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Stomatal Movement and CO_2 Exchange Rate of Sweet Potato Plant (*Ipomoea batatas* Lam.) in Relation to Water Environments

— A Comparison between Native and Improved Varieties —

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We studied the stomatal response to internal and external water environments and clarified its varietal difference by comparing the gas exchange rate between variety Koganesengan (var. Kog) and variety Tsurunasigenji (var. Tsu). The former is an improved variety with high yield and the latter is a native one with low yield. Photosynthesis of leaf was regulated through gas exchange by stomatal aperture degree (SDA), and a high SAD was prerequisite to increase photosynthesis. SAD of var. Kog was high and stable in both wet and dry conditions, while SAD of var. Tsu was low and unstable, After the cut-leaf treatment, var. Kog maintained a higher CO_2 exchange rate (CER) and transpiration rate (TR) during a longer time than var. Tsu. The rigidity of leaf of var. Kog was rapidly lost after this treatment, but a relatively high CER could be maintained. Relative pressure of guard cell to subsidiary cell was suggested to have an important role in stomatal movement; a higher relative pressure was predicted in var. Kog. Also the relative volume of a subsidiary cell to a guard cell in var. Kog was 50% larger than that of var. Tsu. The pretreatment of high humidity air (nearly 100% relative humidity) was effective in increasing TR of var. Tsu. As a whole the gas exchange response of var. Tsu to vapor pressure deficit (VPD) was unclear, but that of var. Kog was much clear; VPD of 2 KPa was a turning point in the gas exchange response. The feature of stomatal movement in the plants grown in a field was recognized as an important criterion for selection of the genotypes with high photosynthesis.

INTRODUCTION

Photosynthesis in a single leaf is identified as a fundamental determinant for the production of various crops. The importance of leaf photosynthesis has been also pointed out with sweet potato plants (Tsuno and Fujise, 1965; Nakatani et *al.,* 1988; Bouwkamp, 1989; Agata et al., 1991; Kubota et *al., 1993).*

The rate of leaf photosynthesis is regulated by two main factors, stomatal aperture on the epidermis and photosynthetic potential in the mesophyll. Stomatal aperture often strongly restricts the photosynthetic rate of a leaf through gas exchange. Of many factors affecting stomatal actions, water is probably a most important factor and closely related to crop production.

So far many of physiological studies have been conducted on stomatal actions in relation to internal or external environmental factors. Despite of much research accumulation, the understanding of stomatal behavior is not yet sufficient. Complicated changes in stomatal movements are frequently observed on sweet potato varieties grown under the field conditions, and there seems to be much unknown realm for the relationship between stomatal behavior and environmental factors.

On the other hand, Jones (1987) examined stomatal behavior in a genetic field and regarded it as an important selection criterion for improvement of crop productivity and drought tolerance. However, limited information is available for sweet potato in this area. In this research, we focused our attention on the varietal difference in response of stomata and gas exchange to water environments. By studying the response feature in relation to the physiological and morphological characters, we clarified the importance of stomatal behavior as a selection criterion for the sweet potato genotype with high photosynthesis and high yield.

MATERIALS AND METHODS

Materials

As experimental materials, two varieties, Koganesengan (var. Kog) and Tsurunasigenji (var. Tsu), of sweet potato, *Ipomoea batatas* Lam., were used. Var.Kog is an improved high yield variety and var. Tsu is a native variety with low yield. The plants grown in pots and field were used.

Growth condition and measurement parameters

Young shoots which had been rooted in sufficiently watered vermiculite for 3 days were transplanted, at the middle of June 1992, in 8.5 L pots (a plant/pot) with sandy soil containing chemical compound fertilizer (N:P:K=16:16:16, 5g/pot), fused phosphate fertilizer (5.3g/pot) and potassium sulfate fertilizer (2.0g/pot). The plants, which were grown outdoors with adequate watering for more than 4 weeks after transplant, were used for treatments and measurements.

Both varieties were also grown in the experimental field (sandy soil) of Kyushu University with a standard cultivation method in 1988, 1989 and 1992. Slaked lime was applied 10 kg/a for soil improvement, and 10 kg/a of chemical compound fertilizer (N:P:K=16:16:16), 3 kg/a of potassium sulfate fertilizer, 1.5 kg/a of fused phosphate fertilizer and 50 kg/a of organic manure were used before young shoots transplanting in each year. The transplant spacing was 60 cm X 70 cm and the growth period was from the middle of June to the late of October. The soil surface was mulched with shading vinyl to prevent weed growth.

Investigated parameters were stomatal aperture degree (SAD), CO_2 exchange rate (CER), transpiration rate (TR), stomatal conductance (GS), water use efficiency (WUE), and leaf and mesophyll water potentials (Ψ_{lF} and Ψ_{ms}, respectively), In addition, influential climatic factors such as vapor pressure deficit (VPD), relative humidity (RH), photosynthetically active radiation (PAR), temperature and the like were measured.

