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THE EFFECT OF TEMPERATURE ON
GROWTH AND DEVELOPMENT
OF PEAS

A thesis presented in partial
fulfilment of the requirements for the degree
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ABSTRACT

The influence of temperature on the growth and development of the garden pea was studied at Massey University during 1978-79. Cultivars with single and multiple (double and triple) podding characteristics were grown in a greenhouse experiment with high, medium and low temperature treatments, a field experiment with four successive sowings and a climate room with alternating high and low temperature treatments between vegetative and reproductive growth phases. Plant response to temperature was examined using growth analysis and component analysis techniques.

High temperature produced a smaller plant with shortened internodes and a delay in pod set. Net assimilation rate was closely linked with final fresh weight yield and harvest index. There was a direct relationship of net assimilation rate and growth duration to yield when net assimilation rate was not limiting; fresh weight yield increased in direct relation to the number of yield components. High temperature effects complicated by flower and pod abortion indicated that the behavior of yield components must be considered along with harvest index as a selection criterion for earliness and high yield in peas.

In all cultivars, the number of yield components decreased as temperature increased, particularly the number of pods per node when high temperature occurred during the vegetative phase. High frequency podding cultivars exhibited the highest instability. Net assimilation rate and competition for assimilates between yield components (sinks) determined the number of yield components that were retained. No one component was identified as the main source of variation in pea yield. Positive interactions between components of yield were identified with yield increases when net assimilation rate was nonlimiting and yield decreases when net assimilation rate was limiting. Negative interactions were associated with yield stability. A balance of negative and positive interactions between components of yield combined with a nonlimiting net assimilation rate (assimilate supply) is needed in high yielding pea cultivars.

INTRODUCTION

The commercial production of peas for processing requires a high yield of green peas at a precise stage of maturity. The final fresh weight yield at this "optimum harvest date" is influenced to a large extent by the temperature of the environment during the growth and development of the pea plant. The influence of temperature on final yield has been well documented, high temperatures in excess of 25 C reduce yield. However, there has been little research into what morphological changes occur and how these changes relate to final yield. Further, most studies have been limited to one or two cultivars with little reference to comparisons between cvs of different node-podding characteristics. For these reasons cvs exhibiting three distinct node-podding characteristics were studied in three experiments. Growth analysis and yield component analysis techniques were used to examine structural and morphological changes that occurred in response to temperature and how these changes related to final yield.

The first experiment examined the growth and development of the pea plant at three temperatures in the greenhouse. The second experiment was an extension of the first and examined the pea plant in a succession of four field sowings. Both studies confirmed the results of many reports that high temperature reduced yield, however the yield obtained is a result of a complex interaction between components of yield and a critical balance in dry weight distribution between vegetative and reproductive growth. Yield component analysis was most useful in assessing the "plastic" nature of the pea plant, namely, how the pea plant adjusted fresh weight yield to prevailing conditions.

The results lead to the third experiment which was concerned with the question of the changes observed in the components of yield and whether these changes were a result of a greater sensitivity to temperature at

some particular developmental phase. Pea plants were grown in climate rooms exposed to high and low temperatures during the vegetative and reproductive phases of growth and development. Component analysis techniques were used to assess the changes in yield components to temperature treatment and how these changes related to final fresh weight yield.

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LIST OF ABBREVIATIONS

<u>Abbreviation</u>	<u>Meaning</u>
AIS	alcohol insoluble solids
C	degrees celsius
cv	cultivar
DF	degrees of freedom
Dp	double-pod cultivar
Dp (Pk)	double-pod cultivar (Puke)
Dp (Vf)	double-pod cultivar (Victory Freezer)
FW	fresh weight
LAR	leaf area ratio
LWR	leaf weight ratio
n	podding node
NAR	net assimilation rate
OHD	optimum harvest date
R	reproductive growth phase
RGR	relative growth phase
SLA	specific leaf area
SE	standard error of mean
Sp	single-pod cultivar (William Massey)
SpI	single-pod leafless cultivar
Tp	triple-pod cultivar (Puget)
V	vegetative growth phase
#	number

CHAPTER 1

Review of Literature

1.1 Classification and Use

Pisum sativum, known simply as peas, is a tendril - climbing, cool season, hardy annual. Peas are grown for the immature fresh, edible green seeds (peas) and for the dry, mature seeds.

Pea cultivars now used in horticulture are classified into two groups according to color: dark green, those with pigment in the skin; and light green, those with less pigment (Anon 1977). Light green cultivars are usually preferred for canning, largely for aesthetic reasons based on appearance of the processed product. Dark green cultivars are only occasionally used for canning and are generally used as fresh market peas.

Pea cultivars are sometimes classified according to seed characteristics; smooth and wrinkled characteristics which are related to the starch type present in the cotyledons (Anon 1977). Smooth seeded cultivars are preferred for dry seed production, wrinkled seeded cultivars for processing in the immature form.

Historically, pea cultivars have also been classified according to plant type, indeterminate and semi-determinate. Generally, semi-determinate cultivars are relatively dwarf in habit and many produce more than one pod at each podding node under favorable conditions. Semi-determinate cultivars which produce their first flower from the fifth to eighth node are early maturing; those which begin flowering from the ninth to eleventh node are late maturing (Tedin and Tedin 1923).

Because of their relatively heavy, concentrated (in time) set of pods and the high ratio of pods to vine weight, semi-determinate cultivars are easier to harvest. They therefore have become the established plant type for commercial production, whether for fresh market or for processing.

1.2 Origin and Breeding Development

Little is known of the ancestry of the garden pea, but it seems likely that its centers of origin are in the Abyssinian and Mediterranean basin regions, though a diversity of forms can also be seen in many Asiatic areas (Yarnell 1962). Peas have been an important crop since the eleventh century, but no extensive breeding was undertaken until the latter half of the nineteenth century when large numbers of cultivars were developed. Cultivated peas that are now commonly grown have probably arisen from a small genetic base.

In order to reduce the loss in potential yield due to the spread in maturity, plant breeders are attempting in several ways to increase the simultaneous development of pods on any given plant. One method involves increasing the number of pods at any given node. The number of pods per node in most present day commercial cultivars rarely exceeds two, but genetic variants are available which have as many as six pods per node (Fell 1976).

