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Correlation between Yielding Ability and Dry Matter Productivity during Initial Seed Filling Stage in Various Soybean Genotypes

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Abstract : The critical developmental stage, during which the genotypic difference in yield is determined, was identified by analyzing the correlations between seed yield and seasonal crop dry matter productivity in optimally managed fields in four seasons. The fields (fluvial sandy loam or clay loam) were managed with irrigation, pest and weed control and canopy support to prevent lodging whenever necessary. The tested genotypes included 11 Japanese old and modern cultivars, five US cultivars and one non-nodulating line. Four to eight cultivars were studied in each year. Seed yield with 15% moisture (Y) in each experimental plot varied from 255 to 498g m^{-2}. The US cultivars and Japanese modern cultivars tended to have a higher yield than the other cultivars grown in the same year. Y significantly and positively correlated with crop growth rate (CGR) during the 20 d period after the beginning of seed filling (R5), i.e. initial seed filling stage, in all four experiments. On the other hand, correlation of seed yield with CGR before or after this period varied with the year from negative to positive correlations. A close correlation was also observed between pod growth rate during the initial seed filling and Y. These results suggest that the critical stage during which seed yield potential of soybean cultivars is determined is the initial seed filling period and the larger dry matter production during this period is closely associated with the satisfactory growth of reproductive organs and high seed yield.

Key words : Cultivar difference, Dry matter productivity, *Glycine max.* L., Initial seed filling, Soybean, Yield potential.

The yield potential of current soybean is lower than that of major cereal crops. Although the low yield of soybean is generally related to protein and lipid accumulation, which requires more photosynthates than carbohydrate accumulation, soybean seems to have a lower yield than high-yielding rice even on a glucose equivalent basis (Shiraiwa, 2002). However the growth processes which limit yield of soybean are not fully understood.

In rice, Horie (2001) proposed that the cultivar differences in yield are closely associated with differences in crop growth rate (CGR) during the two weeks before anthesis. He suggested that growth activity in this period would have a critical impact on the formation of both sink and source including the formation of spikelets viable for grain filling, non-structural carbohydrate to be utilized for initial grain filling and construction of photosynthetic apparatus for assimilate supply during grain filling.

Elucidation of this important period for yield determination will provide insight into the processes that limit the yield potential. In soybean, variation in yield is generally correlated with either pod number or seed number. Several studies that focused on development of reproductive organs revealed that the assimilate supply during flowering and pod set contributed highly to high yield (Schou et al., 1978; Kokubun and Watanabe, 1983; Kokubun, 1988; Egli and Yu, 1991; Board and Harville, 1993; Jiang and Egli, 1995). Recently, a higher number of florets, which would be supported by assimilate supply around the beginning of flowering or even earlier, has been suggested to contribute to improvement of yield (Kohri et al., 1998). In a review of soybean yield potential, Kokubun (2001) stated that assimilate supply during the period from flowering to the beginning of linear seed growth would limit yield mainly through pod formation. These studies suggested the importance of dry matter productivity before the beginning of seed filling. On the other hand, it has been reported that the cultivar difference in seed yield was apparently associated with differences in dry matter production during seed filling when the number of pods is primarily determined (Shiraiwa and Hashikawa, 1995; Specht et al., 1999; Kumudini et al., 2001). Thus the critical stage for yield determination in soybean has not been specified, nor has the existence of such a common stage been confirmed.

This study was conducted to examine whether yield variation among soybean cultivars grown under

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Table 1. Phenological records and seed yield of tested cultivars under optimally managed field conditions at Kusatsu in 1989, Azuchi in 1991, and Kyoto in 2000 and 2001.

