

Gene effects from *Bipolaris maydis* incidence and severity on popcorn

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ABSTRACT: Popcorn suffers severe economic losses resulting from harmful effects caused by several diseases such as southern corn leaf blight (SCLB), which is one of the main leaf diseases able to cause considerable damages to corn crops. The realization conducting genetic studies in order to identify genotypes presenting genetic resistance to this disease it is essential. Accordingly, the aim of the current study is to estimate gene effects and combining abilities in popcorn, with emphasis on the resistance to *Bipolaris maydis*. Full diallel crosses were performed, including reciprocal crosses between eight lines (L76, L88, L70, L77, L55, L61, P1 and P8), in order to produce 56 hybrids (F_1 's and reciprocal hybrids). The experiment followed a randomized block design, with four replicates; in two different cultivation periods (first and second periods), in Campos dos Goytacazes, RJ. Southern corn leaf blight incidence and severity, caused by *B. maydis*, were assessed in each cultivation period. No reciprocal effect was observed for the evaluated characteristics, since the diallel analysis did not find significant effect from this variation source. With respect to SCLB incidence and severity in the two cultivation periods, the mean square of the effects showed that the dominance components were superior to the additivity ones. Hybrids that stood out in the two cultivation periods to the assessed features were: L88 x L61, L88 x L70, L88 x L76, L61 x L77, L61 x P1, L70 x P1, P1 x L76, L77 x L76, and P8 x L77.

Key words: combining ability; genetic resistance; southern corn leaf blight; *Zea mays* L.

Efeitos gênicos da incidência e severidade de *Bipolaris maydis* em milho-pipoca

RESUMO: O milho-pipoca sofre severas perdas econômicas devido aos efeitos danosos da incidência de doenças. A helmintosporiose é uma das principais doenças foliares e representa um considerável potencial de dano à cultura; tornando-se evidente a necessidade de estudos genéticos visando à identificação de genótipos que apresentem resistência genética para essa doença. O estudo teve por objetivo estimar os efeitos gênicos e as capacidades combinatórias em milho-pipoca, com enfoque para a resistência a *Bipolaris maydis*. Foram realizados cruzamentos dialélicos completos, incluindo os recíprocos entre oito linhagens (L76, L88, L70, L77, L55, L61, P1 e P8), para a obtenção de 56 híbridos (F_1 's e recíprocos). Instalou-se experimento em delineamento em blocos ao acaso com quatro repetições, em duas épocas de cultivo, em Campos dos Goytacazes, RJ. Avaliaram-se a incidência e a severidade causada por *B. maydis* para cada época. Observou-se a ausência de efeito recíproco para as características avaliadas, uma vez que não houve efeito significativo desta fonte de variação na análise dialélica. Para a incidência e severidade de helmintosporiose, nas duas épocas de cultivo, o quadrado médio dos efeitos revelou que os componentes de dominância foram superiores aos de aditividade. Os híbridos que se destacaram, nas duas épocas de cultivo, com base no conjunto de características avaliadas, foram: L88 x L61, L88 x L70, L88 x L76, L61 x L77, L61 x P1, L70 x P1, P1 x L76, L77 x L76 e P8 x L77.

Palavras-chave: capacidade combinatória; resistência genética; helmintosporiose; *Zea mays* L.

Introduction

Popcorn is quite consumed worldwide, and although it is intended to human consumption, it is also considered a high-profitability crop, since its final product is widely accepted by the consumers. Thus, interest in grain production has increased in several regions, a fact that turned Brazil into the second largest popcorn producer (Paraginski et al., 2016). However, popcorn cultivation remains modest, mainly due to limitations in finding genotypes able to provide quality, good yield and resistance to diseases. Consequently, it is necessary importing grains, mainly from Argentina and the United States of America (Rinaldi et al., 2007).

Although the limited number of national popcorn cultivars and hybrids is the main barrier for the crop expansion, there has been improvement in both its extension and production capacity. However, the crop lacks genotypes holding other favorable agronomic features, such as the resistance to diseases. Overall, popcorn is less resistant to the main leaf diseases affecting corn crops (Hallauer & Carena, 2009; Ribeiro et al., 2016). This fact, aside from contributing to lower yields, increases the production risks. Hence, developing genetically resistant genotypes is the most viable alternative to control the main leaf diseases (Ayiga-Aluba et al., 2015).

