



Title	窒素処理がサトウキビの成長と光合成速度に与える影響
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# Effects of Nitrogen Supply on Growth Characteristics and Leaf Photosynthesis in Sugarcane

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## Summary

The objective of the present study is to demonstrate the effects of applied nitrogen concentration on the uptake pattern and composition in different parts and investigate the relationship between uptake and physiological activities. We measured leaf number, plant height, leaf nitrogen content, chlorophyll content, and gas exchange rates. Nitrogen concentrations of the six nitrogen levels (0, 1/6, 1/3, 1/2, 1 and 2N) were prepared as 0, 1.5, 3, 4.5, 9 and 18 ml per liter of  $\text{NH}_4\text{NO}_3$  in nutrient solution.

The all parameters measured were increased with increasing levels of nitrogen concentration up to twice of the control. Highest values at 104 days after transplanting in the number of fully expanded leaves, the total leaf number, and plant height, which were observed in the plants grown with 2N solution, were 12, 14.2, and 209cm, respectively. The nitrogen content, SPAD, photosynthesis, and transpiration rates were increased with successive increase in the nitrogen concentration of nutrient solution from 0 to 2 times of the control. The leaf nitrogen content, SPAD, photosynthesis and transpiration were highest in the plant grown with 2N solution and these were 2.28, 39.25, 29.78 and 3.04, respectively.

Nitrogen content in the leaf sheath, mid rib, blade of younger fully expanded leaf of the plant grown with the solution of normal nitrogen concentration were analyzed. The results showed that leaf blade contain highest nitrogen followed by mid rib and sheath. Concentration of nitrogen was higher in top portion as compared with the base. Nitrogen content was highest in the 6th leaf (2.11%), followed by the 5th leaf (2.03%). It might be due to more actives of younger fully expanded leaf, besides these nitrogen concentrations.

The 6th leaf from tip recorded maximum leaf nitrogen content,

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whereas the 5th leaf showed highest SPAD, photosynthesis and transpiration rates. Leaf nitrogen content showed a positive correlation with SPAD and photosynthesis indicating that nitrogen is the dominating factor on these parameter. In the present studies, 3rd leaf from tip, which is younger fully expanded leaf, indicated the higher photosynthetic nitrogen use efficiency, followed by 2nd and 4th leaf.

The optimum temperature of photosynthesis was higher at the 2070  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  of PFD and lowering at 455  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  of PFD. The optimum temperature of photosynthesis was not shifted with nitrogen levels as seen at different PFD. The maximum photosynthetic rate with 0N plants was higher than those of 1/6 and 1/3N plants. In addition, initial slope of the light dependent photosynthetic curves in 0N plants was also higher than those in 1/6N and 1/3N plants.

### Introduction

Sugarcane is an important cash crop catering for about 60 per cent sugar needs of the world. India is the largest producer of sugarcane in the world. Sugarcane is grown in about 3,386 million hectares of land, out of which about 1,129 and 2,257 million hectares are in tropical and sub tropical, respectively. Sugarcane production in tropical zone is about 97,969 million tones and in sub-tropical about 129.09 million tones. The average cane yield of 60t/ha in sub-tropical against 67t/ha for the nation and 100t/ha for tropics is an indication of vast productivity through appropriate production technologies.

Sugarcane crop, producing a heavy tonnage, removes a good amount of plant nutrients from the soil, which needs to be replenished in order to maintain the soil fertility. Large number of factors influences the composition and uptake of nutrients by sugarcane plant. Composition and concentration of nutrient solution also affect the chemical composition of various plant parts, which in turn affects the morphological, anatomical features and physiological processes.

The photosynthetic capacity of a crop is greatly dependent on nitrogen availability. Nitrogen can affect photosynthetic rate per unit leaf area for example, altering the concentrations of photosynthetic pigments or enzymes (Dejong and Doyle, 1985 ; Olensinki et al., 1999). The close association between leaf photosynthetic rate and leaf nitrogen concentration has often been reported in many crops (Keulen and Seligman, 1978). However, often the main effect of nitrogen on photosynthesis is due to changes in the total leaf area and hence light absorption (Sinclair and Horie, 1989). Nitrogen fertility is an important component in gauging the economic and environmental viability of agro-ecosystems. Nitrogen demand and efficiency have been proposed as possible alternative for reducing the cost and reliance upon fertilizer. Nitrogen uptake pattern, distribution and partitioning are influenced by age of the crops and their physiological condition. The objective of the present study is to demonstrate the effects of applied nitrogen concentration on the uptake pattern and composition in different parts and investigate the relationship between uptake and physiological activities.

