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MANIPULATION OF YIELD THROUGH SOURCE-SINK CHANGES IN SOYBEAN [*Glycine max* (L.) Merrill]

A Thesis Presented

by

SHU-HUAN ZHANG

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DEDICATION

To my wife

Wei Wang

whose patience and support allowed me

to complete this project

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CHAPTER 1

INTRODUCTION

Soybean (*Glycine max* (L.) Merrill), an important grain crop in the United States as well as in many other countries of the world, has been studied for many years with regard to yield. Since the supply of water and fertilizer currently is not a problem limiting soybean production in the U.S. and other developed countries, improvement in light utilization by the soybean canopy, usually through planting patterns such as plant density, row width, and intercropping has been intensively investigated. Numerous studies have demonstrated that more efficient light interception by soybean canopy contributes to an increase in soybean yield (Lehman and Lambert, 1960; Blad and Baker, 1972; Willcox, 1974; Cooper, 1977; Johnson *et al.*, 1982; Herbert *et al.*, 1984; Willcott *et al.*, 1984; Duncan,1986; Ikeda, 1992).

Loomis *et al.* (1979) hypothesized that future yield improvements in agricultural crops would come from enhanced partitioning of assimilate to the harvest fraction, and the assimilate partitioning theoretically was accomplished by translocation in the plant. A number of studies on soybean indicated that most light interception by soybean occurs in the top and periphery of the canopy, while most yield occurs in the lower to the middle portions of the plant (Sakamoto and Shaw, 1967; Herbert and Litchfield, 1982). This character suggested that the long - distance assimilate translocation existed in soybean plants through which the assimilates was transported from upper and periphery sources to lower and middle sinks. This further suggested that genetically controlled partitioning of assimilate predominantly determines the distribution pattern of yield in soybean canopy. Detailed analysis on soybean yield components across the node positions would be helpful in the investigation of yield partitioning and yield improvement.

Partitioning of assimilate is affected by the source - sink ratio which was largely responsible for changes in soybean yield (Hick *et al.*, 1969; Beuerlein *et al.*, 1971; Egli and Leggett, 1976; Herbert *et al.*, 1984). Seasonal and daily fluctuation of solar radiation in the field contribute to the variation of source supply to the sink. Pod abscission (abortion), thought to result from inadequate late season photosynthate supply, resulted in a subsequent yield reduction (Mondal *et al.*, 1978). Artificial depodding or defoliation could simulate source - sink variation in soybean plants. Egli and Leggett (1976) stated that pod removal reduced the sink demand in soybeans and resulted in the accumulation of carbohydrate in other plant parts. Reducing the supply of photosynthate by defoliation or shading has been shown to cause reductions in the carbohydrate levels in leaves and other plant parts (McAllister and Krober, 1958; Thorne and

Koller, 1974). Studies by Litchfield (1991) showed the soybean yield could be altered significantly by source - sink manipulation.

This present study investigated the effects of light interception by the soybean canopy during two different growth stages on final yield and compared yield components. Also, the interrelationship among sources and sinks of this indeterminate soybean plant was evaluated by various depodding and defoliation treatments. Yield was analyzed by yield components on a node by node basis. In addition, harvest index and pod harvest index were evaluated to explore how the change in partitioning of assimilate between biological parts and economical parts of soybean plant affect final yield.

CHAPTER 2

LITERATURE REVIEW

2.1 General history of soybean

Soybean (*Glycine max* (L.) Merrill) is one of the oldest of cultivated crops in the world which likely originating in the northeastern provinces of China. As early as 2838 B.C., an ancient Chinese book - Pen Ts'ao Kong Mu - described this leguminous plant. This is believed to be the earliest written record of soybean. In the long history of Chinese civilization, soybean has been one of the five major grains - rice, soybean, wheat, barley and millet. The food made from soybean has always been popular food resource in China and in other oriental countries (Morse, 1950).

Between 200 B.C. and the third century A.D., the cultivated soybean is believed to have disseminated from northern China into Korea, and into Japan (Nagata, 1959). After the Chinese-Japanese war (1894,1895), soybean production gained attention in Japan (Morse, 1950). The introduction of soybeans into Europe dates from 1740, when the missionaries sent soybean seeds from China to the Jardin des Plantes in Paris (Probst and Judd, 1973). In the West, tremendous increase in production and use of soybean occurred after World War II (Synder and Kwon, 1987).

In the United States, soybean was first introduced in the early 1800's, but remained a minor curiosity until the twentieth century. It was not until after 1945 that the value as feed and food oil was recognized (Synder and Kwon, 1987). In 1959, soybean yield in the United States approached the world level recorded by China. In 1960, the soybean yield in the United States surpassed that in mainland China. Since then, the United States has been the country with the largest scale in soybean production and maintained the highest soybean yield in the world.

The steady increase in soybean yields in the United States is attributed to the strong demand as a feed and food resource, and to the rapid progress in modern agricultural science and technology. Probst and Judd (1973) stated that improved adapted varieties, better cultural methods, increased fertility, and improved machinery were important factors in the yield increase per acre. Synder and Kwon (1987) stated that the knowledge about the physiology of soybean had been extremely helpful to the soybean producer. Particularly, knowledge about the maturity group, breeding, diseases and pests, nitrogen and photosynthate assimilate made the management of soybean production much easier. Soybean yields increased with knowledge of plant density, row width, and interplanting. A reasonable planting pattern would enable the crop canopy to intercept much more solar radiation, and reduce competition for water and nutrients. More recently, the source-sink relationship in soybean has been the subject of much investigation.

2.2 Light and light interception in soybean production

Many factors affect soybean growth and final yield including solar radiation, soil fertility, soil aeration, soil and air temperature, carbon dioxide, moisture, weed pressure, insects and pathogens (Litchfield, 1991; Norman, 1978). Solar radiation plays a significant role determining soybean yield, since it supplied solar energy for photosynthesis. Norman (1978) stated that light strongly influenced the morphology of the soybean plants by causing changes in the time of flowering and maturity, which resulted in differences in plant height, pod height, leaf area, lodging, total dry matter production, and grain yield.

One important aspect of light in soybean production is photoperiod that resulted in classification of soybean maturity groups in the United States. There are 11 zones in North America of best adaption for soybean cultivars respectively corresponding to Maturity Group 00 through Maturity Group IX. Soybean cultivars grown in Massachusetts belong to Maturity Group II. However, Group 0 and Group I were usually planted in this area to ensure an earlier harvest. Norman (1978) found that cultivar difference in day length resulted in response in terms of the number of days to flower, the number of days to maturity, plant height, seed weight, pod number, branch number, node number, and others. Flowering occurred when day length became shorter or rather night became longer than the critical value for the cultivar.

The use of maturity groups in the United States plays an important role in increasing soybean yields. Snyder and Kwon (1987) found that soybean yields could be reduced if a maturity group adapted for northern latitudes was planted further south, and vice versa. For the first case, the plant would flower and set pods before it had reached its full vegetative growth; for the later case, flowering would be postponed and easily encounter early frost before the seeds matured.

Another important aspect of light related to soybean growth is light intensity. Light intensity can be altered by many factors like cloud cover, haze, altitude, angle of incidence, competitive shading, and other environmental conditions. Norman (1978) found flower initiation of Biloxi soybeans occurred when the light intensity was above 1076 lux for two consecutive 8-hour photoperiod, but light intensity of less than 1076 lux did not initiate flowering. In a soybean crop, light intensities at the different levels of the canopy varied greatly due to self-shading. Mann *et al.* (1980) suggested that light penetration into a row crop could be modeled by considering the cropping structure (row spacing and orientation, and planting density) as well as the individual plant structure (plant height, leaf area, and leaf angles).

Sunlight must be intercepted by the soybean plant in order to convert the radiant energy of sunlight into the chemical energy stored in carbohydrates. Interception of light is affected by the arrangement and optical properties of the leaves (Kriedeman et al., 1964). Hesketh and Baker (1967) stated that the rate of dry matter accumulation of a crop could be defined as a function of the quantity of light intercepted by the crop and the photosynthetic efficiency of the intercepting tissue. Brougham (1956) concluded that photosynthesis and dry matter production were related to the amount of leaf area present in a crop community, and this relationship was due to the influence of leaf area on the interception of light.

Most light is intercepted by the top level of canopy (Sakamato and Shaw, 1967; Willcott *et al.*, 1984). Light penetration into lower levels of canopy is attenuated (Willcott *et al.*, 1984). Light interception could be described by the different light intensities between two vertical points in a plant community, and could be expressed in the following equation by Monsi and Saeki (1953):

$$I = I_0 e^{-kA}$$

A straight line relationship with slope k is obtained when the equation was expressed in the logarithmic form:

$$\ln(I/I_0) = -kA$$

where I is the light intensity received inside the plant community, I_0 is the light intensity at the top of the plant community, A is the leaf area index, and k is the extinction coefficient which is dependent on the leaf inclination and optical properties of the leaves.

The measurements on light interception in plant communities are usually taken for the total short-wave band (300 to 3000 nanometers) (Anderson, 1964). However, it is more common to measure light using wave bands that are available for photosynthetically active radiation (PAR). PAR is defined as the waveband between 400 and 700 nanometers (Anonymous, 1981).

Light interception in a soybean canopy can be high. Shakamoto and Shaw (1967) found that 90% of the incoming light was intercepted by the top and periphery of the soybean canopy. Singh *et al.* (1968) reported that net radiation at ground level for soybean was 12 - 18% of that above the crop, while Willcott *et al.* (1984) reported it was only 5%. These results were supported by work done by Shaw and Weber (1967). Due to its large leaf area and shorter plant height, soybean has a more closed canopy than other crops such as corn (Litchfield, 1991). The leaves at lower canopy contribute little photosynthate to yield (Shiblesa and Weber, 1965; Johnston *et al.*, 1969). Since the lower leaves are not receiving adequate radiation for photosynthesis, an increase in yield presumably could be achieved by methods that would allow greater light penetration, and were demonstrated in a supplemental light treatment.

Extinction coefficients showed large changes not only with height in the community of one soybean cultivar, but also among different cultivars (Sakamoto and Shaw, 1967; Johnston and Pendleton, 1968; Luxmoore *et al.*, 1971). The variation of light penetration might result from the leaf area distribution, leaf type, leaf angles, and leaf optical properties. Blad and Baker(1972) found leaf area distribution in soybean dependent on plant age, leaf size and number, row width, and orientation. Narrow leaf types had been proposed to allow deeper light penetration into the soybean canopy (Sakamoto and Shaw, 1967), although no yield advantage was found. In a model for simulating photosynthesis, Duncan *et al.* (1967) found that light penetration into the canopy might be increased by adjusting leaf angle. Kriedeman *et al.* (1964) showed that the rate of photosynthesis in soybean leaf was proportional to the cosine of the angle of the incident light.

Numerous studies reported the advantage of narrow rows and high densities for growth and yield of indeterminate soybean cultivars in north and central regions of the United States. (Lehman and Lambert, 1960; Timmons *et al.*, 1967; Cooper, 1977; Koch, 1979; Costa *et al.*, 1980; Parks and Manning, 1980; Spilde *et al.*, 1980; Graves and McCutchen, 1981; Herbert and Litchfield, 1982; Johnson *et al.*, 1982; Willcott *et al.*, 1984). Shibles and Weber (1966) explained that narrow rows and high densities could provide a more rapid development of complete canopy closure by the time plants set pods and fill seeds, with a resultant increase in the interception of solar radiation on a unit land basis accompanied by enhanced photosynthate production.

Herbert *et al.* (1982) reported that more solar radiation was available in more productive years during the seed filling period, and was responsible for yield increase. On the other hand, Taylor *et al.* (1982) reported that a lack of photosynthate supply due to less solar radiation later in the season was a major factor in determining abortion rates of soybean seeds and pods and hence yield. Many researchers conducted investigations about the effects of increased light penetration into, and shading of, the soybean canopy.

Schou *et al.* (1978) imposed various light enrichment or reduction treatments at different stages of soybean development. Two methods of light treatments were used. The first method involved installation of reflectors at 45°

angles to the sample row and installation of black boards of the same dimensions in the same manner. The second method decreased light by 63% using shade cloth. Results showed a increased yield of 6% - 57% from light enrichment treatments, which illustrated that more light was available from opening up the canopy, and that light reflectance resulted in additional advantages. Plants enriched during the period of late flowering to early pod formation had 48% more pods, and 57% more seed yields than controls. The number of pods and the seed yields were 16% and 29% less respectively than controls for the shade treatments imposed during the same development period. Changes in yield by shading during other growth stages were not as significant as during the period from late flowering to early pod formation. The authors postulated that the soybean plants were capable of filling more pods and more seeds due to the rich light condition than were normally produced.

Wahua and Miller (1978) applied shade treatments to soybean plants and caused 20% - 93% reductions in light compared to ambient light. Results showed the highly negative correlation occurred between amount of shading and grain yields, pod number per plant, and percent leaf nitrogen. The loss of the nitrogen fixing ability of the crop as it developed was accelerated by shading.

Johnston *et al.* (1969) used wide-spectrum fluorescent lamps to supplement light on soybean canopies. Results showed that by adding light yields increased by increasing pods per plant and seeds per pod, but seed size decreased. Hongfei (1993) used shade-cloth above the canopy to reduce light and showed a reduction in pod numbers per plant, due to increased flower and pod abscission and to reduced number of flowers per plant. Similar results have been reported by other researchers (Popp, 1926; Lehman, *et al.*, 1960; Pendleton, *et al.*, 1963; Probst, 1945). These studies suggested that solar radiation greatly affects soybean yield. However, more investigation is needed on the vegetative and reproductive growth phases in which light is most influential on the final yield. Season-long light treatments had different effects on soybean yield as hypothesized by Herbert *et al.* (1984) because of light variation during a specific period.

2.3 Source - sink relationship and dry matter partitioning

Generally, organs capable of meristematic activity, additional differentiation, or storage are referred to as sinks, while other organs from which substrates are transported are referred to as sources (Loomis and Connor, 1992). In soybean plant, Egli *et al.* (1989) gave the definition to source and sink: The photosynthetic production of assimilates was undertaken in various chlorophyll containing plant parts which were referred to sources, whereas the seeds were referred to sinks. The soybean yield was dependent on the photosynthetic production of assimilates by sources, the translocation of these assimilates to the sinks, and the utilization of these assimilates to produce storage materials in the sink to give the soybean its economical value (Litchfield, 1991).

To elucidate the movement mechanism of assimilate from source to sink, Gardner *et al.* (1985) stated that:

> "The photosynthetic source cell produces the sugars, which can move symplastically to the sieve tubes. Phloem loading increases the sugar concentration of sieve tubes above that of the apoplast. At the sink, carbohydrates are being absorbed and either actively partitioned into cell constituents (e.g., starches) or changed to other carbohydrates that have little effect on hydrostatic pressure of the phloem. Phloem unloading lowers the concentration of sugars in sieve tubes. The buildup of sugars at the source and the removal of sugars at the sink establish a hydrostatic pressure gradient, which moves water and sugars from source to sinks."

The carbohydrate status of soybean leaves, usually the starch status, affects the interaction between the production of photosynthate and its utilization by the developing seeds and other sinks, and this status is related to the level of final yield (Egli *et al.*, 1980). Some studies proved the feed back effect of starch in leaves, and the high starch concentration could inhibit net leaf photosynthesis, whereas the decreased starch concentration could stimulate photosynthesis (Nafziger and Koller, 1976; Neales and Incoll, 1968).

In indeterminate soybean plants, almost every node provides pod setting and seed development. Belikov and Pirskii (1966) found that the pattern of translocation from each leaf was similar. The greatest amount of assimilate remained in the pods at the node of the applied leaf, and the rest was transported to upper and lower nodes (Gardner *et al.*, 1985).