Observation of stomatal aperture degree

SAD was observed by a portable microscope (Peak, Japan) mentioned in a previous paper (Kubota et al. 1992), and scored with six ranks according to the stomatal aperture from closed (0) to fully open (5). SAD of each leaf was an averaged value of

6-point measurements in a leaf.

Leaf-to-leaf change in stomatal aperture was investigated. SAD on the abaxial side of leaf was scored by microscopic observation under the unclouded conditions on Sept. 8, 1989. Each leaf was equally exposed to the full sun light on the measurement day. The fixed portions of leaf were measured three times, 10:00, 12:00 and 15:00, using the expanded leaves of the 1st (young) to 9th position (old) for var. Kog and of the 1st to 12th position for var. Tsu.

Stomatal density and stomatal pore sizes were measured on young, fully expanded leaves in both varieties. Microscopic observations were made on the leaf-surface replicas which were copied by manicure liquid.

Sizes of guard and subsidiary cells were determined. Microscopic photographs (× 600) of the cross sections of leaf tissues were magnified 400 % by photocopy, and then the parts of guard cell and subsidiary cell were separately cut off from the photocopied papers. The cut-off areas were measured with an automatic area meter (AAM -8, Hayashidenko, Japan).

Measurement of transpiration rate, stomatal conductance and water potential of leaf and climatic factors

Diurnal change in TR, GS and Ψ_{lf} were determined on young, fully expanded leaves of both varieties grown in the field at 30 to 60 min intervals from 6:00 to 20:00 on Aug. 10 and Sept. 3. Aug. 10 was a clear day with precipitation (50mm) in the previous two days, and also Sept.3 was clear but there was no precipitation (no irrigation) for the eight days before.

TR and GS of the abaxial surface of a leaf and climatic factors were measured with a super porometer (LI-1600, Licor, USA), and Ψ_{lf} was measured with a psychrometer (C-51, HR-33T, Wesco, USA). Based on these measurements and the number of stomata, TR and GS of a single leaf (both surfaces) were calculated.

Measurement of gas exchange rate in the controlled vapor pressure deficit and leaf water potential

1) VPD and gas exchange rate

CER, TR and GS of young, fully expanded leaves of the pot-grown varieties were measured in the air with different VPD ranging from 0.3 to 3.5 KPa, using an open system assimilation chamber method. VPD of air supplied to the assimilation chamber was adjusted by dehumidifying the air which had been fully moistened in advance. The intensity of light provided to a leaf was a photosynthetically saturation level (1,500 μmolm^{-2}s^{-1} PAR) and the leaf temperature was 30 ±0.3℃. The psychrometer was used for measurement of Ψ_{lf}. CER and RH in the reference air and sample air were measured with a infrared CO_2 analyzer (URA-23, Shimazu, Japan) and a dew point meter (HMP-112Y, Vaisala, Finland), respectively. Leaf and air temperatures were monitored with a thermoelectric thermometer.

2) Ψ_{lf} and gas exchange rate

Effects of Ψ_{lf} variation from -0.2 to − 1.3 MPa on CER and GS were determined. Ψ_{lf} was varied by restricting water supply to the pot-grown plants. VPD in the assimilation chamber was controlled within a range of 2.2 to 2.7 KPa. CER and the other parameters were measured using the same system mentioned above.

Cut-leaf treatment and measurement of gas exchange rate of a detached leaf

Effect of a cut-leaf treatment (cut of water supply to leaf) on the time courses of CER and GS was investigated using young, fully expanded leaves of both varieties on Sept.20, 1988. A leaf piece of 3.0cm × 3.0cm was cut out off from a leaf with fully opened stomata (5 SAD), immediately after this, the leaf piece was mounted in an assimilation chamber (measurement area, $6.25cm^2 = 2.5cm \times 2.5cm$), and CER and GS were measured with a portable photosynthesis-transpiration system (SBP-H2, ADC, Britain) at 30-sec intervals under sun light or 150 watt halogen lamp. Dry air was supplied to the assimilation chamber at a constant velocity, $400ml/min.6.25cm^2$.

Measurement of CO_2 exchange rate of a peeled leaf and water potential of the mesophyll

A direct measurement of the CER of mesophyll was made on a leaf without epidermis. A young, fully expanded leaf of var. Kog, the abaxial epidermis of which was peeled by a method described in a previous paper (Kubota et *al.*, 1991), was used for the measurement. CER of the abaxial surface was measured with the portable photosynthesis-transpiration system. Leaf area used for the measurement was 6.25 cm^2, and air feeding velocity was constant $400ml/min.6.25cm^2$. The air was humidified up to 85% RH to prevent the mesophyll tissues from suffering desiccation damages. Heat cut light (1,500 $\mu molm^{-2}s^{-1}$ PAR) was provided from a slide projector (HILU-HR, Rikagaku, Japan) with an 1 k watt halogen lamp. Immediately after measurement of CER, Ψ_{ms} was determined with a psychrometer (L-51, HR-33T, Wesco, USA).