### Materials and Methods

The experiment was conducted in a glasshouse at the University of the Ryukyus, Okinawa, Japan. The material used for the experiment was *Saccharum* spp. hybrid cv. NiF8. One bud sugarcane sets were planted in vermiculite bed on 4th September for germination after sterilization over night in 0.05% solution of "Benleet-T" and maintained and/or incubated at 25°C. Uniformly germinated sets were transplanted in pots (1/5000a Wagner pot) on 22nd September 1996. Five pots of each treatment were arranged in a randomized block design with recommended distance. The experiment consisting of six nitrogen levels was planted in pots filled with coral limestone soil (brown red soil), sand and peat at 1:1:1 ratio on volume basis. All nutrients, except nitrogen, in solution form were applied to each pot at weekly interval and nitrogen treatments were also maintained. Composition of nutrient solution is given in Table 1. Nitrogen concentrations of the six nitrogen levels (0, 1/6, 1/3, 1/2, 1 and 2N) were prepared as 0, 1.5, 3, 4.5, 9 and 18 ml per liter of  $\text{NH}_4\text{NO}_3$ . Plants were observed daily and water was supplied as and when needed. The minimum and maximum temperatures and humidity during the cultivation in glasshouse were 15 and 33°C, and 40 and 90%, respectively.

Observations were started on 22nd October 1996. All the five plants were used to measure the number of fully expanded leaf and total leaf, plant height and SPAD at weekly intervals. SPAD of the leaves from tip to bottom and the younger fully expanded leaf were measured at six healthy and unbroken places in the center of the leaf during mid day with a green meter (Model 502, Minolta).

On 104 days after planting, gas exchange measurements were conducted on all the leaves and younger fully expanded leaf by following the method according to Agata et al. (1985), Kawamitsu et al. (1993) and Du et al. (1996). Leaf and air temperatures, relative humidity, photosynthesis, leaf conductance, transpiration, ambient and leaf internal  $\text{CO}_2$  con-

Table 1. Nutrient solution for the experiment in sugarcane.

Compound	Molecular weight	Conc. of stock solution	Stock solution (g/l)	Volume of stock per liter of final solution (ml/l)
$\text{NH}_4\text{NO}_3$	80.04	1.0M	80.04	9
$\text{CaCl}_2$	110.98	1.0M	110.98	6
$\text{K}_2\text{SO}_4$	174.26	0.5M	87.13	12
$\text{KH}_2\text{PO}_4$	136.09	1.0M	136.09	2
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	246.50	1.0M	246.50	2
$\text{H}_3\text{BO}_3$	61.83	25.0mM	1.546	}
$\text{MnSO}_4 \cdot 4\text{H}_2\text{O}$	169.01	10.0mM	1.690	
$\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$	287.54	2.0mM	0.575	
$\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$	249.68	0.5mM	0.125	
$\text{H}_3\text{MoO}_4$	161.97	0.5mM	0.081	
$\text{FeC}_6\text{H}_5\text{O}_7$	244.90	50.0mM	122.45	5

centrations were measured simultaneously. The differences of CO<sub>2</sub> concentration and water vapor between inlet and outlet of the assimilation chamber were analyzed with infrared CO<sub>2</sub> gas analyzer (LI-6251, Li-Cor) and humidity sensor (HMP-113Y, Visala), respectively. An airtight assimilation chamber, in which cross flow fan is installed, was used for all gas exchange measurements. Upper portion of the chamber was covered with fiberglass lid, which opens and closes usually during leaf setting. Sufficient artificial light arrangement was made on the top of the chamber in order to get high photon flux density (PFD) as the sunlight. Transparent water tub was provided between the light source and chamber to control excesses and direct heat of bulb. In order to get the concentration of CO<sub>2</sub> from 0 to 1000 ppm optionally, 5 % CO<sub>2</sub> gas balanced with nitrogen was injected into CO<sub>2</sub> free air containing 21% O<sub>2</sub> by using a mass flow controller (SEC-4400, ESTEC). Humidity control of the air introducing chamber were created by adjusting water temperature within the bubbling circuit, through which introducing air pass. Leaf temperatures in the chamber were maintained with a temperature controller (CTE-82W, Komatsu-Yamato).

To determine the effect of different PFD on gas exchange rate, a different wire nets (neutral filters) and black polythene sheet were used, which eliminated the light from reaching the leaf surface. The filters were installed 30 minutes prior to initiating measurement. A total of 5 younger fully expanded leaves of each treatment were measured. In the PFD response experiment, leaf temperature and vapor pressure difference (VPD) between the leaf and air was  $30.0 \pm 0.2^\circ\text{C}$  and  $18.8 \pm 2.4\text{mb}$ , respectively.

Responses of photosynthesis to leaf temperatures were examined on the younger fully expanded leaf of 1N plants. In the experiment, PFD was maintained at  $2070 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  and leaf temperature was changed from 15.0 to 45.0°C with increasing air temperature in the assimilation chamber.

Leaf area was measured during setting of leaf in the chamber with a meter scale. Average of SPAD value was measured immediately after photosynthesis measurement. To determine the relationship between SPAD and chlorophyll content, 2cm<sup>2</sup> healthy leaf discs were punched out after SPAD measurement and put immediately in 80% acetone solution for chlorophyll extraction. Chlorophyll contents were measured with a spectrophotometer (UV-2200, Shimadzu) at 645 and 663nm according to Arnon (1965).

