Effects of Water Deficit on Photosynthesis in Wheat Plants

VI. Capacitance and resistance of transpiratory water flux in different plant parts*

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Abstract : In order to explore the physiological basis for the difference among plant parts in photosynthetic depression by soil water dieficit, the tissue water status was examined by using an electric circuit analogue. It was found that the tissue water storage capacity per unit volume was larger in the leaf blades than in the ear, and larger in the lower leaves than in the upper ones. In reverse, the tissue water storage resistance was larger in the ear than in the leaf blades, and in the upper leaves than in the lower ones. This suggests that the water loss is easier in the lower parts of a plant than in the upper ones. Furthermore, the percentage change of stomatal resistance per unit leaf water potential decrease was larger in the lower leaves than in the upper ones, and larger in the leaf blades than in the ear, suggesting that stomata close earlier in the lower plant parts as water stress develops. These results account for the difference among plant parts in photosynthetic depression by soil water deficit.

Key words : Electric analogue, Leaf water potential, Photosynthesis, Soil water deficit, Stomata, *Triticum aestivum* L., Water stress, Wheat.

水欠乏がコムギの光合成に及ぼす影響　第6報　植物体内における水の流れに対する抵抗および蓄積容量の部分間差：徐　会連・石井龍一（東京大学農学部）

要　旨：土壌水分欠乏による光合成速度の低下程度は植物体部分によって異なる．その原因を探るため，電気回路アナログによる植物体内の水の流れの解析法により，植物体各部分の水分状態の解析を行った．電気のキャパシタンスに相当する組織内水分蓄積容量は下位葉ほど大きく，穂で一番小さかった．組織内水分蓄積抵抗は下位葉ほど小さく，穂で一番大きかった．さらに水ポテンシャルの単位減少量に対する気孔抵抗の増加割合は，下位葉ほど大きく，穂で一番小さかった．これらの結果から，下位葉が上位葉より，また葉身が穂より土壌水分欠乏により早く光合成・蒸散速度を低下させるのは，土壌水分の低下により，組織内の水を早く失い，また気孔がより小さい水ポテンシャルに感応して開度を小さくするためと考えられた．

キーワード：気孔，光合成，コムギ，電気回路アナログ，土壌水分欠乏，水ストレス，水ポテンシャル．

Water flow from the soil through a plant to the air is usually investigated in the steady state condition, where the transpiratory water loss from the leaf is balanced with the water uptake by the root. This condition can exist only when the soil water content is sufficient to meet transpiratory loss. The change in transpiration rate or soil water uptake will break the steady state of water flow, and induce the change of water status in the plant[1,2,4,5,6,7]. If the soil water is depleted, or if the transpiration is accelerated for any reason, the stored water in the tissue would be released to meet the transpiratory water loss. On the other hand, if the water uptake exceeds the transpiratory water loss, the plant tissue will store the water. This can be simulated to the charge and recharge of a capacitor in an electric circuit, as proposed by Nobel and Jordan[5]. The change of water status in any part of a plant is limited by 1) soil water potential, 2) water source in a plant such as tissue water storage, 3) resistance to water flow, 4) rate of water flow, and 5) transpiratory demand. These factors correspond to 1) battery, 2) electric capacitance, 3) electric resistance, 4) electric current, and 5) electric instrument in an electric circuit, respectively[2,4,5,7]. Among these factors, the storage capacitance and storage resistance are the most important, which can be corresponded to the magnitudes of osmotic adjustment and membrane permeability, respectively[5].

In our previous studies[10,11,12], it was found that the different extent of photosynthetic

depression by soil water deficit between plant parts was due to the different response of photosynthetic factors to water stress, such as stomatal CO_2 diffusion resistance, non-stomatal photosynthetic capacity, and the content of ribulose-1, 5-bisphosphate carboxylase. The changes in these factors due to soil water deficit could be associated with the change of water relations in the tissues of the plant[13]. In this paper, the authors attempted to apply the electric circuit proposed by Nobel and Jordan[5], to the elucidation of the difference between plant parts in photosynthetic depression by soil water deficit.

