Diurnal Change of Photosynthesis and Its Relation to Yield in Soybean Cultivars

Makie KOKUBUN and Shinji SHIMADA

(National Agriculture Research Center, Kannondai, Tsukuba, Ibaraki 305 Japan)

Received July 14, 1993

Abstract : Apparent photosynthetic rates (AP) of plant leaves often decline in midday even when solar radiation is adequate. The objective of this study was to determine whether this phenomenon is responsible for the cultivar differences in growth and yield of soybean (*Glycine max* (L.) Merr.). In a 3 year experiment using nine (1990) or ten (1991, 1992) cultivars, the association of the following parameters with growth and yield of cultivars was examined: APam (AP measured about 10h), APpm (AP measured about 14h), daily mean AP ($[APam + APpm]/2$) or APdec ($APpm/APam$, %) during flowering to early pod-filling. Cultivar differences in these parameters were observed and the ranking among cultivars tended to be consistent, although the significance varied with the day or year. None of the parameters were consistently correlated with growth rates or yields across cultivars. For each cultivar, however, yearly variation in yield closely corresponded to variation in APdec. The results suggest that less decline of midday photosynthesis contributes to yield stability in soybean cultivars.

Key words : Diurnal change, Photosynthesis, Soybean, Yield.

ダイズ品種における光合成速度の日変化と収量との関係: 国分牧衛・島田信二 (農水省農業研究センター)

要 旨 : ダイズ個葉のみかけの光合成速度 (AP) は、晴天日には光強度が十分であるにもかかわらず日中低下することが知られているが、この現象がダイズの収量にどのように関係しているかは不明である。本研究では、収量性の異なるダイズ品種を圃場条件で3年間(1990年: 9品種, 1991年: 10品種, 1992年: 10品種)栽培し、APの午前値 (APam, 10時頃に測定)、午後の値 (APpm, 14時頃に測定)、日平均値 ($[APam + APpm]/2$) あるいは午後の低下程度 (APdec, $APpm/APam$, %) を測定し、これらのパラメーターと生長速度および収量との関係を解析した。APam, APpm, 日平均値及び APdec には、年次や測定日による変動はあるものの、有意な品種間差がみられ、それらの品種間順位は概ね安定していた。APam, APpm, 日平均値及び APdec のいずれのパラメーターも、生長速度及び収量と明瞭な相関関係になかった。しかし、各品種における APdec と収量の年次間変動はよく対応していた。本研究の結果は、日中の光合成速度の低下を軽減することは、ダイズ品種の収量安定性に寄与することを示唆している。

キーワード : 光合成, 収量, ダイズ, 日変化,

Depression of apparent photosynthetic rate (AP) in the late morning or in the early afternoon after its peak in the morning has been observed in rice^{10,16,18}, wheat^{11,13,24,29}, barley²¹, cotton¹, and in other crops. The decline of photosynthetic rate at midday amounted to ca. 26% in rice¹⁰, and ca. 56% in wheat²⁹, even where the plants were well irrigated. Soybean also has exhibited this phenomenon^{8,9,17,20,22,23,26,28}.

This decline of carbon gain, particularly during the flowering to early pod-filling stage, could cause adverse effects on pod-setting and thereby yield which are strongly dependent on the amount of carbon assimilation during that time¹⁴. However, information on how this depression differs among soybean cultivars is very limited^{17,22}, and data on how this phenomenon relates to yield are not available.

In this study, we grew soybean cultivars with different yielding ability in the field for

three years, and examined 1) whether cultivar difference in the degree of the decline exists, and 2) how the difference, if any, associates with differences in growth and yield among the cultivars or years.

Materials and Methods

Experiments were conducted on a loam soil (Aondosol, total N 0.21%, total C 2.08%) at the National Agriculture Research Center (Kannondai, Tsukuba, Ibaraki), during 1990, 1991, and 1992. The three years had contrasting weather during growing season (Table 1). Cultural conditions were the same in the three years. Comparisons of AP, growth and yield were made separately for early-maturity cultivars and late-maturity ones.

