Studies on the reproductive development of Vicia Faba L

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STUDIES ON THE REPRODUCTIVE DEVELOPMENT OF *VICIA FABA* L

A thesis submitted in accordance with the requirements of the University of Durham for the degree of Doctor of Philosophy

by

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b

Frontispiece

Plants of genotype G growing in field plots at Houghall Farm, 1983.

(a) flowering stage

(b) a typical plant at late pod fill stage

ABSTRACT

A series of field trials were performed in order to compare the yield stability of plants of the independent vascular supply (IVS) type peduncle vascular architecture with those of the more usual branched type. The IVS plants gave a low stable, source-limited yield; the plants attained maturity four weeks earlier than those of Maris Bead. The source-sink relationships of the genotypes investigated were established. The potential values of IVS type plants as commercial varieties are discussed.

Studies of the growth and development revealed a difference in pod wall structure and the distribution of stomata and pod hairs: this could be related to pod drying. The growth of all parts of the raceme was studied by plotting fresh and dry weight changes, a sequence of development of tissues was established, the peduncle growing first, then the pedicel, then the pod and finally the seed. Genotypic differences in growth rate were observed. These findings were related to the accompanying vascular development within the raceme. The source of the assimilates rapidly translocated into the seeds during early, rapid growth was established.

The results obtained are discussed and an ideotype constructed on the basis of the information obtained.

INDEX

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CHAPTER 1

INTRODUCTION

1. Biology, origins and classification

The faba bean (Vicia faba L.) is an annual, leguminous herb. The typical phenotype is that of an indeterminate growth habit, having an erect stem up to two metres in height and little or no basal branching. Alleles conferring this plant structure are dominant to those for determinate growth habit and much basal branching. Flowers are borne on axillary inflorescences, these being produced after four to twelve vegetative nodes. Each raceme consists of a short peduncle supporting from two to twenty flowers, the most common floral phenotype having off-white petals with dark spots on the wing petals and dark stripes on the standard petal. White flowers are controlled by recessive genes. The species is normally diploid (2n = 12), although a tetraploid (2n = 4x = 24) has now been described (Poulsen and Martin, 1977).

The origins of the faba bean are somewhat unclear, and, as no wild ancestor is known, this has been a matter of speculation. Of the more recent claims to the geographical region of origin of the species those of Cubero (1974) and Ladizinksy (1975b) that the site of origin was West or Central Asia seems the most likely. The closest known wild relatives of the faba bean are Vicia galilaea (Plitm. et. Zoh) and Vicia narbonensis (Smartt, 1980). Evidence from seed protein profiles and karyotype analysis shows, however, that V. faba is not very closely related to either of the other species (Ladizinsky 1975a). No successful interspecific hybrids between V. faba and V. galilaea or V. narbonensis have been made.

Several intraspecific classifications have been proposed. These are based largely on seed size (Muratova, 1931; Hanlet, 1972). The simplest system was proposed by Cubero (1974), who divided the species into four sub-species on the basis of seed size. The groups are faba (broad), equina (horse), minor (field) and paucijuga (tick); the sub-species faba being commonly known as major.

2. Food value

Faba bean seeds have a high protein level, ranging from 24% to 38%. This protein, as might be expected, is low in the sulphur amino acids cystine and methionine, and high in lysine content (Griffiths, 1983 b). Frequently the food value of the crop is reduced by the presence of anti-nutritive factors such as protease inhibitors, tannins and phytates (Griffiths, 1983 a). In some Mediterranean and African regions the faba bean is among the major sources of protein in human diets. In Western Europe major types are used for human consumption, fresh, frozen or canned (Lawes, 1980). The equina and minor types are mostly used in livestock feed compounds. Faba bean protein isolates are of great potential interest as meat substitutes. Production of such compounds can be performed using processes established in production of soya protein isolates. Production costs compare favourably with those of soya protein (Brown, 1977; Simpson, 1983). Such isolates and concentrates have been used in the United Kingdom and Canada either as textured vegetable protein or as food additives (Jonas, 1981).

3. The faba bean crop, past and present

Domestication of the faba bean is thought to have occurred in Neolithic times (Schultze-Motel, 1972), and during this period cultivation of the crop spread to most Mediterranean regions. Bronze Age remains of the crop have been found in many continental European countries. The earliest finds of faba beans in England were of Iron Age origin (Renfrew, 1973). Since then, with the growth of international trade, the crop has been introduced to most regions of the world (Hawtin and Hebblethwaite, 1983). At present over 60% of the world faba bean crop is grown in China (F.A.O., 1981).

In the mid-nineteenth century the area of faba beens grown in the U.K. was almost equal to the area of wheat. In 1873 the area of beans was 224,000 hectares (Hebblethwaite and Davis, 1969). Owing to the combined effects of the great agricultural depression of the 1880's and 1890's and the influx of cheaper, better quality protein

from abroad, the area of faba beans grown declined rapidly. In 1900 the area was around 100,000 hectares (Hawtin and Hebblethwaite, 1983). Yield instability also played a significant part in bringing about the reduction in popularity of the crop. In the early 1900's, with the recovery of the agricultural industry, the area of beans grown also recovered slightly. Since then, apart from slight recoveries around each of the World Wars, the area grown has slowly declined until, in 1981, there were only 46,000 hectares of field beans grown in the U.K. (Hawtin and Hebblethwaite, 1983). The current national average yield is three tonnes per hectare (Smith and Altrian, 1967). This, however, is extremely unstable and values anywhere between one and nine tonnes per hectare are regularly recorded (Sprent, Bradford and Norton, 1977). Yield instability is the major cause of the lack of popularity of the crop.

4. Some agronomic problems - weeds and pathogens

(a) Weeds

Before the advent of modern selective herbicides faba bean crops frequently harboured flourishing weed populations. Although the problem is now much reduced, there are as yet no selective herbicides to eradicate thistles (Circium sp.), bindweed (Convolvulus arvensis L), or perennial grasses such as couch grass (Agropyron repens). Couch grass competes with the crop, reducing yield (Hewson, Roberts and Bond, 1973): it is also a carrier of Take-all (Gaucomyces gramminis) and other cereal diseases. The value of the field bean crop as a break crop in intensive cereal production can be nullified by infestation with diseased couch grass (Hebblethwaite and Davies, 1971).

(b) Pests

There are many faba bean pests, but most are economically unimportant (Cammell and Way, 1983; Hooper, 1983; Bardner, 1983). Of the aerial pests the blackfly (Aphis fabae Scop.) is the most economically important, causing severe yield loss by direct feeding and by transmission of virus diseases (Cammell and Way, 1983). Damage caused by A. fabae is dependent on the size of the population present. A forecasting system has been devised by Way and Cammell (1973) to

predict aphid levels by monitoring the numbers of eggs found on the over-wintering host, the spindle bush (Euonymus europaeus L). Since 1970 these counts have been used to predict likely infestation levels and facilitate timely application of systemic insecticides (Cammell and Way, 1977). By this method pest control is achieved without harm to the bee population necessary for cross-pollination. The system provides effective control of aphid population, preventing significant economic loss. Current research is aiming to establish similar early warning systems for pests of lesser economic importance, and thus to provide an integrated early warning pest control system (Cammell and Way, 1984). Breeders are also working to find genetic resistance to A. fabae (Bond and Lowe, 1975).

Nematode damage resulting from heavy infestations of Ditylenchus dispaci may be locally severe. Control measures are difficult as the pest is both seed and soil borne, making transmission to future crops easy. Prevention may be achieved by the use of clean seed stocks and good host weed control. Chemical control is possible but expensive. There is no known resistant variety (Hooper, 1983).

(c) Fungal diseases

The major fungal pathogens of faba beans are chocolate spot (Botrytis fabae) and leaf spot (Ascochyta fabae). B. fabae occurs in two forms, aggressive and non-aggressive. The non-aggressive form is visible as small spots on the leaves of most faba bean crops, but causes little damage. The aggressive form may cause serious yield loss in winter sown beans (Hebblethwaite and Davies, 1971). Leaf spot may be either seed borne or spore transmitted; severe infection leads to considerable yield loss (Gaunt, 1983). Other fungal pathogens of faba beans are Uromyces vicae fabae, Peronospora vicae, Sclerotina bifoliorium, Rhizoctonia solari, Fusarium fabae, F. oxysporium. Little genetic variation in disease resistance is found; some cases of partial resistance have been reported (Chapman, 1981b).

Control of these pathogens may sometimes be achieved by chemical means (Litzenberger, 1974), but application may lead to mechanical damage. The best control of Ascochyta is achieved by use of clean seed.

(d) Virus diseases

Around fifty viruses have been reported to infect Vicia faba (Cockbain, 1983). The commonest viruses found are Bean Leaf Roll (BLRV), Bean Yellow Mosaic (BYMV), Broad Bean Stain (BBSV) and Echtes Acherbohnenmosaik (EAMV). BLRV and BYMV are aphid transmitted, especially by Acyrthosiphon pisum, BBSV and EAMV are both seed and weevil transmitted. BLRV is the most serious bean virus infection in Britain (Cockbain, 1980).

(e) Plant Parasites

In hot, dry regions such as Spain and Italy the parasitic plant Orobanche crenata (broomrape) may completely destroy faba bean crops (Cubero, 1983). Two broomrape resistant V. faba lines have been listed (Chapman, 1981b). In humid climates Orobanche is seldom a problem.

5. Factors involved in yield production

The seed yield produced by any plant is influenced by a great many factors. These can be divided into the following groups:-

(a) Intrinsic factors - those variables determined by the genetic constitution of the plant, and, resulting from that, the whole plant physiology and hormone balance.

(b) Environmental factors - influences on yield arising from the environment in which the plant is situated.

Such divisions of the yield producing processes are, of necessity, artificial. In reality yield produced is the result of a great number of these inter-dependent influences and processes. Many of these may be changed either directly or in response to changes made in another factor.

(a) Intrinsic factors

Bud development

The number of buds formed by each plant, and the distribution of those buds, is clearly of great importance as it is the first

stage of yield development. The plant produces more floral buds than will develop into mature pods, a common phenomenon in most crop plants. This functions to prolong the flowering period, should prevailing conditions at the outset of flowering prevent successful reproduction. Thus the chances of the plant's success in terms of progeny production are increased. The abcission of flower buds before reaching anthesis is a commonly observed phenomenon in the faba bean crop. The main occurrences of bud abortion are located at the lower and the apical flowering nodes. Abortion at the lower flowering nodes occurs when the photosynthetic leaf area is insufficient to provide assimilates for both the growing apex and the flower buds. Bud abortion at the apical flowering nodes may be ascribed to the inability of the buds to compete with developing pods lower down the stem for assimilates (Gates et al, 1983).

Pollination and fertilization

The breeding system of the faba bean crop has been extensively investigated (see Kambal, 1969; Hawtin, 1981, for reviews). The breeding behaviour of the crop is intermediate between autogamy and allogamy. The observed partial allogamy is dependent on the timing of production of stigmatic exudates relative to that of anther dehiscence. Self-pollinating "autofertile" plants are protogynous, whilst autosterile plants requiring tripping are protandrous (Paul et al, 1978). The extent of outcrossing reported varies somewhat, the average being 30% (Bond and Pope, 1974; Poulsen, 1975). Bumble bees are the most effective pollinators of the crop, although the presence of honeybees is also of value (Bond and Poulsen, 1983). In the absence of bumble bees pod set is depressed (Free, 1966; Kambal, 1969; Poulsen, 1975; Free and Williams, 1976). Some controversy has arisen over the question of whether all flowers are equally likely to be pollinated and fetilized. Many authors are of the opinion that most flowers, whatever their subsequent fate, are fertilized (Kambal, 1969; Chapman et al, 1979; Gates et al, 1981; Smith, 1982). Stoddard and Lockwood (1984) found that the proportion of fertilized flowers varied

between crop types and situations. In commercial crops spring beans showed 80% to 95% fertilization of at least one ovule per flower, whilst only 50% of winter beans were fertilized. Rowland, Bond and Parker (1983), however, reported only 48% fertilization in spring beans. It is possible that seasonal variation is responsible for the discrepancy between reported values.

Extensive studies by Smith (1982) have shown that yield loss due to flower abcission follows a definite pattern. Abcission is greatest at distal flower positions on the peduncle and in the apical racemes. This is confirmed by Peat (1983) and Jacquiéry and Keller (1978 a). Flower shedding has been shown to be an active physiological process under hormonal control (Gates et al, 1981). Various attempts to produce genotypes with reduced floral wastage have been made. Chapman (1981a) favoured the terminal inflorescence mutant. A plant of semi-determinate growth habit with an independent vascular supply architecture within each raceme was found to reduce floral wastage considerably (Gates et al, 1981: Gates et al, 1983; Smith, 1982).

Pod and seed development

Little work has been done on the processes involved in pod growth. Gehriger and Keller (1979) have shown that efficiency of pod fill is related to leaf area duration. Quantitative aspects of seed growth have been summarised by Peat (1983). As fertilization is unlikely to be a serious yield limitation in many situations (Stoddard and Lockwood, 1984) it is necessary to look to other factors to explain the large number of ovules that either fail to develop or abort early in development. Aborted ovules are most frequently found in positions distal to the stigma (Kambal, 1969; Chapman et al, 1979; Stoddard and Lockwood, 1984). This seems likely to be due to temporal differences in fertilization, the ovules nearest the stigma being fertilized first, and thus obtaining a competitive advantage over those more distal. Lee (1984) proposed that pollen tube growth is under genetic control, genetically 'fitter' pollen growing faster and thus reaching the ovules closest to the stigma in a short time and causing a competitive advantage in terms of assimilate flow to those ovules to be established.

Effect of growth regulators

Newaz and Lawes (1980) showed that the application of the growth regulator TIBA to bean plants brought about an increase in yield via greater pod set on the lower flowering nodes. This was confirmed, and similar effects induced by other growth regulators reported by Chapman and Sadjadi (1981). These growth regulators cause the developing pods to have a competitive advantage for assimilates over the growing apex.

Intra-plant competition

(i) Relationships between sinks

At all stages of yield development in faba beans the reproductive organs compete for assimilates with either vegetative or other reproductive plant parts. Until early pod set the roots are strong assimilate sinks (Crompton et al, 1981). The shoot apex remains a strong assimilate sink until the end of the flowering period (Jacquiery and Keller, 1980), and is thought to be largely responsible for the shedding of young pods (Jacquiery and Keller, 1978a, b, 1980; Gehriger and Keller, 1980).

Once pod development has begun the young pods become the strongest assimilate sinks in the plant. From then on the major competition for assimilates is between the reproductive organs. Competition operates on three levels, inter-raceme, intra-raceme and intra-pod. All such competition may be ascribed to the temporal variation pattern in reproductive development. Inter-raceme competition arises because the flowers of the lower racemes reach anthesis before those on the upper racemes. This affords a developmental advantage, and hence a competitive advantage to the lower racemes. Intra-raceme competition derives from the acropetal pattern of anthesis within each raceme. The flowers occupying positions on the peduncle proximal to the stem are therefore at any time at a more advanced developmental stage than those occupying distal positions, and therefore have a competitive

advantage in terms of assimilate supply (Smith, 1982). In beans with an interdependent or branched vascular supply within each raceme, competition between flowers results in much flower abcission (Smith, 1982; Jacquiéry and Keller, 1978a; Chapman and Sadjadi, 1981). In genotypes with independent vascular supply type peduncles such inter-flower competition is effectively reduced, although still present. Flower and pod shedding is greatly reduced as there is no direct vascular inter-floral linkage to transport abcission promotors within the raceme (Gates et al, 1981; Smith, 1982). Intra-pod competition may be ascribed to temporal differences in fertilization of the different ovules in any one pod as stated in section "Pod and seed development".

Inter-sink competition is thought to be genetically controlled by both additive and non-additive genes (Lawes and Newaz, 1979). Stem apex removal experiments demonstrated increased number of pods at harvest, although fewer seeds were filled in each pod, resulting in little change in final yield. This yield compensation is such that harvest index is a remarkably stable characteristic in the faba bean crop (Gehriger and Keller, 1980).

(ii) Source-sink relationships

An important factor in yield production is the availability of photosynthates to the developing pods. The plant is a complex organism with many inter-related regulation systems. In considering source-sink relationships the following factors must be considered: efficiency of photosynthetic activity, efficiency of translocation, the influence of sink demand on photosynthesis and translocation, and the whole-plant hormone balance.

Attempts have been made to evaluate photosynthetic efficiency by manipulation of leaf areas. McEwen (1972) showed that defoliation of all podded nodes reduced yield

by only 20%, and concluded that under normal conditions leaves functioned at a level well below their maximum photosynthetic potential, and therefore photosynthetic potential was unlikely to be a yield limitation. Similar experiments on French Beans (Binne and Clifford, 1980) were in agreement with this. Experiments involving partial defoliation of soybeans (Egli, Gossett and Leggett, 1976) found that reduced leaf area resulted in increased flower and pod abortion: some adjustment in sink size was made to meet the levels of available photosynthate. Egli and Leggett (1976) showed that partial defoliation of soybeans did not affect the rate of seed growth in retained pods until near the end of the seed fill period. Leaf removal resulted in reduction of seed number and final seed size. Apex removal experiments have been performed, the plant apex being removed either mechanically (Chapman, Guest and Peat, 1978; Chapman, Fagg and Peat, 1979; Binnie and Clifford, 1980; Crompton, Lloyd-Jones and Hill-Cottingham, 1981); or genetically by breeding for terminal inflorescence varieties (Baker et al, 1983, 1984; Austin et al, 1981). These studies show that absence of a vegetative stem apex results in reduced pod loss and increased yield. A greater proportion of assimilates were transferred to the pods. Such experiments do, however, alter the whole-plant hormone balance: this must partially account for the changes in assimilate partitioning. Baker et al (1983) reported that the leaves of terminal inflorescence type plants maintained their photosynthetic activity far longer than those of indeterminate type plants. This prolonged photosynthetic capacity, i.e. increased leaf area duration, gives rise to a longer seed fill period and hence the potential for a higher yield.

The bean seed is composed of approximately 30% protein and 50% carbohydrate, and in examining translocation it is essential to consider both xylem and phloem transported substances. Nitrogenous compounds are xylem transported

throughout the life of the plant (Cooper, Hill-Cottingham and Lloyd-Jones, 1976). Richards and Soper (1979, 1982) have shown that applied nitrogen produces no significant yield increase in faba beans: Day et al (1979) were in agreement with this but did find that increased atmospheric CO_2 gave increased yields. Canney (1975) gave a general review of phloem translocation and advocated that measurement of mass transfer is best studied by dry weights. This is not always appropriate as the origin of mobilised carbohydrate cannot always be traced. From ^{14}C labelling experiments it has been established that current photosynthesis provides most of the carbohydrate for rapidly growing seeds (Kogure, Naka and Asanuman, 1978; Crompton et al, 1981; Jacquiery and Keller, 1978b). This implies the presence of efficient photosynthetic and translocative systems. Similar studies in other leguminous crops are in agreement with this hypothesis (Pate and Minchin, 1980; Flinn and Pate, 1970; Pate and Farrington, 1981; Pate, Layzell and Atkins, 1980).

The influence of sink demand on source activity is difficult to demonstrate and little work has been done in this area. In soybeans Egli, Gossett and Leggett (1976) and Clough, Peet and Kramer (1981) found that sink demand had some control over the rate of translocation of carbohydrates from the leaves to the pods. Flinn (1974) demonstrated regulation of leaflet photosynthesis by developing fruit in the pea.

From the apex removal experiments cited earlier it becomes clear that the role of hormones in the whole plant physiology and in source-sink relationships is important. However, at present no satisfactory mechanism has been described (Herold, 1981). The most likely explanation for the finely co-ordinated source-sink relationships is the genetic determination of photosynthetic rate of leaves at all stages of the plant's life cycle (Herold, 1981).

(b) Environmental factors

The root environment - soil structure, nutrient availability and nodulation

Faba bean roots grow down to a depth of one metre below the soil surface (Dawkins and Brereton, 1984): for this reason good soil structure is of the utmost importance in ensuring good crop growth. Deep cultivation improves soil structure and yield increases of 11.2% have been reported (Warboys, Gooderham and Wilkes, 1979): deep cultivation plus deep fertilizer incorporation resulted in a yield increase of 14.6%. A synopsis of the mineral requirements of legumes is given by Munns and Mosse (1980).

In the presence of an adequate population of symbiotic Rhizobia, added nitrogenous fertilizers have no effect on yield (Richards and Soper, 1982; Day, Roughley and Witty, 1979). Rhizobia are responsible for the fixation of vast amounts of nitrogen essential for crop growth. Management of this symbiotic population is as important as that of the bean crop (Roughley, 1980).

Temperature

Vicia faba does not require vernalization. Soil temperatures above $5^{o}C$ for 1000 degree days are essential for satisfactory dry matter accumulation. High air temperatures during flowering may result in increased flower abcission, and therefore decreased yields (Hadley, Summerfield and Roberts, 1983).

Light

Vicia faba shows a quantitative day length response, requiring a photo-period of at least twelve to thirteen hours for flower expansion (Summerfield, 1980). Shading was found to decrease yield in both Vicia faba (Smith, 1982; Hodgeson and Blackman, 1956) and Pisum sativum (Hole and Scott, 1981).

Planting density

Hodgeson and Blackman (1956) showed that, as planting density increased, so yield components per plant all decreased, whereas

seed yield increased. Seed yield is a direct function of number of mature pods per unit area, not number of mature pods per plant. Similar results have been reported by Soper (1952), Seitzer and Evans (1973), Sprent, Bradford and Norton (1977), Barry and Storey (1979), Keller and Burkhard (1981), and Poulain (1984). Ishag (1973) found that at low planting density the individual plants had 40% more pods and their yield was 80% higher than plants grown at high density; the yield per unit area was, however, 30% higher in the higher planting density. Smith (1982) showed that at high densities the frequency of flower shedding is increased at the middle and upper flowering nodes.

Irrigation

Many authors have reported increased yields in response to added irrigation (Penman, 1962; Sprent, Bradford and Norton, 1977; French and Legg, 1979; Krogman et al, 1980; McEwen et al, 1981; Hebblethwaite, Scott and Kogbe, 1984; Alvino, Zerbi, Frusciante and Monti, 1984). These yield responses may be correlated to the amount of water applied (Krogman et al, 1980; Hebblethwaite, 1981; Day and Legg, 1983). The response of seed yield to irrigation is largely due to increased number of pods, and, to a lesser extent, weight per seed, number of seeds per pod and decreased ovule abortion. The crop is most sensitive to applied irrigation during reproductive growth (French and Legg, 1979; Hebblethwaite, 1981). Thompson and Taylor (1979) devised field plots wherein enviornmental stress was reduced as far as possible. Irrigation was constantly near field capacity; additional nutrients were provided, and pest and disease control was optimal. Under these conditions yield increases of up to 67% were recorded. Similar results were obtained by Thompson and Taylor in 1981.

Waterstress

Water shortage is a common yield limiting factor in faba beans (Jones, 1963; Mériaux, 1972; Sprent et al, 1977; Karamanos, 1984). As a result of this much effort has been put into understanding the water relations of the crop (Kassam and Elston, 1974, 1976; Elston et al, 1976; Karamanos,

1978a). In addition, the effects of waterstress on many aspects of plant growth and development have been examined (El Nadi, 1969, 1970; Sprent, 1972; Karamanos, 1978b; Farah, 1979, 1981; Karamanos et al, 1982). A quantitative investigation of the effects of waterstress was undertaken by Karamanos (1984): from this it was established how stressed crops gave lower yields and lower leaf area duration values.

6. The concept of crop ideotypes

Ever since man started to cultivate crop plants some kind of selection procedure has been in operation to try to achieve better, higher yielding plants for the next year. Plant breeding has "evolved" from such primitive selection. The modern plant breeder has a wide range of techniques available such as mutation breeding, polyploidy, exploitation of hybrid vigour, embryo culture, tissue culture, haploids, genetic manipulation, rapid screening techniques and advanced statistical design and analysis. Until recently, however, plant breeding programmes have been based on either "defect elimination" when dealing with particular agronomic difficulties, or "selection for yield" (Donald, 1968).

In the early 1960's, with increased access to evermore powerful computing facilities, the concept of mathematical modelling of crop plants became popular. Several cereal models were proposed (see Blixt and Vose, 1984, for references). Donald (1968) proposed the use of the word "ideotype" for these models. The early ideotypes were rather strict and inflexible. Evans (1973) favoured an adaptable breeding strategy, arranging her aims to meet the demands of a real situation.

In almost any current crop plant breeding and selection programme it is the phenotype resulting from the genetic composition of the plant, as influenced by the environment in which that plant is growing that is being selected. The more of the genetic control of the phenotype and phenotype x environment interactions we come

to understand, the more accurate and rewarding our efforts at crop improvement will be. It is of importance to understand as much of the genetic composition and variability, and the genetic basis of plant physiological processes as possible; this calls for inter-disciplinary collaboration.

The construction of an ideotype is an essentially subjective process, being based on information which is far from complete and the opinions of those constructing the ideotype. Many factors have to be taken into consideration in order to construct an ideotype that is of practical use in the region for which it is being designed. Some basic considerations are climate, soil type, crop use, cultivation and harvest techniques employed, availability and form of fertilizers, the practicalities of pest, disease and weed control, and the availability of labour. From this it is clear that, for any one crop it is possible to have a core of relatively fixed aims, but many other considerations must be flexible to fit the improved crop into the cropping situation for which it is bred. The key to this type of breeding philosophy must be to have definite aims, but to be prepared to modify those aims in accordance with the state of knowledge at the time.

The best known ideotype for Vicia faba is that proposed by Chapman (1977), a terminal inflorescence type plant with reduced vegetative-reproductive growth competition for assimilates.

7. Aims

The aims of the studies presented here are to investigate pod setting and development in Vicia faba genotypes of differing reproductive vascular architectures. Field studies were made at Scottish Crops Research Institute to investigate the response of pod set and fill to various environmental stresses. At Durham a glasshouse study was done to establish 'normal' growth patterns of the genotypes to be investigated. Physiological and

anatomical studies were performed also in Durham, to establish reproductive tissue growth patterns, vascular development patterns and pod development patterns of genotypes showing various different vascular architectures of their reproductive structures.

The ultimate aim of these studies was to investigate the possibility of constructing a faba bean ideotype based on the independent vascular supply type reproductive architecture, where yield was limited by source activity rather than sink capacity.

CHAPTER 2

MATERIALS AND METHODS

Biological material

Commercial and inbred lines used in both glasshouse experiments and field trials are shown in table 2.1.

Chemicals and histological stains

The chemical materials used in this study are listed in table 2.2.

Microscope specifications

Nikon Diaphot- TMD inverted microscope fitted with TMD-EF epi-fluorescence attachment and appropriate filter cassettes (table 2.3).

Table 2.3 Filter cassettes used for stains employed.

Stain	Filter Cassette	Wavelength
Calcofluor	Ultra-violet	405 nm
Auramine	Blue	495 nm
I_2/KI	-	White light

Statistical analysis

Statistical analysis was performed by computer, using either Statistical Package for the Social Sciences Version 9.0 (Nie et al 1975) or Statistical Package for the Social Sciences Version X (S.S.P.S. Inc. 1983).
Specific tests used are specified in the methods of individual trials.

Glasshouse growth conditions

Seeds were sown in Levingtons Universal Compost in 15 cm. diameter plastic pots under nodulating conditions. Seeds sown in short days were placed under high pressure 400 w. sodium lamps, type SON/T (Anon. 1973), which were suspended 1.5 m. above the bench. This supplementary lighting was used to give plants a sixteen hour day until natural day-length exceeded this.

Table 2.1

Varieties and inbred lines used in experiments.

Variety name or identifier	Source	Identity	Plant and floral architecture, seed size class
Maris Bead	PBI	Commercial variety	Indeterminate growth, little basal branching. Interdependent vascular supply within raceme. Black/purple spot flowers. Minor.
line 22	PBI	Sudanese triple white. Autofertile	Determinate growth, some basal branching. Independent vascular supply within raceme. White flowers, few. Minor/equina.
line F	Durham Breeding Programme	Selected inbred line. (Selection 56/14/F; see Smith 1982) F4	Semi-determinate growth. Semi-independent vascular supply. Black spot flowers. Equina. Some segregating still occuring
line G	Durham Breeding Programme	Selected inbred line. (Selection 56/143/9; see Smith 1982). Autofertile	Semi-determinate growth, some basal branching. Independent vascular supply. White flowers, partially synchronous. Minor.
line A	Durham Breeding Programme	Selected inbred line	As above
line A1V5	Durham Breeding Programme	Selection of line A	As above

Table 2.2

Chemicals and stains used.

Chemical	Source
Acetone	B.D.H. Biochemicals Ltd., Poole, Dorset, U.K.
Iodine	B.D.H. Biochemicals Ltd., Poole, Dorset, U.K.
Potassium iodide	B.D.H. Biochemicals Ltd., Poole, Dorset, U.K.
Glutaraldehyde	E.M. Scope Laboratories Ltd., Ashford, Kent, U.K.
Formaldehyde	E.M. Scope Laboratories Ltd., Ashford, Kent, U.K.
Sodium cacodylate	E.M. Scope Laboratories Ltd., Ashford, Kent, U.K.
Calcofluor white	Polysciences Inc., Warrington, Pennsylvania, U.S.A.
Auramine O	Sigma Chemical Co. Ltd., Poole, Dorset, U.K.

Plants were watered weekly with a commercial nutrient feed, Maxicrop (Maxicrop Ltd.) containing all the necessary elements, including nitrogen. Tap water was used for all other watering. Cool conditions were maintained with a maximum day temperature of 15°C and a minimum night temperature of 10°C. All flowers were tripped at developmental stage 9 (Smith 1982), when the flower was fully open, unless otherwise stated.

Reproductive potential and efficiency

This experiment was performed in order to establish precisely the extent of the yield loss problem in field beans of various floral architectures when no treatment was imposed on the plants. The experiment was set up under glasshouse conditions in order to minimise the influence of environmental fluctuation on development. Ten plants each of genotypes 22, G and Maris Bead were grown and their reproductive development closely monitored. All flowers were hand tripped to ensure pollination. The following yield components were evaluated:-

Number of flowering nodes
Number of buds
Number of flowers
Number of pods set
Number of pods retained
Number of pods 'filled' (bearing seeds)
Number of ovules formed
Number of seeds
Weight of seeds

The location of any abcising reproductive structures on the plant was recorded, the structure collected and dissected to obtain the count for the number of ovules formed. From this data it was possible to estimate absolute theoretical yield potential, inter-genotypic differences at each stage of reproductive development and the relative efficiency of the genotypes examined.

The results obtained were put into the computer and appropriately analysed using S.P.S.S. Analysis on a whole plant basis was performed

using a Mann-Whitney U test as the yield components were not normally distributed and data transformations were inappropriate. In order to examine the inter-genotypic yield component differences more closely, locating the sites of difference on the plant an analysis of yield data at each reproductive node was performed. In this case the data was normally distributed, enabling analysis of variance and least significant differences to be calculated. Plant profiles for each yield component for each genotype were constructed.

