Influence of Soybean Dwarf Virus on Growth and Yield*

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Soybean dwarf disease was found first in the southern Hokkaido area in about 1952 and has been spreading throughout Hokkaido. In 1971, this disease went across the Straits of Tsugaru to be found in Shimokita peninsula, the northern extremity of Honshu area. Tamada *et al.* (1969)⁹⁾ found out that this disease was caused by virus, of which the principal agent of dissemination was the foxglove aphid, *Aulacorthum solani* (Kaltenbach), and named soybean dwarf disease from its typical symptoms.

Although soybean dwarf virus (SDV) does not kill the plant entirely, they reduce greatly yield and quality of seed. It was pointed out by Tamada (1975)⁹⁾ that the disease caused the reduction by about 40 per cent in soybean yield, when 50 per cent of plants became infected in the field. As in most virus disease, essential control practices are to prevent the spread of the agent by insecticide and develop the resistant varieties by breeding.

Almost all soybean varieties are susceptible to SDV and no resistant varieties have been developed up to the present. Also there are little fundamental information of its influence on growth and yield. Not only world-wide search for disease resistant strains but also well understanding of its influence on growth are both necessary for the efficient development of resistant varieties.

Recently some varieties like Adams were found to have various levels of tolerance against SDV⁹⁾. In the present study, using Adams and its F₃ lines as experimental materials, the differences in growth and yield between infected and protected plants were analyzed from the viewpoint of growth

analysis to obtain basic information for better understanding its influences.

MATERIALS AND METHODS

The experiment was conducted at the Experimental Farm, Hokkaido Central Prefectural Agricultural Experiment Station, Naganuma, in 1975. Adams, Yuzuru and their 13 F₃ lines, namely F₃-1, -7, -9, -15, -22, -25, -40, -41, -46, -59, -60, -64 and -66, were used as experimental materials. The seeds were sown in the field with 2 replications in both treatments (mentioned later), on May 15, with 10 cm spaced hills and 60 cm wide rows, as single plant per hill. Fertilizer was applied in the recommended rate (20 kg N, 60 kg P₂O₅, 47 kg K₂O and 13 kg MgO per hectare) at planting.

Soybean dwarf virus was artificially inoculated by 3-5 virulent aphids, *Aulacorthum solani* (Kaltenbach), to Adams, Yuzuru and their F₃ plants in the field at 2-3 leaf stage on June 19. Plants in infected (I) plot were covered with fine mesh nylon cloth up to about one meter height, so that no aphid could cross over plants in protected (P) plot, where insecticide was applied in rows with fertilizer. The infection has been done successfully and the aphids were killed by insecticide one week after the inoculation. The covered cloth was removed on June 30.

Two representative plants of each variety and F₃ line were sampled respectively from two replications in P and I plots on July 17, August 6, August 27 and October 27 (harvesting time). After determination of plant height and node number, sampled materials were divided into leaf blade, stem, petiole

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and pod including seed respectively, measured their fresh weight, and dried in a forced-air circulation oven set at 80°C for two days and recorded their dry weight. Leaf area was measured by an automatic leaf area meter. Nitrogen percentage of leaves was determined by N-C order only with the leaf samples collected on August 27. The measurements of all traits were recorded on single plant basis.

RESULTS and DISCUSSION

1. Effect on growth pattern

The growth patterns of total dry weight (except root) and leaf area per plant in protected (P) and infected (I) plots are presented in fig. 1.

Total dry weight and leaf area of the plants infected with soybean dwarf virus (SDV) were

already lower at first sampling date (July 17) than those in protected ones. The differences between P and I plants were magnified with the progress of the season and the infected plants could not fully recover. One of the parental variety, Adams had higher levels in total dry weight and leaf area throughout growing season in both P and I plots than Yuzuru, another parental variety. Total dry weight and leaf area of Yuzuru were the lowest during the whole growing period in the I plot.

The 13 F_3 lines could be grouped into 4 different types from their growth patterns. F_3 -9 showed almost similar pattern as in Adams; and F_3 -1, -15, -25, -40 and -41 belonged to this type. But some of them (F_3 -1 and -41) had lower levels in I plot than other lines. Others had intermediate patterns between Adams and Yuzuru in P plot, but were variable in I plot.

