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Effects of duration and combination of drought and flood conditions on leaf photosynthesis, growth and sugar content in sugarcane

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ABSTRACT

Global climate change will result in extreme environments, such as droughts and floods. We investigated the individual and combined effects of droughts and floods of varying duration on sugarcane (*Saccharum* spp.) growth using a pot experiment under glasshouse conditions with the following six treatments: drought for 15 d, prolonged drought for 30 d, flood for 15 d, prolonged flood for 30 d, short flood followed by prolonged drought, and prolonged flood followed by prolonged drought. Plants that were subjected to drought conditions, including drought after a flood, had reduced CO₂ assimilation (through stomatal closure) and leaf areas, whereas flood conditions showed no effect. During flooding, some roots died, and adventitious roots with well-developed aerenchyma appeared from the submerged nodes. At the time of harvest, there were no significant differences in stem fresh weight, sucrose content, or sugar yield between the treatments. However, ion content analysis revealed that flood conditions caused an accumulation of sodium in the bottom of stems and adventitious roots. Therefore, under flood conditions, plants may develop adventitious roots, which may offset the negative effects of root death, helping them to maintain their growth and yield.

ABBREVIATION

A, CO₂ assimilation; DAT, days after treatment; F + PD, flood follow by prolong drought; PF + PD, prolong flood follow by prolong drought; LA, leaf area; hr, hour; d, day; mo, month; wk, week

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Adventitious root; CO₂ assimilation; drought; flood; sodium content; sucrose content; sugarcane

Sugarcane (*Saccharum* spp.) is a major economic crop in many tropical and subtropical countries, including Thailand, where production has dramatically increased as a result of the Government encouraging rice (*Oryza sativa*) producers to switch to sugarcane production for better returns (USDA Foreign Agriculture Service, 2014). In Thailand, there are two sugarcane planting patterns: (1) at the end of the rainy season (October–January) and (2) in the early part of the rainy season (April–May) with the selected pattern depending on the topography and climate of the area. However, most of sugarcane plantations are still relying on rain-fed systems, which present challenges for water management.

During the rainy season (May–September), there are two rainfall peaks in May and August, and a dry spell in July (Roongroj & Long, 2006). Consequently, in the worst case, plants could suffer from both flood and drought during a single rainy season. Furthermore, changing from paddy

field to sugarcane production may increase the flood risk and cause problems for cane growers, particularly in the central basin during the rainy season. Sugarcane has four growth phases: germination and emergence (1 mo after planting), tillering and canopy establishment (at 2–3 mo), grand growth (at 4–10 mo), and maturation or ripening (at 11–12 mo) (Gascho, 1985). During the rainy season, sugarcane is 5–6 mo of age and in the grand growth phase, which is important for actual cane formation, elongation, and yield build up. Thus, drought and flood at this time may affect growth and, thus, the yield and quality of sugarcane produced during the maturation or ripening phase.

The amount of flood stress experienced by sugarcane plants depends on the duration of waterlogging, the condition of the floodwater, and soil type (Gomathi et al., 2014). Both cane and sugar yield have been reported to decrease under flood conditions as a result of a reduction in photosynthesis, root development, leaf area (LA), LA index,

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tiller production, stalk height, and sucrose yield (Gomathi et al., 2014; Viator et al., 2012; Webster & Eavis, 1972). It has been found that the application of periodic flooding every mo leads to a 50% reduction in the photosynthesis rate (Viator et al., 2012) and reduced plant growth as a result of a decrease in the metabolic activity of the roots due to hypoxia (Gomathi et al., 2014). However, the plants concurrently develop adventitious roots from the nodes above the soil (Begum et al., 2013) – and when the flood lasts for 3 mo, the sugarcane plants produce adventitious roots with well-developed aerenchyma, which may help plants to continue to take up water and nutrients (Gilbert et al., 2007, 2008).

Drought or a limited water supply usually suppresses the rate of assimilation and leaf extension and promotes leaf senescence (Inman-Bamber, 2004; Smit & Singels, 2006). Roots that grow in drought conditions exhibit profuse growth and are relatively longer with thin rootlets (Hidaka & Karim, 2007). By contrast, there is a reduction in stalk elongation as a result of low rates of leaf development and photosynthesis, which leads to low cane and sucrose yield (Robertson et al., 1999b). Drought that occurs when the leaf canopy is well established will have more serious impacts on total biomass, stalk biomass, and stalk sucrose levels at harvest than drought that occurs in younger crops (Robertson et al., 1999a). Drought stress during the grand growth phase leads to variable reductions in cane and sugar yield depending on the growth stage but a constant reduction in sucrose content (Wiedenfeld, 2000). During the grand growth phase, tiller growth and development occur, alongside height gain and basal sugar accumulation, and so this is known to be a critical stage for drought sensitivity due to plants requiring large amounts of water for growth (Ramesh & Mahadevaswamy, 2000; Zingaretti et al., 2012).

To the best of our knowledge, no previous study on sugarcane has examined the combined effects of flood and drought. The objective of this study was to investigate the effects of various combinations of drought and flood of varying duration on sugarcane growth and yield during the grand growth phase. In addition, morphological and chemical changes in the sugarcane juice and adventitious roots were analyzed to gain a better understanding of their adaptive significance.

Materials and methods

The experiment was conducted in a glasshouse at the University of the Ryukyus, Okinawa, Japan (26°15'N, 127°45'E; altitude 127 m). Sugarcane (*Saccharum* spp. cv. NiF8) seedlings were germinated in a tray on April 3, 2013, and transplanted in pots (1/2,000 a) filled with soil, sand, and peat (2:1:1, v/v). Initially, an automatic drip irrigation

system was used to water the plants for 15 min (495 ml) every morning. The level of irrigation was then doubled at 3 mo by also watering the plants at noon and tripled at 5 mo through the addition of an evening watering. During growth, tillers were removed, and plants were kept in individual pots.

