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GROWTH STUDIES WITH PEAS

A thesis presented in partial fulfilment  
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## ABSTRACT

Two experiments were conducted on vining peas under field conditions and their growth was followed using growth analysis techniques.

In the first experiment, cv Victory Freezer was grown to maturity and the growth parameters total plant dry mass, leaf area and leaf dry mass recorded at weekly intervals for each of four planting densities.

Determination of weekly values of  $\bar{R}$ ,  $\bar{E}$  and  $\bar{F}$  where  $\bar{R}$  is mean relative growth rate,  $\bar{E}$  is mean net assimilation rate and  $\bar{F}$  is mean leaf area ratio, was unsatisfactory due to harvest variability.

By fitting  $\log_e$  values of each parameter over the harvest period to quadratic functions, of the form

$$\hat{Y} = a + bT + cT^2$$

where  $\hat{Y}$  is the derived parameter value, a, b, and c are regression constants and T is time, it was possible to calculate instantaneous values for R, E and F. Calculation of R over the whole of growth by this method was not satisfactory.

A third method of deriving R, E and F was then attempted by fitting the logistic function

$$W = A(1 - e^{-(\lambda + kT)\theta})^{-1/\theta}$$

where W is the required parameter, A is the asymptote, e the base of natural logarithms,  $\lambda$ , k and  $\theta$  are constants and T time. Values of R obtained by this method appeared to more closely approximate to the growth patterns of peas. However, due to the non-asymptotic growth of leaves the method was not suited to derivation of E and F over the whole of growth. Fitting of growth parameters to the model was also difficult where appreciable variability existed in the parameter to be fitted.

At the lower plant densities, Relative Growth Rate was maintained at a higher level for much of the growth period apparently due to a higher net assimilation rate.

In this experiment maximum yield was shown to occur at the highest plant densities. This was despite lower numbers of pods per plant; numbers of peas per pod and individual pea fresh mass being little affected by density.

The second experiment compared three near isogenic lines of cv Dark Skinned Perfection vining pea, differing only in the expression of leaf, tendril and stipule. Each was grown at the same range of densities as in the first experiment. By the time that this experiment was half grown, the weather conditions were unfavourable for growth, with strong winds, heavy rain and low light levels. These conditions were ideal for the spread of fungal disease and the combination of weather and disease made growth very erratic.

Despite the poor conditions recording of growth parameters continued until no further plots were available for harvest. At that stage only a few plots had commenced fruiting and little yield data was obtained.

The very variable growth parameter records made interpretation of  $\bar{R}$ ,  $\bar{E}$  and  $\bar{F}$  almost impossible. The ease of fitting the quadratic function made it seem that this was the only method worth attempting for derivation of R, E and F values over the experimental period. Results obtained showed that in contrast to the first experiment the higher density of planting conferred many benefits to the peas. Higher leaf area ratios in the more closely planted plots led to larger values of R in this experiment.

Weather effects on density were mirrored in leaf reduction where the relative growth rate of the least leafy cultivar was much lower than for the more conventional types, due again to lower values of F.

The difficulty in obtaining meaningful mean values of the derived functions in both experiments suggests that different methods of deriving R, E and F are desirable. Using quadratic regression to derive these functions is limited in following whole of growth changes. Fitting of the logistic model is also difficult particularly where harvest variability is high and where the parameters are not basically asymptotic in form. It is suggested that fitting of functions to data over only part of growth may be advisable.

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## LITERATURE REVIEW

### 1. Pea Physiology

#### 1.1 History

The garden pea, *Pisum sativum* L. belongs to the order Fabales, family Leguminosae. It has been cultivated since the stone age, (Cole, 1961) and is one of the group of plants known collectively as peas, lentils or pulses. Marx (1977) considers that the field pea and the garden pea may be regarded as forms of the one specie. On the grounds of priority this should be known as *P. arvense* but by common usage however the garden pea is called *P. sativum*.

The origin of the garden and field pea is believed to be on the eastern shores of the Mediterranean. Early cultivators probably selected the plant on account of its relatively large seeds, their lack of dormancy and freedom from toxic or bitter principals. These peas are also characterised by their non shattering pods which have no doubt been encouraged by selection.

#### 1.2. Value of Crop

The most important use of the pea is for production of the dry seed. Edwards (1978) quotes global production of 13.4 million tonnes from 10 million hectares grown for dry seed compared to 4.8 million tonnes from 0.8 million hectares for green peas.

The average green pea yield suggested by these figures reflects both their higher moisture content and a higher level of management.

#### 1.3 Description

In cultivation, the pea is a single stemmed upright to scrambling, weak strawed annual herb. The leaves are alternate on the stem usually compound on

long petioles. The lower leaves are much reduced trifid scales while the upper leaves are bi to multi pinnate and are subtended by pairs of large leaf like stipules. The petiole terminates in tendrils, more developed at the upper nodes. Dormant vegetative buds are carried in the leaf axils at the lower nodes while the upper axils bear a flower stem with one or more flowers. The field pea is similar in habit, with pink to purple flowers while the garden pea bears white flowers, (Pate, 1975).

Twelve ovules are usually produced by each flower, not all of which however develop to maturity. The ovules are carried in a single row in the pod. The mature fruit is some five to eight millimetres in diameter, more or less spherical and smooth to wrinkled and varies in colour from greenish to white.

#### 1.4 Development - General

During imbibition the dry seed swells and germination is marked by exsertion of the radicle and then the plumule. Emergence is hypogocal and field emergence is defined by the appearance above ground of the plumule. At germination, six or seven leaf initials are usually present in the embryo, new initials then appear at two or three day intervals. Leaf emergence is typically slower than initiation about three to four days apart. Internode extension proceeds individually for about a week, so that at any time growth proceeds in a wave like fashion, (Birecka and Galston, 1970). The youngest internode grows most rapidly while the penultimate internodes grow at successively slower rates.

Root development normally begins within 48 hours of commencement of imbibition at 25°C (Torrey and Zobel, 1977), and the radicle which makes the first break in the testa continues as the dominant feature of the root, producing a strong tap root. Nodulation following inoculation with *Rhizobium* bacteria may occur

on the main tap root or major laterals as early as ten to twelve days after germination.

Flower initiation may have occurred in the seed embryo in very early cultivars or more commonly from shortly after germination to some weeks later. Flower emergence and development is sequential and once started is compulsive under most conditions, (Murfet, 1977) continuing until the apex senesces and growth ceases.

#### 1.4.1 Leaf Growth

The first leaves to emerge are the trifid scales which are usually produced below the soil surface just above the buried cotyledons. The first true leaves above the soil are bipinnate usually without tendrils, and with only small stipules. Leaves produced from above the fifth node are more complex with additional pairs of pinnae and well developed tendrils as well as large, leaf like stipules.

#### 1.4.2 Branching

While peas are typically single stemmed, dormant vegetative buds are carried in the lower leaf axils which may be stimulated into growth. It has been demonstrated that decapitation will allow axillary growth (Lovell, 1977). Removal of the epicotyl will stimulate growth from the two axillary cotyledonary buds only one of which will persist in dwarf cultivars (Sachs, 1966), while both may grow to maturity in tall cultivars. Decapitation at higher nodes will allow growth from several previously dormant buds until apical dominance is restored by correlative inhibition. At each axil there are three or four buds, only one of which may be expected to grow, (Lovell, 1977).

Planting density is also known to affect branching. At densities of above about 100 plants  $m^{-2}$ , single stemmed plants are usual while at lower densities, branching from both upper and lower nodes may be expected. Low light intensities inhibit branching (Lovell, 1977) while both high light intensity and high nitrogen fertilization reduce apical dominance and thus increase branch product-

ion. Snead, Hobart and Payne (1973) showed that in a freely branching strain a reduction in plant density from 100 to 25 plants  $m^{-2}$  increased branching by 50%. Branches or tillers from the lower nodes may offer advantages in terms of stem numbers per unit area as a component of yield. Branches from the higher nodes however produce flowers at a higher node than on the main stem and increase variability of maturity.

In the intact plant there is a natural release from apical dominance at about the time of flowering with subsequent production of branches and new leaves.

#### 1.4.3 Root Growth

Torrey and Zobel (1977) describe the root growth of the pea as consisting of a primary root formed by elongation of the radicle with secondary and tertiary branches. The primary and secondary roots are of similar length and all are highly branched. Nodulation by *Rhizobium* spp bacterium may take place on the primary or secondary roots beginning as early as ten to twelve days after germination.

Minchin and Pate (1973) suggest the respiration of the roots and in particular the nodules is an important sink for photoassimilate. Prior to flowering almost half of the assimilate is required for root growth and about one quarter of this for the nodules. Growth rate of roots reaches a maximum at about flower initiation and then declines abruptly even before flowering starts (Salter and Drew, 1965). Whole sections of roots were also shown to decay and be lost during flowering.

#### 1.4.4 Flowering

The node at which the first flower is initiated (FN) is designated by counting from the first node above the cotyledonary internode and includes those nodes carrying scale leaves. Murfet (1977) notes that use of the lowest node to begin the count removes confusion arising from arbitrary selections of higher nodes to

begin a count as proposed by some authors. Early cultivars are characterized by a low FN value, usually 6 - 10 (Pate, 1975) or 6 - 13 (Murfet, 1977) where no intermediate class is included. These early cultivars may either have initiated flowers in the seed or initiate them a few days after germination. A typical plastochron of two days (the time between leaf initiations) would indicate that a cultivar of FN 13 would normally initiate flowers by the fourteenth day after germination. Early cultivars would initiate flowers close to field emergence. These early cultivars have been shown to be insensitive to day length (Kopetz, 1938) and to vernalisation, (Barber, 1959). Moore (1964, 1965) suggested that cotyledon excision could increase FN in these cultivars, Murfet (1977) however regarded this effect as due to depletion of reserves. Late cultivars respond to environmental changes with variations in FN although Murfet (1977) suggests that there is an intermediate group of mid season cultivars less influenced by environment than the late group.

The number of flower nodes which may be produced has been shown to be finite (Lockhart and Gottschall, 1961). Even with continuous bud removal the apex eventually senesced.

#### 1.4.4.1 Vernalisation

Cotyledonary response to vernalisation has been demonstrated (Amos and Crowden, 1969; Haupt and Nakamura, 1970; and Reid and Murfet, 1975). Barber (1959) showed that young plants exposed to temperatures of 1 to 7°C for one to four weeks flowered one or two nodes earlier. Moore and Bonde (1962) and Highkin (1958) further showed that exposure to high temperature immediately after vernalisation treatment reversed the effect. Wellensiek (1969) showed that the vernalisation response was greater in later cultivars.

#### 1.4.4.2 Photoperiod

Paton (1971) has demonstrated that the cotyledons are sensitive to photoperiod. There is little evidence to suggest an obligate long day response in peas and Murfet (1977) considers that even those most responsive to long days will eventually flower under short days. The response to day length is most marked in lines with FN of above 13. The cotyledonary response to day length in cv Greenfeast shown by Paton (1971) led him to suggest that the lack of response in cv Massey, which has a low value of FN, is not due solely to time of flower initiation.

Short days and high temperature considerably increase FN (Paton, 1968) while under long days, FN is little affected by temperature.

#### 1.4.5 Vascular Flow

Pate (1975) diagrammatically presented the vasculature of *Pisum* from the description of the similar vascular layout of *Trifolium* (Devadas and Beck, 1972).

The leaf arrangement of the pea is distichous. Of the four vascular bundles, two alternately connect successive nodes so that there is a direct link from mid leaf traces of vertically adjacent leaves on each side of the stem. As well there are secondary links, often from all four vascular bundles, at each node. Within a bundle the central trace directly connects the petiole while two lateral traces each serve a stipule. Axillary shoots or reproductive structures are directly connected to the subtending leaf as well as indirectly to other leaves, (Pate, 1975).

#### 1.4.6 Photosynthesis and Yield

Both leaves and stipules have similar photosynthetic activity, (Flinn, 1969) while the activity of the stems, peduncles, petioles, tendrils and pods, all green organs, is also of varying importance. Maximum photosynthetic activity in the leaf is achieved at about the time of full expansion, losing activity thereafter at

a rate somewhat faster than the loss of chlorophyll, (Smillie, 1962).

#### 1.4.6.1 Vegetative Growth Period

The maximum rate of photosynthesis reached at full leaf expansion is reported to fall rapidly in leaves subtending vegetative nodes. Carr and Pate (1967) showed that the maximum export of photoassimilate from a given leaf coincided with the respective expansion of the next two leaves vertically above it on the stem. By the time of expansion of the fourth highest leaf the output of the older leaf had markedly declined. Until the plant has more than three leaves, downwards export of assimilate dominates vascular flow while in later growth export was mainly upwards with the most recently expanded leaf supplying the greatest amount (Carr and Pate, 1967). Pate (1966) demonstrated that the upper leaves supplied the apex directly with photosynthetically derived amino acids while the lower leaves contributed indirectly by supplying carbon initially to the roots and thence to the apex. Thrower (1967) considered that the older leaves were less dominated by the apex due to separation by distance leading to a reduced contribution of apically produced auxin which was suggested as being the mediating factor.

#### 1.4.6.2 Reproductive Growth Period

Flinn and Pate (1970) have shown that leaves subtending reproductive nodes may retain near maximum rates of photoassimilation for twenty or more days while those subtending vegetative nodes lose activity rapidly. Removal of the developing ovules is reported to reduce activity (Pate, 1975). After flowering, the supply of assimilate to growth is curtailed. The upper nodes bearing reproductive organs supply virtually no assimilate for growth, the output of their leaves and stipules being directed to the pod and seeds while the continued senescence of the lower leaves also limits supply for growth of the apex and the roots.

At fruit filling, as much as 90% of the assimilate produced by the subtending leaf may be directed to its fruit (Linck and Sudia, 1962). Similarly blossom leaflets, stipules and carpels are also heavily committed to seed growth, (Flinn and Pate, 1970; Harvey, 1971). During later stages in pod development, this organ is also believed to contribute significantly to the supply of assimilate to the seed, (Lovell and Lovell, 1970; Flinn and Pate, 1970) as well as recycling carbon respired by the developing seeds. Senescence of the lower leaves during pod filling also frees soluble material from them for pod growth through phloem transport.

#### 1.4.6.3 Temperature on Photosynthesis and Yield

Hellmuth (1971) showed a marked increase in photosynthetic rate at higher temperature. An increase in temperature from 18° to 27°C was shown to double CO<sub>2</sub> uptake rate at normal atmospheric concentrations.

Respiration also increases with temperature, dark respiration being shown to increase from 8 to 27  $\mu\text{g CO}_2\text{dm}^{-2}\text{min}^{-1}$  over the temperature range 18 to 40°C. Light respiration was also shown by Hellmuth (1971) to exceed dark respiration between 18 and 32°C.

Low night temperatures allow more effective conservation of carbon. Stanfield, Ormrod and Fletcher (1966) showed that optimal dry matter production up to the sixth node stage of growth was achieved with day/night temperatures between 21°/10°C and 23°/16°C but from flowering a lower range was optimum, 16°/10°C to 18°/13°C. Brouwer (1959) noted higher pod yields at 10° than at 17°C. High day temperatures of 30°C for three or more consecutive days are also known to reduce yield (Lambert and Linck, 1958) when the plants are beginning to fill the lower pods.

#### 1.4.6.4 Moisture

Salter (1962, 1963) has shown that yield is affected by timing of irrigation at and after flowering

but that under English conditions, irrigation did not affect yield when applied pre flowering. This is considered later (Section 1.5.4.3) with regard to yield and quality of green peas. High day temperatures and low moisture conditions are difficult to separate in their effect on plant growth (Pate, 1977).

#### 1.5 Yield - Components

Hardwick and Milbourn (1967) showed that the yield of green peas for processing is determined by the number of podding nodes, pods per podding node, peas per pod and individual pea fresh mass.

Once over, destructive harvest as required for commercial production requires that the highest yield be obtained at a specified level of maturity, acceptable for freezing, canning or dehydrating, etc. Sequential flowering of the crop is an important limiting factor to yield within acceptable maturity limits.

##### 1.5.1 Number of Podding Nodes

The typical pea plant flowers and sets pods sequentially with some three to four days separating the production of flowers at adjacent nodes. Harvesting usually takes place before the first set, and most mature, peas are unacceptable. Where both canning and freezing peas are produced, the harvested peas may be separated in the processing line thus extending the usable range of maturity.

Marx (1977) suggests that the incorporation of a gene for simultaneous flowering, where flowers at the first three or four reproductive nodes open together, may be practical.

Hardwick and Milbourn (1967) showed that at wider spacing more flower primordia are produced than at closer spacings but that similar numbers of flowers fail to emerge at both spacings. They consider that the loss of the upper reproductive nodes is unimportant in green peas due to immaturity at harvest of the later set pods. Increase in reproductive node number was thus concluded as being ineffective in increasing yield.

### 1.5.2 Pods per Podding Node

Cultivars with one to three or more pods per node are available in commerce although some nodes may fail to produce a pod. In the more common cultivars carrying one or two pods per node, two flower primordia per node are laid down in the leaf axil. Of these, one always develops to a flower while the second may not, producing a blind appendage (Hardwick and Milbourn, 1967), where the flower fails to be produced. Once formed, flowers and pods may later abscise.

Shading has been shown by Meadley and Milbourn (1971) to affect pod retention, low light after flowering reduced pod numbers. Ibarbia and Bienz (1970) showed that pod numbers in single and double podded cultivars were unaffected by day/night temperature regimes of  $15^{\circ}/7^{\circ}\text{C}$  or  $24^{\circ}/15^{\circ}\text{C}$ . Triple podded cultivars however, which produced normal peduncles at the lower treatment level, tended towards indeterminate peduncle growth and variable pod number at the higher regime ( $24^{\circ}/15^{\circ}\text{C}$ ). Waterstress has been shown to reduce pod numbers in multipodded lines (Snoad, Payne and Hobart, 1974), whole pods rather than individual peas being lost, (Marx, 1977).

Planting density has been shown to be positively correlated with pod numbers at the lowest nodes (Hardwick, Andrews, Hole and Salter, 1979). At very high densities however losses, which may be due to rotting in the senescent leaves at the base of the canopy, have been noted, (Hardwick and Milbourn, 1967).

Late planting and reduced pod numbers at higher nodes have been shown to be related (Hardwick et al., 1979). Milbourn and Hardwick (1968) had previously noted that lower yields at later plantings were associated with reduced mean pod numbers..

### 1.5.3 Number of Peas per Pod

Cooper (1938) showed that the pea which is self fertile, has completed pollination before the flower is fully open. The failure of ovules to develop is considered to be rarely due to pollination difficulty but rather to abortion after pollination. Pate and Flinn (1977) note

that in cultivars selected for high ovule number there is no evidence to suggest excessively high rates of ovule loss thus indicating adequate pollination.

Linck (1961) working with cv Alaska showed that embryo failure as high as 30 - 50% was possible in its sharply acuminate pods. Space limitation in the pod has been suggested as the cause of these losses in the ends of the pod. Pate and Flinn (1977) note that blunt podded cultivars are less susceptible to embryo failure than acuminate podded types. High frequencies of unfertilized ovules have been reported as being due to adverse environmental conditions (Pate and Flinn, 1977).

Fresh mass of peas is affected by maturity, cultivar and cultural factors. Due to the successional flowering of the pea, maturity and thus pea mass vary with nodal position, the lowest node bearing more mature peas than the higher, later flowering nodes.

Final dry pea mass at crop maturity for seed peas is affected by cultivar but little by crop spacing (Hardwick and Milbourn, 1967). Fresh pea mass however varies widely and at harvest maturity a sample of peas from a once over harvest will include peas with a range of fresh mass and maturity.

#### 1.5.4.1 Pod Development

Growth of the pod proceeds that of the seed. Initial pod growth is in increase in length and width and it reaches its maximum fresh mass before rapid storage begins in the seed. Initially the pod acts as the major sink for photoassimilate from the leaf and stipules but at a later stage in turn it becomes a donor to the developing seeds as well as recycling respired carbon from the seeds, (Flinn and Pate, 1970; Lovell and Lovell, 1970).

#### 1.5.4.2 Seed Development

The point of maximum fresh mass of the pod corresponds with a change in the seed from cell division to storage of assimilate. In some studies a lag phase is demonstrable between those two phases of growth and storage and this corresponds roughly with green pea harvest

maturity (Carr and Skene, 1961; Flinn and Pate, 1968).

The relationship between pod growth, seed development and maturity has been diagrammatically presented by Pate (1975). This incorporates results for both garden and field pea, both of which show similar growth patterns (Carr and Skene, 1961; Smith 1973) for pod and seed development. After the lag phase a period of accumulation of both starch and protein begins during which maturity increases rapidly.

Starch accumulation is both most rapid and earliest at higher temperatures. Robertson, Highkin, Smydzuk and Went (1962) demonstrated more rapid and earlier accumulation at 17°C compared to 10° and 14°C. Moisture content of the seed was higher at a day/night temperature regime of 14°/10°C than at 17°/10°C and the maximum value was achieved later at the lower temperatures.

#### 1.5.4.3 Irrigation Effects

Both total solids and alcohol insoluble solids (AIS) are related to pea quality (Kertesz, 1934, 1935) and are inversely related to moisture content.

Moisture supply preflowering was not shown to affect yield but irrigations at flowering and early pod swell were effective (Salter, 1962, 1963). Irrigation at flowering increased the number of marketable pods and the number of peas per pod while irrigation at pod swell improved pod retention and increased mean pea fresh mass. Under British conditions, Salter and Williams (1967) were unable to demonstrate that plant populations above six plants per square foot benefitted from irrigation. Stoker (1975) in New Zealand found that with irrigation higher populations could be used to enhance yield. In a greenhouse study, Miller, Manning and Teare (1977) showed that irrigation level was positively related to plant height including when water was only freely available during flowering and early pod filling. Salter (1962) also showed that early irrigation increased haulm growth but not pea yield.

## 1.6 Maturity Determination

Quality of processed peas is related to the maturity of the raw product (Kertesz, 1934, 1935; Makower, 1950). Both subjective and objective tests have been proposed to estimate maturity. Size and colour of the product was related to maturity as well as to cultivar and cultural factors (Makower, 1950). Organoleptic testing, while slow and expensive, is the accepted base for comparison with objective measurement. The acceptable methods for objective measurement are summarized by Makower (1950) as Specific Gravity Texture meter determinations and various solids content.

Of the mechanical methods the Tenderometer (or T value) is most acceptable to industry but is only suitable to raw product, (Makower, 1950). Specific Gravity is commonly used to separate lines as an alternative to seiving. In both cases the separation is followed by a Tenderometer determination. The most convenient method for small scale determination of quality is the determination of Alcohol Insoluble Solids. The advantage of the AIS determination over other solids estimates is discussed by Kertesz (1935) and by Torfason, Nonnecke and Strachan, (1956).

Adam (1958) and Walls and Kemp (1939) have published results relating percentage AIS to T values. Walls and Kemp obtained a curvilinear relationship where

$$Y = -6.15 + 0.24X - 0.00045X^2$$

with Y being the % AIS and X the tenderometer value of canned and raw peas respectively.

Using raw product for both estimates, Adam (1958) however showed that

$$Y = 7.43X + 19$$

$$\text{or } X = 0.122Y - 1.1$$

with X and Y being respectively % AIS and tenderometer reading.

Kertesz (1935), Lee (1941) and Adam (1958) have demonstrated a significant difference between AIS values

obtained from raw and canned product. Lee (1941) ascribed the small variation between the two values in his trials as due to possibly seasonal differences between his and Kertesz's material. Lee (1941) also noted that blanched frozen peas gave inconsistent values for AIS compared to raw or cooked samples suggesting that blanching only partly instituted changes in the pea which could be completed by canning, but not by simple cooking even at elevated temperatures.

#### 1.6.1 Yield at a Standard Maturity

Since the yield of peas increases rapidly with maturity it is necessary for both experimental purposes and for commercial pricing to be able to quote yields at a particular maturity.

To obtain an estimate of yield at a given maturity it is desirable to obtain yield and maturity date both before and after the required maturity is reached. Where the maturity differences are small it is possible to obtain an estimate of yield by direct linear interpolation. Berry (1966) however showed that a more accurate estimate could be obtained by substitution in the formula

$$W' = \frac{(T_2 - T_1)(T' - 70)W_2 + (T_1 - T_2)(T' - 70)W_1}{(T_2 - T_1)(T' - 70) + (T_1 - T_2)(T - 70)}$$

where  $T_1$  and  $T_2$  and  $W_1$  and  $W_2$  are the T value and yield at the first and second harvest respectively and  $T'$  and  $W'$  are the interpolated values of T and W. Extrapolation was regarded by Berry as being acceptable only where the difference between the observed and required values was small.

Pumphrey, Ramig and Allmaras (1975) showed that dry land and irrigated peas differed in their yield/maturity relationships and suggested formulae for estimation of yield in the form

$$\begin{aligned} \text{Dry land Peas } (Y-97.21) &= -14.134(X-100) + 315.14(X_{\frac{1}{2}}-10) \\ \text{Irrigated Peas } (Y-100.43) &= -8.405(X-100) + 200(X_{\frac{1}{2}}-10) \end{aligned}$$

where Y is the percentage yield and X is the observed tenderometer value.

This method is commercially used for yield correlation where only one sample from a field is available. Difficulty may be anticipated in use where rainfall is a variable factor and choice of equation is not clear cut. For standard maturity other than T=100 different relationships would be anticipated. Cultivar may also be expected to affect the relationship which was calculated using cv Dark Skinned Perfection.

Anderson and White (1974) also obtained curvilinear relationship between yield and maturity for cv Victory Freezer in New Zealand. Again, different relationships were obtained between irrigated and non irrigated treatments and were believed to be involved in the response of the yield/maturity relationship. As these equations quote results directly in terms of yield at maturity they of more limited application than the relationship of Pumphrey et al.(1975).

## 2. Leafless Peas

### 2.1.1 Breeding Control of Peas. General

Conventional breeding techniques are described by Donald (1968) as being unable to ever reach the potential maximum yield of crop plants. This, he asserts, is due to the approach normally adopted, where a specific single target is to be looked towards. Maximum yield, in particular, is regarded as being influenced by this approach as the initial screening of potential lines relies on the relative efficiency and competitiveness of single plants. The rationale of this approach is that yield per plant and yield per unit area are positively related and related also to competitive ability. Donald points out that this is not relevant to the crop situation where competitive ability is a positive hindrance to total yield in a closely spaced stand. Of particular concern is the tendency to select for yield through tillering ability and, indirectly, for spreading or semi horizontal leaves. The shading effect of these leaves tend to establish a heterogenous population of both dominant and suppressed individuals. Rice is instanced as a crop in which transplanting has selected a large lax plant adapted to wide hand spaced conditions. Although individually high yielding they are not suitable for close direct drilling spacing.

The possibility is thus raised of breeding to an ideotype in which weak competitive ability is positively selected. It would be expected then that the plant would be upright, single stemmed with more or less upright leaves of high photosynthetic potential and thus able to produce maximum yield under highly competitive pressures.

The success of dwarf rice and wheat has been cited by Snoad and Davies (1972) as an instance of ideotype planning.

### 2.1.2 Ideotype Selection in Peas

Ideotype planning in peas can be considered as a worthwhile project in view of the weaknesses obvious in the current cultivars in their role as crop plants. Of particular interest are the weak strawed spawling habit, indeterminate growth habit and successional flowering and the leafy haulm with its large horizontally exposed leaves and stipules (Snoad and Davies, 1972).

Useful advances in plant type could be achieved by incorporation of dwarf habit particularly with improved straw strength, improved standing ability, reduced leaf area and more vertically oriented surfaces together with determinate growth and simultaneous flowering of increased pod numbers per node.

Useful genes are known in the literature for many of these attributes. Simultaneous flowering has been described by Marx (1977) and Snoad and Davies (1972) as has increased pod numbers per node with up to six being available (Snoad and Davies, 1972). Pea numbers per pod are generally less than the number of ovules available with some current cultivars having a potential for eleven seeds (Snoad and Davies, 1972), usually unrealized in practice.