Other research studies involve the simultaneous development of pods at several successive nodes and there is the continual effort to increase the number of peas per pod beyond the eleven found in the best cultivars. Finally, there is the possibility of exploiting the fasciated condition

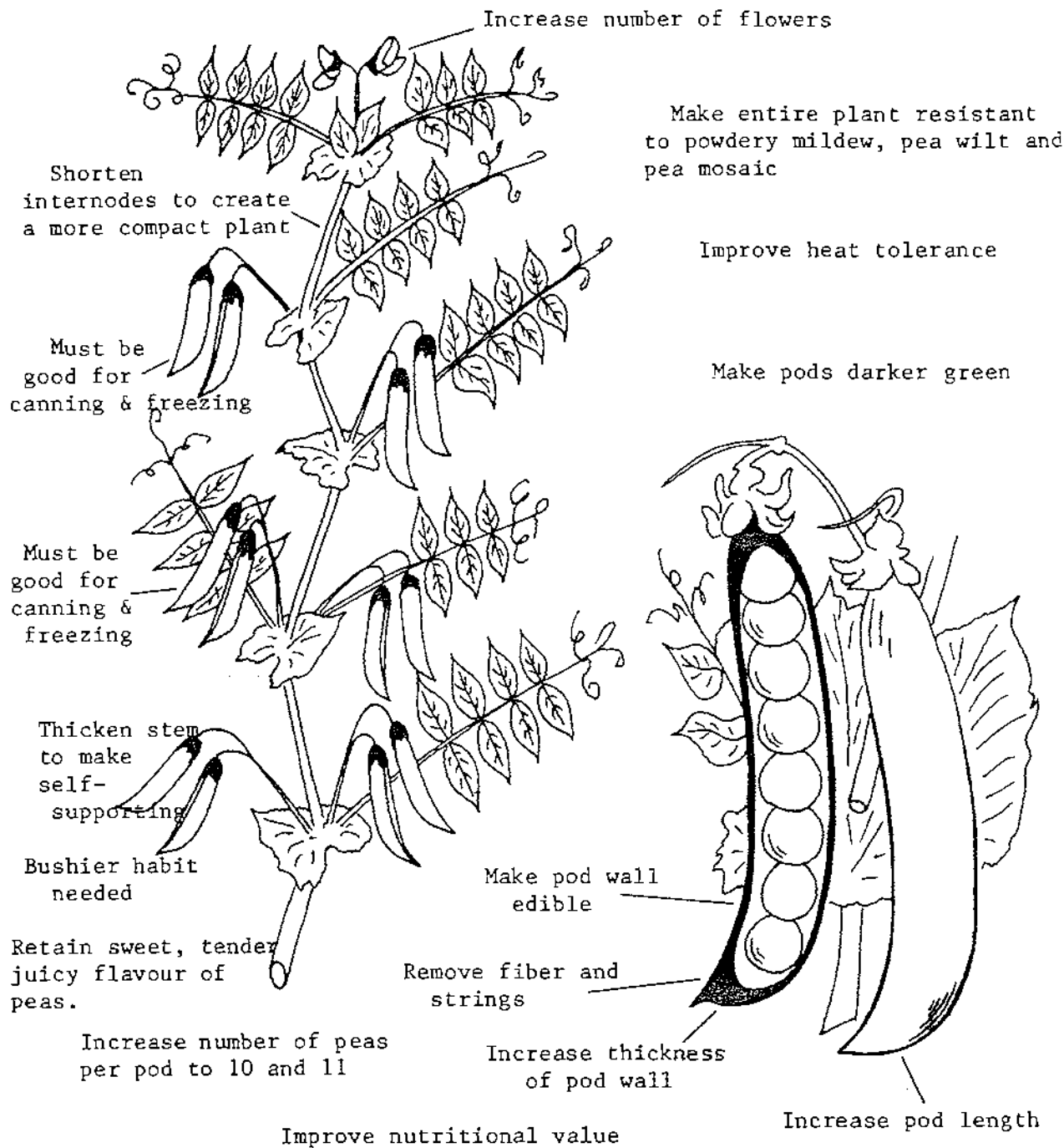


Fig. 1.1 The pea plant of the future

which results in the compaction of the upper nodes and the simultaneous development of many pods (Snoad and Davies 1972).

During the 1940's the requirements for pea breeding changed. Until that time peas were grown mainly for marketing as a green crop and for harvesting as packeted, dried peas; only a small acreage was grown for canning. Breeders sought to increase yield by introducing taller and larger leaved plants.

With the introduction of the once-over mechanical harvest (viners) techniques associated with the development of the quick-freezing industry, entirely new objectives in the breeding of peas were required. The plants now had to be as prolific as possible and much smaller to facilitate easier harvesting. With a once-over method of harvesting, as many seeds as possible had to be at the same stage of development for processing at any given time. Even in current cultivars not all seeds will be at the same stage so that a portion of those harvested will be over-mature and under-mature. The correct stage is determined by taking measurements with a tenderometer or maturometer and considerable effort is devoted to timing to within a matter of hours the precise stage for harvesting (Reynolds 1966). Speed of harvesting is therefore an essential ingredient of success in this part of the industry.

1.3 Growth and Development

There is little information on the inheritance of morphological patterns in roots. Shoot growth affects root growth indirectly because of competition for a limited supply of assimilates (Lovell 1971).

The pea usually has only one dominant shoot (Maurer, Jaffray and Fletcher 1966), however, Husain and Linck (1967) found that low temperatures

Pea Plant (Vegetative)