Field Trials

Introduction

A series of field trials were set up at the Scottish Crops Research Institute at Invergowerie, to investigate the responses of genotypes with different floral architectures to some of the enviornmental stresses commonly found in the field crop situation. The following environmental stresses were selected for investigation:-

High plant competition - systematic density trial

High soil moisture levels - irrigation trial

Lower growth limiting constraints - raised beds

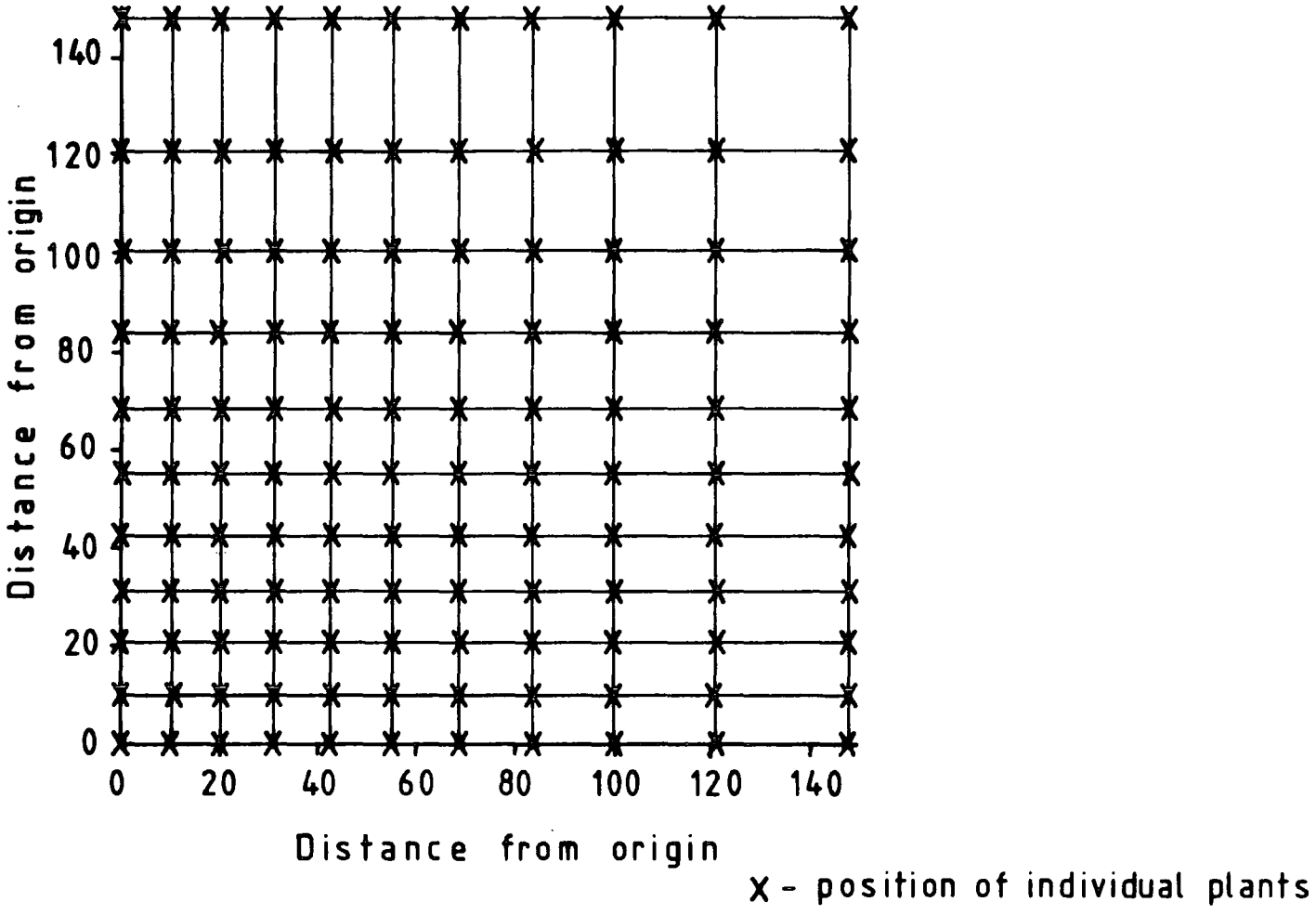
High plant competition/high soil moisture - irrigation and density trial

Low water availability - waterstress experiment

The effects of these stresses on yield and its various components were recorded.

Systematically designed spacing trial

In order to determine the effects of increased inter-plant competition on yield components of field beans of differing floral architectures, a systematically arranged spacing trial was set up. Genotypes A, F, G and Maris Bead were planted. The experimental design (figure 2.1) included planting densities from 10 to 100 plants/metre^2. The experimental design was a square grid plant with increasing spacing on both x and y axes of the planting grid. Four plots of each genotype were planted as a square with the highest planting densities in the centre of the square (figure 2.1, plate 1). Guard plants were planted round each set of plots to eliminate edge effects. If germination



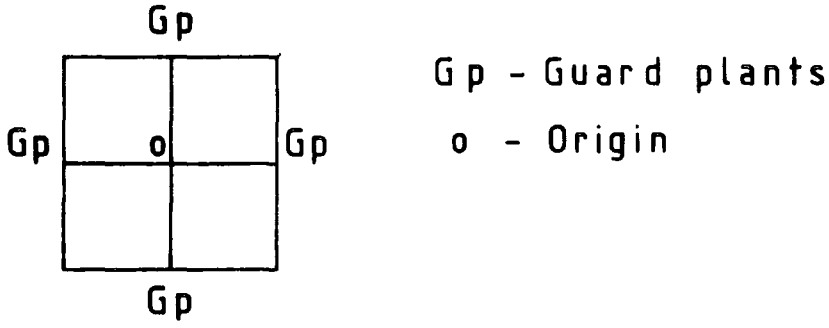


Figure 2.1 Experimental design for the systematically designed plant spacing trial.
(a) Detailed planting grid.
(b) Arrangement of the plots employed for each genotype.

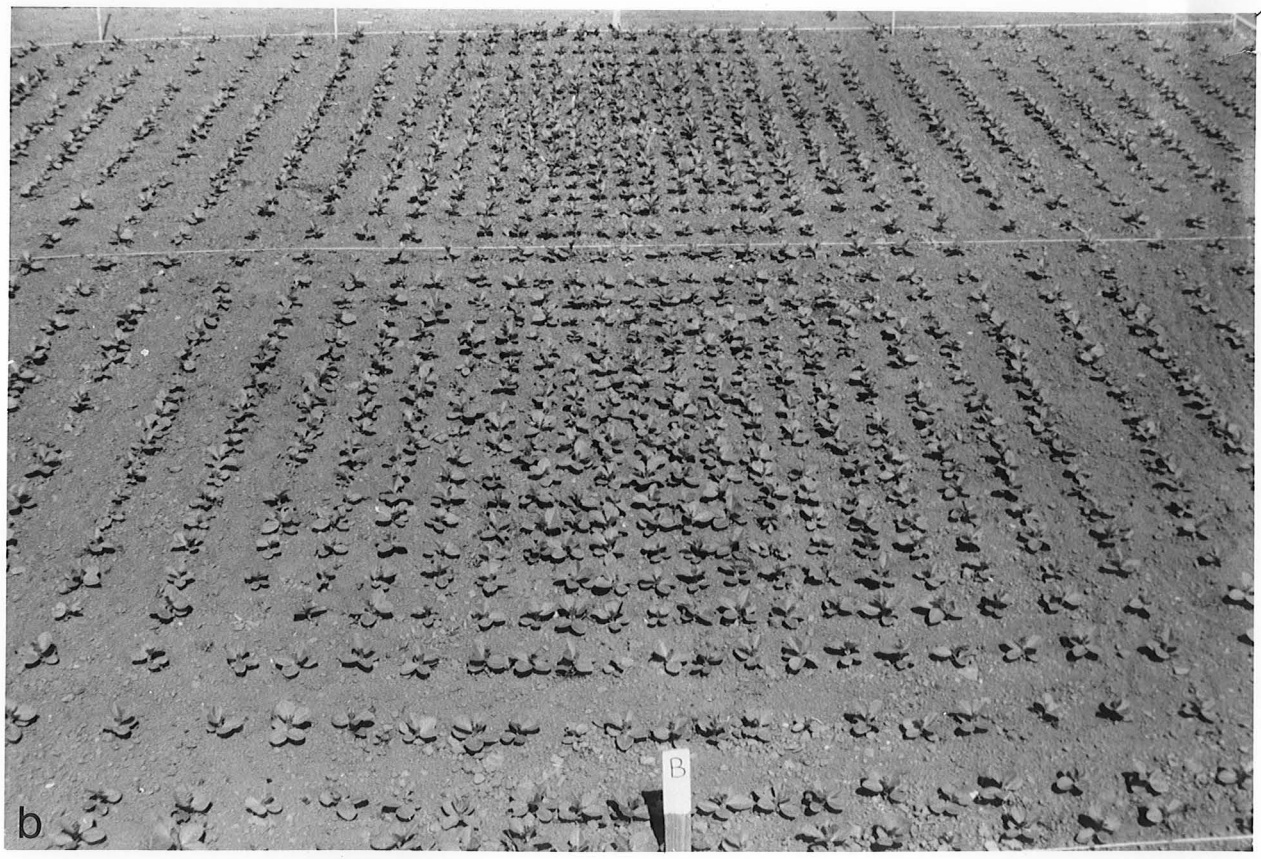
Plate 1

Systematic density trial shortly after seedling emergence.

(a) all plots

(b) close up


a


b
B

failed at any position the gap was filled with a pot grown plant in order to maintain the precise planting densities of the grid. At flowering any rogue plants were tagged in order to quickly identify them at harvest. At harvest (pods dry) each plant was sampled and the following yield components were recorded:-

First flowering node
Number of flowering nodes
Number of flowers
Number of podded nodes
Number of pods set
Number of pods 'filled'
Number of pods per podded node
Number of seeds per pod
Number of seeds per plant
Weight per seed in grammes
Weight of seeds in grammes

Mean values for each yield component of each genotype at each planting density were calculated and plotted. From these the following were calculated:-

Mean number of pods set/metre^2
Mean number of seeds/metre^2
Extrapolated yield in tonnes/hectare at each planting density

These results were plotted and yield component trends relating to differing planting densities examined.

Irrigation trial

An irrigation trial was set up to investigate the effects of high available soil moisture levels on yield components of field beans of different vascular architectures. Genotypes A, G and Maris Bead were tested. The irrigation levels investigated were: control - no irrigation applied, irrigation to 75 centibars soil moisture tension, i.e. water added to a tension between normal field levels and field capacity. The third plot was irrigated to 25 centibars soil moisture tension, close to field capacity. The experimental design used for the trial was based on a fixed and random effects model (figure 2.2), the fixed effects being replicates and irrigations,

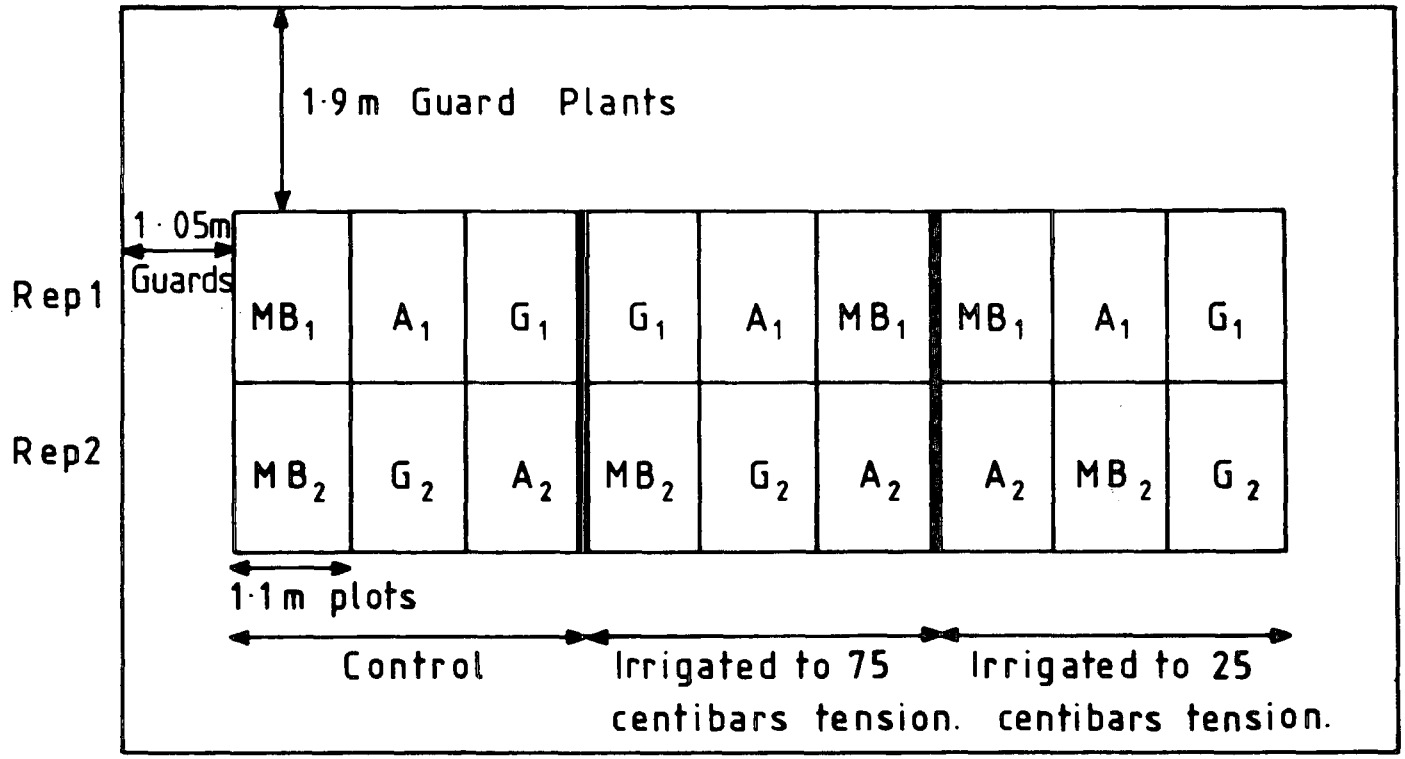


Figure 2.2 The experimental design plan for the irrigation trial.

genotypes were randomised within these constraints. The plants were in double rows with 45 centimetres between double rows, 10 centimetres between individual rows, and 8 centimetre spacings within each row.

From each plot a random sample of 10 plants was taken and the following were recorded:-

Number of stems
Number of podded nodes
Number of pods
Number of seeds
Weight of seeds

Analysis of variancewas carried out using S.P.S.S.X., the data was skewed, so a log transformation was performed to correct the distribution. The results of analysis of variance performed on the transformed data were manipulated by hand in order to obtain the F ratio of each effect investigated against its appropriate error term (Snedecor and Cochran, 1967). Where a significant difference was found, least significant differences were calculated in order to locate the difference. Mean values of each yield component of each genotype at each irrigation were plotted as histograms. At plant maturity the central 0.6 x 1.0 metres of each plot was harvested and the seed yields analysed. In this case the data was normally distributed so no transformations were necessary.

Evaluation of yield components of plants grown with some major growth restraints reduced

Plants of genotypes A, IVSC, AIVS, G, F and Maris Bead were grown in raised beds designed to reduce environmental limitation of plant growth to as low a level as possible. Soil moisture tension was maintained at field capacity by means of trickle irrigation lines laid at frequent intervals in the bed. Mineral nutrition was also supplied via the irrigation lines in order to maintain optimum availability of the various minerals required to maintain healthy plant growth. Soil structure was such that plant root growth was restricted as little as possible. The beds were planted in double rows 45 centimetres apart,

with 10 centimetres between individual rows and 8 centimetre spacings within rows. Three double rows 2 metres long of A, G, F and Maris Bead and one double row 2 metres long of AIVS and IVSC were grown. Maris Bead was also grown as guard plants between rows of lines to be tested and around the plot to eliminate edge effects. Under these growth conditions the plants grew taller than usual and were more susceptible to lodging. To support the plants, nylon netting was placed horizontally across the plants at one and two metres height above soil level. At plant maturity 10 plants of each genotype were randomly sampled and their height, number of stems, number of pods, number of seeds and weight of seeds were recorded. Data analysis was performed using S.P.S.S.X., Least significant differences were used where analysis of variance revealed a significant difference between genotypes in order to determine which genotypes differed significantly from each other.

Irrigation and density trial

To investigate the effects of high inter-plant competition combined with irrigation response a field trial was set up as shown in figure 2.3. A sample of 10 plants was randomly selected from each plot and the following were recorded:-

Plant height
Total stem length
Number of leaves
Dry weight of straw
Number of flowers
Number of pods set
Number of pods 'filled'
Number of seeds
Dry weight of seeds
Number of flowering nodes
Number of podded nodes
Number of nodes with pods 'filled'

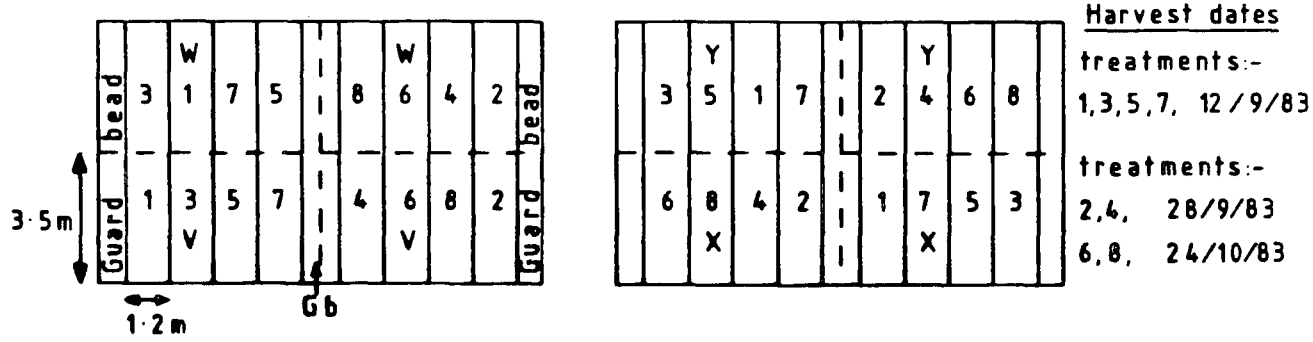
The data was analysed using S.P.S.S. . On examination of plot means plot y was found to give values considerably different from the other

Durham Bean density / Irrigation experiment 1983

Four repeats of eight treatments

1	Genotype G	40 plants / m^2	no irrigation
2	Genotype G	40 plants / m^2	irrigated
3	Genotype G	80 plants / m^2	no irrigation
4	Genotype G	80 plants / m^2	irrigated
5	Genotype MB	40 plants / m^2	no irrigation
6	Genotype MB	40 plants / m^2	irrigated
7	Genotype MB	80 plants / m^2	no irrigation
8	Genotype MB	80 plants / m^2	irrigated

Seed sown in double rows 10 cm apart at 30cm centres (4 double rows)
Within each row seeds sown 8 or16 cm apart (83·3/m^2, 41·6/m^2)
Irrigation lines in plots with even numbers
Tensiometers in plots 4 V, W, X, Y.
Irrigate when first bed reaches 25 cb
(33 mm added $2·5 \times 10^{3}$ megapascals)
Area harvested 2 m x 0·6 m from centre of plot to allow adequate guard plants all around to reduce edge effects.
Plots were harvested at plant maturity, ie:- at same physiological age.



Harvest dates

treatments:-
1,3,5,7, 12/9/83

treatments:-
2,4, 28/9/83
6,8, 24/10/83

Figure 2.3 Experimental plan and treatment regime for the irrigation and density trial.

three plots, therefore plot y was not included in the final analysis tables. When analysis of variance was performed the 4 way interaction of genotype x density x irrigation x plot was non-significant, the interaction sum of squares for the 4 way interaction was therefore pooled with the error sum of squares and the other effects were tested against the resultant mean square. Plant profiles were constructed for each genotype with each treatment for:-

Number of flowers
Number of pods set
Number of pods 'filled'
Number of seeds, at each reproductive node

In order to establish which of the variables measured could best be used as a predictor of high yield in a segregating population growing under field conditions, regression analysis was performed using S.P.S.S.X. A stepwise analysis was performed to show which of the variables contributed significantly to an equation predicting seed yield per plant, and which of these made the highest contribution to the equation. Attempts were made to find the best possible equation to estimate yield by means of standardising data, taking natural logarithms and square roots of the data.

Plot harvest yields were corrected to dry weight and analysed using S.P.S.S.X. The genotype x irrigation x density interaction was insignificant; therefore the resultant sum of squares was added in to the error sum of squares and other variables were tested against the total.

Waterstress trial

In order to establish the effects of waterstress applied at different stages of plant growth, the following trial was set up. Seeds of genotypes G and Maris Bead were sown individually in 7.5 cm. pots in a cool glasshouse. The seedlings were transplanted to 30 cm. pots, 4 seedings to a pot. The pots were stood outside on gravel and were allocated to the following treatments:-

Treatment 1 - G wilted pre-flowering

Treatment 2 - G wilted at flowering/early pod set

Treatment 3 - G wilted at pod fill

Treatment 4 - G control, not wilted

Treatmend 5 - Maris Bead wilted pre-flowering

Treatment 6 - Maris Bead wilted at flowering/early pod set

Treatment 7 - Maris Bead wilted at pod fill

Treatment 8 - Maris Bead control, not wilted

One pot of plants receiving each treatment was allocated to each of four blocks, treatments were randomised within each block. The pots were hand watered daily and given nutrients weekly. The treatments were applied by means of covering the appropriate pots with tinfoil at the following times:-

Treatments 1 and 5 - 24th May/7th July

Treatments 2 and 6 - 7th July/12th August

Treatments 3 and 7 - 12th August/10th September

Treatments 4 and 8 - no treatment applied

At plant maturity (September/October) the following total plant characteristics were recorded:-

Dry weight of straw

Number of stems

Number of flowering stems

Maximum plant height

Total stem length

Total number of leaves

Total number of flowering nodes

Total number of flowers

Total number of pods set

Total number of ovules in pods set

Total number of seeds

Total weight of seeds

The values recorded were analysed using S.P.S.S.X.

Plant profiles were constructed for the main stem of each plant, for this the number of flowers, number of pods set, number of ovules present in pods set, number of seeds and weight of seeds at each node were recorded and plotted for each genotype with each treatment applied.

Studies in pod growth and development

A series of observational studies were undertaken to examine the developmental patterns of pods, especially pod walls, of genotypes 22, G and Maris Bead. Three possible areas of difference between the genotypes were investigated:-

Pod length growth

Pod wall structure

Distribution of hairs and stomate pores on the pod surface

Pod length growth

Ten plants each of genotypes 22, G and Maris Bead were pot grown in the glasshouse. The length of each of the ovaries/pods was recorded every two days from anthesis (day 0) to twenty-four days old and at pod maturity. The measured lengths were plotted as graphs. At each pod age measured, analysis of variance was carried out using S.P.S.S.X. in order to find any significant inter-genotypic differences. Least significant differences were used in order to discover which genotype differed significantly from which other genotype(s).

Pod wall structure

Transverse sections of fully expanded pods of genotypes 22, G and Maris Bead were cut, a fresh razor blade was used for each cut in order to obtain clean cut surfaces. The sections were stained in auramine for thirty seconds, then washed in distilled water for a minute, two further washes were carried out, using fresh water each time. The sections were then stained with calcofluor for ten seconds and the washing procedure repeated. The sections were then each mounted in a drop of distilled water and examined under the fluorescence microscope, which was fitted with an ultra-violet cassette.

The pod wall structure was examined: where present mesocarp lignification was measured using a calibrated eyepiece graticule; the measurement was recorded. The pod wall structure was photographed.

Distribution of hairs and stomate pores on the pod surface

Small areas of pod wall surface of genotypes 22, G and Maris Bead were collected and fixed in 0.1M sodium cacodylate buffer at pH 7.0, plus 2.5% glutaraldehyde, plus 1% formaldehyde for twelve hours, dehydrated through an acetone series, critical point dried with CO_2, coated with gold-palladium alloy and examined in a Cambridge Stereoscan 600 Scanning Electron Microscope (S.E.M.). Further areas of pod wall tissue were stained with calcofluor as previously described, then examined under the fluorescence microscope. The number of stomata and pod wall hairs found in each of ten fields of view at magnification x 100 were counted. Analysis of variance was performed on the data collected using S.P.S.S.X. to ascertain whether there was a significant difference between genotypes for either number of hairs or number of stomata per unit area. Least significant differences were computed to locate significant differences.

Studies of the changes in fresh and dry weights of reproductive tissues during development from anthesis to maturity

A hundred plants each of genotypes Maris Bead, G and 22 were grown in the glasshouse. Flowers were tripped and date tagged at anthesis. When the flowers at flowering node six reached anthesis twenty plants of each genotype were randomly selected and racemes of the same genotype and age were pooled. Racemes were dissected into peduncle, pedicel, pod and seed components. Petals were discarded and seeds dissected from the ovaries and counted. The plant parts were placed on pre-dried, pre-weighed papers and their fresh weight recorded. Then the papers and plant parts were placed in an oven at $105^{o}C$ until constant weight was attained; this was recorded. Harvests were repeated at regular intervals to establish a growth pattern from anthesis to maturity. In the second to the last harvests, owing to

increased weight of plant parts, it was only necessary to harvest ten plants each time.

Fresh and dry weights per unit of tissue were calculated, and for peduncles the weight of peduncle/pod was calculated as this parameter was dependent on the number of pods/peduncle. The resultant weights/part were plotted. In order to establish the increase in weight of each part relative to its initial weight the ratio of:

$$\frac{\text{weight of part at time X}}{\text{weight of part at time 0 (anthesis)}}$$

was calculated. As this ratio yielded relative increases of up to 10^9 the logarithm of the value obtained was taken; these values were plotted.

Studies in the development of the vascular supply within the raceme

Fresh peduncles, pedicels, pods and funicles of Maris Bead at the anthesis stage and at full development were hand sectioned and stained in 0.1% w/v calcofluor white - M2R, washed in distilled water to eliminate background fluorescence and mounted in distilled water. These sections were examined using a fluorescence microscope fitted with an ultra-violet filter cassette. Specimens were photographed using Ilford XP1 film.

Hand sections of stem tissue were also cut; these were from plants either at the beginning of flowering or at pod fill stages. The sections were stained in 1% iodine/10% potassium iodide solution for a minute. Thorough washing followed to remove excess stain and loose debris present on the surfaces of the sections. They were then mounted in distilled water and examined by bright field light microscopy.

CHAPTER 3

RESULTS OF OBSERVATIONS ON REPRODUCTIVE POTENTIAL AND EFFICIENCY

3.1 Whole plant analysis

In all genotypes a high loss of reproductive potential was recorded. Genotype 22 had the lowest values for all yield components (table 3.1.1). Genotypes G and Maris Bead had similar values for most components measured. If values obtained for genotypes 22 and G were calculated as a percentage of the values for Maris Bead, 22 gave consistently low values (table 3.1.2). The values obtained for G fluctuated around those obtained for Maris Bead. The yield of G, however, was 181.51% of that of Maris Bead, a substantially higher value.

An estimate of the efficiency of a plant in producing seed bearing ('full') pods was obtained by calculating the percentage of the number of buds formed present at each stage of development (table 3.1.3). From these values it can be seen that, although Maris Bead appeared most efficient for number of flowers, number of pods set and number of pods retained, it was 22 that filled the greatest proportion of its seeds. When the percentage of ovules yielding seeds was calculated (table 3.1.4) it was clear that genotype 22 filled the greatest proportion of its potential seeds. Genotype G filled the lowest proportion of its potential seeds.

When pairs of genotypes were statistically compared (tables 3.1.5, 3.1.6, 3.1.7) it was seen that genotype 22 was significantly different from both G and Maris Bead for all yield components, mostly at the $p \leq 0.001$ level. Genotypes G and Maris Bead were, however, found to show few significant differences from each other, the only significant values being number of flowering nodes and number of seeds.

Table 3.1.1

Mean values for all yield components. Standard errors shown in parentheses.

	Genotype		
	22	G	Maris Bead
Number of flowering nodes	13.700 (1.086)	22.000 (1.673)	15.700 (0.396)
Number of buds	35.400 (2.725)	99.900 (8.367)	88.200 (5.172)
Number of flowers	11.200 (0.680)	45.500 (3.987)	45.800 (4.268)
Number of pods set	10.100 (0.767)	37.900 (4.159)	42.300 (4.356)
Number of pods retained	8.100 (0.900)	23.900 (2.631)	24.000 (2.700)
Number of pods 'filled'	6.000 (0.596)	10.800 (0.879)	10.400 (0.968)
Number of ovules	86.000 (7.395)	293.400 (25.095)	288.000 (17.978)
Number of seeds	17.900 (10.250)	21.800 (2.489)	30.500 (3.060)
Weight of seeds	4.783 (0.459)	17.096 (10.289)	9.419 (0.996)

Table 3.1.2

Yield component values expressed as percentages of the values for Maris Bead.

	Genotype		
	22	G	Maris Bead
Number of flowering nodes	87.26	104.13	100
Number of buds	40.14	113.27	100
Number of flowers	24.45	99.34	100
Number of pods set	23.88	89.60	100
Number of pods retained	33.75	99.58	100
Number of pods 'filled'	57.69	103.84	100
Number of ovules	29.86	101.88	100
Number of seeds	58.69	71.48	100
Weight of seeds	50.78	181.51	100

Table 3.1.3

Percentage of the number of buds formed present at each stage of yield production.

	Genotype		
	22	G	Maris Bead
Number of buds	100	100	100
Number of flowers	31.64	45.55	51.93
Number of pods set	28.53	37.94	47.36
Number of pods retained	22.88	23.92	27.21
Number of pods 'filled'	16.95	10.81	11.79

Table 3.1.4

Percentage of the number of ovules formed that yield seeds.

	Genotype		
	22	G	Maris Bead
Number of ovules formed	100	100	100
Number of seeds 'filled'	20.81	7.43	10.59

Table 3.1.5

Results of Mann-Whitney U test to detect differences in yield component values between genotypes 22 and G.

Yield component	U value	Z value	2 tailed probability corrected for ties
Number of flowering nodes	8.0	-3.1893	0.0014
Number of buds	0.0	-3.7868	0.0002
Number of flowers	0.0	-3.7853	0.0002
Number of pods set	0.0	-3.7882	0.0002
Number of pods retained	1.5	-3.6718	0.0002
Number of pods 'filled'	6.0	-3.3476	0.0008
Number of ovules	0.0	-3.7839	0.0002
Number of seeds	15.5	-2.6198	0.0088
Weight of seeds	19.0	-2.3434	0.0191

Table 3.1.6

Results of Mann-Whitney U test to detect differences in yield component values between genotypes 22 and Maris Bead.

Yield component	U value	Z value	2 tailed probability corrected for ties
Number of flowering nodes	20.0	-2.2956	0.0217
Number of buds	0.0	-3.7868	0.0002
Number of flowers	0.0	-3.7839	0.0002
Number of pods set	0.0	-3.7868	0.0002
Number of pods retained	1.0	-3.7110	0.0002
Number of pods 'filled'	6.5	-3.3209	0.0009
Number of ovules	0.0	-3.7825	0.0002
Number of seeds	10.0	-3.0374	0.0024
Weight of seeds	5.0	-3.4017	0.0007

Table 3.1.7

Results of Mann-Whitney U tests to detect differences in yield component values between genotypes G and Maris Bead.

