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Flooding Tolerance of Sugarcane in Relation to Growth, Physiology and Root Structure

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Abstract

Different abiotic stresses, such as typhoon, excess water from the torrential rains, flooding during summer in the low lying areas and drought hinder sugarcane productivity. This study was initiated to analyze flooding induced changes in growth, physiology and root structure of sugarcane. A Japanese sugarcane variety, NiF 8, was grown in pots inside a glasshouse under natural light and flooded for one month. Flooding increased root, leaf, stalk and total dry weight. Three different kinds of roots were initiated from the flooded plants, viz. (i) from the aerial nodes (above the water surface), which were reddish-black in color; (ii) from the pre-existing roots primordia, which were developed under water and whitish in color; and (iii) from the newly developed roots, which had upward growth against the gravity and major portion above the water surface, were relatively thinner and pinkish in color. Roots growth showed a positive relationship with that of shoot growth. Photosynthetic rate (Pn) was decreased by flooding, but stomatal conductance (gs) and intercellular CO_2 concentrations (Ci) were increased; thus, indicated a non-stomatal limitation to Pn. Sugar concentration (brix) was found higher in the flood affected plants, especially in the juice of base and middle part of the stalk.
Key words: brix, dry matter, excess water, gas exchange, root structure, *Saccharum* spp.

Introduction

Sugarcane (*Saccharum* spp.) is widely distributed in the tropics and subtropics. This crop plays a major role in the economy of many countries. It is the second most cash earning crop of the farmers, after jute, in Bangladesh. In Japan, sugarcane is the major industry of the Ryukyu Islands, the southern most islands of Japan. The Ryukyu Islands are composed of two prefectures, Kagoshima and Okinawa, which is located between Taiwan and Kyushu, one of four main islands of Japan. It stretches from latitude 24° north (Okinawa Prefecture) to latitude 31° north (Kagoshima Prefecture) in 1000 km long. The crop is the most important crop in the regional economy of the area.

In none of the sugarcane growing countries, however, the farmers are able to har-

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vest the potential cane and sugar yield. There exists a big 'yield gap' between the average yield of the country and that obtained from demonstration trials in the farmers fields. Among many reasons, abiotic stresses, such as typhoon and torrential rains in the Pacific regions, monsoon summer rains, drought and low fertility of soil are behind the low yield of sugarcane. For example, in Bangladesh, about one third of sugarcane is now growing in the low land where the plants remain under water during summer for a considerable long time (HASAN *et al.* 2003). In Japan, sugarcane production has been sluggish because of lack of labor caused by aging of farmers, unstable yield and quality under harsh environments, such as typhoons, drought, torrential rains, etc. (MATSUOKA 2005)

Flooding tolerance is related to many physiological and anatomical adaptations of plants. The tolerant species are able to form aerenchyma, which helps for functioning of the plant processes under anoxia conditions (DREW 1997). GLAZ *et al.* (2004a) concluded from their study that some genotypes of sugarcane can produce constitutive aerenchyma, meaning that plant requires no external stimulus such as flooding for aerenchyma formation, while some genotypes need exposure to flood to form the aerenchyma. Probably, genotypes having the ability to form constitutive aerenchyma perform better under unpredictable short time flooding conditions, such as caused by heavy rains.

Flooding damage in plant is related to several factors, such as flooding depth, duration and flow of water in the field. However, flooding effects on sugarcane physiology and productivity remain inconclusive. GLAZ *et al.* (2004a) and GLAZ *et al.* (2002) reported a higher cane yield or unaffected yield, in some of the genotypes they used, in the wetter field (hypoxia). GASCHO and SHIH (1979) did not find yield differences in two of six cultivars of sugarcane when grown between water table depths of 32-84 cm in lysimeters. GLAZ *et al.* (2004b) also noticed a neutral or positive response of gas exchange characteristics of sugarcane to flooding. Contrary, HASAN *et al.* (2004), RAHMAN *et al.* (1986), and WEBSTER and EAVIS (1972) reported a significant reduction in cane growth under anoxia conditions. More studies are, therefore, needed to make a fruitful conclusion on the sugarcane response to flooding. In this paper, we describe the growth response, photosynthesis and changes in root structure of sugarcane under flooding conditions.

