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A Study on the Change of Photosynthetic Patterns by the Cladode Orientation of *Opuntia lanceolata* Haw.

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부채仙人掌(*Opuntia lanceolata* Haw.)의 葉狀莖方位에 따른 光合成樣式의 變化에 관한 研究

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ABSTRACT

Diurnal acid fluctuation, stomatal resistance, and solar radiation with regard to the cladode orientation were investigated in *Opuntia lanceolata* Haw. growing at Weolryeong-ri, Hallim-eup, Chejudo, Korea.

Diurnal changes of titratable acidity showed the typical CAM pattern in all investigated cladodes. Water tissue in the cladode had the same pattern of acid fluctuation as mesophyll tissue.

Stomatal resistance was low during the night, increased rapidly to be a peak right after sunrise and decreased again thereafter. The southern side of the cladode showed higher stomatal resistance than the northern side during the day time. It suggests that the stomata of the northern side opens under diffuse radiation.

The amount of solar radiation varied depending upon the cladode orientation. It is thought that C_4 acids move inter and intra mesophyll tissues in the cladode through the unknown pathways.

RuBP carboxylase activity in the cladode was very high at 14 : 00, but was not significant at 01 : 00. PEP-carboxylase had high activities both at 14 : 00 and at 01 : 00. The results of this study showed the possibility that *O. lanceolata* Haw. had the C_3, C_4 and CAM photosynthetic patterns under the environmental conditions at Weolryeong-ri.

INTRODUCTION

Orientation of plant leaves critically affects on the interception of photosynthetically active radiation (PAR) and, hence, influences photosynthesis. Such orientation with respect to direct-beam PAR is fixed during development for the massive stems of some CAM plants such as cacti. Since the stems are rigid and opaque, different sides are exposed to quite different radiation environments; thus they make different contributions to the plant's net carbon gain (Nobel, 1982).

Therefore, the question arises as to whether the different sides of a cladode (flattned stem) of platyopunita exhibit any preferential photosynthetic characteristics. The effects of light intensity have been studied on CAM. Malate consumption during the day time is accelerated as light intensity increases, and net dark CO_2 fixation is also increased with high light intensity during the previous light period (Kluge, 1968; Osmond, 1978).

Portulaca oleracea L., a succulent C_4 and CAM, showed that C_4 products assimilated by the PEP carboxylase in leaves moved to stems and were laid up there under insufficient light conditions, and then they were converted into starch by the RuBP carboxylase activated by the sufficient light (Chang & Kim, 1982).

Under the good water status, stomata of CAM plants open even during the day (Chang *et al.*, 1981; James, 1958; Holdsworth, 1971), and also open in response to precipitation (Nobel, 1977; Szarek *et al.*, 1973; Szarek & Ting, 1974; Ting, 1976). In the deserts of the south-western USA, stomata may open during the early part of the light period, but close by midday (Szarek & Ting, 1975). Conde and Kramer (1975) followed stomatal resistance in *Opuntia compressa* as a function of vapor pressure deficit (VPD) of the air and found that the stomata were to be close at high VPD and open at low VPD. (Nobel, 1977; Szarek *et al.*, 1973; Szarek & Ting, 1974; Ting, 1976). Relative humidity has influence on stomatal aperture and stomatal resistance (Lange *et al.*, 1971; Hall & Kaufmann, 1975).

The purpose of this experiment is to show which photosynthetic mode *Opuntia lanceolata* Haw. exhibits under the environment conditions in Weolryeong-ri by investigating diurnal acid fluctuation, stomatal resistance, solar radiation, and organic acid movement according to the cladode orientation in the cladode of *O. lanceolata* Haw. growing at Weolryeong-ri, Hallim-eup, Chejudo, Korea.

MATERIALS AND METHODS

Study area

The study areas were located in the seaside village (N33°23′, E126°9′, Weolryeong-ri, Hallim-eup, Cheju-do, Korea). One site was open area on the basaltic stone fence and the other was under the stone-fence oriented northwest, which was about 10m away from coastline.

