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Combining Ability Estimates of Sulfate Uptake Efficiency in Maize

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Summary. Plant root nutrient uptake efficiency may be expressed by the kinetic parameters, V_{max} and K_m, as well as by normal enzymatic reactions. These parameters are apparently useful indices of the level of adaptation of genotypes to the nutrient conditions in the soil. Moreover, sulfate uptake capacity has been considered a valuable index for selecting superior hybrid characterized by both high grain yield and efficiency in nutrient uptake. Therefore, the purpose of this research was to determine combining ability for sulfate uptake, in a diallel series of maize hybrids among five inbreds. Wide differences among the 20 single crosses were obtained for V_{max} and K_m. The general and specific combining ability mean squares were significant and important for each trait, indicating the presence of considerable amount of both additive and nonadditive gene effects in the control of sulfate uptake. In addition, maternal and nonmaternal components of F1 reciprocal variation showed sizeable effects on all the traits considered. A relatively high correlation was also detected between V_{max} and K_m. However, both traits displayed enough variation to suggest that simultaneous improvement of both V_{max} and K_m should be feasible. A further noteworthy finding in this study was the identification of one inbred line, which was the best overall parent for improving both affinity and velocity strategies of sulfate uptake.

Key words: *Zea mays* L. – Sulfate uptake – Diallel analysis – General and specific combining ability – Nutrient efficiency

Introduction

During the past 50 years maize-breeders have made remarkable progress in enhancing the performance of hybrids (Russell 1974; Duvick 1977). Although a considerable amount of evidence has suggested that hybrid selection based on conventional breeding procedures is effective in improving both plant vigor and adaptation to varying environmental conditions (Sprague and Eberhart 1977), the utilization of such an approach is often time- and resource-consuming. It is, therefore, considered imperative that plant breeders and crop physiologists pursue the goal of identifying better methods for selecting high yielding crops.

Recently, a growing interest has emerged in the use of biochemical and/or physiological indices of performance (for a recent review, see Motto and Salamini 1981).

Among the biochemical markers which can be adopted to facilitate the isolation and selection of improved strains of crop plants, the absorption of nutrient ions from the soil solution may prove useful for future agricultural needs. Frick and Bauman (1978), in a study on excised roots of maize seedlings, suggested a possible relationship between rates of K^+ uptake and yield capacity. Moreover, the ability to increase the rates of K^+ uptake, which is genetically controlled and heritable, showed a significant amount of heterosis (Frick and Bauman 1979). Heterosis has, also, been observed for high sulfate uptake in maize hybrids (Cacco et al. 1978) and a high positive correlation between the V_{max} of the absorption of this nutrient and grain yields has been well documented (Cacco et al. 1980; Saccomani et al. 1981; Landi et al. 1982). Furthermore, in higher plants, maize included, there is considerable evidence supporting the hypothesis that sulfur nutrition has a pronounced effect on nitrogen metabolism (Dijkshoorn and Van Wyk 1967; Stewart and Porter 1969; Bolton et al. 1976; Rending et al. 1976; Rabuffetti and Kamprath 1977; Filner 1978). Friedrich and Schrader (1978) found that nitrate reductase activity is very sensitive to changes in the availability of sulfur and is dramatically reduced in S-deprived maize plants. Reuveny and Filner (1977) reported that ATP-sulfurylase is regulated negatively by an end product of the sulfate assimilation pathway and positively by an end product of the nitrate assimilation pathway. More recently, the existence of a close connection between nitrate and sulfate assimilatory pathways has been suggested (Reuveny et al. 1980). This finding represents a rare case, in higher plants, of two different metabolic pathways reciprocally connected to assure their mutual dependence. Because maize yield depends heavily on nitrogen fertilization it could be that sulfur nutri-

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tion, which plays an important role in nitrogen metabolism, may also affect the final yield of the crop. Therefore, sulfate uptake capacity could represent a valuable index for selecting maize genotypes characterized by high yields and by high nutrient efficiency.

This study was undertaken to gain information on the mode of inheritance of genes controlling the kinetic parameters of sulfate uptake in a number of lines of maize evaluated as F1 hybrids.

