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Plant breeding

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Identifying crisphead lettuce genotypes for a wider range of environments

Identificación de genotipos de lechuga crespa cultivados para un amplio rango de ambientes

Dora Enith Tobar-Tosse[1] **Willame dos Santos Candido**[1] **Lucas da Silva Santos**[1] **Renata Castoldi**[1] **Edgar Henrique Costa Silva**[1] **Leila Trevisan Braz**[1]

[1] Universidade Estadual Paulista "Julio Mezquita de Filho", Câmpus Jaboticabal, São Paulo, Brasil.

*Corresponding: Universidade Estadual Paulista "Julio Mezquita de Filho", Câmpus Jaboticabal, São Paulo, Brasil, Setor de Producão vegetal. tobar30@gmail.com

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Abstract: This work aims to select crisphead lettuce (*Lactuca sativa* L) genotypes superior in production, stability, and adaptability using a mixed model method: restricted maximum likelihood/best linear unbiased prediction. Ten genotypes were grown in different municipalities of the State of São Paulo, Brazil, and seasons of the year, resulting in twelve different environments. The experiment has a randomized complete block design with four repetitions. Genotypes comprise eight breeding lines and two commercial cultivars, Vanda and Vera. The evaluated traits include total production in g/plant, commercial production in g/plant, and numbers of leaves/plant. Analysis of joint deviance indicated that the genotypes responded differently to the environments evaluated. The crisphead lettuce breeding lines that were most productive, stable, and adapted to the twelve lettuce-growing environments, even outperforming the commercial Vanda and Vera cultivars, were lines L_8, L_2, and L_6.

Keywords: Genotype-environment interaction, genotypic values, *Lactuca sativa*, REML/BLUP, stability and adaptability

Resumen: El objetivo de este trabajo fue seleccionar genotipos superiores de lechuga crespa (*Lactuca sativa* L) en términos de producción, estabilidad y adaptabilidad, cultivados en diferentes municipios y estaciones del año en el Estado de São Paulo, Brasil, mediante la metodología de modelos mixtos: máxima probabilidad residual o restringida/mejor predicción lineal no sesgada. El diseño experimental utilizado fue el de bloques completos al azar con cuatro repeticiones y diez genotipos compuestos de ocho líneas y los cultivares comerciales Vanda y Vera, que se plantaron en doce ambientes diferentes. Los caracteres evaluados fueron producción total en g/planta, producción comercial en g/planta y número de hojas/planta. El análisis de desviación conjunta indicó que los genotipos presentaron respuestas diferentes en los diferentes ambientes evaluados. Las líneas de lechuga crespa más productivas, estables y adaptadas a los doce ambientes de cultivo de lechuga que superaron a los cultivares comerciales Vanda y Vera fueron: L_8, L_2 y L_6.

Palabras clave: estabilidad y adaptabilidad, interacción genotipo-ambiente, *Lactuca sativa*, REML/BLUP, valores genotípicos

Introduction

Lettuce, *Lactuca sativa* L. (Asteraceae), stands out as one of the most widely consumed leafy vegetables globally due to its importance as a source of vitamins and minerals, being used mainly in salads for *in natura* consumption. Crisphead lettuce is the preferred type, having a better flavor, more resistance to diseases, ease to handle and transport due to its leaf arrangement, and a longer shelf-life (Santos et al., 2009).

In Brazil, lettuce is the most economically important vegetable. The primary production region is the State of São Paulo, where it is generally cultivated intensively, in all seasons of the year, in conditions of family farming, and in small properties located in peri-urban areas or the green belts of large urban centers (Filgueira, 2008; IEA, 2015).

The diversity of environments in which lettuce is grown in Brazil favors high genotype-environment (G×E) interaction. Having identified G×E interaction as significant, appropriate analyses are needed to efficiently select highly productive, stable, and adapted breeding material (Gualberto et al., 2009). Analysis of G×E interaction alone does not provide sufficient information about the best genotypes for each environment.

Simultaneous selection of productive, stable, and adapted genotypes requires methods based on mixed model equations (REML/BLUP - restricted maximum likelihood/best linear unbiased prediction). Their application has been disseminated in the analysis of information on genotypic stability and adaptability for different vegetables such as carrot (*Daucus carota* L.) (Silva et al., 2011), bean (*Phaseolus vulgaris* L.) (Torres et al., 2015; Torres et al., 2017), strawberry (*Fragaria vasca* L.) (Costa et al., 2015), pepper (*Capsicum annuum* L.) (Pimenta et al., 2016), and recently lettuce (*Lactuca sativa* L.) (Candido et al., 2018; Silva et al., 2019). REML/BLUP orders genotypes based on their genetic values and stability, referring to the BLUP procedure under harmonic means (Resende, 2002). The lower the standard deviation of the genotypic performance between environments, the higher their harmonic mean of genotype values (HMGV); therefore, selection of the highest values of the HMGV implies selection of the traits evaluated and stability (Resende, 2007).

Adaptability refers to the relative performance of genotype values (RPGV) in all environments. In this case, the predicted genotypic values (or the original data) are expressed as a proportion of each environment's general mean, and, subsequently, the mean value of this proportion is obtained across environments. Simultaneous selection of the evaluated traits, stability, and adaptability in the context of mixed models can be performed using the harmonic mean of the relative performance of genotypic predicted value method (HMRPGV) (Resende, 2007; Silva et al., 2011).