The experiment simulated a planting schedule that was similar to the Thailand pattern of planting in the early part of the rainy season (April–May). The flood and dry spell then occurred during the rainy season (May–September), when the sugarcane plants were 4–6 mo of age, i.e. during the grand growth phase. At 6 mo after transplanting (October 1), uniform plants were selected with an average substem length of 263.5 cm. These plants were then subjected to a drought or flood. During the drought, plants received less irrigation, to an equivalent of 15% (v/v) soil moisture, whereas during the flood, plants were submerged up to 35 cm above the soil surface in 45-l plastic buckets. In total, six treatments with varying flood/drought durations and combinations were used along with a control, as follows: drought for 15 d, prolonged drought for 30 d, flood for 15 d, prolonged flood for 30 d, flood for 15 d followed by prolonged drought for 30 d (F + PD), prolonged flood for 30 d followed by prolonged drought for 30 d (PF + PD), and no flood or drought (control). In the combination treatments (F + PD and PF + PD), the plants were drained and then PD was applied by irrigating the plants at 15% (v/v) soil moisture for 30 d.

Each treatment included 18 plants. All plants were fertilized weekly by replacing the irrigation water with 500 ml of Hoagland's nutrient solution, which consists of 4 mM KNO₃, 6 mM Ca(NO₃)₂·4H₂O, 2 mM MgSO₄·7H₂O, 2 mM KH₂PO₄, 0.5 μM CuSO₄·5H₂O, 6.3 μM MnSO₄·5H₂O, 2 μM ZnSO₄·7H₂O, 25 μM H₃BO₃, 0.3 μM Na₂MoO₄·2H₂O, and 0.1 mM Fe(III)-ethylenediaminetetraacetic acid (EDTA). During the flood treatments, this solution was mixed into the floodwater. Plants were arranged with 40 × 90 cm spacing between the plants and rows in a completely randomized design.

Three plants from each treatment were sampled 1 d before the start of treatment (–1), and 15, 30, 45, 60, and 75 d after treatment (DAT). The LA of the whole plant was measured with a LA meter (Li-3,100, Li-COR). For stem sampling, stems were cut from the base, and the substem length (distance from the soil level to the visible auricle of the top visible dewlap leaf (TVD)) and stem weight were measured. Each stem was evenly separated into bottom, middle, and top and squeezed with a three-roller mill to obtain sugarcane juice from each part. For root sampling, adventitious roots appearing from the submerged stem were collected separately and dried in an oven at 80 °C for 48 h to determine their dry weights. Adventitious roots were also sampled at 10, 20, and 30 DAT, by cutting them

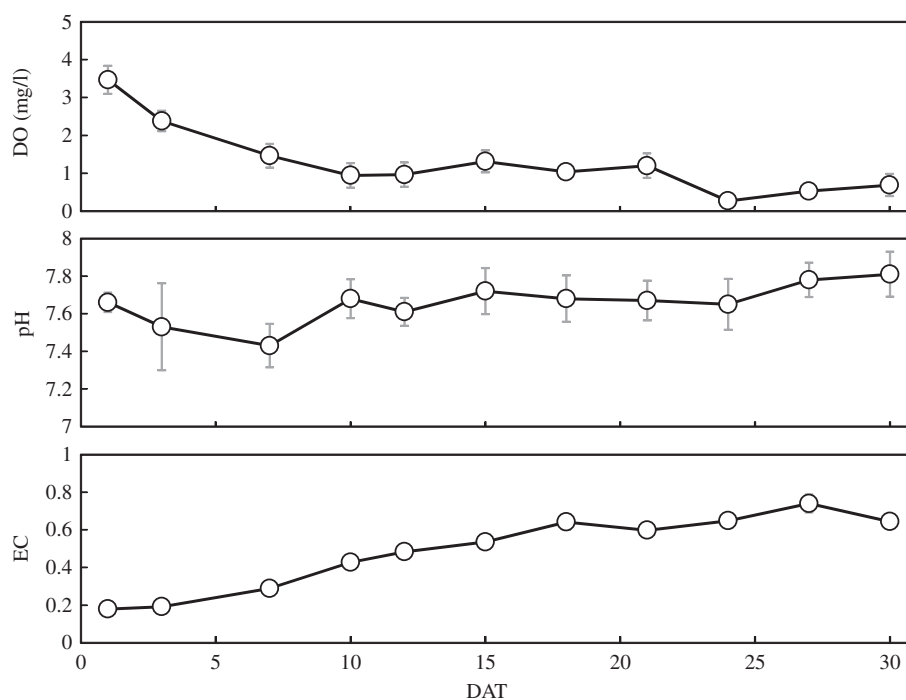


Figure 1. Transition of water in flood treatments during 1–30 DAT included dissolved oxygen (DO) at soil surface or 35 cm water depth, pH, and electronic conductivity (EC). Bar show means \pm SD ($n = 10$). DAT: days after treatment.

1 cm above the tip and fixing them with formalin–acetic acid–alcohol (FAA) solution (50% ethanol:acetic acid:formaldehyde, 18:1:1). These sections were then viewed under light microscope and photographed (ECLIPSE 80i, Nikon). The juice was diluted 50 times with distilled water and filtered with a 0.45- μ m membrane filter (ADVANTEC), following which the sugar content was analyzed with high-performance liquid chromatography (HPLC) (LC-20A, Shimadzu), and anion and cation contents were analyzed with ion chromatography (ICS-1600, Thermo Scientific). Sugar yield was calculated using the following equation:

$$\text{Sugar yield} = \text{sucrose content (\%)} / 100 \\ \times \text{stem weight (g)} \times 0.5$$

where the value 0.5 was the mean efficiency of the squeezing machine, as calculated by $(1 - \text{bagasse weight}) / \text{stem weight}$.

Photosynthesis rates were measured in an upper fully expanded leaf taken from four plants per treatment at –1, 7, 15, 30, 45, and 60 DAT using a portable photosynthesis measurement system (Li-6400XT, Li-COR) equipped with a 2×3 cm² LED chamber (Li-6400–02B, Li-COR). Soil plant analysis development (SPAD) values were then measured on the same leaves with a chlorophyll meter (SPAD-502, Konica Minolta). All measurements were carried out between 10:00 am and 2:00 pm at a photosynthetic flux density (PFD) of 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, leaf temperatures of 25–30 °C, a leaf to air vapor

pressure difference of 1.5–3.5 kPa, and a CO₂ concentration of 400 $\mu\text{mol mol}^{-1}$.

The quality of the floodwater was checked with a dissolved oxygen meter (ID-150, Iijima) at the soil surface, a pH meter (B-71X, Horiba), and an electronic conductivity (EC) meter (B-771, Horiba). Oxygen levels gradually decreased until 10 DAT, after which they remained constant at around 0.8 mg l^{–1}. The pH did not change greatly, while EC increased at a constant rate to a level that was 2.5 times higher by the end of the treatment (Figure 1). The total incident solar radiation in the glasshouse was approximately 1,280 MJ m^{–2}, with an average of 4.9 ± 2.1 MJ m^{–2} d^{–1}. The average daily maximum and minimum temperatures were 38.2 ± 5.8 and 22.7 ± 4.4 °C, respectively.