Total dry weight and leaf area in F_3 -59 (shown in fig. 1) and -7 continued the lowest levels throughout two growth stages (July 18 to Aug. 6 and Aug. 7 to Aug. 27) in I plot as in Yuzuru. Other two different patterns were of F_3 -64 and -46 (shown in fig. 1) types. Total dry weight and leaf area of I plants in F_3 -64 increased steadily throughout two growth stages. But those in F_3 -46 were almost no increase during first stage and then increased rapidly. F_3 -22 and -66 belonged to the former type and F_3 -60 to the later type, respectively.

2. Effect on growth parameters

Differences in crop growth rate per plant (CGR), mean leaf area per plant (LA), net assimilation rate (NAR), specific leaf area (Sp. LA), dry matter and nitrogen percentage in leaves between P and I plots are shown in table 1.

CGR and LA in I plot were very lower during two stages than those in P plot, indicating a parallelism between them. However, the value of NAR in I plot was lower at first stage, but higher at second stage than those in P plot. This may be due to delay of physiological age in photosynthetic apparatus by SDV.

Plants in I plot had lower value for SP. LA than those in P plot, and it was almost same through-

Fig. 1 Growth patterns of total dry weight and leaf area in protected and infected plants among parental varieties and their F_3 lines

Note. ○ : protected plant. ● : infected plant
— : total dry weight
--- : leaf area

Table 1 Differences in three growth parameters and specific leaf area, dry matter and nitrogen percentage in leaves between protected (P) and infected (I) plots

Stage	Treatment	Crop growth rate (g/pl./day)	Mean leaf area* (m ² /pl.)	Net assimilation rate (g/m ² /day)	Specific leaf area* (cm ² /g)	Dry matter percentage in leaves**	Nitrogen percentage in leaves**
I	P	0.70±0.16	0.211±0.035	3.36±0.69	346±26	—	—
	I	0.17±0.12	0.072±0.025	2.10±1.25	196±38	—	—
II	P	0.95±0.28	0.387±0.069	2.42±0.51	342±24	17.0±7.4	5.57±0.28
	I	0.61±0.17	0.136±0.052	4.86±1.50	200±34	35.3±8.6	4.22±0.34

Note. The data are indicated on the average values of all experimental materials.

Stage I: July 18—Aug. 6. Stage II: Aug. 7—Aug. 27

*: Mean values during experiment period

**: The values on Aug. 27

Fig. 2 Relation between crop growth rate and both leaf area (LA) and net assimilation rate (NAR) in protected (P) and infected (I) plots

Note. ○: protected plot

●: infected plot

*: 5%; **: 1%; ***: 0.1% level of significance

out the growth stages. This fact indicated that leaves of plants infected with SDV became extremely thick. In I plot, higher dry matter percentage and lower nitrogen level in leaves than those in P plot were also observed.

CGR are presented by the following formula:

$$\text{CGR} = \text{LA} \times \text{NAR}$$

To find out the main factor to control CGR,

Fig. 3 Differences of seed yield between protected and infected plots

relation between CGR and both LA and NAR were given in fig. 2.

CGR was closely related to LA with continuity between P and I plots in both stages of growth, even though in first stage CGR and LA had no significant correlation in P plot. At stage I, although NAR was correlated with CGR, the regression line differed between P and I plots. Furthermore, in the stage II, NAR in I plot was not correlated with CGR inspite of high positive correlation in P plot.