Materials and Methods

Plant material and growth conditions

Sets of NiF 8, a most popular variety of sugarcane (*Saccharum* spp.) in Japan, were planted on 14 June 2005 in plastic pots of 32cm X 26cm in size, filled with soil, a mixture of 80% loamy soil and 20% compost. After germination of the seedlings, about 10g of NPK mixed fertilizers (14:14:14) were applied to the pots. The pots were kept inside a glasshouse under natural conditions. All the pots were drip-irrigated once daily for 10 minutes using a programmed irrigation system. The drip irrigation was controlled to supply enough water for plants and the soil in the pots did not dried during the periods required.

Treatment imposition

The pots were divided into three groups. In one group, the pots were kept into big buckets filled with water to impose flooding on 16 September 2005 (96 days after planting). The water level in the bucket was about 2cm above the soil surface of the pot. The drip irrigation in the pots of this group continued to compensate the water loss due to evapotranspiration. In the second group, irrigation was cut completely to impose water stress. This treatment was initiated to compare the sugar percentage (brix) and root structures of water stressed plants with that of control and flooded plants. The third group was treated as control. The drip irrigation to this group was continued until harvest on 27 October 2005 (135 days after planting). Flooding was applied for a total of 41 days.

Measurement of plant parameters

Roots

Roots from flooded, water stressed and control plants were collected on 03 October 2005 (16 days after treatment imposition) to study the changes in root structure due to flooding and drought. After collection, the roots were fixed with a solution of ethanol and acetic acid (3:1). Sections were made with a plant microtome (Automatic MT-3, NK system, Japan) and the sections were viewed under microscope and photographed. Sections were made from both root tip and about 2cm above the tip (henceforth be called as 'near-tip').

Relative water content (RWC) and water retention capacity (WRC)

Leaf pieces, about 3cm long and 1cm wide without midrib, from four replicated plants of each treatment, were collected on 18 October 2005 (32 days after flooding) to measure relative water content (RWC) and water retention capacity (WRC). Soon after the collection, fresh weight of the pieces was immediately measured. The pieces were then immersed into deionised water for 8 hours (h) and weighed, after gentle wipe with paper-towel, to get the turgid weight. The pieces were then dried at 80 ℃ for 48 h and weighed for dry weight. The RWC and WRC were calculated as follows:

$$\text{Relative water content (RWC)} = \frac{\text{Fresh weight-Dry weight}}{\text{Turgid weight-Dry weight}} \times 100$$

$$\text{Water retention capacity (WRC)} = \frac{\text{Turgid weight}}{\text{Dry weight}}$$

Gas exchange characteristics

On the day of harvest (135 days after planting), photosynthetic rate (Pn), stomatal conductance (gs) and intercellular concentrations (Ci) were measured with a portable photosynthesis system (Koito Co. Ltd. Tokyo, Model- CIRAS-A), using the uppermost developed leaves, from four replicated plants under control and flooded conditions. During the measurement, the PAR was set to 1500 μ mol $m^{-2}s^{-1}$ and the CO^2 concentration to 370 ppm.

Brix (%)

At harvest, the stalk of control, flooded and water stressed plants was divided into base, middle and top. The brix was measured from each part separately. Three replicated plants were used for brix measurement. Juice from the water stressed plants was collected after pressing the stalk, because the plants were seriously dehydrated.

Plant height and dry weight of different plant parts

The height was measured from the base to the leaf tip of each plant at harvest. Each plant was separated into roots, leaf and stalk. The plant parts were oven dried at 80℃ till the weight was constant. Three replicated plants from both control and flooding conditions were used for the measurement of each parameter.

Results

Morphologically the flooded plants looked similar to the control till the end of the experiment. The lower leaves of water stressed plants turned to yellow after a week of drought and the symptom proceeded to the upper leaves. At the end of the experiment, the plants were almost dead. For flooding, new roots development was initiated just after two days of flooding. Three different kinds of roots were observed in the flooded plants (Fig. 1), *viz*. (i) roots were initiated from the aerial nodes, which were thick, very hard, some were short (about 5-6 cm long) though some extended into water and developed there, the aerial part was in a mixture of reddish and black in color, while the part developed under water was whitish; (ii) roots were initiated from the pre-existing roots primordia and developed under water, which were whitish in color, thick, relatively soft and brittle than the pre-existing older ones; (iii) secondary roots were initiated from the newly developed roots, which were about 3-5 cm long and had upward growth against the gravity, had major portion above the water surface and were relatively thin and pinkish in color. The pre-existing old roots turned into dark brown in color and were hard but living. Roots of the water stressed plants had profuse growth and produced a lot of thin roots hairs.