Unlike cereal grains whose photosynthetic activity by their awns contribute 50% or more of photosynthates required by sinks, the primary site of photosynthesis of soybean plants is in the leaves (Norman, 1978). The green soybean pods apparently did not show any net fixation of atmospheric carbon dioxide, but they could contribute photosynthetically by reassimilating respiratory carbon dioxide from the seeds (Quebedeaux and Challet, 1975). Soybean leaves are the major sources to supply assimilates to sinks.

Leaf area index (LAI: leaf area per unit ground area) is often used to evaluate soybean growth due to its close association with photosynthesis and dry matter production. Shibles and Weber(1965 and 1966) found that until LAI reached its maximum, light interception and dry matter production increased with leaf area development. Further increases in LAI was not associated with decreased rates of dry matter production, indicating that leaf area in excess of that required for full light interception did not cause negative response to productivity.

However, previous studies showed different results about the relationship between soybean yield and LAI. Hicks *et al.* (1969) found no significant difference in seed yield, but found a greater LAI for plants grown in narrow rows. Willcott *et al.* (1984) found that LAI development and dry matter production need not to be greater in the soybean plants for a higher yield, while the efficient interception of light is an important factor in determining final yield.

Soybean yield was a function of differential utilization of photosynthate between vegetative and reproductive structures (Shibles and Weber, 1966). The partitioning of assimilates during the reproductive phase was critical in determining final yield of soybean.

There were predominantly two growth types in soybean plants - determinate and indeterminate species. In determinate species, leaf and stem growth ceased at flowering, while indeterminate species have vegetative and reproductive growth occurring simultaneously. Gardner *et al.* (1985) stated that, depending on the relative strength of their vegetative and reproductive sinks, reproductive yield might be reduced for the indeterminate species when there was more vegetative growth during reproductive development. For the determinate species, the maximum number of leaves was established at the initiation of flowering. Seeds became the dominant sink of plants shortly after pod setting, and the major part of assimilate was used for increasing seed weight during seed filling.

Differences in the time of seed development resulted in different seed yields among varieties and between years (McBlain and Hume, 1980). In addition to leaves, pod walls, stems, and petioles could partially serve as sources of stored carbohydrate for developing seeds in soybean plants (Streeter and Jeffers, 1979; Stephenson and Wilson, 1977). Willcott (1983) suggested that assimilate storage and later redistribution from these additional sources especially from pod walls to developing seeds might effectively lengthen the pod filling period and contribute to final yield.

Loomis *et al.* (1979) hypothesized that future yield improvements in agricultural crops would come from enhanced partitioning of assimilate to the harvest fraction. Assimilate partitioning in the plant theoretically is accomplished by translocation. Blomquist and Kust (1971) used $^{14}CO_2$ to show that translocation from a leaf was limited to its axil and the axil at the next node below it, suggesting short-distance translocation patterns in soybean.

Conversely, Gent (1982) produced Y-shaped soybean plants by removing leaflets and pods from branches and demonstrated the existence of long-distance translocation. Furthermore, constant seed filling rate in the middle phase of seed growth coupled with daily fluctuations in photosynthetic activity, gave additional evidence of long-distance translocation (Thorne, 1979).

Herbert and Litchfield (1982) reported that the most pods were in the central portion of the canopy. However, 90% of the incoming light was intercepted at the top and the periphery of the soybean canopy (Sakamoto and Shaw, 1967). Long-distance translocation of assimilates from top and periphery canopy to the central portion appeared to be necessary for seed development, although Willcott *et al.*(1984) showed that leaves on long petioles were displayed much higher in the canopy than their point of attachment. The uneven pattern of pod distribution pattern may be caused by abscission of flowers and pods and may be due to uneven partitioning of photoassimilates (Wiebold *et al.*, 1981; Heindl *et al.*, 1984). Interplant and intraplant competition for resources, particularly for solar radiation, determines the reproductive abscission and potential yield (Marvel *et al.*, 1993).

To study the mechanism of photoassimilate partitioning and translocation in soybean, many artificial manipulations have been conducted. The common methods used are depodding, defoliation, and branch removal. Generally, pod removal simulated plants which set pods and seeds under unfavorable environmental conditions and experienced more favorable conditions during the seed filling stage; defoliation simulated plants which set large numbers of pods under favorable conditions during the period of early pod set, but encountered unfavorable conditions during the seed filling stage (Litchfield, 1991); branch removal simulated that the intraplant and interplant competition for source supply was reduced, and the mainstem soybean yield could be enhanced by branch removal (Beuerlein, *et al.*, 1971).

McAlister *et al.* (1958) studied the effects of pod removal on total seed yield of 'Lincoln' and 'Hawkeye' soybeans. They found that up to 17% of pods of 'Hawkeye' and 22% of pods of 'Lincoln' could be removed without loss of yield, because seed size increased. Hicks *et al.*(1969) studied flower removal from soybean plants. Seed size increased and yield per plant was not reduced after removing one third of the flowers. However, when two thirds of the flower were removed, the increase in seed size did not compensate for the reduction in the number of pods, and yield per plant was reduced. Beuerlein *et al.* (1971) reported that yield per hector, seed weight, leaf efficiency and leaf density were greater in plants without branches than those with branches. The author stated that the potential increase in soybean yields due to canopy manipulation and changing plant morphology remained an interesting agronomic question. He also suggested that the selection of a non-branching, high harvest index genotypes might merit further investigation.

Source - sink relationship and the assimilate partitioning could be reflected by the term 'harvest index' (Gardner, *et al.*, 1985). Harvest index is the ratio of economical yield to the biological yield. The economical yield in soybean refers to the seed yield, whereas the biological yield is the total yield of plant material (Donald and Hamblin, 1976). However, for practical reasons, root contribution to biological yield is usually ignored.

Harvest index = (economical yield / biological yield) x 100

Crop yield could be improved either by increasing the total dry matter, the proportion of economic yield (the harvest index), or both (Gardner *et al.*, 1985). Schapaugh and Wilcox (1980) indicated that harvest index was influenced by environmental conditions, while Egli (1988) and Spaeth *et al.* (1984) found that harvest index within a cultivar was relatively stable across a range of growing conditions. Harvest maturity was postulated by Hintz and Albrecht (1994) to have a great effect on dry matter partition and yield.

2.4 Soybean yield components

Soybean seed yield is made up by the yield components involving plant density, pods per plant, seeds per pod, and seed size. Environmental conditions affected soybean yield usually by altering one or more of the yield components. Yield changes of soybean plants resulting from variation in solar radiation or changes in source - sink ratio can be studied by detailed investigation on yield components.

Lehman and Lambert (1960) found that the yield component pods per plant was most responsive to changes in the environment. This evidence was supported by a number of studies (Weber *et al.*, 1966; Hick *et al.*, 1969; Fontes and Ohlrogge, 1972; Lueschen and Hicks, 1977; Dominguez and Hume, 1978; Hoggard *et al.*, 1978; Peet and Kramer, 1980). Herbert and Litchfield

(1982) found that increasing plant densities (increasing interplant competition) resulted in fewer pods at final harvest. For the intraplant competition between soybean root and canopy, Marvel *et al.* (1993) also found that pods per plant was the most responsive yield component related to the yield reduction.

Variation in light condition caused obvious changes in pod number per plant. Schou *et al.* (1978) and Johnston *et al.* (1969) found light enrichment during flowering and early pod formation caused more pods per plant at maturity than controls. This evidence could be explained by increased light interception resulting in increased photosynthates available for pod-setting (Kokubun and Watanabe, 1981). Further, this result could be supported by the shading treatment that caused a reduction in pod number per plant (Wahua and Miller, 1978).

Changes in the ratio of source - sink resulting in yield difference might primarily attribute to change in pods per plant. Litchfield (1991) found that sink size in soybean was first regulated by changes in pod numbers and that these changes occurred across all main axis nodes. Caviness and Thomas (1980) found that reduction in the number of pods per plant appeared to be the yield component primarily responsible for yield losses from induced defoliation by inadequate moisture and drought stress.

The yield component seeds per pod was more stable than pods per plant, subject to changes in natural conditions and in artificial manipulation of yield (Lehman and Lambert, 1960; Herbert and Litchfield, 1982; Taylor *et al.*, 1982; Litchfield, 1991). Willcott (1983) reported that the trends for number of seeds per plant tended to be the same as those for number of pods per plant, again suggesting stability in seed number per pod.

However, some other researchers found that seeds per pod could be influenced by changes in row width and plant density (Paudey and Torris, 1973), and in light interception (Kokubun and Watanabe, 1982). On the node-to-node basis, the variation in seed number per pod was most evident at extreme upper and lower node positions (Herbert and Litchfield, 1982). Fewer pods at the extreme node positions containing 1 to 4 seeds resulted in larger deviation from the average seed number per pod of the central nodes.

Seed size is measured by average dry weight per seed. Generally, seed size has not been closely related to yield (Egli *et al.*, 1978), and was the yield component least affected by changes in row width and plant density (Creighton, 1983). However, Herbert and Litchfield (1982) have observed that slight changes in average seed size may account for significant differences in yield between years. The differences in seed size may have resulted from the changes in climatic conditions and photosynthatic supply related to solar radiation between years.

CHAPTER 3

MATERIALS AND METHODS

3.1 General cultural methods

Studies were conducted at the Massachusetts Agricultural Experimental Station farm located in South Deerfield. The soil was a Hadley fine sandy loam (Typic Udifluvents). Muriate of potash was applied prior to cultivation at a rate of 306.45 g ha^{-1}. Prior to planting, 'Evans' soybean seeds were inoculated with a commercial powdered-peat base of granular Brady Rhizobium. Seeds with a 92% germination rate were machine planted in 25 cm rows on May 24, 1994 at a density of 83 seeds m^{-2}. Weeds were controlled by a post-emergence mixture of 2.06 liter ha^{-1} Poast {2-[1-(ethoxyimino)butyl]-5-[2-(ethylthio)propyl]-3-hydroxy-2-cyclohexen} and 2.75 liter ha^{-1} crop oil, plus hand-weeding in the early growth stages of the soybean plants. Final harvest commenced September 27, 1994. The total growth period was about 134 days.

Final yield was determined after maturity by harvesting plants in 4 rows with a length of 3 m. For yield component analysis, 10 plants in each treatment plot were harvested at plant maturity. For each group of ten plants, data were recorded for the whole plant and for each node on the main axis. For the branches, data were recorded for each branch corresponding to the main axis node from which it arose. Node one was the unifoliate node, the first node above the cotyledons. Among the data recorded were pod number, seed number, stem dry weight, pod dry weight and seed dry weight. From these the seed yield components were calculated.

Main plot size was 8 rows, 20 m long. The experimental design was a randomized complete block, split-plot with 4 replications.

3.2 Main-plot treatments: Light enrichment

Light enrichment entailed increasing solar radiation available to the center sample row of each plot. This was achieved by installing a 90 cm tall wire mesh fence on either side of the center sample row, sloping at a 45° angle away from this sample row. The fences were inspected periodically, and all plants behind them were rearranged to prevent undue crowding and allow for normal growth of these fenced border row plants as much as possible. In this way, the plants from the neighboring rows were prevented from encroaching into the growing space of the central sample row thus providing for allowing greater light around the sample row plants. This method was chosen so root competition from the neighboring rows would be relatively unchanged. Once put in place, the fences remained in position until soybean maturity.

Three light treatments were established, LE0, LE1 and LE2. LE0 was the control received no light enrichment. LE1 - light enrichment was applied at the time of the first flower in the soybean plant population. LE2 - light enrichment was applied after flower at the beginning of pod filling.

3.3 Sub-plot treatments: Source - sink manipulation

The following treatments of defoliation and depodding were imposed after most flowers occurring and at the beginning of the pod filling (Figure 3.1):

CK - untreated check plants

CL - removal of the central leaflet from each trifoliate main axis leaf

AP - removal of the pods from alternate main axis nodes

SP - removal of all but one pod from main axis nodes

ALP - removal of the trifoliate leaf and all pods from alternate main axis nodes

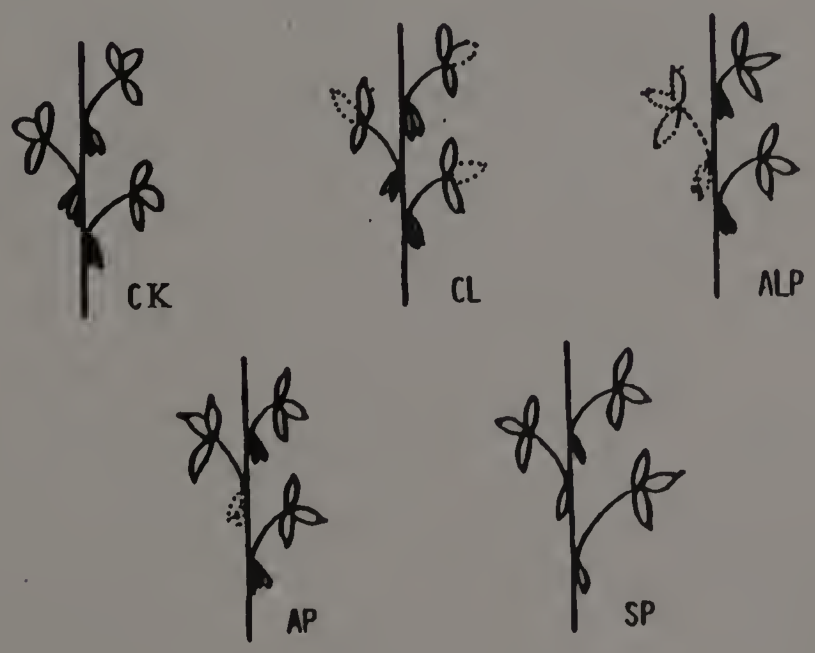

Figure 3.1 Source - sink manipulation treatments in soybean

CHAPTER 4

RESPONSE OF SOYBEAN YIELD COMPONENTS TO INCREASED LIGHT

4.1 Results and discussion

The light intensity at the top of the canopy at the R3 stage (beginning pod) (Herman, 1985) was 13.30 $uEs^{-1}m^{-2}$ and 12.83 $uEs^{-1}m^{-2}$ for LE0 and LE2 respectively, whereas at the base of the canopy it was 0.19 $uEs^{-1}m^{-2}$ and 3.37 $uEs^{-1}m^{-2}$ respectively. Thus, 98.6% and 73.7% of the incoming solar radiation was intercepted by the soybean canopy for LE0 and LE2 respectively. This means that leaves at the base of the soybean canopy in LE2 were receiving more than 25% of available light.

The final yield and yield components of Evans soybean with check treatment in 1994 are shown in Figure 4.1 through Figure 4.11. Results of the analysis of variance are shown in Table 1.

Plants receiving early light enrichment (LE1) yielded more than control plants (LE0); however, those receiving late light enrichment (LE2) did not differ from control (Figure 4.1). Similar results were obtained per plant and per meter of row (Figure 4.2).

Among the yield components, the number of pods per plant was the component most responsible for the yield increase from LE1 (Figure 4.3). This result was similar to that reported by Litchfield (1991), whose experiment also demonstrated that the number of pods per plant was the component largely responsible for the increased yield due to light-enrichment treatments.

The significant difference of pod number per plant due to light treatments suggested that solar radiation became more important in determining pod setting in the early reproductive stage. During flowering, increased solar radiation could afford more photosynthetic assimilate to the development of more pods. Increased solar radiation during flowering is more important for pod formation since soybean usually produces an overabundance of flowers (Dominguez and Hume, 1978; Jiang and Egli, 1993).

Jiang and Egli (1993) reported that the reduction in pod numbers resulting from shade treatment was due both to increased flower and pod abscission and to fewer flowers developed per plant. According to this postulation, the result of increased pod number and increased yield in this LE1 treatment might had resulted not only from an increase in flowering, but also from a reduction in flower abscission. Litchfield (1991) stated that if light enrichment was imposed when flowering was almost complete, an increase in the number of pods per plant resulted from increased pod retention.

Seed number per pod (Figure 4.4) exhibited a similar trend to that of pod number per plant. LE1 resulted in a 15% increase in seeds per pod. Therefore, the increase in the number of seeds per pod was only a small component of the yield increase.