Materials and Methods

Plant materials

The seeds of winter wheat (*Triticum aestivum* L cv. Asakazekomugi) were sown in a 1/2000 Wagner pot in October, 1987. After the plants were grown outdoors with sufficient water supply for three months, they were transferred into the environment controlled greenhouse, where temperature and relative humidity were maintained at 25/20°C (day/night), and 60%, respectively. The uppermost three leaf blades and the ear, which passed 10 days after anthesis, were served for the experiment. The soil water management was made in the same manner as in the previous paper[13].

Application of electric circuit analogue

The concept of the electric circuit analogue proposed by Nobel and Jordan[5] as the model of water flow in a plant is illustrated in Fig.1. Soil water potential (WP_{soil}), which can correspond to the power source in the electric circuit analogue, was measured with a psychrometer (Wescor RH 33T). The transpiratory water loss, which can correspond to electric instrument in the analogue, was estimated from the transpiration rate per unit surface area (Tr) and the transpiratory surface area (A) in each plant part. The Tr was measured with the different plant parts mounted in a acrylic resin chamber by measuring the humidity with a portable photosynthesis - transpiration measuring system (Koito KIP-8510) as reported in the previous paper[10]. The surface area of leaf blade was calculated from the length and the mean width, and the ear surface area was determined by the assumption that ear surface area = length × width × 3.8[12]. The xylem resis-
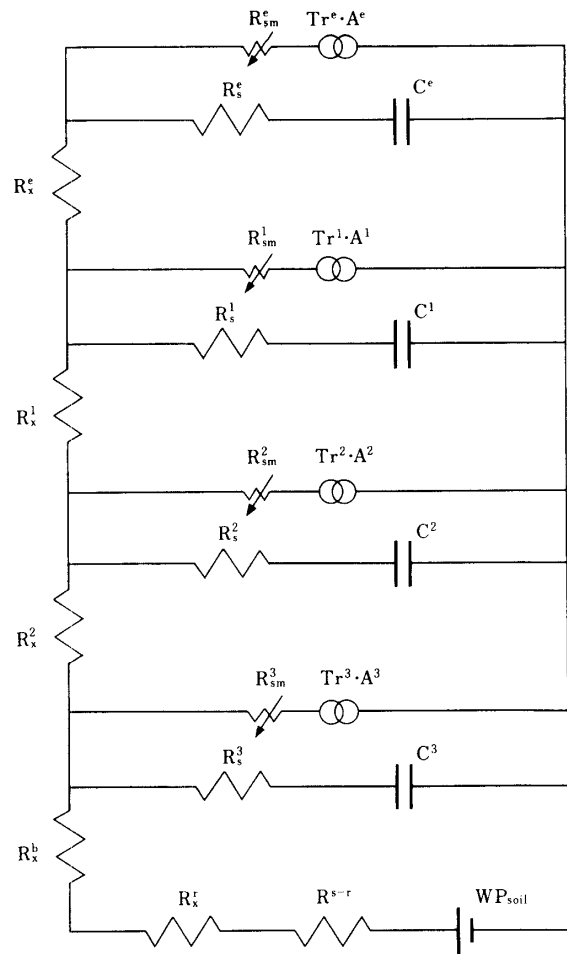

Fig. 1. Electric circuit analogue of the water flow through a wheat plant.
For the meanings and units of the selected symbols, see Table 1.

tance (R_x), therefore, can be obtained from the above mentioned factors by the following equation, assuming that ($Tr \times A$) is equivalent to the transpiratory water flow in the xylen.

$$R_x = \frac{\Delta WP}{Tr \times A} \qquad \cdots\cdots Eq.1$$

Here ΔWP is the difference of water potential between two parts in a plant. The WP was measured according to the method reported in the previous paper[13], with the different plant parts excised just before measurement. Since the R_x in the stem below the third leaf ($R_x{}^b$), in the root ($R_x{}^r$), and in the boundary zone between soil and root xylem (R^{s-r}) cannot be separately determined, the resistances between the 3rd leaf and the soil were combined as in Eq.2.

$$(R_x{}^b + R_x{}^r + R^{s-r}) = \frac{WP_{soil} - WP^3}{\sum (Tr \times A)} \cdots Eq.2$$

where WP^3 is the water potential in the third leaf, and $\sum(\mathrm{Tr}\times\mathrm{A})$ was the total transpiration of ear and the uppermost three leaf blades.