The present work aims to identify crisphead lettuce breeding lines superior in production, stability, and genotypic adaptability in different growing environments in the State of São Paulo, Brazil, using the REML/BLUP method after five and six generations of selections. The second aim is to identify the G×E interaction in these groups of lettuce lines and cultivars.

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Materials and methods

Experimental sites

Twelve experimental trials were carried out in lettuce-producing areas of the State of São Paulo during the autumn-winter, winter, spring, and summer seasons in the municipalities of Monte Alto (MA), São Simão (SS), Aramina (A), Mogi das Cruzes (MC), Biritiba Mirim (BM), and Salesópolis (S), whose climatic conditions are described in table 1. Crisphead lettuce genotypes are composed of eight advanced lines between F_5 and F_6 generations, L_1, L_2, L_3, L_4, L_5, L_6, L_7, L_8, and the commercial cultivars Vanda and Vera.

Tabla 1. Climatic characteristics of the municipalities of the State of São Paulo, where experimental trials were set up to evaluate the production, stability and adaptability of eight lines of crisphead lettuce and the commercial cultivars Vanda and Vera.

Climatic characteristics						
Location	Latitude S	Longitude W	Climatic classification (Köeppen)	Altitude (m)	Average annual temperature (°C)	Average annual rainfall (mm)
Monte Alto	21° 15' 39"	48° 29'45"	Aw	736	21.35	1441.00
São Simão	21° 28' 45"	47° 33' 03"	Cfag	665	18.60	1411.00
Aramina	20º 05' 25"	47º 47' 09"	Aw	614	22.50	1515.00
Mogi-das-Cruzes	23° 31' 22"	46° 11'16"	Cwa	750	20.00	1400.50
Biritiba-Mirim	23° 34' 22"	46° 02' 20"	Cwa	78	19.80	1364.20
Salesópolis	23°31' 55"	45° 50' 45"	Cwa	780	19.80	1256.30

Note. Cfa: Humid tropical climate; Cwa: Humid temperate climate with dry winter and hot summer;
Aw: Tropical climate with dry winter season.
Source: Weather station of institute of Astronomy, Geophysics and Atmospheric Science of the University of São Paulo

Crops were grown in the open field: one crop in autumn winter, five in winter, one in spring, and five in summer. The experimental design for all trials was a randomized complete block with four replications, considering each trial as an environment. The cultivation cycles of each environment from transplantation to harvest are presented in table 2.

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Tabla 2. Twelve different growing environments for crisphead lettuce in the State of Sao Paulo, Brazil

Growing environmensts				
No.	Identification	Municipality	Cultivation cycles	Seasons
1	MA1	Monte Alto	06/2014-08/2014	autumn-winter
2	SS2	São Simão	07/2014-08/2014	winter
3	S3	Salesópolis	08/2014-09/2014	winter
4	BM4	Biritiba Mirin	08/2014-09/2014	winter
5	MC5	Mogi das Cruzes	08/2014-09/2014	winter
6	A6	Aramina	08/2014-09/2014	winter
7	SS7	São Simão	10/2014-11/2014	spring
8	MA8	Monte Alto	12/2014-01/2015	summer
9	BM9	Biritiba Mirin	01/2015-02/2015	summer
10	MC10	Mogi das Cruzes	01/2015-02/2015	summer
11	A11	Aramina	01/2015-02/2015	summer
12	S12	Salesópolis	02/2015-03/2015	summer

Source: Elaborated by the authors

Plant genetic material

The advanced crisphead lettuce lines were obtained using the pedigree method of the crisphead lettuce genetic improvement program, Paulista State University, Brazil (Tobar-Tosse, 2015). They come from the initial crosses between the JAB 4-13-7 line (male parent, possessor of *Bremia lactucae* resistance factor R18) and commercial cultivars: Argelis (A) (possessor of *B. lactucae* resistance factor R38), Vanda (V), Veneranda (Vn), and Solaris (S) (female parents) as presented in table 3.

Tabla 3. Advanced crisphead lettuce lines possessing *Bremia lactucae* resistance factors R18 and R38

Identification	Generation	Origin
L_1	F_5	V X JAB 4-13-7
L_2	F_5	V X JAB 4-13-7
L_3	F_5	Vn X JAB 4-13-7
L_4	F_5	S X JAB 4-13-7
L_5	F_6	A X JAB 4-13-7
L_6	F_6	A X JAB 4-13-7
L_7	F_6	A X JAB 4-13-7
L_8	F_6	A X JAB 4-13-7

Note. Advanced lines of crisphead lettuce obtained from crosses between commercial cultivars Vanda (V), Veneranda (Vn), Solaris (S), and Argelis (A) (resistance factor R38, female parent) with line JAB 4-13-7 (resistance factor R18, male parent).
Source: Elaborated by the authors

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These crisphead lettuce lines have the resistance factors R18 and R38 to the downy mildew races (*Bremia lactucae*) SPBl:01, SPBl:02, SPBl:03, SPBl:04, SPBl:05, SPBl:06, SPBl:07, SPBl: 09, SPBl:10 SPBl:11, and SPBl:12 that arose in the State of São Paulo (Castoldi et al. 2014; Tobar-Tosse et al., 2017). They are characterized by light-green leaves of high frizziness, large plant size, absence of lateral shoots, tolerance to early flowering, and tipburn in the summer season.