The relative water content (RWC) of water stressed plants reduced very much compared to that of control and the flooded plants (Table 1). The RWC of flooded plants was also lower compared to that of the control plants, however, the reduction

Fig. 1. A flooded plant showing roots from the aerial nodes and from water surface (top). Three different kinds of roots were developed from flooded plants, *viz*. roots initiated from the aerial nodes (a), some of which were extended into and developed under water, and aerial portion of the roots was reddish-black in color; roots initiated from the pre-existing roots primordia (b), developed under water and whitish in color; roots developed from the newly developed roots surface (c), had upward growth against the gravity, were relatively thin and short, and pinkish in color (bottom).

Table 1. Relative water content and water retention capacity of sugarcane as affected by flooding and drought for three weeks.

Treatment	Relative water content (%)	Water retention capacity
Control	97.80 ± 0.125	3.68 ± 0.049
Flooding	95.50 ± 0.144	3.80 ± 0.028
Drought	59.25 ± 0.774	4.09 ± 0.037

± : Standard error.

was less than 3%. Water retention capacity was the highest in drought affected plants followed by flooded and control plants, respectively.

Surprisingly, plant height of the flooded plants was noticeably higher than that of the control plants (Fig. 2). Dry weights of roots, leaf and stalk of the flooded plants were conspicuously greater than that of the control plants (Fig. 3a, b, c). An increase of 22%, 4%, and 26%, from the control, of roots, leaf and stalk dry weight, respectively, was observed in the flooded plants. Therefore, the stalk dry weight was the most responsive to flooding. The higher roots, leaf and stalk dry weight contributed to the 16% increase in total dry weight of flooded plants compared to that of the control plants (Fig. 3d).

Flooding affected appreciably the gas exchange characteristics of sugarcane leaf

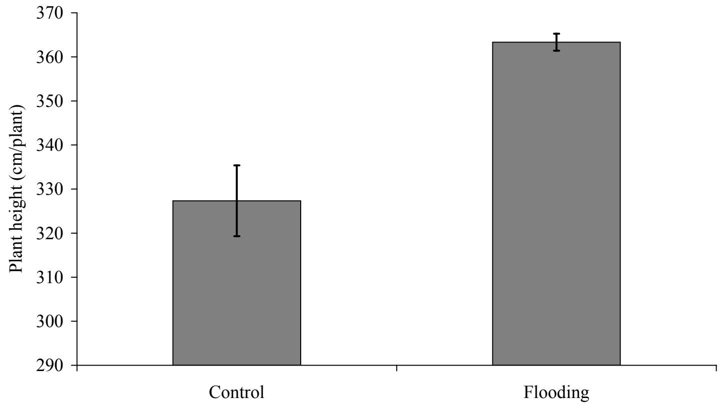

Fig. 2. Effects of flooding for one month on plant height of sugarcane.

