

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

I. Photosynthesis as affected by soil water regime and the above-ground conditions changing with time of day

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Abstract : Wheat plants were grown outdoors and in an environment-controlled walk-in growth chamber under two levels of soil water. The photosynthetic rates of leaf blades (Pn) and ears (Pg) were measured at every one hour intervals in the light stronger than photosaturation point. Photosynthesis was depressed by soil water deficit during the day irrespective of above-ground conditions. The depression was much larger in leaf blades than in ear, and among the uppermost three leaves the lower the leaf position was, the larger the extent of depression was. The aspect of the diurnal variation of Pn depended on above-ground conditions. On clear days with higher air temperature and lower air humidity, Pn decreased with time in the daytime and recovered in the latter half of the afternoon. On rainy day, Pn depression was not apparent. The diurnal variation of Pg of ear was not apparent under all conditions. The extent of Pn depression in the daytime was smaller in the second leaf than in the third leaf and larger in the flag leaf than in the second leaf. Under the soil water deficient condition Pn depression was larger and Pn recovery was smaller than under the well watered condition. The pattern of diurnal variation of Pn seemed to be determined primarily by above-ground conditions and only slightly affected by the soil water regime, which suggested, in a sense, that these two factors affected Pn almost independently. However, in details, the combined effects of the soil water regime and above-ground conditions were mainly additive but partly synergistic.

Key words : Above-ground environment, Diurnal change, Ear, Leaf position, Midday depression, Photosynthesis, Water stress, Wheat.

コムギの光合成に及ぼす土壌水分条件と地上部環境との相互作用 第1報 土壌水分条件と日変化する地上部環境が光合成に及ぼす影響：徐会連・玖村敦彦・山岸 徹・石井龍一（東京大学農学部）

要 旨：戸外および環境制御室内で土壌水分および地上環境の光合成に及ぼす影響を検討した。光合成は上位3葉身、穂に1時間ごとに同化箱を装着し飽和光下で短時間内に測定した。その結果、葉身および穂の光合成速度は地上部環境のいかんにかかわらず、土壌水分欠乏により日中各時刻において低下すること、低下程度は葉身では穂よりも大きく、上位3葉身では葉位が低いほど大きいことがわかった。光合成の時刻的変化のパターンは測定当日の地上環境の推移により強く影響された。戸外では、日中高温、低湿、強日射で植物からの水分損失が多いとみられた日には、日中光合成速度の低下が起り、午後後半にその回復が起こった。曇雨天の日には光合成の日中低下はみられなかった。光合成の日中低下程度は第3葉では第2葉より大きく、第1葉では第2葉より大きく、土壌水分欠乏による光合成の低下とは葉位間順位が異なった。土壌水分レベルの高低に対応し、日中各時刻の光合成速度のレベルに高低がみられたが、光合成の日変化のパターンには土壌水分による差異は小さく、このパターンは主として当日の天候により支配されることがわかった。しかし、詳細に検討すると、土壌水分レベルが低い場合には葉身の光合成速度の日中低下がやや大きく、また夕方における回復がやや小さかった。このことから、土壌の水分状態と地上環境とは光合成に対し主に独立的・相加的に影響するが、両者の複合効果には若干相乗的な傾向もあることがわかった。

キーワード：光合成、コムギ、地上部環境、土壌水分欠乏、日変化、穂、水ストレス、葉位。

Soil water deficit is one of the largest constraints in wheat crop growing all over the world⁹⁾. For this reason, the effects of soil water deficit on photosynthesis have been investigated^{12,13,14,15,16,17,18)}. Under field

conditions, however, soil water deficit does not occur alone but usually together with other environmental stresses such as low air humidity, high air temperature, high solar radiation and sometimes with dry wind. Thus, the authors intended to examine interactive effects between soil water deficit and above-ground

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environmental factors. The objective of the present study was to clarify the combined effects of the soil water regime and the above-ground conditions during the daytime on photosynthesis of leaves and ear.

Materials and Methods

Two experiments (Exp. I and Exp. II) were conducted. Exp. I was conducted under outdoor conditions in 1984/1985. Exp. II was conducted under controlled conditions in the winter of 1985. A winter wheat (*Triticum aestivum* L. cv. Asakaze-komugi) was used in both experiments.