O. lanceolata Haw. which was about 60cm high grew both on the basaltic stone fence and on the basalt bedrock. Soil moistures of each studied areas were 1.03% and 16.12%, respectively.

Field work was conducted from May 20th to May 22nd in 1982, when the time of sunrise and sunset were 05 : 19 and 19 : 38, respectively. And the weather was clear all through the experimental period.

The precipitation of this region is about 1300mm annually and it exceeds 50mm even in dry January. The monthly mean relative humidity ranges from about 70% to 85%. The monthly average max. and min. air temperature are 18.9°C and 10.9°C, respectively. In winter the lowest air temperature ranging from −4°C to −7°C has been recorded.

O. lanceolata Haw. has yellow flowers in June and bears red fruits in November. It is said that it was introduced into Weolryeong-ri about one hundred years ago.

Diurnal acid fluctuation and solar radiation

The cladodes which located on the top and whose sides faced the north, northeast, east, and southwest were selected. Samples were punched out of the cladode with a cork borer at intervals of an hour.

Green mesophyll and water tissues of the samples

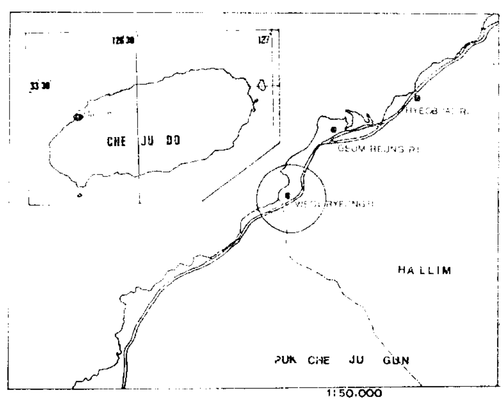

Fig. 1. Geographical map of the study area.

Table 1. The meteorological data in Hallim-eup, Cheju-do, Korea. Central Meteorological Office, Annual Report (1972~1977)

		Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Agu.	Sep.	Oct.	Nov.	Dec.	Annual
Air	Average	5.2	5.5	8.4	13.3	16.5	20.4	25.3	26.3	22.2	17.5	11.9	7.3	15.0
Temper-ature(°C)	Average max.	8.2	9.0	12.4	17.8	21.2	24.8	28.9	30.2	26.3	22.0	15.7	10.7	18.0
	Average min.	1.9	1.8	4.0	8.4	11.6	16.2	21.7	22.6	18.0	12.6	7.7	3.5	10.9
Precipitation(mm)		59.8	80.3	74.0	141.4	133.6	177.1	227.2	152.3	126.1	57.4	71.0	55.4	1344.6
Relative humidity(%)		70.8	71.3	71.0	77.2	80.2	82.0	85.3	84.0	80.3	75.2	70.8	72.2	76.5
Hours with sunshine		126.9	142.6	217.0	205.9	260.9	244.7	250.0	286.6	239.1	223.0	175.4	128.0	2450.9

were separated with a razor blade, carefully rinsed with distilled water, and then extracted. The extracts were titrated to an end point of pH 6.7 using 0.01 N NaOH as described by Hartsock & Nobel (1976) and expressed as μeq/cm^2 of cladode surface area.

At the time of sampling, atmospheric temperature and solar radiation according to the clodode orientation were measured with a thermometer and a temcometer.

Stomatal resistance of clodode

Stomatal resistance was measured with a autoporometer (LI-65, LI-COR) and represented as sec/cm.

Organic acid movements

(1) Inter-mesophyll tissues movement of organic acids

In order to investigate the possibility of organic acids movement between northern and southern mesophyll tissues within the same cladode, the clododes whose sides faced the south and the north were selected, and northern sides were intercepted from sun-light by covering them with opaque aluminum foil. Either a sheet of polyvinyl chloride or a sheet of aluminum foil was inserted between the mesophyll tissues. To prevent water-loss of the clododes they were sealed up with an adhesive tape. Above all, these procedures were done at 4 : 00 in the morning before sunrise. Samples were punched at 08 : 30, 11 : 00, 15 : 00, 19 : 00 and 23 : 00, respectively and titratable acidity was measured for each samples.

