible film: Flaxseed concern coatings. **Coatings** **11**: 1106.
- Badyaev AV (2013) **Maternal inheritance**. 2<sup>nd</sup> edn, Brenner's Encyclopedia of Genetics, Academic Press, p. 320-322.
- Barnes DK, Culbertson JD and Lambert JW (1960) Inheritance of seed and flower colors in flax. **Agronomy Journal** **52**: 456-459.
- Baroux C, Autran D, Gillmor CS, Grimanelli D and Grossniklaus U (2008) The maternal to zygotic transition in animals and plants. **Cold Spring Harbor Symposia on Quantitative Biology** **73**: 89-100.
- Berleth T, Burri M, Thoma G, Bopp D, Richstein S, Frigerio G, Noll M and Nusslein-Volhard C (1988) The role of localization of bicoid RNA in organizing the anterior pattern of the Drosophila embryo. **Embo Journal** **7**: 1749-1756.
- Comstock VE, Ford GH and Gimore EC (1969) Seed quality characters associated with D locus of flax *Linum usitatissimum* L. **Crop Science** **9**: 513-514.
- Cruz CD (1998) Programa GENES: Aplicativo computacional em estatística aplicada à genética (GENES - Software for Experimental Statistics in Genetics). **Plant Genetics and Molecular Biology** **21**: 1.
- Dal'Col Lúcio A, Follmann DN, Emanuelli T, Marchioro VS and Velho JP (2021) Histórico, usos e importância econômica da linhaça. In Velho JP and Dal'Col Lúcio A (eds) **Linhaça: Perspectiva de produção e usos na alimentação humana e animal**. Editora Atena 1: 1-9.
- Dash J, Naik BS and Mohapatra UB (2017) Linseed: a valuable crop plant. **International Journal of Advanced Research** **5**: 1428-1442.
- Diederichsen A and Raney JP (2008) Pure-lining of flax (*Linum usitatissimum* L.) genebank accessions for efficiently exploiting and assessing seed character diversity. **Euphytica** **164**: 255-273.
- Gilsinger JJ, Burton JW and Carter Junior TE (2010) Maternal effects on fatty acid composition of soybean seed oil. **Crop Science** **50**: 1874-1881.
- Green AG and Dribnenki JCP (1995) Linola™ '947' low linolenic acid flax. **Canadian Journal of Plant Science** **75**: 201-202.
- Hall LM, Booker H, Siloto RMP, Jhala AJ and Weselake RJ (2016) Flax (*Linum usitatissimum* L.). **Industrial Oil Crops** **9**: 157-194.
- Kajla P, Sharma A and Sood DR (2015) Flaxseed—a potential functional food source. **Journal of Food Science and Technology** **52**: 1857-1871.
- Laurentin H and Benitez T (2014) Inheritance of seed coat color in sesame. **Pesquisa Agropecuária Brasileira** **49**: 290-295.
- Miart F, Fontaine JX, Mongelard G, Wattier C, Lequart M, Bouton S, Molinié R, Dubrulle N, Fournet F, Demailly H, Roulard R, Dupont L, Boudaoud A, Thomasset B, Gutierrez L, Van Wuytswinkel O, Mesnard F and Pageau K (2021) Integument-specific transcriptional regulation in the mid-stage of flax seed development influences the release of mucilage and the seed oil content. **Cells** **10**: 2677.
- Mittappali O and Rowland G (2003) Inheritance of seed color in flax. **Crop Science** **43**: 1945-1951.
- Parikh M, Maddaford TG, Austria JA, Aliani M, Netticadan T and Pierce GN (2019) Dietary flaxseed as a strategy for improving human health.

- Nutrients** **11**: 1171.
- Popescu F and Marinescu I (1996) Y1-a dominant gene determining yellow seed color in linseed. **Probleme de Genetica Teoretica si Aplicata** **28**: 99-106.