Standing ability and leaf area reduction together with leaf orientation may also be approached in a novel manner through the use of a number of gene pairs for leaf and stipule modification. These have been incorporated in a small number of dried pea cultivars and appear to be worth further consideration for green pea production, (Davies, 1977).

## 2.2 "Leafless" Peas by Genetic Control

### 2.2.1 Leaf Reduction

Leaves of commercial cultivars are controlled by the presence of the gene pairs. Up, Up: Af, Af: Tl, Tl. to produce the typical mix of pinnate leaves with or without tendrils. As described in section 1.4.2 the leaves on the lowest part of the stem are trifid scales usually followed by bipinnate leaves with no tendrils becoming multipinnate with enhanced tendril production on the

higher nodes.

### 2.2.1.1 Leaf Reduction

The gene pair Up or up controls the number of pinnae, Up Up leaves having the normal range of multi-pinnate leaves while the recessive up up reduces all leaves to a single pair of leaflets (Snoad and Davies, 1972; von Rosen, 1944).



Up Up:Af Af:Tl Tl

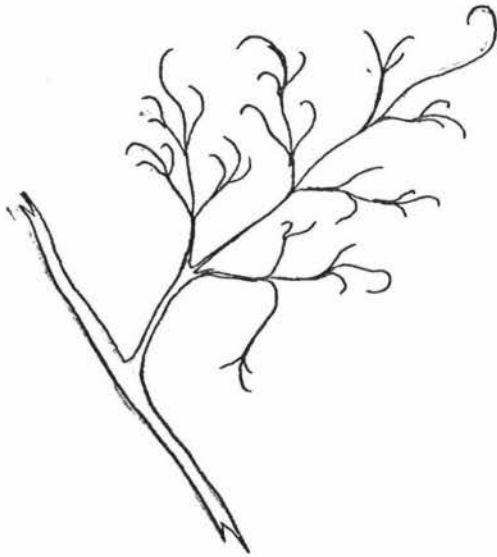


up up:Af Af:Tl Tl

This leaf reduction gene has attracted less attention than some others due possibly to the lack of advantage in leaf orientation, being still basically horizontal and of limited tendril production, (see Section 2.2.1.2).

2.2.1.2 Afila Reduction

The second leaf gene, which has received attention, is the 'afila' or leafless gene which in the recessive form *af af* reduces the leaf lamina to tendrils, (Marx, 1977; Snoad and Davies, 1972; etc.). Not only is the leaf area greatly reduced but by the alternation of the leaf to tendrils the standing ability of the plant is much enhanced. The most usual combination in which this occurs is that of *Up Up, af af, T1 T1* in which the greatest tendril development occurs.



Up Up:af af:T1 T1

2.2.1.3 'Acacia' Leaf

The incorporation of the 'tl tl' recessive gene pair together with the afile characteristics was suggested as a means of improving the photosynthetic area, much reduced by that gene. However the reduced standing ability due to the conversion of the tendrils to small leaflets has led to a complete lack of further interest. In the normal Up Up Af Af configuration, incorporation of the 'tl tl' recessive converts all tendrils to leaflets also (Harvey, 1972; Snoad and Davies, 1972; Marx, 1977).



Up Up:Af Af:tl tl



Up Up:af af:tl tl

#### 2.2.1.4 Leaf Reduction - Other

Other leaf reduction genes are known but are of either little interest or induce sterility such as the 'unifoliate' leaf character (Marx, 1977). The most interesting other methods of leaf 'modification' however are not involved with the true leaves, but with the stipules.

#### 2.2.2 Stipule Reduction

While leaf reduction proper tends to alter the balance of leaflet and tendril, the stipule reduction is affected by the production of vestigial organs. The normal leafy stipule is produced through the presence of the dominant St St pair which in the double recessive st st much reduces the area of the stipule and alters its orientation more towards the vertical as desired (Davies, 1977; Donald, 1968; Marx, 1977) for the preferred ideotype.



Normal Stipule St St

Reduced Stipule st st

The reduced stipule character may be associated with one or more of the recessive leaf reduction genes and in the most extreme form Up Up af af st st there is a reduction of leaflets to tendrils and of stipules to vestiges.

### 2.3.1 Use of Leaf Reduction Genes

Incorporation of the recessive *af af* is regarded (Snoad and Davies, 1972) to have considerable potential in pea breeding in enabling useful reduction of haulm together with enhanced standing ability. Better light penetration of the canopy and improved air circulation to assist in drying of the haulm and of the soil surface are mentioned by Snoad and Davies (1972) as potential advantages in wet seasons. This is of particular importance in the dry pea crop to assist in field drying before harvesting, with or without windrowing. In the green pea crop similar benefits may be anticipated.

### 2.3.2 Herbicide Cover and Weed Growth

The more open canopy of reduced leaf crops may be expected to improve coverage of both the soil and the haulm with spray material. This is of particular importance in weed control where post emergence herbicides may be affected by pea leaf shading. Conversely it has also been suggested (Snoad and Davies, 1972; Davies 1977) however, that due to better light penetration weed control may be poorer, but Davies (1977) suggests that limited trials do not support this. No problems of herbicide sensitivity have been reported and the reduced surface area suggests lessened risk of herbicide damage through capture, (Davies, 1977).

### 2.3.3 Insect Control

While as noted above the reduced surface area of reduced leaf types also reduces spray contact it nevertheless increases the ability of late applied insecticides to penetrate the canopy. Of particular interest for biological insect control is the reduced stipule character where the tortrix moth (*Cnephasia virgauriana*) is discouraged, by lack of terminal stipules, from establishing on the growing point. Snoad and Davies (1972) note the effectiveness of this biological control in reduced stipule compared to normal plants where no reduced plants were damaged of 710 grown compared to 16 out of 186 normal plants affected.

#### 2.4.1 Physiological Aspects

To be commercially acceptable leafless forms must be capable of producing similar yields to normal cultivars and if the ideotype arguments of Donald (1968) can be applied then yield should be enhanced under conditions of increased competitiveness.

Harvey (1972) has shown that tendril bearing plants have a lower proportion of photosynthetically active material than leafy plants. These plants were also less able to utilize low intensity light below  $100 \text{ J m}^{-2} \text{ sec}^{-1}$  suggesting that early in the season they would be at a disadvantage to normal plants but probably comparable later in the season.

At the early stage of breeding of leafless peas from the poor parent types, which provide the source of recessive genes, there was little evidence of yield reduction, (Snoad, 1974) as long as only one factor was included in the breeding line. Combinations with both *af* and *st* reduction genes appear to reduce yield (Snoad, Caston and Negus, 1977). Harvey (1978) considered that this reduction in yield was associated with a delay in attaining maximum pod wall mass. This delay could be expected to increase competition between the pod wall and the developing seed for assimilate. Incorporation of the gene *af* delayed maximal cell wall development while the gene *st* reduced the attainable maximum wall mass. In this context *af* in combination with *st* appears to cause a problem in assimilate competition not evidenced in *af* *St* plants where a greater supply of material may be available at the critical period.

#### 2.4.2 Photosynthetic Ability of Tendrils

As noted in the previous section 2.4.1, Harvey (1972) has shown that tendrils are photosynthetically competent and in a later study (Harvey, 1974) it was demonstrated that they were able to export assimilate in a manner comparable to normal leaves. The measurement of the photosynthetic ability of tendrils is

difficult, (Davies, 1977). due in part to the difficulty in measuring the surface area. Harvey (1972, 1978) established a useful working base for this estimation by assuming the photosynthetic area to be one half the area of a cylinder whose diameter and length product was known. The same assumption is made in this case, that only one half of the leaf surface is illuminated, as is made for flat leaves where the measured area is that of one surface of the leaf only. The measurement of the photosynthetic efficiency of leaves and tendrils has shown (Harvey, 1978) that leaves are more efficient in terms of leaf mass due to structural differences and reduced proportion of photosynthetic tissue in tendrils. It was however shown in the same study that per unit leaf area tendrils were more efficient than leaves in near isogenic lines. The lack of difference in earlier studies (Harvey, 1972) may be due to the variation between lines in those studies. Harvey (1972) also noted that differences occurred in the photosynthetic ability of normal cultivars with older types such as Chemin Long and Thomas Laxton being inferior to newer high yielding cultivars.

#### 2.4.3 Leaf Area Change

Working with near isogenic lines of conventional (AfAfStSt) and leafless (afafstst) cultivars in a greenhouse study, Harvey (1978) was able to follow changes in photosynthetic area near flowering. The conventional line reached a maximum plateau value for leaf and stipule area some ten days before anthesis. Anticipated further gains in leaf production by higher nodes was balanced by losses at lower nodes.

In the leafless phenotype however aggregate tendril area continued to increase at least up to anthesis with a total area of  $168 \text{ cm}^2$  and vestigial stipule area of  $40 \text{ cm}^2$ , less than half the total photosynthetic area of the conventional plant. Tendril area in the leafless plant continued to increase on a node basis with node 16 carrying the largest tendril area while the largest leaf area was carried on node 9 in the conventional plant.

### 3. Plant Spacing

The effect of spacing on crop growth has important practical effects. Spacing relationships between plants may be useful tests for predicting crop yields as well as assisting in interpretation of experimental results. Vegetable crop production is influenced by spacing through both total and marketable yields. Both density of plants per unit area and arrangement of those plants are components of spacing.

#### 3.1 Competition

Changes in plant density affect both yield per plant and per unit area. The changes are due to competition for light, moisture, soil nutrients as well as, on occasions, aerial CO<sub>2</sub> and soil oxygen. Donald (1963) stated that "competition begins when the immediate supply of a single necessary factor falls below the combined demands of the plants".

##### 3.1.1 Light

Competition for light can begin at an early stage of growth due to either inter or intra plant shading. In the more mature plant an estimate of shading may be obtained through the use of the leaf area index (LAI) where

$$LAI = LA/P$$

in which LA is leaf area per plant and P is the "soil area per plant" (Watson, 1947). Where both leaf and soil area are in the same units the ratio is dimensionless.

Watson (1956) suggested that there was an optimal leaf area index and that optimal yield depended on this value being reached most rapidly. Bleasdale (1966b) however claimed that no yield advantage could be expected provided that the initial plant density exceeded that where final yield was constant. Optimal LAI varies with crop and particularly with leaf orientation. Higher values of LAI may be obtained with more

vertically set leaves. Since Watson appeared to be working with crops having generally low values of LAI, his assertions may have been affected by other competition factors preventing full canopy expression rather than limiting light.

### 3.1.2 Moisture

The interaction of density and irrigation are of considerable interest for vegetable production. Salter (1961) showed that in cauliflower

1. Total yield increased with increasing density irrespective of irrigation
2. Irrigation increased total yield at higher densities
3. Marketable yield was much more influenced by irrigation at higher densities than was total yield.

### 3.1.3 Nutrients

Holliday (1960a) noted that there was usually a positive interaction between population and fertilizer or nutrient level. This may be subject to the affects of lodging (cereals and peas).

Nitrogen application has been shown by Lang, Pendleton and Dungan (1956) to increase yield of maize at all densities with the greatest increase at the higher density at which maximum yield was achieved.

### 3.1.4 Carbon Dioxide

Although there are numerous studies on CO<sub>2</sub> supply to plants (Gifford, Bremner and Jones, 1973; Hardman and Brun, 1971; etc.) there appears to be little published information on the effect of spacing on CO<sub>2</sub> depletion in the canopy. It has however been noted that in those crops with axillary influences the upper leaves are the most important contributors to yield. These may be least likely to be affected by restricted air, and thus CO<sub>2</sub> circulation under dense canopy conditions (Evans, 1975).

### 3.2 Effect on Maturity

Density may affect maturity by altering

a.) The time of maturity

or

b.) The spread of maturity

#### 3.2.1 Time to Maturity

This is the less important aspect of spacing on maturity although it can have important consequences in scheduling of harvests.

Nichols (1970) notes that cabbage mature earlier at wider spacings while onions mature later. This may be due to competition for limiting factors being reduced at the wider spacing allowing cabbage to reach a marketable size earlier, while the onion continues to grow longer and larger.

#### 3.2.2 Spread of Maturity

With increased emphasis on non selective harvests in processing crops and reduced harvest labour for all vegetables, variability of harvest maturity is of increasing importance.

Density may affect variability through its influence on tiller number (Sweet Corn, Peas), branching (Snap Beans) and sequential flowering on the main stem (Peas). Jones (1967) noted suppression of axillary branches and their later produced pods in high density planting of snap beans. Snoad, Hobart and Payne (1973) have also reported reduction of tillering in peas at higher density.

### 3.3 Relationship Between Yield and Density

A number of mathematical models have been presented by various authors to quantify the yield/density relationship. The ability of these equations to adequately describe results from various crops varies and more complex models may be required.

### 3.3.1 Holliday

Holliday (1960a,b) suggested that two forms of relationship exist between density and yield. He postulated a parabolic relationship for yield of a 'reproductive' nature and an asymptotic one for 'vegetative' yields.

The parabolic relationship may be written as a quadratic equation

$$Y = a + bX + cX^2 \quad 3.1$$

where Y is the yield per unit area, X is the population and a, b and c are regression coefficients.

The asymptotic relationship may be written as

$$Y = AX/(1 + AbX) \quad 3.2$$

where X and Y have the same values as before, A is the asymptotic or apparent maximum yield per plant and b the linear regression coefficient of the reciprocal of yield per plant and plant population.

### 3.3.2 Shinozaki and Kira

The reciprocal yield equation was expressed directly by Shinozaki and Kira (1956) as

$$W^{-1} = \alpha + \beta\rho \quad 3.3$$

where W is the yield per plant at density  $\rho$  and  $\alpha$  and  $\beta$  are constants. As  $\rho \rightarrow 0$ , then  $1/W \rightarrow B$ , i.e.  $1/\beta$  is a function of the single plant performance, while as  $\rho \rightarrow \infty$  then  $1/W \rightarrow \alpha$  and thus  $\alpha$  is a measure of yield potential of the environment.

### 3.3.2 Bleasdale and Nelder

The reciprocal yield density relationship of Shinozaki and Kira (1956) relates to the same 'total' or 'vegetative' yield of Holliday (1960a,b). This has been extended in the general case of Bleasdale and Nelder (1960) to include the 'reproductive' relationship for plant parts not of this type.

Bleasdale (1967) simplified the relationship

to read

$$w^{-\theta} = \alpha + \beta \rho \quad 3.4$$

which is the general case of the equation of Shinozaki and Kira ( $\theta = 1$ ). The equation also satisfies the parabolic relationship of Holliday (1960a, b) for reproductive growth.

The equation may be used to describe the growth of Red Beet (Bleasdale, 1966b) where  $\theta < 1$ , (parabolic relationship) as well as of carrots (Bleasdale, 1967) and beet tops (Bleasdale, 1966b) where  $\theta = 1$  (an asymptotic relationship).

In agronomic terms this implies that carrot root yield remains constant with increasing density and thus the individual root size falls while in red beets the root yield rises initially with increasing density and then falls together with root size.

#### 3.4 Allometry in Plant Spacing

Allometry in biology involves the study of the growth and development of one part of an organism in relationship to that of another. In general terms the allometric relationship between two plant variates X and Y can be expressed as

$$Y = b X^{\theta} \quad 3.5$$

where X represents some parameter of the size of the whole organism (or some distinct part of it) and Y represents the same for some differentially growing part of it with b, a constant and  $\theta$  the 'allometric constant'. Taking logarithms

$$\log_{10} Y = \log_{10} b + \theta \log_{10} X \quad 3.6$$

which provides a convenient practical method of evaluation. The plot of  $\log Y$  against  $\log X$  will show  $\theta$  as its slope which may be determined by linear regression of  $\log Y$  on  $\log X$ .

Because  $\theta$  can summarize the whole behaviour of X and Y across harvests it is of considerable practical value. Any value of  $\theta$  other than unity implies a change in the relationship of X and Y.

Bleasdale (1967) has shown that  $\theta$  derived from the allometric relationship between total plant mass per plant and yield per plant may be used to fit the reciprocal yield density equation

$$W^{-\theta} = \alpha + \beta \rho \quad 3.4$$

where  $W$  is plant part mass at density  $\rho$  and  $\alpha$  and  $\beta$  are regression constants. If  $\theta$  is equal to unity then there is an asymptotic relationship while  $\theta < 1$  implies a parabolic relationship.

### 3.5 The Competition Model

Implied in the above relationship is the effect of competition between plants. At early harvests there is likely to be little competition. Nichols (1970) has shown that fitting reciprocal yield density relationships over several harvests produces values of  $\alpha$  which will be less at early than at late harvests. That is, the value of  $\alpha$ , which is a measure of the potential of the site, varies in an unacceptable manner.

By assuming a value 'c' for the density at which competition begins and using a method of weighted least squares (Nelder, 1963) Nichols was able to minimize the residual sum of squares for the relationship over a range of values of c. He was thus able to demonstrate that with successive harvests from an early date, competition began at high density and increased with harvest through successively lower densities. The estimates of  $\alpha$  so obtained at the early harvests were also increased to more meaningful values.

### 3.6 Plant Arrangement - Rectangularity

Most horticultural crops have historically been produced in rows (Bleasdale, 1963) and weed technology has only recently reached a stage where alternative cropping systems may be considered as feasible. As a result much of the early work on spacing in both horticultural and agricultural crops has been carried out in rows where rectangularity has been built in to the system.

It has been shown that in many vegetable crops reduced row width has increased yields (Bleasdale, 1963, 1966a; Bleasdale and Thompson, 1966). Frappell (1968) suggested however that for red beet little advantage may be expected from closer rows ( $< 400$  mm).

Berry (1967) has shown that the general relationship of Bleasdale (1967) may be extended to include row width effects using the relationship

$$W^{-\theta} = a + b(1/{}_1X + 1/{}_2X) + C/({}_1X{}_2X) \quad 3.7$$

where  ${}_1X$  and  ${}_2X$  are the intra and inter row spacings respectively and  $a$ ,  $b$  and  $c$  are positive constants while  $0 < \theta \leq 1$ .

or

$$W^{-\theta} = a + b(1/{}_1X + 1/{}_2X) + C\rho \quad 3.8$$

$$\text{since } \rho = 1/{}_1X{}_2X$$

#### 4. Spacing Studies in Peas

Spacing studies in peas have frequently confounded both seeding (and plant) density and rectangularity. This is often the result of use of drilling equipment having fixed inter-row spacing such as grain drills or restricted inter-row variation, e.g. most precision seeders. In an attempt to separate the effect of row width from that of density, Eastin and Gritton (1969) compared three densities at each of three row spacings which was not entirely satisfactory.

Meadley and Milbourn (1970) considered population at a single rectangularity (unity) while other workers have more recently compared densities at a known range of rectangularities (Nichols and Monnecke, 1974). Due to the sprawling nature of the pea little interest appears to have been directed to the use of systematic spacing layouts for this crop.

##### 4.1 Row Spacing

Reynolds (1950) showed that decreasing row width (from 600 to 200mm) gave increasing yield of dry peas. Similar results were reported by Vincent (1958) for green peas by reducing row width from 400 to 100mm at constant density. Bleasdale (1963) showed similar results but indicated that the effect was greatest at higher densities, decreased row spacing having little effect at low density.

##### 4.2 Rectangularity

The increased yield afforded by decreased row spacing is associated also with reduced rectangularity of sowing. In attempting to compare densities at three row spacings, Reynolds (1950) obtained rectangularities varying from 24 to 2.67 while in a similarly motivated study with three densities and three row spacings, Gritton and Eastin (1968) used a range of 1.0 - 12.0

At similar densities Reynolds (1950) data shows that reducing rectangularity from 12 to 5 or from 16 to 4 was accompanied by increased yields of dry peas.

At high density Gritton and Eastin also showed that reduced rectangularity increased yield but that at lower density the effect was less marked.

In contrast, Nichols and Nonnecke (1974) comparing a range of densities at both 1.0 and 4.0 rectangularities were unable to obtain significant arrangement effects. Over the range used they ascribed this lack of response to the sprawling nature of the crop and the maintenance of a high level of both fertilizer and moisture.

#### 4.3 Density at Constant Rectangularity

Using a constant rectangularity (1.0) Meadley and Milbourn (1970) compared growth at three densities. Despite a fourfold difference in density (43 - 172 seeds  $m^{-2}$ ) they were unable to demonstrate significant yield differences at constant maturity.

Significant yield increases were however obtained by Nichols and Nonnecke (1974) with constant rectangularity at from 19 - 384 plants  $m^{-2}$ .

The differences between these two trials is probably associated with the shape of the response curve and to that part of the curve covered by the two sets of experiments. The response curve is considered further below. (See section 4.7).

#### 4.4 Density on Plant Growth

Density has been shown to affect basal branching (Snoad, Hobart and Payne, 1973) and axillary branching of peas. Lateral branch production during late growth effects the leafiness of the plant and may contribute to changes in leaf area index (LAI) during pod fill. Meadley and Milbourn (1970) showed that LAI was affected by density with the highest LAI being achieved soon after flowering at the highest density used. (172 plants  $m^{-2}$ ). At lower densities the peak value was both lower and later while maintaining near peak value longer during pod fill. At high density LAI reached a high early peak and then declined rapidly. Axillary branching may be expected to contribute to the maintenance of LAI at the lower densities.

Mean Net Assimilation Rate ( $\bar{E}$ ) was calculated by Meadley and Milbourn (1970) during growth at each of three densities. At medium and low densities, (97 and 43 seeds  $m^{-2}$ )  $\bar{E}$  remained relatively constant with higher values than at high density. The value of  $\bar{E}$  typically declined initially and was followed by a late increase during the period of maximum increase in pod dry matter.

Eastin and Gritton (1969) calculated leaf area ratio (F) for the three densities used (55 - 166 plants  $m^{-2}$ ) and showed that the highest density had the highest value of F. The peak value was reached at similar dates in each density and fell rapidly during flowering and pod fill.

Specific Leaf Area (SLA) was also calculated in this comparison with a peak value being obtained at full bloom corresponding to maximum LAI. The highest density in this experiment had both the highest SLA and the highest LAI.

Crop growth rate (C) increased with time at all densities used by Meadley and Milbourn (1970) reaching a peak a week before flowering at the highest densities. At the lowest density it continued to rise for a further two weeks and maintained a high level until vining harvest.

No values for the effects of density on relative growth rate (R) appear to be available for peas in the literature.

#### 4.5 Density on Pea Yield

The effect of density on maturity is recorded as being either non significant (Gritton and Eastin, 1968) or advancing maturity by one to three days (Salter and Williams, 1967). Similar density treatments were used by both groups but with different cultivars.

Nichols and Nonnecke (1974) showed that at high density the relationship of tenderometer value (T) to yield changed rapidly due to a more concentrated pod set. At lower density a greater range of pod maturity existed and over the range  $T = 90$  to  $T = 110$  yield

increased slowly. This effect is due to both increased pea mass with maturity and increased numbers of peas at higher nodes being included in harvestable yield with time.

Using a smaller range of densities Meadley and Milbourn (1970) were unable to demonstrate either significant differences in fresh or dry mass of peas. This was ascribed by them to the rapid fall in LAI at high density during pod filling. Salter and Williams (1967) obtained inconsistent effects of density on pea yield over three years of trials. The effect in this case was shown to be due to greater variability in yield per plant at the higher density. It was further suggested that date of sowing had an important influence on yield and at the higher densities this may have been different to that at lower densities.

Higher density was shown (Gritton and Eastin, 1968) to positively influence yield over the range 55 - 166 plants  $m^{-2}$  which was also correlated with higher LAI and LAR.

#### 4.6 Density and Components of Yield

The components of yield have been shown (Hardwick and Milbourn, 1967) to be related such that

$$\text{Yield} = \text{Number of Podding Nodes} \times \text{Pods Node}^{-1} \times \text{Peas Pod}^{-1} \times \text{Mass Pea}^{-1}$$

Density has been shown to affect yield through these components in different ways.

Meadley and Milbourn (1970) showed that the number of flowers plus pods reached a peak and then declined at all densities used. At the highest density this peak was earliest and highest but by harvest some four weeks later the number of flowers plus pods was similar at all densities. Much of the early difference was lost due to abscission of pods. At low densities the number of single and double pods per square metre was similar during the period but at the highest density the proportion of single pods rose sharply thus reducing the average number of pods per podding node.

Gritton and Eastin (1968) also showed that the number of pods per plant fell with increasing density. The number of flowering nodes was not affected.

Increased density has been shown to reduce the number of peas per pod (Gritton and Eastin, 1968; Meadley and Milbourn, 1970). At lower densities more pods filled at the upper nodes and these contained more peas (Meadley and Milbourn, 1970).

Mean pea fresh mass did not change over the range of planting densities studied by Meadley and Milbourn (1970). Gritton and Eastin (1968) determined that seed size index was not affected by spacing or population but suggested that it and mean pea mass were not consistently related.

#### 4.7

#### Yield Density Relationship

While it has been generally accepted that the yield density relationship in peas is parabolic (Holliday, 1960a; Stoker, 1975) there is evidence that this may not be correct. Nichols (1972) suggested that the parabolic relationship may be due to the use of constant row spacings which can convert an asymptotic relationship at square spacing to a parabolic one over a range of rectangularity.

Nichols and Nonnecke, (1974) obtained values for the constants  $K$  and  $\theta$  from the allometric relationship

$$\log W = \log K + \theta \log {}_1W \quad 3.6$$

where  $W$  is total plant dry mass and  ${}_1W$  the mass of a plant part, in this case pea and pod yields. The value of  $\theta$  so derived was shown to be different to unity for both plant parts and was used to fit the yield density relationship for pea and pod yield.

## 5. Growth Analysis

Early interest in growth of plants involved tabulation of changes in mass, length and volume and recording of flowering dates, number of branches, numbers of fruit, etc. To quantify changes however it is important not only to measure the magnitude of the change but its relation to existing plant material.

### 5.1 Relative Growth Rate

Blackman (1919) proposed an efficiency index of plant growth which may be written

$${}_2W = {}_1We^R({}_2T - {}_1T) \quad 5.1$$

where  ${}_1W$  and  ${}_2W$  are measures of plant material at times  ${}_1T$  and  ${}_2T$ ,  $e$  the base of natural logarithms and  $R$ , the efficiency index.

Fisher (1920) represented this equation in calculus notation as

$$R = \frac{1}{W} \cdot \frac{dW}{dT} \quad 5.2$$

and called  $R$  the efficiency index of Blackman, Relative Growth Rate or Specific Growth Rate.

#### 5.1.1 Derivation of Relative Growth Rate

The value of  $R$  expressed in equation 2 is not readily determined directly but a mean value may be readily calculated from equation (1). For convenience this equation may be written in this form

$$1-2\bar{R} = (\log_e {}_2W - \log_e {}_1W) / ({}_2T - {}_1T) \quad 5.3$$

where the measured values are expressed as their natural logarithms. Since the value of  $\bar{R}$  is the average change of  $\log_e W$  between  ${}_1T$  and  ${}_2T$  it is only the same as  $R$  (from equation 2) when growth is exponential (Hunt, 1978).

Although  $W$  is conventionally expressed as total dry mass, equivalent calculations may be performed for other plant components.

### 5.2 Net Assimilation Rate (NAR) or (E)

Gregory (1918) suggested that the use of 'net gain in weight per unit of leaf area' might provide more

information on efficiency of growth. Briggs, Kidd and West (1920a and b) termed it the unit leaf rate or net assimilation rate (E). Gregory (1926) expressed this as

$$E = 1/L_A \cdot dW/dT \quad 5.4$$

where  $L_A$  is the leaf area of the plant at time T.

Calculation of the mean value may be obtained from

$${}_{1-2}\bar{E} = ({}_2W-{}_1W)/({}_2T-{}_1T) \cdot (\log_{e2}L_A - \log_{e1}L_A)/({}_2L_A-{}_1L_A). \quad 5.5$$

where W and  $L_A$  are linearly related during time  ${}_2T-{}_1T$  (Hunt, 1978).

