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Citation: Kyoto University (京都大学)

Issue Date: 2015-03-23

URL: https://doi.org/10.14989/doctor.k19051

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Textversion: ETD

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The Effects of Developmental Traits on Genetic Variation of Green Stem Disorder in Soybean [Glycine max (L.) Merr.]

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1. Introduction

Soybean [Glycine max (L.) Merr.] is a typical monocarpic plant species that loses green color and stem moisture as the seeds mature. However, these plants occasionally maintain stem greenness, stem moisture and leaf color at seed maturity, and this phenomenon was termed as green stem disorder (GSD). The severity level in plants has been described from entirely green plants to leafless plants with a yellow-green stem. Because GSD plant causes a reduction of harvesting efficiency and negatively impacts seed appearance when combine harvester is employed, GSD is regarded as an unfavorable phenomenon that should be prevented. The occurrence of GSD seems to be induced by biotic and abiotic stress. But, the reproducibility of experimental result is uncertain, and GSD plants appear even under appropriately managed condition. Hence, any reliable countermeasures through modifying cultivation methods have not been established. On the other hand, variability in the severity of GSD in soybean cultivars has been reported, and thus use of GSD resistant cultivars would be effective to prevent the occurrence of GSD. This study identified inherited plant characteristics related to GSD, and analyzed how the heritable traits are associated with the severity of GSD to provide a reliable countermeasure.

2. Genetic Variation of the Susceptibility to Green Stem Disorder in Japanese and US Soybean Cultivars

Assessment of variability of GSD severity in soybean cultivars is fundamental for the breeding of cultivars resistant to GSD. But, the evaluation using a wide variation of soybean genotypes has not been conducted. In Japan, introduction of combine harvester has started in 1970s, while combine has been utilized since early twentieth century in USA. Therefore, US soybean cultivars may accumulate suitable plant properties for
mechanical harvesting. In this chapter, various Japanese and US cultivars were used, and the severity of GSD was evaluated with developmental traits at the same location (Kyoto) over two years (2009 and 2011). The severity of GSD was recorded using a 5-point scale evaluation method proposed by Furuya and Umezaki (1993), which evaluates the degree of synchronous senescence (DSS) between vegetative and reproductive organs. A lower DSS represents more severe symptoms of GSD.

Both the Japanese and US cultivars exhibited wide variations of DSS. Means of DSS were significantly different between 2009 and 2011, but the DSS values showed correlation between the years, suggesting that the severity of GSD was genetically controlled. Mean DSS of the US cultivars was significantly higher than that of the Japanese cultivars, and thus the US cultivars likely have favorable properties against GSD. Late flowering cultivars with determinate stem growth habit (D-type) tended to have high DSS compared to early flowering cultivars, while DSS of cultivars with indeterminate stem growth habit (I-type) was much higher than that of the D-type cultivars with the same flowering time as I-type cultivars. In the US cultivars, early flowering cultivars were with I-type stem growth habit and late cultivars had D-type stem growth, which seemed to be the cause of DSS difference between the Japanese and US cultivars. This analysis suggested that developmental traits such as stem determination type and earliness of flowering have significant effects on DSS in a wide variation of cultivars.

3. Verification of the Effects of Stem Determination and Earliness of Flowering on Green Stem Disorder of Soybean against Genetic Background and Environment

Developmental traits such as stem determination and earliness of flowering were suggested as major genetic factors which influence DSS. But, the cultivation area of I-type cultivars is entirely different from that of D-type cultivars, as well as earliness of flowering. Hence, it is suspicious these traits certainly influence DSS. To verify their effects on DSS, two sets of recombinant inbred line (RIL) populations segregating stem determination and flowering time were tested at two different locations (Kyoto and Akita) over two years. One population was developed from a cross between the Stressland (US I-type) and Tachinagaha (Japanese D-type) cultivars, and the other was derived from a
cross between the Ohsuzu (Japanese D-type) and Athow (US I-type) cultivars.