1. Plant material

Nine (1990) and ten (1991, 1992) cultivars selected on the basis of high- or low-yielding ability (Table 2) were sown on June 14

Table 1. Monthly mean air temperature and monthly precipitation during the growth season for three years (Kannondai, Tsukuba).

	1990			1991			1992		
	July	Aug.	Sep.	July	Aug.	Sep.	July	Aug.	Sep.
Temperature, °C	23.8	26.9	23.1	24.6	23.8	22.3	23.7	25.4	21.3
Precipitation, mm	52.0	90.5	195.5	127.0	184.0	419.0	74.5	45.5	81.0

Table 2. Year released, dates of initial flowering (50% plants) and maturity, and grain yield of cultivars used.

Cultivar	Released year*	Flowering			Maturity			Yield		
		1990	1991	1992	1990	1991	1992	1990	1991	1992
Early maturity								gm ⁻²		
Harosoy	1951	Jul 18	Jul 18	Jul 20	Sep 24	Sep 30	Sep 20	273a	337ab	268b
Beeson	1968	—	Jul 17	Jul 19	—	Oct 1	Sep 20	—	313bc	257b
Amsoy	1966	Jul 19	Jul 18	Jul 20	Sep 25	Oct 2	Sep 21	267a	337ab	245b
Norin No. 2	1940	Jul 26	Jul 28	Jul 30	Sep 29	Oct 5	Sep 26	289a	323b	304b
Peking	IC	Aug 1	Aug 2	Aug 3	Sep 27	Oct 10	Sep 26	267a	268c	268b
Enrei	1971	—	Jul 27	Jul 29	—	Oct 10	Oct 1	—	366a	380a
Tosan No. 89	BL	Jul 27	—	—	Sep 28	—	—	257a	—	—
Late maturity										
Tachinagaha	1986	—	Jul 27	Jul 30	—	Oct 20	Oct 9	—	373a	334a
Tachiyutaka	1987	—	Jul 29	Jul 31	—	Oct 20	Oct 8	—	336ab	306a
Nanguntakedate	IC	Jul 27	—	—	Oct 20	—	—	263a	—	—
Akazaya	IC	Aug 2	Aug 4	Aug 7	Oct 21	Oct 26	Oct 19	318a	362a	298a
Sogazairai	IC	Aug 1	Aug 3	Aug 5	Oct 23	Oct 26	Oct 22	317a	329b	262a
Bragg	1963	Aug 8	—	—	Nov 6	—	—	311a	—	—

* ; Year released in USA or Japan. IC ; Indigenous cultivar, BL ; Breeding line.

Within columns of each maturity group, values followed by the same letter are not significantly different by Duncan's multiple range test ($p=0.05$).

(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 gN , $10 \text{ g P}_2\text{O}_5$, $10 \text{ g K}_2\text{O m}^{-2}$) 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.

2. Measurement of Photosynthetic rate

AP of intact leaves (terminal leaflet) was 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. In 1991, leaves 3 nodes below the most recently expanded leaves were also measured in Peking and Sogazairai.

In 1990, in order to determine the time of a day for the measurement of AP, the diurnal change of AP of cv Tachinagaha was measured on several days. For the cultivar comparison, AP of all the cultivars was measured twice a day (ca. 10h, 14h) on several sunny days (Tables 3 and 4).

3. Measurement of growth and yield

For the measurements of growth parameters, subsamples of plants were harvested on July 17 and Aug. 28 for all the cultivars in 1991. In 1992, plants were sampled on July 24 and Aug. 11 for early-maturity cultivars, and

Table 3. Cultivar difference in leaf photosynthetic rate measured in the morning (APam).

