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Relationship between the agronomic and anatomical characteristics of the leaf with a view to indirect selection in maize plants[1]

Relação entre caracteres agronômicos e anatômicos da folha visando seleção indireta de plantas de milho

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ABSTRACT - In crops such as maize, the leaf is directly related to dry-matter accumulation in the grain, and directly affects plant yield. The aim of this study was to verify the existence of a correlation between the agronomic and anatomical characteristics of the maize leaf, as well as to verify the effects of these characteristics on grain production using path analysis. The agronomic characteristics used in the analysis were plant height, height of ear insertion, relative position of the ear, lodging, plant breakage and grain yield. The following anatomical characteristics were evaluated: total leaf area, thickness of the bulliform cells, thickness of the adaxial and abaxial epidermis, thickness of the mesophyll, area of the xylem, phloem and sclerenchyma, and mean area of the vascular bundles. In analysing the genotypic correlation, associations were seen at 1% significance between mesophyll thickness and plant height, mesophyll thickness and height of ear insertion, and mesophyll thickness and plant breakage, indicating the possibility of indirect selection for these agronomic characteristics. From the path analysis, it was found that the agronomic characteristics of lodging and breakage, and the anatomical characteristics of thickness of the adaxial epidermis, area of the xylem and area of the sclerenchyma had the greatest direct effect on grain yield, indicating the additional possibility of indirect selection for yield during the earliest stages of the plant. These results can afford faster selection of superior genotypes within the various breeding programs of the species.

Key words: Correlation. Association. Plant breeding. *Zea mays* L.

RESUMO – Em culturas como o milho, a folha está diretamente relacionada ao acúmulo de matéria seca nos grãos, interferindo assim diretamente na produção da planta. Objetivou-se no presente trabalho verificar a existência de correlação entre caracteres agronômicos e anatômicos da folha em milho, bem como verificar os efeitos desses caracteres na produção de grãos pela análise de trilhas. Os caracteres agronômicos utilizados para análise foram: altura da planta, altura de inserção da espiga, posição relativa da espiga, acamamento, quebramento de planta e produtividade de grãos. Os caracteres anatômicos avaliados foram: área total da folha, espessura das células buliformes, espessura da epiderme adaxial, espessura da epiderme abaxial, espessura do mesofilo, área do xilema, área do floema, área do esclerênquima e área média dos feixes vasculares. Na análise da correlação genotípica foram observadas associações a 1% de significância entre os caracteres espessura do mesofilo e altura de plantas, espessura do mesofilo e altura de inserção da espiga, e espessura do mesofilo e quebramento de planta, indicando a possibilidade de seleção indireta para tais caracteres agronômicos. Na análise de trilha observou-se que os caracteres agronômicos: acamamento e quebramento, e anatômicos: espessura da epiderme adaxial, área do xilema e área do esclerênquima foram os que apresentaram maior efeito direto sobre a produção de grãos em milho, indicando a possibilidade de seleção indireta também para o rendimento nos estágios mais precoces da planta. Tais resultados podem proporcionar maior rapidez na seleção de genótipos superiores dentro dos diferentes programas de melhoramento da espécie.

Palavras-chave: Correlação. Associação. Melhoramento de plantas. *Zea mays* L.

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INTRODUCTION

The maize leaf is directly associated with yield, since it is responsible for the metabolic activity of carbon and nitrogen that results in the accumulation of dry matter in the grain through specific anatomical structures that are related to the photosynthetic capacity of the plant (WANG *et al*., 2016).

Several breeding programs have invested in a study of the association between characteristics in order to maximise efficiency in selecting superior individuals through the indirect selection of correlated traits. These studies can also provide for the simultaneous selection of various characteristics, and for the selection of characteristics with low heritability and with problems of measurement due to the need for specific environments or the extremely long waiting time necessary for evaluation, such as characteristics that are expressed only at the end of the crop cycle. (FISCHER; REBETZKE, 2018).

Most studies of the association between the anatomical and agronomic characteristics of a plant are linked to tolerance to pests and diseases (GALINDO-CASTAÑEDA *et al*., 2019), and plant adaptation to adverse environmental conditions (WU *et al*., 2020).

Among the methods of multivariate analysis that aim to study the relationship between different characteristics, path analysis is widely used to estimate the direct and indirect effects of traits on a basic variable, estimates of which are obtained through regression equations, where the basic variables have previously been standardised (CRUZ *et al*., 2012).