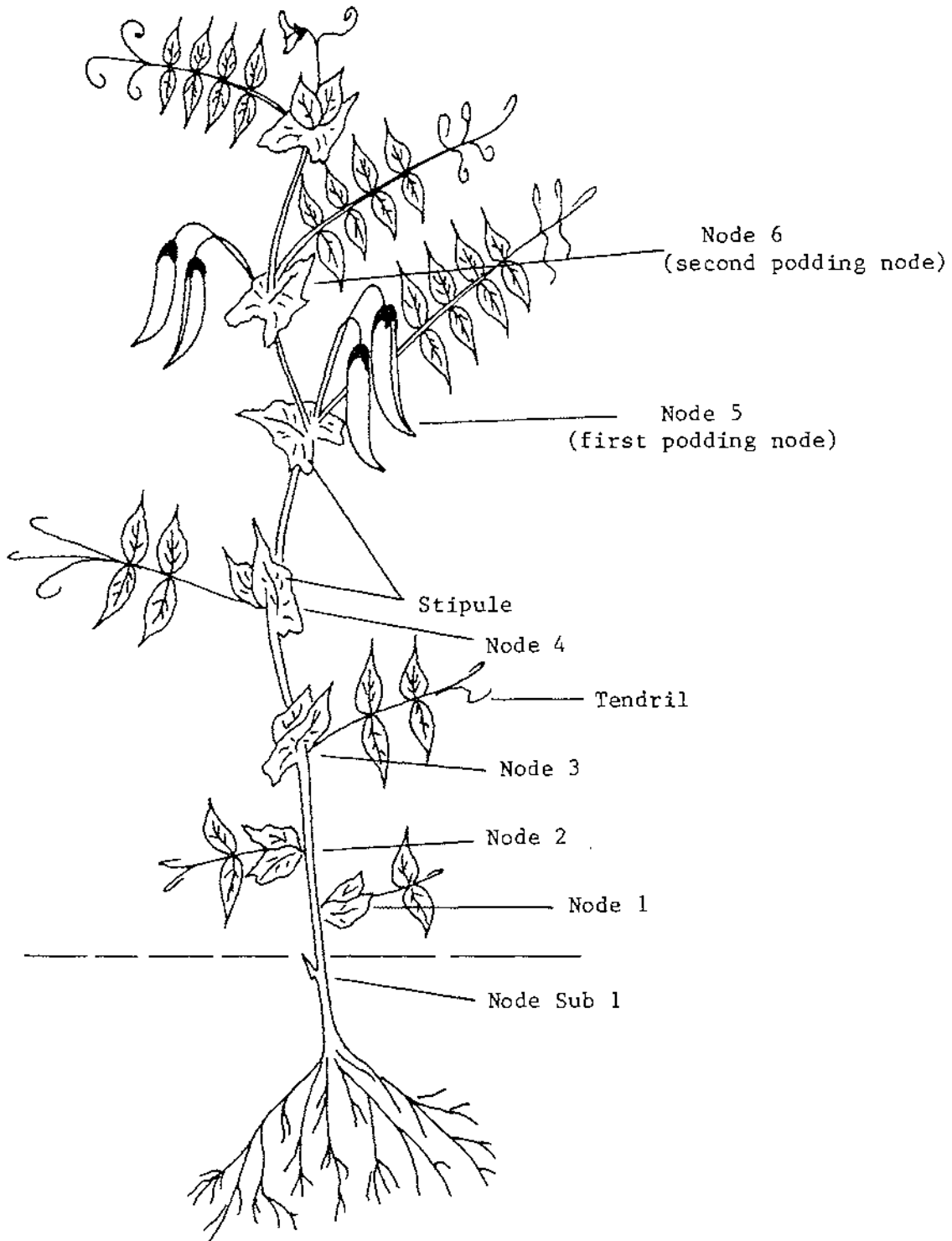


Fig. 1.2 The morphology of the pea plant relevant to the definition of development stages

reduce growth rates and a short period of cooling inhibits apical dominance and causes the plant to throw laterals; the effect is not reversed when the plants are returned to higher temperatures. Auxin transport may be involved. Generally, the first two nodes from which tillers may originate are found below the soil surface producing vestigial leaves. They are normally designated as node one. Growth of the stem is affected dramatically by simple genetic factors. Stem length is affected by flowering time (Wellensiek 1973). It was once believed that tall cultivars which tend to flower later than short-stemmed cultivars produced a growth stimulating factor which was synthesized at a higher rate in tall cultivars. However, reciprocal grafts between tall and short cultivars supports the theory that growth can be interpreted as a balance between growth stimulatory and growth inhibitory processes in the plant (Brian 1957).

Successive nodes develop as the stem elongates. A compound leaf develops at each node and it can be considered growth and elongation at a given node is completed as each compound leaf is fully expanded (Anon 1977). Patterns of leaf development are genetically controlled and breeders speculate that lamina expansion is physiologically controlled independently of the branching system of the leaf axis and main veins. Smillie (1962) observed that during the early vegetative growth of peas the first-formed leaves each established a period of approximately five days when they maintained a near maximal activity in photosynthesis. The attainment of the maximum rate of CO_2 uptake often coincided with the completion of leaf expansion. Pea leaves reach their maximum photosynthetic activity at the time of full expansion, losing activity thereafter at a rate somewhat faster than the loss of chlorophyll (Smillie 1962). The longevity of the optimum period for later leaves is variable and is affected by genetic and environmental factors. The maximum rate of CO_2 uptake attained by each successive leaf of peas

appears to be a basic characteristic of the genotype and not markedly influenced by the transition from vegetative to reproductive phase. This does not exclude the possibility that developing pods can increase the overall output of adjacent leaves by increasing the period which they function at near maximum activity (Smillie 1962).

More recent evidence has indicated that growth of fruit influences markedly the photosynthetic potential of the subtending leaf. There are two phases of markedly increased rate of net CO_2 uptake, one corresponding with the attainment of maximum elongation of the pod, the other with the main period of swelling of the seeds (Flinn 1974).

Stipules are found at the petiole base of each foliage leaf; with upper leaves the terminal and sometimes subterminal leaflets are present as tendrils. Photosynthetic activity of stems and petioles does not appear to have been studied but stipules (Flinn 1969) and tendrils (Snoad and Davies 1972) are reported to be as efficient in photosynthesis (measured as CO_2 uptake) as sister leaflets.

With increase in size and complexity of leaves there is a corresponding increase in length and diameter of successive internodes, this trend being evident at least until flowering is under way. The development which takes place between nodes follows a set pattern and by describing stages between nodes it is possible to relate the effect of environment to the growth and development of pea plants over relatively short time intervals.

At about the time of initiation of flower primordia, root growth reaches a maximum and then begins to decline as flowering commences (Salter and Drew 1965). Reproduction is by means of auxiliary inflorescences bearing one or more flowers, the basic pattern of fruit maturation

being therefore a sequential one (i.e. the peas contained in the pods in the lower nodes are larger and more mature than those appearing at succeeding nodes). Shoot morphology and reproductive behaviour may be greatly influenced by genotype and environment (Evans 1975). It would seem, however, that much of the variation in flowering behaviour in peas is regulated through an unknown flower promoter-inhibitor balance (Murfet 1973).

The pea is self-fertile and its flowers are usually self-pollinated (Cooper 1938). Pollination takes place in the late bud stage, 24-36 hours before the flower is fully open, and by the time of full blossom, fertilization has taken place (Cooper 1938). It is usual for all ovules of a pea pod to be fertilized, but a considerable proportion of them may fail to develop into mature seeds. Linck (1961) showed that space restrictions in the pod may cause ovule abortion. High frequencies of ovule abortion at the pre-fertilization stage has been observed in peas grown under adverse environmental conditions (Linck 1961).

Rapid increases in pod length and width occur during early growth and these are accompanied by a thickening of the pod wall. Gas exchange on the pod's outer surface is facilitated by the presence of stomata, although their density is much lower than on the surfaces of stipules or leaflets (Flinn 1969).

The initial increases in length and width and then in wall thickness of the pod allow for maximum fresh weight before the contained seeds become active in laying down starch and sugar storage reserves (Flinn and Pate 1968). After this pods lose dry matter and final drying out is accompanied by a rapid loss of chlorophyll and photosynthetic capacity.

1.4 Components of Yield

The pea is a highly plastic plant (capable of altering its pattern of growth and development) which possesses a number of physiological mechanisms by which it adjusts its yield to prevailing conditions. These changes considerably complicate the picture of yield production, but because of the plastic responses, once made, cannot be reversed, they are preserved in the plant's structure until harvest.

1.4.1 Branches

Lateral branches from the main stem under normal commercial conditions contribute only a small fraction of the total yield (Hardwick and Milbourn 1967). The amount of branching is a cultivar characteristic which is plastic, branches are completely suppressed at high plant densities. Branches arise at the basal nodes of the main stem or at a later stage, just below the first podding node. The pods on both types of branches are younger than those on the main stem and when cultivars with a propensity to branch are grown at low density, they may yield well, but will also have a wider range of pea maturity than is commercially desirable. Branching is therefore unlikely to be a desirable breeding characteristic unless the lag in development of branch pods can be overcome (Singh and Singh 1972).

