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Studies on Leaf Water Stress in Fruit Trees

II. Relationship between Climatic Factors and Leaf Water Potential of Satsuma Mandarin (*Citrus unshiu* Marc.) Trees during the Winter

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Summary

Relationships between climatic factors and leaf water potential of satsuma mandarin trees during the winter were studied. The climatic factors were summarized as $U^{1/2}$ (wind speed)$\cdot \Delta C$ (the difference in water vapor concentration between the leaf surface and the ambient air).

Under conditions where soil water was adequate, leaf water potential before sunrise, which usually showed a fairly constant value around −3 atms during the summer, varied widely from less than −38 atms to −10 atms during the winter, depending upon meteorological factors.

The diurnal changes of leaf water potential are of interest in two ways. In the first place, leaf water potential was affected significantly by wind of high velocity. Secondly, leaf water potential was closely related to $U^{1/2}\Delta C$ when stomata were closed.

When a low temperature coincided with wind of high velocity the stomata were usually opened. Under other conditions, such as when the weather was windy but warm, or it was cold but calm, few stomata' if any, were opened.

Introduction

Cold wind injury to citrus trees has been a serious problem during the winter in Japan, since defoliation resulting from this injury affects the growth of trees in early spring. In citrus areas where the damage has been extensive, the crowns of trees are usually wrapped with straw mats as a protection against the cold wind.

The cold wind injury to citrus trees has been studied by many workers (6). From the viewpoint of water relations, it is generally believed that defoliation results from an unbalance between transpirational flux brought forth by high wind velocity and water absorption by roots (6).

The purpose of the present study is to determine the relationship between leaf water potential and environmental factors in Satsuma mandarin trees during the winter.

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Materials and Methods

The main experiments were performed on a mature tree of Owari which was grown in the Citrus Field Station at Mihara City, Hiroshima Prefecture. Cultural methods were similar to those used at the Citrus Field Station, except that machine oil was not sprayed on the leaves. Most data were obtained between Feb. 21 and Feb. 27.

1. *Measurement of leaf temperature*

The leaf temperature was determined with 0.1 mm copper-constantan thermocouples as described by Takechi *et al.* (9). The thermocouples were attached with chloroprene cement to the interveinal area of a leaf. The leaf temperature was measured 3 times with leaves supported horizontally without movement.

2. *Measurement of other environmental factors.*

The air temperature and the relative humidity were recorded by an aspiratory psychrometer at about 1.5 m above the ground, wind velocity was measured with an anemometer at about 2 m above the ground, and solar radiation was measured with the Noshi-Denshi type pyrheliometer.

3. Measurement of soil temperature and soil matric potential

The soil temperature was measured with a thermometer at depths of 10, 20 and 30 cm within a tree canopy. Soil matric potential was measured with a tensiometer at 30 cm depth.

4. Measurement of stomatal aperture

To determine whether stomata are open or not, the penetration of a drop of isobutyl alcohol, applied to the lower side of a leaf, was observed. Moreover, to determine the opening status of the stomata, the epidermis, peeled off from the lower surface of leaves and immediately transferred into absolute ethyl alcohol, were examined under the microscope.

5. Measurement of leaf water potential

Water potential of current spring leaves was measured with a pressure chamber. Pressure from a tank of compressed nitrogen was applied at the rate of 0.35 atm/sce(8). The leaf water potential and climatic data were taken from the side of the canopy exposed to the wind. The air temperature, vapor pressure, leaf temperature and wind velocity were recorded successively. The notations of climatic factors were reduced to $U^{1/2}\Delta C$.

Haseba *et al.*(2) have show that the transpiration rate from citrus leaves can be expressed by the following equation neglecting the terms of transfer by free convection ;

$$W \doteqdot (\varepsilon_s + 2\varepsilon_c) Df \cdot \Delta C$$

Where W is the transpiration rate, ε_s and ε_c are the efficiencies of the stomatal and the cuticular transpiration, respectively, Df is the coefficient of vapor transfer by forced convection from the leaf surface and the ambient air, and $Df \cdot \Delta C$ is the parameter that is approximately equivalent to the intensity of the climatic factors associated with the transpiration rate.

