



Physiological bases of genetic gains in sugarcane yield in Argentina



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ABSTRACT

Breeding and management efforts during the 20th century have increased sugar yield in almost all sugarcane areas worldwide. However, a close analysis of the trends during the last decades reveals that the rate of increase in sugar yield has been actually slowing down since the 1980s. An experiment was conducted to compare sugarcane varieties representing different eras of genetic improvement in Argentina (one widely grown self-pollination variety, 11 released sugarcane hybrids and one advanced breeding hybrid) during the 2010/11, 2011/12 and 2012/13 growing seasons under rainfed field conditions in Tucumán, the main sugarcane area of Argentina. The aim of the experiment was to quantify the achievements in sugarcane breeding since 1940 in Tucumán, by identifying the main crop physiological bases responsible for yield increases. Genetic gains for sugar yield were 0.08 and 0.14 Mg ha⁻¹ y⁻¹ for plant and ratoon cane, respectively. There was a linear increase in sugar yield, cane yield, sugar content and average stem weight with the year of release of the varieties throughout the period from 1940 to 2010. The increase in sugar yield was linearly and positively related to cane yield, sugar content and average stem weight, whereas the increase in cane yield was associated to average stem weight and not to the number of stems. Breeding also increased the total above ground dry biomass and the dry stem weight. However, the partitioning of total above ground dry biomass to stems or to sugar were not increased by breeding. These findings reveal that the varieties continuously released by Argentine sugarcane breeding programs have not reached a “plateau” in sugar yield.

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1. Introduction

Genetic improvement has played an important role in yield increment in almost all the sugarcane producing countries. Although breeders have selected new varieties with important objectives, such as ratooning ability, disease resistance or fibre content, their main goal is sugar yield through the main yield components: cane yield and sugar content.

Breeding and management efforts during the 20th century have increased sugar yield from 4 to 14 Mg of sugar ha⁻¹, depending on the environment, with records being documented from Colombia (Cock, 2003), Hawaii (Wu and Arcinas, 2004), USA (Edmé et al., 2005), Australia (Jackson, 2005; Ming et al., 2006; Cox and Stringer, 2007) and Argentina (Fernandez de Olivari et al., 2009). These increases led to genetic gains ranging from 0.09 to 0.18 Mg of sugar ha⁻¹ y⁻¹. Almost all these genetic gains in sugar yield were

mainly associated with cane yield, whereas there was little progress in sugar content (Jackson, 2005). However, a close analysis of the trends in all these studies during the last decades reveals that the rate of increase in sugar yield has been actually slowing down since the 1980s.

In Argentina, increases in sugar production during different periods of the last century were due to the expansion of sugarcane cultivated areas and intensified use of inputs. These factors are not likely to occur at present due to economic and environmental constraints. Therefore, future sugar production increases with the consequent improved yield gains required for satisfying world sugar demands will strongly rely on genetic improvement.

In this context, breeding strategies using physiological knowledge could play an important role in yield gain. An alternative for identifying prospective physiological traits useful in yield improvement has been the analysis of the physiological traits that were instrumental in the breeding achievements made in the past (Reynolds et al., 2001).

Many studies have explored the physiological bases associated with genetic gains in different crops, such as wheat (Austin et al., 1980), barley (Wych and Rasmusson, 1983), maize (Tollenaar,

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Table 1
Sugarcane varieties grown, indicating year of release in Argentina, country of origin, and period in which the varieties were grown commercially.

Variety	Year of release in Argentina ¹	Country of origin	Commercial growth period	Relative maximum proportion of cultivated area in Argentina
TUC 26–45	1940	Argentina	1940–1960	+50% (1950) [*]
CP 34–120	1950	USA	1950–1970	wd
NCO 310	1960	South Africa	1960–Present	wd
NA 56–79	1964	Argentina	1964–Present	46% (1977) [*]
CP 48–103	1970	USA	1970–1880	7% (1977) [*]
NA 56–30	1970	Argentina	1970–1980	19% (1977) [*]
NA 63–90	1977	Argentina	1977–Present	25% (1987) [*]
CP 65–350	1987	USA	1987–1990	20% (1990) [*]
CP 65–357	1989	USA	1989–Present	33% (1998) [*]
TUCCP 77–42	1994	Argentina	1994–Present	32% (1998) [*]
LCP 85–384	2001	USA	2001–Present	77% (2010) ^{**}
RA 87–3	2005	Argentina	2005–Present	8% (2008) ^{**}
FAM 91–209	–	Argentina	–	–

wd = without published data (recommended by sugarcane breeders R.A Sopena and/or R. Fernández Ullivarri).

