

# Evaluation of root aerenchyma area in sugar cane (*Saccharum* spp.) as feature of tolerance to hypoxia

## Evaluación del área de aerénquima radical en caña de azúcar (*Saccharum* spp.) como característica de tolerancia a hipoxia

Carlos Andrés Unigarro Muñoz<sup>1</sup>, Jorge Ignacio Victoria Kafure<sup>2</sup>, and Oscar Eduardo Checa Coral<sup>3</sup>

<sup>1</sup>Agronomist Engineer, Student of Master in Agricultural Sciences, Universidad de Nariño. Pasto, Colombia. <sup>2</sup>Agronomist Engineer, Ph.D. Director of the Variety program of Cenicaña. Cali, Colombia. <sup>3</sup>Associated professor, Agronomist Engineer. Ph.D. Faculty of Agricultural Sciences. Universidad de Nariño. Research Group on Andean Crops. Pasto, Colombia. Corresponding author: andresunigarro@gmail.com

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### Abstract

The research was developed at the experiment station San Antonio (EESA) of Cenicaña located in the village of San Antonio de los Caballeros (Florida, Cauca Valley). Two experiments were conducted: one on semi-dry conditions and another on wet conditions, each one with a design completely randomized block design with three replications. The aerenchyma observed in the fibrous roots of 13 varieties of sugarcane was evaluated (*Saccharum* spp.) at 4, 6 and 8 months after planting. Agronomic variables as height, diameter, population, stalk weight of total plot, sucrose (% cane) and yield of sucrose per plot were evaluated at harvesting time. It was found that there was a differential response between environments because of the lack of oxygen (hypoxia) in soil. On wet conditions, the aerenchyma occupied 55% of the total area in the root tissues although did not show statistical differences between varieties, whereas the opposite occurred on semi-dry conditions where it only occupied 33%. The aerenchyma was not associated with any of the agronomic traits evaluated. The variety CC 01-1884 had the best agronomic performance in the evaluations.

**Keywords:** Drought stress, fibrous roots, flooding stress, soil waterlogging, sugarcane.

### Resumen

La investigación se desarrolló en la Estación Experimental San Antonio (EESA) de Cenicaña ubicada en el corregimiento de San Antonio de los Caballeros (Florida, Valle del Cauca). Se realizaron dos experimentos denominados condición húmeda (con lisímetros para el manejo artificial del nivel freático) y condición semiseca (en campo), utilizando un diseño de bloques completos al azar con tres repeticiones. Se evaluó el aerénquima presente en las raíces fibrosas de 13 variedades de caña de azúcar (*Saccharum* spp.) a 4, 6 y 8 meses después de la siembra y las variables agronómicas altura de planta, diámetro de tallo, población de tallos, peso de tallos por parcela y producción de sacarosa por parcela al momento de la cosecha. Se encontró una respuesta diferencial entre condiciones a causa de la falta de oxígeno (hipoxia). En condiciones húmedas el aerénquima ocupó 55% del área total de los tejidos en la raíz, sin diferencias estadísticas entre variedades; mientras que en condiciones semisecas sólo ocupó 33%. En ambas condiciones, el aerénquima no mostró asociación con las variables agronómicas evaluadas, no obstante la variedad CC01-1884 presentó el mejor comportamiento agronómico.

**Palabras clave:** Anegamiento del suelo, caña de azúcar, estrés de inundación, estrés de sequía, raíces fibrosas.

## Introduction

At the valley of Cauca river there are approximately 61,000 ha sown on sugarcane in wet zones, this area has been classified into 70 agroecological zones that are characterized for their diverse type of soils and conditions of medium, high and very high humidity according to the Fourth Approximation to Agroecological Zoning of sugarcane (Cenicaña, 2008). In very humid or inundated soils, the plant growth is negatively affected by the loss of soil nutrients (Kozłowski and Pallardy, 1984), low macronutrient absorption and lack of oxygen in the roots (Pardos, 2004). The oxygen deficit causes in plants a physiological stress known as hypoxia, that reduces their growth and production (Pardos, 2004). According to Bailey and Voesenek (2008) the hypoxia is presented when the concentration of oxygen dissolved in water is between 0.1 and 20.9%, at 20 °C. However, some plants can tolerate hypoxia by mechanisms that involve transport and supply of oxygen to the organs submerged in water, among them, it is important to notice the formation of aerenchyma tissue in roots, stems and leaves (Armstrong *et al.*, 1994).