ΔC is defined (2) by

$$\Delta C = (E_L/\Theta_L - eA/\Theta_A)/Rw$$

where E_L is the saturated vapor pressure at leaf temperature (dyne/cm^2), eA is the vapor pressure of the atmosphere (dyne/cm^2), Θ_L is the leaf temperature (°K), Θ_A is the air temperature (°K) and Rw is the gas constant (8.314×10^7 erg/mole °K).

Df is expressed(4) as follows :

$$Df = 0.0380 \cdot Sc^{1/3} \cdot Re^{1/2} \cdot d/1$$

where Sc is the Schmidt number, Re is Reynold's number ($Re = 1 \cdot U/\nu$), d is the molecular diffusivity of water vapor to the air (cm^2/sec), ν is kinematic viscosity of air (cm^2/sec), U is wind speed (cm/sec) and 1 is the characteristic dimension of the leaf and may be approximated by the mean linear dimension (cm).

In the present study, Schmidt's number was treated as a constant because it is slightly affected by temperature, humidity and pressure (3). Therefore,

$$Df \cdot \Delta C = 0.0380 \cdot Sc^{1/3}(1 \cdot U/\nu)^{1/2} d/1 \cdot \Delta C$$
$$= U^{1/2}\Delta C (0.0380 \cdot Sc^{1/3}(1/\nu)^{1/2} d/1)$$

That is, $0.0380 \cdot Sc^{1/3}(1/\nu)^{1/2} d/1$ is constant, and $U^{1/2}\Delta C$ is the parameter that is approximately equivalent to the intensity of the climatic factors and has a large effect on the transpiration rate.

Results

Table 1 indicates the relationship between soil matric potential and the leaf water potential before sunrise (ψ_{max}) on a 6-year-old tree of Sugiyama Unshiu grown at the Fruit Tree Research Station at Akitsu. The soil temperature and the soil matric potential were measured at a soil depth 15 cm. During the summer ψ_{max} was related well to the soil matric potential(5, 7), whereas there was no close relation between ψ_{max} and soil matric potential during the winter. When soil water was adequate in amount during the summer, ψ_{max} showed around −3 atms(7), but it varied from less than −20 atms to about −10 atms during the winter. This suggests that other factors besides soil moisture (*i. e.* soil temperature or meteorological elements) should considerably influence the plant water status during the winter. Because the rate of water uptake is

Table 1. Relationship between leaf water potential and soil matric potential.

Date	Dec. 2	Dec. 3	Dec. 4	Dec. 5
Leaf water potential (atms)	−21.8	−12.4	−10.1	−7.8
Soil matric potential (atm)	−0.01	−0.02	−0.03	−0.04
Soil temperature (°C)	9.5	9.7	10.3	11.5

dependent upon soil temperature but the fluctuation of soil temperature in the present study is fairly small (Table 1), the fluctuation of leaf water potential should be reasonably correlated with meteorological elements that affect transpiration.