Field experiment descriptions

Each experimental plot consisted of four rows 1.75 m long with a distance between plants of 0.25 m in a triangular arrangement, totaling 28 plants per plot and evaluating the six central plants. Cultivation practices were followed according to the needs of the crop and the horticulturist recommended management practices.

Data collection

When lettuce reached market maturity, approximately 35 (spring-summer) and 45 days after transplanting (autumn-winter), the following characteristics were assessed:

i) Total production in g/plant (TP): The average of the fresh mass of the aerial part of six plants (without removing the outer leaves)

ii) Commercial production in g/plant (CP): The average of the fresh mass of the aerial part of six plants, after removing the outer leaves and remaining stem of the plant

iii) Number of leaves/plant (NL): The number of leaves counted, considering those longer than 1.5 cm

REML/BLUP analyses

Stability and adaptability were evaluated using the Selegen program (Resende, 2016), which employs the REML/BLUP methodology, considering statistical model 51 for the genetic evaluation by the highest values of the HMGV. The significance of the model's effects was estimated by deviance analysis, and the genetic parameters according to Resende (2007).

Model 51 considers the randomized complete block experimental design. In the model, the ten genotypes of crisphead lettuce in twelve growing environments were included (Equation 1).

$$Y = Xr + Zg + Wp + Ti + e \qquad (1)$$

where Y = data vector; r = vector of repetition effects (fixed) in addition to the general mean; g = vector of genotypic effects (random); p = vector of plot effects (random); i = vector of G×E interaction effects (random); e = vector of the error or residuals (random). Capital letters represent the incidence matrices for the purposes above.

The values of HMGV for stability, RPGV for adaptability, and HMPRGV for productivity, stability, and adaptability simultaneously, for all genotypes, were obtained according to Resende (2007) (Equations 2, 3, and 4):

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$$\text{HMGV} = \frac{l}{\sum_{i=1}^{l} \frac{1}{GV_j}} \qquad (2)$$

$$\text{RPGV} = \frac{1}{l}\left(\frac{\sum GV_j}{M_j}\right) \qquad (3)$$

$$\text{MHPRVG} = \frac{l}{\sum_{l=1}^{l} \frac{1}{RPGV_j}} \qquad (4)$$

where l = number of environments; GV = genotypic value; j = genotypes.

Results and discussion

Components of variance and genetic parameters

The genotype selection precision parameter (Acgen) defined by Resende and Duarte (2007) varied from high (0.71) for CP to very high (0.95) for NL, indicating a high correlation between the predicted and actual genotypic values. These results are like those obtained by Silva et al. (2019) for an Acgen of 0.98 for NL and 0.80 for yield in lettuce cultivars under different environmental conditions in Mossoró, RN, Brazil (table 4).

Table 4. Estimation of variance and genetic parameters for total production (TP), commercial production (CP), and number of leaves/plant (NL) in crisphead lettuce

Parameter	TP (g/plant)	CP (g/plant)	NL (number of leaves/plant)
V_g	131.74	81.22	2.15
V_{plot}	619.24	435.68	1.46
V_{g*e}	873.77	714.66	2.00
V_e	3143.29	2603.00	12.00
V_{ph}	4768.07	3834.00	17.51
h^2_g	0.03	0.02	0.12
c^2_{plot}	0.13	0.11	0.08
c^2_{g*a}	0.18	0.19	0.11
h^2_{mg}	0.58	0.51	0.90
Acgen	0.76	0.71	0.95
r_{gloc}	0.13	0.10	0.52
CVgi%	4.21	3.70	6.15
CVe%	12.41	12.11	7.78

Note. V_g: genotypic variance; V_{plot}: environmental variance between plots; V_{g*e}: variance of the G×E interaction; V_e: residual variance; V_{ph}: individual phenotypic variance; h^2_g: individual heritability in the broad sense, that is, of the total genotypic effects; c^2_{plot}: coefficient for determining the plot effects; c^2_{g*e}: coefficients of determination of the G×E interaction effects; h^2_{mg}: heritability of the genotype mean, assuming complete survival; Acgen: precision of genotype selection, assuming complete survival; r_{gloc}: genotypic correlation between performance

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in various environments; CVgi%: coefficient of genotypic variation; CVe%: coefficient of environmental variation.
Source: Elaborated by the authors.

The effect of genotypes was significant ($P < 0.05$) for TP, CP, and NL, indicating differential performance among lettuce genotypes (table 5). The production observed in this research was higher than the one observed by Candido et al. (2018) for the same genotypes but in seven different cropping systems during two seasons in the municipality of Jaboticabal, SP, Brazil.

Tabla 5. Global analysis of joint deviance (ANADEV)

Effect	**TP** (g/plant)		**CP** (g/plant)		**NL** (number of leaves/plant)	
	Deviance	LRT	Deviance	LRT	Deviance	LRT
Complete model	25502.9		24961.84		10100.47	
Genotype	25992.1	489.2**	25418.72	456.88**	10378.28	277.81
Plot	25656.0	153.1**	25084.41	122.57**	10177.14	76.67**
Genotype*environment	25793.0	290.1**	25255.19	293.35*	10253.69	153.22**
General mean	272.53		243.52		23.83	

Note. ** and *: significance at 1 and 5 % probability, respectively, by mixed models' likelihood ratio test (LRT).
Source: Elaborated by the authors.