All samples for nitrogen and carbon estimation were dried in oven for 48 hours at 80 °C and then ground with a vibrating sample mill (TI-100, CMT). 20-30 mg ground sample was used to estimate nitrogen and carbon concentration with N/C analyzer (NC-90A, Shimadzu).

## Results and discussions

### Effects of N concentration on growth attributes

Variations due to nitrogen level were observed in respect of plant height and leaf numbers. The attributes were increased with increasing levels of nitrogen concentration up to twice of the control (1N). Highest values at 104 days in the number of fully expanded leaves, the total leaf number, and plant height, which were observed in the plants grown with 2N solution, were 12, 14.2, and 209cm, respectively (Table 2, Figs. 1~3). All attributes

Table 2. Effect of nitrogen application on growth attributes at 104 days after planting.

Treatment	Leaf number		Plant height (cm)
	Fully expanded	Total	
0N	7.2	9.6	110.2
1/6N	9.8	12.0	148.6
1/3N	11.0	13.2	183.4
1/2N	11.2	13.2	189.3
1N	11.6	13.8	202.4
2N	12.0	14.2	209.0

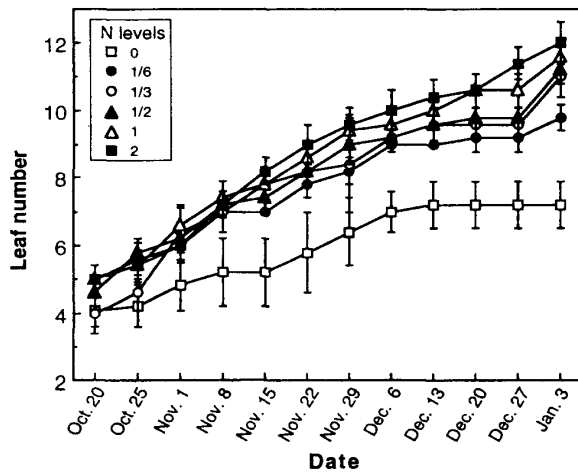


Fig. 1. Time changes in leaf number of younger fully expanded leaf under different nitrogen supply in Sugarcane (NiF8). Bars in the figure indicate standard deviation.

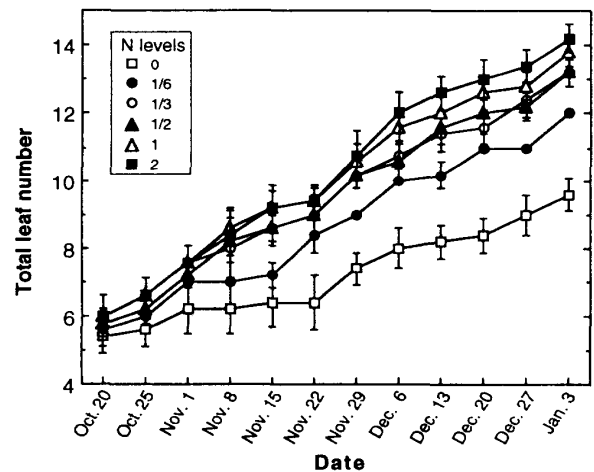


Fig. 2. Time changes in total leaf number under different nitrogen supply in Sugarcane (NiF8). Bars in the figure indicate standard deviation.

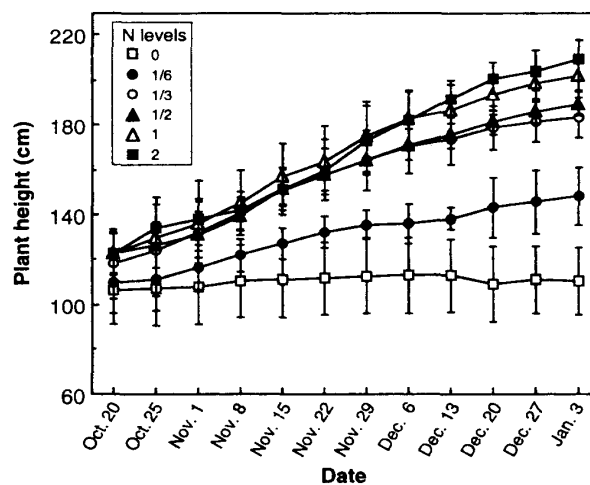


Fig. 3. Time changes in plant height under different nitrogen supply in Sugarcane (NiF8). Bars in the figure indicate standard deviation.

were increased with increasing duration from 20th October to 3rd January and trend was almost similar. Nitrogen applications to plants have been reported to have direct and indirect effects on the growth of plants. Biemond and Vos (1992) and Hattak et al. (1999) have reported that nitrogen fertilization results in high nitrogen in the leaves and maintains high level of growth leading to high leaf and stem dry weight, leaf area and plant height and this is in agreement with our data in Figs. 1~3. Thus nitrogen directly acts on the apical meristem of the plant to enhance process that results in cell division and initiation. In the indirect effect, nitrogen acts through the derivatives of nitrogen with a delaying effect on leave senescence (Trewavas, 1983). This results in low respiration and consequently to a better use of carbon dioxide and high yield (Andrews and McKenzie, 1991). Goodwin et al. (1978) also reported a relationship between nitrogen in plants and endogenous cytokinin levels. The increase in the number of leaves and plant height was therefore a confirmation to these previous reports.

