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Effects of Water Deficit on Photosynthesis in Wheat Plants

IV. Response of photosynthesis to exogenous abscisic acid in different plant parts*

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Abstract : As a physiological basis for the difference among parts of a wheat plant in photosynthetic depression by soil water deficit, the stomatal response to abscisic acid (ABA) was examined in an ABA-sprayed plant. An additional experiment was also conducted in order to confirm whether there is a direct inhibitory effect of ABA on non-stomatal mediated photosynthesis.

About 1 hour after ABA was sprayed, photosynthesis (PS) and transpiration (Tr) in the leaf blades, the stem and the flag leaf sheath decreased to as low level as less than 10% of the initial rates. But, in the ear, the decreases of PS and Tr were not as much as in such parts as above-mentioned. This means that the stomata in the ear are less sensitive to ABA, which accumulates in water stress condition, than those in other plant parts.

Non-stomatal photosynthesis was not inhibited by ABA addition to the reaction mixture in any part of a plant. It was suggested that photosynthetic depression by soil water deficit was not caused by the direct inhibition of photosynthetic mechanism by ABA, but by stomatal sensitivity to accumulated ABA.
Key words : Abscisic acid, Ear, Leaf position, Photosynthesis, *Triticum aestivum.* L., Water stress, Wheat.

水欠乏がコムギの光合成に及ぼす影響　第4報　アブシジン酸に対する光合成の反応の植物体部分間差：
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要　旨：土壌水分欠乏による気孔の閉鎖には，水ストレスにより蓄積するアブシジン酸（ABA）が関与しているとされている．そこで，土壌水分欠乏に対する光合成の反応の植物体部分間差の原因を解明するため，外与 ABA に対する気孔の反応を，植物体各部分で調べた．ABA 散布1時間後の光合成と蒸散速度は，葉身，茎および葉鞘において大きく減少したが，穂では非常に小さかった．このことから，穂の光合成が水ストレスに対して強いのは，ABA に対する反応が小さいためと思われた．さらに，気孔の影響が除去された光合成に及ぼす ABA の影響はほとんど認められなかったことから，ABA の光合成に対する影響の植物体部分間差は，主に気孔の ABA に対する反応を通じて起こるものと考えられた．
キーワード：アブシジン酸，気孔，光合成，コムギ，土壌水分欠乏，穂，水ストレス，葉位．

It was found in the previous papers that the degree of photosynthetic depression by soil water deficit was different among plant parts, and that stomatal and mesophyll CO_2 diffusion resistances increased to different extent among plant parts by soil water deficit treatment[18,19,20]. As for the stomatal CO_2 diffusion resistance, it is known that stomatal behavior is controlled by ABA [1,2,4,5,6,9,11], which accumulates in water stress condition[8].

It is, therefore, reasonably considered that different amount of the accumulated ABA can cause a difference among the plant parts in the depression of stomatal mediated photosynthesis by soil water deficit. However, it is discussed whether ABA also has a direct effect on non-stomatal mediated photosynthesis[12,14,15,17]. Cummins et al[3] suggested that ABA had no inhibitory effect on photosynthesis other than to reduce the supply of available CO_2 to CO_2 fixation sites through stomata. On the other hand, it is reported by many researchers that ABA treatment reduced ribulose-1, 5-bisphosphate carboxylase activity and consequently CO_2 assimilation[12,14,15].

In this paper, We examined the effect of exogenous ABA on stomatal mediated photosynthesis in different parts of a plant, to know whether the stomatal sensitivity to ABA gives the physiological basis for the difference in photosynthetic depression by soil water deficit. Secondly, we tried to clarify whether there is a direct effect of ABA on non-stomatal

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photosynthetic O_2 evolution in the ABA-incubated tissue sections.

Materials and Methods

1. Plant materials

Winter wheat (*Triticum aestivum* L. cv. Asakaze-komugi) was sown in 1/2000 a Wagner pots on October 20, 1986. They were grown outdoor under sufficient soil water condition until the next spring.

2. Measurement of stomatal mediated photosynthesis

The well watered plants were sprayed with 0, 10, 100 ppm ABA solutions on the 15th day after anthesis. Tween 20 was used as the adhesive. Photosynthesis and transpiration were measured with the gas exchange rate measuring system by the method as described in the previous paper[18], in 1, 24 and 72 hours after ABA was sprayed. The surface area of the leaf blade, leaf sheath and stem was measured by the method as described in the previous paper[18], and the ear surface area was determined according to the following equation by Qiu et al[13]

$$\text{Area} = 3.8 \times \text{Length} \times \text{Width}$$

3. Measurement of non-stomatal photosynthesis

Non-stomatal mediated photosynthesis (NSP) was determined by the oxygen electrode method as described in the previous paper[20]. 2, 4-cis-tr-ABA (Sigma) was dissolved in a small amount of methanol, and then diluted to 30 ppm with the photosynthetic reaction medium. The tissue sections were infiltrated with the photosynthetic measuring medium containing ABA for 15 min. The measurement was made at 25°C with an illumination of 900 μmol PPFD m^{-2} s^{-1} using a 500 W projector lamp.