Although correlation is an intrinsic feature of two characteristics in any given experimental situation, in path analysis, the breakdown depends on the set of characteristics under study, which are usually evaluated based on prior knowledge of the researcher regarding their importance and possible interrelationships (CRUZ *et al*., 2012).

The aim of this study, therefore, was to verify the existence of a correlation between the agronomic and anatomical characteristics of the maize leaf with a view to indirect selection, as well as check the effect of characteristics related to yield, using linear genetic correlation and path analysis.

MATERIAL AND METHODS

Evaluation of the agronomic characteristics

The study was carried out in the field during the 2009/2010 harvest and during the off-season harvest in 2010 in the district of Jaboticabal in the state of São Paulo (21º15'17" S, 48º 19' 20" W, altitude 605 m), and during the 2009/2010 harvest in Campo Alegre de Goiás in the state of Goiás (17º37'59" S, 47º46'42" W, altitude 877 m). Each combination of location and sowing time was considered a separate environment, resulting in three environments.

Thirteen synthetic maize populations were used, provided by the School of Agricultural and Veterinary Sciences of the State University of São Paulo (UNESP). The experimental design was of randomised blocks, with three replications and plots of four rows of five metres, with the two central rows considered the working plot. The spacing was 0.20 m between plants and 0.90 m between rows, corresponding to a population of approximately 50 plants per plot.

Evaluations began when the majority of the plants in each plot released pollen. The agronomic characteristics evaluated in the field were plant height (PH, in cm) - distance from the ground to the flag leaf (youngest leaf on the plant); height of ear insertion (EH, in cm) - distance between the ground and the insertion of the main ear; relative position of the ear (RPE) - relationship between the height of ear insertion and plant height; lodging (LG, in %) - percentage of plants inclined at less than 45° relative to the vertical, or lying on the ground at the time of harvesting; and plant breakage (PB, in %) - percentage of plants broken below the main ear.

Grain yield (GY, in kg.ha^{-1}) was obtained by weighing the grain from each plot after harvesting the material, and included the lodged plants. The humidity was then corrected to 13% and the yield converted to tonnes per hectare.

Evaluation of the anatomical characteristics of the leaf

The synthetic populations evaluated in the field were replanted during 2014 at the School of Agricultural and Veterinary Sciences of UNESP in Jaboticabal, in two-litre shaded polythene bags containing a mixture of industrial substrate (Bioplant) and a Eutrophic Red Latosol (EMBRPHA, 2018) at a ratio of 1:1. Three seeds were used per bag, and were later thinned out to leave one plant.

The experimental design was of randomised blocks, with nine replications, each plastic bag being considered one plot.

The leaves were collected when the plants reached the six-leaf stage (V6). The third youngest leaf of each plant was cut near the centre, and approximately 0.5 cm² of the central rib was removed and fixed for 48 hours in a solution of formaldehyde, acetic acid and 50% ethanol (FAA 50) (JOHANSEN, 1940), at a volume corresponding to 10 times the volume of the samples.

The alcoholic battery described by Johansen (1940) was then used to remove existing water from the tissue, and the material subsequently infiltrated through an ethanol-xylolic series (1:1).

The material was transferred to aluminium moulds containing molten paraffin, and placed in an oven at 60 °C for 12 hours, with the paraffin changed every 4 hours while the material remained in the oven.

The paraffin blocks were later assembled using small, pre-waxed paper boxes, the material from the aluminium moulds being transferred longitudinally to the boxes, which were already properly labelled.

The blocks remained at room temperature until completely solid; the following day, the paraffin ribbons were sectioned to a thickness of 12.5 µm using a sliding microtome. The resulting slides rested on a heating plate at 40 °C to distend the ribbon, which allowed better fixing of the sections. After confirming the quality of the slides under an optical microscope, the paraffin was removed using xylol, and the slides were rehydrated via an ethanol-xylolic series (3:1), as described by Johansen (1940).

The slides were stained with Toluidine in a fume cupboard for 2 minutes, then washed in running water and left to dry at room temperature. Coverslips were used with one drop of Entellan to preserve the slides, and evaluation began after the slides had completely dried. To evaluate the characteristics, the material was photographed with a digital camera coupled to an optical microscope, at one photo per slide. The anatomical structures were measured with the aid of the Image Motic software, calibrated using a microscopic scale and captured at the same magnification as the photographs.