### 5.3 Leaf Area Ratio (LAR) or (F)

Briggs, Kidd and West (1920a and b) defined the index of leafiness of the plant as the ratio of total leaf area to whole plant dry mass or

$$F = L_A/W \quad 5.6$$

This may be obtained as a point value direct from field data or as a mean value  $\bar{F}$  from the equation

$${}_{1-2}\bar{F} = ({}_2L_A-{}_1L_A)/({}_2W-{}_1W) \cdot (\log_{e2}W - \log_{e1}W)/(\log_{e2}L_A - \log_{e1}L_A) \quad 5.7$$

By definition, since E and F are subdivisions of R,

$$R = E \times F \quad 5.8$$

or

$$W^{-1} \cdot (dW/dT) = L_A^{-1} \cdot (dW/dT) \quad L_A \cdot W^{-1} \quad 5.9$$

however since the mean values are rarely related

$$\bar{R} \neq \bar{E} \times \bar{F} \quad 5.10$$

### 5.4 Instantaneous Values of R - Curve Fitting

Goodall (1949) made early use of curve fitting by use of polynomials applied to growth of Cacao. In this case however he used the fitted curve to obtain revised estimates of  $\bar{R}$ . Subsequent workers have used smoothing curves to obtain instantaneous values of R which have useful theoretical advantages.

Vernon and Allison (1963) fitted a quadratic function to data obtained from post tasselling harvests in maize. This had the form

$$\hat{W} = a + bT + cT^2 \quad 5.11$$

where  $\hat{W}$  is the derived value of  $W$  at time  $T$  and  $a$ ,  $b$  and  $c$  are regression constants. From this equation may be calculated.

$$R = (b+2cT) (a+bT+cT^2)^{-1} \quad 5.12$$

after Radford (1967). This direct approach is limited in usefulness by the necessity for homoscedacity of data. Where originally used over a relatively short period the variance of the data did not change greatly. Even so, Vernon and Allison accepted the variability of the data and attempted to improve statistical validity by using pooled log variance over the period of growth. Over longer term growth, heteroscedacticity or increased variance of the data renders this method unsuitable.

Hughes and Freeman (1967) recognized the problem in using long term data and were able to reduce variance to an acceptable level by converting their data to natural logarithms. By using the natural logarithm of the dry mass per plant they were able to fit a cubic polynomial and more simply obtain the relative growth rate.

Hunt and Parsons (1974) using a similar method suggested that one of a range of polynomials could be used to obtain an acceptable fit for the  $\log_e$  data. The range of polynomials suggested by these groups cover the range from cubic to linear functions and may be written in a unified style as

$$\log_e \hat{W} = a + bT + cT^2 + dT^3 \quad \text{cubic} \quad 5.13$$

$$\log_e \hat{W} = a + bT + cT^2 \quad \text{quadratic} \quad 5.14$$

$$\log_e \hat{W} = a + bT \quad \text{linear} \quad 5.15$$

$R$  can be directly calculated from these functions using the correlation coefficients,  $b$ ,  $c$  or  $d$  at time  $T$  in

$$R = b + 2cT + 3dT^2 \quad 5.16 \text{ from } 5.13$$

$$R = b + 2cT \quad 5.17 \text{ from } 5.14$$

$$R = b \quad 5.18 \text{ from } 5.15$$

Richards (1959) suggested that a smoothing curve could be fitted to data using a generalisation of the logistic function.

$$W = A(1 \pm be^{-kT})^{-1/n} \quad 5.19$$

where  $W$  is plant dry mass at time  $T$ ,  $A$  is the asymptote and  $b$ ,  $k$  and  $n$  are constants.

Nelder (1961) has presented a method for fitting this curve by iteration of least squares by computer. To obtain starting values for the computation Nelder suggests a semi graphical method of calculation of  $A$  and  $n$  in the represented form of this equation

$$W = A(1 - e^{-(\lambda + kT)\theta})^{1/\theta} \quad 5.20$$

where  $\lambda$ ,  $k$  and  $\theta$  are the constants and  $\theta$  is positive.

Causton (1969) has also presented a simplified method for obtaining starting values by direct computer analysis.

Suitable choice of constants enables a range of curves to be fitted by use of this function and Hunt (1978) likens it to an adjustable spanner to be used on a range of nuts (the raw data).

Relative Growth Rate may be readily derived from 5.20 by restating

$$W = A(1 - e^{-(\lambda + kT)\theta})^{1/\theta}$$

as the differential equation

$$R = 1/W \cdot dW/dT = K [1 - (W/A)^\theta] \quad 5.21$$

Radford (1967) also used an exponential function to describe the growth of tall fescue,

$$\hat{W} = a + be^{\delta T} \quad 5.22$$

where  $\hat{W}$  is the derived dry mass at time  $T$ ,  $e$  is the base of natural logarithms and  $a$ ,  $b$  and  $\delta$  are constants.

By weighing each point according to the inverse of its variance he was able to obtain

$$R = b\delta e^{\delta T} (a + be^{\delta T})^{-1} \quad 5.23$$

### 5.5 Use of Fitted Curves

As well as obtaining fitted growth curves for total dry mass, similar functions may be used to describe changes in leaf area ( $L_A$ ), leaf dry mass ( $L_W$ ) and other growth data such as changes in leaf protein or leaf nitrogen etc.

By definition

$$R = E \times F \quad 5.8$$

$$\text{where } F = L_A/W \quad 5.6$$

$$\text{and } E = 1/L_A \cdot dW/dT \quad 5.4$$

Knowing instantaneous values for  $L_A$  and  $W$  any of these functions may be calculated as instantaneous values.

### 5.6 Net Assimilation Rate (E)

Instantaneous values of  $E$  may be calculated directly from growth formula regression coefficients or more conveniently by difference knowing  $R$  and  $F$ . Use of instantaneous values of  $E$  allows for conditions of non linearity between  $L_A$  and  $W$  which preclude calculation of mean values.

Variations in  $E$  may occur with time, changes in light intensity and duration, temperature (Blackman and Wilson, 1951) and between species (Heath and Gregory, 1938; Grime and Hunt, 1975). It is little affected by nutrient level over a wide range (Watson, 1952).

### 5.7 Leaf Area Ratio (F)

Instantaneous values of  $F$  may readily be calculated from both field data and smoothing curve values, (equation 5.6). In practice it is convenient to calculate  $R$  and  $F$  and to obtain  $E$  by difference.

Leaf area ratio varies with time and is inversely related to light intensity (Blackman and Wilson, 1951) and varies between species.

The components of  $F$  are of possibly more interest than is  $F$  itself, being respectively measures of leaf density (SLA) and leafiness of the plant (LMR). The relationship may be written

$$F = \text{SLA} \cdot \text{LMR} \quad 5.24$$

$$\text{where SLA} = L_A / L_W \quad 5.25$$

$$\text{and LMR} = L_W / W \quad 5.26$$

### 5.8 Specific Leaf Area (SLA)

Evans (1972) showed that SLA was affected by most aspects of environmental change. There is a strong inverse relationship between light intensity and SLA (Hughes and Evans, 1962). Ontogenetic drift in specific leaf area is also marked.

As shown by various authors (Jarvis and Jarvis, 1964; Hunt, 1978) there are considerable differences between species in leaf density and thus SLA.

### 5.9 Leaf Mass Ratio (LMR)

Evans (1972) notes that this is much less affected by environment and ontogenetic drift than SLA. Changes in LMR may be expected during the reproductive stage of growth and near maturity due to leaf senescence. Large differences in LMR have been obtained between species.

### 5.10 Leaf Area Index (LAI) or (L)

Watson (1947) suggested that a useful index of leafiness could include land area rather than plant dry mass as in LAR. This he defined as the Leaf Area Index where

$$L = L_A P^{-1} \quad 5.27$$

where  $P$  is the unit of land per plant. Where both  $L_A$  and  $P$  are in terms of the same unit,  $L$  is dimensionless. Watson suggested that an optimum value of  $L$  is that which supports the maximum rate of dry matter increase when the lowest and least illuminated leaves are just able on average to maintain a positive carbon balance.

Leaf area index is affected by plant density and by leaf orientation. In those plants with more vertical leaves, higher levels of LAI may be obtained than in those with more lax or spreading leaves.

Optimum LAI for dry matter production is strongly positively affected by the level of radiation (Black, 1963).

#### 5.11 Crop Growth Rate (CGR) or (C)

The product of E (Net Assimilation Rate) and L (Leaf Area Index) may be written as

$$C = E \times L \quad 5.28$$

or

$$C = L_A^{-1}(dW/dT) \quad (L_A P^{-1}) = P^{-1}(dW/dT) \quad 5.29$$

In general terms C can be stated as the product of the efficiency of leaves and leafiness in much the same way as can the relative growth rate R. The change in C with time then depends upon the relative changes in E. and L. Defoliation studies with Kale (Watson, 1956) showed increases in C and E with moderate loss of leaf. With sugar beet C was reduced at all levels of defoliation despite increase in E.

#### 5.12 Problems with Curve Fitting

The fitting of smoothing curves to field data has been considered by Nicholls and Calder (1973) and by Hurd(1977).

Nicholls and Calder noted that the use of more complex regressions to obtain growth curves increased the standard error (SE) of the derived function and may also lead to spurious values of those functions. To obtain the simplest function which would adequately fit observed data, Hunt and Parsons (1974) presented a range of polynomials. Hurd (1977) noted that choice of the simplest curve applied over a large range of data led to production of a confusing range of functions. He therefore suggested that within such a body of data, a unified approach to curve fitting was desirable.

Both over fitting and over simplification of functions should be considered in analysing data.

THE EFFECT OF DENSITY ON THE GROWTH OF VINING PEAS6. INTRODUCTION

The objects of this study was to examine the effects of plant density on the growth and development of three near isogenic lines of peas with differing leaf and stipule growth.

Two experiments were planned, the first to examine the effects of density on the conventional pea cultivar and to determine what methods of growth analysis were appropriate to follow growth and development changes. A second experiment using the three near isogenic lines was then to extend the results and methods.

7. EXPERIMENT No. 17.1 The Effect of Density on the Growth of Vining PeasMaterials and Methods

The experimental site was on Manawatu silt loam in the Department of Horticulture and Plant Health's vegetable trial area at Massey University. Vigorous growth of grasses and weeds were killed by application of Glyphosate herbicide ( $9 \text{ l ha}^{-1}$ ) in late September, 1978. This was followed fourteen days later by mould-board ploughing on the 13th October.

After ploughing, the trial area was marked out into beds and subsequent cultivation by rotary hoe was confined to these areas to reduce in-plot compaction by wheel traffic. Fertilizer was broadcast on the 20th October at  $17 \text{ kg ha}^{-1}\text{N}$ ,  $45 \text{ kg ha}^{-1}\text{P}$  and  $60 \text{ kg ha}^{-1}\text{K}$  and rotary hoed in. A preplanting herbicide, trifluralin ( $1.5 \text{ l ha}^{-1}$ ), was applied on the 23rd October by boom spray and incorporated to 100mm depth by rotary hoe.

Seed of the cv Victory Freezer (VF) was sown by hand on the 25th October at four densities in a randomised block layout. Densities used were (A) 400, (B) 200, (C) 100, (D) 25 plants per square metre, with rectangularity of unity (square spacing). Each sample plot of nine seeds was surrounded by approximately 300mm of guard plants at the same density and rectangularity. Twelve harvest dates were allowed of each treatment. To obtain random harvest pairs this required 22 plots of each treatment in a block of 88 plots.

The block was duplicated giving two replications and a total of 176 plots.

Irrigation was applied as required during growth with particular attention paid to early flowering and early pod swell as suggested by Salter (1962, 1963).

Soon after emergence pea plants raised in individual compartment trays in a greenhouse were transplanted to fill vacant spaces in the plots. Each transplant was delineated by a permanent visible marker if in the harvest area of the plot. To aid in selection of

plants for harvest, the central plant of each plot was also marked with a bamboo stake, 60cm long.

At each harvest, the marked plant and the surrounding plants (of the nine plot plants), were dug by fork, the marked transplants and any unguarded plot plants being discarded. The roots were then carefully washed free of soil and the plants placed in plastic bags and transferred to a cool store. All recording of fresh material was done on the harvest day.

At each harvest the following data were obtained from each plot:

- A. Before podding
  - (i) Number of plants
  - (ii) Fresh mass of whole plants
  - (iii) Dry mass of roots, leaves and stipules, and stem
  - (iv) Area of leaves and stipules by digital photoelectric meter(leaf area).
  - (v) Number of flowers per node
- B. After Podding
  - (i) - (v) as above
  - (vi) Number of pods per node
  - (vii) Number of peas per node
  - (viii) Fresh mass of peas per node
  - (ix) AIS of sample of peas per node
  - (x) Dry mass of pods and peas per node.

## 7.2 Results

At each harvest date, average per plant results were calculated for

- (a) plant total dry mass (W)
- (b) leaf area (L<sub>A</sub>)
- and
- (c) leaf dry mass (L<sub>W</sub>)

Apart from the first (H<sub>1</sub>) and last (H<sub>12</sub>) harvests, two independent estimates of these three parameters were available for each density and replicate. At H<sub>12</sub> no leaf data was recorded due to defoliation.

### 7.2.1 Total Dry Mass (W)

The average values of the natural logarithms of total plant dry mass at each harvest were plotted for each density against time (Figure 1). These tended to follow a logistic pattern. An analysis of variance at each harvest showed no significant differences between densities at the early harvests but from harvest six ( $H_6$ ) onwards significant differences ( $P < 5\%$ ) were present.

### 7.2.2 Leaf Area ( $L_A$ )

A graph of the natural logarithms of leaf area for each density against time indicated that the growth patterns followed a parabolic form, reaching a peak then falling rapidly to low levels as the plants reached maturity (Figure 2). Analysis of variance at each harvest showed no significant differences between treatments from  $H_1$  to  $H_5$ . Significant ( $P < 5\%$ ) differences were shown from  $H_6$  onwards with the lowest density having the largest leaf area.

### 7.2.3 Leaf Dry Mass ( $L_W$ )

The graph of the natural logarithms of leaf dry mass against time produced similar curves for the four treatments to those obtained from  $\log_e L_A$ . (Figure 3).

### 7.2.4 Relative Growth Rate (R)

Mean relative growth rates were determined for each time period and density, by substitution in the formula

$${}_{1-2}\bar{R} = (\log_{e2} W - \log_{e1} W) / ({}_2T - {}_1T) \quad 5.3$$

where  ${}_{1-2}\bar{R}$  is the mean relative growth rate of plant dry mass  $W$  between time  ${}_1T$  and  ${}_2T$ .

The values obtained are shown in Table 1. There is a considerable variation in those values of  $\bar{R}$  although it is possible to detect an overall fall with time. The scatter shown by the mean values suggests

that a smoothing curve should be fitted to the field data for  $\log_e W$  and that instantaneous values of  $\bar{R}$  be calculated.

### 7.3 Choice of Smoothing Curve

Although the graph of  $\log_e W$  against time is logistic in shape, the  $\log_e L_A$  and  $\log_e L_W$  curves are parabolic. The fitting of polynomial functions to both total plant and leaf parameters is comparatively robust and can be expected to cope with harvest variability shown in this experiment.

#### 7.3.1 Polynomial Curve Fitting

When fitting of a polynomial to the data for  $\log_e W$ , the method of Hughes and Freeman (1967) produces a cubic function while Hunt and Parsons (1974) include also quadratic and linear functions for consideration. To choose an appropriate curve the data was submitted to an analysis of variance over harvest using the Teddy Bear programme of S.B. Wilson (1979) which showed that > 98% of harvest variance was accounted for by linear (92%) and quadratic (6%) regression.

Using the method of Little and Hills (1975) the regression constants for the equation

$$\hat{Y} = a + bT + cT^2 \quad 5.14$$

where  $\hat{Y}$  is the derived value of  $\log_e W$  at time  $T$  and  $a$ ,  $b$  and  $c$  are the regression constants, were calculated and graphed (Figure 1).

From these constants Relative Growth Rate,  $R$  may be calculated as

$$R = b + 2cT \quad 5.17$$

Analysis of variance of the derived values showed that there were initial significant differences in  $R$  between treatments ( $P < 1\%$ ), which did not relate to the mean data ( $\bar{R}$ ). As well the initial values obtained for  $R$  were higher (0.1 to 0.14  $\text{day}^{-1}$ ) than for  $\bar{R}$  (0.08  $\text{day}^{-1}$ ).

The straight lines for  $R$  produced by the use of this method (figure 7) are unsatisfactory in following whole of growth changes. If both early and late

relative growth rate are expected to be similar then there can be no differences during growth.

### 7.3.2 Fitting the Logistic Curve

It was considered desirable to fit a logistic function of the form suggested by Richards (1959) to the field data so that

$$W = A (1 - e^{-(\lambda + kT)^\theta})^{1/\theta} \quad 5.20$$

where  $W$  is plant dry mass (or desired parameter)  $A$  is the asymptote,  $e$  the base of natural logarithms,  $\lambda$ ,  $K$  and  $\theta$  constants and  $T$  chronological time. This relationship is derived from the differential equation

$$dW/dT = KW [1 - (W/A)^\theta] \quad 7.1$$

of which the logistic curve is a particular case. The fitting of the curve was demonstrated by Nelder (1961) and a computer programme described by Berry (1964) was used in the calculation of the constants. It will be seen that the constant  $\theta$ , as written above is the inverse of that used by Nelder (1961) but is in accord with Berry (1964).

Considerable difficulty was experienced in fitting the data using this method. Since the constants produced on the successful runs suggested that  $\theta$  of the recalcitrant plots was approaching unity, this value  $\theta = 1$  was set as a first approximation and a set of constants produced.

These were substituted in the derived formula from equation 7.1

$$R = W^{-1} dW/dT = K [1 - (W/A)^\theta] \quad 5.21$$

using the value of  $W$  derived from solving equation 5.20. Analysis of variance by harvest of the data obtained showed a significant ( $P < 1\%$ ) difference at the initial harvests ( $H_1$  to  $H_8$ ). While the differences during mid growth were desirable the early differences were unexpected and again not in line with the mean values or with observed changes in  $\log_e W$ .

In a further attempt to reduce the significant difference in  $R$  at  $H_1$ , a mean value for  $K$  was

determined by fitting the logistic function to harvest mean values of  $W$  and obtaining mean constants. The fitting of the derived values of  $W$  by this method are shown graphically in figure 2. Since  $K$  is related closely to the initial relative growth rate (Nichols, 1971) use of a constant value for this constant in fitting the logistic function could be expected to reduce the variance in  $R$  at the early harvests.

The new values of  $R$  obtained by this technique were again subjected to analysis of variance by harvest and while the variance at  $H_1$  was reduced it was still significant ( $P < 5\%$ ). The new values did however show significantly higher relative growth rates for the lower densities ( $P < 5\%$ ) during the mid period of growth which was a marked improvement on the fitting of the linear functions of  $R$  (figures 7 and 8).

#### 7.4 Leaf Area and Leaf Mass in Growth Analysis

The natural logarithms of leaf area ( $\log_e L_A$ ) and of leaf dry mass ( $\log_e L_W$ ) were plotted against time and as noted (section 7.2) were both of similar parabolic outline.

Analysis of variance by harvest had showed that significant differences in the logarithmic values existed between treatments from the fourth ( $\log_e L_W$ ) or sixth ( $\log_e L_A$ ) harvest.

#### 7.5 Net Assimilation Rate (E)

Mean net assimilation rate was calculated using the equation

$${}_{1-2}\bar{E} = ({}_2W - {}_1W) / ({}_2T - {}_1T) \cdot (\log_e {}_2L_A - \log_e {}_1L_A) / ({}_2L_A - {}_1L_A) \quad 5.5$$

where  ${}_1W$  and  ${}_2W$  are plant dry mass and  ${}_1L_A$  and  ${}_2L_A$  are leaf area at time  ${}_1T$  and  ${}_2T$  respectively and  ${}_{1-2}\bar{E}$  is the mean net assimilation ratio over that harvest interval.

There was considerable between harvest variation in the mean values obtained but it was possible to note a tendency for  $\bar{E}$  to fall and then rise with time (table 2).

### 7.6.1 Polynomial Curve Fitting of $L_A$

Using the same method as used for fitting a polynomial function to plant dry mass, it was first determined that a quadratic accounted for > 98% of the variability due to harvest.

Calculated values for the regression coefficients  $a^1$ ,  $b^1$  and  $c^1$  of the equation

$$\hat{Y} = a^1 + b^1 T + c^1 T^2$$

where  $\hat{Y}$  is the derived value of  $\log_e L_A$  at time  $T$  were then determined as before and new values of  $\log_e L_A$  obtained (figure 3).

Instantaneous values for  $E$  for each treatment were obtained by first determining  $F$  (Leaf Area Ratio) from the equation

$$F = \text{antilog}_e (\log_e L_A - \log_e W) \quad 5.6$$

and knowing  $R$  from the previous determination, substituting in the equation

$$E = R/F \quad 5.8$$

The derived values of  $E$  were graphed against time and clearly showed a 'U' response (figure 9).

The instability in  $E$  noted after  $H_9$  was similar to that of the mean determination ( $\bar{E}$ ) and is common in peas, corresponding to post flowering leaf loss together with rapidly increasing peas and pod mass.

### 7.6.2 Logistic Curve Fitting

Although the initial curve fitting for  $\log_e W$  was by the use of polynomial regression for reasons of its robustness it was also noted that the curve for  $\log_e L_A$  was parabolic in shape. This suggested that use could be made of a family of similar regressions. As noted above however, once leaf area began to fall, the value of  $E$  became unstable. Accordingly it was decided to delete the leaf data of  $H_9$  to  $H_{11}$  and to fit a logistic regression to  $L_A$  in the same manner as for  $W$  (section 7.3.2) and to examine the value of  $E$  obtained.

Fitting the logistic function was again difficult and despite as a first approximation setting

$\theta$  to equal 1, to facilitate fitting, results were unsatisfactory. Mean values of the regression constants were obtained and it was noted that  $\theta$  obtained by this fitting was lower than previously used. ( $\theta = 0.85$ ). Using the same approach as for that used in fitting the plant mass data, the common value of K was used in new determinations. The new fitting was satisfactory and using the derived values of  $L_A$ , F and then E were calculated as above (equation 5.6 and 5.8).

The values of E were then graphed against time (figure 10) and again showed an 'U' shaped response curve.

### 7.7 Leaf Area Ratio

Mean values for leaf area ratio ( $\bar{F}$ ) were calculated by substitution in the equation

$$1-2\bar{F} = (2^{L_A} - 1) / (2^W - 1) \cdot (\log_{e2} W - \log_{e1} W) / (\log_{e2} L_A - \log_{e1} L_A) \quad 5.7$$

using the same values of W and  $L_A$  as for determination of E. The values were tabulated (Table 3) and showed much less variation than did the values of  $\bar{R}$  or  $\bar{E}$ . Analysis of variance by harvest showed that there were significant differences (< 5%) during early growth ( $H_2 - H_7$ ).

#### 7.7.1 Curve Fitting - Instantaneous Values of F

The fitting of a quadratic regression to  $\log_e L_A$  and derivation of instantaneous values of F has already been detailed (section 7.6.2). New values of F were also obtained as an intermediate stage in determination of E from the fitting of the logistic function to  $L_A$ . The values obtained were plotted against time (figures 11 and 12).

### 7.8 Components of Leaf Area Ratio

The changes in F may be considered both through direct inspection or by consideration of its components derived from the relationship

$$F = SLA/LMR$$

where SLA is the specific leaf area ( $L_A/L_W$ ) and LMR is the leaf mass ratio ( $L_W$  being the leaf dry mass).

Mean values of  $L_W$  may be used to derive mean SLA and mean LMR using the equations

$${}_{1-2}SLA = ({}_2L_A - {}_1L_A) / ({}_2L_W - {}_1L_W) \cdot (\log_{e2}L_W - \log_{e1}L_W) / (\log_{e2}L_A - \log_{e1}L_A) \quad 7.2$$

and

$${}_{1-2}LMR = ({}_2L_W - {}_1L_W) / ({}_2W - {}_1W) \cdot (\log_{e2}W - \log_{e1}W) / (\log_{e2}L_W - \log_{e1}L_W) \quad 7.3$$

Analysis of variance by harvest showed significant differences between treatments ( $P < 5\%$ ) in value of SLA after  $H_{1-2}$  (table 4). The mean values for LMR were also analysed by harvest but showed no significant treatment differences (table 6).

## 7.9 Curve Fitting to Leaf Mass

### 7.9.1 (a) Polynomial

Using analogous methods to those applied to curve fitting to leaf area it was shown that 98% of harvest variability could be accounted for by quadratic regression which was then fitted to  $\log_e L_W$ . The values obtained were then graphed against time. (figure 5).

This derived value was then used to calculate instantaneous values of SLA and LMR using the relationships

$$SLA = L_A / L_W \quad 5.25$$

$$LMR = L_W / W \quad 5.26$$

Analysis of variance by harvest of both parameters showed similar results to that obtained from the mean values.

### 7.9.2 (b) Logistic

Using the same methods as were used to fit the logistic function to leaf area, new constants and derived values of leaf mass were obtained from  $H_1$  to  $H_9$ , (figure 6). New values for SLA and LMR were calcu-

lated using the data obtained by the same methods for  $W$ ,  $L_A$  and  $L_W$  and were tabulated against time (Tables 5 and 6).

#### 7.10 Leaf Area Index (LAI) or (L)

Using the relationship

$$L = L_A/P \quad 5.27$$

where  $L_A$  is the leaf area and  $P$  is the unit ground area per plant, the leaf area index was calculated for each treatment at each harvest. Analysis of variance at each harvest showed significant treatment effects ( $P < 1\%$ ), at each of the first seven harvests. Peak values were obtained at the three highest densities at  $H_7$  while the highest value for the lowest density was obtained at  $H_9$  ( $P < 5\%$ ).

#### 7.11 Green Pea Yields

##### 7.11.1 Alcohol Insoluble Solids ( % AIS)

The accepted standard method of determining the % AIS of peas involves the use of large (200g) samples of canned material. As there were neither sufficiently large samples nor canning facilities it was necessary to determine the % AIS on small (20g) samples of fresh frozen peas.

The method used for determination was after Kertesz (1935) but modified for sample size and for fresh peas. Both Kertesz (1935) and Lee (1941) noted that the % AIS of fresh peas is higher at a given maturity than the % AIS for canned peas. The difference is not great but varies between seasons (Lee, 1941) so that is not possible to apply a correction. Both workers found however a good correlation between the % AIS of fresh and canned product in any particular season.

Lee (1941) also comments on the variability of % AIS when using frozen peas, but this is related to the blanching given his samples. The material used in the

current determination was not blanched before freezing. The peas were stored in moisture resistant packs while frozen and did not lose significant mass.

### 7.11.2 Pea Yields

Samples of peas were obtained from all treatments on three occasions, H<sub>10</sub> to H<sub>12</sub>. At each harvest % AIS was calculated for samples of peas from each reproductive node.

To obtain mean fresh pea mass at optimum maturity ( % AIS = 12) it was necessary to obtain the regression of mean pea mass on % AIS by node over more than one harvest (figure 17). Using data from a single harvest necessitated some extrapolation which could be avoided by using data from other harvests. Berry (1966) has shown that interpolation by linear regression can give adequate estimate of yield at standard maturity.

Calculation of regressions using data from only H<sub>10</sub> to H<sub>11</sub> gave the best correlation. When the regression was extended to include data from H<sub>12</sub> the correlation was much poorer.

The mean mass of green peas at standard % AIS is shown in table 8. . Using the relationship

Yield = Mean Pea Mass X No. of Peas per Plant  
yield per plant was calculated. From this the yield per square meter for each density was also determined.

