HAVE WE REACHED PEAK CCS?

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KEYWORDS: Sucrose Content, Carbon Partitioning, Breeding, Physiology, Molecular Biology.

Abstract

AN INCREASE in commercial cane sugar (CCS) is up to 1.8 times more valuable than a sucrose yield increase due to improved cane yield, because increased CCS does not attract high marginal costs in harvesting, transport and milling as does increased cane yield. Despite the priority in research and development investment to increasing CCS in past decades, industry mean CCS has fluctuated between 13 and 14% over the past 15 years with no obvious trend upward or downward. In this paper we consider limits to CCS and sucrose content in sugarcane and what may be done to address these limits. The maximum CCS in commercial cane delivered to mills in Australia appears to be about 18% and, while levels of sucrose in internode tissue measured in carefully controlled glasshouse conditions is only 3% units higher, we suggest that future efforts concentrate on the gap of 4 to 5% units between the highest observed CCS levels and the industrial average. This gap arises because of genetic responses to environmental factors and age, in contrast to a bio-physical limit to sucrose content already reached, and because of extraneous matter with little or no CCS. There is an opportunity to manage crops and select varieties that have higher CCS earlier in the season, and with better response to environmental factors reducing CCS. There is some evidence suggesting high CCS genotypes may be sensitive to factors affecting stem elongation. Moderate reductions in expansive growth will reduce cane volume and weight without sacrificing photosynthesis, leading to improved CCS. Ripeners could be re-evaluated with a better understanding of ripener, water, temperature and genotype interactions possibly using controlled conditions of the glasshouse. Reasons for the apparent limited progress in breeding programs in leading to increased industry CCS are not clear, but some suggestions are made for a re-evaluation of past approaches.

Introduction

In Australia, commercial cane sugar (CCS) is a measure of recoverable sugar and mean industry CCS has fluctuated between 13 and 14% over the past 15 years with no obvious trend upward or downward (Anon, 2009). CCS is highly correlated with and of similar magnitude to sucrose content on a fresh weight basis when both exceed 10% (Muchow *et al*., 1993). However, CCS may be substantially lower than sucrose content in immature cane or suckers due to high levels of reducing sugars relative to sucrose. An increase in sucrose yield due to improved CCS is up to 1.8 times more valuable from a 'whole of industry' perspective than a sucrose yield increase due to improved cane yield (Jackson *et al.,* 2000) because increased cane yield attracts marginal costs in

harvesting, transport and milling whereas the marginal costs are much less for increased CCS. Even if the Australian sugar industry, as expected, moves progressively toward obtaining increased revenue from energy to supplement that from sugar, the latter is still widely expected to be the most valuable component of sugarcane biomass for several decades.

In this paper, we consider all levels of research from molecule to mill in order to assess limits to CCS in sugarcane. We also provide perspectives on the question posed in the title, and suggestions on approaches to overcome constraints to achieving higher CCS.

CCS determined at the mill

What is the highest CCS measured at the mill?

In the Burdekin region, which has the highest CCS levels in the Australian industry, weekly CCS determined at the mill exceeded 16% for 1 in 5 weeks of September and for 1 in 10 weeks of August and October during 1992 to 2003 (Figure 1). Over this period 770 tonnes were delivered with CCS>17.5% but none had CCS>18%. CCS was highest during August to October and lowest from December to May when less than 7% of total cane tonnage was crushed. Median CCS was 14.7%, which is similar to the long-term industry mean. Thus, 18% appears to be about the limit for CCS delivered to the mill in the Burdekin though individual consignments may have achieved slightly higher CCS than this.

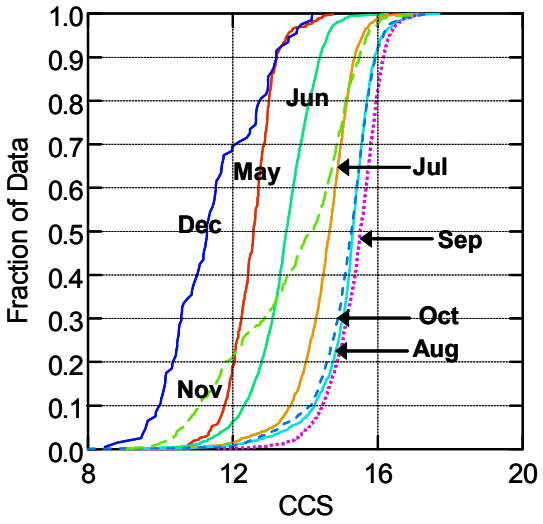

Fig. 1—Cumulative frequency distribution of weekly mean CCS at Burdekin mills for 1992 to 2003.