Results are given as means \pm standard deviations. Mean values for each treatment were compared using Fisher's least significance difference (LSD) test with a 5% level of significance.

Results

Growth of shoots and yield

Plants that experienced drought and prolonged drought exhibited a yellowing of the lower leaves, which proceeded to the upper leaves when drought conditions were extended. Eventually, some of the leaves died, resulting in the LA decreasing by 15.0% in drought conditions and 32.2% in prolonged drought conditions at 30

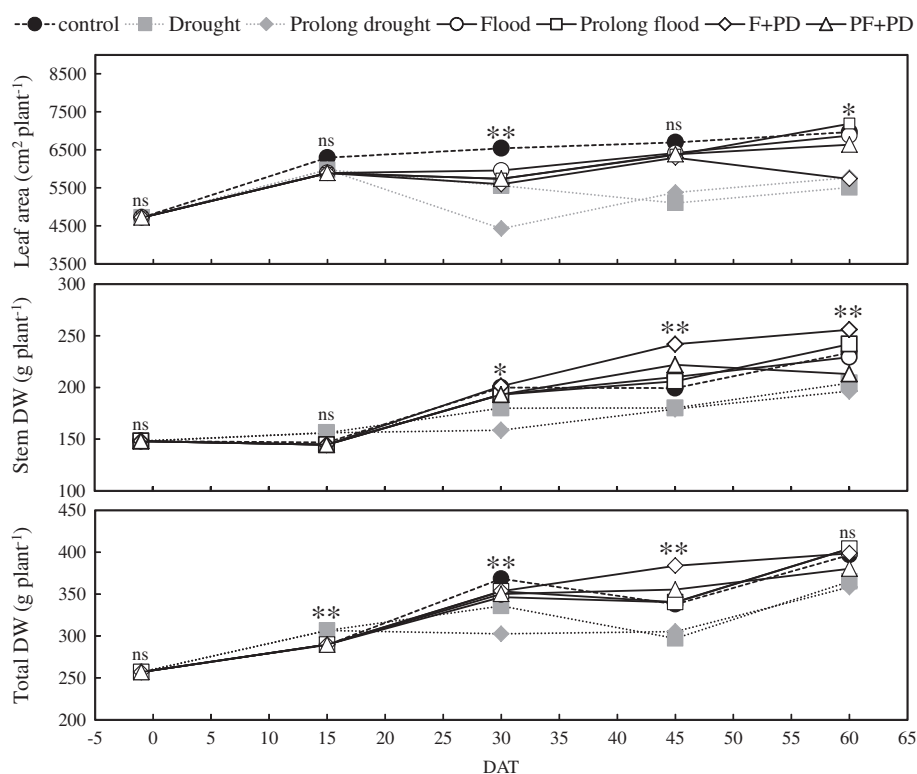


Figure 2. LA, stem DW (dry weight), and total DW of sugarcane cv. NiF8 compared with 7 treatments as control, drought (15 d), prolonged drought (30 d), flood (15 d), prolonged flood (30 d), F + PD (flood + prolonged drought), and PF + PD (prolonged flood + prolonged drought) at sampling date: 1 d before treatment (–1), 15, 30, 45, and 60 DAT.

Notes. *, ** indicate significant effect of treatments in each sampling at $P \leq 0.05$ and 0.01 , respectively. ns indicates not significant ($n = 3$). DAT: days after treatment.

DAT. Furthermore, even re-irrigated plants had a lower LA than control plants during the experiment. The stem and total dry weight of plants that experienced drought and prolonged drought conditions were also lower than in the control plants, following a similar pattern to that observed for LA (Figure 2). By contrast, flooded plants, including flood, prolonged flood, and combination (F + PD and PF + PD) treatments, did not exhibit any change in leaf color, but LA did slightly decrease by 12.2–14.4% at 30 DAT (Figure 2). Following flooding, the stem and total dry weight increased in a similar manner to control plants, except when prolonged flooding was followed by prolonged drought (PF + PD), which led to a reduction in stem weight (Figure 2).

In the control plants, the sucrose content of the sugarcane juice started to increase from 15 DAT, following which the accumulation gradually accelerated (Figure 3), demonstrating that the treatment occurred just before the period of accumulation began. Plants that were exposed to the first drought treatment, which was applied until 15 DAT, experienced a 14% increase in sucrose content. By contrast, the sucrose content was maintained at a low level or decreased as a result of prolonged drought until 30 DAT. The sucrose content was not

affected by the flood treatments, and subjecting plants to prolonged drought after a flood (F + PD) may even have facilitated the accumulation of sucrose. The analysis of the concentration of various ions in the juice showed that sodium levels increased significantly in all flood and combination treatments (Figure 4), and also remained high following re-irrigation. During flooding, sodium mostly accumulated in the bottom parts of the plant, whereas the upper parts retained the same low concentration as was seen in the other treatments (Figure 5).

At the time of harvest (75 DAT), substem length, stem fresh weight, sucrose content, and sugar yield did not differ between treatments (Table 1).

Root growth and development

The root dry weight of plants decreased by 10% under drought conditions and 20% under prolonged drought conditions and remained lower than the control even after re-irrigation (Figure 6). A decrease in root dry weight was also observed in flooded plants, including the combination treatments (flood = 24.0%, prolonged flood = 25.3%, F + PD = 20.4%, and PF + PD = 25.3%), as a result of some of the roots rotting. The root growth in plants exposed to

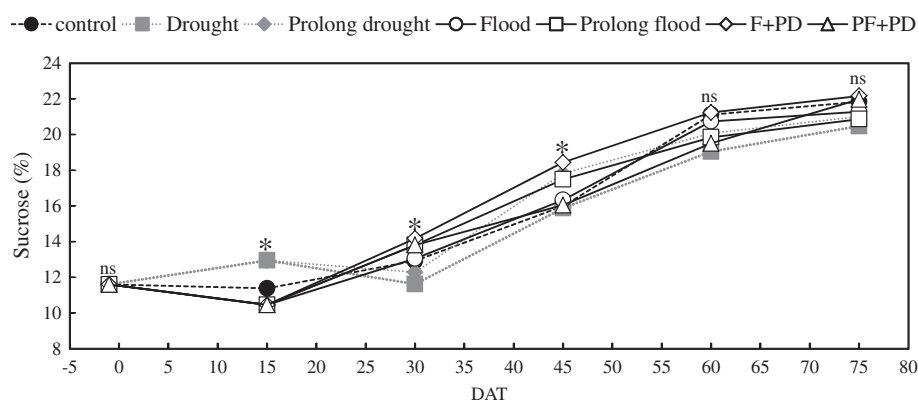


Figure 3. Percentage of sucrose of sugarcane cv. NiF8 compared with 7 treatments as control, drought (15 d), prolong drought (30 d), flood (15 d), prolong flood (30 d), F + PD (flood + prolong drought), and PF + PD (prolong flood + prolong drought) at sampling date: 1 d before treatment (–1), 15, 30, 45, 60, and 75 DAT.