Southern Corn Leaf Blight (SCLB) caused by the fungus *Bipolaris maydis* (Nisik.) Shoemaker [synonym *Helminthosporium maydis* Nisik and Myiake], stands out among the main leaf diseases affecting popcorn crops. This fungus may drastically reduce crop stand and yield depending on the resistance level of some cultivars, the crop management system and the climate conditions during cultivation; yield losses may reach 70% (Altaf et al., 2016). According to Negeri et al. (2011), the use of quantitative resistance to SCLB may help mitigating the disease in pathogen-vulnerable regions, besides avoiding the use of expensive, highly harmful to the environment, fungicides. The case gains relevance in Brazil due to lack of records concerning specific fungicides able to control this pathogen.

Accordingly, several techniques have been suggested in order to help selecting parents to produce hybrids able to present favorable agronomic features. Among the aforementioned techniques, the diallel cross has been widely used to give many genetic information it may provide to breeders (Oliboni et al., 2013). The methodology by Griffing (1956) allows estimating genetic parameters, such as combining abilities, in order to support the indication of breeding strategies and the recommendation of promising genotypes.

Studies about popcorn genetic resistance to leaf diseases are scarce; most of these assessed such resistance based on intervarietal diallels. Among them, it is worth mentioning Rangel et al. (2007) and Vieira et al. (2009). On the other hand, Pinto et al. (2007), Pajic et al. (2008), Silva et al. (2010), Viana et al. (2011), Vieira et al. (2011), Moterle et al. (2012) and Cabral et al. (2013) stand out when it comes to studies providing information about the diallel cross between popcorn lines.

However, there is limited information about the genetic resistance of the herein addressed crop to *B. maydis*. Thereby, the aim of the study was to investigate the existence of reciprocal effect, in order to estimate the combining ability of popcorn parents and hybrids according to the method by Griffing (1956), as well as to indicate the best combinations able to enhance plant resistance to southern corn leaf blight.

Materials and Methods

Eight popcorn (S₁) lines (P1, P8, L55, L61, L70, L76, L77 and L88) produced by the Popcorn Reproduction Program from the State University of Northern Rio de Janeiro, were previously identified as of interest for the accomplishment of this research in the study developed by Kurosawa et al (2017), and when submitted to complete diallel cross; it was possible to make 56 hybrid combinations, including reciprocal hybrids. Evaluations were conducted at the Antônio Sarlo State Agricultural College, located in Campos dos Goytacazes - RJ, Brazil. Eight parents, along with 56 hybrids and 6 controls (IAC 125, Angela BRS, UENF 14, UFV M2-Barão de Viçosa, L70 x L54 hybrid and P8 x L54 hybrid) were evaluated in two growth periods: the first one from October 2014 to January 2015, with variable temperature between 24 °C and 25 °C and the relative air humidity ranging from 70 to 76%; and the second one from May to August 2015, with temperature between 21 °C and 23 °C and air humidity from 79% to 85%.

The experiment followed a randomized block design, with four replicates. Each plot consisted of a 5 m-long row holding 25 plants spaced 0.90 m between rows and 0.20 m between plants. Sowing comprised 3 grains per pit, placed 0.05 m down in the soil; thinning was performed 30 days after the sowing and left one plant per pit. The plots were fertilized at sowing using 60 kg ha⁻¹ of K₂O, 30 kg ha⁻¹ of N, and 60 kg ha⁻¹ of P₂O₅, in addition to 100 kg ha⁻¹ of N as topdressing, 30 days after the sowing.

Treatments reaction to leaf diseases was monitored through the manifestation of symptoms by natural field infection. Assessed features were *B. maydis* incidence (BMI) and severity (BMS) on the plant. The BMI assessment that considers the rate of damaged leaves in the whole plant by using all leaves was performed employing the Agrocere (1996) rating scale, with grades ranging from 1 to 9, where grade 1 indicates 0% incidence; 2 - 0.5% incidence; 3 - 10% incidence; 4 - 30% incidence; 5 - 50% incidence; 6 - 70% incidence; 7 - 80% incidence; 8 - 90% incidence and 9 - 100% leaf incidence; James's (1971) diagrammatic scale, with percentage values of 1, 5, 25 and 50 of the injured leaf area, was employed to measure BMS considering only the upper ear leaf in the plant. The 5 firsts and lasts plants were excluded from the assessment; only the 15 central plants were considered as useful plot. The first plant in each useful plot was marked and assessed; the subsequent 2 were omitted; with this procedure being repeated until the last plant. Thereby, 5 plants were assessed in each plot.