#### Effects of leaf nitrogen content on SPAD, photosynthesis, and water use efficiency

The nitrogen content, SPAD, photosynthesis, and transpiration rates were increased with successive increase in the nitrogen concentration of nutrient solution from 0 to 2 times of the normal level (Table 3). The leaf nitrogen content, SPAD, photosynthesis and transpiration were highest in the plant grown with 2N solution and these were 2.28, 39.25, 29.78 and 3.04, respectively.

These effects of applied nitrogen on leaf nitrogen, photosynthesis and transpiration have similarly been reported by several researchers. Nitrogen have been reported to have both metabolic and osmotic effects on plant growth (McIntyre, 1997). In the report of Millard and Mackerran (1986), they observed that most of the applied nitrogen accumulated in the leaf vacuole and in the roots. The accumulation of the nitrogen in the leaf and roots exerts an osmotic effect, which results in better water absorption and water use efficiency. Under good moisture conditions therefore, the leaves become turgid leading to an opening of the stomata and this can accelerate transpiration. Nitrate reductase, the first enzyme in the pathway leading to assimilation of nitrate into pigments is well known to be nitrate inducible and its activity is thought to be a rate-limiting step in nitrate assimilation. Hattak

Table 3. Effect of nitrogen application on leaf nitrogen content, SPAD, photosynthesis, transpiration and water use efficiency at 110 days after planting in sugarcane (NiF8).

Treatment	Nitrogen (%)	SPAD	Photosynthesis ( $\mu\text{mol} \cdot \text{m}^2 \cdot \text{s}^{-1}$ )	Transpiration ( $\text{mmol} \cdot \text{m}^2 \cdot \text{s}^{-1}$ )	Water use efficiency ( $\mu\text{mol} \cdot \text{mmol}^{-1}$ )
0N	0.81	23.37	26.26	2.91	9.02
1/6N	1.54	32.62	20.74	1.62	15.15
1/3N	1.59	33.22	18.30	1.63	11.20
1/2N	1.84	35.23	24.60	2.39	10.29
1N	1.92	37.43	26.14	2.61	10.02
2N	2.28	39.25	29.78	3.04	9.79

et al. (1999) have reported that nitrate reductase activity increases with applied nitrogen levels in the leaves of plants.

Apart from enhancing the formation of chloroplast components such as carbon assimilatory enzymes and chlorophyll-protein complexes per unit area, Evans (1983) and Robinson (1996 and 1997a, b) increased nitrogen supply has also been reported to increase total carotenoid on leaf area basis to a greater extent especially at high irradiance. This coupled with the effect of applied nitrogen on leaf area expansion were factors to explain the increased photosynthesis with increased applied nitrogen. Booij (1996) have reported that applied nitrogen results in increased leaf area which leads to higher light interception for increased photosynthesis.

The value of photosynthesis and transpiration rates was higher at 0N level as compared to 1/6 N level. It might be due to less number of active leaves and translocation of all the nutrients that were available in those leaves. Alternatively, it might be thought that the sugarcane grown with the low levels of nitrogen dependent on the nitrogen supplying from  $N_2$  fixing bacteria (Yoneyama et al., 1997). Also, the plants that were grown on 0N level had most of their leaves falling down below the plant. These leaves decompose with time and supply nitrogen to the plants and this might have led to the young leaves having some amount of nitrogen. The above two factors could therefore be probable causes for the high photosynthesis in the 0N plants than some of the N treated plants. There is no defined relationship between trend water use efficiency and the nitrogen levels, except 1/6N (Table 3).

#### Partitioning of nitrogen and carbon content in different portion of leaf

Nitrogen content in the leaf sheath, mid rib (base and top), blade (base and top) of younger fully expanded leaf of the plant grown with the solution of normal nitrogen concentration were analyzed (Fig. 4). The results showed that leaf blade contain highest nitrogen followed by mid rib and sheath. Concentration of nitrogen was higher in top portion as compared with the base. It might be due to the ontogenetic characteristics of the sugarcane leaf including activity of the photosynthesis. Similar trend was also noticed with carbon

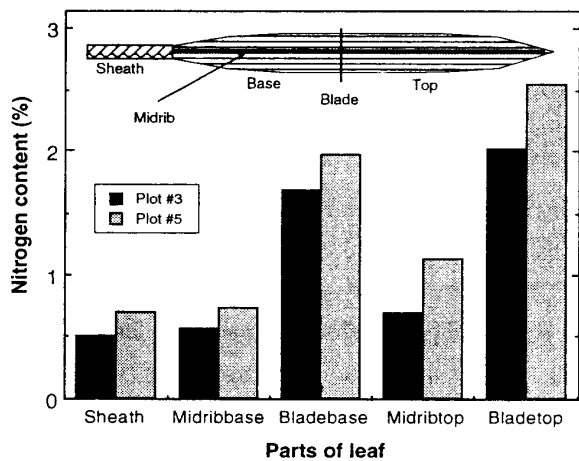


Fig. 4. Nitrogen content in different part of leaf of Sugarcane (NiF8) under normal nitrogen supply (1N).

