第6卷 第4期 大 豆 科 学 Vol. 6 No. 4
1987年 11月 SOYBEAN SCIENCE Nov.. 1987

SEED GROWTH AND DEVELOPMENT IN SOYBEAN

D. B. Egli

(*Dep. of Agronomy, Univ. of Kentucky, Lexington, KY U. S. A.*)

INTRODUCTION

Reproductive development in the soybean begins with the development of the flower primordia and continues through anthesis, development of the pod and seed, accumulation of dry matter by the seed and ends at physiological maturity (maximum seed dry weight), when the fruit matures. The study of seed growth and development in soybean is complicated by the extended period of flowering (up to 4 weeks long), which means that at any time there are fruits of many different stages of development on the plant. The objective of this brief review is to discuss the general patterns of pod and seed growth in soybeans, the factors influencing seed growth and the relationship between seed growth characteristics and yield.

POD AND SEED DEVELOPMENT

The initial development of the soybean fruit after pollination has been described in detail by Carlson (1973). The development of the pod and seed structures are usually complete within 15 to 20 days after anthesis. At this time the pod has reached its maximum length and width and cell division in the cotyledons has stopped (Egli et al., 1981). Thus, all structural development is complete before the seed begin its rapid accumulation of dry weight as it accumulates storage materials, primarily oil and protein. Since cell number in the cotyledons is constant during most of seed growth, the increase in seed size is a result of cell expansion (Egli et al., 1985).

The vascular tissue antamoses extensively throughout the seed coat

but there is no vascular connection between the seed coat (maternal tissue) and the embryo (hypocotyl-radicle axis and cotyledons) (Thorne, 1981). Movement of assimilate into the cotyledons requires unloading from the phloem in the seed coat, diffusion from the seed coat to the cotyledons and uptake by the cotyledon cells. (Thorne, 1985; Litchner and Spanswick, 1981). Sucrose is the primary source of carbohydrate for the developing seed while the bulk of the nitrogenous material in exudate from the seed coat was glutamine and asparagine, with ureides present only at very low levels (Rainbird et al., 1984; Hsu et al., 1984). The ability of soybean cotyledons to grow normally in culture systems with only sucrose and glutamine or asparagine as sources of carbon and N, (Thompson et al., 1977) confirms the suggestion that soybean seeds require only simple forms of C and N from the mother plant for normal growth.

After an initial lag phase, the soybean seed accumulates dry matter at a constant rate (linear phase of seed growth) until the rate of dry matter accumulation decreases and reaches zero at physiological maturity (Egli, 1975; Fraser et al., 1982). This pattern of dry matter accumulation is consistent across genotypes and environments and is also characteristic of seeds or kernels of many other plant species (Egli, 1981). Since cell division is complete early in seed development and the accumulation of dry weight is primarily a result of the accumulati n of storage materials, it is not surprising that the rate of dry matter accumulation is constant during most of seed growth.

Seed water content (mg H_2O $seed^{-1}$) increases throughout seed growth and reaches a maximum before the seed reaches physiological maturity. Seed water concentration is initially very high (>80% fresh weight basis) and declines steadily during development reaching approximately 55% at physiological maturity (Fraser et al., 1982). The concentration of H_2O in the seed at physiological maturity is very constant across genotypes and environments and it has been suggested that the moisture status of the seed plays an important regulatory role in seed development (Adams and Rinne, 1980; Fraser et al., 1982). This hypothesis is made more attractive by the fact that the increase in seed size during developmedt is a result of cell expansion which requires a net uptake of water by the cotyledonary cells.

FACTORS INFLUENCING SEED GROWTH

Seed growth rate-The seed growth rate (SGR) is defined as the rate of accumulation of dry matter by an individual seed during the linear phase of seed growth. We usually measure SGR by marking pods that are full size and contain seeds that are approximately 3mm long and then harvesting these pods at approximately weekly intervals. This insures that the pods that are sampled are at the same developmental stage.

Genotypic differences in SGR are constant across years (Table 1) suggesting that these differences are under genetic control (Egli et al., 1978, 1981). The SGR's of seven genotypes varied from 3.9 to 10.9mg seed^{-1} day^{-1} in a field experiment in 1979. The genotypic differences in SGR were maintained when SGR's were measured in an *in vitro* culture system with concentrations of sucrose and asparagine in the nutrient medium that were above those required to maximize SGR (Egli et al., 1981). The correlation between SGR's on the plant and in the *in vitro* culture system was $r=0.89$ (significant at $\alpha=0.01$). The fact

Table 1 Genotypic differences in seed growth rate

Genotype	SEED GROWTH RATE			
	1977[1]	1978[1]	1979[2]	1980[3]
	mg seed^{-1} day^{-1}			
Kanrich	6.8	9.7	7.6	—
Williams	5.6	6.2	5.9	6.0
Essex	3.6	3.7	3.9	4.2

	DURATION OF SEED FILL		
	1977[4]	1978[5]	1979[5]
	days		
Williams	48	40	35
Lincoln	43	28	27

1 From Egli et al., 1978.
2 From Egli et al., 1981.
3 From Egli et al., 1985.
4 From Gay et al., 1980, time from growth stage R_4 to R_7.
5 From Boon-Long, 1980, time from growth stage R_5 to R_7.

that genotype differences in SGR were maintained with saturating levels of sucrose and asparagine in the nutrient solution indicates that the genetic differences in SGR are controlled by the seed, not by the ability of the plant to supply assimilate to the seed.