Yield component	U value	Z value	2 tailed probability corrected for ties
Number of flowering nodes	10.0	-3.0514	0.0023
Number of buds	37.0	-0.9834	0.3254
Number of flowers	47.5	-0.1893	0.8499
Number of pods set	39.0	-0.8325	0.4051
Number of pods retained	50.0	0.0	1.0000
Number of pods 'filled'	42.5	-0.5746	0.5656
Number of ovules	46.0	-0.3025	0.7623
Number of seeds	22.5	-2.0819	0.0373
Weight of seeds	32.0	-1.3607	0.1736

3.2 Individual node analysis

Plant profiles for each yield component (figures 3.2.1, 3.2.2, 3.2.3, 3.2.4, 3.2.5, 3.2.6, 3.2.7, 3.2.8) gave a characteristically shaped curve for each yield component for each genotype. When analysis of variance was carried out for each yield component at each reproductive node significant inter-genotypic differences were revealed (tables 3.2.1, 3.2.2, 3.2.3, 3.2.4, 3.2.5, 3.2.6, 3.2.7, 3.2.8) These could be ascribed to differences between particular genotypes by use of least significant differences.

List of figure headings

Figure 3.2.1

Plant profiles of each genotype to show the mean number of buds formed at each node.

Figure 3.2.2

Plant profiles of each genotype to show the mean number of flowers formed at each node.

Figure 3.2.3

Plant profiles of each genotype to show the mean number of pods set at each node.

Figure 3.2.4

Plant profiles of each genotype to show the mean number of pods retained at each node.

Figure 3.2.5

Plant profiles of each genotype to show mean numbers of pods 'filled' at each node.

Figure 3.2.6

Plant profiles of each genotype to show mean numbers of ovules formed at each node.

Figure 3.2.7

Plant profiles of each genotype to show the mean number of seeds at each node.

Figure 3.2.8

Plant profiles of each genotype to show mean weight of seeds at each node.

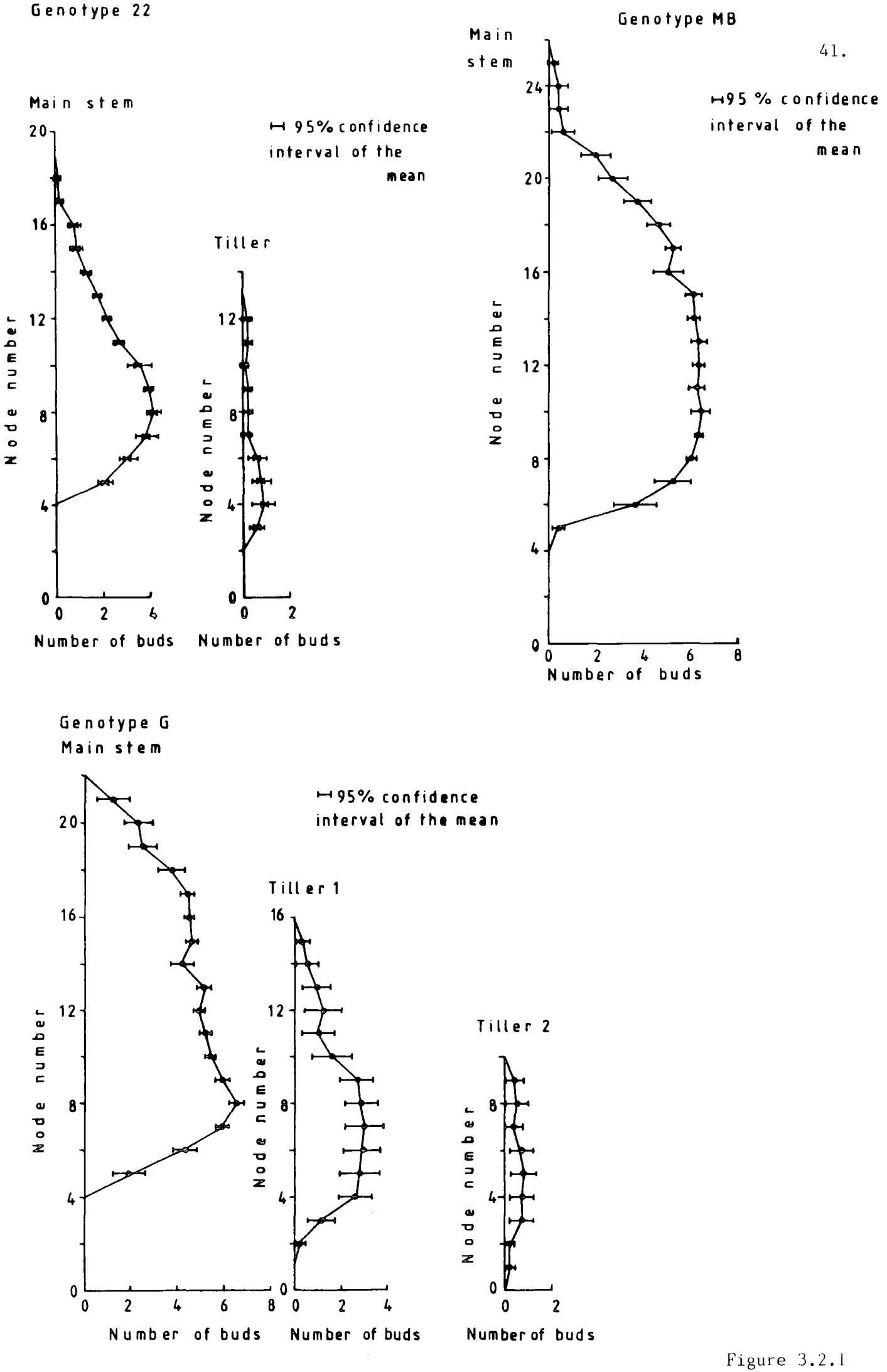

Genotype 22
Main stem
95% confidence interval of the mean
Tiller
Node number
Number of buds
Genotype MB
Main stem
95 % confidence interval of the mean
Node number
Number of buds
Genotype G
Main stem
95% confidence interval of the mean
Tiller 1
Tiller 2
Node number
Number of buds

Figure 3.2.1

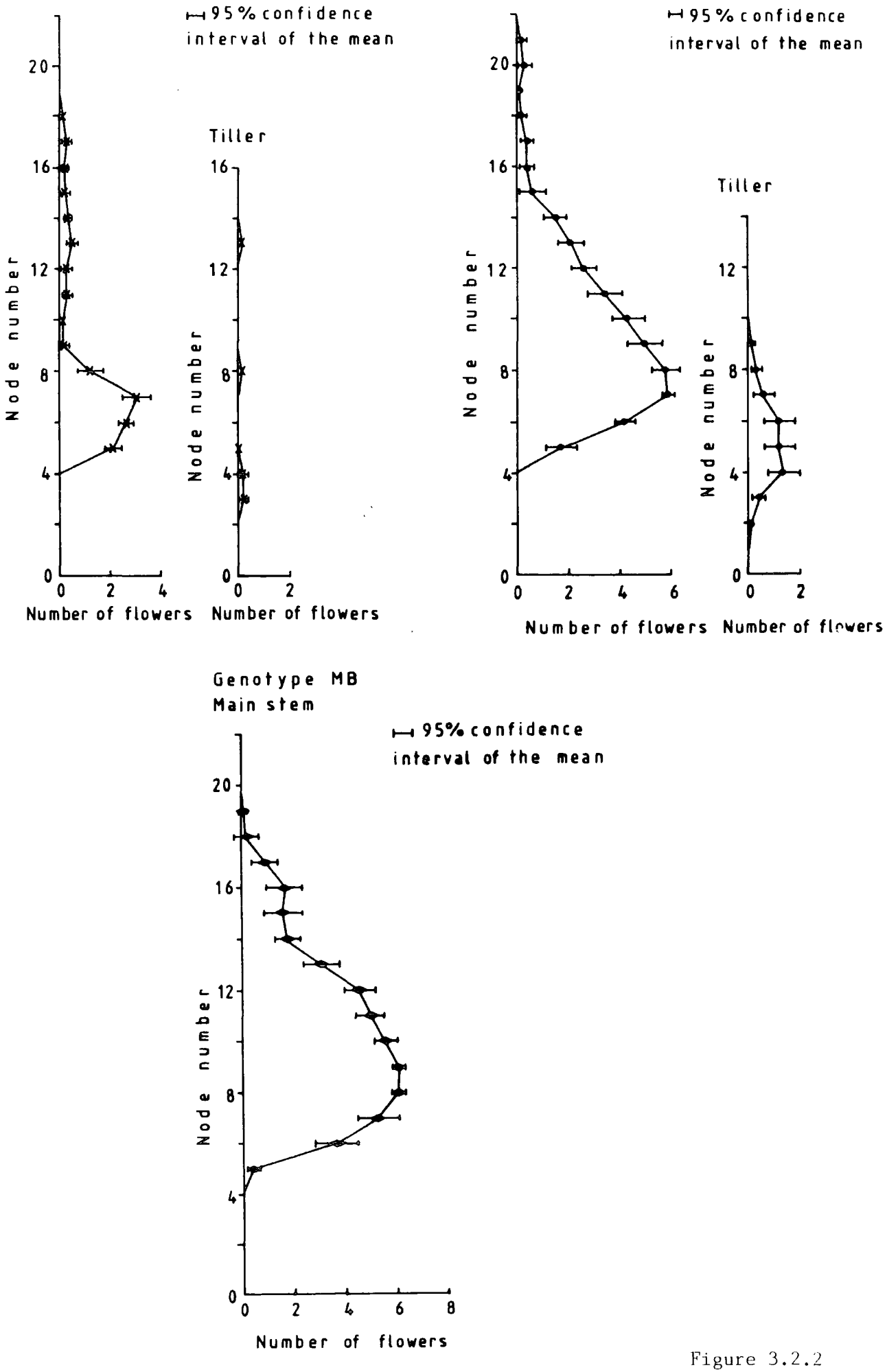
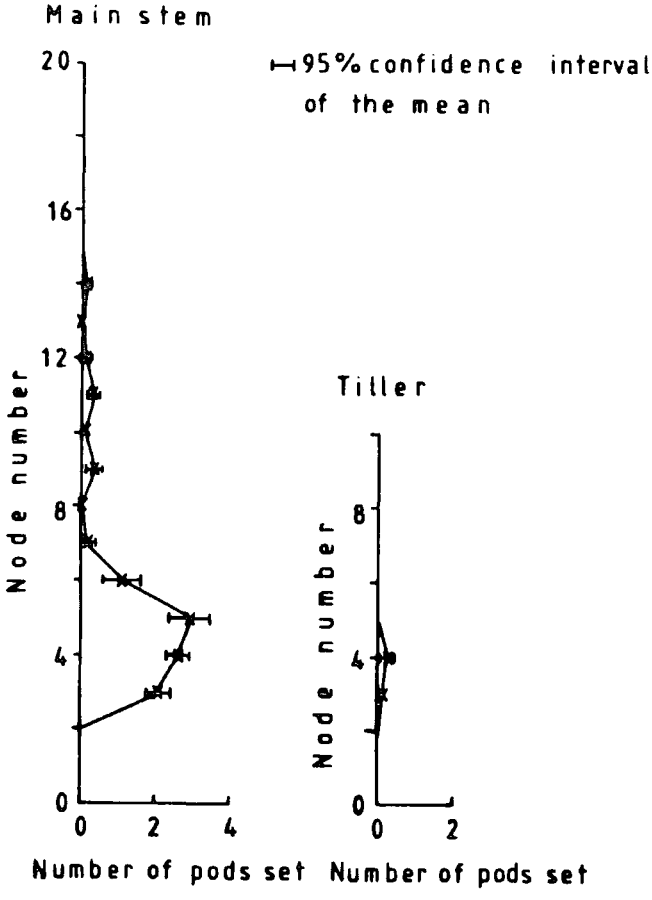
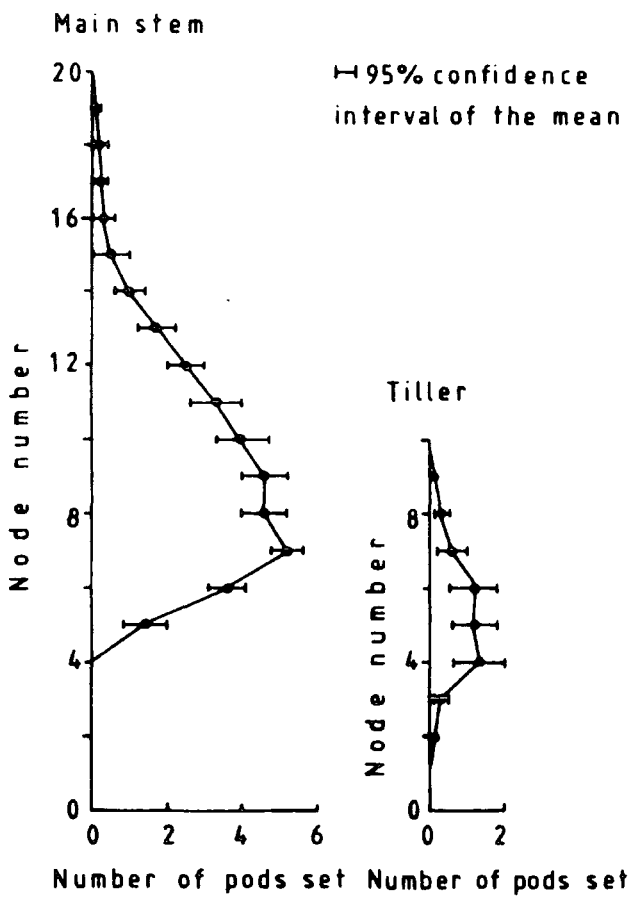

Genotype 22
Main stem
95% confidence interval of the mean
Node number
Number of flowers
Tiller
Genotype G
Main stem
95% confidence interval of the mean
Node number
Number of flowers
Tiller
Genotype MB
Main stem
95% confidence interval of the mean
Node number
Number of flowers

Figure 3.2.2

Genotype 22



Genotype G



Genotype MB

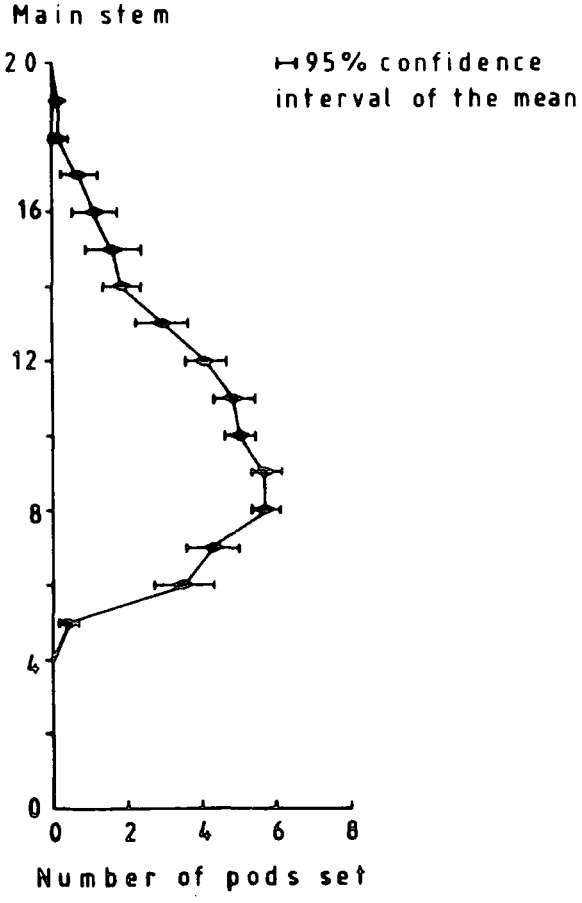
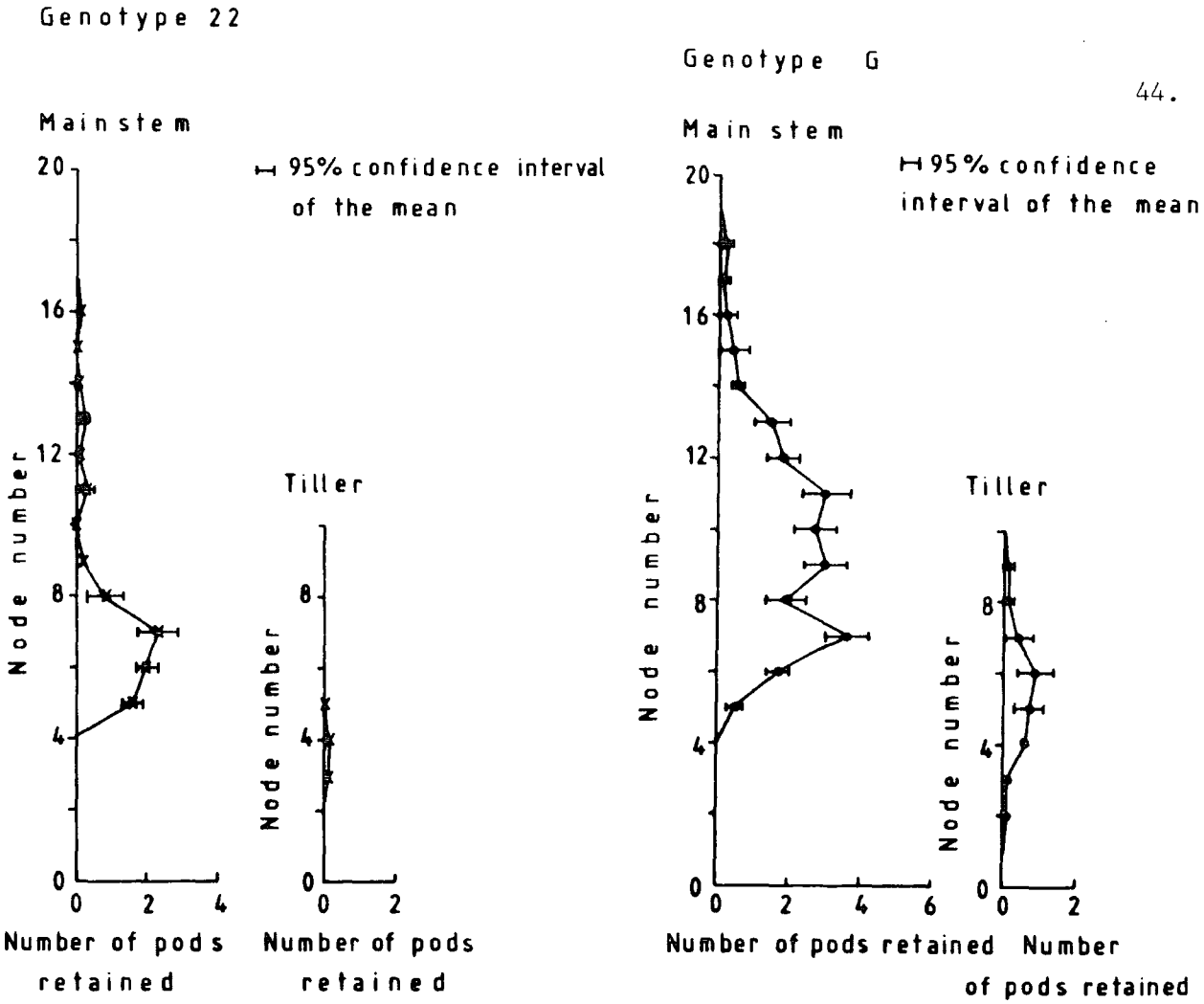


Figure 3.2.3


Genotype 22
Main stem
95% confidence interval of the mean
Node number
Number of pods retained
Tiller
Node number
Number of pods retained
Genotype G
Main stem
95% confidence interval of the mean
Node number
Number of pods retained
Tiller
Node number
Number of pods retained

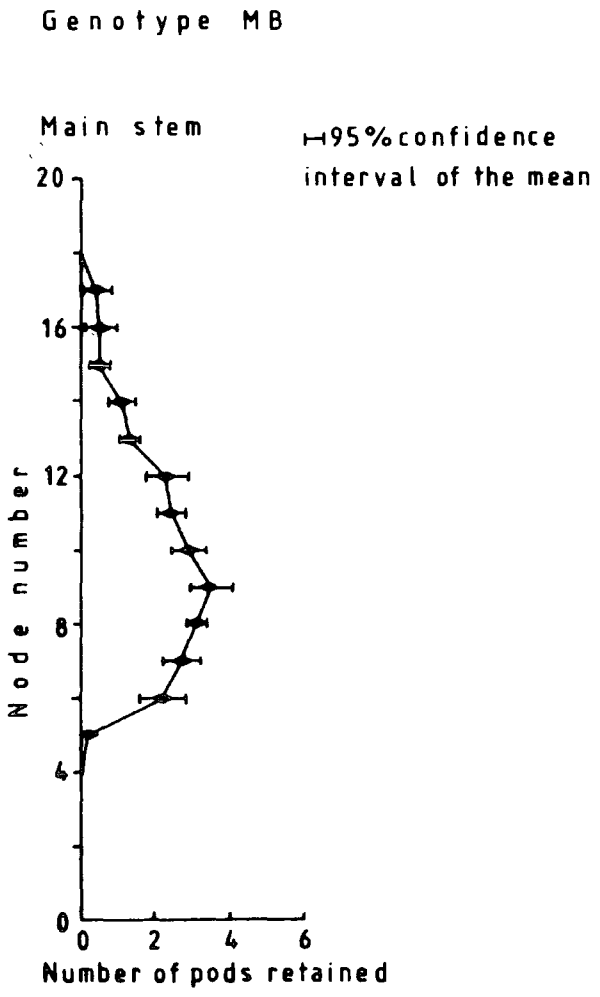
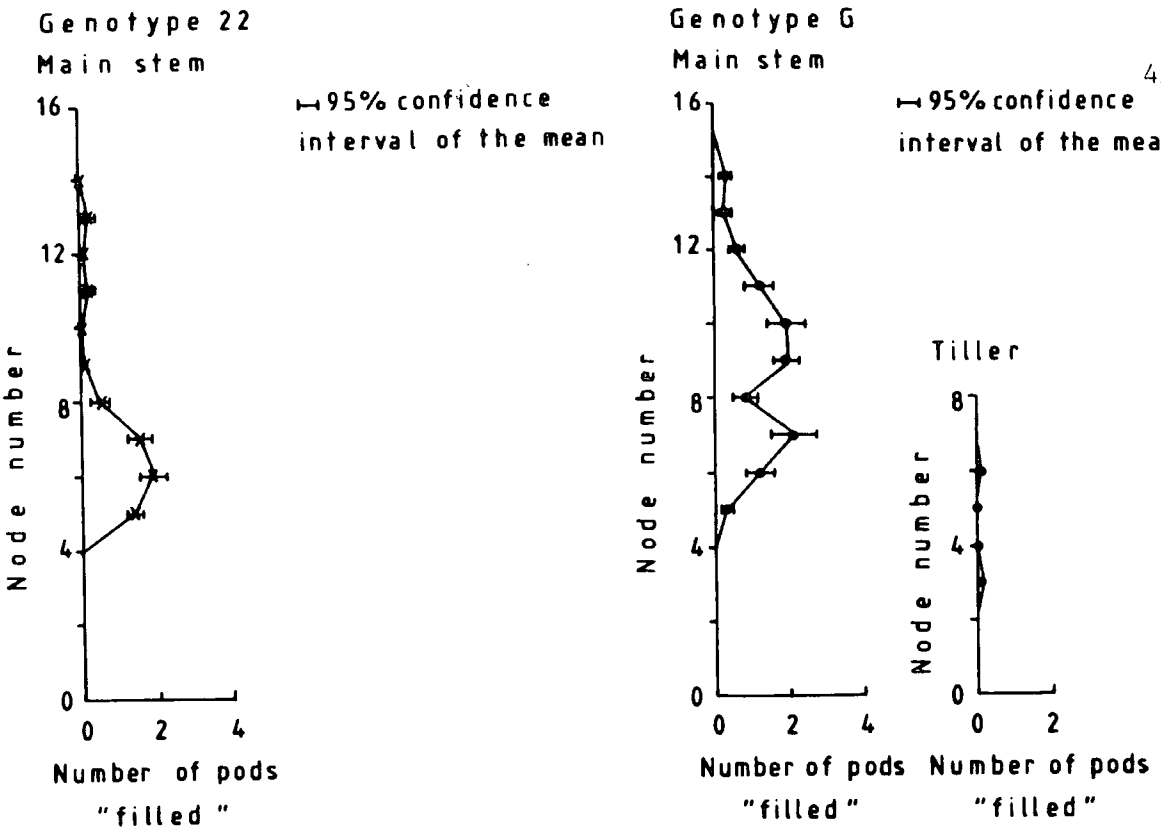

Genotype MB
Main stem
95% confidence interval of the mean
Node number
Number of pods retained

Figure 3.2.4


Genotype 22
Main stem
95% confidence interval of the mean
Node number
Number of pods "filled"
Genotype G
Main stem
95% confidence interval of the mean
Tiller
Node number
Number of pods "filled"
Number of pods "filled"

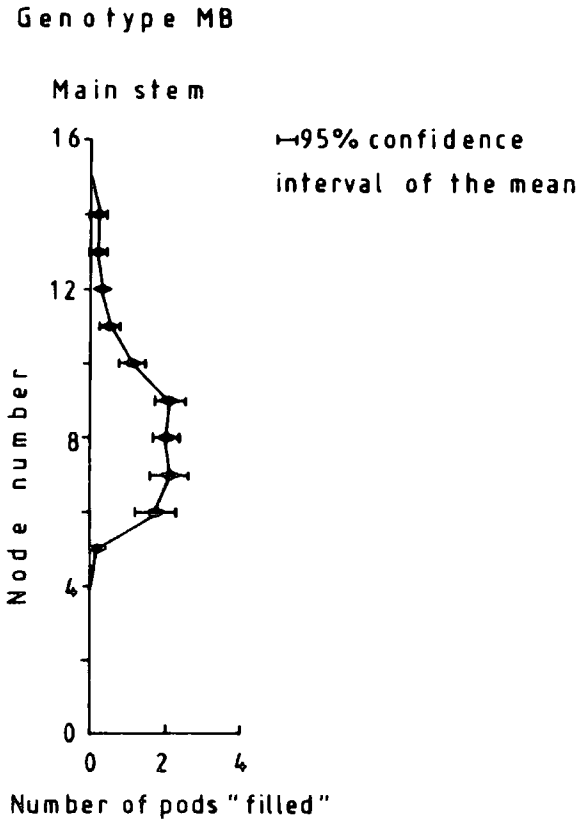

Genotype MB
Main stem
95% confidence interval of the mean
Node number
Number of pods "filled"