^{*} From Ahmed et al. (2007).

^{**} From Ostengo et al. (2012).

1991) soybean (Morrison et al., 1999), rice (Peng et al., 2000) and sunflower (de la Vega et al., 2007). However, to the best of our knowledge, no study has reported the physiological bases associated with genetic gains in sugarcane. This lack of studies in sugarcane might contribute to the slowing down in sugar yield gains worldwide. Such studies could help to determine the rate of return from investment in breeding programs, but they could also lead to faster progress in sugar yield gains.

As sugarcane is one of the most important energy sources for humans (FAO, 2010), we aimed to quantify the achievements made by sugarcane breeding since 1940 in Tucumán, the main growing area in Argentina, by identifying the main crop physiological bases responsible for such achievements. For this purpose, representative varieties released from the 1940s to the beginning of the 21st century were grown during three consecutive seasons.

2. Materials and methods

2.1. General

An experiment was carried out under rainfed field conditions in the province of Tucumán, the main sugarcane producing area of Argentina. The experiment was conducted in Famaillá (27°03'S, 65°25'W, 363 m.a.s.l.), in the experimental fields of the National Institute of Agricultural Research (INTA) during the 2010/11, 2011/12 and 2012/13 growing seasons. The soil is fertile and is classified as Aquic Argiudoll.

Rainfall from planting to 2011 harvest was 1417.1 mm; from 2011 harvest to 2012 harvest it was 992.3 mm; and from 2012 harvest to 2013 harvest it was 1069.3 mm. Soil N–NO₃ content after winter was approximately 45 kg ha⁻¹ (range 35–56) in all years. Fertilizers were broadcasted at tillering, applying 110 kg N ha⁻¹ in 2011/12 and 2012/13, whereas no fertilization was used in 2010/11.

2.2. Treatments and design

Sugarcane varieties that were important for the development of sugarcane breeding in Argentina (Table 1) were compared. They were selected or introduced to the production system by the breeding programs of “Obispo Colombres” Experimental Station of Tucuman, “Chacra Experimental” of Colonia Santa Rosa, Salta, and INTA of Tucuman that planted 80,000, 200,000 and 25,000 seedlings per year, respectively (R. Sopena, personal communication). These programs are characterized by sugar production (cane yield and sugar content) and diseases resistant as selection criteria.

The varieties included a widely grown self-pollination variety (TUC 26–45), 11 released sugarcane hybrids selected due to their success during at least one decade in farm crops in Tucumán, and an advanced breeding hybrid of INTA's sugarcane breeding program performing consistently well in several comparative trials.

Treatments were arranged in a randomised complete block design with three replications. Plots, consisting of five 10-m long rows that were 1.60 m apart, were planted at commercial cane densities on 24 August 2010 (Romero et al., 2009). Commercial harvests were performed on 20 September 2011, 26 August 2012 and 29 August 2013.

Weeds and insects were controlled or prevented using recommended products. Ratoon stunting disease was prevented using seed cane from treated nurseries or by treating the seed cane with hydrothermotherapy. Other bacterial or viral diseases that commonly occur in Tucuman (leaf mosaic virus or red stripe) were not considered because they are controlled only genetically. Rust was not present during the trials.

2.3. Sampling and measurements

Plant samples were taken from all experimental units at ripening. Samplings were performed on 30 June, 02 July and 10 June for the growing seasons 2010/11, 2011/12 and 2012/13, respectively. These dates are around the optimum harvest date for Tucuman.