Data concerning each cultivation period were individually subjected to analysis of variance. The means of the treatments

were grouped through the Scott-Knott test at $p > 0.05$. Based on the analysis of variance results, the treatments sum of squares were decomposed into general and specific combining ability and reciprocal effects, according to the methodology by Griffing (1956), Method 1 (parent, F_1 's hybrids with reciprocal hybrids) and Model B (fixed genotype effects). Analyses were performed in the statistical software Genes (Cruz, 2013).

Results and Discussion

The analysis of variance applied to the first cultivation period did not show significant variance ($p < 0.01$) in genotype variation sources GCA and SCA, except for BMI (Table 1). These results indicate that all hybrid combinations were similar to the mean of the parents; therefore, the chances of finding a superior hybrid combination for the herein assessed set of hybrids in this cultivation period were limited. Possibly, the effect of the pathogen on the leaves at the first cultivation period may have been small or absent, which results in the impossibility of discriminating the genotypes.

The second cultivation period showed significant differences ($p < 0.01$) in genotype variation sources, GCA and SCA, in both herein assessed features (Table 1), and it indicated the existence of additive and non-additive effects controlling these features. Significant effect on combining abilities revealed variability resulting from both effects. With these results, it was possible to conclude that the evaluation performed in this environment with significant presence of the pathogen on plants, favored significant variability among the genotypes in the evaluated characteristics; this variability resulted from the combining ability effects. Incidence and severity of fungal diseases are aggravated, depending on climatic conditions, especially through the temperature and air humidity present in the region. Weather conditions in Campos dos Goytacazes are not well defined, according to the imposed sowing season. Infestation and proliferation of southern corn leaf blight causing pathogens may vary due to existing climate instability. Environmental influence on GCA and SCA estimates for disease resistance and agronomic

characteristics have been reported by Parodas & Hayes (1971) and Pixley & Bjarnason (1993). This fact is intensified in tropical regions, where interaction is of particular interest, as there is a significant variation between locations, even when they are nearby. Variations in latitude, length of day, humidity and temperature are greater in these regions, changing what is expected to be found in disease assessments when differences in growing seasons

Estimates of means of the squares from effects found SCA values to be higher than the GCA ones (Table 1); it indicated that the gene actions and genetic structure of the evaluated hybrids favored manifestation of non-additive gene effects. Studies indicate that genetic resistance to southern corn leaf blight in Corn is predominantly determined by additive effect genes (Kumar et al., 2016; Li et al., 2018). However, the existence of non-additive effects on *B. maydis* control has also been reported in the literature (Carson et al., 2004). Non-additive effects are very important to popcorn breeding because they directly affect the hybrid varieties exploitation. On the other hand, if one was interested in developing corn lines, these results would indicate that the selection based on the herein assessed features would be more efficient in advanced generations when the dominance effects are less pronounced.

Absence of reciprocal effects on the herein assessed features indicated lack of differentiation in the male parent selection to express the features. These results are of significant importance for popcorn breeding programs, since there was no information about reciprocal hybrids resistance to southern corn leaf blight so far. Then again, field corn resistance to southern corn leaf blight caused by *B. maydis* may be related to the parent at crossing. Hence, there is reciprocal influence on the resistance/susceptibility depending on the order of the parent at crossing. A historical example of it was the severe epidemic that took place in the United States of America in 1970, in which corn cultivars containing T cytoplasm were highly susceptible to T-fungus, fact that led to the loss of more than 1 billion dollars in that year (Costa et al., 2014). In this case, there was effect relation involving cytoplasmic genes

Table 1. Analysis of variance applied to the general (GCA) and specific combining abilities (SCA) and mean squares of the GCA and SCA effects on *Bipolaris maydis* incidence (BMI) and severity (BMS), assessed in 8 parents and 56 popcorn hybrids intercrossed with the reciprocal hybrids in full diallel, in the first harvest (from October 2014 to January 2015) and the second harvest (from May to August 2015), in Campos dos Goytacazes, RJ.

