Soybean yield and yield component distribution across the main axis in response to light enrichment and shading under different densities

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ABSTRACT

A 2-year field experiment was conducted under light enrichment and shading conditions to examine the responses of seed yield and yield components distribution across main axis in soybean. The results showed that the maximum increase in seed yield per plant by light enrichment occurred at 27 plants/m^2, while the most significant reduction in seed yield per plant by shading occurred at 54 plants/m^2. Light enrichment beginning at early flowering stage decreased seed size on average by 7% while shading increased seed size on average by 9% over densities and cultivars, resulting in a fewer extent compensation in seed yield decrement. Responses to light enrichment and shading occurred proportionately across the main axis node positions despite the differences in the time (15–20 days) of development of yield components between the high and low node positions. Variation intensity of seed size of three soybeans was dissimilar as a result of changes in the environment during the reproductive period. The small-seed cultivar had the greatest stability in single seed size across the main axis, followed by moderate-seed cultivar, while large-seed cultivar was the least stable. Although maximum seed size may be determined by genetic potential in soybean plants, our results suggested that seed size can still be modified by environmental conditions, and the impact can be expressed through some internal control moderating the final size of most seeds in main stem and in all pods. It indicates that, through redistributing the available resources across main stem to components, soybean plants showed the mechanism, in an attempt to maintain or improve yield in a constantly changing environment.

Keywords: light enrichment; shading; yield component; seed size

Environmental conditions prevailing during the reproductive period, especially intensity and quality of solar radiation intercepted by the canopy, are important determinants of soybean yield and yield components (Myers et al. 1987, Board and Harvill et al. 1996). Increased seed yield of soybean through narrow rows, can be attributed to increased light interception during reproductive period (Costa et al. 1980, Herbert and Litchfield 1982, Board et al. 1992, Board and Harville 1996). Light enrichment initiated at late vegetative or early flowering stages increased plentiful pod number, resulting in a 144% to 252% increase in seed yield (Mathew et al. 2000). Shading resulted in lengthening of internodes, decreasing of the number of pods and seeds per plant, the seeds yield per plant, the aerial part biomass per plant significantly (Ephrath et al. 1993, Jiang and Egli 1993, Li et al. 2006). In addition, influence of shading on seeds yield per area depends on duration of shading (Jiang and Egli 1995).

Adjusting planting density is an important tool to optimize crop growth and the time required for

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canopy closure, and to achieve maximum biomass and grain yield (Liu et al. 2008). High populations provide a way to optimize grain yields in short-season production systems (Liu et al. 2006b). The breeding and selection of semi-dwarf cultivars and adoption of narrow row spacing made high densities possible, and thus increased soybean yield (Svecnjak et al. 2006). Purcell et al. (2002) proposed that a decrease in radiation use efficiency was responsible for the yield ceiling usually observed in population density experiments.

The seed yield of soybean consists of several components, including the number of plants per unit area, pods number per plant, seeds per pod, and seed size. Theoretically, enriched light in field conditions could permit an increase in the number of plants per unit area, which leads to responses of other components. However, interaction of light enrichment with population is less investigated, and no information is available for the distribution of yield components cross main axis under light enrichment and shading condition. Our objective of the current research was to investigate the differential responses of yield and yield components distribution to light enrichment and shading under different densities.

MATERIALS AND METHODS

This study was conducted in the Hailun Agroecological Experimental Station, China in 2007 and 2008. The research site (47°26'N, 126°38'E, altitude 240 m) is in the north temperate zone and continental monsoon area (cold and arid in winter, hot and rainy in summer), has an average annual precipitation of 530 mm with 65% in June–August, and an average annual temperature of 1.5°C. Annual sunshine is around 2600–2800 h, total annual solar radiation is 113M J/cm^2 and annual average available accumulated temperature ≥ 10°C is 2450°C. The area is the typical Mollisol (Black soil) region with about 260 000 ha of land under cultivation. The textural class of the black soil is silty clay loam or silty clay with about 40% clay.

