Studies on Matter Production in Pineapple Plant

II. Effects of soil moisture on the gas exchange of pineapple plants*

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Crassulacean acid metabolism (CAM) is generally recognized as an adaptive character of plants to drought^{13,23,30}. In this sense, the mechanism of drought tolerance of CAM plants have already been clarified to some extent^{1,10,16,19,22,23,27,28,30}. Only a few studies, however, have so far been done on optimum soil moisture conditions to increase the matter production of CAM plants^{15,24,25}. As for pineapple plants, investigations into optimum soil moisture conditions for further matter production is more important than those into drought tolerance. Studies on relationships between the growth of pineapple and soil moisture percentage have also been done by only a few investigators. Using three kinds of soils, SIDERIS and KRAUSS²⁶ investigated into relations between soil moisture percentage (to dry weight) and the growth of pineapple, and they have concluded that the maximum growth rate is obtained under 20% to 30% of soil moisture percentage. SHIROMA²⁵ observed that the elongation rate of leaf blade declined as soil moisture decreased, and he qualitatively indicated that the decrease of soil moisture delayed the vegetative growth of pineapple plants.

The present studies were carried out in an attempt to find the effects of soil moisture on the gas exchange of the top of pineapple plants. In order to compare the soil

moisture characteristics of plants other than CAM plants, gas exchange measurements were carried out at four levels of soil moisture contents that are conventionally referred to.

Materials and Methods

Plant material used was the "Mitsubishi-kei Yuryo Keito" selected from the cultivar Smooth Cayenne. Crowns of winter fruits were obtained from the Gogayama Experiment Farm, Okinawa Agricultural Experiment Station. One crown in one pot was planted in Oct. 27, 1977, using WAGNER pots (1/2000 a) filled with acid lithosols of Kunigami gravel formation. With sufficient water supply, the plants were grown in a vinyl house in the campus of the University of the Ryukyus, Naha, Japan, following the standard culture methods in Okinawa Prefecture. Plant sizes during the measurements are shown in Table 1.

Four Blocks of soil moisture condition were established ranging from pF 1.0 to pF 4.5 of soil moisture tension. Each soil moisture condition at measurements is shown in Table 1. Hereinafter, the blocks of soil moisture will be expressed in mean pF value as shown in Table 1. In accordance with the drying in the soil, water treatment on each soil moisture block was practiced during Jan. 7, 1978 and Feb. 13, namely, during the 72nd day and 109th day after planting. The regulation of soil moisture was done by weighing method, using GIBO's soil moisture-pF curve⁵ and another soil moisture-pF curve confirmed again by the authors at the time of soil collection. The

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Table 1. Soil moisture conditions and characters of pineapple plants for each gas exchange measurement.

Exp. No.	Soil moisture tension (pF)			Characters of plants			
	Start	End	Mean	(1)	(2)	(3)	(4)
I	1.3	1.3	1.3	79	28.6	35.60	89.2
	2.1	2.5	2.3	60	26.5	31.96	88.8
	3.5	3.8	3.7	73	23.4	26.80	89.3
	4.3	4.6	4.5	73	25.8	34.38	88.2
II	1.3	0.9	1.1	75	29.7	37.05	89.1
	2.4	2.7	2.6	73	31.2	40.30	88.9
	3.6	4.0	3.8	71	32.2	42.68	88.4
	4.3	4.7	4.5	73	29.7	39.35	88.1

(1)...leaf number, no/plant, (2)...leaf area, dm²/plant, (3)...leaf dry weight, g/plant, (4)...leaf water percentage on fresh weight base, %.

acid lithosols used to grow the material plants were collected at the same location as those used in GIBO's experiments.

