Genetic control of viviparity in common bean

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ABSTRACT: In common bean (*Phaseolus vulgaris*) harvesting is carried out in the field. It is therefore necessary that cultivars be tolerant to viviparity, i.e., germination of grains still in the pods. Study of the percentage of germination of beans in the pods under laboratory conditions, where humidity content is high, has been proposed. Furthermore, under question is whether the thickness of the pod wall affects water uptake by the pods and, consequently, viviparity. Thus, the aim of the present study was to verify if there is variance among progenies for viviparity and if it is influenced by pod thickness. We assessed the parents, Pérola and ESAL 686, the F1, and a number of segregating generations in two crop seasons, in relation to the percentage of germination of seeds in the pods (PGSP) and pod wall thickness (PWT), and data on individual plants were obtained. The same traits were also assessed using the $F_{2:3}$, $F_{3:4}$ and $F_{4:5}$ progenies. Taking into account the genetic and phenotypic parameters estimates, especially the level of high heritability, selection to less viviparity in common bean has to be carried out to evaluate PGSP in progenies.

Keywords: *Phaseolus vulgaris*, plant breeding, pre-harvest sprouting, genetic components, heritability

Introduction

The cultivation of common bean (*Phaseolus vulgaris*) in Brazil is highly diverse in terms of management systems, especially at harvest. In the case of family farms, after harvesting, the plants are spread out up to the time of threshing in the field. At the other extreme, large corporate farms use mechanical harvesting and even where this is the case plants are often left in the field to dry or they are cut and threshed at the same time.

Under any of these management systems, if harvesting coincides with a rainy period, which is frequent in various common bean crop seasons in Minas Gerais, especially if the plants are left in the field, germination of seeds may begin while still in the pods or the seeds may become spotted, which reduces their commercial value. To mitigate the damage arising from rainfall coinciding with harvesting, one of the alternatives is to use cultivars in which early germination of the seeds in the pods, a phenomenon known as viviparity, is as limited as possible. This phenomenon has already been intensively studied in other crop species, and the existence of certain genes involved in expression of the trait has been observed in crops such as maize (Neuffer et al., 1997; Suzuki et al., 2006) and wheat (Gubler et al., 2005; Tan et al., 2006; Zhang et al., 2014).

In the case of common bean, studies on this topic are few. Pryke (1978) observed variation in early germination in a series of common bean crosses grown in a greenhouse. Lima et al. (2012) evaluated 95 common bean lines related to tolerance to excess moisture at harvest time. They observed that the main difficulty in selection of common bean lines for tolerance to high moisture at harvest is repeatability of the environmental conditions in the field from one crop season to another. For this reason, the determination of percentage of ger-

mination of seeds in the pods (PGSP) has been proposed, and conducted under laboratory conditions, where moisture levels and temperature may be controlled. Questions also arise as to whether pod wall thickness (PWT) affects water absorption by the pods and, consequently, the PGSP. No information was found on genetic control of pod wall thickness associated with viviparity. The only report on genetic control of this trait had another purpose, related to snap beans (Yuste-Lisbona et al., 2014).

This study was carried out for the purpose of obtaining information on genetic control of PGSP and PWT, and on the possible association between them, as well as verifying if there is a difference in efficiency of selection if it is performed on individual plants or progenies.

Materials and Methods

The experiments were carried out in a greenhouse and in the field in an experimental area in the city of Lavras, located in the southern region of the state of Minas Gerais at an altitude of 918 meters, 21°58′ South latitude and 42°22′ West longitude.

The lines ESAL 686 and Pérola were used as parents. ESAL 686 has a determined growth habit, upright plant architecture, and large seeds of yellow color. It has an early cycle (approximately 65 days) and belongs to the Andean gene group, the Nova Granada race. It has pod walls of greater thickness.

The Pérola line, with carioca grains (cream colored with brown streaks) has an indeterminate growth habit, semi-upright plant architecture, and a 90-day cycle. It is of Mesoamerican origin and its pod wall is not so thick.

Hybridization was carried out between the parents, Pérola (P_1) and ESAL 686 (P_2), and the F_1 generation was obtained. So it was possible to generate the F_1RC_{11}

$(F_1 \times P_1)$, F_1RC_{21} $(F_1 \times P_2)$, F_2, F_2RC_{11}, F_2RC_{21}, and F_3 generations.