The heritability of the genotype mean, assuming complete survival (h^2_{mg}), was estimated when the means of the blocks were used as genotype evaluation or selection criteria. The h^2_{mg} values found in this work ranged from medium for CP (0.51) to high for NL (0.90); the greater this value, the better the reliability in selecting genotypes based on genotype values. These results agree with the ones found by Silva et al. (2019) in crisphead, American, mimosa, and smooth lettuce genotypes for NL with a high h^2_{mg} value of 0.96 (table 4).

On estimating the individual heritability in the broad sense (h^2_g), considering the total genotypic effects, low values were found for the production characteristics evaluated, varying from 0.02 for CP to 0.12 for NL, as shown in table 3. Similarly, Candido et al. (2018) on evaluating the identical genotypes of crisphead lettuce in the municipality of Jaboticabal, SP, Brazil, in seven different cropping systems, found low h^2_g values for TP (0.001 + 0.004), CP (0.001 + 0.004), and NL (0.132), which is consistent with the polygenic nature and therefore quantitative inheritance of these characteristics.

The phenotypic value of a trait generated in field trials is composed of the genetic effect, environment effect, and interaction effect of a genotype in a specific environment. Thus, the sum of the genotypic variance (V_g), the environmental variance between plots (V_p), the variance of the G×E interaction (V_{g*e}), and residual variance (V_e) results in individual phenotypic variance (V_{ph}).

This study confirmed that the environmental component contributed the most to the expression of productive characteristics (table 4), as verified by Candido et al. (2018) in identical genotypes and Silva et al. (2019) in different types of lettuce for the yield characteristic Mg/ha, except in NL, where the genetic component made the biggest contribution to phenotypic variance.

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The G×E interaction effect in TP and CP was more significant than the genotypic effect, while for NL, the genotypic effect was greater than the G×E interaction (tables 4 and 5). These results agree with those obtained by Candido et al. (2018) and Silva et al. (2019). The significant effect of the G×E interaction indicates a differential behavior of the lettuce genotypes across the different growing environments, commonly found in the evaluation of lines and cultivars adapted to several geographical regions in Brazil (Blind & Silva, 2015; Candido et al., 2018; Gualberto et al., 2009; Luz et al., 2009; Silva et al., 2019).

The c^2_{plot} component quantifies how much of the phenotypic variance is explained by the environmental variance component between plots, and the c^2_{g*e} quantifies how much of the phenotypic variance is explained by the variance component of the G×E interaction. The environmental variance between plots and the G×E interaction have more effect on TP and CP, explaining 12.9 % and 11.3 % for c^2_{plot} and 18.3 % and 18.6 % for c^2_{g*e} of the phenotypic variance, respectively, and the c^2_{plot} and c^2_{g*e} for NL was the lowest, 8.3 % and 11.4 %, respectively (table 4).

The mean genotypic correlation (r_{gloc}) of the genotypes' performance in the environments shows how constant the order of the genotypes is and, therefore, the magnitude of the complex interaction. In this parameter, the r_{gloc} estimates were low for TP (0.131) and CP (0.102) and moderate for NL (0.517). These correlations corroborate the previously mentioned results of Ve for TP, CP, and NL, indicating that G×E interaction is vital for TP and CP but not for NL.

Genotypic values

According to the classification order by genotypic value of the joint analysis presented in tables 6 and 7, most breeding lines outperformed the commercial Vanda and Vera cultivars in TP and CP. Conversely, L_5 ranked together for TP with the commercial cultivars among the three worst-performing genotypes. Meanwhile, the lines that outperformed the commercial cultivars in NL were L_7, L8, L_6, L_4, and L_2; the other lines barely surpassed Vera and were classified among the five least productive genotypes.

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Table 6. Genotypic values (GV) for total production/plant (TP) and their rankings in parenthesis (order of sorting by the highest genotypic values) of ten genotypes of crisphead lettuce, including eight advanced lines and two commercial cultivars in twelve growing environments, in the State of São Paulo, Brazil.

