Studies on Matter Production in Pineapple Plants

III. Effects of nitrogen nutrition on the gas exchange of shoots*

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It is well known in many C_3 and C_4 plants that the nitrogen concentration in culture medium and the nitrogen content in leaf blades affect the photosynthetic activity on the plant^{1,5,8,15}. In CAM plants having CO_2 fixation pathway similar to C_4 photosynthesis, only a few studies have so far been done on the effects of nitrogen nutrition on the photosynthetic activity of CAM plants¹⁷.

Using plants cultured under the conditions of different nitrogen source and amount, SIDERIS et al. investigated the effects of nitrogen nutrition on the growth and chemical composition in leaf blades of pineapple plants^{9,10,11,12,13}. WATANABE¹⁶ has shown that the nitrogen nutrition greatly affected the growth rate of pineapple plants. In the studies reported previously, however, it had not been recognized that pineapple plants exhibit CAM type of photosynthesis. Consequently, the effects of nitrogen nutrition on the photosynthetic characteristics of pineapple plants have not so far been proved sufficiently.

From the reasons mentioned above, the present study was carried out to examine the effects of nitrogen concentration in culture medium on the gas exchange of pineapple plants. Two experiments were done in August to November 1979, and October 1980 to February 1981. Since the two experiments gave the same results, the results for 1980 to 1981 is reported in this paper.

Materilas and Methods

Plant materials used were the "Hawaii N-72" selected from *Ananas comosus* (L.) Merr. cv. Smooth cayenne. Crowns of autumn fruits were obtained from Nago Experiment Branch, Okinawa Agricultural Experiment Station, Nago, Okinawa.

Crowns were submerged for ten minutes in a sterilizer with "Mannebu-daisen" solution diluted to one thousandth with water, and they were dried in the shade for ten days. Then, one crown on one pot was planted, using Wagner pots (1/2,000a) filled with 13 liters of SIDERIS's culture solution¹³. pH of the culture solution was maintained at 5.0 with 0.1 N HCl and 0.1 N NaOH solution using pH test paper, Brom Cresol Green, every three days. Aeration into the culture solution was done continuously.

Nitrogen concentrations in the culture solution for six nitrogen treatments used in the present experiment were 554, 277, 137, 69, 28 and 14 ppm, respectively. As a nitrogen source, $Ca(NO_3)_2$ was used. The composition of nutrition elements in the culture solution other than nitrogen was same with six nitrogen treatments, 1.8 mM KCl, 1.0 mM $MgSO_4 \cdot 7H_2O$, 1.0 mM $NaH_2PO_4 \cdot 7H_2O$, 0.1 mM $FeSO_4 \cdot 7H_2O$, 0.05 mM $MnSO_4 \cdot 7H_2O$, 0.05 mM $ZnSO_4 \cdot 7H_2O$, and 0.05 mM $K_2B_4O_7 \cdot 7H_2O$. Since 277 ppm nitrogen concentration corresponded to the recommended rate of fertilizer application in Okinawa Prefecture, 0.36 grams nitrogen per plant, the 277 ppm plants are named 1 N in the present paper. Plants 554, 138, 69, 28 and 14 ppm are also named briefly 2 N, 1/2

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N, 1/4 N, 1/10 N and 1/20 N, respectively. SIDERIS's culture solution corresponds to treatment 1/10 N.

Plants were cultured in SIDERIS's solution for the first 44 days, and they were cultured on the six nitrogen treatments afterwards. The SIDERIS's solution in pretreatment was renewed on the 21th day since the water culture began. The culture solution in nitrogen treatment was not exchanged in this experiment.

Two examination were carried out during the 14th day and 28th day (Exp. I), and during the 35th day and 49th day (Exp. II) after the beginning of nitrogen treatment. In Exp. I and Exp. II, number of leaves was 48 ± 6 and 58 ± 6 , respectively, and leaf area $23.65 \pm 2.41 \text{ dm}^2$ and $24.77 \pm 2.84 \text{ dm}^2$, respectively.

