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THE EFFECT OF PLANT DENSITY ON LEAF AREA INDEX AND YIELDS OF *PISUM SATIVUM* L.

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SUMMARY

A study was made of the effects of plant density on canopy development, light interception and yield of peas. The critical leaf area index was then estimated with a view to the possible manipulation of plant spacings through the season as a method of maintaining optimum yields. It was found that at leaf area index of 5.3 or above, in excess of 95% of incoming visible solar radiation is intercepted by the canopy.

The relationship of crop growth rate in the rapid growth phase to mean leaf area index was investigated over a range of leaf area index values up to 8.6 and even at these high values, only slight reductions in growth rates were recorded.

Green pea yields were found to increase up to leaf area index values approximating the critical value. At levels above this, yields were depressed. To achieve optimum yields, it was necessary to increase planting rates from 170 kg ha⁻¹ in early season, to over 270 kg ha⁻¹ for late season production.

I. INTRODUCTION

In a plant community where water and nutrients are not limiting, the biological yield is largely determined by the utilization of available solar radiation. The production of vegetable crops is usually carried out under conditions of high nutrient and water availability. However, under existing cultural practice, the spatial distribution of plants is largely determined by accessibility for routine cultural practices which include weed control, fertilizer application, pest and disease control and harvesting. Under such conditions, the utilization of incoming radiation is a major factor limiting production. In the production of peas, the advent of mechanical harvesting has removed such restrictions and the plants are placed so as to form a continuous canopy. This crop therefore offers considerable scope for the establishment of a canopy that can most efficiently use the available solar radiation.

The effect of plant density on the production of peas has been investigated by a number of workers (Larson 1943, Reynolds 1950, Vincent 1958, and King 1967). Most of these results indicate optimum yields from plant populations in the range 100 to 200 plants m^{-2} . Kornilov and Kostina (1965) investigated plant density responses under a wide range of climatic conditions and found optimum yields from sowing rates which gave maximum Leaf Area Index (L) values of 4.5 to 5.7.

In south-east Queensland, peas are grown over an extended period from April to October. Decreased yields of late season crops were found by Kruger (1973) to be associated with reductions in plant weight, number of leaves and plant height. These changes which result in reduced interplant competition were attributed to increasing late season temperatures. An investigation has been made of the effects of plant density on the growth and yield of peas with a view to obtaining maximal use of incoming radiation and improving late season production.

II. MATERIALS AND METHODS

The experimental area was located at the Redlands Horticultural Research Station on a typical krasnozem soil. The investigation involved seven experiments which were conducted in the years 1965 (EA1-3), 1966 (EB1-3) and 1967 (EC). The three experiments in each of the series EA and EB were planted in May, July and September and were designed to investigate plant growth and yield responses. In EC, which was planted in August, an investigation was made of canopy development and light interception.

The row spacing for all experiments was 7 in. (17.78 cm) and differential plant populations were achieved by using within row plant spacings of 1 in. (2.54 cm), 2 in. (5.08 cm), 4 in. (10.16 cm), and 8 in. (20.32 cm) which gave populations of 221.5 (D4), 110.7 (D3), 55.4 (D2), and 27.7 (D1) plants m^{-2} respectively.

A complete fertilizer with a composition of 5% nitrogen, 8% phosphorus and 2% potassium was incorporated at a rate of 2 500 kg ha^{-1} to a depth of 10 cm prior to sowing. The variety Fiesta was used and seed was hand planted and a 10% over-sowing was made. The plants were thinned at the three-leaf stage to the desired stand.

The effect of competition from weeds was removed by the use of herbicides and regular hand weeding. Supplementary irrigation was applied by oscillating Skinner lines and the requirements were calculated from rainfall, open-pan evaporation and percentage ground cover by the crop.

In each of these experiments, four harvests were made during the growth of the crop. Datum areas of 0.9 m^2 were replicated four times. At each harvest, plant number and green weight data were recorded and subsamples of 10 plants were taken for morphological measurements, and determination of leaf area and dry weight. As peas approached maturity, samples from guard areas were tested

with a maturometer (Lynch and Mitchell 1950) and when a Maturity Index (MI) of 250 was reached, the final harvests were made and yields determined. In this study, a MI of 250 was considered to indicate the Optimum Harvest Time (OHT).

Leaf area was determined by a leaf punching technique. Circular leaf discs of a known area were weighed and the dry weight per unit area for each sample was used to calculate the leaf area. A planimetric method was used as a standard.

At each growth harvest in experiment EC, the height of the surface of well-determined canopy of leaves was determined. Sampling was also made by the 'stratified clip method' (Stern and Donald 1962). The corner of each plot to be harvested was pegged and steel wires were inserted to define the vertical distribution of foliage in 10 cm zones. The foliage in each zone was carefully cut using broad blade shears so that all material could be collected.

Determinations of photosynthetically active radiation (PhAR) in EC were made using two tube solarimeters as described by Szeicz, Monteith and Dos Santos (1964). These instruments are sensitive to radiation in the wavelength range of 0.4 to 2.0 micron. By inclusion of a Kodak Wratten 88A gelatin sheet filter over the sensing elements of one tube, the sensitivity range is reduced to 0.75 to 2.0 micron. The two tubes were located side by side and after levelling, readings were taken by alternate switching to a microammeter. PhAR was then calculated in terms of $\text{cal cm}^{-2} \text{min}^{-1}$ by subtracting the two readings. A series of six readings was made in each plot. All readings were made on cloudless days about local noon and the time required for a complete set of measurements was approximately 1 h.

III. RESULTS AND DISCUSSION

1. Vegetative growth

Plant density had little effect on the reduction of plant population except at the highest density. This effect was most severe for the first two plantings in each of the EA and EB series. In each case, the population was reduced from 221.5 plants m^{-2} to approximately 188 plants m^{-2} at the final harvest.

Plant dry weight (g m^{-2}) is presented for EA in figure 1 and for series EB and EC in figure 2. At each sampling, the production of dry matter has increased with increasing plant density. On no occasion during the course of these experiments were significant decreases in plant dry weight recorded as a result of increasing plant densities. The results indicate that, as planting is delayed, there is a decrease in the maximum dry weight and the number of days from sowing until the final harvest.

L values of the four plant densities at each planting are presented in figure 3 (EA) and figure 4 (EB and EC). The general trend is for L to increase to a maximum during pod development and then decrease as maturity is approached. Maximum values recorded for EA, EB and EC were 7.45, 7.52 and 9.95 respectively. In all cases, the swards with the higher plant densities recorded the greatest leaf area development.