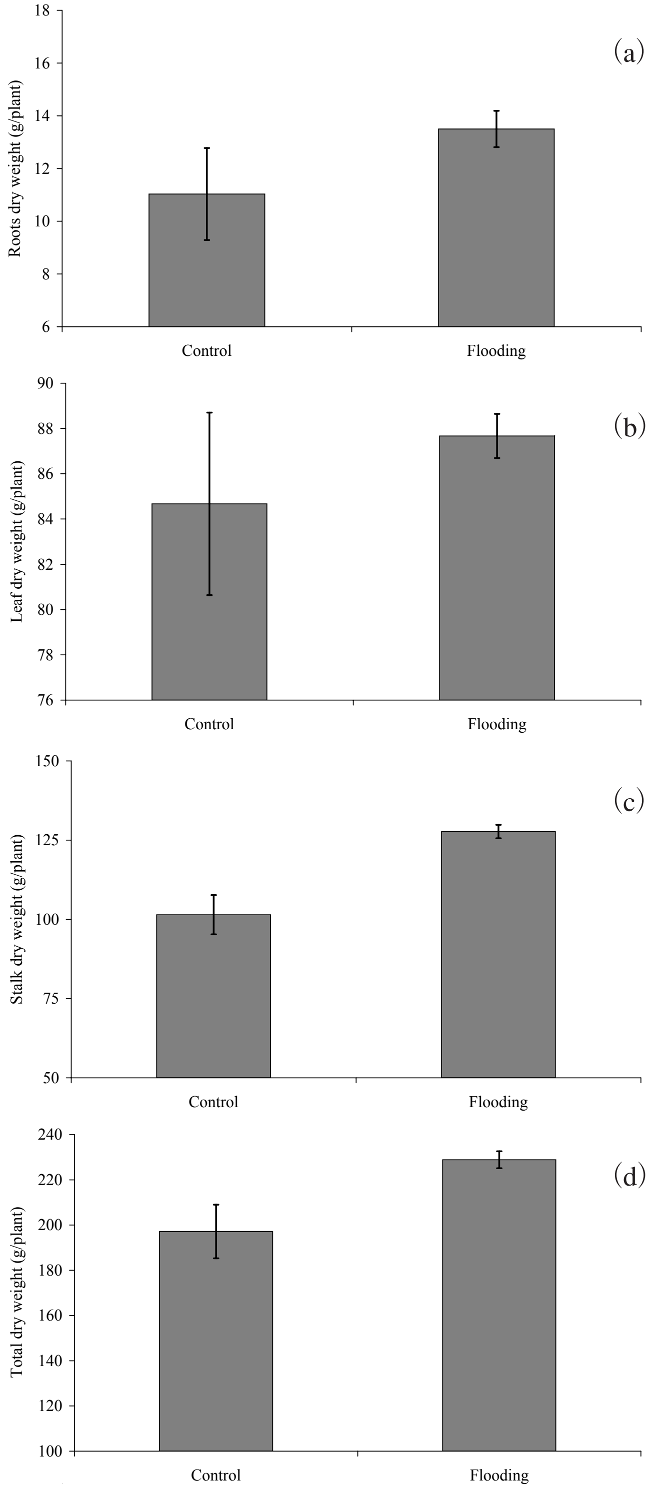

Fig. 3. Effects of flooding for one month on roots dry weight (a), leaf dry weight (b), stalk dry weight (c) and total dry weight (d) of sugarcane. Bar indicates standard error (±).

(Fig. 4a, b, c). A reduction in photosynthesis (9%) was noticed in the flooded plants. Surprisingly, flooded plants had several fold higher stomatal conductance than that of the control plants. Similarly, flood affected plants had higher intercellular CO_2 concen-