High humidity air treatment on leaves and measurement of transpiration rate

Plants of both varieties were placed in a high humidity air in advance, and its effect on TR was investigated. A whole plant was covered with a vinyl bag during one night (12 hr). RH in the bag was held at near 100%. In the following morning TR of a young, fully expanded leaf was measured with the portable photosynthesis-transpiration system.

RESULTS AND DISCUSSION

1. Stomatal aperture and gas exchange rate under the field conditions

Diurnal change in TR, GS and Ψ_{lf}

Figure 1 and Fig. 2 show diurnal changes in TR, GS and Ψ_{lf} of the field-grown plants and climatic factors measured on Aug.10 and Sept. 3, respectively. On both days, the highest solar radiations were 1,700 to 1,800 $\mu molm^{-2}s^{-1}$ PAR, maximal air temperatures were 29 to 32℃ and RHs during the mid days were 60 to 70%. Weather conditions of these days seem to be suitable for photosynthesis and growth of sweet potato plant. However, water status in plants and soil was different between both days. Plants and soil were highly moistened on Aug. 10 because much precipitation was given directly before the day, while there was no precipitation for several days before Sept. 3.

On Aug. 10 TR maintained a high value, around 7.0 $mmolH_2O\,m^{-2}s^{-1}$, at 11:00 to 14:00, GS gradually decreased from 0.8 to 0.1 $mmolm^{-2}s^{-1}$ with time from morning to

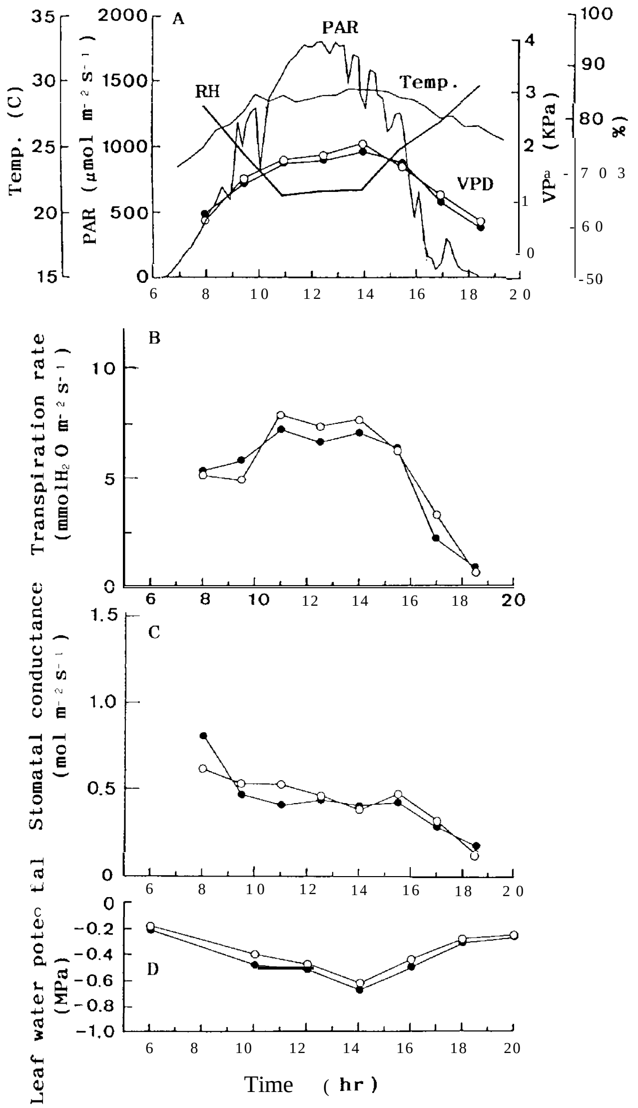

Fig. 1. Diurnal changes in climatic factors (A), transpiration rate (B), stomatal conductance (C) and leaf water potential (D) in var. Kog (●) and var. Tsu (○) on Aug. 10, 1992.

Temp., air temperature; PAR, photosynthetically active radiation; VPD, vapor pressure deficit; RH, relative humidity.