Materials and Methods

Plant Materials

Five commonly used inbred lines of maize (B14, B37, Oh43, W22, and W64A) were the source material for this experiment; these lines are maintained by the Maize Section of the Experiment Institute of Cereal Research, at Bergamo. Crosses to produce diallel genotypes, including reciprocals, were made at Bergamo during the summer of 1981. From each of the 20 single-cross hybrids, two random samples of 30 seeds each were used for the sulfate uptake experiments. These were performed at five solution concentrations as described below.

Growth Conditions

Thirty seeds from each F1 and their reciprocals were surface-sterilized by soaking in 1% sodium hypochlorite solution for 10 min, and were germinated in plastic pots containing quartz sand. Six seeds were planted in each pot. Two replications were used. Pots for each genotypes were placed in a controlled-environment room. The conditions in the room were day/night temperatures of 25 °C/18 °C with a relative humidity of 70/90%. The light intensity for the 14-h day was 60 W/m^2. The pots were watered daily with Hoagland's solution (Arnon and Hoagland 1940). On the fifth postgermination day, the nutrient solution was deprived of sulfate and the anion was replaced with chloride. Four days later, plants were removed from pots and transferred to 100 ml of sulfate solution. The absorption solutions were similar to the previous solution; however $MgSO_4$ was replaced by $MgCl_2$ and K_2SO_4 by 5, 10, 25, 50, 100 μM ^{35}[S]labelled K_2SO_4. The incubation mixture was maintained at 27 °C, for 10 min, in a Dubnoff shaker and oxygenated by continuous air bubbling.

Chemical Assays

At the end of the absorption period, the incubated roots were rinsed with 0.1 nonradioactive K_2SO_4, at 0 °C, for 10 min. Roots were then removed and homogenated in an Ultraturrax apparatus. Aliquots of each homogenate were used to determine apparent ion uptake. This was measured by liquid scintillation spectrometry with Instagel, using a Packard Tricarb spectrometer. The transport kinetic parameters, V_{max} and K_m, of the uptake process were derived from the double reciprocal plots (Lineweaver-Burk) of the uptake rate and SO_4^{2-} concentrations. The K_m parameter was expressed as μeq. l^{-1}, while the V_{max} parameter was expressed per unit of both fresh weight and protein and indicated as V_{max_1} (neq $SO_4^{2-} \cdot min^{-1} \cdot g\ fr \cdot wt^{-1}$) and V_{max_2} (neq $SO_4^{2-} \cdot min^{-1} \cdot mg^{-1}$ protein), respectively. Protein was determined by the method of Lowry et al. (1951).

Statistical Procedures

All data were analyzed by conventional analysis of variance. The diallel analyses were computed on all crosses and their reciprocals according to Griffing's (1956), method 3, model 1, which provides estimates of general combining ability (GCA), specific combining ability (SCA) and reciprocal effects. The F1 reciprocal variation was partitioned into maternal and nonmaternal sources according to Cockerham (1963). Phenotypic correlations were also computed between all pairs of traits from the entry means.

Results

The mean values of the kinetic parameters of sulfate uptake for all possible single-cross combinations derived from the five parental lines are presented in Table 1. The magnitude of phenotypic variations was appreciably large for each of the traits examined. In fact, the means of replications for the V_{max} parameters expressed per unit either of fresh weight or protein ranged, respectively, from 4.177 and 1.425 for the cross W64A × B37 to 9.195 and 2.694 neq $SO_4^{2-} \times min^{-1}$ for W22 × B14, while the K_m values ranged from 21.50 for W64A × B37 to 65.50 μeq × l^{-1} for W64A × W22. The line means of data for inbreds used as both male and female parents show that B37 has the lowest, while B14 and W22 has the highest values for the V_{max} and K_m kinetic parameters of sulfate uptake. Hence, the range of differences in adequate to illustrate the relative importance of various types of gene action conditioning sulfate uptake among the crosses tested.

The variation attributable to differences among crosses was significant in every instance (Table 2). Moreover, the combining ability analysis suggested the presence of significant variation due to general (GCA) and specific ability (SCA) for each of the traits tested, indicating the presence of considerable amounts of both additive and nonadditive gene effects in the control of sulfate uptake. In addition, maternal and nonmaternal components of F1 reciprocal variations had a pronounced effect on both V_{max} per unit of protein and K_m, while the maternal component had effects only on the V_{max} per g fresh weight, as shown by the relative sizes of the mean squares for maternal and nonmaternal reciprocal effects.