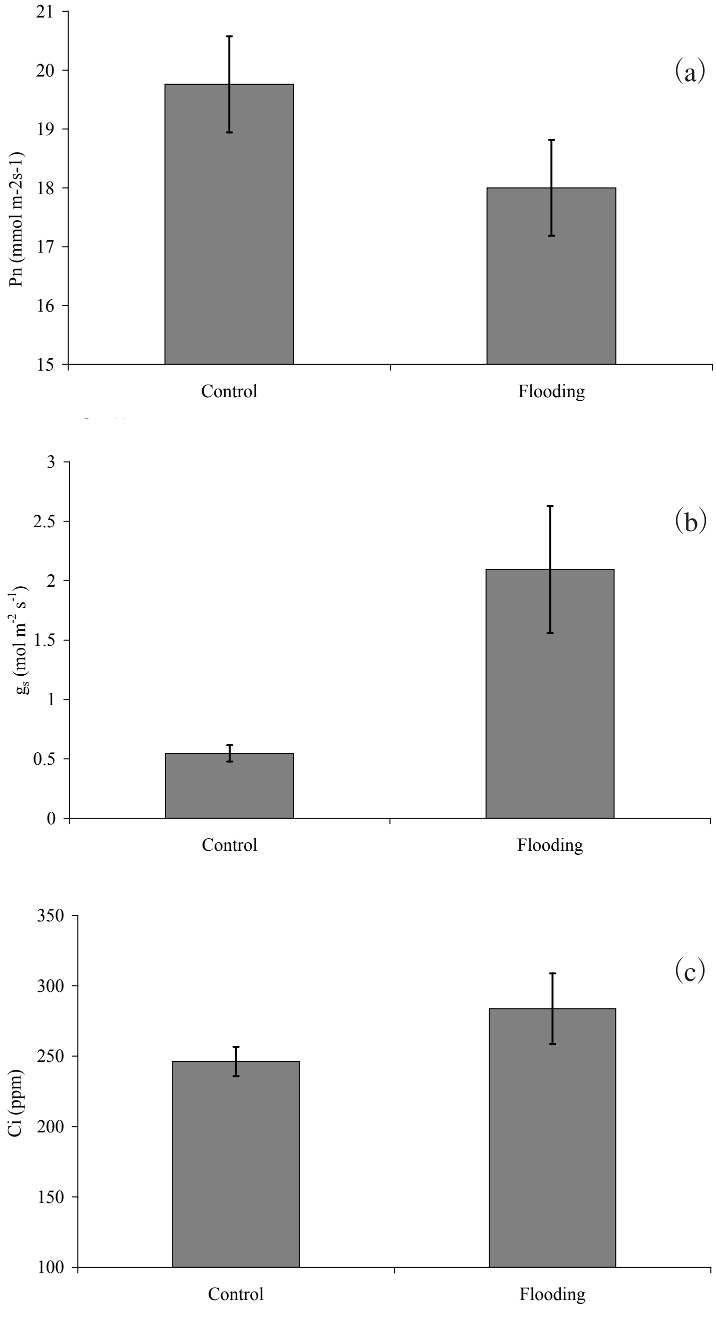

Fig. 4. Effects of flooding for one month on photosynthetic rate (Pn) (a), stomatal conductance (g_s) (b), and intercellular CO_2 concentrations (Ci) (c) of sugarcane. Bar indicates standard error (±).

tration (15%) than that of the control plants.

The brix of juice of the base of stalk was much higher than that of the mid and top, irrespective of the treatments imposed (Table 2). Interestingly, the juice of base of flooded plants had significantly higher brix than that of control or water stressed

Table 2. Brix in juice of different parts of sugarcane stalk as affected by flooding and drought for one month.

Treatments	Base	Mid	Top
Control	16.73 ± 0.694	12.87 ± 0.750	7.00 ± 0.3
Flooding	19.80 ± 0.115	13.33 ± 0.851	6.87 ± 0.306
Drought	14.27 ± 0.395	11.23 ± 0.302	10.47 ± 0.184

± : Standard error.

plants. There was a little difference in brix of mid portion among the treatments, though the juice of the flooded plants showed relatively higher brix compared to that in other two treatments. However, the juice of the top of water stressed plants had appreciably higher brix than that of control and flooded plants.

The root systems developed under different treatments condition are shown in Fig. 5. Roots system of flooded plants was spreading type, shorter and had thick but less number of roots compared to that in the other treatments; it had many new roots, which were thin and pinkish in color with upward growth as described before. Root system of water stressed plants was profuse in growth, relatively longer, had a lot of

Fig. 5. Roots of control (left), water stressed (center) and flooded (right) plants of sugarcane. There were a lot of hairy roots in controlled and water stressed plants, however, few hairy and more bigger roots were seen in the flooded plants, which contributed to the root weight of the plants.

thin rootlets, and many roots in number compared to that of control root system. The flooding and water stress also changed the roots structure (Fig. 6). Root hairs were observed in tip and near-tip of the roots of control plants (6a). There were a few gas-filled spaces in several places of the near-tip of control plant roots, but the shape of the spaces was irregular (6b). Tip of the water stressed roots had also hairs and the cells were relatively round (6c); the near-tip of these water stressed roots had also hairs,

