Indian Journal of Plant Sciences ISSN: 2319–3824(Online)
An Open Access, Online International Journal Available at http://www.cibtech.org/jps.htm
2016 Vol. 5 (2) April-June, pp.19-25/Basuchaudhuri
Review Article

SOURCE-SINK RELATIONSHIPS IN SOYBEAN

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ABSTRACT
It is interesting to know in details about the source-sink relationships in soybean. Here, it was tried to elaborate the source and sink concepts and the dependence to each other. It is important to know the relationships perspective to productivity of soybean. As the soybean yield is not high enough, it is of special interest. Changes in leaf photosynthesis with the variation of source and environmental changes had been discussed. Similarly, sink strength and its variations also been discussed. But, the complex nature of assimilate supply at different stages of growth and environment, translocation and remobilization of assimilates are not clearly understood especially when both source and sink may be limited i.e. co-limited.

Keywords: *Soybean, Source Strength, Sink Strength, Leaf Photosynthesis, Seed Growth Rate*

INTRODUCTION
Soybean is a grain legume crop. As food and feed soybean plays an important role throughout the different countries of the world. It provides oil as well as protein to the living beings. This very useful crop is grown in many countries but land coverage is highest in United States of America though it is known that the origin of soybean is in East Asia. The crop cannot tolerate water logging, salinity and acidity of the soil. Thus, liming of the soil is one concept for better productivity of the soybean in acid soils. Apart from these, climatic factors severely affect root growth and nodulation in soybean.

Growth of soybean is vigorous. However, growth in the early vegetative stage is slow. Interesting aspect is that the flowering continues for a long time hence the pod set also. Another important aspect is the leaf shading at physiological maturity. After few days of leaf shading the harvesting is done and dried to achieve the soybean yield. In spite of adequate researches on soybean and with the available management practices the productivity of the soybean is not high. During reproductive phase though vegetative growth is high enough, the light interception by leaves are comparatively less. Hence, photosynthesis in reproductive phase took place in a diffused light condition.

It is noted that the productivity of soybean is related with the number of seeds per square meter and the weight of the seeds. Hence, high number of seeds and the high seed weight are important for high productivity. Medium duration and medium height plants are most favored. Average production is about 2 t/ha.

As it is a leguminous plant much nitrogen fertilization is not necessary. Early stage weed management is one important concept. Soybean is usually grown under rainfed condition but if necessary irrigation can be arranged. Microbial inoculation no doubt enhances appreciably the health and productivity of the soybean crop. It is a typical C_3 plant and photosynthetic rate of leaves changes widely depending on the environmental changes.

Soybean seed oil is good in respect of quality. Protein content in the seed is much higher in seeds than cereals and many pulses. This is a good quality food raw material and the finished products serve as food for human consumption.

Feed is the byproduct of soybean food industries and used as important ingredient. Soybean, one of nature's most versatile crops, is increasingly becoming an important food and cash crop in the tropics due to high protein content (40%), high oil content (20%) and adoptability to various growing environments (Smith *et al.,* 1995). The crop has a variety of uses including for human food, livestock feed, vegetable oil, and many industrial products and is a major crop in several developing and developed countries (McKevith, 2005).

In plant system, source-sink relationship is a complex phenomenon. In many plants source is limiting and in other plants sink may be limiting, in some source as well as sink may be limiting. With the emergence of high yielding plant types in crops, the changes had been arranged from those of traditional varieties so that the source and sink had been balanced. It is interesting to understand the under laying basis of source and sink in soybean plant as both source and sink strength under different agro-climatic conditions and under abiotic stress may affect the yield of soybean. In this crop, it is necessary to optimize the source for maximizing the yield through manifestation of yield contributing components or enhance the sink strength to an extent so that source may be a limiting, which can be further manipulated by the efficient cultural management practices. Thus, an attempt has been made to elaborate the source-sink relationships in soybean.

