Effects of the Temperature Lowered in the Daytime and Night-time on Sugar Accumulation in Sugarcane

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Abstract: Sugarcane (Saccharum spp.) is a major crop grown for sucrose production. In Japan, its sucrose concentration is highest in winter. We examined the effects of the temperature lowered in the daytime and night-time (LDT and LNT, respectively) on sugar assimilation. Since photosynthetic and respiration rates change with temperature, we assumed that plants under LNT (LNT plants) would have low respiration rates and thus high sugar yields, whereas those under LDT (LDT plants) would have low rates of photosynthesis and thus low sugar yields. However, because of their acclimatisation to the reduced temperatures, LNT and LDT plants had sugar yields that were similar, or superior, to those of control plants. Sugar yield depends on biomass and sugar concentration; the stems of LNT and LDT plants did not grow as tall as those of the controls, but the sucrose concentrations in their stems were higher than in the controls.

13C analysis revealed no difference in the partitioning of photosynthates to the soluble sugar fraction between control plants and those treated with low temperature. Control plants had higher glucose concentrations in the stem than treated plants, in which new photosynthates appeared to be partitioned preferentially into sucrose. Low temperature enhanced the sucrose concentration in the sugarcane stem not by improving the carbon budget, but by promoting the partitioning of carbon to stored sucrose.

Key words: 13C, Internode, Photosynthesis, Respiration, Sucrose, Translocation.

Sugarcane is an important source of biomass for ethanol production. It is also a major crop grown for sucrose production, providing up to 60% of the world’s sugar supplies (Grivet and Arruda, 2002). In Japan, the sugar concentration and sugar yield of sugarcane increase in late autumn and winter (Terauchi et al., 1999b, 2000).

Sugar yield depends on two factors: plant biomass and stem sucrose concentration (Ebrahim et al., 1998). Since more carbohydrate is needed to grow a bigger biomass and to store sucrose at higher concentrations, a good whole-plant carbon budget would seem to induce a higher sugar yield. Carbohydrate is produced in the leaves and translocated to the stem (Moore, 1995). Photosynthesis and respiration gain and consume carbon, respectively, and both are affected by temperature (Yamori et al., 2005). So if the daytime temperature remains optimal, a lower temperature in the night-time may promote net carbon gain; conversely, a lower temperature in the daytime may decrease carbon gains.

Several researchers reported the effects of the difference between daily maximum and minimum temperature on crop yield (Sato and Ikeda, 1979; Nicholls, 1997; Dhakhwa and Campbell, 1998; Gent and Ma, 1998; Wilkens and Singh, 2001; Peng et al., 2004; Lobell, 2007; Lobell and Ortiz-Monasterio, 2007). A large range of diurnal change in temperature reduces crop yield owing to water and heat stresses and harm induced by hot days (Dhakhwa and Campbell, 1998; Lobell, 2007). On the other hand, the positive effect of a large diurnal temperature range is earlier fruit set, earlier ripening, and an increase in fruit size in tomato (Gent and Ma, 1998), and an increase in yield in soybean (Sato and Ikeda, 1979). However, few reports have considered the carbon budget changes that may result from a lowered temperature.

Even if the whole plant has a good carbon budget, growth and storage compete for substrates (Hatch and Glaziov, 1969; Bonnett et al., 2006; Inman-Bamber et al., 2008). Therefore, it is important to know into which organ or fraction (e.g. soluble sugars, structural components) new photosynthates are partitioned. Although several researchers have predicted the partitioning of photosynthate in sugarcane (Bonnett et al., 2006; Inman-Bamber et al., 2008), it has not been measured directly. 13C analysis is useful for measuring the partitioning of photosynthates, and other data, such as those on photosynthesis and carbon budgeting, can be added for various analyses (Sasaki et al., 2005, 2007).