The low concentration of oxygen at the rhizosphere stimulates the production of ethylene in the roots, which, because of its low diffusion rate in water, is accumulated and induces in the root cortex cells a process of programmed cell death that forms a specialized tissue called aerenchyma; this tissue comprises longitudinal channels filled with air by which the oxygen is transported from the atmosphere to the roots (Drew, 1997; Visser and Voesenek, 2004; Bailey and Voesenek, 2008). Mathematical models and direct experimentation show that the oxygen can dissolve itself from the aerial stems to the roots through the aerenchyma in order to satisfy the respira-

tory needs of the tissues (Jackson, 2008). Jackson (1985) points that the aerenchyma allows a rapid diffusion of oxygen in the buds, to the roots which helps the plant to survive the hypoxia. The development of the aerenchyma tissue in the stems and roots, and the development of adventitious roots are morphological changes common in the response to hypoxia in sugarcane (Gilbert *et al.*, 2007). Srinivasan and Batcha (1962) when evaluating 68 clones of *Saccharum* spp. Found that the ones tolerant to flooding had abundant adventitious roots and aerenchyma. Between 60 and 80% of the sugarcane root system under wet conditions is composed of fibrous roots (Morris and Tai, 2004), which, according to Dillewijn (1975) have a diameter smaller than 1 mm. The ability of the Canal Point (CP) varieties to produce constitutive aerenchyma in the stem under no hypoxic conditions, could be a mechanism for the plants to survive flooding (Glaz *et al.*, 2004); however, despite this, the selection programs discard these materials because they reduce the weight of the sugarcane, due to the formation of empty spaces in the stem which is not desirable for the sugar industry. The root aerenchyma is constitutive in sugarcane (Ray and Sinclair, 1999), however, its role in hypoxia processes has not been studied in detail. The objective of this research was to evaluate the behavior of the aerenchyma area in the fibrous roots of 13 sugarcane varieties under wet and semi-dry conditions and, to determine how this tissue affects the tolerance to hypoxia and some agronomical traits of the plant.

## Materials and methods

The research was done in the Experimental Station San Antonio (EESA) from Cenicaña located at 3° 21' N and 76° 18' W, at 1024 MASL in the town Florida (Valle del Cauca).

The annual mean temperature is 23 °C, with an annual average rainfall of 1160 mm and relative humidity 77%. The soil corresponds to the agroecological zone 11H1 (Quintero *et al.*, 2008). Sowing was done on December the 10<sup>th</sup>, 2008 and harvest on July 28<sup>th</sup>, 2009.

A completely randomized block design with three replicates and 13 treatments (varieties) was used, each experimental plot was composed for five plants sown at 0.30 m between spots and 1.50 m between rows of each one of the studied varieties. The useful area of the experimental plot was 1.50 m<sup>2</sup> discarding the plants are the extreme of the rows. The varieties used were Cenicaña Colombia (CC): CC 84-75, CC 92-2198, CC 92-2804, CC 93-3826, CC 93-4181, CC 93-4418, CC 00-3993, CC 00-4586, CC 01-1817, CC 01-1884 and RD 75-11. The variety CC 93-4418, with low productivity under wet conditions, is considered susceptible; whereas the varieties of the series 00 and 01 at the third stage of varietal selection done by Cenicaña are tolerant to wet conditions. The absolute control was the CC 85-92 variety that is the most cultivated in the geographical area of the Cauca river valley (Cenicaña, 2008). These characteristics were taken into account for the development of the two experiments, named wet condition (with lysimeters or structures for the artificial management of the water table) and the semi-dry condition (in the field), that contrasted the behavior of the varieties between a condition of hypoxia (oxygen deficit) and a normal condition, respectively. In wet conditions, hypoxia was induced by saturating the soil with water till the water table was 10 cm over the soil surface, where it was kept once the fourth month ended till the harvesting time. Each day the water table was determined and when it was at a deeper level, water was added to the lysimeter until the established level. Soil preparation under wet conditions was done manually to avoid alteration of the wall of the lysimeter, whereas under semi-dry conditions was prepared mechanically using one pass of

plow and one pass of rake. The weed control was done manually 45 days after sowing in the lysimeters and by machine in the field.