Notes. *, ** indicate significant effect of treatments in each sampling at $P \leq 0.05$ and 0.01 , respectively. ns indicates not significant ($n = 3$). DAT: days after treatment.

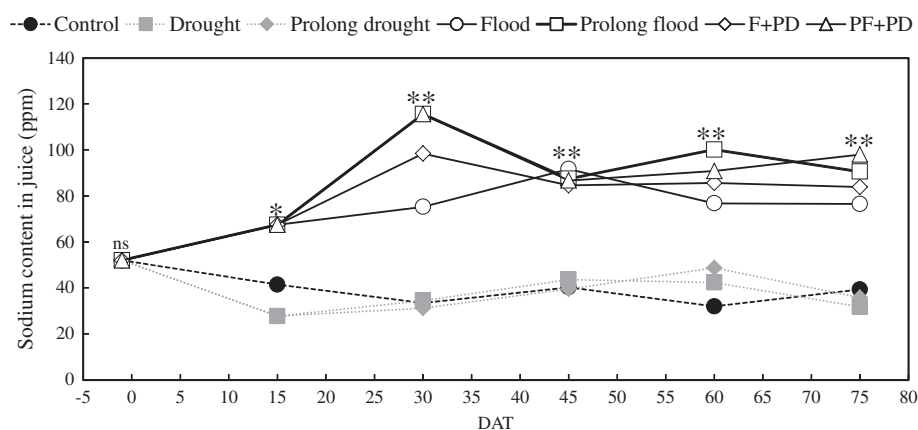


Figure 4. Total sodium concentration in juice of sugarcane cv. NiF8 compared with 7 treatments as control, drought (15 d), prolong drought (30 d), flood (15 d), prolong flood (30 d), F + PD (flood + prolong drought), and PF + PD (prolong flood + prolong drought) at sampling date: 1 d before treatment (–1), 15, 30, 45, 60, and 75 DAT.

Notes. *, ** indicate significant effect of treatments in each sampling at $P \leq 0.05$ and 0.01 , respectively. ns indicates not significant ($n = 3$). DAT: days after treatment.

all of these treatments had recovered by 75 DAT, however, with no significant differences from the control plants.

Flooded plants produced three types of adventitious roots after flooding, an increased number of which were observed during prolonged flooding (Figure 7). The first type of root appeared from the nodes under the water a few d after flooding and was initially white in color but then changed to pink. These roots were most developed in length and size at the top node, decreasing toward the bottom nodes. A second type of root then developed from the first type, which were numerous, small in size, thin, grew upward against gravity, and pink in color. Under prolonged flooding, a third type of root then emerged at the

aerial nodes, commonly being found at the 1st–3rd nodes above the water. These roots were few in number, hard, and short (3–5 cm length), with a deep red color and slow growth. It was also found that the growth of adventitious roots increased under prolonged flooding, with the dry weight of roots being 80.2% higher under the prolonged flooding and PF + PD treatments than under the normal flooding and F + PD treatments, with significant differences at 30 DAT (Figure 6). Aerenchyma was developed in the cortex of these roots, increasing their porosity under prolonged flooding (Figure 8). However, once the plants had been drained, these roots no longer grew, and they dried up.

