Active and Passive Behaviours of the Guard Cells for Stomatal Opening and Closing in *Heteromeres arbutifolia* and *Ferocactus acanthodes*

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Heteromeres arbutifolia 와 *Ferocactus acanthodes*의 氣孔 開閉를 위한 孔邊細胞의 能受動的 行動

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ABSTRACT

Stomatal resistances of the leaves in *Heteromeres arbutifolia* and of the stems in *Ferocactus acanthodes* were studied to estimate active and passive behaviors of the guard cells on a theoretical basis. Active and passive stomatal responses to light and water deficit were observed. When the change rate of existent water due to variation of osmotic potential in the guard cells and the loss rate of transpirational water from the guard cells are Δw_i and Δw_l, respectively, the water accumulation rate, Δw, in the guard cells is equal to $\Delta w_i - \Delta w_l$. When leaves with open stomata in the light were darkened and those with stomata closed in the dark were illuminated, the guard cells in leaves of *H. arbutifolia* were under only the condition of $\Delta w_i > \Delta w$ and leaded to active behaviors for opening and closing stomata. However, when stems of *F. acanthodes* with stomata closed under the solar irradiation were covered with black cloth and then taken off, behaviors of the guard cells occurred in the condition of $\Delta w_i < \Delta w_l$ and were passive. Under the condition of $\Delta w_i < \Delta w_l$ due to cutout from stems, passive behaviors of the guard cells in *H. arbutifolia* and *F. acanthodes* always occurred in spite of the solar irradiation and darkness, respectively. The transpirational resistance coefficients of the guard cells in stems of *F. acanthodes* (0.380) and *Opuntia bigelovii* (0.135) were much higher than in leaves of *H. arbutifolia* (0.034). Moreover, stomatal opening in stems of *F. acanthodes* during the daytime could be induced by watering. Those results are interpreted as that since the guard cells in desert Crassulacean acid metabolism (CAM) plants always exist in the state of stomatal opening, nocturnal stomatal opening and daytime stomatal closing are exhibited by passive behaviors of the guard cells in the alternant conditions of $\Delta w_i > \Delta w_l$ and $\Delta w_i < \Delta w$, respectively.

INTRODUCTION

Although the stomata of most plants are opened during the daytime and closed at night, the CAM plants are characterized by diurnal changes in tissue acidity and nighttime stomatal opening(Szarek *et al.* 1973, Szarek and Ting 1975, Raven *et al.* 1976, Nobel 1976, Hartsock and Nobel 1976, Kluge and Ting 1978). Accompanying the uptake CO_2 and O_2 by stomatal opening, there must also be an increased loss of water vapor, as long as the water potential of the external atmosphere is lower than that of the leaves. When such loss of water approaches the level of water stress injury, the stomata are to close in order to reduce the rate of water loss cuticular transpiration. They have become adapted to this function by means of a guard cell structure which leads to closure when loss of water from these cells lowers their turgor pressure to a sufficient degree (Lange *et al.* 1976). Enhanced stomatal opening during cool nights, the red-

uced transpirational water loss at low tissue temperatures, and the relatively low temperature optimum for dark CO_2 fixation combine to maximize the water use efficiency for CAM plants in the desert habitat (Nobel 1977).

The interesting study by Szarek and Ting(1975) indicated that nocturnal stomatal opening for *Opuntia basilaris* in natural stands was initiated following rainfall, and stomata remained open during the daytime. Nobel (1976) reported that although no natural stomatal opening *Agave deserti* occurred in the summer, it could be induced by watering. In this case, the stomatal opening is an important adaptive strategy for the CAM plants in desert environments.

Therefore, the following study investigated active and passive behaviors of the guard cells to elucidate water and light influences on stomatal opening and closing. *Heteromeres arbutifolia* as a C_3 plant and *F. acanthodes* as a desert CAM plant were selected for this study and a comparison between the active and passive behaviors due to the stomatal resistances in leaves and stems was carried out experimentally and theoretically.

THEORY

When the guard cells are more turgid than the surrounding epidermis cells, stomata open and when the guard cells are less turgid, stomata close. Turgor is maintained or lost due to influx and efflux of water in or out of the guard cells (Fig. 1). The water movements in the guard cells are divided into active and passive behaviors.