The root sampling was done 4, 6 and 8 months after sowing; the simple extraction was done with a modified auger that reduced the mechanical damage at sampling; the roots were washed and fixed on a F.A.A. solution (formaldehyde + 70% alcohol + acetic acid) (Silva *et al.*, 2003), then they were stored at 7 °C (Muñoz *et al.*, 2006). From the samples per experimental plot were selected three roots with a diameter between 0.4 and 0.6 mm in which transversal sections were done using dissecting blades. Sections were mounted on microscope slides with a semi-permanent solution of water-glycerin (1:1) and observed under microscope at 10X; then they were microphotographed at 3 megapixels resolution. Pictures were analyzed by the software ImageJ (Rasband, 1997) that calculated the aerenchyma, parenchyma and cortex areas. These areas were transformed to percentages for their evaluation (Visser and Bögemann, 2003). The agronomical variables of plant height, stem diameter and population or number of stems/plot were quantified at the harvesting time using meters and calibrators. The harvested stems per plot were weighted using an electric balance. Sucrose production was calculated in the lab with the weight of the stem per plot and the concentration of sucrose obtained by the direct-Cenicaña (DAC) method (Larrahondo and Torres, 1989).

In the mathematical model of the variables aerenchyma, parenchyma and cortex area were taken into account the subsampling characteristics and for that an analysis of variance was performed with the stratum PROC MIXED (SAS Institute, 2004) using the blocks as random effects and the variables as fixed effects; mean comparisons were done by the Tukey's test ( $Pr > F = 0.05$ ). For the analysis of variables such as height, diameter, population and sucrose production was used the stratum PROC GLM (SAS Institute, 2004), the multiple

comparison test was done by Duncan ( $P > F = 0.05$ ). The relation between the variables was performed by calculating the Pearson correlation coefficient using the stratum PROC CORR (SAS Institute, 2004).

## Results and discussion

### Behavior of aerenchyma, parenchyma and cortex area of the root

**Wet condition.** At the fourth month of the experiment, lysimeters had a semi-dry condition (point zero), since the water table in them was at 83 cm of the soil surface. In this month the aerenchyma:parenchyma ratio (A:P) was 1:1, showing that the differential rates between parenchyma and the aerenchyma formation were under equilibrium (Table 1). The aerenchyma in the sugarcane is a constitutive characteristic that is developed with or without hypoxia (Ray and Sinclair, 1999). There were highly significant differences found between the varieties ( $P < 0.001$ ) in the aerenchyma, parenchyma and cortex zone formation (Table 1). However, for the characteristics above mentioned, these differences were determined by the moment in which the parenchymal cells were evaluated and the

change they were experiencing and not, by the result of the variety tolerance to lack of oxygen. From this moment, the different varieties in the lysimeters were subjected to an induced hypoxia, placing the water table at 10 cm of the soil surface.

In the Figure 1 is observed that the aerenchyma proportion at the sixth month, with a general average of 38%, was statistically superior to the one found at the fourth month. That increase changed the ratio (A:P) from 1:1 in the fourth month to 3:2 in the sixth (Table 1). Among varieties there were no significant differences in aerenchyma, pointing at a general response of the varieties to the hypoxia (Table 1). The parenchyma in the sixth month was reduced in 3% in comparison the fourth month but, there was no statistical difference among them (Figure 1); however, there were highly significant differences between the varieties at the sixth month (Table 1), which indicates that the cortical zone had different proportions in the varieties. This was proved when observing that there are differences among varieties ( $P < 0.05$ ) for the cortex zone variable (Table 1).