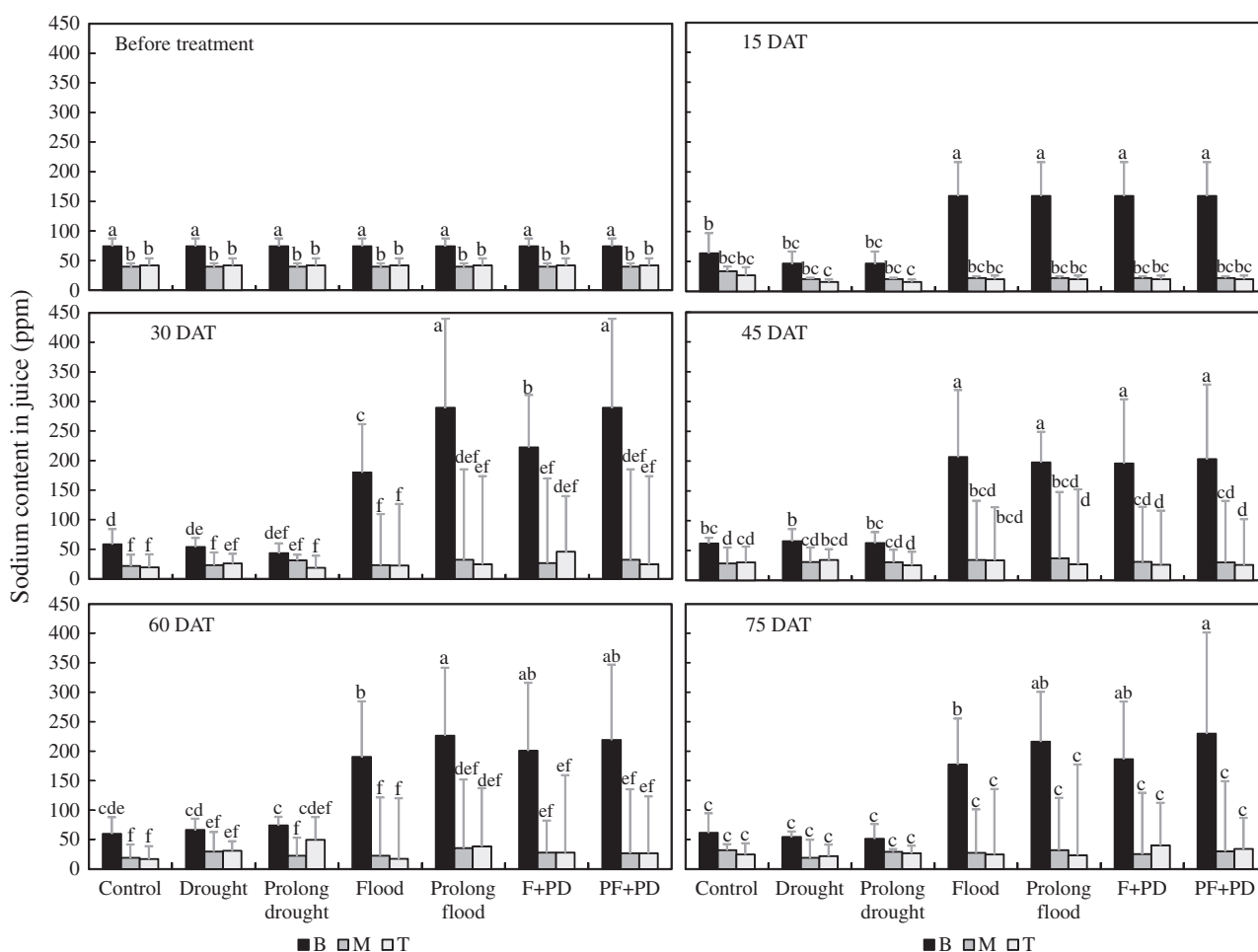


Figure 5. Sodium concentration in juice separated by bottom (B), middle (M) and top (T) of stem compared with 7 treatments as control, drought (15 d), prolong drought (30 d), flood (15 d), prolong flood (30 d), F + PD (flood + prolong drought), and PF + PD (prolong flood + prolong drought) at sampling date: 1 d before treatment, 15, 30, 45, 60, and 75 DAT.

Notes. Mean with the same letter in each sampling indicates not statistically different ($P \leq 0.05$) as determined by LSD multiple comparison test ($n = 3$). Bar shows means \pm SD ($n = 10$). DAT: days after treatment.

Table 1. Substem length, stem fresh weight, LA, total dry mass, percentage of sucrose, percentage of total sugar and sugar yield of sugarcane cv. NiF8 under drought, flood, and combination treatment.

Treatment	Substem length (cm plant ⁻¹)	Stem fresh weight (g plant ⁻¹)	LA (cm ² plant ⁻¹)	Total dry mass (g plant ⁻¹)	Sucrose (%)	Total sugar (%)	Sugar yield (g stem ⁻¹)
Control	320.0a	1,515.7a	7,852.9a	450.5a	21.8a	22.2ab	165.6a
Drought	318.7a	1,368.7a	5,367.0d	395.9a	20.5a	21.0c	140.0a
Prolong drought	326.3a	1,464.7a	6,815.9ab	420.0a	21.0a	21.3bc	153.8a
Flood	316.0a	1,428.3a	6,164.4bcd	426.5a	21.3a	21.6abc	152.1a
Prolong flood	328.0a	1,566.3a	6,413.2bcd	430.8a	20.7a	21.3bc	163.7a
F + PD	318.7a	1,515.0a	6,649.7bc	459.5a	22.2a	22.7a	167.9a
PF + PD	311.3a	1,414.7a	5,683.1 cd	434.0a	21.2a	22.3ab	155.3a

Notes. Treatments included control, drought (15 d), prolong drought (30 d), flood (15 d), prolong flood (30 d), F + PD (flood + prolong drought), and PF + PD (prolong flood + prolong drought) at harvest (75 DAT). DAT: days after treatment. Mean with the same letter in each column indicates not statistically different ($P \leq 0.05$) as determined by LSD multiple comparison test ($n = 3$).

CO₂ assimilation

Under drought conditions, CO₂ assimilation and transpiration ceased in accordance with the stomatal closure (Figure 9). Plants that were exposed to drought and prolonged

drought conditions had a 66% lower CO₂ assimilation rate than control plants at 15 DAT but then recovered following re-irrigation. By contrast, the flooding and prolonged flooding treatments only slightly affected the photosynthesis of the plants; and photosynthesis was unaffected

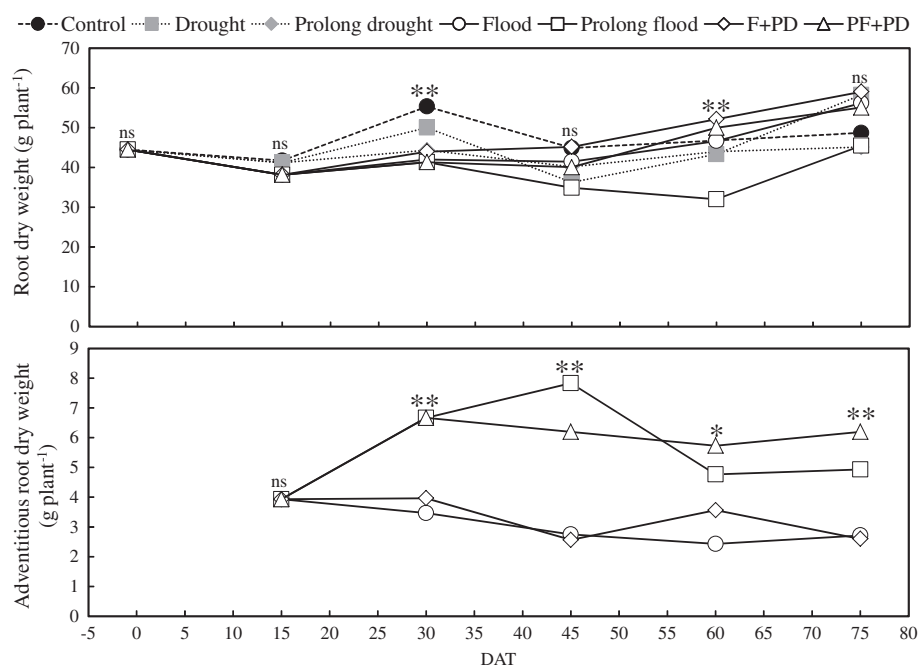


Figure 6. Root dry weight and adventitious root dry weight of sugarcane cv. NiF8 compared with 7 treatments as control, drought (15 d), prolong drought (30 d), flood (15 d), prolong flood (30 d), F + PD (flood + prolong drought), and PF + PD (prolong flood + prolong drought) at sampling date: 1 d before treatment (–1), 15, 30, 45, 60, and 75 DAT of root dry weight and 15, 30, 45, 60, and 75 DAT of adventitious root dry weight.