Results

Table 1 shows the rates of photosynthesis (PS) and transpiration (Tr) measured with the gas exchange rate measuring system, under the field condition in 1 hour after ABA was sprayed. PS in the leaf blades, the stem and the flag leaf sheath decreased as low as less than 10% of the initial rates, but PS of the ear showed only 20 and 40% reduction from the control by 10 ppm and 100 ppm ABA treatment, respectively. Tr also showed a similar change to PS by ABA treatment, although the degree of depression of Tr was not so great as that of PS. These results suggest that the stomata in the ear are less sensitive to ABA than those in other parts.

Fig. 1 shows the time course change of PS and Tr of the flag leaf after ABA was sprayed. At the time of one hour after ABA was sprayed, there was practically no difference in PS and Tr, between 10 and 100 ppm ABA treated leaves, but, afterwards, the difference was apparent and getting larger. This might be due to more ABA remaining in the leaf treated with higher concentration of ABA. The time course trends of the decreasing and recovering process of gas exchange rate in the second leaf, the stem and the leaf sheath were similar to those in the flag leaf. However, the time course change in the ear was different from those in other parts of a plant (Fig. 2). At any time, the depression of PS and Tr was smaller in the ear than in the flag leaf.

In order to know whether the depression of PS could be attributed to the direct effect of ABA on photosynthetic machinery, the effect of ABA incubation on non-stomatal photosynthesis (NSP) was examined by oxygen electrode method. As shown in Table 2, the decrease in NSP by ABA incubation was less than 10% in all the plant parts. There is no significant difference in the decreasing extent of NSP among plant parts. From these results, it was concluded that photosynthetic depression by ABA was mainly attributed to stomatal closure and not to non-stomatal photosynthetic inhibition.

Discussion

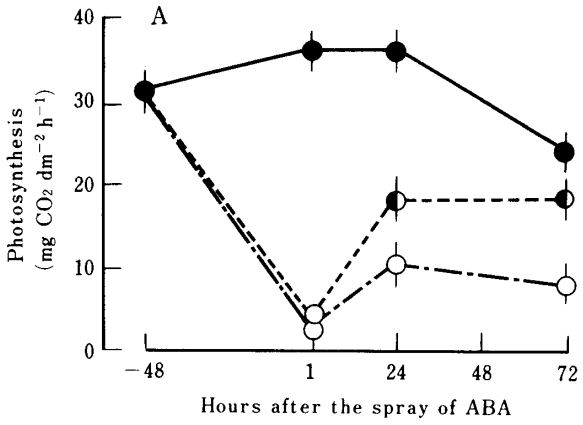
It was found in the previous papers that PS in the ear was less sensitive to soil water deficit than other parts of a plant [18,19,20]. The results in the present work suggested that less depression of photosynthesis in the ear, was partly attributed to less sensitivity of stomata to the accumulated ABA in water stress condition.

The present study showed that the decrease of NSP by ABA incubation was very small in all the parts of a plant. Therefore, it can be concluded that the photosysthetic reduction by ABA is resulted mainly from ABA-dependent stomatal closure, and not from the non-stomatal photosynthetic inhibition. At least, it is concluded that there was no immediate (incubated with ABA solution for 15 min) effect of ABA on non-stomatal mediated

Table 1. The effect of ABA spray treatments on the photosynthesis and transpiration of the different parts of a wheat plant.

Plant part	Photosynthesis ($mg\ CO_2\ dm^{-2}\ h^{-1}$)			Transpiration ($g\ H_2O\ dm^{-2}\ h^{-1}$)		
	Control	ABA 10 ppm	ABA 100 ppm	Control	ABA 10 ppm	ABA 100 ppm
Flag leaf blade	35.0 ±2.1	3.5 ±0.7 (10)	2.9 ±0.8 (8)	6.9 ±0.3	1.6 ±0.2 (23)	0.7 ±0.2 (10)
2nd leaf blade	27.4 ±2.7	2.8 ±0.6 (10)	1.5 ±0.5 (5)	4.9 ±0.2	1.5 ±0.3 (31)	1.0 ±0.3 (20)
Ear	6.6 ±0.3	5.2 ±0.2 (79)	3.9 ±0.1 (59)	0.8 ±0.1	0.6 ±0.2 (75)	0.5 ±0.1 (63)
Stem	13.5 ±1.8	3.4 ±0.8 (25)	1.7 ±0.6 (13)	4.0 ±0.3	1.3 ±0.3 (33)	0.8 ±0.2 (20)
Flag leaf sheath	11.4 ±1.2	1.9 ±0.6 (17)	1.2 ±0.4 (11)	3.4 ±0.2	1.4 ±0.2 (41)	0.7 ±0.2 (21)

Values are means of five measurements with standard errors.
Figures in the parenthesis are relative values to control.