Cultivar	Code	Type	Beginning of seed filling (R5)				Maturity (R8)				Grain yield (g m^{-2} with 15% moisture)			
			1989 Kusatsu	1991 Azuchi	2000 Kyoto	2002 Kyoto	1989 Kusatsu	1991 Azuchi	2000 Kyoto	2002 Kyoto	1989 Kusatsu	1991 Azuchi	2000 Kyoto	2002 Kyoto
Enrei	E	Jpn. modern det.*	16 Aug.	22 Aug.	11 Aug.	-	7 Oct.	14 Oct.	12 Oct.	-	461	381	288	-
Tachinagaha	Tc	Jpn. modern det.	16 Aug.	22 Aug.	11 Aug.	16 Aug.	25 Oct.	24 Oct.	22 Oct.	17 Oct.	418	376	289	329
Akazaya	Ak	Jpn. old det.	25 Aug.	30 Aug.	-	-	23 Oct.	20 Oct.	-	-	354	334	-	-
Mizukuguri	M	Jpn. old det.	23 Aug.	1 Sept.	23 Aug.	-	24 Oct.	26 Oct.	25 Oct.	-	374	279	335	-
Tamahomare	Tm	Jpn. modern det.	26 Aug.	-	22 Aug.	-	26 Oct.	-	30 Oct.	-	439	-	498	-
Ayakogane	Ay	Jpn. modern det.	-	-	14 Aug.	-	-	-	17 Oct.	-	-	-	385	-
Tozan194	Tz	Jpn. modern det.	-	-	27 Aug.	-	-	-	31 Oct.	-	-	-	424	-
Lee(-)	L	Non-nod** det.	-	-	1 Sept.	-	-	-	2 Nov.	-	-	-	255	-
Shin-Tanbaguro	Tn	Jpn. old det.	-	-	3 Sept.	-	-	-	20 Nov.	-	-	-	329	-
Suzukari	Sz	Jpn. modern det.	-	-	-	14 Aug.	-	-	-	9 Oct.	-	-	-	401
Ryuhou	R	Jpn. modern det.	-	-	-	13 Aug.	-	-	-	8 Oct.	-	-	-	352
Hatayutaka	H	Jpn. modern det.	-	-	-	20 Aug.	-	-	-	18 Oct.	-	-	-	373
Athow	At	USA modern	-	-	-	11 Aug.	-	-	-	5 Oct.	-	-	-	344
Ina	I	USA modern indet.	-	-	-	12 Aug.	-	-	-	14 Oct.	-	-	-	406
Spry	Sp	USA modern det.	-	-	-	20 Aug.	-	-	-	13 Oct.	-	-	-	403
Stressland	St	USA modern indet.	-	-	-	15 Aug.	-	-	-	11 Oct.	-	-	-	404
Mean			-	-	-	-	-	-	-	-	409	342	350	377
LSD(0.05)			-	-	-	-	-	-	-	-	44	31	80	60

favorable field conditions is associated with dry matter production during a particular period.

Materials and Methods

Differences among cultivars were examined under field conditions in four seasons. The total number of tested cultivars was 16 (Table 1), in which three old-type cultivars and one non-nodulating line were included in order to observe diverse genotypes with different yield potentials. The old cultivars were Mizukuguri, a local line, Akazaya, released in 1915 and Shin-Tanbaguro, a pure line selected from a local line. The others were commercial cultivars released later than 1970 and were designated as modern cultivars in this study.

In 1989, two old and three modern Japanese cultivars, all determinate type, were grown on an upland field (silty clay loam) at Shiga Prefectural Junior College, Kusatsu. Seeds were sown on 13 July into rows 0.7m apart with a 0.14m intra-row spacing. The above cultivars excluding cv. Tamahomare were grown in 1991 on a drained paddy field (clay loam) at Shiga Prefectural Agricultural Experiment Station, Azuchi being sown on 29 June at a 0.65m by 0.15cm plant spacing. In 2000, seven Japanese cultivars and one non-nodulating line, a half of which were the same as those mentioned above, were grown on an upland field (sandy loam) at Kyoto University, Kyoto. Sowing date was 16 June and plant spacing was 0.65m by 0.2m. In 2002, eight cultivars including four Japanese determinate types, three US indeterminate types and one US determinate type were sown on 27 June in 0.65m rows with a 0.1m intra-row spacing at the same field as in 2000. In all experiments, cultivars were arranged in a randomized complete block design with three replications. The subplot sizes for each cultivar were 23, 47, 26 and $10m^2$, in 1989, 1991, 2000 and 2002, respectively.

The fields were fertilized before sowing with P_2O_5 and K_2O at 100 to 120kg ha^{-1} and were managed as optimally as possible with irrigation and pest and weed controls whenever necessary. For evaluation of potential crop productivity, lodging was prevented during late growing periods by setting up a net of 0.25 by 0.25m mesh horizontally above the plant for the cultivars that were likely to lodge, around the flowering period. The plants grew up passing through the net, and the net did not substantially affect the natural shape of mature canopies.