Notes. *, ** indicate significant effect of treatments in each sampling at $P \leq 0.05$ and 0.01 , respectively. ns indicates not significant ($n = 3$). DAT: days after treatment.

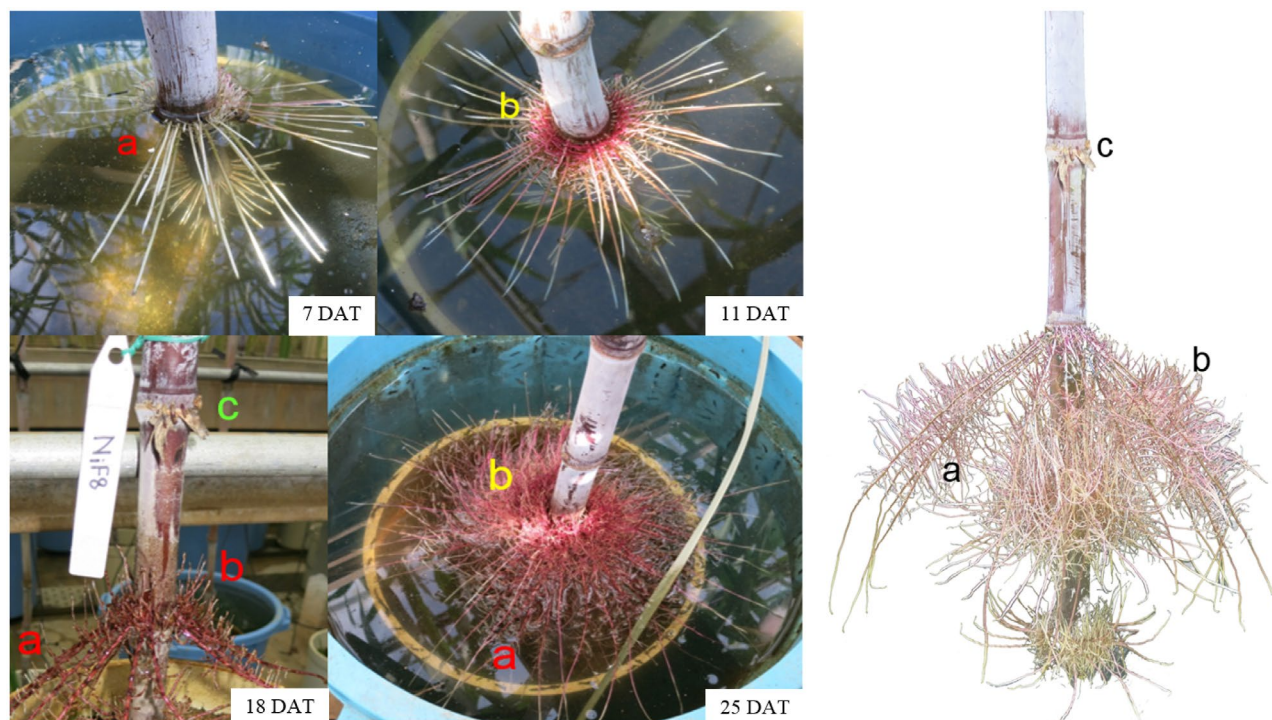


Figure 7. Development of adventitious root at 7, 11, 18, and 25 d under flood condition. Three types of root were emerged, the letter a indicated the first type of roots appeared from the nodes under the water a few d after flooding and were initially white in color but then changed to pink. These roots were most developed in length and size at the top node, decreasing toward the bottom nodes. Afterward, b type of roots was developed from a type with numerous, small in size, thin and grew upward against gravity, and pink in color. Under prolong flood, c roots were third type of root that emerged at the aerial nodes, commonly being found at the 1st–3rd nodes above the water. These roots were few in number, hard, and short (3–5 cm length), with a deep red color and slow growth. DAT: days after treatment.

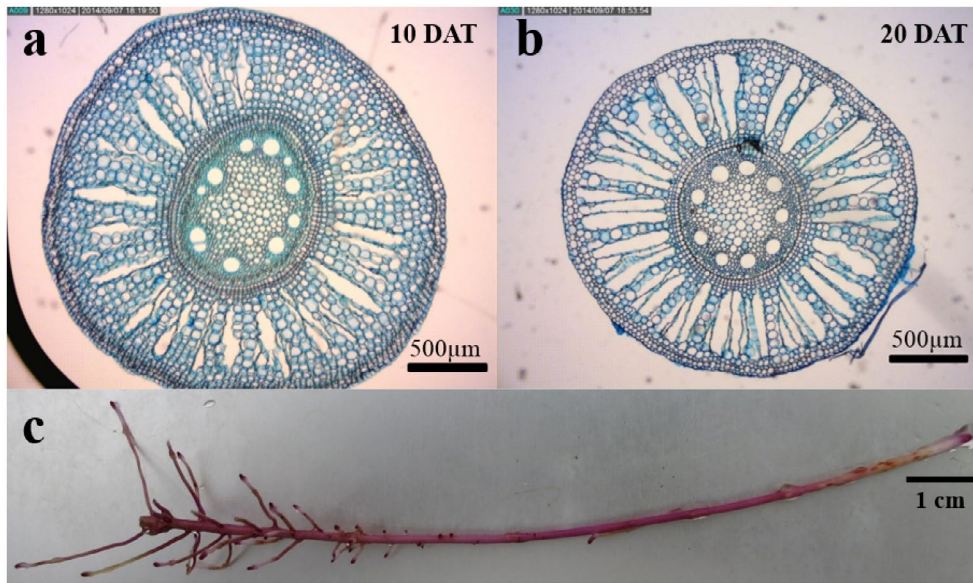


Figure 8. Development of aerenchyma increased porosity in the cortex of adventitious during flood. Cross section was made at 1 cm above the tip at 10 and 20 DAT (pictures a, b, and c). Picture c indicates adventitious root at 10 DAT.