We analyzed the effects of the temperature lowered...
Hoagland’s solution (6 mM Ca(NO₃)₂, 12 mM KNO₃, leaving just one stem. Fertilizer in the form of 300 mL ash soil). All tillers were removed as they emerged, 3.8-L plastic pots filled with field soil (black volcanic 2005 and 28 April 2006. On 30 May 2005 and 30 May a greenhouse at the University of Tokyo on 21 April officinarum L. cv. NiF8) were placed in vermiculite in 2006, rooted seedlings were transplanted singly into 2 mM KH₂PO₄, 2 mM MgSO₄, 25 MnSO₄, 2 μM H₂MoO₄, 10 μM H₃BO₃, 10 μM CuSO₄, 0.5 μM ZnSO₄, 0.5 μM MnSO₄, 2 mM KH₂PO₄, 2 mM MgSO₄, 25 μM H₂BO₃, 10 μM MnSO₄, 2 μM ZnSO₄, 0.5 μM CuSO₄, 0.5 μM H₂MoO₄ and 0.1 mM FeC₆H₅O₇ ) was applied to each pot and 4. Whole-plant respiration rate

The schedule and number of replications for measurement of whole-plant respiration rate were the same as those for the measurement of whole plant photosynthesis rate. In both years, the whole-plant respiration rate was measured in an open chamber system with an infrared gas analysis system (SPB-H5, ADC BioScientific Ltd., Herts, England) (Fig. 1). Since the sugarcane plant is too big, the whole plant was divided into several pieces and Vaseline was then put on to their transverse section. In a preliminary experiment with sugarcane, we confirmed that whole-plant respiration rate did not change before and after dividing. The plants were placed in a 22.3 L chamber

Table 1. Mean daytime and night-time temperatures during the 4-week treatment period in sugarcane.

| Treatment | 2005 Daytime | Night-time | 2006 Daytime | Night-time |
|-----------|--------------|------------|--------------|------------|
| Control   | 33.7 ± 0.4   | 26.2 ± 0.3 | 30.9 ± 0.6   | 23.8 ± 0.4 |
| LNT       | 33.7 ± 0.4   | 15.3 ± 0.2 | 30.9 ± 0.6   | 15.5 ± 0.2 |
| LDT       | 26.6 ± 0.5   | 26.2 ± 0.3 | 24.0 ± 0.7   | 23.8 ± 0.4 |

Values are means of data for 4 weeks ± SE. LNT: lowered night-time temperature; LDT: lowered daytime temperature.
plants were divided into leaf blades, leaf sheaths, stems and roots. Leaf blades, leaf sheaths and stems were frozen in liquid nitrogen and stored at −80°C, and then freeze-dried. Roots were carefully cleaned under running water to remove soil and other matter, and then freeze-dried.

7. Extraction of structural and non-structural carbohydrates

The freeze-dried plant materials were weighed and then ground to a fine powder. Samples (approximately 500 mg) were incubated in 80% ethanol at 80°C for 1 hr, and then centrifuged at 3000 × g for 10 min, after which the ethanol-soluble fraction was decanted.

The ethanol-soluble fraction was dried in a centrifugal dryer in a vacuum (CVE-200D, EYELA, Tokyo, Japan) and then further fractionated with a mixture of 2 mL distilled water and 2 mL chloroform. The aqueous phase was passed through a cation-exchange resin (Dowex-50, Dow Chemical, Midland, Michigan, USA) to remove amino acids. The efflux was collected and used as the soluble sugar fraction. Distilled water was added to the ethanol-insoluble fraction, which had been dried in a centrifugal dryer in a vacuum, and the suspension was boiled for 4 hr. Twenty units of glucoamylase in 0.5 mL of 100-mM acetate buffer (pH 4.6) was added to the suspension, which was then incubated for 2 hr at 60°C to digest the starch into glucose. After centrifugation of the suspension at 3000 × g for 10 min, the water-soluble fraction was collected, then passed through Dowex-50 and a nitrocellulose filter (Advantec, Tokyo, Japan) to remove proteins. The filtrate was collected and used as the insoluble sugar fraction (i.e., starch). The water-insoluble fraction (structural components) was washed twice with distilled water and dried in an electric oven at 80°C.

8. Measurement of \(^{13}\text{C}\) content

The total carbon and \(^{13}\text{C}\) contents were determined with an elemental analyzer (NC2500, Thermoquest, San Jose, CA, USA) and a mass spectrometer (Delta Plus System, Thermoquest). Each fraction was dried completely and its \(^{13}\text{C}\) content was determined. The \(^{13}\text{C}\) content in each organ was calculated by equation 1:

\[
^{13}\text{C content} = (\text{total carbon atom content}) \times (\text{^{13}C atom excess %}) \times 13
\]

where \(^{13}\text{C}\) atom excess % is the difference in the ratio of \(^{13}\text{C}/(^{12}\text{C}+^{13}\text{C})\) between the plants supplied with \(^{13}\text{CO}_2\) and those supplied with ordinary \(^{12}\text{CO}_2\). The \(^{13}\text{C}\) content was expressed as a percentage of the \(^{13}\text{C}\) that was incorporated immediately after \(^{13}\text{CO}_2\) feeding.