Seed size exhibited significant increase for both LE1 and LE2 over LE0 (Figure 4.5). When light enrichment occurred after most of the flowers had set (LE2), there was no significant increase in the number of pods per plant or the number of seeds per pod, in contrast to the significant increase in the number of pods per plant and the number of seeds per pod by earlier light enrichment (LE1). The capacity of sink size (number of pods or seeds) in LE2 was less than that in LE1. Therefore, increased photosynthetic assimilate from subsequent increased light condition could cause a larger seed size in LE2 than that in LE1.

Previously Litchfield (1991) found no increase in seed size for the LE1 treatment. The 16% significant increase in seed size for the LE1 in this experiment indicated that yield increase due to improved light condition in the early reproductive growth stage could be partially attributed to the seed-size increase in addition to the change in the pod number per plant and seed number per pod. This result might help explain the variance in seed size among years of the same genotype grown in the same field.

The results of the analysis of pod harvest index (PHI) for different light treatments are shown in Figure 4.6. No matter when the light enrichment was imposed, dry matter distribution between pod shell and seed at final harvest was not significantly affected. No significant difference in pod harvest index was observed for LE1 or LE2 against LE0. This result indicated that the pod harvest index in Evans soybean was controlled genetically and was constant, regardless of how much change occurred in environmental conditions and subsequent changes in the final yield.

Harvest index (HI) showed no significant difference. However, light enrichment treatments resulted in the tendency of increased harvest index (Figure 4.7). As stated previously, soybean yield could be enhanced either by increasing the total dry matter accumulation or by increasing the proportion of economic yield (the harvest index) or both (Gardner et al., 1958). The yield increase which resulted from an improvement in solar radiation on the soybean canopy, especially during early reproductive growth (LE1), could be contribute not only to the increase in total plant dry matter (Figure 4.8) but also to the harvest index (Figure 4.7). Enhancement in harvest index implied an improvement in partitioning to the sinks of economic significance, and it could be reached by an improved light condition.

The results of the analysis of the number of pods across main axis node positions are shown in Figure 4.9. The majority of pods were born on lower-central region of the plants. Improvement in light conditions altered the pattern of distribution, and LE1 greatly increased the number of pods per node in the central portion of the plant. An interesting finding was that nodes in the central region (e.g., node 6,7,8) had the largest number of pods; however, all nodes, except the extreme upper and lower nodes showed a large increase in pod number with added light at LE1. Previous studies (Egli, 1988; Litchfield, 1991; Jiang, 1993) also suggested that nodes in central region in soybean plant had the highest yield potential. Based on this evidence, therefore, selection of a soybean genotype with high yield potential across all the main axis nodes might merit further investigation.

Seed number per pod was relatively constant across node positions, and distribution was not affected by light treatments (Figure 4.10). This result suggests that the pod formation and the pod anatomical organization were controlled genetically rather than environmentally. In the study by Litchfield (1991), the relatively constant seeds per pod across node position was suggested to be the result of approximately constant proportion of 1-, 2-, 3-, and 4-seeded pods produced at each node. In this experiment, increased solar radiation did not largely improve the mean seed number in the pod across main stem nodes. However, the slight change in seeds per pod between LE1 and LE0 indicated that, improved light condition at an early reproductive growth stage caused a relatively sufficient source supply to the newly formed zygotes, embryos or young seeds that otherwise in poor light conditions might fail to develop during the process of meiosis.

The big variance in seeds per pod at upper extreme node position occurred because the number of sampled pods at these node positions was far less than that in other regions of the plant. A fewer pods with extreme seed number (e.g. 1 or 4) at the extreme node position could easily cause anomalies in the statistical results (mean seeds per pod).

Seed size on a nodal basis according to light treatments is presented in Figure 4.11. Within each light treatment, seed size was relatively constant across the main axis except for extreme node position. This result might suggest that the partitioning of assimilate to each individual seed was relatively equivalent to each other. As mentioned before, Evans soybean is indeterminate which continues vegetative growth when some parts of the plant are experiencing reproductive growth. Complex mechanisms were involved in assimilate partitioning during the grain-filling period, due to different sources, e.g. leaves, green parts of stem, and pod walls, from which the photosynthate was deposited in seeds. The rate of partitioning of assimilate into developing seeds born at upper stem nodes must surpass that into developed seeds at middle and lower nodes, in order to develop a constant seed size at harvest. Bils and Howell (1963) and Egli *et al.* (1981) stated that cell division in the cotyledons was usually complete early in seed development, and much of seed growth was related to cell expansion. The constant seed size across main stem nodes in this experiment suggests that seed size was under genetic control in the soybean plant, presumably, controlled by the constant cotyledon cell numbers.

The consistent increase in seed size occurred at all node positions in response to both light enrichment treatments (Figure 4.11), even though time of seed fill varied greatly between lower and upper node position. Egli et al. (1978) reported that seed size of soybean was a function of the rate and duration of dry weight accumulation in the seed fraction. Consequently, environmental factors influencing that rate would have a direct influence on yield. In our experiment, the increased seed size in both LE1 and LE2 was caused by improved light condition, and thus by the resultant increased dry matter accumulation rate during seed filling period.

4.2 Summary

The yield of Evans soybean can be enhanced by increasing light during the early reproductive stages. Optimizing the light condition at the early reproductive stage would be more effective in determining final yield than at the beginning of pod filling. Yield increases are largely the result of increasing the number of pods per plant, although increase in seed size and the number of seeds per pod also contribute to the increased final yield. The change in yield components occurs across all the main axis node position. Seed size usually is not related closely to yield variation. However, the significant change in seed size by both light enrichment treatments can help explain the yield variance among years in the same field. Seed size was consistent across main axis nodes regardless of light changes. Pod harvest index remained constant showing the consistent assimilate partitioning among pod shells and seeds, and the harvest index was enhanced by higher light and thus the increased partitioning of assimilates to reproductive sinks can contribute to yield increase.

Table 1. Results of analysis of variances

	df	F	P>F
Seed Yield (g/plant)	2	24.63	0.0013
Pods/Plant	2	21.52	0.0018
Seeds/Pod	2	5.67	0.0415
Seed Weight	2	25.78	0.0011
Pod Harvest Index	2	5.11	0.0506
Harvest Index	2	4.78	0.0573
Plant Dry Weight	2	67.48	0.0146
Yield/Meter of Row	2	199.89	0.0001

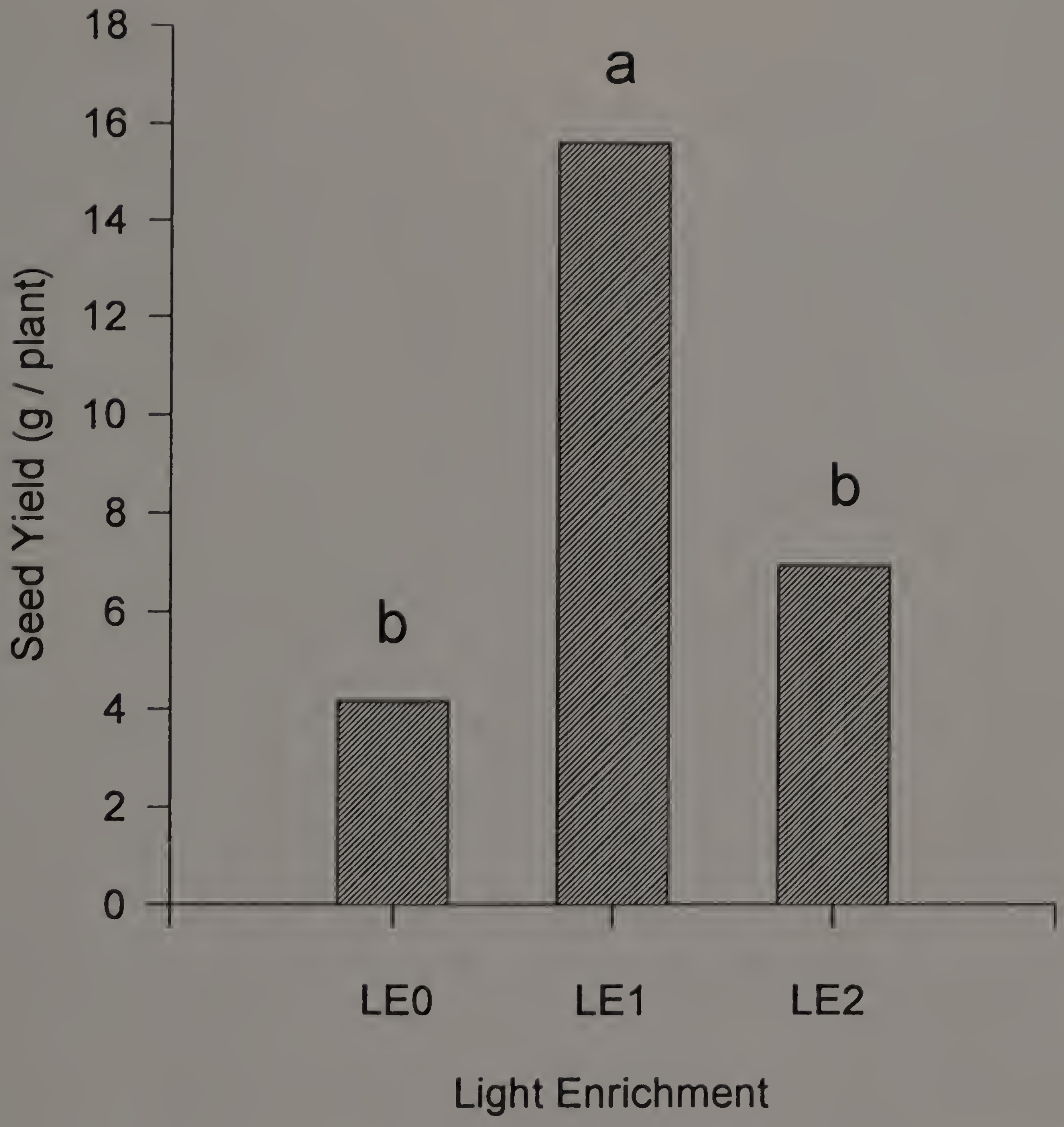

Figure 4.1 Seed yield per plant in response to light treatments.
LE0: Control light enrichment; LE1: Light enrichment 1; LE2: Light enrichment 2.
Mean separation by Duncan's New Multiple Range Test, P=0.05.

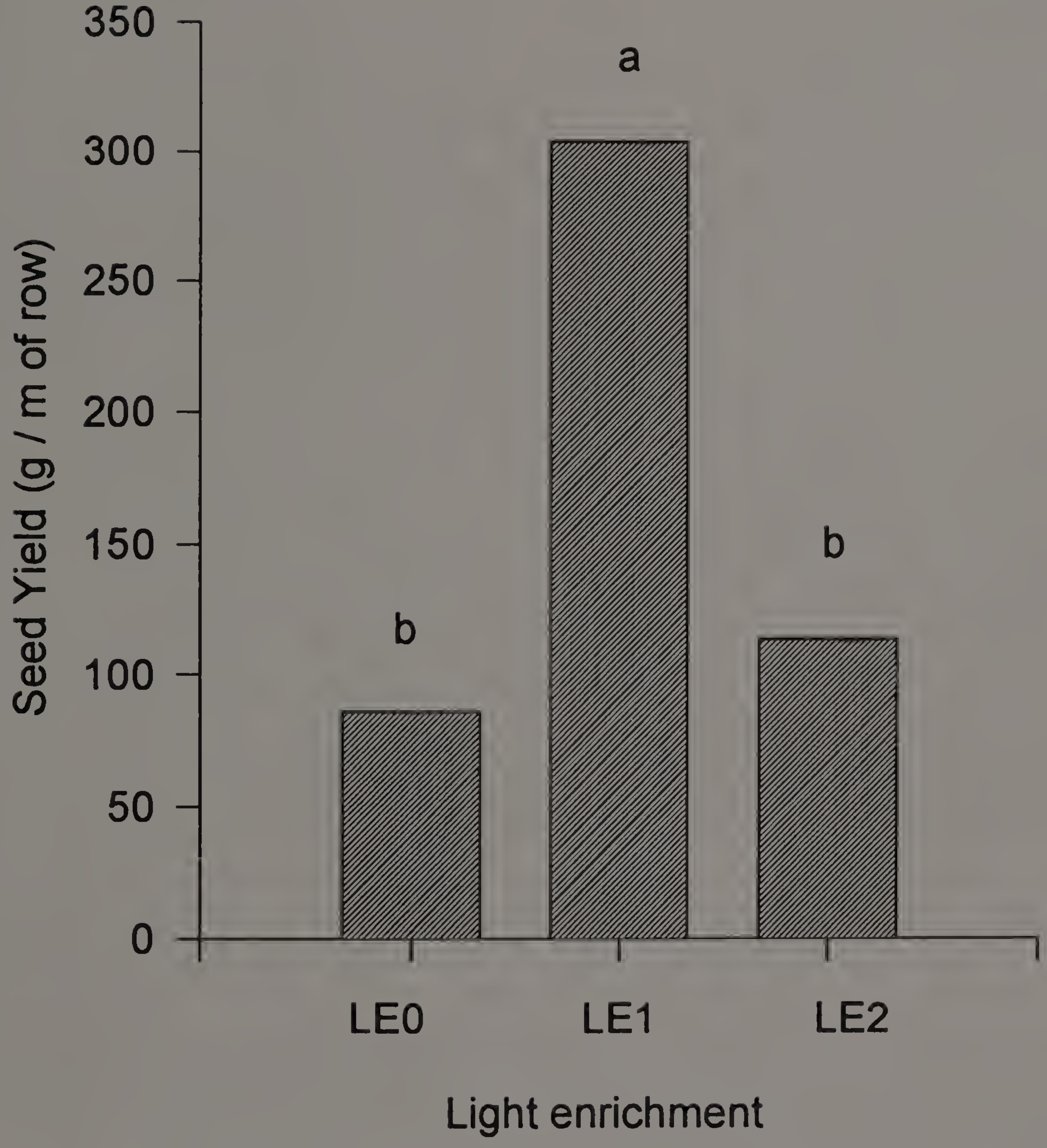

Figure 4.2 Seed yield per meter of row in response to light treatments.
LE0: Control light condition; LE1: Light enrichment 1; LE2: Light enrichment 2.
Mean separation by Duncan's New Multiple Range Test, P=0.05.

