コムギの光合成に及ぼす土壌水分欠乏と地上部環境との相互作用(2)

土壌水分欠乏と低空気湿度の複合効果

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Interactive Effects of Soil Water Regime with Above-Ground Conditions on Photosynthesis in Wheat Plants

II. Combined effects of soil water deficit with low air humidity

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Abstract : Effects of soil water deficit, low air humidity and in combination were examined at the milky stage under controlled conditions. Low air humidity which plants experienced prior to measurement affected leaf photosynthesis in a manner different from effects of soil water deficit, in regard of the order of depression extent among leaves, i.e., photosynthetic depression by soil water deficit was in the order of flag leaf<2nd leaf<3rd leaf, while that by low air humidity, flag leaf>2nd leaf<3rd leaf. Stomatal (g_s) and mesophyll (g_m) conductances for CO_2 diffusion, and Rubisco content varied in parallel with photosynthesis, though there was one exception. It was suggested that the above-mentioned responses of photosynthesis were caused by the corresponding depression in stomatal aperture and photosynthetic activity of mesophyll. Among the three leaves examined, little difference was observed in decrease of leaf water potential (ψ) caused by soil water deficit, while the decrease in ψ by precedent low air humidity was especially large in the flag leaf. The lower the leaf position, the larger the sensitivity of g_s, g_m, and Rubisco content to decrease in ψ was. Thus, difference in the extent of photosynthetic depression by soil water deficit among the uppermost three leaves was attributed mainly to different sensitivity to decrease in ψ, while that by dry air was attributed to the difference in the extent of decrease of ψ in addition to sensitivity differences. The effect of low soil water and low air humidity on photosynthesis seemed to be additive when combined.
Key words : Humidity, Leaf position, Photosynthesis, Ribulose 1, 5-bisphosphate carboxylase/oxygenase, Soil water deficit, Stomatal conductance, Water stress, Wheat.

コムギの光合成に及ぼす土壌水分欠乏と地上部環境との相互作用　第2報　土壌水分欠乏と低空気湿度の複合効果：徐　会連・山岸　徹・和田義春・石井龍一・玖村敦彦（東京大学農学部）

要　旨：土壌水分欠乏，光合成測定に先立つ生育環境の低空気湿度および両者の複合が光合成とその関連要因に及ぼす影響を葉位別に検討した．実験は乳熟期の材料を用い，規制環境下で行われた．光合成低下程度の葉位間の順位からみて，低空気湿度の影響のしかたは土壌水分欠乏のそれと異なった．すなわち，土壌水分欠乏による光合成低下程度は，止葉<第2<第3葉の順位であったのに対し，低空気湿度によるそれは，止葉>第2葉<第3葉であった．気孔伝導度（g_s），葉肉伝導度（g_m），Rubisco 含量の変動は光合成の変動とほぼ並行していた．この事実から，土壌水分欠乏および低空気湿度の上記のような葉位別光合成に対する影響は，気孔開度と葉内光合成活性の対応する変動を基礎として起こることが示唆された．土壌水分欠乏による葉内水ポテンシャル（ψ）の低下程度は上位3葉間ではほとんどちがわなかった．これに対し，低空気湿度によるψの低下程度はとくに止葉で顕著であった．ψの低下に対する g_s，g_m，および Rubisco の感受性は下位葉ほど大であった．これらのことから，土壌水分欠乏による光合成低下程度の葉位間差異は主として，ψの低下に対する気孔，葉肉光合成機構の感受性の差異にもとづくこと，低空気湿度による光合成低下程度の葉位間差異にはこの感受性の差異に加え，ψの低下程度の葉位間差異が密度に関係することがわかった．土壌水分欠乏と低空気湿度が複合した場合には，両者それぞれの効果がほぼ相加的にあらわれた．
キーワード：RuBP カルボキシラーゼ/オキシゲナーゼ，光合成，コムギ，土壌水分欠乏，水ストレス，葉位．

In the previous work[12], the authors examined diurnal changes of leaf photosynthesis in outdoor conditions, with leaves irradiated by artificial light higher than the photosaturation point at measurement. The results showed that photosynthetic rate decreased continually until a time in the late afternoon, and that the extent of depression was larger on hot-dry days with high solar radiation than on cool-humid days with lower solar radiation. This suggests that photosynthetic depression in the daytime was induced by

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above-ground conditions which accelerate water loss from the plant tissues. The extent of photosynthetic depression by such above-ground conditions varied with positions of leaves on a stem, i.e. flag leaf > 2nd leaf < 3rd leaf. On the other hand , extent of photosynthetic depression by soil water deficit in the same experiment was flag leaf < 2nd leaf < 3rd leaf. Similar tendencies were observed in other experiments [16,17].