Exp. I

Seeds were sown in 1/2000 a Wagner pots on 15 November 1984. Compound fertilizer (N : P₂O₅ : K₂O = 13 : 12 : 10) was applied 6 g per pot. The seedlings, after established, were thinned to 10 plants per pot. A plastic pipe having many small holes at the side wall was inserted vertically into the soil of a pot, and the soil was supplied with water through the small holes as evenly as possible. The plants were grown outdoors with sufficient water supply until the anthesis stage in the next year. Then, the pots were transferred into a vinyl house and divided into two groups. In one of them, water was withheld for three days to reduce the soil water content to 40% of field capacity. After that the soil water content was controlled at the level of 40% in the daily average by supplying an appropriate amount of water every evening. The plot having this soil water regime was named "soil water deficit plot".

In the other group, the soil water content was regulated to 75% of the field capacity in the daily average. This plot was named "control plot".

On the 6th (May 9), 8th (May 11), and 11th (May 14) day from the start of soil water deficit treatment, the photosynthetic rates of the uppermost three leaf blades and ear were measured under outdoor conditions at one-hour intervals according to Kuroda et al.¹⁰. At the time of measurement, sample leaves were temporarily irradiated with an artificial light, the intensity of which was larger than the photosaturation point (1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in photosynthetic photon flux). At other times, the leaves were in natural light. A transparent acrylic water bath was put between the assimilation chamber and the lamp, in order to minimize the irradiation heat. Temperature inside the assimilation chamber was not controlled and so changed with the ambient air temperature (23–30°C). The assimilation chamber was supplied with air containing definite CO₂ (350 ppm). The air humidity at the inlet of the assimilation chamber was 4 mg H₂O/L. The humidity at the outlet varied with the transpiration rate, with the maximum of 11 mg H₂O/L. The time required for one measurement was 3–5 min. Since the measurement time was so short, the authors regarded the obtained photosynthetic rate as that close to the photosynthetic activity under the internal condition of leaves just before attaching the assimilation chamber. Ear photosynthesis was measured using a cylindrical assimilation chamber fitting ear (200 mm long with a 25 mm diameter). The flow rate of air into the assimilation chamber was 1.5 L/min.

The photosynthetic activity of leaf blade was expressed as apparent photosynthetic rate, because the rate of respiration was negligible compared with that of photosynthesis. The photosynthetic activity of ear was expressed as gross one because the respiration rate was not negligible (70% of the gross photosynthesis). Respiration rate of ear was measured after measuring photosynthesis. The light respiration was not measured, and the above-mentioned respiration refers to dark respiration only.

Water potential (ψ) of leaf blade and ear was determined by the pressure chamber method⁴) at two-hour intervals. Stomatal (g_s) and mesophyll (g_m) conductances for CO₂ transfer were calculated according to the ordinary procedure^{8,10,16}).

Climatic factors, such as air humidity, air temperature, and solar radiation were recorded continuously on days when photosynthesis was measured under outdoor conditions.

Exp. II :

Seeds were sown in 1/5000 a plastic pots on August 20, 1985. Compound fertilizer (N : P₂O₅ : K₂O = 13 : 12 : 10) was supplied with 2 g per pot. The seedlings were thinned to 6 plants per pot at an early stage of growth. The plants were grown outdoors with sufficient water supply until the booting stage (November 5), and then transferred into a cabinet in the Center of Environment Regulation System for

Biology of the University of Tokyo, where the temperature and light intensity were controlled at 25/20°C (day/night) and 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively.

Two days after anthesis (November 30), the pots were divided into two groups differing in soil water content as in Exp. I. The photosynthetic rate of the uppermost three leaf blades and ear, and the respiration rate of ear were measured by the same method as in Exp. I. The measurement was conducted in the growth cabinet on December 9. Light intensity at the time of measurement was 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Temperature inside the assimilation chamber was not controlled but near to the cabinet air temperature ($25 \pm 2^\circ\text{C}$). The CO_2 concentration and humidity of the supplied air were similar to those in Exp. I. Water potential was determined by the same method as in Exp. I.