(2) Intra-mesophyll tissue movement of organic acids

In order to investigate the possibility of organic acids movement between the left side and right side within the same cladode, one was incised nearly to the base and aluminum foil was inserted in the middle of the cladode vertically to the cladode side. One half side was intercepted from light and the other half was exposed to natural light conditions. Another cladode with the same light treatment was left intact without surgical treatment. Each experiment had a control.

Enzyme assays

RuBP carboxylase and PEP carboxylase were prepared and assayed as follows; samples were punched out of the 1st, 2nd, 3rd and 4th cladode from the top at 01 : 00 and 14 : 00. And then they were assayed by using of $NaH^{14}CO_3$ as described by Chang *et al.* (1981).

The extraction media used to prepare PEP carboxylase and RuBP carboxylase extracts consisted of 50mM Tris-HCl at pH 8.3, 20mM $MgCl_2$, 0.1mM Na_2-EDTA, 5mM D-isoascorbate, and 2% PVP-40.

PEP carboxylase was assayed as ^{14}C-incorporated reaction mixture containing 5mM PEP, 10mM $NaH^{14}CO_3$, 5mM DTT, 10mM $MgCl_2$ and 50mM Tris-HCl buffer at pH 8.3. RuBP carboxylase was assayed as ^{14}C-incorporated in a medium including 0.5mM RuBP, 20mM $MgCl_2$, 0.1mM Na_2-EDTA, 20mM $NaH^{14}CO_3$, 5mM DTT, and 50mM Tris-HCl (pH 8.3). The reaction was initiated with RuBP after a 10 min. preincubation in the assay medium.

RESULTS

Acid fluctuation according to the cladode orientation

Diurnal fluctuation of titratable acidity, stomatal resistance and solar radiation according to the cladode orientation are shown in Fig. 2, Fig. 3, Fig. 4, and Fig. 5, respectively. Titratable acidity shows maximum value at 06 : 00∼08 : 00, and minimum value at 10 : 00 in all of the investigated cladodes. In the initial stage of the light period, deacidification rate of the cladode side exposed to direct sun ray earlier was faster than that of the other side. However, both sides indicated the minimum values of acidity at the same time in the end of the light period. In all of the investigated cladodes, the water tissues show the obvious diurnal acid fluctions. These data agreed well to those of Chang *et al.* (1981) who experimented with potted *O. lanceolata* Haw. The data from the area under the northwest oriented stone fence are shown in Fig. 6. Titratable acidity began to increase from sunset and reached its maximum value at 10 : 00 in the next morning. These results were different from those of the open area. It is assumed that the steep decrease of titratable acidity after 10 : 00 is due to the sudden increase of solar radiation and stomatal resistance (stomatal closure).

In Fig. 4, deacidification rate of northern mesophyll tissue that was irradiated only by the diffuse solar radiation was as high as that of southern mesophyll tissue that was irradiated by direct radiation. Without considering the C_4 acids movement, this result would mean that deacidification rate under 7,000 lux of light is sufficiently as high as that of southern mesophyll tissue, which is different from the results of Kluge (1968). Therefore, as being inferred from the experiment of Kluge (1968) and the data of Fig. 6, it is assumed that the organic acids in northern mesophyll tissue move to the sou-