Thus, although varietal differences in CGR could be explained by LA, covering all experimental materials in P and I plots, NAR also controlled partly CGR. However, from the fact that the relation between NAR and CGR differed in P and I plots, it may be suggested that SDV may

Table 2 Correlation coefficients between seed yield and total dry weight (TDW), leaf area (LA), specific leaf area (Sp. LA) and net assimilation rate (NAR)

Traits		Protected plot	Infected plot
TDW	(Aug. 27)	0.253	0.686**
LA	(July 17)	-0.187	0.766**
LA	(Aug. 6)	0.478	0.729**
LA	(Aug. 27)	0.244	0.623*
Sp. LA	(July 17)	-0.153	0.814***
Sp. LA	(Aug. 6)	0.167	0.725**
Sp. LA	(Aug. 27)	-0.154	0.333
NAR	(Stage I)	0.441	0.340
NAR	(Stage II)	-0.257	-0.346

Note. *: 5%; **: 1%; ***: 0.1% level of significance

influence physiologically and anatomically on photosynthetic apparatus, resulting in decrease in photosynthetic activity on thick leaves.

3. Effect on seed yield

Differences in seed yield per plant between P and I plots with parental and F_3 lines are given in fig. 3. All the F_3 lines produced higher yield than both parental varieties in P plot, but lower in I plot than Adams. The range of reduction in seed yield was the lowest in Adams. Some F_3 lines had yielded relatively higher than F_3 average, indicating resistance to some extent against SDV.

As shown in table 2, seed yield in I plot indicated positive significant correlation with total dry weight on August 27, LA at 3 sampling dates and Sp. LA on July 17 and August 6 and non-significant correlation with NAR at both stages. However, in P plot, they did not correlate significantly with seed yield. Among the traits indicating positive significant correlation with seed yield, total dry weight on August 27, LA on August 6 and Sp. LA on July 17 indicated parallelism with seed yield in the inhibition rate $((1-I/P) \times 100; \%)$.

Ghosh *et al.* (1975)¹³ observed that the growth stage about two weeks before full leaf expanding stage was better period for screening resistant plants against SDV. From the results described above, Sp. LA at early growth stage and LA at middle stage of growth might be also useful to screen

Table 3 Simple correlation coefficients between relative leaf growth rate and net assimilation rate (NAR), distribution ratio of total dry weight to leaf (DL) and specific leaf area (Sp. LA)

Parameter	Stage I		Stage II	
	P	I	P	I
NAR	0.953***	0.917***	0.866***	0.798***
DL	0.361	-0.149	0.688**	0.500
Sp. LA	0.102	0.679**	0.607*	-0.428

Note. P: protected plot. I: infected plot.

*: 5%; **: 1%; ***: 0.1% level of significance

SDV resistant plants.

4. Analysis on leaf area development

As shown in fig. 2 and table 3, CGR and final seed yield in I plot were highly correlated positively with LA at each sampling date and stage. These results may suggest that the decrease in growth and yield in I plot may be due to decrease in LA. Variety with better relative leaf growth rate (RLGR) from the beginning of growth has advantage for vigorous growth in vegetative stage and higher yield at harvesting time. So it is necessary to analyze the influences of SDV on the leaf area development.

RLGR was presented by three parameters from the following formula¹³:

$$\text{RLGR} = \frac{1}{\Delta t} \cdot \frac{\Delta A}{A} \\ = \left(\frac{1}{\Delta t} \cdot \frac{\Delta W}{A} \right) \times \left(\frac{\Delta L}{\Delta W} \right) \times \left(\frac{\Delta A}{\Delta L} \right)$$

where ΔA , ΔW , ΔL and Δt were increased values in LA, total dry weight, leaf dry weight and days during experiment period respectively and A was LA. Also, $1/\Delta t \cdot \Delta W/A$, $\Delta L/\Delta W$ and $\Delta A/\Delta L$ were equal to NAR, distribution ratio (%) of total dry weight to leaf blade (DL) and Sp. LA, respectively.

Therefore, the formula presented above are rewritten as:

$$\text{RLGR} = \text{NAR} \times \text{DL} \times \text{Sp. LA.}$$

Then, to analyze the interrelationship between leaf area development and these three parameters, simple correlation coefficients between RLGR and NAR, DL and Sp. LA were calculated and presented in table 3.

RLGR indicated high positive significant correlation with NAR in both P and I plots at both stages. In I plot at stage I, Sp. LA was correlated significantly with RLGR, indicating also high positive significant partial correlation with RLGR ($r=0.728^{**}$). Although in P plot at stage II, DL and Sp. LA were related positively to RLGR, partial correlation was significant only between NAR and RLGR.