When influx and efflux of water(w_i) depend on active behaviors of the guard cells, w_i is the function of soil water potential(Ψ_s), osmotic potential (Ψ_o) turgor potential(Ψ_t), matric potential(Ψ_m) and time(t);

$$w_i = W_i(\Psi_s, \ \Psi_o, \ \Psi_t, \ \Psi_m, \ t) \qquad (1)$$

where W_i is a signal of a function. When the values of w_i is increased by photoactive and scotoactive stomatal behaviors, it indicates that water is absorbed by the guard cells from the surrounding cells.
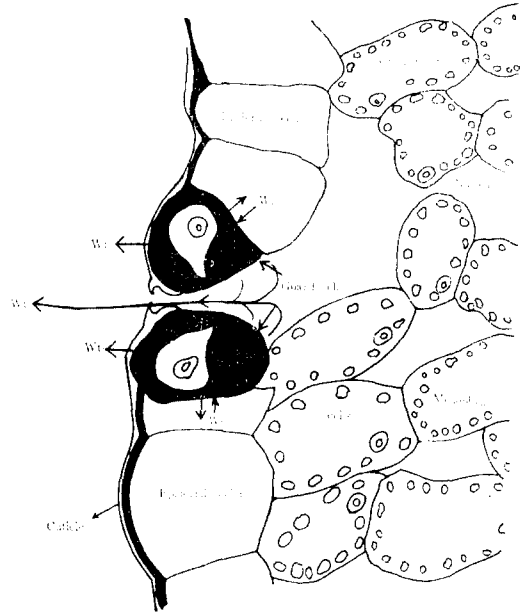

Fig. 1. A diagram of the active water influx and efflux (w_i) and the passive water loss (w_t) due to transpiration in the guard cells of a leaf to derive the mathematical theory of water accumulation (w).

However, when w_i is decreased, efflux of water occurs in the guard cells. In these active behaviors, energy is extended in the preferential accumulation and loss of solute that create the gradients. The major solute responsible for the gradients is a potassium ion (Humble and Hsiao 1970, Humble and Raschke 1971, Fischer 1971). The relationship between the soil water potential and stomatal resistance of desert CAM plants was studied by Szarek and Ting (1975), Nobel (1976) and Nobel (1977), respectively. According to Turner and Begg (1973), the following equation was used to determine the turgor potential; $\Psi = \Psi_o + \Psi_t + \Psi_m$ where Ψ is the leaf water potential.

The transpirational water loss (w_t), which is a kind of water efflux from the guard cells, depends on leaf and air temperature (t_e), water vapor pressure (Ψ_v) on the leaf surface and time;

$$w_t = W_t(t_e, \ \Psi_v, \ t) \qquad (2)$$

where W_t is a signal of a function. This relationship was reported by Nobel(1978), Nobel and Hartsock(1979), Morrow and Slatyer (1971), Szarek

et al. (1973), and Hall and Kaufmann (1975), respectively.

Therefore, total water accumulation(w) in the guard cells is

$$w = w_i - w_t \tag{3}$$

When time interval from t_1, t_0, t_2 is Δt, the equations (1) and (2) become

$$\Delta w_i = W_i(\Psi_s, \Psi_o, \Psi_t, \Psi_m)_i \Delta t \tag{4}$$

and

$$\Delta w_t = W_t(t_o, \Psi_v)_t \Delta t \tag{5}$$

The total water accumulation rate (Δw) in the guard cells are equal to the difference between Δw_i and Δw_t;

$$\Delta w = \Delta w_i - \Delta w_t \tag{6}$$

In the case of $\Delta w_i > \Delta w_t$, the equation(6) is defined as $\Delta w > 0$.

$$\Delta w = \Delta w_i - \Delta w_t > 0 \tag{7}$$

Hence, the guard cells are to perform photoactive and scotoactive stomatal opening and closing due to preferential accumulation and loss of solute.

However, in case of $\Delta w_i < \Delta w_t$, the equation (6) has the negative value;

$$\Delta w = \Delta w_i - \Delta w_t < 0 \tag{8}$$

The guard cells in this condition continue the water loss in spite of their high osmotic values. It is the passive behavior of the guard cells.