The light conditions during the gas exchange measurement were as follow: The light period was 11 hours from 07:00 to 18:00, and the dark period 13 hours of the rest. Three conditions of average light intensity were designed for each nitrogen condition throughout the Exp. I and Exp. II. They were $56.1 \pm 3.4 \text{ klx}$ (55 klx block), $25.4 \pm 1.0 \text{ klx}$ (25 klx block), and $9.6 \pm 1.5 \text{ klx}$ (10 klx block) on the plant top. Leaf temperature for the light period and dark period was kept at $24.8 \pm 0.8^\circ\text{C}$ and $18.9 \pm 1.1^\circ\text{C}$, and air temperature at $24.3 \pm 0.8^\circ\text{C}$ and $19.3 \pm 1.1^\circ\text{C}$, and air humidity at $61.5 \pm 7.1\%$ and $76.0 \pm 3.1\%$, respectively. Air into the assimilation chamber was ventilated 7.44 ± 0.71 liters per minute throughout the experiment. Air ventilation was measured with an automatic differential pressure meter (Yokogawa electric Co., d/p cell). Other conditions during the gas exchange measurement except for those described above were the same as in the previous report⁴⁾.

The content of chlorophyll, soluble protein, and total nitrogen were measured with ARNON's method³⁾, LOWERY's method¹⁴⁾, and KJELDAHL's method, respectively.

Results

Effects of nitrogen in culture medium on gas exchange of pineapple plants

Diurnal CO_2 exchange pattern (Fig. 1-A) showed typical CAM type of photosynthesis,

which is depressed in the middle part of light period, and is activated in the latter part of light period and dark period. OSMOND⁶⁾ has classified the diurnal gas exchange pattern into four phases: dark period as phase 1, morning as phase 2, noon as phase 3, and the rest of light period as phase 4. In reference to this classification, the effects of the nitrogen in the culture medium to gas exchange of shoots were compared among various nitrogen treatments. It was clearly recognized that nitrogen concentration in culture medium affected the CO_2 influx rate in phase 4 and phase 1 under three different light intensities. The CO_2 influx rate in 2 N plants showed a minimum value in phase 4 and 1. The maximum value in phase 4 was observed in 1/2 N plants, and that in phase 1 was observed in 1 N and 1/2 N plants.

Transpiration rate of each nitrogen treatment under each light condition was higher in phase 4 than in other phases (Fig. 1-B). In comparison of transpiration rate among six nitrogen treatments, difference was not clearly found among them, except for 2 N plants where the rate was low in phase 4. As for water vapour exchange coefficient (G_s), which was calculated from transpiration rate, leaf temperature, and air temperature⁴⁾, difference among the six treatments was not clearly recognized. Only 2 N plants, however, transpiration rate and G_s in phase 4 were smaller than that obtained in other treatments.

Fig. 2 shows the effect of nitrogen concentration in culture medium on the CO_2 gain in four gas exchange phases of pineapple plants. The X, Y and Z axes in the figure show nitrogen concentration in culture medium, average light intensity and CO_2 balance, respectively. CO_2 balance per full one day attained a maximum value in 1 N plants (277 ppm nitrogen) under average light intensity of 55 klx and 25 klx, and in 1/2 N plants (138 ppm) under 10 klx. The CO_2 balance decreased as nitrogen concentration become higher than that of 1 N, or lower than that of 1/2 N. CO_2 gain in phase 1 showed a maximum in 1 N plants under low light intensity, same as the daily balance. In phase 4, the maximum value of CO_2 gain was obtained in 1/2 N plants.

Fig. 1. Effects of nitrogen concentration in culture medium on CO_2 exchange (A), transpiration (B) and water vapour exchange coefficient (C) of pineapple plants.

Figures 55, 25 and 10 in the figure show the average light intensity of light period on the plant top.

● : 2 N, 554 ppm, $\triangle$: 1 N, 277 ppm, $\times$: 1/2 N, 138 ppm, $\circ$: 1/4 N, 69 ppm, $\blacktriangle$: 1/10 N, 28 ppm, $\square$: 1/20 N, 14 ppm. Results in this figure were obtained in Exp. II.

Nitrogen treatments showing the maximum and minimum value of CO_2 gain in three phases corresponded to nitrogen treatments where the maximum and minimum value of CO_2 exchange rate were obtained in corresponding phases (Fig. 1).

Next, Fig. 3 showed the effect of nitrogen concentration in culture medium on total nitrogen, soluble protein, and chlorophyll content in leaves. Total nitrogen values in the figure are the values obtained from the mixture of whole leaves, and the values from leaves D (mixture of three leaves), both leaves were used for gas exchange measurement in the present experiment. The leaf D means the longest leaf of fully-expanded leaves in the shoot¹⁰⁾. The contents of soluble protein and chlorophyll were measured in leaves D.