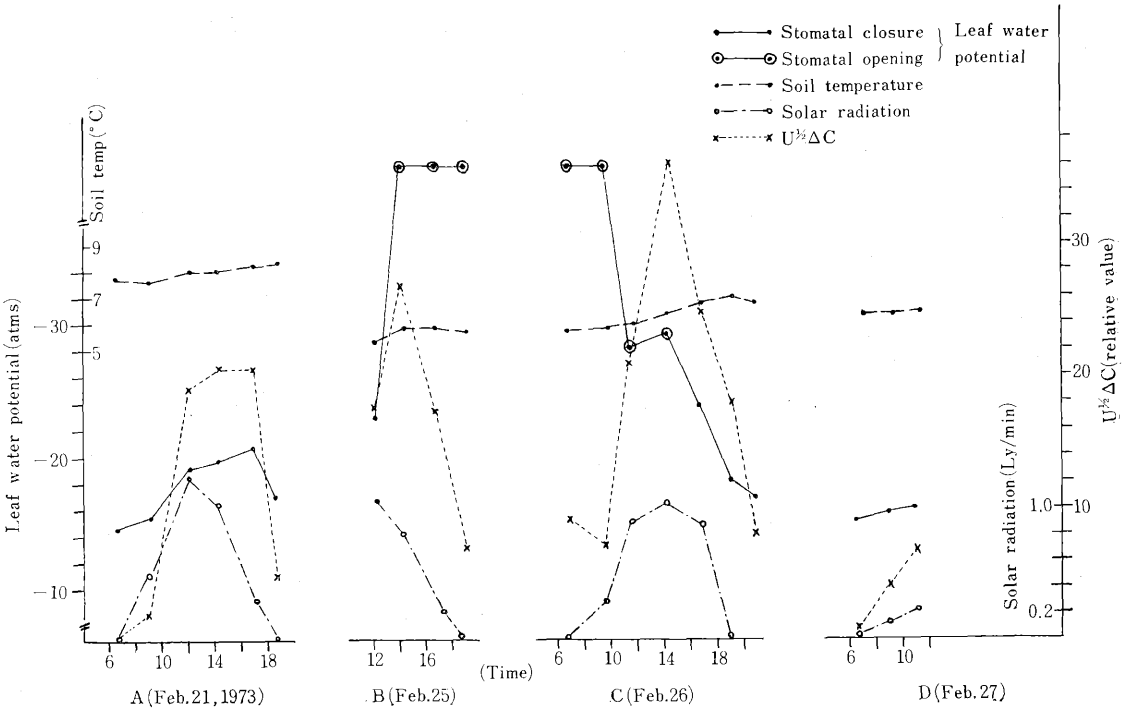

Fig. 1. Diurnal changes in leaf water potential and environmental factors.

Table 2. Other climatic conditions at the same experiment shown in Fig. 1.

Date	Time	Air temperature (°C)	Wind speed (cm/sec)	Stomatal opening leaves (%)	Leaf water potential (atms)	Soil matric potential (atm)
Feb. 21, 1973	6 : 30 a. m.	1. 0	11	0	−14. 1	−0. 01
	9 : 00	4. 0	23	0	−14. 9	
	12 : 00	10. 4	110	0	−18. 6	
	2 : 00 p. m.	12. 1	79	0	−19. 7	
	4 : 30	11. 2	72	0	−20. 8	
	7 : 00	7. 0	26	0	−16. 8	
Feb. 25, 1973	12 : 00 a. m.	4. 7	111	20	−22. 7	−0. 01
	2 : 00 p. m.	5. 8	136	100	below −38	
	4 : 30	4. 9	98	100	below −38	
	7 : 00	3. 9	30	100	below −38	
Feb. 26, 1973	6 : 30 a. m.	4. 5	78	83	below −38	−0. 01
	9 : 30	5. 8	34	42	below −38	
	11 : 30	8. 6	138	15	−27. 6	
	2 : 00 p. m.	11. 3	128	9	−28. 8	
	4 : 30	11. 5	62	0	−23. 7	
	7 : 00	7. 8	38	0	−18. 0	
	9 : 00	5. 1	85	0	−16. 9	
Feb. 27, 1973	6 : 30 a. m.	2. 5	14	0	−14. 7	−0. 02
	9 : 00	4. 6	56	0	−15. 6	
	11 : 00	6. 5	43	0	−15. 9	

The relationship between leaf water potential and $U^{1/2}\Delta C$ was examined for a mature Owari tree grown at the Citrus Field Station. The results are shown in Fig. 1 and Table 2.

Feb. 21 (Fig. 1-A) was a clear and relatively warm day with gentle wind. Because of rain on the previous day, the soil moisture tension was 0.01 atm, but leaf water potential before sunrise was −14.1 atms. Thereafter, leaf water potentials continued to change throughout the day with changes in $U^{1/2}\Delta C$. The stomata remained closed during the period.

Feb. 25 (Fig. 1-B) was a cold and windy day ; the average wind velocity was 111 cm/sec until 12 : 00 a. m., at that time there were a few leaves with stomata that were opened and the average leaf water potential attained −22.7 atms. The average wind velocity was 136 cm/sec between 12 : 00 a. m. and 2 : 00 p. m. At 2 : 00 p. m. the stomata of all the leaves were opened, and leaf water potential was less than −38 atms (the lowest measurable limit of the pressure chamber is 40 atms).

Feb. 26 (Fig. 1-C) started as a calm day. At 11 : 30 a. m. the stomata began to close and leaf water potential was −27.6 atms, which indicates that the plant had partially recovered from the severe water stress of the previous day. Between 11 : 30 a. m. and 2 : 00 p. m. the plant encountered wind of high velocity (the average wind velocity was 138 cm/sec), but stomata continued to close and leaf water potential hardly declined. The air temperature from 12 : 00 a. m. to 2 : 00 p. m. on Feb. 25 was 4.7 to 5.8°C and that from 11 : 30 a.m. to 2 : 00 p. m. on the following day was 8.6 to 11.3°C, whereas the wind velocity was nearly equal. Difference in the behavior of stomata at those two periods, therefore, seemed to be attributed to the difference in air temperature. Thereafter, leaf water potential changed with relation to $U^{1/2}\Delta C$ and the stomata of all the leaves remained closed.