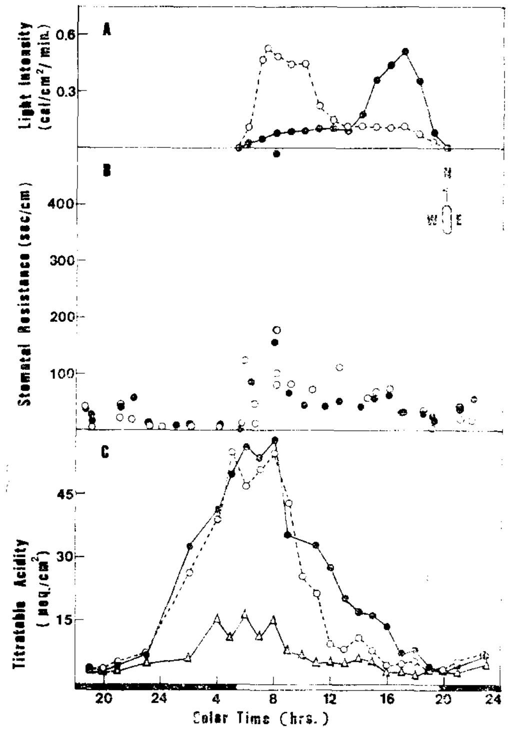

Fig. 2. Solar radiation (A), stomatal resistance (B), and titratable acidity fluctutation (C) were measured during a day in the eastern and western sides of the cladode of *O. lanceolata* Haw. growing at habitat in Weolryeong-ri, Hallim-eup, Chejud-do, Korea. The shaded lines indicate night.
○······○ : eastern side of the cladode
●——● : western side of the cladode
△——△ : water tissue of the cladode

thern mesophyll tissue. The maximum air-temperature reached 29.5°C at 14 : 00 and the minimum temperature was 7.0°C at 05 : 00.

The air temperature during the night ranged from 7°C to 18°C.

Stomatal resistance (Rs) of cladode

Rs value during the night was about 10 sec/cm, indicating completely opening of the stomata, Rs in an hour after sunrise was very high (150 sec/cm or more), indicating a tighter closing of the stomata, and then became about 50 sec/cm indicating a

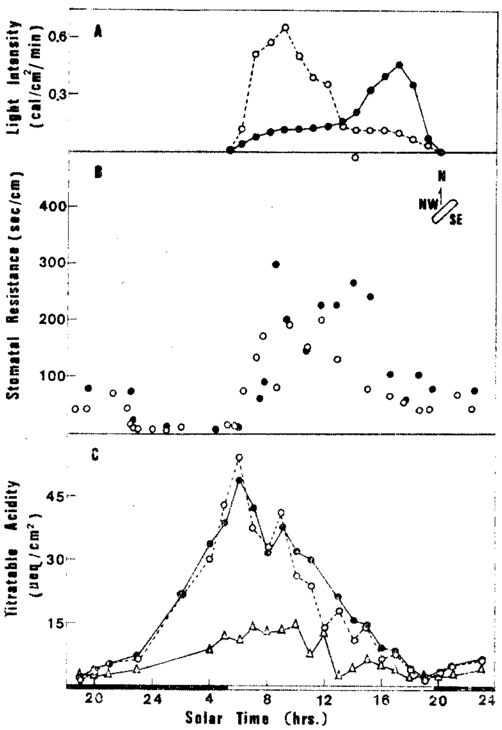

Fig. 3. Solar radiation (A), stomatal resistance (B), and titratable acidity fluctuction (C) were measured during aday in the northwestern and southeastern sides of the cladode of *O. lanceolata* Haw.