Wide variations in DSS were observed for ST and OA RILs, but many lines normally senesced in Akita. Although DSS of each line differed considerably between the locations, the scores showed significant correlations among the environments. Therefore, the susceptibility to GSD is relatively consistent even at different locations. Quantitative trait locus (QTL) analysis revealed a strong and consistent QTL for GSD severity in ST RILs across the environments near the $Dt1$ locus, which governs stem determination, and the determinate growth genotypes showed more evident symptoms of GSD. However, QTLs were not detected near the $Dt1$ locus in OA RILs. Thus, it was unclear if the responsible gene was identical to the stem determination gene. The early flowering lines showed more severe symptom of GSD in both populations, but this trend was evident only in the D-type lines. The effect of another QTL detected in OA RILs also depended on the allele near the $Dt1$ locus. Thus, the genetic factor near the $Dt1$ locus seemed to interact with the other genetic factors in relation to DSS. These results indicated that the genetic factor at the $Dt1$ locus and the factor controlling flowering time influenced DSS under every environment, and that their effects and interaction complicated the genetic control of GSD.

4. Analysis of the Effect of the Genetic Factor near the $Dt1$ Locus on Source and Sink Balance and Its Relationship to the Severity of Green Stem Disorder of Soybean

In soybean, depodding is known to delay the senescence of vegetative organs, and thus imbalance of reproductive sink organs and assimilate supply (source) is believed to be a possible cause of GSD. In this analysis, the effect of the genetic factor near the $Dt1$ locus was investigated from a viewpoint of source and sink balance using near isogenic lines (NILs) segregating stem growth habits. These NILs were derived from the Clark, Harosoy, Williams and Elf cultivars. Because the amount of vegetative growth differs between I-type and D-type genotypes, source and sink balance was standardized in the node-basis.

The D-type showed more severe symptom of GSD than the corresponding I-type in all of the genetic backgrounds, the allele at the $Dt1$ locus which induced GSD symptom was
compatible with the D-type. Leaf area index (LAI) at the beginning of seed filling of the I-type was about twice as large as that of the D-type. It is reported that photo-assimilate supply to reproductive organs during flowering and pod setting positively correlates with the number of pods and seeds. The amount of available source per node in the D-type would be larger than the I-type due to smaller LAI. Because the number of pods per node, the number of seeds per node and seed weight per node at seed maturity were not different between the stem determination types, the D-type seemed to be under source and sink imbalance. The D-type has less small number of flowers per node, and this mainly resulted from decreased number of flowers per primary raceme. The responsible gene of stem determination turned out to be an ortholog of Arabidopsis *TERMINAL FLOWER1*, which is known to associate with the continuation of stem apical meristem and inflorescence development. Therefore, the stem determination gene of soybean may also affect the morphology of inflorescence. This result suggested that the I-type stem growth habit secured the number of flowers per node which prevent the occurrence of source and sink imbalance. If the genetic variation in the severity of GSD is associated with the number of flowers per node, the genetic factor near the *Dt1* locus influencing DSS might be identical to the stem determination gene.

5. **Verification of the Impact of Genetic Variation in Flower Production on the Severity of Green Stem Disorder in Soybean**

A genetic factor near the *Dt1* locus was suggested to influence source and sink balance through the number of flowers per node, and to be associated with the severity of green stem disorder (GSD) of soybean. But, further investigation is needed to verify the relationship between the number of flowers per node and the severity of GSD. In the study, the relationship between the number of flowers per node and DSS were analyzed at two different environments. Selected lines from ST and OA RILs were used, and they segregated for DSS.

Wide variation in the number of flowers per node was observed in ST and OA RILs, and the number was environmentally stable, and thus the number of flowers per node would be genetically controlled. The line with large number of flowers per node tended
to have high DSS score. Therefore, it was suggested that the number of flowers per node influenced DSS. The variation of the number of flowers per node was wide in the D-type lines of ST and OA RILs compared with that in the I-type lines, but the number of flower per node was relatively high in the I-type lines. In addition, the late flowering lines tended to have large number of flowers per node as compared with early flowering lines especially in the D-type lines. The genes influencing flowering time are associated with the maintenance of stem apical meristem (SAM) activity. This result suggested that these genes also associated with the continuation of inflorescence meristem activity. These associations in the flower production might explain the variation of DSS caused by the genetic factor near the $Dt1$ locus and earliness of flowering.

6. General discussion

The genetic factor near the $Dt1$ locus and its interaction with flowering time genes are considered as major determinant factors to cause genetic variation in DSS in soybean. This study also revealed these genetic factors would govern the number of flowers per node. Excess source supply relative to sink size is known to induce the symptom of GSD. Increased flower number was suggested to ameliorate the source and sink imbalance. The other genetic factor(s) which increases flower production would contribute the improvement of GSD characteristic without altering stem growth habit and flowering time.