In the $\Delta w_i = \Delta w_t$, the water content of the guard cells is not changed;

$$\Delta w = \Delta w_i - \Delta w = 0 \tag{9}$$

If the studied materials are sampled at a certain plot, position and time, the equations (4) and (5) are simplified as;

$$\Delta w_i = (W_i) \ \Psi_s, \ \Psi_o, \ \Psi_t, \ \Psi_m, \ t \ \Delta t \tag{10}$$

and

$$\Delta w_t = (W_t) \ t_o, \ \Psi_v, \ t \ \Delta t \tag{11}$$

The change of the water concentrations in the guard cells by the equation(10) can be represented as follows;

$$w_i \longrightarrow w_{i1}$$

where the initial concentration $w_1 = w_i(O)$ and $w_i = O$. The previously derived equation is given by

$$\frac{dw_i}{dt} = -\frac{dw_{i1}}{dt} = -kw_{i1} \tag{12}$$

where k is a coefficient of the change of the water concentration in the guard cells. The integration of

this equation is performed easily after separation of variables and taking the antilogarithm yields

$$w_i(t) = w_i(O) \ \exp \ (-kt) \tag{13}$$

According to the equation (13), photoactive and scotoactive stomatal opening and closing can be detected.

Water concentrations inside and outside the guard cells are expressed as w_{ti} and w_{to} ($w_{ti} \geqq w_{to}$), and the volume and surface area of the guard cells are V and A, respectively. Transpirational water concentration per unit time, dw_t/dt, is proportional to A and $w_{ti} - w_{to}$;

$$\frac{dw_t}{dt} = CA(w_{ti} - w_{to}) \tag{14}$$

or

$$\frac{dw_{ti}}{dt} V = CA(w_{ti} - w_{to}) \tag{15}$$

where C is the transpirational coefficient of the guard cells. The integration of the equation (15) with the initial water concentration of $w_{to} = O$ at $t = O$ is given by

$$ln(1 - \frac{w_{to}}{w_{ti}}) = -\frac{CA}{V}t \tag{16}$$

Taking the antilogarithm yields

$$w_{to}(t) = w_{ti}[1 - exp(-C\frac{A}{V}t)] \tag{17}$$

According to the equation (17), passive behaviors of the guard cells by water loss can be detected.

MATERIALS AND METHODS

Plant Materials; *Ferocactus acanthodes*(Lemaire) Britton and Rose having 13 ribs, and *Opuntia bigelovii* Engelm having 2 stems were transplanted from natural stands of plants at the University of California's Philip L. Boyd Deep Canyon Desert Research Center near Palm Desert, California, U.S.A. (116°24′ W,33°38′N) and then maintained in desert soils of pots on the roof garden of the laboratory building in order to take the same orientations as the desert. Twenty mm of water were uniformly sprinkled on the soil surface at 3 day intervals. *Heteromeles arbutifolia* M. Roemer planted on the campus of the University of California at Los Angeles was used for this study. This tree is known in California, U.S.A., as "tollon", "Christ-

mas-berry", and "California holly".

Stomatal Resistance, Photosynthetically Active Radiation (PAR) and Temperature; The diffusive resistance to water loss from the stomata was directly measured by using a Lambda Instruments LI-60 diffusive resistance porometer with an LI-208 sensor. Solar irradiation for PAR (400 to 700nm) was determined with a Lambda Instruments LI-19 0S quantum sensor, and air temperature was measured with a Barnes Engineering PTR·10TR field thermometer.

Stomatal Resistance Analysis; The stomatal resistance(R) for water vapor loss from leaves and stems per unit area and volume is inversely proportional to the turgid or water concentration gradients of the guard cells. The stomatal resistances calculated from the equations(13) and (17) can be substituted into the expression yielding

$$R_i(t) = R_i(O)exp(-kt) \qquad (18)$$

and

$$R_{to}(t) = R_{ti}[1 - exp(-Ct)] \qquad (19)$$

where R_i, R_{to} and R_{ti} are $a \cdot \dfrac{1}{w_i}$, $b \cdot \dfrac{1}{w_{to}}$ and $d \cdot \dfrac{1}{w_{ti}}$, and a, b and d are the proprtional constants, respectively. In the equations(18) and (19), k and C are coefficient of the change of stomatal resistance in the guard cells and a transpirational resistance coefficient of the guard cells as compared with the equations (13) and (17), respectively.