1.4.2 Podding Nodes

The inflorescence of the pea is racemose, bearing one or more flowers in the axil of each leaf in the upper part of the stem which is of variable length. The number of nodes on the lower or vegetative part of the stem (i.e. below the first podding node) is genetically determined and in mid-summer cultivars at least, the number of vegetative nodes cannot be altered by day length treatments (Moore 1964).

The number of flowering nodes on the upper flowering part of the stem can again vary between cultivars, but it also varies with plant density. Harwick and Milbourn (1967) observed that widely spaced plants produced more flower primordia than closely spaced plants. The number of nodes that eventually bear flowers is less than the number laid down earlier. This must reflect competition within the plant, possibly for assimilates (Lockhart and Gottschall 1961). The abortion in upper nodes may appear to represent a loss of potential yield, but had they been retained they would only have contributed small, immature peas with a resultant increased range in maturity of the harvested sample. As the pea is harvested when young, an increase in the component "number of podding nodes" causes only a relatively small increase in yield, and this component is only worth increasing in the vining crop if the lag between nodes can be reduced.

1.4.3 Number of Pods per Node

The number of pods per node is an important yield component. Most cultivars in current commercial use carry either one or two pods per node. Early workers in pea breeding programmes recognized that one of the best ways to increase yield of peas which mature at the same time was to increase the number of pods produced at each node (Wellensiek 1925; Lamprecht 1952).

The environmental contribution to variability of pod number per node has been shown to be considerable (Clay 1935; Lamprecht 1952; Ibarbia and Bienz 1970). Fluctuations in the number of pods at each node must be the outcome of differences either in number of pods produced or in numbers lost. Pods are produced by the apical meristem as flower primordia, in regular succession, starting when the plant enters the phase of ripeness to flower. From this stage onwards, pairs

of primordia are laid down in the axil of every node produced. Of the pairs of primordia the first primordium always becomes a flower; but the second may develop into either a flower or a blind stalk-like appendage. The failure of the second primordia to develop represents a loss of potential yield and is of considerable commercial importance.

Potential yield may be reduced secondarily if pods, once formed, abscise. At commercial plant densities most flowers turn into pods and few are abscised. Up to forty percent losses of pods have been observed in very dense populations of peas, but it is not clear how far this can be ascribed to true abscission and how far it is the result of pods becoming casualties in the mass of rotting leaves which develop at the base of the crop (Hardwick and Milbourn 1967).

However, breeding multipod cultivars of the normal type has not lost its practical importance. Though the influence of pod number on the uniformity of maturity is slight, that on the yield per plant is large (Drijfhout 1972). Drijfhout noted that with a good pod frequency and about an equal number of seeds per pod the yield can increase almost proportionally to the number of pod places.

1.4.4 Number of Peas per Pod

Multiple regression analysis indicated that the number of seeds per pod was an important yield component and accounted for great variability in seed yield of forty pea cultivars (Singh and Singh 1972). When a pea pod is shelled it is often found to contain, in addition to the fully grown peas, a few aborted ovules at either end of the pod which have not developed (Cummings 1914). The maximum number of peas per pod is a cultivar characteristic which can be manipulated by the plant breeder. The manipulation of pea number will be to the advantage

of yield, provided that a high number of peas per pod is not achieved at the expense of the other components of yield.

1.4.5 Weight per Pea

Individual pea weight is quite unlike the other components of yield. It cannot be assumed that an increase in the value of this component will cause a corresponding increase in yield because the vining pea is harvested at a date decided by the stage of maturity of the crop. Stage of maturity is a function of pea weight and if the stage of maturity is fixed then pea weight is not free to vary (Hardwick and Milbourn 1967).

The situation is further complicated by the pea's indeterminate growth habit which results in the crop being made up of a range of pods at different stages. To use pea weight as a component of yield is an oversimplification; there is in fact a range of pea weight, decreasing by an approximately constant amount at each succeeding node (Hardwick and Milbourn 1967).

The range of pea weights that occurs at the vining stage does suggest that some potential yield is foregone by once-over picking. If the plant breeder could produce a cultivar having a smaller lag between nodes, the yield would be increased by a larger contribution from the upper nodes and the product would be much more homogeneous.

1.5 Pea Maturity

The relationship between yield and maturity is of considerable economic importance. In the past it has not been possible to find a simple universal curve which would relate yield and maturity. The

relationship varies between seed rates and between seasons (Ottoson 1958; Berry 1966). It is suggested that this is because the age of the pod population varies. It has been found that if the differences in this respect between populations are taken into account by comparing nodes separately, a repeatable relationship emerges between maturity and pea weight (Hardwick and Milbourn 1967).

1.6 Influence of the Environment

1.6.1 Light (day length)

Kopetz (1941, 1943) observed that early cultivars were essentially day-neutral whereas the flowering of late cultivars was significantly delayed by short days. Haupt (1957, 1969) suggested that the absence of a photoperiod response in early cultivars was not so much a consequence of a particular genetic situation but rather followed automatically because flower initiation takes place so rapidly after germination that there is no opportunity for the seedling to respond to photoperiod. Barber (1959) and Aitken (1971) classed the pea as a long-day plant which will bloom in continuous light. Early maturing cultivars are the least sensitive to photoperiod while mid and late season cultivars respond and are induced to bloom earlier by an increased day length. The latter are impeded by short days with respect to both number of pods and days required to bloom (Aitken 1971). Barber (1959) and Marx (1969) found that flowering of late peas showed little change as the photoperiod decreased from 24 to approximately 20 hours but as the photoperiod further decreased the flowering process began to rise slowly at first and then more steeply between a photoperiod of 16 and 12 hours. Aitken (1978) later found that flowering in peas was related to photoperiod and also temperature. Aitken measured the development rate in peas and saw that it was controlled directly by temperature. She found that in each successive sowing from spring to winter as the

temperature increased there was an increasing sensitivity to photoperiod and a lesser sensitivity to temperature. Along with the increasing temperatures pods grew less efficiently with respect to respiratory CO_2 efflux (Hole and Scott 1983) and as earlier observed by Phumphrey, Ramig and Allmaras (1979), yield in peas as a result decreased as temperature increased.

There is clear evidence that the photoperiod response is reduced by low temperatures (Barber 1959; Wellensiek 1969) and may even be nullified if vernalization is followed by continued cold nights (Murfet and Reid 1974). Flowering response to temperature has been interpreted under the "balance" concept noted by Murfet (1971). It is assumed that the reaction producing inhibitor has a higher temperature coefficient than the reaction controlling the formation of promoter, and secondly, that inhibitor production is suppressed by continuous light.