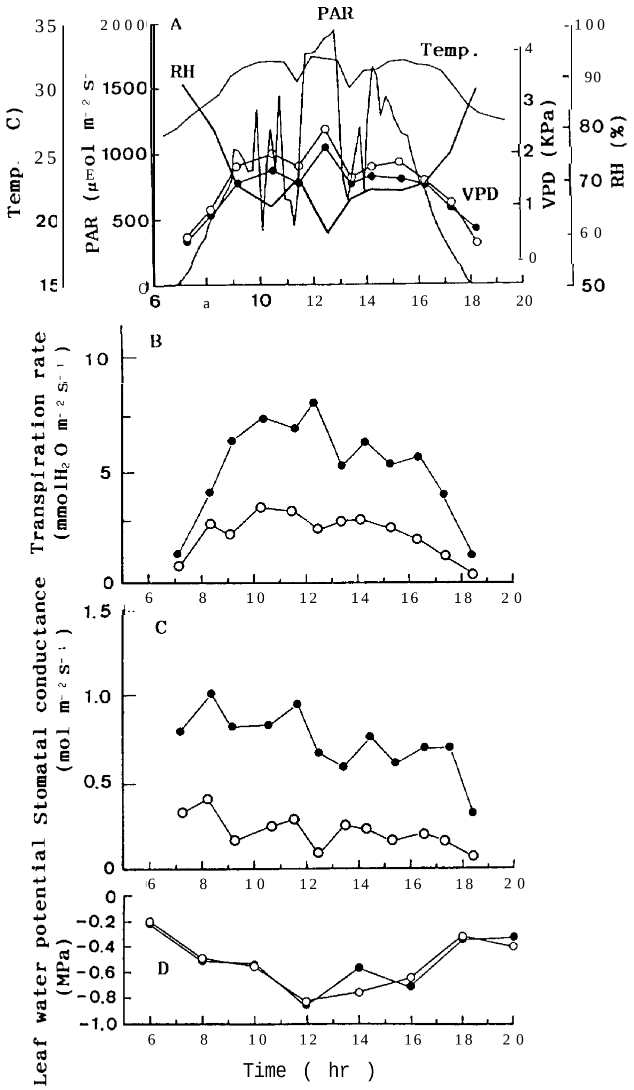

Fig. 2. Diurnal changes in climatic factors (A), transpiration rate (B), stomatal conductance (C) and leaf water potential (D) in var. Kog (●) and var. Tsu (○) on Sept. 3, 1992.

Temp., air temperature; PAR, photosynthetically active radiation; VPD, vapor pressure deficit; RH, relative humidity.

evening, and Ψ_{lf} had a bottom level, -0.7 MPa, at 14:O0. There was no or little varietal difference in TR and GS here. While there was a clear varietal difference in the values measured on Sept. 3; TR and GS of var. Tsu were less than 40% of those of var. Kog. As contrasting the values in Fig. 1 with those in Fig. 2, it is evident that stomata of var. Kog was less affected by moisture conditions and showed a stable and high openness under dry conditions.

Variation in SAD with leaf position

Changes in SAD with leaf position are compared between both varieties in Fig. 3. There was a striking varietal difference here. The 4th to 9th leaves of var. Kog had a high and stable SAD ranging from 3.5 to 5 and the variation with time was small. Contrary, SAD of var. Tsu was lower as a whole and showed complicated time-to-time and leaf-to-leaf variations. In addition, a patchy aperture of stomata was more frequently observed in leaves of var. Tsu.

The vascular bundle system in leaf is divided into two types, the homobaric and heterobaric types (Terashima, 1992). Horizontal gas expansion through mesophyll is prevented in the heterobaric leaf such as a sweet potato leaf, because there is no intercellular space on the vascular bundle sheath extension. Patchy aperture of stomata is considered to be less beneficial for photosynthesis in a sweet potato leaf.

Starch grains are formed in chloroplasts as a result that photosynthetic productivity (source) exceeds the exporting capacity of phtotosynthate from chloroplast to other organs (sink). This causes a physical and physiological depression in photosynthetic function, leading to stomatal closure (Thorne and Koller, 1974; Nafziger and Koller, 1976). It has been known the sink capacity of var. Tsu is greatly restricted as compared with var. Kog (Nakatani et al. 1988). Photosynthetic depression shown in var. Tsu is partially caused by the inferior capacity of photosynthate transport, but a quick movement and patchy aperture of stomata can not be sufficiently explained by the sink-source balance theory. Water environment is considered to play a more effective role on stomatal action. In the following sections, the stomatal movement or

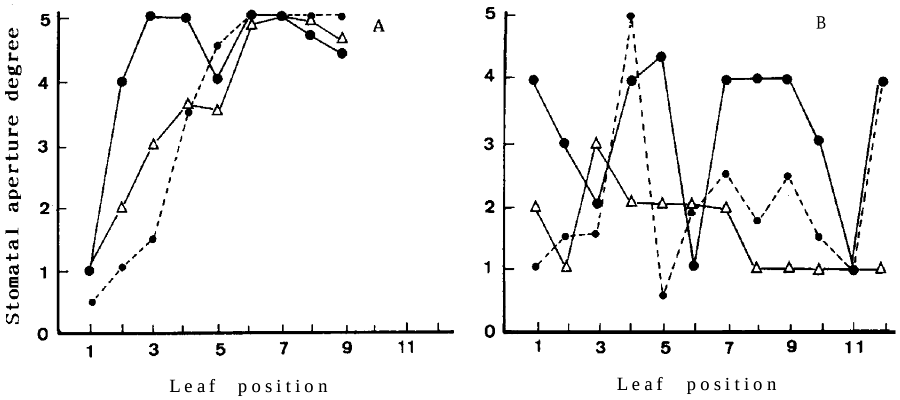

Fig. 3. Changes in stomatal aperture degree with leaf position in var. Kog (A) and var. Tsu (B).
Measurement times were 10:00 (●),12:00(•) and 15:00 (△).

gas exchange and its varietal difference are discussed in relation to internal and external water environmental conditions.