Figure 3.2.5

Genotype 22

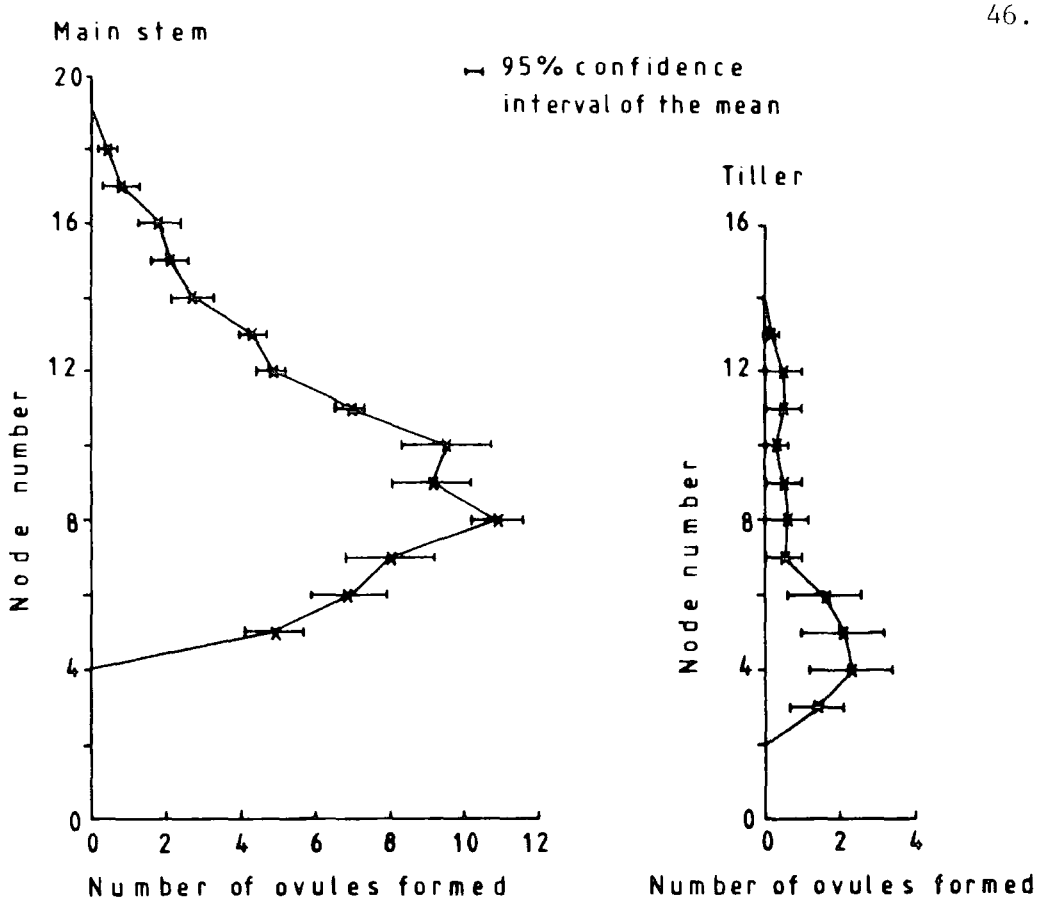


Figure 3.2.6

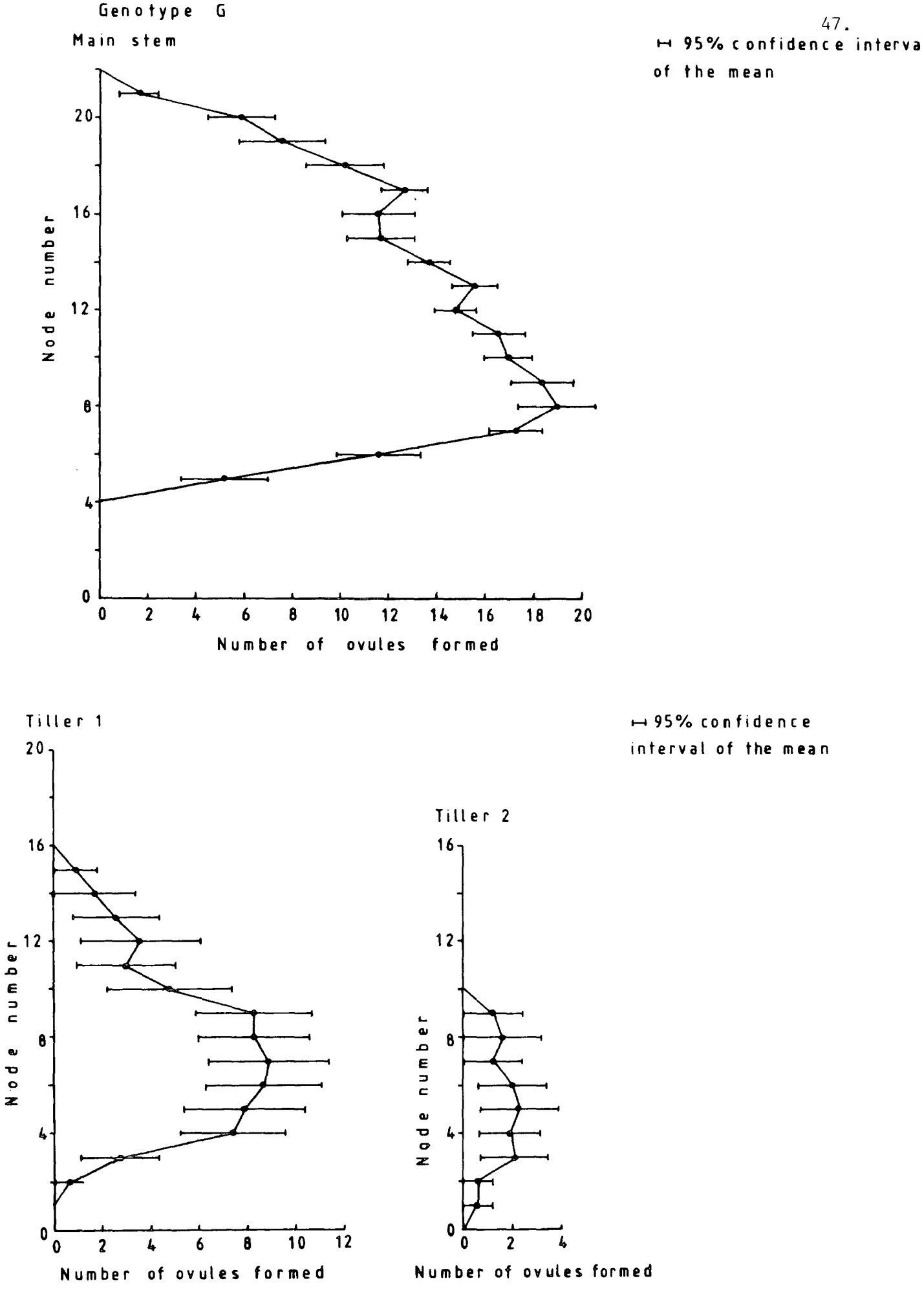


Figure 3.2.6 continued

Genotype MB

⊢ 95% confidence interval of the mean

Main stem

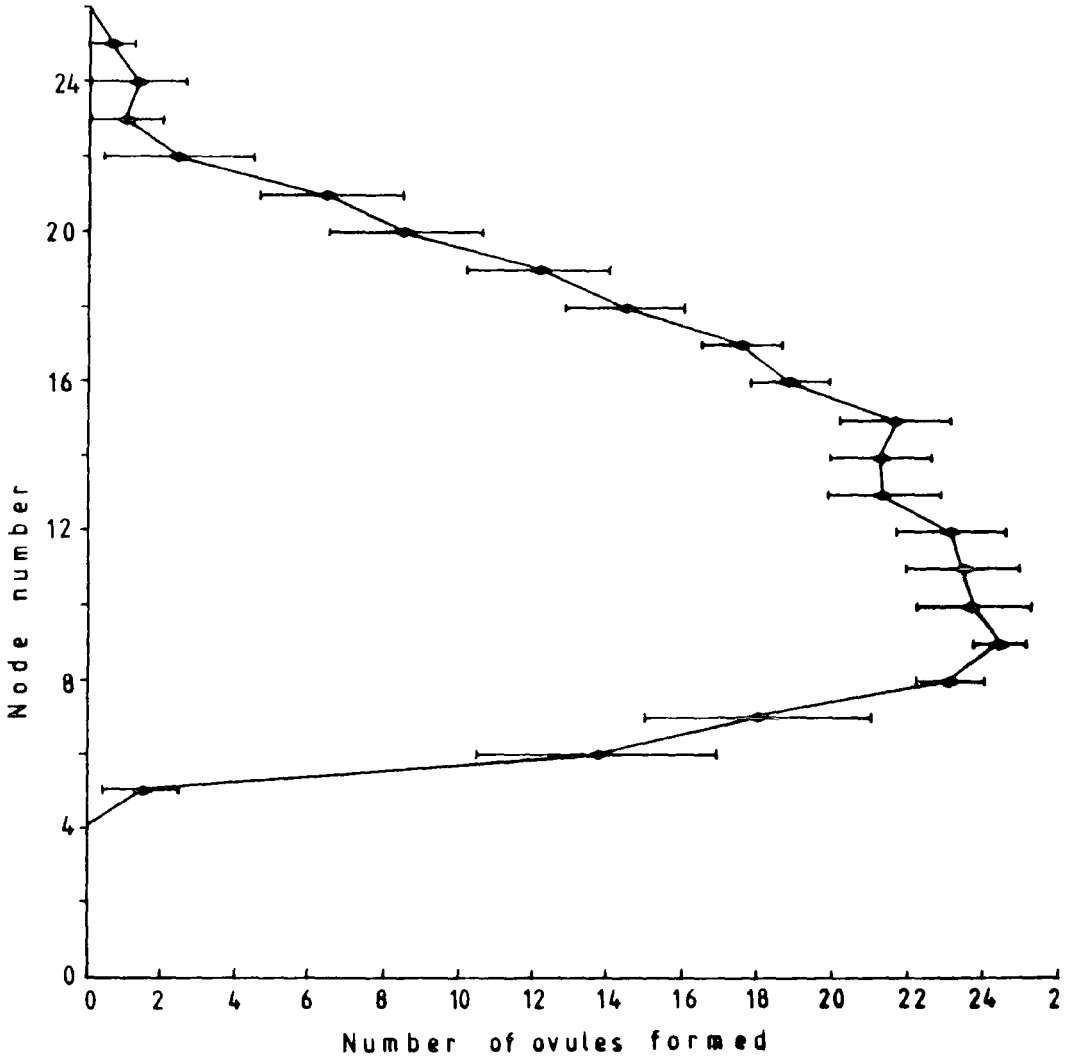
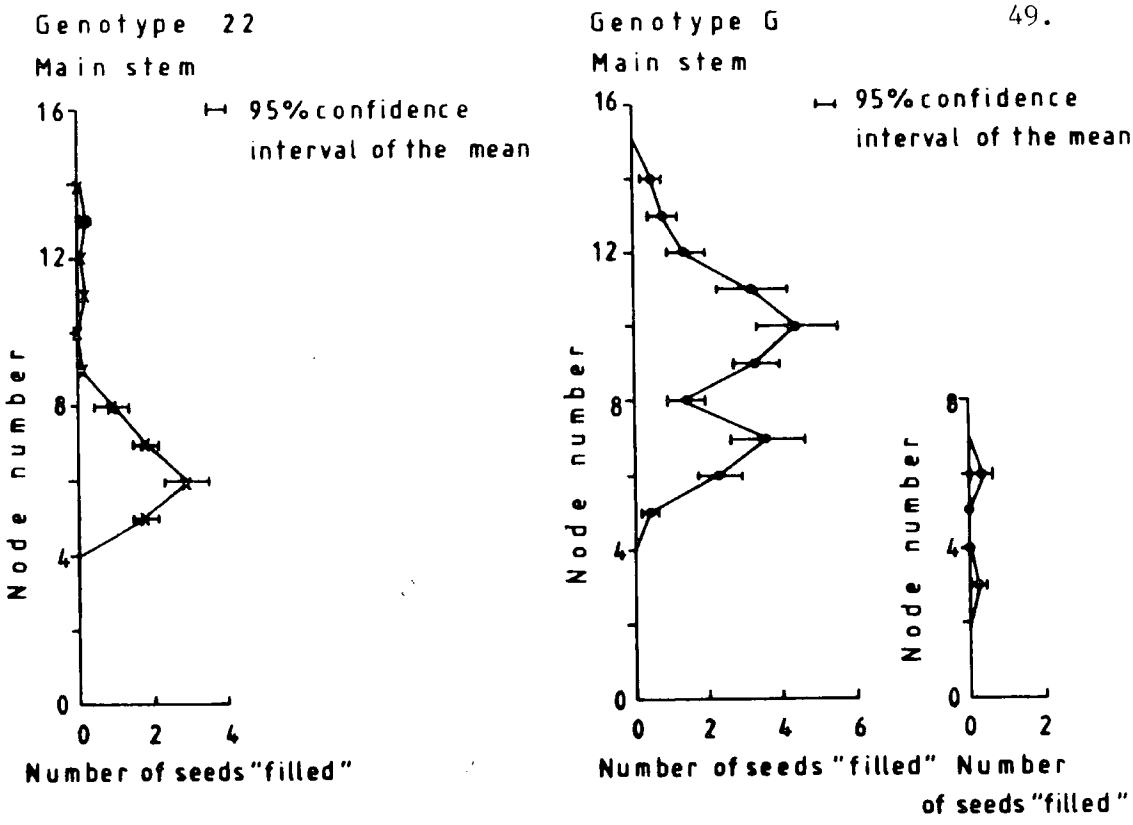


Figure 3.2.6 continued


Genotype 22
Main stem
95% confidence interval of the mean
Node number
Number of seeds "filled"
Genotype G
Main stem
95% confidence interval of the mean
Node number
Number of seeds "filled"
Number of seeds "filled"

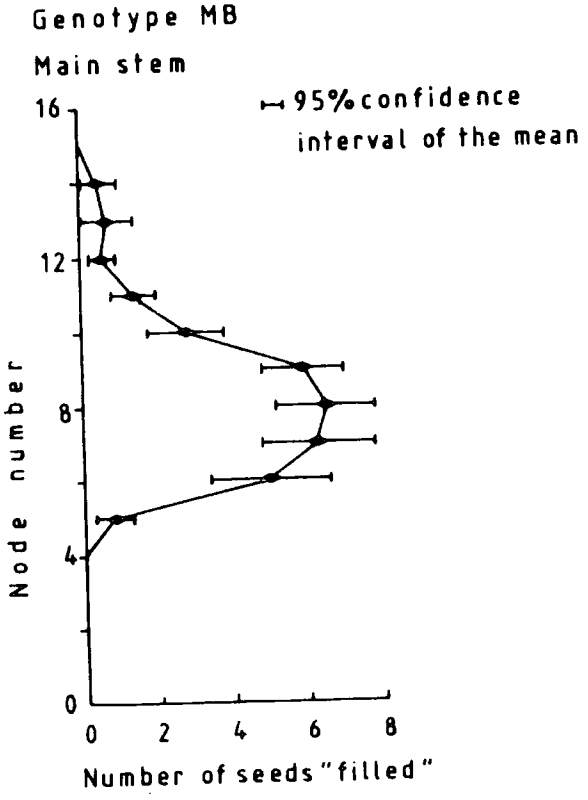

Genotype MB
Main stem
95% confidence interval of the mean
Node number
Number of seeds "filled"

Figure 3.2.7

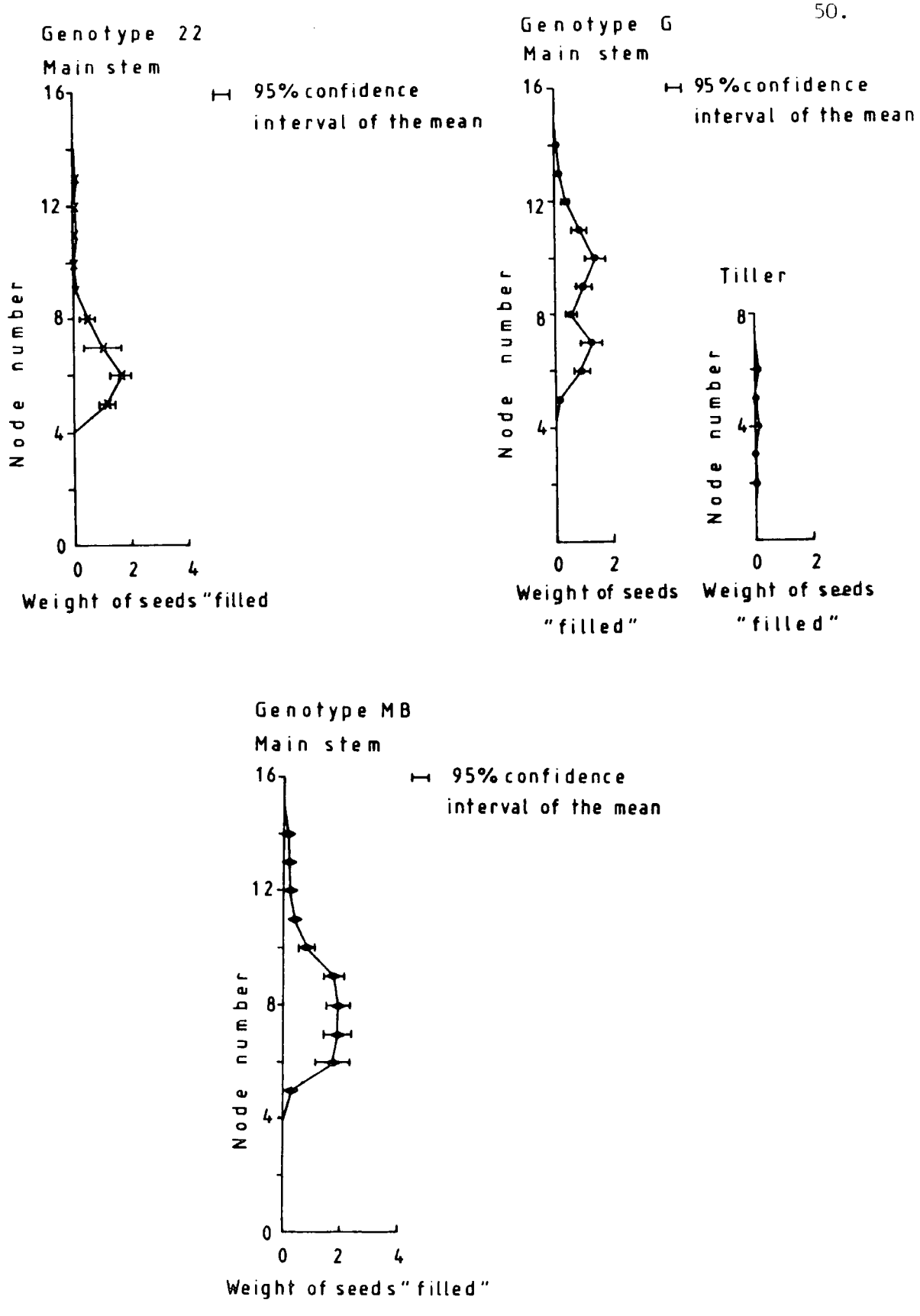

Genotype 22
Main stem
95% confidence interval of the mean
Node number
Weight of seeds "filled
Genotype G
Main stem
95% confidence interval of the mean
Node number
Weight of seeds "filled"
Tiller
Node number
Weight of seeds "filled"
Genotype MB
Main stem
95% confidence interval of the mean
Node number
Weight of seeds "filled"

Figure 3.2.8

Table 3.2.1

Results of analysis of variance to identify inter-genotypic differences for number of buds formed at each node.

Node Number	F Ratio	F Probability
21	0.689	n.s.
20	0.205	n.s.
19	2.301	n.s.
18	30.928	***
17	99.537	***
16	29.884	***
15	87.131	***
14	46.428	***
13	80.333	***
12	94.814	***
11	44.813	***
10	14.725	***
9	35.549	***
8	19.414	***
7	3.311	n.s.
6	0.925	n.s.
5	4.466	*

n.s. non significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.2

Results of analysis of variance to identify inter-genotypic differences for number of flowers of each node.

Node Number	F Ratio	F Probability
21	1.000	n.s.
20	1.000	n.s.
19	0.00	n.s.
18	0.148	n.s.
17	0.788	n.s.
16	2.884	n.s.
15	1.791	n.s.
14	3.682	*
13	6.799	**
12	25.008	***
11	20.153	***
10	35.191	***
9	57.155	***
8	37.647	***
7	6.660	**
6	1.807	n.s.
5	4.500	*

n.s. non significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.3

Results of analysis of variance to identify inter-genotypic differences for number of pods set at each node.

Node Number	F Ratio	F Probability
18	0.692	n.s.
17	1.481	n.s.
16	1.804	n.s.
15	2.415	n.s.
14	4.822	*
13	6.814	**
12	20.925	***
11	17.763	***
10	33.750	***
9	43.894	***
8	22.448	***
7	3.917	*
6	0.878	n.s.
5	4.727	*

n.s. non significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.4

Results of analysis of variance to identify inter-genotypic differences for number of pods retained at each node.

Node Number	F Ratio	F Probability
18	2.250	n.s.
17	0.765	n.s.
16	0.616	n.s.
15	0.904	n.s.
14	4.783	*
13	4.381	*
12	7.389	**
11	10.337	***
10	14.455	***
9	13.754	***
8	6.225	**
7	1.563	n.s.
6	0.318	n.s.
5	11.736	***

n.s. non significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.5

Results of analysis of variance to identify inter-genotypic differences for number of pods 'filled'

Node Number	F Ratio	F Probability
15	0.904	n.s.
14	1.105	n.s.
13	0.123	n.s.
12	2.311	n.s.
11	4.017	*
10	7.269	**
9	12.270	***
8	7.058	**
7	0.350	n.s.
6	0.753	n.s.
5	14.778	***

n.s. non significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.6

Results of analysis of variance to identify inter-genotypic differences for number of ovules formed at each node.

Node Number	F Ratio	F Probability
21	4.413	*
20	1.120	n.s.
19	2.878	n.s.
18	29.375	***
17	94.059	***
16	60.753	***
15	61.204	***
14	86.648	***
13	68.612	***
12	85.194	***
11	58.439	***
10	32.395	***
9	55.009	***
8	29.487	***
7	8.866	**
6	1.756	n.s.
5	2.597	n.s.

n.s. non significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.7

Results of analysis of variance to identify inter-genotypic differences for number of seeds at each node.

Node Number	F Ratio	F Probability
14	0.776	n.s.
13	0.455	n.s.
12	3.445	*
11	5.235	*
10	6.975	**
9	16.289	***
8	13.807	***
7	4.646	*
6	1.756	n.s.
5	3.545	*

n.s. non significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.8

Results of analysis of variance to identify inter-genotypic differences for weight of seeds at each node.

Node Number	F Ratio	F Probability
14	0.651	n.s.
13	0.200	n.s.
12	3.623	*
11	4.915	*
10	6.783	**
9	11.113	***
8	6.563	**
7	1.760	n.s.
6	1.029	n.s.
5	11.069	***

n.s. non significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.9

A closer examination of significant differences between genotypes at each node in order to determine which genotypes differ significantly from others - number of buds.

(a) Node 5

		Genotype		
Mean	Genotype	22	G	Maris Bead
2.10	22			
1.90	G			
0.40	Maris Bead	*	*	

(b) Node 6

No significant differences detected.

(c) Node 7

		Genotype		
Mean	Genotype	22	G	Maris Bead
3.90	22			
5.90	G	*		
5.20	Maris Bead			

(d) Node 8

		Genotype		
Mean	Genotype	22	G	Maris Bead
4.20	22			
6.50	G	***		
6.10	Maris Bead	***		

(e) Node 9

		Genotype		
Mean	Genotype	22	G	Maris Bead
4.00	22			
5.90	G	***		
6.40	Maris Bead	***		

Table 3.2.9 continued

(f) Node 10

			Genotype	
Mean	Genotype	22	G	Maris Bead
3.60	22			
5.40	G	**		
6.50	Maris Bead	***		

(g) Node 11

			Genotype	
Mean	Genotype	22	G	Maris Bead
2.80	22			
5.20	G	***		
6.30	Maris Bead	***	**	

(h) Node 12

			Genotype	
Mean	Genotype	22	G	Maris Bead
2.20	22			
4.90	G	***		
6.40	Maris Bead	***	***	

(i) Node 13

			Genotype	
Mean	Genotype	22	G	Maris Bead
1.80	22			
5.10	G	***		
6.40	Maris Bead	***	**	

(j) Node 14

			Genotype	
Mean	Genotype	22	G	Maris Bead
1.30	22			
4.20	G	***		
6.20	Maris Bead	***	***	

Table 3.2.9 continued

(k) Node 15

			Genotype	
Mean	Genotype	22	G	Maris Bead
0.90	22			
4.60	G	***		
6.20	Maris Bead	***	***	

(l) Node 16

			Genotype	
Mean	Genotype	22	G	Maris Bead
0.80	22			
4.50	G	***		
5.10	Maris Bead	***		

(m) Node 17

			Genotype	
Mean	Genotype	22	G	Maris Bead
0.20	22			
4.40	G	***		
5.30	Maris Bead	***	*	

(n) Node 18

			Genotype	
Mean	Genotype	22	G	Maris Bead
0.10	22			
3.70	G	***		
4.70	Maris Bead	***		

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.10

A closer examination of significant differences at each node in order to determine which genotypes differ significantly from others - number of flowers.

(a) Node 5

		Genotype		
Mean	Genotype	22	G	Maris Bead
2.10	22			
1.70	G			
0.40	Maris Bead	**	*	

(b) Node 6

No significant differences detected.

(c) Node 7

		Genotype		
Mean	Genotype	22	G	Maris Bead
3.00	22			
5.90	G	**		
5.30	Maris Bead	*		

(d) Node 8

		Genotype		
Mean	Genotype	22	G	Maris Bead
1.20	22			
5.80	G	***		
6.10	Maris Bead	***		

(e) Node 9

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.20	22			
5.00	G	***		
6.10	Maris Bead	***		

Table 3.2.10 continued

(f) Node 10

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.10	22			
4.30	G	***		
5.60	Maris Bead	***		

(g) Node 11

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.30	22			
3.40	G	***		
5.00	Maris Bead	***	*	

(h) Node 12

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.20	22			
2.60	G	***		
4.60	Maris Bead	***	**	

(i) Node 13

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.50	22			
2.10	G	*		
3.10	Maris Bead	**		

(j) Node 14

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.30	22			
1.50	G			
1.80	Maris Bead	*		

Table 3.2.10 continued

(k) Node 15

No significant differences detected.

(l) Node 16

Mean	Genotype	22	G	Maris Bead
0.20	22			
0.40	G			
1.70	Maris Bead	*		

(m) Node 17

No significant differences detected.

(n) Node 18

No significant differences detected.

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.11

A closer examination of significant differences between genotypes at each node in order to determine which genotypes differ significantly from others - number of pods set.

(a) Node 5

		Genotype		
Mean	Genotype	22	G	Maris Bead
2.10	22			
1.40	G			
0.40	Maris Bead	**		

(b) Node 6

No significant differences detected.

(c) Node 7

		Genotype		
Mean	Genotype	22	G	Maris Bead
2.90	22			
5.20	G	**		
4.30	Maris Bead			

(d) Node 8

		Genotype		
Mean	Genotype	22	G	Maris Bead
1.10	22			
4.60	G	***		
5.70	Maris Bead	***		

(e) Node 9

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.20	22			
4.60	G	***		
5.70	Maris Bead	***		

Table 3.2.11 continued

(f) Node 10

			Genotype	
Mean	Genotype	22	G	Maris Bead
0.00	22			
4.00	G	***		
5.00	Maris Bead	***		

(g) Node 11

			Genotype	
Mean	Genotype	22	G	Maris Bead
0.30	22			
3.30	G	***		
4.80	Maris Bead	***		

(h) Node 12

			Genotype	
Mean	Genotype	22	G	Maris Bead
0.10	22			
2.50	G	***		
4.10	Maris Bead	***	*	

(i) Node 13

			Genotype	
Mean	Genotype	22	G	Maris Bead
0.30	22			
1.70	G			
2.90	Maris Bead	**		

(j) Node 14

			Genotype	
Mean	Genotype	22	G	Maris Bead
0.10	22			
1.00	G			
1.80	Maris Bead	**		

Table 3.2.11 continued

(k) Node 15

Mean	Genotype	Genotype 22	G	Maris Bead
0.00	22			
0.50	G			
1.63	Maris Bead	*		

(l) Node 16

No significant differences detected.

(m) Node 17

No significant differences detected.

(n) Node 18

No significant differences detected.

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.12

A closer examination of significant differences between genotypes at each node in order to determine which genotypes differ significantly from others - number of pods retained.

(a) Node 5

		Genotype		
Mean	Genotype	22	G	Maris Bead
1.60	22			
0.50	G	**		
0.20	Maris Bead	***		

(b) Node 6

No significant differences detected.

(c) Node 7

No significant differences detected.

(d) Node 8

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.80	22			
1.90	G			
3.10	Maris Bead	**		

(e) Node 9

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.20	22			
3.00	G	***		
3.50	Maris Bead	***		

(f) Node 10

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.00	22			
2.70	G	***		
2.90	Maris Bead	***		

Table 3.2.12 continued

(g) Node 11

Mean	Genotype	22	Genotype G	Maris Bead
0.30	22			
3.00	G	***		
2.40	Maris Bead	**		

(h) Node 12

Mean	Genotype	22	Genotype G	Maris Bead
0.10	22			
1.80	G	**		
2.30	Maris Bead	**		

(i) Node 13

Mean	Genotype	22	Genotype G	Maris Bead
0.20	22			
1.50	G	*		
1.30	Maris Bead	*		

(j) Node 14

Mean	Genotype	22	Genotype G	Maris Bead
0.10	22			
0.50	G			
1.10	Maris Bead	**		

(k) Node 15

No significant differences detected.

(l) Node 16

No significant differences detected.

Table 3.2.12 continued

(m) Node 17

No significant differences detected.

(n) Node 18

No significant differences detected.

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.13

A closer examination of significant differences between genotypes at each node in order to determine which genotypes differ significantly from others - number of pods 'filled'.

(a) Node 5

		Genotype		
Mean	Genotype	22	G	Maris Bead
1.40	22			
0.30	G	***		
0.20	Maris Bead	***		

(b) Node 6

No significant differences detected.

(c) Node 7

No significant differences detected.

(d) Node 8

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.50	22			
0.80	G			
2.00	Maris Bead	**	**	

(e) Node 9

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.10	22			
1.90	G	***		
2.10	Maris Bead	***		

(f) Node 10

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.00	22			
1.90	G	***		
1.10	Maris Bead	*		

Table 3.2.13 continued

(g) Node 11

Mean	Genotype	Genotype 22	G	Maris Bead
0.20	22			
1.20	G	*		
0.50	Maris Bead			

(h) Node 12

Mean	Genotype	Genotype 22	G	Maris Bead
0.10	22			
0.60	G	*		
0.30	Maris Bead			

(i) Node 13

No significant differences detected.

(j) Node 14

No significant differences detected.

(k) Node 15

None

(l) Node 16

None

(m) Node 17

None

(n) Node 18

None

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.14

A closer examination of significant differences between genotypes at each node in order to determine which genotypes differ significantly from others - number of ovules formed.

(a) Node 5

No significant differences detected.

(b) Node 6

		Genotype		
Mean	Genotype	22	G	Maris Bead
6.90	22			
11.60	G			
13.70	Maris Bead	*		

(c) Node 7

		Genotype		
Mean	Genotype	22	G	Maris Bead
8.00	22			
17.30	G	**		
18.90	Maris Bead	***		

(d) Node 8

		Genotype		
Mean	Genotype	22	G	Maris Bead
10.90	22			
19.00	G	***		
23.30	Maris Bead	***	*	

(e) Node 9

		Genotype		
Mean	Genotype	22	G	Maris Bead
9.10	22			
18.40	G	***		
24.40	Maris Bead	***	***	

Table 3.2.14 continued

(f) Node 10

			Genotype	
Mean	Genotype	22	G	Maris Bead
9.50	22			
17.00	G	***		
23.70	Maris Bead	***	***	

(g) Node 11

			Genotype	
Mean	Genotype	22	G	Maris Bead
6.90	22			
16.60	G	***		
23.40	Maris Bead	***	***	

(h) Node 12

			Genotype	
Mean	Genotype	22	G	Maris Bead
4.80	22			
14.80	G	***		
23.10	Maris Bead	***	***	

(i) Node 13

			Genotype	
Mean	Genotype	22	G	Maris Bead
4.30	22			
15.60	G	***		
21.30	Maris Bead	***	***	

(j) Node 14

			Genotype	
Mean	Genotype	22	G	Maris Bead
2.70	22			
13.70	G	***		
21.20	Maris Bead	***	***	

Table 3.2.14 continued

(k) Node 15

		Genotype		
Mean	Genotype	22	G	Maris Bead
2.10	22			
11.70	G	***		
21.60	Maris Bead	***	***	

(l) Node 16

		Genotype		
Mean	Genotype	22	G	Maris Bead
1.80	22			
11.60	G	***		
18.80	Maris Bead	***	***	

(m) Node 17

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.80	22			
12.70	G	***		
17.50	Maris Bead	***	***	

(n) Node 18

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.40	22			
10.20	G	***		
14.40	Maris Bead	***	*	

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.15

A closer examination of significant differences between genotypes at each node in order to determine which genotypes differ significantly from others - number of seeds.

(a) Node 5

		Genotype		
Mean	Genotype	22	G	Maris Bead
1.80	22			
0.80	G			
0.80	Maris Bead	*		

(b) Node 6

No significant differences detected.

(c) Node 7

		Genotype		
Mean	Genotype	22	G	Maris Bead
1.80	22			
3.60	G			
6.30	Maris Bead	**		

(d) Node 8

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.90	22			
1.40	G			
6.50	Maris Bead	***	***	

(e) Node 9

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.10	22			
3.30	G	**		
5.90	Maris Bead	***	*	

(f) Node 10

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.00	22			
4.40	G	**		
2.80	Maris Bead	*		

(g) Node 11

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.20	22			
3.20	G	**		
1.40	Maris Bead			

(h) Node 12

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.10	22			
1.40	G	*		
0.60	Maris Bead			

(i) Node 13

No significant differences detected.

(j) Node 14

No significant differences detected.

(k) Node 15

None.

(l) Node 16

None.

(m) Node 17

None.

(n) Node 18

None.

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 3.2.16

A closer examination of significant differences between genotypes at each node in order to determine which genotypes differ significantly from others - weight of seeds.

(a) Node 5

		Genotype		
Mean	Genotype	22	G	Maris Bead
1.17	22			
0.16	G	***		
0.24	Maris Bead	***		

(b) Node 6

No significant differences detected.

(c) Node 7

No significant differences detected.

(d) Node 8

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.53	22			
0.48	G			
1.87	Maris Bead	**	**	

(e) Node 9

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.08	22			
1.03	G	*		
1.76	Maris Bead	***		

(f) Node 10

		Genotype		
Mean	Genotype	22	G	Maris Bead
0.00	22			
1.38	G	**		
0.79	Maris Bead	*		

Table 3.2.16 continued

(g) Node 11

Mean	Genotype	Genotype 22	G	Maris Bead
0.09	22			
0.86	G	**		
0.34	Maris Bead		*	

(h) Node 12

Mean	Genotype	Genotype 22	G	Maris Bead
0.02	22			
0.37	G	*		
0.17	Maris Bead			

(i) Node 13

No significant differences detected.

(j) Node 14

No significant differences detected.

(k) Node 15

None.

(l) Node 16

None.

(m) Node 17

None.

(n) Node 18

None.