At the eight month, the aerenchyma, parenchyma and cortical zone variables did

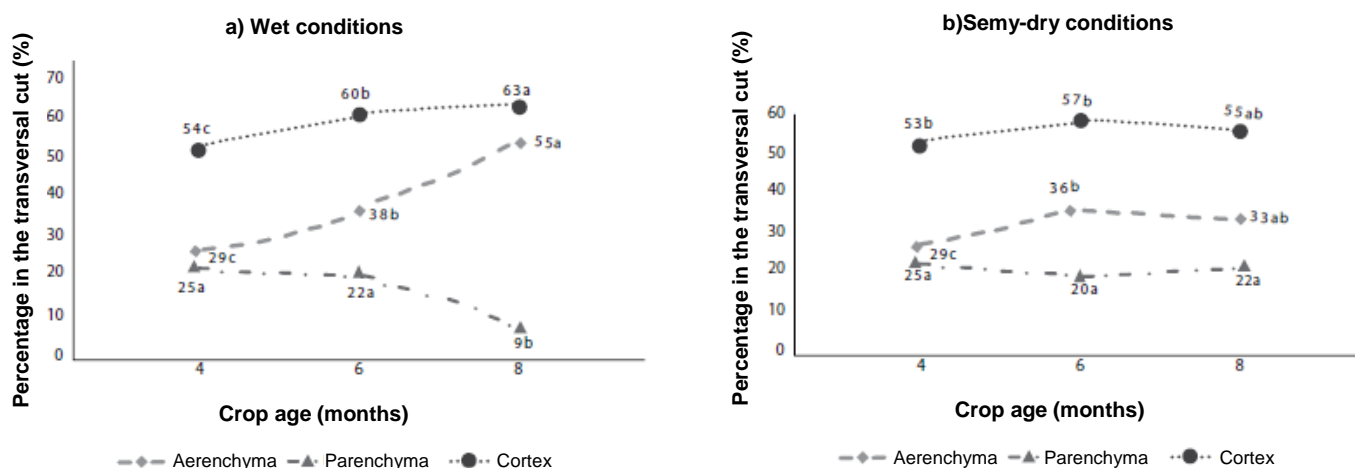
**Table 1.** Analysis of variance for the values of the root variables in 13 sugarcane varieties at different ages (months) in wet and semi-dry soil conditions. Valley of Cauca river, Colombia.

Variable	Month 4 (w.t.= 80 cm)			Month 6 (w.t.= 10 ± 5 cm)			Month 8 (w.t. = 10 ± 5 cm)		
	Aerenc.	Paren.	Cortex	Aerenc.	Paren.	Cortex	Aerenc.	Paren.	Cortex
<b>Wet conditions</b>									
MSE (variedad)	97.4**	76.2**	14.2**	23.1 ns	26.6**	17.7*	33.6 ns	21.3 ns	15.4 ns
Mean	29.0	25.0	54.0	38.0	22.0	59.0	55.0	9.0	63.0
A:P ratio	1.0	1.0	–	3.0	2.0	–	6.0	1.0	–
C.V.	14.0	12.0	8.0	8.0	7.0	10.0	13.0	5.0	11.0
<b>Semi-dry conditions</b>									
MSE (variedad)	89.5*	90.5*	25.7**	35.2**	36.5**	11.1**	99.6**	95.5**	18.5**
Mean	28.0	25.0	53.0	36.0	20.0	57.0	33.0	22.0	55.0
A:P ratio	1.0	1.0	–	3.0	2.0	–	3.0	2.0	–
C.V.	13.0	12.0	11.0	9.0	8.0	8.0	15.0	13.0	10.0

\*\* ( $P < 0.01$ ), \* ( $P < 0.05$ ). ns = no significant.

w.t. = water table. Aerenc. = aerenchyma, Paren. = parenchyma.

MSE = Mean square error, A:P = aerenchyma:parenchyma ratio



**Figure 1.** Behavior and multiple comparison by Tukey ( $P > F = 0.05$ ) for the aerenchyma (%), parenchyma (%) and cortical zone (%) in sugarcane roots under wet and semi-dry soil. Valley of Cauca river, Colombia.

not show statistical differences between varieties (Table 1). This confirms the results at the sixth month, when it was found that the average values by variety for the aerenchyma variable were statistically the same when those traits were evaluated under wet conditions. At the eighth month, the general average for aerenchyma was 55%, whereas for parenchyma was 9%, therefore the ratio between both variables (A:P) was 6:1 (Table 1). Justin and Armstrong (1987) when evaluating the roots of 91 species grown un wet zones found that they have between 10% and 20% of aerenchyma under normal conditions, while under hypoxia this value was two or three times higher. Visser *et al.* (2000a) found similar values in the monocot *Carex acuta*.