Active and passive behaviors of the guard cells for leaves of *H. arbutifolia* and stems of *F. acanthodes* and *O. bigelovii* was detected with the k and C coefficients for examining influences on light, dark, water deficit and water resupply. At 10~14 o'clock, the stomatal resistances for the 8th leaf from the unfolded top leaf of *H. arbutifolia* and for the 2nd-4th nodes form the top node of *F. acanthodes* were measured under the solar irradiation and in darkness intercepted by black cloth. Twenty mm of water were uniformly sprinkled on the surface soil of the pots in the early morning, and the time course of the stomatal resistances for the 2nd-4th nodes of *F. acanthodes* and the 1st stems of *O. bigelovii* was investigated after cutout from

the roots and the 2nd stem at the midnight. After the twigs of *H. arbutifolia* were cut out, the changes of the stomatal resistance in course of time were measured in the 8th leaf at 10~14 o'clock and then when these twigs were transferred to the bottled water, the same experiment was carried out. The diurnal changes in the stomatal resistances for *F. acanthodes* were observed at various time after rainfall and watering. Those data were analyzed by the equations (18) and (19), and the active and passive behaviors of the guard cells distinguished.

The magnitudes of k and C for those data were obtained from the slope of the straight line in a semilogarithmic plot of the stomatal resistance versus time. The time for the stomatal resistance to change from any given value to one-half of that value can be obtained from the equation (18);

$$R_{i1}(t_{1/2}) = R_{i1}(O)/2 = R_{i1}(O) \ exp \ (-kt_{1/2})$$

or

$$exp(kt_{1/2}) = 2$$

and taking the logarithm yields

$$t_{1/2} = ln2/k = 0.693/k \qquad (20)$$

and

$$k = 0.693/t_{1/2} \qquad (21)$$

The coefficient C of the equation (19) can be obtained from the following set of solution;

$$R_{to}(t) = R_{ti} - R_{ti}exp(-Ct)$$

The change of stomatal resistances of the water vapor accumlation on the leaf or stem surface is

$$R_{ti}(t) = R_{ti}(O)exp(-Ct) \qquad (22)$$

where $R_{ti}(t)$ and $R_{ti}(O)$ are the stomatal resistances at an arbitrary time and the initial stomatal resistance, respectively. Therefore, the coefficient C is similar to

$$C = 0.693/t_{1/2} \qquad (23)$$

RESULTS AND DISCUSSION

1. Active and Passive Behaviors of the Guard Cells by the Light Irradiation

When the 8th green leaf from the top of *H. arbutifolia* with open stomata in the light were darkened, the cessation of photosynthesis in this leaf

occurred and the stomatal resistances led to increase exponentially from 18.0 sec cm⁻¹ to 92.1 sec cm⁻¹(Fig. 2). In this case, the k value was equal to 0.038 at the minute unit. It suggests that this stomatal movement is similar to the proposing of Lange *et al.* (1976) with scotoactive closing which may require the expense of the accumulated nicotinamide adenine dinucleotide reduced (NADPH) and adenosine tri-phosphate (ATP).

When the leaf of *H. arbutifolia* with stomata closed in the dark was illuminated, their stomatal resistances were decreased exponentially from 92.1 sec cm⁻¹ to 18.5 sec cm⁻¹ (Fig. 2). According to Lange *et al.* (1976), the photoactive stomatal opening in this case was set in motion by the initial steps of photosynthesis of the photoelectron transport leading to NADP⁺ reduction and the accompanying proton transport leading to ATP formation. The k value was expressed as 0.042.
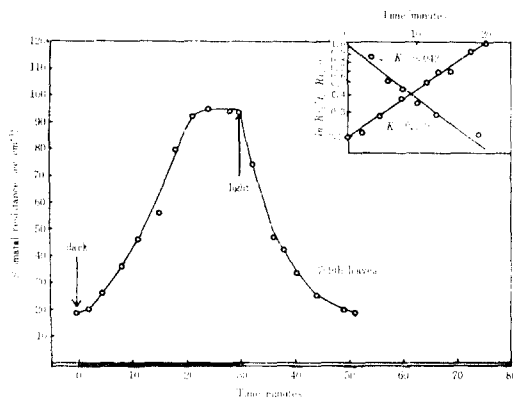

Fig. 2. The time courses of the stomatal resistances in the 8th leaves of *H. arbutifolia* trees when leaves with open stomata under the solar irradiation were darkened and with stomata closed in the dark were illuminated. The stomatal resistances were measured at the maximum PAR of 1,698 μEm⁻² sec⁻¹ and the maximum air temperature of 26.9°C on attached leaves of trees on 21∼22 March, 1979. The logarithms of the normalized stomatal resistances were plotted against time and the slopes were equal to the positive and the negative of the rate coefficient k.