9. Statistics

For all statistical analyses we used Fisher’s protected least significant difference (PLSD) test, included in
Results

To estimate the carbon budget, in 2005 we measured the gas exchange rates in a whole plant at different temperatures before the start of treatments (Fig. 2). The dark respiration rate in the plant at 17ºC, which corresponded approximately to the night-time temperature of an LNT plant (see Table 1), was only about 60% of that in the plant at 27ºC, which corresponded to the night-time temperature of a control plant. The photosynthetic rate in the plant at 27ºC, which corresponded to the daytime temperature of an LDT plant, was only about 85% of that in the plant at 32ºC, which corresponded to the daytime temperature of a control plant.

We investigated sugar yield and related characters, including stem length, stem fresh weight and sucrose concentration, before and after the temperature treatment (Table 2). At the end of the 4-wk treatment period the control stems had grown by 21 cm, but the LNT and LDT stems had grown only slightly; this difference was significant (P < 0.05). Stem fresh weight followed the same pattern: it increased by 58 g in control plants, but the LNT and LDT plants had significantly lighter stems (P < 0.05). Although the difference of stem fresh weight between LNT and LDT plants seemed to big, this difference was not significant. Sucrose concentration in the juice extracted from the stem increased in all groups, but LNT plants (13.8%) and LDT plants (16.5%) each had significantly greater sucrose concentrations than the controls: temperature lowered in the daytime or night-time promoted sucrose concentration in the juice. Sugar yield in sugarcane is dependent on stem fresh weight and sucrose concentration, so although LNT plants had a significantly greater mean sucrose concentration than the controls, because of their lower stem fresh weight they did not have a higher sugar yield. In contrast, because the LDT plants had a 67% higher mean sucrose concentration than the controls, LDT plants had a significantly higher (by 20%) sugar yield (P < 0.05). Thus, the observed sugar yields were different from the carbon gain and loss changes.

| Table 2. Effect of low temperature on sugar yield components in sugarcane in 2005. |
|-----------------|-----------------|-----------------|-----------------|-----------------|
| After treatment | Stem length (cm) | Stem fresh weight (g) | Sucrose concentration (%) | Sugar yield (g) |
| Control        | 120±1 a         | 223±15 a        | 9.9±0.7 c         | 18.8±1.6 b     |
| LNT            | 100±5 b         | 165±7 b         | 13.8±0.7 b        | 17.5±0.7 b     |
| LDT            | 102±4 b         | 190±14 b        | 16.5±0.5 a        | 23.4±1.8 a     |

The stem from the ground to the base of the uppermost leaf was used for evaluation of length and fresh weight. ‘Sucrose concentration’ is the percentage of sucrose (w/v) in juice. Values are means ± SE of five plants. Means followed by different letters differ significantly (P < 0.05, Fisher’s PLSD). LNT, lowered night-time temperature; LDT, lowered daytime temperature.

| Table 3. Partitioning of fed ^13C in each organ 2 wk after feeding in sugarcane in 2005. |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Treatment      | Leaf            | Leaf sheath     | Stem            | Root            | Whole plant     |
|                 | %               | %               | %               | %               | %               |
| Control        | 12.8±0.7        | 9.0±2.0         | 55.3±3.4 a      | 5.8±0.4 b       | 82.9±2.0        |
| LNT            | 13.3±1.3        | 10.3±1.3        | 45.8±1.8 b      | 8.3±0.7 b       | 77.7±2.6        |
| LDT            | 14.3±2.3        | 7.1±0.6         | 41.9±1.3 b      | 14.1±1.6 a      | 77.3±0.8        |

The total amount of ^13C in a whole plant immediately after feeding was regarded as 100%. Values are means ± SE of four plants. Means followed by different letters differ significantly (P < 0.05, Fisher’s PLSD). LNT, lowered night-time temperature; LDT, lowered daytime temperature.
predicted from the photosynthetic and respiration rates (Fig. 2).

Sugarcane plants were supplied with $^{13}$CO$_2$ 2 wk after the start of the treatments to examine the partitioning of photosynthates to different organs (Table 3). 2 wk after the feeding of $^{13}$C, whole control plants had 82.9% $^{13}$C. Although there were no significant differences in whole-plant $^{13}$CO$_2$ contents among treatments, LNT and LDT had only about 77% $^{13}$C; thus, the ratio of consumed carbon to fixed carbon in these plants tended to be larger than that in control plants. Furthermore, both LDT and LNT plants had significantly less $^{13}$C in the stem than did the control plants (P < 0.05). In LDT plants significantly more fed $^{13}$C was partitioned to the roots than in the other two groups (P < 0.05).