Estimates of GCA effects for the five lines tested indicated that several lines gave noteworthy genetic contributions (Table 3). Inbred B14 contributed, on the average, additive genetic effects which, in hybrid combinations, significantly improved the kinetic parameters of sulfate uptake. By contrast, the genetic contribution of B37 led to a reduced sulfate uptake, and to the highest GCA estimates for the K_m parameters. Oh43 displayed positive effects in the V_{max} expressed for g of fresh weight and on the affinity for sulfate uptake. On

Table 1. Mean values of the kinetic parameters (V_{max} and K_m) of sulfate uptake by maize roots

Male inbred	Variable[a]	Female inbred					Line[b] mean
		B14	B37	Oh43	W22	W64A	
B14	V_{max_1}	–	7.484	9.049	7.361	7.820	7.964 a[c]
	V_{max_2}	–	2.295	2.575	2.495	2.443	2.377 a
	K_m	–	33.5	27.0	38.5	46.0	39.00 b
B37	V_{max_1}	7.374	–	6.197	6.171	4.177	6.034 c
	V_{max_2}	2.059	–	2.038	2.243	1.425	1.961 c
	K_m	34.0	–	37.5	40.5	21.5	36.81 b
Oh43	V_{max_1}	9.000	6.161	–	6.676	7.351	7.065 b
	V_{max_2}	2.479	2.124	–	1.986	2.311	2.158 b
	K_m	33.0	41.0	–	37.5	49.0	37.25 b
W22	V_{max_1}	9.195	4.623	6.352	–	5.879	6.728 c
	V_{max_2}	2.694	1.472	2.028	–	2.084	2.195 b
	K_m	63.50	36.0	37.50	–	47.50	45.81 a
W64A	V_{max_1}	6.428	6.088	5.736	7.566	–	6.381 d
	V_{max_2}	1.971	2.029	1.722	2.556	–	2.068 bc
	K_m	36.50	50.50	35.5	65.50	–	44.00 a

[a] L.S.D. at 5%: $V_{max_1}=0.631$; $V_{max_2}=0.324$; $K_m=5.377$
[b] Lines means were computed from the single crosses for each inbred used as both female and male parent
[c] Any two means, within the same variable, not followed by the same letter differ at $P_{.01}$ according to Duncan's Multiple Range Test

Table 2. Mean squares for general (GCA) and specific combining ability (SCA) and reciprocal, maternal (Mat. E.), and non-maternal (Nonmat. E.) reciprocal effects from the kinetic parameters (V_{max} and K_m) of sulfate uptake by maize roots

Source	d.f.	Mean squares		
		V_{max_1}	V_{max_2}	K_m
Hybrids	19	3.609**	0.242**	230.4**
GCA	4	8.745**	0.384**	267.2**
SCA	5	3.331**	0.264**	235.2**
Rec. E.	10	1.693**	0.173**	213.1**
Mat. E.	4	0.440*	0.105*	146.8**
Nonmat. E.	6	0.144	0.327**	257.2**
Error	19	0.091	0.024	6.6

*, ** Significant at the 0.05 and 0.01 levels of probability, respectively

the other hand, W22 showed reduced affinity for sulfate while V_{max} was not significant.

Estimates of SCA and reciprocal effects are presented in Table 4. W64A×W22 had the highest estimates of SCA effects for the V_{max} parameter both per unit of fresh weight and protein. By contrast, B14×W64A gave negative effects for these two traits. Four out of ten crosses gave favourable significant SCA for K_m, while the others gave unfavorable or not significant effects. Although, the SCA effects of B14×Oh43, B37×W22, B37×W64A and W22×Oh43 did not differ significantly, W22×Oh43 involving a poor×poor general combiner revealed the highest SCA effects for K_m. Estimates of reciprocal effects for the three kinetic parameters exhibited significant differences for most of the crosses involving W22 and W64A.

Simple correlation coefficients between the kinetic parameters of sulfate uptake were obtained from cross means (Table 5). The V_{max} parameters, as expected, were closely related. Moreover, it is interesting to note that the K_m parameter showed a sizeable positive correlation with the V_{max} per unit of protein, whereas a lack of relationship was observed between the former trait with the V_{max} expressed per unit of fresh weight.

