

Relation between Midday Depression of Photosynthesis and Leaf Water Status in Soybean Cultivars

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Abstract : Physiological attributes relating to cultivar difference in midday depression of apparent photosynthetic rates (AP) of soybean leaves were examined in terms of leaf water status. In a 3-year experiment with 9 (1990) or 10 (1991, 1992) cultivars grown on the naturally rain-fed field and rain-intercepted field, the following parameters were measured twice a day (0900–1100 h, 1300–1500 h) : AP, stomatal conductance (Gs), water potential (Ψ_w), osmotic potential (Ψ_s), pressure potential (Ψ_p), relative water content (RWC) and exudation rate (Ex) during flowering to early podfilling. The degree of midday decline of AP (APdec), which was expressed as a ratio of AP measured at 1300–1500 h to AP at 0900–1100 h, was significantly correlated with the decline of Gs on 5 out of 9 occasions. On an occasion where the vapor pressure deficit was extremely large, the cultivar with the highest APdec (Peking) maintained higher Ψ_w compared with cultivars with lower APdec (Sogazairai etc.). When soil water availability was restricted by intercepting rainfall, Peking tended to have lower RWC and to maintain higher Ψ_p by lowering Ψ_s than Sogazairai, suggesting that leaf water status was responsible for the cultivar difference in APdec. On occasions where there was adequate rainfall, however, midday decline of AP often occurred with little decline of Ψ_w . A positive correlation of Ex with APdec and Gsdec among cultivars was observed. Thus, cultivar difference in the degree of midday depression of photosynthesis appeared to be associated with leaf water status, although other physiological attributes could often predominate, probably depending on the environmental conditions.

Key words : Cultivar difference, Diurnal change, Exudation rate, Photosynthesis, Soybean, Water potential.

ダイズ品種における光合成速度の日中の低下と葉の水分状態との関係 : 国分牧衛・島田信二 (農水省農業研究センター)

要 旨 : ダイズ個葉の光合成速度の日中の低下程度 (APdec : 午後の値/午前の値) の品種間差に關与する生理的要因を葉の水分状態に着目して解析した。ダイズ 10 品種を圃場条件で 3 年間 (1990~1992) 栽培し、葉のみかけの光合成速度 (AP), 気孔コンダクタンス (Gs), 水ポテンシャル (Ψ_w), 浸透ポテンシャル (Ψ_s), 圧ポテンシャル (Ψ_p), 相対含水率 (RWC) および茎基部からの出液速度 (Ex) を午前 (9–11 h) と午後 (13–15 h) 測定した。APdec は Gs の低下程度 (Gsdec) と 9 回の測定中 5 回品種間で有意な相関がみられた。供試品種中 APdec のもっとも大きい品種 (Peking) の Ψ_w は、飽差 (VPD) の大きい条件 (1990 年) では、APdec のもっとも小さい品種 (宗賀在来) を含む 2, 3 の他の品種に比べて高く維持されたことから、 Ψ_w の差が APdec や Gsdec の品種間差に寄与しているように思われた。降雨遮断処理条件では、Peking は宗賀在来に比べ、RWC が低く、 Ψ_s が低下して Ψ_p の低下を少なくする傾向がみられた。しかし 1991, 1992 年 (多雨条件) には、 Ψ_w の低下がほとんどなくとも AP が低下する場合がみられた。Ex と APdec および Gsdec との間には、品種間で正の相関が認められた。これらの結果は、光合成速度の日中の低下程度の品種間差は、葉の水分状態や水分吸収能と密接な関係にあるが、それ以外の要因が支配的な場合もあることを示している。

キーワード : 光合成速度, 出液速度, ダイズ, 日変化, 品種間差, 水ポテンシャル。

Decline of apparent photosynthetic rate (AP) in the late morning or in the early afternoon of sunny days, after AP peaked earlier in the day, has been observed in rice^{7,13,14}, wheat^{8,9,23}, oats¹⁶, cotton¹ and some other crops. In soybean as well, this phenomenon has been found by several workers^{6,15,17,18,20,22}. The reduction of AP amounted to 25.6% in rice which was grown in flooded conditions⁷, or 56% in well-irrigated wheat²³. We observed ca. 35% of the

reduction in naturally rain-fed soybean¹¹.