Cultivar	1990		1991				1992				
	Aug 7	Jul 24	Aug 2	Aug 16	Aug 26	Av.	Aug 7	Aug 10	Aug 15	Aug 26	Av.
$\mu \text{ mol m}^{-2} \text{ s}^{-1}$											
Early maturity											
Harosoy	25.0a	21.5bc	23.9b	28.8a	25.2a	24.8a	28.9bc	25.9a	27.0a	20.8ab	25.7a
Beeson	—	23.5ab	24.3ab	29.1a	24.4a	25.3a	30.2ab	24.9ab	26.3a	18.7bc	25.0ab
Amsoy	24.4ab	24.7a	24.8ab	27.6ab	24.9a	25.5a	31.8a	24.7ab	27.2a	19.0bc	25.7a
Norin No. 2	22.7ab	19.5c	25.7ab	26.9abc	21.4b	23.4a	26.9cd	21.9bc	23.4b	20.9ab	23.3ab
Peking	21.2b	19.1c	23.5b	24.7c	24.2a	22.9a	24.9de	25.1ab	25.2ab	23.0a	24.6ab
Enrei	—	19.4c	27.1a	25.5bc	23.9ab	24.0a	23.0e	20.1c	19.3c	16.0c	19.6b
Tosan No. 89	21.1b	—	—	—	—	—	—	—	—	—	—
Late maturity											
Tachinagaha	—	19.3ab	24.9ab	24.0ab	23.3ab	22.9ab	23.7a	19.9b	21.9a	16.7ab	20.6a
Tachiyutaka	—	21.3a	27.4a	25.9a	26.4a	25.3a	24.5a	24.4a	21.6a	19.7a	22.6a
Nanguntakedate	22.2a	—	—	—	—	—	—	—	—	—	—
Akazaya	16.1b	17.9b	23.4b	19.5c	17.9c	19.7b	22.6a	19.1b	16.8b	17.0ab	18.9a
Sogazairai	15.3b	20.7a	23.8b	22.8b	20.3bc	21.9ab	22.6a	19.6b	19.2ab	15.7b	19.3a
Bragg	19.7ab	—	—	—	—	—	—	—	—	—	—

Av.: Average of all the measurements of each year.

Within columns of each maturity group, values followed by the same letter are not significantly different by Duncan's multiple range test ($p=0.05$).

Table 4. Cultivar difference in leaf photosynthetic rate measured in the early afternoon (APpm).

Cultivar	1990		1991				1992				
	Aug 7	Jul 24	Aug 2	Aug 16	Aug 26	Av.	Aug 7	Aug 10	Aug 15	Aug 26	Av.
$\mu \text{ mol m}^{-2} \text{ s}^{-1}$											
Early maturity											
Harosoy	18.3ab	21.3ab	23.9a	26.9a	25.0a	24.3a	20.6ab	23.8ab	21.6ab	18.6b	21.2ab
Beeson	—	22.5a	24.2a	25.6abc	25.0a	24.3a	21.6ab	20.7bc	23.8a	19.6b	21.4ab
Amsoy	21.8a	20.9ab	23.3a	26.6ab	25.5a	24.1a	23.7a	24.6a	23.7a	20.9ab	23.2a
Norin No. 2	15.6b	20.5b	22.9a	22.6cd	21.2b	21.8a	19.5b	18.9c	20.3ab	20.9ab	19.9bc
Peking	21.8a	19.7b	22.6a	23.6bcd	23.4a	22.3a	21.7ab	23.4ab	21.5ab	23.0a	22.4ab
Enrei	—	20.4b	24.2a	21.3d	21.0b	21.7a	19.1b	18.3c	18.0b	15.3c	17.7c
Tosan No. 89	17.8ab	—	—	—	—	—	—	—	—	—	—
Late maturity											
Tachinagaha	—	19.2a	22.1ab	21.0ab	21.3ab	20.9ab	20.5a	18.9b	20.7a	13.4ab	18.4a
Tachiyutaka	—	20.0a	24.1a	23.2a	22.6a	22.5a	21.0a	22.1a	21.5a	17.1a	20.4a
Nanguntakedate	16.4a	—	—	—	—	—	—	—	—	—	—
Akazaya	12.1ab	18.6a	21.1b	18.8b	16.5b	18.8b	19.3a	16.2b	15.1b	12.7b	15.8a
Sogazairai	9.5b	18.8a	19.7b	19.7b	17.5b	18.9b	20.8a	16.2b	16.8b	12.9b	16.7a
Bragg	16.6a	—	—	—	—	—	—	—	—	—	—

Av.: Average of all the measurements of each year.