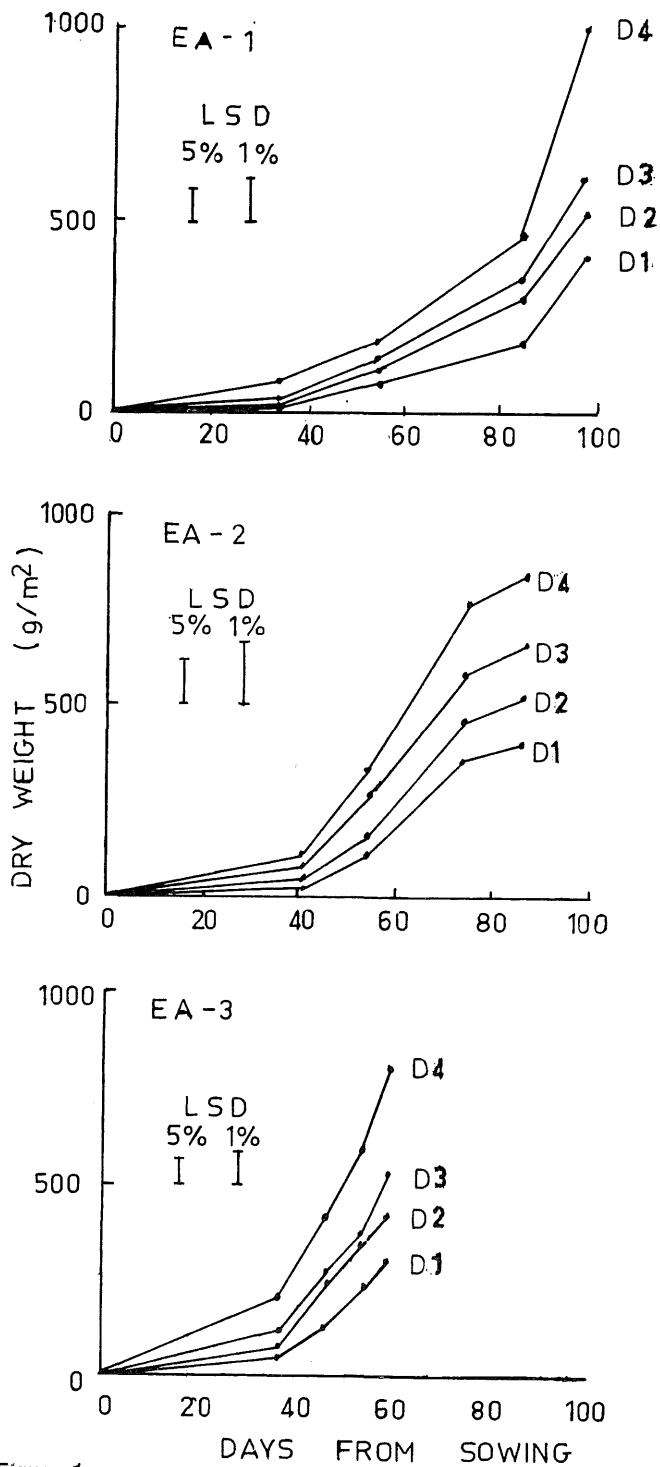


Figure 1

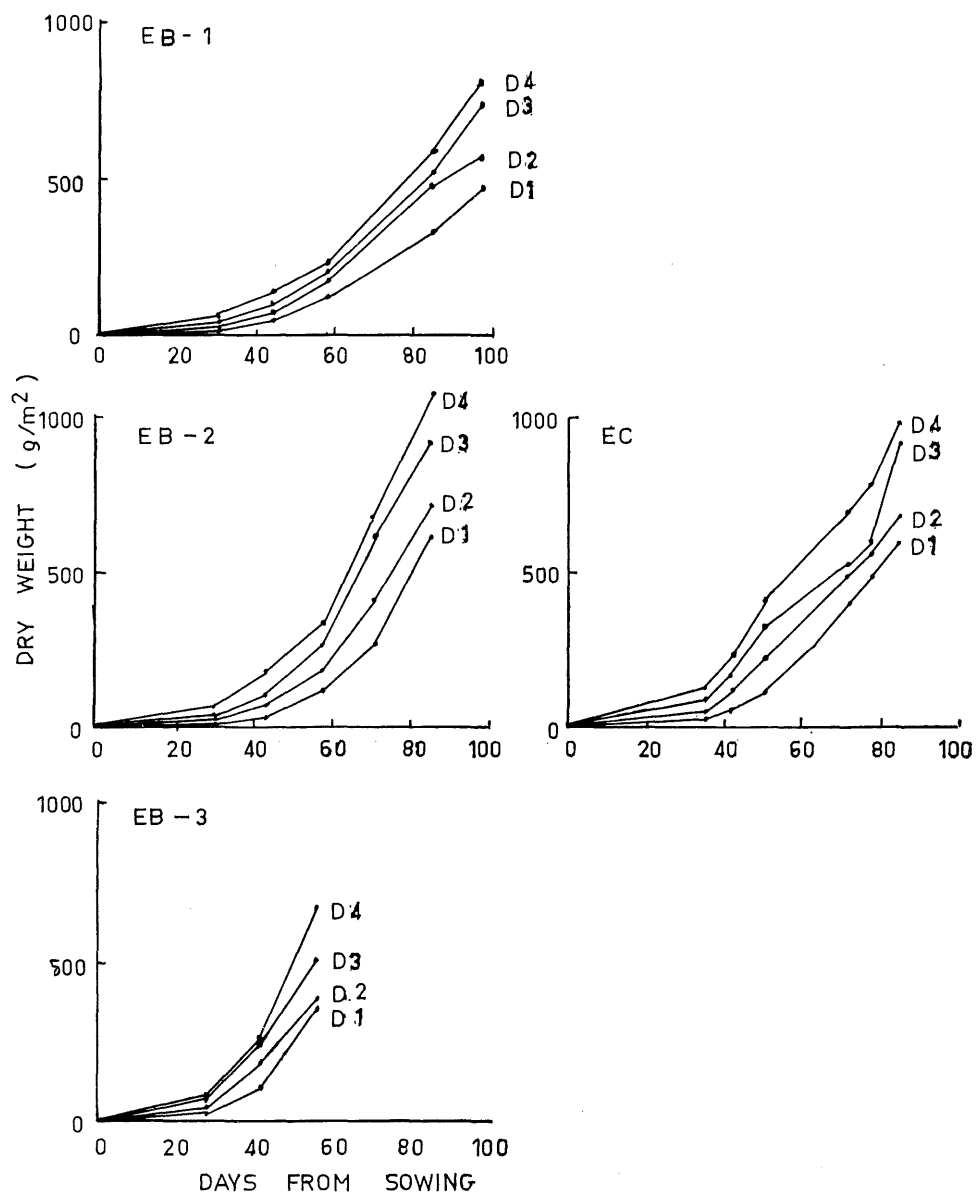


Figure 2

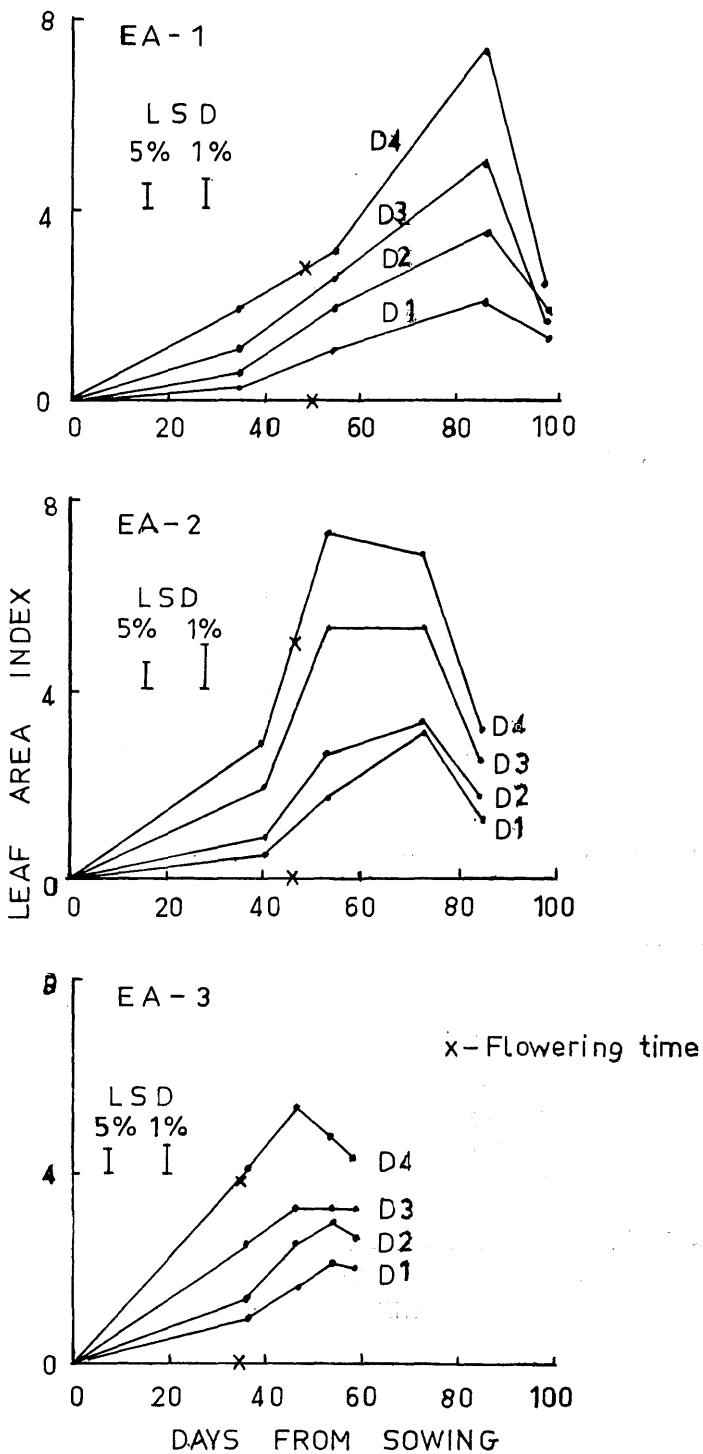


Figure 3

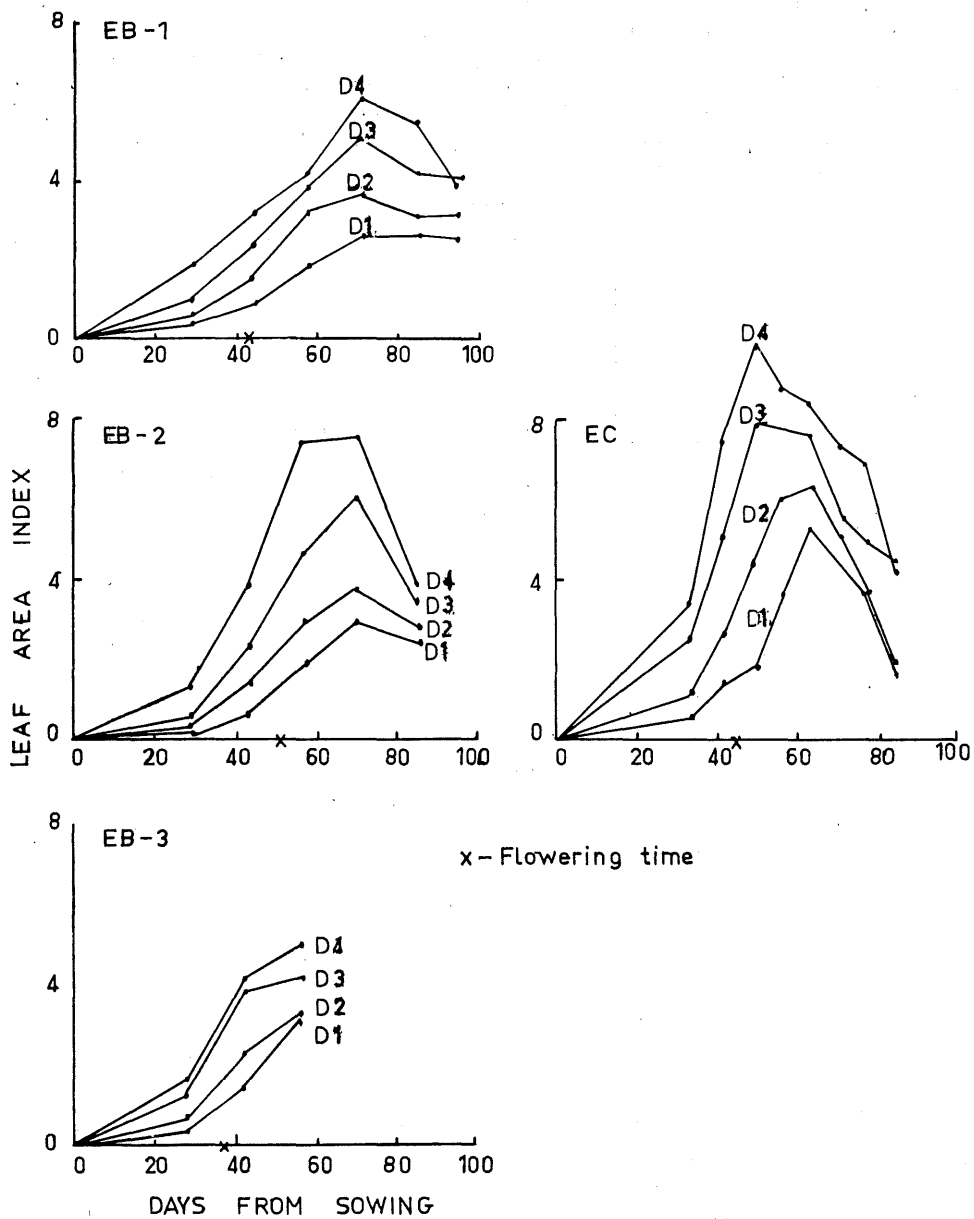


Figure 4

These differences in L represent the summary effects of the several changes in plant morphology brought about as a result of plant competition. The mean number of leaves produced per plant for EA and EB is given in table 1. The number of leaves per plant is reduced by both increases in plant density and delay in planting time. The effect of treatment on the number of nodes with leaves contributing to L was recorded at maturity for series EB (table 1). For earlier plantings and at higher densities, the senescence of older leaves was accelerated as the plants matured resulting in a reduction of the number of nodes with leaves contributing to L. Tillering is another aspect of the morphological development of plants on which treatments have had considerable effect. Reduction in plant density has resulted in increased development of laterals.

TABLE 1
MEAN NUMBER OF LEAVES—EA AND EB AND NUMBER OF LEAVES CONTRIBUTING TO
LEAF AREA INDEX—EB

Treatment	EA		EB	
	Mean No. Leaves		Mean No. Leaves	No. Leaves Contributing to L.
Time of Planting				
1	15.4		18.1	11.6
2	16.5		17.4	9.8
3	14.3		15.4	13.9
L.S.D.				
5%	0.50		0.41	0.98
1%	0.67		0.63	1.48
Plant Density				
D 1	16.7		18.1	11.0
D 2	15.9		17.6	10.0
D 3	14.9		16.6	7.8
D 4	14.1		15.6	6.4
L.S.D.				
5%	0.57		0.48	1.13
1%	0.77		0.72	1.71

TABLE 2
MEAN NET ASSIMILATION RATE (E), RELATIVE GROWTH RATE (R) AND CROP GROWTH
RATE (C) OVER THE WHOLE GROWING PERIOD IN RELATION TO TIME OF PLANTING AND
PLANT DENSITY.

Treatment	E (g m ⁻² day ⁻¹)		R (g g ⁻¹ day ⁻¹)		C (g m ⁻² day ⁻¹)	
	EA	EB	EA	EB	EA	EB
Time of Planting						
1	7.00	5.10	0.044	0.048	9.26	9.64