There was no significant difference between the k value of stomatal closing which occurred when leaves with open stomata in the light were darkened and that of stomatal opening which occurred when leaves with stomata closed in the dark were illuminated, but their directions of the scotoactive and photoactive behaviors of the guard cells were opposite each other. Therefore, those results indicate that under the condition of $\Delta w_i > \Delta w_t$, the active behaviors of the guard cells occurs. It is similar to the hypothesis that in leaves under the sufficient water absorption, potassium and an accompanying anion comprise the major, osmotically, active solutes in the guard cells of open stomata (Fisher 1971, Humble and Hsiao 1970, Humble and Raschke 1971). Kriedemann (1971) reported that variation in leaf resistance induced by moisture status, or by cyclic oscillations in stomatal aperture, was associated with changes in both photosynthesis and transpiration. Most of the studies on the stomatal movements belong to the photoactive and scotoactive stomatal opening and closing, but there are no studies on the passive behaviors of the guard cells.
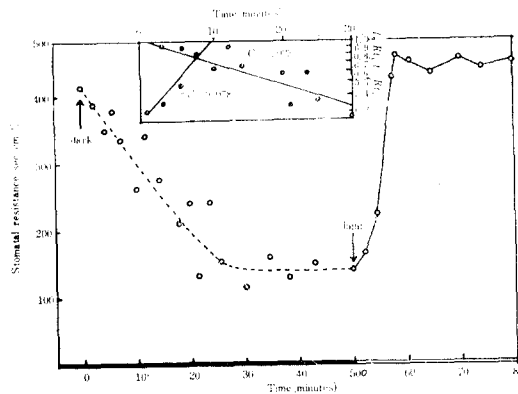

Fig. 3. The time course of the stomatal resistances in stems of *F. acanthodes* when stems with stomata closed in the light were darkened and with open stomata in the dark were illuminated. The stomatal resistances were determined at the maximum PAR of 1,700 μE m⁻² sec⁻¹ and the maximum air temperature of 30.5°C on the stem surface on March 21, 1979. Semilogarithmic plot between the logarithm of the normalized stomatal resistances and minutes represents the rate coefficient C of the transpirational resistance.

As shown in Fig. 3, when stems of *F. acantho-des* with stomata closed in the light were darkened, the stomatal resistances for opening were gradually decreased from 412 sec cm^{-1} to 140 sec cm^{-1} while these values had the large variations. The slope which was made by semilogarithmic plot between the logarithm of the normalized stomatal resistances and minutes was equal to 0.023.

However, when stems with open stomata in the dark were illuminated, the stomatal resistance was increased very rapidly from 140 sec cm^{-1} to 455 sec cm^{-1} during 8.3 minutes and its coefficient value was 0.078 (Fig. 3). In Figure 3, the rate coefficient value of the former differs from that of the latter. The great difference between 0.023 and 0.078 indicates that the stems covered by black cloth could not absorb the light energy but might be affected on air temperature and thus the minimum value of stomatal resistances in this condition did not go below 112 sec cm^{-1}. These results suggest that in spite of the active behavioral conditions of the light and dark as compared with *H. arbutifolia*, the stomatal movements of *F. acanthodes* are not active but passive because of the condition of $\Delta w_i < \Delta w_t$.

2. The Passive Behaviors of the Guard Cells Withheld and Resupplied Water

The passive behaviors of the guard cells depended upon soil water uptake were investigated using leaves of *H. arbutifolia*, and stems of *F. acanthodes* and *O. bigelovii*. The time courses of the stomatal resistance in leaves and stems as soon as cut out the stems and roots were presented in Figure 4. Before the twigs and stems were cut out from stems, the stomatal resistances in leaves of *H. arbutifolia* during the daytime and in stems of *F. acanthodes* and *O. bigelovii* at the midnight were 10, 14 and 17 sec cm^{-1}, respectively. The transpirational resistance coefficient of the guard cells in leaves of *H. arbutifolia* was 0.034 but those in *F. acanthodes* and *O. bigelovii* stems were 0.380 and 0.135. It is a physiologically important feature for adaptation in desert environments that the transpirational resistance coefficients in the stems of cacti are much higher than that in *H. arbutifolia* leaves.