Within columns of each maturity group, values followed by the same letter are not significantly different by Duncan's multiple range test ($p=0.05$).

on July 30 and Aug. 19 for late-maturity cultivars, respectively. After harvest of 10 plants of each plot at each sampling time, leaf areas and dry weights of the plant parts were determined, following drying them at 70°C. Crop growth rates (CGR) and net assimilation rates (NAR) were calculated on a shoot dry weight basis. At maturity, seed yields were measured on the central 4.2 m² of each plot.

Results

1. Climate, growth stage and yield

In 1990, it was very hot and rained less than usual until early pod-filling but substantial rain occurred during late pod-filling and maturity (Table 1). The hot and dry conditions appeared to cause severe water stress in plants and reduced the yields considerably. In contrast there was constant rainfall during the

growing season in 1991, so that yields were highest among the three years, although heavy rain occurred at maturity. In 1992, it rained less than usual throughout the growing season resulting in the lowest yield in the three years for some cultivars.

Plants tended to initiate flowering earlier in 1990 than in 1991 and 1992 (Table 2). Maturity time was earlier in 1990 and 1992 than 1991, probably because the dry conditions shortened the pod-filling duration in the former two years.

Yields tended to be higher in 1991 than in 1990 and 1992, reflecting the differences in rainfall during flowering to early pod-filling (Table 2). In comparison with 1990 and 1992, yields of late-maturing cultivars were higher in 1990 than in 1992, probably due to differences in rainfall at the late pod-filling stage.

2. APam, APpm and APdec

Diurnal course of AP and PPFD measured on July 27 and August 14 of 1990 is illustrated in Fig. 1. AP in the late morning tended to be higher than that of the early afternoon even though PPFD (photosynthetic photon flux density) was comparable in the two durations. PPFD incident on the leaf chamber ranged from 1,700 to 2,200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during 9-15h, which should be greater than the light saturation requirement for AP¹⁴. The daily maximum of AP tended to be around 8h, but the duration exhibiting the maximum value was not long enough to measure all the cultivars. Therefore, 10h and 14h were selected for the cultivar comparison. Each measurement of 9 or 10 cultivars (6 leaves for each cultivar) took about 40 minutes.

On many occasions, there were significant differences in APam among cultivars. In 1990, in early-maturity cultivars, APam of Harosoy exceeded that of Peking and Tosan No.89, while in the late-maturity group Nanguntakedate exceeded Akazaya and Sogazairai (Table 3). In 1991, APam of Harosoy, Beeson and Amsoy tended to be higher than that of Norin No.2, Enrei, and Peking, although the cultivar difference was not statistically significant as an average of four occasions. In 1991, Tachiyutaka had the highest APam among the late maturity-cultivars, followed by Tachinagaha with Akazaya having the lowest APam. The results in 1992 were generally

Fig. 1. Diurnal course of apparent photosynthetic rate (AP) and photosynthetic photon flux density (PPFD). Measurements were made on recently developed leaves of soybean (cv Tachinagaha) on two sunny days (July 27, August 14) in 1990.

similar to those of 1991. Thus ranking of APam among cultivars appeared to be relatively consistent through the three years.

There were cultivar differences in APpm, although they were not always statistically significant (Table 4). Through the three years, Harosoy, Beeson, Amsoy and Peking of the early-maturity cultivars, and Tachiyutaka of the late-maturity cultivars had higher APpm values than the other cultivars. The cultivar ranking of APpm tended to be similar to that of APam.

AP tended to decline in early afternoon, and the degree of the decline (APdec) varied with cultivar and year (Table 5). The yearly variation reflected the weather condition of each year; the decline was moderate in 1990 and 1992 but slight in 1991. In 1990, AP declined remarkably in all cultivars measured. Sogazairai had the lowest APdec (62%) whereas Peking had the highest (103%), although the cultivar difference was not statistically significant. In 1991 APdec values tended to be high with only small differences among cultivars, however, Sogazairai had smaller average values than Harosoy, Amsoy and Peking which had values close to 100%. In 1992 APdec values were intermediate between 1990 and 1991. Cultivars with the

Table 5. Cultivar difference in midday decline of leaf photosynthetic rate (APdec).