Source Strength

In a plant system to understand the source-sink relationship it is necessary to know the source strength. In soybean plant sources are usually the leaf area which is better represented by leaf area index i.e. leaf area per unit of land area. However, the source strength is the product of leaf area index and the efficiency of photosynthetic capacity of the leaves. Sometimes net assimilation rate is also considered as the photosynthetic capacity. Thus, source strength may be given as; source strength = Leaf area index X photosynthetic capacity or net assimilation rate. Egli and Zhenwen (1991) suggested that seeds per unit area were related to canopy photosynthesis during flowering and pod set and canopy photosynthesis rate is determined through Leaf area index (LAI) and Crop growth rate (CGR). A plant with optimum LAI and Net assimilation rate (NAR) may have higher biological yield as well as seed yield (Mondal *et al*., 2007).

Leaf Area Index (Source Size)

Soybean genotypes differ significantly in leaf area index at different growth stages. However, leaf area index of soybean within the range of 4.5 – 5.5 is better correlated with high seed yield. Leaf area index followed a typical sigmoid pattern with respect to time and increased with age till 80 days after sowing in most of the genotypes followed by a decline in green leaves because of abscission of old leaves and at physiological maturity suddenly all leaves dry and heavy leaf shading occurs. Another aspect is that the changes of leaf area index in soybean have a differential pattern at different growth stages. But, the leaf area index changes along up the height at pod setting stage is of sigmoid type, maximum leaf area being at three-fourth of plant height decreasing sharply down the canopy (Basuchaudhuri, 1987). This causes a mutual shading of sun light in the canopy and reduced photosynthesis by the full grown leaves. Hence, leaf area index and the plant architect are important in consideration of source of soybean plant.

Photosynthetic Capacity (Source Activity)

In soybean biological yield depends on source-strength by photosynthetic capacity (Egli and Crafts – Brandner, 1996). Increasing canopy photosynthesis by increasing levels of atmospheric CO_2 (Hard-man and Burn, 1971) or irradiance (Schou *et al*., 1978) increased pod and seed number, while reducing photosynthesis by shading (Egli and Zhenwen, 1991; Andrade and Ferreiro, 1996) or defoliation (Board and Tan, 1995) decreased pod and seed number. In Soybean a significant negative correlation exists between leaf photosynthetic carbohydrate (sources of starch) content and photosynthetic rate (Sawada *et al*., 1986; Kasai, 2008). There have also been findings of photosynthetic carbohydrate-mediated decrease in the activity or the amount of Rubisco, the CO_2 fixing enzyme in leaves (Paul and Pellny, 2003), although the detailed mechanism is still unclear. On the other hand, the reproductive stage of growth may be attributed to excessive mutual shading as the leaf area was maximum during this period and increased number of old leaves could have lowered the photosynthetic efficiency (Salam *et al.,* 1987). In grain legume, excess LA was reported to have lower relative growth rate and resulted in a decrease of dry matter production and net assimilation rate, which probably resulted from excessive mutual shading (Pandey *et al.,* 1978).

Sink Strength

Sink is the plant part where the assimilates moves to be utilized without synthesizing in situ. Growing and developing leaves, stems are also the sink. Seeds are the major sink. On the other hand, developing buds are also sink. Roots are potential sink through out the life span of the plant. So, the concept of sink at different stages of growth is different and is complex. For simplicity here we will consider seeds as the sink especially at reproductive stage.

Sink Size

Number of seeds is the sink size. There are variations among genotypes in average number of seeds per plant. However, management practices such as plant density, nutrient management, season also have some influences on seeds per square meter of land area. Though, pod and seed size varies occasionally, Mehta *et al.*, (2000) observed that seed yield of soybean had no positive relationship with pod and seed size. In a study, among the genotypes, BAU-70 produced the highest seed yield per plant (9.95g) and per ha (3.31t) due to production of higher number of pods per plant (31.23) and greater dry matter partitioning to seeds (harvest index 37.73%) though it produced slightly smaller seed size than he others (Malek *et al*., 2012). So, it is necessary to optimize the management practices to obtain maximum seeds per unit land area to achieve the highest yield in soybean (Basuchaudhuri *et al.*, 1986).