Table 3. Estimates of general combining ability effects for the kinetic parameters (V_{max} and K_m) of sulfate uptake by maize roots

Inbred line	General combining ability estimates		
	V_{max_1}	V_{max_2}	K_m
$\bar{X}$	6.835	2.152	40.575
B14	1.506**	0.300**	−2.100*
B37	−1.067**	−0.255**	−5.016**
Oh43	0.308**	0.009	−4.434**
W22	−0.142	0.058	6.983**
W64A	−0.605**	−0.112*	4.567**
L.S.D. at (5%)	0.257	0.132	2.195

*, ** Significantly different from zero at the 0.05 and 0.01 levels of probability, respectively

Table 4. Estimates of specific combining ability (above diagonal) and reciprocal effects (below diagonal) for kinetic parameters of sulfate uptake by maize roots

Inbred	Variable	Inbred				
		B14	B37	Oh43	W22	W64A
B14	V_{max_1}	–	0.155	0.376**	0.079	–0.611**
	V_{max_2}	–	–0.020	0.066	0.084	–0.133*
	K_m	–	0.291	–4.041**	5.541**	–1.791
B37	V_{max_1}	0.055	–	0.103	–0.228*	–0.030
	V_{max_2}	0.118	–	0.175**	–0.097	–0.053
	K_m	–0.250	–	8.125**	–4.291**	–4.125**
Oh43	V_{max_1}	0.024	0.018	–	–0.486**	0.006
	V_{max_2}	0.176	–0.043	–	–0.211**	–0.032
	K_m	–3.000*	–1.750	–	–5.625**	1.541
W22	V_{max_1}	–0.917**	0.774**	0.162	–	0.634**
	V_{max_2}	–0.099	0.386**	–0.023	–	0.222**
	K_m	–12.500**	2.250	0.000	–	4.375**
W64A	V_{max_1}	0.696**	–0.955**	0.808**	–0.844**	–
	V_{max_2}	0.236**	–0.304**	0.155	–0.236**	–
	K_m	4.750**	–14.500**	6.750**	–9.000**	–

	V_{max_1}	V_{max_2}	K_m
L.S.D. at 5% (S.C.A.)	0.257	0.132	2.195
L.S.D. at 5% (Rec. E.)	0.315	0.162	2.688

*, ** Significantly different from zero at the 0.05 and 0.01 levels of probability, respectively

Table 5. Correlation coefficients between the kinetic parameters (V_{max} and K_m) of sulfate uptake by maize roots

Variable	V_{max_2}	K_m
V_{max_1}	0.903**	0.307
V_{max_2}	–	0.501*

*, ** Significantly different from zero at 0.05 and 0.01 levels of probability, respectively

Discussion

The efficiency by which crops utilize soil nutrients is affected by several plant characteristics which may be related to root morphology and distribution and to physiological mechanisms regulating ion uptake within the roots (for a review, see Clarkson and Hanson 1980). Moreover, experimental results indicate that the level of selectivity in nutrient uptake is genetically controlled (Epstein and Jefferies 1964; Läuchli 1976) and varies extensively among and within crop species (Läuchli 1976; Vose 1963; Dunlop and Tomkins 1976; Bruetsch and Estes 1976; Spear et al. 1978).

In maize plants the genetic regulation of sulfate uptake by root tissues has been repeatedly reported (Ferrari and Renosto 1972; Cacco et al. 1976, 1977, 1978, 1979). Additional research in this area has also shown that ATP-sulfurylase, the first enzyme of the sulfate metabolic pathway, is associated in its variation and inheritance, to sulfate transport in roots (Cacco et al. 1978).

In agreement with these findings, the data presented here have shown that sizeable differences in sulfate uptake occur among genotypes. Moreover, the levels of GCA and SCA reported in this paper indicate that additive and nonadditive gene actions are important in the control of the kinetic parameters of transport. Therefore, selection procedures based on the accumulation of additive effects should be successful in improving the sulfate uptake capacity. However, the maximum advantage of selection should be obtained by using procedures which are known to be effective in shifting gene frequency when additive and nonadditive genetic variations are important.