The parents and the F_1, F_2, F_1RC_{11}, and F_1RC_{21} generations were evaluated in the field, with sowing in Feb 2013. In July 2013, in addition to the parents and the F_1, F_2, and $F_1 RC_{11}$ and F_1RC_{21} generations, the F_3 and F_2RC_{11} and F_2RC_{21} were also evaluated in the field. In both seasons a complete randomized block design with two replicates was used. The plants were harvested individually and dried in the sun.

Afterwards, the pods were removed. Part was used for measuring pod wall thickness (PWT), and the other part was used for evaluating the percentage of germination of seeds while still in the pods (PGSP).

For the PWT measurement of PWT, three pods/plant/plot were selected at random in both crop seasons. The seeds were removed and a valve of the pods was subjected to measurements of thickness by an external digital micrometer, DIGIMESS brand, code 110.284, 0-25 mm capacity, with a precision of $\pm$ 0.002 mm. Measurements were taken at the center of one of the valves of each pod.

The PGSP was obtained using two pods/plant/replication. Two replications were evaluated. For this purpose, the pods were rolled up, two by two, in sheets of germination paper previously moistened with distilled water and identified with watercolor pencils. The rolls were kept in germinators at 25 °C with 12 h of light in the Seed Analysis Laboratory. The total number of seeds and germinated seeds were counted on the seventh day so as to obtain the PGSP. A germinated seed was considered as one that exhibited radicle protrusion.

Data were subjected to analysis of variance. From the results of the analyses of variance, the accuracy estimate $(r_{gg'})$ was obtained using the following expression: $r_{gg'} = \sqrt{1-(1/F)}$. In which F: Progenies mean square/ Residual mean square.

The mean values and the variances between plants per plot were obtained for all generations. Using these values, the Mather and Jinks (1982) methodology was followed. The joint scale test was applied as described by Rowe and Alexander (1980). The mean genetic parameters were estimated using the weighted least squares method, according to the procedure presented. Considering no epistasis and the generations P_1, P_2, F_1, F_2, F_3, F_1RC_{11}, F_1RC_{21}, F_2RC_{11}, F_2RC_{21}:

$$\hat{\beta} = \left(C'NS^{-1}C\right)^{-1}(C'NS^{-1}Y)$$

in which:

$$\hat{\beta} = \begin{bmatrix} \hat{m} \\ \hat{a} \\ \hat{d} \end{bmatrix},$$

where, $\hat{m}$ is the mean value; $\hat{a}$ refers to the deviation of homozygotes for the average, additive effect and $\hat{d}$ represents the contribution of heterozygotes loci, the dominance effect.

C refers to the model matrix, in the present situation becoming:

$$C = \begin{bmatrix} 1 & 1 & 0 \\ 1 & -1 & 0 \\ 1 & 0 & 1 \\ 1 & 0 & 0.5 \\ 1 & 0 & 0.25 \\ 1 & 0.5 & 0.5 \\ 1 & -0.5 & 0.5 \\ 1 & 0.5 & 0.25 \\ 1 & -0.5 & 0.25 \end{bmatrix}$$

NS^{-1} is the weighting matrix to reduce the variance heterogeneity between the different population; N is the diagonal populations number matrix, S the diagonal populations variance matrix, and Y the means of each population vector.

The components of phenotypic variance (V_E, V_A and V_D) were estimated by the iterative weighted least squares method (Mather and Jinks, 1984), adopting the following model:

$$\hat{\beta} = \left(Q'W^{-1}Q\right)^{-1}(Q'W^{-1}Z)$$

$$\hat{\beta} = \begin{bmatrix} \hat{V}_E \\ \hat{V}_A \\ \hat{V}_D \end{bmatrix},$$

where $\hat{V}_E$ is the environmental variance, $\hat{V}_A$ represents the additive variance estimate and $\hat{V}_D$ is the dominance variance estimate.