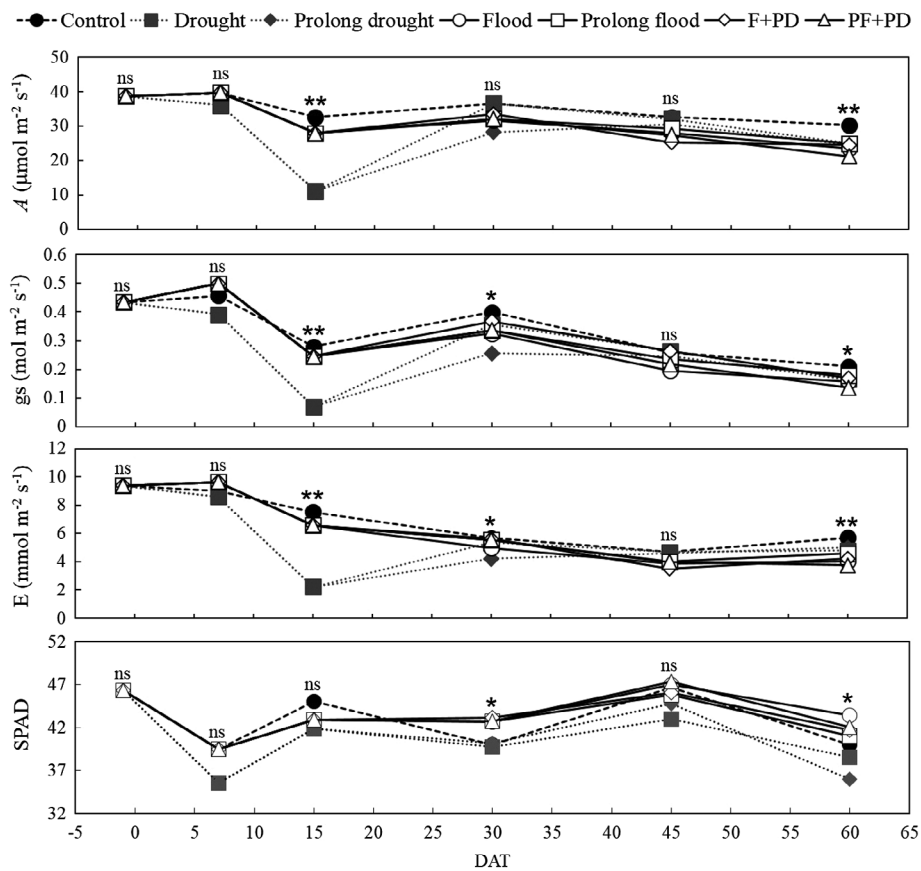


Figure 9. CO₂ assimilation (A), stomatal conductance (gs), transpiration (E), and SPAD of sugarcane cv. NiF8 compared with 7 treatments as control, drought (15 d), prolong drought (30 d), flood (15 d), prolong flood (30 d), F + PD (flood + prolong drought), and PF + PD (prolong flood + prolong drought) measured at 1 d before treatment (–1), 15, 30, 45, and 60 DAT.

Notes. *, ** indicate significant effect of treatments in each sampling at $P \leq 0.05$ and 0.01 , respectively. ns indicates not significant ($n = 3$). DAT: days after treatment.

when the soil was dehydrated after flooding (F + PD and PF + PD). Drought conditions reduced SPAD, and it was found that these effects may continue even after re-irrigation (Figure 9). By contrast, SPAD was maintained at a fairly high level for all other treatments (flood, prolonged flood, F + PD, and PF + PD).

Discussion

CO₂ assimilation and the transpiration rate were dramatically reduced when plants were subjected to drought (Figure 9) due to the stomata closing to prevent transpiration loss, which reduced the amount of CO₂ required for photosynthesis (Cornic & Massacci, 1996; Koonjah et al., 2006). The finding that stomatal conductance reduced alongside CO₂ assimilation matches the findings of a previous study on severe drought, which showed that stomatal conductance and water use efficiency declined by 5% and 7% of the control, respectively (Joseph & Leon, 2009). CO₂ assimilation, stomatal conductance, and transpiration rate in plants that were exposed to drought and prolonged drought treatments increased and recovered following re-irrigation, however (Figure 9). By contrast, the flood and combination treatments slightly reduced CO₂ assimilation compared with the control. The CO₂ assimilation in plants that were exposed to flood and prolonged flood treatments was no different from the control plants at 30 DAT, and plants that were exposed to the treatments that combined flooding with prolonged drought may use the moisture remaining in the drained soil together with the low level of irrigation water to maintain CO₂ assimilation until re-irrigation. These results are consistent with a previous study that reported the positive response of sugarcane gas exchange rates to periodic 7-d flooding (Glaz et al., 2004) and another study which reported that periodic flooding every mo did not affect CO₂ assimilation of Ho 01-12 (energy cane), HoCP 96-540 (sugarcane), or L99-226 (sugarcane), with only L79-1002 (energy cane) experiencing a 50% reduction in cane plants and a 48% reduction in ratoon cane (Viator et al., 2012). However, in the combination treatments (F + PD and PF + PD), CO₂ assimilation was reduced during prolonged drought but then increased when the plants were re-irrigated. In the early stages of flooding (7 DAT), stomatal conductance and transpiration increased to higher levels than control plants. However, when the flooding was extended, stomatal conductance and transpiration reduced in the same way as CO₂ assimilation and were lower than the control (Figure 9). This matches a previous study that showed that a 41-d flood reduced CO₂ assimilation, while stomatal conductance was higher than control plants (Hidaka & Karim, 2007).

Plants that were exposed to drought and prolonged drought experienced a reduction in growth. This matches

the findings of a previous study, which demonstrated that water deficit resulted in a reduction in turgor pressure, the interruption of water flow from the xylem to the surrounding elongation cells, and a slowing down of the growth process, particularly in terms of a decrease in cell elongation and cell volume, an increased concentration of cell sap, and the progressive dehydration of the protoplasm (Larcher, 2003; Nonami, 1998). Low biomass accumulation under water stress has been attributed to a reduction in light interception, plant extension rate, and photosynthesis (Koonjah et al., 2006). However, following re-irrigation, the drought plants exhibited slightly increased LAs, stem dry weights, and total dry weights, although these were still lower than the control plants. By contrast, the flood and combination treatments resulted in plants initially having a slightly reduced growth rate than control plants and then a slightly higher growth rate than the control plants, even under prolonged flooding. This is consistent with the previous finding that the total dry weight of the roots, leaves, and stalks of flood plants was 16% higher than control plants (Hidaka & Karim, 2007). The F + PD and PF + PD treatments resulted in plants having slightly reduced growth, but this then increased when the plants were re-irrigated (Figure 2). At the time of harvest, the sub-stem length, stem fresh weight, and total dry weight had recovered for all treatments, while LA was still affected and different between the treatments (Table 1).