Aboveground plant parts were harvested from 0.5 to $1.0m^2$ land area four (1989), seven (1991), nine (2000) and two (2002) times during growing period and dry matter weights were measured. CGR was calculated for 20 days (d) before R5 stage (flowering and pod set), 20 d after R5 (initial seed filling) and 18 d from 13d after R5 to 31d after R5 (mid seed filling). CGR was calculated in 1989 and 2001 from difference of top dry weight (TDW) between two dates, but for 1991 and 2000 it was calculated by the linear regression between TDW at three or four dates and days. The linear regression was used to mitigate inevitable experimental errors of CGR assessment, and its r square exceeded 0.8 in about 80 percent of total calculations.

At the maturity stage, the seed yield was determined for $1.0m^2$ or larger area as winnowed seeds with aborted seeds excluded. The yield was expressed by the weight of seeds with a moisture content of 15%.

Results and Discussion

The mean air temperatures during experiments in 1989 and 1991 conducted at Kusatsu and Azuchi in Shiga Prefecture were slightly lower than those conducted in 2000 and 2002 at Kyoto. The mean daily solar radiation was highest in 2000 at Kyoto and lowest

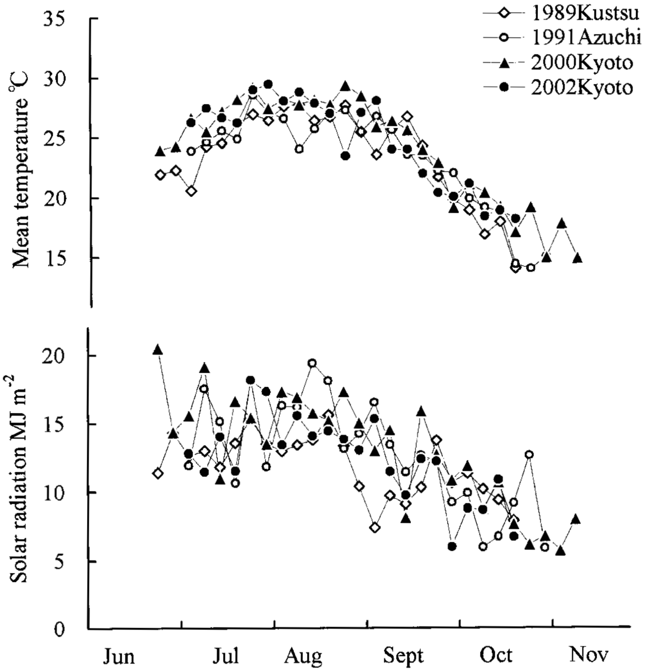

Fig. 1. Five-day means of daily mean air temperature and solar radiation for each experimental period.

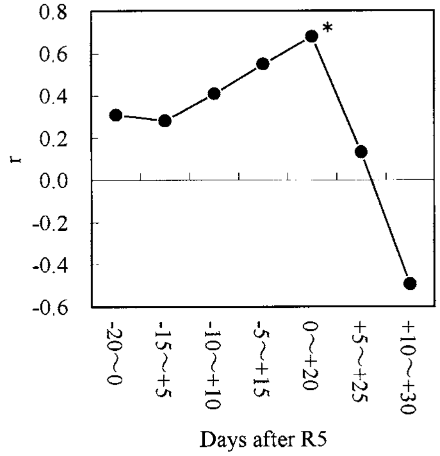

Fig. 2. Correlations (r) of seed yield with CGR's calculated for 20 days in various growing periods, from the cultivar comparison in 2000 at Kyoto. * : significant at the P=0.05 level.

Table 2. Correlations between seed yield and crop growth rates (CGR) during 20 days before/after R5 and mid seed-filling period. * and ** : significant at the P=0.05 and 0.01 levels, respectively.

	Correlation coefficient		
	R5-20d ~ R5	R5 ~ R5+20d	Mid seed-filling[a]
1989 Kusatsu	0. 97**	0. 94*	no data
1991 Azuchi	−0. 01	0. 97**	0. 85
2000 Kyoto	0. 31	0. 68*	−0. 59
2002 Kyoto	no data	0. 74*	no data

in 1989 at Kusatsu (Fig. 1).