Total nitrogen content of whole leaves (Fig. 3-B) attained a maximum value in 1 N

plants in Exp. I and 1/2 N plants in Exp. II; the content decreased when nitrogen concentration in culture solution became higher than that of 1 N or lower than that of 1/2 N. The results of total nitrogen in leaves D (Fig. 3-A) were similar to those obtained in whole leaves, although maximum values were obtained in 1/2 N and 1 N plants in Exp. II. The relationships between soluble protein and nitrogen concentration in culture medium were different in Exp. I and Exp. II. In other words, in Exp. I, soluble protein contents did not show distinct difference among five nitrogen treatments, except in 1/20 N plants where smaller values of the content were found. In Exp. II, however, soluble protein content attained the maximum value in 1 N plants. Next, the relationships between chlorophyll content and nitrogen concentration in culture medium were the same as those found in the case of total

Fig. 2. Effects of nitrogen concentration in culture medium and average light intensity at light period on CO_2 balance of the top of pineapple plants.

A : full one day, B : phase 1, C : phase 4. Results in the figure were obtained in Exp. II.

Fig. 3. Effects of nitrogen concentration in culture medium on total nitrogen (A, B), chlorophyll content (C), and soluble protein (D).

○ : Exp. I, ● : Exp. II, A, C and D : contents analyzed on D leaves, B : content analyzed on all leaves used for gas exchange measurements. Vertical line in figure shows the standard deviation.

nitrogen content, although chlorophyll content showed relatively low value in 1 N plants in Exp. II (Fig. 3-C).

The reason that a different tendency of nitrogen components was showed between Exp. I and Exp. II (Fig. 3) is regarded to be derived from the difference in the duration of the nitrogen treatment.

Relationships between leaf nitrogen components in leaves and gas exchange

Base on the relationships between leaf nitrogen components and gas exchange characteristics of pineapple plants, the role of nitrogen nutrition in CAM type of photosynthesis of pineapple plants is examined herein after.

Total nitrogen contents of whole leaves and leaves D showed a positive and a statistically significant correlation to CO_2 balance in full one day and in phase 1 under three light intensity conditions (Fig. 4). Although CO_2 gain in phase 4 showed a correlation of 0.45 to leaf nitrogen content under 25 klx light intensity, it was not significant.

Correlation between CO_2 balance and soluble protein content was in the same pattern as in the case of total nitrogen content of leaves (Fig. 5-A). Correlation between CO_2 balance and chlorophyll content was also similar to the relationship between soluble protein and total nitrogen content (Fig. 5-B).

CAM type of photosynthesis is characterized best with CO_2 influx in dark period. In other words, the more the ratio of CO_2 influx in phase 1 to daily CO_2 balance, the more the CAM type of photosynthesis is characterized. Consequently, defining the degree of CAM ability as the ratio of CO_2 influx in phase 1 to CO_2 balance in full one day

Fig. 4. Relationships between total nitrogen concentration in leaves and CO_2 balance of the shoots.

○, △ and ● : CO_2 balance of full one day, phase 1, and phase 4, respectively. A : total nitrogen content analyzed on all leaves used for gas exchange measurements. B ; total nitrogen content analyzed on D leaves. Figure 55, 25 and 10 : average light intensity (klx) of light period on the plant top. ***, ** and * : statistical significance at 0.1, 1.0 and 5.0% level, respectively. n.s. : non of significant.

Fig. 5. Relationships between CO_2 balance of the shoot and each of soluble protein (A) and chlorophyll content (B) of D leaves.

Symbols and figures are the same as in Fig. 4.

enables the easier evaluation of the effect of various treatment to CAM type of photosynthetic CO_2 exchange. Based on the CAM ability expressed as mentioned above, relations between CAM ability and total nitrogen content of whole leaves (Fig. 6) showed positive and significant correlations under each light condition. In other words, as total nitrogen content of leaves increased, CAM ability increased along with the activated CO_2 influx in phase 1. Further, the degrees of CAM ability under three light conditions increased as light intensity decreased, shown as the increase in the interception of Y-axis with the increase in light intensity.

Although water vapour exchange coefficient (G_s), which exhibits the degree of

stomatal aperture, is not directly related to leaf nitrogen components, the relationships between G_s and CO_2 exchange will be briefly mentioned hereinafter. Under the light condition of 55 klx, the relationship between G_s and CO_2 influx rate in phase 1 did not show significant correlation. Under the light condition of 25 klx and 10 klx, however, correlations were significant; while the degrees of correlations were as low as 0.566 and 0.451, respectively. Next, the relationships between G_s and CO_2 influx rate in phase 4 showed high significant and positive correlation (Fig. 7-B). The facts observed above show that stomatal aperture regulated CO_2 influx rate more in phase 4 than in phase 1.