The aerenchyma percentage at the eight month was higher than the one at the sixth month (Figure 1). In such Figure is observed a trend for the aerenchyma to increase, whereas the parenchyma is decreasing. The increase in the cortical zone allows deducing that the tissues at the stele and epidermis reduced their proportion to favor the formation of aerenchyma. Visseret *et al.* (2000b) consider that the intercellular spaces like the aerenchyma reduce the diameter of the vascular system in the root that transport water and nutrients.

The roots, in the months 6 and 8, despite of growing at similar water tables (10 cm depth) showed a growth difference in the amount of aerenchyma, so, at the eight month, there was a 17% increase in comparison to the sixth month (Figure 1). A possible explanation to this phenomenon could be the high elongation rates of the roots at the sixth month. Negi *et al.* (1972) in India studied the root system of the sugarcane variety BO3 with tolerance to humidity and observed that the growth rate of the roots per unit of area was 12, 24 and 3 at 12, 24 and 36 weeks, respectively; which allows deducing that approximately at the sixth month of development, there is a significant translocation of energy to the root elongation processes, that in turn, competes with the aerenchyma formation which is costly but required for plant survival (Bailey and Voeselek, 2008). Based on the above mentioned, it is possible to assume that in the sixth month there is an equilibrium between the high root elongation rates and the aerenchyma formation, reason why there is not a total expression of the aerenchyma in the cortical zone, contrary to what happened at the month eight, when the elongation could be reduced and the plant could devote more energy to the increase of aerenchyma as resource to tolerate hypoxia.

The combined analysis of variance for wet conditions (Table 2) showed highly significant differences ( $P < 0.001$ ) between months for all the varieties evaluated, whereas the sources variety and the interaction month x variety were not significant. The above means that even though there is a response of the aerenchyma area to hypoxia, it is a general response without differences between the genotypes, therefore, the phenotypic difference observed in

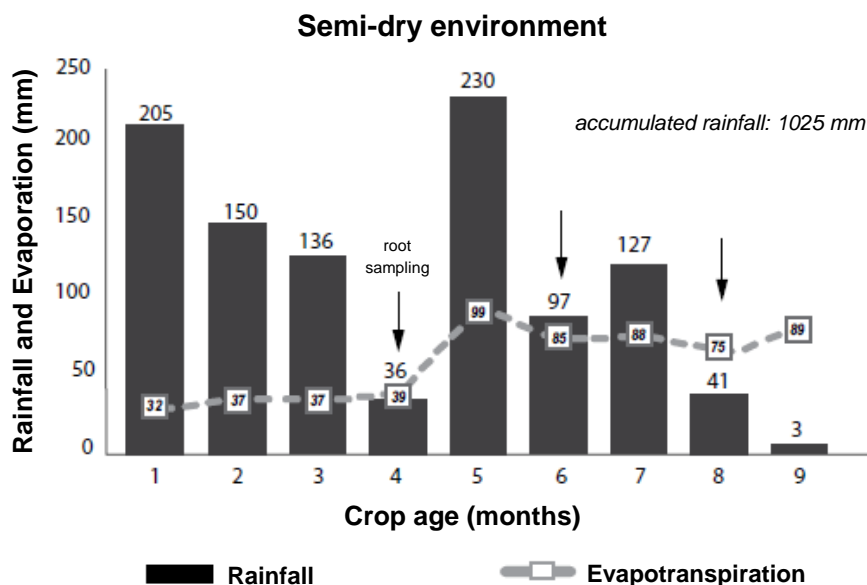
its production is due to the interaction of the aerenchyma with other characteristics such as root length or metabolism.

**Semi-dry condition.** The variables of aerenchyma and parenchyma percentage under this condition are included in Table 1. At the fourth month the A:P ratio was 1:1 but, at the sixth and eight month this ratio increased till 3:2, which happened due to rainfall at the fifth month (Figure 2) that

**Table 2.** Combined analysis of variance for the 4, 6 and 8 months for the aerenchyma, parenchyma and cortical zone variables in 13 sugarcane varieties in wet and semi-dry soil conditions. Valley of Cauca river, Colombia.