Sink Activity

The greater plasticity of soybean seeds for establishing final seed sink potential may be the most important trait behind its higher seed dry weight response to increased assimilate availability during seed filling. The efficiency of remobilization of assimilates temporarily stored in plant for seed production may be an important aspect determining seed dry weight response when assimilate availability is reduced. Seed growth rate (SGR) is considered as the sink activity. Experiments suggest that soybean SGR is generally sink limited if photosynthesis increases during seed filling, but source limited if photosynthesis is reduced. Usually under normal conditions of growth photosynthesis at seed filling stage is slightly reduced. Absolute growth rate of seeds is thus important which creates potential sink and SGR is positively associated with seed yield. Thus, seed number as well as SGR combination is the sink strength.

Source-Sink Interactions

Limitations to crop yields are frequently sought in either photosynthesis, the source of assimilates or in the sink, the site of assimilate utilization. This division recognizes the two major processes involved in the accumulation of grain yield, the production of assimilates in the leaves and utilization of this assimilates by the developing seed. Focusing on sources and sinks provides what appears to be a simple two-component system; unfortunately, analysis of this system does not always clearly identify the yield limiting processes (Evans, 1993). Modification of source activity of soybean during flowering and pod set usually results in a corresponding change in pod and seed number, indicating a source limitation. Increasing canopy photosynthesis by increasing levels of atmospheric CO_2 (Hardman and Brun, 1971) or irradiance (Schou *et al*., 1978) increased pod and seed number, while reducing photosynthesis by shading (Egli and Zhen-wen, 1991) or defoliation (Board and Tan, 1995) decreased pod and seed number. The effects of source-sink alterations during seed filling, after pod seed numbers are fixed, are more complex. De-poding to increase assimilate supply to the remaining seed usually increases seed size (weight per seed) (McAllister and Krober, 1958; Hicks and Pendleton, 1969; Egli *et al*., 1976; Munier-Jolain *et al*., 1998), but does not always change individual seed growth rates (SGR) (Egli *et al*., 1985; Munier-Jolain *et al*., 1998). Reducing assimilate supply by defoliation (McAllister and Krober, 1958; Egli *et al*., 1976; Board and Harville, 1998) reduced seed size, but the effect of shade was more variable (Egli *et al*., 1985; Egli, 1999). Source limitations during seed filling seem to be relatively common based on changes in seed size, but SGR is not as responsive to changes in source activity and can be sink limited. Recent analysis of changes in starch levels in soybean leaves during seed filling supports this contention by suggesting that intermittent sink limitation can occur (Egli, 1999). The response of the sink (the seed) to source-sink alterations during seed filling depends upon the effect on the assimilate level in the seed and the ability of the seed to respond to a change in assimilate supply (Jenner *et al*., 1991). The response could be manifested in change in SGR or seed fill duration, with their interaction determining final seed size. The response of seed fill duration to assimilate availability is not well understood.

In a study, in Iran to know the effects of changes in source-sink on the yield and yield components of soybean cultivars planted at different dates as the main plot (June 6, June 27), cultivars (Line 032, 033, Sare or JK and Telar or BP) as the sub-plot, and five levels (including the removal of the top, the middle and bottom one thirds of the leaves, removal of one third of the flowers, and the control treatment as the sub-sub plot. Seed yield at the first planting date (184.03 gm^{-2}) was 11/18% lower than that of second planting date (163.45 gm^{-2}). The highest seed yield was obtained in Line 033 with 219.96 gm^{-2}, which was statically different from those of all other cultivars except Line 032, which produced 186.19 gm^{-2}. The higher seed yield in Line 033 as compared with other treatments were accompanied by the highest 1000 seed weight (242.93g), the highest number of pods per plant on the main stem (43.31) and on the auxillary stems (33.37) and the relatively high number of seeds per pod (2.37). Results of applying limitations of sink-source treatments on seed yield showed that the highest seed yield was obtained in the control plants (212.17gm^{-2}). With the removal of top one third of the leaves, the yield decreased severely (138.08gm^{-2}) about 35% less than that of control. In removing one third of leaves in the middle and one third of flowers, the seed yield was reduced by 28.5 and 1.8% respectively than control. The least effect on seed yield was observed in the treatment of removing the bottom one third of the leaves, in which the yield was 201gm^{-2}, only 5.25% less than that of control. The least seed yield associated with the removal of top one third of leaves was accompanied by the least 1000 seed weight (199.59g), the fewest number of seeds per pod (2.27), the fewest number of pods per main stem (30.62) and the fewest number of pods per plant (53) (Yasari *et al.*, 2011).

