AGRO-PHYSIOLOGICAL CHARACTERISTICS UNDERLYING THE SUCROSE ACCUMULATION PATTERN OF EARLY AND LATE VARIETIES

AR NAYAMUTH, BF CHEEROO-NAYAMUTH AND GC SOOPRAMANIEN

Sugar Industry Research Institute, Reduit, Mauritius.

Abstract

In Mauritius, sugarcane (Saccharum officinarum) is harvested between June and November. The first crops harvested have low sucrose contents and juice punties, which result in low milling efficiencies. In order to improve the selection of varieties with higher sucrose contents for the start of the crop season, a better understanding of sucrose accumulation is necessary. A large scale trial was therefore implemented under non-limiting water and nutrient conditions to study sucrose accumulation with respect to the crop's agronomic and physiological characteristics. The results presented in this paper pertain to a first ratoon crop of one typical early variety (M 13/56) and one late variety (R 570) harvested in July and October respectively.

The results showed that the early variety differed agronomically and physiologically from the late variety. The early variety produced fewer tillers and had an earlier formation of stalks. A higher number of shorter internodes with smaller leaves were produced in the early variety. This resulted in a lower leaf area index (LAI), a less dense canopy and reduced light interception. The early variety also exhibited a more efficient partitioning of above-ground dry matter into cane as well as into sucrose. This was associated with lower levels of reducing sugars and a lower reducing sugar to sucrose ratio.

The early variety accumulated higher amounts of cane and sucrose at the onset of winter, in about May. After May, the late variety had higher rates of cane and sucrose accumulation. It was concluded that sucrose accumulation was more genetically determined in the early variety. Selection procedures may therefore need to be adjusted so that varieties with early sucrose accumulation are not rejected because of comparatively low cane and sucrose yields, if selection takes place later in the harvest season.

Introduction

In Mauritius (20.5°S and 57.5°E), the sugarcane harvest season extends from mid-June to November, with peak sucrose contents in most varieties being reached around the months of September and October. Hence, as in most cane growing countries, the first fields harvested have not attained optimum maturity. The juice quality from such cane is poor, contributing to lower milling efficiencies. Cultural practices, such as chemical ripening and drying-off, are used to improve sucrose content early in the harvest season and breeders have attempted to select varieties with relatively high sucrose contents for the early part of the season. The quest for true early varieties, however, remains difficult and a better understanding of the mechanism of sucrose accumulation could assist with this.

The sugarcane crop cycle has been reported to comprise distinct vegetative (tillering and elongation) and ripening (sucrose accumulation) phases (Soopramanien, 1979). Under Mauritian conditions, the ripening phase is considered to start with the onset of winter, about the month of May. Sucrose accumulation patterns, however, have been reported to differ between varieties, these differences being attributed to their genetic potential, the environment, or both. According to Hebert and Rice (1971), early varieties produce more sugar per ton of cane at the start of the crop season than late varieties, but accumulate less sugar during the subsequent ripening phase. Cuenda and Mariotti (1986) confirmed this finding when they obtained a strong negative association between early sucrose content and the subsequent rate of ripening. Julien and Delaveau (1977) stressed that determination of cane maturity on a fresh weight basis could be erroneous and explained the ripening process in terms of cane dry matter. Most studies have followed sucrose accumulation after the onset of the ripening phase and few detailed studies have reported on sucrose accumulation during the vegetative phase.

In this paper, sucrose accumulation in the first ratoon crops of one early and one late ripening variety, grown under non-limiting water and nutrient conditions, will be discussed in terms of total dry matter produced and its partitioning into different plant parts. The relationship between sucrose accumulation and different agronomic and physiological characters is also discussed.

Materials and Methods

The trials were planted at Belle Vue (BV) with six commercial varieties (M 13/56, M 555/60, M 695/69, M 292/70, R 570 and S 17) recommended for different harvest dates over the local harvesting season. The row spacing was 1.62 m. The sets were subjected to hot water and fungicide treatments before planting. Fertilizer was applied at planting and
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about one month after harvesting the plant crop, based on the expected cane yield and assuming that 1.2 kg of N, 0.6 kg of P₂O₅, and 1.8 kg of K₂O were utilised per ton of cane. Full crop water requirements, based on the formula of Penman (1963) were provided daily by drip irrigation. In order to eliminate the differential effects of water stress on ripening between the varieties, drying-off was not practised. Half of the field was harvested during the second week of July (H1) and the other during the first week of October (H2). A split-plot design with four replicates was adopted with harvest dates as the main plots and varieties as the split-plots. The plot size was 6 rows of 49 m. Detailed agronomic and growth analysis data were collected at four to six week intervals.