Genotypes	Total production (g/plant)												
	MA1[1]	SS2	S3	BM4	MC5	A6	SS7	MA8	BM9	MC10	A11	S12	Joint analysis
	Genotypic value (GV)[2]												
L_1	479.70(8)	484.85(7)	281.96(3)	405.14(4)	387.53(4)	245.48(8)	193.82(10)	215.58(4)	188.25(3)	170.82(6)	79.92(9)	91.37(8)	268.70(7)
L_2	589.11(1)	525.23(1)	278.32(4)	379.19(8)	377.31(5)	246.15(7)	251.89(3)	203.20(9)	184.21(4)	172.38(4)	100.27(4)	111.26(2)	284.88(1)
L_3	564.20(3)	513.53(2)	290.99(2)	410.27(3)	370.89(7)	264.08(4)	261.27(2)	204.77(8)	138.12(10)	166.14(8)	91.56(8)	87.29(9)	280.26(4)
L_4	565.96(2)	498.45(5)	245.68(6)	397.03(5)	368.21(8)	254.05(5)	194.20(9)	212.69(5)	203.14(1)	170.85(5)	100.74(3)	120.87(1)	277.66(6)
L_5	438.82(10)	464.09(8)	220.70(9)	356.57(9)	372.89(6)	248.16(6)	227.05(6)	216.17(3)	179.35(5)	167.60(7)	76.73(10)	86.93(10)	254.59(9)
L_6	533.18(5)	490.19(6)	235.82(8)	389.39(6)	432.73(1)	294.30(1)	226.16(7)	230.81(2)	158.72(7)	165.65(9)	96.24(5)	106.01(4)	279.93(5)
L_7	542.46(4)	500.29(4)	263.19(5)	433.28(1)	410.25(2)	275.95(3)	273.04(1)	195.38(10)	155.87(8)	157.85(10)	94.01(6)	97.56(6)	283.26(3)
L_8	527.05(7)	510.13(3)	297.17(1)	426.87(2)	406.91(3)	285.97(2)	237.59(5)	210.55(7)	139.87(9)	175.31(3)	100.77(2)	92.99(7)	284.27(2)
Vanda	528.55(6)	405.08(10)	242.70(7)	389.32(7)	325.20(9)	237.33(9)	249.21(4)	211.87(6)	178.58(6)	175.53(2)	109.57(1)	109.57(3)	263.54(8)
Vera	450.51(9)	426.56(9)	219.88(10)	336.90(10)	293.97(10)	233.69(10)	211.81(8)	234.39(1)	199.72(2)	179.23(1)	92.48(7)	98.97(5)	248.17(10)
General mean	521.95	481.84	257.64	392.39	374.59	258.52	232.60	213.54	172.58	170.14	94.23	100.28	

Note. [1]: Growing environments: MA1-Monte Alto 1, 06/2014-08/2014 (autumn-winter); SS2 - São Simão 2, 07/2014-08/2014 (winter); S3-Salesópolis 3, 08/2014-09/2014 (winter); BM4-Biritiba Mirin, 08/2014-09/2014 (winter); MC5-Mogi das Cruzes 5, 08/2014-09/2014 (winter); A6-Aramina 6, 08/2014-09/2014 (winter); SS7-São Simão 7, 10/2014-11/2014 (spring); MA8-Monte Alto 8, 12/2014-01/2015 (summer); Biritiba Mirin-9, 01/2015-02/2015 (summer); MC10-Mogi das Cruzes 10, 01/2015-02/2015 (summer); A11-Aramina 11, 01/2015-02/2015 (summer); S12-Salesópolis 12, 02/2015-03/2015 (summer). [2]: Genotypic values = ((uj+g+gem): General mean plus the genotype effect and the mean interaction for total production in g/plant.
Source: Elaborated by the authors.

Table 7. Genotypic values (GV) for commercial production/plant (CP), and their rankings in parenthesis (order of sorting by the highest genotypic values) of ten genotypes of crisphead lettuce, including eight advanced lines and two commercial cultivars in twelve growing environments, in the State of São Paulo, Brazil.

Genotypes	Commercial production (g/plant)												
	MA1[1]	SS2	S3	BM4	MC5	A6	SS7	MA8	BM9	MC10	A11	S12	Joint analysis
	Genotypic value (GV)[2]												
L_1	434.22(8)[3]	446.93(7)	251.38(3)	359.99(4)	345.94(5)	220.12(7)	161.06(10)	161.06(10)	152.04(5)	144.20(3)	70.68(10)	76.16(8)	237.53(7)
L_2	528.69(1)	484.61(1)	239.63(4)	339.36(8)	336.96(6)	218.43(8)	207.97(4)	207.97(4)	153.84(4)	142.26(5)	88.96(4)	94.59(2)	251.12(4)
L_3	507.80(3)	477.28(2)	256.30(2)	370.15(3)	333.65(7)	237.42(4)	216.38(2)	216.38(2)	108.12(10)	131.35(10)	81.36(8)	71.65(10)	247.41(5)
L_4	512.06(2)	458.29(5)	219.30(6)	357.09(6)	331.15(8)	230.43(6)	166.46(9)	166.46(9)	170.13(1)	138.61(7)	91.38(3)	103.39(1)	247.10(6)
L_5	413.61(10)	441.39(8)	204.38(9)	334.11(9)	349.04(4)	233.94(5)	205.99(5)	205.99(5)	156.37(3)	144.20(4)	71.01(9)	75.34(9)	235.31(8)
L_6	488.75(6)	454.30(6)	206.37(8)	358.05(5)	401.47(1)	271.98(1)	193.76(7)	193.76(7)	131.83(7)	134.23(8)	87.16(5)	91.04(4)	251.85(3)
L_7	497.55(4)	464.94(3)	236.82(5)	394.98(1)	374.09(2)	255.51(3)	236.24(1)	236.24(1)	128.42(8)	131.62(9)	85.52(6)	81.52(6)	254.76(2)
L_8	491.34(5)	459.52(4)	269.90(1)	392.65(2)	367.34(3)	262.57(2)	205.96(6)	205.96(6)	114.88(9)	144.53(2)	91.96(2)	78.02(7)	255.15(1)
Vanda	470.02(7)	366.80(10)	210.04(7)	345.08(7)	295.20(9)	212.30(10)	209.01(3)	209.01(3)	143.32(6)	141.92(6)	99.47(1)	91.67(3)	230.82(9)
Vera	414.84(9)	396.22(9)	197.92(10)	310.38(10)	268.70(10)	216.63(9)	184.88(8)	184.88(8)	166.46(2)	153.40(1)	84.99(7)	87. 98(5)	224.09(10)
General mean	475.89	445.03	229.2	356.18	340.35	235.93	198.77	198.77	142.54	140.71	85.25	85.14	