For a further examination of the effects of leaf nitrogen components on the degree of

stomatal aperture in phase 4, the relationships between the maximum G_s and leaf nitrogen components are summarized in Table 1. Maximum G_s in phase 4 did not show a significant correlation to any one of total nitrogen, soluble protein, and chlorophyll content.

Since significant correlations between total nitrogen and soluble protein, and those between total nitrogen and chlorophyll content (Fig. 8) were obtained in the present experiment, the close relationships among them in pineapple leaves were clearly demonstrated, as mentioned in the previous studies^{11,12}.

Nitrogen use efficiency

BROWN¹⁾ defined the nitrogen use efficiency of plants as biomass production of CO_2 assimilation rate per unit nitrogen content of the plant, mainly in leaves, and he showed that C_4 plants exhibited higher efficiency for nitrogen use than C_3 plants. The nitrogen use efficiency in full one day, phase 1, and phase 4, under high light condition of 55 klx (Fig. 9-A) ranged from 1.9 to 1.2 mgCO_2/mgN , 1.3 to 0.9 mgCO_2/mgN , and 0.6 to 0.2 mgCO_2/mgN , respectively. In addition, total nitrogen content for all the measured leaves showed a positive correlation to nitrogen use efficiency in phase 1, and a negative one for full one day and phase 4. The degrees of those correlations, however, were relatively low, and they were not statistically significant.

Fig. 9-B was drawn to show the correlation between leaf total nitrogen content and maximum CO_2 influx rate per unit leaf nitrogen both in phase 4 and in phase 1. Correlation was positive in phase 1, and negative in phase 4. The maximum value of nitrogen use efficiency obtained in the present experiment ranged from 0.09 to 0.13 $\text{mgCO}_2/\text{mgN}/\text{h}$, and 0.06 to 0.15 $\text{mgCO}_2/\text{mgN}/\text{h}$, in phase 1 and phase 4, respectively.

Discussion

It became clear that nitrogen concentration in culture medium affected CAM type of gas exchange of pineapple plants (Fig. 1). Particularly, CO_2 balance for full one day attained a maximum value with 277 ppm

Fig. 6. Relationships between CAM ability and total nitrogen contents in leaves. Figures 55, 25 and 10 klx show the average light intensity at light period on the plant top. **: significant at 1.0% level. n.s.: non of significant.

Fig. 7. Relationships between CO_2 influx rate and water vapour exchange coefficient in phase 1 (A) and phase 4 (B).

Figures following A and B in the figure indicated average light intensity at light period. Symbols in the figure are the same as in Fig. 1. Results in the figure were obtained in Exp. II. ***: significant at 0.1% level. n.s.: non of significant.

nitrogen concentration in culture medium, and it decreased on both side of this nitrogen concentration (Fig. 2). Total nitrogen contents and soluble protein in leaves decreased in 2 N plants (Fig. 3).

SIDERIS et al.⁹⁾ cultured pineapple plants for nine months on twelve species of solution with different concentrations but with the same ratio in nutrition element composition, and they published that maximum plant weight was obtained with 847 ppm nitrogen treatment. On the other hand, according to the manual for pineapple culture edited by Okinawa Prefecture, Japan, the recommended amount of nitrogen in basal dressing is 3.6 grams per plant, and the amount is equal to total nitrogen contained in culture medium on treatment 1 N in the present experiment.

The reason for the discrepancy between SIDERIS' result and that of the present experiment is seemed that the absorption of nitrogen nutrition into the leaf was hampered by the law of minimum for nutrition of plants under high nutrition condition, 2 N (Fig. 3), and that this resulted in the reduction of gas exchange.

It is well known that CO_2 assimilation rate in C_3 and C_4 plants is affected by nitrogen components in leaves^{1,5,8,15)}, but only a few studies have so far been done on the relationships between leaf nitrogen components and the characteristics of gas exchange in CAM plants including pineapple. In the present experiment, it was shown that CO_2 balance for full one day and in phase 1 was closely related to total nitrogen, soluble protein, and chlorophyll content in leaves. In phase 4, however, correlation between CO_2 gain and leaf nitrogen components was not significant (Figs. 4 and 5). In addition to it, the degree of stomatal conductance affecting CO_2 exchange, water vapour exchange coefficient (G_s), showed a positive and significant correlation to CO_2 influx rate in phase 4. Correlation between G_s and CO_2 influx rate in phase 1 was also significant, but the correlation was not necessarily high (Fig. 1, Table 1). In brief, these facts show that CO_2 exchange of pineapple plants was mainly affected by leaf nitrogen components in phase 1, and by the degree of stomatal aperture in phase 4.