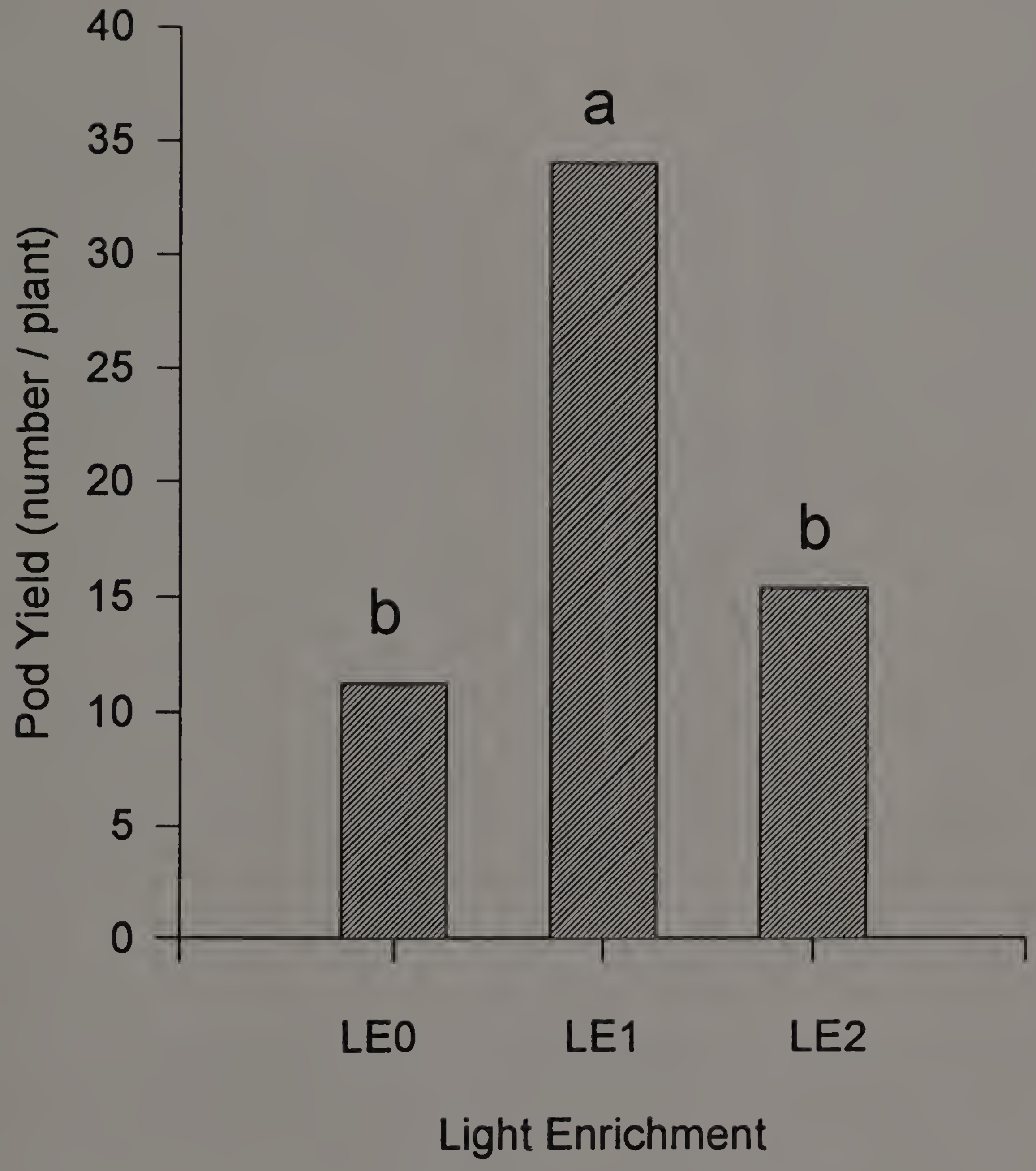

Figure 4.3 Pod number per plant in response to light treatments.
LE0: Control light condition; LE1: Light enrichment 1; LE2: Light enrichment 2.
Mean separation by Duncan's New Multiple Range Test, P=0.05.

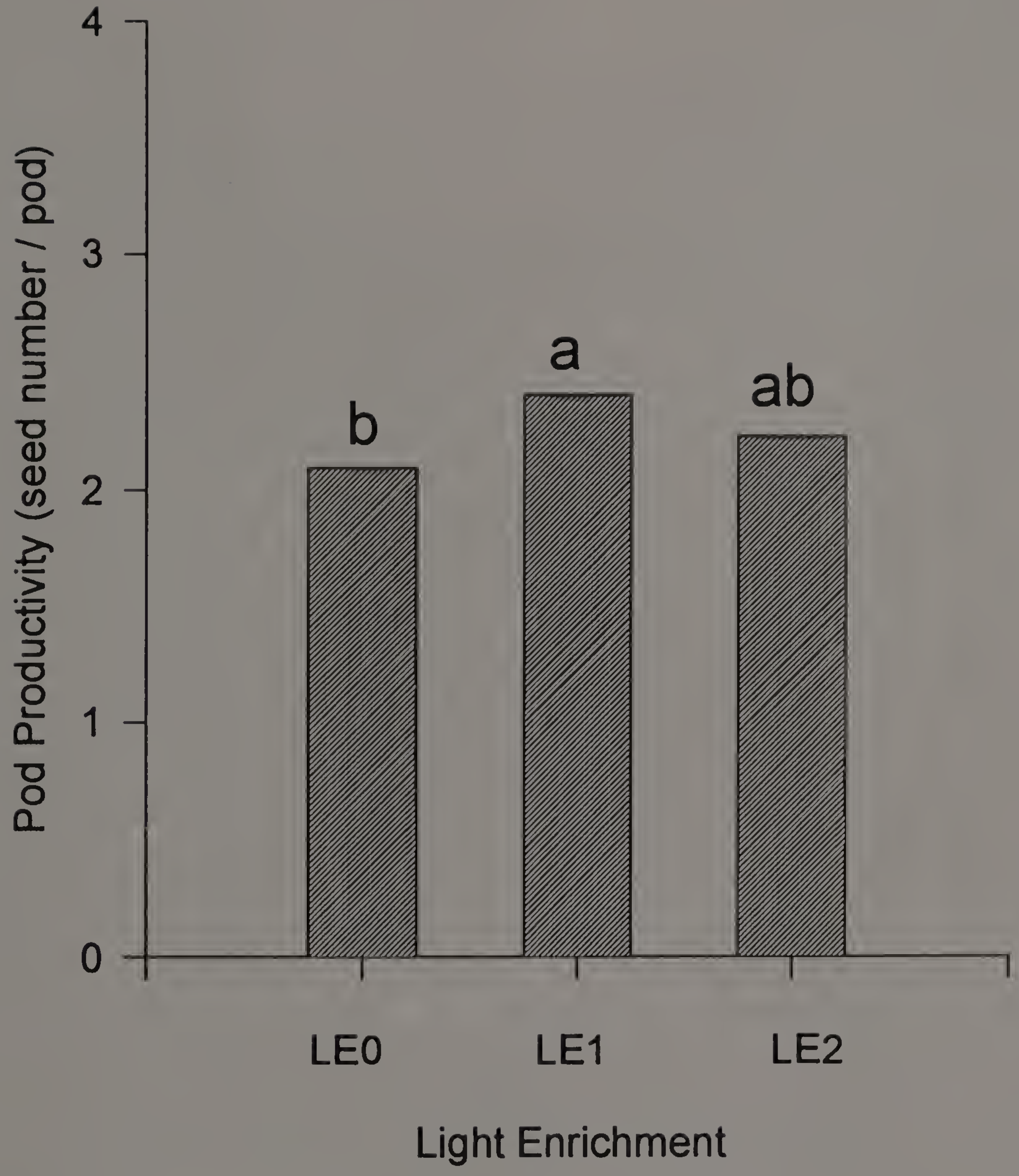

Figure 4.4 Seeds per pod in response to light treatments.
LE0: Control light condition; LE1: Light enrichment 1; LE2: Light enrichment 2.
Mean separation by Duncan's New Multiple Range Test, P=0.05.

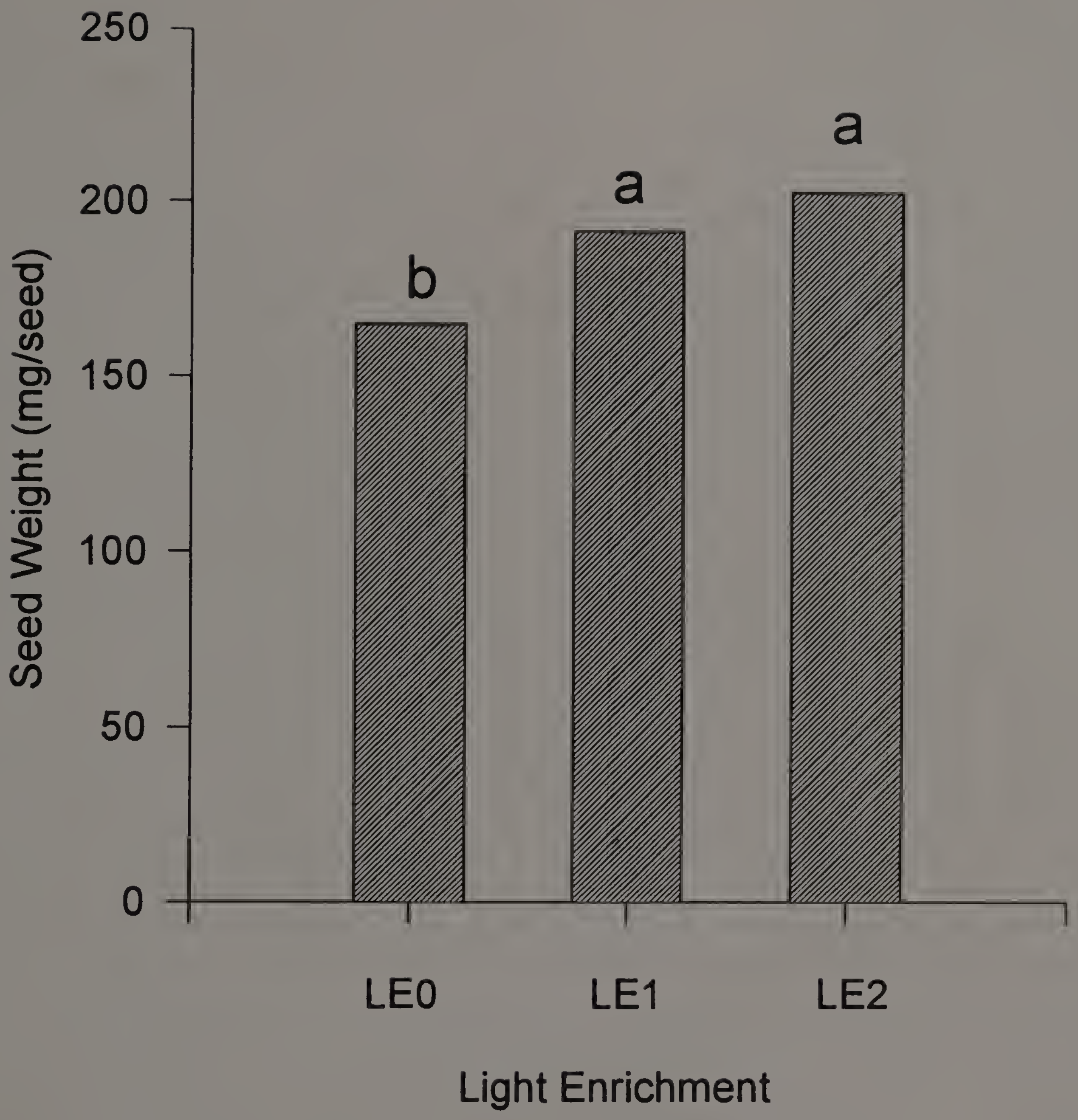

Figure 4.5 Seed size in response to light treatments.
LE0: Control light condition; LE1: Light enrichment 1; LE2: Light enrichment 2.
Mean separation by Duncan's New Multiple Range Test, P=0.05.

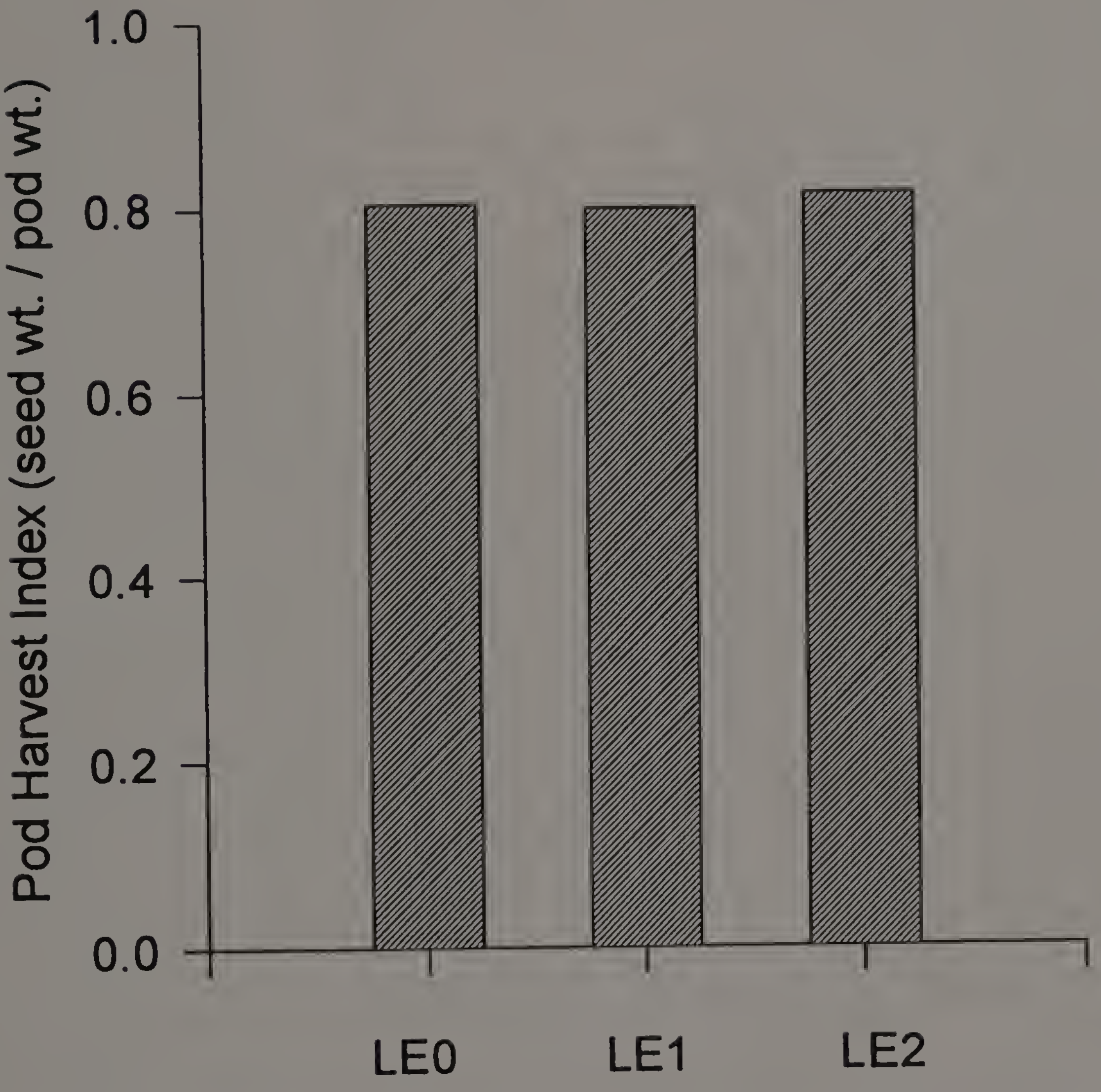

Figure 4.6 Pod harvest index in response to light treatments.
LE0: Control light condition; LE1: Light enrichment1; LE2: Light enrichment 2.
Light enrichment treatments did not affect pod harvest index significantly.