2. Internal water environments and gas exchange properties

Effect of the cut-leaf treatment on CER and TR

TR and CER were monitored at short intervals after the cut-leaf treatment in order to examine the stomatal movement after stop of the water supply to leaf. Time courses of TR and CER in both varieties are compared in Fig. 4. In a high light intensity (1,500 μmolm^{-2}s^{-1} PAR), TR and CER reduced with time. The reduction rate was higher in var. Tsu. Water loss by transpiration during the measurement time of 6 min was 64.8g /m^2 for var. Kog, while that of var. Tsu was 25.9g/m^2. The leaf rigidity of var. Kog was rapidly lost after the treatment, but TR remained relatively high. Contrary, the leaf rigidity of var. Tsu was maintained, but TR was quickly reduced. This means that stomata of var. Tsu readily closed to preserve water content in leaf. A similar trend was also detected in lower light intensities. Stomatal movement of var. Kog was less sensitive to water deficits in leaf.

It is an interesting evidence that GS and CER of var. Kog were relatively high in the wilted leaf. A temporary increase in TR shown after the cut-leaf treatment is known as Ivanoff effect; this is because negative-pressure in the apoplastic space is loosened by cutting the vascular bundles (Meidner, 1965).

The turgor pressure of guard cell is important for stomatal action, and in addition

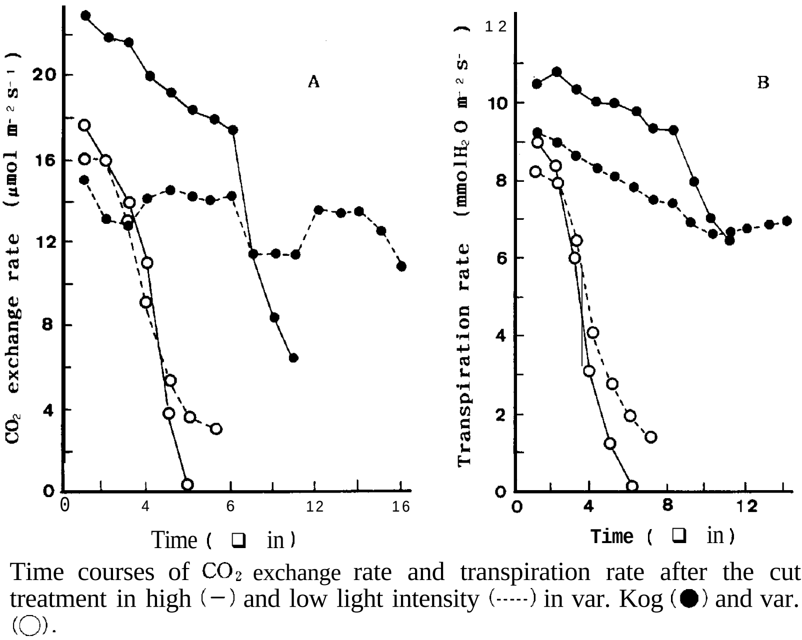

Fig. 4. Time courses of CO_2 exchange rate and transpiration rate after the cut-leaf treatment in high (—) and low light intensity (-----) in var. Kog (●) and var. *Tsu* (○).

High light intensity, 1,500 μ mol m^{-2}s^{-1}; Low light intensity, 900 - 1,400 μ mol m^{-2}s^{-1}

the relative turgor pressure of guard cell to subsidiary cell is also regarded as a determinant for stomatal movement (Maier-Maercker, 1983). When a leaf is a little wilted by rapid transpiration as often observed on var. Kog, the loss of leaf rigidity may become a cause of increasing the relative turgor pressure of guard cells, which is effective in preventing the stomata from closing.

Effect of Ψ_{lf} on GS and CER

Changes in GS and CER with Ψ_{lf} are shown in Fig. 5 A and B, respectively. Both GS and CER decreased with decrease in Ψ_{lf} from -0.31 to $-$ 1.25 MPa, and through the whole range of Ψ_{lf} both parameters were higher in var. Kog.

