Ecological Analysis of Photosynthesis of Barley and Wheat

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Winter cereals in Japan are six-rowed barley, two-rowed barley, wheat, rye and oats. The author and co-researchers have carried out ecological studies on the photosynthesis of these winter cereals.^{2,8-12}) In this report, results on barley and wheat obtained from these studies will be presented. These studies were conducted at the Second Division of Plant Physiology (Kitamoto, Saitama), National 'nutitute of Agricultural Sciences, to which 'he author had belonged formerly.

Relation between photosynthesis and temperature during growth period¹¹⁾

Relation between the photosynthesis of the inter cereals and temperature had been investigated by several authors^{6,7)}, using samples of young seedlings. For example, Murata and Iyama⁶⁾ reported that most of the crops belonging to 'northern type' showed the highest apparent photosynthetic rate at 10° to 15°C. Sawada⁷⁾ found, by using wheat seedlings grown in different seasons, that the optimum temperature of photosynthesis rose in parallel with the rise of the mean air temperature under which the plants had been grown.

Our experiment was carried out using the samples which were collected from the plants growing in fields during a growth period. The samples were collected in the morning, and apparent photosynthetic rates of the leaf blades were measured in assimilation chambers with artificial illumination. During the period before April, the samples used were in a state which enables water absorption through roots during the measurement. However, in and from April onward, separated leaves were used so that the measurements were made with leaf blades absorbing water through leaf sheaths.

As given in Fig. 1, the relation between the photosynthetic rate and leaf temperature showed different patterns at different stages in a growth season. The optimum leaf temperature for apparent photosynthesis in barley and wheat was about 15° C in the winter, and $20^{\circ}-25^{\circ}$ C in April or May, under the condition of artificial illumination of 0.6 ly.

Photosynthesis under field condition in winter^{2,8,11)}

Daily air temperature in the fields where experimental materials were grown was usually lower than 10°C in the winter. So that it was assumed that the apparent photosynthetic rate under the field condition in the winter must be at a depressed level, a little less than the optimum value. Actually the following experiments proved that the degree of depression of apparent photosynthetic rates in many clear days in the winter was much larger than expected.

The experiments were consisted of (1) diurnal changes in photosynthesis of tworowed barley under field condition^{8,11}, and (2) photosynthesis of wheat under artificial conditions of low temperature simulating the actual winter season¹¹⁾.

Some typical diurnal changes in photosynthetic rates are shown in Fig. 2. The rates were measured with assimilation chambers. The chambers were placed over the plants ten minutes before each sampling of air for the measurement, and then removed soon after the air sampling, for the purpose of keeping the plants under natural conditions as far as possible. The air temperature inside the chamber was higher than the ambient air temperature, especially at midday with differences of 5° to 8°C.

By comparing the apparent photosynthetic rates of Dec. 22, Jan. 13 and Jan. 21 to that of Dec. 23, it was made clear that the apparent photosynthetic rate was depressed to a great extent on Jan. 21, and depressed until about noon on Dec. 22 and Jan. 13. Although air temperature inside the chambers on Jan. 21 was almost similar to that on Dec. 22 and Jan. 13, the freezing of soil lasted until evening on Jan. 21, until about noon on Dec. 22 and Jan. 13, whereas no soil freezing occurred on Dec. 23.

It is assumed based on the above results and other reports^{3,4,7)} that there are four types of relationships between the apparent photosynthesis and the temperature (from the preceeding night to the daytime of a day) under field conditions in the winter.

(1) When the air temperature from night to daytime is rather high and the soil is not frozen, the photosynthetic activity may be kept to be normal, judged from the relation observed between photosynthesis and temperature as shown in Fig. 1.

(2) When the air temperature from night to daytime is low, the depression of photosynthesis may be large and continues until evening.

(3) When air temperature is kept below 0° C for a long time from the night to the morning the soil surrounding the main root zone may be frozen. When the freezing of soil continues until daytime, the depression of photosynthesis may be large and continues until evening, in spite of rising of air temperature.

(4) When the minimum air temperature in the morning is below 0°C but the soil freezing does not continue for long time, the depression of photosynthesis may occur only in the morning.

On the other hand, Koh et al.⁴⁾ examined an after-effect of low night temperature on photosynthesis in the following daytime, and attempted to determine the mechanism of depression in apparent photosynthesis. They concluded that the depression of apparent photosynthesis was attributable not to the acceleration of photorespiration, but to the depression of photosynthesis itself, and that this depression was caused by both decreases in the stomatal aperture and the photosyn-



Fig. 1. Changes of relationship between leaf temperature and apparent photosynthesis of leaf blades by growth stages in two-rowed barley and wheat

- Note: 1) Photosynthetic rates are expressed by the ratio to the photosynthetic rate at optimum temperature.
 - 2) Numerals in the figure indicate the leaf position on a main stem.
 - 3) A: Jan. 16~24, 1973, B: Feb. 24~27, 1972, C: Mar. 30~Apr. 1, 1972, D: May 2~4, 1972, E: May 16~17, 1972.



Fig. 2. Apparent photosynthesis (open circles) and air temperature inside the chambers (closed circles) in relation to solar radiation under field condition, in two-rowed barley (1969 \sim 1970).