### 7.11.3 Yield Density Relationship

The calculated yields were used to fit the reciprocal yield density equation (Bleasdale, 1967).

$$W^{-\theta} = A + Bp$$

where W is green pea yield at density p and A, B and  $\theta$  are constants. Where p is the only variable,  $\theta$  is the measure of the effect of changes in plant density on relative distribution of plant parts and may be calculated from the allometric relationship.

$$\log_{10} W = \log_{10} K - \theta \log_{10} W^1 \quad 3.6$$

with W total plant dry mass, W<sup>1</sup> the plant part mass and K and  $\theta$  constants.

Using  $W^1$  to equal green pea fresh mass from the calculation of yield above, the relationship was fitted for each harvest,  $H_{10} - H_{12}$ . The value of  $\theta$  so obtained varied from 0.98 to 1.05 and to fit the reciprocal yield density equation was taken as  $\theta = 1$ .

Fitting the relationship showed that in density A (400 plants  $m^{-2}$ ) one replication had an exceptionally high yield. This was because the number of peas at  $H_{11}$  was greatly in excess of that at  $H_{10}$  and  $H_{12}$ . This plot was deleted and the number of peas in the equivalent plot at  $H_{12}$  was substituted in further calculations.

Number of peas per pod and per plant, number of pods per plant and pea seed fresh mass were tabulated and an analysis of variance performed for each. From these results the yield per plant and per square metre were calculated for each treatment.

From the reciprocal yield density relationship taking  $\theta$  as being equal to one,

$$W^{-1} + A + Bp$$

where  $W$  is the yield per plant at AIS = 12% at density  $p$ , estimates of yield at each density were obtained and tabulated. Analysis of variance showed significant differences between density treatments for both yield per plant and per square metre.

## DISCUSSION

### RELATIVE GROWTH RATE

Three methods were used to measure the relative growth rate at the four density treatments in this first experiment. The fitting of the mean relative growth rate  $\bar{R}$  was unsatisfactory due to variation between harvest dates over the twelve weeks of harvest. Mean values could possibly have been of use over shorter periods in growth in a manner similar to that of Hunt and Parsons (1977) where growth over a long period was segmented for analysis. Also unsatisfactory was the derivation of linear functions to describe  $R$  from quadratic regression of  $W$  against time. To enable similar values of  $R$  to be obtained at early and late harvests while separating effects at mid growth it is obviously unsatisfactory to use linear functions.

The third method of deriving  $R$  was not wholly satisfactory in that differences were indicated at early harvests which were not shown in the original data. Even so, this method did allow for separation of treatment effects during mid growth.

Although not justified by analysis of variance, the inclusion of a cubic term in the regression of  $W$  against time would have allowed for  $R$  to be described by a quadratic function which may have allowed more meaningful results to have been obtained. Alternatively a segmentation method as discussed by Hunt and Parsons (1977) may have been useful in separating the effects of the four densities.

Examination of the graphs of  $R$  against time from the logistic function (figure 8) indicate that  $R$  was initially similar in all treatments, except for treatment A (400 plants  $m^{-2}$ ), and later differences became apparent progressively in the order of decreasing density. That is to say that treatment B (200 plants  $m^{-2}$ ) began to fall soon after emergence followed by treatment C (100 plants  $m^{-2}$ ) but that treatment D (25 plants  $m^{-2}$ ) continued to grow at a near constant rate until around the sixth harvest.

Differences in plant dry mass were due to changes in the time of reduction in R from its initial rate as well as to the rate of fall. Both density A (400 plants  $m^{-2}$ ) and density B (200 plants  $m^{-2}$ ) fell from their initial rate of R soon after emergence but both then continued to fall slowly to their minimal value. In contrast density C (100 plants  $m^{-2}$ ) and density D (25 plants  $m^{-2}$ ) fell later but then more rapidly from their initial value of R.

#### NET ASSIMILATION RATE E

Three methods of determining E for the four density treatments were again compared in a similar manner to that used for determination of changes in R with time.

The least satisfactory method of following changes in E was by determination of mean values. The variability of the field data was reflected in the mean value of E and little could be gained from them although there were significant differences between treatments ( $P < 5\%$ ). The overall mean values for harvests suggested that E fell from its initial value, remained more or less constant for most of growth, then rose sharply during pod fill.

Both methods of obtaining instantaneous values of E confirmed an initial fall in E for each treatment followed by a late rise as the plants flowered and set. The quadratic regression method indicated that E for treatment C (100 plants  $m^{-2}$ ) became unstable at the last harvest, falling dramatically while the remaining treatments continued to rise in values. Use of the logistic function to derive E suggested that E fell in all treatments as the pods began to swell. Both methods also suggested that initial values of E were greater than final values. This was in contrast to the mean values ( $\bar{E}$ ) where final values tended to be greater than initial figures.

When changes in Net Assimilation Rate were compared with changes in Leaf Area Index (LAI) it could

be seen that the logistic method indicated a rise in  $E$  while LAI rose from  $H_4$  to  $H_7$  or  $H_8$  and that the subsequent fall in  $E$  paralleled the fall in LAI. In contrast the quadratic regression suggested that  $E$  continued to rise while LAI fell.

High initial values of  $E$  are related to the low photosynthetic area measured in newly emerged peas. The expanded leaf area is small and those leaves may be expected to be at their maximum photosynthetic ability. As well there is a significant photosynthetic area in stems and petioles which is not measured in conventional growth analysis but which may be expected particularly at early harvests, to contribute significantly to assimilation.

With time there are several changes which may be expected to alter the measured Net Assimilation Rate. As the number of leaves increases there is a small proportion of the total which are at peak photoassimilation capacity and with increasing individual leaf area at higher nodes, the proportion of non measured photosynthetic area falls. These changes may be expected to allow a fall in net assimilation rate to a more or less steady rate during the non reproductive phase of growth.

After flowering it is known that leaves subtending reproductive nodes continue to produce assimilate at a near optimum level for up to twenty days in contrast to the early formed leaves at the non reproductive nodes. There are therefore two effects during this period. The earlier formed leaves (non reproductive) initially fall in photoassimilatory rate while maintaining a high value for leaf area while the newer formed leaves maintain a high level of activity (peak LAI). There is thus an increasing loss of photosynthetic area as the lower leaves senesce, shown by the fall in LAI, while the remaining leaves continue to produce assimilate at a constant rate. The third stage occurs as the area of non measured photosynthetic surface increases with pod enlargement.

During this period there is initially an increase in leaf area together with a rise in level of assimilation so that  $E$  begins to rise. This would be followed by a more rapid rise in  $E$  as  $L_A$  falls and assimilation increases to a plateau rate with mainly reproductive node leaves contributing assimilate. Following this there is a period where  $L_A$  is being underestimated and the apparent value of  $E$  continues to rise rapidly.

The significant differences in  $E$  between the two high density treatments, 400 and 200 plants  $m^{-2}$  and the low density treatments, 100 and 25 plants  $m^{-2}$  at the early harvests is difficult to interpret. As already shown there are initially no differences in  $\bar{R}$  between densities and the differences in  $E$  must be due to changes in  $F$ , the leaf area ratio.

Significant differences ( $P < 5\%$ ) between  $F$  at different densities has been demonstrated at the early harvests and this appears to be due to the lower values for SLA at the lower densities (100 and 25 plants  $m^{-2}$ ).

If this effect is real, it would imply that even at the first harvest there was a degree of mutual protection at the higher densities. Since on the field data the differences in SLA at  $H_1$  were not significant, the effects noted may have been due to experiment error. At the second harvest ( $H_2$ ) however there was significant difference between the SLA for the different treatments which persisted to the sixth harvest. ( $H_6$ ).

Confirmation of the existence of a difference in SLA and thus in  $E$  at this early harvest would be desirable. This would also allow determination of the existence of early differences in  $R$  as shown by the instantaneous methods used in this experiment. Real differences in  $R$  at this early stage would be expected to have important consequences in determining density and final plant size.

Net Assimilation Rate is affected by both Relative Growth Rate and by Leaf Area Ratio during the period  $H_2$  to  $H_6$ . At the lowest density (25 plants  $m^{-2}$ ) the initial rate of  $R$  was maintained for a considerable

time (up to  $H_6$  or  $H_7$ ) as shown by the logistic function method. During this period F had the main effect on E, the initial rise in F being mirrored in a fall in E. Not until the value of R began to fall after  $H_7$  does the late rise in E caused by the fall in F slow and then reverse itself.

At the higher densities (100 to 400 plants  $m^{-2}$ ) it would appear that the initial rise in F also dominated the change in E but to a lesser extent than at the lowest density. The fall in R from soon after emergence at above 200 plants  $m^{-2}$  is reflected by the low initial value for E and the low minimum value shown by these treatments.

Maximum values of Leaf Area Index were attained in this experiment for the three highest density treatments at  $H_7$ . At the lowest density (25 plants  $m^{-2}$ ) the peak value was not attained until  $H_9$ . The differences between the high densities (100 to 400 plants  $m^{-2}$ ) and the low density (25 plants  $m^{-2}$ ) in this regard was due to considerable growth of axillary shoots at the low density. These shoots were produced after apical dominance was interrupted by flowering and pod set. This late growth was reflected in the high late value of F shown by this treatment as well as by the slow rise in E at the later harvests.

Yield of green peas was obtained by initially determining average pea fresh mass at a standard % AIS equivalent to freezing maturity. From this and the number of peas per plant in each treatment the yield per plant and per unit area were calculated.

There was no significant difference determined in the average pea mass at 12% AIS between any of the treatments. This was not altogether unexpected as while there were differences between densities in the number of podding nodes the range of pea maximum and minimum fresh masses were similar at each treatment. While differences in time of achieving an optimum average maturity may have been expected to vary, the average pea mass at that maturity did not vary significantly.

Differences in yield were thus related to number of peas per plant and to number of plants per unit area at the standard maturity.

No significant difference was detected between number of peas per pod at each density treatment. This result is in line with that of Snoad, Hobart and Payne (1973) who suggested that under stress entire pods were more likely to be aborted than individual peas within a pod.

Significant differences ( $P < 5\%$ ) were determined in number of pods per plant between treatments. At the higher densities fewer pods per plant were matured than at lower densities.

Significant differences in yield per plant and per unit were also demonstrated ( $P < 1\%$ ), with the highest yield being obtained at the highest density (400 plants  $m^{-2}$ ). This yield (2.23  $kg/m^{-2}$ ) was almost four times (3.7 X) that from the lowest density treatment. The seed rate had however been increased from 25 to 400 seeds  $m^{-2}$ , a factor of 16 X, to achieve this increased yield.

Halving the maximum seed rate to 200 seeds  $m^{-2}$  (B) resulted in a reduction in estimated yield from 2.200 to 1.900  $kgm^{-2}$  or approximately 15%.

The choice of optimum seed rate is determined not only by the maximum obtainable yield, which in this trial was obtained at the highest density used, but also by the relative cost of seed and return for peas. Since all other inputs were the same in this experiment the ratio of seed cost to pea return over the density range investigated would have had to be 1 : 4 greater to warrant the use of the higher seed rate. Between the two higher densities a ratio of almost 1 : 7 would be required to warrant the use of the maximum seed rate in this experiment.

#### WEED CONTROL

An effect of planting density not directly measured in this experiment is that of weed suppression. Use of a pre-emergence herbicide allowed sufficient time for the higher density treatments to achieve a high enough leaf area index to effectively shade out late germinating weed seed. At the lowest density

however the maximum LAI attained was 3.5 at H<sub>9</sub> which was inadequate to prevent weed growth. The three high density treatments (100 - 400 plants m<sup>-2</sup>) all reached their maximum LAI by H<sub>7</sub> (LAI = 8-15) and effectively suppressed weeds.

As weeds compete for all environmental inputs, water, fertilizer, light, etc. their suppression by the crop is a useful extension of other weed control practice.

## CONCLUSION

Peas of the cultivar Victory Freezer were sown in Spring at four planting densities from 25 plants to 400 plants per square metre. Harvests were taken at weekly intervals from shortly after emergence to senescence.

Total dry mass, leaf area and leaf dry mass were recorded at each harvest and at the later harvests, flower and pod data including pea yield and maturity were also recorded.

The growth data obtained was used to derive mean values of relative growth rate, net assimilation rate and leaf area ratio. Variability in the recordings made interpretation of these mean values difficult. Instantaneous values of relative growth rate, net assimilation rate and leaf area ratio were then calculated by two separate methods. The first involved fitting the natural logarithms of the measured data to polynomial function and the second fitting the data to the logistic model.

The polynomial method has the benefit of simplicity of calculation and is relatively robust however the derived functions, particularly relative growth rate, failed to adequately describe growth of the crop at the different plant densities. By fitting the logistic model more usable derived functions were obtained. Notwithstanding it was still difficult to relate relative growth rate to early growth in the field.

Net assimilation rate was shown to follow a 'U' shaped curve with time. Similar responses have been recorded elsewhere. It is considered that the high early and late values are due in part to under estimation of photosynthetic area. The stems and petioles of peas make up a large proportion of the photo-assimilating area soon after emergence while during ripening the pods also add considerably to this area. In the present study neither area was included as photosynthetic or 'leaf' area.

Yield of peas was affected by planting density with the highest yield being obtained at the most dense planting. Components of pea yield affected by plant density were number of pods per plant and number of plants per unit area. Number of peas per pod and mean pea mass were not affected.

Plant density was shown to affect specific leaf area soon after emergence giving rise to early differences in leaf area ratio.

Use of alternative techniques to obtain relative growth rate over the whole of growth is suggested. It may be necessary to consider growth in separate stages, for example, examining vegetative and reproductive growth as distinct segments and fitting appropriate functions to each.

Greater attention should be paid to determining accurate measures of plant mass and leaf area during early growth to improve estimation of relative growth rate and other derived functions during this period. Changes during germination and early emergence, not followed in this trial, may be expected to alter the function derived during vegetative growth.

EXPERIMENT No. 28.1 The Effect of Planting Density on the Growth of Peas with Modified LeavesMaterials and Methods

The second experiment was sited 100 metres to the north of the first experiment on a similar soil type. The site was prepared by spraying a green manure crop with glyphosate herbicide ( $9 \text{ l ha}^{-1}$ ) on 12th January, 1979. Ten days later when the green crop was dying back the area was rotary hoed to a depth of 100mm and then divided into beds and subsequent soil preparation and spraying was conducted so as to avoid wheel working on the area to be cropped.

Fertilizer was applied broadcast as a proprietary mixture at the rate of  $17 \text{ kg ha}^{-1}$  N,  $45 \text{ kg ha}^{-1}$  P and  $60 \text{ kg ha}^{-1}$  K and rotary hoed to a depth of 150mm.

Seed used in this experiment was supplied by Dr. E. T. Gritton, University of Wisconsin, Madison, U.S.A. This seed comprised three near isogenic lines of Dark Skinned Perfection (DSP), the parent line, and two derived lines *afila* (*af*) and *leafless* (*afst*). The derived lines varied from DSP in the presence of recessive genes for leaf to tendrill conversion (*af*) and stipule reduction (*st*) as indicated. In the comparison DSP is used as a normal leafed canning cultivar including genes *Af* for multipinnate leaves, *Tl* for tendrill expression and *St* for normal stipule production. The combination of the recessive form *af* with the dominant *Tl* in the line *afila* produces a plant where the leaflets are converted to tendrills. In the *leafless* line there is the further use of the recessive *st* gene giving a plant with both converted leaves and reduced stipules.

Planting density was the same as that used in the first experiment being (A) 400, (B) 200, (C) 100 and (D) 25 plants  $\text{m}^{-2}$ , with a rectangularity of unity. Each harvest plot was of nine seeds hand sown on the 1st and 2nd February and surrounded by guard plants at the same density and rectangularity.

Because of limited seed a split plot layout was used with density and cultivar being main plots and harvest date as sub plots. This allowed use of common guards between adjacent sub plots. Except for the leafless line all plots were surrounded by 300mm of guards, shortage of seed allowing only 200mm of guard for this line.

Eleven harvest dates were allowed assuming rapid growth of the peas during the summer. Duplicate harvests thus required twenty sub plots randomized within each of the twelve main plots. The main treatments, four densities and three cultivars, were randomized in each of two blocks. Of the 480 sub plots, half, being one block, was sown on each of the two successive days.

After sowing the area was lightly irrigated, the weather being hot and dry. Fine nylon threads were strung across the plots next day to discourage bird attacks on the germinating seedlings.

Using container grown plants any misses were made good by transplanting some 14 days after sowing. These replacement plants were marked and discarded at harvest. The centre of the sub plots was also marked by a 600mm bamboo stake as a harvest aid at the same time.

A week later the plot was sprayed with metribuzin ( $350\text{g ai ha}^{-1}$ ) herbicide to control seedling weeds. Heavy rain the next day resulted in leaf scorch in the peas, however weed control was excellent.

From late March the to last harvest on 30th April, the weather was unusually cool with frequent rain and strong winds. Heavy cloud cover reduced light levels well below normal. The conditions favoured slugs, for which frequent baiting was required, as well as leaf and stem diseases, particularly *Mycosphaerella pisi*.

Although the eleven weeks of harvest were expected to include the period of pea maturity for commercial harvest, only the normal and semi leafless (af) lines produced any usable peas. Guard plants left

after completion of the experiment were observed for some weeks and it was noted that flowering of the leafless genotype was much delayed. Both the other lines also continued to produce new flowers and pods until the site was destroyed in mid July suggesting that the weather had adversely affected all lines.

Harvests were taken weekly by digging the nine marked plants in the plot area with a fork and discarding any replacements as well as any plants not guarded on four side. The remaining plants were then washed to remove soil, bagged in plastic and held at 5° C until measured.

As required, the samples were removed from the cool store and the following data was recorded.

A. Prior to Podding

- (i) Number of Plants out of nine
- (ii) Total fresh mass
- (iii) Photosynthetic area for each line by digital photoelectric meter as
  - (a) DSP-leaf and stipule combined
  - (b) reduced leaf lines tendril and stipule separately
- (iv) Dry mass of root and stems separately
- (v) Dry mass of photosynthetic material as separated under (iii).

B. After Podding the additional measurements

- (vi) Number of pods at each node
- (vii) Number of peas at each node
- (viii) Fresh mass peas at each node
- (ix) AIS of sample of peas at each node
- (x) Dry mass of pods and peas at each node.

Petioles in all lines were included in measurements of stem mass. The mass and area of tendrils in the normal line were regarded as being insignificant compared to the total 'leaf' area and were measured with leaf. No differentiation between leaflets and stipules was made in the normal line the information to be so gained although of interest, was not regarded as being essential.

## 8.2 Results

At each harvest date, per plant results were calculated for total plant dry mass ( $W$ ), leaf dry mass ( $L_W$ ), and leaf (photosynthetic) area ( $L_A$ ).

Both  $W$  and  $L_W$  were obtained from their components, including leaf, stipule or tendrill mass where appropriate. Calculation of  $L_A$  is less straight forward as Harvey (1972) has shown that the measured tendrill area is the longitudinal cross section ( $LXD$ ) of a cylinder. From the formula

$$A = L \times D \times \pi$$

$A$ , the surface area may be calculated knowing the product of  $L$  the length and  $D$  the diameter with  $\pi$  having its conventional value. Since however only one surface of a flat leaf is usually measured only the half surface of the cylinder is calculated by obtaining the product of  $L \times D$  (as measured) and  $\pi/2$ . Leaflet and stipule area were used as measured together with the recalculated area of tendrill as required to determine  $L$ .

At each harvest, two independent assessments of  $W$ ,  $L_A$  and  $L_W$  were thus available for each main plot except for the first ( $H_1$ ) and last ( $H_{11}$ ) harvests.

### 8.2.1 Total dry mass

The values of  $\log_e$  total dry mass against time are shown in figures 14,15. Despite considerable variation the resultant graphs approximate to a logistic function similar to that obtained in the first experiment. Because of variation however it was decided not to attempt to fit the logistic function but to use the more robust polynomial approach.

There was no difference between the three highest density treatments but the lowest density  $D$  (25 plants  $m^{-2}$ ) was significantly lower ( $P < 5\%$ ) in value from harvest 8 ( $H_8$ ) to harvest 11 ( $H_{11}$ ). This effect was opposite to that found in the first experiment. Significant cultivar effects were also found on all occasions with DSP being significantly greater than afst.

### 8.2.2 Leaf Area ( $L_A$ )

$\log_e L_A$  was plotted against time as shown in figures 16,17. The overturning type curves found for  $\log_e L_A$  in the first experiment were not so obvious due to termination of the harvest before maturity of the plants.

At all except the first harvest ( $H_1$ ) the lowest density (25 plants  $m^{-2}$ ) gave significantly lower values of  $\log_e L_A$  (<5%) than the higher densities.

Cultivar differences in  $\log_e L_A$  were significant ( $P < 1\%$ ) at each harvest with the leafless line having significantly lower values.

### 8.2.3 Leaf Dry Mass ( $L_W$ )

Plotting of  $\log_e L_W$  by harvest for cultivar and density (figures 18,19). showed significant differences between densities ( $P < 5\%$ ) and between cultivars ( $P < 1\%$ ). At the lowest density, 25 plants  $m^{-2}$ , the value of  $\log_e L_W$  was significantly lower ( $P < 5\%$ ) than at higher densities while that of the leafless line was also significantly lower ( $P < 1\%$ ) than the semi leafless or conventional line.

### 8.3 Curve Fitting

Harvest variability was accounted for by linear and quadratic regression to a similar extent (>97%) for each of  $\log_e W$ ,  $\log_e L_A$  and  $\log_e L_W$ . Using the method of Little and Hills (1975) described in the first experiment, quadratic coefficients were calculated and new values of  $\log_e W$ ,  $\log_e L_A$  and  $\log_e L_W$  obtained from the formula

$$\log_e \hat{Y} = a + bT + cT^2 \quad 5.14$$

where  $\hat{Y}$  is the new value of  $W$ ,  $L_A$  or  $L_W$  at time  $T$  and  $a$ ,  $b$  and  $c$  are regression coefficients.

From the regression coefficients obtained it was then possible to calculate instantaneous values for Relative Growth Rate ( $R$ ), Net Assimilation Rate ( $E$ ), and Leaf Area Ratio ( $F$ ) for the different densities and cultivars.

#### 8.4 Relative Growth Rate

Calculation of mean values of relative growth rate ( $\bar{R}$ ) showed that as in the first experiment, harvest variability caused large fluctuations in value. This was predominantly due to weather caused fluctuations in growth including the initial check following the herbicide application (Table 9 ).

Using the formula

$$R = b + 2cT \quad 5.17$$

where b and c are regression coefficients at time T, instantaneous values of relative growth rate (R) were obtained and graphed (figure ). As this is a linear function, there was shown to be difficulty in obtaining useful information over the whole growth of the crop in the first experiment. The shorter period of harvest in this experiment, which terminated during growth rather than at senescence, allowed for useful curves of R to be produced.

From the fourth harvest ( $H_4$ ) onwards the value of R for the plants 25 plants  $m^{-2}$  (D) treatment was significantly less ( $P < 5\%$ ) than for the higher densities. The leafless cultivar (afst) was also shown to have significantly lower value of R ( $P < 5\%$ ) from  $H_4$  than the semi leafless and normal cultivars.

#### 8.5 Net Assimilation Rate (E)

Harvest variability also affected the values of mean net assimilation rate ( $\bar{E}$ ) in a similar way to that of  $\bar{R}$ , (Table 10 ).

Instantaneous values of E were calculated in the manner described in the first experiment by first determining R and F, the leaf area ratio, and then determining E from

$$E = R/F \quad 5,8$$

Differences in E due to density were small at the early harvests being non significant up to  $H_7$ . After  $H_7$  however the lowest density (D) 25 plants  $m^{-2}$  showed a significantly lower value of E which continued to fall with later harvests. Only at density B, (200

plants  $m^{-2}$ ) was there a rise in E which is usually attributed to pod and seed development.

Variations in E due to cultivar differences were significant with the leafless line being initially very high but falling to a low level at the later harvests. There was no significant differences between the normal and semi leafless lines.

#### 8.6 Leaf Area Ratio (F)

Mean values of leaf area ratio ( $\bar{F}$ ) were calculated and significant differences between densities and cultivars ( $P < 1\%$ ) could be demonstrated.

Similar results were obtained by analysis of instantaneous values of F. In both cases the lowest density (D) 25 plants  $m^{-2}$ , had significantly ( $P < 1\%$ ) lower values of leaf area ratio during the greater part of the experiment. The leafless (afst) cultivar also was significantly lower ( $P < 1\%$ ) at all harvests in the value of F.

#### 8.7 Specific Leaf Area (SLA)

Since SLA is defined as

$$SLA = L_A/L_W \quad 5.25$$

changes in 'leaf' thickness particularly in the proportion of dense tissue such as tendrils to leaves and stipules may be expected to be reflected in the values of SLA. Both mean and instantaneous values of SLA were calculated.

The effect of density was shown by significant differences ( $P < 5\%$ ) between treatments from  $H_3$  to  $H_{10}$  with the lowest density (D), 25 plants  $m^{-2}$  having the lowest SLA. Cultivar differences were significant at each harvest with the leafless line (afst) being of significantly lower ( $P < 1\%$ ) value.

#### 8.8 Leaf Mass Ratio (LMR)

Environmental factors usually have little affect on LMR and this was demonstrated in this experiment, density having little effect on either mean or instantaneous values.

Cultivar effects were however significant during early growth  $H_1$  to  $H_6$ , with the lowest values being obtained in the leafless (afst) plants.

#### 8.9 Green Pea Yields

Yields of usable peas were obtained at  $H_{10}$  and  $H_{11}$  from some density treatments only, in either the normal (DSP) or semi leafless (af) plots. No yield was obtained from any of the leafless treatments at either harvest. The paucity of information obtained made it impossible to draw conclusions on the effect of density on cultivars in this trial.

## DISCUSSION

The effect of density upon growth of peas in this trial was contrary to that expected either from literature or from the first trial. No significant differences were demonstrated between the three highest density treatments (100 to 400 plants  $m^{-2}$ ) in average plant mass, average leaf area or average leaf mass. The lowest density treatment however showed frequent variation, the plants being smaller with thicker leaves.

From the conditions of the experiment it would appear that weather was the main modifying factor in altering the response of the plants to density of planting. In particular the effect of wind on the lowest density planting could be expected to have been severe. The response of the plants in terms of specific leaf area would suggest that exposure had resulted in thickening of the leaves as well as in overall reduction of average leaf area. At the early growth stages no significant differences were detected in value of SLA between density treatments at a time when both inter-plant competition and mutual support were minimal.

During the mid and late period of growth however the mutual support of the denser planted treatments would appear to have allowed more rapid growth to continue than at the lowest density. It was not determined in this experiment whether the effect of low planting density was due to wind directly or to lower temperatures, either as a consequence of enhanced evaporation from leaf surfaces or radiation of heat from the bare soil.

Cultivar differences were interesting in that there was generally little difference between the normal leaves (DSP) and semi leafless (af) lines. Average  $\log_e W$  was not significantly different between these two lines nor was  $\log_e L_A$  or  $\log_e L_W$ . Relative growth rate, net assimilation rate and leaf area ratio were accordingly not significantly different under the

conditions of the experiment. The reason for the lack of difference between these two lines is not able to be directly determined. Since the individual area of leaflet, stipule and tendril were not determined for normal plants, it is not possible to state whether the stipule area in the af genotype was increased. Harvey, (1978) has stated that the photoassimilating efficiency of leaf and stipule is similar to that of tendrils in terms of unit surface area. This would appear to be the case in this comparison as shown by the similar figures for net assimilation rate and 'leaf' area ratio of the two lines.

Again under the conditions of the experiment the leafless line (afst) was often at a disadvantage compared to the normal plant. Although the value of  $\log_e W$  did not initially vary between lines, after the seventh harvest ( $H_7$ ) the leafless line had significantly ( $P < 5\%$ ) lower values than the normal line. In terms of  $\log_e L_A$  the leafless line had significantly ( $P < 5\%$ ) lower values than the normal line at all but the first harvest.