Much time and effort has been devoted over the years to the search for the endogenous substances believed to regulate flowering in peas. Despite these efforts, the flowering hormones have remained elusive. However, it is proposed that the level of these hormones may vary in a quantitative manner with flowering being evoked by the gradual achievement at the apex, of a balance (or ratio) of promoter to inhibitor in excess of a critical ratio (Murfet 1971). Leaves are believed to play a prime role in the formation of the flowering hormones, yet the relative proportions of the hormones contributed by a leaf might be expected to vary with the genotype, the physical environment in which the leaf is functioning and possibly the age of the leaf (Paton 1971). Back in 1968, Paton showed that the number of green foliage leaves at flower initiation was related to a quantitative leaf requirement. Leaf requirement was least in continuous light. Dolan (1973) found that the greatest degree of flowering and vegetative growth in peas was obtained with the combination of long days with high light

intensity. He indicated that optimum conditions for pea growth would combine medium temperature, long day length and high light intensity.

Wellensiek (1973) observed that the number of nodes per stem of young vegetative plants is not affected by day length. In older plants node numbers tend to increase with day length but the rate of node formation decreases with flower formation. Internode length increases with day length even in very young plants and shows a further considerable increase when flower formation starts. Hence, flower formation clearly marks changes in the growth pattern, consisting of a decrease in node formation and an increase in internode length.

1.6.2 Temperature

1.6.2.1 Germination

Pea seeds are not long-lived, nor do they exhibit after-ripening or secondary dormancy. As with other species, viability decreases markedly at high storage temperatures and high seed moisture content.

Germination tests on peas carried out at optimal laboratory temperature are often very poorly correlated with ability to germinate and become established in the field, partly due to varying tolerance of prolonged exposure to damp, cold conditions and partly to attack by pathogens whose growth may be stimulated by solutes exuded by seeds (Torfason and Nonnecke 1959). Most of the leaked solutes come from the cotyledons; Larson (1968) and Perry and Harrison (1970) have suggested that it is the sudden inrush of water during imbibition which causes the injuries resulting in leakage. Simon and Harun (1973) considered that drying out of the embryo during seed ripening causes cell membranes to lose their integrity, thus rendering cellular

contents susceptible to leaching. Losses can involve substantial fractions of the sugar, amino acid and inorganic solutes of the seed so that particularly leaky seeds may give rise to poor crop establishment (Larson and Kyagaba 1969).

The major problem in pea seed emergence and establishment is the poor emergence of some commercially available seed lots which are in a poor physiological condition, especially in cold wet soils (Jones 1931; Clark and Little 1955). This seed condition reveals itself in the poor retention of solutes (when seeds are placed in water) and in low respiration. Poor solute retention appears to be attributable to defective membranes within the cells (Mathews and Carver 1971).

Although death from the direct effect of the inadequate provision of the physiological requirements of the emerging seed, such as oxygen and water, might occur under some extreme circumstances, the more important cause of failure to emerge appears to be infection by the soil-borne fungus *Pythium ultimum* before or just after germination (Perry and Harrison 1970). The suggestion was made that low temperatures and high soil moistures combine to both prolong the time when the seed is vulnerable to infection and increase the susceptibility of the seed to the pathogen. Low resistance to infection in the cotyledons of seeds that are in poor physiological condition is considered more important than the leaching of nutrients into the soil which might stimulate fungal growth. It is suggested that seeds which are viable but in poor physiological condition are produced by the harvesting and drying of immature seeds and by prolonged storage in unfavourable conditions (Powell and Mathews 1977).

Electrical conductivity of the leachate has been shown to be a reliable method to predict field emergence of pea cultivars whether

round or wrinkled seeded (Bedford 1974). A high conductivity is indicative of poor emergence.

The epigeal pattern of germination, the large and rich cotyledon reserves and the overall sensitivity of pea seeds to factors in the soil environment are likely to create some serious problems for the agronomist. Much has to be overcome before germination and establishment of pea crops becomes as reliable as it is with most other species.

1.6.2.2 Root Growth

Ying (1966) found pea root growth rate depended on temperature and was greatest at 20 and 25 C. Kung and West (1968) found that extension growth of pea roots attained its maximum at 20 C and at 30 C was forty percent less.

The relation between root growth and temperature shows an optimum at a lower temperature than the same relation for shoot growth. The root is most active and produces the highest shoot weight per gram of weight where growth is optimal (Brouwer 1962).

1.6.2.3 Shoot Growth

Boswell (1926) summarized the results of successional sowings at weekly intervals over three years. As temperatures increased at later plantings, less time was required to reach each stage of development and the weight of plant, weight and number of pods and the number of peas per plant was lower.

Later, work by Ibarbia and Bienz (1970) confirmed Boswell's report that pod number is temperature sensitive. They found that single and

double podded parent lines were extremely uniform producing almost 100 percent single and double pods respectively at both temperature regimes (7 C night, 15 C day; 15 C night and 24 C day). The triple podded parent produced mainly three-podded determinate nodes at the lower temperature but tended to produce indeterminate nodes, with two, three and four pods at the higher temperature. Variability of pod number in the field (Fletcher, Ormrod, Maurer and Stanfield 1966) and in controlled environments (Stanfield, Ormrod and Fletcher 1966) had been demonstrated. Variations in the number of pods per node between successive sowings of Dark Skin Perfection was found to be partly due to variation in the frequency of formation of single and double flowers; flower initiation and subsequent loss setting the potential or upper limit for pod number (Milbourn and Hardwick 1968).

There are several conflicting views on causes of flower and pod loss. Many young pods fail to survive to maturity. This suggests some form of competition is occurring to limit the eventual number of pods. Support for this view comes from the observation that flower failure within an inflorescence is not at random (Clay 1935; Lamprecht 1952; Ibarbia and Bienz 1970). The basal flowers are commonly the most successful, presumably because they are the first to open and have an advantage over the rest.

In pea cultivars incapable of producing more than two flowers per node, flower number per node was negatively correlated with temperature during the period of flower initiation (Ormrod, Maurer, Mitchell and Eaton 1970; Hole and Hardwick 1974). When multiflowered cultivars were tested, they produced more flowers at high temperature than they did at low temperature (Hole and Hardwick 1974). This response was the opposite of that shown by the two-flowered cultivars. Analysis of soluble sugar levels suggested that the availability of assimilate

was an endogenous factor involved in the temperature control of flower number. Assimilate level was not implicated in the variation of stability of flower number per node to temperature change (Hole and Hardwick 1974; Hole 1977).

Boswell (1929) could not point out any one specific period during which high temperatures were most critical for pod set. Using controlled light and temperature conditions, Karr, Linck and Swanson (1959) found the critical period for pea plants given high temperature treatments only during the light period was nine to eleven days after full bloom; while the critical period for those given high temperature treatments only during the dark period was six to nine days after bloom. The critical period found by Karr et al (1959) was similar to the period of five to ten days after full bloom found to be critical by Lambert and Linck (1958).

High temperatures reduced number of pods and some cultivars showed a reduced pea size as well. The deleterious effects of high temperature on these components of yield agree with reports by Reath and Wittwer (1952); Karr et al (1959); Ormrod et al (1970); Nonnecke, Adedipe and Ormrod (1971).

