

Yield and yield components responses of old and new soybean cultivars to source-sink manipulation under light enrichment

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ABSTRACT

Limited information is available regarding the source-sink alterations on soybean yield under whole plant light enriched conditions. The differential responses of yield components for two old and two new cultivars were investigated. The yield sensitivity of the old cultivars to the changes in source strength and light enriched conditions was much greater than that of the two new cultivars. The yield of the new cultivars was more likely sink-limited, and source-limited for the old cultivars. The increased yield by light enrichment was in part due to an increased branch contribution. Pod number per plant was more responsive than seed number per pod. The reduction in pod number by source-sink manipulation was more severe in the old cultivars. Light enrichment increased pod number in the two old cultivars but not in the two new cultivars. Seed size was responsive to changes in the source-sink ratio and changes in the environment. Both pod number or seed size may be increased or decreased if environmental conditions for seed filling are altered.

Keywords: soybean; yield and yield components; source-sink alterations; light enrichment

The seed yield of soybean consists of several components, including the number of plants per unit area, pods per node, seeds per pod, and seed size. These parameters are determined at different stages of reproductive growth (Herbert and Litchfield 1982, Egli et al. 1985, Board et al. 1995). The production of assimilate by photosynthesis, translocation of the assimilate to reproductive sinks, and utilization of the assimilate by the developing seeds to produce the storage materials is the function of yield in a grain crop (Egli et al. 1989, Egli 1999). Thus, the concept of photosynthetic source and sink is fundamental to yield of a grain crop (Liu and Herbert 2000). Charles-Edwards et al. (1986) stated that the assimilate requirement of an individual seed plays an important role in determining total seed number because the total assimilate requirement of all of the seeds on the plant must be in balance with the available assimilate supply. Equilibrium, therefore, will be maintained between source and sink during plant growth and development (Liu and Zhang 1992). For the past three decades, source-sink alterations on

soybean yield were extensively studied (Kollman et al. 1974, Egli and Leggett 1976, Egli et al. 1985, Crafts-Brandner and Egli 1987, Board et al. 1994, Board et al. 1995, Board and Harville 1998, Wang and Liu 1999, Egli and Bruening 2001). Improved understanding of yield responses to alterations in assimilate availability during different phenological phases has been a major advance in crop physiology (Borras et al. 2004).

Light is the major energy source of plants. Enhancement of source level through light enrichment using lamps or reflectors increased the yield of soybean (Johnson et al. 1969, Schou et al. 1978), while reducing source by imposing shade during seed fill reduced seed yield (Egli et al. 1980, Jiang and Egli 1993). Mathew et al. (2000) indicated that light enrichment initiated at early flowering stage by installing wire mesh fencing increased seed yield from 144 to 252% in different genotypes and environmental conditions. The improvement in yield was primarily due to an increased pod number. Light enrichment imposed at early pod formation increased seed size from 8 to 23%, result-

ing in a 32 to 115% increase in seed yield. However, limited information is available where whole plant light enrichment is used to quantify the source-sink relationship, especially yield and its components responses between old and new cultivars.

New or modern cultivars were reported to have more dry matter production during seed filling period (Shiraiwa and Hashikawa 1995, Kumudini et al. 2001, Liu et al. 2005), and yield gain in soybean was made through the production and allocation of photosynthate to more seeds or larger seeds per unit area (Morrison et al. 1999). Although seed number per unit land area is the most important yield determinant, there is a differential response of yield components to changes in environmental conditions (Herbert and Litchfield 1982). Seed dry weight is also an important contributor to seed yield, because for any given seed number there is a wide range in achievable yield due to variations in mean seed dry weight (Borras et al. 2004). More studies are required to better understand the dynamic of yield components response to the ever-changing environmental conditions. The objective of the current research was to compare the differential response of yield components of old and new soybean cultivars to the assimilate availability at an early reproductive stage of growth under light enriched conditions.

MATERIAL AND METHODS

Studies were conducted at the University of Massachusetts Agronomy Farm in 2002 and 2003. Altona of maturity group 0 and Evans of maturity group I, which are referred to as old cultivars hereafter, and other two cultivars Northup King S19-V2 of maturity group I and Northup King S28-V8 of maturity group II, both Roundup Ready, which are referred to as new cultivars hereafter, were used separately. In 2002, Altona and Northup King S19-V2 were planted on May 18. In 2003, the other two cultivars, Evans and Northup King S28-V8, were planted on May 16. The previous crop in both years was corn (*Zea mays* L.) harvested for silage. The soil is a Hadley fine sandy loam (Typic Udifluent).