The anatomical characteristics under evaluation were thickness of the bulliform cells (TBC, in µm), thickness of the adaxial epidermis (TAD, in µm), thickness of the abaxial epidermis (TAB, in µm), thickness of the mesophyll (TME, in µm), area of the conducting vessels of the xylem (AXV, in µm^2), area of the phloem (APH, in µm^2), area of the sclerenchyma (ASC, in µm^2) and area of the vascular bundle (AVB, in µm^2). To determine the thickness of the adaxial and abaxial epidermis, and of the mesophyll, four measurements were taken in random areas of the slide. For the area of the conducting vessels of the xylem, phloem, sclerenchyma and vascular bundle, measurements was taken on the most developed of the vascular bundles.

Statistical analysis

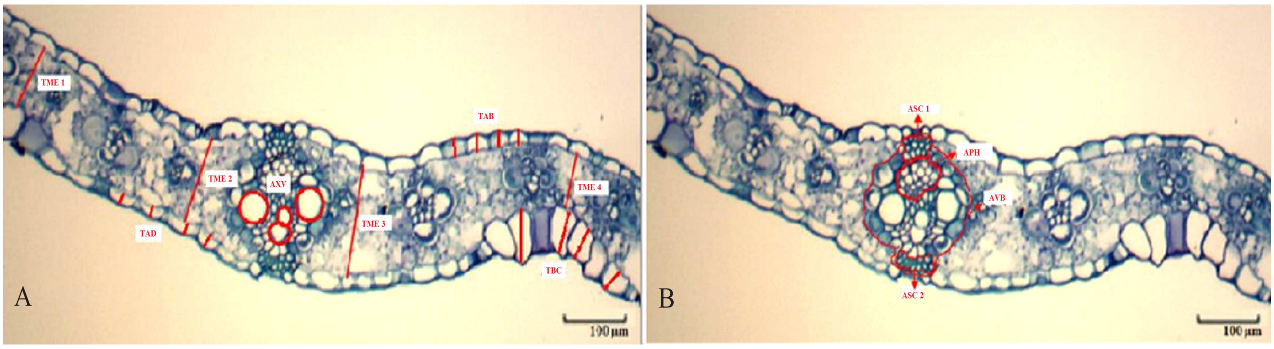
Once the data of the agronomic and anatomical characteristics were obtained, the analysis of variance was carried out and the genetic parameters estimated; a joint analysis of variance for the agronomic characteristics was also conducted.

Additionally, a study was made of multicollinearity between the characteristics of each group (CRUZ *et al*., 2012), homogeneity of variance by the Cochran and Bartlett test and an evaluation of normality by the Lilliefors test (PEGORARA *et al*., 2020) to verify the assumptions of the analysis of variance. Characteristics that did not meet any of the assumptions were transformed according to the nature of the obtained data (CRUZ *et al*., 2012), with lodging (LG) transformed to $\sqrt{(x)}+1$ and the area of the xylem (AXV) transformed to Log(x)+1.

To assess the association of GY with the other agronomic and anatomical characteristics, a path analysis was carried out by a breakdown of the direct and indirect effects, as described by Sánchez (2019).

Each statistical analysis was carried out using the GENES computer software (CRUZ, 2016).

Figure 1 - Detail of cross sections of the leaf of synthetic maize populations in which the measured organs are identified: A. Thickness of the abaxial epidermis (TAB), Thickness of the adaxial epidermis (TAD), Thickness of bulliform cells (TBC), Thickness of the mesophyll (TME1, TME2, TME3 and TME4) and Area of the conducting vessels of the xylem (AXV); B. Area of the sclerenchyma (ASC1 and ASC2), Area of the phloem (APH) and Area of the vascular bundle (AVB)



RESULT AND DISCUSSION

Based on the joint analysis of variance, it could be seen that the effects of the genotype x environment interaction were not significant at a level of 5% for the agronomic characteristics under evaluation (Table 1), indicating that the relative behaviour of the genotypes was hardly influenced by the environmental conditions where the experiments were developed.

A lack of genotype x environment interaction for the characteristics under evaluation would facilitate recommending cultivars for the regions under study (CRUZ *et al*., 2012), since the indicated genotype would present uniform yield for all the locations in question.