○……○ : southestern side
●——● : northwestern side
△——△ : water tissue

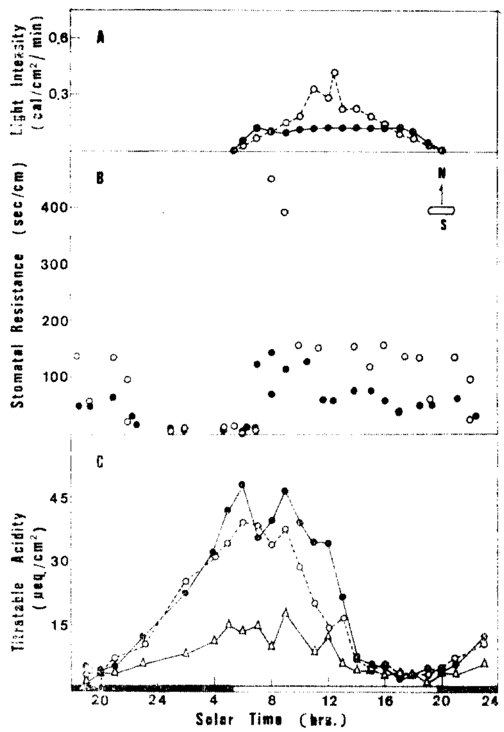

Fig. 4. Solar radiation (A), stomatal resistance (B), and titratable acidity fluctuation (C) were measured during a day in the northern and southern sides of the cladode of *O. lanceolata* Haw.

○……○ : southwestern side
●——● : northeastern side
△——△ : water tissue

little opening of the stomata.

In Fig. 6, Rs value was increasing at 10 : 00, five hours after sunrise. It is assumed that this phenomenon results from high soil water content (16.12%) and direct solar radiation which was shielded by the northwest oriented stone fence until 10 : 00. In Fig. 4, Rs value of the southern side was 150 sec/cm after 10 : 00, while that of the northern side was 60 sec/cm. This suggests that the northern side under the diffuse radiation open its stomata more widely than the southern side.

The movement of organic acids

The data for the organic acids movement within the same clodode are shown in Fig. 7 and Fig. 8. In Fig. 7-I, the tendencies of acidity change of both sides are almost the same. However,. as shown in Fig. 7-II, the deacidification rate of the southern side was much reduced. In Fig. 7-III and 7-IV, the amplitudes of deacidifications of northern side are lower than those in Fig. 7-I and 7-II.

The difference between Fig. 7-III and 7-IV is not detected. Both A side and B side of Fig. 8-III have the same deacidification rate.

This result means that A side of the cladode is deacidified under the light free condition. A side of Fig. 8-II has far less deacidification than those of Fig. 8-I and 8-III. These results suggest that C_4 acids move between the opposite sides of a cladode

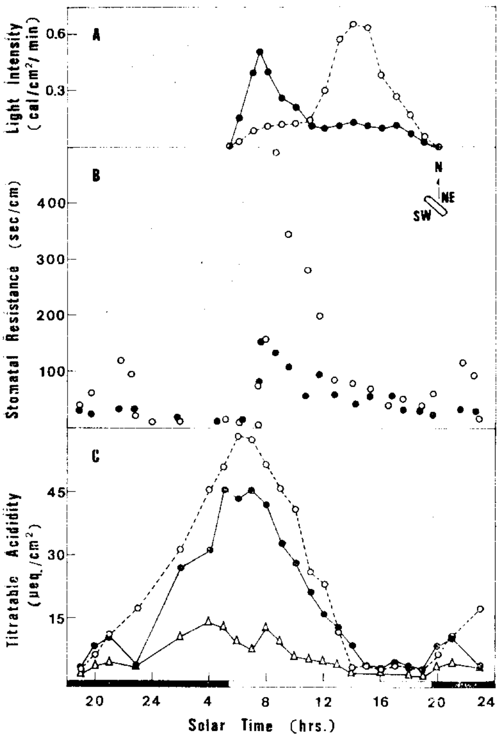

Fig. 5. Solar radiation (A), stomatal resistance (B), and titratable acidity fluctuation (C) were measured during a day in the northeastern sides of the cladode of *O. lanceolata* Haw.