Note. [1]: Growing environments: MA1-Monte Alto 1, 06/2014-08/2014 (autumn-winter); SS2 - São Simão 2, 07/2014-08/2014 (winter); S3-Salesópolis 3, 08/2014-09/2014 (winter); BM4-Biritiba Mirin, 08/2014-09/2014 (winter); MC5-Mogi das Cruzes 5, 08/2014-09/2014 (winter); A6-Aramina 6, 08/2014-09/2014 (winter); SS7-São Simão 7, 10/2014-11/2014 (spring); MA8-Monte Alto 8, 12/2014-01/2015 (summer); Biritiba Mirin-9, 01/2015-02/2015 (summer); MC10-Mogi das Cruzes 10, 01/2015-02/2015 (summer); A11-Aramina 11, 01/2015-02/2015 (summer); S12-Salesópolis 12, 02/2015-03/2015 (summer). [2]: Genotypic values = ((uj+g+gem): General mean plus the genotype effect and the mean interaction for commercial production in g/plant.
Source: Elaborated by the authors

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In the joint analysis of the twelve environments, the three genotypes with the highest genotypic value were lines L_2, L_8, and L_7 for TP; L_8, L_7, and L_6 for CP; lines L_7, L_8, and L_6 and for NL. On verifying these lines' performance across the environments, and according to c^2_{gxa} and r_{gloc} values, we observed the predominance of the complex component of G×E for TP and CP and a medium genotypic correlation for NL. Thus, the order of the genotypes across the environments for TP, CP, and NL varied moderately (table 8).

Table 8. Genotypic values (GV) for number of leaves/plant (NL) and their rankings in parenthesis (order of sorting by the highest genotypic values) of ten genotypes of crisphead lettuce, including eight advanced lines and two commercial cultivars in twelve growing environments, in the State of São Paulo, Brazil.

Genotypes	Number of leaves												
	MA1[1]	SS2	S3	BM4	MC5	A6	SS7	MA8	BM9	MC10	A11	S12	Joint analysis
	Genotypic value (GV)[2]												
L_1	27.27(9)	25.37(8)	28.56(5)	24.62(7)	24.19(6)	20.86(5)	25.75(9)	21.15(8)	24.30(7)	21.60(8)	11.51(9)	19.32(8)	22.87(8)
L_2	28.64(6)	26.38(5)	29.46(4)	24.29(8)	24.07(7)	20.59(6)	28.93(3)	21.95(7)	24.87(5)	22.44(4)	12.81(7)	23.63(1)	24.01(5)
L_3	29.47(5)	25.68(7)	28.22(6)	24.02(9)	23.27(9)	20.54(8)	26.16(8)	20.53(9)	21.23(10)	21.14(9)	13.83(3)	18.90(9)	22.75(9)
L_4	28.57(7)	26.87(4)	27.89(8)	25.38(4)	24.68(5)	20.56(7)	26.64(7)	22.50(5)	27.47(1)	22.12(6)	13.65(4)	22.37(3)	24.06(4)
L_5	27.77(8)	26.20(6)	28.08(7)	24.91(5)	25.08(4)	21.55(4)	28.88(4)	23.00(3)	25.86(3)	21.95(7)	12.67(8)	20.74(6)	23.81(7)
L_6	31.47(2)	27.93(3)	27.74(9)	26.22(3)	25.96(2)	22.16(3)	27.57(6)	22.56(4)	22.59(8)	22.53(3)	13.08(5)	21.13(5)	24.25(3)
L_7	31.98(1)	30.59(1)	31.36(2)	29.41(1)	27.10(1)	23.71(1)	32.33(1)	23.77(1)	25.65(4)	24.54(1)	14.19(1)	22.62(2)	26.44(1)
L_8	31.37(3)	29.94(2)	32.39(1)	28.33(2)	25.70(3)	22.71(2)	28.34(5)	23.33(2)	22.30(9)	23.42(2)	14.04(2)	21.49(4)	25.28(2)
Vanda	29.80(4)	25.15(9)	29.90(3)	24.84(6)	23.61(8)	20.22(9)	29.57(2)	22.23(6)	26.02(2)	22.29(5)	12.91(6)	20.37(7)	23.91(6)
Vera	24.74(10)	24.01(10)	23.50(10)	20.84(10	20.12(10)	17.72(10)	24.55(10)	19.81(10)	24.83(6)	20.36(10)	11.38(10)	18.72(10)	20.88(10)
General mean	29.11	26.81	28.71	25.29	24.38	21.06	27.87	22.08	24.51	22.24	13.01	20.93	