In each year a random complete block experimental design with three replications was used. Soybean cultivars Hai339, Heinong35 and Kennong18 were planted in 14, 27 and 54 plants/m^2 in 2007 and in 27 and 40 plants/m^2 in 2008. Each plot consisted of seven rows 8.5 m long with an inter-row spacing of 0.67 cm. The seeds were planted on May 7, 2007 and May 6, 2008. Carbamide 50 kg/ha (N 46%), and diammonium phosphate of 50 kg/ha (N 18%, P_2O_5 46%), and composite fertilizer of 150 kg/ha (N 18%, P_2O_5 16%, K_2O 16%) were applied before seeding. Weeds were controlled by hand and usual field management was conducted.

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 late vegetative or early flowering stage, 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

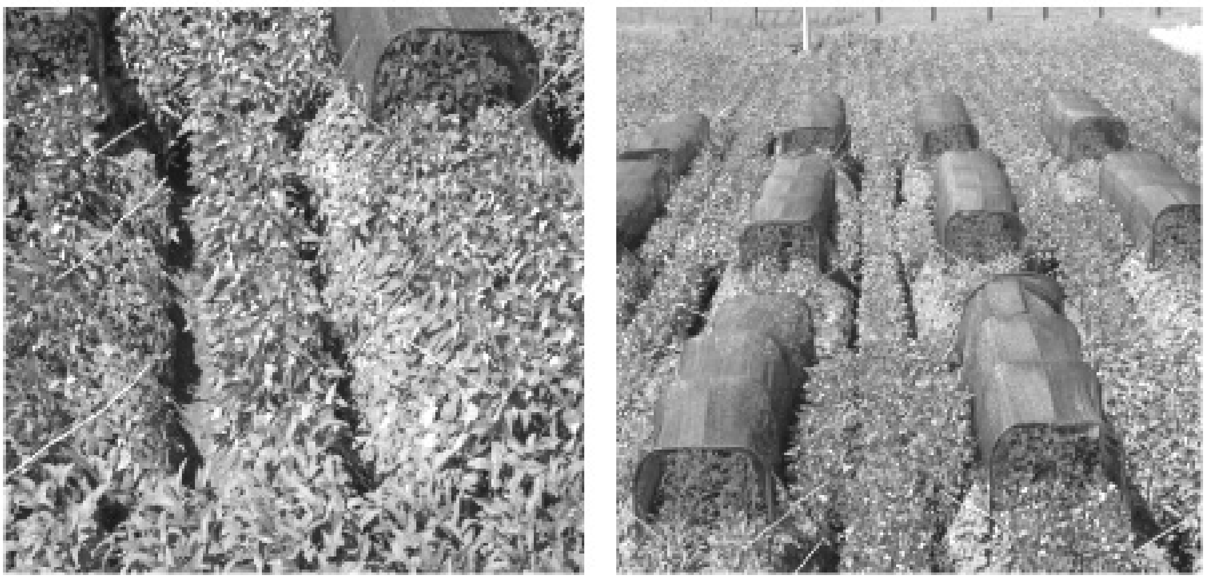

Figure 1. Light enrichment and shading treatment experimental design

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 receiving more than 25% ambient light. Shading was provided by black polypropylene fabric installed 0.5 m above the soybean canopy. Shade cloth was attached to metallic posts, which resulted in 25% light reduction compared to the ambient light (Figure 1). These treatments will not result in big changes for canopy temperature, humidity as well as air circulation.

In each plot, 50 plants were tagged and 15 plants were allocated randomly to each treatment. To obtain a detailed analysis of yield components, data were recorded for all the treated plants. For each group of plants, data were recorded according to node position on the main axis and for each branch corresponding to the main axis node from which it arose. Node 1 was the unifoliate node, being the first node above the cotyledons. Among the data recorded, there were pod number, seed number 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 make-up. Statistical analysis of data was performed by using PROC ANOVA (analysis of variance), and Duncan's multiple range tests were used for mean comparison (SAS Institute, Inc. 1996).