Gas exchange of the top of material plants was measured at three levels of average light intensity and at four levels of soil moisture regulated as mentioned above. Two series of experiments, namely Exp. I and Exp. II, were carried out from Feb. 14, 1978 to Mar. 23, 1978, during the 110th day and 147th day after planting. Exp. I consisted of the measurements from Feb. 14 to Mar. 2, and Exp. II consisted of those from Mar. 9 to Mar. 23. Gas exchange of the top of plants was measured in the open system and by the same method as in the previous experiments²⁰⁾, using acrylic assimilation chambers with the dimension of 40 cm×60 cm×40 cm ($w \times l \times h$). The light period was 11 hours from 7:30 to 18:30, and the dark period 13 hours of the rest. The leaf temperature was kept at $29.4 \pm 0.7^\circ\text{C}$ and $23.3 \pm 1.1^\circ\text{C}$, and air humidity at $50.2 \pm 8.8\%$ and $62.8 \pm 4.3\%$, in light and dark period, respectively. Air was ventilated 7.5 ± 0.3 liters per minute throughout the experiment. Average light intensity of 10 klx, 30 klx, and 60 klx were designed for each soil moisture condition. Actual light intensities are shown in Table

2. In order to keep the soil moisture conditions constant, 50 ml/pot of water was supplied every morning through an intake at the bottom of the pot.

Results

Diurnal gas exchange pattern

The diurnal patterns of gas exchange and transpiration rate of pineapple top at each soil moisture condition at three levels of light intensity are shown in Fig. 1. The results were obtained in Exp. II. OSMOND²³⁾ has classified the diurnal gas exchange of CAM plants 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. Following OSMOND's classification, a comparison of the effect of soil moisture on gas exchange has been done as follows: Firstly, the rise of CO₂ influx rate in the last half of light period (phase 4) occurred earliest in pF 2.6 block, and latest in pF 4.5 block. The order of soil moisture levels in maximum CO₂ influx rate in phase 4 was also the same as that in the time when the rise of CO₂ influx occurred. Both of the diurnal pattern and the order of magnitude in transpiration rate were also the same as those in CO₂ exchange rate. Transpiration rate in phase 4 at three levels of soil moisture except for pF 4.5, however, was the highest among those in four phases of the day.

Secondly, CO₂ influx rate in the first half

Table 2. Average light intensity (klx) in light period on top of the plant for each gas exchange measurement.

Exp. No.	Light intensity			
	(1)	10	30	60
I	1.3	12.1	36.1	61.9
	2.3	11.7	32.8	63.3
	3.7	9.9	33.2	69.1
	4.4	10.2	32.4	65.0
II	1.1	10.5	31.2	58.9
	2.6	14.0	31.9	56.8
	3.8	12.6	36.7	64.8
	4.5	12.3	38.0	66.0

(1)...Soil moisture block, pF.

of dark period (phase 1) was largest at pF 2.6, and smallest at pF 4.5. The maximum of CO₂ influx rate in this phase was the highest throughout the day at each soil moisture condition. It is particularly interesting that CO₂ influx rate at pF 4.5 was far larger in phase 1 than in phase 4. The order of soil moisture levels in CO₂ influx rate at light intensity of 10 klx was also partly different from those at other light intensities where they showed the same order. Transpiration rate in phase 1 has been slightly larger at pF 2.6 than at other soil moisture levels, but this difference between each soil moisture level has not shown so much clear difference as in CO₂ exchange in this phase. In addition to it, transpiration rate in this phase at each soil moisture level is as low as that in phase 3.

Fig. 2 shows the daily pattern of water vapour exchange coefficient for the top obtained in Exp. II. The change of water vapour exchange coefficient (D) is expressed by following formula^{4,29,32,33}.

$$D = T / (e_{int} - e_a)$$

where, T denotes transpiration rate, e_{int} water vapour in the leaf, e_a water vapour in the surrounding air. Since the diffusion

resistance of boundary layer (r_a) is affected by air turbulence, leaf shape and leaf size^{4,29}, it is considered that water vapour exchange coefficient for the whole of a single plant contains complex factors. In the present investigations, fan speed in the assimilation chamber was constant in every measurement, and plant size at every measurement was almost the same. Therefore, r_a was assumed to have had the same value at every measurement. Consequently, D in these experiments is regarded to have expressed the stomatal conductance of gas diffusion system on a whole single plant.