Since the previous experiments were conducted in outdoor conditions, it was difficult to know precisely the effect of individual environmental factors on photosynthesis. Thus, in the present study, an experiment was conducted under controlled conditions to elucidate the effects of two specific factors, i.e. air humidity and soil water content on photosynthesis.

We think the effects of low air humidity can be divided into two categories. One is direct effects brought about by current low air humidity[5,7,8,12,13,14,15]. The other is effects caused by low air humidity prior to the time concerned. Considering the results obtained so far by many authors, there is a possibility that the manner and mechanisms for the two effects are very different [6,15]. Thus, the authors intended to examine them separately, and in the present paper, the latter, i.e. after-effects of low air humidity, will be dealt with.

The effects of low air humidity were evaluated by measuring photosynthesis under the same conditions in a leaf chamber using the plants which had experienced different air humidity. Therefore, in the present study, the effects of low air humidity mean aftereffects of low air humidity prior to measurement of single leaf photosynthesis.

The examination was mainly focused on peculiarities of the soil water deficit and low air humidity in the effect on photosynthesis of the uppermost three leaves, the mode of combined effects of these two factors, and the physiological basis for them.

Many studies on the effects of soil water deficit and low air humidity on photosynthesis have been conducted. However, as far as we know, no one is focusing on the above-mentioned question.

Materials and Methods

1. Plant materials, soil water and air humidity

The experiment was conducted in 1985/1986. The seeds of a winter wheat (*Triticum aestivum* L. cv. Asakaze-komugi) were sown in 1/2000 a Wagner pots filled with loamy soil on November 1, 1986. Compound fertilizer (N : P_2O_5 : K_2O = 15 : 14 : 12%) was supplied at the rate of 6 g per pot. After the seedlings established, they were thinned out to 10 plants per pot. The plants were grown outdoors with sufficient water supply until the anthesis stage in the next year. The pots were then transferred to an environment-controlled growth cabinet in the Center of Environment Regulation System for Biology, the University of Tokyo, where the temperature and light intensity were controlled at 25/20°C (12 h day/12 h night) and 600 μmol m^{-2} s^{-1} (400−700 nm), respectively.

A plastic pipe with many small holes on the side wall was inserted vertically into the pot, and water was supplied through the pipe. Two days after the pots were transferred into the cabinet, the pots were grouped into two soil water regimes, 75% (control plot) and 40% (water stressed plot) of the field capacity. In the water stressed plot, watering was withheld for four days and when the soil water content decreased to 40% of the field capacity, the pots were watered to 45%. On the next evening, when the soil water content decreased to about 35%, the pots were rewatered to 45%. In this way, daily soil water was regulated at about 40% on average. In the control plot, the watering was made in the same way as in the water stressed plot, except that the soil water content before and after rewatering was ca 65% and ca 85% respectively, and so ca 75% on average. Two days after the expected soil water content was reached, air humidity treatments, 80±5% (high air humidity, HAH) and 33±3% (low air humidity, LAH) in relative humidity, were commenced. Combining the two air humidities with the two soil water regimes, the following four growth conditions were prepared : high soil water with high air humidity (HSW-HAH), low soil water with high air humidity (LSW-HAH), high soil water with low air humidity (HSW-LAH), and low soil water with low air humid-

ity (LSW-LAH). Three days after the air humidity treatments were started, photosynthesis was measured. The content of ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) was determined the next day.

2. Measurement of photosynthesis

Photosynthetic rates of the uppermost three leaf blades were measured by the gas exchange method according to Kuroda et al[9]. Photosynthesis of plants grown under four environmental conditions was measured in the growth chamber controlled at $80\pm5\%$ of relative humidity and 25/20°C of air temperature, three hours after the beginning of the light period. Plants grown under low air humidity were transferred to the above-mentioned growth chamber 15 min before measurement.