In the unsteady state when the soil water is short or excessive to transpiratory demand, water will be released or stored somewhere in the water flow pathway. In such a case, the storage capacitance (C) will function as a preventor of large changes of water flow. The concept of storage capacitance can be defined as the ratio of change in water volume ΔV at a certain plant part against the change of water potential (ΔWP) [5].

$$C = \Delta V/\Delta WP \quad \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots \mathrm{Eq.3}$$

Since the density of water is constant, V can be replaced by RWC [3,4] and so Eq.3 can be modified to Eq.4.

$$C_v = \Delta RWC/\Delta WP \quad \cdots\cdots\cdots\cdots\cdots\cdots \mathrm{Eq.4}$$

Here, C_v is the capacitace per unit volume of tissue water at full hydration, and it can be practically obtained from the slope of the relation curve between imposed balance pressure and RWC [5,9], as shown in Fig. 2. The pressure-RWC curve was obtained by the following way: After the plant part was hydrated by putting the cut surface into the water for 24 hours, it was put in a small polyvinyl bag and set in the pressure chamber.
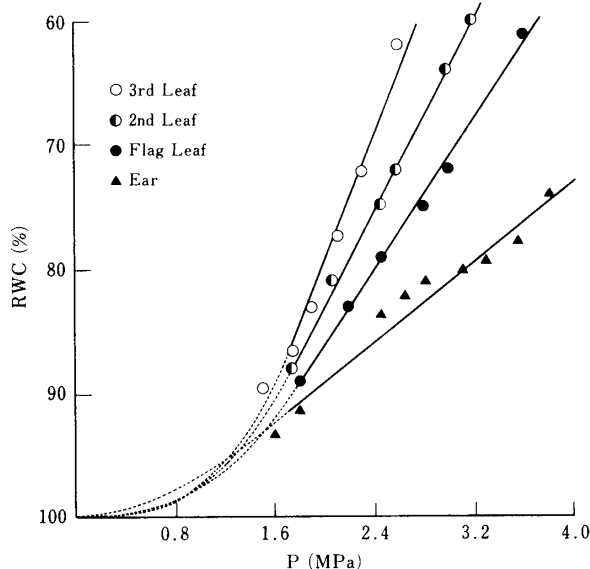
A pressure was imposed until the water exuded from the cut surface, and the water was completely absorbed with a filter paper. Then the pressure was lowered to the level at which water exudation ceased. This lowered pressure is called balance pressure. When exudation stopped, the tissue was taken out and the change in weight was determined. The change in weight is supposed to indicate the water loss induced by the decrease of water potential corresponding to the balance pressure. A higher pressure was imposed again and another change in weight was determined. By repeating this procedure, the data were obtained as shown in Fig. 2. As the change in balance pressure (P) is considered to correspond to the decrease of water potential, Eq.4 can be rewritten to Eq.5

$$C_v = \Delta RWC/\Delta P \quad \cdots\cdots\cdots\cdots\cdots\cdots\cdots \mathrm{Eq.5}$$

Here C_v is shown as the relative value. To obtain the absolute capacitance (C), the total water volume of a plant part should be multiplied with C_v.

$$C = C_v \times WC_{FH} \quad \cdots\cdots\cdots\cdots\cdots\cdots\cdots \mathrm{Eq.6}$$

where WC_{FH} is the water content of a plant part at full hydration.