The seed yield (Y) varied with the year and cultivar from 255 to 498 g m^{-2}. The yields of modern cultivars were consistently higher than that of old cultivars in 1989 and 1991, but in 2000, the two modern cultivars, Enrei and Tachinagaha, gave lower yields than the others. In 2000, they showed a typical symptom of delayed stem maturation (Furuya et al., 1988) which might have been related to the low yield. In 2002, three US cultivars tended to show higher yields than the Japanese cultivars.

Fig. 2 shows the results for 2000 when TDW was measured most frequently. In this year, CGR during each 20-d period from flowering to late seed filling was obtained by linear regression. The correlation between Y and the CGR during each period was highest at the 20-d period after R5 (initial seed filling). As shown in Table 2, Y positively correlated with CGR during the 20 days after R5 in all four experiments, with r=0.94, 0.97, 0.68 and 0.74 in 1989, 1991, 2000 and 2002, respectively. However, the correlation coefficients between Y and CGR of the period during the 20d before R5 or in the mid-seed filling stage varied with the experiments from negative to positive correlation. Seed yields were plotted against CGR during 20d after R5 in Fig. 3. It was proved that the quantitative relations between the two variables were similar in the four years. Cultivars Enrei and Tachinagaha in 2000 that exhibited delayed stem maturation showed exceptionally low yields relative to their CGR. If these cultivars were excluded from the 2000 data set, the correlation coefficient between CGR and Y in this year was as high as 0.93. The factor that caused delayed stem maturation is unknown. However, in 2000, these relatively early-maturing cultivars showed this symptom widely in central and western Japan, and an extensive survey suggested, the involvement of unusually dry and warm weather in mid-summer as a factor (Fukui Prefecture Agricultural Experiment Station, 2002[†]).

The relationship between seasonal growth rate and yield would vary with the plant size at the season. In our study, the mean of aboveground dry weight at 20 d before R5 (approximately R1) among tested cultivars ranged from 91g m^{-2} in 1991 to 233g m^{-2} in 2000 and that at R5 from 352g m^{-2} in 2002 to 539g m^{-2} in 2000. Irrespective of this variation in plant size, a close relationship was observed between CGR during the

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[†] Fukui Prefecture Agricultural Experiment Station 2002. Special Report : Factors and Possible Remedy for Delayed Stem Maturation in Soybean. Fukui Prefecture, 1-160 (In Japanese).

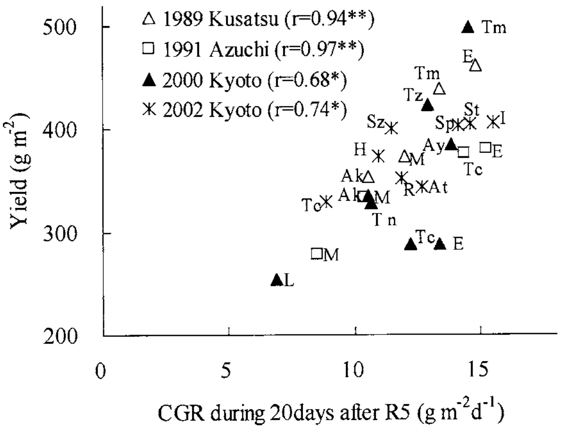

Fig. 3. Relationship between CGR during initial seed filling and yield. Letters attached to symbols are cultivar codes defined in Table 1. * and ** : significant at the P=0.05 and 0.01 levels, respectively.

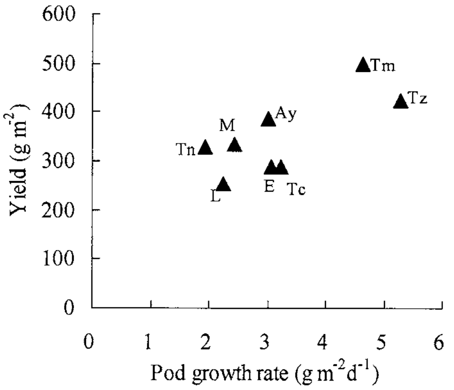

Fig. 4. Relationship between mean growth rate of pod (pod wall+seed) during 15 days after R5 and seed yield. From the experiment in 2000 at Kyoto. Letters attached to symbols are cultivar codes defined in Table 1. * : significant at the P=0.05 level.

initial seed filling period and Y. In contrast to this, the correlation between CGR during the 20d before R5 and Y was not consistently observed among years.