In this experiment the leafless line (afst) showed an initial very high level of net assimilation rate suggesting that the photosynthetically active area of the plant was being underestimated. Inspection of these small plants shows that in the absence of well developed leaflets and stipules, the green stem area is large in relation to the measured tendril area. This suggests that it would be desirable to measure the entire green and thus presumably photosynthetic area of seedlings to enable a more meaningful estimate of leaf area and thus of net assimilation rate during early growth. In this line it would be interesting to obtain a record of the whole surface of the plant for the entire life of the plant in order to determine the possible photosynthetic contribution of 'stem' area.

One effect of the poor weather conditions which is not possible to measure which may have been of some consequence is the low light intensity response of leafless cultivars described by Harvey (1972). Below  $100 \text{ J m}^{-2}$

sec<sup>-1</sup> the leafless lines were shown to be at a disadvantage to normal lines, a situation which may have been encountered for much of this experiment. The low values of E shown in the late harvests may be expected to be at least partly due to this.

Overall consideration of this experiment is however difficult due to the considerable variability consequent upon adverse weather during much of its growth.

## CONCLUSION

Peas of three near isogenic lines of Dark Skinned Perfection (DSP) were obtained differing only in the presence or absence of leaf and stipule modifying genes. The lines were:

- 1) normal leaved DSP
- 2) leaflets converted to tendrils
- 3) leaflets converted to tendrils and stipules reduced

All three lines were sown in late summer at four planting densities, 25, 100, 200 and 400 plants per square metre. At weekly intervals nine plants were harvested from different plots beginning shortly after emergence and continuing until all plots had been measured. Total dry mass, leaf and tendril area and dry mass were recorded at each harvest. Where flowers and fruit were present data was recorded on numbers of both per node, fresh and dry mass of peas and pods and maturity of peas.

Growth data obtained was used to derive mean values of relative growth rate, net assimilation rate and leaf area ratio. Mean relative growth rate was not easy to follow due to excessive harvest variability.

Due to the poor growth and extreme variability of the observed data due to the inclement weather and high levels of disease it was decided to attempt to fit polynomial functions only. This method had been previously shown to be robust and to reflect well the growth patterns of the pea.

The effect of density on plant growth in this experiment showed that at low density (25 plants  $m^{-2}$ ) plant growth was much reduced. Because measurement of the crop ceased well before senescence it was possible to show that relative growth rates varied between density treatments with the lowest density having a significantly lower relative growth rate for much of the term of the experiment.

Mean and instantaneous values of net assimilation rate and leaf area ratio were calculated. Significant density effects could be demonstrated for both instantaneous and mean value of leaf area ratio but not with mean net assimilation rate. At low density both E and F were significantly lower.

There was little apparent difference between the normal and semi leafless lines which varied only in the leaf form as measured by any growth function. The fully leafless line was however significantly different with lower values of relative growth rate. The effect on net assimilation rate was to initially greatly increase and then to rapidly decrease values. This could probably be due to an early underestimation of photosynthetic area and later to reduced photoassimilation under the poor weather conditions.

The effect of weather may be expected to have altered the response of the crop to plant density as seen in the opposite reaction in the two experiments. Under the inclement weather and shorter days of the second experiment, more widely spaced plants were unable to utilize the reduced competition as they had in the first experiment. Similarly the poor performance of the leafless line would be expected to be more a function of the weather than of the genetic difference between it and the two near isogenic lines with normal stipules and either normal or reduced leaflets.

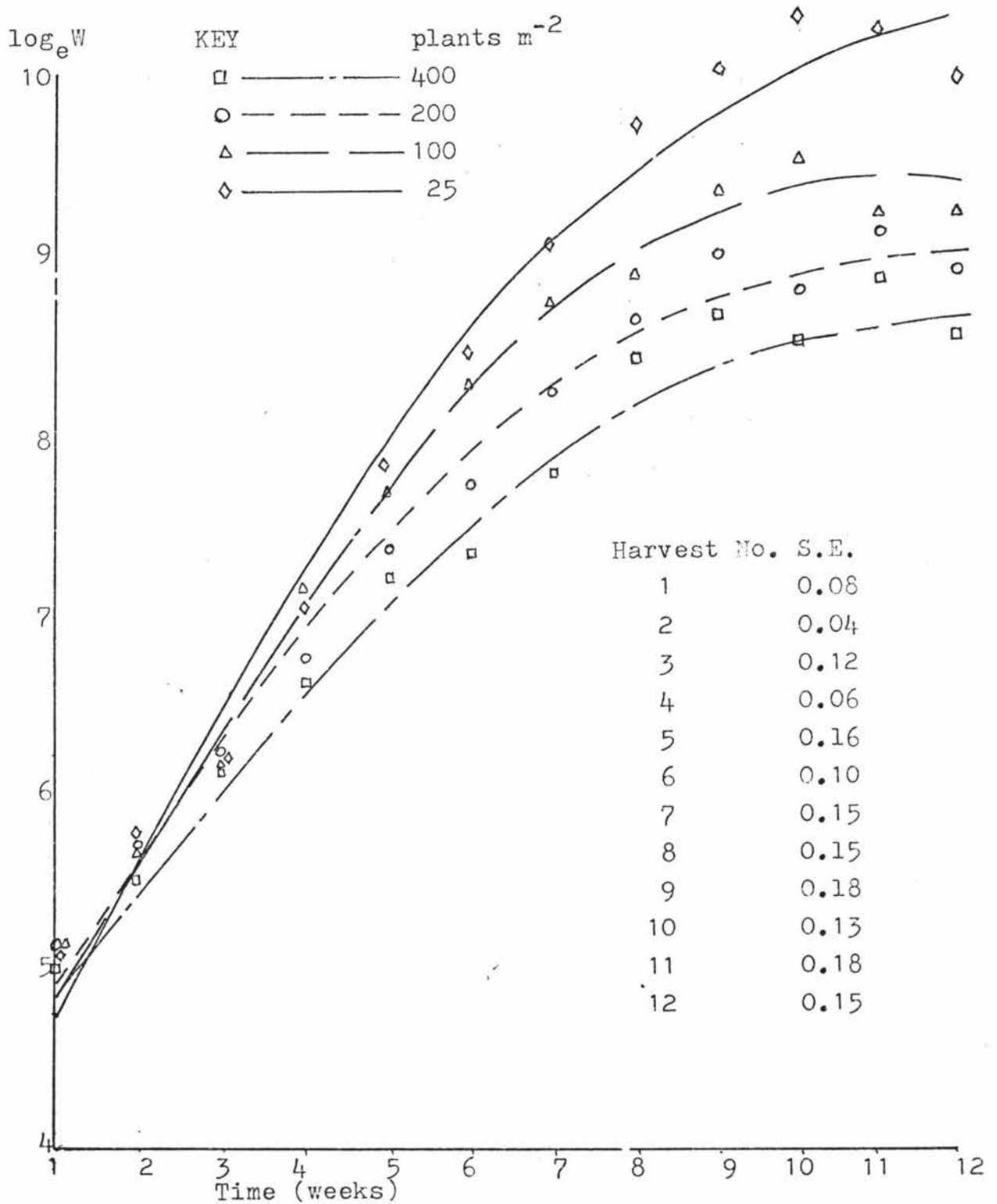


Fig 1.

Effect of plant density and harvest date on total plant dry mass of peas, fitted to quadratic functions.

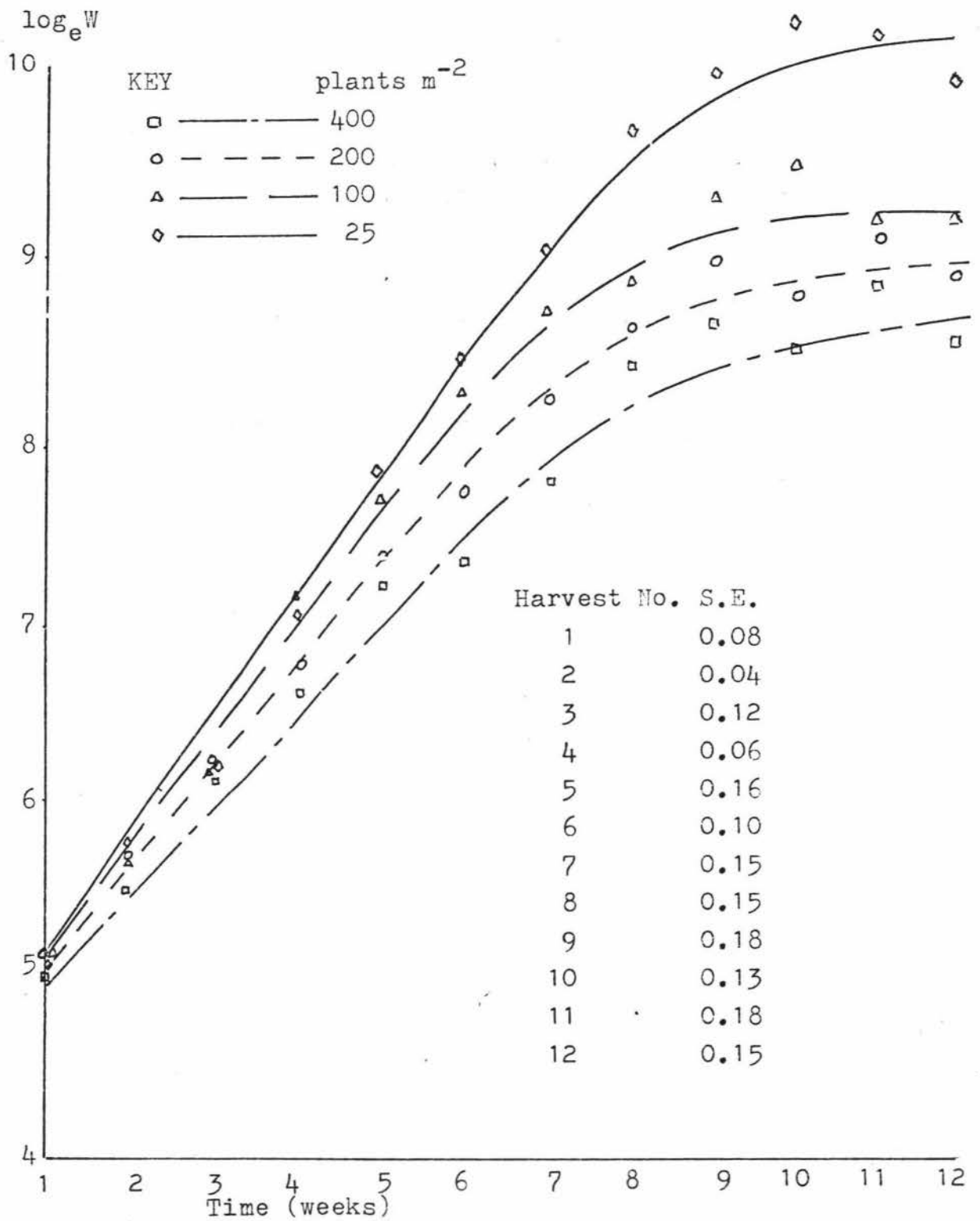


Fig 2.

Effect of plant density and harvest date on total plant dry mass of peas, fitted to logistic functions

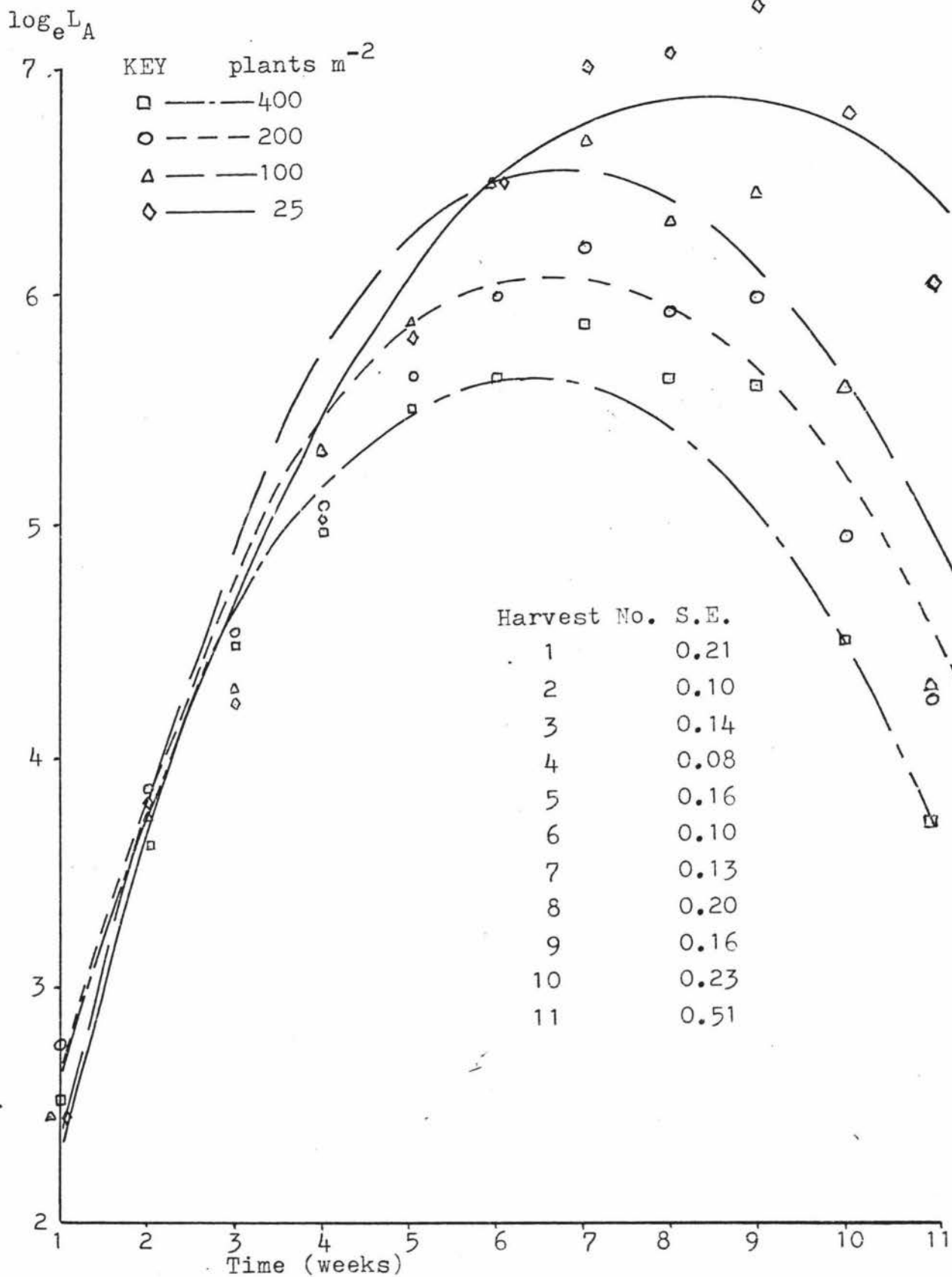


Fig 3.

Effect of density and harvest date on leaf area of peas, fitted to quadratic functions.

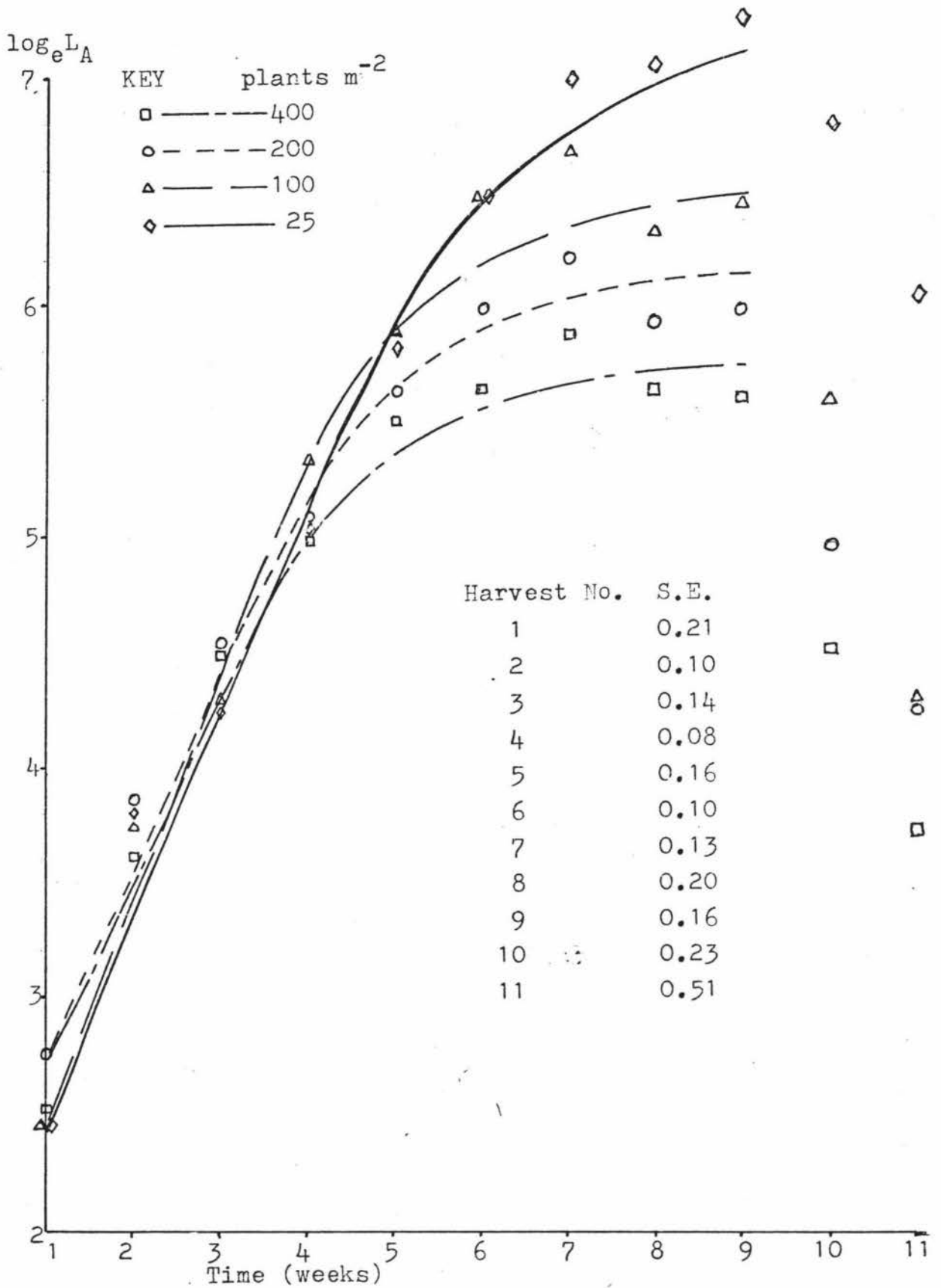


Fig 4.

Effect of plant density and harvest date on leaf area of peas, fitted to logistic functions.

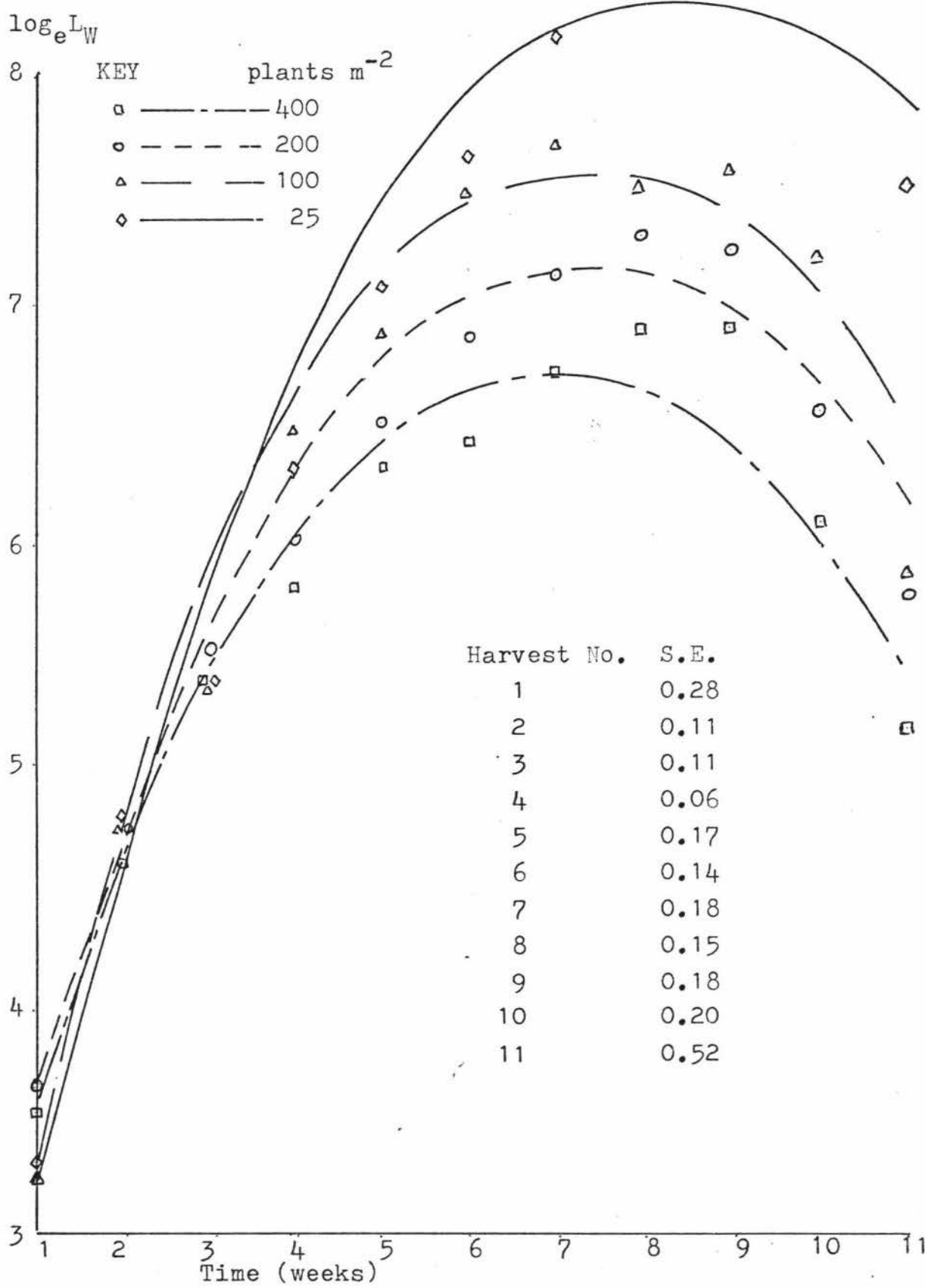


Fig 5.  
 Effect of plant density and harvest date on leaf dry mass of peas, fitted to quadratic functions.

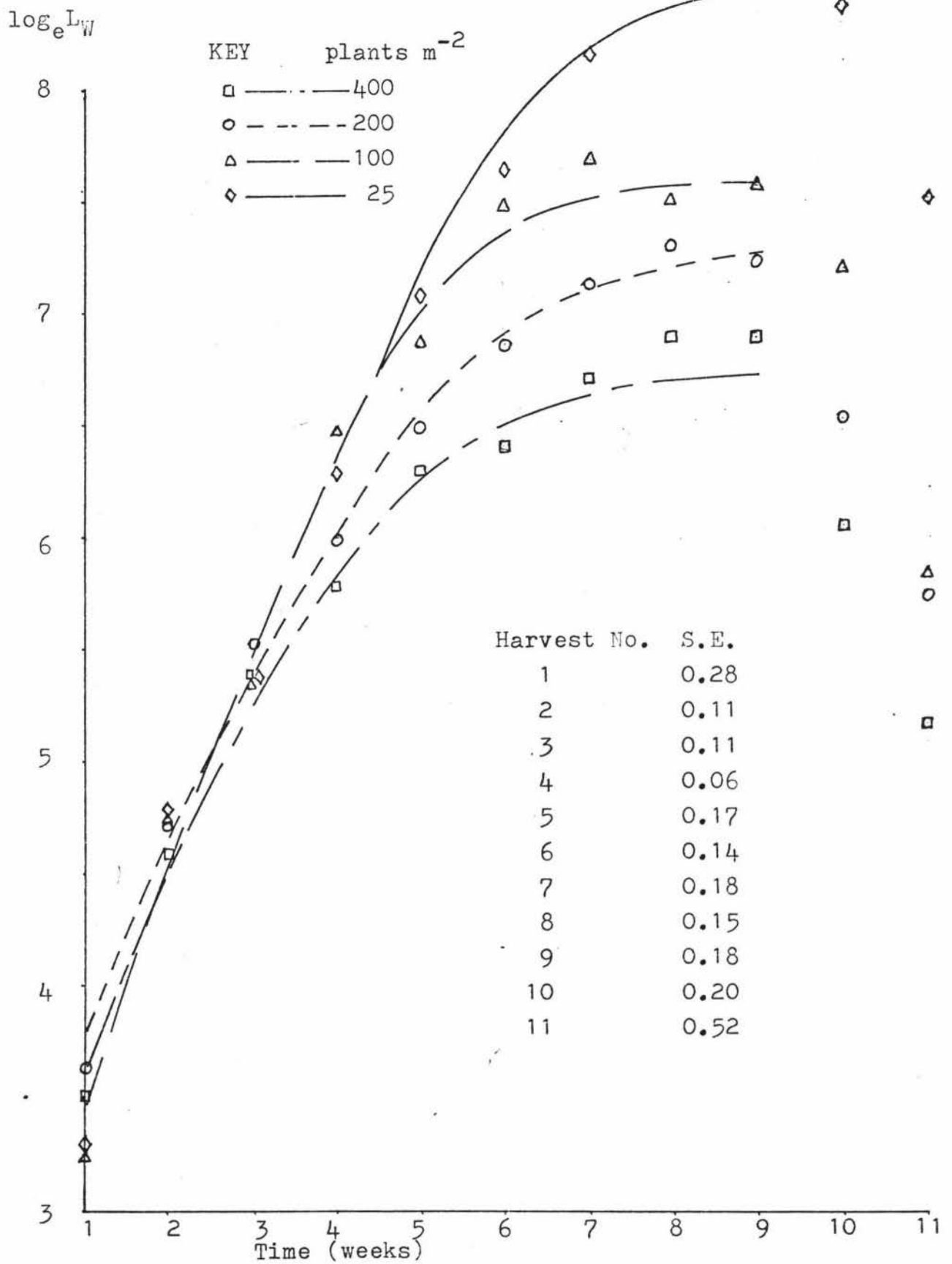


Fig 6. Effect of plant density and harvest date on leaf dry mass of peas, fitted to logistic functions.