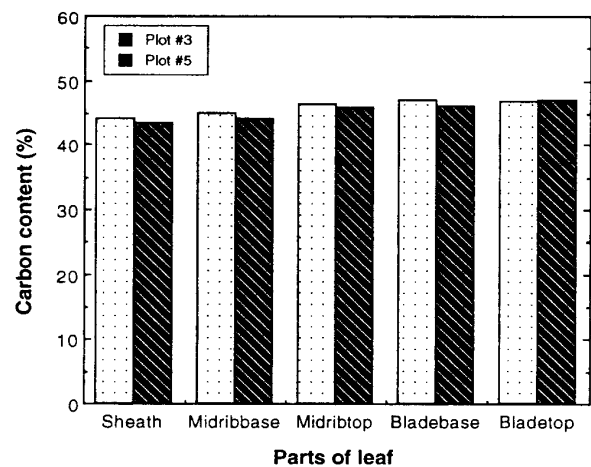


Fig. 5. Carbon content in different part of leaf of Sugarcane (NiF8) under normal nitrogen supply (1N). See Fig. 4 for the parts of leaf.



content (Fig. 5), but the differences were less.

#### Effect of growing duration on SPAD value under different nitrogen supply

It is clear that nitrogen supply was positively correlated with SPAD value (Table 3 and Fig. 6). Higher SPAD values were recorded with successive increase of nitrogen concentration but differences were less at each successive increase as compared to previous one. There was fluctuation in SPAD value for each week but effect of nitrogen concentration was same.

It is because of fluctuation in environmental conditions (Thompson et al., 1996). The maximum SPAD value was recorded at twice of the normal nitrogen level in beginning and decreased with advancement of age after some time. The SPAD value-decreasing rate was higher in 0N than the higher one.

The above mentioned relationship was observed only at 110 days after transplanting. Chlorophyll concentration was highly related with SPAD value (Fig. 7), coincident with that of Thompson *et al.* (1996). Lower and higher value of SPAD and chlorophyll were recorded 23.3 and 3.1, and 51.0 and 9.3, respectively.

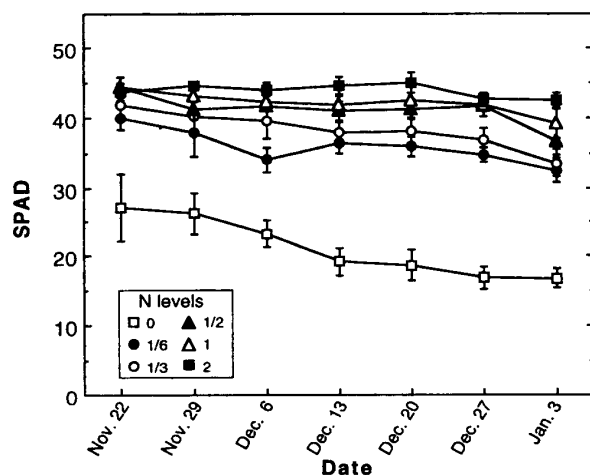


Fig. 6. Time changes in SPAD values under different nitrogen supply in Sugarcane (NiF8). Bars in the figure indicate standard deviation.

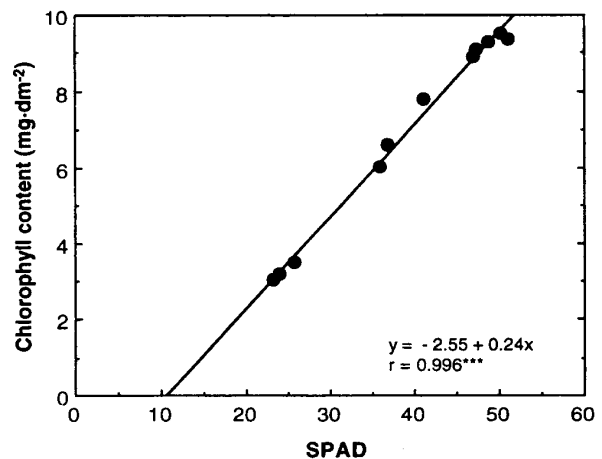


Fig. 7. Relationship between chlorophyll content and SPAD in Sugarcane (NiF8). See Materials and Methods for the estimation of chlorophyll contents.