- Possobom MTFD, Ribeiro ND, Domingues LS and Casagrande CR (2015) Genetic control of iron concentration in Mesoamerican and Andean common bean seeds. **Pesquisa Agropecuária Brasileira** **50**: 383-391.
- Saeidi G and Rowland GG (1999) The effect of temperature, seed colour and linolenic acid concentration on germination and seed vigour in flax. **Canadian Journal of Plant Science** **79**: 315-319.
- Shaw FJ, Khan AR and Alam M (1931) Studies in indian oilseeds. V. The inheritance of characters in Indian linseed. **Indian Journal of Agricultural Sciences** **1**: 1-57.
- Singh KK, Mridula D, Rehal J and Barnwal P (2011) Flaxseed: A potential source of food, feed and fiber. **Critical Reviews in Food Science and Nutrition** **51**: 210-222.
- Singh J, Clavijo MJA, Gezan SA, Lee H and Vallejos CE (2017) Maternal effects on seed and seedling phenotypes in reciprocal F1 hybrids of the common bean (*Phaseolus vulgaris* L.). **Frontier Plant Science** **8**: 42.
- Sudarshan GP, Kulkarni M, Akhoy L, Ashe P, Shaterian H, Cloutier S, Rowland G, Wei Y and Selvaraj G (2017) QTL mapping and molecular characterization of the classical d locus controlling seed and flower color in *Linum usitatissimum* (flax). **Scientific Reports** **7**: 15751.
- Tammes T (1922) Genetic analysis, schemes of co-operation and multiple allelomorphs of *Linum usitatissimum*. **Journal of Genetic** **12**: 19-46.
- Tomaszewska-Gras J, Islam M, Grzeca L, Kaczmarek A and Fornal E (2021) Comprehensive thermal characteristics of different cultivars of flaxseed oil (*Linum usitatissimum* L.). **Molecules** **26**: 1958.
- Tong ZB, Gold L, Pfeifer KE, Dorward H, Lee E, Bondy CA, Dean J and Nelson LM (2000) Mater, a maternal effect gene required for early embryonic development in mice. **Nature Genetics** **26**: 267-268.
- Troshchynska Y, Bleha R, Kumbarová L, Sluková M, Sinica A and Štětina J (2019) Discrimination of flax cultivars based on visible diffusion reflectance spectra and colour parameters of whole seeds. **Czech Journal of Food Science** **37**: 199-204.
- Venglat P, Xiang D, Qiu S, Stone SL, Tibiche C, Cram D, Alting-Mees M, Nowak J, Cloutier S, Deyholos M, Bekkaoui F, Sharpe A, Wang E, Rowland G, Selvaraj G and Datla R (2011) Gene expression analysis of flax seed development. **BMC Plant Biology** **11**: 74.
- Xu W, Dubos C and Lepiniec L (2015) Transcriptional control of flavonoid biosynthesis by MYB–bHLH–WDR complexes. **Trends Plant Science** **20**: 176-185.
- Zare S, Mirlohi A, Saeidi G, Sabzalian MR and Ataie E (2021) Water stress intensified the relation of seed color with lignan content and seed yield components in flax (*Linum usitatissimum* L.). **Scientific Reports** **11**: 23958.
- Zhi-wen L, Ting-dong F, Jin-xing T and Bao-yuan C (2005) Inheritance of seed colour and identification of RAPD and AFLP markers linked to the seed colour gene in rapeseed (*Brassica napus* L.). **Theoretical and Applied Genetics** **110**: 303-310.
- Wolf JB and Wade MJ (2009) What are maternal effects (and what are they not)? **Philosophical Transactions of the Royal Society B** **364**: 11071115.
- You FM, Duguid SD, Lam I, Cloutier, S, Rashid KY and Booker HM (2016) Pedigrees and genetic base of flax cultivars registered in Canada. **Canadian Journal of Plant Science** **96**: 837-852.