The genetic differences in SGR among the seven genotypes were significantly correlated ($r=0.93$) with the number of cells in the cotyledons, suggesting that cell number plays an important role in controlling genetic differences in SGR (Egli et al., 1981). Recent research in our laboratory has suggested that cell number in the cotyledons may be influenced by environmental conditions (Swank et al., 1987). If this is true, it provides another mechanism by which environmental conditions could influence SGR. We initially reported a positive correlation between SGR, final seed size, and the number of cells in the cotyledons (Egli et al., 1981). However, subsequent work with a larger number of genotypes has demonstrated that SGR and seed size are not always highly correlated (Swank et al., 1987). It was possible to identify genotypes that have large seeds, but have only moderate SGRs and numbers of cells in the cotyledons. Thus, it seems that there is no absolute relationship between final seed size and SGR; although, it should be noted that a large seed with a low seed growth rate would require an excessively long seed filling period.

In a series of field and greenhouse experiments (Egli et al., 1985), removal of approximately 75% of the fruits on the plant increased SGR by 15 to 63%. The fruit removal treatments were applied after the pods had reached their maximum size and cell division in the cotyledons was complete so the treatments would not affect cell division or pod size. Reducing insolation during seed filling by approximately 60% with shade cloth reduced SGR by 12 to 27%. These results are consistent with *in vitro* culture experiments with varying concentrations of sucrose or amino acids in the nutrient media (Thompson et al., 1977) that demonstrated that SGR was affected by the substrate concentration.

Seed growth rate is also sensitive to temperature, with higher rates (7.9mg seed^{-1} day^{-1}) at 27/22 C (day/night) than at 18/13 C (6.1 mg seed^{-1} day^{-1}) in phytotron experiments (Egli and Wardlaw, 1980). There was no change in SGR as the temperature increased to 33/28 C.

Seed growth rates are relatively insensitive to plant water stress. Field experiments involving moisture stress treatments applied at different plant growth stages, which reduced yield and the number of seeds m^{-2}, had no significant effect on SGR (Meckel et al., 1984). Severe stress would probably affect SGR; however, these data suggest that SGR is less sensitive to moisture stress than some other plant processes.

Seeds usually contain relatively high levels of plant hormones. It has been suggested that hormones (primarily abscisic acid) may play a significant role in controlling SGR (Schussler et al., 1984; Hein et al., 1984). However, the mechanisms involved in this potential control, or its significance has not been clearly determined.

Duration of seed fill-The duration of seed fill is frequently estimated by the effective filling period (EFP) (Daynard et al., 1971) which is calculated by dividing the final seed size by SGR. This estimate is useful because it eliminates the need to accurately determine the beginning and end of seed growth. The duration of seed fill can also be estimated on a whole plant basis as the time from growth stage R_5 (beginning seed fill.) to R_7 (physiological maturity).

Genotypic differences in the duration of seed fill that are consistent across years (Table 1) suggest that the duration of seed fill is under genetic control. In a field experiment with 59 genotypes, the EFP ranged from 13 to 57 days and there were a number of genotypes that had an EFP longer than the cultivars currently grown in Kentucky (Egli et al., 1984). We have consistently found a significant genotype x environment interaction for the duration of seed fill that indicates that environmental conditions have a significant effect on this character.

The duration of seed fill in soybean was not very sensitive to temperature (Egli and Wardlaw, 1980; Egli et al., 1984; Egli et al., 1987). Moisture stress during seed filling shortened the seed filling period (Egli et al., 1984; Meckel et al., 1984) and the duration of seed fill was also affected by variations in assimilate supply created by source-sink alterations. Increasing assimilate supplies by depodding lengthened the duration of seed fill and decreasing assimilate supplies by shading also tended to lengthen the duration of seed fill (Egli et al., 1985).

RELATIONSHIP TO YIELD

We have not been able to demonstrate any relationship between SGR and yield (Egli, 1975, 1981; Egli et al., 1978). The SGR is an estimation of the daily assimilate requirement of the seed. Assuming a constant level of assimilate supply from photosynthesis, fewer seeds with a high SGR would be required to equal the total assimilate supply than for seeds with a low SGR. This relationship assumes no feedback control between sink strength (SGR) and photosynthesis. It predicts an inverse relationship between SGR and the number of seeds m^{-2} which suggests that one should not expect any relationship between SGR and yield in soybeans. This argument is consistent with the reciprocal relationship between seed size and seed number frequently encountered by plant breeders (Egli et al., 1978).