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

CHAPTER 4

RESULTS OF FIELD TRIALS - INVESTIGATIONS OF THE RESPONSES OF GENOTYPES OF DIFFERING FLORAL ARCHITECTURES TO VARIOUS ENVIRONMENTAL STRESSES

4.1 Systematically designed spacing trial

During the course of this trial the pods of genotype A split during early seed development, no further growth occurred, consequently no yield component data were recorded for A. The remaining genotypes did respond differently to increasing planting density for the yield components plotted. The number of the first flowering node is different for each genotype but does not change with increasing planting density (figure 4.1.1). In all genotypes the number of flowering nodes fell with increasing planting density (figure 4.1.2), though the rate of this fall varied between genotypes. The same pattern was observed for number of flowers per plant (figure 4.1.3), the scatter of data points was, however, wider than that for the number of flowering nodes. The pattern observed for number of podded nodes (figure 4.1.4) was similar to that for number of flowering nodes. The number of pods per podded node also fell with increasing planting density for each genotype (figure 4.1.5). In each genotype a greater number of pods per plant was set than was filled (figure 4.1.6), the number of both pods set and pods filled fell with increasing planting density. The number of seeds per plant also fell at higher plant populations (figure 4.1.7). The values for number of seeds per pod were unaffected by plant population in all three genotypes tested (figure 4.1.8). The individual seed weight also seemed not to change with increasing planting densities (figure 4.1.9). Seed yield per plant fell with increasing population in all three genotypes tested (figure 4.1.10). The calculated values for pods set per metre^2 at each planting density revealed a different pattern in each of the genotypes tested (figure 4.1.11). The number of seeds per

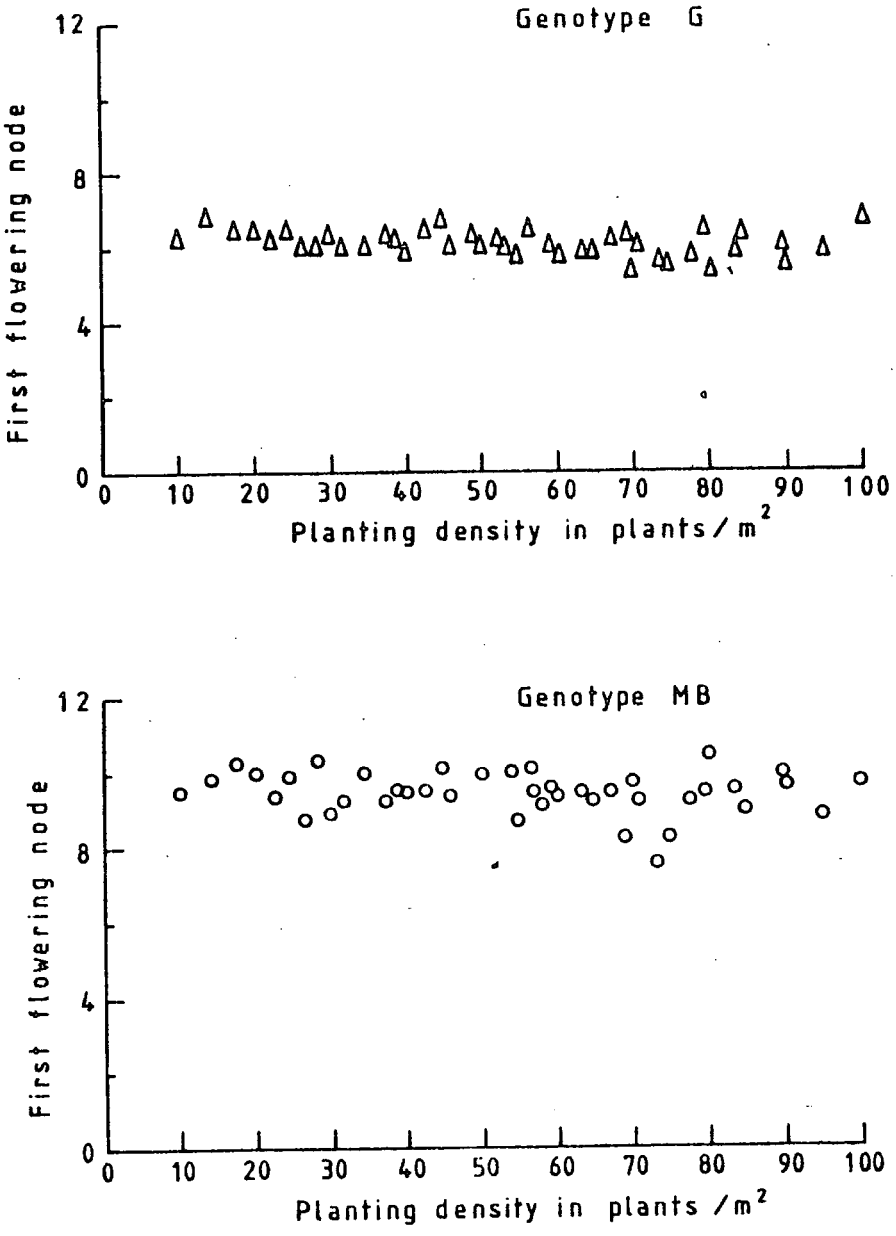


Figure 4.1.1 The effect of different planting densities on the mean number of the first flowering node in genotypes F, G and Maris Bead (MB)

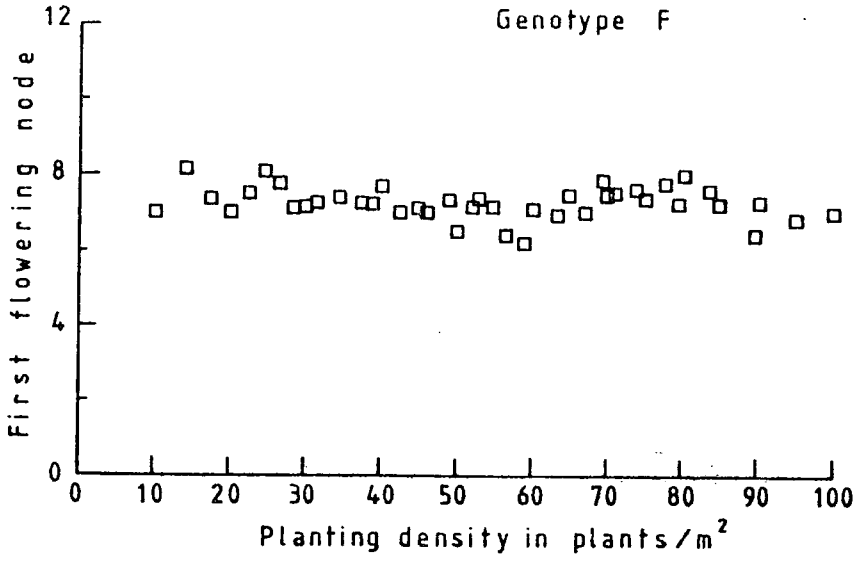


Figure 4.1.1 continued

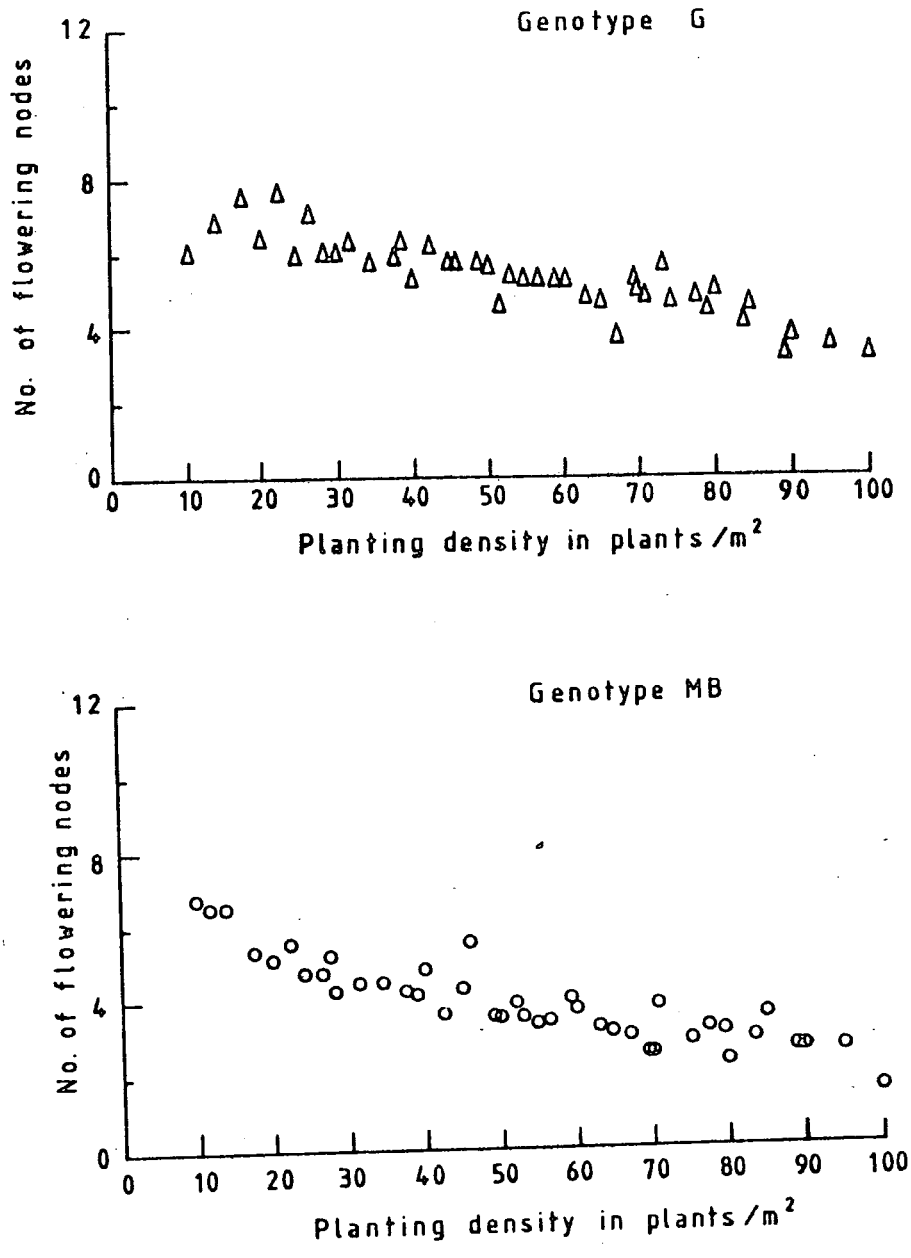


Figure 4.1.2 The effect of different planting densities on the mean number of flowering nodes per plant in genotypes F, G and Maris Bead (MB)

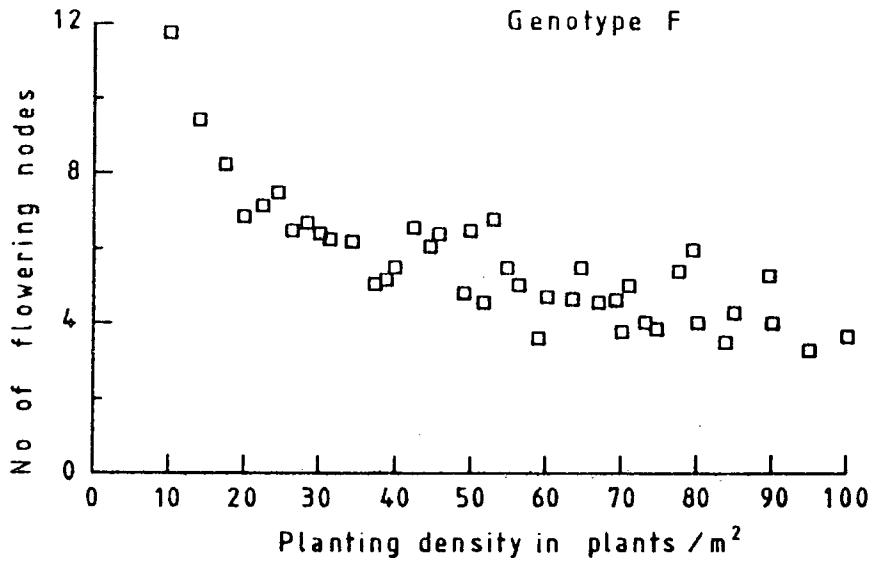


Figure 4.1.2 continued

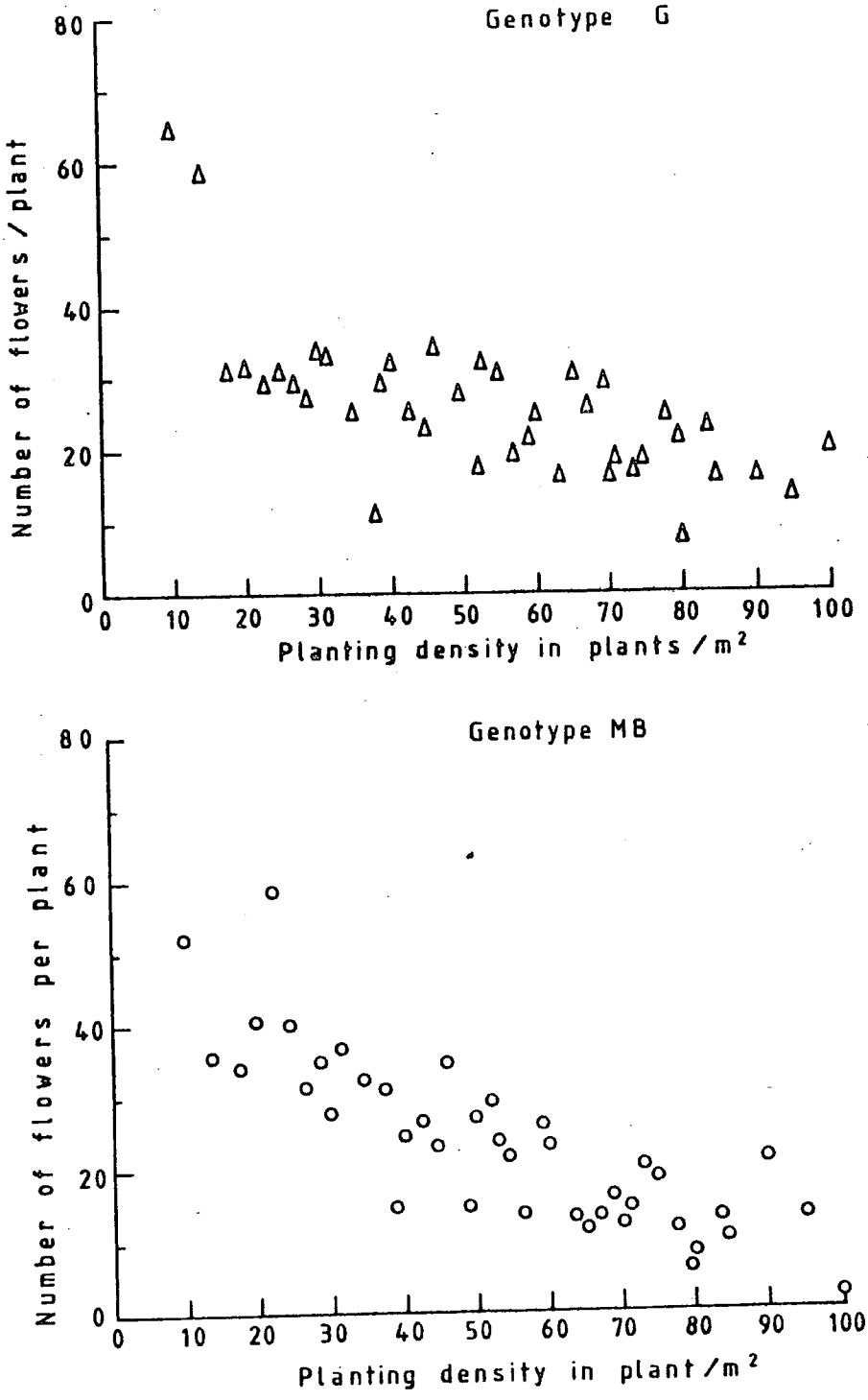


Figure 4.1.3 The effect of different planting densities on the mean number of flowers per plant in genotypes F, G and Maris Bead (MB)

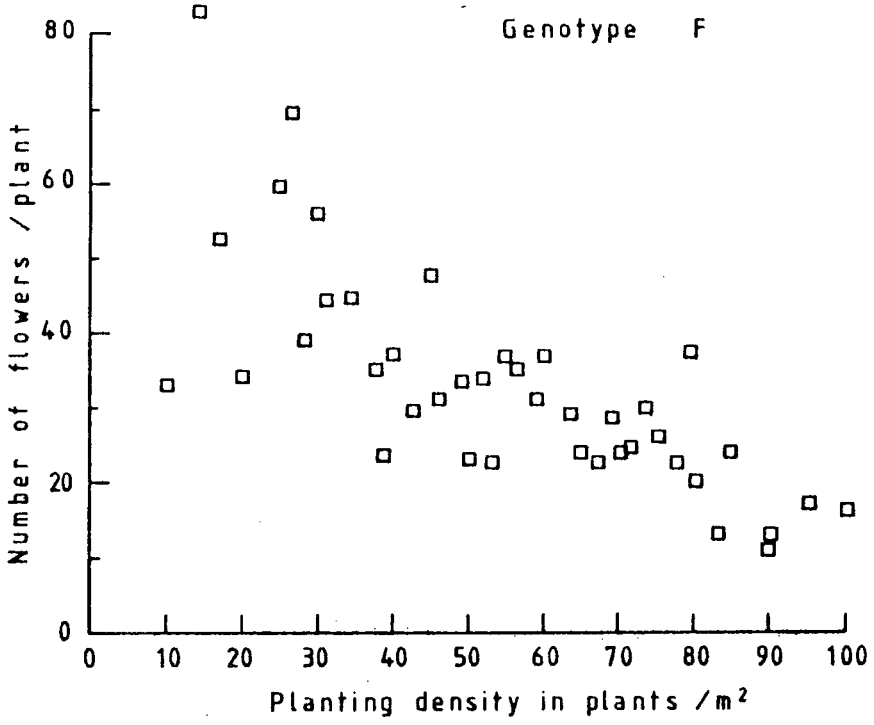


Figure 4.1.3 continued

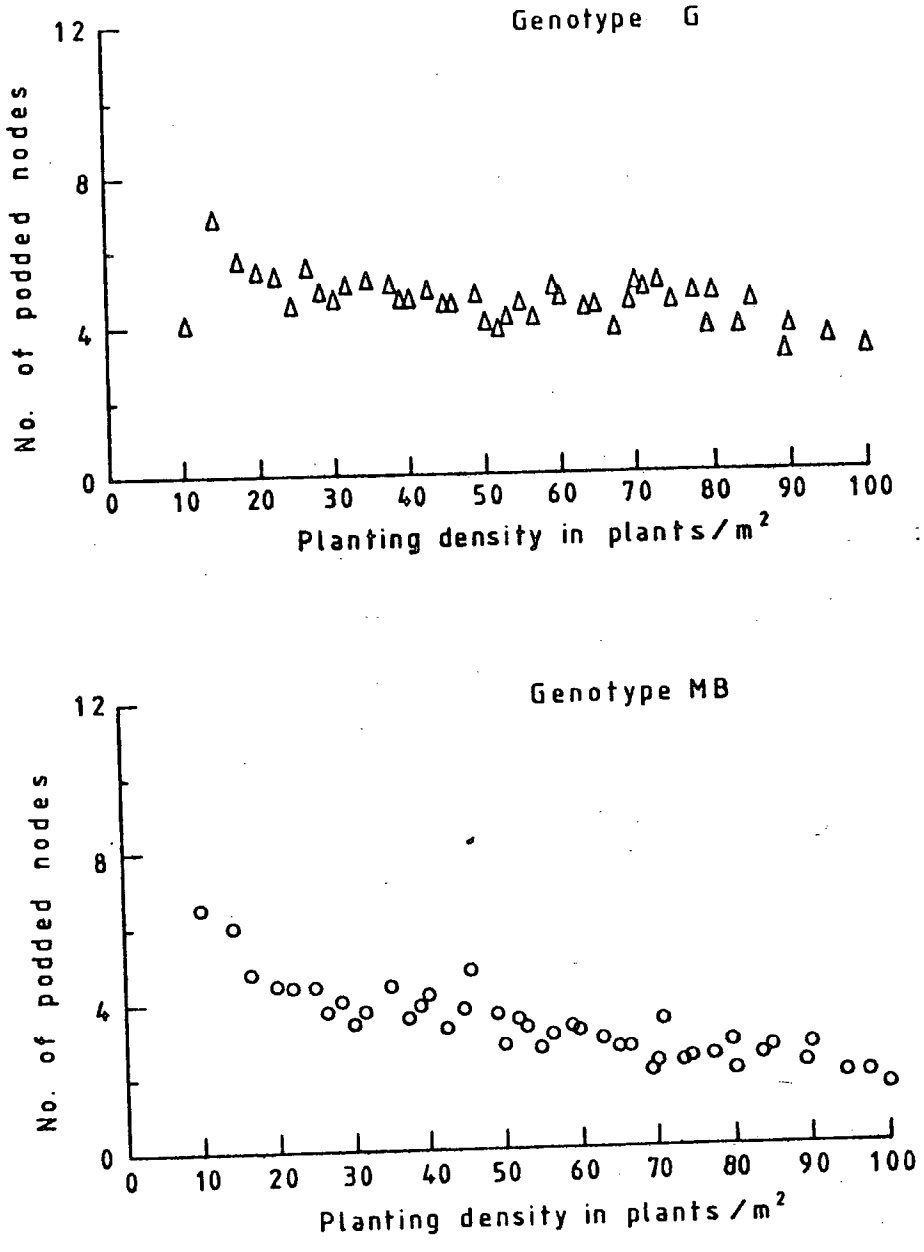


Figure 4.1.4 The effect of different planting densities on the mean number of podded nodes per plant in genotypes F, G and Maris Bead (MB)

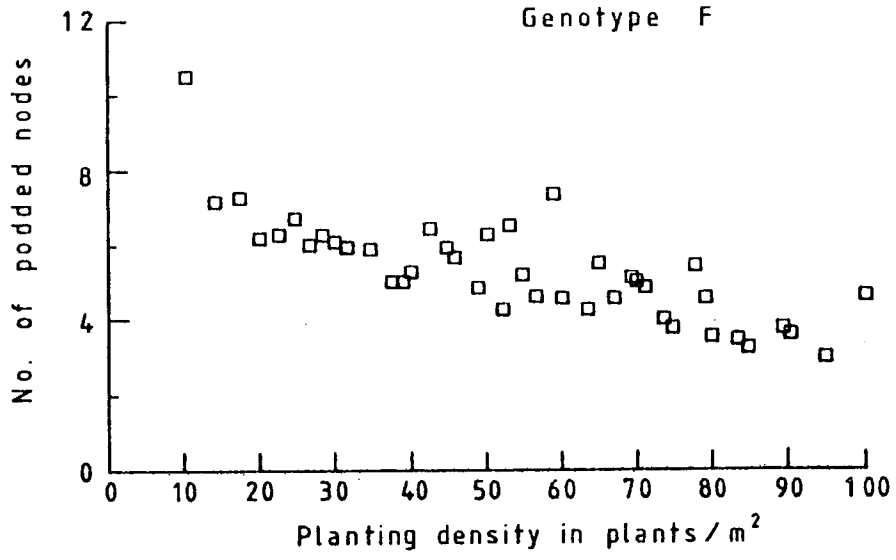


Figure 4.1.4 continued

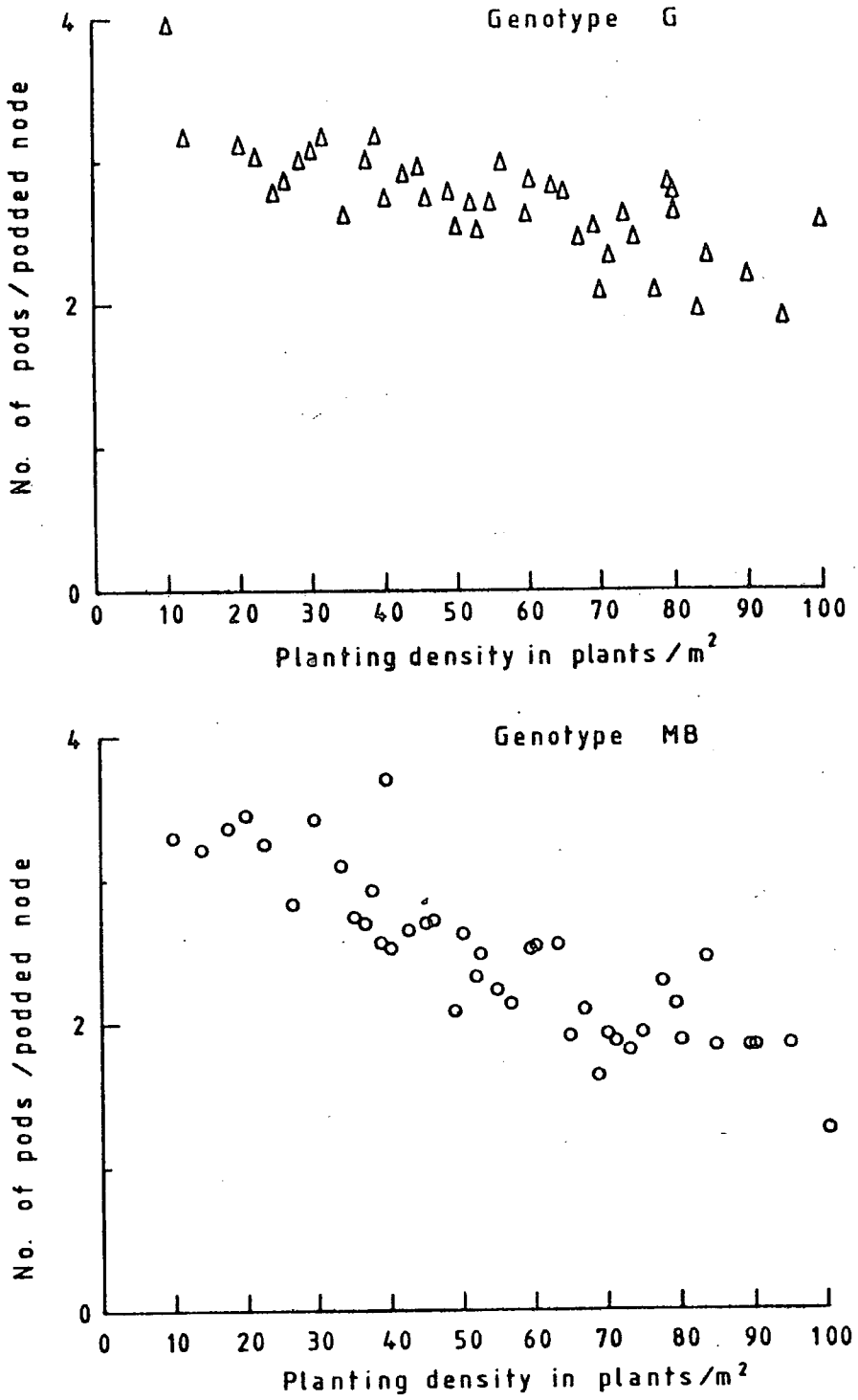


Figure 4.1.5 The effect of different planting densities on the mean number of pods per podded node per plant in genotypes F, G and Maris Bead (MB)

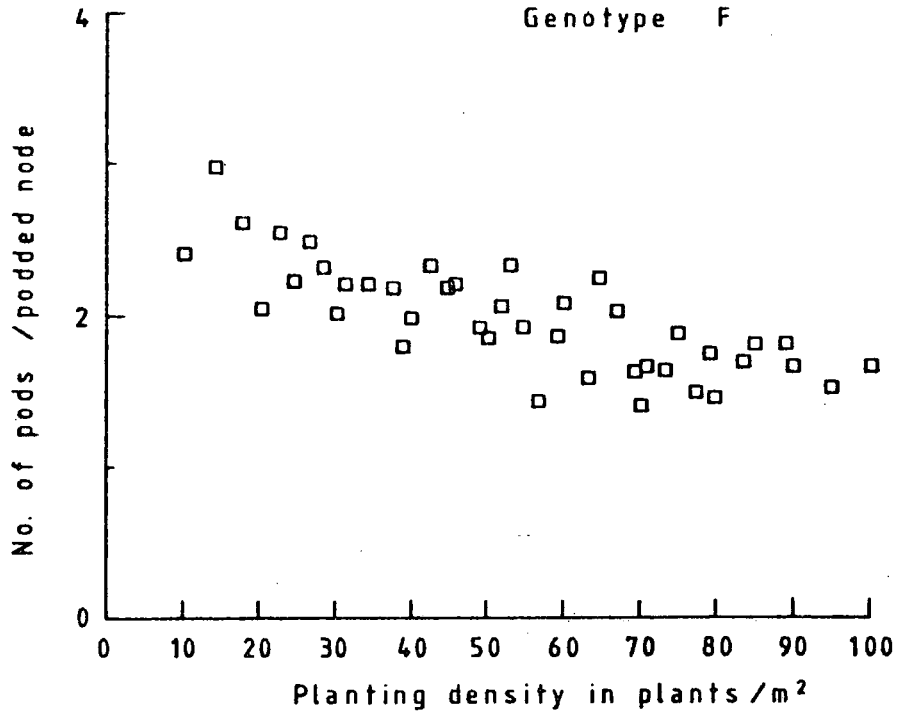


Figure 4.1.5 continued

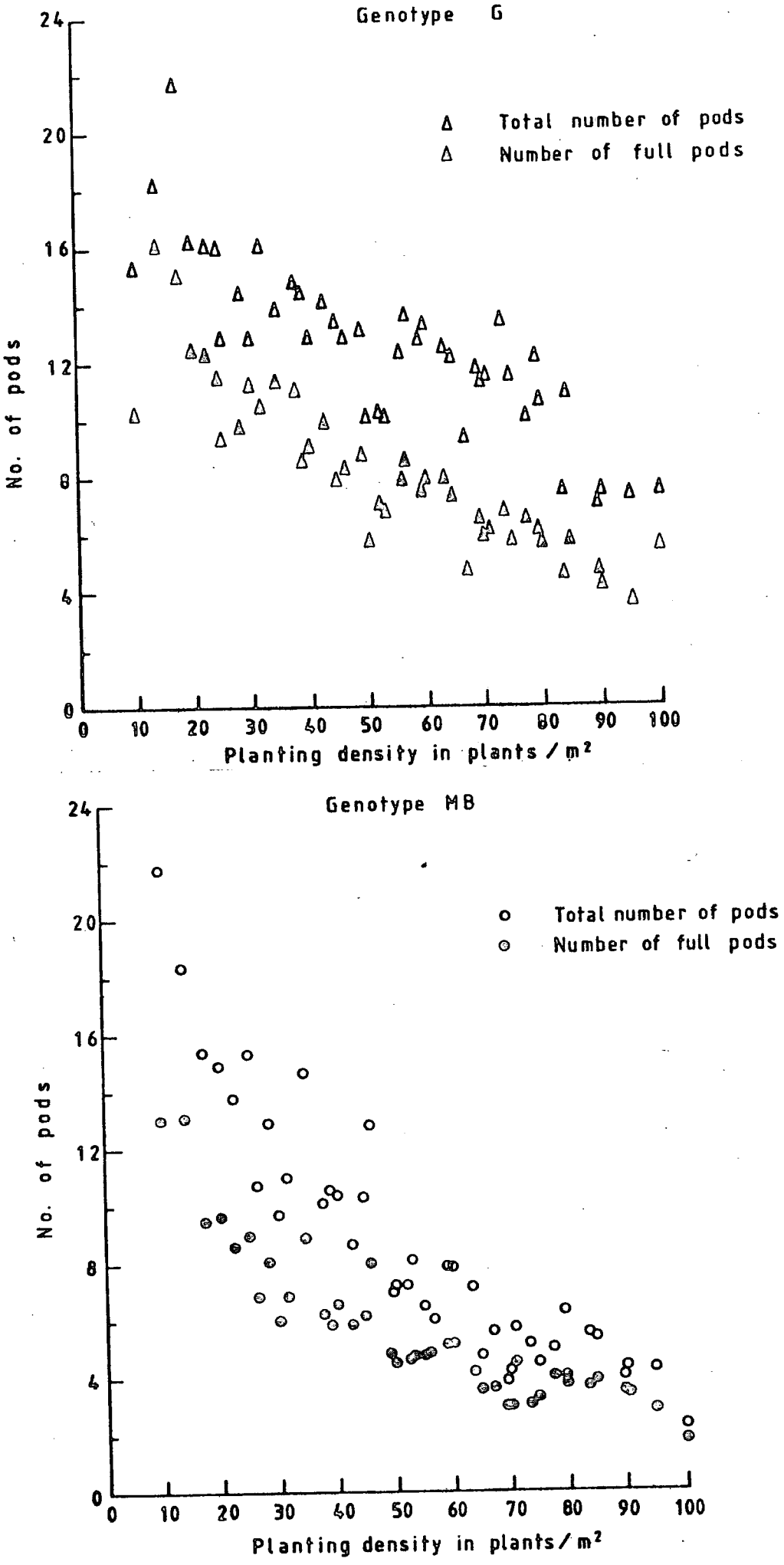


Figure 4.1.6 The effect of different planting densities on the mean number of pods set and mean number of pods filled (seed bearing pods) per plant in genotypes F, G and Maris Bead (MB)