Fig. 8. Relationships between total nitrogen content and each of soluble protein (A) and chlorophyll content (B).

*** : significant at 0.1% level.

Table 1. Correlation coefficients between maximum water vapour exchange coefficient and nitrogen components in leaves.

Light block	N in total leaves	N in D leaves	Sol. prot.	Chl.
50	-0.220	-0.177	0.085	-0.680
	n.s.	n.s.	n.s.	0.05
30	0.404	0.416	0.547	0.458
	n.s.	n.s.	n.s.	n.s.
10	0.113	0.192	0.322	0.165
	n.s.	n.s.	n.s.	n.s.

n.s. : non of significant. 0.05 : significant at 5.0% level.

From experiments using *Kalanchoë pinnate*, WINTER et al.¹⁷⁾ have published that the activity ratio of ribulosebisphosphate carboxylase (RuBP-C) to phosphoenolpyruvate carboxylase (PEP-C) was not influenced by nitrogen treatments. Their results suggest that nitrogen treatment equally affected the CO_2 gain both in phase 1 and phase 4, and it also suggests that the treatment did not affect the CAM ability, the ratio of CO_2 influx in phase 1 to CO_2 balance for full one day. In the present experiment, the CAM ability of pineapple plants increased as total nitrogen content in leaves increased (Fig. 6).

In other words, in phase 1 and phase 4, the unique relationships between G_s as well as leaf nitrogen components and CO_2 influx rate, and the increase in CAM ability both appear to be due to the difference in the potential activity of CO_2 fixation enzyme in each phase. It is known that the CO_2 affinity

Fig. 9. Relationships between total nitrogen content and nitrogen use efficiency.

A: relations calculated from nitrogen use efficiency per full one day (○), phase 1 (●) and phase 4 (△). B: relations calculated from maximum nitrogen use efficiency in phase 1 (○) and phase 4 (△). *: significant at 5.0% level. n.s.: non of significant.

of PEP-C, the CO₂ fixation enzyme in phase 1, is several times to ten times higher than that of RuBP-C in phase 4²⁾. Consequently, it appears that the lower CO₂ affinity of RuBP-C made the control of CO₂ influx rate by Gs more salient in phase 4, and that the higher CO₂ affinity of PEP-C made the relationship between CO₂ influx rate and leaf nitrogen components more salient in phase 1. In addition to it, it also appears that the CAM ability increased in present experiment, since the increase in RuBP-C activity following the increase in nitrogen nutrition did not exceed stomatal resistance to gas flux.

BROWN¹⁾, and SCHMITT and EDWARDS⁸⁾ reported that the nitrogen use efficiency in C₄ plants was higher than in C₃ plants. CAM plants have a carbon fixation scheme similar to C₄ photosynthesis, but not much has been known about the nitrogen use efficiency of CAM plants. Maximum nitrogen use efficiency of pineapple obtained in the present experiment ranged from 93 to 120 μgCO₂/mgN/h, and 65 to 150 μgCO₂/mgN/h, in phase 1 and phase 4, respectively; and these values are one fiftieth of the efficiency of C₃ plants and one hundredth of C₄ plants^{6,8)}. Therefore, it may be concluded that CAM type of photosynthesis of pineapple is extremely inefficient as to nitrogen

use efficiency. BROWN regards the high nitrogen use efficiency of C₄ plants as evolutionary significance. Such a significance, however, was not found in the present experiment of CAM type photosynthesis of pineapple plants. In addition, pineapple plants showed such behaviors that they increased CAM ability and improved water use efficiency even under the high nitrogen condition, while C₃ and C₄ plants reduce water use efficiency and their growth becomes more active under the same nitrogen nutrition conditions. In brief, concerning the increase in CAM ability and low nitrogen use efficiency under high nitrogen conditions, the advantage of CAM type photosynthesis may be found in drought tolerance alone, as indicated by OSMOND⁶⁾.