The diurnal changes in leaf water potential reported above are of interest in the following two ways : First, there was the large effect of high wind velocity on leaf water potential. Second, leaf water potential was related fairly closely to $U^{1/2}\Delta C$ when stomata were closed, whereas the relationship became poor when the stomata were opened.

The relationship between leaf water potential, $U^{1/2}\Delta C$ and stomatal movement are presented in Fig. 2. When the stomata were closed, leaf water potential (·mark) appeared to be correlated in a curvilinear manner with $U^{1/2}\Delta C$, but there was no relation between leaf water potential and $U^{1/2}\Delta C$ when the stomata were opened.

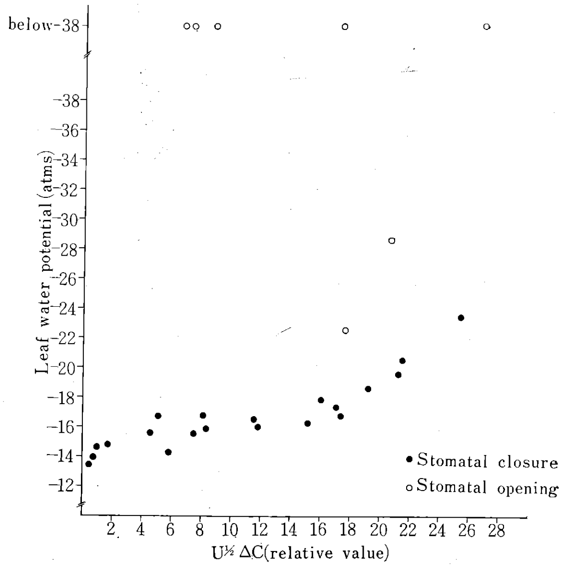

Fig. 2. Relationship between leaf water potential and $U^{1/2}\Delta C$.

Table 3. Effect of climatic conditions on stomatal behavior.

Location	Stomatal aperture	Air temperature (°C)	Saturation deficit (mmHg)	Wind speed (cm/sec)	Solar radiation (Ly/min)
Mihara	opened	12.5	5.0	111	0.60
〃	〃	1.7	1.8	156	0.26
〃	〃	4.7	3.1	111	1.02
〃	〃	3.9	2.3	97	0.20
Akitsu	〃	4.3	2.8	165	—
〃	〃	13.2	6.6	176	0.73
〃	〃	5.0	2.0	86	0.00
〃	〃	7.8	3.7	150	0.04
〃	〃	5.7	3.9	247	—
〃	〃	−0.9	0.7	215	—
〃	〃	6.2	4.1	150	0.78
Mihara	closed	10.2	4.0	110	1.19
〃	〃	1.0	0.7	11	0.00
〃	〃	2.5	1.0	14	0.00
〃	〃	12.1	5.0	79	1.01
〃	〃	11.5	4.9	62	0.43
Akitsu	〃	11.0	5.4	213	—
〃	〃	11.9	—	138	—

Table 4. Effect of climatic conditions on stomatal opening.

Tree No.	Feb. 7 4 : 30 p. m. Stomata		Feb. 8 10 : 00 a. m. Stomata		Feb. 10 10 : 00 a. m. Stomata	
	opened	closed	opened	closed	opened	closed
	(Leaf number)		(Leaf number)		(Leaf number)	
1	4	3	1	6	0	7
2	5	2	3	4	0	7
3	5	2	1	6	0	7
4	1	6	0	7	0	7
5	7	0	2	5	0	7
6	5	2	3	4	1	6
7	5	2	2	5	0	7
8	7	0	3	4	0	7
9	7	0	4	3	0	7
10	5	2	5	2	0	7
11	6	1	4	3	0	7
12	7	0	4	3	1	6
13	4	3	3	4	1	6
14	6	1	3	4	0	7
15	6	1	3	4	0	7
16	6	1	1	6	0	7
17	5	2	1	6	0	7
18	7	0	2	5	0	7
19	5	2	2	5	0	7
20	7	0	1	6	1	6
mean (%)	79	21	34	66	3	97
Wind speed (cm/sce)	233		33		Gentle wind	
Air temperature (°C)	6. 3		1. 3		Relatively warm	