In this case, the stomatal opening and closing are passive behaviors of the positive and negative directions of the guard cells under the condition of $\Delta w_i < \Delta w_t$. However, these stomatal movements were observed in CAM plants (Szarek *et al.* 1973, Szarek and Ting 1975, Nobel 1975, Nobel 1976) and are predicted in C$_3$ and C$_4$ plants at the noon of the hot summer and during the drought season. In spite of the active regulation of the guard cells, the passive behaviors under the condition of $\Delta w_i < \Delta w_t$ occur without consumption of ATP.

Figure 5 shows that the course of changes in the stomatal resistance in leaves of *H. arbutifolia* after
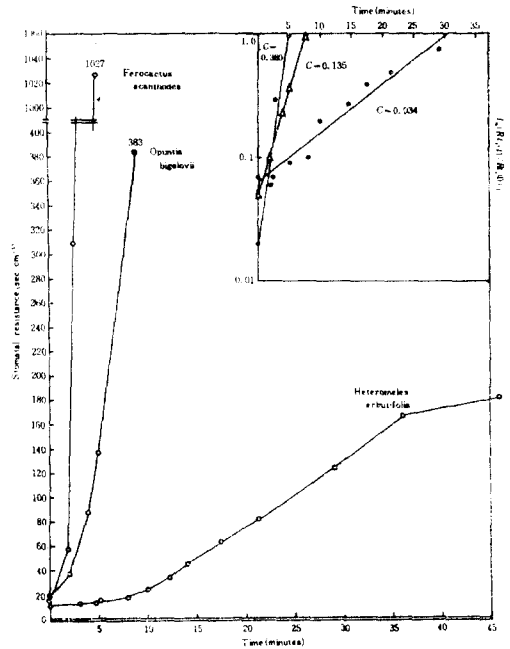

Fig. 4. The time course of the stomatal resistances in stems of *F. acanthodes* and *O. bigelovii* cut out from the roots and stems at the midnight, and in leaves of *H. arbutifolia* twigs cut out form stems at the daytime. The stomatal resistances were measured at the maximum PAR of 1.683 μEm^{-2} sec^{-1} and the maximum and minimum air temperatures of 30.4°C on the leaf surface and 7.8°C on the stem on 22~23 March, 1979. The logarithm of the normalized stomatal resistances was plotted against minutes and the slope is equal to the positive of the transpirational resistance coefficient C.
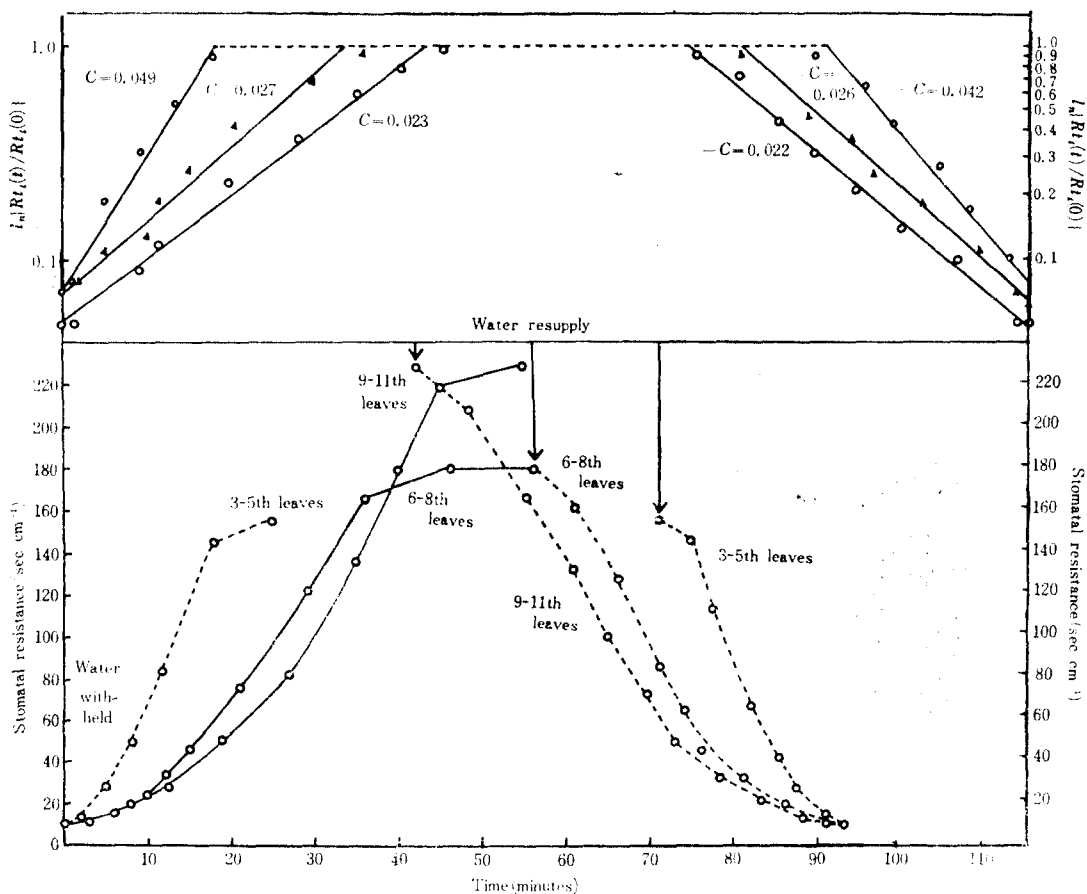
Fig. 5. The time course of the stomatal resistances in the 3~5, 6~8 and 9~11th leaves from the top of *H. arbutifolia* twigs withheld and resupplied water under the solar irradiation. The stomatal resistances were determined at the maximum PAR of 1,683 μE m^{-2} sec $^{-1}$ and maximum air temperature of 30.4°C on the leaf surface on March 23, 1979. The logarithms of the normalized stomatal resistances were plotted against minutes and the slopes are equal to the positive and negative of the transpirational resistance coefficient C.