	1990		1991				1992				
Cultivar	Aug 7	Jul 24	Aug 2	Aug 16	Aug 26	Av.	Aug 7	Aug 10	Aug 15	Aug 26	Av.
	%										
Early maturity											
Harosoy	73a	104a	100a	95abc	99a	100a	71c	92a	77a	90b	83a
Beeson	—	96a	100a	88abc	103a	97a	72c	84a	91a	106a	88a
Amsoy	89a	97a	95ab	97a	102a	98a	75bc	96a	86a	111a	92a
Norin No. 2	69a	105a	89b	84bc	102a	95a	72c	85a	87a	100ab	86a
Peking	103a	103a	97a	96ab	97ab	98a	88a	97a	86a	100ab	93a
Enrei	—	106a	89b	84c	89b	92a	85a	91a	85a	96ab	89a
Tosan No. 89	85a	—	—	—	—	—	—	—	—	—	—
Late maturity											
Tachinagaha	—	100ab	89a	88a	92a	92ab	86a	96a	95a	81a	89a
Tachiyutaka	—	95ab	88a	90a	86a	90ab	86a	91a	100a	88a	92a
Nanguntakedate	74a	—	—	—	—	—	—	—	—	—	—
Akazaya	75a	108a	90a	97a	91a	97a	86a	79a	93a	73a	83a
Sogazairai	62a	91b	83a	87a	89a	88b	93a	87a	88a	76a	86a
Bragg	84a	—	—	—	—	—	—	—	—	—	—

APdec; $[(APpm)/(APam)] \times 100$. Av.; Average of all the measurements of each year.

Within columns of each maturity group, values followed by the same letter are not significantly different by Duncan's multiple range test ($p=0.05$).

greatest average values were Amsoy, Peking among the early-maturity group, and Tachiyutaka for the late-maturity cultivars. Harosoy, Norin No.2, Akazaya, and Sogazairai had the lowest APdec values. Through the three years, Peking had the highest APdec, followed by Amsoy, whereas Sogazairai had the lowest APdec among all of the cultivars.

In the study comparing leaves 3 nodes (N-3) below the most recently expanded leaves (N), APdec of N-3 was about 10% points lower than N for both cultivars (Table 6).

3. Relation of APam, APpm, mean AP and APdec to growth parameters and yield

Correlations among cultivars between APam, APpm, daily mean AP ($[APam + APpm]/2$) or APdec and CGR, NAR, or yield were calculated for each maturity group (Table 7). APam, APpm, mean AP and APdec were averages of four dates both in 1991 and 1992 (as shown in Tables 3, 4, 5). CGR and NAR were calculated from the data on July 17 and Aug. 28 in 1991, on July 24 and Aug. 11 in 1992 for the early cultivars, and on July 30 and Aug. 19 in 1992 for the late cultivars. The periods correspond to the stage of early flowering to early pod-filling which is very critical for yield determination¹⁴.

The correlation of APam with growth parameters or yield was generally poor. There was a positive correlation between APam and

Table 6. Effect of leaf position on APam, APpm and APdec for two cultivars.

Cultivar	N	N-3
Peking		
APam, $\mu\text{mol m}^{-2}\text{s}^{-1}$	24.7 ± 0.53	18.6 ± 2.31
APpm, $\mu\text{mol m}^{-2}\text{s}^{-1}$	23.6 ± 0.74	15.5 ± 1.25
APdec, %	95.5	83.4
Sogazairai		
APam, $\mu\text{mol m}^{-2}\text{s}^{-1}$	22.8 ± 1.21	18.9 ± 2.59
APpm, $\mu\text{mol m}^{-2}\text{s}^{-1}$	19.8 ± 1.33	14.7 ± 3.53
APdec, %	86.5	77.9

Mean $\pm$ se ($n=6$).

Measurements were made of two leaf positions (N: most recently developed leaf, N-3: leaf on the three nodes lower than N) of each cultivar on Aug. 16, 1991.

NAR but the correlation was significant only for the early-maturity group of 1991. A negative correlation between APam and yield of the early-maturity cultivars was detected only in 1992. This correlation reflects the contrasting performance of a few cultivars: Peking maintained relatively higher APam with the lowest yield, whereas Enrei performed reverse. However, this correlation was not observed in 1991.