RESULTS AND DISCUSSION

Seed yield response. Yield of soybean plants and yield components under light enrichment and shading conditions obtained from the two experimental years were summarized in Tables 1–3. Light enrichment increased seed yield per plant compared with that of the ambient light in two years. In 2007, under low, moderate and high density conditions, light enrichment increased Hai339 (H339) seed yield per plant by 57.2%, 71.7% and 18.0%; that of Heinong35 (HN35) by 48.0%, 53.1%, 10.8% and that of Kennong18 (KN18) by 26.2%, 27.7%, and 61.4%, respectively. Maximum yield increase for H339 and HN35 was observed under moderate density, but in high density for KN18. The increased seed yield per plant for H339 and HN35 under high density in 2007 by light enrichment was not significant (Tables 1–2). Significant difference was observed for KN18 with 61.4% yield gain. This means that three soybean cultivars differ in yield sensitivity to light enrichment, which might be due to their differences in physiological character and canopy structure. Therefore, it is proposed that light is not the limiting factor for H339 and HN35 under high density. However, light might be a main factor influencing seed yield per

Table 1. Effects of light enrichment and shading on yield and yield components of Hai339 at three densities

Yield component		2007			2008	
		D14	D27	D54	D27	D40
Yield plant (g/plant)	LE	36.0^{a}	21.8^{a}	9.5^{a}	24.3^{a}	17.2^{a}
	CK	22.9^{b}	12.7^{b}	8.1^{a}	12.5^{b}	10.0^{b}
	S	14.4^{c}	7.0^{c}	3.9^{b}	8.7^{c}	4.9^{c}
Pods plant (No./plant)	LE	59.3^{a}	40.2^{a}	15.9^{a}	46.8^{a}	28.2^{a}
	CK	39.3^{b}	23.5^{b}	13.3^{b}	21.4^{b}	17.2^{b}
	S	21.5^{c}	12.3^{c}	7.73^{c}	14.4^{c}	8.4^{c}
Seeds pod (No./pod)	LE	2.36^{a}	2.05^{a}	2.22^{a}	1.96^{a}	2.21^{a}
	CK	2.17^{b}	1.93^{a}	2.14^{ab}	2.04^{a}	1.94^{b}
	S	2.28^{b}	1.98^{a}	2.01^{b}	1.94^{a}	1.80^{c}
Seed size (mg/seed)	LE	255^{b}	263^{b}	271^{a}	265^{c}	276^{c}
	CK	273^{b}	287^{a}	290^{a}	287^{b}	298^{b}
	S	302^{a}	292^{a}	239^{b}	313^{a}	322^{a}

Values followed by different letters within the row are significantly different from different light treatments under the same density within a year (P < 0.05). D14, D27 and D54 are 14 plants/m^2, 27 plants/m^2 and 54 plants/m^2, respectively. LE, CK and S are light enrichment, natural light and shade treatments, respectively

Table 2. Effects of light enrichment and shading on yield and yield components of Heinong35 at three densities

Yield component		2007			2008	
		D14	D27	D54	D27	D40
Yield/plant (g/plant)	LE	23.2^{a}	15.4^{a}	9.0^{a}	14.4^{a}	11.7^{a}
	CK	15.7^{b}	10.1^{b}	8.1^{a}	10.4^{b}	8.1^{b}
	S	9.4^{c}	6.6^{c}	3.7^{b}	6.3^{c}	4.8^{c}
Pods/plant (No./plant)	LE	58.1^{a}	41.4^{a}	24.0^{a}	39.7^{a}	31.6^{a}
	CK	44.8^{b}	29.3^{b}	22.6^{a}	30.0^{b}	25.2^{b}
	S	25.6^{c}	16.7^{c}	11.0^{b}	17.0^{c}	13.8^{c}
Seeds/pod (No./pod)	LE	2.26^{a}	2.13^{a}	2.19^{a}	2.08^{a}	2.15^{a}
	CK	1.93^{b}	1.78^{b}	2.00^{a}	1.83^{b}	1.84^{b}
	S	2.15^{b}	2.07^{a}	1.87^{b}	1.88^{b}	1.86^{b}
Seed size (mg/seed)	LE	178^{a}	177^{b}	172^{a}	174^{b}	172^{b}
	CK	184^{a}	191^{a}	179^{a}	189^{a}	175^{b}
	S	174^{a}	185^{a}	177^{a}	196^{a}	187^{a}

Values followed by different letters within the row are significantly different from different light treatments under the same density within a year ($P < 0.05$). D14, D27 and D54 are 14 plants/m^2, 27 plants/m^2 and 54 plants/m^2, respectively. LE, CK and S are light enrichment, natural light and shade treatments, respectively

plant under high density to KN18. This implies that single plant nutrient area of three soybean cultivars is different and is also helpful for making decision on optimum density to certain soybean.