Thus, leaf area development was supported mainly by NAR, but Sp. LA had also great influence on RLGR in I plot at stage I. These facts indicate that not only decrease in photosynthetic activity but also anatomical changes in leaves, due to the direct influences of SDV, constrain leaf area development.

Soybean dwarf virus is pointed out to be a phloem invading virus like barley yellow dwarf virus⁹⁾. It is also transmitted by aphids which are phloem feeders and produce systemic symptoms of a vascular infection. The results obtained in the present experiment, such as decrease in net assimilation rate, thickness of leaves, high dry matter percentage and low nitrogen level in leaves in infected plants, may suggest that SDV infection interferes with physiological functions and metabolisms and disrupts normal translocation as reported on barley yellow dwarf virus and tobacco etch virus^{2),3),4),6),7)}.

SUMMARY

To obtain some information for the influence of soybean dwarf virus, differences in growth and yield between infected (I) and protected (P) plants were analyzed from the viewpoint of growth analysis, using varieties Adams, Yuzuru and their 13 F_3 lines as experimental materials.

Total dry weight (except root) and leaf area in infected plants were lower at the first sampling date (July 17) than protected ones and the differences between P and I plots increased with time. Adams had more total dry weight and leaf area than Yuzuru in P and I plots. Four different growth patterns, showing same and/or intermediate patterns between parental varieties,

were found among F_3 lines (fig. 1).

Values of crop growth rate (CGR) and mean leaf area (LA) per plant in I plot were very lower than those in P plot, showing parallelism between them. Net assimilation rate (NAR) in I plot was lower at stage I (July 18—Aug. 17), but higher at stage II (Aug. 18—Aug. 27) than those in P plot. Plants in I plot had lower value for specific leaf area (Sp. LA) than those in P plot. Plants in I plot had also higher dry matter percentage and lower nitrogen level in leaves than those in P plot.

CGR was closely related with LA. NAR was also significantly correlated with CGR in stage I, but the regression line differed between P and I plots. In stage II, NAR in I plot was not correlated with CGR, though in P plot there was high positive correlation. From these facts, it was suggested that photosynthetic apparatus was greatly influenced physiologically and anatomically due to soybean dwarf virus.

Seed yield in I plot was highly correlated with leaf area, indicated that the decrease in growth and yield in I plot was mainly due to leaf area. Relative leaf growth rate (RLGR) had high positive correlation with NAR in P and I plots. In I plot at stage I, Sp. LA was also correlated significantly with RLGR. Thus leaf area development was supported mainly by NAR, but in I plot Sp. LA had also great influence on RLGR.

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〔和 文 摘 要〕

ダイズ矮化病ウイルスの生育・収量に及ぼす影響について

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ダイズ矮化病ウイルスの生育・収量に及ぼす影響を明らかにするため、品種アダムス、ゆうづるおよびその F₃ 系統 13 系統を供試し、接種区および防除区における生育・収量の差異について比較、検討した。

1) 接種区における全乾物重および葉面積は、ウイルス接種約 1 ヶ月後の 7 月 17 日において、すでに防除区に比し劣り、その差は生育とともに拡大した。

2) 生育期間中の個体当乾物増加速度および葉面積は接種区が劣ったが、純同化率は 8 月 6 日を中心に前期では防除区が、後期では接種区がまさった。また、接種区では比葉面積および葉身の窒素含有率が低く、乾物率は逆に高い傾向を示し、ウイルス感染による葉の肥厚、転流の阻害が認められた。

3) 接種区における個体当平均子実重は防除区に比べ約 70% 減少した。また、接種区では子実重と各生育時期における葉面積との間に有意な正の相関関係が認められ、子実収量の系統間差異は葉面積の差によることが明らかとなった。

4) 相対葉面積生長率が純同化率および比葉面積と有意な正の相関を示すことから、接種区における葉面積の減少は、ウイルス感染による光合成率の低下と葉の肥厚に起因するものと考えられる。