Breeding progress, or not?

Using CCS determined at the mill, Cox and Stringer (2007) reported a gain of about 0.03 CCS units per year between 1970 and 2004 and Burnquist *et al.* (2010) reported a gain of 0.04 units per year between 1983 and 2006 for the Australian sugarcane breeding program. The same studies also reported cane yield gains of about 1.6% per year assuming a starting cane yield of 80 t/ha. Considering the high emphasis given to CCS in the Australian breeding program, apparent genetic gains reported for CCS may be considered to be small compared to advances in other traits such as disease resistance.

Direct comparisons of historical sequences of cultivars in field trials have also been done, but only on a very small scale, and none recently. Wallis (2001) reported on results from a trial in the Atherton region which showed no discernable increases in CCS in released cultivars since the

1960s, but important gains in cane yield. Similar results were found in field trials conducted by CSR Limited on historical sequences of varieties (Jackson, 2005).

Underlying genetic gain in breeding programs may be best documented by examining rates of gain in breeding values of parents. Breeding value is a measure of the mean performance of progeny from a parent clone. Rattey *et al.* (2004) reported low or zero gains in breeding value for both economic value and CCS of parents since the 1960s, with some old parents (before 1970) still producing commercial cultivars and having high breeding values compared with the best, more recent parents. Inspection of recent data (not reported here) suggests no obvious changes to conclusions by Rattey *et al.* (2004). Several reasons for lack of progress in breeding programs for CCS have been hypothesised (Jackson, 2005), but actual reasons remain unclear. However, the lack of clear progress suggests that alternative approaches to parental improvement and mating designs to those applied in recent decades should be considered and evaluated.

Despite a general picture of limited progress from breeding for higher CCS reported above, some examples of 'one-off' contributions from recently released cultivars are apparent. Q200$^{\phi}$ was released in far north Queensland in 2000 and has since provided a mean CCS of 14.3% at the mill compared with 13.0% for the average of all other cultivars (Berding and McIntyre, 2010). Productivity data on KQ228$^{\phi}$, released in 2005 in the Burdekin region, also shows a marked improvement of 2 units in early season CCS over other cultivars, although CCS for this variety then declined more rapidly later in the 2010 season compared with other varieties, due at least in part to its suckering propensity (Figure 2).

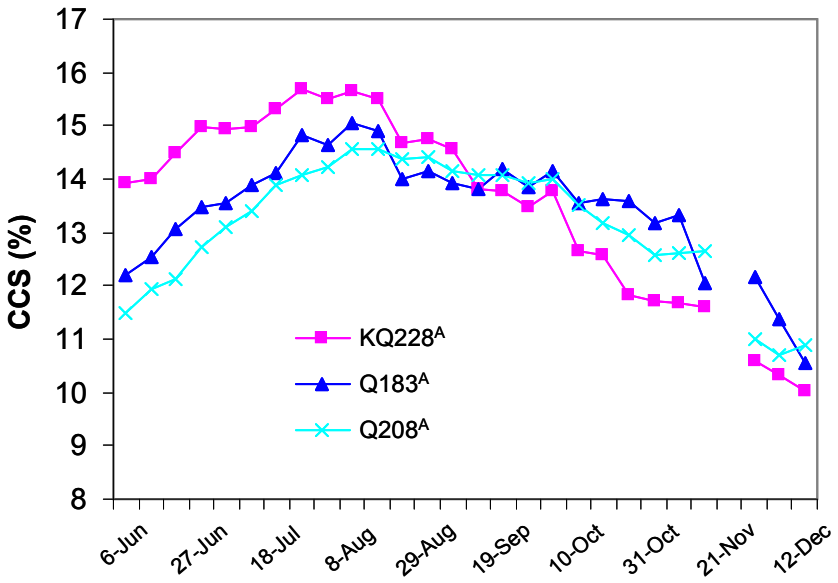

Fig. 2—CCS data from 2010 in the Burdekin region, for the three major varieties (KQ228$^{\phi}$, Q183$^{\phi}$ and Q208$^{\phi}$).