The illumination at the time of measurement was adjusted to 900 μmol m^{-2} s^{-1} (photosynthetically active photon) at the leaf-level concerned. Since air in the assimilation chamber was stirred by a fan, air humidity in the assimilation chamber was near to that at the outlet, about 60% with a little difference according to the transpiration rates. The assimilation chamber was heated during photosynthetic measurement due to strong illumination but every time one measurement had been finished, the heated chamber was cooled with ice water and then the next measurement was started. Thus, the air temperature inside the assimilation chamber was near to the air temperature in the growth cabinet (25 ± 2°C). Leaf temperature was 0.5−1.0°C below the air temperature. The CO_2 concentration of the supplied air was adjusted to 350 ± 15 ppm.

3. Estimation of g_s and g_m

Stomatal (g_s) and mesophyll (g_m) conductances for CO_2 diffusion were estimated in the same way as in the previous work[17].

4. Determination of Rubisco content

Rubisco was extracted according to the method by Makino et al[10]. One gram of fresh tissue material was cut out from the central part of each leaf blade. The tissue was homogenized with a mortar and pestle in a buffer (pH 7.8) containing 50 mM Tris-HCl, 10 mM $MgCl_2$, 0.1 mM EDTA-Na 2 mM dithiothretol (DTT) and a small quantity of acid washed sand on ice. The homogenate was filtered through four layers of cheesecloth and centrifuged at 30,000 g for 30 min at 0°C. The supernatant was collected as the enzyme extract and was used for determining Rubisco content by the method of single radial immuno diffusion according to Matsuhashi et al[11]. The gel used for diffusion contained 1.2% (w/v) agarose, 100 mM Tris (pH 8.6, ion density 0.05), 25 mM HCl and 0.1% (w/v) NaN_3. Purified Rubisco (Sigma) was used as the standard protein. Wells with 3 mm diameter were punched on the gel plate and 4 μmol of the enzyme extract or the standard protein was injected into each well. A standard curve was plotted beforehand and the content of Rubisco was calculated from the regression line.

5. Measurement of leaf water potential

Water potential of leaf blades was determined by a pressure chamber[1] just after photosynthetic measurement.

Results and Discussion

1. Peculiarity of the effects of soil water deficit and of those of low air humidity

We can evaluate the extent of depressant effects of soil water deficit on photosynthesis under high air humidity as the difference between values for HSW-HAH and those for LSW-HAH. The extent of photosynthetic depression due to soil water deficit under low air humidity can be estimated as the difference between values for HSW-LAH and those for LSW-LAH.

Likewise, the effects of low air humidity under high and low soil water content can be evaluated as the difference between HSW-HAH and HSW-LAH, and that between LSW-HAH and LSW-LAH, respectively.

(1) Depressant effects of soil water deficit on photosynthesis

Under both high and low air humidity, the lower the leaf position, the larger the extent of depression (Tables 1 and 2). This trend is consistent with that seen in the previous work under outdoor conditions[17]. In the previous paper we reported that leaf photosynthesis was depressed in the daytime on hot-dry days under field conditions, and the extent of the depression was larger in the flag leaf and the 3rd leaf than in the 2nd one. The results obtained under controlled conditions in this study suggest that the major factor to bring about such a trend was low air humidity in the

Table 1. Photosynthetic rate (Pn, mg dm^{-2} h^{-1}), stomatal (g_s, cm s^{-1}) and mesophyll (g_m, cm s^{-1}) conductances, Rubisco content (RC, mg g^{-1} FW), and leaf water potential (ψ, $-$ MPa) in the plants developed under various conditions of soil water content combined with air humidity.

Factor	Leaf	Treatment			
		HSW-HAH	LSW-HAH	HSW-LAH	LSW-LAH
Pn	Flag	21.7±0.7	19.5±0.4(−10)	19.7±0.5(−9)	16.8±0.6(−23)[−4]
	2nd	21.6±0.5	17.4±0.6(−19)	20.9±0.9(−3)	17.0±0.6(−21)[1]
	3rd	15.2±0.9	9.2±0.4(−39)	13.9±1.1(−8)	8.3±0.9(−45)[3]
g_s	Flag	0.526	0.435(−17)	0.475(− 9)	0.286(−46)
	2nd	0.385	0.278(−28)	0.370(− 4)	0.263(−32)
	3rd	0.270	0.170(−37)	0.250(− 7)	0.122(−55)
g_m	Flag	0.135	0.126(− 7)	0.121(−10)	0.106(−21)
	2nd	0.147	0.119(−19)	0.138(− 6)	0.122(−17)
	3rd	0.095	0.058(−39)	0.077(−19)	0.056(−41)
RC	Flag	14.3±0.4	13.3±0.4(− 7)	13.7±0.4(− 4)	11.0±0.4(−23)
	2nd	12.5±0.5	10.7±0.6(−14)	12.4±0.5(− 1)	10.3±0.5(−18)
	3rd	11.7±0.3	9.5±0.4(−19)	11.4±0.7(− 3)	8.6±0.3(−26)
ψ	Flag	0.68±0.04	1.52±0.05(0.84)	1.15±0.05(0.47)	2.05±0.12(1.37)
	2nd	0.59±0.05	1.40±0.09(0.81)	0.89±0.06(0.30)	1.72±0.10(1.13)
	3rd	0.48±0.03	1.35±0.06(0.87)	0.70±0.05(0.22)	1.60±0.08(1.12)