Water storage resistance (R_S) was determined by Eq.7 according to the method by

Fig. 2. Relationship between balance pressure (P) imposed to the tissue and the relative water content (RWC)

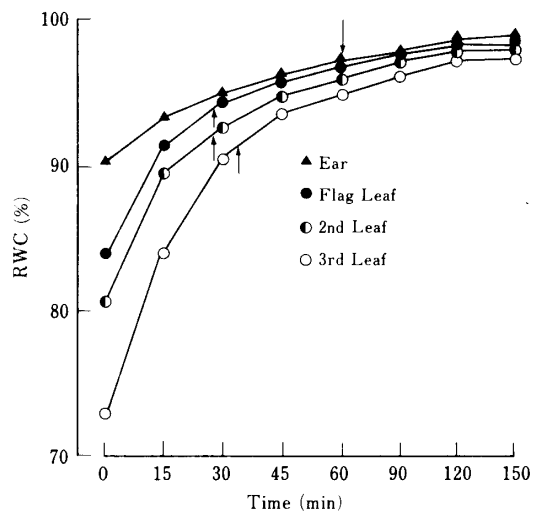The slope of the linear part is defined as water storage capacitance (See text for the details).

Fig. 3. Time course change of the recovery of relative water content (RWC) in the different parts of a water stressed plant when the cut trace was immersed in the water.

The arrows show the point of 63% recovery of lost RWC, the time (second) at which was defined as time constant (See text for the details).

Smith and Nobel[7], and Hunt and Nobel[4].

$$R_s = t/c \quad\quad\quad \text{Eq.7}$$

The time constant of a plant part (t) can be easily determined by the rehydration kinetics of RWC as shown in Fig. 3. As soon as the wilting symptoms appear in the leaves of the plant subjected to soil water deficit, the leaves and the ear were excised at their bases, and immersed in water. The increasing rate of RWC enabled to estimate the time constant (t), which is defined as the time (second) required for 63% recovery of RWC[5].

Variability of stomatal resistance (R_{sm}), which can correspond to the variable resistance in the electric circuit, was theoretically defined as

$$R_{sm} = \frac{dr_s}{d\text{WP}} = \frac{\Delta r_s}{\Delta \text{WP}} \quad\quad \text{Eq.8}$$

where r_s is the absolute value of stomatal resistance. R_{sm} can be expressed more correctly as follows.

$$R_{sm} = \frac{r_s[\text{WP}_{TP=0}] - r_s[\text{WP}_{max}]}{\text{WP}_{max} - \text{WP}_{TP=0}} \quad \text{Eq.9}$$

or

$$R_{sm} = \frac{r_s \int_{\text{WP}_{TP=0}}^{\text{WP}_{max}} f(\text{WP}) d\text{WP}}{\text{WP}_{max} - \text{WP}_{TP=0}} \quad\quad \text{Eq.10}$$

where $r_s[\text{WP}_{max}]$ and $r_s[\text{WP}_{TP=0}]$ are the stomatal resistance at maximum WP, and at zero turgor, respectively.

It is reasonable to suppose that r_s at zero turgor will be as large as it can reach, while r_s at WP_{max} will be as small as it can attain in each plant part. Therefore, we can assume r_s at zero turgor, and that at WP_{max} as 100, and for the relative values. In other words, the total change of $r_s \int_{\text{WP}_{TP=0}}^{\text{WP}_{max}} f(\text{WP}) d\text{WP}$, can be supposed as 100 on the relative basis. So, Eq.11. can be obtained.

$$R_{sm.r} = \frac{100}{\text{WP}_{max} - \text{WP}_{TP=0}} \quad\quad \text{Eq.11}$$

where $R_{sm.r}$ means the percentage change of stomatal resistance per unit water potential decrease.

Turgor potential was calculated from the difference between water potential and osmotic potential which was determined by the method described in the previous paper[13].

The selected symbols and their units were

Table 1   Selected Symols and their units.