the twigs were cut from stems to withhold water-supply and were transferred to bottled water to resupply water. The older leaves of *H. arbutifolia* against the water deficit and resupply responded differently from the younger leaves. The values of the transpirational resistance coefficients in the leaves of the 3-5, 6-8 and 9-11th leaf orders from the top of the twigs cut out from stems were 0.0 49, 0.027 and 0.023, and those of the twigs tran-

sferred to bottled water were 0.042, 0.026 and 0. 022, respectively. The maximum values of the stomatal resistance in the 3-5, 6-8 and 9-11th leaves were 156, 180 and 229 sec cm^{-1}, while the minimum value in all the leaves was 10 sec cm^{-1}. Those results indicate that the stomatal resistances in the younger leaves are higher than the older leaves but the cuticular resistances are lower. Turner and Begg(1973) reported that the diurnal
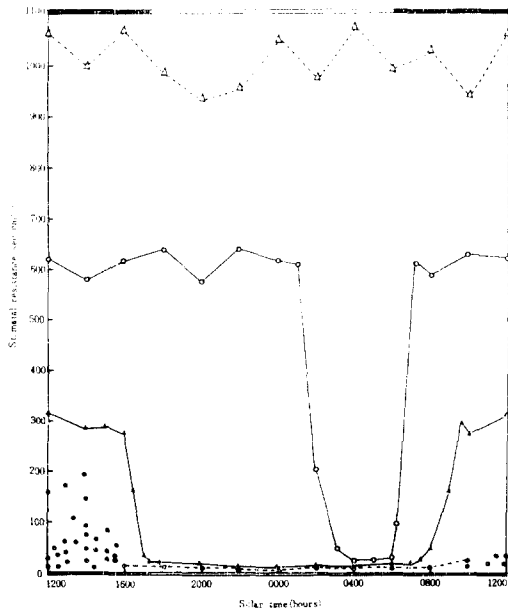
Fig. 6. Diurnal changes in the stomatal resistances at various times after daytime stomatal opening induced by watering. No stomatal opening of 2nd-4th nodes in stems of *F. acanthodes* experienced 6 weeks without rainfall and watering (△) was observed. After 20mm of water splinkled on the surface soils of the pots at an interval of 3 hours during a week (●), after a day without watering (▲) and after 2 weeks without watering (○), its stomatal opening was maintained during the daytime as well as the nighttime, 10 hours at night and 2 hours at only night, respectively. The diurnal stomatal resistances were measured on 20~26 April 1979 under clear, sunny weather conditions.

range of stomatal resistance variables was greater for leaves in the upper canopy of maize, sorghum and tobacco under the vertical profiles of irradiance incident than for those in the lower canopy. However, this result seems to depend upon the stomatal movements due to light intensity and leaf ages in the vertical profiles of the canopy. The results of Figure 5 suggest that under the condition of $\varDelta w_i < \varDelta w_t$ during the hot noon and drought season, passive behaviors of the guard cells in young leaves of the C_3 and C_4 plants can be observed as

the decreasing photosynthetic rate and increasing stomatal resistance.