The ultimate effect of high temperature is reduced pea yield. Lambert and Linck (1958) hypothesized that the high temperature reduced yield by causing an increase in respiration or by reducing translocation of assimilates into the pods and peas. High temperatures also may have interfered with the balance of nitrogenous compounds and the synthesis of proteins. Other conditions such as the effect of high temperature on genetic expression may have also influenced the yield of peas. However, because of the complexity of conditions in the environment, it is often impossible to identify these causes.

1.6.3 Moisture

1.6.3.1 Humidity

Reports that relative humidity may influence development of peas are few. Nagy (1966) found that the development of peas was adversely affected by low humidity; Parek, Sivanayagam and Heydecker (1969) indicated that high humidity resulted in small and thin leaves. Nonnecke et al (1971) reported that humidity has no significant effect, irrespective of cultivar, however, relative humidity effects on pea yield were closely related to air temperature when soil moisture is limiting.

1.6.3.2 Soil Moisture

Research dealing with morphological responses of peas to water stress is somewhat limited, most have dealt with water sensitive stages of growth on seed yield (Sprent 1957; Stanhill 1957; Brouwer 1959; Frohlick and Henkel 1961; Salter 1962; Salter 1963; Salter and Goode 1967; Behl, Sowhney and Moolani 1968; Gautum and Lenka 1968; Pumphrey and Schwanke 1974). It has been shown that on green pea yield, the flowering phase of plant development is more sensitive to water stress than the vegetative phase (Monson 1942; Salter and Goode 1967). Brouwer (1959); Maurer, Ormrod and Fletcher (1968) found that high water regimes were essential to high yields. They also observed that high water regimes increased plant height and internode length, number of nodes, increased foliage yield and fresh vine weight of peas. Further studies by Miller, Manning and Teare (1977); Stoker (1977); Martin and Tabley (1981) and White, Sheath and Meijer (1982) found that irrigation increased pea yield. Both White et al (1982) and Miller et al (1977) showed that vine height increased with a resulting

increase in total plant dry weight as soil moisture levels increased. White et al further showed that pea yield increased as a result of increased number of pods per plant, seeds per pod and seed weight. It was the flowering period to pod filling that was most critical in irrigation and yield (Stoker 1977; Falloon and White 1978; Cannell, Gales, Snaydon and Suhail 1979; Jackson 1979 and White et al 1982). Once soil conditions became waterlogged leaf senescence increased, growth decreased and consequently there were fewer podding nodes and yield decreased (Cannell et al 1979; Jackson 1979 and Belford, Cannell, Thomson and Dennis 1980). Further, water stress reduced branching and McIntyre (1971) and Falloon and White (1978) suggested that it may be necessary to seed in early spring thereby avoiding the effects of water stress with later sowings if irrigation is not available. Miller et al (1977) also observed that the number of nodes per plant remained constant but internode length varied in relation to water level and irrigation scheduling. Plant height was significantly reduced with decreasing water levels for constant water regimes. They found that with the exception of stem diameter there were no definite, observable changes in the tissue systems of the stem or pod nodes that could be identified with soil water stress. Thickness of the leaflet blade was significantly less in plants grown at 100 percent field capacity than those grown at 80 to 60 percent to 60 to 40 percent of field capacity in a greenhouse soil mix (3 Palouse loam: 3 sand: 2 parts peatmoss). Plants grown at 40 to 20 percent of field capacity had significantly thinner leaflets than did those grown at higher moisture regimes.

1.6.4 Planting Date

In the earliest reported studies of environmental effects on pea yields, Boswell (1926) reported that late season plantings required

less time to reach any particular stage of development but higher temperatures had an increase depression on pod set. There was no reduction in number or weight of peas per pod with later plantings. Wang (1962) indicated that the combination of a warm spring (during the seedling stage) and a cool summer (during the reproductive period) produced a high yield while the combination of a cool spring and a hot summer produced a low yield. He observed similar effects of temperature on yield components as Boswell.

Studies by Fletcher et al (1966) indicated that where temperatures exceeded the optimum for most growth characteristics in late plantings, the mean of maximum temperature was negatively correlated with total dry matter yield, peas per pod and pea yield; was positively correlated with branching and had no effect on pods per plant. Where temperatures were sub-optimum for early plantings and approached optimum for the later plantings, the mean of maximum temperatures was positively correlated with total dry matter yield, but had no effect on peas per pod or branching. A seasonal mean maximum of 20 to 22 C was considered to be optimum for peas.

Porjazov (1970) measured in time and integrated temperature the requirements for five garden pea cultivars sown on five dates at fifteen day intervals. Delayed sowing shortened the growing period, sowing to emergence being the most affected and flowering to maturity the least. The length of the growing season expressed in days varied little in mid season whereas expressed as integrated temperature requirements the early cultivars showed little variation.

1.7 Growth Analysis

1.7.1 Introduction

The continuing pressure to produce higher yielding cultivars has

stimulated interest in physiological factors contributing to final yield and in the possibilities of using such factors in selection. Growth analysis attempts to describe the form of growth a plant takes and if the mode of growth is known then it is possible to concentrate efforts into areas that will produce high yielding cultivars.

The classical methods of growth analysis involve a series of relatively infrequent large harvest (with much replication or measurement) and the derivation of growth parameters, using the formulae (Gregory 1917; Blackman 1917; Briggs, Kidd and Went 1920):

mean relative growth rate

$$\text{RGR} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$

mean net assimilation rate

$$\text{NAR} = \frac{W_2 - W_1}{t_2 - t_1} \times \frac{\log_e L_2 - \log_e L_1}{L_2 - L_1}$$

mean leaf weight ratio

$$\text{LWR} = \frac{LW_2 - LW_1}{W_2 - W_1} \times \frac{\log_e W_2 - \log_e W_1}{\log_e LW_2 - \log_e LW_1}$$

leaf area ratio

$$\text{LAR} = \frac{L_2 - L_1}{W_2 - W_1} \times \frac{\log_e W_2 - \log_e W_1}{\log_e L_2 - \log_e L_1}$$

specific leaf weight

$$\text{SLW} = \frac{L_2 - L_1}{LW_2 - LW_1} \times \frac{\log_e LW_2 - \log_e LW_1}{\log_e L_2 - \log_e L_1}$$

W = dry plant weight; L = leaf area per plant; LW = leaf weight per plant; t = time. The subscripts 1,2 denote first and second harvests.