Mathew et al. (2000) showed that light enrichment initiated at early flowering stages increased seed yield by 144–252%, mainly by increasing pod number. In our experiment, the highest value was only 71.7%. Two possible reasons may result in the difference. First, soybean cultivars in their experiment were more profusely branching ones, while cultivars used in our studies were main axis ones without branches. More branches produced by light enrichment resulted in more pods in the low region of soybean plants. Second, row width was 25 cm in their experiment, while row width was 67 cm in our study. Thus, it is obvious that light enrichment effect in narrow row is much greater than that in wide row. Soybean plant has self regulation mechanism of redistributing the

Table 3. Effects of light enrichment and shading on yield and yield components of Kennong18 at three densities

Yield component		2007			2008	
		D14	D27	D54	D27	D40
Yield/plant (g/plant)	LE	21.5^{a}	19.3^{a}	11.3^{a}	21.0^{a}	19.1^{a}
	CK	17.0^{b}	15.1^{b}	7.0^{b}	12.5^{b}	13.3^{b}
	S	9.2^{c}	7.6^{c}	4.1^{c}	7.2^{c}	6.8^{c}
Pods/plant (No./plant)	LE	63.7^{a}	60.5^{a}	34.6^{a}	66.4^{a}	56.4^{a}
	CK	52.9^{b}	45.4^{b}	24.1^{b}	41.8^{b}	44.4^{b}
	S	27.7^{c}	25.4^{c}	14.3^{c}	23.9^{c}	23.6^{c}
Seeds/pod (No./pod)	LE	2.13^{a}	2.14^{a}	2.08^{a}	2.05^{a}	2.06^{a}
	CK	2.17^{a}	2.11^{a}	1.89^{b}	1.91^{b}	1.84^{b}
	S	1.97^{b}	1.78^{b}	1.75^{b}	1.78^{c}	1.73^{c}
Seed size (mg/seed)	LE	158^{ab}	149^{b}	155^{a}	155^{b}	164^{a}
	CK	149^{b}	159^{ab}	154^{a}	157^{b}	163^{a}
	S	161^{a}	166^{a}	161^{a}	168^{a}	169^{a}

Values followed by different letters within the row are significantly different from different light treatments under same density within a year ($P < 0.05$). D14, D27 and D54 are 14 plants/m^2, 27 plants/m^2 and 54 plants/m^2, respectively. LE, CK and S are light enrichment, natural light and shade treatments, respectively available assimilates to components, in an attempt to maintain or improve yield. In addition, profusely branching cultivars and mainstem style ones may have different mechanisms.

Shading imposed in anthesis reduced flower production and increased flower and pod abscission, resulting in reduced pod number and yield (Jiang and Egli 1993, Sharma et al. 1996). The impact of shading on seed yield depends on duration of shading (Jiang and Egli 1995). In our experiment, shading decreased seed yield per plant compared with that of the ambient light in two years. In 2007, under low, moderate and high density conditions, shading decreased H339 seed yield per plant by 37.1%, 45.3% and 51.1%; that of HN35 per plant by 39.9%, 34.4%, 55.0% and that of KN18 per plant by 46.1%, 49.7%, and 41.7%, respectively (Tables 1–3). Thus, the yield reducing effect by shading was quite lower than the yield increasing effect by light enrichment. However, yield sensitivity of different cultivars to shading condition was very uniform.

Yield components response. Pod number per plant was the most responsible component for yield change under light enrichment and shading in the 2-year study. This suggests that light enrichment and shading imposed during early flowering stage would change assimilates availability to the developing reproductive structures, influence flowering, and flower and pod abscission number with a resultant change in final pod number at harvest. Pod number per plant as the yield component was most influenced by change in cultural and environmental conditions (Herbert and Litchfield 1982, Board et al. 1992).