Firstly, in phase 4, the order of soil moisture in water vapour exchange coefficient (D) has the same trend as that in CO₂ exchange rate in all light blocks tested (Fig. 1), and D is largest at pF 2.6 and smallest at pF 4.5. In the three blocks except for pF 4.5, the maximum of D in this phase has been the highest throughout the day. At pF 4.5, the rise in D in this phase is little.

In the next place, D in phase 1 has been the largest at pF 2.6 and the smallest at pF 4.5. D at pF 4.5, however, increased more in phase 1 than in phase 4. The way in

Fig. 1. The effects of soil moisture on the diurnal gas exchange of pineapple plants. A, B, and C in the figure show 60 klx, 30 klx, and 10 klx light block in average light intensity, respectively.

○...pF 1.1, △...pF 2.6, ×...pF 3.8, ●...pF 4.5. Values for the figure are shown in detail in Table 1 and Table 2. Results in the figure were obtained in Exp. II.

Fig. 2. The effects of soil moisture on diurnal pattern of water vapour exchange coefficient of the top of pineapple plants.

The alphabet and symbols in the figure are the same as in Fig. 1. Results in the figure were obtained in Exp. II.

Fig. 3. The effects of soil moisture and light intensity in light period on the CO_2 balance of the top of pineapple plants.

A...Daily CO_2 balance, B... CO_2 balance in phase 1, C... CO_2 balance in phase 4, ○...Exp. I, ●...Exp. II.

which D changed as the phase moved on from phase 4 into phase 1 was also differed from those at other three moisture levels. In other words, it shows that stomata at pF 4.5 almost closed in phase 4, and opened gradually in phase 1 (dark period). It also appears that stomata at other three blocks opened even in phase 4, and the degree of aperture in the phase was larger than in

phase 1 (dark period).

The results of gas exchange and water vapour exchange coefficient mentioned above were almost the same as Exp. I.

CO_2 balance

Fig. 3 shows the relationships among CO_2 balance, soil moisture tension, and average light intensity obtained in these experiments. A in the figure shows daily CO_2 balance, B

the balance in the phase 1, and C the balance in the phase 4. Closed circles in the figure show the results in Exp. I and open circles those in Exp. II. All the values were obtained by integration of the values in Fig. 1. In Fig. 3-A, daily CO_2 balance at each light intensity reached a maximum at pF 2.3 in Exp. I, and at pF 2.6 in Exp. II. The CO_2 balance declined towards the both sides of the soil moisture. Similar results of CO_2 balance were found in phase 1 and phase 4.

Water use efficiency

Taking carbon balance, which supports growth, as a major topic, the results of the experiments were shown in the previous sections. Hereinafter, the effects of soil moisture and light intensity on transpiration ratio (transpiration/ CO_2 flux) as an index of drought tolerance will be described in this section. Fig. 4 shows the relationships among transpiration ratio, soil moisture condition, and light intensity for one day, in phase 1, and phase 4. The results shown in this section were obtained from Exp. II and they were calculated from the integral values of CO_2 exchange and transpiration in each phase. It is difficult to find a certain relation between soil moisture and transpiration ratio at each light intensity. Transpiration ratio at each moisture tension, however, increased in each phase as light intensity decreased. Peculiar values at pF 4.5 may be due to characteristic phenomena caused by a strong water stress^{13, 27)}. In brief, it appears that transpiration ratio under weak water stress is mainly regulated by light intensity.

Discussion

Four soil moisture levels established in the present investigations are equivalent to some soil moisture constants⁷⁾ which have already been referred to for investigations into other crop plants except for CAM plants. In other words, pF 4.4 and pF 4.5 correspond to permanent wilting point, pF 3.7 and 3.8 to first wilting point, pF 2.3 and pF 2.6 total readily available moisture between field capacity and depletion of moisture content for optimum growth,

Fig. 4. The relationships among transpiration ratio (TR), soil moisture, and light intensity in light period.