Note. [1]: Growing environments: MA1-Monte Alto 1, 06/2014-08/2014 (autumn-winter); SS2 - São Simão 2, 07/2014-08/2014 (winter); S3-Salesópolis 3, 08/2014-09/2014 (winter); BM4-Biritiba Mirin, 08/2014-09/2014 (winter); MC5-Mogi das Cruzes 5, 08/2014-09/2014 (winter); A6-Aramina 6, 08/2014-09/2014 (winter); SS7-São Simão 7, 10/2014-11/2014 (spring); MA8-Monte Alto 8, 12/2014-01/2015 (summer); Biritiba Mirin-9, 01/2015-02/2015 (summer); MC10-Mogi das Cruzes 10, 01/2015-02/2015 (summer); A11-Aramina 11, 01/2015-02/2015 (summer); S12-Salesópolis 12, 02/2015-03/2015 (summer). 2: Genotypic values = ((uj+g+gem): General mean plus the genotype effect and the mean interaction for the number of leaves per plant.
Source: Elaborated by the authors.

On comparing the values of the general means of the environments in autumn and winter seasons with the environments in spring and summer seasons, we noted that the lettuce crop is more adapted to autumn and winter conditions (environments: MA1, SS2, S3, BM4, MC5, and A6) (tables 6 and 7). The lines L_1, L_2, L_3, L_4, L_5, L_6, L_7, and L_8 have resistance factors R18 and R38 to *B. lactucae* races and show promising results for cultivation during winter where the appearance of lettuce downy mildew disease is frequent. In particular, the L_8 line stands out among the three most productive in the set of twelve environments and, specifically, in most of the environments with the autumn-winter season.

Some genotypes showed specific adaptability to the environment in which they were grown. For example, the L_2 line for TP with the best genotypic performance in the MA1 and SS2 environments was the worst-performing in MA8. For CP, the L_7 line with the best genotypic performance in the S3 environment ranked among the worst performers in the BM9 environment. The cultivar Vera performed better in the MA8, BM9, and MC10 environments, having a higher resistance to early flowering in summer cultivation (Feltrim et al., 2009). Perhaps, cultivar Vera has some tolerance to warmer temperatures that remains to be investigated.

The three best genotypes prominent in the joint analysis across environments had excellent performance in specific environments. It was found that the L_2 line stood out among the three best-performing genotypes in at least four environments (MA1, SS2, SS7, and S12) for TP; L_8 stood out among the top three genotypes in six environments (S3, BM4, MC5, A6, MC10, and A11) for TP and CP and the SS2 environment only for TP. The L_7 line stood out in four environments (BM4, MC5, A6, and SS7) among the three superior genotypes, and in the SS2 and MA8 environments only for CP; and the L_6 line in at least two environments (MC5 and A6) for CP (tables 6 and 7). The L_7 and L_8 genotypes were superior genotypes in the twelve environments for NL, except the BM9 environment for the L_7 line and the SS7, BM9, and S12 environments for the L_8 line. The L_6 line behaved similarly in half of the environments evaluated (table 8).

The superiority of the commercial cultivars compared to the lines was generally noticeable in the environments with the summer season (MA8, BM9, MC10, A11, and S12). Breeding line L_8 stood out among the three best genotypes along with one or both commercial cultivars in environments A11 and MC10 for TP and CP. Meanwhile, breeding line L_4, although not outstanding in the joint analysis, was the most productive genotype for TP and CP in the S12 environment and TP, CP, and NL in the BM9 environment. Breeding lines L_8 and L_4 are possibly more tolerant to early flowering than the others.

The lettuce crop is better adapted to winter months and shows differential responses to different cultivation environments (cultivation systems, municipalities, seasons) (Brzezinski et al., 2017; Candido et al., 2018; Feltrim et al., 2009; Gualberto et al., 2009; Queiroz et al., 2014; Sediyama et al., 2009; Silva et al., 2019). The lack of adaptation of lettuce to conditions of high temperature and higher number of light hours may accelerate the reproductive phase and, therefore, the early elongation of the flower stem. This phenomenon is also known as early bolting and makes lettuce unfit for consumption due to the production of milky latex that gives the leaves a bitter taste (Luz et al., 2009).

However, the cultivation of genotypes in a wide range of sites or conditions (environments) is of interest to seed producers of lettuce and other vegetables. It would increase their profitability by targeting several environments for cultivar release. Identifying productive lettuce genotypes with the highest stability and adaptability in the twelve environments evaluated would attenuate the G×E interaction (Torres et al., 2017). In the context of mixed models, the HMRPGV-BLUP technique allows incorporating stability, adaptability, and the mean value of the characteristics of interest into a single genotypic data model (Resende, 2002) that can be used for selection (table 9).