Seed number per pod was less affected by change in light regime in our experiment, compared with the pod number per plant (Tables 1–3). Seed number per pod is a minor component determining the yield of soybean (Schou et al. 1978, Herbert and Litchfield 1982). The effect of shading on seed number per pod was larger than that of light enrichment in D54 of HN35 in 2007, D14 and D27 of KN18 in 2007, respectively, while the effect was smaller than that of light enrichment in D14 of H339 in 2007, D14 of HN35 in 2007, D27 and D40 of HN35 in 2008, D54 of KN18 in 2007. However, there was a tendency of increased seed number per pod under light enrichment and decreased seed number per pod under shading. This indicated that seed number per pod is strongly determined by the internal genetic mechanism, and is influenced by environment condition to some extent.

Seed size was negatively impacted by light enrichment. In case of cultivar H339, seed size was 8% decreased by light enrichment under moderate density in 2007 and 7% decreased under low density by light enrichment in 2008. Less assimilates available to fill the single seeds may contribute to the smaller seed size. Decrease of seed size in D27 of H339 in 2007 and D27 of H339 in 2008 might be caused by the greater increase of seed number per plant than increase of available amount of photosynthate synthesized per plant under the light enrichment condition.

Liu et al. (2006a) noticed that shading (52% light reduction) lowered seed size while Egli et al. (1985) reported that shading (60% light reduction) during the linear phase of seed development lowered seed growth rate but did not affect final seed size because of a longer duration of seed growth. In our study, shading (25% light reduction) increased seed size by 7 to 11%, which might be a compensation mechanism to yield loss. The influence of shading on seeds yield per plant depends on duration of shading (Jiang and Egli 1995). Therefore, the response of seed size to shading is closely related to shading intensity and a threshold of shading intensity is existed to influence seed size.

Distribution of yield components across the main axis. Light enrichment and shading treatments resulted in proportional changes in pod number across all node positions (Figure 2). This is true for three cultivars under different densities. Most pods were produced at the nodes in the middle parts of the plants. Differences in pod distribution curve between densities and cultivars were observed. Under densities of 14 and 27 plants/m^2, the space among pod distribution curves in different light treatments was wider than densities of 40 and 54 plants/m^2. This indicated that under low and moderate densities light had much stronger effect on pod number per node in main axis than that of high densities. The increase and decrease in pods due to light enrichment and shading occurred relatively consistent across every node in the main axis. This showed that light enrichment and shading initiated from the early flowering influenced the final pod number through changing flower and pod abscission at all nodes. Pod number per plant as the yield component was most influenced by changes in cultural and environment conditions (Board and Tan 1995, Egli 2005). Heindl and Brun (1984) reported that in indeterminate soybean, there is only a slight variation in the number of flowers formed at each node, and high rate of flower abscission was the major factor determining the pod number per node. Whether light influence on final pod num-