HSW, high soil water content; LSW, low soil water content; HAH, high air humidity; LAH, low air humidity. The values are the means of five measurements with standard errors. As for the figures in parentheses and brackets, see text.

Table 2. Effect of low soil water content on photosynthesis (Pn) and internal factors of leaf, i. e., stomatal (g_s) and mesophyll (g_m) conductances, Rubisco content (RC), and water potential (ψ) under the conditions of high air humiditty (HAH) and low air humidity (LAH).

Leaf	Under HAH					Under LAH				
	Pn	g_s	g_m	RC	ψ	Pn	g_s	g_m	RC	ψ
Flag	−10	−17	− 7	− 7	0.84	−15	−40	−12	−20	0.90
2nd	−19	−28	−19	−14	0.81	−19	−29	−12	−17	0.83
3rd	−39	−37	−39	−19	0.87	−40	−51	−27	−25	0.90

The effects are expressed in percentage changes (values for HSH−HAH=100) in g_s, g_m and RC, and absolute changes in ψ (MPa).

daytime.

(2) Depressant effects of low air humidity on photosynthesis

The extent of depression due to low air humidity was consistently the largest in the flag leaf, followed by the 3rd leaf, and the smallest in the 2nd one under both the soil water regimes (Tables 1 and 3). As a result, it is clear that low air humidity affects photosynthesis in a manner different from that of soil water deficit, in regard to the order of depression among leaves.

Table 3. Effect of low air humidity on photosynthesis (Pn) and the internal factors of leaf, i. e., stomatal (g_s) and mesophyll (g_m) conductances, Rubisco content (RC), and water potential (ψ) in leaf blades under the conditions of high (HSW) and low soil water content (LSW).

Leaf	Under HSW					Under LSW				
	Pn	g_s	g_m	RC	ψ	Pn	g_s	g_m	RC	ψ
Flag	−9	−9	−10	−4	0.47	−14	−34	−16	−17	0.53
2nd	−3	−4	− 6	−1	0.30	− 2	− 5	3	− 4	0.32
3rd	−8	−7	−19	−3	0.22	−10	−28	− 3	− 9	0.25

See Table 2.

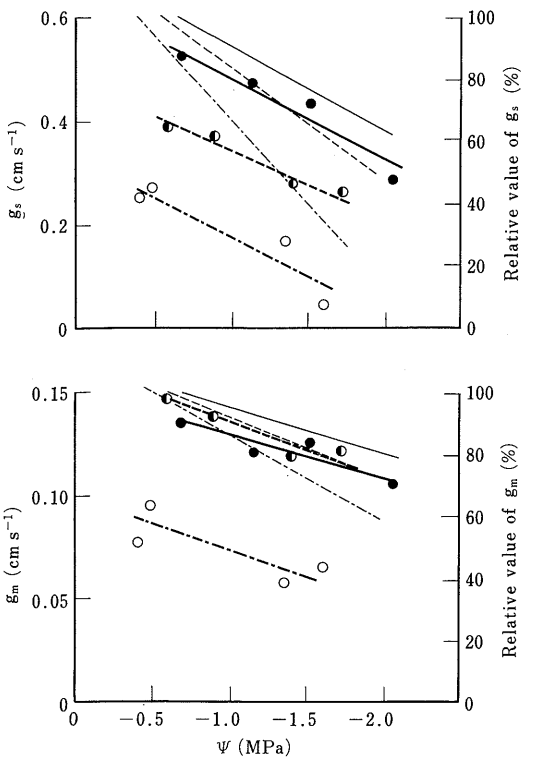

Fig. 1. Decreases of stomatal (g_s) and mesophyll (g_m) conductances as water potential (ψ) decreased.
——, ----, and ——— show flag, the 2nd, and the 3rd leaves, respectively. The thin lines show the relative values. For the detail, see the text.