○……○ : southwestern side
●——● : northeastern side
△——△ : water tissue

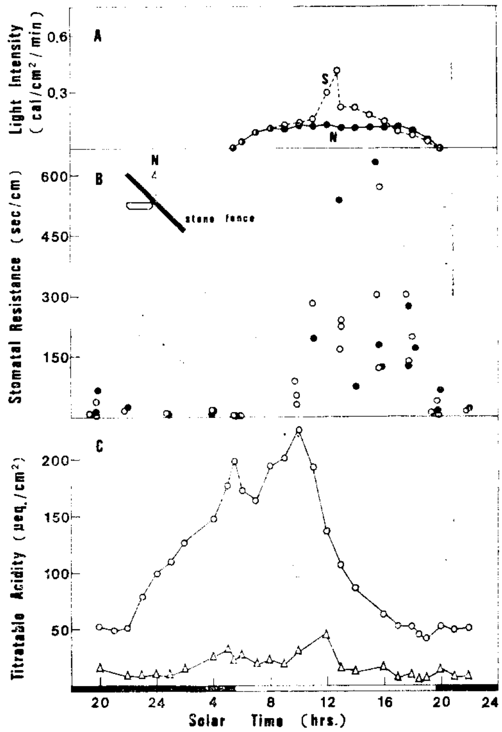

Fig. 6. Solar radiation (A), stomatal resistance (B), and titratable acidity fluctuation (C) were measured in the cladode of *O. lanceolata* Haw. at the area with a northwest oriented stone fence northeastwardly.

○——○ : total titratable acidity
△——△ : water tissue
○……○ : southern side of the cladode
●——● : northern side of the cladode

via the water tissue, and also intra mesophyll tissue of the same side of a cladode.

Activities of RuBP carboxylase and PEP carboxylase

The data are shown in Table 2. RuBP carboxylase activity was high at 14 : 00, while it was not significant at 01 : 00. These results indicate the possibility of C_3 photosynthetic mode under stomatal opening and CO_2 uptake. However, PEP carboxylase activities were high both at 01 : 00 and 14 : 00. Based on PEP carboxylase activities in addition to diurnal acid fluctuation, modes of C_4 and CAM photosynthesis are also able to be proposed in *O. lanceolata*.

Table 2. The carboxylase activities from the cladode extracts of *Opuntia lanceolata* Haw. activity in μmole/cm^2 hr

Enzyme / Cladode order \ Time	RuBP carboxylase		PEP carboxylase	
	01 : 00	14 : 00	01 : 00	14 : 00
1	N.S.*	265. 4	487	932
2	N.S.	229. 8	323	439
3	N.S.	172. 0	493	405
4	N.S.	268. 3	527	737

* Not significant

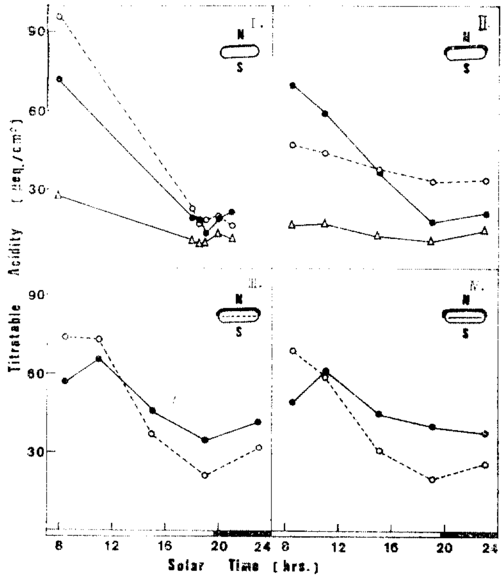

Fig. 7. Experiment of C_4 acids movement between the opposite sides of the cladode of *O. lanceolata* Haw. I. Both sides were normally irradiated. II. Only northern side was intercepted from light. III. Only northern side was intercepted from light and a sheet of transparent poly vinyl chloride was inserted between the mesophyll tissues. IV. Only northern side was intercepted from light and a sheet of aluminum foil was inserted between the mesophyll tissues.