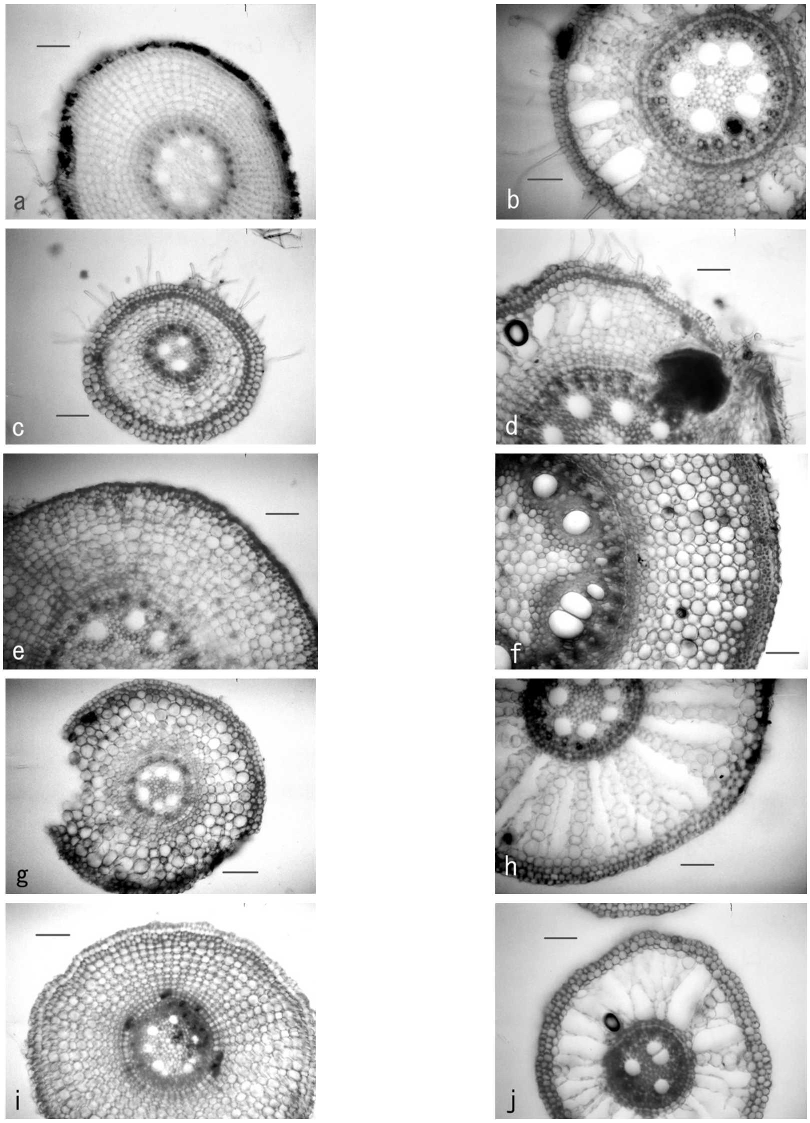

Fig. 6. Photographs of tip (a) and near-tip (b) of the roots of control plant; tip (c) and near-tip (d) of the roots of water stressed plant; tip (e) and near-tip (f) of the roots developed from aerial nodes of the flooded plant; tip (g) and near-tip (h) of the roots initiated from primordia of the pre-existing roots and developed under water of the flooded plant; tip (i) and near-tip (j) of the roots developed from the new roots surface and had upward growth of the flooded plant. Note that, the gas-filled spaces of the roots developed from flooded plants were much larger and connected from the outer layer to the cambium layer, while that of the control and water stressed roots were irregular in shape and not connected between the two layers. The near-tip of the aerial root had no gas-filled space. See the text for detailed explanation. (bar = 0.1 mm)

compact cells, a few gas-filled spaces of irregular shape, and had signs of new rootsdevelopment (6d). The tip of the roots developed from aerial nodes of the flooded plants had no hair, thick cell walls and hard outer cell layers (6e); the near-tip of these roots had no gas-filled spaces, relatively round and larger cells, and had very thick outer layers (6f). The tip of the roots, initiated from the primordia of pre-existing roots and developed under water, had thin outer layer, more intercellular spaces and no root hairs (6g); the near-tip of these roots had very large gas-filled spaces, larger than any of the roots studied, alternate with one or more rows of radial lines of intact large sized living cells, and the spaces were connected from the outer layer to the cambium layer (6h). The tip of the roots, developed from the new roots and had upward growth, did not have roots hair but had thin outer layers (6i); the near-tip of this type of roots had mostly gas-filled spaces, which were connected from the outer layer to the cambium layer, and there were a few radial lines of the intact cells between the two spaces (6j).

Discussion

The purpose of this study was to analyze the response of sugarcane to flooding. The results indicated that the growth was favored by the flood for one month. The positive growth of sugarcane due to flooding reconfirms the earlier reports of Glaz *et al.* (2004a) and Glaz *et al.* (2002) who noticed a higher yield of sugarcane, in one of nine cultivars, from the wetter field than that from low depth of water table one. They, however, noticed a high variations in yield among the genotypes; some genotypes were unaffected or even had low yield under wet conditions. Carter and Floyd (1971) did not notice differences in yield of sugarcane due to variations of water table depth. They, however, did not consider a treatment with water level above the soil surface. Contrary, Hasan *et al.* (2003), Rahman *et al.* (1986) and Webster and Eavis (1972) reported deleterious effects of flooding on sugarcane yield. Therefore, it is rather difficult to make a general conclusion on the growth response of sugarcane to flooding. However, the results of our study and that of the previous ones imply that sugarcane, in general, can tolerate flooding for a long time and there are high genotypic variations in flooding tolerance; some genotype may produce significantly higher yield under anoxia or hypoxia conditions.