Q is the model matrix, that in the present situation becomes:

$$Q = \begin{bmatrix} 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 1 \\ 1 & 1 & 1 \\ 1 & 1 & 2 \\ 1 & 2 & 1.5 \\ 1 & 1.5 & 0.75 \end{bmatrix}$$

W is the weight diagonal matrix derived from the variance of variance estimates (Mode and Robinson, 1959):

$$\hat{Var}(\hat{V}) = \frac{2(\hat{V})^2}{DF+2};$$

in which DF is the degree of freedom of each variance estimate, Z: populations variance vector.

Using the estimates of the components of variance, narrow sense heritability (h_r^2) was obtained for all the traits, according to the estimator described by Bernardo (2010).

The phenotypic correlations of the traits (r_{XY}) were obtained with the F_2 generation as a reference, using the estimator:

$$r_{XY} = \frac{COV_{XY}}{\sigma_X \cdot \sigma_Y}$$

in which:

COV_{XY} is the covariance between the variable X and Y, where X represents PWT and Y becomes PGSP; and σ_X and σ_Y are the phenotypic deviations of the X and Y variables, respectively.

The second step of the experiment consisted of an evaluation of the progenies. The same cross was used, and in this case, a sample of the plants harvested in the F_2, F_3, and F_4 generations was taken, thereby obtaining 32 $F_{2:3}$, 29 $F_{3:4}$, and 32 $F_{4:5}$ progenies. These progenies and the following controls: RP1, Majestoso, Small White, and Radiante were evaluated in an experiment conducted in Feb 2014, the complete randomized block with 2 replicates was implemented. The plants of each progenie or control were harvested at the point of maturity and dried in the sun, and the pods were removed.

To evaluate the progenies, the procedure for measuring the PWT was the same as had been adopted for individual plants. However, in this case, there was no separation of individuals. Three pods per plot/progeny were removed at random.

For the $PGSP$ evaluation, 15 pods per plot were removed at random. Three replications per plot with five pods were made, i.e., six replications in all. The experimental procedure was similar to that described above, except that the rolls were kept in a mist chamber in the Department of Biology. Humidity and temperature were controlled by a thermo-hygrometer, "temperature and humidity datalogger", model HT-500. The data were subjected to analysis of variance, considering a completely randomized design.

To estimate the broad sense heritability (h^2) of the progenies from the analysis of variance, estimates of the mean squares of progenies (MSP) and mean square error (MSE) were used:

$$h^2 = \frac{MSP - MSE}{MSP}.$$

The errors associated with the estimate of h^2 were estimated using the expression from Knapp et al. (1985):

$$LL = \left\{ 1 - \left[\left(\frac{MSP}{MSE} \right) F_{1-\alpha/2} \left(DF_{ERROR}; DF_{Progenies} \right) \right]^{-1} \right\}$$

$$UL = \left\{ 1 - \left[\left(\frac{MSP}{MSE} \right) F_{\alpha/2} \left(DF_{ERROR}; DF_{Progenies} \right) \right]^{-1} \right\}$$

LL: Lower limit, UL: Upperlimit; F: table values of F distribution with DF (degrees of freedom) progenies and DF error, where $\alpha = 0.05$.

The gain expected from selection (GS) was estimated considering all the progenies, using the expression described by Bernardo (2010):

$$Gs = sd \cdot h^2$$

sd: selection differential; sd = selected progenies mean – all progenies mean; h^2: has already been described.

Phenotypic correlation (r_{XY}) was estimated between the mean values of the progenies for PWT (X) and PGSP (Y), using the same estimator described above.

The correlated response $RC_{Y(X)}$ in trait Y ($PGSP$) was estimated by selecting the best 10 % of progenies with the greatest PWT (X), in a way similar to the model proposed by Falconer and Mackay (1996):

$$RC_{Y(X)} = h_Y^2 \cdot sd_{Y(X)}'$$

in which $sd_{Y(X)}'$ represents the selection differential of the progenies selected by the PWT, taking their PGSP as a reference.

$$sd_{Y(X)} = M_{S_{Y(X)}} - M_{O_Y}$$

All the statistical analyses were conducted using the R software (R Core Team, 2014).

Results and Discussion

Observing the mean values obtained by the different generations, when individual plants were evaluated in reference to the PWT, it may be observed that the results were quite similar over the crop seasons (Table 1). The level of accuracy obtained in the experiments ($r_{gg'}$ = 98 %; 94 %) was high. The pod wall thickness of P_1, "Pérola", was always less than that of "ESAL 686", P_2. The mean value of the F_1 generation was intermediate in the parents, and the F_2 generation was similar to that of the F_1. In principle, the absence of dominance in expression of the trait may be inferred from this condition.