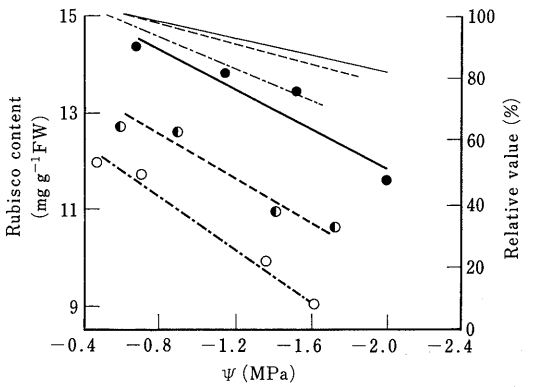

Fig. 2. Decreases of Rubisco content as water potential (ψ) decreased.
As for symbols, see the note of fig. 1.

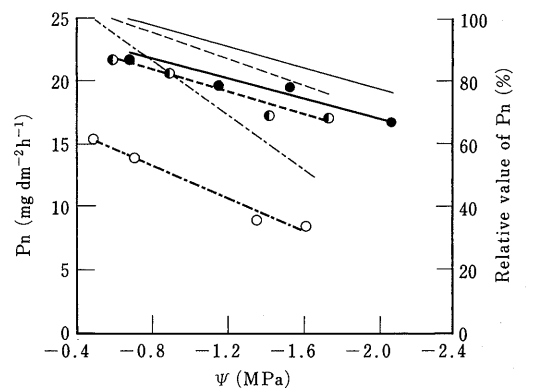

Fig. 3. Decreases of photosynthesis (Pn) as water potential (ψ) decreased.
As for symbols, see the note of Fig. 1.

2. Effects of soil water deficit and low air humidity on g_s, g_m, and Rubisco content.

(1) Effects of soil water deficit

From the results presented in Table 1, the extent of depression in Pn, g_s, g_m, and Rubisco content under high and low humidity were expressed in percentage changes (Table 2).

Under high air humidity, the extent of depression in g_s, g_m, and Rubisco content were all in the order of 3rd leaf > 2nd leaf >

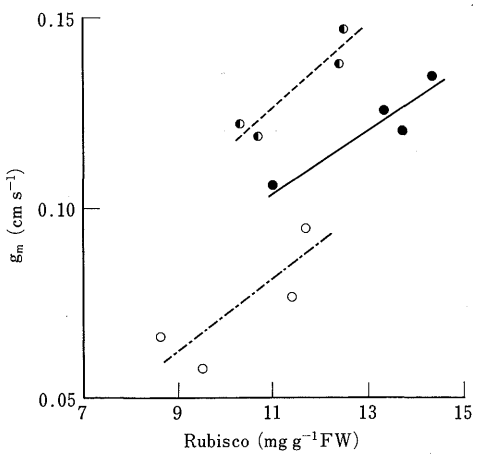

Fig. 4. Dependence of mesophyll conductance (g_m) on Rubisco content.
As for symbols, see the note of Fig. 1.

flag leaf. Under the low air humidity, the extent of depression in g_s, g_m, and Rubisco content were all the largest in the 3rd leaf as in the case under high air humidity, whereas the order of the extent of depression between the 2nd and the flag leaf was a little different from that under the high air humidity.

Thus, variations in g_s, g_m and Rubisco content among leaf positions were parallel to those in photosynthesis though there was one exception. This demonstrates the trend of depression in photosynthesis due to soil water deficit in the order of 3rd leaf > 2nd leaf > flag leaf is caused by corresponding depression in stomatal aperture and photosynthetic activity of mesophyll.

(2) Effects of low air humidity

The extent of depression in g_s, g_m, and Rubisco content due to low air humidity was all in the trend of flag leaf > 2nd leaf < 3rd leaf in both high and low soil water levels without exception (Tables 1 and 3). This shows that the above-mentioned order of depression in photosynthesis is attributable to the mode of depression in stomatal aperture and photosynthetic activity of mesophyll as described here.