Soil type and climate

BV is located at an altitude of 69 m and its long-term annual rainfall is 1 400 mm. The soil is a low humic latosol of basaltic origin (Parish and Feillafé, 1965), i.e. a tropic haptosol in the USDA System (Aridige and Wong You Cheong, 1975). It is a dark reddish brown, silty clay or clay with low bulk density (1.1 g/cm³), high clay content (25-75%), high iron content (21-25 w/w Fe₂O₃) and a mean depth of 1.0-1.7 m. Iron oxide bonds the clay into sillo-sized particles, so the soil is free draining and has a saturated hydraulic conductivity of 1 mm/day. Long term monthly means of rainfall, temperatures and solar radiation are given in Table 1.

Table 1. Long term climatic data from the Belle Vue trial site.

<table>
<thead>
<tr>
<th>Month</th>
<th>Rainfall (mm)</th>
<th>Max temp (°C)</th>
<th>Min temp (°C)</th>
<th>Radiation (Langleys)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan</td>
<td>188.2</td>
<td>30.6</td>
<td>22.6</td>
<td>678.8</td>
</tr>
<tr>
<td>Feb</td>
<td>218.3</td>
<td>30.6</td>
<td>22.7</td>
<td>556.5</td>
</tr>
<tr>
<td>Mar</td>
<td>202.1</td>
<td>29.1</td>
<td>22.5</td>
<td>594.4</td>
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<tr>
<td>Apr</td>
<td>147.7</td>
<td>27.6</td>
<td>21.5</td>
<td>501.5</td>
</tr>
<tr>
<td>May</td>
<td>89.4</td>
<td>26.0</td>
<td>19.3</td>
<td>466.3</td>
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<tr>
<td>Jun</td>
<td>63.8</td>
<td>25.3</td>
<td>17.2</td>
<td>414.7</td>
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<td>Jul</td>
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<td>25.3</td>
<td>16.6</td>
<td>446.6</td>
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<td>Aug</td>
<td>67.5</td>
<td>26.2</td>
<td>16.8</td>
<td>511.6</td>
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<tr>
<td>Sep</td>
<td>54.9</td>
<td>27.4</td>
<td>17.4</td>
<td>556.6</td>
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<td>Oct</td>
<td>42.5</td>
<td>28.9</td>
<td>18.7</td>
<td>666.0</td>
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<td>49.6</td>
<td>29.8</td>
<td>20.6</td>
<td>677.5</td>
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<tr>
<td>Dec</td>
<td>133.8</td>
<td>28.1</td>
<td>21.4</td>
<td>674.7</td>
</tr>
<tr>
<td>Mean</td>
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<td>28.1</td>
<td>19.7</td>
<td>563.3</td>
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<td>SD</td>
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<td>0.3</td>
<td>0.3</td>
<td>227.1</td>
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<td>CV %</td>
<td>30.0</td>
<td>1.0</td>
<td>1.6</td>
<td>3.4</td>
</tr>
</tbody>
</table>
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Antoine and Froberville (1964) and De Saint Antoine (1968). Juice from another sub-sample was extracted in a hydraulic press (200 bars/2 minutes) and stored in a freezer after the addition of 0.5 cm³ of mercuric chloride as preservative per liter of juice. The thawed juice was analysed for sucrose content using the Jackson and Gillis modification (method IV) of the Clerget Method (Anon, 1991) and for reducing sugar content using the alkaline iodosyanide colorimetric method (Chiranjivi Rao and Asokan, 1974).

Tiller density, the fraction of dry matter in the different components of the above-ground biomass, and cane quality parameters were used to convert the fresh weight of the different plant components to yield per hectare on a dry weight basis and various ratios were computed.