3. Stomatal Opening during the Daytime Induced by Watering

The changes in the stomatal resistances during the course of 24 hour periods at various times depended upon different water contents of soils were presented in Figure 6. *Ferocatus acanthodes* in the pot had experienced 6 weeks without rainfall and watering, and no stomatal opening of stems was observed. After 20 mm of water uniformly sprinkled on the surface soils of the pots at an interval of 3 hours during a week, the minimum decrease (<11 sec m^{-1}) of the stomatal resistances occurred in stems and stomata remain open during the daytime. After a day without watering, stomata were open from 17 : 10 to 07 : 05 (<15 sec cm^{-1}). After 2 weeks without watering, the stomatal resistances went below 25 sec cm^{-1} for only 2 hours at the nighttime. Those results indicate that the water loss ($\varDelta w_t$) from the guard cells was not compensated by water uptake from the soils, and so during the night period of low stomatal resistances decreased, the stomatal opening occurs passively. Szarek and Ting(1975) reported that nocturnal stomatal opening in stems of *Opuntia basilaris* was initiated following rainfall and that stomatal opening remained during the daytime. Moreover, stomatal movements of *Agave deserti* at a hot and dry time of year could be induced by watering (Nobel 1976). Nobel (1977) reported that after 7 months of drought and consequent unreplenished water loss from a plant, diurnal stomatal activity was not observed. Therefore, in general, since the guard cells in CAM plants exist always in the state of the stomatal opening, the nocturnal stomatal opening and the daytime stomatal closing of CAM plants which have the higher values of the transpirational resistance coefficient C are led to passive behaviors of the guard cells under the alternant condition between $\varDelta w_i > \varDelta w_t$ and $\varDelta w_i < \varDelta w_t$. This passive stomatal opening during the nighttime periods permits the increases of efficiency of water use in desert environments and of atmospheric CO_2 assimilation by organic acid synthesis.

要　約

本 硏究는 *Hateromeles arbutifolia*의 잎과 *Perocactus acamthodes*의 줄기에서 氣孔저항을 測定하여 孔邊細胞의 能動的 受動的 運動을 理論的 기반하에서 硏究하는데 그 目的이 있다.

빛과 물의 損失에 대한 氣孔의 能動的 受動的 反應이 觀察되었고 孔邊細胞의 內外의 물의 得失率을 各各 Δw_i와 Δw_t라고 하였을 때 그곳에 蓄積되는 물의 蓄積率은 $\Delta w_i - \Delta w_t$로 표시된다. 빛의 存在하에서 氣孔이 열린 잎을 暗처리시키고 어두운 곳에서 氣孔이 닫힌 잎에 빛을 주었을때 *H. arbutifolia*잎의 孔邊細胞는 $\Delta w_i > \Delta w_t$인 狀態만을 나타냈고 氣孔開閉는 能動的이었다. 그러나 自然光下에서 氣孔을 닫는 *F. acanthodes*의 줄기에 검은 천을 덮었다가 벗겼을때 孔邊細胞의 運動은 $\Delta w_i < \Delta w_t$ 狀態에서 일어 났으며 受動的이었다.

줄기에서 떨어짐으로 인해 $\Delta w_i < \Delta w_t$ 狀態를 나타내는 *H. arbutifolia*와 *F. acanthodes*의 孔邊細胞의 運動은 光의 有無에 無關하게 언제나 受動的으로 일어 났다. *F. acanthodes*와 *Opuntia bigelovii*의 줄기에 있는 孔邊細胞의 증산저항계수는 각각 0.380과 0.135였으며 이둘은 0.034의 값을 나타내는 *H. arbutifolia*잎의 경우보다 훨씬높다. 더우기 낮동안에 *F. acanthodes*의 줄기에서 氣孔이 열리는 현상은 물을 줌으로써 誘導될 수 있었다. 이 結果들로부터 沙漠의 CAM植物들은 언제나 氣孔을 여는 狀態이나 밤동안은 $\Delta w_i > \Delta w_t$이고 낮동안은 $\Delta w_i < \Delta w_t$가 되므로 밤에 기공이 열리고 낮에는 닫히는 受動的 運動을 하게된다고 解釋된다.

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