As there was no genotype x environment interaction in the joint variance analysis for the agronomic characteristics (Table 1), in order to increase the accuracy of the path analysis using the same number of replications for both the agronomic and anatomical characteristics, it was decided to conduct a new analysis of variance where each combination of block and environment represented one replication, resulting in nine replications for the agronomic as well as the anatomical characteristics (Table 2).

The source of variation, the populations, showed a difference at 1% significance for each of the agronomic and anatomical characteristics of the leaf, proving the variability of the populations in terms of the characteristics under study, the only exception being RPE, which was eliminated from the

Table 1 - Mean squares and significance of the joint analysis of variance in the agronomic characteristics of 13 maize populations

SV	DF	PH	EH	RPE	LG	PB	GY
Blocks/environment	6	85.85	50.40	0.01	0.88	63.49	1.05
Environment (E)	2	13418.01	3729.06	0.01	1.96	2734.01	39.78
Genotype (G)	12	1387.67	845.68	0.01	3.44	72.92	3.75
GxE Interaçtion	24	268.78^{ns}	149.65^{ns}	0.01^{ns}	0.63^{ns}	36.03^{ns}	0.26^{ns}
Mean		205.65	118.19	0.58	2.07	7.04	3.97
Mean error	72	167.99	93.53	0.01	0.72	22.51	0.20
CV%		6.30	8.18	9.78	40.96	67.37	11.22

PH: plant height (in cm), EH: height ear insertion (in cm), RPE: relative position of the ear (in cm), LG: lodging (transformed data), PB: plant breakage (in %), GY: grain yield (in t ha^{-1}). ns: Not significant at 5% by F-test

Table 2 - Mean squares and significance of the agronomic and anatomical characteristics in 13 maize populations

SV	DF	Agronomic Characteristics							
		PH	EH	RPE	LG	PB	GY		
Blocks	8	3.4x10^{3}	970.08	0.002	1.16	731.12	10.73		
Populations	12	1.4x10^{3}**	845.67**	0.003^{ns}	3.44**	72.92**	3.75**		
Residual	96	202.54	112.13	0.003	0.70	30.24	0.21		
Mean		205.65	118.19	0.57	2.07	7.04	3.97		
CV%		6.92	8.96	9.93	40.29	78.08	11.64		
		Anatomical Characteristics							
		TBC	TAD	TAB	TME	AXV	APH	ASC	AVB
Blocks	8	404.03	57.62	90.53	534.76	0.047	5.0x10^{5}	1.8x10^{6}	3.4x10^{7}
Populations	12	280.35**	80.28**	169.92**	533.02**	0.037**	6.8x10^{5}**	1.6x10^{6}**	3.4x10^{7}**
Residual	96	70.49	13.56	18.40	92.23	0.006	1.2x10^{5}	4.0x10^{5}	5.0x10^{6}
Mean		46.18	21.94	25.05	94.55	4.49	1.5x10^{3}	2.5x10^{3}	1.6x10^{4}
CV%		18.18	16.79	17.12	10.16	1.75	22.42	25.18	13.95

PH: plant height (in cm), EH: height of ear insertion (in cm), RPE: relative position of the ear, LG: lodging (transformed data), PB: plant breakage (in %), GY: grain yield (in t ha^{-1}), TBC: thickness of the bulliform cells (in µm), TAD: thickness of the adaxial epidermis (in µm), TAB: thickness of the abaxial epidermis (in µm), TME: thickness of the mesophyll (in µm), AXV: area of the xylem conducting cells (in µm^{2}), APH: area of the phloem (in µm^{2}), ASC: area of the sclerenchyma (in µm^{2}), AVB: mean area of the vascular bundles (in µm^{2}). ns: Not significant, **: Significant at 1% by F-test parameter estimates and path analysis (Table 2) as it did not show a significant difference between populations.

For the coefficient of variation (CV%) of the agronomic characteristics, lodging and plant breakage showed high values, something already seen by other authors, since such characteristics are easily related to uncontrolled environmental factors such as the wind and rain (JIFAR *et al.*, 2017). For the anatomical characteristics, despite the absence of similar studies in the literature for comparison, it was found that the coefficients of variation ranged from 10.16% (TME) to 25.18% (ASC), which according to Begun *et al.* (2016), could fit as the median variation for agricultural experiments, while the area of the xylem, at 1.75%, had a low coefficient of variation.