The results of the PWT were quite consistent in the two crop seasons in regard to the magnitude of the estimates of the mean components (Table 2). The fit of the

Table 1 – Mean value of pod wall thickness (PWT) (mm × 100) obtained in the different populations evaluated. Sowing in Feb and July, 2013.

Generations	Feb	July
	(mm × 100)	(mm × 100)
P_1	17.596	16.758
P_2	23.072	22.387
F_1	21.319	20.200
F_2	20.434	19.288
F_1RC_{11}	17.144	17.107
F_1RC_{21}	19.535	18.822
F_2RC_{11}	-	17.763
F_2RC_{21}	-	20.437
F_3		19.370
Accuracy (r_{gg})	98 %	94 %

P_1: Pérola; P_2: ESAL 686.

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additive-dominant model was high, with estimates of R^2 greater than 99 %. It was observed that the "d" component, which estimates the deviation of the heterozygote in relation to the mean, did not differ from zero. In other words, there is no dominance in the expression of the trait. The estimate of "a", the contribution of the homozygotes in relation to the mean, was different from zero. The fact that the estimate was negative is a result of using a parent of less thickness as P_1. In this case, in addition to d not being different from zero, allele frequency is 0.5 and, therefore, as only the a component differed from zero, the predominance of the additive effect in control of the trait may be inferred (Bernardo, 2010).

The predominance of the additive effects obtained may be confirmed from the estimates of the components of genetic additive variance (V_A), which was different from zero, and this did not occur with the dominance variance (V_D). The estimates of heritability (h_r^2) for PWT were greater than 59 % (Table 2). This result is in agreement with estimates of heritability obtained for certain traits of snap beans for another purpose, among them thickness, the estimate of which, h^2 was greater than 50 % (Yuste-Lisbona et al., 2014).

Using progenies, the evaluations of PWT showed results which coincided well with those obtained from individual plants. Accuracy was high, greater than 80 %, indicating good precision in the evaluation. For the trait in question, both the evaluation of individual plants and the evaluation of progenies allow for estimates of genetic and phenotypic parameters with good precision (Table 3).

The h^2 when considering all the progenies, was high, 62 %, similar to the h^2 when considering each type of progeny. This being the case, the better option is to select regardless of progeny type. The genetic gain was expressive for both traits (Table 4).

In relation to the percentage of germination of seeds in the pods (PGSP), the first question is what the ideal time of pod exposure to high moisture conditions would be. That is because if this time is too short, there is a risk of not allowing germination to come about. If many days

Table 2 – Estimates of the mean and variance genetic components of the pod wall thickness (PWT) trait. Sowing in Feb and July, 2013.

Mean Genetic Component	Feb		July	
	Estimate	Standard Deviation	Estimate	Standard Deviation
$\hat{m}$	19.5280	0.253 **	19.225	0.1463 **
$\hat{a}$	-2.4020	0.235 **	-2.603	0.1611**
$\hat{d}$	0.0058	0.487	-0.396	0.3570
[1]R^2 (%)	100		100	
Variance Component	Feb		July	
	Estimate	Standard Deviation	Estimate	Standard Deviation
$\hat{V}_E$	4.7045	0.800**	1.7890	0.4089**
$\hat{V}_A$	6.8310	1.988*	5.1154	0.6464**
$\hat{V}_D$	-2.9355	1.6	1.7410	0.7921
[1]R^2(%)	98		98	
h_r^2	79		59	

[1]Coefficient of determination of the model; *estimate different from zero at the level of 7 % probability by the t test; **estimate different from zero at the level of 1 % probability by the t test.

Table 3 – Variance analyses summary for pod wall thickness (PWT) (mm × 100) and percentage of germination of seeds in the pod (PGSP) from progenies and checks. Lavras, 2014.