Results

The results obtained from the early variety M 13/56 and the late variety R 570, which were most contrasting in their sucrose accumulation pattern, are presented. The other varieties were intermediate in their behaviour.

AGRONOMIC CHARACTERISTICS

Tiller density

The pattern of tiller density (Figure 1) showed that for either harvest date, peak tiller density was attained at about the same time in both varieties but the late variety produced significantly more tillers. A higher tiller mortality rate was recorded in the late variety but it maintained a slightly higher tiller density up to harvest. Furthermore, the late variety exhibited a distinct tillering phase followed by a distinct elongation phase. By contrast, in the early variety the first tillers started to elongate during the tillering phase itself.

Stalk height at apex

Irrespective of harvest date, stalks were taller in the early variety during the first part of the season (up to about five months after harvest) than in the late variety (Figure 2). This was due to an earlier start of elongation of a few older tillers in the early variety. Tiller elongation in the late variety began later but then exhibited a higher rate of elongation, and this resulted in longer millable stalks at harvest.

Number and length of internodes

Data recorded in May showed that the early variety had a higher rate of production of internodes and leaves and had produced about eight internodes more than the late variety in the July and October harvested crops respectively. At both harvest dates the late variety had longer internodes (Figure 3).

Figure 1. Tiller density in 1R crops of early maturing variety M13/56 and late maturing variety R570.

Figure 2. Evolution of stalk height in 1R crops of early maturing variety M13/56 and late maturing variety R570.
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Figure 3. Number and length of internodes of M13/56 and R570 in May.

Canopy characteristics
Although the rate of leaf production was greater in the early variety, the maximum numbers of green leaves (± 10) maintained per stalk in the two varieties were similar. Maximum leaf size in the early variety was considerably smaller (400 cm²) than in the late variety (650 cm²). The smaller leaf size and lower tiller density of the early variety resulted in a lower LAI in this variety irrespective of harvest date (Figure 4). The difference in LAI between the early and late variety was of the order of 2.0 and this resulted in higher light interception in the late variety (about 10% in the stable canopy phase).

Physiological characteristics
Dry matter accumulation and partitioning
Similar trends in the rate of accumulation of total above-ground biomass at the two harvest dates were recorded in the two varieties but the late variety had accumulated more biomass at both harvest dates (Figure 5). This difference was attributed mainly to more light being intercepted in the late variety. Additionally, it appeared that, in contrast to the late variety, the growth rate of the early variety was checked by the fall in temperature associated with the onset of winter, from approximately the start of May.

Of the total above-ground biomass, more dry matter was partitioned into stalks in the early variety than in the late variety. This difference was maintained throughout the crop cycle irrespective of harvest date (Figure 6). Within the cane fraction, the early variety partitioned more dry matter into sucrose compared with the late variety.

Juice quality
Irrespective of harvest date, there was a lower proportion of reducing sugars in the juice of the early variety throughout the crop cycle (Figure 7). This difference was greatest during the early part of the season but gradually decreased as the crop aged. Differences were still recorded between the two varieties at the July harvest but there was little difference at the time of the October harvest.

The rate of increase in sucrose % juice (Figure 8) showed that, for the early harvest date, sucrose content was higher in the early variety throughout the crop cycle and the difference was greatest at the start of the crop cycle. The early variety had already accumulated substantial amounts of sucrose when the late variety started accumulation. Both varieties maintained similar rates of sucrose accumulation up to the time when daily temperatures started to fall at the onset of winter in May. From that time, the late variety accumulated sucrose at a slightly greater rate. For the later harvest, a similar relationship between the sucrose contents of the two varieties was observed but, in this case, the initially greater
rate of sucrose accumulation of the early variety eventually disappeared completely and at harvest the late variety had a higher sucrose content.

Cane and sucrose yields
Cane and sucrose yields and sucrose contents just before the onset of winter, i.e. in 10-month old July harvested and 7-month old October harvested crops, are compared in Figure 9 with harvest data for 12-month crops. These data show that the early variety maintained its advantage in terms of sucrose yield over the late variety up to the pre-harvest dates, despite the late variety producing a significantly higher cane yield. The higher sucrose production up to the onset of winter (i.e. the start of the maturation phase) in the early variety was attributed to a significantly higher sucrose content. This advantage had disappeared at the July harvest due to the higher cane yield of the late variety. As expected, the productivity of the late variety exceeded that of the early variety for the late harvest date because of both its higher cane yield and final sucrose content.