Field to mill CCS

In the wet tropics, CCS was shown to be about 3% units less than the sucrose content of sound stalks predominantly through the dilution effect of damaged stalks and extraneous matter (Berding *et al.,* 2002). Sound stalks making up 54 to 63% of the crop in the field contained 15.5 to 16.5% CCS. Damaged stalks, comprising about 16 to 20% of the crop, contained 7 to 12% CCS, and CCS was negligible in extraneous matter which comprised nearly 19% of the crop in the field and 13 to 19% in mill consignments (Berding *et al.,* 2002). Berding *et al.* advocated a cleaning

process either in the field or at the mill to reduce the amount of extraneous matter being delivered, but the economics of such a system was not considered. The rapid decline in CCS that sometimes occurs at the Tully mill was thought to arise from these dilution effects (Lawes and Lawn, 2005). Kingston (2002) accounted for 47 to 55% of the weekly variation in CCS at two mills in the tropics and two in the subtropics on the basis of temperature and rainfall as well as day-of-year which seems to have accounted for some unknown seasonal variable. However, Kingston's empirical formula could not account for the rapid decrease in CCS toward the end of the season, which was blamed on suckering. When lodging was prevented with scaffolding, CCS increased by 3 to 12%, the response decreasing with time after lodging due to the declining influence of dead stalk material in the sample (Singh *et al.,* 2002). Harvesting soon after lodging may be advised if suckering is the main cause of reduced CCS but delaying harvesting may be a better option if stalk death is the main cause (Singh *et al.,* 2002) because the contribution of suckers to consignments would tend to increase with time after lodging while the contribution of dead stalks would tend to decline.

Given the large influence of lodging, stalk damage and extraneous matter on CCS, it may be important for breeders to consider these traits along with CCS of sound stalks in the selection program. Currently, predictions of economic value in breeding programs are biased by measuring the weight of commercially harvested cane yield in plots but assuming all yield has the CCS of whole sound stalks. The impact of this assumption should be reviewed in the light of disappointing genetic gains in CCS.

CCS in field plot experiments

Age and season

The effects of crop age, time of year, and their interaction on sucrose content was investigated in field plots in the Burdekin by ratooning crops throughout the year and sampling them at 32, 40, 48, 52, 56 and 60 weeks later (McDonald, 2006). Sucrose content of whole sound stalks peaked at 19% in September for the 60-week old Q96 treatment and exceeded 16.5% for all treatments of Q96 older than 32 weeks sampled at this time.

In January and February sucrose content was about 15% in the 56 and 60-week old crops and only 7% in the 40-week crop. Season had the dominant effect during August to October but there was a marked effect of crop age early in the calendar year. The dominating climatic factors causing the time of year effect appear to be temperature and soil water working together. Thus, when Q96 was dried off for 4 months, sucrose content reached a maximum of 18% in August compared to only 14% for plots that were irrigated regularly (Inman-Bamber, 2004).

Ripeners

CCS can be enhanced in many varieties through the application of cane ripeners (Morgan *et al*., 2007). For example, 31 of the 42 Australian varieties tested in 2000 and 2001 showed significant responses in sucrose content to a combination treatment of Ethrel® and Fusilade®. The most responsive variety, Q117, showed an increase of 2.1 units to this ripener application. CCS gains with ripeners were often variety dependent but many other factors including type of ripener or ripener combination (Rostron, 1985), time of application and crop maturity (Clowes, 1978), application rate (Donaldson, 1989), and treatment to harvest interval (Dusky and Alvarez, 1986) also affect the responses seen.

Understanding the physiology of sucrose accumulation

Recent research using a controlled temperature glasshouse known as the Tall Plant Facility (TPF) helped to explain the physiology of the genotype x environment (GxE) interaction in regard to sucrose accumulation. The research focussed on three mechanisms that may be responsible for

differences in genotypes: photosynthesis, storage capacity in the cane stalk and dry matter partitioning. The climatic variables considered were water stress and temperature, both of which were varied independently in the controlled conditions of the glasshouse.

Dry matter distribution was regulated by reducing expansive growth as a sink for photo-assimilate, with reduced irrigation. Hourly plant extension rate (PER) was the measure of stalk volume and leaf (sink) growth, and photosynthesis was the measure of assimilate supply (source). Water stress reduced total biomass gain by 19%. The reduction was proportionately greater in leaves plus cabbage or tops (37%), than in stalks (14%). Sucrose accumulation, however, increased by 27%. Water stress reduced whole plant photosynthesis by 18% thus largely accounting for the 19% reduction in biomass accumulation and it reduced PER by 41% thus largely accounting for the 37% reduction in mass of tops (Inman-Bamber *et al.*, 2008).