A randomized block design was used with three replications in 2002 and four replications in 2003. In both years, seeds were all machine planted with a density of 50 plants/m² with plot size of 8.5 meters in length and 7 rows 25 cm apart. Light enrichment consisted of making an increased solar radiation available to the center row of each plot

by installing 90 cm tall wire mesh fencing (mesh hole size 4–5 cm) adjacent to the center row and sloping away at a 45° angle. Fences were installed at the onset of flowering, which is the growth stage R1 (Fehr and Caviness 1977), and were left in place for the remainder of the growing season. Fences prevented encroachment of plants from neighboring rows into the growing space, and thus increased the radiation interception area of the sample row. The fences were inspected periodically and all plants in rows bordering the center row were pushed behind the fences to prevent encroachment on the sample row. Light intensity measurements, using a Licor line quantum sensor (LI-188B), placed parallel to and beside the center row plants, showed that leaves at the base of the canopy in light-enriched plots were always receiving more than 25% ambient light.

The following treatments were initiated when all cultivars reached the growth stage R1:

- CK – check plants (no manipulation)
- SP – removal of all but one pod from main axis nodes
- AP – removal of pods from alternate main axis nodes upon emergence
- CL – removal of the central leaflet from each trifoliate main axis leaf upon emergence
- ALP – removal of the trifoliate leaf and all pods from alternate main axis nodes upon emergence

In each plot, 50 plants were tagged whereas 10 plants were allocated randomly to each treatment. All treated plants were tagged with different colors of wire for a differentiation during reproductive growth and at harvest. In order to obtain a detailed analysis of yield components, data were recorded for all the treated plants. Collected data included pod number, seed number, stem dry weight and seed dry weight. The final data analysis consists of a detailed separation of the yield components by treatment in order to discern the effects of the independent variables upon component makeup. Experimental data were analyzed using PROC ANOVA (analysis of variance), and Duncan's multiple range tests were used for mean comparison (SAS Institute 1996).

RESULTS AND DISCUSSION

Seed yield

Seed yield showed a significant response to source-sink manipulation and light enrichment

Table 1. Analysis of variance of final harvest yield components for light enrichment and source-sink manipulation treatments of two cultivars in each year

Yield components	Source of variation	2002	2003
Yield/plant	manipulation (M)	**	**
	cultivars (Cul)	NS	NS
	light enrichment (LE)	**	**
	M × LE	NS	NS
	M × Cul × LE	NS	NS
Pods/plant	M	**	*
	Cul	*	*
	LE	**	**
	M × LE	NS	NS
	M × Cul × LE	*	*
Seeds/pod	M	**	*
	Cul	NS	NS
	LE	*	NS
	M × LE	*	*
	M × Cul × LE	NS	NS
Seed size	M	**	**
	Cul	**	**
	LE	NS	*
	M × LE	*	*
	M × Cul × LE	NS	NS

*significant at $P = 0.05$, **significant at $P = 0.01$, NS – not significant

(Table 1). Decreasing the photosynthetic source by removing central leaflets from all leaves (CL) reduced yield both in ambient and enriched light conditions. However, cultivars responded to CL treatment differently (Table 2). Under ambient light conditions, compared to check plants, CL reduced yield averagely by 57 and 17% for the two old cultivars and the two new cultivars, respectively. The corresponding values of CL for the light enriched conditions were 31 and 26%, respectively. This result indicated that yield sensitivity of old cultivars to the conditions where source was limited during reproductive period was much greater than that of new cultivars. The two new cultivars had higher seed yields and showed more yield stability to the available source. The significant yield response of cultivars to source availability in our study may have implications for developing higher yielding genotypes and may also be helpful criteria for stable genotypic selection (Board et

al. 1995). The current study also confirmed the earlier reports that soybean yield is affected more by source strength rather than sink activity and is controlled by the availability of assimilates during the reproductive period (Hardman and Brun 1971, Taylor et al. 1982, Jiang and Egli 1993, Board and Tan 1995, Wang and Liu 1999). This, however, was true for the old cultivars. Under ambient light conditions, reducing sink size through removing pods from alternate main axis nodes (AP) or thinning pods to only one per main axis node (SP) showed no significant effect on seed yield of the old and the new cultivars (Table 2). This indicated that remainder sinks were able to respond to the extra source now available to them.