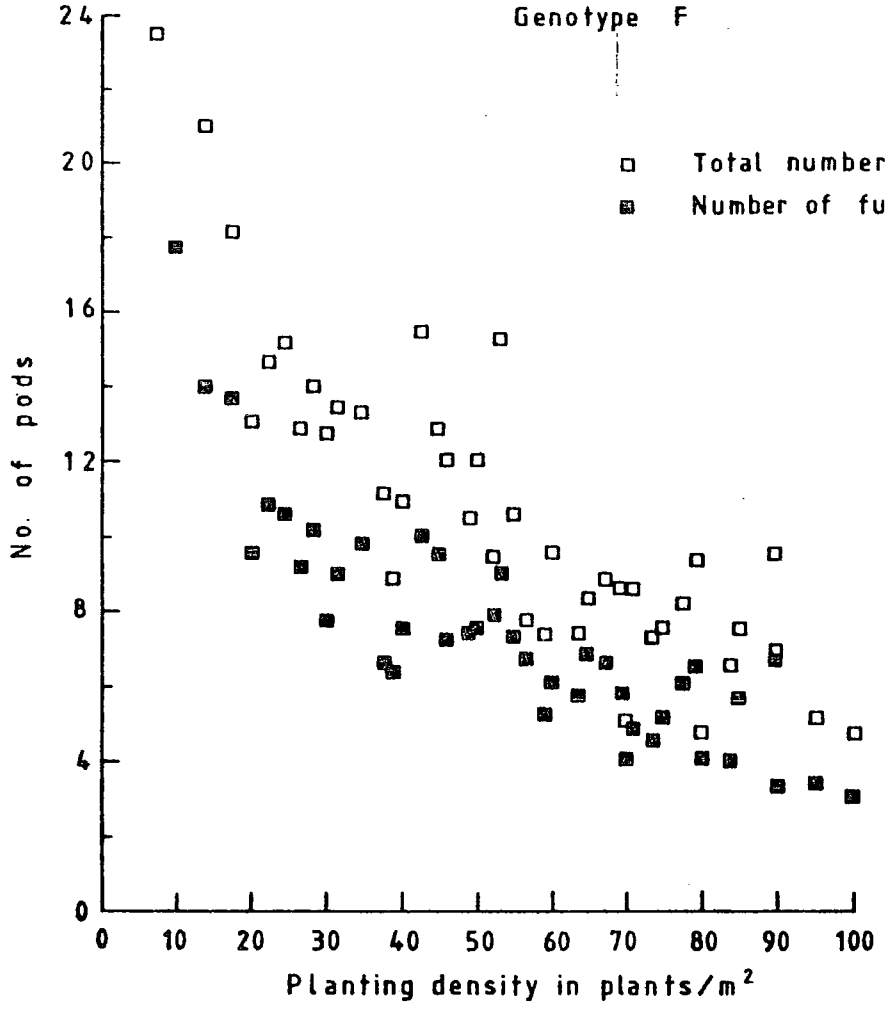


Figure 4.1.6 continued

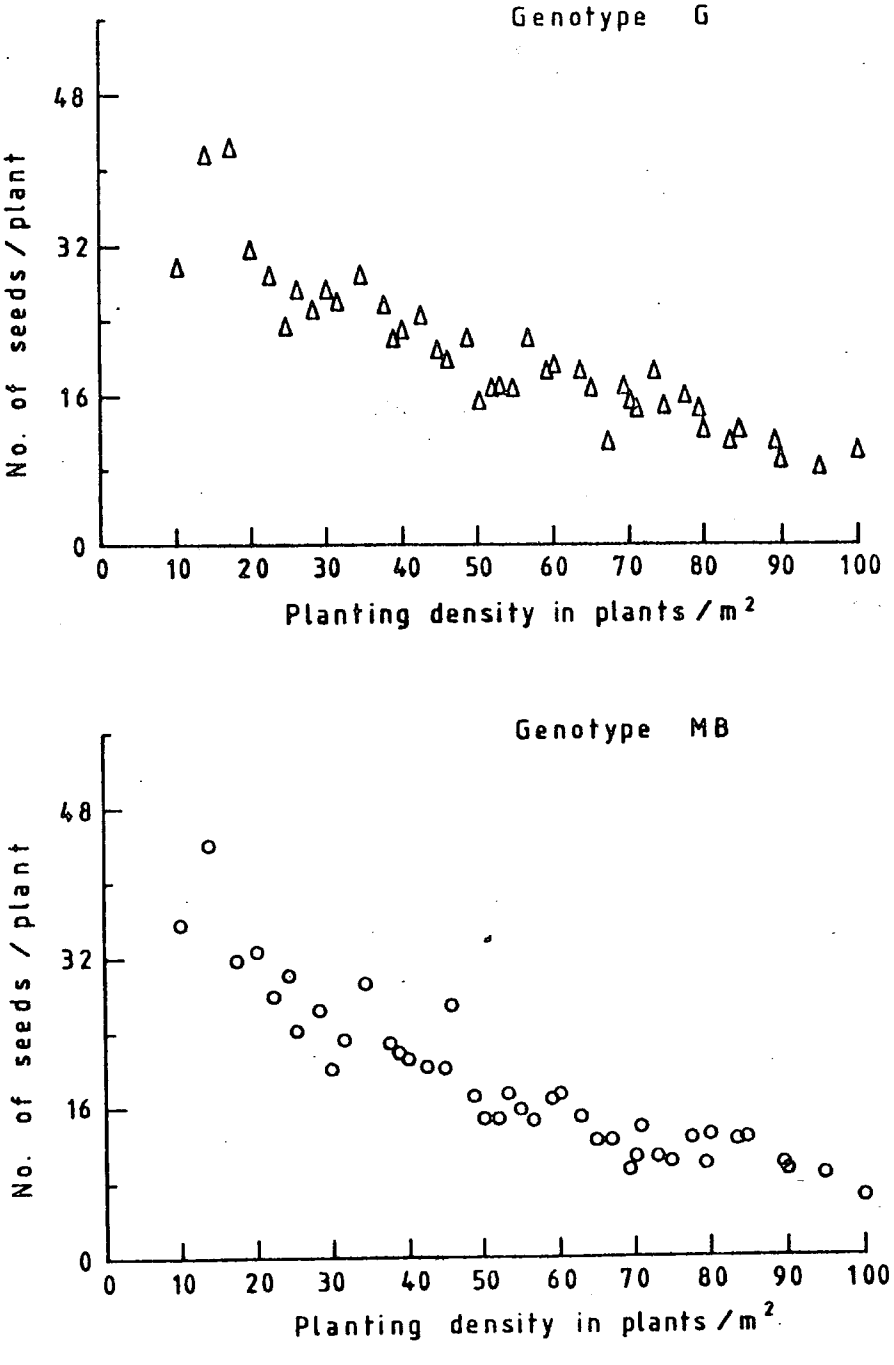


Figure 4.1.7 The effect of different planting densities on the mean number of seeds per plant in genotypes F, G and Maris Bead (MB)

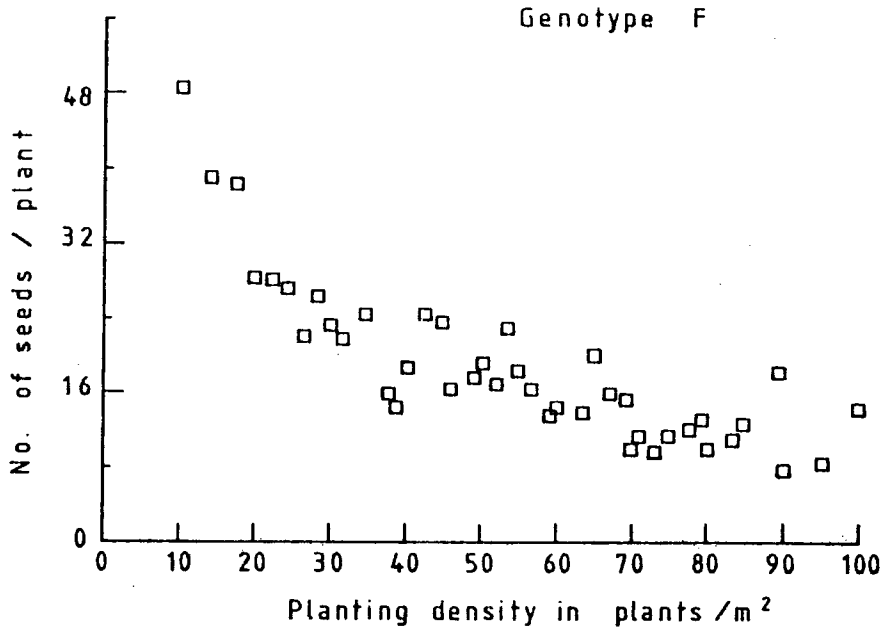
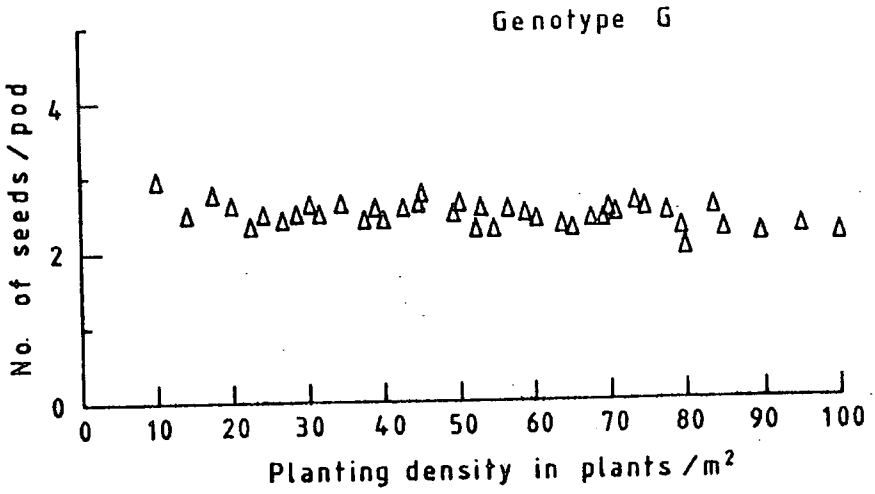


Figure 4.1.7 continued



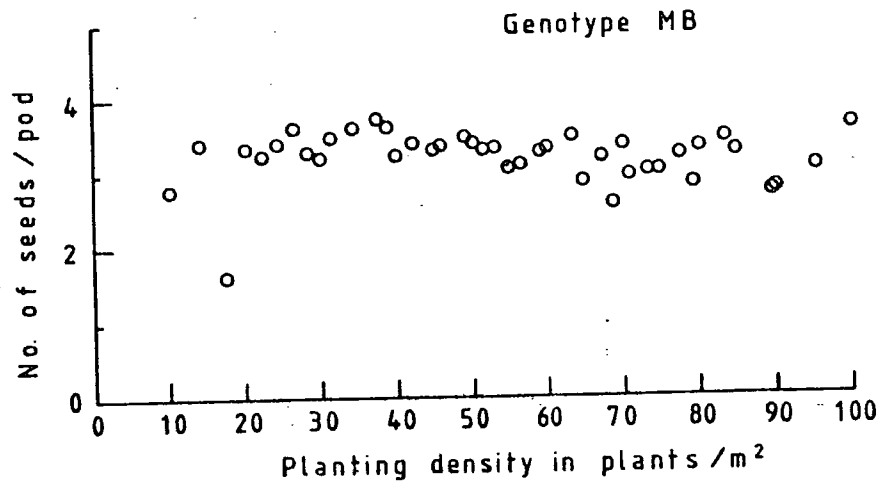


Figure 4.1.8 The effect of different planting densities on the mean number of seeds per pod in genotypes F, G and Maris Bead (MB)

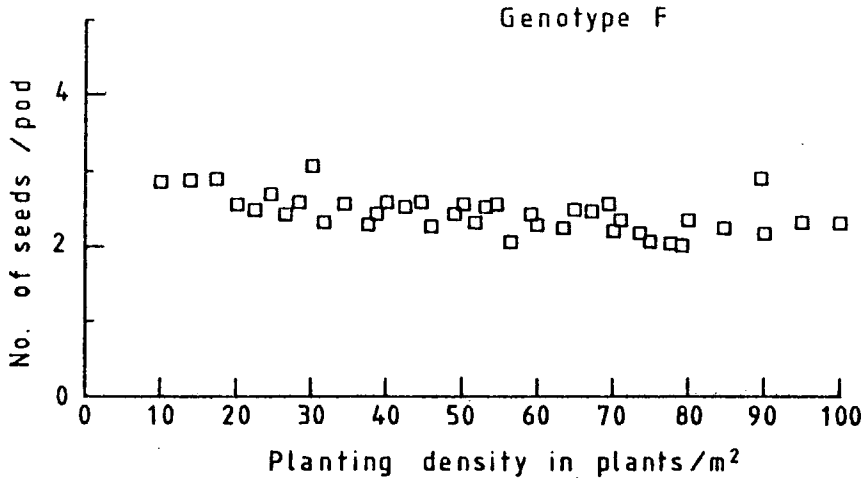


Figure 4.1.8 continued

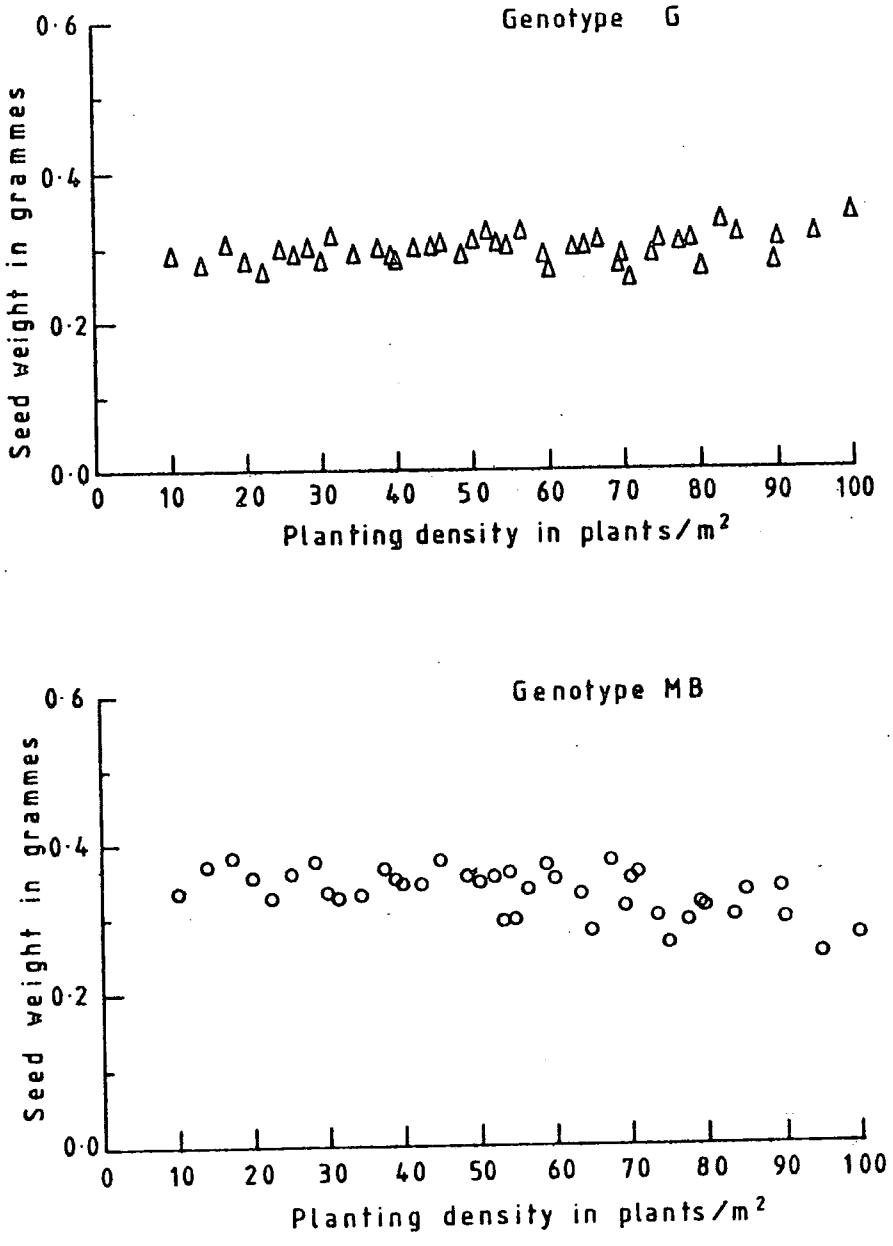
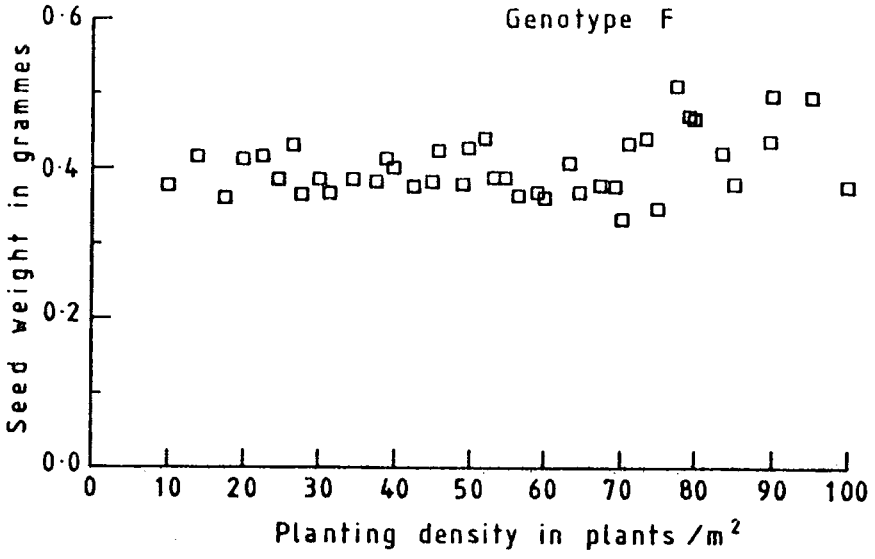


Figure 4.1.9 The effect of different planting densities on the mean individual seed weight in grammes in genotypes F, G and Maris Bead (MB)



Eigure 4.1.9 continued

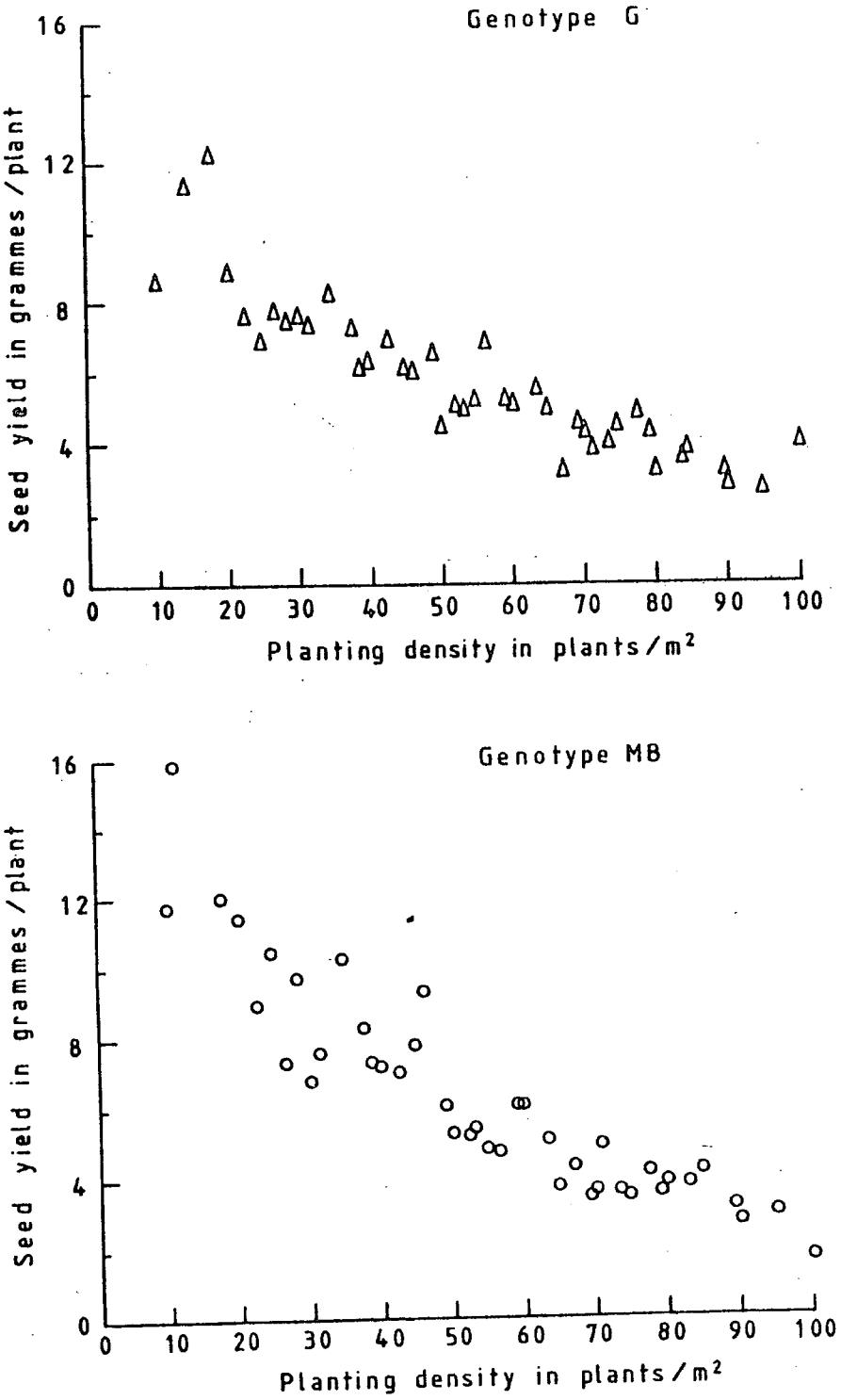


Figure 4.1.10 The effect of different planting densities on the mean seed yield in grammes per plant in genotypes F, G and Maris Bead (MB)

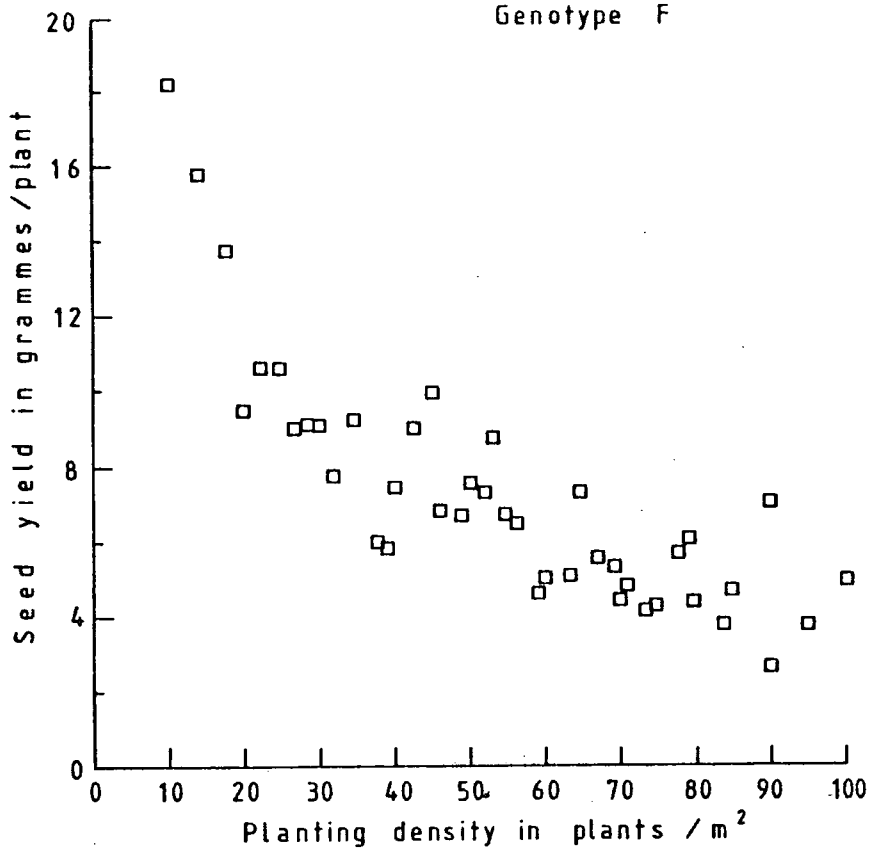


Figure 4.1.10 continued

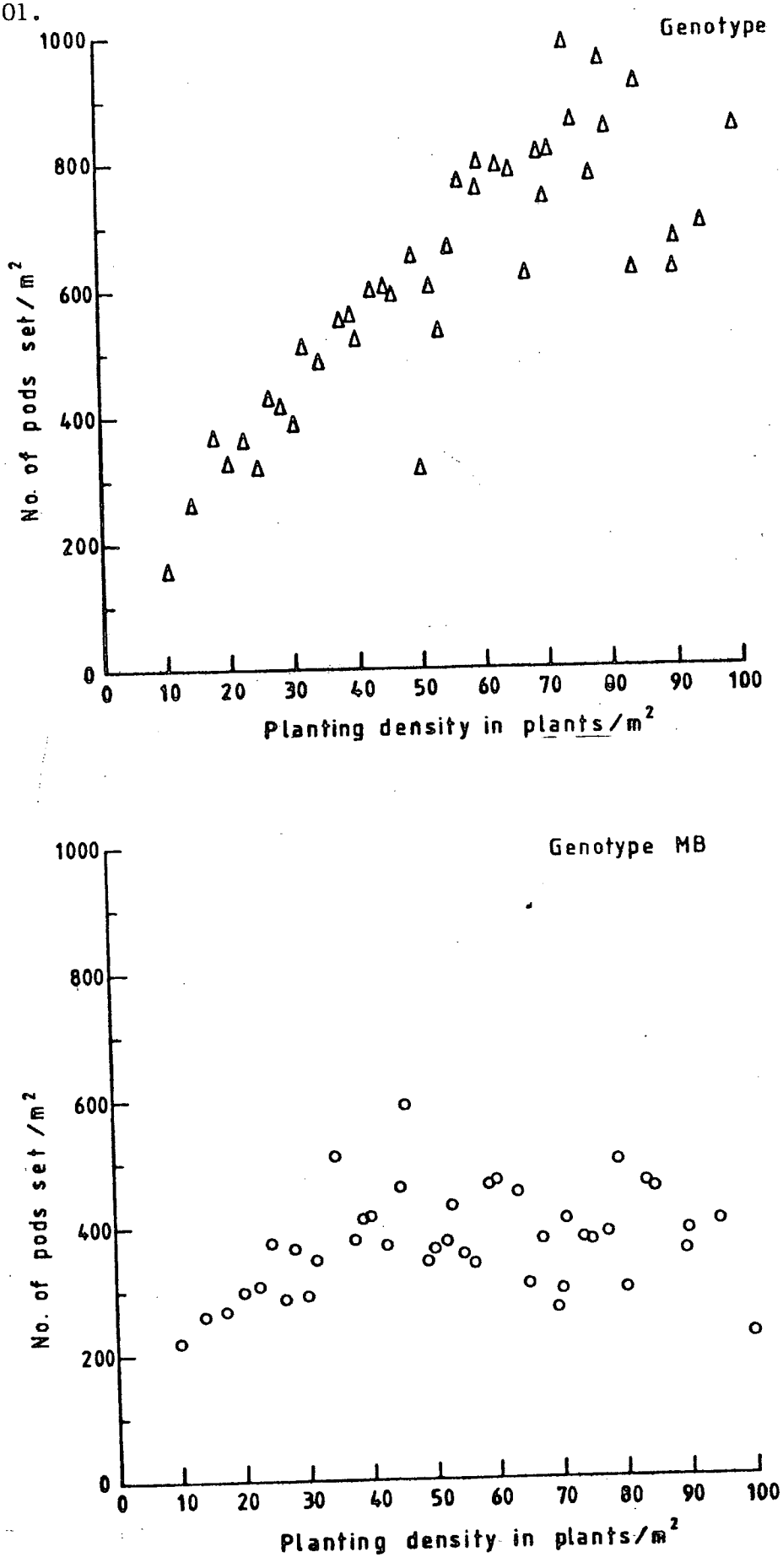


Figure 4.1.11 The effects of different planting densities on the mean number of pods set per square metre in genotypes F, G and Maris Bead (MB)

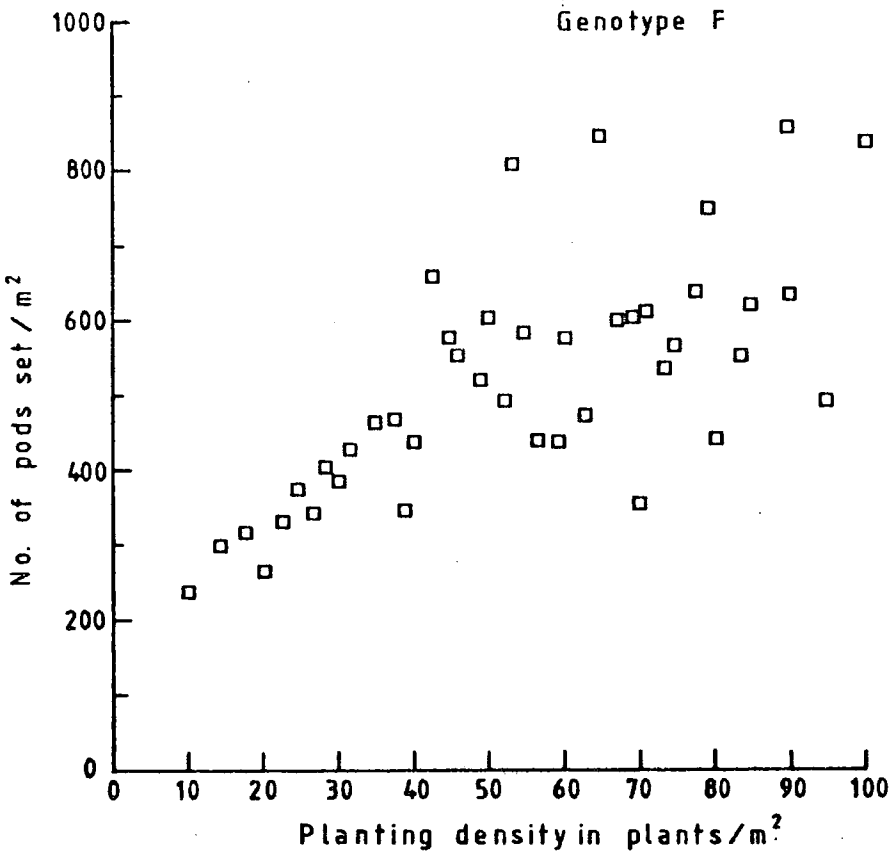


Figure 4.1.11 continued

metre^2 as calculated at each planting density follows a different pattern in the three genotypes tested (figure 4.1.12). The values for extrapolated yield in tonnes per hectare reveals a slightly different response to increasing plant population in each genotype (figure 4.1.13).