Source of Variation	DF	PWT (mm × 100)		DF	PGSP (%)	
		MS	F		MS	F
Treatments	98	10.62	2.95**	99	1439.52	4.71**
Between Types	2	11.55	3.21**	2	824.46	2.70**
Between Progenies	92	9.39	2.61**	93	1326.63	4.34**
$F_{2:3}$	31	10.18	2.83**	31	968.11	3.17**
$F_{3:4}$	28	9.99	2.78**	29	1868.51	6.12**
$F_{4:5}$	31	7.93	2.20**	31	1210.64	3.96**
Between Checks,	5	18.76	5.21**	5	2737.10	8.96**
Checks vs Prog	1	82.11	22.80**	1	5454.89	17.85**
Residual	99	3.60		100	305.56	
Accuracy ($r_{gg}\prime$)		81 %			88 %	

**estimate different from zero at the level of 1 % probability by the t test.

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pass, germination is nearly total and would not discriminate the genotypes. It should be noted that in the germinator and/or mist chamber, humidity is more expressive than under field conditions. That is because even when the harvest coincides with rainfall, high humidity is almost never continuous, as occurs in the laboratory. On consulting the Regulations for Seed Analysis (Regras para Análise de Sementes - RAS) (MAPA, 2009), the first germination scoring for common bean (*Phaseolus vulgaris*) is indicated after five days in the germinator at 25 °C, and the final scoring after nine days. Thus, the choice was made to evaluate the percentage of germination on the seventh day when the test was conducted in germinators at 25 °C, and individual plants were evaluated. When progenies were evaluated in a mist chamber with a mean temperature of 20 °C and 98 % relative humidity, there was monitoring through control. Thus, every day a roll containing a control was opened and the percentage of germination was verified. Adopting this strategy, it may be concluded that, in this case, scoring germination would be made on the sixth day. The strategy adopted was efficient, i.e., there was discrimination of the progenies with a high degree of accuracy (Table 3).

Differences were also observed between the populations ($p \leq 0.01$) for PGSP (Table 5). As expected, the variance in the segregating populations was greater than

that of the parents. It was observed that the seeds still in the pods of the plants showed wide variation in the percentage of germination, ranging from 0 to 100 %, but with greater concentration in the class of higher percentages. The mean values of the F_1 generations in the two periods of evaluation were less than those of the parents and of the F_2 generation. In principle, this result, in contrast with what occurred with thickness, indicates the occurrence of dominance. The estimate of heterosis of the F_1 generation, in relation to the mean value of the parents, was -75 % in the sowing conducted in Feb 2013, and -37 % in the other period of evaluation (Table 5). It should be noted that the mean percentage of germination of the parent with lower pod thickness, Pérola (P_1), was greater than that observed for the line ESAL 686 (P_2) with greater pod thickness.

In the evaluations of individual plants for the PGSP, the additive-dominant model, as had occurred for the PWT, explained a large part of the variation (R^2 greater than 97 %) (Table 6). In this case, considering one locus, a is the deviation of homozygotes for the mean. When $\hat{p} = \hat{q} = 1/2$ a corresponds to an additive effect and $\hat{d}$ is the deviation of the heterozygote in relation to the mean, the dominance effect. Both components were different from zero. As the estimate of d was negative, it may be inferred that the dominance was in the direction of reducing expression of the trait. In the first period of evaluation, only the component of environmental variance (V_E) was different from zero, a fact that may be explained by the large magnitude of associated errors. In the second period, there was greater consistency with the results of the mean components, and in this case, both V_A and V_D differed from zero. For this trait, the estimate of heritability (h^2) for the first period of evaluation was very low ($h^2 = 1$ %), but in the second period, the estimate was higher ($h^2 = 24$ %). It may be inferred that the evaluation of this trait from the pods of individual plants shows low precision (Table 6).

The use of progenies proved to be more efficient than the use of individual plants in the PGSP evaluation, with heritability greater than 75 %. One of the reasons is that, in this case, more pods were available and it was possible to use five pods per plot with three replications. In a similar study involving 95 common bean lines, with the use of ten pods per plot, the accuracy of the percentage of germination of seeds while still in the pods was similar to that obtained in the present study, i.e., 62 % (Lima et al., 2012).