Table 9. Harmonic mean of genotypic values (HMGV), relative performance of genotypic values (RPGV), RPGV*general mean (GM), harmonic mean of the relative performance of genotype values (HMRPGV) and HMRPGV*general mean (GM) for total production, commercial production, and number of leaves/plant

Genotypes	Total production (g/plant)				
	HMGV	**RPVG**	**RPGV*GM**[1]	**HMRPVG**	**HMRPGV*GM**
L_1	195.96(9)[2]	0.9778	266.47(8)	0.9706	264.51(8)
L_2	215.72(1)	10.428	284.18(1)	10.393	283.24(1)
L_3	198.60(8)	10.029	273.31(6)	0.9935	270.75(6)
L_4	214.90(2)	10.280	280.17(3)	10.193	277.78(3)
L_5	188.71(10)	0.9349	254.78(10)	0.9293	253.25(10)
L_6	209.25(4)	10.221	278.54(4)	10.170	277.16(4)
L_7	205.37(6)	10.213	278.34(5)	10.152	276.68(5)
L_8	206.86(5)	10.289	280.41(2)	10.207	278.16(2)
Vanda	211.94(3)	0.9966	271.60(7)	0.9885	269.39(7)
Vera	199.16(7)	0.9447	257.46(9)	0.9331	254.30(9)
	Commercial production (g/plant)				
L_1	168.90(9)	0.9669	235.45(9)	0.9587	233.46(9)
L_2	186.38(2)	10.297	250.76(2)	10.261	249.86(1)
L_3	168.44(10)	0.9840	239.62(6)	0.9725	236.82(6)
L_4	187.74(1)	10.263	249.93(4)	10.170	247.65(5)
L_5	170.41(8)	0.9685	235.85(8)	0.9618	234.22(8)
L_6	182.85(3)	10.264	249.95(3)	10.201	248.41(3)
L_7	179.20(6)	10.257	249.77(5)	10.187	248.07(4)
L_8	180.13(5)	10.317	251.24(1)	10.223	248.95(2)
Vanda	182.42(4)	0.9802	238.69(7)	0.9718	236.65(7)
Vera	177.91(7)	0.9606	233.93(10)	0.9481	230.88(10)
	Number of leaves/plant				
L_1	21.69(9)	0.9572	22.81(8)	0.9560	22.78(8)
L_2	22.93(5)	10.074	24.01(5)	10.058	23.97(5)
L_3	21.89(8)	0.9570	22.81(9)	0.9546	22.75(9)
L_4	23.16(3)	10.130	24.14(4)	10.111	24.10(4)
L_5	22.83(6)	10.026	23.89(6)	10.016	23.87(6)
L_6	23.15(4)	10.170	24.24(3)	10.152	24.20(3)
L_7	25.19(1)	11.075	26.40(1)	11.065	26.37(1)
L_8	24.10(2)	10.598	25.26(2)	10.566	25.18(2)
Vanda	22.75(7)	10.009	23.85(7)	0.9994	23.82(7)
Vera	19.98(10)	0.8776	20.92(10)	0.8747	20.85(10)

Note. [1]: General mean; [2:] Order of sorting by the highest values of HMGV, RPGV*GM, and HMRPGV*GM.
Source: Elaborated by the authors.

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Stability of genetic values (MHVG)

HMGV is a parameter that allows selection based on production and stability. According to this parameter, the L_2, L_4, and Vanda genotypes stood out for TP; lines L_4, L_2, and L_6 were higher for CP; and lines L_7, L_8 and L_4 stood out for NL.

Adaptability of genetic values (RPGV)

Adaptability is the ability of the genotype to respond positively to the best environment (Silva et al., 2019). RPGV is used to identify this characteristic, which capitalizes the response of each genotype to the best environments. The results were similar to HMGV; thus, for TP, the best genotypes were lines L_2, L_8, and L_4; for CP, L_8, L_2 and L_6, L6; and for NL, L_7, L_8, and L_6.

Stability and adaptability of genetic values (HMRPGV)

The HMRPGV method, based on the genotypic values predicted by mixed models, groups together production, stability, and adaptability in a single statistic, facilitating the selection of superior genotypes uniquely (Resende, 2007). The HMRPGV*MG provided the genotypic value of each genotype penalized for instability and capitalized for adaptability in the unit of measurement of the characteristic concerned. Most of the lines outperformed the commercial cultivars, except lines L_5 and L_1 for PT and PC and L_3 and L_1 for NL (table 9).

For TP, the L_2, L_8, and L_4 lines with the best performance responded with mean values of 1.0393, 1.0207, and 1.0193 times, respectively, to the mean of the environment where they were cultivated. For CP, the L_2, L_8, and L_6 lines with the best performance responded with a mean value of 1.0261, 1.0223, and 1.0201 times, respectively, and for NL, the L_7, L_8, and L_6 lines were superior, responding 1.1065, 1.0566, and 1.0152 times, respectively, to the mean of culture environments. Lines L_6 and L_8 were also reported by Candido et al. (2018) as the most productive, stable, adapted, and superior to commercial cultivars in eight different growing environments in the municipality of Jaboticabal State of São Paulo, Brazil.

REML/BLUP can be useful when selecting yield-related traits (CP, TP, and NL) but remains to be identified if the model can be helpful when selecting other traits against lettuce diseases and pests targeted by breeding programs.

Conclusions

According to the discrimination of genotypes using the REML/BLUP mixed model methodology, crisphead lettuce breeding lines L_2, L_8 and L_4 were the most productive, stable, and adapted for total production, L_2, L_8, and L_6 for commercial production and L_7, L_8, and L_6 for the number of leaves. The lettuce lines mentioned above outperformed Vanda and Vera commercial cultivars regarding these characteristics in lettuce-growing environments in Sao Paulo, Brazil.

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Disclaimers

All authors made significant contributions to the document and agreedwith its publication. They state that there are no conflicts of interest in this study.

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