Samples consisted of all plants at one meter from the three central rows and were taken on both sampling dates. The samples were used to determine the number of stems, average stem weight, cane yield, sugar content and sugar yield on a fresh basis (as sugarcane commercial final products are the fresh stems) (Eqs. (1)–(3)). During the 2010/11 and 2011/12 seasons total above ground dry biomass, dry stem weight, and the partitioning of total above ground dry biomass to stems and to sugar, and the partitioning of dry stem weight to sugar were also determined (Eqs. (4)–(6)).

$$\text{Sugar yield} = \text{Cane yield} \times \text{Sugar content} \quad (1)$$

$$\text{Cane yield} = \text{Number of stems} \times \text{Average stem weight} \quad (2)$$

$$\text{Sugar yield} = \text{Number of stems} \times \text{Average stems weight} \times \text{Sugar content} \quad (3)$$

$$\begin{aligned} \text{Partitioning of total above ground dry biomass to stems} \\ = \text{Dry stem weight} / \text{Total above ground dry biomass} \end{aligned} \quad (4)$$

Table 2
Mean squares of sugar yield, cane yield, sugar recovery, number of stems and average stem weight in three environments: 2010/11, plant cane; 2011/12, ratoon cane; 2012/2013, ratoon cane).

Source of variation	Sugar yield	Cane yield	Sugar content	Number of stems	Average stem weight
Environments (E)	164.47***	8845.05***	25.15***	78.60***	0.04
Variety (V)	79.70***	6966.37***	3.39***	46.05***	0.49***
E × V	6.70	625.17	0.54	6.02	0.02
Error	7.94	663.09	0.83	5.66	0.02

Significant at * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

$$\text{Partitioning of dry stem weight to sugar} \\ = \text{Sugar yield/Dry stem weight} \quad (5)$$

$$\text{Partitioning of total above ground dry biomass to sugar} \\ = \text{Sugar yield/Total above ground dry biomass} \quad (6)$$

Sugar content was measured by crushing the canes with an experimental mill of 10.5 kg cm^{-2} of pressure and 50% of juice extraction. The juice was analysed for brix (%; soluble solids) using a digital brixometer. After clarifying the juice using lead sub acetate, pol in juice (%; juice sucrose concentration) was determined using a digital polarimeter. Purity (%) was calculated by the quotient of pol in juice and brix (Eq. (7)), and pol in cane (%; cane sucrose concentration) was calculated from pol in juice and the Java's factor of 0.80 (Eq. (8)). Sugar content was calculated as in Eq. (9).

$$\text{Purity} = \text{Pol in juice/Brix} \times 100 \quad (7)$$

$$\text{Pol in cane} = \text{Pol in juice} \times \text{Java's factor}(0.80) \quad (8)$$

$$\text{Sugar content} = \text{Winter's factor} \times \text{Pol in cane} \\ \times \text{Sucrose extraction efficiency} \\ \times \text{Industrial efficiency} \quad (9)$$

where Winter's factor = $1.4 \times 41.51/\text{Purity}$ in first extraction juice; sucrose extraction efficiency = $\text{Purity in mix juice}/\text{Purity in first extraction juice} = 0.978$; industrial efficiency = 0.82.

Data from the three environments were subjected to an ANOVA. Genetic gains of sugar yield and other traits as well as associations between yield and its determinants were estimated by fitting the data to linear ($Y = a + b \times X$) or bi-linear ($Y = a + b \times X$ ($X \leq c$) + $b \times c$ ($X > c$)) regression models by means of curve-fitting software (Jandell, 1991), where a is the intercept, b the slope and c the X value at which maximum Y is reached. Then, bi-linear regressions were not used because they did not perform significantly better than the linear models.

When data were plotted against year of release it was assumed that the hybrid FAM 91–209 was released in 2010 because this

was the year in which this hybrid officially entered the external comparative trials of the breeding programme.

3. Results

In general, there were significant effects of environments and varieties for all the attributes analysed in the study, whereas their interaction was not significant (Tables 2 and 3). Based on this result and on the fact that yields from plant cane and ratoon cane are often very different, we present results for plant cane and for the average of first and second ratoon canes.

Genetic gains for sugar yield were 0.08 and $0.14 \text{ Mg ha}^{-1} \text{ y}^{-1}$ for plant and ratoon cane, respectively ($r > 0.71$; $P < 0.01$). Their 95% confidence limits were 0.04 and $0.11 \text{ Mg ha}^{-1} \text{ y}^{-1}$ for plant cane and 0.12 and $0.18 \text{ Mg ha}^{-1} \text{ y}^{-1}$ for ratoon cane.

There was a linear increase in sugar yield, cane yield and sugar content with the year of release of the varieties throughout the period from 1940 to 2010 (Fig. 1a–c). Thus, there were positive and linear associations between sugar yield and cane yield or sugar content. The association between sugar yield and cane yield was stronger than that of sugar yield and sugar content (Table 4).