#### Effects of leaf positions on nitrogen content

Nitrogen content, SPAD, photosynthesis, transpiration and water use efficiency were measured individual leaves at 110 days after transplanting (Table 4). Highest value of SPAD (41.9) and photosynthesis ( $32.9 \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ) were observed in 5th leaf. Nitrogen content was highest in the 6th (2.11%), followed by the 5th (2.03%). It might be due to more actives of younger fully expanded leaf, besides these nitrogen concentrations. Nitrogen content has been reported to decrease down the canopy of plants and several factors have been implicated in the nitrogen profile in plant canopies. Hirose et al. (1988) indicated that the light reduction the canopy could be a factor. An association between nitrogen vertical distribution and light was also found in many studies. For example, Werger and Horose

(1991) and Lemaire et al. (1991) have reported that leaves in the upper parts of canopies exposed to more light had high nitrogen contents. No definite trend was detected in the variation of transpiration and water use efficiency, although the values varied from 2.01 to 3.14 and from 6.41 to 10.52, respectively.

Effects of leaf positions on leaf nitrogen content, SPAD, photosynthesis and transpiration at different nitrogen concentration were also observed. The 6th leaf from tip recorded

Table 4. Effect of leaf position on leaf nitrogen content, SPAD, photosynthesis, transpiration and water use efficiency at 110 days after planting in sugarcane (NiF8).

Position	Nitrogen (%)	SPAD	Photosynthesis ( $\mu\text{mol} \cdot \text{m}^2 \cdot \text{s}^{-1}$ )	Transpiration ( $\text{mmol} \cdot \text{m}^2 \cdot \text{s}^{-1}$ )	Water use efficiency ( $\mu\text{mol} \cdot \text{mmol}^{-1}$ )
3rd*	1.79	35.08	26.15	2.66	9.84
4th	1.83	35.57	29.29	2.97	9.86
5th	2.03	41.86	32.87	3.14	10.46
6th	2.11	40.30	30.94	2.94	10.52
9th	1.86	36.10	12.86	2.01	6.41

Note: \*The younger fully expanded leaf.

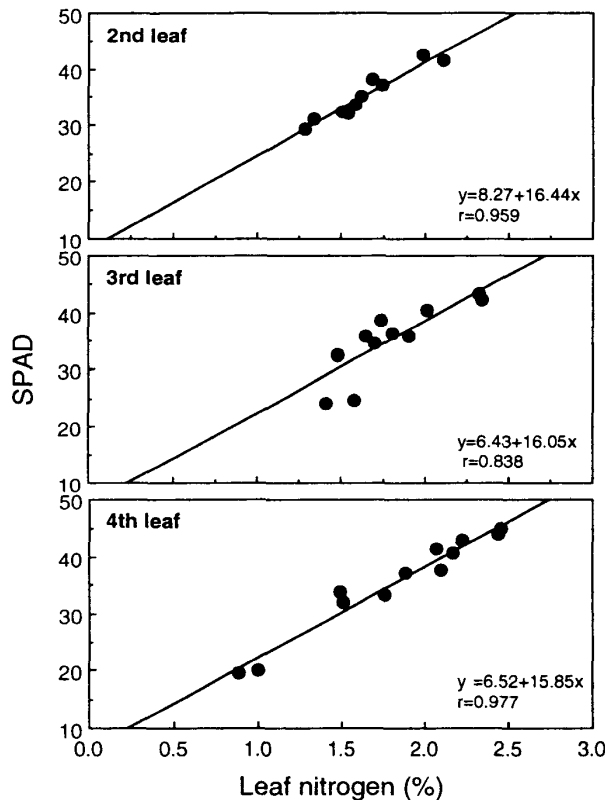


Fig. 8. Relationship between leaf nitrogen content and SPAD in 2nd, 3rd and 4th leaf from tip in Sugarcane (NiF8).

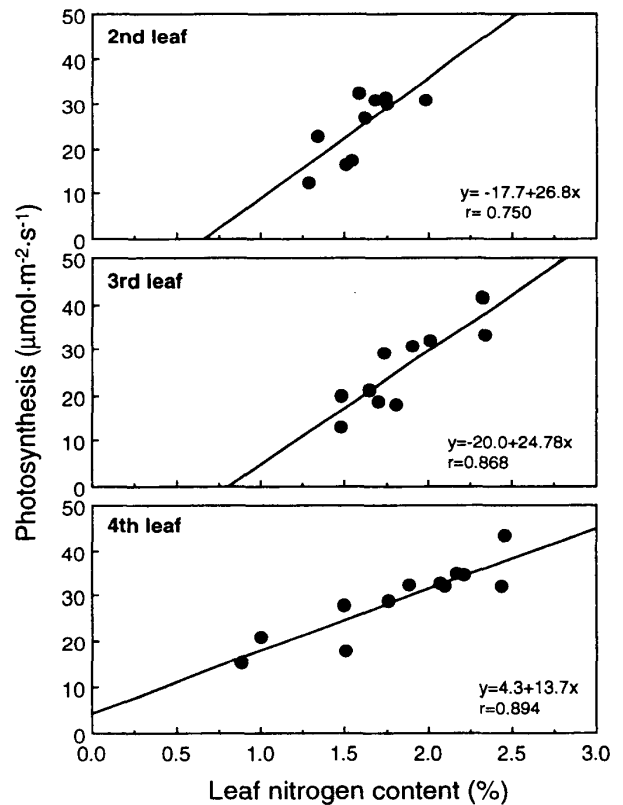


Fig. 9. Relationship between leaf nitrogen content and photosynthesis in 2nd, 3rd and 4th leaf from tip in Sugarcane (NiF8).