The correlations of APpm and daily-mean AP with growth parameters or yield were relatively more significant than APam, but the

Table 7. Correlations between APam, APpm, mean AP or APdec and growth parameters or yield. Correlations were calculated across cultivars of each maturity group (early or late). APam, APpm, mean AP and APdec are averages of four measurements (1991: Jul.24, Aug.2, Aug.16, Aug.26; 1992: Aug.7, Aug.10, Aug.15, Aug.26), and growth parameters are the values of the period from early flowering to pod elongation.

	Cultivar	1991			1992		
		CGR	NAR	Yield	CGR	NAR	Yield
APam	Early maturity	0.05	0.97**	0.45	-0.78	0.50	-0.98**
	Late maturity	-0.64	0.39	-0.22	0.11	0.60	0.45
APpm	Early maturity	-0.43	0.89**	0.01	-0.85*	0.44	-0.95**
	Late maturity	-0.12	0.36	-0.36	0.89*	0.97**	0.79*
Mean AP	Early maturity	-0.22	0.96**	0.23	-0.83*	0.49	-0.99**
	Late maturity	-0.52	0.40	-0.26	0.12	0.64	0.46
APdec	Early maturity	-0.81	0.38	-0.53	-0.31	-0.08	-0.06
	Late maturity	-0.01	0.15	0.78	0.39	0.78	0.45

*, **: Significant at 5, 1% level, respectively.

Mean AP: (APam + APpm) / 2.

tendency was not consistent among maturity groups or years. The only consistent correlation was between APpm or mean AP and NAR, although it was not always significant.

There was no significant correlation between APdec and growth parameters or yield in either maturity group or year.

For each cultivar, however, yearly variation in yield clearly corresponded to that of APdec (Fig. 2).

Discussion

Since ranking of APam, APpm and APdec among cultivars tended to be consistent regardless of growth stage and year (Tables 3, 4, 5), APam, APpm and APdec can be evaluated as genetic traits.

APam, APdec and yield of six cultivars which were commonly evaluated in the three years are summarized in Fig. 2. Among cultivars used, both Harosoy and Amsoy possessed highest APam with less yearly variation, but Amsoy showed higher APdec than Harosoy. Sogazairai was characterized as having the lowest APam and with a substantial variation in APdec. Norin No.2 and Peking showed intermediate APam, and APdec of Peking varied much less than Norin No.2 or any other cultivars.

APdec of 1990, which was measured only on Aug. 7, was lowest in the three years,

Fig. 2. Yearly change of yield (bars), APam and APdec for six soybean cultivars.

probably reflecting the least rainfall in August. The yields of 1990, however, were not necessarily lower than those of 1992, where rainfall in August was similarly very limited. Much rainfall recorded in September might have alleviated the yield reduction in 1990, particularly in the late-maturity cultivars.

Factors affecting midday depression of AP in soybean have been examined by many workers. Under controlled environments, AP decline at midday appeared to be induced by an endogenous rhythm²⁰⁾, or accumulation of carbohydrates²⁸⁾. However, in the field where environmental factors fluctuate with time, clear explanation seems to be difficult. Plant water deficits, which often occur due to strong atmospheric demand of transpiration, could be responsible for the midday decline of

AP^{9,17,22}). From many measurements of diurnal changes of AP and water potential of plants, Rawson et al.²²) described several types of diurnal patterns of AP vs. leaf water potentials. Some reports showed that the magnitude of midday decline of AP varied with cultivar²⁶) or irrigation/nonirrigation condition⁹). In both studies, a more extensive rooting system, due to cultivar differences or growth under rain-fed conditions rather than irrigated conditions, alleviated the degree of the decline. These results suggest that the leaf water status, which should be closely associated with the extent of the rooting system, was responsible for the midday depression of AP. Nevertheless, we do not ascribe the AP decline solely to leaf water status, because recent evidence indicates leaf photosynthesis can be affected by changes in soil water status with no detectable change in leaf water status²⁷). In fact, AP decline was not always accompanied by concurrent decline of leaf water potential in the present study (data are not shown).