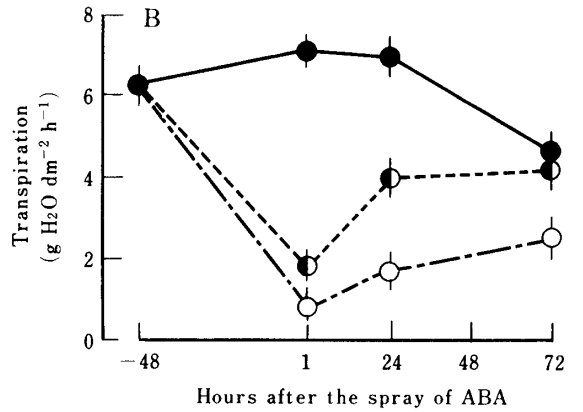
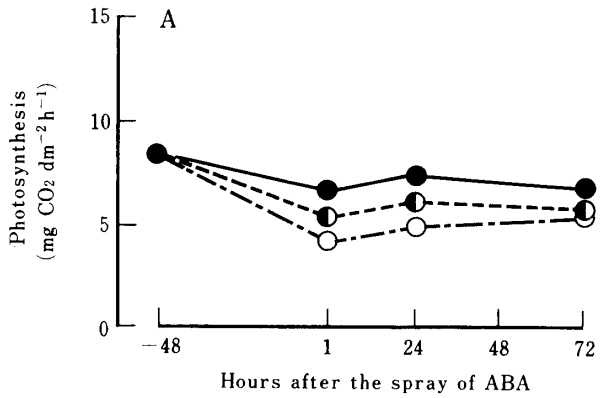


Fig. 1. Time course change of photosynthesis (A) and transpiration (B) in the flag leaf of a wheat plant after ABA spray treatmennt.
●——●, control; ◐--------◐, 10 ppm ABA; ○——○100 ppm ABA.



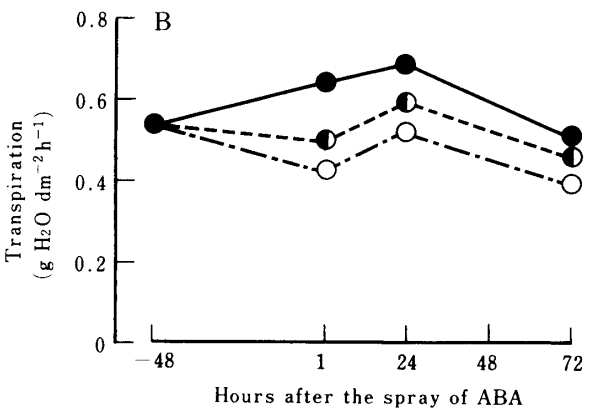


Fig. 2. Time course change of photosynthesis (A) and transpiration (B) in ear of a wheat plant after ABA spray treatment.
●——●, control; ◐--------◐, 10 ppm ABA; ——○, 100 ppm ABA.

Table 2. The effect of ABA incubation on the non-stomatal mediated photosynthesis (NSP) in the different Parts of a wheat Plant.

Plant part	NSP (μmol O_2 dm^{-2} h^{-1})	
	Control	ABA treated
Flag leaf blade	310 ±5	284 ±4 (92)
2nd leaf blade	290 ±290	277 ±6 (96)
Ear	297 ±4*	280 ±5 (94)*
Stem	200 ±5	195 ±4 (98)
Flag leaf sheath	190 ±4	175 ±7 (92)

Values are means of three measuremets with standard errors.
* μmol O_2 (100 spikelets)$^{-1}$ h^{-1}
Fingures in the parenthesis are relative values to the control.

photosynthetic mechanism.

As for the difference between plant parts in PS response to ABA, the mechanism is not well understood. But, it is well known that anatomical structure in the ear is different from those in other plant parts. Furthermore, in the ear, there are various photosynthetic tissues such as glumes, awn, and pericarp, which are different from those in leaf blades in the structure and frequency of stomata [10,16]. The pericarp of grain has a much higher photosynthetic activity than other tissues, and almost no stomata are observed on it[16]. The different stomatal response of the ear to other plant parts is probably attributed to the different stomatal structure or different stomatal frequency of the tissues of the ear.

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*In Japanes with English summary ; **In Chinese.