Under light enriched conditions, yield was decreased significantly in response to sink reduction in the two new cultivars and remained relatively unchanged in the older cultivars. This suggests that yield of the new cultivars during the reproductive

Table 2. Effects of source-sink alteration under ambient and enriched light on seed yield per plant (g/plant)

Cultivars	Light treatments	Source-sink treatments				
		CK	SP	AP	CL	ALP
Altona	ambient light	7.7a	6.5ab	7.7a	4.0b	3.9b
	light enriched	8.4ab	9.8a	10.7a	5.6b	4.6b
Evans	ambient light	7.9a	8.7a	8.7a	2.7b	3.7b
	light enriched	12.9a	9.4b	12.7a	9.1b	5.3c
S19-V2	ambient light	9.6a	8.4ab	9.3a	8.5ab	6.8b
	light enriched	14.9a	11.3b	12.3b	11.8b	10.4b
S28-V8	ambient light	8.5a	6.9ab	7.5ab	6.7ab	5.7b
	light enriched	13.2a	9.0b	11.8b	9.2b	8.3b

Values followed by the same letter within the row for different treatments are not significantly different ($P \leq 0.05$) CK – check plants, SP – removal of all but one pod from main axis nodes, AP – removal of pods from alternate main axis nodes upon emergence, CL – removal of the central leaflet from each trifoliate main axis leaf upon emergence, ALP – removal of the trifoliate leaf and all pods from alternate main axis nodes upon emergence

period may be sink-limited, while the old cultivars may be more source-limited. Thus, the new cultivars had greater capacity to produce higher yields with more sink available to utilize extra source, compared to the old cultivars (Table 2). However, there have been no clear conclusions regarding whether the yield is source or sink limited. Source and sink both may limit yield, as they are not independent (Evans 1993). Soybean yield can be limited either by the activity of the source or by the

ability of the sink to utilize assimilate produced by the source (Egli 1999). Soybean yield under most field conditions was shown to be source restricted during the late reproductive period (Shibles et al. 1987, Egli and Crafts-Brandner 1996). At the same time the source and sink limitations appeared to exist, as reported by Board and Harville (1998). The lower seed yield of the old cultivars would be consistent with a hypothesis that the old cultivars are source-limited for assimilates during seed filling

Table 3. Effects of source-sink alteration under ambient and enriched light conditions on total number of pods per plant

Cultivars	Light treatments	Source-sink treatments				
		CK	SP	AP	CL	ALP
Altona	ambient light	20.4a	14.9b	17.1a	13.1b	11.4b
	light enriched	20.5b	20.8b	26.5a	14.3c	12.1c
Evans	ambient light	23.9a	20.8ab	24.5a	11.7c	18.5b
	light enriched	36.2a	25.1b	35.3a	29.5b	17.4c
S19-V2	ambient light	24.9a	14.9c	19.6b	25.2a	17.8bc
	light enriched	39.7a	22.8b	28.3b	34.9a	26.7b
S28-V8	ambient light	27.9a	14.9d	20.1bc	23.8ab	16.4cd
	light enriched	35.0a	17.2d	28.1b	30.2b	21.4c

Values followed by the same letter within the row for different treatments are not significantly different ($P \leq 0.05$) CK – check plants, SP – removal of all but one pod from main axis nodes, AP – removal of pods from alternate main axis nodes upon emergence, CL – removal of the central leaflet from each trifoliate main axis leaf upon emergence, ALP – removal of the trifoliate leaf and all pods from alternate main axis nodes upon emergence