The number of stems was significantly different among varieties (Table 2); these differences were not associated with their year of release (Fig. 1d). However, the average stem weight increased with the year of release of the variety (Fig. 1e). Thus, cane yield increase was not associated with number of stems, but it was linearly and positively related to average stem weight (Table 4).

An analysis of the main components of sugar content, juice sucrose concentration (pol in juice) and purity, revealed that the increases in sugar content with the year of release of the varieties was due to increases in pol in juice ($r > 0.58$; $P < 0.05$) for plant and ratoon canes, and in purity ($r = 0.63$; $P < 0.05$) only for plant cane (Fig. 2b–f).

Total above ground dry biomass and dry stem weight increased with the year of release of the varieties ($r > 0.71$; $P < 0.01$ and $r > 0.68$; $P < 0.05$, respectively) (Fig. 3a and b). There were linear and positive associations between total above ground dry biomass or dry stem weight and sugar yield or cane yield, whereas total above ground dry biomass or dry stem weight were only and poorly related with sugar content for plant cane (Table 3).

Breeding did not increase the partitioning of total above ground dry biomass to stems or to sugar (Fig. 3c and e) nor the partitioning of dry stem weight to sugar (Fig. 3d).

Table 3
Mean squares of total above ground dry biomass, dry stem weight, partitioning of total above ground dry biomass to stems and to sugar, and partitioning of dry stem weight to sugar in two environments: 2010/11, plant cane; 2011/12, ratoon cane).

Source of variation	Total above ground dry biomass (TAGDB)	Dry stem weight	Partitioning of TAGDB to stems	Partitioning of Dry stem weight to sugar	Partitioning of TAGDB to sugar
Environments (E)	17,118.72***	8885.81***	14.95	17,160.14***	8040.75***
Variety (V)	330.30***	163.01***	24.34	210.29	128.58
E × V	86.58	40.32	33.29	159.90	90.42
Error	67.49	37.52	30.14	276.54	103.17