maximum leaf nitrogen content, whereas the 5th leaf showed highest SPAD, photosynthesis and transpiration rates. Leaf nitrogen content showed a positive correlation with SPAD and photosynthesis indicating that nitrogen is the dominating factor on these parameter. There were a positive correlation between leaf nitrogen content and SPAD, and between leaf nitrogen content and photosynthesis, irrespective of the leaf position (Figs. 8 and 9). Water use efficiency also had almost similar results.

$C_4$  species show a higher photosynthetic nitrogen use efficiency as compared to the  $C_3$  species (Brown, 1985). In  $C_4$  species, there are some variations in photosynthetic nitrogen use efficiency due to growth conditions, gas exchange measurement conditions, leaf ages, and genotypes. In the present studies, 3rd leaf from tip, which is younger fully expanded leaf, indicated the higher photosynthetic nitrogen use efficiency, followed by 2nd and 4th leaf.

#### Effects of leaf temperature and PFD on photosynthesis and transpiration

Responses of photosynthesis and transpiration to leaf temperature were measured at different PFD (Fig. 10). The optimum temperature of photosynthesis was higher at the 2070  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  of PFD and lower at 455  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  of PFD. It might be due to disturbance in stomatal conductance and photosynthetic enzyme activities altered with nitrogen contents. The optimum temperature of photosynthesis was not shifted with nitrogen levels as seen at different PFDs (Sage and Pearcy, 1987). Transpiration was increased linearly with increasing temperature up to 44°C. At 17 to 20°C, transpiration was zero presumably due to the setting of dew point temperature before the assimilation chamber.

The response curves of photosynthesis to PFD at different nitrogen supply (Fig. 11) showed that the saturation one for leaf of the lower nitrogen content and non-saturated one for leaf of the higher nitrogen content. It was also shown that a light saturated region for PFD about 940  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , confirming the result of Vadell et al. (1993). Average leaf photosynthesis at saturation PFD was highest in 2N (28.64) followed in order by 1N (28.4), 1/2N (21.0), 1/3N (23.5) and 1/6N (22.7). Again, maximum photosynthetic rate with 0N plants was higher than those of 1/6N and 1/3N plants. In addition, initial slope of the light dependent curves in 0N plants was also higher than those in 1/6N and 1/3N

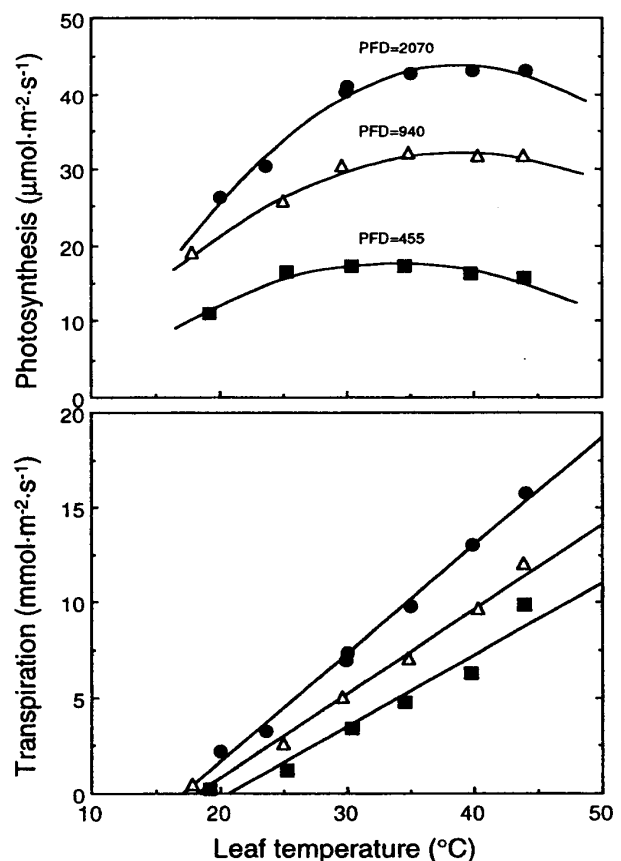


Fig. 10. Temperature response curves of photosynthesis and transpiration for fully expanded leaf of Sugarcane (NiF8) under normal nitrogen supply (1N).  $\text{CO}_2$  was set at 350 ppm and PFDs were set at 2070, 940 and 455  $\mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ .

plants. It seems possible to speculate the plants grown with the low levels of nitrogen obtained actively from  $N_2$  fixing bacteria (Yoneyama et al., 1997).