○……○ : titratable acidity of southern side
●——● : titratable acidity of northern side
△——△ : titratable acidity of water tissue

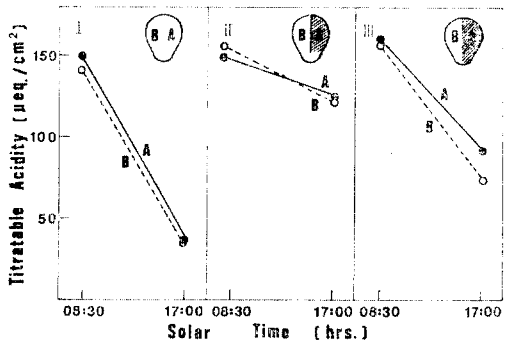

Fig. 8. Experiment of C_4 acids movement in the same side of a cladode.

I. The cladode was under the natural light condition.
II. A sheet of aluminum foil was inserted in the middle of the cladode in parallel with to the cladode side. One half (A) was intercepted from light and the other half (B) was under the natural light condition.
III. One half (A) was intercepted from light and the other half (B) was under the natural light condition. This cladode was not blocked up in the middle.

DISCUSSION

O. lanceolata Haw. growing at Weolryeong-ri shows the typical CAM characteristics, diurnal acid fluctuation (Chang *et al.*, 1981; Szarek & Ting, 1974). Malate consumption during the daytime is accelerated by increased light intensity (Kluge, 1968; Osmond, 1978). In Kluge's experiment (1975) with *Kalanchoe tubiflora* deacidification rate at 8,000 lux light intensity was lower than that at 17,000 lux and titratable acidity at 8,000 lux did not reach the minimum point which was as low as that at 17,000 lux. But in this experiment, though the light intensity of the diffuse radiation was about 7,000 lux, titratable acidities of both sides of all of the investigated cladodes reached the lowest value at the same time regardless of the cladode orientation. Especially, northern side of a cladode was irradiated by the only diffuse radiation, while southern side of a cladode was irradiated by the direct radiation whose maximum intensity was 0.4cal/cm²/min. In spite of it, both southern and northern mesophyll tissues of a cladode had the same deacidification rate. This suggests that organic acids in the northern mesophyll tissue move to the southern mesophyll tissue. It gives us another proof of organic acids movement that water tissues in the middle layer of a cladode show the same titratable acidity fluctuation as that of mesophyll tissue regardless of the cladode orientation. Kluge and Ting (1978) said that CAM would be expected to occur in those plant tissues where the key processes of CAM, namely malate synthesis, storage of it in large vacuoles, and final conversion of malate to carbohydrates via photosynthesis, were located in the same cell, and that in *Aloe arborescence* Mill, organic acids did not move between water tissue and mesophyll tissue and only mesophyll tissue had the CAM charateristics (Kluge *et al.*, 1979). But in *O. lanceolata* Haw., water tissue had the remarkable acidity fluctuation. The results in Fig. 7 suggest that organic acids in the northern mesophyll tissue move to the southern mesophyll tissue irradiated sufficiently and the results in Fig. 8 indicate the possibilitty of organic acids movement between the left and right of the same cladode side. The pathway, however, is unknown. It has not also known whether organic acids move through the water tissue or through the bundle between mesophyll tissue and water tissue. In *Portulaca oleracea* L., under the little or insufficient light condition, C_4 products assimilated by PEP carboxylase in leaves moved to the stems, where they were stored up and then were fixed by RuBP carboxylase activated by the light (Chang & Kim, 1982).

One of the significant features of CAM plants is the stomatal behavior that they may open at night and close during the day. Stomatal movements of CAM plants are affected by the age of the plant (Hanscom & Ting, 1977; Ting *et al.*, 1967), and the environmental factors such as temperature (Nishida, 1963; Ting *et al.*, 1967), light (Queiroz, 1974), water stress (James, 1958; Holdsworkth, 1971; Nobel, 1977; Szarek *et al.*, 1973) and so on.