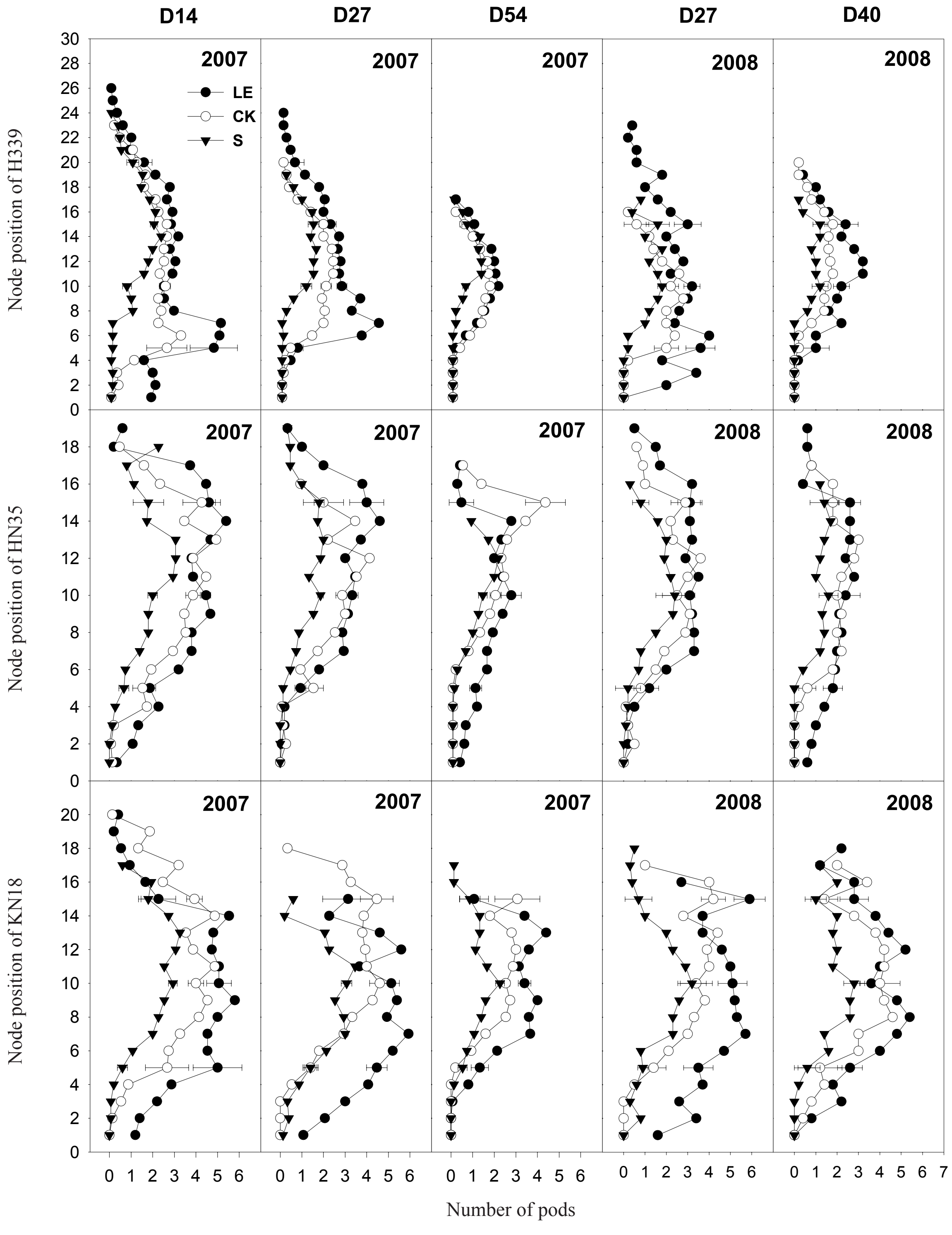

Figure 2. Distribution of pods in the main stem of different cultivars treated with light enrichment and shading at three densities. H339, HN35 and KN18 are Hai339, Heinong35 and Kennong18, respectively. Bar indicates standard error of the mean

ber is from variation of flower or change of pod abscission is still unclear.

As is shown in the Figure 3, seed number per pod was less affected by change in light regime, compared with the pod number per node across the main axis. This indicated that the proportion of one, two, three and four seeded pods produced at each node was relatively constant. However, there was a tendency for HN35 in 2007 and KN18 in 2008 that seed number per pod was increased under light enrichment. This suggests that there might be two mechanisms for soybean plants to