A...TR for a whole day, B...TR in phase 4, C...TR in phase 1. Symbols in the figure are the same as in Fig. 1. Results in the figure were obtained in Exp. II.

pF 1.1 and pF 1.3 to excessive moisture. Fig. 3 shows that CO_2 balance of the top of pineapple plants reached a maximum under a soil moisture condition of total readily available moisture and it declined as soil moisture changed towards the both sides of the condition. Consequently, it appears that drought is not necessarily suitable for the growth of CAM plants^{22, 24)}, and it is found that the optimum soil moisture for the growth of pineapple plants is equivalent to that recognized suitable to plants other than CAM plants. From the fact that pineapple plants exhibits a positive CO_2 balance even at soil moisture levels of so called the first wilting point and permanent wilting point, however, it appears that the pineapple as a CAM plant has a strong drought tolerance. On the other hand, CO_2 balance decreases under excessive soil moisture conditions of pF 1.1 and pF 1.3. This may indicate paradoxical characteristics for the drought tolerance of CAM plants. In this respect, SHIROMA²⁵⁾ has observed the same phenomena. It has been believed from experience that yield of pineapple from the field of excessively high soil mois-

ture and ill-drainage is low due to disease. The results of the present investigations suggest that physiological drawback in growth also occurs in the field of excessively high soil moisture.

It has been recognized in CAM plants that CO_2 influx is depleted first in phase 4 as water depletion begins and that it declines afterwards in phase 1^{1,10,12,16,17,18,19,22,23,28,30}. In the present investigation, it was observed that the fall in CO_2 influx in both phase 1 and phase 4 occurred simultaneously under weak water stress (Fig. 1 and Fig. 3). CO_2 influx in phase 4 kept on falling further as soil moisture decreased from pF 3.8 to pF 4.5. During this process, however, the decrease in CO_2 influx in phase 1 was not much appreciable. In brief, it is considered that CO_2 balance in phase 1 and phase 4 in pineapple plants decreases together under weak water stress, and that the CO_2 balance in phase 4 is suppressed further as water stress increased. Consequently, it is suggested that soil moisture levels resulting in large depletion in CO_2 influx are in the range between the first wilting point and permanent wilting point.

As described above, it appears that the relationships between CO_2 balance of pineapple plants and soil moisture conditions are different from those of other crops belonging to C_3 and C_4 plants. Based on the results described above, a few comments on the mechanism of some phenomena observed in the present experiments will be mentioned hereinafter. Firstly, as for water content on fresh weight base of plant, it has been observed that CO_2 balance decreased when water content on fresh weight base of photosynthetic organ declined from 85.7% to 80.2% in *Tillandsia usneoides*¹⁰, and from 95.6% to 94.5% in *Dudleya farinosa*¹¹. CO_2 balance in the present experiments was observed to decline when water content on fresh weight base of the top of pineapple plants decreased to 88.1% to 88.2% (Table 1 and Fig. 3). The range of the change in water content on fresh weight base was as small as 1.1% in Exp. I and 1.0% in Exp. II. The fact that a clear difference in CO_2 balance, as shown in Fig. 3, was caused by

such a small change in water content suggests that the CO_2 exchange of pineapple plants responds sensitively to water condition of photosynthetic organs and that this range of water content on fresh weight base is threshold values for water stress.

Water vapour exchange coefficient (D) indicating the aperture of stomata changed in phase 1 and phase 4 in the same trend as CO_2 exchange did (Fig. 1 and 2). Fig. 5 shows the relationships between D and CO_2 exchange rate in phase 1 and phase 4 in Exp. II. Under the same light conditions, a significant positive correlation was observed between D and CO_2 exchange rate in both of the phases. Comparing D for each soil moisture stress under each light condition, D was largest at pF 2.6 (triangle in Fig. 5), smallest at pF 4.5 (closed circle), and medium values were observed at pF 1.1 and pF 3.5. In other words, D at each soil moisture block has a singular value. The phenomena described above indicate that CO_2 exchange rate in these investigations was strongly affected by D, that is by stomatal aperture, and that the stomatal aperture was regulated by soil moisture conditions. In brief, it appears that the effects of soil moisture on CO_2 balance shown in Fig. 1 and 3 were mainly resulted through stomatal resistance in gas diffusion system.