Under a controlled environment, indigenous rhythm¹⁵ or accumulation of carbohydrates²² was assumed to be responsible for the midday depression of AP. In a field where temperature can be very high with low humidity, plant water deficits, which may be caused by excessive transpiration and/or inadequate absorption of soil water, appeared to cause the midday decline of AP^{6,17}. Rawson et al.¹⁷ illustrated diurnal courses of AP for various

levels of Ψ_w from the concurrent measurements of AP and leaf water potential (Ψ_w) of field-grown soybeans. The degree of the midday decline of AP differed among cultivars²⁰⁾ or among growing conditions whether the plants were irrigated or not⁶⁾. In these observations, the AP reduction was less in a cultivar of larger root system or in a rain-fed condition which resulted in a larger root system, suggesting that high capacity for soil water absorption by extensive root system may contribute to alleviate the reduction. In the former experiment²⁰⁾, only two cultivars were compared, therefore it is not adequate to discuss the cultivar difference. On the other hand, difference in grain yield among old and new soybean cultivars was associated with cultivar differences in water-maintaining capacity⁵⁾ or water-absorbing capacity³⁾. In these studies, however, AP was not measured but estimated from other data showing the relationships between AP and leaf water status.

In the previous paper¹¹⁾, we reported that the degree of midday decline of AP differed among cultivars and that decline was associated with yield stability of a cultivar. The present study was conducted to clarify whether leaf water status is associated with the midday depression of AP in soybean cultivars.

Materials and Methods

Two experiments (Exp. 1, 2) were conducted on a loam soil (Andosol, total N 0.21%, total C 2.08%) at the National Agriculture Research Center (Kannondai, Tsukuba, Ibaraki). In Exp. 1, soybean cultivars were field grown under naturally rain-fed conditions in 1990, 1991 and 1992. Conditions of culturing remained the same in the three years. In Exp. 2, soybeans were grown on a set of framed fields (each field: 3×3 m), part of which can be automatically covered by roof whenever it rains. Exp. 2 was conducted in 1992.

1. Plant material

In Exp. 1, 9 (1990) or 10 (1991, 1992) cultivars selected on the basis of high- or low-yielding ability were sown on June 14 (1990), June 12 (1991) and June 10 (1992). Seedlings were thinned after establishment to give a plant density of 14.3 m^{-2} . Calcium carbonate (100 gm^{-2}) and compound fertilizer (3 g N, 10 g P_2O_5 , 10 g K_2O m^{-2}) were applied

before seeding. Each plot consisted of 6 rows \times 12 m long and 0.6 m apart between rows, arranged in a randomized block design with three replications.

In Exp. 2, two cultivars (Peking and Sogazairai) which revealed contrasting characteristics of AP in Exp. 1 were sown on June 23, in 50 cm row spacing with 10 cm (Peking) or 15 cm (Sogazairai) intra-row width. Calcium carbonate (100 gm^{-2}) and compound fertilizer (3 g N, 10 g P_2O_5 , 10 g K_2O m^{-2}) were applied before seeding. Each plot consisted of 1.5 m^2 with two replications. From Aug. 1 to Aug. 25, for a half of the plots, water supply was withheld by covering the plots with automatically removable roof whenever it rained. The other half was irrigated, in addition to rainfall, several times with each time supplied 10–15 mm of water. Total amount of irrigation was 75 mm and rainfall was 45.5 mm during the period.

2. Measurements

AP of intact leaves (terminal leaflet) were measured in the field using a portable CO_2 analyzer (LCA-2) with a leaf chamber (PLCB, enclosed area: 6.25 cm^2), air supply unit (ASUM2), and data logger (DL2) (The Analytical Development Co. Ltd, Hoddesdon, UK.). Air for the chamber was fed at a flow rate of 500 ml min^{-1} , through a mast that sampled air from 5 m above the canopy. Measurements of recently expanded leaves on the main stem (6 plants per plot) were made during the flowering to early pod-filling stage. The measurements of AP were undertaken twice a day (0900–1100 h, 1300–1500 h) on several (Exp. 1: 9, Exp. 2: 1) sunny days¹¹⁾. During the measurements, temperature and humidity in the plant canopy were monitored with a digital humidity meter (HN-K model, Chino Corporation, Tokyo). Soil moisture was detected diurnally by a tensiometer (DIK-3130 model, Daiki Rika, Tokyo).