The environmental factors associated with stomatal opening obtained from the experiments on the Owari and the Sugiyama trees are summarized in Tables 3 and 4. Tables 3 and 4 indicate that the stomata opened only when low temperature coexisted with wind of high velocity. In other words, there were few leaves, if any, with the opened stomata when it was windy and warm, or cold and calm. It seems that solar radiation had a minor effect on the stomatal opening. Under a microscope, even when stomata were judged to be opened as a result of the penetration of isobutyl alcohol into a leaf, stomatal aperture of the leaf was generally small and open stomata surrounded by closed ones were sporadically observed on the leaf surface under the climatic conditions mentioned above.

Discussion

In the previous paper(7), we demonstrated that during the summer leaf water potential was highly correlated with either saturation deficit or with solar radiation. In that study (7), maximum leaf water potential was observed before sunrise and minimum leaf water potential was reached between 12 : 00 a. m. and 2 : 00 p. m., corresponding with maximum solar radiation. As the radiation decreased in the afternoon, leaf water potential increased rapidly, reaching a maximum about midnight. The diurnal patterns of leaf water potential during the winter, however, were much more complex than those during the summer.

Leaf water potential may be expressed as follows :

$$\psi = f_{(w-r)} \qquad (A)$$

where ψ is leaf water potential, w is transpiration rate and r is water uptake rate. If r can be considered constant, equation (A) may be expressed as $\psi = f_{(w)}$. During stomatal closure, w is equal to

$$2\,\varepsilon_c (0.0380 \cdot Sc^{1/3} (1/\nu)^{1/2} d/1)\, U^{1/2} \Delta C.$$

Therefore, ψ becomes the function of $U^{1/2}\Delta C$. Since leaf water potential correlated well with $U^{1/2}\Delta C$ (Fig. 2), it may be concluded that water uptake rate through roots may be roughly constant under the ranges of soil temperature encountered in this study. When stomata are opened and r is kept constant, ψ becomes the function of $(\varepsilon_s + 2\,\varepsilon_c) U^{1/2}\Delta C$; hence, ψ was poorly correlated with $U^{1/2}\Delta C$ (Fib. 2).

It is generally accepted that stomatal reaction is sensitive to light intensity during the summer, and at night when stomata are closed and transpiration rate is low, leaf water potential fully recovers from the reduction in potential during the day. During the winter, however, solar radiation exerts only a minor effect on the behavior of stomata. Even under conditions of stomatal closure during the winter the increase in leaf water potential was very slow, presumably because of high root resistance to water absorption at low soil temperatures(1).

Kubo(6) reported that the defoliation of citrus leaves during the winter was closely related to both the maximum wind velocity and the mean air temperature, and that the cold wind injury of the citrus trees resulted from an unbalance between transpiration rate and water uptake rather than leaf water content. The climatic conditions under which stomata opened in the present study seem to agree with those where defoliaton occurred as described by Kubo (6). However, the plant water stress results from an unbalance between the rates of transpiration and absorption. We infer that Kubo could not measure the water stress developing in citrus leaves because he (6) indicated this unbalance on the basis of leaf water content instead of leaf water potential. If he had used a pressure chamber, he would have been able to measure the water stress in citrns leaves.

It is generally assumed that under conditions of low air temperatures, low solar radiation or of high moisture stress in leaves, stomatal opening become negligible. However, there are instances of stomata which have opened under unfavorable conditions. Tamai *et al.* (10), for example, reported that the stomata, usually closed in the winter, abnormally opened when roots were artificially cooled between 6.5°C and 8.7°C, and closed again when soil temperature reached above 10°C. Furthermore, Uegaki (11) reported that the stomata of new leaves of tea (*Thea sinensis* L.) in the winter were hardened and opened.

It is possible, therefore, that under some conditions there are other factors that are associated with stomatal opening. Because of the importance of controlling cold wind injury to the successful management of citrus orchards further studies are needed to reveal the mechanism of stomatal opening under unfavorable weather conditions.