Var. Kog maintained relatively high values in CER, around 5 μ mol m^{-2}s^{-1}, at Ψ_{lf} of below $-$1.2MPa, while CER of var.' Tsu was almost zero at $-$ 1.0 MPa Ψ_{lf}. Gs in both varieties came close to zero level at Ψ_{lf} of $-$ 1.0 to $-$ 1.2 MPa, but a varietal difference was found. A slight difference in GS may result in making a large difference in CER. Particularly, an increase in GS from 0 to 0.1 mmolm^{-2}s^{-1} is highly effective for increasing CER.

Stomatal density and stomatal pore size are also regulating factors for gas exchange. The values of these factors are shown in Table 1. Var. Kog had a higher

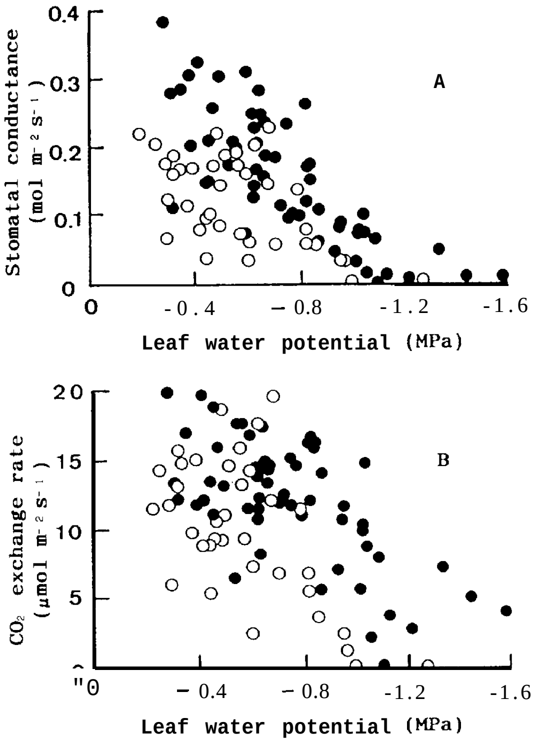

Fig. 5. Effects of leaf water potential on stomatal conductance (A) and CO$_2$ exchange rate (B) in var. Kog (●) and var. Tsu (○).

Table 1. Stomatal density and size in var. Kog and var. Tsu.

	The number of stomata (No. ／mm^2)					Stomatal pore (μm)	
	Abaxial side Average	SE	Adaxial side Average	SE	Total	Long axis	Short axis
Var. Kog	254.7	15.3	32.5	3.5	287.2	21.1	12.5
Var. Tsu	208.4	6.6	80.6	3.3	289.0	22.5	12.2

SE, standard error.

stomatal density (254.7/mm^2) on the abaxial surface than var. Tsu (208.4/mm^2), while the total numbers of stomata on the abaxial and adaxial surfaces were around 290/mm^2, little different between the two varieties. The long axis of stomatal pore was a little longer in var. Tsu, but no difference was detected in stomatal pore size (long axis x short axis) between the varieties.

Effect of Ψ_{ms} on CER of a leaf without the epidermis

Photosynthetic rate of mesophyll tissues can be measured on a leaf the epidenrmis of which has been peeled. Fig. 6 shows change in the abaxial surface CER of peeled and unpeeled leaves with Ψ_{ms}. The CER exponentially decreased from 10 to 2 umol $m^{-2}s^{-1}$ according to decrease in Ψ_{ms} from 0 to $-$ 3.0 MPa. CER of mesophyll maintained a relatively high level at low Ψ_{ms}, as compared with CER (abaxial + adaxial sides) shown in Fig. 5.

CER of an unpeeled leaf shown in Fig. 6 reduced to below 2 μmolm^{-2}s^{-1} at $-$ 0.6 MPa Ψ_{ms}, but a several-fold increase in CER was obtained by peeling the epidermis. This fact suggests that CER reduction frequently observed on water-stressed plants mainly depends on the gas exchange restriction by stomatal closure; being less affected by the reduction of mesophyll photosynthesis. Plants like var. Kog having a dull sensitivity in stomatal movement are able to maintain a relatively high and stable photosynthesis in both wet and dry environments.

Sizes of guard cell and subsidiary cell.

A physiological inter-function between guard and subsidiary cells is closely related to stomatal movement, and their physiological function is considered to be variable with volume of both cells. Cross sectional areas of guard and subsidiary cells of var. Kog and var. Tsu are compared in Table 2. The guard cell area of var. Tsu was significantly larger at $P < 0.01$ than that of var. Kog. While there was no varietal difference for subsidiary cell area. The areal ratio of a subsidiary cell to a guard cell was 2.46 for var. Kog and 1.84 for var. Tsu. This means that the relative volume of subsidiary cell of var. Kog was around 50% larger than that of var. Tsu. Subsidiary cell functions as a pool of solution including chemical substances which are exported to or imported from guard cell, and hence a large volume of subsidiary cell might be beneficial to maintain the turgor pressure of guard cell and stomatal openness.