The present study has also brought out the importance of significant reciprocal effects, probably due to heritable cytoplasmic effects, and to the interaction of nuclear and cytoplasmic effects.

A further noteworthy point is that kinetic parameters of sulfate uptake, V_{max} and K_m, are also useful indexes of the level of adaptation of the genotypes to the nutrient conditions in the soil (Crowley 1975). The different genotypes may have developed an "affinity strategy" (low K_m) or a "velocity strategy" (high V_{max}). The ever increasing costs of fertilizers has recently stimulated interests in breeding crops that exploit available inorganic resources more efficiently (Jackson et al. 1975). Therefore, these genotypes should be characterized by a high V_{max} and low K_m of ion uptake. However, our data showed that the relationships between K_m and V_{max} when expressed per unit of protein, although significant, are not very large. Moreover, both traits displayed sufficient variation to suggest that simultaneous improvement in the "affinity strategy" and "velocity strategy" should be possible. In this respect, it appears that among the materials considered B14, which was effective in transmitting high V_{max} and low K_m, would probably be the best for breeding programs. Finally, we point out that only a few inbreds where tested in this study; there may be other genotypes that would provide a sulfate uptake capacity in their crosses superior to those manifested by the lines used in this study.

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Literature

Arnon, D.I.; Hoagland, D.R. (1940): Crop production in artificial culture solution and in soils with special reference to factor influencing yields and absorption of inorganic nutrients. Soil Sci. **50**, 463–483

Bolton, J.; Nowakowski, T.Z.; Lazarus, W. (1976): Sulphur-nitrogen interaction effects on the yield and composition of protein-N, non protein-N, and soluble carbohydrates in perennial ryegrass. J. Sci. Food Agric. **27**, 553–560

Bruetsch, T.F.; Estes, G.O. (1976): Genotypic variation in nutrient uptake efficiency in corn. Agron. J. **68**, 521–523

Cacco, G.; Ferrari, G.; Lucci, G.C. (1976): Uptake efficiency of roots in plants at different ploidy levels. J. Agric. Sci. **87**, 585–589

Cacco, G.; Saccomani, M.; Ferrari, G. (1977): Development of sulfate uptake capacity and ATP sulfurylase activity during root elongation in maize. Plant Physiol. **60**, 582–584

Cacco, G.; Ferrari, G.; Saccomani, M. (1978): Variability and inheritance of sulfate uptake efficiency and ATP sulfurylase activity in maize. Crop Sci. **18**, 503–505

Cacco, G.; Ferrari, G.; Saccomani, M. (1979): Coordination of sulfate uptake, ATP sulfurylase and O-acetylserinesulphydrylase activities in maize roots as affected by the Ht mutation. Maydica **24**, 247–254

Cacco, G.; Ferrari, G.; Saccomani, M. (1980): Pattern of sulfate uptake during root elongation in maize: its correlation with productivity. Physiol. Plant **48**, 375–378

Cockerham, C.C. (1963): Estimation of genetic variances. In: Statistical genetics and plant breeding (eds. Hanson, W.D.; Robinson, H.F.), pp. 53–94. N.A.C.-N.R.C. Publ.

Clarkson, D.T.; Hanson, J.B. (1980): The mineral nutrition of higher plants. Ann. Rev. Plant Physiol. **31**, 239–298

Crowley, A.H. (1975): Natural selection and the Michaelis constant. J. Theor. Biol. **50**, 461–475

Dijkshoorn, W.A.; Van Wyk, A.I. (1967): The sulphur requirements of plants as evidenced by the sulphur-nitrogen ratio in organic matter. A review of published data. Plant Soil **26**, 129–157

Dunlop, J.; Tomkins, B.D. (1976): Genotypic differences in potassium translocation in ryegrass. In: Transport and transfer processes in plants (eds. Wardlow I.F.; Passioura, J.B.), pp. 145–152. New York: Acad. Press

Duvick, D.N. (1977): Genetic rates of gain in hybrid maize yields during the past 40 years. Maydica **22**, 187–196

Epstein, E.; Jefferies, R.L. (1964): The genetic basis of selective ion transport in plants. Ann. Rev. Plant Physiol. **15**, 169–184