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Literature Cited

1. ELFVING, D. C., M. R. KAUFMANN and A. E. HALL. 1972. Interpreting leaf water potential measurements with a model of soil-plant-atmosphere continuum. Physiol. Plant. 27 : 161—168.
2. HASEBA, T. and O. TAKECHI. 1966. Studies of transpiration in relation to the environment (1) Diurnal change in transpiration from citrus leaves (in Japanese with English summary). J. Agric. Met. (Tokyo) 22 : 1—6.
3. ——— • ——— and D. ITO. 1967. Do(2). Annual change in transpiration from citrus leaves (in Japanese with English summary). Ibid. 23 : 19—24.
4. ———. 1973. Water-vapor transfer from leaf-like surfaces within canopy models (in Japanese with English summary). Ibid. 29 : 25—33.
5. KAUFMANN, M. R. and D. C. ELFVING. 1972. Evaluation of tensiometers for estimating plant water stress in Citrus. HortScience. 7 : 513—514.
6. KUBO, S. 1966. Studies on the cold wind injury of the citrus unshyu (in Japanese with English summary). Bull. Nat. Inst. Agric. Sci. (Japan) Ser. A No. 13 : 1—80.
7. MAOTANI, T. and Y. MACHIDA. 1973. Studies on leaf water content in fruit trees. 3. Some factors affecting the water stress in satsuma mandarin leaves (in Japanese). Abstr. Spring Meet. 1973. Jap. Soc. Hort. Sci. pp. 66—67.
8. MACHIDA, Y. and T. MAOTANI. 1974. Studies on leaf water stress in fruit trees. 1. Evaluation of the pressure chamber method for estimating leaf water potential of Citrus unshiu trees (in Japanese with English summary). Jour. Jap. Soc. Hort. Sci. 43 : 7—14.
9. TAKECHI, O., T. HASEBA, I. TOMARI and T. AKIMOTO. 1962. Studies on the leaf temperature (1) Influences of solar radiation and wind velocity on the leaf temperature of citrus. J. Agric. Met. (Tokyo) 18 : 89—91.
10. TAMAI, T., S. JODO and K. SINOHARA. 1957. Natu-kan no kisetsuhenka to konbu-reikyaku ni tomonau ijō-kaiko ni tsuite. Abstr. Autumnal Meet. 1957. Jap. Soc. Hort. Sci. pp. 8.
11. UEGAKI, T. 1954. Cha-ju no jōsan ni kansuru kenkyu. Ondo oyobi kikō to jōsan ni tsuite. Nogyo Gijutsu. 9 : 27—28.

果樹の葉内水分欠乏に関する研究（第2報）

冬季における温州ミカン葉の Water potential と気象要因との関係

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摘　要

広島果試柑橘試験地の尾張系温州の成木および果試安芸津支場の6年生杉山温州を用い，土壌水分が多い条件下での冬季の葉の water potential (ψ) と気象要因および気孔の開閉について調査を行なった．気象要因は，風速の 1/2 乗 ($U^{1/2}$) と葉面水蒸気濃度差 (ΔC) の積 ($U^{1/2}\Delta C$) で表わした．この $U^{1/2}\Delta C$ は葉面からの水蒸気輸送を決定する近似的気象因子である．

（1） 冬季の日出前の葉の $\psi(\psi_{max})$ は土壌水分が多い場合でも，低地温による根の吸水不足のために，常時 −10 atms 前後以下という低い水分状態に置かれていた．

（2） 冬季の葉の ψ の日変化は，夏季のように一般的なパターンを示すことは困難であった．これは風速が大きく影響するためと思われた．しかし冬の葉の ψ の動きを次の二つに分類することが出来た．第1は，$U^{1/2}\Delta C$ と関係をもって葉の ψ が変化する場合，第2は，$U^{1/2}\Delta C$ と対応しないで ψ が変化する場合である．前者は気孔が閉じている時であり，後者は気孔が開いている時であった．

（3） 冬季において気孔が開く気象条件は，強風と低気温が重なった時であった．このように強寒風下で気孔が開くことは，きわめて奇妙な現象であるが，これによって葉の ψ は低下し，植物体は強度の water stress に落ち入ると思われた．冬季の季節風による落葉現象を水分生理の面から見るならば，強寒風ー気孔の開孔の結果，植物体の water stress が増大するものと思われた．