Most of the genotypic quadratic components were superior to the components of environmental variance for mean value, which indicates high genetic variability in the populations, except for LG, ASC and AVB, where the genotypic quadratic component was inferior to that of environmental variance (Table 3). The genotypic coefficients of determination in the plots ranged from 13.5% (PB) to 64.8% (GY) for the agronomic characteristics, and from 24.66% to 47.77% for the anatomical characteristics (Table 3), demonstrating the possibility of selecting for GY (CRUZ *et al.*, 2012).

For the coefficients of genetic variation (CVg), most of the agronomic and anatomical characteristics showed a good indication of the genetic potential of the germplasm for breeding, which according to Rodrigues *et al.* (2011), in maize under the conditions of Brazil, has to be greater than 7%, with the only exceptions being PH and AXV (Table 3).

GY was the only characteristic with a CVg to CVe ratio greater than 1 (Table 3), a favourable condition for selection, together with the high value of the quadratic genotypic component (VENCOVSKY; BARRIGA, 1992).

The genotypic correlation between the agronomic and anatomical characteristics was significant at a level of 5% between TBC and LG (0.63), TAD and LG (0.62), TAD and GY (-0.62), TAB and GY (-0.69), ASC and LG (-0.60), and ASC and PB (-0.69) (Table 4). The negative correlation between TAD and GY and TAB and GY shows that selecting plants where the epidermis is less thick can result in an increase in plant productivity, thereby taking early advantage of the indirect selection of the characteristic.

Table 3 - Estimates of the phenotypic quadratic components in the mean values of the populations (ϕ_P), components of environmental variance for mean value (σ^2_{Ex}), genotypic quadratic components (ϕ_G), genotypic coefficients of determination per plot (H^2), coefficients of genetic variation (CVg) and ratio between the genetic and environmental coefficients of variation (CVg/CVe) for the characteristics under evaluation in 13 maize populations

Parameter	Agronomic Characteristics				
	PH	EH	LG	PB	GY
Φ_P	154.19	93.96	0.38	8.10	0.42
σ^2_{Ex}	22.50	12.46	0.78	3.36	0.02
ϕ_G	131.69	81.50	0.30	4.74	0.39
H^2	39.40	42.09	30.31	13.56	64.78
CVg	5.58	7.64	26.57	30.92	15.79
CVg/CVe	0.81	0.85	0.66	0.40	1.36

Parameter	Anatomical Characteristics							
	TBC	TAD	TAB	TME	AXV	APH	ASC	AVB
Φ_P	31.15	8.92	18.88	59.22	0.004	7.5×10^4	1.7×10^5	3.9×10^6
σ^2_{Ex}	7.83	1.51	2.04	10.25	0.001	1.3×10^4	4.4×10^4	5.6×10^5
ϕ^G	23.32	7.41	16.83	48.98	0.003	6.2×10^4	1.3×10^5	3.4×10^6
H^2	24.86	35.35	47.77	34.69	35.54	33.60	24.66	40.16
CVg	10.46	12.41	16.38	7.40	1.30	15.95	14.41	11.43
CVg/CVe	0.58	0.74	0.96	0.73	0.74	0.71	0.57	0.82

PH: plant height (in cm), EH: height of ear insertion (in cm), RPE: relative position of the ear (in cm), LG: lodging (in %), PB: plant breakage (in %), GY: grain yield (in t ha^{-1}), TBC: thickness of the bulliform cells (in µm), TAD: thickness of the adaxial epidermis (in µm), TAB: thickness of the abaxial epidermis (in µm), TME: thickness of the mesophyll (in µm), AXV: area of the xylem conducting cells (in µm^2), APH: area of the phloem (in µm^2), ASC: area of the sclerenchyma (in µm^2), AVB: mean area of the vascular bundles (in µm^2)

Despite having no direct association with grain yield, mesophyll thickness was correlated with plant height, height of ear insertion and plant breakage, characteristics directly related to plant yield (Table 4). Changes in mesophyll thickness can influence the quantity or quality of the substances produced, interfering directly in crop productivity, since among the tissues that make up the mesophyll are the chlorophyll-containing parenchyma, which includes cells with an ample number of chloroplasts and intercellular spaces that are responsible for carrying out photosynthesis, and with the presence of nutritious substances, which allow vital plant metabolism (REN *et al*., 2016). Ren, Weraduwage and Sharkey (2019), reviewing the effects of the anatomical characteristics of the leaf on photosynthesis, noted that a large cell space in the mesophyll avoids excessive contact between cells, increasing the surface area of the mesophyll and of the chloroplast exposed to the intercellular air space per unit area of leaf, improving mesophyll conductance and consequently, photosynthesis.