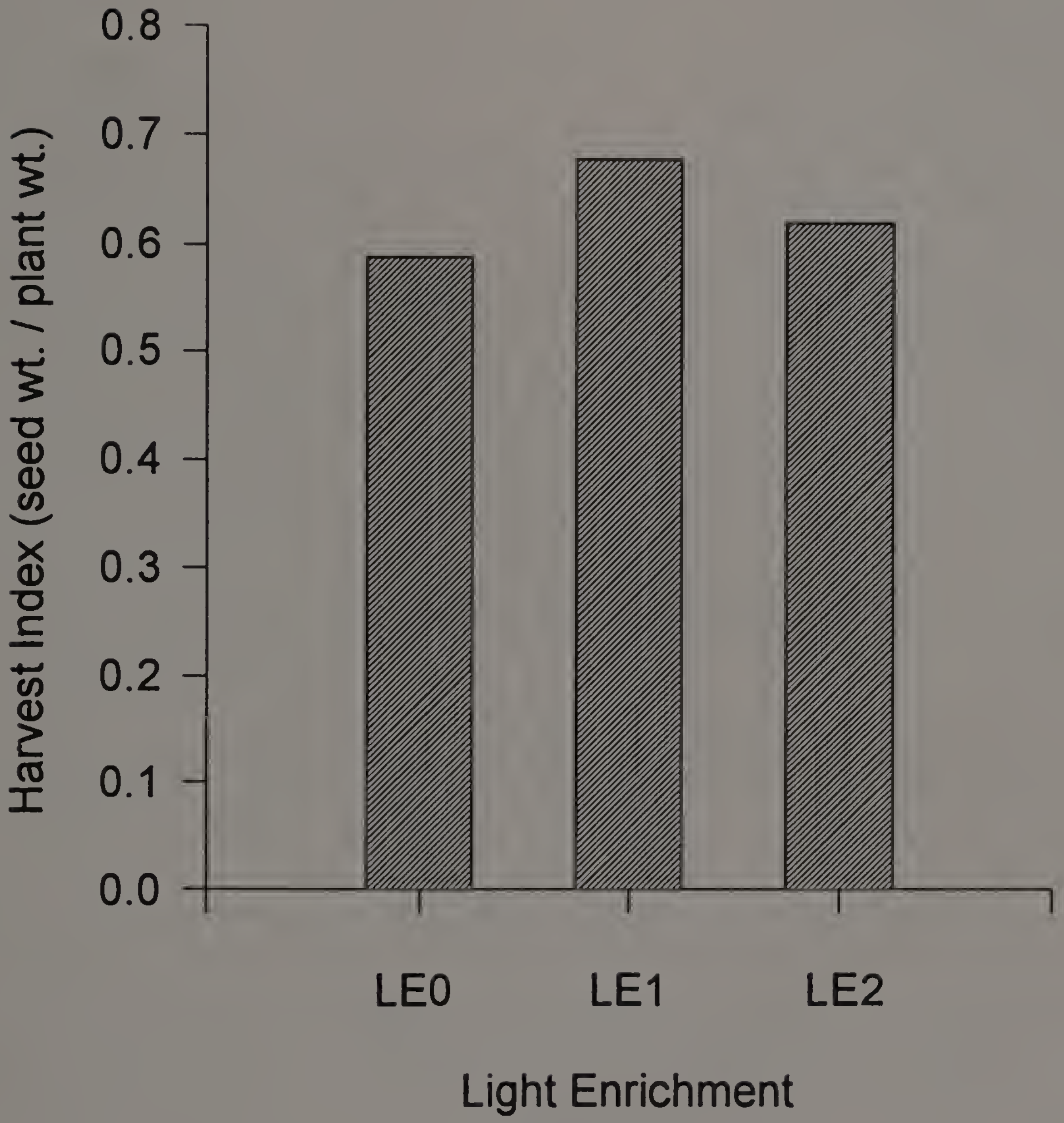

Figure 4.7 Harvest index in response to light treatments.
LE0: Control light condition; LE1: Light enrichment 1; LE2: Light enrichment 2.
Light enrichment treatments did not affect harvest index significantly.

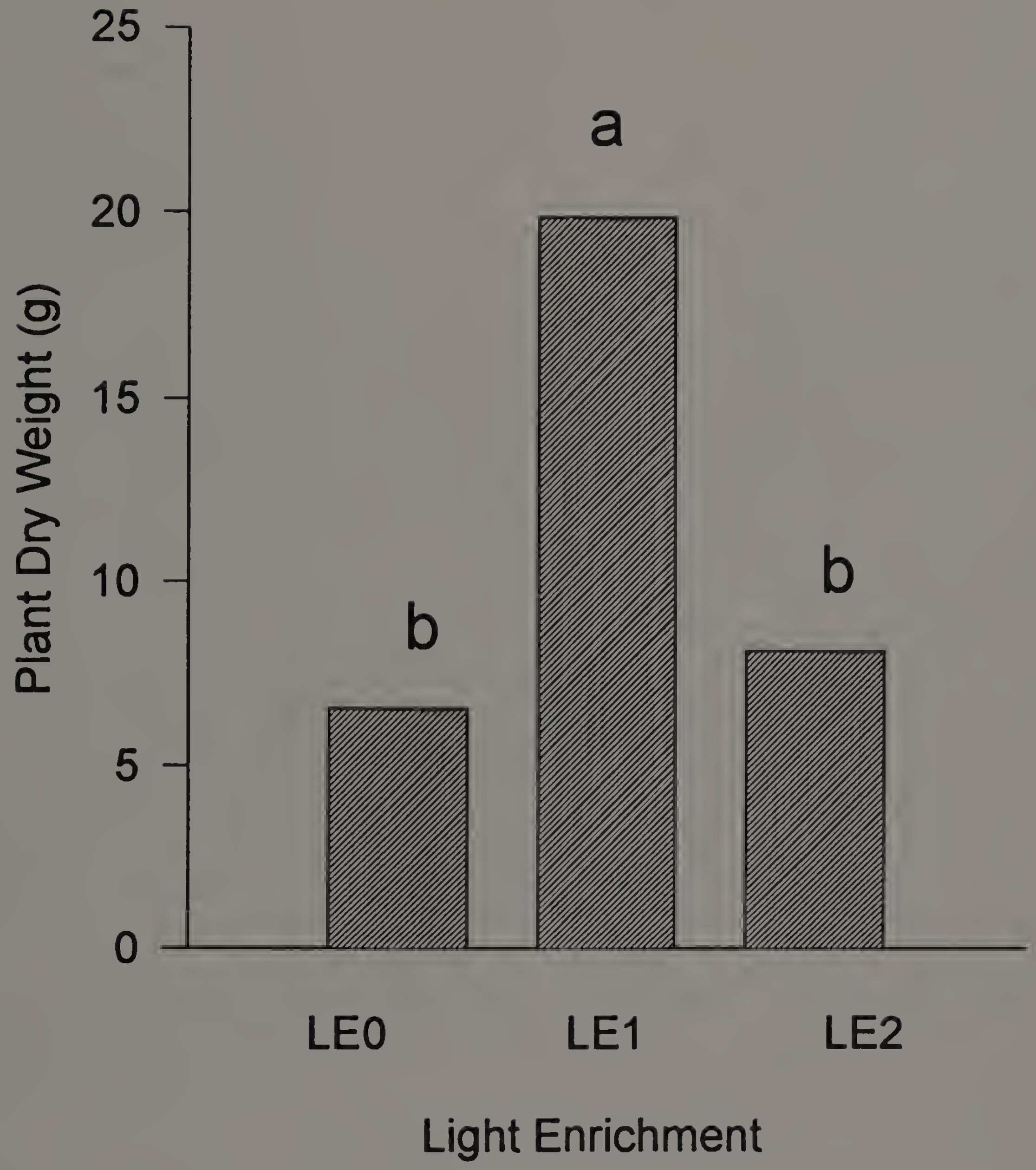

Figure 4.8 Plant dry weight in response to light treatments.
LE0: Control light condition; LE1: Light enrichment 1; LE2: Light enrichment 2.
Mean separation by Duncan's New Multiple Range Test, P=0.05.

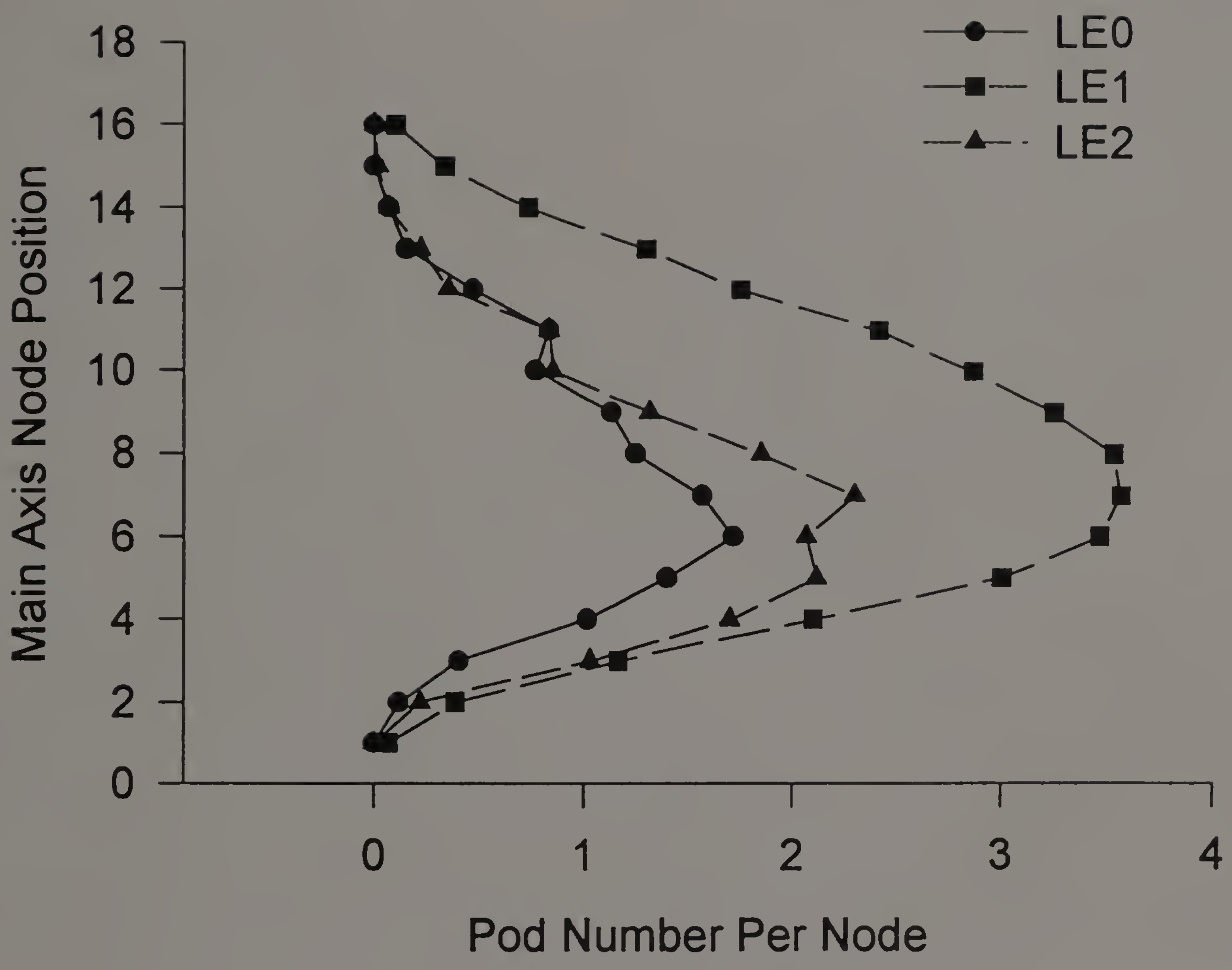

Figure 4.9 Pod number per main axis node position in response to light treatments.
LE0: Control light condition; LE1: Light enrichment 1;
LE2: Light enrichment 2.

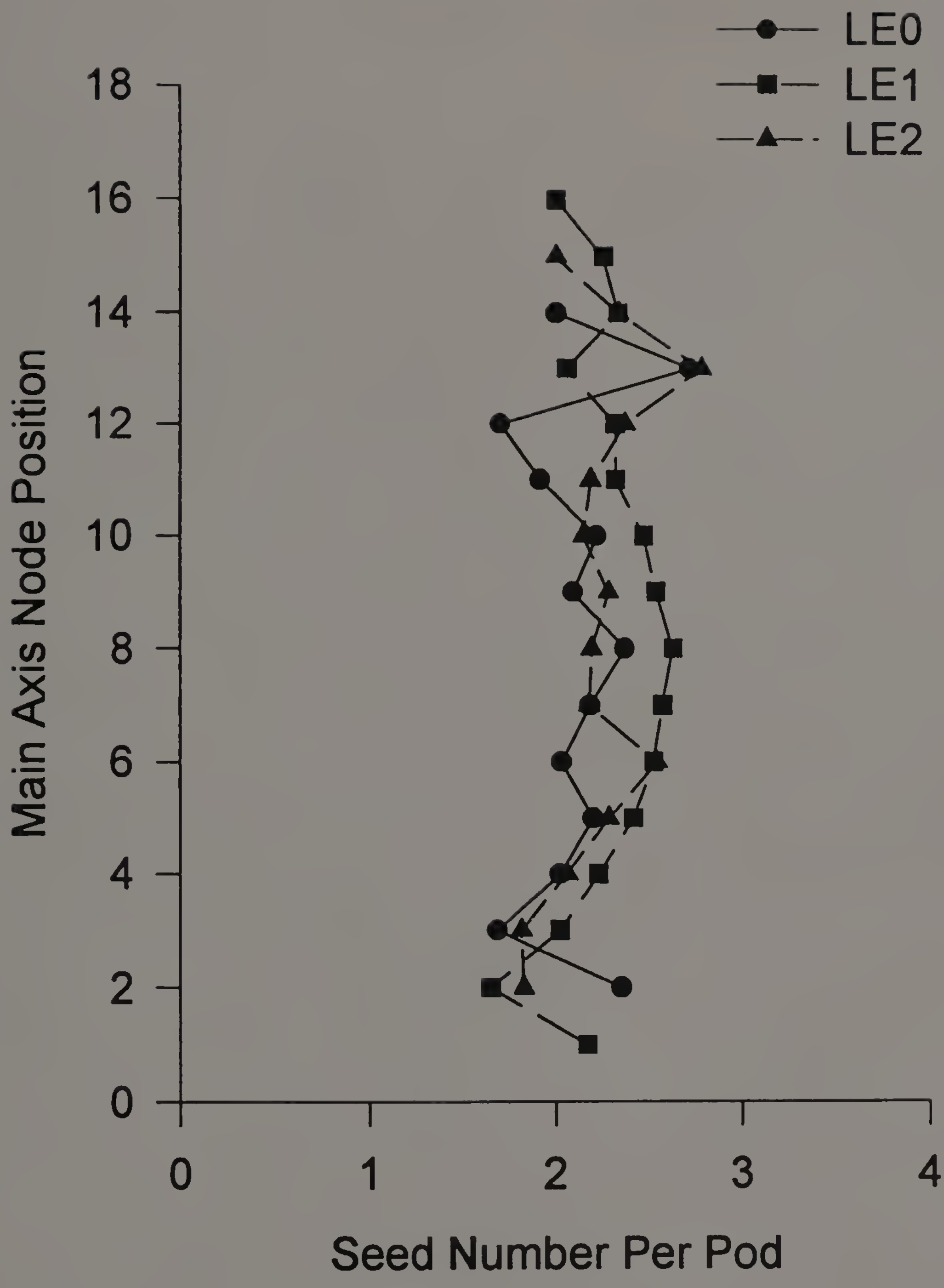

Figure 4.10 Seeds per pod across main axis node position in response to light treatments.
LE0: Control light condition; LE1: Light enrichment 1; LE2: Light enrichment 2.