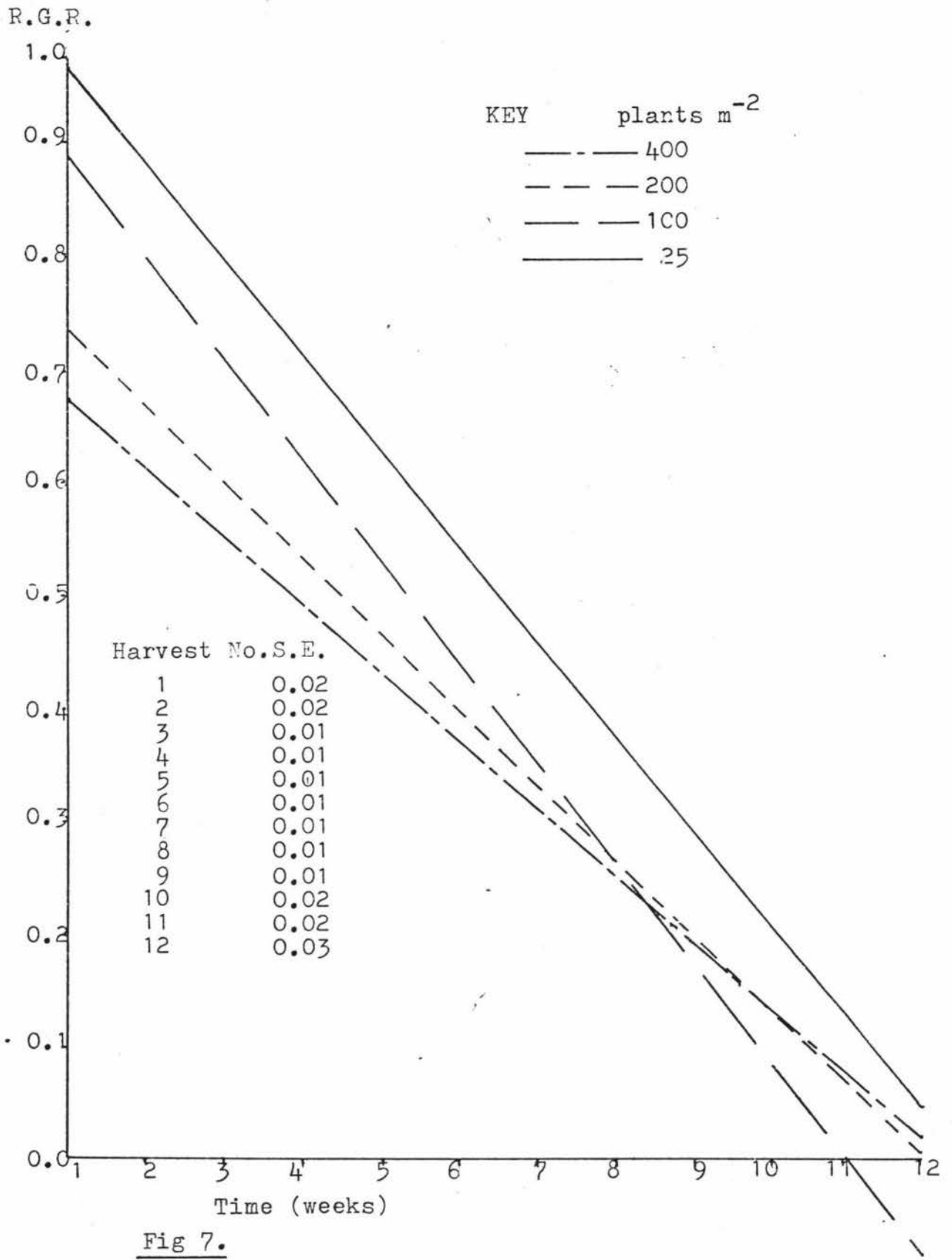


Fig 7.

Effect of plant density and harvest date on Relative Growth Rate of peas, derived from quadratic functions.

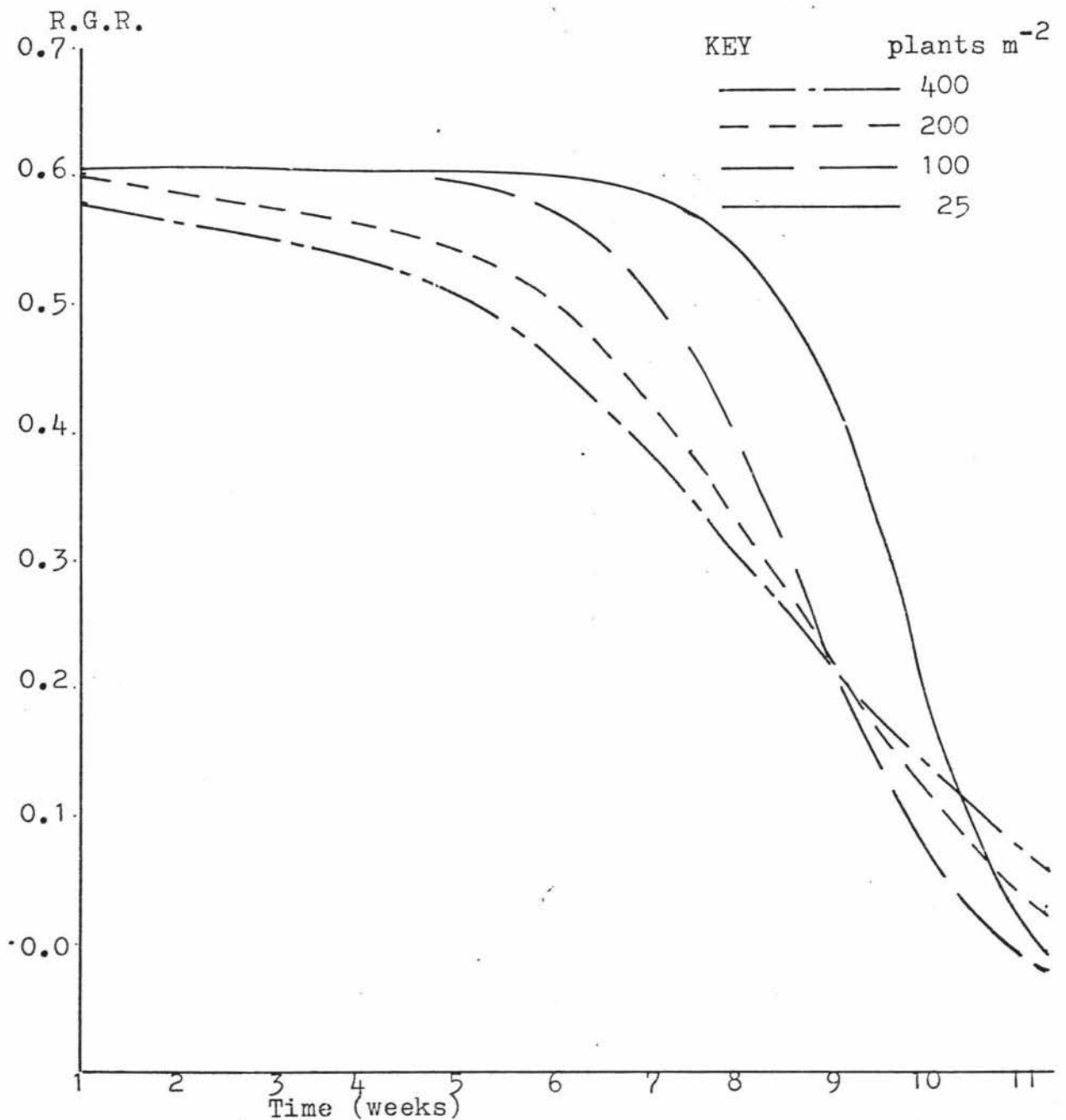


Fig 8.

Effect of plant density and harvest date on Relative Growth Rate of peas, derived from logistic functions.

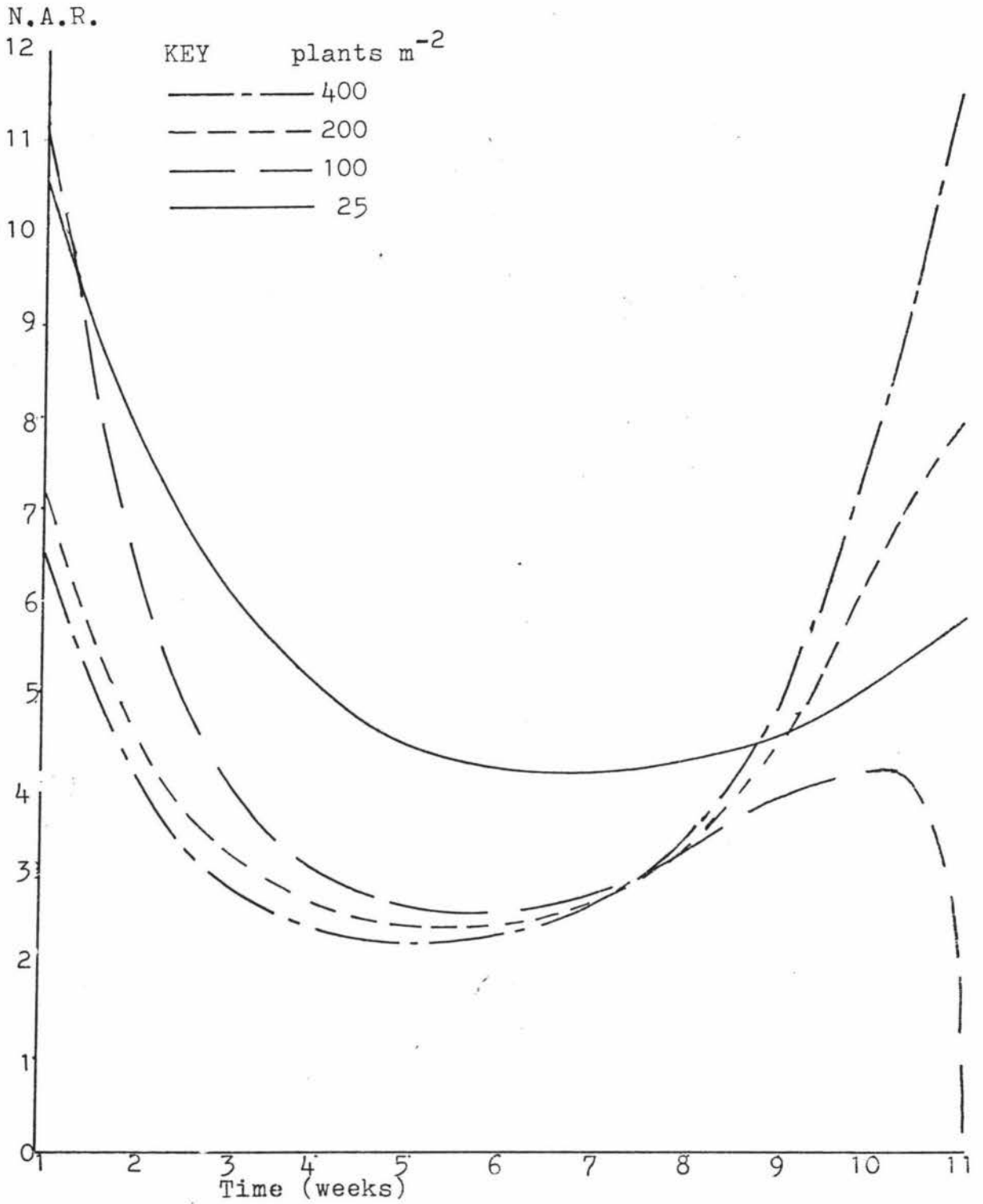


Fig 9.

Effect of plant density and harvest date on Net Assimilation Rate of peas, derived from quadratic functions.

N.A.R.

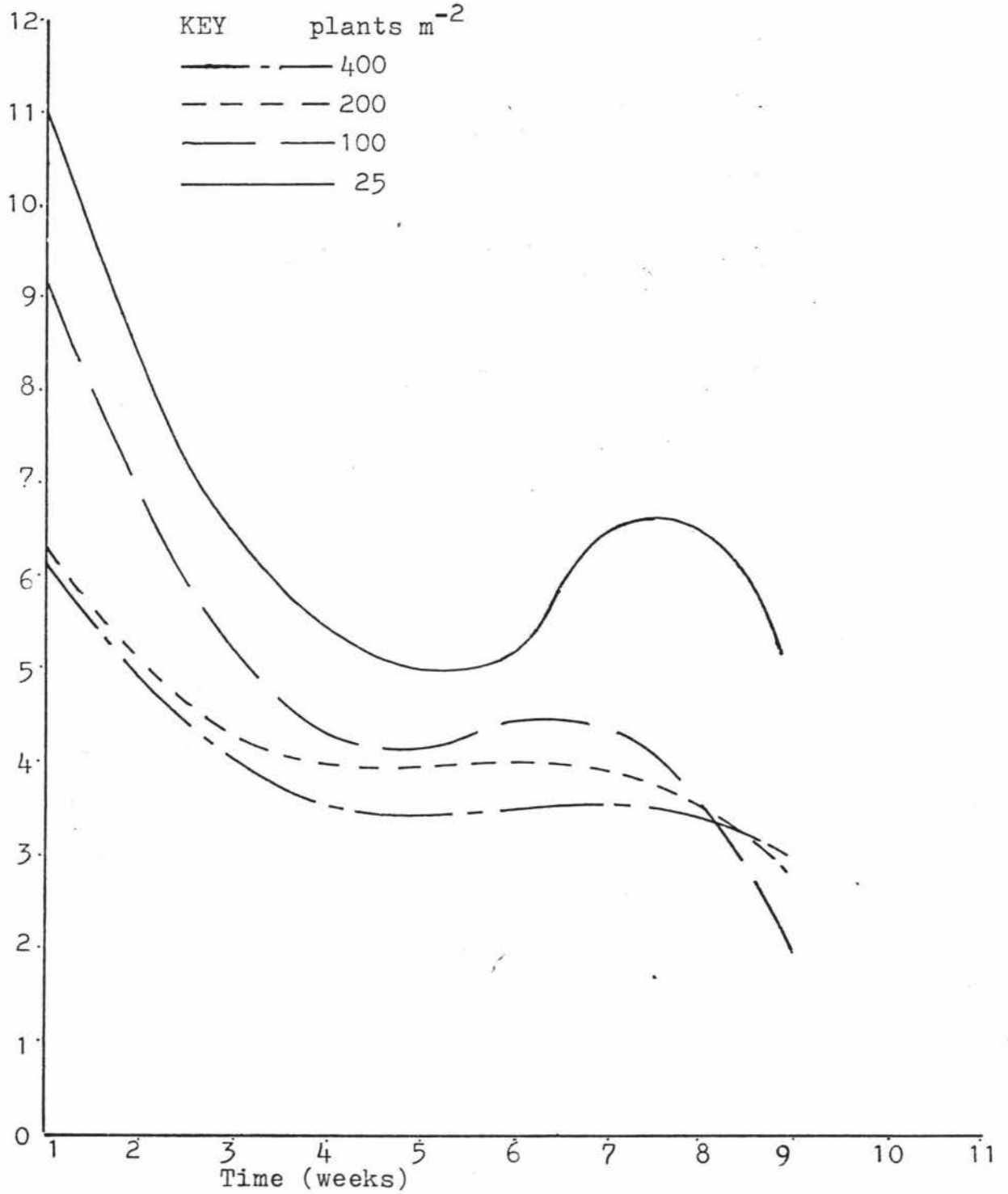


Fig 10.

Effect of plant density and harvest date on Net Assimilation Rate of peas, derived from logistic functions.

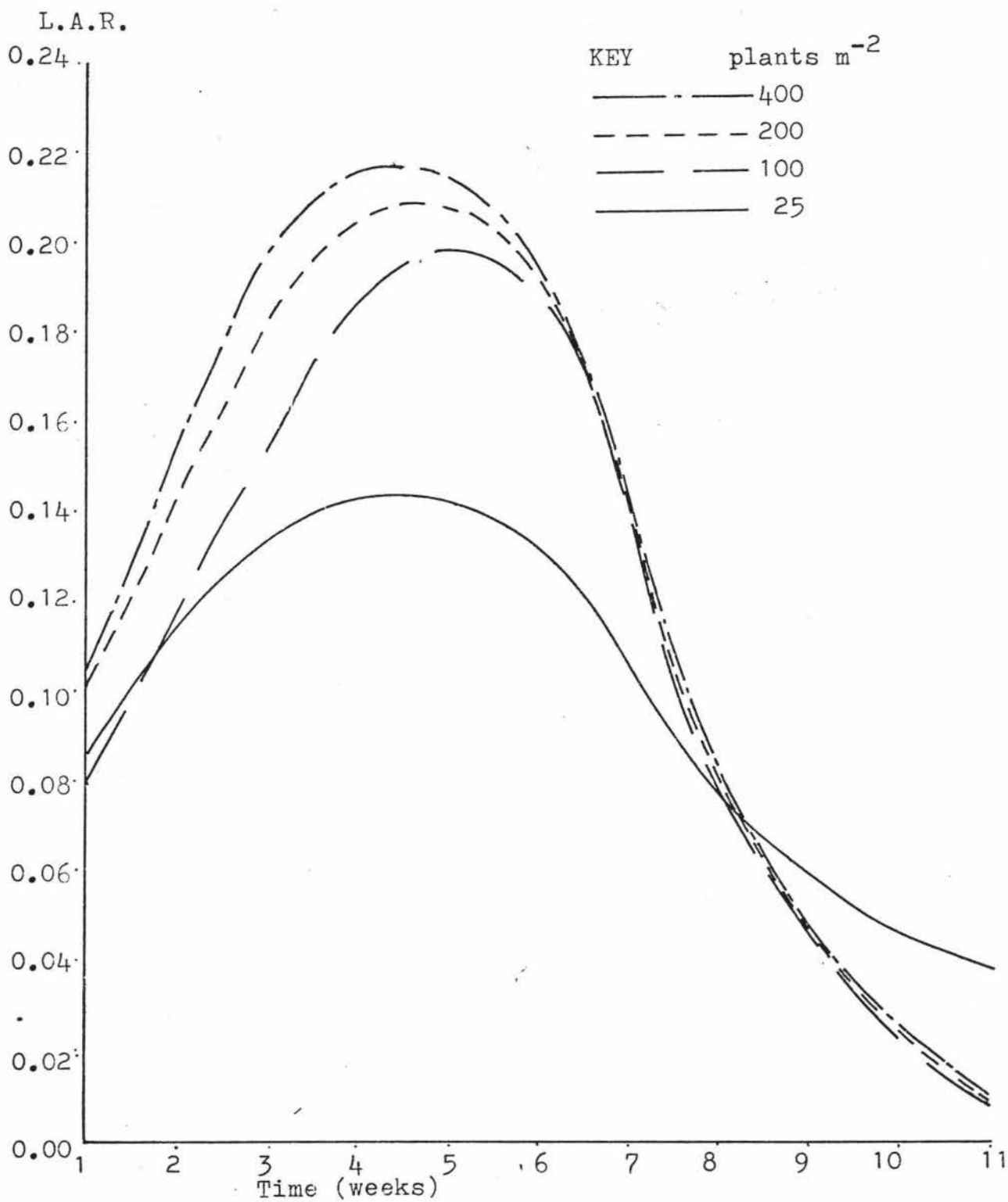


Fig 11.

Effect of plant density and harvest date on Leaf Area Ratio of peas, derived from quadratic functions.

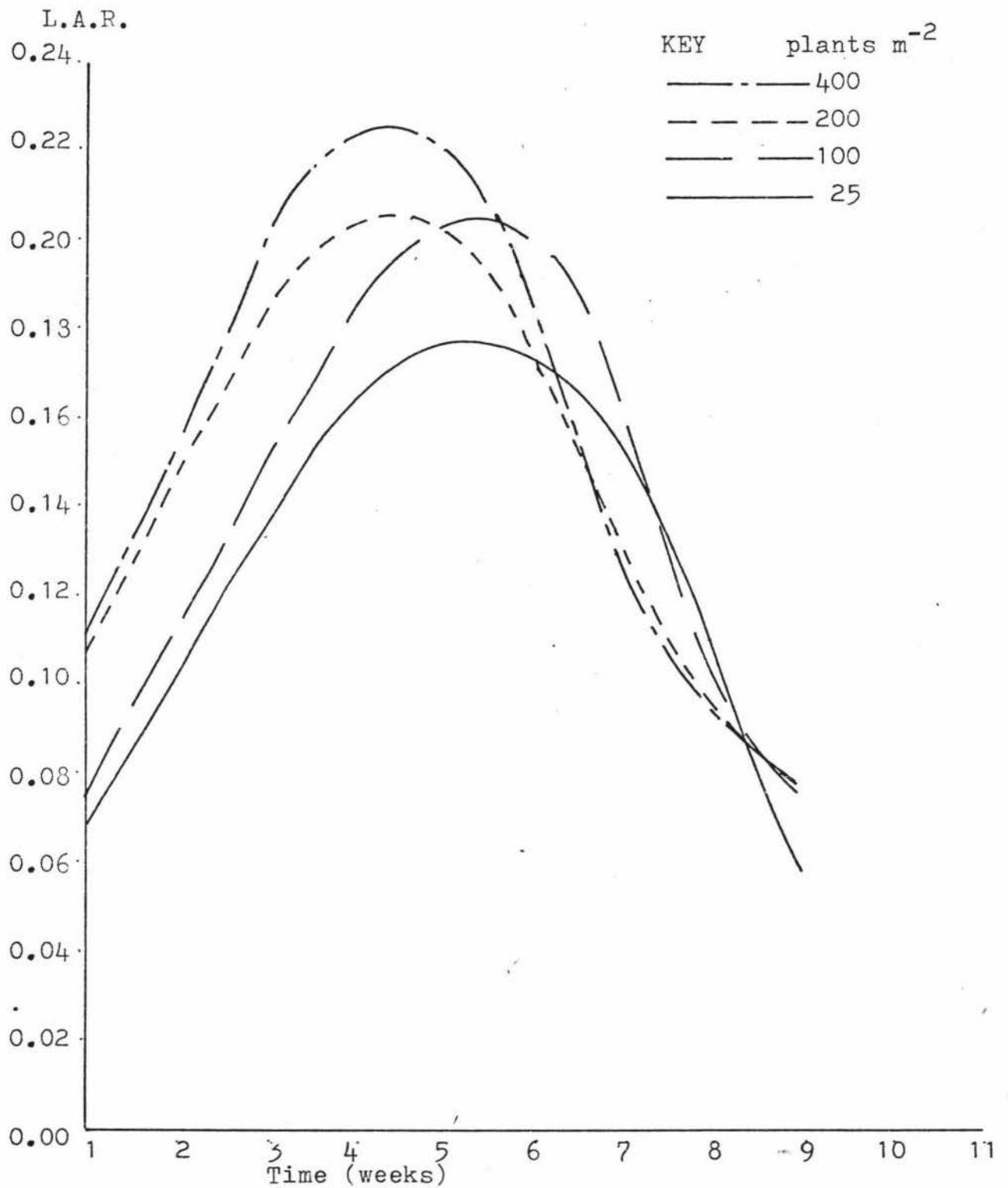


Fig 12.

Effect of plant density and harvest date on Leaf Area Ratio of peas, derived from logistic functions.

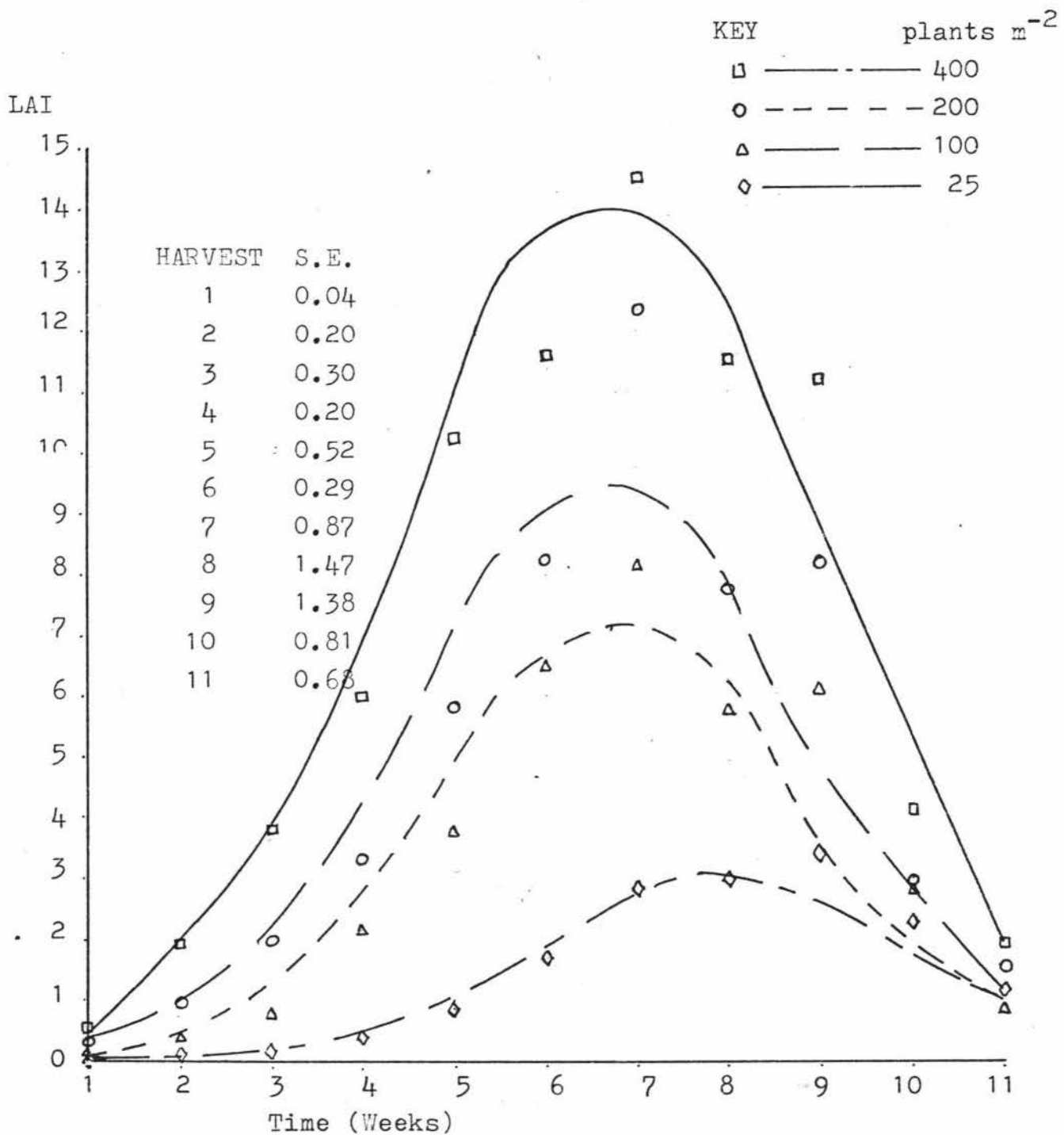


Fig. 13

Effect of plant density and harvest date on Leaf Area Index of peas, derived from quadratic functions.

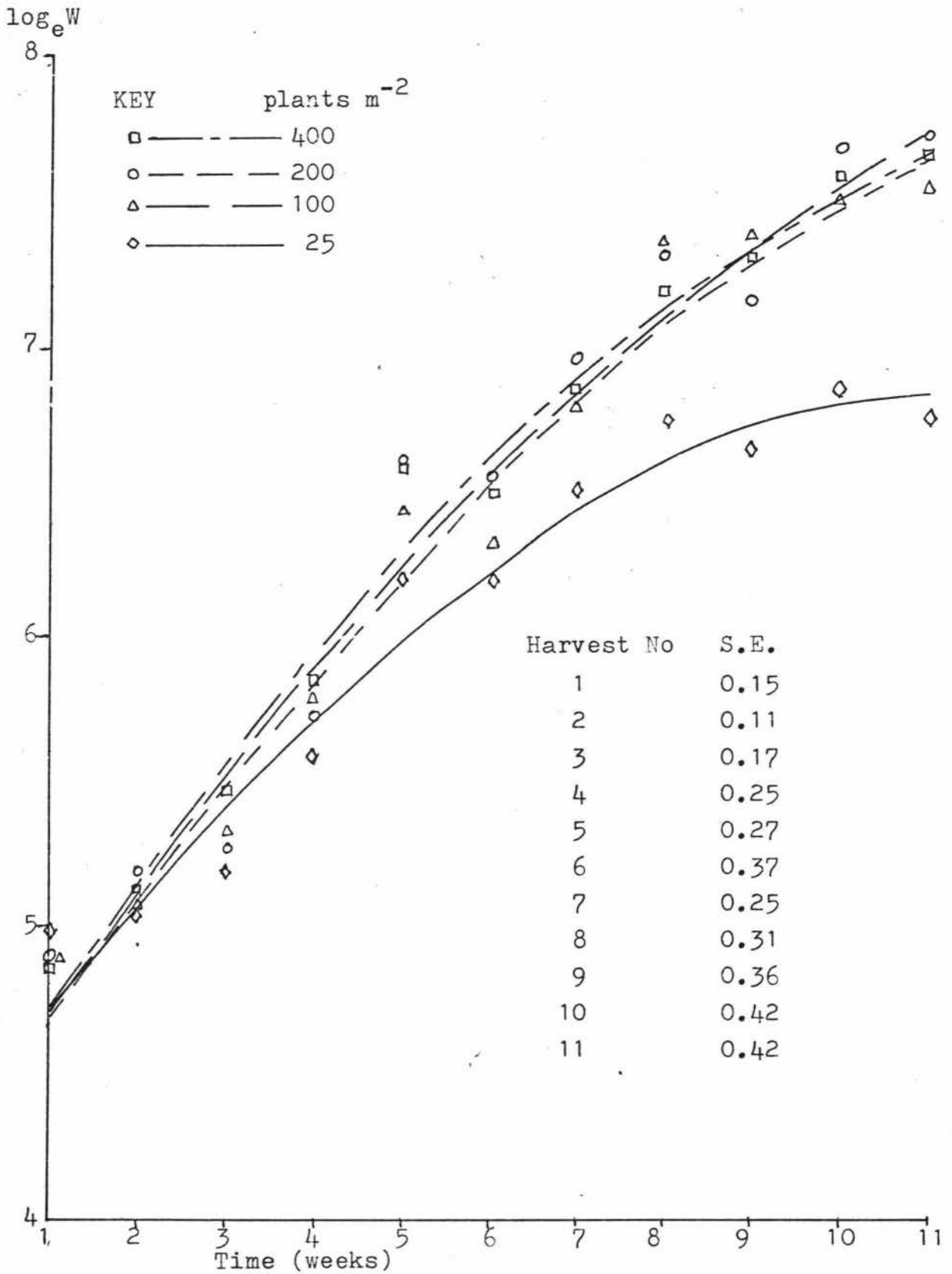


Fig 14.