4.2 Irrigation trial

4.2.1 Analysis of data from plants sampled from each plot

Analysis of variance revealed which of the sources of variation contained significantly differing components in each of the parameters tested. In the case of plant height irrigations, genotypes and the replicates x irrigations x genotypes interaction were found to contain significant differences. Only the genotypes differed significantly from each other in terms of number of pod bearing stems. The data for number of podded nodes, number of pods, number of seeds and weight of seeds all contained significant differences between genotypes and between irrigations x genotypes interactions. (See tables 4.2.1.1, 4.2.1.2, 4.2.1.3, 4.2.1.4, 4.2.1.5 and 4.2.1.6.)

Examination of means for each of the significantly different sources of variation enabled the differences to be located. From the means for plant height (table 4.2.1.7) it was apparent that the difference due to irrigations was due to the value of the control plot being much lower than those of either of the irrigated plots. The plant height means for genotypes showed that Maris Bead had a higher value than genotypes A and G, whose mean values were similar to each other (figure 4.2.1). Examination of the means for the replicates x irrigations x genotypes interaction revealed that different replicates of different genotypes responded differently to the irrigations tested. In genotype A irrigation to 75 centibars soil moisture tension increased plant height in both replicates to a similar extent, at the higher

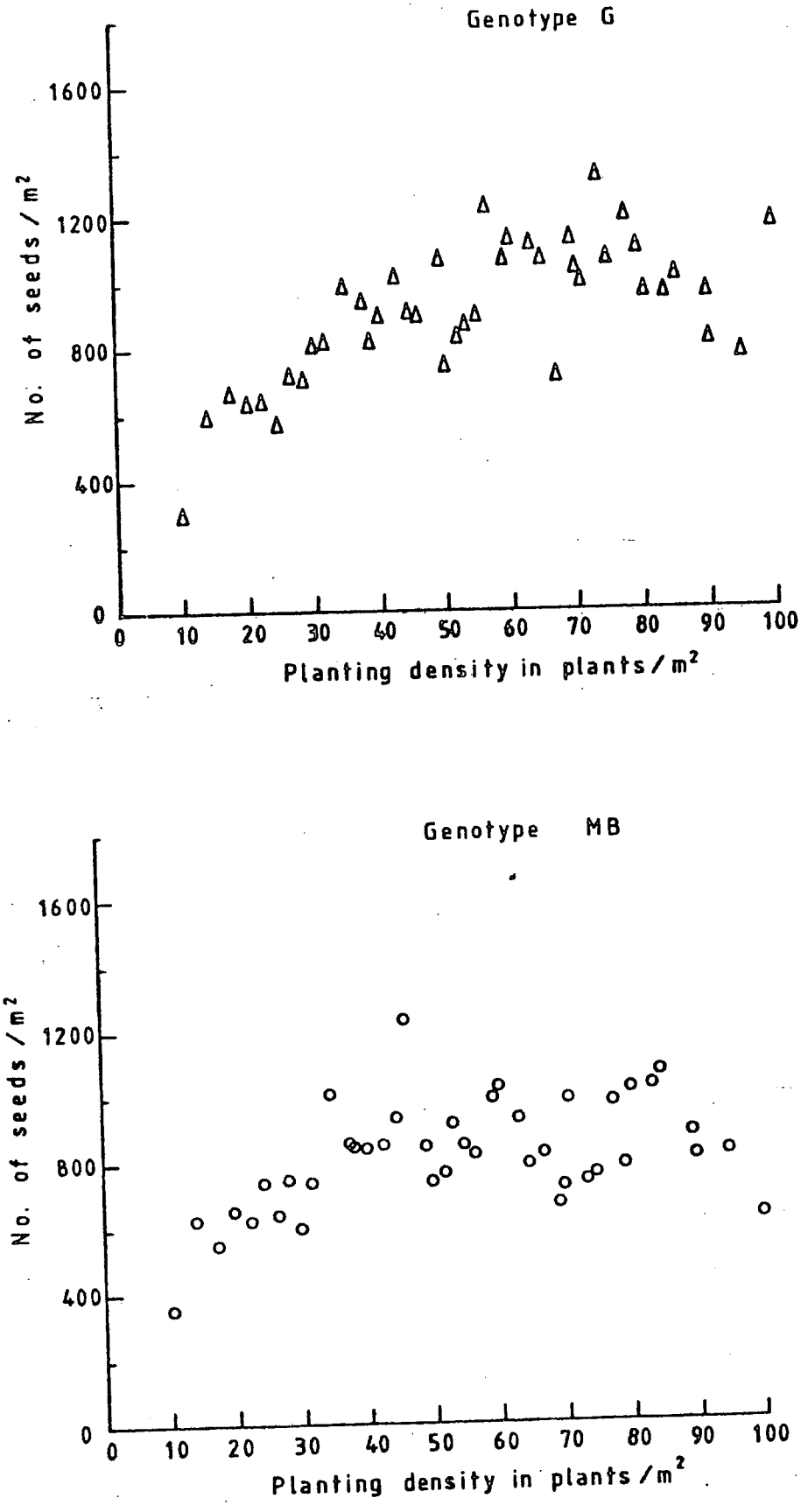


Figure 4.1.12 The effects of different planting densities on the mean number of seeds per square metre in genotypes F, G and Maris Bead (MB)

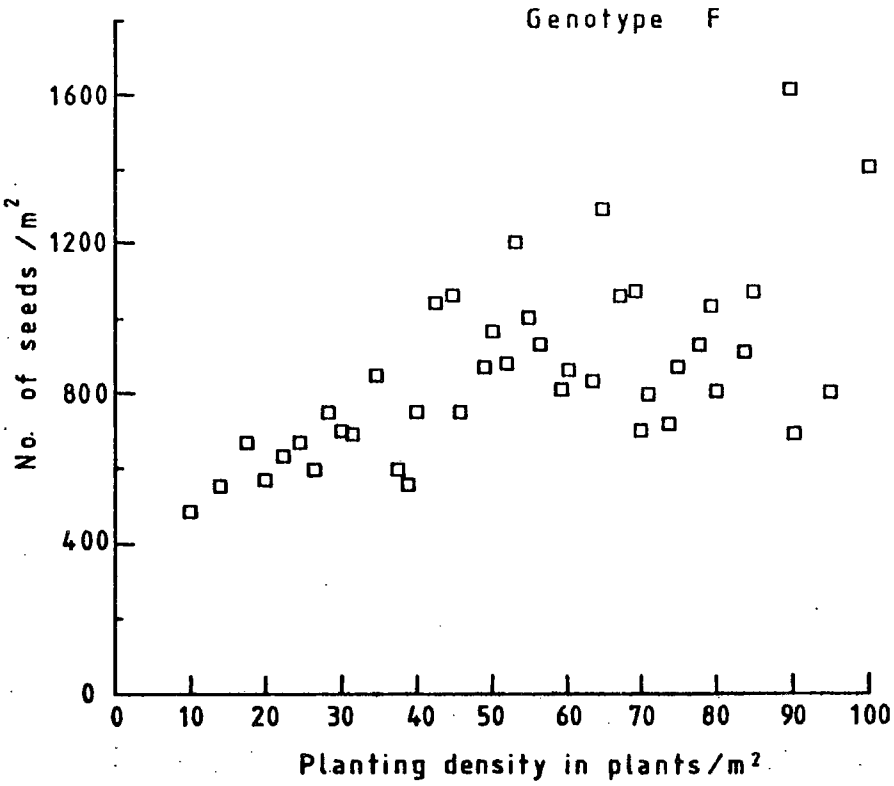


Figure 4.1.12 continued

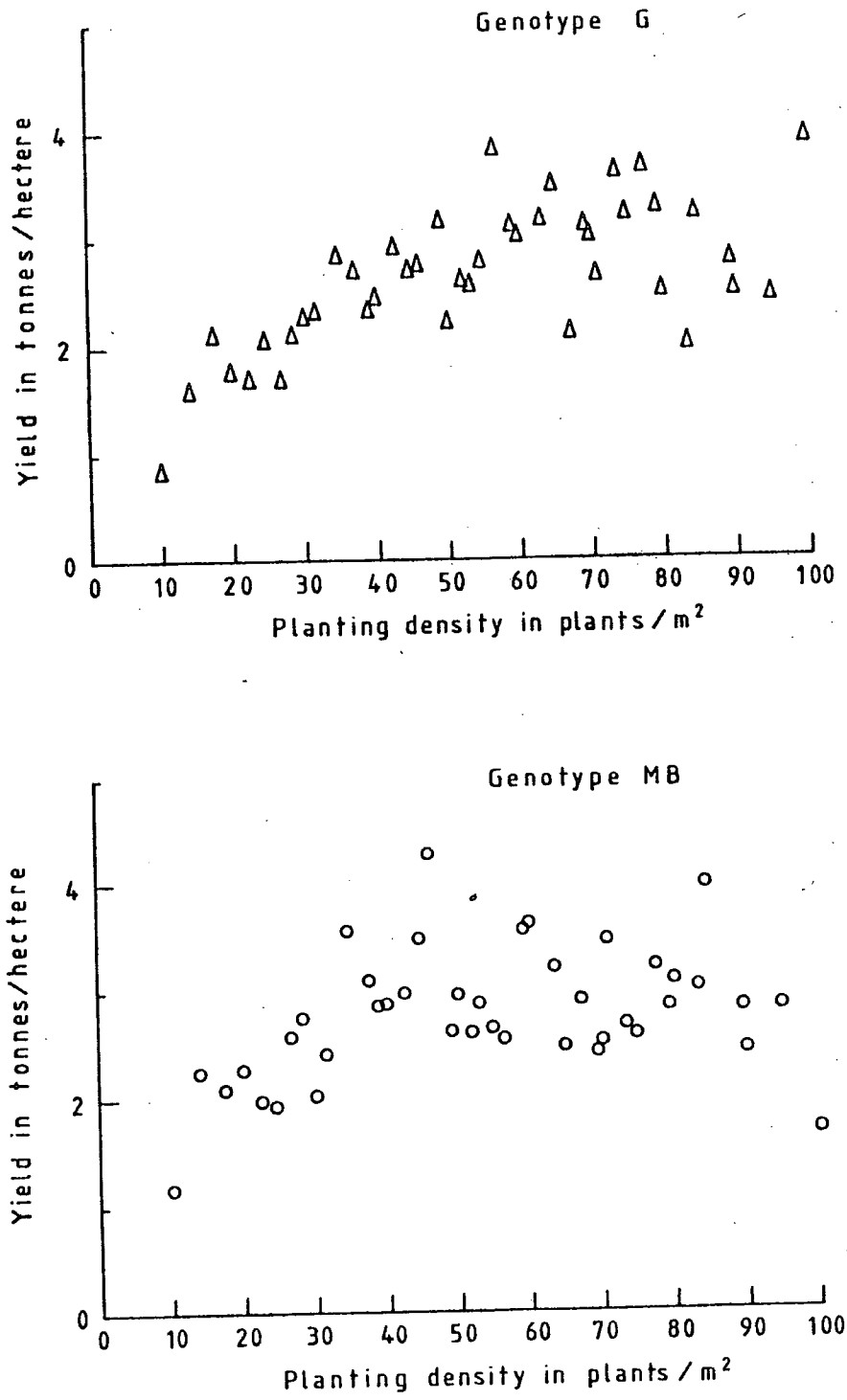


Figure 4.1.13 The effects of different planting densities on the extrapolated yield in tonnes per hectare for genotypes F, G and Maris Bead (MB)

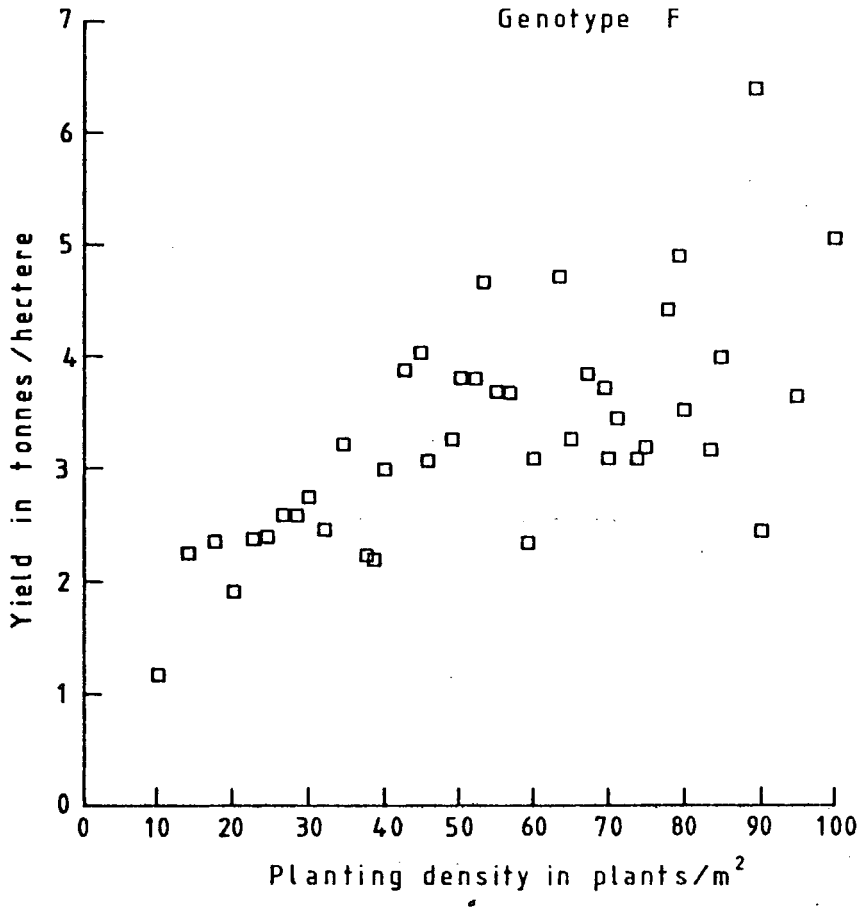


Figure 4.1.13 continued

Table 4.2.1.1

Analysis of variance for plant height in irrigation experiment.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	Significance of F
Replicates	1	0.000	0.000	0.000	n.s.
Error 1	6	0.062	0.010		
Irrigations	2	0.655	0.328	14.909	**
Error 2	8	0.179	0.022		
Genotypes	2	1.029	0.514	64.25	***
Replicates x Irrigations	2	0.002	0.001	0.125	n.s.
Replicates x genotypes	2	0.031	0.016	2.00	n.s.
Irrigations x genotypes	4	0.148	0.037	4.625	n.s.
Error 3	4	0.031	0.008		
Replicates x irrigations x genotypes	4	0.031	0.008	4.00	**
Error 4	142	0.341	0.002		
Corrected Total	159	2.089	0.013		

n.s. non-significant

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.2.1.2

Analysis of variance for number of stems in the irrigation experiment.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	Significance of F
Replicates	1	0.011	0.011	2.750	n.s.
Error 1	148	0.554	0.004		
Irrigations	2	0.001	0.001	0.250	n.s.
Error 2	150	0.535	0.004		
Genotypes	2	0.027	0.013	3.250	*
Replicates x Irrigations	2	0.004	0.002	0.500	n.s.
Replicates x genotypes	2	0.021	0.010	2.500	n.s.
Irrigations x genotypes	4	0.002	0.001	0.250	n.s.
Error 3	146	0.533	0.004		
Corrected Total	159	0.607	0.004		

n.s. non-significant

* $p \leq 0.05$

Table 4.2.1.3

Analysis of variance for number of podded nodes in the irrigation experiment.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	Significance of F
Replicates	1	0.003	0.003	0.111	n.s.
Error 1	148	3.932	0.027		
Irrigations	2	1.127	0.563	1.291	n.s.
Error 2	4	1.745	0.436		
Genotypes	2	0.635	0.317	11.809	***
Replicates x irrigations	2	0.022	0.011	0.413	n.s.
Replications x genotypes	2	0.007	0.003	0.128	n.s.
Irrigations x genotypes	4	1.745	0.436	16.228	***
Error 3	146	3.925	0.027		
Corrected Total	159	7.262	0.046		

n.s. non-significant

*** $p \leq 0.001$

Table 4.2.1.4

Analysis of variance for number of pods in the irrigation experiment.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	Significance of F
Replicate	1	0.002	0.002	0.049	n.s.
Error 1	148	6.100	0.041		
Irrigations	2	0.745	0.372	0.684	n.s.
Error 2	4	2.177	0.544		
Genotypes	2	2.864	1.432	34.095	***
Replicates x irrigations	2	0.054	0.027	0.643	n.s.
Replicates x genotypes	2	0.036	0.018	0.428	n.s.
Irrigations x genotypes	4	2.177	0.544	12.952	***
Error 3	146	6.063	0.042		
Corrected Total	159	11.722	0.074		

n.s. non-significant

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.2.1.5

Analysis of variance for number of seeds in the irrigation experiment.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	Significance of F
Replicates	1	0.033	0.033	0.541	n.s.
Error 1	148	9.070	0.061		
Irrigations	2	0.749	0.374	0.766	n.s.
Error 2	4	1.952	0.488		
Genotypes	2	7.670	3.835	62.338	***
Replicates x irrigations	2	0.017	0.009	0.140	n.s.
Replicates x genotypes	2	0.088	0.044	0.719	n.s.
Irrigations x genotypes	4	1.952	0.488	7.932	***
Error 3	146	8.982	0.062		
Corrected Total	159	19.220	0.121		

n.s. non-significant

*** $p \leq 0.001$

Table 4.2.1.6

Analysis of variance for weight of seeds in the irrigation experiment.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	Significance of F
Replicates	1	0.176	0.176	2.256	n.s.
Error 1	148	11.488	0.078		
Irrigations	2	0.534	0.267	0.539	n.s.
Error 2	4	1.980	0.495		
Genotypes	2	9.332	4.666	60.597	***
Replicates x irrigations	2	0.004	0.002	0.026	n.s.
Replicates x genotypes	2	0.178	0.089	1.148	n.s.
Irrigations x genotypes	4	1.980	0.495	6.389	***
Error 3	146	11.310	0.077		
Corrected Total	159	23.590	0.148		

n.s. non-significant

*** $p \leq 0.001$

Table 4.2.1.7

Cell mean values of significantly differing sources of variation found in table 4.2.1.1 - plant height - log values.

(a) Irrigations

Control	Irrigated to 75 centibars	Irrigated to 25 centibars
2.04	2.16	2.18

(b) Genotypes

A	Maris Bead	G
2.06	2.23	2.09

(c) Replicates x irrigations x denotypes

Irrigations	Genotypes					
	A		Maris Bead		G	
	Rep. 1	Rep. 2	Rep. 1	Rep. 2	Rep. 1	Rep. 2
Control	2.01	2.01	2.08	2.09	2.03	2.00
Irrigated to 75 centibars	2.10	2.08	2.30	2.25	2.08	2.14
Irrigated to 25 centibars	2.09	2.03	2.32	2.32	2.13	2.17

Table 4.2.1.8

Cell mean values of significantly differing sources of variation found in table 4.2.1.2 - number of pod bearing stems - log values.

Genotypes

A	Maris Bead	G
0.03	0.00	0.01

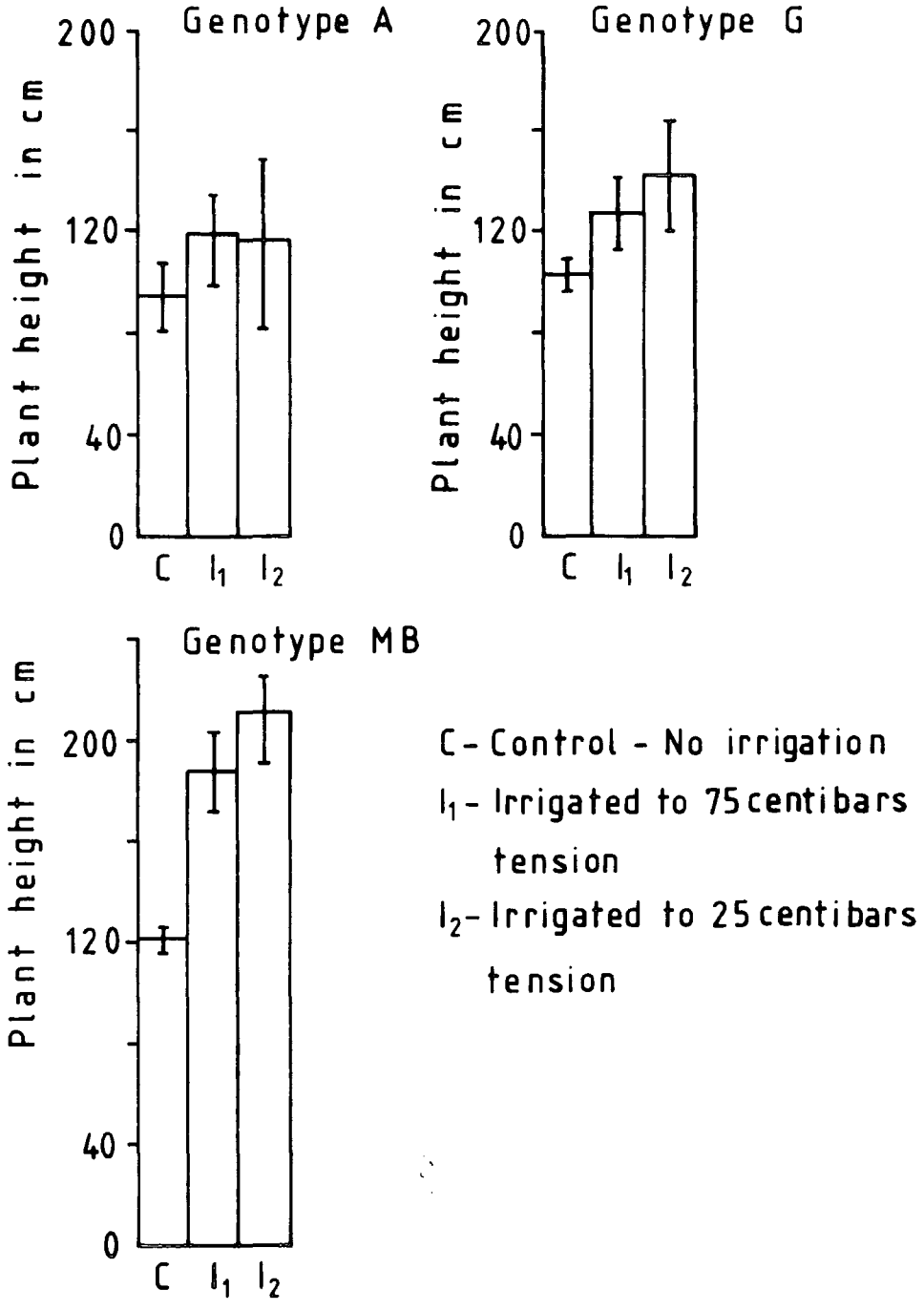


Figure 4.2.1 The effects of irrigation on mean plant height of each of the genotypes tested. Bar = standard deviation.

irrigation level; however, replicate 1 was of similar height to that found at the lower irrigation level, whereas the height of replicate 2 fell to a level similar to that of the control. In Maris Bead the values of the control and the higher level of irrigation were similar; at the lower irrigation level, however, replicate 1 had a higher value than replicate 2. The mean values of the replicates for genotype G differed at each of the irrigation levels tested. In the control replicate 1 was higher than replicate 2; at the lower irrigation level the situation was reversed, both replicates increased in height, but replicate 2 increased to a mean height greater than that of replicate 1. At the higher level of irrigation both replicates increased in height; replicate 1 showed the greatest increase.

Mean values for the number of pod bearing stems (table 4.2.1.8) showed that, whilst Maris Bead had only one such stem, both G and A had pod bearing branches in addition to the main stem; A had the greatest number of such branches (figure 4.2.2).

The cell means for number of podded nodes (table 4.2.1.9) showed that, although the value for G is lower than that of Maris Bead, both of these values were considerably higher than that of A. Examination of the means involved in the irrigations x genotypes interaction showed that each genotype responded differently to irrigation. Genotype A gave no response to the lower level of irrigation and a decrease in the number of podded nodes at the higher level. There was a substantial increase in number of podded nodes in response to the lower level of irrigation in Maris Bead. Further irrigation resulted in another slight increase in number of podded nodes. In genotype G the lower level of irrigation resulted in an increase in number of podded nodes. Further irrigation, however, resulted in a decrease in number of podded nodes to a value similar to that of the control (figure 4.2.3).

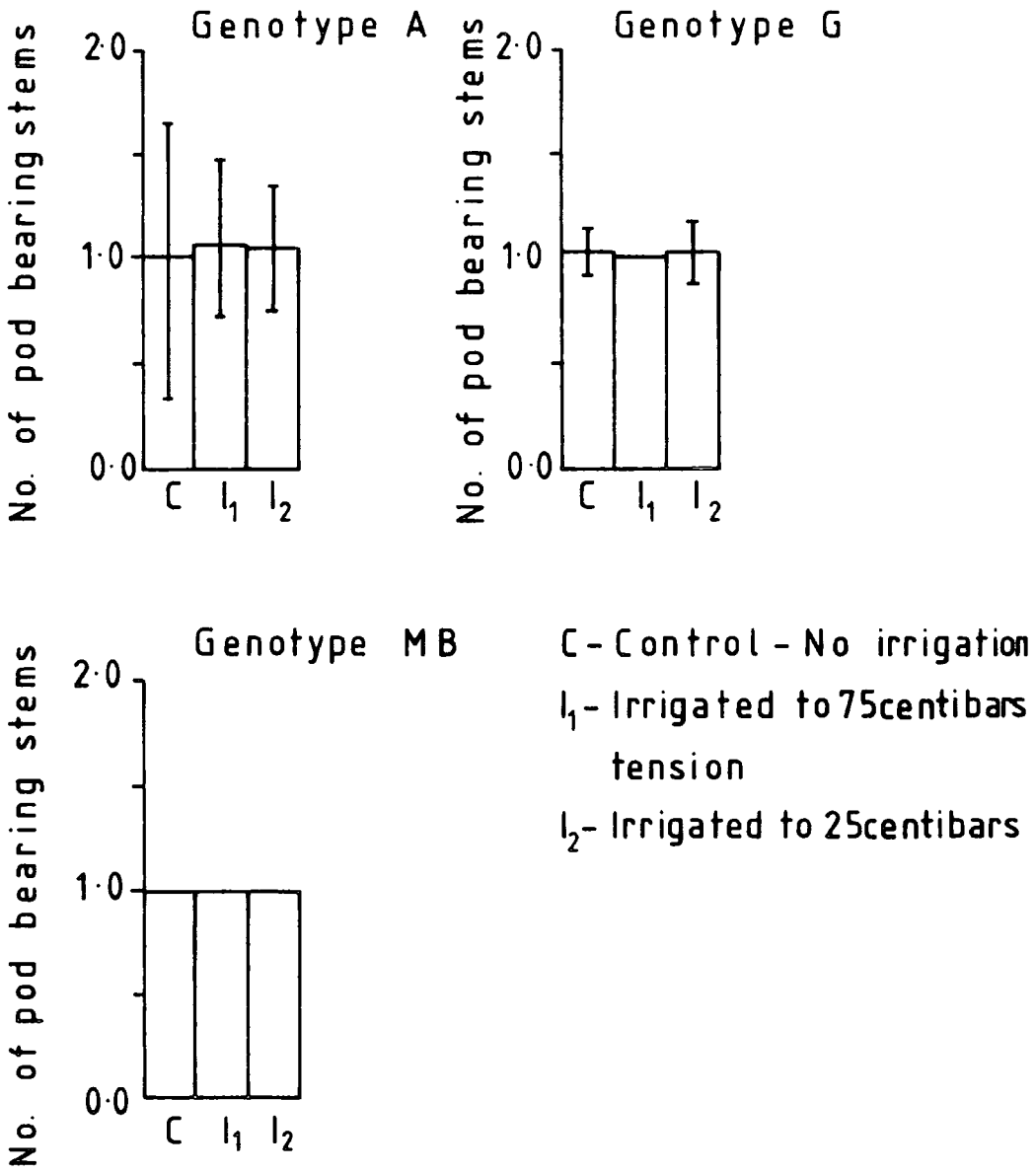


Figure 4.2.2 The effects of irrigation on the mean number of pod bearing stems of each of the genotypes tested. Bar = standard deviation.

Table 4.2.1.9

Cell mean values of significantly differing sources of variation found in table 4.2.1.3 - number of podded nodes - log values.

(a) Genotypes

A	Maris Bead	G
0.63	0.76	0.72

(b) Irrigation x genotypes

	Genotypes		
Irrigations	A	Maris Bead	G
Control	0.70	0.46	0.69
Irrigated to 75 centibars	0.69	0.86	0.81
Irrigated to 25 centibars	0.55	0.94	0.67

Table 4.2.1.10

Cell mean values for significantly differing sources of variation found in table 4.2.1.4 - number of pods - log values.