Ferrari, G.; Renosto, F. (1972): Comparative studies on the active transport by excised roots of inbred and hybrid maize. J. Agric. Sci. **79**, 105–108

Filner, P. (1978): Regulation of inorganic nitrogen and sulfur assimilation in cell suspension cultures. In: Frontiers of plant tissue culture (ed. Thorpe T.A.), pp. 437–442. Calgary: The International Association for Plant Tissue Culture

Frick, H.; Bauman, L.F. (1978): Heterosis in maize as measured by K uptake properties of seedling roots. Crop Sci. **18**, 99–103

Frick, H.; Bauman, L.F. (1979): Heterosis in maize as measured by K uptake properties of seedling roots: pedigree analyses of inbreds with high or low augmentation potential. Crop Sci. **19**, 707–710

Friedrich, I.W.; Schrader, L.E. (1978): Sulfur deprivation and nitrogen metabolism in maize seedlings. Plant Physiol. **61**, 900–907

Griffing, B. (1956): Concept of general and specific combining ability in relation to diallel crossing system. Aust. J. Biol. Sci. **9**, 463–493

Jackson, W.A.; Knezek, B.D.; Van Schilfgarrde, J. (1975): Water, soil and mineral input. In: Crop Productivity ... Research imperatives (eds. Brown, A.W.A.; Byerly, T.C.; Gibbs, M.; San Pietro, A.), pp. 201–274. East Lansing, Michigan: Michigan-Kettering

Landi, S.; Saccomani, M.; Cacco, G. (1982): Correlation between grain yield and efficiency of K^+ and SO_4^{2-} uptake. Agrochimica (In press)

Läuchli, A. (1976): Genotypic variation in transport. In: Encyclopedia of plant physiology, New Series, Vol. 2 (eds. Lüttge, U.; Pitman, M.G.), pp. 372–393. Berlin, Heidelberg, New York: Springer

Lowry, O.H.; Rosebrough, N.J.; Farr, A.L.; Randall, R.J. (1951): Protein measurement with the Folin phenol reagent. J. Biol. Chem. **193**, 265–375

Motto, M.; Salamini, F. (1981): Genetic basis of physiological traits related to maize productivity. Riv. Agron. **15**, 3–19

Rabuffetti, A.; Kamprath, E.J. (1977): Yield, N, and S content of corn as affected by N and S fertilization on coastal plain soils. Agron. J. **69**, 785–788

Rending, V.V.; Oputa, C.; McComb, E.A. (1976): Effects of sulfur deficiency on non-protein nitrogen, soluble sugars and N/S ratios in young corn plants. Plant Soil **44**, 423–437

Reuveny, Z.; Filner, P. (1977): Regulation of adenosine triphosphate sulfurylase in cultured tobacco cells; effects of sulfur and nitrogen sources on the formation and decay of the enzyme. J. Biol. Chem. **252**, 1858–1864

Reuveny, Z.; Dougall, K.D.; Trinity, P.M. (1980): Regulatory coupling of nitrate and sulfate assimilation pathways in cultured tobacco cells. Proc. Natl. Acad. Sci. USA **77**, 6670–6672

Russell, W.A. (1974): Comparative performance of maize hybrids representing different eras of maize breeding. Proc. 29th Ann. Corn and Sorghum Res. Conf. **29,** 81–101

Saccomani, M.; Cacco, G.; Ferrari, G. (1981): Efficiency of the first steps of sulfate utilisation by maize hybrids in relation to their productivity. Physiol. Plant. **53,** 101–104

Spear, S.N.; Asher, C.J.; Edwards, D.G. (1978): Response of Cassava, sunflower, and maize to potassium concentration in solution II. Potassium absorption and its relation to growth. Field Crops Res. **1,** 363–373

Sprague, G.F.; Eberhart, S.A. (1977): Corn breeding. In: Corn and corn improvement (ed. Sprague, G.F.), pp. 305–362. Madison (WI, USA): Am. Soc. Agron. Inc. Publ.

Stewart, B.A.; Porter, L.K. (1969): Nitrogen sulfur relationships in wheat, corn, and beans. Agron. J. **61,** 267–271

Vose, P.B. (1963): Varietal differences in plant nutrition. Herbage Abstr. **33,** 1–13

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