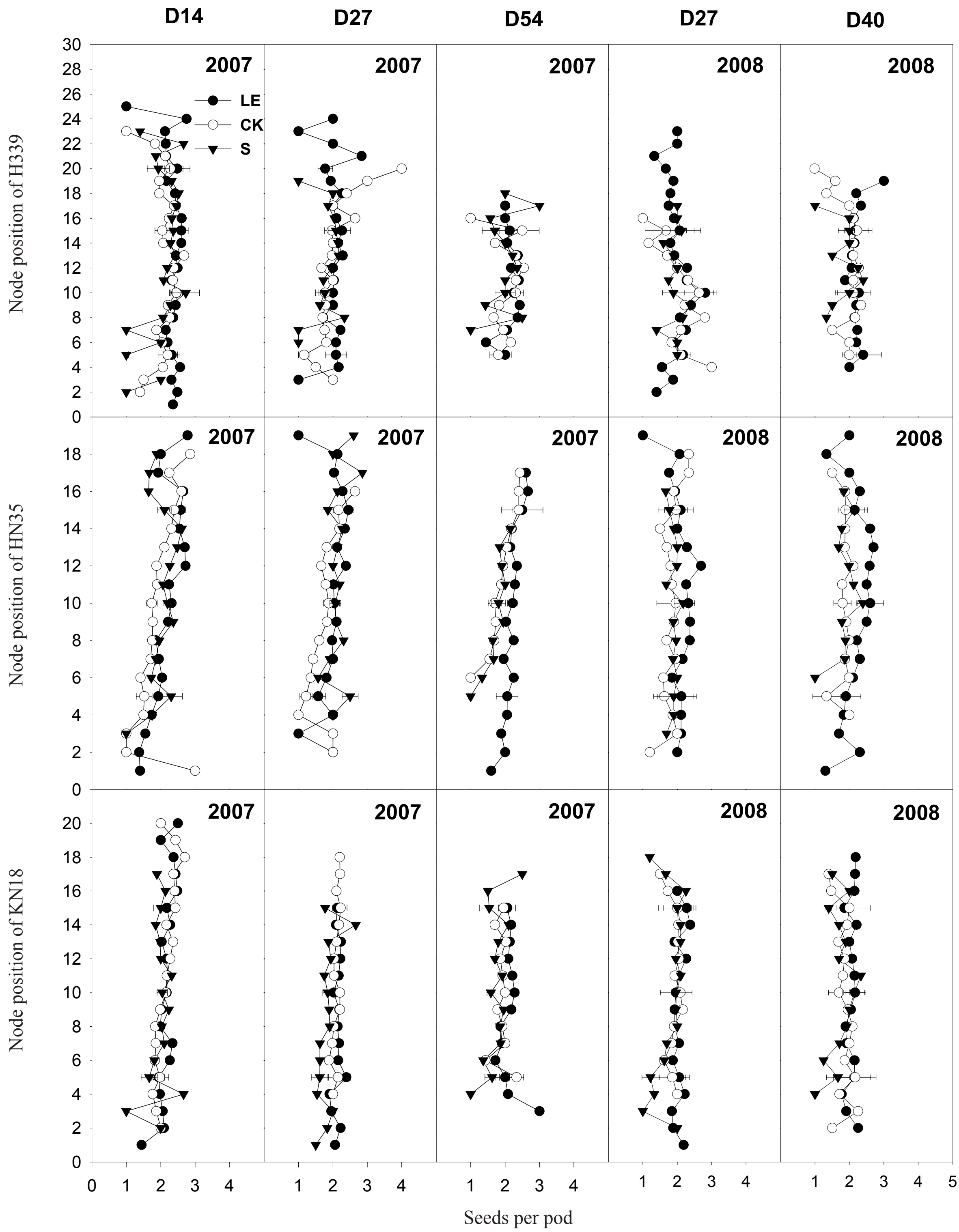

Figure 3. Distribution of seeds per pod in main stem of different cultivars treated light enrichment and shading at three densities. H339, HN35 and KN18 are Hai339, Heinong35 and Kennong18, respectively. Bar indicate standard error of the mean

respond the extra available source. That is either to increase pod number per plant or seed number per pod. Liu et al. (2006b) suggested that some internal factors rather than external input regulate the seed number per pod in some cultivars. The variation in seed number per pod observed at the extreme node positions was much greater than that at the middle mainstem nodes of soybean plants. It is mostly due to the small number of these pods borne at these extreme node positions, so the presence