2	7.07	9.70	0.053	0.061	12.08	14.11
3	6.86	7.66	0.066	0.082	17.26	15.58
L.S.D.						
5%	1.02	1.68	0.0044	0.0111	2.84	2.59
1%	1.56	2.55	0.0068	0.0168	4.30	3.92
Plant Density						
D 1	8.48	9.20	0.065	0.077	8.65	10.40
D 2	7.32	7.53	0.057	0.066	11.09	10.99
D 3	6.04	6.71	0.048	0.057	12.77	14.04
D 4	6.07	6.50	0.048	0.056	18.95	17.01
L.S.D.						
5%	1.18	1.94	0.0052	0.0128	3.27	2.99
1%	1.79	2.94	0.0078	0.0194	4.96	4.52

The effects of planting time and plant density on net assimilation rate (E), relative growth rate (R) and crop growth rate (C) are presented in table 2. These indices were calculated for each growth period and are presented as means for the whole growing period. Delays in planting have resulted in significant increases in both R and C. However, E, although showing no significant differences in EA, does reflect the seasonal response in EB with a maximum at the second planting. At higher plant densities, both E and R have been depressed, but dry matter accumulation as represented by C has been increased.

Of particular interest is the effect of L on the rate of dry matter accumulation. This relationship is illustrated in figure 5 using data from the exponential growth phase of each planting in EA, EB and EC. A line of best fit $y = 3.90 + 2.62x$ (in the least squares sense) was derived from these data. This linear regression contributed significantly ($p < 0.01$) towards explaining the relationship between crop growth rate and leaf area index. These data give no indication of the rate of dry matter accumulation reaching a maximum value or decreasing over the range of L values developed in these plantings.

2. Light interception