Significant at * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

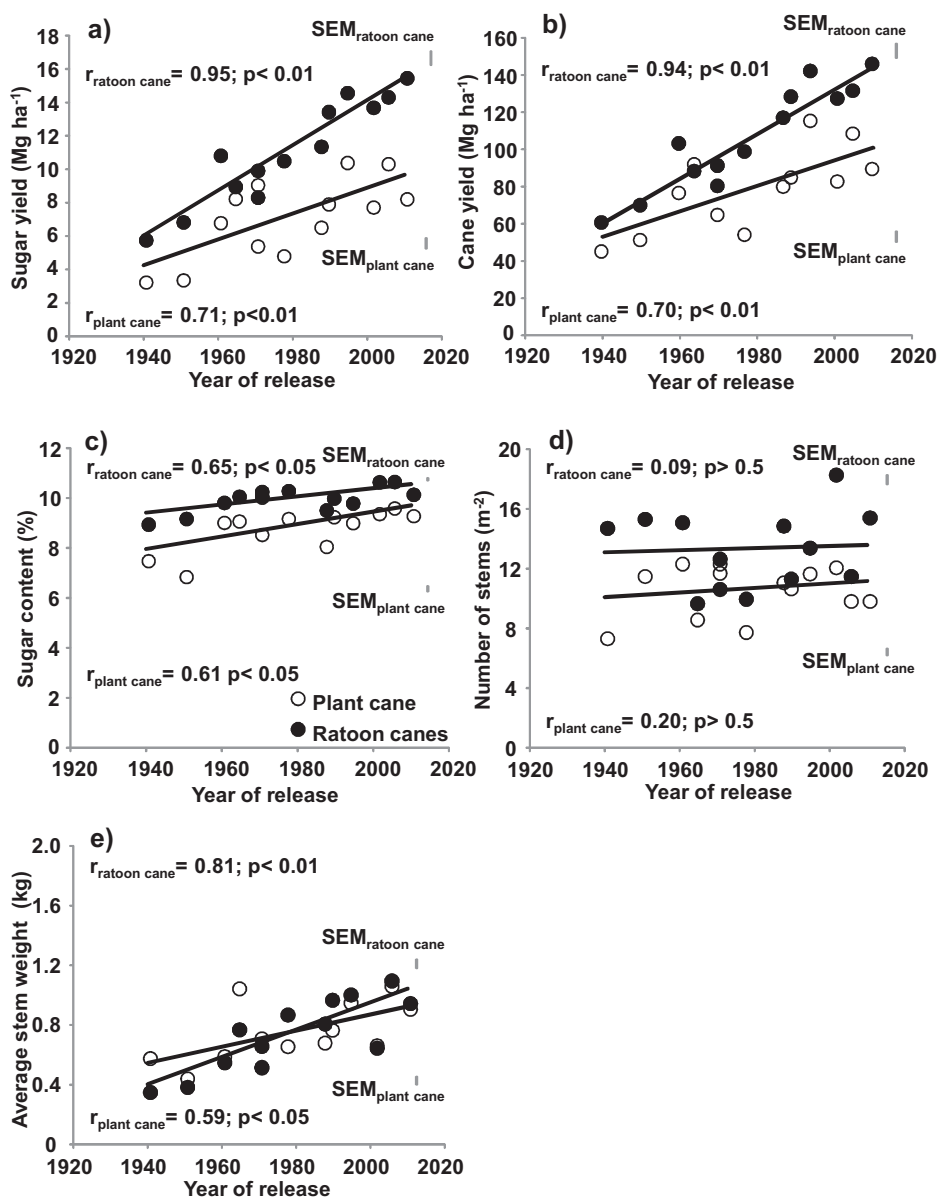


Fig. 1. Trends in sugar yield (a), cane yield (b), sugar content (c), number of stems (d) and average cane weight (e) with the year of release of sugarcane varieties grown at plant and ratoon ages. S.E.M stands for standard error of the means for each age.

Table 4

Correlation coefficients between sugar yield, cane yield, sugar recovery, number of stems, average stem weight and total above ground dry biomass for plant and ratoon cane.

	Plant cane						
	Sugar yield	Cane yield	Sugar content	Number of stems	Average stem weight	Total above ground dry biomass	
Sugar yield	–						
Cane yield	0.98**	–					
Sugar content	0.79**	0.67*	–				
Number of stems	0.32	0.34	0.16	–			
Average stem weight	0.82**	0.82**	0.59*	0.24	–		
Total above ground dry biomass	0.91**	0.88**	0.63*	0.40	0.62*	–	
	Ratoon cane						
	Sugar yield	Cane yield	Sugar content	Number of stems	Average stem weight	Total above ground dry biomass	
Sugar yield	–						
Cane yield	0.99**	–					
Sugar content	0.64*	0.58*	–				
Number of stems	0.15	0.42	0.10	–			
Average stem weight	0.82**	0.81**	0.58*	0.42	–		
Total above ground dry biomass	0.93**	0.91**	0.12	0.42	0.75**	–	

Significant at * $P < 0.05$ and ** $P < 0.01$.