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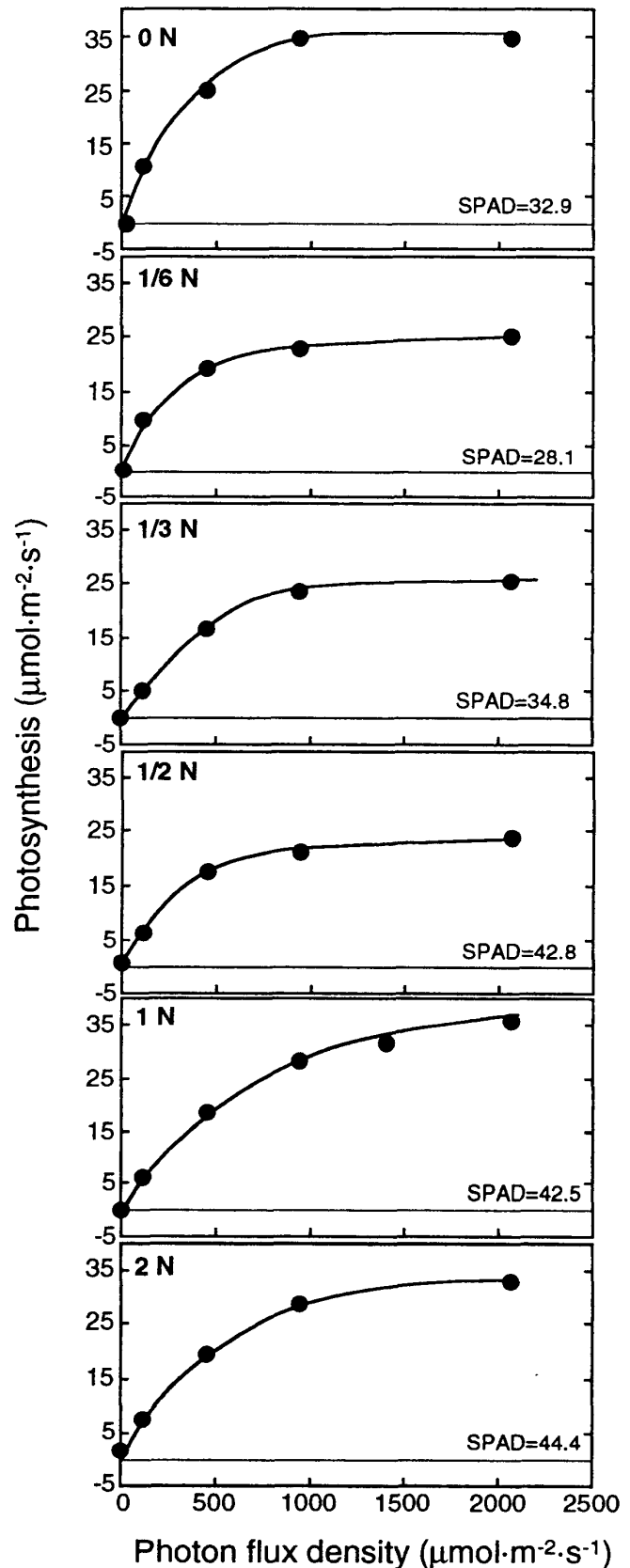


Fig. 11. Light response curves of photosynthesis for younger fully expanded leaf at different nitrogen supply in Sugarcane (NiF8).

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## 窒素処理がサトウキビの成長と光合成速度に与える影響

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### 要 旨

サトウキビはC<sub>4</sub>型光合成経路を有し、光合成からみた窒素利用効率は極めて高いと云われる。本研究では、サトウキビの成長と光合成速度に与える窒素処理の影響を調べた。処理は水耕液中に含まれる窒素源としての硝酸アンモニウム(NH<sub>4</sub>NO<sub>3</sub>)の濃度を6段階に分け、与えた。

葉の窒素含量は処理濃度に比例して増大した。0N区の葉の窒素含量は0.81%で、2N区のそれは2.28%であった。また、草丈、葉数も窒素処理濃度が上昇するにつれ増大した。処理開始後104日目に比較したところ、0N区の草丈は2N区の約半分であった。光合成速度及び蒸散速度の最大値は2N区で見られ、最小値は0N区ではなく1/3N区で認められた。

1N区の葉身を用いて葉の各部位の窒素含量を比較したところ、葉身上部が基部に比較して高く、中肋は葉鞘とほぼ同じであった。

SPADとクロロフィル含量との間には、極めて高い正の相関関係が認められた。しかし、両者間の回帰式の傾きは葉位によって異なり、サトウキビの葉にSPADを用いる場合、注意を要する。

“光-光合成曲線”に対する窒素含量の影響を調べたところ、低窒素区では飽和型に、高窒素区では不飽和曲線となった。0N区の最大光合成速度は2N区のものに匹敵し、窒素を与えていないにも関わらず高い値を示した。

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