The gain expected from selection involving all the progenies and selecting the 10 % with the lowest PGSP was -61 % (Table 4). One of the objectives of this study was to verify which of the two traits evaluated would allow for greater efficiency in selection. The estimate of correlation between PWT and PGSP was practically zero when individual plants were used; however, when the averages of the progenies was used, the estimate of correlation was negative and different from zero (r = -0.5**). Based on this last result, it may be inferred that the greater the pod wall thickness, the lower the germination.

Table 4 – Estimates of gain expected from selection (GS) and correlated response (CR$_{Y(X)}$) obtained for the traits of pod wall thickness (PWT) and percentage of germination of seeds while still in the pods (PGSP). Lavras, 2014.

Indices evaluated	Trait under selection		
	PWT (mm × 100)	PGSP (%)	CR$_{(PWT)(PGSP)}$
Mean of the progenies (Mo)	16.25	26.19	26.19
Mean selected	20.23	5.61	12.69
h^2	62 %	77 %	-
GS	2.47	-15.85	-10.40
GS%	15	-61	-40*

*Correlated response of selection carried out in PWT and gain in PGSP (CR$_{(PWT)(PGSP)}$).

Table 5 – Mean value of the percentage of germination of seeds in the pods (PGSP) obtained for the different populations evaluated. Sowing in Feb and July, 2013.

Generations	DF	Feb	DF	July
		Mean %		Mean %
P_1	25	88.325	43	96.519
P_2	29	71.983	19	67.932
F_1	53	45.825	60	59.956
F_2	188	60.487	229	69.056
F_1RC_{11}	95	57.561	137	75.855
F_1RC_{21}	90	53.382	123	59.670
F_2RC_{11}	-	-	217	62.589
F_2RC_{21}	-	-	317	63.487
F_3	-	-	610	62.689
Accuracy (r_{gg})		91 %		93 %
Heterosis		-75 %		-37 %

P_1: Pérola; P_2: ESAL 686.

Table 6 – Estimates of the mean and variance components of the trait, percentage of germination of seeds while still in the pods (PGSP). Sowing in Feb and July, 2013.

Mean Genetic Component	Feb		July	
	Estimate	Standard Deviation	Estimate	Standard Deviation
$\hat{m}$	78.2612	2.7846**	73.230	1.3374**
$\hat{a}$	8.2016	2.7404**	18.391	1.4548**
$\hat{d}$	-37.1106	5.2105**	-17.632	3.5453**
[1]R^2 (%)	99.71		97.34	
Variance Component	Feb		July	
	Estimate	Standard Deviation	Estimate	Standard Deviation
$\hat{V}_E$	826.178	112.952**	254.583	45.536**
$\hat{V}_A$	13.000	323.262	289.492	72.974**
$\hat{V}_D$	437.822	302.050	659.134	103.478**
[1]R^2(%)	98		96	
h_r^2	1		24	

[1]Coefficient of determination of the model; **estimate different from zero at the level of 1 % probability by the t test.

Finally, considering that in the two methodologies there is similar difficulty of evaluation, use of the germination in the pod test, in principle, proved to be more promising. Unfortunately, there is difficulty in showing that this trait reflects tolerance to high moisture under field conditions, above all, due to the lower experimental precision in the evaluations under field conditions. This fact contributed so that the correlated response by selection in PWT and expected gain in PGSP was less than that directly seen in the trait, though still expressive (Table 4).

Viviparity in common bean has been little studied, and in the studies already undertaken, the emphasis was on identification of the variation between lines for the trait (Yuste-Lisbona, 2014). In the corn crop, studies are more numerous, and different genes involved in expression of viviparity have been identified. These genes act in different manners, above all by production of the hormone abscisic acid (ABA) (McCarty, 1991; Neuffer et al., 1997; Suzuki et al., 2006). In wheat, there is growing concern about early seed germination, because early germination also brings about expressive economic losses. It is known that for this crop, the main resistance to viviparity is associated with overcoming seed dormancy. However, in spite of the various studies published, information in relation to genetic control is still in the early stages (Flintham, 2000; Groos et al., 2002; Li et al., 2004; Gubler et al., 2005; Tan et al., 2006; Rikiishi and Maekawa, 2010; Lan et al., 2012; Zhang et al., 2014).

Conclusions

Taking into account the genetic and phenotypic parameters estimates, especially the high heritability, selection for less viviparity in common bean has to be done evaluating the PGSP in progenies.

Acknowledgements

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