Analysis of the partitioning of fed $^{13}$C from each fraction (soluble sugars, starch and structural components) 2 wk after feeding revealed that relatively large amounts of $^{13}$C were partitioned to the structural component in each organ (about 35% of the whole plant total) (Fig. 3). The highest proportion of $^{13}$C was partitioned to the soluble sugar fraction in the stem (about 26%), and there were no significant differences in $^{13}$C content of this fraction in the stem among treatments. Analysis of the content in soluble sugars in stem revealed that control plants had larger proportions of glucose (12.6%) and fructose (10.2%) to total soluble sugars than did LNT or LDT plants; the soluble sugar content of the stems of LNT and LDT plants was almost all sucrose (LNT: 94.1%, LDT: 87.4%) (Table 4).

As the carbon budget seemed to differ from that predicted from the pre-treatment photosynthetic and respiration rates, to confirm acclimatisation in whole plants, in 2006 we examined the effects of lowered temperature in our experimental system (Figs. 4, 5). The photosynthetic rate in LNT plants measured at 31ºC after the treatment was clearly lower than that measured before the treatment, but that in the control plants was similar to that measured before the treatment (Fig. 4). The photosynthetic rate in LDT plants measured after the treatment was similar to that measured before the treatment. The respiration rate in LNT plants measured at 16ºC after the treatment was similar to that measured before the treatment and to that in control plants measured at 24ºC after the treatment. In LDT plants, the respiration rate measured at 24ºC after the treatment was lower than that measured before the treatment though not significantly. Thus, in LDT plants, the respiration rate but not photosynthetic rate, seemed to increase after the treatment. On the other hand, in LNT plants, the photosynthetic rate, but not respiration rate, seemed to decrease after the treatment.

### Discussion

Because photosynthetic and respiration rates in sugarcane are affected by temperature (Fig. 2), we hypothesised that suppression of respiration through temperature lowering in the night-time would enhance both the carbohydrate content of the whole plant and the sugar yield. However, acclimatisation to low temperatures in the daytime induced higher respiration rates at night (Fig. 5), as Yamori et al. (2005) reported in curves of respiration temperature in spinach. Energy supply by respiration may be necessary for sucrose synthesis activated by low temperature. Photosynthesis was also suppressed by acclimatization to low temperatures at night (LNT) (Fig. 4), perhaps because pyruvate phosphate dikinase, one of the

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**Table 4. Effect of temperature treatments on proportions of soluble sugars in sugarcane stem in 2005.**

| Treatment | Sucrose | Fructose | Glucose |
|-----------|---------|----------|---------|
| Control   | 77.2±2.2 c | 10.2±1.0 a | 12.6±1.3 a |
| LNT       | 94.1±0.6 a  | 3.0±0.3  a  | 2.9±0.3  c  |
| LDT       | 87.4±1.4 b  | 5.9±0.6  b  | 6.7±0.8  b  |

The total amount of soluble sugars (sucrose, fructose, glucose) was regarded as 100%. Values are means±SE of five plants. Means followed by different letters differ significantly (P < 0.05, Fisher’s PLSD). LNT : lowered night-time temperature ; LDT : lowered daytime temperature.
The values at 31 and 24°C before treatment were calculated from the curve of photosynthesis plotted against temperature (ref. Fig. 2). Bars indicate SE of four replications. Means followed by different letters differ significantly (P < 0.05 by Fisher’s PLSD). LNT, lowered night-time temperature; LDT, lowered daytime temperature.

The deterioration in the carbon budget of LNT plants is supported by the fact that less 13C remained in the LDT plants than in control plants (Table 3). A lowered daytime temperature tended to lower the photosynthetic rate (Figs. 2, 4) and acclimatisation to low temperature in the daytime increased the respiration rate at night (Fig. 5). Furthermore, although LDT plants were placed outside without shading in the daytime, less 13C remained in the LDT plants than in control plants (Table 3). Although we cannot define the optimum temperature for the carbon budget from these experiments, the results indicate that a lowered temperature—whether in the daytime or at night—causes deterioration in the carbon budget.