As described above, it is concluded from the present investigations that the relationships between CO_2 balance and soil moisture condition was resulted from the behavior of stomatal aperture. Further, as discussed in previous sections, water content on fresh weight base of photosynthetic organ also decreased slightly, although not much, as soil moisture decreased. According to the facts so far clarified by other investigations, it is known that there are two routes through which soil moisture conditions affect on CO_2 exchange of plant. One of them is that the effect of stomatal aperture and CO_2 fixation on CO_2 exchange is brought about due to the decrease of water content^{6,14}, and the other way is a direct effect on the degree of stomatal aperture due to the hormonal balance of cytokinin and

Fig. 5. Correlations between water vapour exchange coefficient and CO₂ influx rate in phase 1 and phase 4.

A...60 klx in phase 1, B...30 klx in phase 1, C...10 klx in phase 1,

D...60 klx in phase 4, E...30 klx in phase 4, F...10 klx in phase 4.

Symbols in the figure are the same as in Fig. 1. ***...significant at 0.1% level.

Results in the figure were obtained in Exp. II.

abscisic acid etc^{8,23}). It is difficult to determine route through which the soil moisture conditions affected stomatal resistance in the present investigations. From the fact that the change in water content on fresh weight base of plant was very little, it appears that the result obtained in these investigations were due to hormonal balance. Further investigations, however, will be necessary to confirm this conception.

The above discussion was concerned with the relation between drought tolerance and CO₂ exchange in pineapple plants. Following is another discussion on transpiration

ratio (transpiration/CO₂ balance: TR) as an index of drought tolerance of plants. TR values obtained in the present investigations are in the range of other values so far obtained in CAM plants including the pineapple^{2,9,18,23,26,30}. Although the pathway of carbon fixation in phase 4 has been regarded to be "C₃-like"^{3,11,20,21,23,30}, TR in phase 4 is positively smaller than that of C₃ plants²) (Fig. 4-B). This fact is also considered to exhibit a characteristic drought resistance of gas diffusion system in pineapple as a CAM plant.

Next, under the same light conditions,

Fig. 6. Correlations between transpiration ratio and water vapour exchange coefficient in phase 1 and phase 4.

A...pF 1.1 in phase 1, B...pF 2.6 in phase 1, C...pF 3.8 in phase 1, D...pF 4.5 in phase 1, E...pF 1.1 in phase 4, F...pF 2.6 in phase 4, G...pF 3.8 in phase 4, H...pF 4.5 in phase 4, ○...60 klx, △...30 klx, ●...10 klx. Values in the figure are shown in detail in Table 1 and Table 2.

Results in the figure were obtained in Exp. II.

TR was not significantly affected by soil moisture conditions. The same finding has been obtained in *Echeveria pumila* Van Houtte (crassulaceae)¹⁵⁾. MEIZER and RUNDEL¹⁵⁾ attributed this cause to genetic characteristics, but details are unknown. On the other hand, it has been proved in the present investigations that TR was regulated by light intensity. Based on this fact, a discussion that TR in the top of pineapple plants is regulated by light intensity will be mentioned as follows: Fig. 6 shows correlation between TR and water vapour exchange coefficient (D) as light intensity changes under each soil moisture condition. TR in three soil moisture blocks except for pF 4.5 exponentially decreases while it ap-

proaches to a constant value as D increases. In addition, D becomes larger and larger as light intensity increases. In other words, under the same soil moisture conditions, D increases as light intensity in light period increases, and TR decreases simultaneously. TOTSUKA³¹⁾ has reported contrary results that the TR of sunflower, a C₃ plant, increased as light intensity increased. Although some discrepant results have been obtained in the relation of TR and light intensity, comments based on the relationships between TR and D obtained from the present investigations are as follows:

In brief, it is regarded that D has an additional resistance to the resistance caused by water vapour and CO₂ transfer that are

both the components of transpiration ratio ($r_{s,CO_2} = 1.7 \times r_{s,H_2O}$, r_s : stomatal resistance⁴⁾). Consequently, it is difficult to regard that the exponential decrease in TR described above was caused by D only. In other words, it appears that large transpiration ratio at small D was brought about by the multiple effects that the fall in light intensity makes CO_2 influx rate small, since the influx rate is a denominator in the fraction denoting transpiration ratio. In addition, it is also regarded that the convergence of TR at large D is resulted from the saturation of CO_2 influx rate in high light intensity and from the saturation of D in gas diffusion systems. In other words, the reason why water use efficiency was regulated by light intensity rather than by soil moisture conditions may be due to the fact that as far as the present experiments are concerned, soil moisture was simply a factor to affect D only, although light intensity affected transpiration ratio in geometrically increasing rate through both D and CO_2 influx rate.