Symbol	Unit	Definition
A	(m^2)	Transpiratory surface area
C	(m^3 MPa^{-1})	Tissue water storage capacitance
C_v	(% MPa^{-1})	Capacitance per unit water volume
e		Superscript for ear
P	(MPa)	Balance pressure for pressure-volume curve
R_s·	(MPa s m^{-3})	Tissue water storage resistance
R^{s-r}	(MPa s m^{-3})	Resistance of the boundary zone between soil and root
$r_{s.TP=0}$	(s m^{-1})	Stomtal resistance at zero turgor
$r_{s.min}$	(s m^{-1})	The minimum stomatal resistance under steady state condition
R_{sm}	(s m^{-1} MPa^{-1})	Change in stomatal resistance per unit change of water potential
$R_{sm.r}$	(% MPa^{-1})	Percentage change in stomatal resistance per unit change of water potential
R_x	(MPa s m^{-3})	Xylem resistance to water flow
R^b_x	(MPa s m^{-3})	Xylem resistance below the 3rd leaf
R^r_x	(MPa s m^{-3})	Xylem resistance in root
T	(s)	Equlibrium time of rehydration kinetics
t	(s)	Time constant for the equlibrium of rehydration kinetics
Tr	(m^3 m^{-2} s^{-1})	Transpiration rate per unit surface area
TP	(MPa)	Turgor potential
WC_{FH}	(m^3)	Total water content of plant part at full hydration
WP	(MPa)	Water potential
WP_{max}	(MPa)	Maximum water potential under steady state
WP_{soil}	(MPa)	Soil water potential
$WP_{TP=0}$	(MPa)	Water potential at zero turgor
1, 2, 3		Superscript for the position of internodes or of leaves counted from the top

shown in Table 1.

Results

Table 2 shows the various parameters of water status in the different plant parts. The water potential in the steady state of water (WP_{max}) was lower in the upper parts of the plant than in the lower parts, indicating that WP gradients occurs from the lower parts to the upper parts of the plant. Xylem resistance (R_x) was larger in the upper position (R_x^e) than in the lower position (R_x^1, R_x^2). This means that as the water moves up to the upper parts in a plant, it meets more xylem resistance, resulting in the development of WP difference between two parts.

Storage capacitance per unit water volume (C_v), which was calculated from the slope of the relationship between imposed balance pressure and RWC (Fig. 2), was larger in the lower leaves than in the upper, with the smallest value in the ear. This suggests that water in the tissue can be more easily lost in the lower leaf blades than in the upper leaf blades or the ear. In other words, the ear and the upper leaf blades can sustain the stored water in the tissue. The absolute capacitance (C) was the largest in the ear and larger in the lower leaves than in the upper ones. Since the absolute capacitance is largely dependent on the total water volume (Wc_{FM}), it is not important for the comparison of water maintaining ability.

Water storage resistance ($R_{s.v}$), which was obtained from the time constant (t) and the water storage capacitance per unit water volume (C_v) was, in reverse to C_v, the largest in the ear, and larger in the upper leaves than in the lower ones. This was consistent with the result of C. The storage resistance (R_s) obtained from the absolute capacitance was also the larger in the upper leaves, but R_s in the ear was lower than that in the flag leaf. This is due to the high water volume in the ear as seen in WC_{FH}.

The absolute stomatal resistance at zero turgor, $r_{s.TP=0}$ was not different among leaf positions, although the r_s at maximum leaf water potential was a little higher in the lower leaves. The averaged value of change in r_s per unit change in water potential (R_{sm}) was higher in the lower leaves.

The result in $R_{sm.r}$, which was calculated as the percentage change of stomatal resistance per MPa of WP change, suggests that the stomata in the lower parts close earlier than in the upper parts as the water stress condition develops. This might be due to the early loss of turgor in the lower parts of a plant.

Discussion

Nobel and Jordan pioneered to apply the electric analogue to the analysis of interspecific difference in plant water relations[5]. However,

Table 2. Parameters of the electric circuit analogue in each plant part.