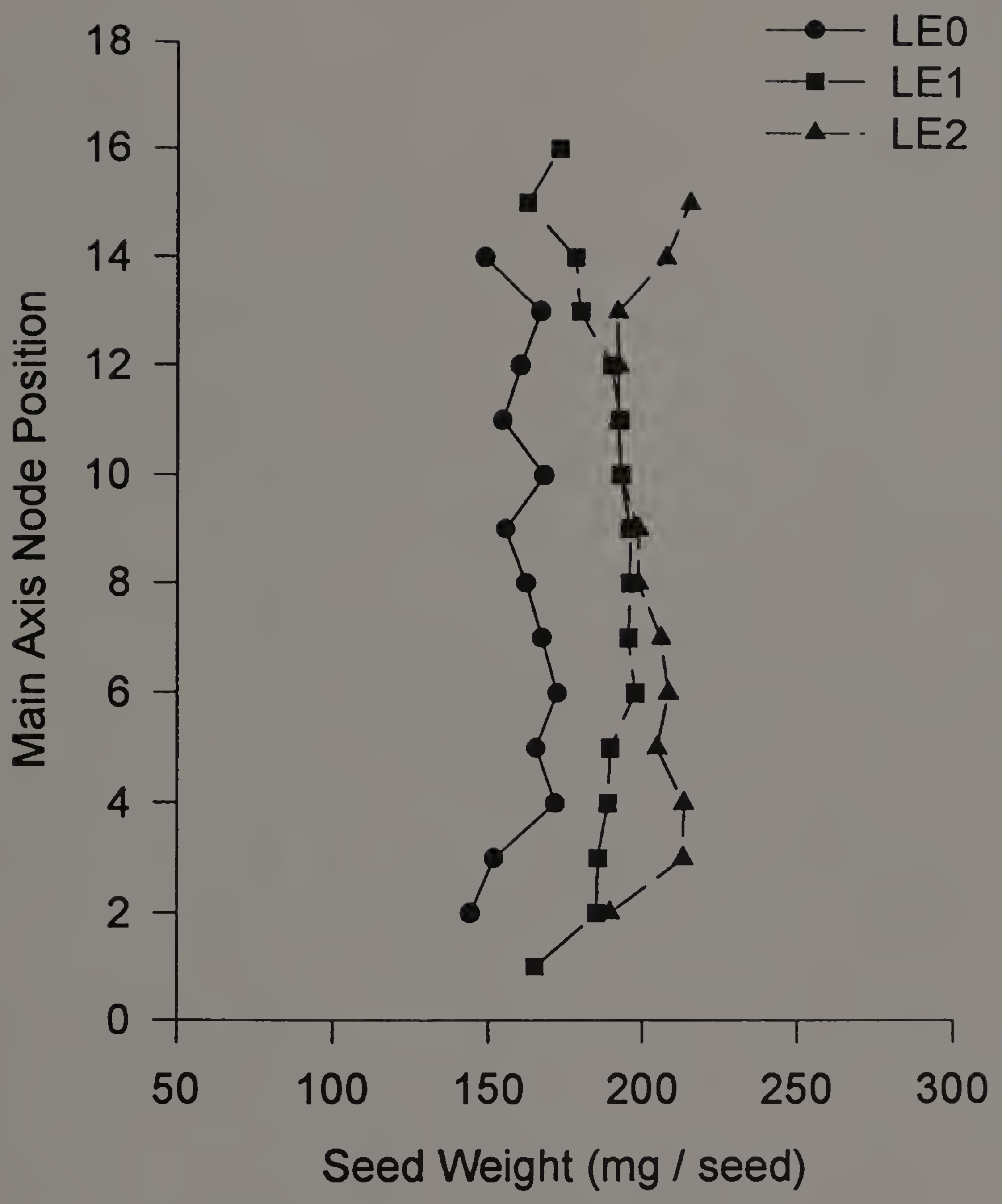

Figure 4.11 Seed size across main axis node position in response to light treatments.
LE0: Control light condition; LE1: Light enrichment 1; LE2: Light enrichment 2.

CHAPTER 5

RESPONSE OF SOYBEAN YIELD COMPONENTS TO SOURCE - SINK MANIPULATIONS

5.1 Results and discussion

Manipulation treatments were imposed so that the patterns of resultant changes in yield components could be studied in detail (Table 2). Manipulation and light enrichment interacted to affect seed yield per plant, pods per plant, and seeds per pod.

5.1.1 Effects of source - sink manipulation on yield components based on whole plants

5.1.1.1 Seed yield per plant

The effects of source-sink manipulation on final seed yield per plant are showed in Figure 5.1. Under control light conditions, manipulation did not significantly affect seed yield per plant.

Under LE1 conditions, all the four manipulation treatments of pod and/or leaf removal (CL, SP, AP, ALP) significantly reduced seed yield compared to check plants (CK).

Under LE2 conditions, all manipulation treatments caused the reduction in final seed yield except that removing pods from alternate main axis nodes (AP) did not affect the yield. The increased seed yield by remaining main axis nodes compensated for the loss of yield from depodded nodes in plants of AP within LE2 treatment. This compensation could be contributed by the 7% more pods retaining in the remaining main axis nodes (Figure 5.2), and by the 5% greater seed size (Figure 5.4). In contrast, ALP treatment caused a significant decrease in seed yield per plant, suggesting no compensation of seed yield by remaining main axis node position.

Regardless of the light conditions, the trends of seed yield due to manipulation treatments were similar. In addition, the close similarity between Figure 5.1 and Figure 5.2 indicated that the decrease in final seed yield per plant was mainly contributed by the changes in the pod number per plant.

5.1.1.2 Pod number per plant

Pods per plant showed a highly significant difference in response to the light enrichment (L), to the source - sink manipulation (M), and to the interaction between light treatment and manipulation (L*M). The effect of source - sink manipulation on pod number per plant are shown in Figure 5.2. As stated before, the close similarity between Figure 5.1 and Figure 5.2 indicated that seed yield variation was mainly caused by the changes in pod number per plant.

5.1.1.3 Seed number per pod

Seed number per pod showed a significant difference in response to the light treatments, highly significant difference in response to the manipulation treatments, and significant difference in the interaction between light treatment and manipulation. The effects of light treatment and source - sink manipulation on seed number per pod were smaller than the changes in pod number per plant (Figure 5.2, Figure 5.3).

Under control light conditions (LE0), the manipulation of CL, AP, and ALP caused no significant difference in seeds per pod compared with check plants (Figure 5.3). However, thinning pods to only one per main axis node (SP) caused a significant increase in seeds per pod by 13%. This result demonstrated that increasing source/sink ratio by thinning pods to only one per main axis node would be able to supply more assimilates to the remaining single pod at each node, and therefore more seeds could be produced that might fail to develop in the normal level of source/sink ratio.

For the light-enrichment treatment beginning from the early reproductive stage (LE1), no manipulation treatment was different from the check (Figure 5.3). AP resulted in significantly fewer seeds per pod than ALP. The relatively constant seeds per pod for all the manipulation treatments in LE1 indicated that, under early light enrichment condition (LE1), the proportion of 1, 2, 3, and 4 seeded pods was rarely affected by the change in source - sink ratio.

Within the LE2, both AP and ALP caused slight but significant reduction in seeds per pod. It was difficult to give explanation on this point, since either the increase in source/sink ratio due to AP or the relatively stable source/sink ratio due to ALP did not prohibit the supply of photosynthetic assimilate to seed development. The abnormal results might come from experimental error. For all light conditions and all manipulation treatments, the relatively constant number of seeds per pod indicate that the proportion among 1-, 2-, 3-, and 4-seeded pods was genetically controlled in Evans soybean, and this characteristics was rarely affected by the change in source-sink ratio.

5.1.1.4 Seed size

Seed size showed highly significant difference in response to light treatment, manipulation, but no significant difference in response to the interaction of light treatment and manipulation. Means of manipulation treatments (combining the three light treatments) are presented in Figure 5.4.

Reducing sink size by removing pods (SP and AP treatments) significantly increased seed size, whereas reducing the source by removing central leaflet (CL) significantly decreased seed size. In contrast to treatments CL, AP and SP, reducing both source and sink size (ALP) resulted in a non-significant change in seed size. Presumably source (leaves) removal lessened the effect of sink (seeds) removal.

These results were similar to previous studies on both Altona and Evans soybeans by Litchfield (1991).

5.1.1.5 Pod harvest index

ANOVA results on pod harvest index showed no significant difference in response to light treatments, manipulation treatments, and the interaction between light enrichment and manipulation (Figure 5.5). Generally, the partitioning of assimilates between the pod shell and seeds at final harvest is not greatly affected by the change in source-sink ratio due to manipulation, light variation, or both. Genetic control exerted the predominant role in pod harvest index regardless of environment impaction.

5.1.1.6 Harvest index

Harvest index showed highly significant difference in response to manipulation treatments but showed no significant difference in response to the light treatments and the interaction between light treatments and manipulation. By combining three light treatments, all the four manipulation treatments (CL, SP, AP, ALP) were significantly lower than check plants (CK). This suggested the manipulation treatments reduced the partitioning of assimilate to seeds. In general, the seed yield reduction due to source-sink manipulation compared with check plants could be partially attributed to the decrease in harvest index (Figure 5.1, Figure 5.6).

5.1.2 Effects of source - sink manipulation on yield components across main axis node position

The analysis of yield components across main axis nodes are showed in Figure 5.7 through Figure 5.9. The patterns of yield components in response to manipulation treatments across main axis nodes were similar to each other for LEO, LE1 and LE2. For brevity and convenience, the remaining discussion was focused on the manipulation treatments within LE1 treatment.

The distribution of main axis pods across nodes showed that most pods were produced at the nodes in the lower and central sections of the plants. Contribution of nodes 2 - 12 to total pod number ranged from 92% in SP plants to 95% in AP plants. Thinning pods to only one at each node (SP) showed relatively consistent results except for the lack of productivity of extreme node positions, and therefore the absence of pods at extreme node positions in some sampled plants. Decreasing photosynthetic sources by removing central leaflets (CL) caused relatively consistent decrease in node productivity across all nodes in contrast to check plants (CK). The increase in node productivity of remaining node position due to removal of alternate pods (AP) or alternate pods and leaves (ALP) was primarily occurred at node 2, 4, and 6, which might be contributed by the increase in branch node productivity. However, the increase in node productivity in AP and ALP plants within LE0 and LE2 occurred across all the main axis node, indicating less contribution from basal branches. Under the control light condition (LE0), the increase of node productivity in plants with AP and ALP treatments over check plants occurred across all the main axis node.

Seed number per pod was mostly constant across node position regardless of manipulation treatments and light-enrichment treatments (Figure 5.8). Some variation of seeds per pod at the extreme node position resulted from small number of pods produced at extreme node position, especially node 14, 15, and 16. On most of the main axis nodes, the proportion of 1-, 2-, 3-, and 4-seeded pods was therefore relatively constant. No consistent variation in the number of seeds per pod across main axis node position was observed due to manipulation treatments. These results elucidated that seeds per pod was the most stable yield component being least susceptible to changes in source-sink ratio and in canopy position.

Seed size is shown on a nodal basis according to light treatments and manipulation treatments in Figure 5.9. Within each manipulation and light treatment, seed size was quite constant at the majority of nodes. Within LE1, the changes in seed size due to any manipulation treatment occurred consistently at all but extreme node positions. The significant decrease in seed size resulting from reduced photosynthetic area by removing central leaflets from all nodes (CL) was relatively consistent across all main axis nodes. This was also true for seed size increase by reducing sink capacity in both SP and AP treatments. However, reducing both source and sink size (ALP) resulted in little variation in seed size compared to check treatment because source removal perhaps offset the effect of sink size removal.

5.2 Summary

This research has demonstrated that source-sink changes in soybean plants can cause variation in soybean yield components and in total yield. Among these yield components, the pod number per plant is most responsible for yield change. In contrast, the seed number per pod has been slightly affected. Seed size increase when sink strength decrease, whereas seed size decrease when source strength decrease. All the changes in final yield components are reflected through the node-to-node positions. Pod harvest index and harvest index show no significant difference in response to the interaction of light treatment and manipulation treatments.

Table 2. Analysis of variance of final harvest yield components for light treatments and source - sink manipulation treatments

		Pods per plant		Seeds per pod		Seed size	
Source	df	F	P>F	F	P>F	F	P>F
L	2	118.19	0.00	6.90	0.03	38.61	0.00
M	4	19.09	0.00	7.30	0.00	26.70	0.00
L*M	8	553.99	0.01	2.77	0.03	1.68	0.15

		Pod harvest index		Harvest index		Yield per plant	
Source	df	F	P>F	F	P>F	F	P>F
L	2	0.51	0.62	3.36	0.10	107.64	0.00
M	4	2.14	0.14	22.97	0.00	12.36	0.00
L*M	8	1.42	0.24	1.71	0.15	3.50	0.01

M denote source - sink manipulation treatments
L denote light enrichment treatments

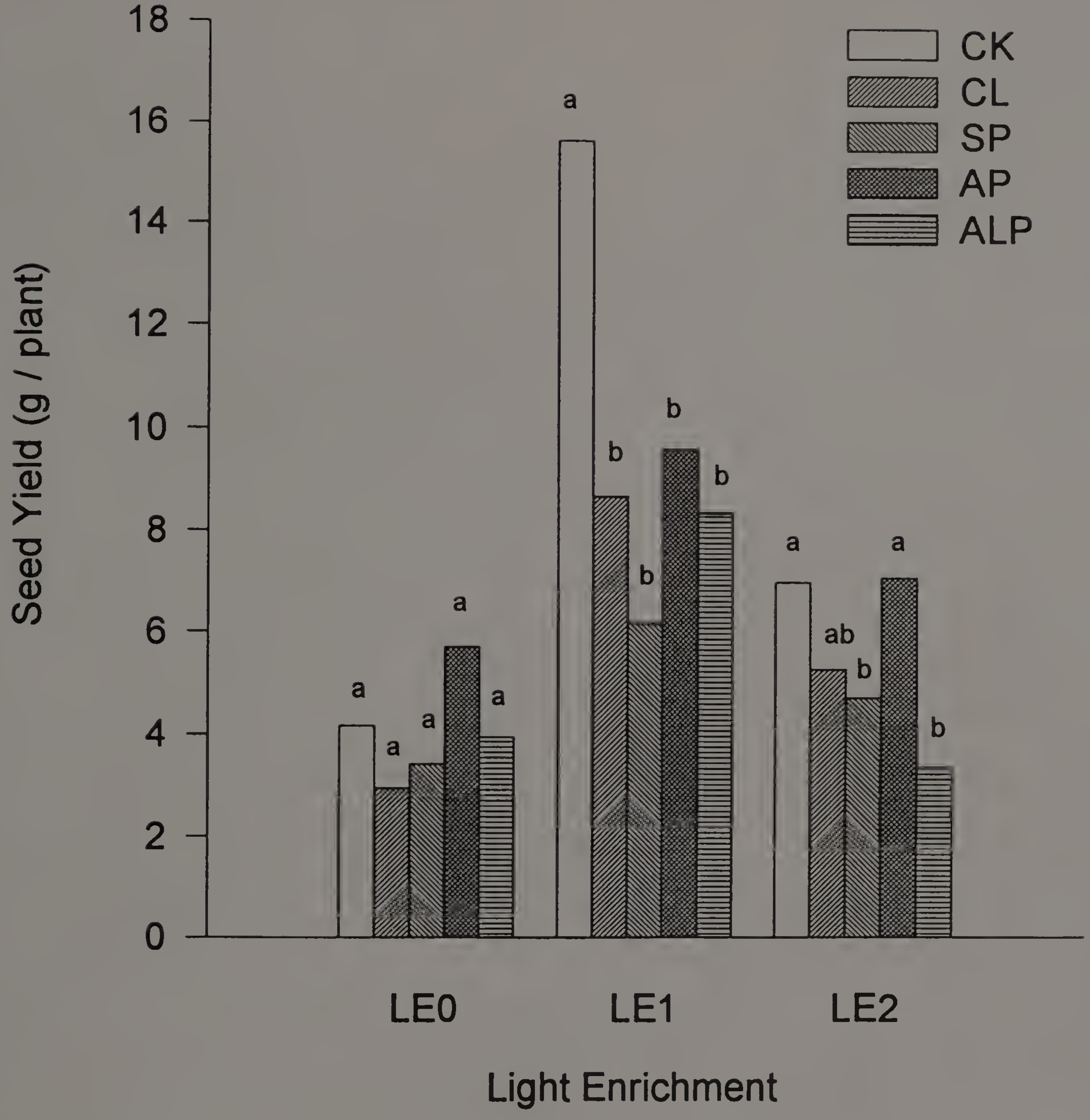

Figure 5.1 Seed yield per plant in response to light treatments and manipulation treatments.

LE0: Control light condition;LE1: Light enrichment 1; LE2: Light enrichment 2. Mean separation within LE treatment by Duncan's New Multiple Range Test, P=0.05.