Effect of plant density and harvest on total dry mass of peas, fitted to quadratic functions.

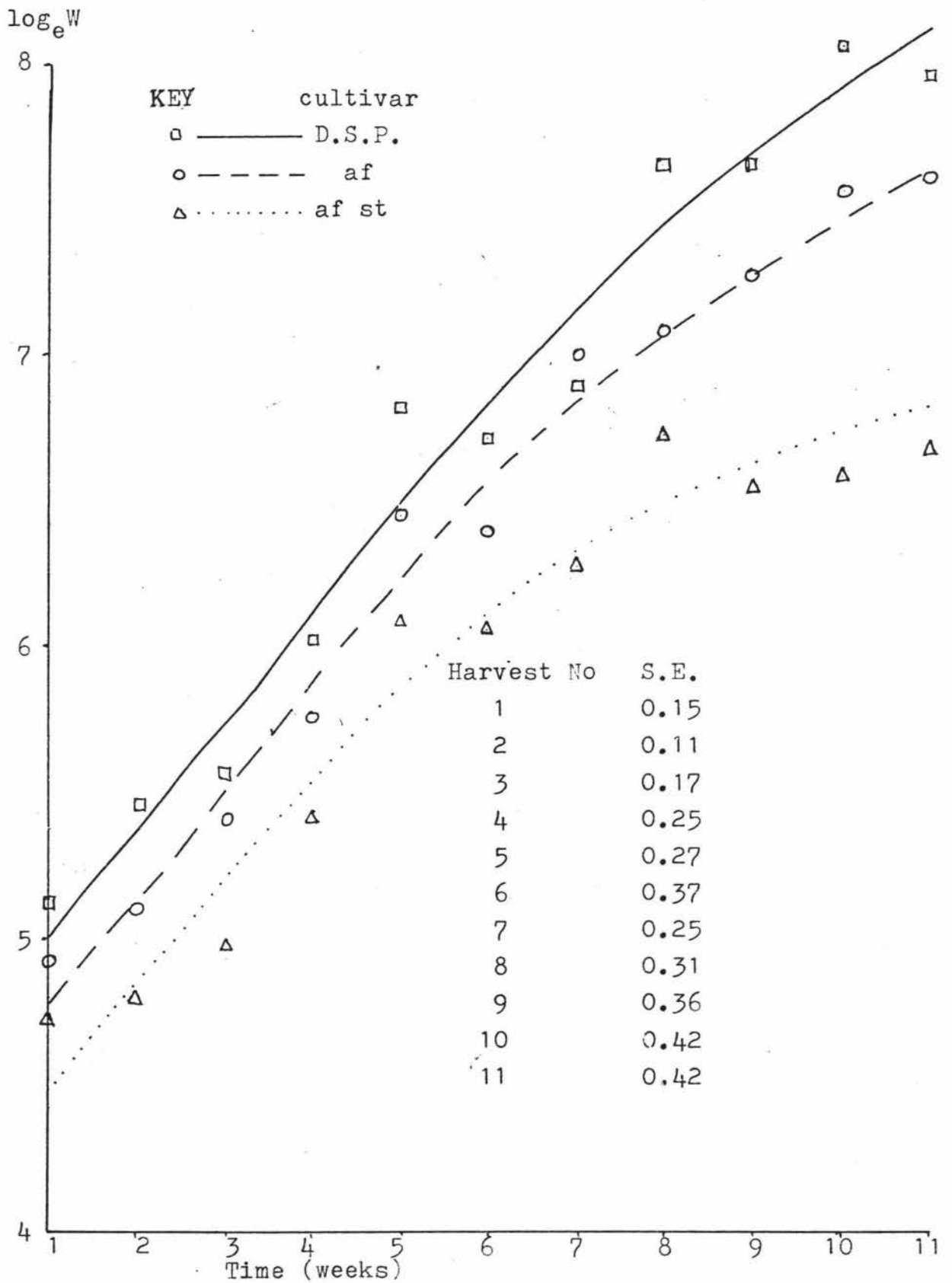


Fig 15.

Effect of cultivar and harvest on total dry mass of peas, fitted to quadratic functions.

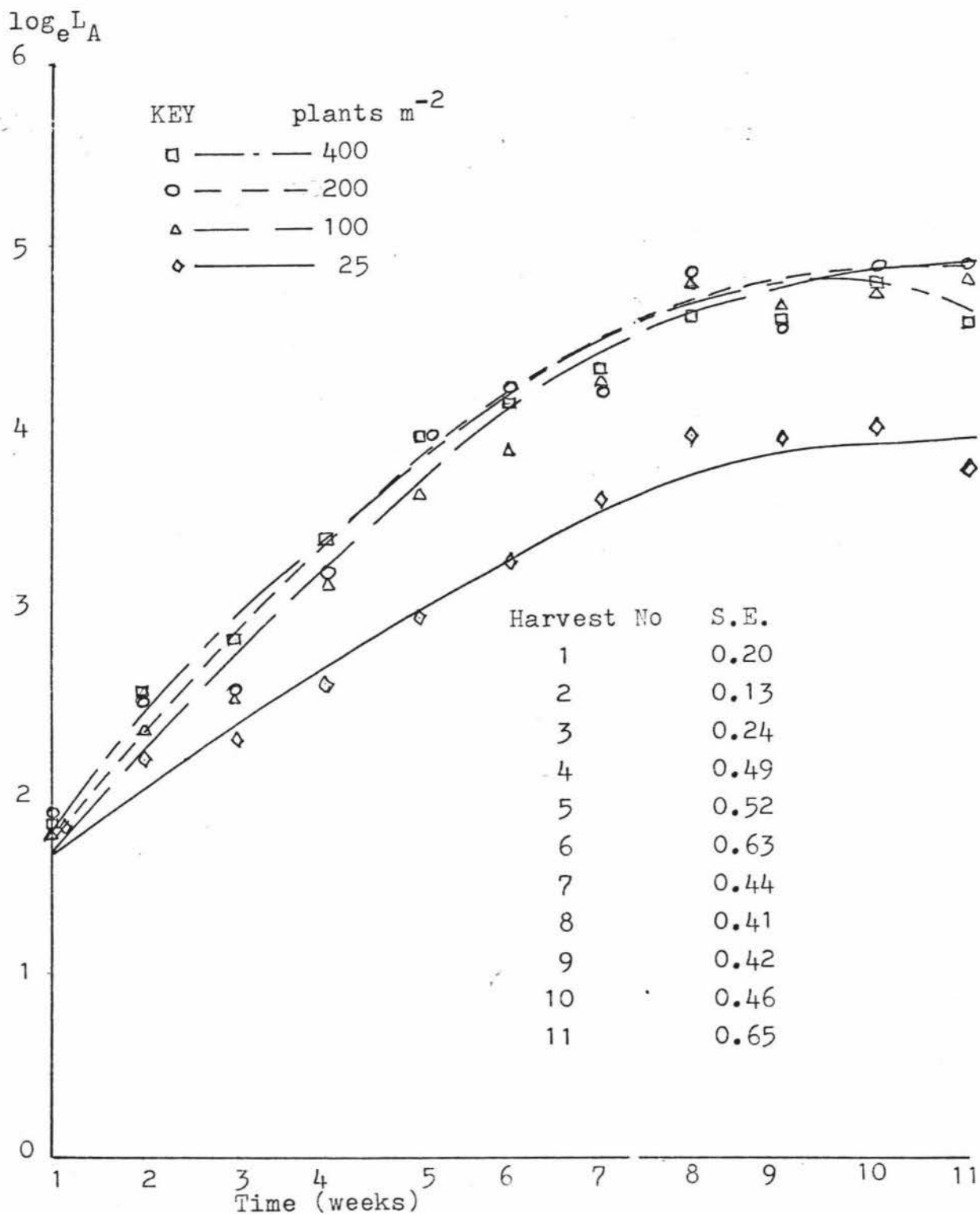


Fig 16.

Effect of plant density and harvest on leaf area of peas, fitted to quadratic functions.

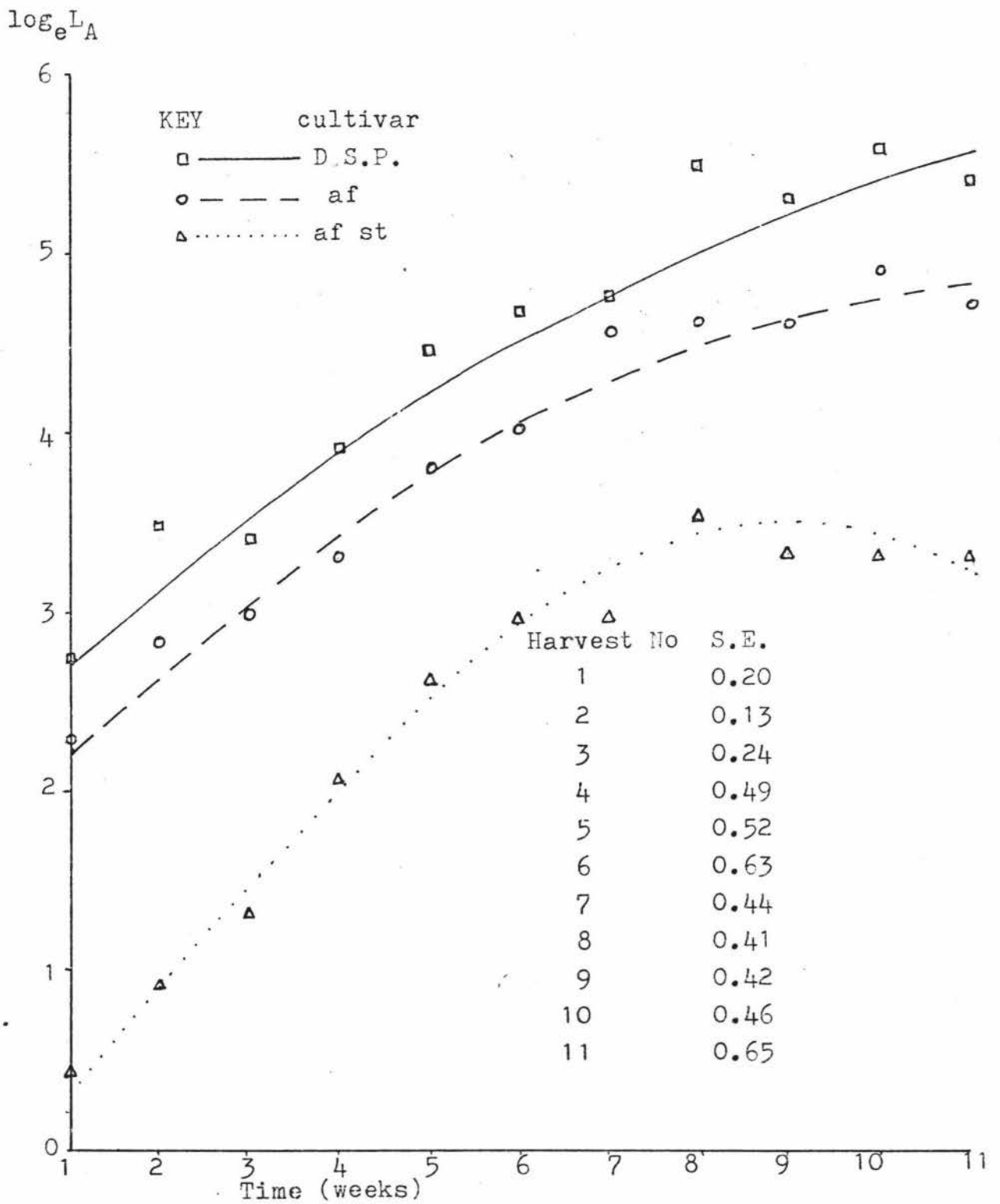


Fig 17.

Effect of cultivar and harvest on leaf area of peas, fitted to quadratic functions.

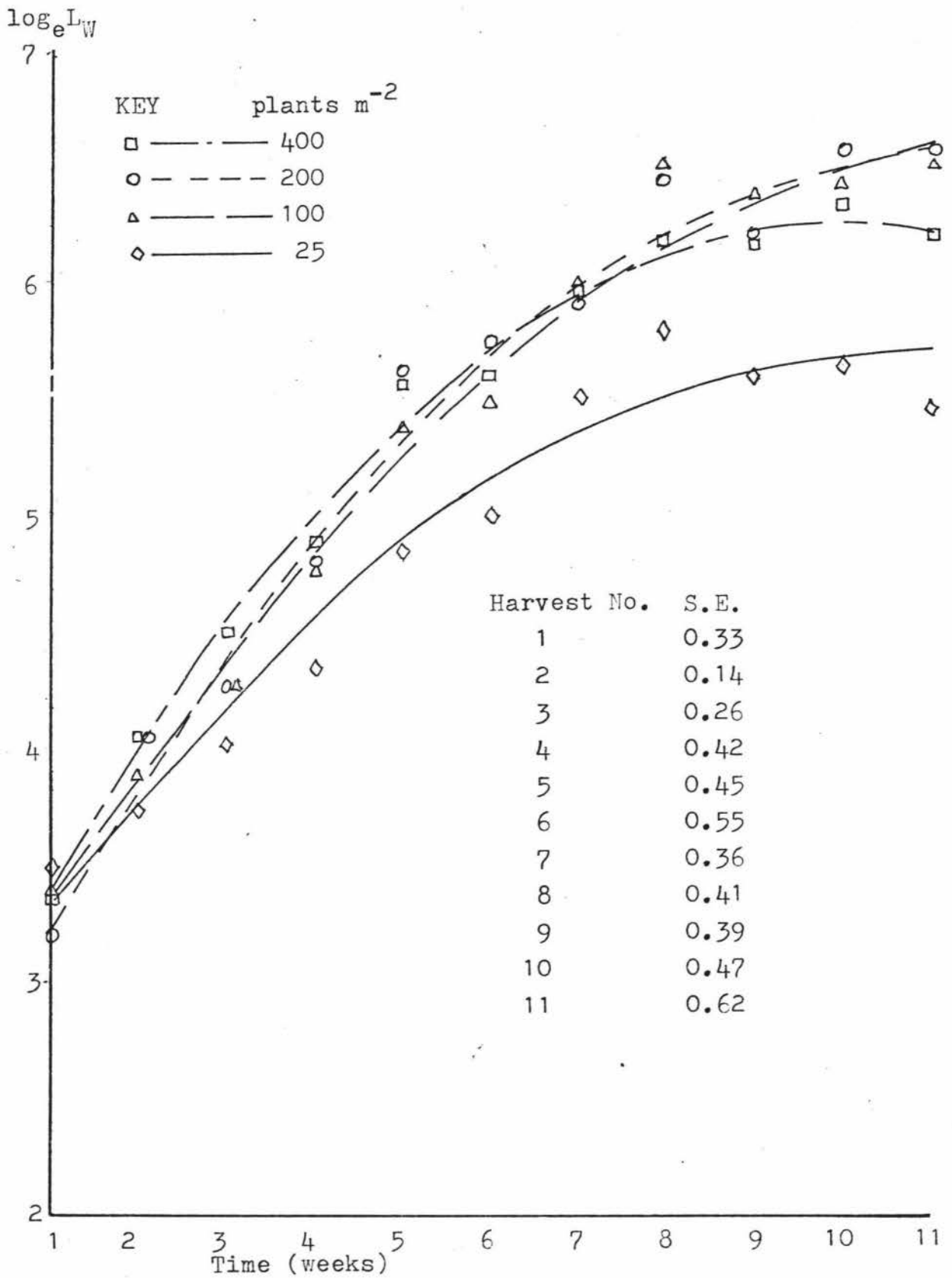


Fig 18.

Effect of plant density and harvest on leaf dry mass of peas, fitted to quadratic functions.

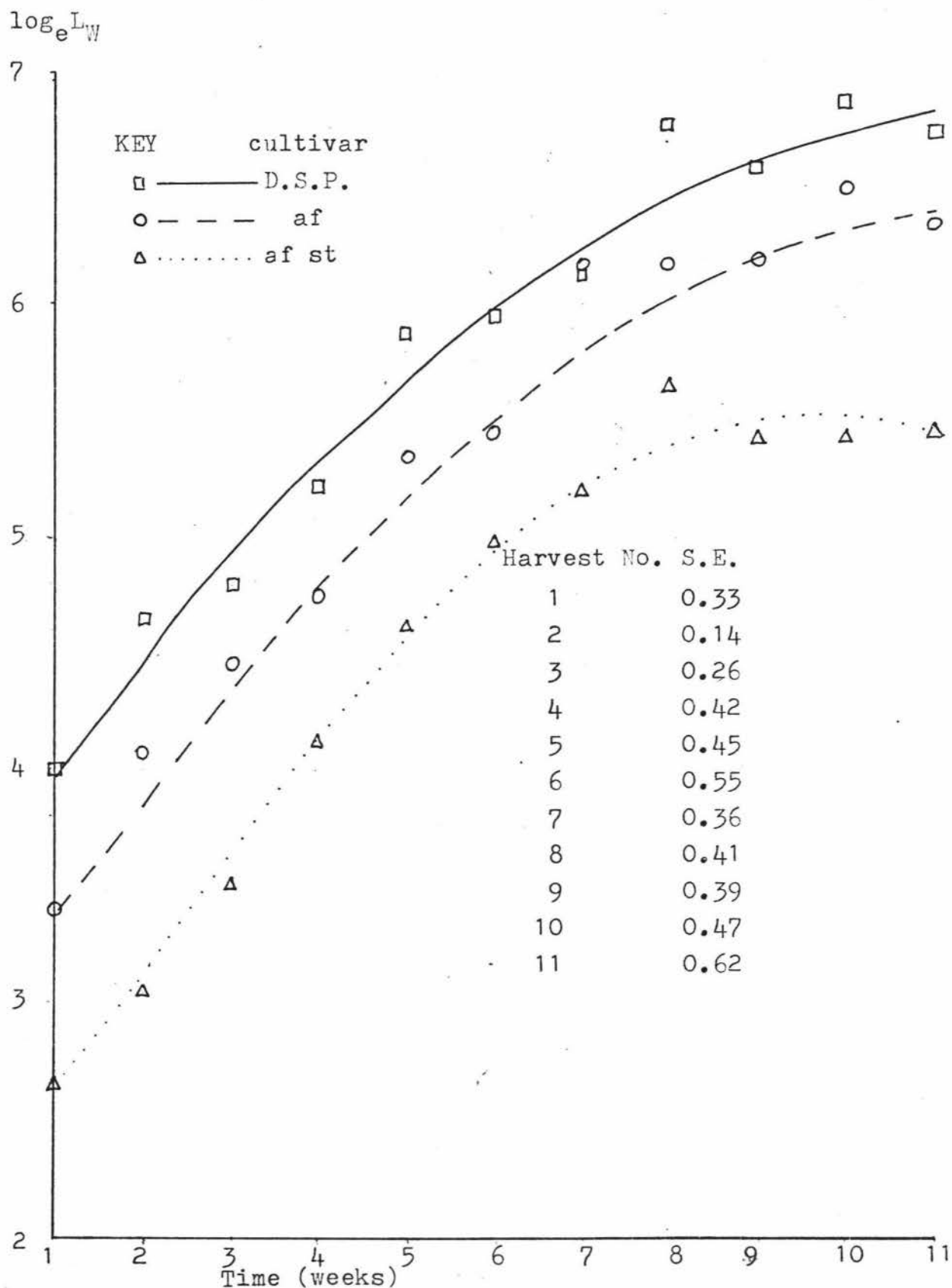


Fig 19.

Effect of cultivar and harvest on leaf dry mass of peas, fitted to quadratic functions.

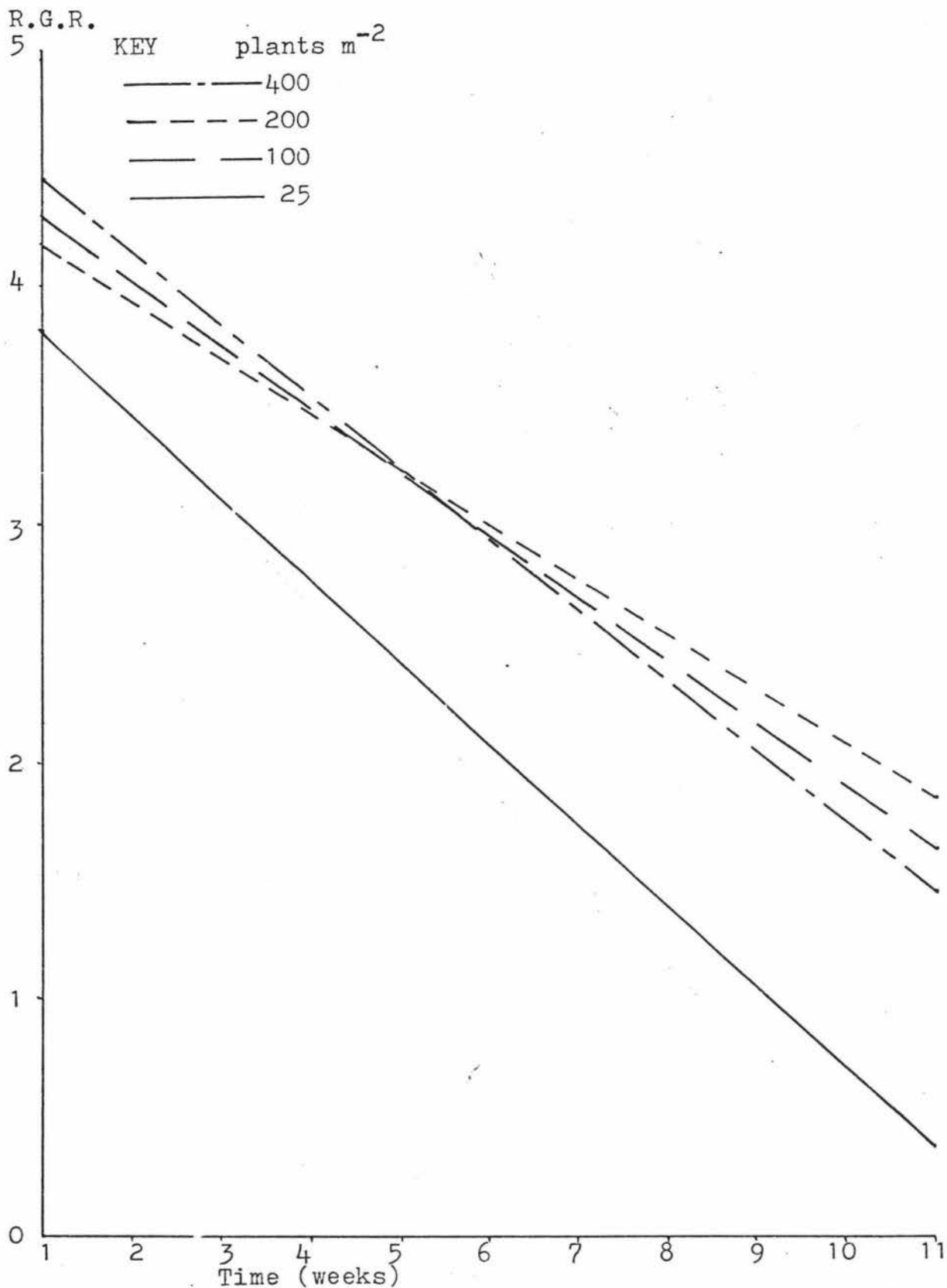


Fig 20.

Effect of plant density and harvest date on Relative Growth Rate of peas, derived from quadratic functions.

R.G.R.

5

KEY cultivar

———— D.S.P.

- - - - - af

..... af st

4

3

2

1

0

1 2 3 4 5 6 7 8 9 10 11  
Time (weeks)

Fig 21.

Effect of cultivar and harvest date on Relative Growth Rate of peas, derived from quadratic functions.

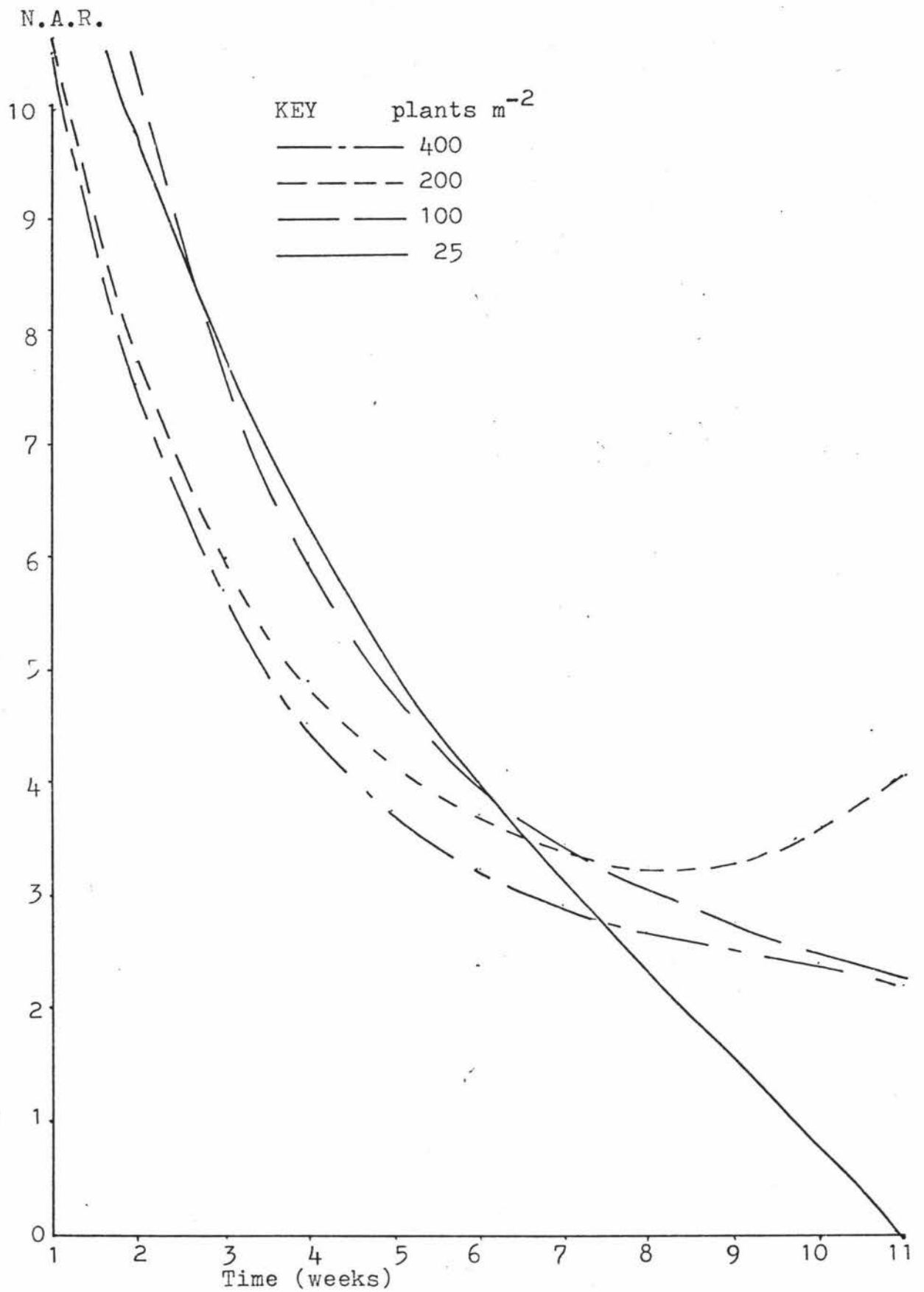


Fig 22.