Note) Numerals in the figure indicate the time of day.

thetic activity within mesophyll.

Photosynthetic ability of various organs in ripening stage^{9,10,11,12)}

One of the interesting characters related to the photosynthetic production in winterbarley and -wheat is that photosynthetic activity of various organs other leaf blades become to be conspicuous in a later growing stage. After the experiments by Thorne^{13,14)}, photosynthetic rates of the various organs have been measured directly by many workers.

Photosynthetic ability of various organs is shown in Fig. 3 and Fig. 4. All samples were collected from the field, separated from adjacent organs, and their photosynthetic rates were measured. These rates represent gross photosynthesis measured under controlled conditions in assimilation chambers with artificial illumination of 0.6 ly·min⁻¹ and with surface temperature of each organ kept at $18^{\circ} \sim 23^{\circ}$ C, and were referred to "photosynthetic ability" in this experiment.

In the ripening stage, as shown in Fig. 3, the gross photosynthetic ability of leaf blades per productive tiller decreases more drastically than that of other photosynthetic organs.

The contribution of each organ to the total gross photosynthesis of a productive tiller is shown in Fig. 4, calculated from Fig. 3 on an assumption that every organs are equally illuminated. Awn photosynthesis in barley



Fig. 3. Gross photosynthesis of various organs per productive tiller in the ripening stage, in six-rowed barley (sown in 1969) and wheat (sown in 1970).
Note) ○——○: Ear, ○……○: Leaf blade, ●——●: Leaf sheath, ●……●: Culm





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occupies greater part of ear photosynthesis, especially in the early and middle ripening stage. On the contrary, the photosynthetic ability of awn in wheat is nearly nothing. Thus, the contribution of ears is clearly found to be greater in barley than in wheat. The contribution of leaf blades is high in the early ripening stage, but decreases drastically at the later stage, in both crops.

Next, the contribution of various organs to grain production in barley was calculated by simulation experiments as follows.

A basic model for simulation of dry-matter growth of six-rowed barley was designed and formulated, using the modified structure taken from the model by Iwaki¹⁾. It was assumed in the structure of the model that all of the ears are distributed in the top layer of the canopy, and the daily gross photosynthesis of the canopy was calculated by the equations obtained by modifying the equation of Kuroiwa5). The contribution of each organ to grain production was calculated by eliminating the photosynthetic ability of organs other than leaf blade. It was 28% for ear, 35% for leaf sheath and culm, and 37% for leaf blade, in case of neglecting redistribution of photosynthate. The contribution of ears in wheat has not been calculated directly, but is assumed to be about $10 \sim 15\%$.

Growth analysis of dry-matter production^{9,11)}

Watson et al.¹⁵⁾ calculated leaf area index (L) including the green surface of sheaths and the exposed stems in wheat, and then calculated net assimilation rate by using L.

In our experiment, a new index LAI* was introduced by the following equation.

LAI*=LAI×	total gross photosynthesis per productive tiller							
	gross blades	phot	productive	of tille	leaf er			

Where, LAI is an index of leaf blade surface area.

Net assimilation rate calculated by using LAI* was referred to NAR*.

The difference between LAI* and LAI indicates an assumptive leaf blade surface which expresses the photosynthetic ability of various organs other than leaf blade in terms of an additional leaf area.

As shown in Table 1, the difference in barley is about 0.8 at ten days before the

	balley and wheat, sown in 1970									
		DEC. 24	JAN. 19	FEB. 23	APR 2	. APR 14	2. API 24	R. MA 14	Y JUN 4	
Dry-matter	Barley	6	32	64	256	458	3 94	7 1, 11	6	
g • m ⁻²	Wheat	19	40	81	285	422	2 81	0 1,20	6 1,499	
LAI B	Barley	0. 20	0.35	0. 73	4. 23	3. 72	2 2.7	6 0.3	4	
	Wheat	0.25	0.42	0. 90	3. 82	4.00	3.6	0 2.6	4 0.10	
LAI* E	Barley					4. 45	8 4.6	0 0.9	7	
	Wheat						4.9	3 3.9	4 0.40	
RGR	Barley	0.	178	0. 139	0. 255	0.340	0. 390	0.068		
week ⁻¹	Wheat	0.	202	0. 140	0. 232	0. 234	0.349	0. 165	0.047	
NAR(NAR*)	Barley	j	16. 1	12.4	17.8	(27.1)	(57.1)	(25.0)		
g·m ⁻² ·week ⁻¹	Wheat	1	17.3	13. 0	18.3	20. 5	(47.0)	(36. 3)	(29.8)	

Table 1. Growth analysis of dry-matter production in six-rowed barley and wheat, sown in 1970

Germinating date: November 5

Heading date of the barley: April 24

Flowering stage of the wheat: April 30

heading date and about 2.3 at the heading date, and that in wheat is about 1.3 from a week before the flowering stage to the middle ripening stage. This result clearly shows that the various organs other than leaf blades play an important role for the grain production in both crops.

Moreover, it can be recognized from Table 1 that NAR* in a period from middle to late April is more than 3.6 times of NAR shown in the winter in both crops. It seems reasonable to conclude that winter-barley and -wheat cannot manifest fully their photosynthetic ability because of unfavorable environment of winter in fields, especially low temperature.

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