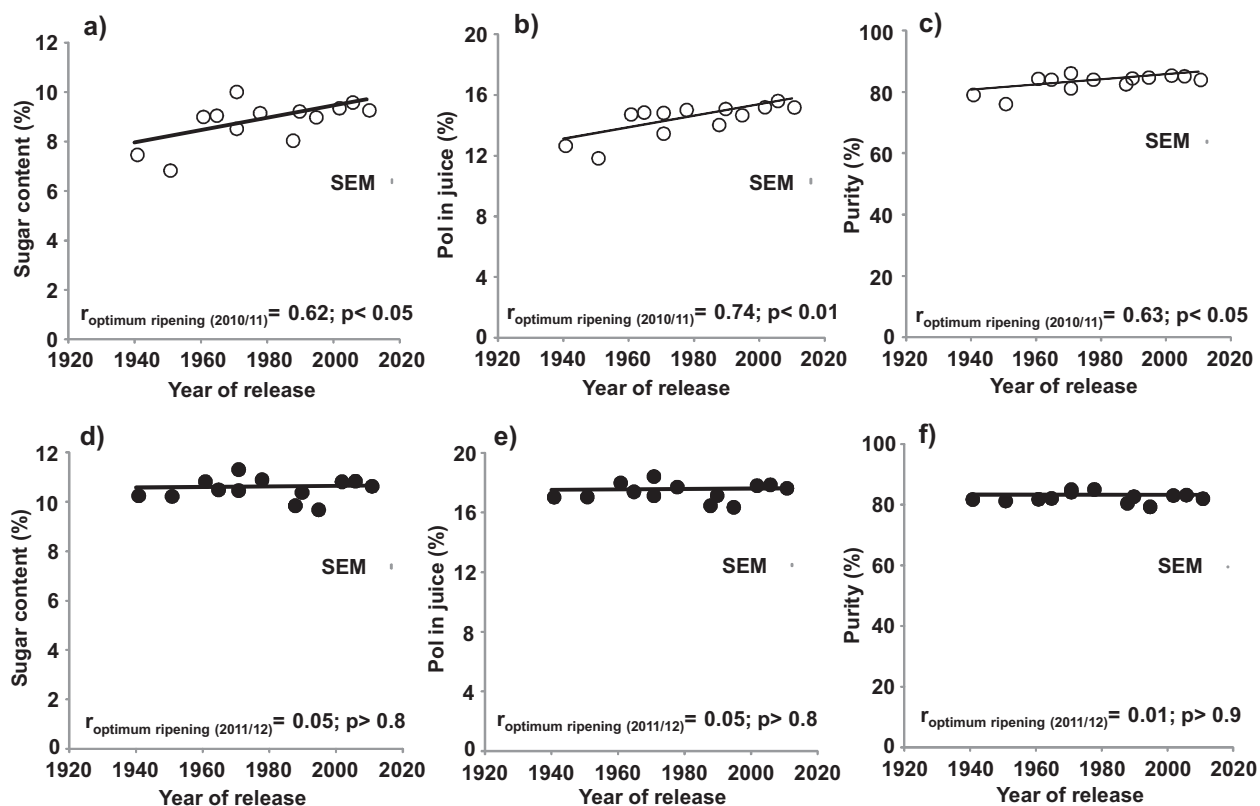


Fig. 2. Trends in sugar content (a and d), pol in juice (b and e) and purity (c and f) with the year of release of sugarcane varieties for plant (a–c) and ratoon canes (d–f). S.E.M stands for standard error of the means for each attribute and age.

4. Discussion

This is the very first study reporting the physiological bases for genetic gains in sugarcane during the last 75 years in Argentina. Genetic gains in sugar yield in Tucumán were 0.08 and 0.14 Mg ha⁻¹ y⁻¹ for plant and ratoon cane, respectively. Many other studies conducted during the last century reported increases in genetic gains ranging from 0.09 to 0.18 Mg of sugar ha⁻¹ y⁻¹ in different environments, such as Colombia (Cock, 2003), Hawaii (Wu and Arcinas, 2004), USA (Edmé et al., 2005), Australia (Jackson, 2005; Ming et al., 2006; Cox and Stringer, 2007) and Argentina (Fernandez de Ulivarri et al., 2009).

Genotypic by environment interaction was not significant. However, the fact that trend lines on Figs. 1–3a are not parallel indicates possible interactions that would have not been detected because of the small sample size (4.8 m²) that resulted in an average CV for all attributes of 19%. Larger sample size would have produced smaller CV (Thomas et al., 1993).

There was a linear increase in sugar yield with the year of release of the varieties throughout the period from 1940 to 2010. Comparing the quotient 2010 to 1940 for sugar yield and its main determinants (values calculated with the linear equation for each attribute and for the average of plant and ratoon canes) we relativize breeding progress. Sugar yield increased 2.44 times mainly associated with an increase in average stem weight (1.97 times), since sugar content increased only 1.15 times and number of stems slightly varied (1.08 times).

Surprisingly, there was not a positive association between number of stems and the year of release of the varieties cultivated in the Tucumán sugarcane area. As cane yield was positively associated with the year of release of the varieties, cane yield and number of stems were not related. The probable reason for the lack of improvement in the number of stems could be the higher number of stems