Leaf water potentials (Ψ_w) of the same leaflets with AP were measured. After the measurement of AP, the leaf discs of 6 mm diameter were sampled and immediately placed in a C-52-SF sample chamber (Wescor Inc., USA). The samples were allowed to equilibrate in the chamber for three hours at 25°C , then Ψ_w was measured with a Wescor model HR-33T dewpoint microvoltmeter. In Exp. 2, the leaf chambers were frozen at

Table 1. Summary of apparent photosynthetic rate (AP) and its midday decline (APdec) of all the cultivars used, and environmental variants during the measurements (Exp. 1).

Year	Date	Time	AP		APdec		Environmental variants				Soil moisture	
			Average	Range	Average	Range	PPFD*	Temp.	RH	VPD	20cm	60cm*
			$\mu\text{mol m}^{-2}\text{s}^{-1}$		%		$\mu\text{mol m}^{-2}\text{s}^{-1}$	$^{\circ}\text{C}$	%	mmHg	pF	
1990	Aug. 7	AM	20.8	25.0—15.3			2026 ± 9	31.7	59.6	18.9	2.9	2.5
		PM	17.0	21.8—11.0	80.2	95.4—65.0	2026 ± 13	37.7	40.1	39.1	2.9	2.5
1991	July 24	AM	20.7	24.7—17.9			1886 ± 19	34.3	66.0	18.4	2.1	2.1
		PM	20.7	24.0—18.8	100.4	107.5—91.0	2159 ± 30	36.5	63.5	22.3	2.2	2.2
	Aug. 2	AM	24.9	27.4—23.4			2177 ± 22	32.4	75.5	11.9	2.9	2.4
		PM	22.8	24.2—19.7	92.1	99.9—82.7	2141 ± 17	37.1	58.1	26.4	2.9	2.4
	Aug.16	AM	25.5	29.1—19.5			2346 ± 39	27.7	73.0	10.0	2.3	2.7
		PM	23.0	26.9—18.8	90.6	97.0—83.6	2233 ± 12	27.5	64.0	13.2	2.3	2.7
	Aug.26	AM	23.2	26.4—17.9			2107 ± 10	28.2	66.2	12.9	2.1	1.8
		PM	22.0	25.5—16.5	94.9	103.1—85.8	2043 ± 24	30.4	62.5	16.3	2.1	1.7
	Aug. 7	AM	25.9	31.8—22.6			1897 ± 17	32.5	68.0	15.7	2.9	2.6
		PM	20.8	23.7—19.1	81.0	92.0—71.1	1941 ± 8	32.8	67.0	16.4	2.8	2.5
	Aug.10	AM	22.6	25.9—19.1			2255 ± 8	30.8	60.5	17.5	2.9	2.7
		PM	20.3	24.6—16.2	89.8	99.6—82.7	2233 ± 20	31.9	58.0	19.9	2.9	2.8
1992	Aug.15	AM	22.8	27.2—16.8			2373 ± 10	32.2	71.0	13.9	2.9	2.8
		PM	20.3	23.8—15.1	89.5	99.4—80.1	2341 ± 9	34.4	67.0	17.9	2.9	2.9
	Aug.26	AM	18.7	23.0—15.7			2131 ± 8	34.1	60.0	21.4	2.9	2.9
		PM	17.4	23.0—12.1	91.9	109.9—74.6	1850 ± 52	34.4	58.0	22.8	2.9	2.9

APdec = (AP measured at PM) / (AP measured at AM), %.

*Mean \pm SE. *Depth from the soil surface.

—20°C in a freezer, followed by thawing for two hours at 25°C, then osmotic potentials (Ψ_s) were measured in the same way with Ψ_w . Pressure potentials (Ψ_p) were calculated by subtracting Ψ_s from Ψ_w . In Exp. 2, 10 leaf discs of 10 mm diameter were sampled concurrently with the sampling for Ψ_w , and relative water contents (RWC) were determined. For the measurement of RWC, the discs were collected in tared sample bottles, and after the determination of fresh weight (W_f), were floated for 4 hours at a light level of $10 \mu\text{E m}^{-2} \text{s}^{-1}$, surface dried, and weighed to give the turgid weight (W_t). After oven drying at 85°C and weighing (W_d), RWC was determined: $\text{RWC} = 100(W_f - W_d) / (W_t - W_d)$.