Summary

Using pineapple plants, a cultivar selected from the Smooth cayenne and grown in cultural solution, the effect of nitrogen (NO₃-N) nutrition on the gas exchange of the plants was investigated. Six nitrogen treatments in culture medium contained 14, 28, 69, 138, 277 and 554 ppm of nitrogen concentration, respectively. The concentration of other elements except for nitrogen was same in the six treatments. The obtained results were as follows:

1. The CO₂ influx occurred in dark period (phase 1, after OSMOND) and the last half of light period (phase 4) on every nitrogen treatment, and CO₂ influx rate was different each other among each treatment.

2. Maximum CO₂ balance for full one day and phase 1 was obtained in nitrogen treatments of 277 and 138 ppm. Maximum CO₂ balance in phase 4 was obtained in 138 ppm plants (Fig. 2).

3. Total nitrogen, soluble protein, and chlorophyll content in leaves showed maximum value in 138 and 277 ppm nitrogen plants and decreased in 557 ppm plants (Fig. 3).

4. CO₂ balance for full one day and in phase 1 showed positive and statistically significant correlations to total nitrogen, soluble protein, and chlorophyll content in leaves. CO₂ balance in phase 4 did not significantly correlate to leaf nitrogen compo-

nents (Figs. 4 and 5).

5. Correlation between CO_2 influx rate and water vapour exchange coefficient was positive and significant in phase 1 and 4. The degree of correlation in phase 4 was particularly high (Fig. 7). Consequently, it appears that CO_2 influx in phase 1 was mainly affected by factors related to nitrogen content in leaves, and that CO_2 influx in phase 4 was regulated with the degree of stomatal aperture.

6. CAM ability, the ratio of CO_2 balance in phase 1 to CO_2 balance for full one day, increased as total nitrogen in leaves increased (Fig. 6).

7. Nitrogen use efficiency for one day in pineapple plant was as small as 1.9 to 1.2 $\text{mgCO}_2/\text{mgN}/\text{day}$. In addition, maximum nitrogen use efficiency calculated from maximum CO_2 influx rate in phase 1 and 4 was extremely small, showing the value of 93 to 120 $\mu\text{gCO}_2/\text{mgN}/\text{h}$ in phase 1 and 65 to 150 $\mu\text{gCO}_2/\text{mgN}/\text{h}$ in phase 4 (Fig. 9).

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** In Japanese

〔和文摘要〕

パイナップルの物質生産に関する研究

第3報 窒素栄養が地上部のガス交換に及ぼす影響

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パイナップル (スムーズ・カイエン種 ハワイ系 N-76) を水耕栽培し、窒素栄養 (硝酸態窒素) が地上部のガス交換に及ぼす影響を検討した。根圏の窒素濃度区として、14, 28, 69, 138, 277, 552 ppm の6処理区を設定した。得られた結果は、以下のとおりである。

1. いずれの窒素区においても、明期の後半と暗期に CO_2 吸収が生じるという、CAM 型 CO_2 交換を示した (第1図)。
2. 全日と暗期の CO_2 収支は、277 と 138 ppm の窒素区で最大となった。明期の後半の CO_2 吸収は、138 ppm 区で最大となった (第2図)。
3. 葉身の全窒素含量・可溶性タンパク含量・クロロフィル含量は、138 と 277 ppm 区で最大となり、554 ppm 区では減少した (第3図)。
4. 全日と暗期の CO_2 収支は、葉身の全窒素、可溶性タンパク、クロロフィルと正の有意な相関を示した。明期の後半の CO_2 吸収量は、調査した葉身の窒素要因とは有意な相関を示さなかった (第4, 5図)。
5. CO_2 吸収速度と水蒸気交換係数は、明期の後半と暗期の両方で正の有意な相関を示し、特に前者での相関の程度が高かった (第7図)。従って、暗期の CO_2 吸収は葉内の窒素関連要因によって主に制御をうけ、明期の後半の CO_2 吸収は気孔コンダクタンスによって主に制御されるものと推察された。
6. CAM 性 (全日の CO_2 収支に占める暗期の CO_2 吸収の割合) は、葉身の全窒素含量の増大とともに上昇した (第6図)。
7. パイナップルの CO_2 吸収における窒素利用効率は、1日当りでは $1.9 \sim 1.2 \text{ mgCO}_2/\text{mgN}$ と小さかった。暗期と明期の最大 CO_2 吸収速度から求めた最大窒素利用効率は、暗期で $93 \sim 120 \mu\text{gCO}_2/\text{mgN/h}$ 、明期で $65 \sim 105 \mu\text{gCO}_2/\text{mgN/h}$ と極めて小さかった (第9図)。