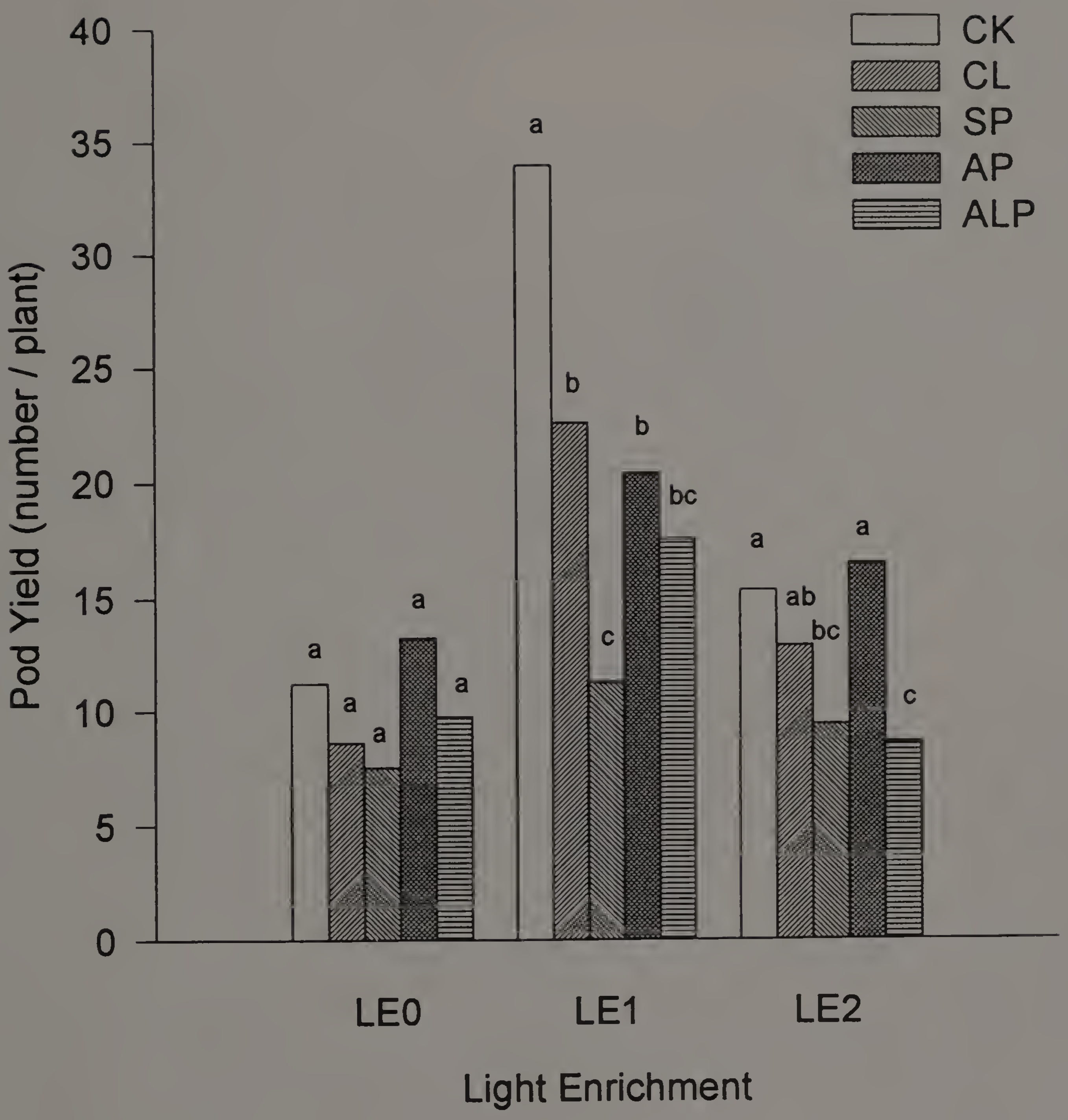

Figure 5.2 Pod number per plant in response to light treatments and manipulation treatments.

LE0: Control light condition; LE1: Light enrichment 1; LE2: Light enrichment 2. Mean separation within LE treatment by Duncan's New Multiple Range Test, P=0.05.

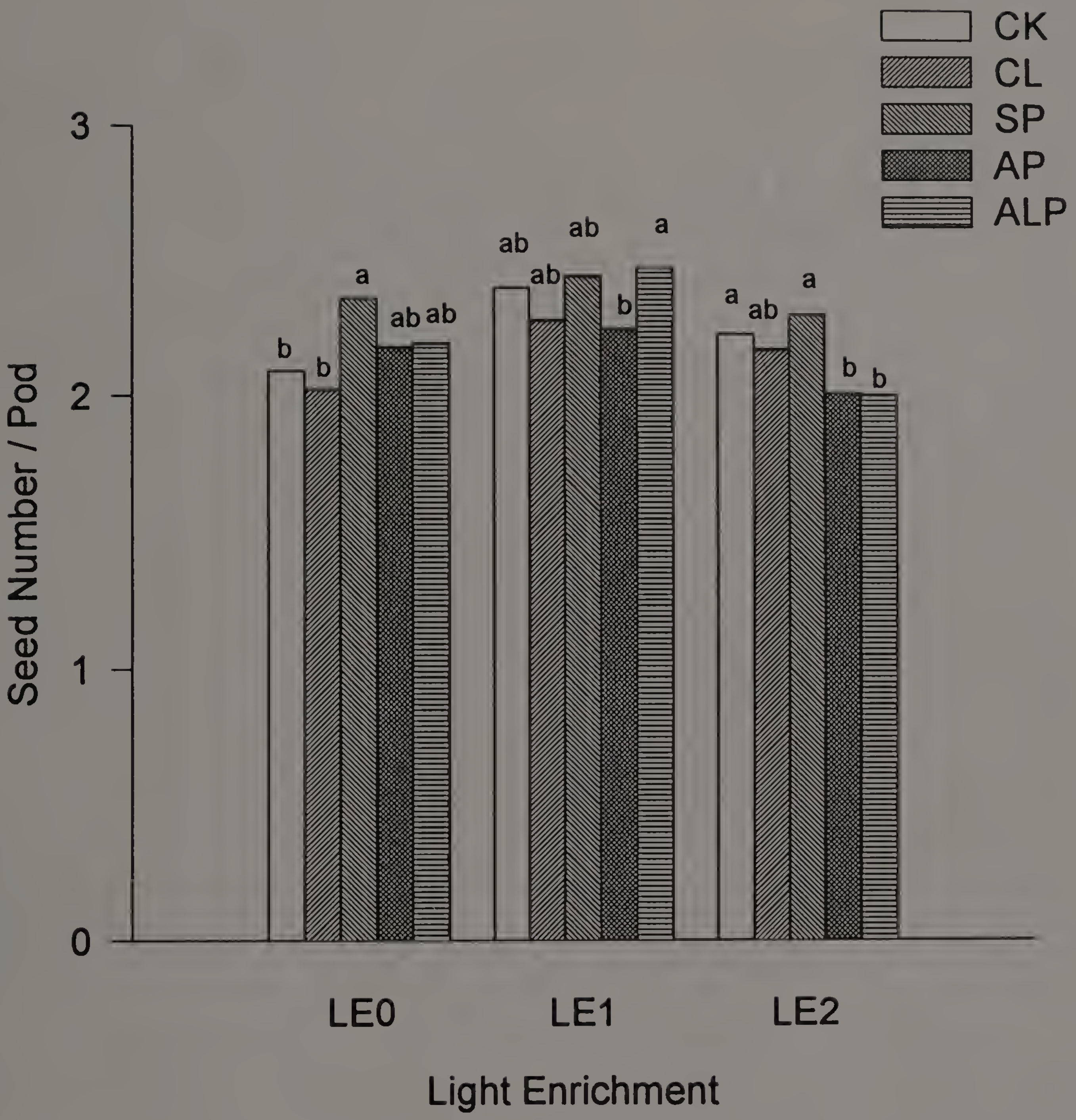

Figure 5.3 Seed number per pod in response to light treatments and manipulation treatments.
LE0: Control light condition; LE1: Light enrichment 1; LE2: Light enrichment 2.
Mean separation within LE treatment by Duncan's New Multiple Range Test, P=0.05.

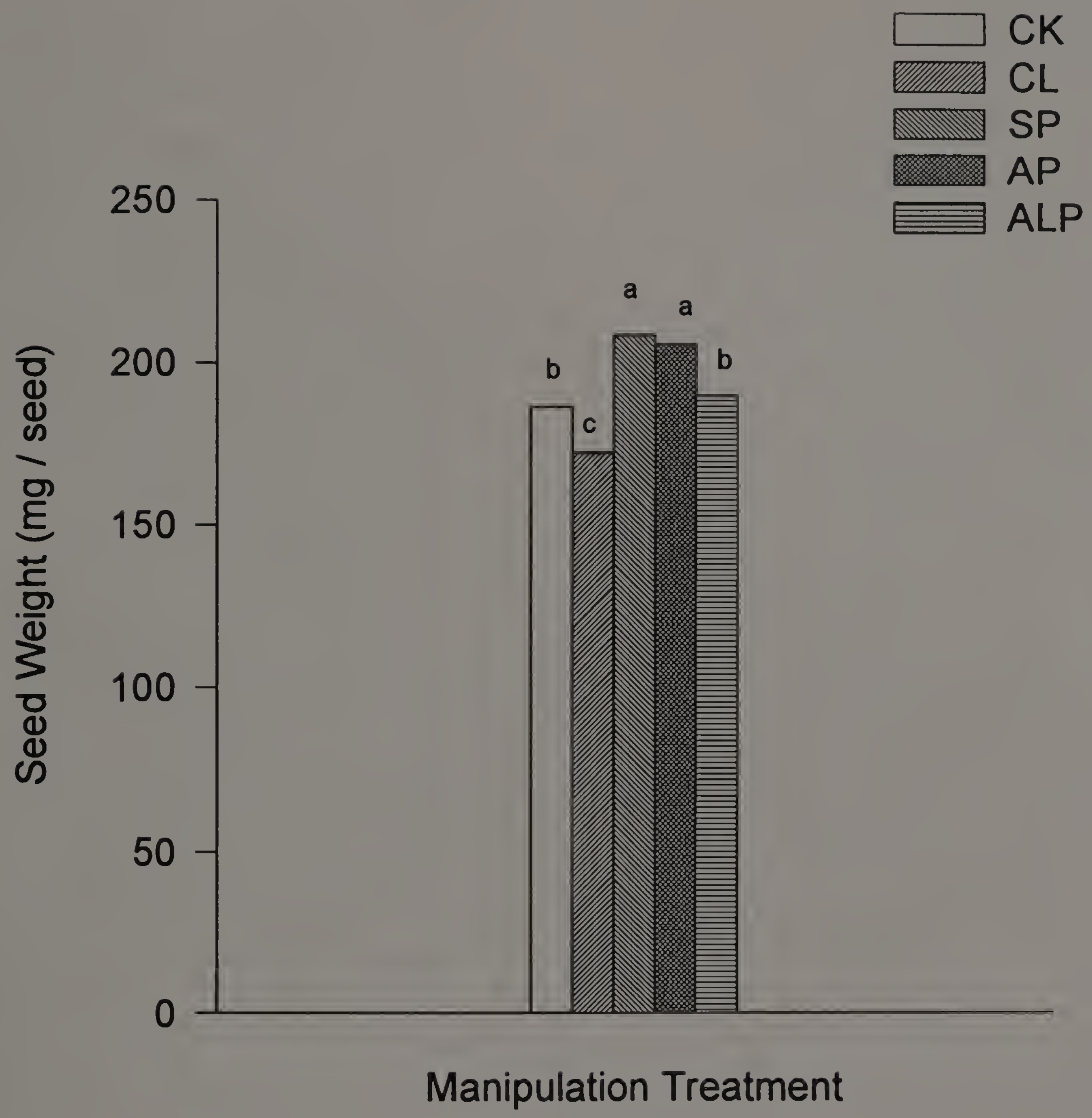

Figure 5.4 Seed size in response to manipulation treatments with combined light condition.
Mean separation by Duncan's New Multiple Range Test, P=0.05.

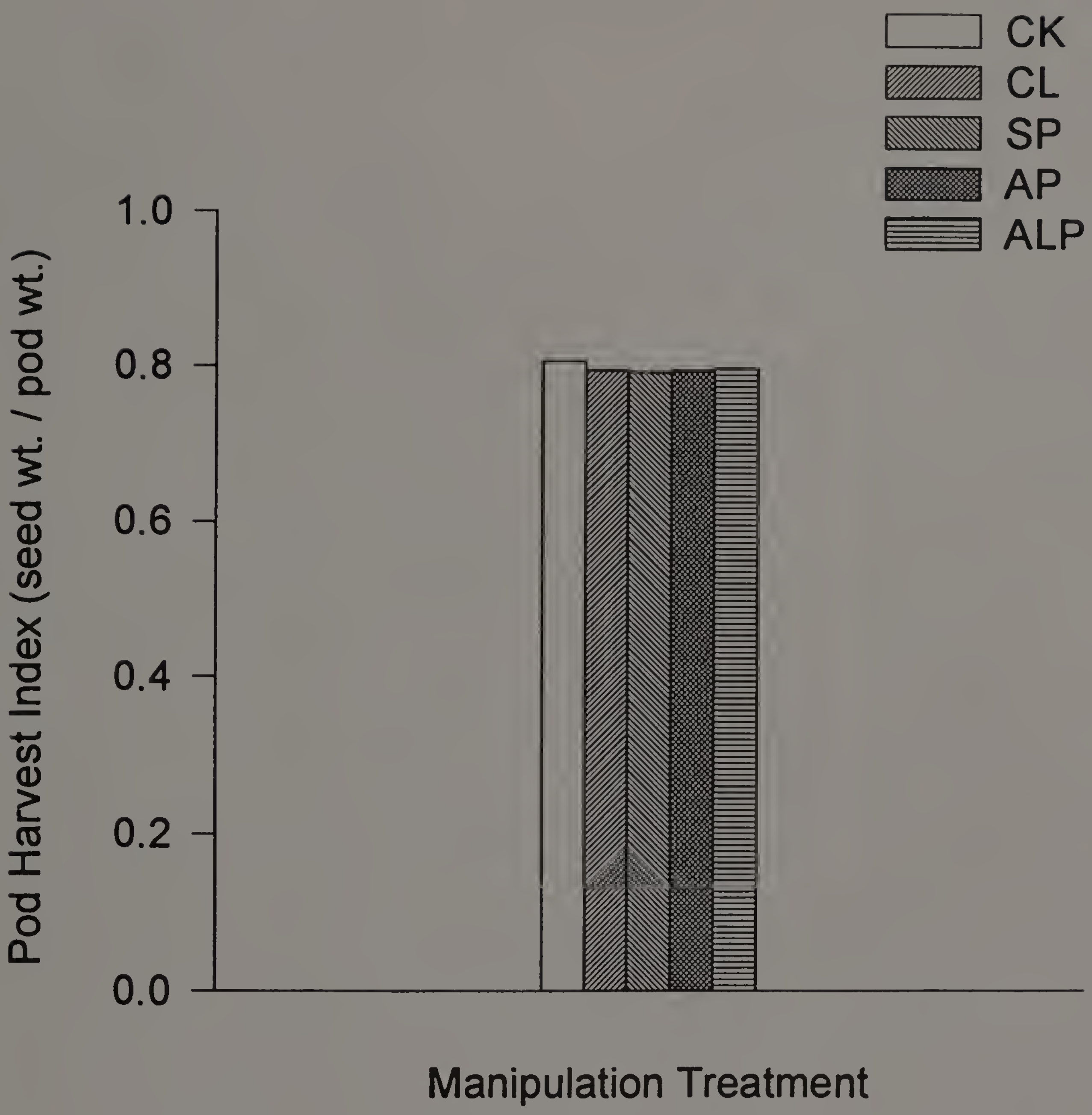

Figure 5.5 Pod harvest index in response to manipulation treatments with combined light condition.

Manipulation treatments did not affect pod harvest index significantly.