3. Effects of soil water deficit and low air humidity on water potential, and sensitivity of the uppermost three leaves to decrease in water potential (ψ)

(1) Effects of soil water deficit

Little difference was observed in decrease of ψ among the three leaves (Tables 1 and 2). Fig. 1, which was prepared using the data obtained in four treatments, shows relationships between ψ and conductances. Here, the thick lines represent the relationship between ψ and g_s or g_m in absolute values. The thin lines in this figure represent relative values of g_s and g_m, which are expressed in the percentage based on the values for ψ in the HSW+HAH treated plants. Thus, the slope of a thin line represents the relative sensitivity to decease in ψ of the leaf concerned. From the comparison of the slopes for the uppermost three leaves, it seemed that the lower the position of leaf, the larger was the sensitivity of both g_s and g_m to decrease of ψ.

The similar relationship was observed in the case of Rubisco content (Fig. 2).

Fig. 3 shows the dependence of photosynthesis on ψ, which is expressed in the same form with those in Fig. 1 and 2. As expected form the trends of g_s, g_m and Rubisco content, the lower the position of leaf, the larger the sensitivity of photosynthesis to decrease in ψ.

From the above, it is suggested that the larger depression in photosynthesis due to soil water deficit in the lower leaves is attributable mainly to the larger sensitivity of stomatal aperture and mesophyll photosynthetic activity to decrease in ψ.

(2) Effects of low air humidity

When leves were exposed to dry air, the higher the position of leaf, the larger the decrease in ψ (Tables 1 and 3). The decrease in ψ was especially large in the flag leaf. It is thus certain that the large depression of photosynthesis in the flag leaf compared with that in the 2nd leaf is caused by the larger decrease in ψ in the former leaf.

Comparing the 2nd and the 3rd leaves, the extent of decrease in ψ seemed to be larger in the former, but the difference was small. Thus, the larger photosynthetic depression due to dry air in the 3rd leaf may be attributable to the larger sensitivity of stomatal aperture and mesophyll photosynthetic activity.

In conclusion, differences in the extent of photosynthetic depression due to dry air among the uppermost three leaves were attributable to differences in the extent of decrease in ψ on the one hand and those in the sensitivity on the other. As for the extent of decrease in ψ, there was a trend that the higher the position of leaf, the larger this was. The sensi-

tivity of photosynthesis to decrease of ψ was the larger in the lower leaves. As the result of combination of these two trends, the trend that flag leaf>2nd leaf<3rd leaf for the photosynthetic depression came out.

4. Relationship between Rubisco content and g_m

The g_m represents the photosynthetic activity of the mesophyll as a whole, which is estimated from the gas exchange rates. Rubisco is well known as the key enzyme in the photosynthetic mechanism[6,8].

Fig. 4 shows the existence of a fairly close correlation between g_m and Rubisco content in each leaf. However, the level of the regression line was different from leaf to leaf. The above-mentioned facts show variations of g_m brought about by those in soil water and air humidity are attributable to the difference in Rubisco content, but differences in g_m between leaves are based on other internal factor (s).

5. Combined effects of low soil water and low air humidity

In Table 1, figures in parentheses represent percentage depression of photosynthesis caused by soil water deficit, dry air and the both. The figures for LSW-LAH denote the combined effect of low soil water and low air humidity. If the effect of these two is "additive", the figures must be equal to the sum of the percentage depression for LSW-HAH and that for HSW-LAH. If there is an interaction between the effects of soil water deficit and dry air, the real percentage depression must be larger or smaller than the sum. So, the difference between the actual depression and the sum is thought to be the interactive part of the combined effect. In Table 1, the differences calculated are shown in brackets.

Compared with the total combined effect (figures in parenthesis), the magnitude of interactive effect (figures in brackets) is very small though the value for the flag leaf might not be negligible. From this, it can be concluded that the manner of the effects of low soil water and low air humidity on photosynthesis is additive though there may be a possibility that a small positive interaction exists between the effects of these two, in the case of the flag leaf.

6. Basis for the different response of leaf water potential to soil water deficit and dry air among leaves.

Soil water deficit and dry air both result in a decrease in leaf ψ. However, the former caused no difference in leaf positions while the latter induced a larger decrease in the flag leaf, and it was shown that this was the basis for the different response of leaves to soil water deficit and dry air in photosynthesis. Thus, the final question is why the uppermost three leaves responded differently to soil water deficit and dry air in respect of ψ. This is an essential problem to be solved in the future. At present, one possible explanation for the largest decrease of ψ in the flag leaf under low air humidity conditions is the largest exposure to dry air. In this experiment, plants were situated in a small stand. So, the flag leaf was directly exposed to dry air while the lower leaves were not. However, this must be proved through comparing ψ of leaves at different positions on plants situated in a stand and under isolated conditions.

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* Japanese with English summary.
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