The relationship between light interception and leaf area is presented in figure 6. These data represent recordings for the four plant densities on five sampling dates during the growth of series EC. The curve of best fit, $y = -18.96 + 85.84x - 0.5x^2 - 15.75x^3$, has been drawn. It is indicated that 95% light interception will be achieved at L of approximately 5.3. Where L exceeds this value, the extra foliage could well be below compensation point.

Light penetration into the canopy has been investigated in relation to L and is presented in figure 7. It has been found that the data are adequately described by an equation of the form $I/I_0 = e^{-KL}$ where (I/I_0) is the fraction of light penetrating a layer of foliage (L) and k is the extinction coefficient. The value of k calculated for these data is 0.51 ± 0.03 .

An investigation of the vertical leaf area distribution in relation to light interception was made by stratified sampling at flowering and pod enlargement (Figure 8). These data allow an assessment of the effective L at each plant density. As plant density increases from D1 to D4, the percentage of light reaching lower levels is reduced. A comparison of the vertical distribution of leaf area development at these two stages indicates the effect of lodging experienced at higher plant densities. At the lowest density, D1, there has been further leaf area development in the 50 to 70 cm zone, while at higher densities, D3 and D4, there have been decreases in the upper zones and increases in the lower zones.

3. Reproductive growth

Yield data (kg ha^{-1}) for all plantings are presented in figure 9. With the exception of EA-2 and EB-1, maximum yields of approximately 6500 kg ha^{-1} were recorded for all plantings. The maximum yields were recorded from progressively higher densities as planting was delayed. The yield depressions of the above two plantings are attributed to damage from frost which was not severe enough to cause foliar symptoms, but flowers and young pods were damaged.