Parameter		Ear	Flag leaf	2nd leaf	3rd leaf
WP_{max}	(MPa)	-0.66	-0.61	-0.52	-0.45
Tr	(m^3 m^{-2} s^{-1})	2.5×10^{-8}	11.4×10^{-8}	10.6×10^{-8}	-9.4×10^{-9}
A	(m^2)	4.5×10^{-8}	1.9×10^{-3}	2.5×10^{-3}	2.1×10^{-3}
WC_{FH}	(m^3)	14.8×10^{-7}	2.9×10^{-7}	4.3×10^{-7}	3.7×10^{-7}
R_x	(MPa s m^{-3})	4.4×10^8	2.7×10^8	1.2×10^8	5.6×10^8
		(R_x^e)	(R_x^1)	(R_x^2)	($R_x^b + R_x^r + R^{s-r}$)
C_U	(% MPa^{-1})	8.2	15.4	18.2	25.8
C	(m^3 MPa^{-1})	12.1×10^{-8}	4.5×10^{-8}	7.8×10^{-8}	9.6×10^{-8}
t	(s)	3.6×10^3	1.8×10^3	1.8×10^3	2.0×10^3
R_s	(MPa s m^{-3})	3.0×10^8	4.0×10^8	2.3×10^8	2.1×10^8
$R_{s.U}$	(MPa s)	4.4×10^4	1.2×10^4	1.0×10^4	0.8×10^4
$WP_{TP=0}$	(MPa)	-2.65	-2.50	-2.20	-1.80
$r_{s.TP=0}$	(s m^{-1})	——	3.1×10^7	3.0×10^7	3.0×10^7
$r_{s.min}$	(s m^{-1})	——	2.7×10^6	3.0×10^6	4.0×10^6
R_{sm}	(sm^{-1} MPa^{-1})	——	1.2×10^7	1.3×10^7	1.4×10^7
$R_{sm.r}$	(% MPa^{-1})	52	53	60	74

See Table 1 and text for the selected symbols.

their experiment was conducted on the level of a whole plant. In the present paper, the authors tried to apply this to the analysis of the difference in water relations among plant parts. In our previous papers[10,11,12,13], it was made clear that less photosynthetic depression in the upper parts of a plant was attributed to higher maintenances of RWC and turgor potential rather than to the level of WP. It was found in the present study that higher maintenances of RWC and turgor potential in the upper parts of a plant was attributed to higher storage resistance and lower storage capacitance per water volume. The upper leaves and the ear with lower capacitance per water volume and higher storage resistance are able not only to absorb the water more strongly from the soil, but also to prevent water loss from their tissue under soil water deficit conditions. However, the lower storage resistance and the higher storage capacitance in the lower plant parts made them lose tissue water easier than in the upper parts. Therefore, it seems that the mechanism of storage resistance is the most important factor to understand the water status in the different plant parts. As the storage resistance will be closely associated with the membrane permeability of the cells and the water adsorbing force by the chemicals in cell sap, the comparison of the chemical and physical properties of cell membrane in different plant tissues would be needed.

It was reported that the stomatal resistance (r_s), and the critical point of WP for stomatal closure were different between plant parts[8]. This is consistent with our results in the present paper. As R_{sm} modeled as the variable resistance in the electric circuit analogue, the average values of both absolute (R_{sm}) and relative change of stomatal resistance per unit WP change $(R_{sm.r})$ were used in this paper, to compare the sensitivity of stomata to the water deficit condition. Larger R_{sm} or $R_{sm.r}$ in the lower parts suggested that the early closure of stomata due to the reduced WP led to a larger decrease of photosynthesis and transpiration than in the upper parts. The result that r_s at a given level of leaf water potential was much larger in the lower leaves than in the upper ones will support the above-mentioned suggestion (Fig. 4)
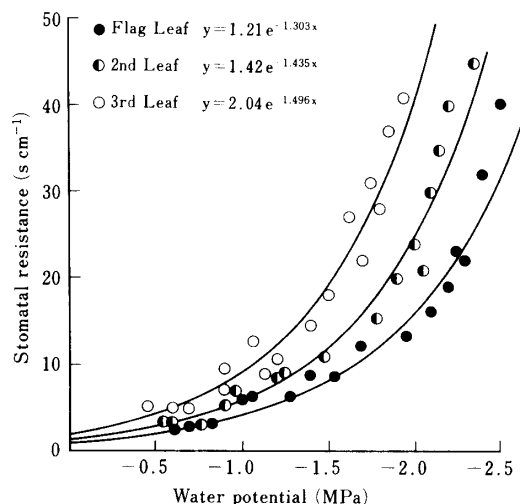

Fig. 4.   Relation between stomatal resistance and water potential in the differently positioned leaves.

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