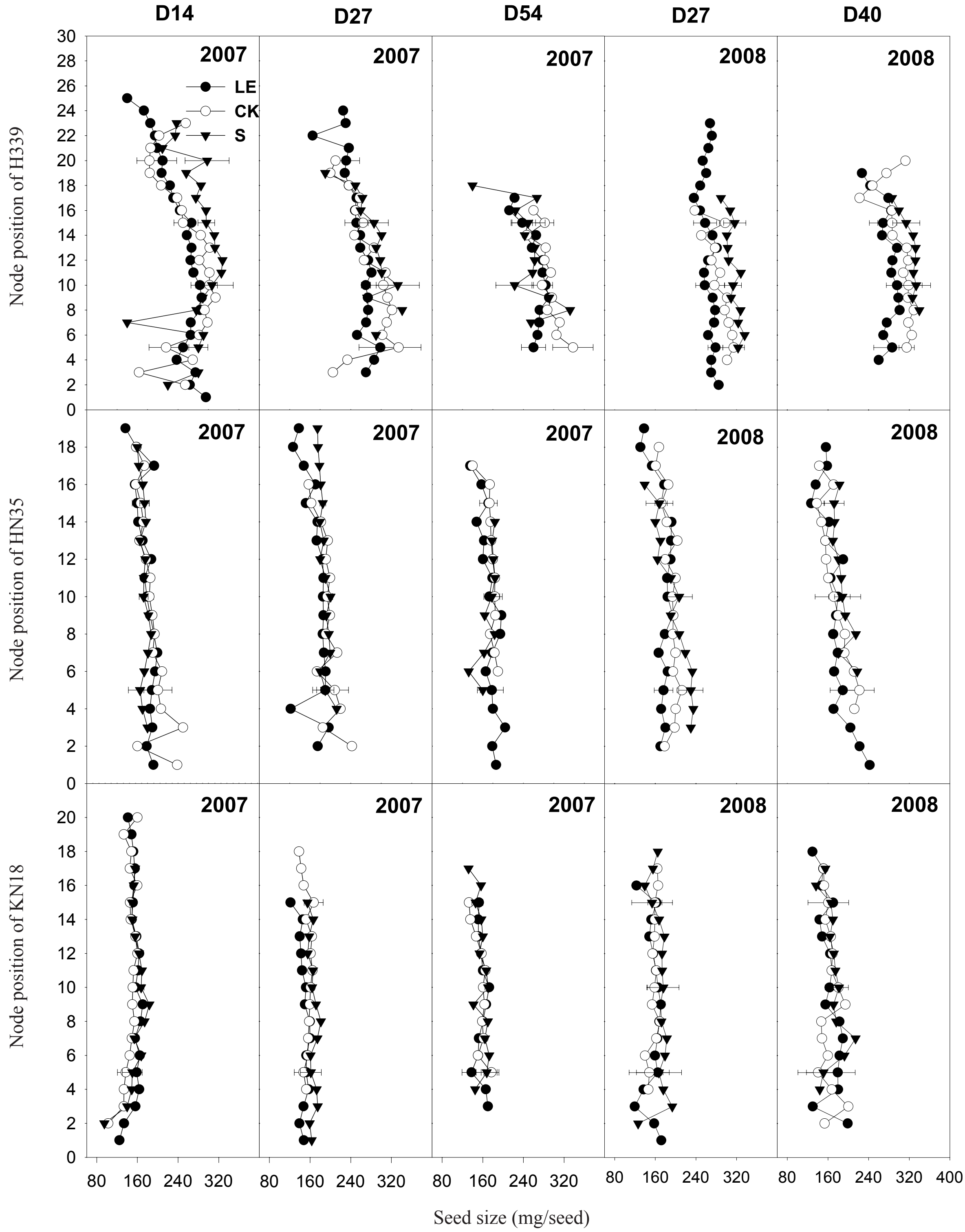

Figure 4. Distribution of seed size in main stem of different cultivars treated with light enrichment and shading at three densities. Bar indicates standard error of the mean. H339, HN35 and KN18 are Hai339, Heinong35 and Kennong18, respectively. Bar indicate standard error of the mean

of a one and four seeded pod unduly weighted the average number of seeds per pod, causing variation in the calculation of mean seed number per pod.

In soybean plants, when the lowermost nodes start filling seeds, the uppermost nodes are still in the process of producing flowers. Despite the difference (about 15–20 days) in the duration of seed filling between the lowermost and uppermost node, seed size was mostly constant across mainstem nodes (Figure 4). Spaeth and Sinclair

(1984) reported that the duration of seed filling decreases from the lowermost nodes to the uppermost nodes of the soybean plant. As a result of simultaneity of the seed produced on the lowermost and the uppermost nodes reaching physiological maturation, it is doubtless that seed produced on the uppermost nodes has higher seed average growth rate than that produced on the lowermost nodes (Egli et al. 1985). Cotyledon cell number and cotyledon cell volume are two main components determining seed size (Mathew 2000). We postulate that seeds produced on the uppermost nodes have relatively higher number of cotyledon cells and much smaller or lighter cotyledon cell volume, while seeds produced on the lowermost nodes have relatively a lower cotyledon cell number but much bigger cotyledon cell volume, making seeds produced on the lowermost and uppermost node quite uniform.

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