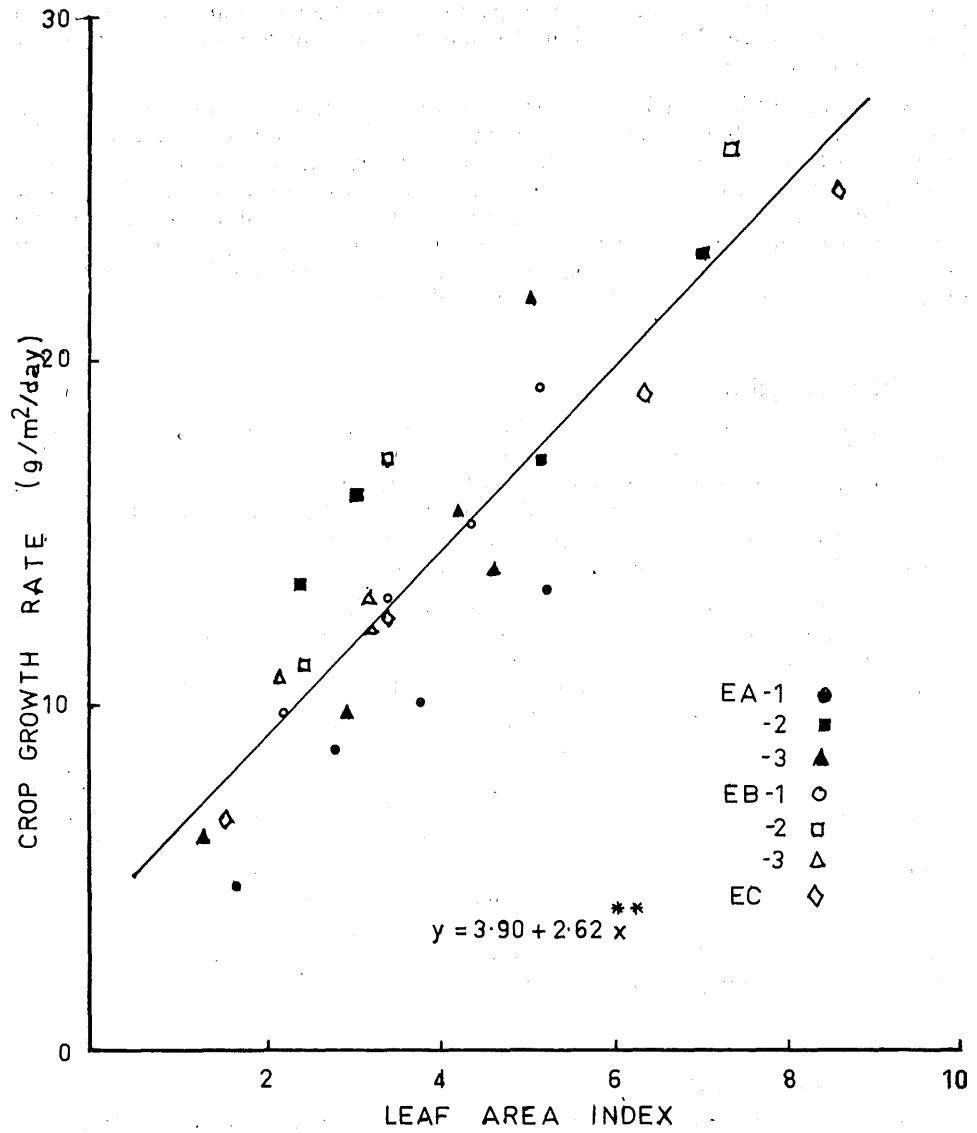


Figure 5

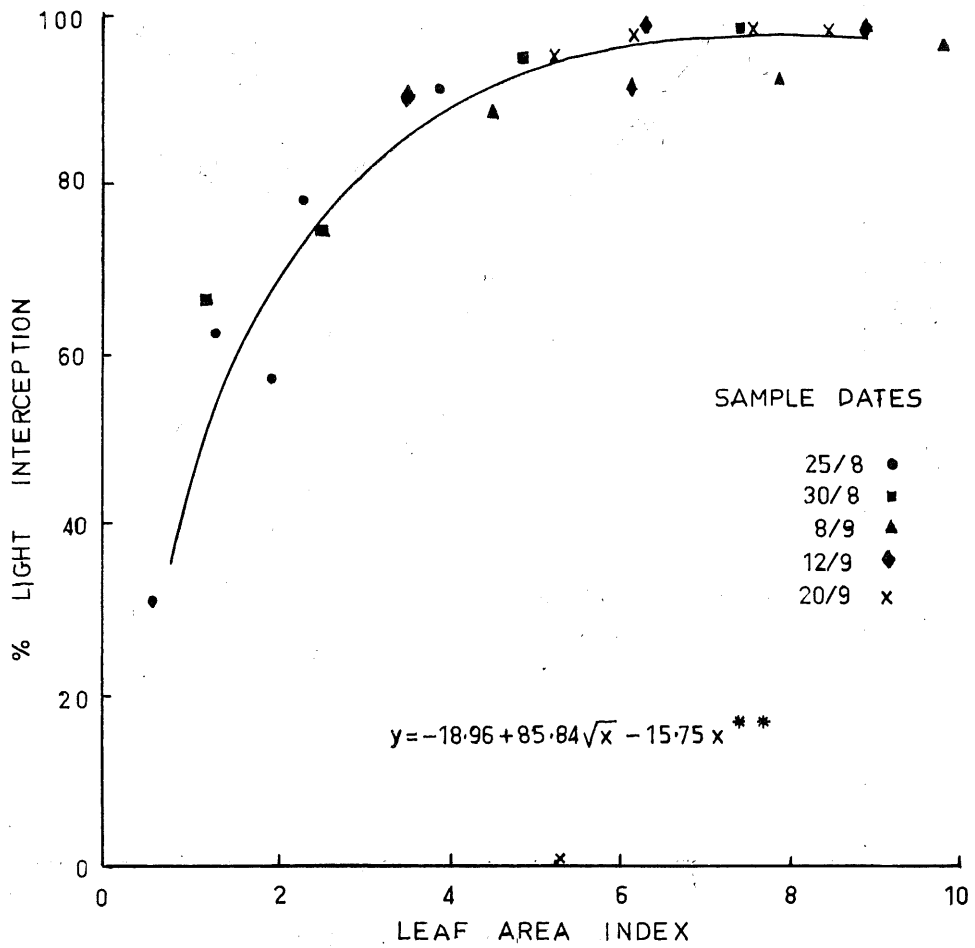


Figure 6

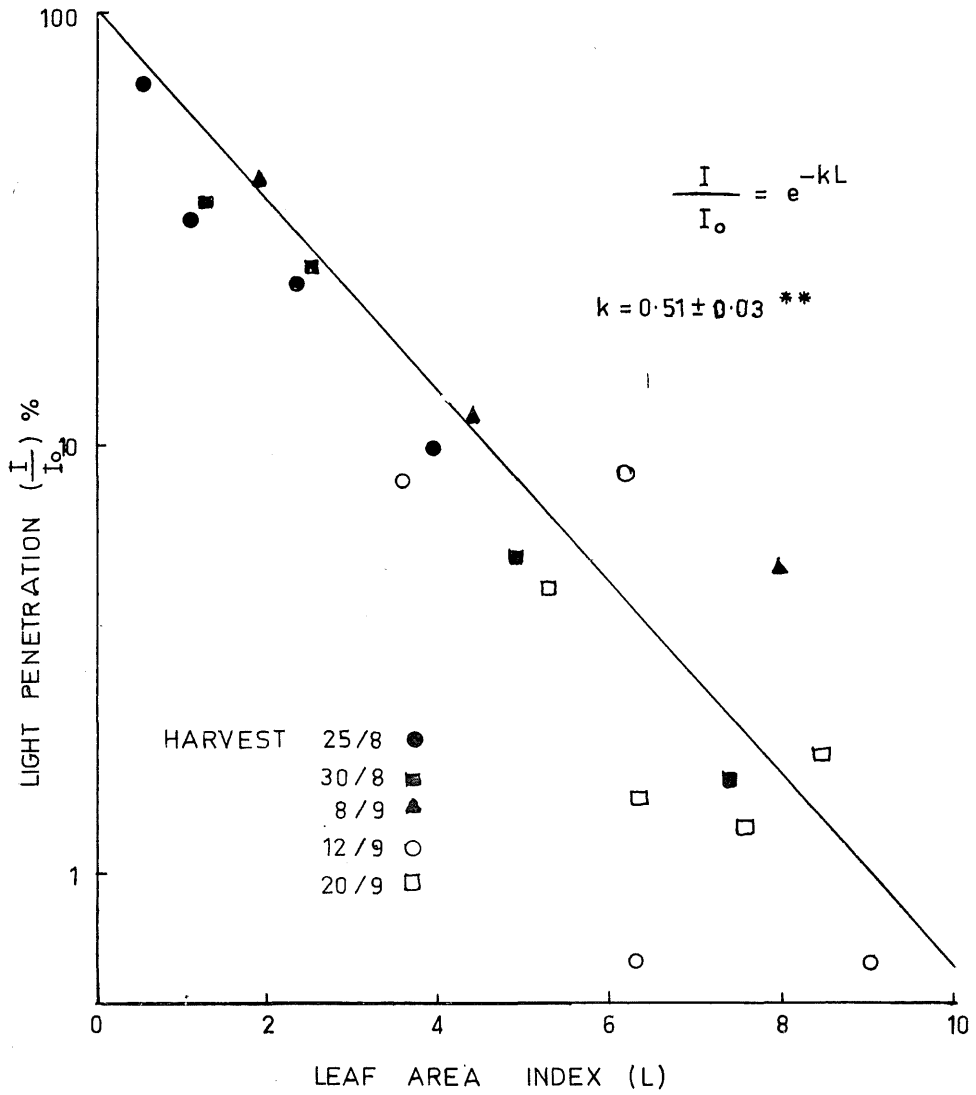


Figure 7

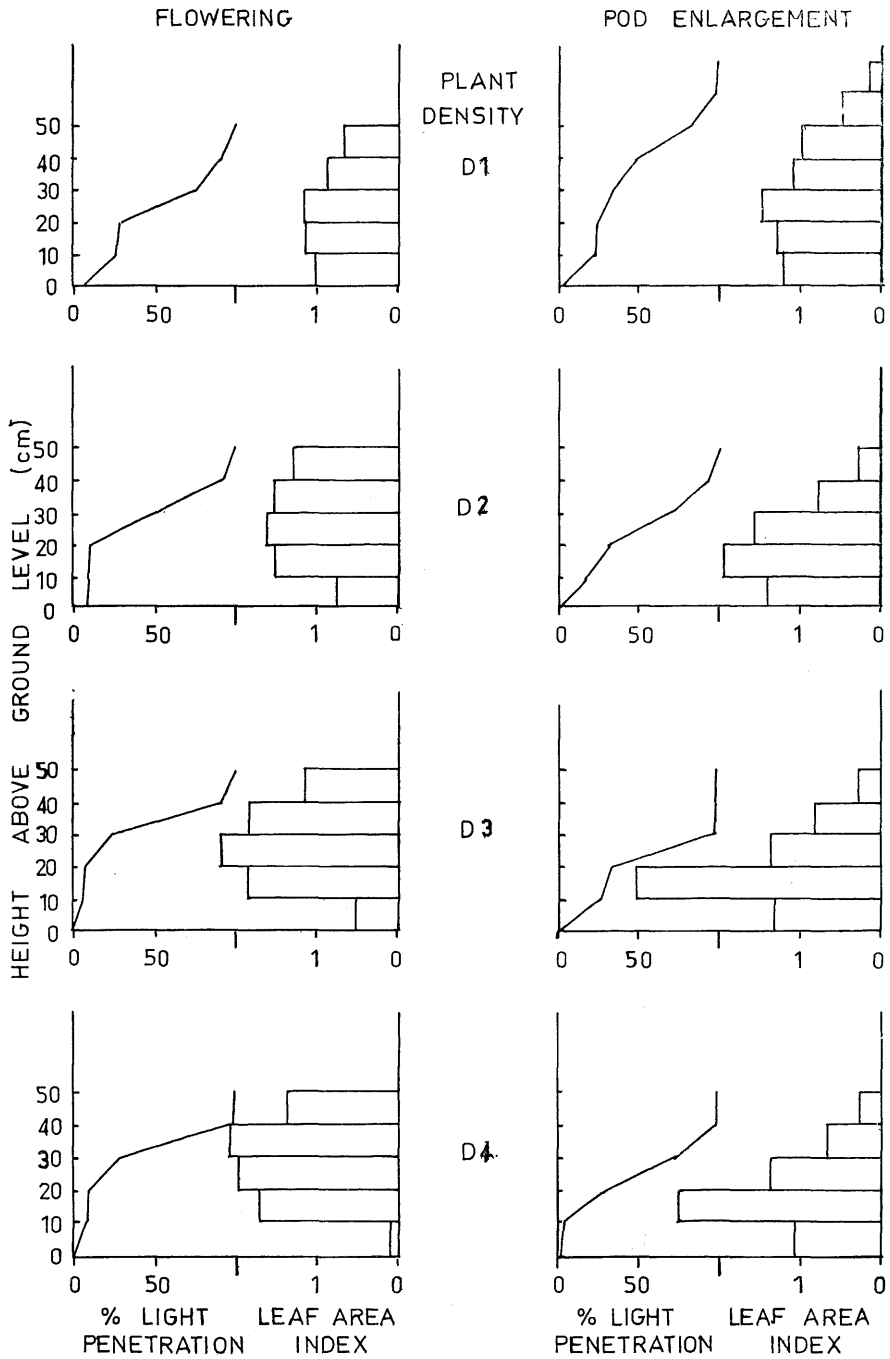


Figure 8

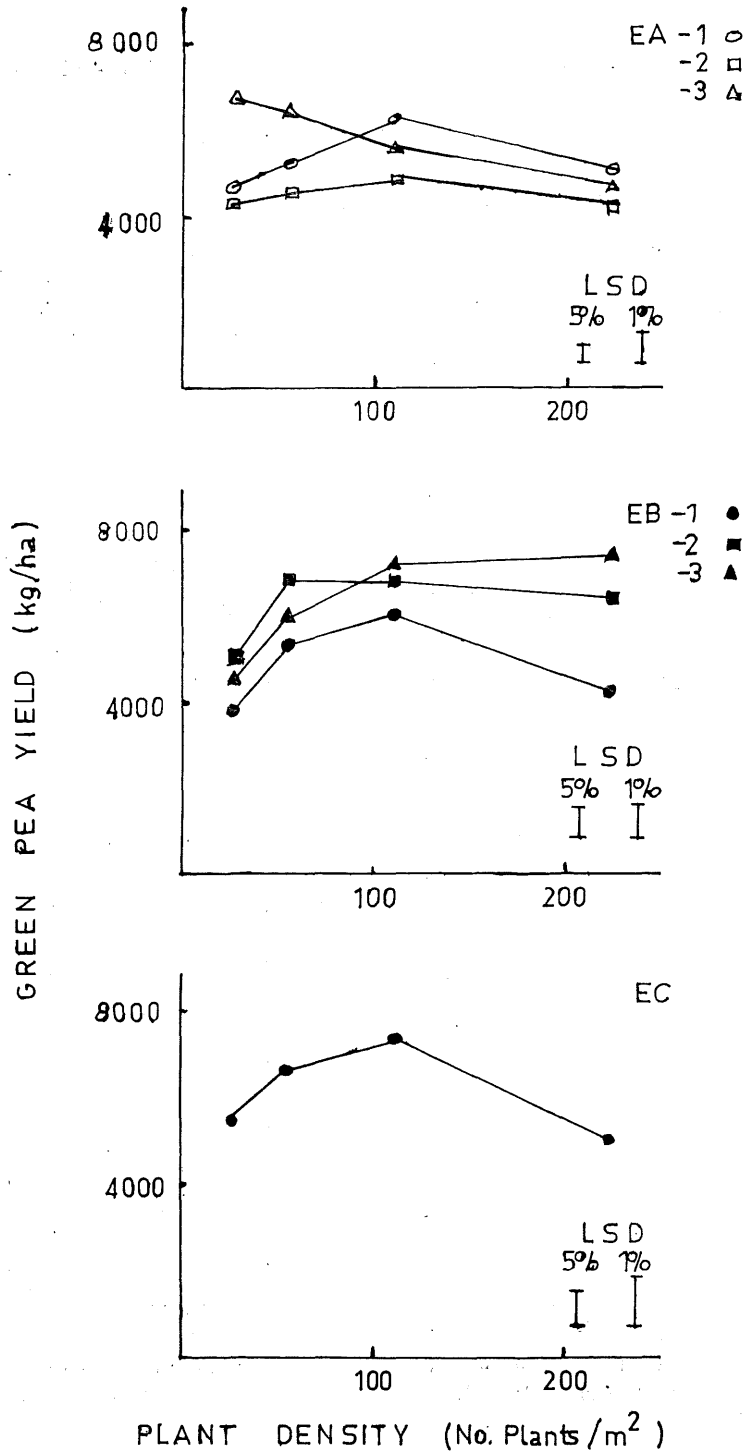


Figure 9

The effects of treatments in series EB affected the following components of yield: number of pods per plant, mean green pea weight, number of peas per pod, percentage of marketable pods, percentage of nodes with double pods, number of stems per plant and per cent marketable pods on lateral stems. The correlation of these factors with yield is presented in table 3. These results