In both the experiments, the pots were arranged so close that plants formed a stand similar to those in fields. The plant materials used for measuring photosynthesis and water potential were sampled from the central parts of the pots.

The climatic conditions were considerably different among measuring days as shown in Fig. 1.

Results

1. Effects of the soil water regime on photosynthesis

As shown in Figs. 2, 3, 4, 5 and 6, curves representing photosynthesis of soil water deficit plot always ran lower than those of control plot. In order to evaluate the extent of depres-

sion in photosynthesis caused by soil water deficit, percentage depression of photosynthesis was calculated as $100 \times [(\text{Daily mean of control plot}) - (\text{Daily mean of soil water deficit plot})] / (\text{Daily mean of control plot})$. In all the four cases, depression of photosynthesis was much larger in leaf blades than in ear. Comparing the leaves at different positions, the lower the position was, the larger was the extent of depression. These are consistent with our previous results¹⁵⁾. The depression of photosynthesis by soil water deficit was accompanied by the decreases of g_s , g_m and ψ .

2. Effects of the above-ground environment on photosynthesis

1) *Leaf photosynthesis* In Exp. I, the pattern of diurnal changes of leaf photosynthesis (P_n) varied from day to day. On the clear days, i. e. May 9 and 11, P_n decreased with the time of day but it turned to increase at a time in the afternoon. Of these two days, the extent of depression and recovery was much larger on May 11, which was characterized by higher air temperature, lower air humidity and stronger solar radiation (Fig. 1). On the heavily cloudy day, i. e. May 14, the variation of P_n in daytime was very small and no midday depression was detected (Fig. 4).

In the processes of depression and recovery of P_n , ψ , g_s , and g_m also showed depression and recovery. However, it seemed that there was a difference in the correspondence of P_n to two kinds of conductance between depression and recovery. In the process of depression of P_n , percentage depression of g_s was larger than that of g_m in most cases (Table 2). On the other hand, in the process of the recovery

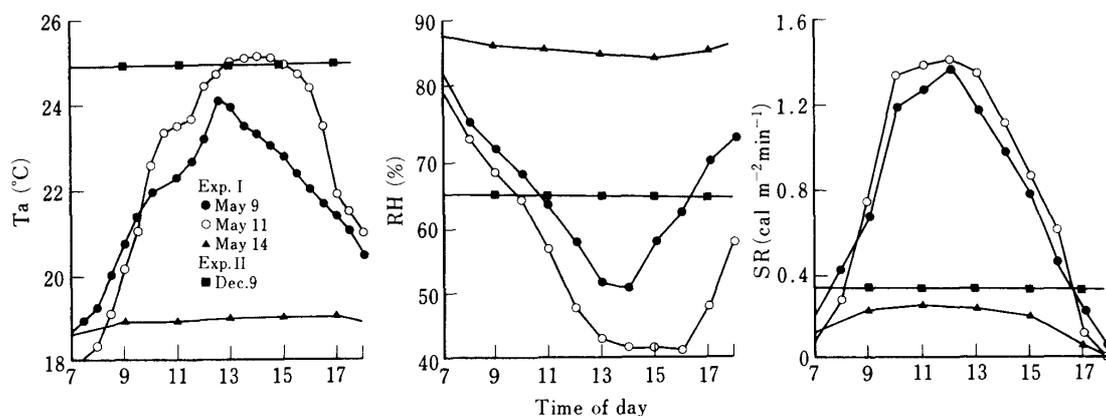


Fig. 1. Diurnal changes of air temperature (T_a), air humidity (RH) and solar radiation (SR) on measuring days.