In Exp. 1, exudation rates (Ex) from basal node of the stem were measured on Aug. 17, 1991. After cutting off the internode between 1st and 2nd trifoliate leaf node, the exudation from the section was collected into cotton wool stuffed in a 100 ml polyethylene bottle. The bottles were covered with aluminum foil to avoid solar irradiance. The cutting-off was

undertaken at 0900 h and the exudation was collected twice; 0900–1100 h and 1300–1500 h, from the same section. Ex was estimated from an increase of cotton wool weight during the two hours. Five plants were used for a cultivar.

Results and Discussion

Table 1 summarizes AP, APdec (expressed as AP at 1300–1500 h/AP at 0900–1100 h, %), and environmental conditions during the measurements. The average AP for all the cultivars was always higher in the morning than in the afternoon except on July 24, 1991. Cultivar differences in AP were significant on most occasions with the largest difference being ca. $10 \mu\text{mol m}^{-2}\text{s}^{-1}$. Harosoy, Beeson and Amsoy showed the highest AP, whereas Akazaya and Sogazairai showed the lowest. When APdec was compared over the 3 years, it was lowest in 1990, whereas it was highest in 1991, and intermediate in 1992. This yearly difference in APdec may reflect changing environmental conditions. There were cultivar

Table 2. Correlation coefficients among cultivars between AP and Gs, both of which were measured in the morning and in the afternoon (Exp.1).

Year	Date	AM	PM	Decline*
1990	Aug. 7	0.53	0.93**	0.12
1991	July 24	0.24	0.65**	0.24
	Aug. 2	0.12	0.53	-0.16
	Aug.16	0.75**	0.86**	0.75**
	Aug.26	0.53	0.85**	0.58*
1992	Aug. 7	0.49	0.55*	0.83**
	Aug.10	0.90**	0.80**	0.27
	Aug.15	0.94**	0.70*	0.74**
	Aug.26	0.92**	0.99**	0.71*

*Correlations between APdec (PM value/AM value) and Gsdec (PM value/AM value).

***Significant at $P=0.05$, 0.01 , respectively.

differences in APdec, and the largest difference amounted to ca. 30% (Aug. 7, 1990). Peking and Amsoy showed the highest APdec, whereas Sogazairai showed the lowest (for data of each cultivar, refer to the previous paper¹¹⁾).

Photosynthetic photon flux density (PPFD) was more than $1,800 \mu\text{mol m}^{-2}\text{s}^{-1}$, which is estimated to be the level of light-saturation¹⁰⁾. Since PPFD in the morning was similar to that in the afternoon, PPFD may not be responsible for the AP decline in the afternoon. In the afternoon, air temperature was higher and relative humidity was lower, which brings about a higher vapor pressure deficit (VPD) than in the morning. On Aug. 7 in 1990, VPD rose up to 39 mm Hg in the afternoon from 18.9 mm Hg in the morning. This large VPD appeared to cause the lowest APdec of the afternoon. On the other days in 1991 and 1992, VPD ranged between 10 and 26 mmHg and the decline of VPD was not apparently associated with APdec. Soil moisture was higher on July 24 and Aug. 26 in 1991. This higher soil moisture appeared to be the reason for the higher APdec on the 2 days. However, since soil moisture did not differ remarkably between the morning and the afternoon, this did not appear to be associated with the midday decline of AP. The CO_2 concentration over the plant canopy tended to decrease at midday by ca. 20%, which also may have

affected the midday AP decline to some extent. Thus diurnal change in VPD and CO_2 concentration appeared to be responsible for the diurnal change in AP on some occasions to some extent. However, a single environmental factor could not clearly explain the AP decline.

Table 2 shows correlation between AP and stomatal conductance (Gs) among cultivars. There was a significant correlation between AP and Gs on 4 (AM) or 8 (PM) out of 9 occasions. On the other hand, APdec was significantly correlated with the midday decline in Gs in 5 out of 9 measurements, and correlation tended to be closer at a later growth stage.