indicate that plant density increases have resulted in a reduction in the number of pods per plant, number of peas per pod and the number of stems per plant. The negative correlation of these factors with yield suggest that increased plant numbers at higher densities offsets these reductions and high yields are maintained. This effect is also demonstrated in yield component data for series EC (table 4) where the number of pods is expressed on a unit area basis.

TABLE 3
COMPONENTS OF YIELD—EB

Treatment	Variate	No. Pods per Plant	Mean Green Pea Wt. (g)	No. Peas per Pod	% Marketable Pods	% Nodes with Double Pods	No. Stems per Plant	% Marketable Pods on Laterals
Time of Planting								
	EB-1 ..	8.15	0.42	5.63	69.9	1.4	1.45	3.6
	EB-2 ..	8.96	0.45	5.03	87.0	16.8	1.31	20.9
	EB-3 ..	7.08	0.46	4.19	90.00	6.0	1.45	12.1
L.S.D.	5% ..	0.34	0.03	0.15	3.84	2.07	0.11	3.17
	1% ..	0.46	0.04	0.21	5.18	2.80	0.16	4.29
Plant Density								
	D 1 ..	12.71	0.46	5.42	76.4	10.0	2.00	15.4
	D 2 ..	9.27	0.45	5.27	82.8	10.5	1.58	12.4
	D 3 ..	5.88	0.43	4.71	87.4	8.7	1.04	15.6
	D 4 ..	4.39	0.44	4.39	83.1	3.0	1.00	5.3
L.S.D.	5% ..	0.39	0.04	0.18	4.43	2.4	0.13	3.7
	1% ..	0.53	0.05	0.24	5.99	3.2	0.18	4.9
Correlation with Yield		-0.47**	0.18	-0.54**	0.75**	0.33	-0.57**	0.27
**—Sig. 1%								