It is, however, difficult to conclude that the relationships between TR and light intensity obtained in these investigations will hold true under field conditions as well. This is because increase in light intensity in field condition will possibly result in the increase in leaf-air vapour pressure deficit due to the increase in leaf temperature and fall in air humidity and consequently, transpiration rate will be possibly promoted under such conditions. This may be an aspect to solve the discrepancy between TOTSUKA's results^{3,1)} and those of the present investigations.

Summary

Using pineapple plants, a cultivar selected from the Smooth Cayenne, the effects of soil moisture on the gas exchange of the top of the plants were investigated. Soil moisture levels under which the present experiments were carried out four soil moisture constants conventionally referred to in plants except for CAM plants: They were the condition of excessive water, total readily available moisture, first wilting

point, and permanent wilting point. The following results have been obtained:

1. The CO_2 influx occurred in dark period and the last half of light period under every soil moisture condition (Fig. 1).
2. The CO_2 balance in the last half of light period, in dark period, and for a whole day reached a maximum at total readily available moisture condition of pF 2 to pF 3 (Fig. 3).
3. Pineapple plants, which belong to the CAM plant, exhibited a positive CO_2 balance even under the first wilting point to permanent wilting point for other plants (Fig. 1 and 3).
4. CO_2 influx in the last half of light period decreased much under soil moisture condition between first wilting point and permanent wilting point. Decrease in CO_2 balance in dark period, however, was not so large under the same soil moisture conditions.
5. The time course of water vapour exchange coefficient of the whole top of a single plant was similar to that of CO_2 exchange (Fig. 2).
6. Transpiration ratio, in each phase of the CO_2 exchange, that is in last half of light period, dark period, and a whole day was regulated by light intensity in light period rather than soil moisture conditions (Fig. 4).
7. It was found that the effect of soil moisture obtained in the present investigations was resulted from the regulating action of stomatal aperture.

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[和 文 摘 要]

パイナップルの物質生産に関する研究

第2報 土壌水分がパイナップルのガス交換に及ぼす影響

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パイナップル（スモース カイエーン 三菱系優良系統）を用い、地上部のガス交換に及ぼす土壌水分の影響を調査した。土壌水分条件は、今までに CAM 植物以外の植物で明らかにされてきた4種の土壌水分条件、すなわち過湿、生長有効水分域、初期萎凋点、永久萎凋点を設定した。得られた結果は以下のとおりである。

1. いずれの土壌水分下でも昼の後半と夜に CO_2 を吸収した（第1図）。
2. 昼の後半、夜および1日の CO_2 収支は pF 2 から pF 3 にかけての生長有効水分域で極大値を示した（第3図）。
3. CAM 植物の一種であるパイナップルでは初期萎凋点や永久萎凋点といわれる土壌水分域でも正の CO_2 収支を示した（第1図、第3図）。
4. 昼の後半の CO_2 吸収は、初期萎凋点から永久萎凋点にかけての土壌水分域で大きく減少することが認められた。しかし、このときの夜の CO_2 収支の低下は、それほど大きくなかった。
5. 地上部全体について求めた水蒸気交換係数は CO_2 交換の推移と同様な動きを示した（第2図）。
6. CO_2 交換の日変化の各相（昼の後半、夜、1日）で求めた蒸散比は、土壌水分よりも昼間の光強度により律速されるものであった（第4図）。
7. 本実験で得られた土壌水分の影響は、主に気孔開度の調節を通して生じたことが明らかにされた。