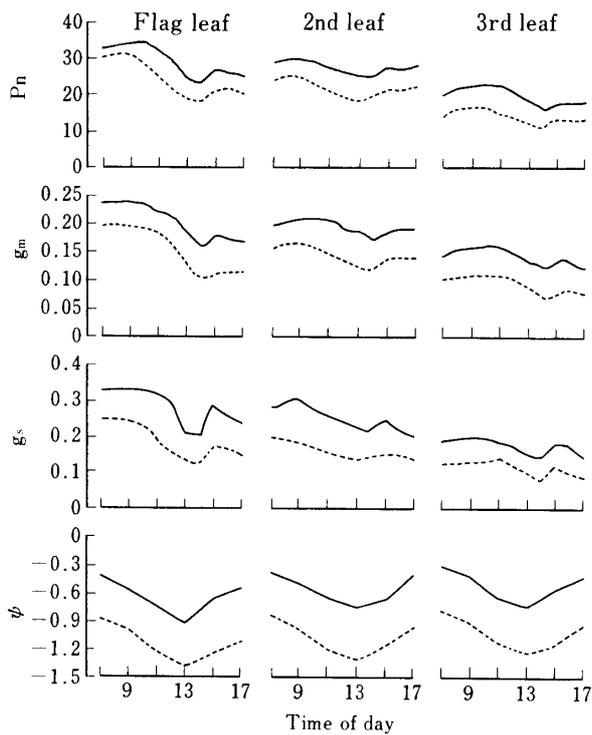


Fig. 2. Diurnal changes of photosynthesis (P_n), stomatal (g_s) and mesophyll (g_m) conductances, and water potential (ψ) in the uppermost three leaves of well watered (solid line) and water stressed (broken line) plants (May 9, Exp. I). P_n , $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$; g_m and g_s , cm s^{-1} ; ψ , MPa.

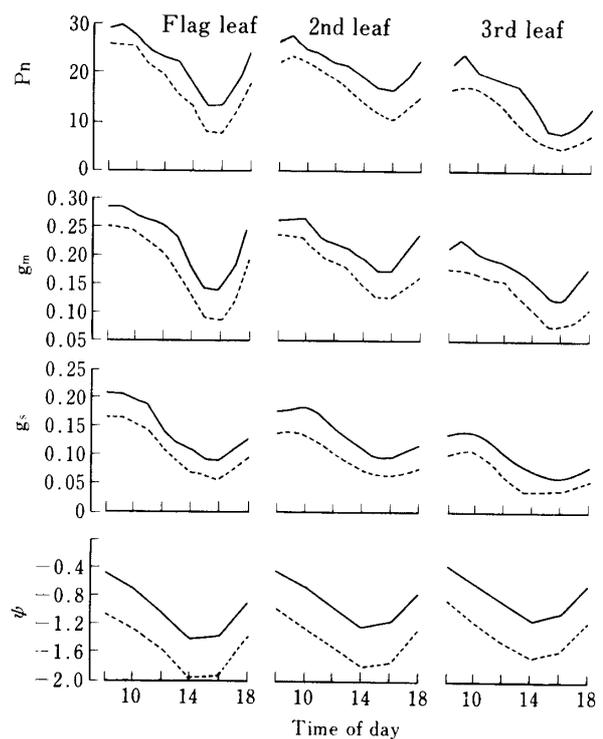


Fig. 3. Diurnal changes of photosynthesis (P_n), stomatal (g_s) and mesophyll (g_m) conductances, and water potential (ψ) in the uppermost three leaves of well watered (solid line) and water stressed (broken line) plants (May 11, Exp. I).

See Fig. 1.

of P_n on May 11, when midday depression and recovery of P_n were most outstanding, percentage recovery of g_m was much larger than that of g_s in most cases (Table 3).

Comparing the three days in Exp. I, the extent of P_n depression was the largest on May 11 followed by May 9 and May 14 in this order, reflecting the patterns of diurnal changes of P_n described above (Table 2). The difference in the extent of depression of P_n among the three days perfectly corresponded to variations of g_s , g_m , and ψ , i. e., the extent of depression of these leaf factors was in the order of May 11 > May 9 > May 14.

In Exp. II, P_n continued to decrease gradually during the light period, being accompanied by depression of g_s , g_m , and ψ .

The extent of depression of P_n was also different among leaf positions. Interestingly, it was consistently smaller in the second leaf than in other two leaves on all of the four measuring days. The difference in the extent of depression of P_n among leaf positions did

not correspond to the variation of ψ as shown in Table 2. The extent of recovery of P_n after midday depression seemed to be also different among leaf positions. On May 11 when diurnal variation of P_n was the most outstanding, the higher the leaf positions, the larger was the degree of recovery.