of the oldest varieties (15 stems m⁻² for ratoon cane for the average of the three oldest and three newest varieties). The linear increase in sugar yield through the period 1940 to 2010 found in the present study differed from findings of Cock (2003), Wu and Arcinas (2004), Edmé et al. (2005), Jackson (2005), Ming et al. (2006), Cox and Stringer (2007) and Fernandez de Ulivarri et al. (2009) that reported for many sugarcane areas of the world that actually there has been a slowing down in sugar yield increases since the 1980s. The difference in sugar yield trends between the present study and those reported elsewhere could be explained by the association of sugar yield with both, cane yield (through average stem weight) and sugar content in our study, whereas in the other studies sugar yield was mainly, if not only, associated with cane yield, with little progress in sugar content. The varieties released in Argentina, however, had low sugar content (Fig. 4) that probably facilitated breeding increase of sugar content. The exception of the reported studies was that of Edmé et al. (2005), who found an increase of sugar yield associated with cane yield and sugar content for sugarcane growing in USA from 1968 to 2000. However, they reported genetic progress through analysis of huge datasets compiled from different experiments and years and not from experiments exploring the varieties commercially grown in the same environment during a single period. Although both methods are valid, determining genetic gains and associated attributes by conducting experiments with the varieties representative of yield progress during a single period and under the same experimental conditions, appears to be the best alternative in order to minimize the effect of management on genetic gains (e.g. Austin et al., 1980; Wych and Rasmusson, 1983; Tollenaar, 1991; Morrison et al., 1999; Peng et al., 2000; de la Vega et al., 2007).

There is little or no association between cane yield and sugar content under different environments and sets of varieties. This can be observed in Fig. 4, which shows the analysis of the results