VS	DF	First Harvest		Second Harvest	
		BMI	BMS	BMI	BMS
Genotype	63	24438.1439**	6.8788 ^{n.s.}	57378.0724**	368.9778**
GCA	7	101714.4614 ^{n.s.}	10.1684 ^{n.s.}	384486.2704**	1769.8194**
SCA	28	25385.1855**	8.5268 ^{n.s.}	31368.6386**	373.2015**
Reciprocal	28	4172.0229 ^{n.s.}	4.4083 ^{n.s.}	1610.4566 ^{n.s.}	14.5436 ^{n.s.}
Residual	189	4632.2361	6.5320	24.9434	59.5202
Mean squares of effects					
GCA		1516.9098	0.0568	5933.9371	26.72343
SCA		5188.2373	0.4987	6663.5858	78.42034
Reciprocal		-57.5266	-0.2655	-387.9799	-5.62207

VS = variation source, DF = degrees of freedom, GCA = general combining ability, SCA = specific combining ability, ** = significant at 1% probability level, ^{n.s.} = non-significant at 1% probability level.

in the control of the resistance expressed by this feature; thus, the epidemic affected genotypes presenting a certain cytoplasm type.

SCA is more important than GCA in some corn culture diseases. Nihei & Ferreira (2012) used corn lines to investigate several leaf diseases, in a study based on diallel analysis, and found that the dominant effects were more important to the resistance against *E. turcicum*. Such result differs from the responses found by Paterniani et al. (2000), Carson (2006) and Vivek et al. (2010). It may happen when crossing using non-related lines, since it increases the possibility of not finding similarity between the loci controlling the feature; consequently, it increases the possibility of finding a genetic complementation in hybrids expressing gene dominance effects, thus decreasing the GCA effect. This study recorded higher non-additive effects, meaning that, in this case, complementation between hybrids in the loci showed some dominance degree. Therefore, breeding procedures based on hybridizations are the best alternative to explore the gene-complementation effect, since it may generate superior genetic gains (Freitas Junior et al., 2006).

With respect to the estimates concerning the \hat{g}_i effects on the studied features, the current study recorded values whose sign ranged from positive to negative depending on the used parent (Table 2). It is noteworthy that the selection lies on individuals showing high \hat{g}_i estimates and positive-sign value; however, negative-sign \hat{g}_i values may be more convenient depending on the feature, as in the case of disease resistance-related features.

In the first harvest, it was not possible to indicate potential parents for the IBM and SBM characteristics, since they had no significant effect for CGC in the analysis of variance (Table 1). On the other hand, in the second harvest, parents who expressed the highest negative estimates of overall combining ability for the characteristics related to *B. maydis* (IBM) and *B. maydis* (SBM) were: L61, L70 and L76 (Table 2). L61 parent had the highest negative estimate for the characteristics, IBM (-91.2664) and SBM (-4.9361). Since this current study addresses disease resistance, it is possible stating that the genotype presenting negative GCA is potentially superior to be used in breeding programs (Cruz et al., 2012). Genotypes L70 and L61 recorded negative BMI and BMS estimates for

Table 2. Estimate of the general combining ability (\hat{g}_i) assessed in a full diallel cross comprising 8 parents, in the first harvest (from October 2014 to January 2015) and the second harvest (from May to August 2015), Campos dos Goytacazes, RJ.

Parents	First Harvest		Second Harvest	
	BMI	BMS	BMI	BMS
L88	61.8709	0.2734	115.8905	1.8470
P8	22.5184	-0.2222	63.3211	11.0089
L61	-57.3891	-0.3572	-91.2664	-4.9361
L70	-51.0828	-0.3028	-78.8658	-4.1280
L77	24.0309	0.8603	39.3680	1.1508
L55	14.3134	-0.1316	-40.5027	-2.7005
P1	-5.9253	-0.0147	54.5161	1.7452
L76	-8.3366	-0.1053	-62.4608	-3.9873

the second harvest, thus constituting a powerful resistance source to be used in breeding programs.

Genotypes L61, L70 and L76 are relevant parents in the production of superior segregant genotypes in advanced generations, since these lines are more prone to hold alleles resistant to southern corn leaf blight. On that account, they are recommended to be used in crosses aimed at reducing southern corn leaf blight levels in crops. Hence, using these parents in hybridizations increases the possibility of finding hybrid combinations showing favorable s_{ij} estimates for all features.