In the present study, we failed to detect a clear relation between cultivar differences in AP_{am}, AP_{pm}, daily-mean AP or AP_{dec} and differences in CGR or NAR, all of which were measured during the growth period most critical to yield determination. In a year or maturity group, there were significant correlations between the photosynthetic parameters and growth parameters or yields, but the correlations were not observed in the other year or maturity group. This lack of consistent correlation between AP_{am} and CGR or NAR has been observed in other studies^{5,12,15}), but the relation of AP_{dec} to the growth parameters has not been reported.

Cultivar difference in AP_{am} or AP_{dec} did not correspond to that of yield. This obscure association of AP_{am} or AP_{dec} with yield appears to reflect a similar poor relation of these parameters to the growth parameters. Correlations between AP_{am} and yield across cultivars have been found to be significantly positive^{3,19}) or nonsignificantly correlated^{4,5,7,15}). Our results agree with the latter group of reports.

In an experiment comparing old and new cultivars, Boyer et al.²) examined the association of afternoon water deficits with yield and found that new cultivars with higher yields experienced smaller afternoon water deficits

than old cultivars having lower yields. In that study, AP was not measured but was estimated from the relation between AP and leaf water potentials which was drawn from another experiment. In another experiment comparing the drought tolerant cultivar PI416937 with Forrest under drought conditions, Slone et al.²⁵) found that PI416937 retained higher turgor potential and relative water content, by lowering leaf osmotic potential. The authors suggested that this may have contributed to the smaller yield reduction of this cultivar under water-stressed conditions. In that experiment leaf water potentials were not different between the two cultivars. Frederich et al.⁶) compared the water status of old and new soybean cultivars. They found that the new cultivars (Williams 82, Clark) maintained higher leaf water potentials and leaf osmotic potentials than did an old cultivar (Dunfield) regardless of irrigation/nonirrigation, but turgor potentials did not differ among the cultivars. Thus factors affecting cultivar difference in productivity under water-stressed condition have not been clearly identified, so that more detailed research is required.

In this study, we observed no association between cultivar differences in AP_{am} and AP_{dec} and grain yield. It is notable, however, that yearly variation in yield corresponded to that of AP_{dec}, that is, a higher AP_{dec} brought about a higher yield within cultivars, as shown in Fig. 2. Therefore, we conclude that reducing the afternoon decline in AP, either genetically or agronomically, can cause yield stability but not necessarily bring about yield increase in soybeans.

Acknowledgments

We thank H. Shibata, M. Sato, T. Nishizawa, S. Yamashita for their help with the measurements.

References

1. Baker, D.N. 1965. Effects of certain environmental factors on net assimilation in cotton. *Crop Sci.* 1: 83—87.
2. Boyer, J.S., R.R. Johnson and S.G. Saupe 1980. Afternoon water deficits and grain yields in old and new soybean cultivars. *Agron. J.* 72: 981—986.
3. Buttery, B.R., R.I. Buzzell and W.I. Findlay 1981.