In the path analysis (Table 5), a high degree of multicollinearity was found between characteristics in the phenotypic correlation matrix of the explanatory variables. As such, path analysis with ridge regression was chosen, in which path analysis with collinearity is suggested without the need to eliminate variables. In this strategy, a constant (*k*) is used, the value of which should be as small as possible to stabilise the path coefficients and keep the variance inflation factor below 10 for each of the explanatory variables (AZEVEDO *et al*., 2016).

The result of the path analysis for GY based on the explanatory variables TBC, TAD, TAB, TME, AXV, APH, ASC, AVB, PH, AE, LG and PB is shown in Table 5, with a value for *k* of 0.04. The coefficient of determination of the path analysis model (R^2) was equal to 0.85, characterising that 85% of the variation of the dependent variable GY in the model is explained by the variables used in the causal diagram.

The direct effects of the variables under analysis proved to be superior to the effect of the residual variable (0.38) for the characteristics LG (-0.531) and PB (-0.526), and very close for TAD (- 0.379), AXV (0.371) and ASC (-0.311), indicating that an increase in GY is directly related to the effects of these variables. It can therefore be concluded that these variables are the main determinants of GY, making indirect selection for an increase in GY possible. The thickness of the adaxial epidermis (TAD) is directly linked to effective gas exchange in the plant to carry out photosynthesis and transpiration, and should guarantee the continuous passage of air for efficient gas exchange in the leaves (BAILLIE; FLEMING, 2020). The direct negative effect between TAD and GY indicates a tendency towards greater productivity in plants where the adaxial epidermis is less thick, probably as it allows an increase in the photosynthetic capacity of the plant and consequently, in its productivity.

The direct effect seen in the AXV path analysis in relation to GY indicates the large influence of this characteristic on the yield of maize plants.

In maize, studies of the importance of the xylem in ear development with a view to increasing the agricultural yield of the plant are few and not specific. In fruit trees, the greater participation of the xylem or phloem in transporting water for fruit formation depends on the development stage of the plant. Brüggenwirth, Winkler and Knoche (2016), evaluating xylem flow, phloem flow, and transpiration during fruit development in the wild cherry, found that the daily phloem flow was small during stage II of the fruit (the stage of cherry development), but increased markedly during stage III (increase in pulp cells). Xylem flow exceeded that of the phloem during stage II, but steadily decreased in stage III to almost zero

Table 4 - Estimates of the genotypic correlations between the variables obtained in the 13 synthetic maize populations

Characteristic	TBC	TAD	TAB	TME	AXV	APH	ASC	AVB
PH	0.26	0.39	-0.04	0.81**	0.40	-0.01	-0.36	0.46
EH	0.30	0.46	0.20	0.77**	0.22	-0.16	-0.45	0.37
LG	0.63*	0.62*	0.56	0.48	0.23	-0.13	-0.60*	0.27
PB	0.47	0.56	0.56	0.85**	0.21	-0.24	-0.69*	0.16
GY	-0.53	-0.62*	-0.69*	-0.42	-0.02	0.06	0.56	-0.15

TBC: thickness of the bulliform cells (in µm), TAD: thickness of the adaxial epidermis (in µm), TAB: thickness of the abaxial epidermis (in µm), TME: thickness of the mesophyll (in µm), AXV: area of the xylem conducting cells (in µm^2), APH: area of the phloem (in µm^2), ASC: area of the sclerenchyma (in µm^2), AVB: mean area of the vascular bundles (in µm^2), PH: plant height (in cm), EH: height of the ear insertion (in cm), RPE: relative position of the ear (in cm), LG: lodging (in %), PB: plant breakage (in %), GY: grain yield (in t ha^{-1}).*, **: significant at 5% and 1% respectively by t-test; values with no asterisk are not significant at harvest; different to that seen by Chen *et al*. (2019) who, assessing interruption of the xylem function during maturation of *Syzygium jambos*, found that the xylem remained fully functional until the fruit fell, with a sharp reduction in vessel function towards the distal end of the fruit only after separating from the plant.