The \hat{s}_{ij} estimates were positive for both features in the two cultivation periods, except for BMI in the first cultivation period, when parents L88, P8 and L55 were used (Table 3). Thus, negative dominance deviations were recorded; consequently, there was unidirectional dominance. Therefore,

Table 3. \hat{s}_{ij} estimate and \hat{s}_i effects, assessed in a full diallel cross using 8 parents, the reciprocal crosses included, in the first harvest (from October 2014 to January 2015) and the second harvest (from May to August 2015), Campos dos Goytacazes, RJ.

Effects (\hat{s}_{ij}), (\hat{s}_i)	Assessed features			
	First Harvest		Second Harvest	
	BMI	BMS	BMI	BMS
L88 X L88	217.2116	-0.9172	187.5583	2.2767
L88 X P8	-5.5009	-0.4866	19.1877	4.7148
L88 X L61	-63.2784	-0.5816	-48.0348	-1.5202
L88 X L70	-34.7247	-0.2209	-52.1255	-0.5733
L88 X L77	-21.7134	-1.1141	-31.2342	-4.8720
L88 X L55	-29.3559	2.3428	-80.7536	-2.0758
L88 X P1	-21.5422	0.9809	25.8077	3.2836
L88 X L76	-41.0959	-0.0034	-20.4055	-1.2339
P8 X P8	74.0166	-0.0759	108.9470	37.0230
P8 X L61	-44.9859	0.1441	-50.1555	-10.9920
P8 X L70	-19.6422	0.4797	-21.4311	-9.7602
P8 X L77	-24.5259	-0.9134	-11.9148	0.4211
P8 X L55	19.0016	-0.0616	-12.1042	-7.5927
P8 X P1	31.9553	-0.0184	39.9713	13.1853
P8 X L76	-30.3184	0.9322	-36.8719	-18.0734
L61 X L61	99.8416	0.7741	214.7563	27.4616
L61 X L70	37.6053	-0.0053	86.5219	16.3003
L61 X L77	-5.3534	-0.2584	-81.1131	-11.0328
L61 X L55	-36.5909	-0.1916	-10.9717	2.7623
L61 X P1	-9.3922	-0.0484	-75.0355	-2.4183
L61 X L76	22.1541	0.1672	-11.8736	3.1942
L70 X L70	119.2791	0.5653	102.8208	5.9267
L70 X L77	-56.0797	-0.7028	20.0220	-0.9870
L70 X L55	-10.1222	-0.2009	-22.1673	1.2742
L70 X P1	-31.4934	-0.1178	-54.1911	-2.3164
L70 X L76	-4.8222	0.2028	-17.7092	2.6661
L55 X L55	92.4366	-0.1272	164.3445	4.0717
L55 X P1	55.9397	-0.1991	-26.9292	-0.4639
L55 X L76	1.9066	-0.3384	5.1727	2.5036
P1 X P1	113.4841	0.4091	158.0570	7.2005
P1 X L76	-19.6947	-0.3653	-20.7211	-0.7570
L76 X L76	102.0366	0.0703	111.1308	4.4955
L77 X L55	18.6641	-1.2241	-16.5911	-0.4795
L77 X P1	-7.3772	-0.6409	14.3902	-0.1052
L77 X L76	-30.1659	-0.6653	-34.4430	-1.4777

Continues...

Table 3. Continuation.