Roots play a very important role on the survival of plant and its productivity under flooding conditions (Drew 1997, Drew *et al.* 1979). Three different kinds of roots were developed from the flooded plants, besides the pre-existing ones. The roots that developed from the aerial nodes and remained above the water surface hardly produced any aerencyma. Some adventitious roots were initiated from the pre-existing roots primordia and developed under water; this type of roots had large interconnected gas-filled spaces. The third types were developed from the newly developed roots surface and had upward growth against the gravity. This types of roots also formed large interconnected gas filled. All these roots, that developed by the influence of flood, helped in maintaining roots activity under flooding conditions by supplying necessary oxygen (Drew 1997). The newly developed roots might contribute for the higher dry matter accumulation in the cane under flooding conditions, however, further experiments under different revels of water supply should be needed. It is not clear why the flood affected plants had lower relative water content and higher water retention capacity compared to that of the control plants, although the former had higher root mass than the latter one. The role of newly developed roots on water uptake under flooding conditions remains to be elucidated in further studies. Moreover, the roots that developed from the aerial nodes and remained above water surface had no gas filled spaces. Therefore, their role on flooding tolerance needs to be clarified.

The dry matter accumulation in roots, leaf and stalk of the flooded plants was 22%, 4, and 26%, respectively, higher than that of the control plants (Fig. 3a, b, c). The variation in the distribution indicated that roots and stalk of flooded plants received relatively more dry matter than that of the leaf. Perhaps current photosynthesis, which was lower under flooding conditions (Fig. 4a) than the control, was supporting more the stalk and roots development compared to the leaf development.

Flooding lowered the photosynthetic rate (Pn), though increased the stomatal conductance (g_S) and intercellular CO_2 concentrations (Ci). The results partially corroborated with that of Glaz *et al.* (2004b), who observed a neutral or positive response of photosynthetic rate, transpiration and stomatal conductance of sugarcane leaf to flood. According to Liao and Lin (1994), the Ci elevation under flooding conditions might have been attributed to a reduced Pn, a higher respiratory CO_2 evolution rate than the CO_2 fixation rate, and an increase in stomatal resistance. In this experiment the stomatal resistance was, however, lower in the flood affected plants, as indicated by the several fold higher g_s than that of the control plants. The higher Ci as well as g_s of the flooded plants indicated that the low Pn was not due to the lack of CO_2. Rather, non-stomatal factors, e.g. low ATP supply, were presumably responsible for the lower Pn under flooding conditions.

The brix of the juice from base of the flood affected plants was significantly higher compared to that of control and water stressed plants (Table 2). The difference in the brix of the mid portion was narrow among the treatments, though flood affected plants had higher brix. Brix of the top was, however, higher in the water stressed plants. Moreover, there was a little difference in brix among base, mid and top of the water stressed plants compared to that of the plants under flooded and control conditions. As already mentioned that leaves of the water stressed plants were almost dead and the plants stopped the growth completely at harvest. It might happened that photosynthetic activities of water stressed plants were stopped long before it was permanently wilted, and the plants had to live on reserved food. Consequently, the sugar content of the water stressed plants might have depleted (lower brix) and well distributed among top, middle and base compared to that in other treatments. Hasan *et al.* (2003) noticed a higher brix from waterlogged sugarcane plant compared to that of well aerated plant. In a study of Rahman *et al.* (1985), the flood affected plants had higher level of sucrose, glucose and fructose, though they did not find a relationship between sugar levels and flooding tolerance of different sugarcane species. Contrary, the sugar yield was higher in the well drained sugarcane field than that of flooded one in the study of GLAZ *et al*. (2004a). Like growth, there might have high genotypic differences in sugar content in response to flooding.

In conclusion, we have demonstrated the flooding induced changes in growth, physiology and root structure in sugarcane. The growth was enhanced by the flooding. However, the growth of roots and stalk was relatively higher than that of leaf growth. Three different kinds of roots were developed from the flooded plants. Except the aerial one, which developed from the nodes above the water surface, the other two types of roots had large gas-filled spaces, which were more than the space occupied by the root cells. Photosynthesis was reduced by flooding. However, the enhanced Ci and g_s due to flooding indicated a non-stomatal limitation to Pn. Flooding also increased brix of juice form base and mid, but not from that of the top. Drought affected plants had well balanced brix in base, mid and the top compared to that of other treatments.

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