Wet conditions			
Source	Aerenchyma	Parenchyma	Cotical zone
Month	0.001**	0.004*	0.014*
Variety	0.287 ns	0.231 ns	0.692 ns
Month x Variety	0.500 ns	0.126 ns	0.074 ns
C.V.	11	8	9
Semi-dry conditions			
Source	Aerenchyma	Parenchyma	Cotical zone
Month	0.090 ns	0.261 ns	0.229 ns
Variety	0.030*	0.173 ns	0.025*
Month x Variety	0.152 ns	0.203 ns	0.421 ns
C.V.	13	11	9

\*\* ( $P < 0.01$ ), \* ( $P < 0.05$ ). ns = no significant.



**Figure 2.** Hydrological and root sampling conditions at the Experimental Station San Antonio at Cenicaña, plot 13B and agroecological zone 11H1, Florida, Valle del Cauca, Colombia



avored the development of aerenchyma. The results show that the highest percentage of this tissue was at the sixth month, being higher than the one of the fourth month although similar to the one found at the eighth month. These results and the fact that the aerenchyma percentages in the last month were slightly smaller, show that the ratio between aerenchyma (Figure 1) and the rainfall (Figure 2).

The parenchyma percentage did not have statistical differences between the evaluated months (Table 2), however it slightly decreased at the sixth month (Figure 1). The range of the percentage for the mean was < 5% (Figure 1), which means that the proportion of tissue was relatively constant in the time under the semi-dry condition of this study. The cortical percentage had a similar behavior to the aerenchyma percentage (Figure 1) which was due, apparently, to the rainfall at the

fifth month that influenced the aerenchymal proportion observed at the sixth month. These results show the adjustments that the roots experience even with relatively low water table. For varieties there were statistical differences during all the months of the study for the aerenchyma, parenchyma and cortical zone variables (Table 1) due to the specific water conditions at a determined space and time but, not due to a particular characteristic of tolerance to flooding soils.

The combined analysis of variance in Table 2 shows that the source of variation month has differences ( $P < 0.05$ ) in the variable aerenchyma percentage but, not for the parenchyma and cortex. The month x variety interaction was not significant for the evaluated variables. The source variety had differences in aerenchyma and cortical zone. These differences were found because of the variability in the aerenchyma under semi-dry due to the different conversion

**Table 3.** Analysis of variance and multiple comparison by Duncan ( $P < 0.05$ ) for the mean of the height (cm), stem diameter (mm), population (no. stems/plot) and production (kg of fresh stems/plot) variables, for 13 sugarcane varieties. Valley of Cauca river, Colombia.

Variety	Diameter (cm)	Height (m)	Population (no. stems/parcela)	Production (kg de stems/plot)
CC 00-3993	2.36 e	2.09 ba	31 a	33 bac a
CC 00-4586	2.96 a	1.66 dc	20 b	24 bc
CC 01-1817	2.67 bdc	1.90 bdac	30 a	37 baa
CC 01-1884	2.75 bac	2.08 ba	32 a	44 aa
CC 84-75	2.49 edc	1.83 bdac	30 a	30 bca
CC 92-2198	2.84 ba	1.76 bdc	20 b	26 bc
CC 92-2804	2.49 edc	1.54 d	26 ba	22 c
CC 93-3826	2.97 a	2.23 a	24 ba	35 baca
CC 93-4181	2.64 bdc	1.69 bdc	27 ba	27 bc
CC 93-4418	2.47 ed	1.63 dc	25	25 bc
CC 93-7510	2.53 edc	1.89 bda	32 a	34 baca
RD 75-11	2.58 edc	2.08 ba	26 ba	30 bac
CC 85-92 (control)	2.60 bedc	2.04 bac	26 ba	34 baca
Mean	2.64	1.88	27	31
Pr  t	0.0001**	0.012**	0.044*	0.048*
R <sup>2</sup>	0.75	0.67	0.55	0.53
C.V. (%)	0.51	1.16	17.3	23.8

Values on the same column followed by the same letters do not statistically differ ( $P < 0.05$ ), according to Duncan's test ( $Pr > F = 0.05$ ). R<sup>2</sup> = coefficient of determination; C.V. = coefficient of variation.

rates that occur at the parenchyma at a specific moment.