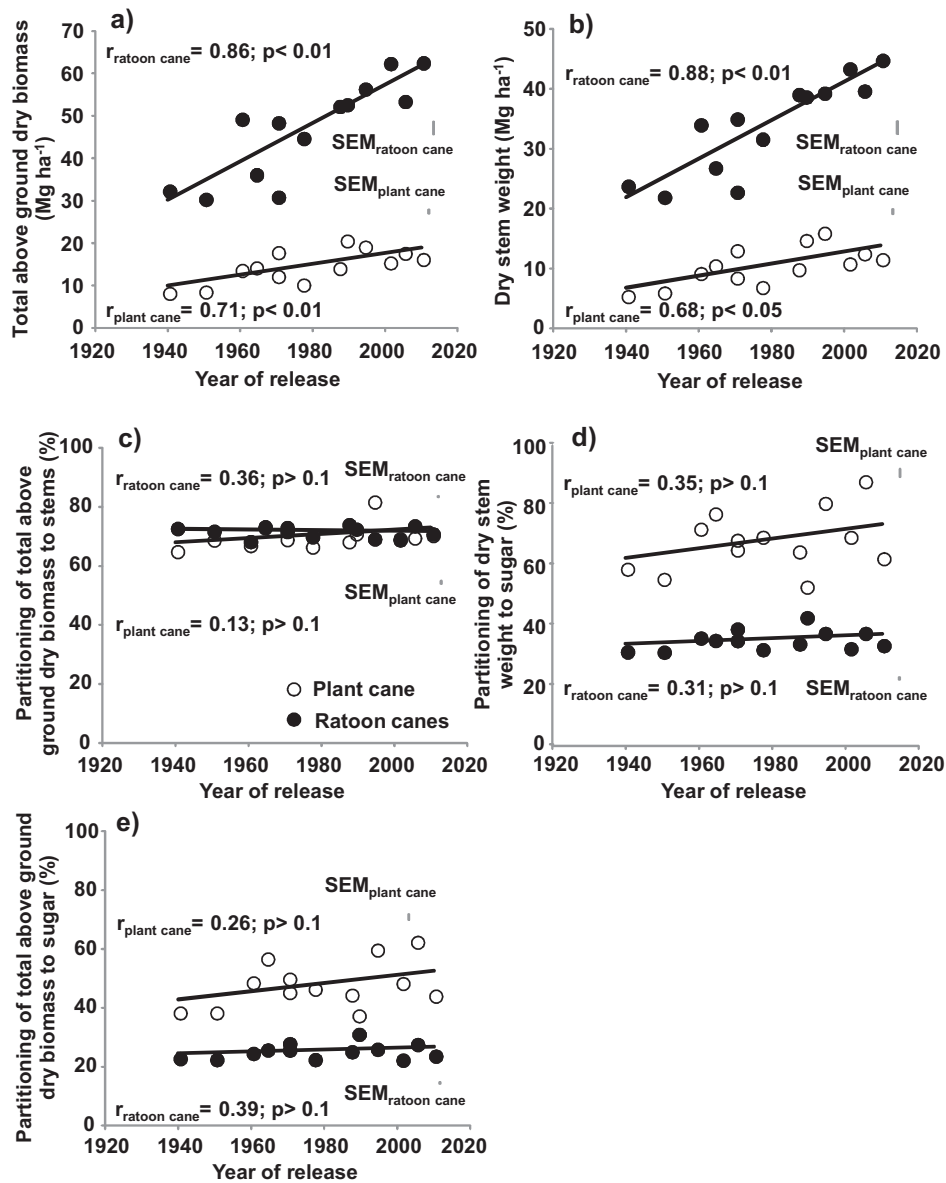


Fig. 3. Trends of total above ground dry biomass (a), dry stem weight (b), partitioning of total above ground dry biomass to stems (c), partitioning of dry stem weight to sugar (d), and partitioning of total above ground dry biomass to sugar (e) with the year of release of sugarcane varieties grown at plant and ratoon ages. S.E.M stands for standard error of the means for each age.

of the present study and those reported by De Silva and De Costa (2004), Jackson (2005) and Singh et al. (2006).

Different genetic basis could explain the lack of association between cane yield and sugar content. For instance, the most important contributor of high sucrose is *Saccharum officinarum*, whereas *Saccharum spontaneum* is responsible of increments in cane yield (Jackson, 2005). As hybrids cultivated nowadays contain germplasm of both species, selecting for increases in cane yield does not necessarily imply increases in sugar content.

Sugar yield increases were associated with increases in total above ground dry biomass and dry stem weight and not with increases in total above ground dry biomass partitioning to stems or to sugar, nor to the partitioning of dry stem weight to sugar. This is in agreement with findings of Russell (1991) and Tollenaar (1991) for maize (also a C4 species), who reported that yield increases were mainly associated with increases in total above ground dry biomass rather than with the partitioning of total above ground

dry biomass to harvested organs. However, Echarte and Andrade (2003) comparing maize hybrids released in different eras showed high dry matter partitioning to harvested organs per plant in modern maize hybrids. In many other crops, such as wheat (Austin et al., 1980), barley (Wych and Rasmusson, 1983), soybean (Morrison et al., 1999) or rice (Peng et al., 2000), yield increase was associated with increases in the partitioning of total above ground dry biomass to harvested organs.

The absence of increments in the partitioning of total above ground dry biomass to stems in our study could be associated with the already high values that old varieties show for this variable (ca. 70%).

These findings revealed that the varieties continuously released by sugarcane breeding programmes in Argentina have not reached a “plateau” in sugar yield. The main crop physiological bases responsible for such increments were firstly the average stem weight and secondly sugar content, since the number of stems

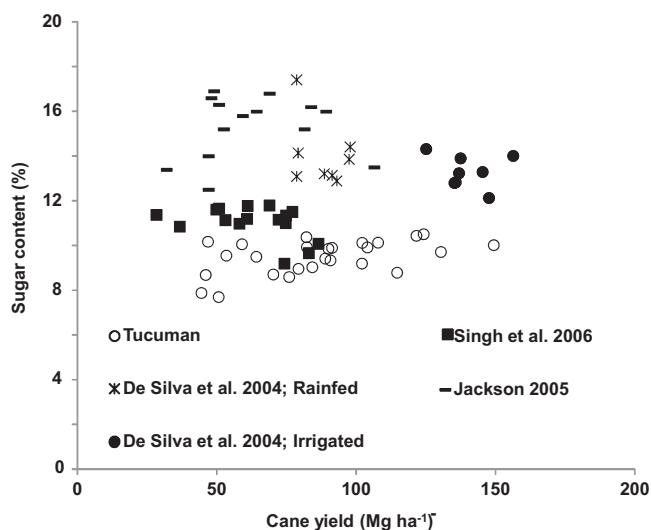


Fig. 4. Comparison between sugar content and cane yield for the results of the present study (Tucuman) and those reported in the literature.

varied only slightly. The average stem weight increased in association with the total above ground dry biomass and not with the partitioning of the total above ground dry biomass to stems or sugar, nor to the partitioning of dry stem weight to sugar.

If breeders include more physiological attributes in their selection process, they would increase sugar yield by strides instead of steps. This attributes could be the partitioning of total above ground dry biomass to stems and sugar, the partitioning of stem weight to sugar, and attributes related to the resource capture and use efficiency such as nitrogen and water use efficiency, as can be seen in the second part of this paper.

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