There is evidence that midday depression of AP or Gs is associated with leaf water status^{2,17)}. In Table 3. AP, Gs and Ψ_w , which were measured on 3 representative occasions (Aug. 7, 1990; Aug. 2, 1991; Aug. 10, 1992) are shown. In this table, 3 or 4 contrasting cultivars are shown; Peking had the highest APdec, whereas Sogazairai showed the lowest APdec, and that of Tachinagaha or Akazaya was intermediate. On Aug. 7 in 1990, Ψ_w decreased remarkably at midday, and the decrease was accompanied by the midday decline of AP and Gs. Comparing cultivars, Peking possessed higher Ψ_w with less decline in the afternoon than the other cultivars. This characteristic of leaf water status appeared to be associated with higher AP, Gs or APdec of this cultivar. On Aug. 2 in 1991, Ψ_w was relatively higher and the decline at midday was less than on Aug. 7 in 1990. The Ψ_w on Aug. 10 in 1992 was intermediate between the two days.

Boyer²⁾ reported that AP of soybean leaves, when the plants were gradually dehydrated, initiated to decline below -1.1 MPa of Ψ_w . In the present experiment, since Ψ_w of the cultivars except Peking decreased below -1.1 MPa in the afternoon, the difference in APdec between Peking and the other cultivars are likely to be due to the difference in Ψ_w . In contrast, 1991 and 1992, although Ψ_w of all the cultivars was maintained above -0.7 MPa all day, AP and Gs decreased considerably (except Gs of Tachinagaha on Aug. 2, 1991). This result cannot be explained from the Boyer's observation.

There is increasing evidence that when

Table 3. Leaf water potential (Ψ_w), AP and Gs measured in the morning and in the early afternoon on fine days (Exp.1). Measurements were made of selected cultivars on several occasions for three years. Data are expressed as mean \pm se of five plants.

Year Date Cultivar	Ψ_w		AP		Gs	
	AM	PM	AM	PM	AM	PM
	MPa		$\mu\text{molm}^{-2}\text{s}^{-1}$		$\text{molm}^{-2}\text{s}^{-1}$	
1990 Aug. 7						
Peking	-0.59 ± 0.03	-0.90 ± 0.04	21.4 ± 2.4	20.5 ± 2.3	0.61 ± 0.08	0.42 ± 0.06
Akazaya	-0.93 ± 0.06	-1.33 ± 0.07	16.1 ± 2.2	12.6 ± 1.7	0.33 ± 0.48	0.19 ± 0.27
Sogazairai	-0.80 ± 0.07	-1.33 ± 0.06	13.9 ± 2.8	9.0 ± 1.8	0.22 ± 0.07	0.16 ± 0.05
1991 Aug. 2						
Peking	-0.24 ± 0.03	-0.37 ± 0.02	23.5 ± 1.1	22.6 ± 0.7	0.59 ± 0.03	0.52 ± 0.01
Akazaya	-0.27 ± 0.05	-0.31 ± 0.05	23.4 ± 0.9	21.1 ± 0.5	0.52 ± 0.01	0.48 ± 0.01
Sogazairai	-0.42 ± 0.06	-0.61 ± 0.09	23.8 ± 1.4	19.7 ± 1.1	0.55 ± 0.02	0.47 ± 0.01
Tachinagaha	-0.34 ± 0.05	-0.39 ± 0.02	24.6 ± 1.0	22.1 ± 1.0	0.44 ± 0.03	0.47 ± 0.02
1992 Aug. 10						
Peking	-0.32 ± 0.02	-0.64 ± 0.03	25.1 ± 1.0	23.4 ± 1.1	0.67 ± 0.04	0.58 ± 0.01
Sogazairai	-0.43 ± 0.05	-0.66 ± 0.10	19.6 ± 1.1	16.2 ± 0.9	0.42 ± 0.03	0.32 ± 0.02
Tachinagaha	-0.52 ± 0.06	-0.65 ± 0.04	19.9 ± 0.8	18.9 ± 0.7	0.43 ± 0.01	0.35 ± 0.02

Table 4. Comparison of two contrasting cultivars in leaf water potential (Ψ_w), leaf osmotic potential (Ψ_s), leaf turgor potential (Ψ_p) and leaf relative water content (RWC) under the irrigated or rain-intercepted condition (Exp. 2). Measurements were made at around 1400 h on Aug.25 in 1992. Mean \pm se of 5 plants.