TABLE 4
COMPONENTS OF YIELD—EC

Plant Density	% Total Pod Dry Wt. as Pea	No. Pods m ⁻²	No. Pods per Plant	Mean Pea Dry Wt.	No. Peas per Pod
D 1	60.3	407	13.9	0.22	5.5
D 2	56.3	476	9.7	0.20	5.1
D 3	61.3	571	5.5	0.22	4.1
D 4	65.3	771	4.5	0.23	4.5
L.S.D.	5%	7.6	64.5	1.78	1.01
	1%	10.9	92.7	2.56	1.45

At higher planting rates, the number of surviving plants was reduced as growth progressed. This effect was not observed in the late season plantings EA-3 and EB-3. Such relationships have been studied by Holliday (1953) who concluded that with increasing plant densities, the original linear relationship between number of seeds planted and number of plants at establishment is modified to a curvilinear relationship as plants develop, as a result of death of plants from interplant competition. As the curved relationship was observed in some of these plantings, it indicated that maximum seeding rates were being approached. However, with delay in planting date, the reduction in plant numbers was not observed, thus reinforcing the suggestion that higher seeding rates are warranted for optimum development of late season crops.

The leaf development for each planting is illustrated in figures 3 and 4, and shows maximum values for plantings at the highest plant density. However, this maximum is modified by planting time, showing a general trend to decrease with delays in planting. This maximum development occurred during pod enlargement and thereafter declines as maturity is approached. In late season plantings, this decline is rapid, the L for EB-3 being reduced to almost zero 5 days after maturity and consequently no data were recorded. This reduction results from a combination of reduced rate of leaf production and increased leaf senescence. The rate of leaf senescence has been found to be increased at earlier plantings and for higher plant densities (table 1).

The relationship of L to light interception was determined in EC (figure 6) and it is found that 95% interception of PhAR, that is, the critical value using the terminology of Brougham (1956), was achieved at an L of approximately 5.3. From this, it is inferred that any leaves in excess of this critical L value will be below compensation point. This value is in agreement with the results of Kornilov and Kostina (1965) who found optimum yields of peas from L values in the range of 4.5 to 5.7.

Stratified samplings which were carried out at the stages of flowering and pod enlargement show the vertical distribution of foliage in relation to light penetration. At higher densities, leaf area development was greatest towards the top of the plant while, at lower densities, there was a more even leaf distribution over the full height of the plant. By the time of pod enlargement, this distribution had been modified as a result of lodging. This effect was most severe at the higher densities.

The penetration of light into a plant canopy was found by Monsi and Saeki (1953) to be successfully described by Beer's Law. When this relationship was tested on the data from these experiments (figure 7), a response significant at the 1% level was obtained. This indicates that the model satisfactorily describes these experimental data. The extinction coefficient (k) in this case is 0.51. Brown and Blaser (1968) reviewed this subject and found that, in species with almost horizontal leaves, k values approach or even exceed 1.0 while, in species with more inclined leaves such as perennial grasses, lower values in the range 0.4 to 0.7 are recorded.

The relationship of C in the rapid growth phase to mean L for the period is given in figure 5 and a straight line has been fitted. A quadratic equation was also fitted but no increased significance was obtained. From these results, it could be expected that no decrease in vegetative growth rates will be recorded at L values up to approximately 9.0. As canopy densities in commercial practice seldom approach this level, it is considered that reductions in vegetative growth as a result of high L values will not occur. As this relationship does not describe an optimum value it corresponds to an 'ascending' type response.

The investigation of light interception in relation to L has shown that 95% of available PhAR was intercepted at L of 5.3 and this is termed the 'critical leaf-area index'. It could be expected that vegetative growth would be retarded when leaf area development exceeded the critical value. Such an hypothesis would assume a linear proportionality between L and respiratory load. Williams, Loomis and Lepley (1965) present evidence from their work that no such proportionality existed at high densities. They showed that leaf area per unit leaf weight increased with increasing density and suggest that, if respiration is more closely related to leaf weight than leaf area, as could be expected, then respiration per unit leaf area could decline with increasing L. These authors therefore suggest that an optimum, critical or ascending type relationship may be obtained depending on the distribution of dry matter within a crop and its relative contribution to increases in respiration. These conclusions are supported by the results of translocation studies with many plants in which lower, shaded, old leaves have been found not to import assimilates from upper young leaves.

In their work with subterranean clover, Stern and Donald (1962) found that the optimum L value increased with increasing levels of radiation. Assuming that there is little difference between the optimum and the critical L values in defining maximum energy interception, as suggested by Shibies and Weber (1965), it can well be expected that the L of 95% light interception would increase with increasing levels of radiation. As the light interception data in this work were recorded for a midseason planting, it is suggested that the critical L value would be reduced for earlier plantings and elevated for late-season plantings.

The economic interest in this crop is related to a unit of reproductive growth. Yield response in relation to plant density (figure 9) shows a parabolic relationship as opposed to the 'ascending' relationship described for vegetative growth. The data of Reynolds (1950) and Vincent (1958) for yield of peas in relation to plant density also show the same type of parabolic response. Such a distinction in vegetative and reproductive growth responses in relation to plant density has been discussed by Holliday (1960) who considered it to be the typical response of most plants.

A consideration of green pea yields shows that, after disregarding the results for EA-2 and EB-1 which were damaged by frost, the plant density producing the highest yield increased as planting was delayed. However, maximum vegetative growth rate was obtained at the highest plant density in all plantings. These conditions which result in optimum vegetative yields do not necessarily promote optimum reproductive yields.

High green pea yields were recorded for populations where L values in the vegetative phase approached the critical value. Where leaf area development was in excess of critical value, the plants were much smaller with fewer pods and a trend towards reduced numbers of seed per pod and yields were depressed. At lower populations where L values were below the critical value, yield reductions were also recorded. This was probably associated with the fact that light interceptions in these populations was not complete. To achieve the critical L value in these experiments, it was necessary to increase planting rates from 170 kg ha⁻¹ in early season, to over 270 kg ha⁻¹ for late season production. Although optimum yields can be maintained by adjusting the sowing rates, the higher temperatures encountered by late season plantings will result in the earlier development of starch phosphorylase giving greatly accelerated maturation rates.

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