The extent of depression and recovery of P_n varied with the soil water regimes. Except for May 14 when the diurnal change in P_n was negligible, the extent of depression of P_n was larger in the soil water deficit plot without exception (Table 2). The extent of recovery of P_n after midday depression on May 11 was smaller in the soil water deficit plot than in the control plot in all of the three leaves (Table 3).

2) *Ear photosynthesis* The pattern of diurnal change of ear photosynthesis was rather inverse to that of leaves, i. e. it increased first and then decreased. Generally, the extent of variation in photosynthesis was much smaller than that of leaf photosynthesis. In Exp. II,

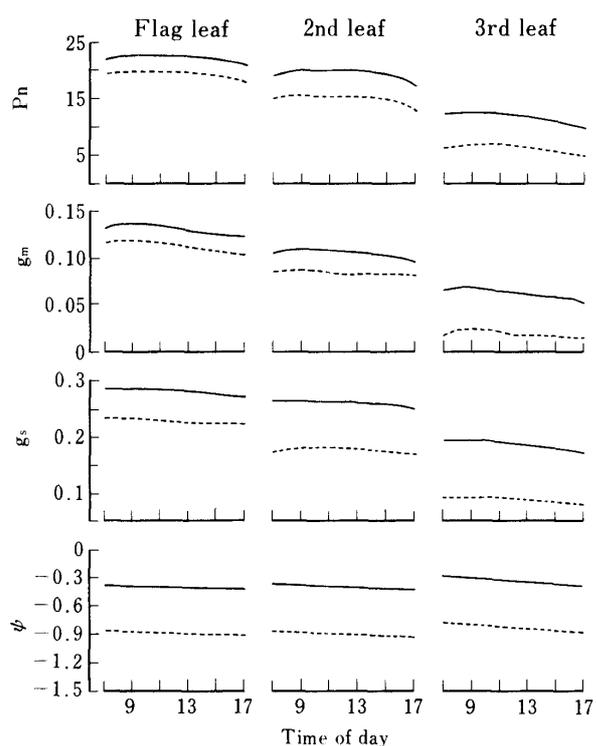


Fig. 4. Diurnal changes of photosynthesis (P_n), stomatal (g_s) and mesophyll (g_m) conductances, and water potential (ψ) in the uppermost three leaves of well watered (solid line) and water stressed (broken line) plants (May 14, Exp. I).

See Fig. 1.

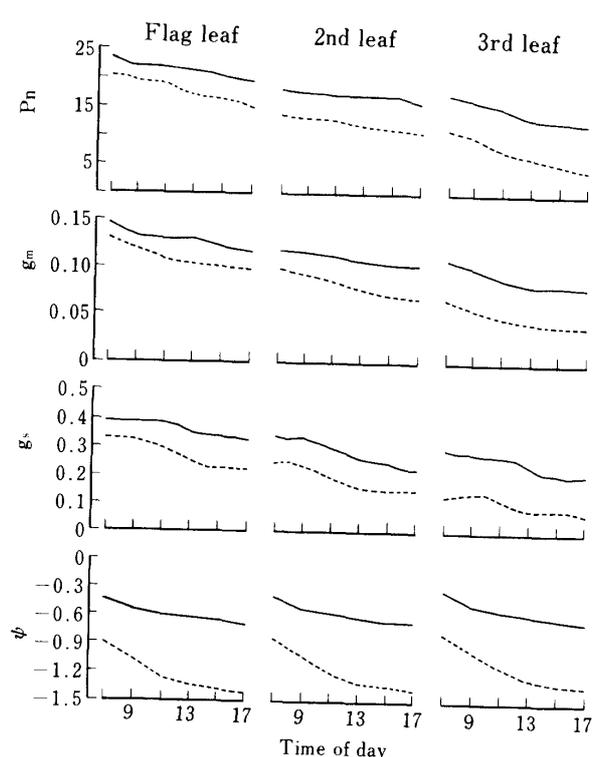


Fig. 5. Diurnal changes of photosynthesis (P_n), stomatal (g_s) and mesophyll (g_m) conductances, and water potential (ψ) in the uppermost three leaves of well watered (solid line) and water stressed (broken line) plants (Exp. II).
See Fig. 1.