**Height, diameter, population and production under wet conditions**

Under wet soil conditions, the varieties CC 93-3826, CC 00-4586, CC 92-2198 and CC 01-1884 presented the largest values with stem diameters between 2.97 and 2.75 cm, which were higher ( $P < 0.05$ ) than the control variety CC 85-92. The variety CC 00-3993 had the smaller diameter (Table 3). The stem high ranged from 1.54 m for the CC 92-2804 variety and 2.23 m for the CC 93-3826 variety (Table 3). The population in stems/plot was different among varieties ( $P < 0.05$ ) with an average of 27 stems/plot. The varieties CC 01-1884, CC 01-1817, CC 84-75, CC 93-7510 and CC 00- 3993 had between 30 and 32 stems/plot and were superior to the varieties CC 00-4586 and CC 92-2198, while the control CC 85-92 only had 26 stems/plot (Table 3). The production (kg of green stems/plot) had differences ( $P < 0.05$ ) with a coefficient of variation (17%) that is acceptable for this kind of experiments. The CC 01-1884 variety (44 kg of sucrose/plot) was the best and statistically superior to the CC 92-2804, CC 93-4418, CC 84-75, CC 92- 2198, CC 00-4586 and CC 93-4181 varieties, whereas the CC 85-92 (34 kg sucrose/plot) was statistically the same to CC 01-1884 and to CC 92-2804 which has the lowest production of the experiment (Table 3).

**Correlation between the evaluated variables**

The aerenchyma, parenchyma and cortical zone did not show any correlation with the height, diameter, population and plant production variables (Table 4). However, there were correlations among the contrasting groups, the production variable positively correlated with height and stem population. Viveros *et al.* (2008) using a path analysis found that the height was a fundamental trait selecting varieties for wet locations.

The percentage of aerenchyma variable correlated negatively with the percentage of parenchyma. The cortex percentage presented a positive and highly significant correlation with the aerenchyma percentage. These results indicate that the increase in the aerenchyma percentage results also in an increase in the root cortical area with a reduction in the other root tissues, showing the importance of forming aerenchyma for the plant survival under hypoxic conditions. The aerenchyma and parenchyma percentages in group form the root cortical area, located between the exodermis and the endodermis in the root. Both structures had an inverse relation since the processes that form aerenchyma are the division and expansion of neighboring cells (schizogenous aerenchyma) (Drew, 1997) or the death and dissociation of the cells (lysogenous aerenchyma) in the parenchymatous tissue (Pennell and Lamb, 1997)

**Table 4.** Correlations between the aerenchyma (5), parenchyma (5) and cortical zone (%) variables with height (cm), stem diameter (mm), population (no. stems/plot) and production (kg of fresh stems/plot) variables, for 13 sugarcane varieties. Valley of Cauca river, Colombia.

Variable		Diameter	Height	Population	Production	Aerenchyma	Parenchyma	Cortex
Production	r Person	0.25	0.53	0.68	1	-0.18	0.23	-0.01
	Pr> r	0.13 ns	0.001**	<0.0001**	-	0.29 ns	0.16 ns	0.94 ns
Aerenchyma	r Person	-0.12	-0.06	-0.15	-0.18	1	-0.77	0.69
	Pr> r	0.48 ns	0.70 ns	0.36 ns	0.29 ns	-	<0.0001**	<0.0001**
Parenchyma	r Person	0.19	0.19	0.09	-0.17	-0.77	1	-0.07
	Pr> r	0.24 ns	0.24 ns	0.57 ns	0.31 ns	<0.0001**	-	0.67 ns
Cortex	r Person	0.04	0.12	-0.13	-0.03	0.69	-0.07	1
	Pr> r	0.82 ns	0.47 ns	0.44 ns	0.88 ns	<0.0001**	0.67 ns	-

\*\* ( $P < 0.001$ ), \* ( $P < 0.05$ ). ns = no significant



## Conclusions

- The aerenchymal area of the sugarcane roots was statistically the same in all the varieties, therefore, it is not recommended to be used as a tool for variety selection. Nonetheless, a general response of the varieties to hypoxia was found, which consists in increasing the aerenchymal area causing the reduction in other tissues and, demonstrating the importance of the characteristic in the survival of the plant to wet conditions.
- The CC 01-1884 variety presented the best agronomical characteristics for this experiment.

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