Effects ($\hat{\sigma}_{ij}$), ($\hat{\sigma}_{ij}$)	Assessed features			
	First Harvest		Second Harvest	
	BMI	BMS	BMI	BMS
Reciprocal				
P8 X L88	28.6150	0.1350	-25.8100	3.4100
L61 X L88	3.3700	-0.0750	-10.5000	-0.3600
L70 X L88	8.9400	0.4900	-17.0600	-1.7150
L77 X L88	-31.4150	0.4300	-5.6850	0.1750
L55 X L88	-21.9050	-3.3650	6.6750	-0.3600
P1 X L88	-51.9200	1.4900	6.1250	1.2250
L76 X L88	8.6950	-0.0350	-24.9350	0.2450
L61 X P8	-5.6200	-0.0050	6.5600	-0.2800
L70 X P8	13.1700	-0.7750	-5.6850	-0.5900
L77 X P8	5.5000	-0.1150	-10.9350	-2.8700
L55 X P8	-2.6700	-0.2350	13.1250	1.6250
P1 X P8	18.9650	-0.0350	-21.0000	-3.1200
L76 X P8	14.3500	-0.2450	1.7500	-0.0100
L70 X L61	-56.2200	0.2550	2.1900	0.1650
L77 X L61	52.9350	0.0950	17.0600	0.2650
L55 X L61	-1.4000	0.2900	-4.9200	-0.7750
P1 X L61	12.2900	0.0600	-13.1250	-0.1300
L76 X L61	-22.4450	0.1650	20.5600	-0.0600
L77 X L70	-3.7050	-0.3150	-14.4350	0.0450
L55 X L70	19.9950	-0.0850	-20.1250	-0.0950
P1 X L70	15.5750	0.1150	-22.7500	0.1700
L76 X L70	-23.7750	-0.1150	-6.1250	0.1500
L55 X L77	-20.8250	-0.0750	-10.9350	0.5200
P1 X L77	4.3750	-0.1650	-8.3150	-3.4400
L76 X L77	-2.2750	-0.4900	-21.8750	-0.1850
P1 X L55	-13.3850	-0.0950	11.3750	0.3000
L76 X L55	12.3800	0.2150	7.0000	0.2250
L76 X P1	-3.8200	0.2350	-9.6250	0.6200

the dominant genes helped reducing the southern corn leaf blight incidence and severity expression.

According to Griffing (1956), depending on the aim of the breeding program, the best combination should show the highest SCA estimate and at least one of the parents should record high GCA. So, with respect to features related to *B. maydis* incidence and severity, the $\hat{\sigma}_{ij}$ results showed that 9 combinations were negative for both features. Combinations L88 x L61, L88 x L70, L88 x L76, L61 x L77, L61 x P1, L70 x P1, P1 x L76 and L77 x L76 stood out, since they all showed negative SCA estimate and at least one of the parents displayed negative $\hat{\sigma}_{ij}$ values. This result showed that the parents, who were highlighted according to their $\hat{\sigma}_{ij}$ values in Table 2, were actually able to generate superior individuals when it came to *B. maydis* incidence and severity, since at least one of the parents were used in the herein presented combinations. A single combination - P8 x L77 - recorded positive $\hat{\sigma}_{ij}$ estimate. However, the two parents composing the hybrid combination had satisfactory performance; they recorded high negative $\hat{\sigma}_{ij}$ estimate to the analyzed features; this result showed that this combination presented better parental GCA than the expected, since the parents composing such combination did not record negative $\hat{\sigma}_{ij}$ estimate.

Severity is often associated with production losses (Belasque et al., 2005); thus, some studies just consider

severity at the time to estimate genotype resistance or susceptibility to diseases. This study not only assessed, but also indicated, promising hybrids based not only on disease severity, but also on its incidence. Hence, hybrids displaying superior results for disease incidence in the plant and severity in the leaf were selected and indicated according to $\hat{\sigma}_{ij}$.

It is worth emphasizing that these combinations also derived from at least one parent showing $\hat{\sigma}_{ij}$ estimate strong enough to reduce *B. maydis* incidence and severity, fact that may explain the superiority of these combinations. Therefore, it is possible predicting that the allele accumulation found in the parents composing the hybrid combinations will probably happen as a desirable genetic complementation in the hybrids used to reduce southern corn leaf blight incidence and severity rates.

Conclusions

It was not possible to highlight favorable parents to reduce the incidence and severity of southern corn leaf blight in the first harvest.

Genetic control for the characteristics related to resistance to southern corn leaf blight, in the second harvest were influenced by the additive and non-additive effects, and the non-additive effects were higher for this set of parents.

Assessments for reciprocal effect showed that there is no difference when a genotype is used as donor or recipient of pollen, since there is presence of nuclear genes effect for the characteristics related to resistance to *B. maydis*.

Hybrids that stood out in the two harvest on the resistance to southern corn leaf blight, and are thus recommended for cultivation, were L88 x L61, L88 x L70, L88 x L76, L61 x L77, L61 x P1, L70 x P1, P1 x L76 and L77 x L76.

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