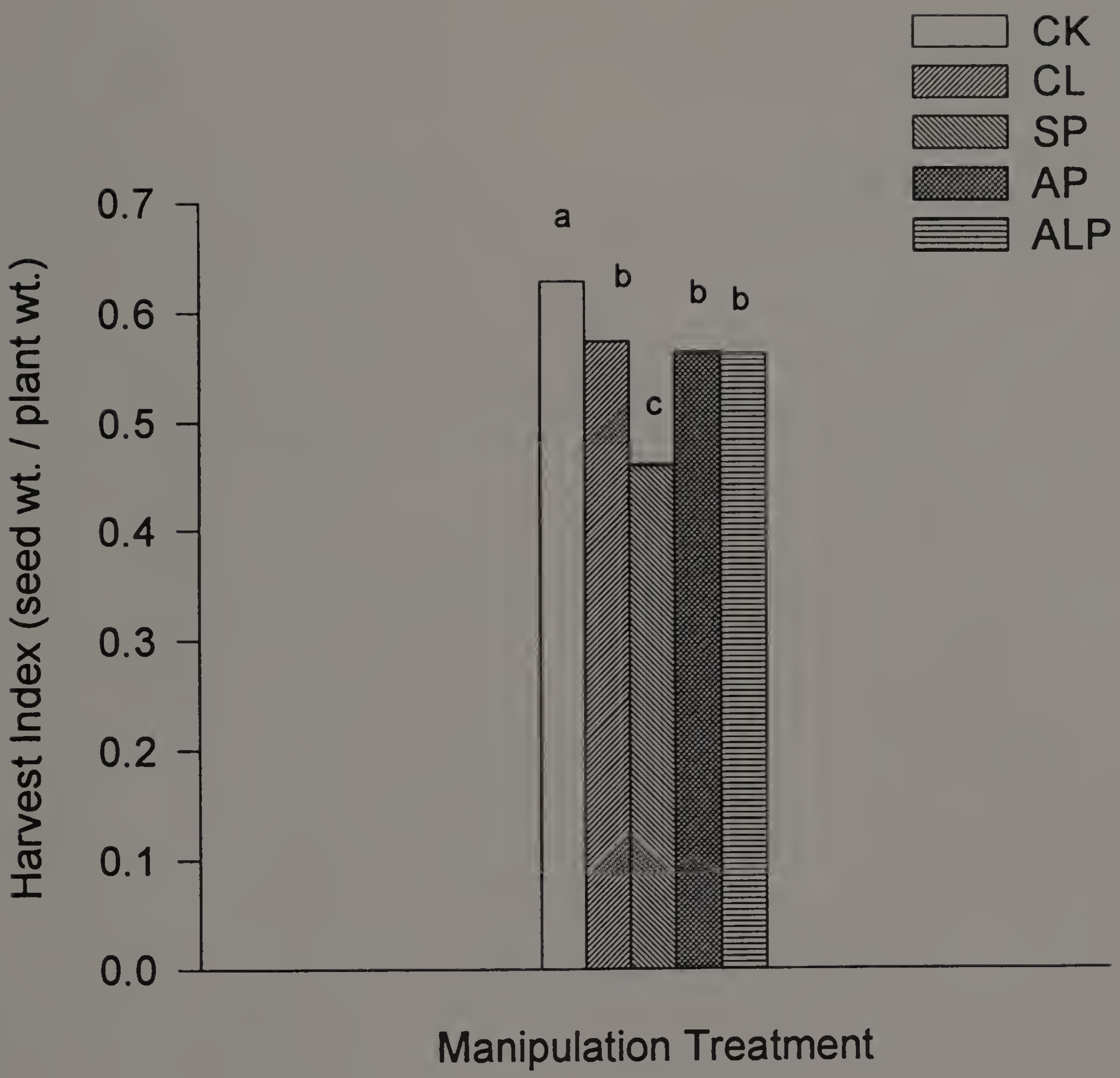

Figure 5.6 Harvest index in response to manipulation treatments with combined light condition.
Mean separation by Duncan's New Multiple Range Test, P=0.05.

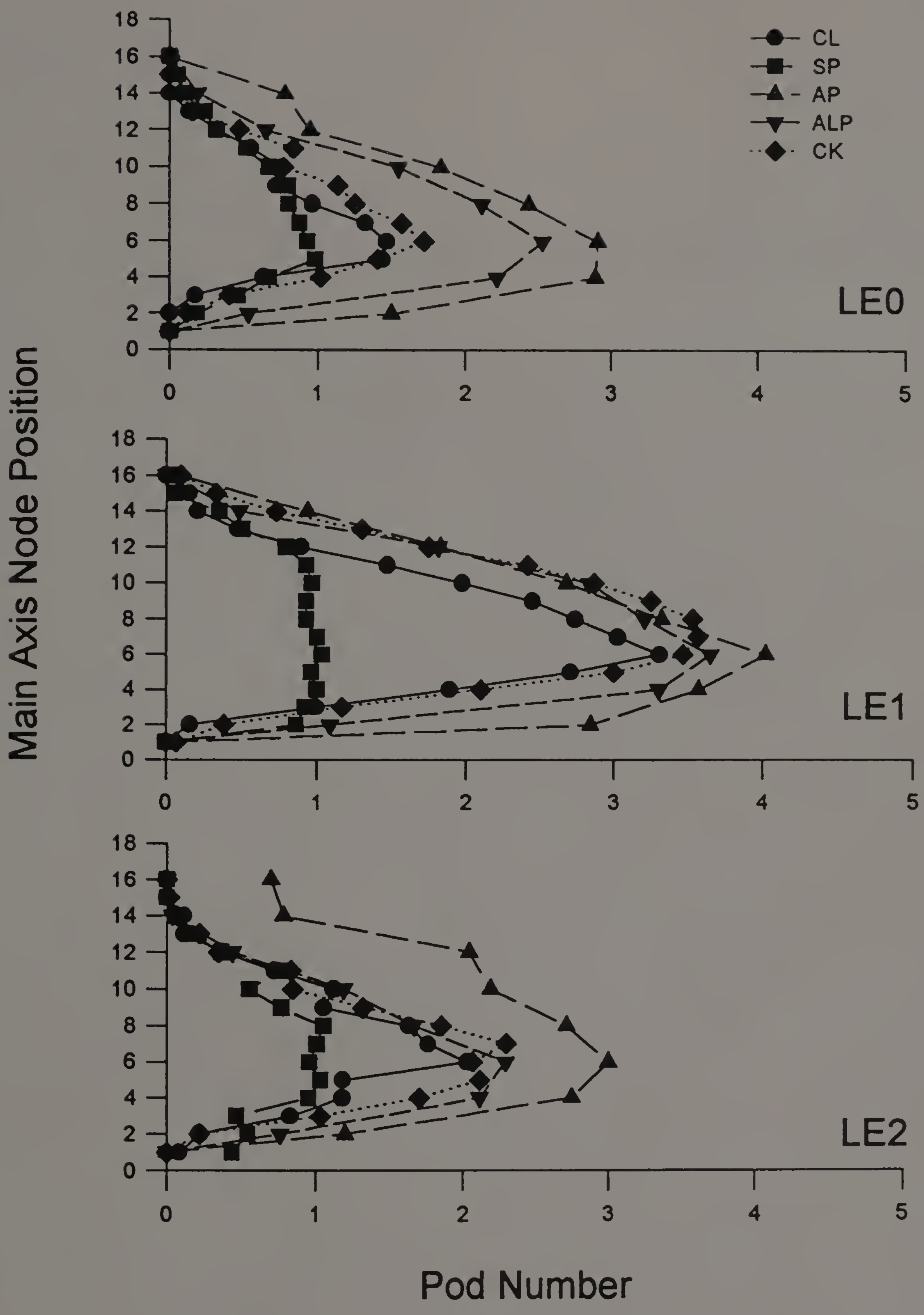

Figure 5.7 Pod number per main axis node in response to light treatments and manipulation treatments.
LE0: Control light condition; LE1: Light enrichment 1;
LE2: Light enrichment 2.

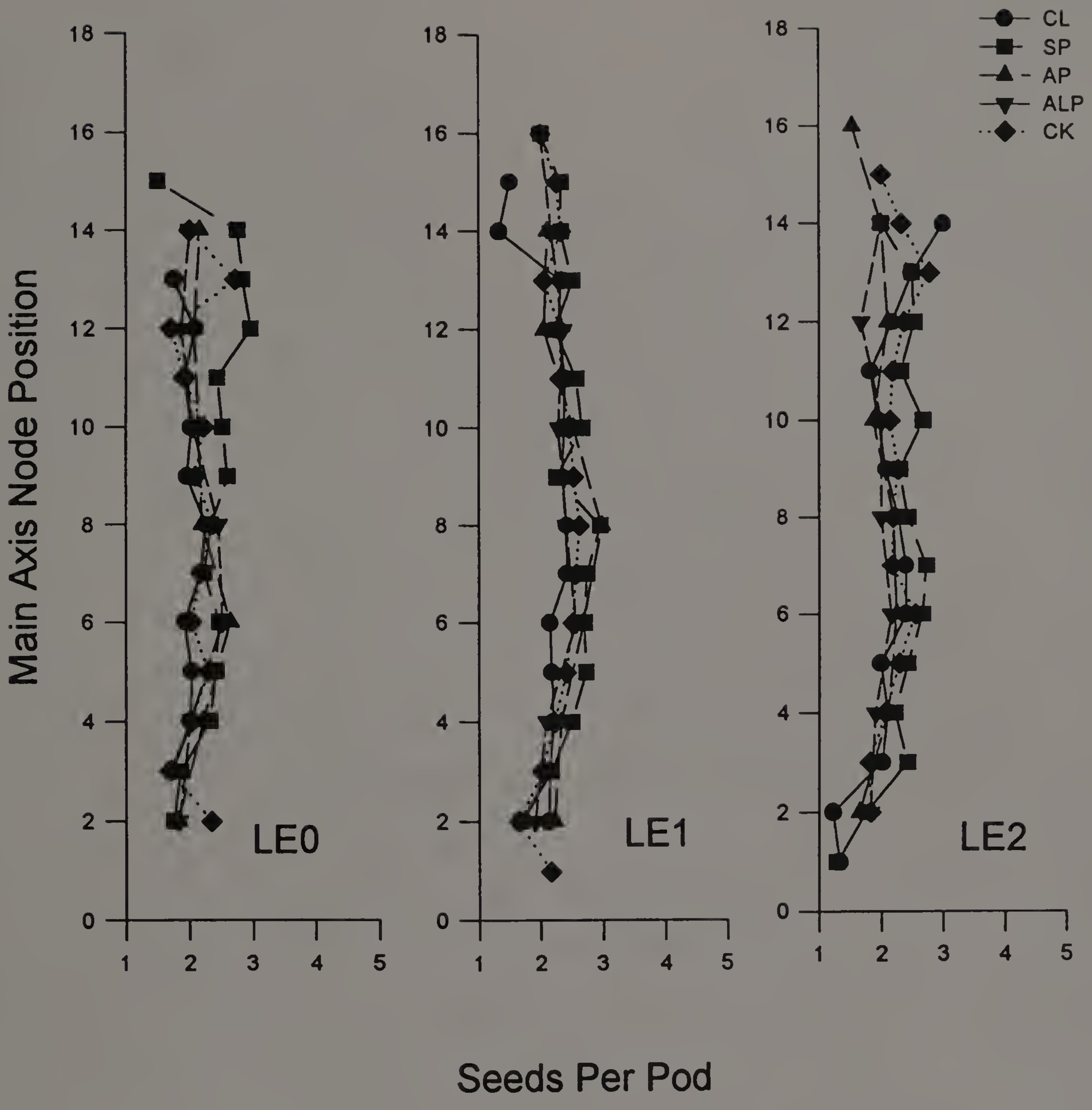

Figure 5.8 Mean seed number per pod across main axis node position in response to light treatments and manipulation treatments.
LE0: Control light condition; LE1: Light enrichment 1;
LE2: Light enrichment 2.

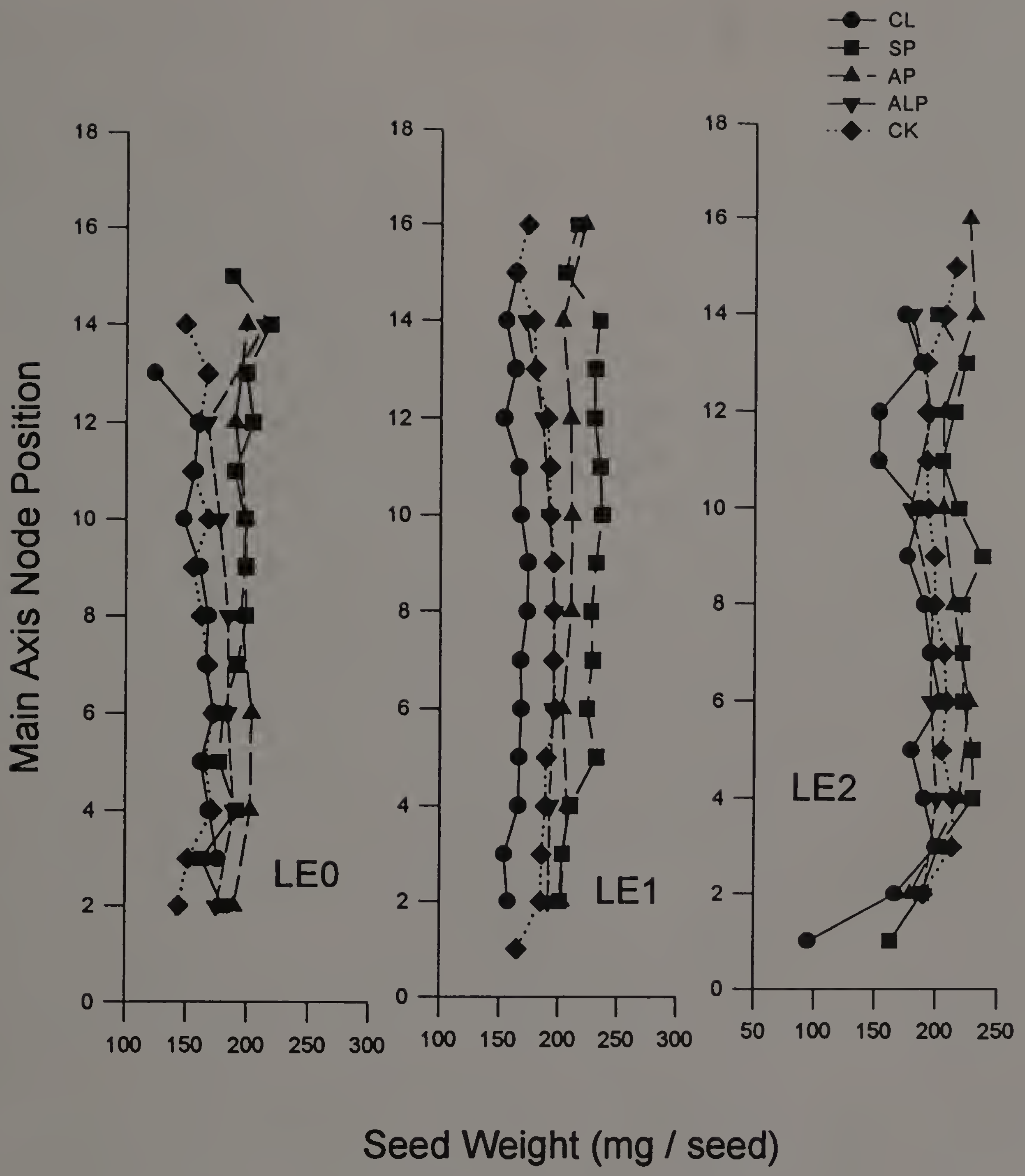

Figure 5.9 Seed size of mainstem seeds across main axis nodes in response to light treatments and manipulation treatments. LE0: Control light condition; LE1: Light enrichment 1; LE2: Light enrichment 2.

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