If one abandons the commitment to calculations on the classical harvest interval method, than several advantages accrue if one is able to adopt what Radford (1967) has called the dynamic approach to plant growth analysis (Hunt 1978). Mathematical functions by regression techniques are fitted to experimental data and describe the relationship between data and time. From these functions (growth curves), fitted values of data are extracted which may subsequently be plotted as fitted instantaneous values. The regression technique utilizes information from all available harvests in determining values at any point of time whereas the classical method only uses data from the two immediate harvests. Also, pairing of plants across the harvest interval becomes unnecessary and small deviations from the overall trend of the original experimental data against time are "smoothed" often making the final results less erratic (Hunt 1973). The only assumption necessary for the adoption of this approach is that the fitted growth curves adequately describe the trends in the raw data. This in turn depends on the assumption that the raw data adequately describes what is really happening in the plants under investigation.

1.7.2 Application to Peas

Early attempts to find differences between crop species in terms of growth analysis, in particular NAR, were largely unsuccessful (Heath and Gregory 1938). Later work by Watson and Witts (1959) on beets; Muramoto, Heskieth, El-Sharkway (1965) on cotton; Stoy (1965) on wheat and Cannell (1967) on cereals, showed little difference between cultivars in terms of NAR or of net photosynthetic rate. Watson (1952) stated that although there were differences between and within species in NAR, productivity was much more closely related to the leaf area component of growth analysis.

Buttery and Buzzell (1972) working with soybeans found that plants

with a low LAR had a larger "sink" for their photosynthetic products than did leaves in plants with a high LAR, low LAR may therefore favour high rates of photosynthesis. Eastin and Gritton (1969) investigated the leaf area relationship in peas and observed that during the period just prior to bloom through canning stage and especially while the pods were filling, a given unit of leaf area was more efficient in producing above ground dry matter than at the immediately earlier growth stages. They postulated that the increase in efficiency may have been due to: 1. a diversion of growth from the roots to the tops, 2. photosynthesis of chlorophyllous pods which were not included in the leaf area measurements or 3. a positive effect of the physiological status of plant parts other than the leaf in the photosynthesis of a given unit of leaf area. Eastin and Gritton believed that it was sink size that had a positive effect on photosynthesis. The effect could be by preventing accumulation of assimilates in the leaves, by providing some positive stimulatory factor or preventing accumulation of an inhibitor. Later reports on other crops supported the theory that highest photosynthetic rates and enzyme activities occur when growth and sink demand are highest (Blenkinsop and Pate 1974; Pate 1975). This implied that high growth rates caused high photosynthetic rates rather than vice versa.

All evidence suggests that the pea leaf exhibits a normal C_3 pattern of photosynthesis (Hellmuth 1971). CO_2 uptake by pea leaves increased as temperature increased. Further studies by Hellmuth (1971) indicated that leaf temperature markedly influenced the magnitude of the maximum rate of net CO_2 uptake in relation to light intensity. The compensation point and saturation value for light were found to be markedly dependent on leaf temperature,

Photosynthesis in peas is subject to both environment constraints

and internal regulation which takes the form of source/sink feedback control over carbon dioxide assimilation. The effect of sinks on photosynthesis has been documented as have current reports on enzyme and hormone regulatory effects (Wareing and Patrick 1973; Kriedmann, Loveys, Possingham and Satoh 1976). Thus an increase in demand of a sink may result in a rise in the assimilation rate of the source organ; a decrease in demand may lead to a fall in the assimilation rate.

In the pea the onset of flowering and subsequent growth of the fruit leads to a rapid doubling in the photosynthesis of the whole plant (Lawrie and Wheeler 1974). Studies by Flinn (1974) suggests that leaflet photosynthesis rises and falls in response to the swings in demand for assimilates by the developing pod, but responds to a lesser extent to the demand for assimilates by the maturing seed, a primary component of yield. The results suggest that the presence of seeds in a pod may exercise a stimulatory effect on pod activity in translocation and possibly a stimulus also to its photosynthetic performance.

Pea response to environment measured in the behavior of yield components is a complex subject still under study. Studies to date on component behaviour have shown that pea yield increased as component number increased. However, such behaviour has been shown to markedly decrease the growth of first formed fruit (Hole and Scott 1983). Hole and Scott also noted that the actual proportion of dry matter allocated to different fruit were not changed by an increasing number of competing fruit if assimilate supply was adequate. If assimilate supply was limited, however, two fruits on the same or successive nodes competed significantly for assimilates (Salter, Hole and Scott 1979).

Gifford and Evans (1981) stated that the leaves were the primary source of assimilates and that demand by sinks for assimilates can also determine photosynthetic supply. Falloon and White (1978) earlier stated that photosynthetic supply in a pea plant can be limited by insufficient active photosynthetic tissue capable of producing adequate supplies of assimilates and/or that competition between vegetative and reproductive growth for the available assimilates exists. With any decrease in the amount of assimilates Hole and Scott (1983) observed that there was a decreased fruit growth rate and that fruits at lower reproductive nodes on the pea plant were less affected. Mahon and Hobbs (1983) observed that lower reproductive nodes were dominant sinks and that even within individual nodes there was considerable variation in total sink strength. Mahon and Hobbs also observed that seeds in the same pod developed at different rates and that final pod weight was highly correlated with the rate of pod filling and both were significantly related to seed yield per plant. Therefore, plants with strong seed sinks were generally more likely to attain a high harvest index (Hedley and Ambrose 1980).

Pea yield decreased by seed abortion which was linked to sink demand and when demand for assimilates exceeded the supply seed in the pods aborted (Hedley, Smith and Hayward 1982). Falloon and White (1978) found that the number of ovule initials per pod were predominantly under genetic control, however, photosynthetic area may have influenced development of ovules within pods, therefore, any decrease in the photosynthetic area of the pea plant after flowering increased the percentage of ovule failure. The abscission of any plant part was enhanced by water deficit, a decrease or increase in

photoperiod and temperature extremes and any differences between cultivars in number of structures lost under such conditions may be related to ability to maintain a higher photosynthetic area per reproductive structure (Falloon and White 1978). Hobbs and Mahon (1982) concluded that in areas with short growing seasons, rapid growth for a limited period with more assimilates being placed into seeds (high harvest index) may be desirable. Combination of such characters in pea cultivars might produce maximum yield potential in the short time available.

There is evidence from several species that a consuming organ (sink) can exercise a controlling influence over the production and export of assimilates by "source" organs such as photosynthesizing leaves. Lovell, Oo and Sagar (1972) have found that the rate of C^{14} export from pea leaves can be greatly increased if, 20 hours before feeding, all other leaves are removed from the shoot. Since this increase in export is not evident if root or shoot apices are removed at the time of defoliation, it appears to be the demand for assimilates by these sinks which sets the tempo of export. Competition for assimilates is likely to result in organs of low competing power functioning at less than full capacity. Then if a dominant sink be removed, assimilates are likely to become readily available to less favoured organs. Evidence of such a diversion of assimilates has been shown in tracer studies in peas by Hasain (1967) and Morris and Thomas (1968).

Studies by Harvey (1973) indicated that a leaf at a reproductive node exported assimilates principally to its subtended fruit, but a leaf at a vegetative node exported mainly to the nearest fruit above it on the same side of the haulm. Genetically induced changes in leaf morphology did not markedly affect the translocation potential

or pattern of partitioning of assimilates in the plant. Harvey postulated that new foliage forms would be unlikely to exhibit any large scale imbalance in dry matter accumulation in vegetative or reproductive organs.