Cultivar	Treatment	Ψ_w	Ψ_s	Ψ_p	RWC
		MPa	MPa	MPa	%
Peking	irrigated	-0.42 ± 0.07	-1.31 ± 0.08	0.89 ± 0.05	76.8 ± 0.8
	rain int.	-0.58 ± 0.03	-1.40 ± 0.03	0.82 ± 0.02	73.3 ± 0.8
Sogazairai	irrigated	-0.39 ± 0.06	-1.31 ± 0.07	0.92 ± 0.02	82.1 ± 0.9
	rain int.	-0.58 ± 0.05	-1.32 ± 0.02	0.74 ± 0.04	80.1 ± 0.7

irrigated : Plants were irrigated several times during Aug. 1 to Aug. 25 (rain ; 45.5, irrigation ; 75mm).

rain int. : Rain was intercepted during Aug. 1 to Aug. 25.

plant roots sense water deficits chemical signals such as abscisic acid produced in the roots and translocated to the leaves can play a predominant role in stomatal closure of the plants^{4,21}). In the present experiment, since soil moisture did not significantly vary with time of day or with cultivar, it is not likely that chemical signals—the production of which might be triggered by the change in soil moisture—brought about the midday depression of AP and Gs. In our experiment, however, soil moisture was measured between rows, and intra-row moisture was not detected. Root

morphology varies with cultivar, therefore we do not abandon a possibility of signals-mediated depression of AP or Gs. Further studies are needed in this respect.

In Exp. 2, soil moisture was altered, either being irrigated or water supply being restricted by an interception of rainfall. By this treatment, Peking tended to have lower RWC, and to maintain Ψ_p higher by lowering Ψ_s under the water-restricted condition (Table 4). This osmoregulation observed in Peking could alleviate the depression of AP or Gs under dry soil condition¹²).

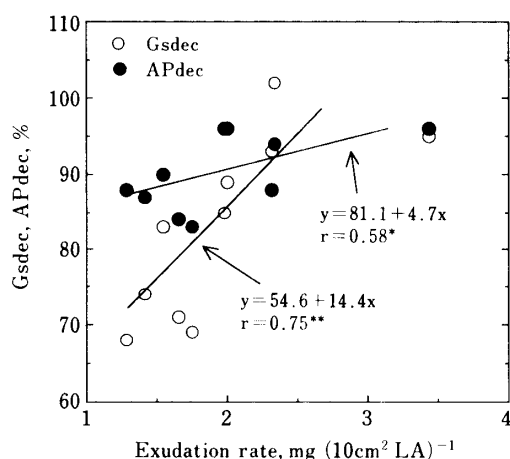


Fig. 1. Relation of exudation rate to Gsdec or APdec. Exudation of sap was collected for 2 hours (1300–1500 h) from the stem section topped between 1st and 2nd trifoliate leaf node (Exp. 1).

In soybeans, exudation rates (Ex) of sap from cut stems were positively correlated with plant water conductances, which were estimated from the measurement of transpiration rates and water potential differences between leaves and soil¹⁹⁾. In the present study, there was a clear difference in Ex among cultivars; Amsoy, Beeson, and Harosoy showed higher Ex, whereas Sogazairai and Enrei showed lower Ex. In every cultivar, Ex clearly decreased in the afternoon compared to that of the morning, but there was a positive correlation between morning and afternoon Ex among cultivars. It is noticeable that Ex was significantly correlated with APdec and Gsdec among cultivars (Fig. 1). Since the volume of exudation is only a small percentage of the total volume lost by transpiration in actively transpiring plants, the importance of the exudation is estimated to be low in the water budget of the whole plants¹²⁾. However, the positive correlation of Ex to APdec or Gsdec observed here suggests that the lesser midday depression of AP of a cultivar is attributed, to some extent, to its higher capacity of water absorption in midday.

Among the cultivars used in this study, Peking showed highest AP or Ψ_w in midday under water-stressed conditions. Nevertheless, grain yield of this cultivar was less than that of most other cultivars, particularly in years where there was plenty of rainfall¹¹⁾, as observed in our previous study. These results indicate that a cultivar with a stable AP under

water-stressed conditions does not necessarily bring about a high yield under adequate soil water conditions. In Japan, soybeans are grown predominantly on fields originally used as paddy fields, where soil water is under control. Therefore, breeding a cultivar for higher AP under optimal water conditions, rather than for stabler AP under water-stressed conditions, may result in higher grain yield.

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- * In Japanese with English summary.
** In Japanese with English abstract.
*** Translated from Japanese by the present authors.