Effect of density and harvest date on Net Assimilation rate of peas, derived from quadratic functions.

N.A.R.

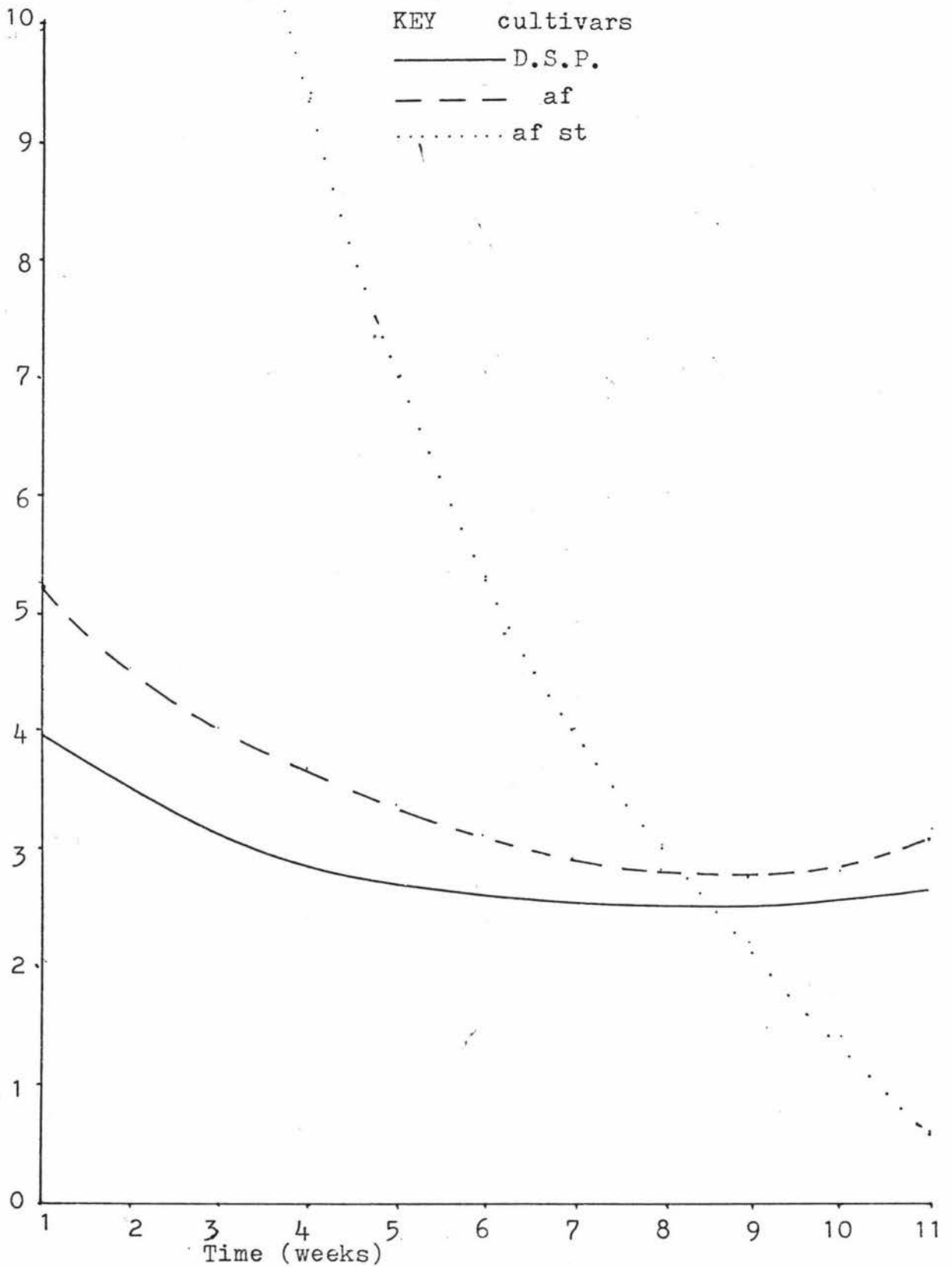


Fig 23.

Effect of cultivar and harvest date on Net Assimilation Rate of peas, derived from quadratic functions.

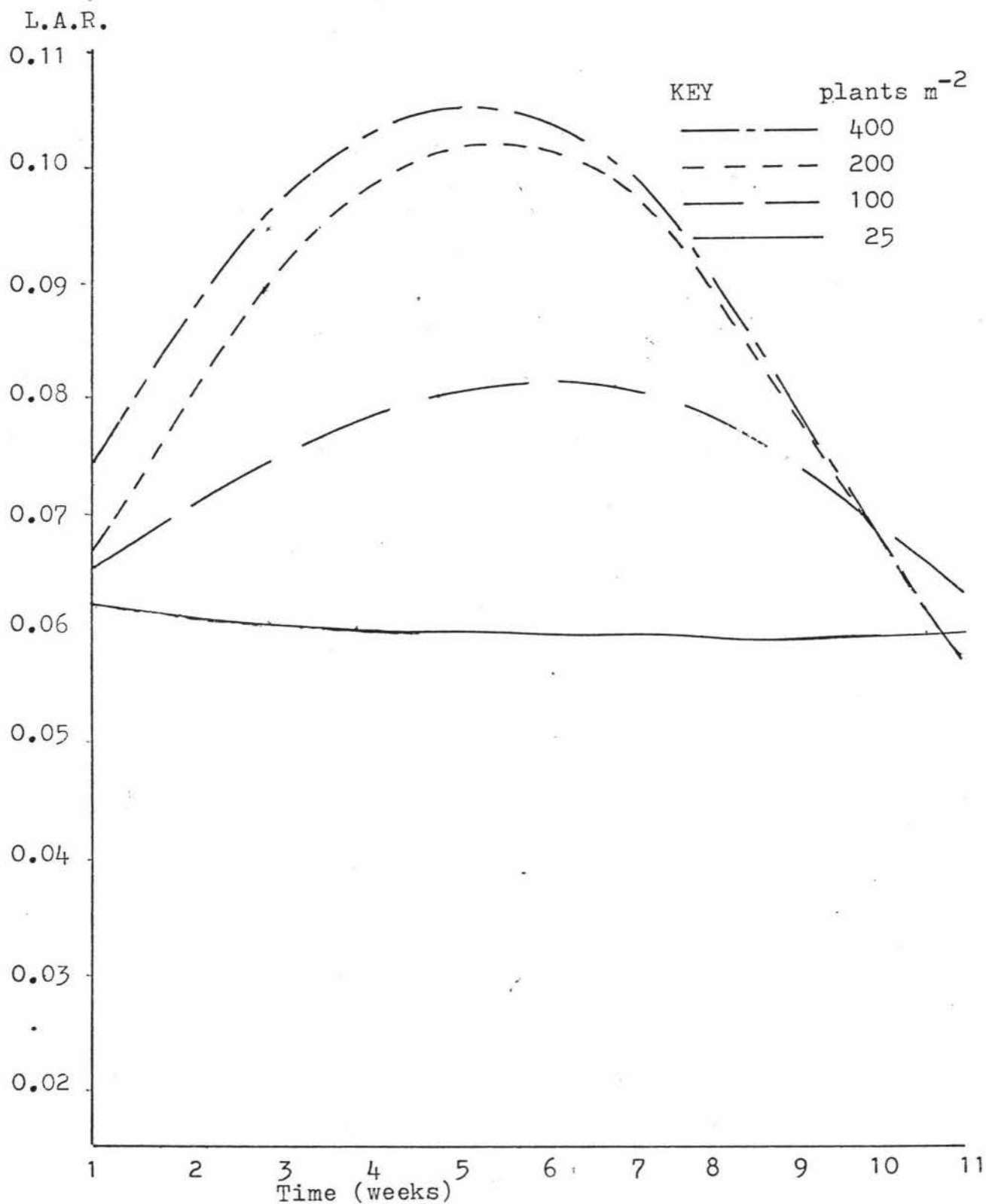


Fig 24.

Effect of density and harvest date on Leaf Area Ratio of peas, derived from quadratic functions.

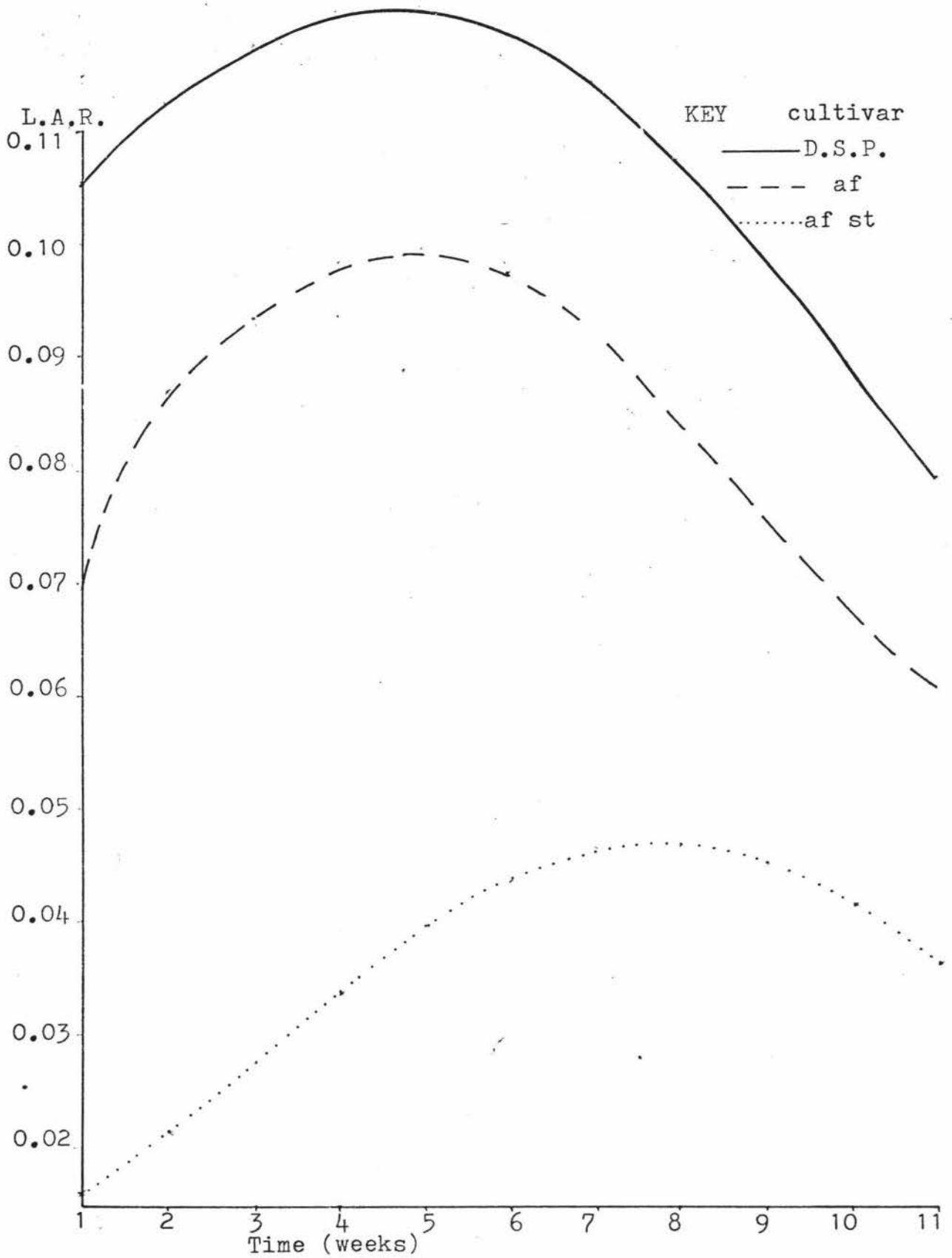


Fig 25.

Effect of cultivar and harvest date on Leaf Area Ratio of peas, derived from quadratic functions.

TABLE 1.

Effect of four plant densities and harvest date on the R.G.R. of peas.

Harvest	$\bar{A}$	$\bar{B}$	$\bar{C}$	$\bar{D}$	S.E.
1	0.0739	0.0669	0.0781	0.0807	0.007
2	0.0940	0.0636	0.0642	0.0608	0.013
3	0.0736	0.0612	0.1147	0.1316	0.036
4	0.0672	0.0812	0.0400	0.1192	0.028
5	0.0231	0.0428	0.0647	0.1196	0.019
6	0.0862	0.0674	0.0533	0.0820	0.056
7	0.0725	0.0564	0.0270	0.0838	0.033
8	0.0255	0.0548	0.0806	0.0608	0.055
9	-0.0207	-0.0246	0.0237	0.0485	0.007
10	0.0437	0.0731	-0.0574	0.0301	0.039
11	-0.0517	-0.0296	-0.0045	-0.0031	0.055

TABLE 2.

Effect of four plant densities and harvest date on the N.A.R. of peas.

Harvest	$\bar{A}$	$\bar{B}$	$\bar{C}$	$\bar{D}$	S.E.
1	0.5366	0.5080	0.7223	0.7058	0.133
2	0.4804	0.3597	0.4096	0.4324	0.085
3	0.3618	0.3524	0.6606	0.9668	0.269
4	0.3366	0.4356	0.2293	0.8483	0.153
5	0.1190	0.2325	0.3865	0.8349	0.106
6	0.5366	0.3747	0.3547	0.6378	0.394
7	0.6334	0.5487	0.2592	0.9012	0.369
8	0.4759	0.9421	1.3137	0.8251	0.868
9	-0.6457	-0.6512	0.6439	1.2452	0.724
10	3.2987	6.4835	-4.1130	1.1094	3.256

TABLE 3.

Effect of four plant densities and harvest date on the  $\bar{L.A.R.}$  of peas.

Harvest	$\bar{A}$	$\bar{B}$	$\bar{C}$	$\bar{D}$	S.E.
1	0.0865	0.0933	0.0721	0.0717	0.013
2	0.1968	0.1663	0.1552	0.1492	0.023
3	0.2056	0.1874	0.1599	0.1458	0.009
4	0.1998	0.1956	0.1600	0.1337	0.010
5	0.1928	0.1851	0.1759	0.1412	0.007
6	0.1897	0.1861	0.1679	0.1401	0.010
7	0.1567	0.1625	0.1354	0.1319	0.009
8	0.0703	0.0695	0.0809	0.0734	0.005
9	0.0489	0.0534	0.0538	0.0620	0.004
10	0.0196	0.0224	0.0208	0.0303	0.004
11	0.0063	0.0078	0.0079	0.0164	0.005

TABLE 4.

Effect of four plant densities and harvest date on the S.L.A. of peas derived from quadratic functions.

Harvest	$\bar{A}$	$\bar{B}$	$\bar{C}$	$\bar{D}$	S.E.
1	0.4080	0.3959	0.3997	0.4138	0.016
2	0.4361	0.4172	0.4008	0.3736	0.006
3	0.4520	0.4282	0.3960	0.3409	0.006
4	0.4545	0.4279	0.3857	0.3141	0.009
5	0.4432	0.4163	0.3700	0.2917	0.012
6	0.4191	0.3942	0.3499	0.2732	0.013
7	0.8843	0.3633	0.3260	0.2578	0.012
8	0.3417	0.3259	0.2994	0.2452	0.011
9	0.2948	0.2846	0.2709	0.2351	0.008
10	0.2466	0.2420	0.2416	0.2276	0.004
11	0.2002	0.2004	0.2124	0.2227	0.004

TABLE 5.

Effect of four plant densities and harvest date on the S.L.A. of peas, derived from logistic functions.

Harvest	$\bar{A}$	$\bar{B}$	$\bar{C}$	$\bar{D}$	S.E.
1	0.4045	0.3900	0.3940	0.3780	0.007
2	0.4256	0.4070	0.3853	0.3662	0.007
3	0.4563	0.4284	0.3756	0.3499	0.009
4	0.4717	0.4390	0.3641	0.3267	0.009
5	0.4463	0.4227	0.3535	0.2963	0.013
6	0.4048	0.3870	0.3515	0.2647	0.015
7	0.3743	0.3517	0.3537	0.2412	0.015
8	0.3572	0.3264	0.3550	0.2284	0.016
9	0.3485	0.3107	0.3554	0.2229	0.017

TABLE 6.

Effect of four plant densities and harvest date on the L.M.R. of peas, derived from quadratic functions.

Harvest	$\bar{A}$	$\bar{B}$	$\bar{C}$	$\bar{D}$	S.E.
1	0.2478	0.2521	0.1959	0.2184	0.02
2	0.3506	0.3513	0.3506	0.3097	0.03
3	0.4415	0.4390	0.4176	0.3990	0.04
4	0.4940	0.4916	0.4996	0.4672	0.05
5	0.4910	0.4930	0.5235	0.4972	0.04
6	0.4334	0.4425	0.4805	0.4807	0.02
7	0.3402	0.3555	0.3862	0.4223	0.01
8	0.2379	0.2557	0.2719	0.3371	0.02
9	0.1487	0.1648	0.1676	0.2446	0.02
10	0.0834	0.0952	0.0905	0.1613	0.02
11	0.0422	0.0494	0.0428	0.0966	0.01

TABLE 7.

Effect of four plant densities and harvest date on the L.M.R. of peas, derived from logistic functions.

Harvest	$\bar{A}$	$\bar{B}$	$\bar{C}$	$\bar{D}$	S.E.
1	0.2647	0.2745	0.1875	0.1899	0.03
2	0.3604	0.3637	0.2765	0.2707	0.03
3	0.4505	0.4439	0.4005	0.3782	0.03
4	0.4918	0.4828	0.5421	0.5041	0.02
5	0.4577	0.4604	0.6026	0.6073	0.03
6	0.3776	0.3939	0.4840	0.6131	0.03
7	0.2973	0.3205	0.3229	0.4986	0.02
8	0.2370	0.2643	0.2317	0.3504	0.02
9	0.1971	0.2289	0.1995	0.2546	0.02

TABLE 8.

Harvest results; fresh green peas at optimum maturity (A.I.S.= 12% ) as affected by density of planting.

DENSITY	400 p.m <sup>-2</sup>	200 p.m <sup>-2</sup>	100 p.m <sup>-2</sup>	25 p.m <sup>-2</sup>	S.E.
<u>Pea fresh mass mg seed<sup>-1</sup></u>	411	390	437	397	25.4
<u>Pea yield g plant<sup>-1</sup></u>	5.57	10.83	11.38	31.11	1.89
<u>Pea yield g m<sup>-2</sup></u>	2230	2167	1138	778	218.5
<u>Number of peas per pod</u>	3.65	4.23	3.62	4.74	0.61
<u>Number of peas per plant</u>	13.6	27.9	26.1	79.5	9.42
<u>Number of pods per plant</u>	3.7	6.6	7.3	16.8	1.9

TABLE 9.

Effect of four plant densities, three cultivars  
and harvest date on  $\overline{R.G.R.}$  of peas.

Harvest	$\overline{DSP}$	$\overline{af}$	$\overline{af\ st}$
1	0.0511	0.0310	0.0025
2	0.0136	0.0522	0.0150
3	0.0450	0.0605	0.0511
4	0.0938	0.1062	0.0812
5	-0.0069	-0.0139	-0.0058
6	0.0198	0.0922	0.0205
7	0.0970	0.0580	0.0331
8	-0.0109	0.0643	-0.0339
9	0.0571	0.0753	-0.0148
10	-0.0567	0.0383	0.0199

Harvest	$\overline{A}$	$\overline{F}$	$\overline{C}$	$\overline{D}$
1	0.0455	0.0404	0.0161	0.0108
2	0.0575	0.0137	0.0223	0.0143
3	0.0406	0.0603	0.0609	0.0470
4	0.0944	0.1266	0.0884	0.0655
5	-0.0076	0.0104	-0.0249	-0.0132
6	0.0701	0.0243	0.0578	0.0243
7	0.0638	0.0612	0.0987	0.0270
8	-0.0137	-0.0109	0.0218	0.0290
9	0.0274	0.0943	-0.0105	0.0850
10	0.0237	0.0036	-0.0216	-0.0035

TABLE 10.

Effect of three cultivars, four plant densities and harvest date on N.A.R. of peas.

Harvest	$\overline{\text{DSP}}$	$\overline{\text{af}}$	$\overline{\text{af st}}$
1	0.4459	0.3084	0.0349
2	0.1212	0.4501	0.5948
3	0.4137	0.6646	1.5899
4	0.9130	1.4283	2.6414
5	-0.0617	-0.3226	-0.3096
6	0.1187	1.0876	0.5721
7	0.8499	0.6644	0.7029
8	-0.1184	0.8220	-0.9299
9	0.7697	1.1837	0.3054
10	0.0386	0.4391	0.6574

Harvest	$\overline{\text{A}}$	$\overline{\text{B}}$	$\overline{\text{C}}$	$\overline{\text{D}}$
1	0.9140	0.4184	-0.2480	-0.0321
2	0.6594	0.2645	0.2136	0.4172
3	0.4697	0.9260	1.0115	1.1505
4	1.1960	1.6207	1.5664	2.2604
5	-0.2823	0.2160	-0.4505	-0.4083
6	0.7824	0.1719	0.8211	0.5958
7	0.5767	0.5567	1.2342	0.5885
8	-0.6998	-0.2208	0.2360	0.3828
9	0.4924	1.4815	-0.1458	1.1836
10	0.6632	0.9715	-0.1977	0.0766

TABLE 11.

Effect of three cultivars, four plant densities  
and harvest date on  $\overline{\text{L.A.R.}}$  of peas.

Harvest	$\overline{\text{DSP}}$	$\overline{\text{af}}$	$\overline{\text{af st}}$
1	0.1598	0.0754	0.0357
2	0.1240	0.0962	0.0228
3	0.1108	0.0921	0.0301
4	0.1066	0.0785	0.0355
5	0.1209	0.0860	0.0388
6	0.1235	0.0927	0.0393
7	0.1135	0.0880	0.0386
8	0.1081	0.0832	0.0411
9	0.0923	0.0660	0.0411
10	0.0810	0.0687	0.0364

Harvest	$\overline{\text{A}}$	$\overline{\text{B}}$	$\overline{\text{C}}$	$\overline{\text{D}}$
1	0.1065	0.0757	0.0688	0.1102
2	0.0944	0.0844	0.0771	0.0680
3	0.0917	0.0837	0.0758	0.0595
4	0.0942	0.0825	0.0690	0.0483
5	0.0956	0.0956	0.0787	0.0576
6	0.1002	0.0964	0.0883	0.0557
7	0.0877	0.0892	0.0820	0.0620
8	0.0792	0.0859	0.0760	0.0688
9	0.0721	0.0689	0.0673	0.0575
10	0.0600	0.0626	0.0660	0.0595

TABLE 12.

Effect of three cultivars, four plant densities and harvest date on S.L.A. of peas, derived from quadratic functions.

Harvest	$\overline{DSP}$	$\overline{af}$	$\overline{af\ st}$
1	0.2917	0.3245	0.1184
2	0.2814	0.2908	0.1212
3	0.2739	0.2682	0.1336
4	0.2688	0.2520	0.1257
5	0.2658	0.2394	0.1273
6	0.2647	0.2289	0.1284
7	0.2654	0.2198	0.1291
8	0.2679	0.2120	0.1292
9	0.2723	0.2061	0.1289
10	0.2785	0.2027	0.1281
11	0.2874	0.2029	0.1271

Harvest	$\overline{A}$	$\overline{B}$	$\overline{C}$	$\overline{D}$
1	0.2485	0.2844	0.2275	0.2191
2	0.2470	0.2595	0.2165	0.2014
3	0.2453	0.2458	0.2080	0.1885
4	0.2434	0.2375	0.2016	0.1794
5	0.2414	0.2315	0.1968	0.1737
6	0.2392	0.2259	0.1935	0.1707
7	0.2369	0.2202	0.1915	0.1704
8	0.2344	0.2144	0.1908	0.1726
9	0.2318	0.2090	0.1913	0.1776
10	0.2294	0.2048	0.1927	0.1856
11	0.2271	0.2028	0.1961	0.1972

TABLE 13.

Effect of three cultivars, four plant densities and harvest date on L.M.R. of peas, derived from quadratic functions.

Harvest	$\overline{DSP}$	$\overline{af}$	$\overline{af\ st}$
1	0.3624	0.2647	0.1335
2	0.3998	0.3060	0.1742
3	0.4289	0.3458	0.2184
4	0.4476	0.3801	0.2626
5	0.4543	0.4050	0.3024
6	0.4484	0.4171	0.3334
7	0.4304	0.4147	0.3521
8	0.4017	0.3985	0.3558
9	0.3647	0.3710	0.3445
10	0.3222	0.3364	0.3199
11	0.2769	0.2990	0.2853

Harvest	$\overline{A}$	$\overline{B}$	$\overline{C}$	$\overline{D}$
1	0.2691	0.2401	0.2539	0.2510
2	0.3165	0.2890	0.2946	0.2732
3	0.3592	0.3378	0.3335	0.2936
4	0.3928	0.3818	0.3679	0.3112
5	0.4132	0.4157	0.3952	0.3248
6	0.4179	0.4345	0.4127	0.3333
7	0.4058	0.4354	0.4188	0.3362
8	0.3783	0.4173	0.4125	0.3333
9	0.3385	0.3827	0.3943	0.3249
10	0.2909	0.3361	0.3656	0.3119
11	0.2402	0.2835	0.3290	0.2955

TABLE 14.

Effect of three cultivars, four plant densities and harvest date on L.A.I. of peas, derived from quadratic functions.

Harvest	$\overline{DSP}$	$\overline{af}$	$\overline{af\ st}$
1	0.2768	0.1965	0.0251
2	0.4646	0.3495	0.0511
3	0.7480	0.5875	0.0962
4	1.1495	0.9243	0.1716
5	1.6801	1.3526	0.2632
6	2.3319	1.8351	0.3800
7	3.0771	2.3069	0.4981
8	3.8689	2.6896	0.5994
9	4.6545	2.9209	0.6570
10	5.3909	2.9728	0.6611
11	6.0536	2.8615	0.6156

Harvest	$\overline{A}$	$\overline{B}$	$\overline{C}$	$\overline{D}$
1	0.3792	0.1760	0.0883	0.0212
2	0.6695	0.3192	0.1348	0.0302
3	1.1190	0.5435	0.2038	0.0425
4	1.7600	0.8733	0.3018	0.0587
5	2.5945	1.2873	0.4340	0.0787
6	3.5773	1.7818	0.6022	0.1014
7	4.6165	2.2962	0.8038	0.1263
8	5.6047	2.7548	1.0328	0.1515
9	6.4360	3.0835	1.2818	0.1752
10	7.0622	3.2285	1.5462	0.1962
11	7.4912	3.1733	1.8298	0.2133

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