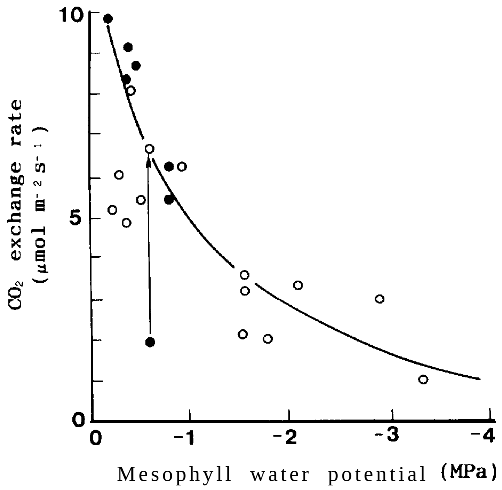

Fig. 6. Change in CO_2 exchange rate of peeled (○) and unpeeled leaves (●) with mesophyll water potential in var. Kog. CO_2 exchange rates were measured on the abaxial side in both peeled and unpeeled leaves. The vertical arrow shows an increase of CO_2 exchange rate by peeling the epidermis.

Table 2. Cross sectional area of guard cell and subsidiary cell in var. Kog and var. Tsu.

	Guard cell (μm^2)	Subsidiary cell (μm^2)	B/A
Var. Kog	17.5 ± 1.1	43.0 ± 4.7	2.46 ± 0.15
Var. Tsu	22.2 ± 1.1	40.9 ± 2.7	1.84 ± 0.09

Values were expressed as average ± standard error.

3. External water environments and gas exchange properties

Effect of the high humidity treatment on GS and TR

Figure 7 shows the effect of the pretreatment of the high humidity air on GS and TR in both varieties. There was no difference in both GS and TR between treated and control plants of var. Kog. On the other hand, an apparent treatment effect was detected for var. Tsu; the treated leaf showed significantly higher values for both GS and TR than the control one.

Ψ_{lf} in both treated and control leaves ranged within -0.3 to -0.4 MPa, being little affected by the treatment. This suggests that humidity or VPD in the ambient air is a factor mainly affecting the water status of epidermis and strongly regulating stomatal action.

Effects of VPD and Ψ_{lf} on gas exchange

VPD-dependent changes in GS, CER, TR, WUE and Ψ_{lf} are shown in Fig. 8 A to E, respectively. In var. Kog, both GS and CER decreased with increase in VPD. TR showed a monopeaked curve having the highest values (around 9 mmol H_2O $m^{-2}s^{-1}$)

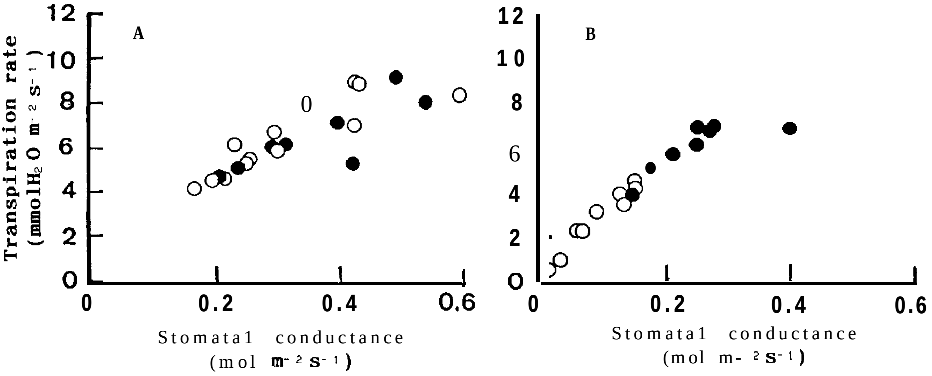

Fig. 7. Effects of the pretreatment of high humidity air on stomatal conductance and transpiration rate in var. Kog (A) and var. Tsu (B).
●, treated; ○, control.