Shading of all side leaflets of a determinate soybean cultivar during pod filling significantly increased rates of photosynthesis in the un-shaded centre leaflets, compared to centre leaflets of controls. Higher rates were associated with both higher stomatal and mesophyll conductances, and were reversible within 2 days when shades were removed. These higher rates of photosynthesis were not associated with decreased percentage enhancement by low oxygen, indicating that treatment effects were probably not associated with changes in photorespiration relative to photosynthesis. Percentage enhancement did, however, increases as the plants approached physiological maturity, chiefly because of a decrease in photosynthesis. Inspite of these increases in rates of photosynthesis seed weight per plant was decreased by 37% in plants with side leaflets shaded for the entire pod filling period and by 28% in plants shaded for only the second half of the period. In plants where shades were removed during the second half of pod filling seed yield was reduced by only 19% because shade removal delayed leaf senescence. The four treatments reduced yield by different mechanisms. Plants shaded continuously during pod filling produced fewer seeds than controls, but the weight per seed was similar. When shading was applied during second half of pod fillings seed number was unchanged but weight per seed was significantly reduced. In contrast when shades were removed for second half of pod filling seed number remained similar to that of continuously shaded plants, but seed weight increased.

Although all shading treatments reduced yield, the reduction was not proportional to the 63% reduction in leaf area available for photosynthesis (Peet and Kramer, 1980).

Defoliation treatments decreased yield in soybean in following order as 100% defoliation, 50% defoliation of top leaves, defoliation of top 4 leaves, defoliation of top 3 leaves, 50% defoliation of based leaves and defoliation of top 1 or 2 leaves did not affect yield. With defoliation of either 1 or 2 top leaves, yield production remained same as compared to control. This indicates that reduced source size and strength might have proportional changes on sink activities (Islam *et al*., 2014).

An experiment on the effect of shading, defoliation and seeding rates on source and sink reactions, in two determinate and two indeterminate cultivars and consisted of three different seeding rates, shade at two different periods during reproduction, and manipulation of the canopy during the reproductive period. Five plants from each treatment were taken at intervals from R5 to maturity. Biomass of entire plants and individual pods were measured along with pods per plant. As grow AG5605 was the least source limited at all locations. Treatments that were source limited varied some by locations, however, both the defoliated and non defoliated low seeding rate, the high seeding rate, and the medium seeding rate shaded late all exhibited source limitations at each location. In another experiment conducted to investigate the effect of defoliation on some morphological characters and seed yield in two soybean varieties viz. BARI Soybean-5 and BARI Soybean-6. Four defoliation treatments were imposed at flower initiation stage viz (i) control (no leaf removal), (ii) 25% leaf removal, (iii) 50% leaf removal and (iv)

75% leaf removal. All morphological and yield attributes had shown significant differences among the treatments in two soybean varieties. Morphological characters such as plant height, root length, leaf area, total dry matter and yield attributes such as pod number, pod length, seeds per pod and seed yield decreased with increasing defoliation levels where as reverse trend was observed in number of branches per plant, nitrate reductase activity, photosynthesis and harvest index. The higher morphological and yield contributing characters were recorded in control and 25% defoliation which resulted higher seed yield, there after further increment of defoliation decreased significantly yield attributes and seed yield in soybean (Ali, 2011).

In a determination of starch, sucrose and triose phosphate in a whole homogenate sample and non aqueously isolated chloroplast sample from plants of different source-sink ratios, the amounts of starch in chloroplasts, the number of starch granules per chloroplast and their size in the sink limited treatment were significantly higher then in the source limited and normal treatments. Thus, it could be concluded that starch acts as a messenger from sink to source and there by act as a regulator of source-sink relationships. Although there are some indications of regulation by triose phosphate and sucrose their role is less clear (Bandara, 1992).