The above results do not agree with the well recognized concept that pod or seed number and hence yield depend on assimilate supply during a period before R5 (Shou et al., 1978; Kokubun and Watanabe, 1983; Egli and Yu, 1991; Board and Harville, 1993; Jiang and Egli, 1995). Our results rather support the view of Specht et al. (1999) and Shiraiwa and Hashikawa (1995), who reported that higher yields in modern cultivars than in old cultivars correlated with their greater dry matter production during the seed filling period. This study also showed a close association of Y with the growth rate during the initial seed filling period.

One possible reason for the above inconsistency between studies may be the fact that we conducted experiments avoiding any disturbance of crop canopies, supporting canopies to observe the potential performance of the crop without lodging. Our results agree in part with those of Shou et al. (1978), who extensively examined the effect of assimilate supply on pod formation and seed yield. They found the greatest reduction in yield by shading the canopy shortly after R5. Although they also found that light enrichment by using a reflector before R5 had a greater effect on yield than that after R5, the light enrichment inside the canopy using a reflector might not only increase assimilate supply, but also have a photomorphogenic effect on pod development (Heindl and Brun, 1983).

Yoshida et al. (1983) observed the dimensional growth of reproductive organs in field-grown determinate and indeterminate cultivars, and showed that pods reached maximal length and width within a few weeks after R5. Egli et al. (1985) reported the number of developing seeds, i.e. seeds viable as sink, ceased to increase one or two weeks after R5. In a determinate type cultivar Enrei, Sameshima (2000) characterized the initial growth period of seeds on a whole plant basis as an exponential growth phase before the linear growth. The period of the exponential phase was 10 days after R5, and CGR during which closely correlated with the number of seeds finally produced. It is well known that soybean plants lose a substantial portion of reproductive organs during flowering, pod set and initial seed development (Kato and Sakaguchi, 1954; Kato et al., 1955). Recently, it was reported that the final stage in seed abortion corresponded with the time when seed length reached approximately 80% of the final value (Duthion and Pigeaire, 1991). At the whole plant level, this stage would be near R6 or later according to the field observation of dimensional growth of individual seeds (Yoshida et al., 1983). Combining these facts, the 20-d period after R5 would correspond to the final stage of the production of viable reproductive organs, which function as assimilate sink during the major period of linear seed growth.

As shown in Fig. 4, the growth rate of pod dry matter weight during 15d after R5 also significantly correlated with seed yield in the 2000 experiment in Kyoto. Unlike the relation between CGR and Y (Fig. 3), data points for cultivars Enrei and Tachinagaha were not exceptional. This result combined with the above knowledge suggests that the growth of reproductive organs mediates the close relation between CGR during initial seed filling and Y. Considering the previous finding that pod and seed growth depended mainly on crop growth rate rather than assimilate partitioning to reproductive parts (Egli et al., 1985), a high CGR during initial seed filling would be required to achieve satisfactory production of viable reproductive organs.

Finally, the cultivar difference in growth rate and yield might depend on the weather condition experienced by respective cultivars rather than on the potential productivity of genotypes. For example, mean daily solar radiation during 20d after R5 varied across cultivars and years from 12.7 to 15.1 MJ m^{-2} due not only to the yearly change in weather but also to different phenological traits of cultivars. To assess how this affected observed productivity, we conducted a multiple regression analysis with mean air-temperature and solar radiation during 20d after R5 as independent variables and with CGR as dependent variable for each of four year data-sets. However, the r square as a whole was as low as less than 0.68 in three of four years, and even in the data set with exceptionally high r^2 (0.99 in 1991), the partial regression coefficient for solar radiation was negative (-7.5). These facts indicate that there was not any substantial association between cultivar performance and weather condition specifically experienced by each cultivar. In any way, full-scale analyses of genotype by environment interaction, which is not allowed in this study, remains to be pursued for determination of genetic traits that limit soybean productivity.

In conclusion, the cultivar difference in soybean yield under favorable conditions was associated with dry-matter productivity during initial seed filling stage. According to the literature, the number of reproductive organs viable as sinks would be finally determined during the initial seed filling period, at least during the period including this period.

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