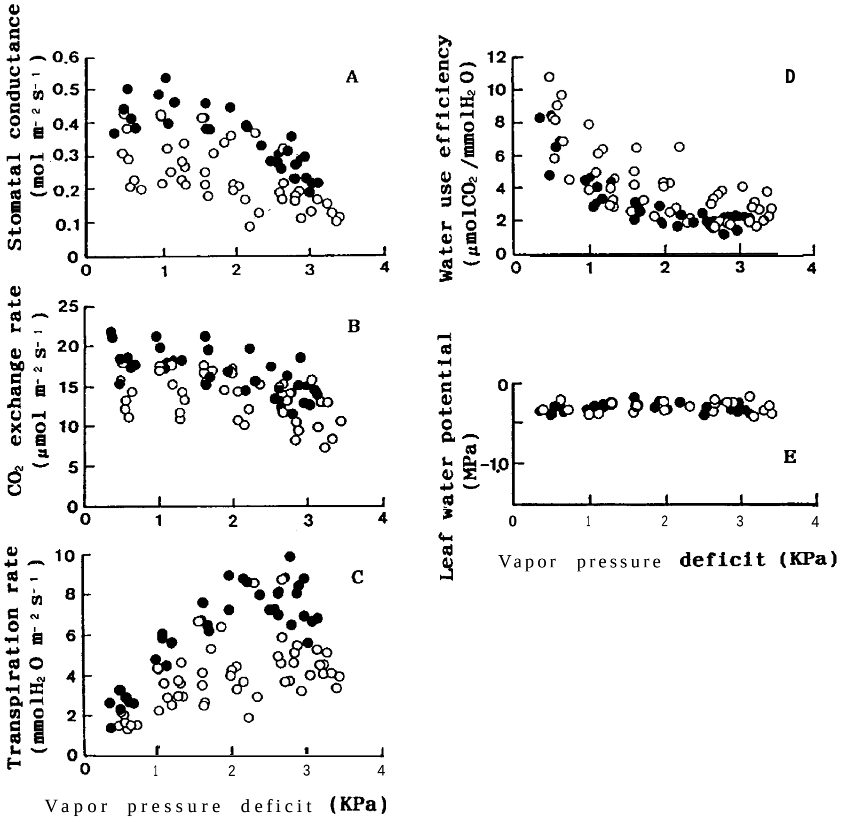

Fig. 8. Effects of vapor pressure deficit on stomatal conductance (A), CO_2 exchange rate (B), transpiration rate (C), water use efficiency (D) and leaf water potential (E) in var. Kog (●) and var. Tsu (○).

at VPD of 2 KPa or a little more. WUE exponentially decreased with increase in VPD, and showed a turning point at ca. 2KPa. VPD of 2 KPa is equivalent to 52.9% RH at 30°C and regarded as an important point for gas exchange and water management to plants. El-Sharkaway and Cock (1984) also pointed out that 1.8 to 2.0 KPa was a turning point of the gas exchange response to VPD in a cassava leaf.

GS, CER and TR of var. Tsu were lower as a whole than those of var. Kog through a given range of VPD from 0.3 to 3.1 KPa. Although the responses of var. Tsu to VPD were unclear, yet these seemed roughly similar to those of var. Kog. While Ψ_{lf} of both varieties was little affected by VPD; its variation was limited within a range of 0.25 to 0.45 MPa.

As mentioned above, a varietal difference in stomatal action was evident in the materials used here.. Particularly, stomata of var. Tsu often showed a complicated movement independently of environmental conditions. Regulating process for stomatal action and mesophyll photosynthesis seems to vary with species and with environmental factors (Osonubi and Davies, 1980; El-Sharkaway and Cock, 1984; El-Sharkaway *et al.*, 1984; Schulze, 1986; Hirasawa *et al.*, 1988; Nonami *et al.*, 1990).

CONCLUSION

Recently sweet potato has been grown with various purposes other than food stuff supply, accordingly the breeding of this crop is conducted toward various directions. Even in such a circumstance it may be recognized that high yield or high photosynthesis is still an important aim of the breeding.

In this research, we detected a clear difference in stomatal behavior and gas exchange between the two varieties. Var. Kog, an improved variety having high yield, had high photosynthesis with high SAD. Contrary, var. Tsu, a native variety having low yield, had low and unstable SAD. The ability of maintaining stomatal aperture in var. Kog is regarded as a character which was introduced and fixed in the process of breeding of this variety. Stomatal aperture is taken up as the main determinant for photosynthesis of a single leaf and can be used as a selection criterion at the early step of high yield breeding. On the occasion that many leaves are required to be investigated in a short time in a breeding field, a quick scoring of SAD can be done by using a 97.5% ethanol filtration method (Kubota *et al.*, 1992).

It may be predicted that a plant with high SAD is readily susceptible to drought. But the relationship between stomatal behavior and drought tolerance has not been clarified in this experiment.

Stomatal movements are fundamentally explained by the turgor pressure theory of guard cell, and physiological studies in this area have been accumulated. However, many of the studies have been made using simplified experimental materials and systems. There are many internal and external factors which function as the regulators for guard cell actions in plants grown in changing environments. Particularly, field crops such as sweet potato are intermittently subjected to mild to hard water stresses during summer season, even if the field is frequently irrigated. Under such conditions, stomata show complicated movements, and it is almost impossible to identify what factor is the determinant of stomatal movement. Recently a concept of accumulative signals which are informed from roots to leaves or stomata has been demonstrated (Davies and Zhang, 1991). When we intend to use stomatal aperture as a selection criterion for the improvement of photosynthesis and productivity of crops, it is important to recognize stomatal actions as an integrated expression of environmental effects in the field where the plants are grown.

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