Two clones from each extreme of the sucrose content range from an F1 population were irrigated fully in one chamber of the TPF and partially in the other so as to reduce PER by about 50% (Inman-Bamber *et al.*, 2009). One of the low sucrose clones (C2) growing under limited irrigation developed a sucrose content profile similar to that of two high sucrose clones (C3 and C4) growing with unlimited irrigation (Figure 3). In addition, sucrose content of internodes 2, 4 and 6 of C2 was similar to corresponding internodes of C3 and C4 when expansive growth was limited in all these clones (Figure 3). These data suggest that environment and genotype effects are additive in determining sucrose content and that there is no pre-set upper limit causing differences in sucrose content between high and low sucrose clones. Under limited irrigation, the sucrose content of the high sucrose clones (C3 and C4) reached 21% by fresh weight (67% by dry weight, Inman-Bamber *et al.*, 2009) and sucrose content of C2 reached 17% in the oldest internode (Figure 3).

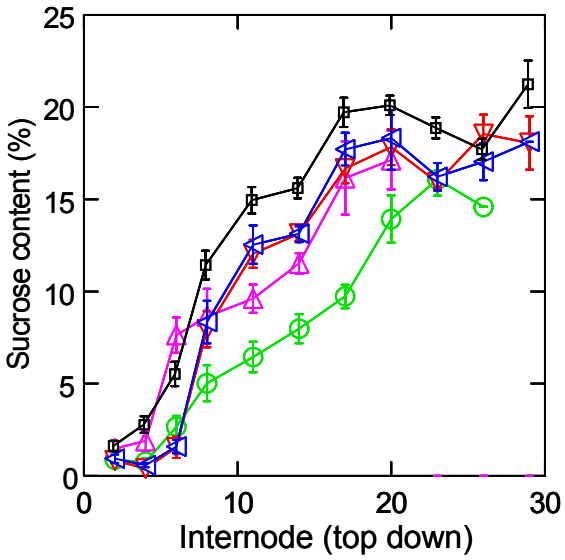

Fig. 3—Sucrose content for internodes of two low sucrose clones, C1 (○) and C2 (△) grown with limited irrigation, two high sucrose clones, C3 (◁) and C4 (▽) grown with unlimited irrigation and means for C3 and C4 grown with limited irrigation (□). Bars are 2 x standard error of the mean.

PER of the two low sucrose clones was less responsive to changes in soil water content and temperature than the two high sucrose clones (Inman-Bamber *et al.,* 2009, 2010).

Photosynthesis determined in the TPF showed that the low sucrose clone, C2, had the highest whole plant photosynthesis and the highest leaf area but the second lowest photosynthesis

per unit leaf area (Inman-Bamber *et al.,* 2009). The clones ranked the same with respect to photosynthesis and leaf area per pot but they tended to rank in reverse order with respect to photosynthesis per unit leaf area. The high- and low sucrose clones were not distinct in terms of leaf area or any measure of photosynthesis.

Based on a limited number of clones, this research suggests that competition for photo-assimilate within the plant for expansive growth versus storage is responsible for differences in sucrose content rather than differences in photosynthesis or upper limits in storage capacity of internodal tissue. Any factor such as irrigation, temperature or hormones/ripeners that reduces competition for assimilate from leaf or stalk fibre will increase CCS. Measurements of photosynthesis and PER can be used to assess the relative impact of the extent of such modification. Genetic modification could also be considered in this regard. High CCS clones appear to be more responsive to environmental factors which reduce competition from leaf and stalk fibre.

Breeding and physiology

Combining extensive knowledge from the plant improvement program with more limited knowledge of the physiology of the GxE interaction, two 'dimensions' of variation among genotypes may be distinguished conceptually. The first, and by far the greatest proportion of total genetic variance, is a general difference among genotypes in overall level of CCS, regardless of environment or maturity level. These genetic differences show up very early in stalk development, even when sucrose content is very low (Jackson and Morgan, 2003; Fong Chong *et al*., 2010, pers. comm.) This suggests a constitutive cause of genetic variation in sucrose content, such as anatomical variation in storage cells. The second dimension is associated with different responses of genotypes to the environment and to maturity. These differences tend to be more subtle than the first, but can also be commercially important. Examples include the responses of different genotypes to environmental manipulation in Figure 3, and the contrast in maturity profiles of KQ228$^{\phi}$ (high early CCS) and Q208$^{\phi}$ (relatively lower early, but high later) (Figure 2).

Understanding sucrose accumulation at the molecular level

Research to understand the molecular level of sucrose accumulation started with the discoveries of the enzymes involved in sucrose storage processes in plants in the 1950s (Cardini *et al*., 1955). The hypothesis that increasing the activity of those enzymes involved in synthesis or reducing the activity of those involved in degradation of sucrose would result in increased sucrose content, was tested once suitable molecular tools had been developed. This approach was supported by biochemical studies that correlated sucrose content to the activity of sucrose-phosphate synthase (Grof *et al.,* 2007) or the balance between the enzymes with synthetic and hydrolytic activity (Zhu *et al.*, 1997; Lingle, 1999). However, the manipulation of single genes encoding one component of the pathway has rarely given the desired phenotype. An exception has been the down-regulation of the gene encoding pyrophosphate:fructose 6-phosphate 1-phosphotransferase (PFP) which did lead to an increase in sucrose content in immature internodes but not in older internodes (Groenewald and Botha, 2008).