As shown in Fig. 2, Fig. 4 and Fig. 5, it is thought that *O. lanceolata* Haw. loses the typical characteristics of CAM and follows C_3 photosynthetic metabolism based on the stomatal opening after 10 : 00. It was reported that stomata of CAM plants opened even during the day-time under the good water status and that stomata opened in response to precipitation (James, 1958; Holdworth, 1971; Lange *et al.*, 1971; Hall & Kaufmann, 1975; Nobel, 1977). Kluge and Ting (1978) said that if atmospheric humidity was retained to be high, cactus stomata would be kept open throughout the day. The precipitation of the study region is about 1,300mm annually, and it exceeds 50mm even in dry January.

The monthly mean relative humidity of air ranges from about 70 to 85%. These data indicate that the climate of study area is very humid, compared to that of a desert. It was reported that *Agave deserti* growing at the desert opened its stomata during the day time and had the C_3 photosynthetic pattern under the good water status (Nobel & Hartsock, 1978). There is a close relationship between CO_2 uptake and stomatal opening (Nishida, 1963; Kluge & Ting, 1978). In CAM plants, stomatal opening during the day time is followed by the CO_2 uptake, and this suggests the possibility that *O. lanceolata* Haw. has C_3 or/and C_4 photosynthetic pattern weakly.

In Fig. 4, northern side of a cladode had the Rs value of about 60 sec/cm, which meant that its stomata opened a little, while southern side closed its stomata, in which Rs value was about 150 sec/cm. And in Table 2, activities of PEP-carboxylase were high both at 01 : 00 and at 14 : 00 with little difference between them. Therefore, it is thought that at the northern mesophyll tissue under diffuse radiation CO_2 may be assimilated into C_4 acids, and then transferred to the southern mesophyll tissue which has closed stomata under disect radiation, and at there they may be refixed through the C_3 cycle. This is thought to be C_4 photosynthetic pattern, for there is a spacial separation in primary CO_2 fixation pathway.

From the above results, the following is suggested. CAM photosynthetic pattern prevails from sunrise to 14 : 00, when *O. lanceolata* Haw. close its stomata and is deacidified. From 14 : 00 to 19 : 00, the cladodes with southern and northern sides have C_4 photosynthetic patterns and the other cladodes inhales CO_2 direct through the open stomata, showing C_3 photosynthetic pattern.

Therefore, it is concluded that *O. lanceolata* Haw. growing at Weoiryeong-Ri has CAM, C_3 and C_4 photosynthetic patterns according to the irradiated condition of the cladode under the good water status.

摘 要

濟州道 北濟州郡 翰林邑 月令里에서 生育하고 있는 부채仙人掌(*Opuntia lanceolata* Haw.)의 葉狀莖의 方位에 따른 酸度의 日變化, 氣孔抵抗 및 太陽輻射 energy의 變化에 대하여 調査하였다.

方位에 關係없이 葉狀莖의 酸度의 日變化는 典型的인 CAM의 性格을 나타내었으며, 葉狀莖의 貯水組織 역시 分明한 酸度의 日變化를 나타내었다.

氣孔抵抗値는 밤에는 約 10 sec/cm 程度로 낮았고, 日出直後에 높아졌다(150 sec/cm 以上)가 다시 約 50 sec/cm 程度로 떨어졌다. 散亂光만 받는 葉狀莖의 北面은 直射光線을 받는 南面보다 낮동안에 낮은 氣孔抵抗値(約 60 sec/cm)를 보여 散亂光下의 北面에서는 氣孔을 열고 있음을 알 수 있다. 太陽의 輻射 energy는 葉狀莖의 方位에 따라 많은 차이가 관찰되었다. C_4 有機酸은 葉狀莖의 南・北面의 葉肉組織間과 同一面의 葉肉組織間에도 移動하였다. RuBP carboxylase의 活性度는 14時에 매우 높았으나, 1時에는 거의 無視할 程度로 낮았다. PEP carboxylase의 活性度는 14時와 1時에 똑같이 높게 나왔다. 이 結果로 月令里의 부채仙人掌은 C_3, C_4 및 CAM型의 光合成樣式이 環境條件에 따라 나타난다는 것을 알 수 있었다.

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