Seed filling and yield of soybean under water and radiation deficits were investigated. Treatments were irrigations (I, I_2, I_3 and I_4 for irrigation after 60, 90, 120 and 150 mm evaporation from class A pan, respectively) in main plots and light interceptions (L_1- 100%, L_2-65% and L_3-25% of sunlight) in sub-plots. Seeds per plant under I_1 and I_2 decreased, but under I_3 and I_4 increased as a result of irrigation deficit. Maximum seed weight and seed filling duration of plants under 25% light interception were higher than those under full sunlight (L_1) and 65% light interception (L_2). In contrast, plants under full sunlight had the highest seed filling rate, particularly under water stress. Seed filling duration under severe light deficit (L_3), was about 9 days longer than that under full sunlight (L_1), leading to 15.8% enhancement in maximum seed weight. Decreasing seed yield of soybean under well watering and mild water stress and improving it under moderate and severe water deficit due to low solar radiation are directly related with changes in seed filling duration and consequently in seed weight and number of seeds per plant under these conditions. It is noted that early pod development of soybean is characterized by active cell division in the young ovules and is marked by rapid pod expansion; both processes are very sensitive to drought stress. Drought induced carbohydrate deprivation and change in the concentration of endogenous abscisic acid of the plants could have significant effects on pod growth and development, and may thus be involved in inducing pod abortion (Liu, 2004). It had also been noted that fruiting soybean plants at 24^0C had close to double the CO_2 uptake rates of barren plants; whereas at 27^0C the rates were the same. Removing the pods reduced the CO_2 uptake at 24^0C to close to that of barren plants. Sink activity appeared to limit CO_2 uptake over a very narrow temperature range below optimum temperatures for growth, whereas at optimum temperatures CO_2 uptake appeared to limit growth (Hofstra, 1984).

Kobraee *et al*., (2011) showed that in soybean, grain yield limited by the sink, while fewer changes in 100 seed weight at the seed filling period resulted that seed growth and seed yield were not sink limited. High change in seed weight may not always be indicated of source limitation.

Regulatory mechanism of plant photosynthesis under sink limitation occurring under various environmental conditions is still insufficient. In a study two different degrees of sink limitation were imposed on soybean plants by removing either half or all developing pods and after that, photosynthetic rate and various other characteristics were investigated in fully expanded source leaves of the depodded and control plants. It was found that a larger degree of pod removal (sink limitation) resulted in lower leaf photosynthetic rate, stomatal conductance and activation ratio (a percentage of initial activity to total activity) of Rubisco and higher leaf sucrose and starch contents without decreasing leaf intercellular CO_2 concentration and affecting leaf water, chlorophyll, total protein and Rubisco protein contents. In addition, there were agreements between activation ratios of Rubisco and photosynthetic rates of the depodded plants relative to controls. These results showed that a down regulation mechanism of leaf photosynthetic rate in soybean which depends on a decrease in activation ration of Rubisco rather those leaf Rubisco content or leaf intercellular CO_2 concentration under sink limitation (Kasai, 2008).

The regulation of carbon partitioning between source and sink tissues in higher plants is not only important for plant growth and development, but insight into the underlying regulatory mechanism is also prerequisite to modulating assimilates partitioning in transgenic plants.

Hexoses, as well as sucrose, have been recognized as important signal molecules in source-sink regulation. Components of the underlying signal transduction pathways have been identified and parallels, as well as distinct differences, to know pathways in yeast and animals have become apparent. There is accumulating evidence for crosstalk, modulation and integration between signaling pathways responding to phytohormones, phosphate, light, sugars and biotic and abiotic stress related stimuli. These complex interactions at the signal transduction levels and coordinated regulation of gene expression seen to play a central role in source-sink regulation (Roitsch, 1999).

Conclusion

Source-sink relationship is a very complex regulation processes in considering assimilate supply, translocation and remobilization systems operating side by side. In soybean both source and sink may be limiting and affect the seed yield.

Thus, soybean is known as co-limited crop plant. But in common soybean crop shows source limited until environment is of disadvantage.

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