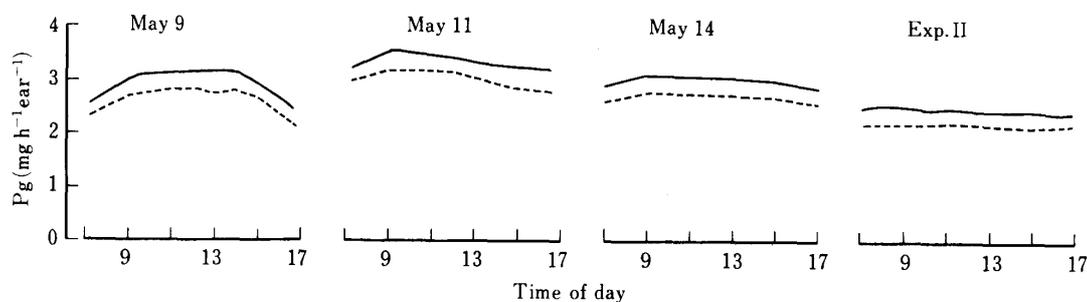


Fig. 6 Diurnal changes of gross photosynthesis (P_g) in ears of well watered (solid line) and water stressed (broken line) plants (May 9, 11 and 14 in Exp. I, and Dec. 9 in Exp. II).

Table 1. Percentage depressions [$100 \times (\text{Maximum} - \text{Minimum}) / (\text{Maximum})$] of photosynthesis (P_n), stomatal (g_s) and mesophyll (g_m) conductances, and absolute decrease of water potential (ψ) by soil water deficit.

Day		Flag leaf				2nd leaf				3rd leaf				Ear
		P_n	g_m (%)	g_s	ψ (MPa)	P_n	g_m (%)	g_s	ψ (MPa)	P_n	g_m (%)	g_s	ψ (MPa)	P_g (%)
Exp. I	May 9	19	16	25	0.52	24	20	32	0.52	32	32	34	0.54	8
	May 11	20	22	23	0.55	25	25	27	0.58	35	37	36	0.56	7
	May 14	11	13	15	0.50	24	20	32	0.51	45	43	52	0.53	6
Exp. II	Dec. 9	18	15	23	0.65	30	33	32	0.64	49	45	55	0.62	9

Table 2. Percentage depressions $[100 \times (\text{Maximum-Minimum}) / (\text{Maximum})]$ of photosynthesis (Pn), stomatal (g_s) and mesophyll (g_m) conductances, and absolute midday decrease of water potential (ψ) in the daytime.

Day	Water regime		Flag leaf				2nd leaf				3rd leaf			
			Pn	g_m (%)	g_s	ψ (MPa)	Pn	g_m (%)	g_s	ψ (MPa)	Pn	g_m (%)	g_s	ψ (MPa)
Exp. 1	May 9	WW	36	32	43	0.49	22	20	27	0.34	35	33	40	0.44
		WS	45	57	60	0.49	29	34	43	0.45	38	50	50	0.44
	May 11	WW	56	52	57	0.95	39	33	44	0.81	64	48	53	0.76
		WS	70	72	68	0.88	54	46	50	0.83	67	65	66	0.80
	May 14	WW	5	4	6	0.05	5	5	4	0.06	9	15	5	0.10
		WS	6	9	8	0.08	3	6	2	0.07	7	11	7	0.12
Exp. 11	Dec. 9	WW	21	20	21	0.26	14	12	20	0.26	32	25	40	0.32
		WS	26	24	31	0.48	22	28	27	0.51	45	53	42	0.55

WW, well watered ; WS, water stressed.

 Table 3. Percentage recovery $[100 \times (\text{Final-Minimum}) / (\text{Minimum})]$ of photosynthesis (Pn), stomatal (g_s) and mesophyll (g_m) conductances, and water potential (ψ) (May 11).

Water regime	Flag leaf				2nd leaf				3rd leaf			
	Pn	g_m (%)	g_s	ψ (MPa)	Pn	g_m (%)	g_s	ψ (MPa)	Pn	g_m (%)	g_s	ψ (MPa)
WW	68	80	27	0.58	63	73	29	0.55	47	68	33	0.51
WS	58	70	35	0.63	36	41	27	0.60	23	22	25	0.52

WW, well watered ; WS, water stressed.

where leaf photosynthesis decreased with time, ear photosynthesis was kept almost constant throughout the light period (Fig. 6).