- Relationships among photosynthetic rate, bean yield and other characters in field-grown cultivars of soybean. *Can. J. Plant Sci.* 61 : 191—198.
4. Curtis, P.E., W.L. Ogren and R.H. Hageman 1969. Varietal effects in soybean photosynthesis and photorespiration. *Crop Sci.* 9 : 323—327.
 5. Ford, D.M., R. Shibles and D.E. Green 1983. Growth and yield of soybean lines selected for divergent leaf photosynthetic ability. *Crop Sci.* 23 : 517—520.
 6. Frederick, J.R., J.T. Wooley, J.D. Hesketh and D. B. Peters 1990. Water deficit development in old and new soybean cultivars. *Agron. J.* 82 : 76—81.
 7. Gay, S., D.B. Egli and D.A. Reicosky 1980. Physiological aspects of yield improvement in soybeans. *Agron. J.* 72 : 387—391.
 8. Gao, H., Q. Zhou and B. Cheng 1992. The different types of diurnal course of photosynthesis of soybean (*Glycine max* (L.) Merr.) leaves and related factors. *Soybean Sci.* 11 : 219—225.***
 9. Huck, M.G., K. Ishihara, C.M. Peterson and T. Ushijima 1983. Soybean adaptation to water stress at selected stages of growth. *Plant Physiol.* 73 : 422—427.
 10. Ishihara, K. and K. Saitoh 1987. Diurnal courses of photosynthesis, transpiration, and diffusive conductance in the single-leaf of the rice plants grown in the paddy field under submerged condition. *Jpn. J. Crop Sci.* 56 : 8—17.*
 11. Johnson, R.C., R.E. Witters and A.J. Cihra 1981. Daily patterns of apparent photosynthesis and evapotranspiration in a developing winter wheat crop. *Agron. J.* 73 : 414—418.
 12. Kaplan, S.L. and H.R. Koller 1977. Leaf area and CO₂-exchange rate as determinants of the rate of vegetative growth in soybean plants. *Crop Sci.* 17 : 35—38.
 13. Koh, S. and A. Kumura 1973. Studies on matter production in wheat plant. I. Diurnal changes in carbon dioxide exchange of wheat plant under field conditions. *Proc. Crop Sci. Soc. Jpn.* 42 : 227—235.*
 14. Kokubun, M. 1988. Design and evaluation of soybean ideotypes. *Bull. Tohoku Natl. Agric. Exp. Stn.* 77 : 77—142.*
 15. ———, H. Mochida and Y. Asahi 1988. Soybean cultivar difference in leaf photosynthetic rate and its relation to seed yield. *Jpn. J. Crop Sci.* 57 : 743—748.
 16. Kuroda, E. and A. Kumura 1989. Single leaf photosynthesis of rice plants under field conditions. III. Variation in single-leaf photosynthesis with time of day and its physiological base. *Jpn. J. Crop Sci.* 58 : 617—622.**
 17. Larson, E.M., J.D. Hesketh, J.T. Woolley and D. B. Peters 1981. Seasonal variations in apparent photosynthesis among plant stands of different soybean cultivars. *Photosynthesis Res.* 2 : 3—20.
 18. Murata, Y. 1961. Studies on the photosynthesis of rice plants and its culture significance. *Bull. Natl. Inst. Agric. Sci.* D9 : 1—169.*
 19. Ojima, M. 1972. Improvement of leaf photosynthesis in soybean varieties. *Bull. Natl. Inst. Agric. Sci.* D23 : 97—154.*
 20. Pallas, J.E., Jr. 1973. Diurnal changes in transpiration and daily photosynthetic rate of several crop plants. *Crop Sci.* 13 : 82—84.
 21. Pitman, M.G., U. Luttge, A. Lauchli and E. Ball 1975. Diurnal changes in photosynthetic capacity of barley leaves. *Aust. J. Plant Physiol.* 2 : 101—103.
 22. Rawson, H.M., N.C. Turner and J.E. Begg 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits. IV. Photosynthesis, transpiration and water use efficiency of leaves. *Aust. J. Plant Physiol.* 5 : 195—209.
 23. Sakamoto, C.M. and R.H. Shaw 1967. Apparent photosynthesis in field soybean communities. *Agron. J.* 59 : 73—75.
 24. Sawada, S. 1978. On midday depression of photosynthesis in wheat seedlings. *Jpn. J. Crop Sci.* 47 : 18—24.
 25. Slone, R.J., R.P. Patterson and T.E. Carter, Jr. 1990. Field drought tolerance of a soybean plant introduction. *Crop Sci.* 30 : 118—123.
 26. Turner, N.C., J.E. Begg, H.M. Rawson, S.D. English and A.B. Hearn 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits. III. Components of leaf water potential, leaf conductance, ¹⁴CO₂ photosynthesis and adaptation to water deficits. *Aust. J. Plant Physiol.* 5 : 179—194.
 27. ——— 1986. Crop water deficits : A decade of progress. *Adv. Agron.* 39 : 1—51.
 28. Upmeyer, D.J. and H.R. Koller 1973. Diurnal trends in net photosynthetic rate and carbohydrate levels of soybean leaves. *Plant Physiol.* 51 : 871—874.
 29. Xu, H., A. Kumura, T. Yamagishi and R. Ishii 1990. 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. *Jpn. J. Crop Sci.* 59 : 830—837.

* In Japanese with English summary.

** In Japanese with English abstract.

*** In Chinese with English summary.