The available evidence from DNA marker studies is that genetic variation in sucrose content is under the complex control of numerous small genetic effects (e.g. Aitken *et al.,* 2006). When trying to increase sucrose content through manipulation of endogenous genes, it has been hoped to exert an influence beyond the natural variation. This has not been successful and may in part be because the control of the sucrose synthesis and degradation pathways is shared by multiple steps and not just one (Uys *et al.,* 2007). More recent advances in experimental technology have allowed experiments to be conducted where the expression level of many genes can be compared in different tissues or genotypes, in the one experiment. Sequencing of expressed genes provided the

resource to develop the arrays for such experiments. From this sequencing, it was clear from comparing immature internodes to internodes that were in the phase of rapidly accumulating sucrose that, while there were many genes up-regulated in the older tissue, very few appeared to be directly related to sucrose metabolism (Casu *et al*., 2003).

There are two lines of evidence that suggest that there may be some internal control over the level of sucrose that can be accumulated and that the plant has a way of sensing the level of sucrose. The level of total sugars was increased to 27% on a fresh weight basis by the expression of a transgene that encoded for the synthesis of isomaltulose (Wu and Birch, 2007). With these results and their subsequent analysis of cells with the modification, Wu and Birch (2010) indicate that perturbation in the processes that control sucrose accumulation and sensing may lead to higher levels of sucrose. Similarly, potential limitation of photosynthesis through feedback inhibition caused by the accumulation of hexoses in leaves and internodes has been proposed as a potential limitation to sugarcane productivity (McCormick *et al*., 2008). This conflicts somewhat with higher level studies reported above where high and low sucrose clones have similar rates of photosynthesis.

We suggest that new knowledge from whole plant level studies is considered when planning molecular manipulation in future. It may be possible to insert dwarf type genes that slow internode elongation down, much like reduced water and temperature effects, leading to enhanced CCS and reduced lodging.

Conclusions

The maximum CCS in commercial cane supplied to mills currently is about 18%, which is close to the maximum sucrose content of internode tissue (21%) measured when carefully controlling expansive growth to enhance sucrose content. While a small fraction of consignments are near to this observed upper level, the industrial average has fluctuated between 13 and 14% without increase for many years. This indicates that most industry cane consignments are not close to the biological upper level. The shortfall of 4 to 5% units between consignments with the highest CCS and the industry average arises due to two reasons.

Firstly, it is due to responses of current cultivars to environmental factors acting to divert assimilate to growth rather than storage of sucrose, rather than an inherent upper bio-physical limit already attained in these cultivars. This is particularly so for cane harvested outside the time of the year when CCS is highest. Consequently, there is a further opportunity to both manage crops and select varieties that have higher CCS earlier in the season. However, the apparent slow general progress in breeding programs and agronomic research in leading to industry outcomes justifies a re-think of past approaches.

Results from recent physiological experiments point to source/sink balances as being important for maximising CCS. There is some evidence suggesting high CCS genotypes may be sensitive to factors affecting stem elongation. Moderate reductions in expansive growth that reduce cane volume and weight without sacrificing photosynthesis lead to improved CCS. Re-evaluation of ripeners with a better understanding of ripener, water, temperature and genotype interactions possibly using controlled conditions may be useful.

Secondly, industry CCS is reduced by extraneous matter, as is well known. This is an issue related to economic optimisation of harvester design and operation, variety selection and milling season. Current biases in predicting economic value of varieties in breeding programs arises because sound whole stalks are used as a measure of variety CCS and this may be inhibiting the rate of genetic gain in mill CCS to the extent that there is important genetic variation in suckering and in other traits affecting extraneous matter.

The final way of increasing CCS would be to raise the potential CCS to get beyond the measured limit (21%). This will require exploiting genes that are not yet in the commercial germplasm pool and molecular intervention to break internal physiological limits where the highest reported concentration of sugars in transgenic plants is about 27% on a fresh weight basis (Wu and Birch, 2007).

Acknowledgements

We thank Sucrogen Australia Pty Ltd for use of their mill data. Funding for much of the research cited was from by the Australian Federal Government and Sugar Industry through the Sugar Research and Development Cooperation.

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