Many researchers have reported a positive correlation between the duration of seed growth and yield in soybeans (Egli and Leggett, 1973; Gay et al., 1980). Thus, the selection for longer seed filling periods may be one way of increasing soybean yields. This avenue for yield improvement is particularly attractive because, in many environments, soybeans do not use all of the available growing season in producing yield, and also because there has been little effort in the past to use this character in plant breeding programs. The relatively large genotype by environment interactions reported for this character may hamper its use as a selection criteria, but it should be possible to minimize this problem with the proper experimental techniques. Although the duration of seed fill is potentially a useful selection criteria to increase yield, whether it is more effective than selecting for yield itself, remains to be determined.

REFERENCES

[1] Boon-Long, Preeda. 1980. The relationship between photosynthesis and nitrogenous components in soybean [*Glycine max* (L.) Merrill] leaves during reproductive growth. Ph. D. dissertation, Dep. of Agronomy, University of Kentucky, Lexington, KY.

[2] Carlson, J. B. 1973. Morphology. p. 17—95. *In* B. E. Caldwell (ed.) Soybeans: Improvement Production, and Uses. American Society of Agronomy, Madison, WI.

[3] Egli, D. B. 1975. Rate of accumulation of dry weight in seed of soybeans and its relationship to yield. Canad. J. Plant Sci. 55: 215—219.

〔4〕 Egli, D. B. 1981. Species differences in seed growth characteristics. Field Crops Res. 4：1—12.
〔5〕 Egli, D. B., Joanna Fraser, J. E. Leggett, and C. G. Ponsleit. 1981. Control of seed growth in soya beans (*Glycine max* (L.) Merrill). Ann. Bot. 48：171—179.
〔6〕 Egli, D. B., R. D. Guffy, L. W. Meckel, and J. E. Leggett. 1985. The effect of source-sink alterations on soybean seed growth. Ann. Bot. 55：395—402.
〔7〕 Egli, D. B. and J. E. Leggett. 1973. Dry matter accumulation patterns in determinate and indeterminate soybeans. Crop Sci. 13：220—222.
〔8〕 Egli, D.B., J. E. Leggett, and J. M. Wood. 1978. Influence of soybean seed size and position on the rate and duration of filling. Agron. J. 70：127—130.
〔9〕 Egli, D. B., J. H. Orf, and T. W. Pfeiffer. 1984. Genotypic variation for duration of seed fill in soybean. Crop Sci. 24：587—592.
〔10〕 Egli, D. B. and J. F. Wardlaw. 1980. Temperature response of seed growth characteristics of soybeans. Agron. J. 72：560—564.
〔11〕 Fraser, Joanna, D. B. Egli, and J. E. Leggett. 1982. Pod and seed development in soybean cultivars with differences in seed size. Agron. J. 74：81—85.
〔12〕 Gay, Scott, D. B. Egli, and D. A. Reicosky. 1980. Physiological Aspects of yield improvement in soybeans. Agron. J. 72：387—391.
〔13〕 Hein, M. B., M. L. Brenner, and W. A. Brun. 1984. Concentration of indole-3-acetic acid and abscisic acid in soybean seeds during development. Plant Physiol. 76：951—954.
〔14〕 Hsu, F. C., A. B. Bennett, and R. M. Spanswick. 1984. Concentrations of sucrose and nitrogenous compounds in the apoplast of developing soybean seed coats and embryos. Plant Physiol. 75：181—186.
〔15〕 Litchner, F. T., and R. M. Spanswick. 1981. Sucrose uptake by developing soybean cotyledons. Plant Physiol. 68：693—695.
〔16〕 Meckel, L., D. B. Egli, R. E. Phillips, D. Radcliffe, and J. E. Leggett. 1984. Effect of moisture stress on seed growth in soybeans. Agron. J. 76：647—650.
〔17〕 Rainbird, R. M., J. H. Thorne, and R. W. F. Hardy. 1984. Role of amides, amino acids, and ureides in the nutrition of developing soybean seeds. Plant Physiol. 74：329—334.
〔18〕 Schussler, J. R., M. L. Brenner, and W. A. Brun. 1984. Abscisic acid and its relationship to seed filling in soybeans. Plant Physiol. 76：301—303.
〔19〕 Swank, J. C., D. B. Egli, and T. W. Pfeiffer. 1987. Seed growth characteristics of soybean genotypes differing in duration of seed fill. Crop Sci. 27：85—89.
〔20〕 Thompson, J. F., J. T. Madison, and A. E. Muenster. 1977. *In Vitro* culture of immature cotyledons of soya bean (*Glycine max* (L.) Merr.). Ann. Bot. 41：29—39.
〔21〕 Thorne, J. H. 1981. Morphology and ultrastructure of maternal seed tissues of soybeans in relation to import of photosynthate. Plant Physiol. 67：1016—1025.

大豆籽粒的生长和发育

肯塔基大学 D. B. Egli

提 要

大豆〔*Glycine Max* (L.) Merrill〕籽粒产量的粒成是同化物生产，转运，及在籽形中合成贮藏物质的复杂过程。因为大豆的花期较长，在生殖生长时期，植株上存在不同发育阶段的豆荚，所以，带来了对大豆籽粒生长和发育的研究的复杂性。本文主要根据作者的研究，讨论了大豆豆荚和籽粒的生长模式，影响籽粒生长的因素，及籽粒生长特性与产量的关系。