Prolonged drought reduced the root dry weight by 19.9% at 30 DAT, which matches the previous finding that the hypocotyl length, and the fresh and dry masses of shoots and roots of alfalfa (*Medicago sativa*) decreased under water deficit (Zeid & Shedeed, 2006). Similarly, prolonged flooding and the PF + PD treatment reduced the dry root weight by 25.3% at 30 DAT (Figure 6). These results are consistent with a previous study on roots under flooded conditions, which demonstrated that the root hairs died and the original roots became blackened and rotten, leading to the arrest of root respiration and affecting important metabolic activities of the plants (Gomathi et al., 2014). However, the plants compensated for this by producing adventitious roots that emerged from the root primordia at nodes under the water and from aerial nodes, with increased numbers being seen when prolonged flooding had occurred (Figure 6). These roots developed as a result of the hormonal imbalance that is induced by hypoxia due to the low oxygen supply to the submerged tissue and were located in the upper layer of water, which has a higher oxygen content (Gomathi et al., 2014). Three types of roots were produced after flooding: the first type emerged from the nodes that were located under the water, the second type developed from these first roots and grew upward against gravity, and the third type emerged from aerial nodes above the water (Hidaka &

Karim, 2007). As a result of this growth, the root dry weight was 41.0% higher under prolonged flooding compared with normal flooding (Figure 6).

These roots also exhibited an increased porosity as a result of aerenchyma developing in the cortex (Figure 8). It has previously been reported that flooding for 3 mo led to a 4–15 times increase in root development, a 108% greater aerenchyma pipe extension, and a 115% greater aerenchyma pipe diameter (Gilbert et al., 2007), while flooding for 120 d to a level 30 cm above the top of the soil led to sugarcane clone I 6–04 having the highest root dry weight at 28.3 g/plant (Begum et al., 2013). During floods, plants produce roots and exhibit ethylene-dependent death and lysis, which lead to the formation of continuous gas-filled channels (aerenchyma) that help the plants to maintain their root activity and supply the necessary oxygen (Drew, 1997). Thus, the numerous roots that grow during floods are better adapted to these conditions than the original roots, containing well-developed aerenchyma (Laan et al., 1991). Since root elongation was closely related to the oxygen concentration in the root zone, the internal aeration of the plants may have been achieved by increasing the root porosity and developing aerenchyma, which may have helped the plants to continue to take up water and nutrients, and may have offset any losses associated with flooding (Begum et al., 2013; Gilbert et al., 2007; Gomathi et al., 2014). However, following drainage, it was found that some of the original roots were damaged, and the adventitious roots dried out and became non-functional. Thus, the flooded plants required time to develop new roots to support and recover their growth.

The sucrose content of the sugarcane juice increased during the early stages of drought but then decreased under prolonged drought conditions when the plants were placed under extreme stress. These findings support those of a previous study that showed that sucrose content increased during a period of low rainfall or under dry-land conditions but was reduced under extreme drought conditions (Robertson et al., 1999a); and similarly, a 6-wk drought during the grand growth phase was found to reduce the sucrose content by an average of 4.7% and sugar yield by 11.7–19.1% (Wiedefeld, 2000). In this study, however, sucrose content increased again following re-irrigation. In plants that were exposed to the flood and combination treatments, the sucrose content decreased in the early stages of flooding and then dramatically increased to reach levels that were similar to the control plants, even during prolonged flooding or where flooding was followed by drought (Figure 3). These results are consistent with the previous finding that sugar yield was not affected in cultivar CP 72-1210 when grown with a water table depth of 45 or 75 cm (Pitts et al., 1990), while 2-d periodic floods in each of eight 14-d cycles per year increased the cane

and sucrose yield in cultivars CP 72-2086 and CP 80-1827 (Glaz & Gilbert, 2006). However, in this study, all treatments had an increased sucrose content once the treatments had finished.

During flooding, the concentrations of various ions, such as NH_4^+ , K^+ , Mg^+ , Cl^- , PO_4^- , and SO_4^- , were reduced in the sugarcane juice and remained at a lower level than the control even once the water had been drained and the conditions had returned to normal. Both Ca^+ and F^- also increased during flooding but then returned to similar levels to the control following drainage (data not show). By contrast, the concentration of sodium (Na^+) was higher in the flooded plants than in the control and drought plants. Furthermore, during prolonged flooding, the sodium content of plants was 245.5% higher than in the control plants, representing a 71.3% increase as a result of flooding, which was maintained even after the water had been drained or the plants had been placed under prolonged drought conditions (Figure 4). The highest sodium content was found in the bottom part of the stem, and it was here that the levels increased during prolonged flooding, while the middle and top parts of the stem had similar sodium concentrations as the control plants (Figure 5). However, there is still a lack of information about this increase in sodium content in the juice of flooded sugarcane plants, and so its role in flood tolerance remains unclear. Thus, further study on the relationship between sodium accumulation and physiological changes under flood conditions may help to explain this phenomenon in the future.

Conclusion

Our study showed that CO_2 assimilation was reduced dramatically in sugarcane plants that were exposed to drought and prolonged drought treatments but recovered once the plants were re-irrigated. By contrast, the flood and combination treatments did not affect CO_2 assimilation, even when the water was drained or the plants were subsequently exposed to prolonged drought. During flooding, adventitious roots with well-developed aerenchyma were produced, the number of which increased under prolonged flooding, which may help plants to offset the losses associated with flooding. The expansion of LA was interrupted by drought and remained at a low level even after re-irrigation, while this increased once the flood and combination treatments had finished. The stem and total dry weight increased as a result of the flood and combination treatments but reduced during the drought treatments. At the time of harvest, there were no significant differences in stem fresh weight, sucrose content, or sugar yield between treatments. Flooding induced the accumulation of sodium in sugarcane juice at the bottom of stem, with a particularly high accumulation following

prolonged flooding, and this remained even after the soil water had been drained and re-irrigated. Therefore, it is concluded that the formation of adventitious roots may offset the negative effects of root death and help plants to maintain their growth and yield of sugarcane during a flood.

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Disclosure statement

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