Sclerenchyma tissue offers mechanical support, and substances such as calcium crystals and phenolic compounds may be stored in the leaves. The inverse association between ASC and GY seen in the path analysis indicates that plants where the area of the sclerenchyma is smaller are more productive; this may have been due

Table 5 - Estimation of the direct and indirect effects on grain yield (GY) of the characteristics thickness of the bulliform cells (TBC), thickness of the adaxial epidermis (TAD), thickness of the abaxial epidermis (TAB), thickness of the mesophyll (TME), area of the xylem (AXV), area of the phloem (APH), area of the sclerenchyma (ASC), mean area of the vascular bundles (AVB), plant height (PH), height of ear insertion (EH), relative position of the ear (RPE), lodging (LG) and plant breakage (PB)

Direct effect on GY	TBC	TAD	TAB	TME	AXV	APH
	-0.014	-0.379	-0.169	-0.117	0.371	-0.214
Indirect via TBC		-0.009	-0.011	-0.001	-0.008	-0.003
Indirect via TAD	-0.243		-0.202	-0.164	-0.171	0.010
Indirect via TAB	-0.127	-0.090		0.017	-0.015	0.041
Indirect via TME	-0.007	-0.051	0.012		-0.033	-0.046
Indirect via AXV	0.209	0.168	0.032	0.105		0.176
Indirect via APH	-0.044	0.005	0.052	-0.085	-0.102	
Indirect via ASC	0.000	0.049	0.078	0.074	-0.139	-0.145
Indirect via AVB	0.108	0.121	0.023	0.107	0.164	0.110
Indirect via PH	0.035	0.058	-0.007	0.122	0.059	-0.005
Indirect via EH	0.020	0.032	0.015	0.055	0.016	-0.012
Indirect via LG	-0.241	-0.261	-0.244	-0.200	-0.094	0.046
Indirect via PB	-0.169	-0.201	-0.223	-0.296	-0.099	0.079
TOTAL (Pearson Corr.)	-0.472	-0.572	-0.650	-0.387	-0.037	0.028
Direct effect on GY	ASC	AVB	PH	EH	LG	PB
	-0.311	0.206	0.186	0.087	-0.531	-0.526
Indirect via TBC	0.000	-0.007	-0.003	-0.003	-0.006	-0.005
Indirect via TAD	0.060	-0.224	-0.119	-0.138	-0.186	-0.144
Indirect via TAB	0.043	-0.019	0.007	-0.030	-0.078	-0.072
Indirect via TME	0.028	-0.061	-0.077	-0.074	-0.044	-0.066
Indirect via AXV	0.166	0.296	0.118	0.068	0.066	0.070
Indirect via APH	-0.100	-0.115	0.006	0.029	0.018	0.032
Indirect via ASC		-0.141	0.091	0.110	0.152	0.185
Indirect via AVB	0.093		0.079	0.064	0.046	0.030
Indirect via PH	-0.054	0.072		0.175	0.058	0.128
Indirect via EH	-0.031	0.027	0.082		0.037	0.067
Indirect via LG	0.259	-0.118	-0.166	-0.227		-0.281
Indirect via PB	0.312	-0.078	-0.363	-0.408	-0.278	
TOTAL (Pearson Corr.)	0.452	-0.155	-0.153	-0.346	-0.768	-0.601
Coefficient of determination	0.85					
Residual effect	0.38					
Value for k used in the analysis	0.04					

to a smaller area resulting in more intercellular space per unit area of leaf, reducing the density of the mesophyll cells and affording more-efficient photosynthesis (REN; WERADUWAGE; SHARKEY, 2019).

Various studies using the method of path analysis have been developed with the aim of verifying the effects of agronomic characteristics on plant productivity. Begum *et al*. (2016), in evaluating the variability and association between characteristics of the plant and the ear through the use of path analysis, found that plant height, ear length and rows of grains per ear had a highly significant positive direct effect on grain yield, a fact that was not found in this study.

CONCLUSIONS

1. According to the analysis of genotypic correlation, the characteristics plant height, height of ear insertion, lodging, plant breakage and grain production are related to the anatomical characteristics thickness of the bulliform cells, thickness of the adaxial and abaxial epidermis, area of the sclerenchyma and thickness of the mesophyll, allowing indirect selection for the agronomic characteristics via the anatomical characteristics;
2. Based on the path analysis, the thickness of the adaxial epidermis, area of the xylem and area of the sclerenchyma, as they have a greater direct effect on grain yield, can be used for indirect selection for this characteristic in breeding programs of the species.

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