Discussion

1. *Characteristics of and physiological bases for depression of photosynthesis caused by soil water deficit.*

The trend of photosynthesis well coincided with those of g_s and g_m , i. e., g_s and g_m were decreased by soil water deficit and the extent of decrease was larger in the lower leaves.

Leaf water potential was also decreased by soil water deficit. However, the extent of decrease in ψ was little different among the three leaf positions. Therefore, the extent of decrease in ψ did not account for the difference in the extent of Pn depression among the three leaf positions. The authors have suggested that the larger photosynthetic depression by soil water deficit in lower leaves was not due to the larger decrease in ψ but probably attributable to the lower adjusting abili-

ty^{16,17,18}). The result obtained in the present paper seems to support this view.

Ear photosynthesis was less affected by soil water deficit than that of leaves. This is consistent with the results reported in our other paper¹⁵).

2. *Characteristics of and physiological bases for the effects of above-ground environmental conditions on photosynthesis*

The pattern of diurnal change in leaf photosynthesis was quite different among the four measuring days, where the diurnal changes of the above-ground conditions were largely different. From this, the pattern of diurnal change of leaf photosynthesis is considered to be primarily decided by that of the above-ground environmental conditions.

Comparing the time courses of Pn and ψ in Figs. 2—5, correspondence between Pn and ψ is not necessarily perfect, particularly in Fig. 2. However, on the whole, Pn varies in nearly parallel with ψ , which suggests that the pattern of diurnal change in the former is primar-

ily determined by the diurnal variation of leaf water status. This further suggests that the above-ground environmental condition affects Pn mainly through leaf water status.

Comparing the above ground environmental conditions on May 9, 11 and 14 in Exp. I, it is certain that water loss from leaves was the largest on May 11, followed by May 9 and 14 in this order. Corresponding to this, the extent of decrease of ψ showed the same order (Table 3). From this, the decline of ψ in the daytime is thought to be brought about by a force of the above-ground environment to take water away from leaves, which is large at high air temperature, low air humidity and strong solar radiation. Thus it seems that a kind of water stress given by such an above-ground environment causes decrease of ψ .

However, the aspect of Pn depression brought about by such above-ground environmental conditions differs from that by soil water deficit. As described above, the extent of Pn depression caused by soil water deficit was larger in the 2nd leaf than in the flag leaf. Contrasting to this, the extent of Pn depression in the daytime, which was striking on clear days, was consistently larger in the flag leaf than in the 2nd leaf. This trend was difficult to be accounted for by ψ because the correspondence between Pn and ψ was not consistent (Table 2).

One possible explanation for the larger Pn depression in the flag leaf might be an injury of the photosynthetic mechanisms by strong solar radiation. Since plants were arranged so close as to form a stand in our experiments, it is certain that flag leaves were exposed to stronger solar radiation than the second ones were. If such a situation resulted in an injury of photosynthetic mechanisms of the flag leaf, it could be a reason for the larger depression of Pn in this leaf on clear days. It is known that strong irradiation brought about an injury of photosynthetic mechanisms of mesophyll^{1,2,3,5,6,7,11}). However, we have to make further examination to reveal this point.

3. The combined effects of the above-ground condition and the soil water regime

Roughly viewing, Pn curves representing water deficit plots always run parallel with those for control plots under various above-ground conditions. So, it seems that the soil water regime and the above-ground condition

affect photosynthesis almost independently, or in other words additively (Figs. 2—5).

Examining the details, however, the extent of depression of Pn in the daytime or the light period was larger in water deficit plots than in control plots consistently (Table 2). Further, the extent of recovery of Pn after midday depression was smaller in the water deficit plot on May 11, Exp. I (Table 3). These facts show that a part of the combined effect of the soil water regime and the above-ground conditions is synergistic.

From the above, we conclude that the soil water regime and the above-ground condition affect leaf photosynthesis mainly additively but partly synergistically in the way that Pn depression caused by the above-ground condition is enhanced by soil water deficit.

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* Chinese with English abstract.

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