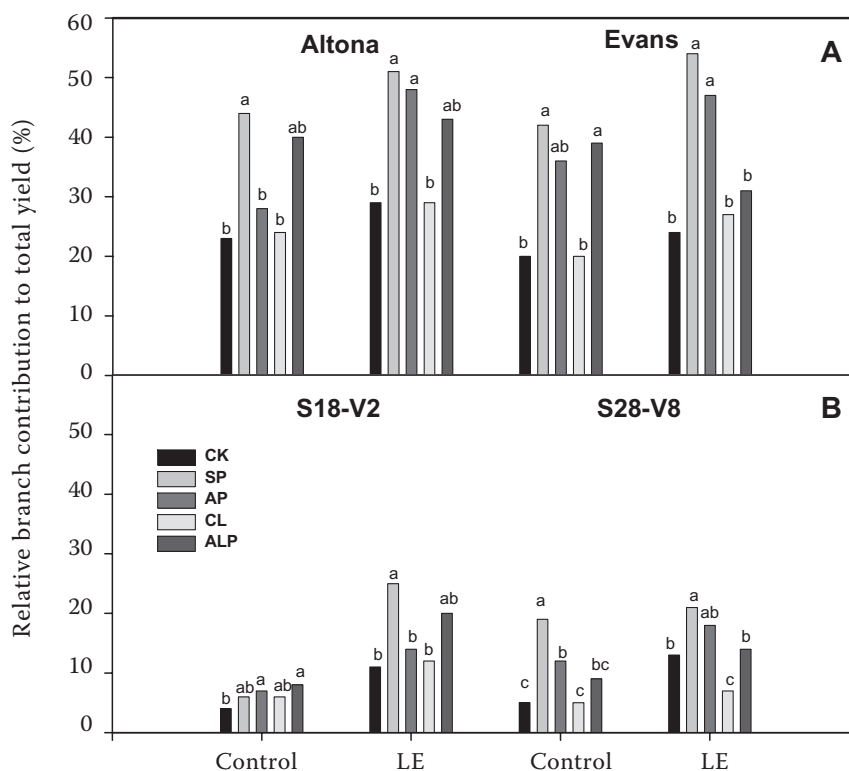


Figure 1. Relative contribution of branch to total yield in different source-sink manipulations under ambient and light enriched (LE) conditions for two old cultivars (A) and two new cultivars (B)

CK – untreated check, SP – removal of all but one pod from main axis nodes single, AP – pods removed from alternate main axis nodes, CL – central leaflet removed from each leaf, ALP – pods and trifoliolate leaf removed from alternate main axis nodes; bars with no common letter are significantly different at the 5% level

period (Spaeth et al. 1999). Whether soybean yield is source or sink limited will depend on genotype and cultural conditions.

Under both light regimes, the yield reduction due to removal of the trifoliolate leaves and pods from alternate main axis nodes (ALP) where average reductions were 51 and 32% for old and new cultivars, respectively. Since source-sink ratio in ALP treatment was unchanged, the similar yield decline in both light conditions was reasonable.

Overall, yields of source-sink manipulation treatments under light enrichment were greater compared to their corresponding treatments under ambient light conditions (Table 2). The results are consistent with those reported by Mathew et al. (2000). The yield increase due to light enrichment in all manipulation of source-sink treatments (except ALP for Evans) was in part due to increased branch contribution (Figure 1). The SP treatment had the greatest branch contribution to the yield under both ambient and enriched light conditions (except for S18-V2 under ambient light). This suggested that the loss of yield from depodded

nodes in main axis was compensated partly by higher contribution of branches to the yield. As less assimilate was demanded by pods on the main axis, the available assimilate was most likely used to form more branches and seed on the branches. Figure 1 also indicated that the old cultivars had greater ability to produce branches than the new cultivars.

Yield components

Pod number per plant exhibited significant responses to the cultivars, source-sink manipulation, and light enrichment (Table 1). As expected, plants produced or retained more pods under light enriched conditions compared to the ambient light condition (Table 3). Plants that received more light were not forced to abort pods due to source limitations. With source restriction in the CL treatment pod number was significantly reduced compared to untreated plants in both light regimes. The reduction in pod number, re-

Table 4. Effects of source-sink alteration under ambient and enriched light conditions on seed number per pod of main stem pods

Cultivars	Light treatments	Source-sink treatments				
		CK	SP	AP	CL	ALP
Altona	ambient light	2.23a	2.13ab	2.21a	1.93b	1.99b
	light enriched	2.30a	2.25ab	2.22ab	2.32a	2.14b
Evans	ambient light	2.36a	2.32a	2.16ab	1.89b	1.99b
	light enriched	2.33a	2.21ab	2.18ab	2.17ab	2.10b
S19-V2	ambient light	2.67b	3.00a	2.69b	2.61b	2.62b
	light enriched	2.63b	2.82a	2.69ab	2.62b	2.67ab
S28-V8	ambient light	2.38b	2.68a	2.48ab	2.27b	2.39b
	light enriched	2.46b	2.68a	2.52ab	2.40b	2.52ab

Values followed by the same letter within the row for different treatments are not significantly different ($P \leq 0.05$) CK – check plants, SP – removal of all but one pod from main axis nodes, AP – removal of pods from alternate main axis nodes upon emergence, CL – removal of the central leaflet from each trifoliate main axis leaf upon emergence, ALP – removal of the trifoliate leaf and all pods from alternate main axis nodes upon emergence

regardless of light condition, was more severe in the two old cultivars compared to the two new cultivars. Average reductions in pod number for the two old cultivars were 44 and 24%, and for the two new cultivars were 7 and 13% in ambient and enriched light conditions, respectively. Several reports showed that modification of the environmental conditions to reduce photosynthates during

reproductive growth stage caused a reduction in pod number and consequently yield (Schou et al. 1978, Board and Harville 1993, Egli 1993, Jiang and Egli 1993). Pod number was more responsive to altered source strength than other yield components including seeds per pod and seed size (Board et al. 1995, Mathew et al. 2000). However, the negative effect of reduced source strength on