Carr and Pate (1967) studied the effects of leaf age on translocation from leaves and found that distribution and quantity of assimilates change as the leaf ages. As further leaves unfold so an older leaf becomes further and further removed from the influence of the apex it is less likely to respond to demands from the apical sinks. Pate (1966) believed that auxin produced in the apex regulated leaf production and export of assimilates. This was supported by the findings of Seth and Wareing (1967) and Davidson (1971).

In terms of assimilate origin, Flinn (1969) found that the stipule and the subtending leaf had a similar photosynthetic efficiency per unit area and a similar surface area. Despite this the stipules were somewhat important contributors during the very early stages of pod growth. Flinn (1969) showed that the stipules contributed two-thirds of the total assimilate requirement of the seed borne at the node, the remainder was presumed to come from elsewhere in the plant to the seed.

Flinn and Pate (1970) and Harvey (1972, 1974) have shown that although each blossom leaf is deeply committed to supplying assimilates to its subtended fruit, during its early life it supplies quite sizeable amounts of photosynthate to other parts of the plant. Stipules make a larger contribution to the subtended fruit than do the companion leaflets, not necessarily because the stipules are less active photosynthetically, but because the stipules participate more than

leaflets do in transporting assimilates up and down the stem. This is because stipules possess less direct vascular connections with the fruit stalk than do leaflets (Brennan 1966).

Unlike the blossom leaf, the pod is entirely committed to transport to its seeds, the extent of this involvement increasing in proportion to the mass of seeds present (Lovell and Lovell 1970). Seeds do not seem to be capable of significant photosynthesis while in their pod despite their intense green color (Flinn 1969).

To use the classical technique of growth analysis, in which the growth of the crop is analysed in terms of leaf area and leaf activity is one approach to the problem of crop yield. Although this method is valuable in the analysis of the vegetative phase of pea growth, it has proved less useful when the crop is in the reproductive phase. For example, at flowering much of the leaf canopy is senescent and likely to be past its peak activity (Smillie 1962). Also, during the reproductive phase of growth, the true leaf area is difficult to estimate for at this time leaf loss proceeds faster than leaf production. Estimation of effective photosynthetic area is further complicated by the considerable area of stem and green pods present in the crop. Finally, the complexity of the source/sink relationships and the internal and external influences on photosynthesis make interpretation of growth analysis on pea growth and development difficult.

In view of these problems, Hardwick and Milbourn (1967) turned their attention instead to component yield analysis, that is, analysis of the number and size of the "sinks" at which photosynthates and proteins are stored as the final product. This approach is based on an

extension of the method of Engledow and Wadham (1923) in which final yield for the whole plant is factorized into components at each node separately:

$$\text{yield} = \text{number of podding nodes} \times \text{number of pods per node} \times \\ \text{number of peas per pod} \times \text{weight per pea}$$

The contribution of each component is the result of a number of physiological processes. By analysing the yield from crops grown under a range of conditions, one can assess the contribution of each component and process to final yield. The question remains of how this knowledge is to be used. Because of lags between nodes the detailed picture is very complex and its dynamics are further complicated by interactions between components.

1.8 Yield - Tenderometer Relationship

To interpolate yields for a given maturity, a knowledge of the form of the yield - tenderometer relationship is necessary. The relationship between the yield of shelled peas per plant (W) and the tenderometer value (T) is generally a curvilinear relationship in which the increase of W per unit increase in T declines with T , particularly for higher values of T (Berry 1966).

A model for this relationship of the form

$$\left(\frac{T - T_0}{W} \right)^\theta = A + B (T - T_0)$$

where θ , T_0 , A and B are constants, was given by Berry (1963), together with a method of fitting. The relationship described by the equation is such that the yield at tenderometer value T_0 is zero and for $\theta = 1$ the yield approaches an upper limit for increasing values of T . For $\theta < 1$ the yield reaches a maximum and then declines for higher values of T .

Experience in fitting the relationship has shown that the fit is not very sensitive to variations in $\theta = 1$ (Berry 1966). In so far as the tenderometer value is only obtainable in a range of the order of 60 to 180 it may be argued that the behaviour of the relationship outside this range is of no consequence. Berry (1966) found that the relationship given by the equation with $\theta = 1$ and $T_o = 70$ fitted his data satisfactorily in the majority of cases. Pollard, Wilcox and Peterson (1947) gave data which showed no sign of approaching an upper limit to yield for a tenderometer value as high as 160. Therefore, the model with $\theta = 1$ and $T_o = 70$ values between 70 and 180 is suggested in best relating the yield of shelled peas to maturity.

In 1981 Martin tested six methods used to relate yield and tenderometer reading and he found that whatever method he used there was little variation between results. Martin stated that linear interpolation has the advantage of not being based on any preconceived idea of yield-tenderometer relationships and is simple to use. Berry's (1966) method was better because of the curvilinear relationship between yield and tenderometer reading especially if there is a wide range in tenderometer values or if upper tenderometer readings are high.

1.9 AIS - Tenderometer Relationship

The correlation of tenderometer and AIS (alcohol insoluble solids) on raw peas has been studied extensively by Adam (1958). Adam observed that the relationship between tenderometer reading and AIS was constant in seven years of trial. From these studies, he arrived at regression lines as follows; where y is the tenderometer reading and x the AIS constant.

$$y = 7.42x + 19$$

$$x = 0.122y - 1.1$$

Thus for an AIS content (x) of 15% the most probable tenderometer reading (y) would be 131; or for a tenderometer reading (y) of 120 the AIS content (x) would be 13.5%. From these equations, AIS maturity results can be converted to tenderometer readings and vice versa.

1.10 Harvest Index

Component analysis of yield begins with the expression of yield into two major components, namely accumulation of assimilate and partitioning of assimilate. Assimilate accumulation is most easily measured as total plant dry weight or biological yield (Donald 1962; Wallace 1973). Biological yield is a direct outcome of the extent and duration of photosynthesis, subject only to the addition of minerals and losses by respiration. Environmental factors which influence total yield such as temperature, do so because it influences either directly or indirectly the rate of duration of photosynthesis. The highest photosynthetic rates occur when growth and sink demand are high (Donald 1962; Blenkinsop and Pate 1974; Pate 1975). Therefore, total plant dry weight (biological yield) is a measure of overall photosynthetic efficiency (Wallace 1973).

Partitioning of assimilates is a physiological component of yield, little is known concerning the mechanisms controlling the partitioning. The partitioning of assimilates as seed weight is defined as economic yield (Donald 1962; Wallace 1973). The ratio of economic yield to biological yield is commonly called the harvest index (Donald 1962). Hardwick (1970) defined harvest index in peas as:

$$\text{harvest index} = \frac{\text{dry weight pod + peas}}{\text{dry weight stem + leaves}}$$