Discussion
Hatch et al. (1963) described the enzymatic control of sucrose accumulation in sugarcane storage tissue and Haten and Glasziou (1963) demonstrated a linear relationship between acid invertase activity and the rate of elongation of immature internodes as well as between neutral invertase activity and sucrose storage. This study confirms these findings in the late variety but not the early variety. In fact, the early variety accumulated a major part of its sucrose during the stalk elongation phase, when conditions were conducive to growth rather than ripening. This could be attributed to a higher efficiency of sucrose accumulation in the early variety. These results agree with those of Singh and Venkatarama (1983).

From the start of the crop cycle, the partitioning of photosynthate in the two varieties differed considerably. Whereas a major proportion of the dry matter was diverted towards the formation of tillers in the late variety, in the early variety some of the photosynthate was diverted to the formation of internodes that were available as 'sinks' during the tillering phase. The higher rate of tiller mortality in the late variety is also indicative of a poorer utilisation of photosynthate.

The early variety produced shorter internodes with smaller leaf blades more rapidly than the late variety. This could be an indication of the presence of smaller storage cells in the early variety favouring sucrose accumulation (Macecoli, 1971). It is also possible that, throughout the crop cycle, less photosynthate was utilised to maintain the lower leaves in the early variety, thus leaving more for storage.
The less extensive root system of the early variety, reported by Larcie (1995), might also have contributed to the more efficient partitioning of dry matter into cane and sucrose. This poorer root system might also have limited the availability of nutrients, thus causing stress that could have favoured the partitioning of dry matter into sucrose. This might have been associated with lower auxin levels in the early variety (Sacher and Glasziou, 1962).

This study confirms the findings of Julien and Delaveau (1977) that early varieties are more efficient in partitioning cane dry matter into sucrose during the initial part of the crop cycle and with little increase in the ripening phase. Conversely, late varieties require the colder temperatures of the ripening phase to stimulate the rapid accumulation of sucrose towards the end of the harvest season.

This study also showed that the 'variety by environment' interaction that is apparent at harvest can be separated into genetic and environmental components with regard to ripening. It appears that sucrose accumulation is mostly genetically controlled in early varieties, in contrast to it being predominantly influenced by the environment in late varieties.

Moreover, since early varieties maintain their quality and yield advantages over late varieties only up to May, it is apparent that, if selection is undertaken after that date, the 'real' early varieties will be discarded, since the main selection criteria are cane and sucrose yield. Accordingly, the timing of selection should be adjusted so as not to lose this potential. The commercial exploitation of early varieties is of the utmost importance in sugarcane producing countries that have long crop seasons and in countries where conditions are not conducive to ripening.

**Conclusions**

This study has shown that the early and late varieties differed agronomically, physiologically and biochemically. Tillering and stalk elongation occurred in distinct phases in the late variety, whereas in the early variety the primary shoots started to elongate first followed by the successive production of tillers. The early variety produced shorter stalks with higher numbers of internodes at harvest. Both varieties maintained similar numbers of green leaves per stalk, but the tiller density and mean leaf size of the early variety were smaller. This resulted in a smaller LAI and lower light interception efficiency in the early variety. Despite these limitations, the early variety was more efficient at partitioning biomass into cane and sucrose. The combination of earlier stalk elongation, more efficient partitioning of dry matter and a lower reducing sugars to sucrose ratio contributed to higher cane and sucrose yields of the early variety in the first half of the 12-month crop cycle. These findings point to the possibility...
of different enzymatic and hormonal balances in early and late varieties.

The early variety accumulated substantial sucrose during the first half of the cycle, i.e., in the period more favourable for vegetative growth in most varieties. In contrast, the late variety accumulated sucrose most rapidly after the onset of winter, when conditions were no longer conducive to growth. This indicates that sucrose accumulation is more genetically determined in the early variety, in contrast to the predominately climatic determination of sucrose accumulation in the late variety. The timing of selection for early ripening needs to be adjusted so that this is not overlooked.

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