Table 5. Effects of source-sink alteration under ambient and enriched light conditions on seed size (mg/seed) of seeds in the main stem pods

Cultivars	Light treatments	Source-sink treatments				
		CK	SP	AP	CL	ALP
Altona	ambient light	168b	203a	204a	160b	171b
	light enriched	177b	208a	183b	167b	174b
Evans	ambient light	143b	179a	164a	123c	135bc
	light enriched	153ab	169a	166a	141b	146b
S19-V2	ambient light	145c	190a	176b	130d	146c
	light enriched	145c	186a	165b	130d	148c
S28-V8	ambient light	128c	173a	152b	123c	148b
	light enriched	154c	200a	169b	134c	155c

Values followed by the same letter within the row for different treatments are not significantly different ($P \leq 0.05$) CK – check plants, SP – removal of all but one pod from main axis nodes, AP – removal of pods from alternate main axis nodes upon emergence, CL – removal of the central leaflet from each trifoliate main axis leaf upon emergence, ALP – removal of the trifoliate leaf and all pods from alternate main axis nodes upon emergence

pod number of soybean was not similar for all cultivars in our study. The results indicated that the impact of reduced source on pod number, like their effect on seed yield, was also dependent on cultivar and light availability.

Results for AP and SP (increased source/decreased sink) indicated that the two old cultivars showed greater growth of branches and production of branch pods under stressful conditions when main axis pod production was restricted (Table 3). A similar percentage of reduced pod number in the SP treatment was obtained for both light conditions for the two new cultivars (40 and 43% for S19-V2, and 47 and 50% for S28-V8, respectively under ambient and enriched light conditions). This indicated that light enrichment had no significant effect on the capacity of new cultivars to compensate for a reduction of pods through producing more pods on other main axis nodes and/or branches.

The response of seed number per pod to light enrichment and source-sink treatments was smaller compared to changes in pod number per plant (Table 4). The SP and AP treatments did not improve the seed number per remaining pod for the two old cultivars, but slightly increased seed number per pod for the two new cultivars in both light conditions. Reducing source in the CL treatment significantly lowered the seed number per pod in the old cultivars but not in the new cultivars under ambient light (Table 4). This shows the two new cultivars were able to maintain or increase the number of seeds per pod in their main axis under a limited source condition compared to the two old cultivars. However, under light enrichment no significant differences were found among CL and check plants in all cultivars. Thus, the old cultivars in this enriched light conditions, were able to utilize the added light to compensate for reduced leaf area.

The effects of source-sink manipulation on seed size resulted in some larger changes than for seed number per pod (Table 5). Smallest seeds were consistently obtained in the CL treatment for all cultivars. Egli (1999) indicated that increased number of pods and seeds by the plant in response to the lessened photosynthetic area resulted in less available photosynthate to fill the seeds. Our results were consistent with that report. Defoliation studies during the reproductive stage of growth have shown that seed size is affected when source strength is decreased (Egli and Leggett 1976, Ingram et al. 1981). This is mainly because the photosynthetic activity by crop canopy declines

gradually during the effective filling period and current photosynthesis (rather than remobilization of stored carbohydrate) is considered to be the main source for seed growth in soybean (Liu et al. 2004). In all cultivars, reducing sink size through the SP and AP treatments on the main axis resulted in a significant increase in seed size of remainder seeds (Table 5). The heaviest seeds were produced in the plants of SP treatment. In SP treatment, compared to control plants, average seed increase in size was 23 and 33% for old cultivars and new cultivars respectively under ambient light conditions. Egli et al. (1985) stated that increased assimilate supplies created by partial fruit removal can increase rates of dry matter accumulation, duration of seed growth and therefore, final seed size. An increase in seed size compensated for the decreased pod load was also reported by several other researchers (McAlister and Krober 1958, Schonbeck et al. 1986, Board and Harville 1998).

Light enrichment did not further increase the seed size of the cultivars except for S28-V8. Smaller seed size of this cultivar compared to other cultivars may be responsible for its significant response. The lack of response of seeds of other cultivars to extra source suggests that adjustment in yield is primarily taking place via other components, specifically pod number per plant. This has been shown in other studies where adjustments to light enrichment imposed at R1 or earlier are through increased pod number where light enrichment imposed at the beginning of pod fill resulted in an increase of seed size (Mathew et al. 2000). The cultivar response for seed size to light enrichment needs further investigation.

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