Sugar yield depends on sucrose concentration and stem fresh weight, and a poor carbon budget is thought to suppress stem growth and sugar concentration. Sun and Chow (1949) reported that low temperatures at night suppressed stem elongation in sugarcane. Regardless of whether it occurred in the daytime or at night, a lowered temperature decreased both stem length and stem fresh weight (Table 2), but it enhanced the sucrose concentration despite the suppression of stem growth. Bonnett et al. (2006) suggested that sugarcane partitions less carbon to stored sucrose when grown under high compared with low temperature conditions. We therefore suggest that regardless of whether it occurred in the daytime or at night, a lowered temperature might partition new carbohydrate not to stem elongation, but to sucrose storage in the stem.

We used 13C to clarify the partitioning of newly fixed carbon. Regardless of the temperature treatment, some 13C was partitioned to structural components such as the cell membrane and cell wall (Sasaki et al., 2005, 2007). However, about 26% of fixed 13C was partitioned to soluble sugars (including sucrose, fructose and glucose) in the stems. Control plants had more glucose, a growth substrate, in the stem than LNT and LDT plants (Table 4). However, LNT and LDT plants had more sucrose stored in the stem than control plants. Although the 13C content of sucrose and glucose could not be separated, control plants tended to have more newly fixed photosynthates in the form of glucose in the stem, whereas LNT and LDT plants had more in the form of sucrose. These results support our suggestion that the lowered temperature might partition new carbohydrate not for use as a growth substrate, but for sucrose storage in the stem.

Several researchers have reported the effects of diurnal temperature variations on crop yield (Sato and Ikeda, 1979; Nicholls, 1997; Dhakhwa and Campbell, 1998; Gent and Ma, 1998; Peng et al., 2004; Wilkens and Singh, 2001; Lobell, 2007; Lobell and Ortiz-Monasterio, 2007). LDT and LNT treatments in this experiment corresponded to small and large variations, respectively. However, the diurnal temperature variations in these reports were almost all related to the maximum or average daytime temperature. Furthermore, the effects of diurnal temperature differences on crop yield have been discussed from the viewpoint of agriculture rather than plant physiology. Although the positive effect of a large diurnal temperature change is earlier fruit set and ripening and an increase in fruit size in tomato (Gent and Ma, 1998), and increased yield in soybean (Sato and Ikeda, 1979), these reports have never considered the changes in the carbon budget that result from the temperature change. We hypothesised that sugar yield would change because LNT and LDT would...
induce better and worse carbon budgets, respectively.
However, sucrose storage in the stem was accelerated
neither by improvement in the budget nor by diurnal
fluctuation of temperature. Bonnett et al. (2006)
suggested that the sugarcane partitions less carbon to
stored sucrose when grown under high compared with
low temperatures such as we suggested. So how does
the lowered temperature promote storage of sucrose
in the stem? A low temperature increases sucrose
production in Arabidopsis by promoting fructose-1,6-
bisphosphatase and sucrose phosphate synthase (SPS),
the two key regulated enzymes in sucrose synthesis
that shifts in carbon partitioning to sucrose
(Strand et al., 1999; Stitt and Hurry, 2002). The
activity of enzymes in the sucrose synthesis pathway
increases during cold acclimatization in the leaves
of spinach (Martindale and Leegood, 1997), winter
wheat, rye and rape (Hurry et al., 1994, 1995), and
in walnut wood (Margel et al., 2001). Post-transcriptional
activation of SPS occurs in potato tubers (Hill et al.,
1996; Deting et al., 1998; Krause et al., 1998), apple
fruits (Duque et al., 1999) and cabbage seedlings
(Sasaki et al., 2001) exposed to low temperatures.
Terauchi et al. (1999a, 2000) reported that lowered
temperature promotes SPS activity in the stem of
sugarcane. On the other hand, Inman-Bamber et
al. (2008) suggested that reduced plant extension
resulted in reduced demand for photo-assimilate by
tops thus allowing excess assimilate to accumulate
in the form of sucrose. Certainly, stem length was
shorter in LNT and LDT plants than in the control
plants (Table 2). Therefore, we suggest that since the
stem growth is suppressed and the sucrose synthesis
pathway is activated by a lowered temperature whether
in the daytime or night-time, more photosynthate is
partitioned to sucrose.

We conclude that a lowered temperature enhanced
the sucrose concentration in the stem of sugarcane
not by improvement of the carbon budget, but by
promotion of partitioning of carbon into sucrose.

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We measured 13C by mass-spectrometry at Asia Natu-
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