(a) Genotypes

A	Maris Bead	G
0.77	1.09	0.92

(b) Irrigations x genotypes

	Genotype		
Irrigation	A	Maris Bead	G
Control	0.83	0.83	0.97
Irrigated to 75 centibars	0.83	1.17	1.04
Irrigated to 25 centibars	0.69	1.24	0.75

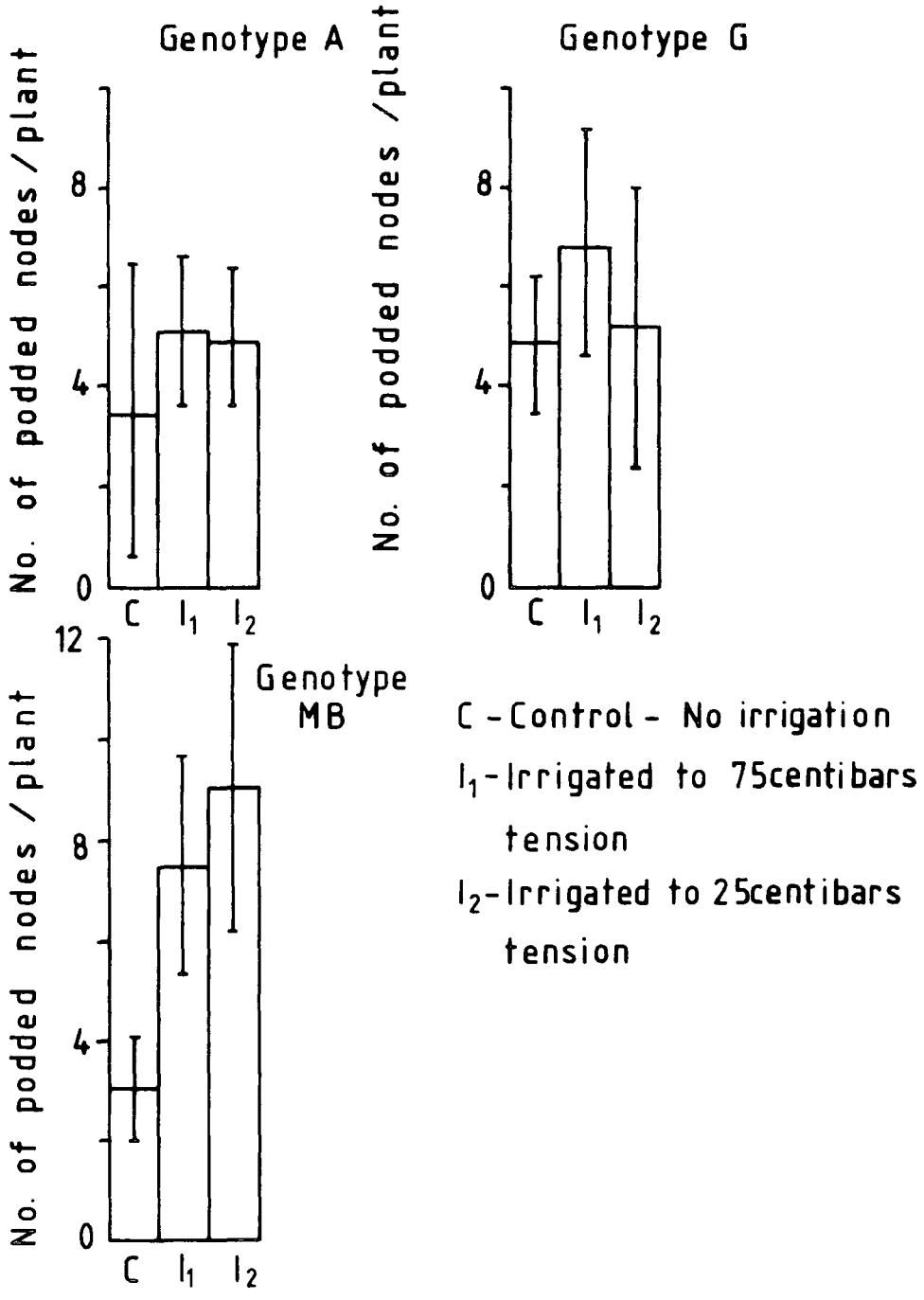


Figure 4.2.3 The effects of irrigation on the mean number of podded nodes per plant of each of the genotypes tested. Bar = standard deviation.

The means for number of pods (table 4.2.1.10) follow a pattern similar to that for number of podded nodes. (figure 4.2.4).

A slightly different pattern emerged on examination of the means for number of seeds (table 4.2.1.11). The mean for each genotype differed considerably from that of either of the other two. The interaction means showed the pattern occurring in A to be one of increased number of seeds at the lower level or irrigation applied, and a fall in number of seeds at the higher irrigation level to a value between those of the control and the first irrigation level. In Maris Bead the response pattern was similar to that seen before, a large increase with the lower irrigation level than a smaller increase at the higher irrigation level. In G the lower irrigation level produced very little response, further irrigation resulted in a decrease in number of seeds to a value lower than the control (figure 4.2.5). The pattern observed for weight of seeds (table 4.2.1.12) was very similar to that for number of seeds (figure 4.2.6).

The mean number of pods per podded node for each genotype at each irrigation level was calculated and plotted (figure 4.2.7). From this it was seen that number of pods per podded node was a less variable yield component than either number of podded nodes or number of pods per plant. In each genotype the number of pods per podded node was relatively unaffected by irrigation. The mean number of seeds per pod for each genotype at each irrigation was also calculated and plotted (figure 4.2.8). The mean values for number of seeds per pod were different for each of the three genotypes tested. The response to irrigation differed between genotypes. In genotype A irrigation resulted in an increase in number of seeds per pod, whereas in both genotypes G and Maris Bead the lower level of irrigation produced

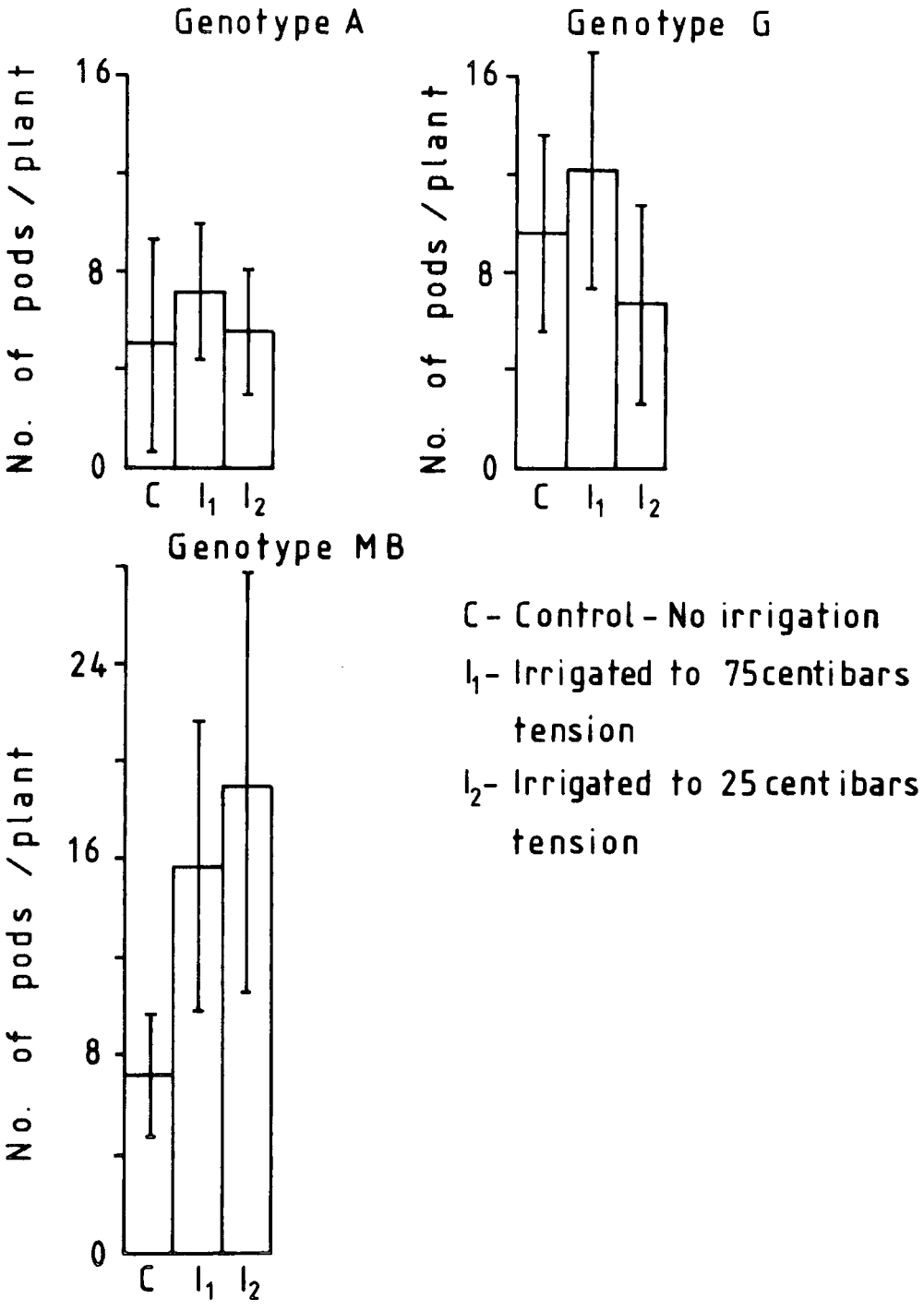


Figure 4.2.4 The effects of irrigation on the mean number of pods per plant of each of the genotypes tested. Bar = standard deviation.

Table 4.2.1.11

Cell mean values for significantly differing sources of variation found in table 4.2.1.5 - number of seeds - log values.

(a) Genotypes

A	Maris Bead	G
1.08	1.62	1.34

(b) Irrigations x genotypes

	Genotype		
Irrigation	A	Maris Bead	G
Control	0.96	1.37	1.40
Irrigated to 75 centibars	1.15	1.68	1.45
Irrigated to 25 centibars	1.06	1.77	1.17

Table 4.2.1.12

Cell mean values for significantly differing sources of variation found in table 4.2.1.6 - weight of seeds - log values.

(a) Genotypes

A	Maris Bead	G
0.51	1.12	0.83

(b) Irrigations x genotypes

	Genotypes		
Irrigation	A	Maris Bead	G
Control	0.47	0.91	0.93
Irrigated to 75 centibars	0.56	1.19	0.94
Irrigated to 25 centibars	0.49	1.23	0.61

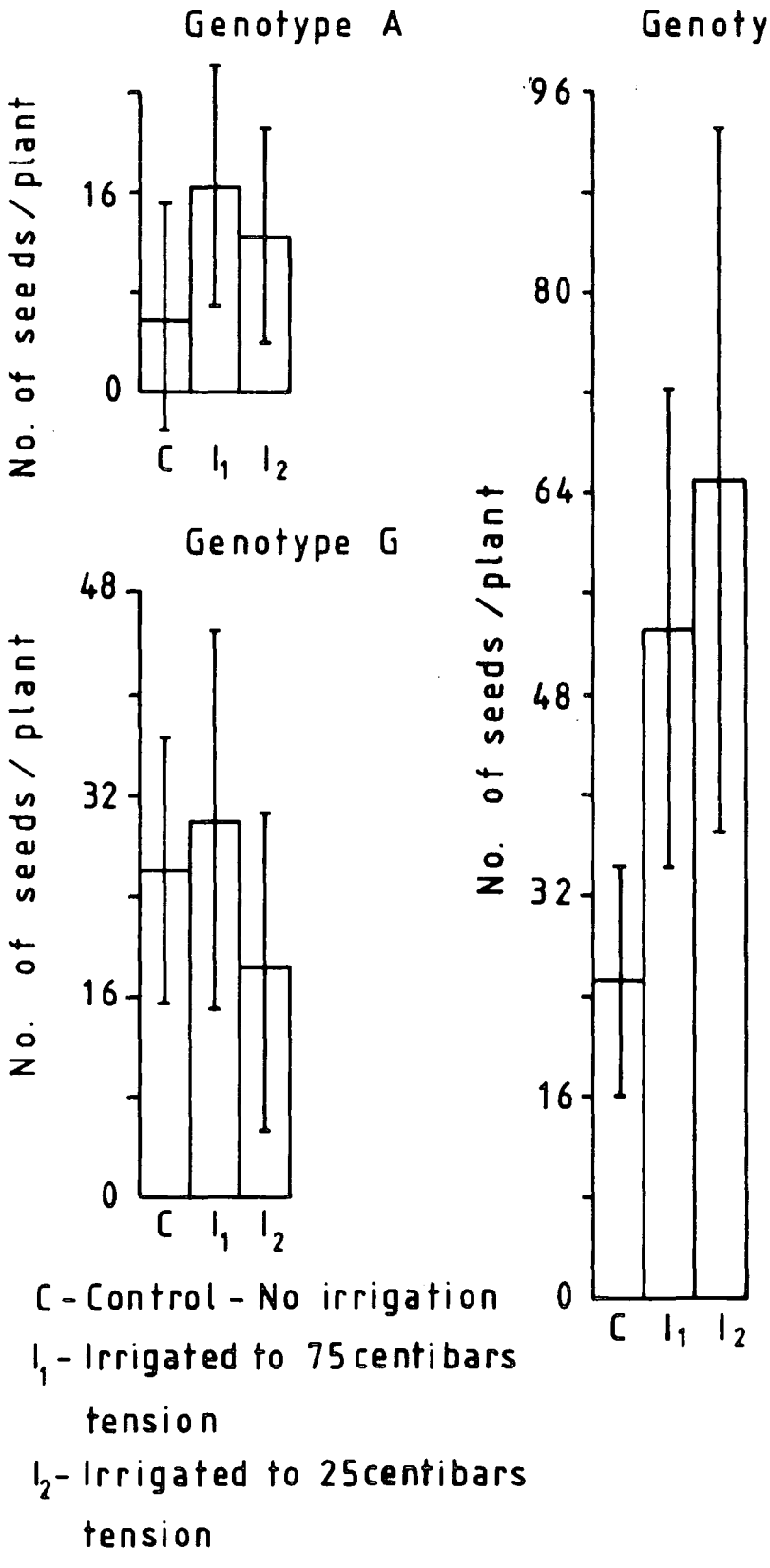


Figure 4.2.5 The effects of irrigation on the mean number of seeds per plant of each of the genotypes tested. Bar = standard deviation.

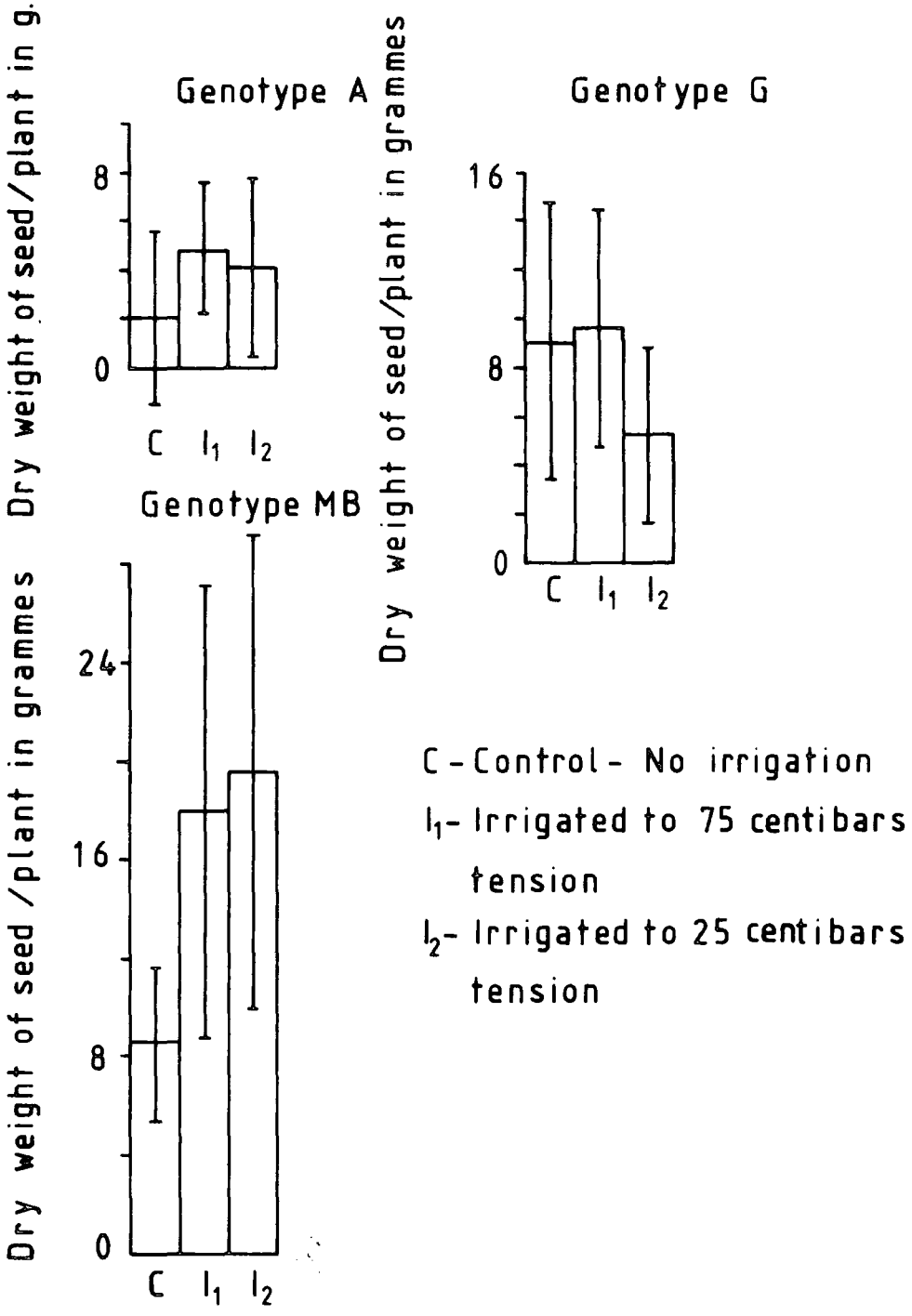


Figure 4.2.6 The effects of irrigation on the mean dry weight of seeds per plant of each of the genotypes tested. Bar = standard deviation.

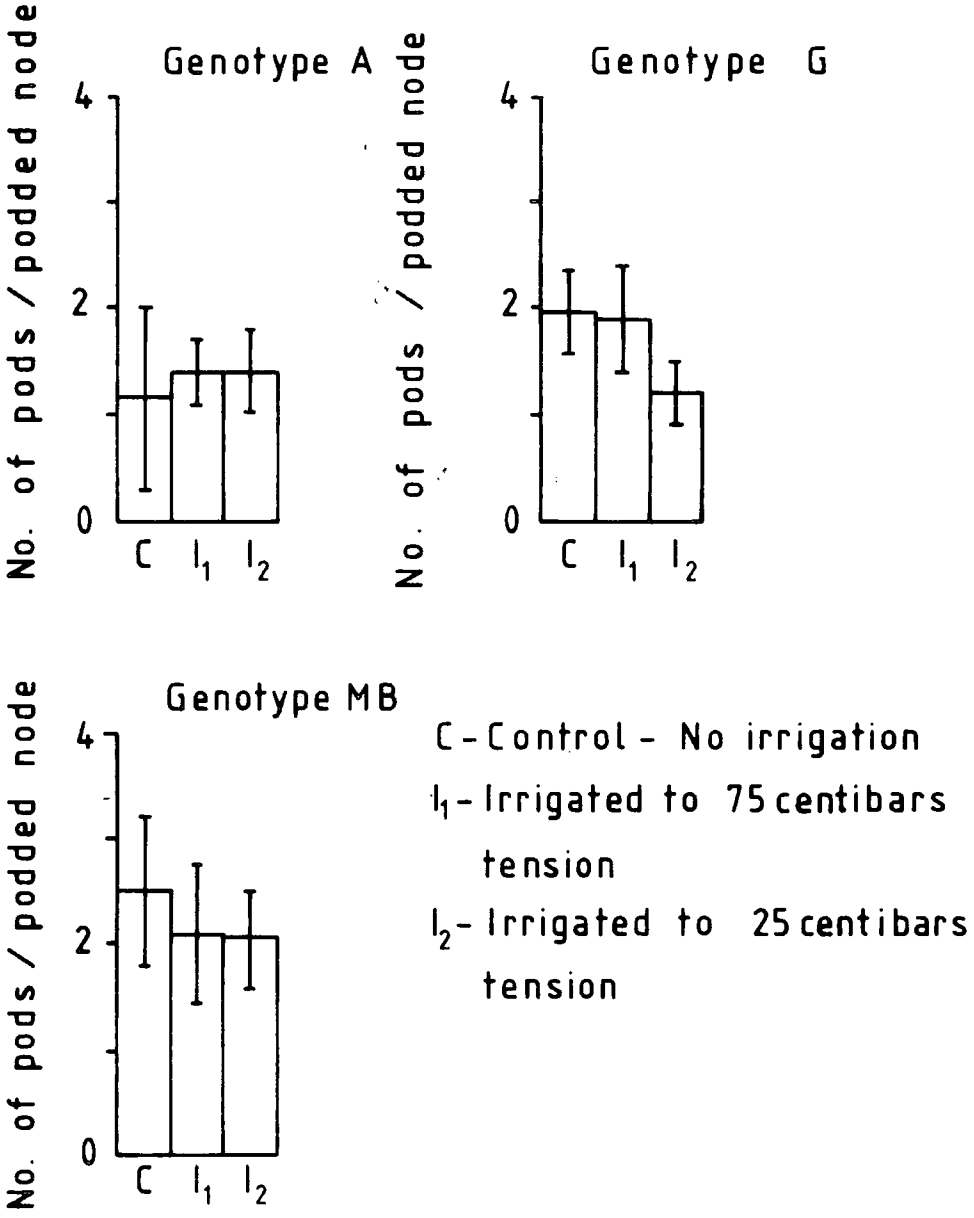


Figure 4.2.7 The effects of irrigation on the mean number of pods per podded node of each of the genotypes tested. Bar = standard deviation.

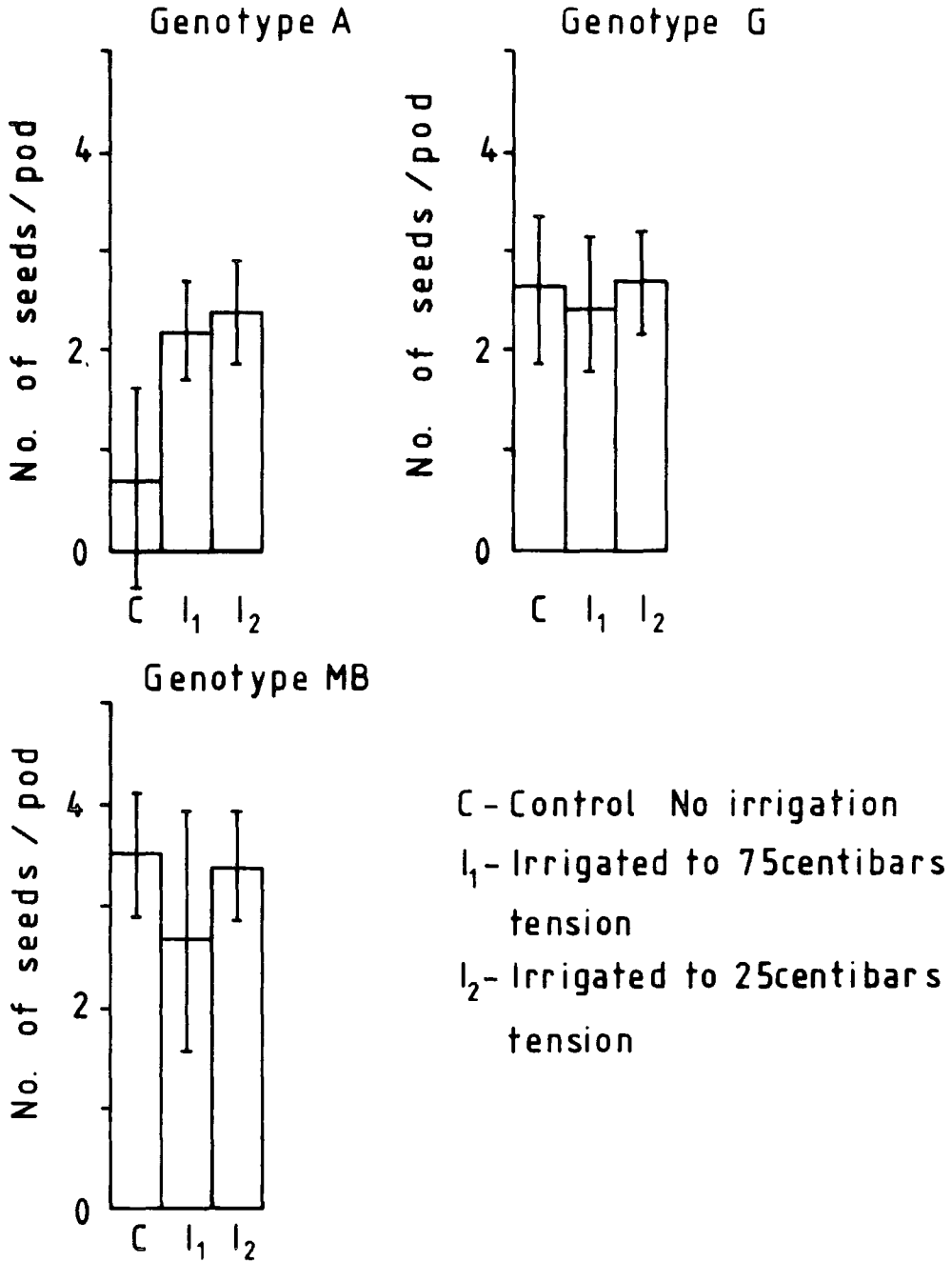


Figure 4.2.8 The effects of irrigation on the mean number of seeds per pod of each of the genotypes tested. Bar = standard deviation.

a decrease, but this was restored at the higher irrigation level. The calculated weight per seed (figure 4.2.9) revealed the mean values to be similar within each genotype irrespective of the treatment applied. The standard deviation levels found in genotype A were very high.

4.2.2 Analysis of plot yield data

Analysis of variance revealed significant differences between genotypes, there were also significantly differing irrigations x genotypes interaction (table 4.2.2.1). Examination of mean yield values for genotypes using least significant differences showed that all genotypes differed from each other to varying levels of significance (table 4.2.2.2). The means involved in the irrigations x genotypes interaction showed the same general pattern in all three genotypes. When irrigated to 75 centibars soil moisture tension the yield was greater than that of the control. With irrigation to 25 centibars soil moisture tension the yield decreased. The extent of the increase and decrease in yield due to irrigation varied between genotypes, this variation produced the significant interaction value on the F table.

4.3 Yield components of plants grown under conditions of reduced environmental stress

Analysis of variance revealed significant inter-genotypic differences in plant height, number of pods, number of seeds and weight of seeds (table 4.3.1). When the least significant difference values for plant height were examined in detail it was seen that Maris Bead was significantly taller than any other genotype tested, genotype F was also taller than some of the other genotypes. The independent vascular supply plants were shorter than the non-independent vascular supply type plants (table 4.3.2). In all of the yield components recorded the same overall pattern of differences was seen (tables 4.3.3, 4.3.4, 4.3.5).

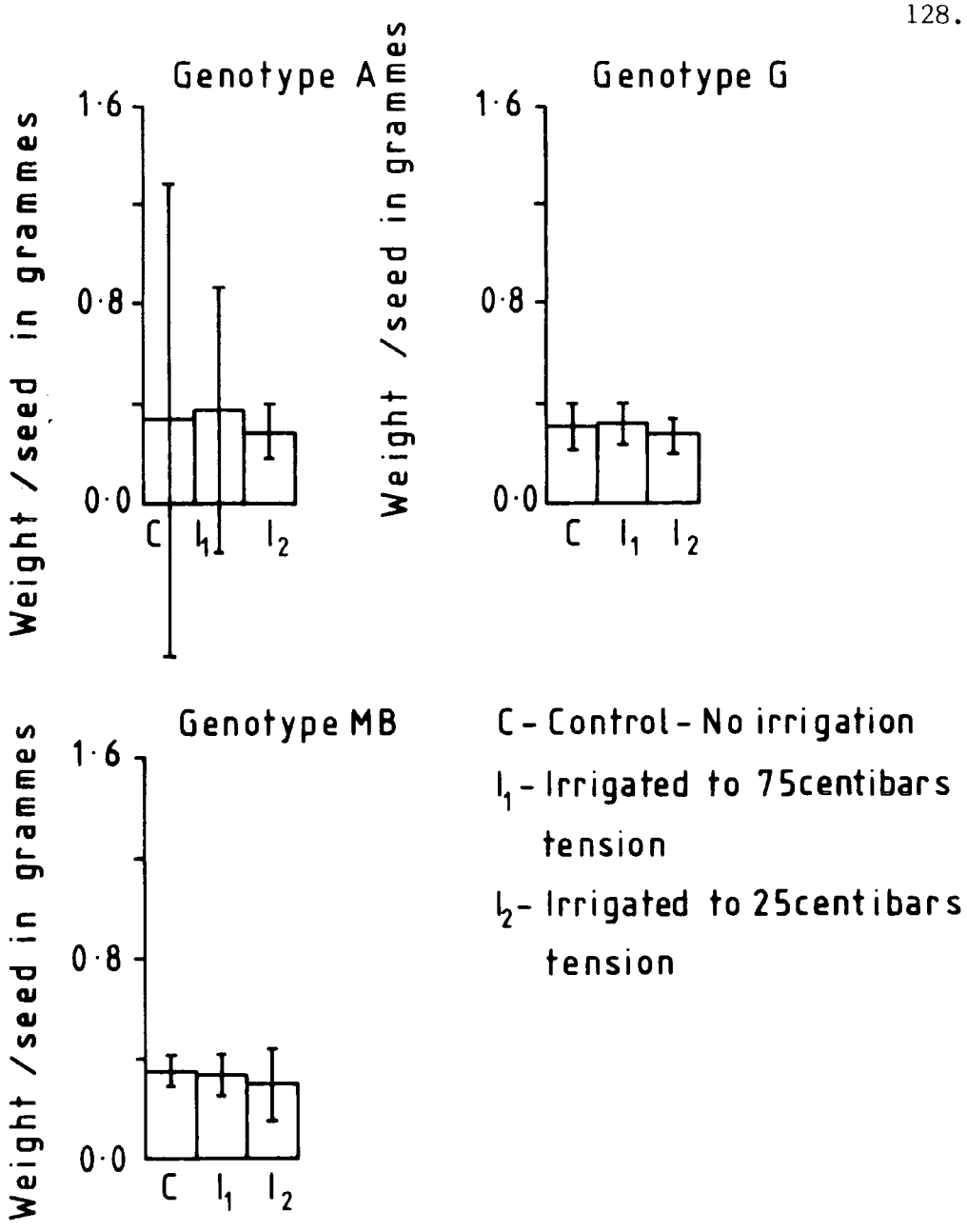


Figure 4.2.9 The effects of irrigation on the mean weight per seed of each of the genotypes tested. Bar = standard deviation.

Table 4.2.2.1

Analysis of variance for irrigation experiment plot yield.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	Significance of F
Replicates	1	1820.257	1820.257	0.319	n.s.
Error 1	6	34158.800	5693.133		
Irrigations	2	194998.333	97499.166	1.083	n.s.
Error 2	4	359956.336	89989.084		
Genotypes	2	1816987.083	908493.541	387.670	***
Replicates x irrigations	2	4304.000	2152.000	0.9182	n.s.
Replicates x genotypes	2	24784.916	12392.458	5.288	n.s.
Irrigations x genotypes	4	359956.336	89989.084	38.399	**
Error 3	4	9373.884	2343.471		
Corrected Total	17	2412224.808	141895.577		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.2.2.2

Results of investigations into significant differences found by analysis of variance in table 4.2.2.1.

(a) Differences between genotypes

Mean	Genotype	A	Genotype Maris Bead	G
124.34	A			
892.86	Maris Bead	***		
402.38	G	**	***	

** $p \leq 0.01$

*** $p \leq 0.001$

(b) Irrigations x genotypes - cell means

Irrigation	Genotypes A	Maris Bead	G
Control	96.72	487.00	438.75
Irrigated to 75 centibars	155.58	1138.25	491.57
Irrigated to 25 centibars	120.71	1053.31	276.82

Table 4.3.1

Results of analysis of variance of each parameter recorded under conditions of reduced environmental stress.

Yield Parameter	F Ratio	F Probability
Plant height	16.5606	***
Number of stems	0.8822	n.s.
Number of pods	4.6369	**
Number of seeds	7.1614	***
Weight of seeds	5.7247	***

n.s. non-significant
** $p \leq 0.01$
*** $p \leq 0.001$

Table 4.3.2

Significant inter-genotypic differences in plant height shown by least significant differences.

		Genotypes					
Mean	Genotype	A	AIVS	F	G	IVSC	Maris Bead
164.10	A						
178.50	AIVS						
190.20	F	*					
163.80	G			*			
147.70	IVSC		**	***			
236.10	Maris Bead	***	***	***	***	***	

* $p \leq 0.05$
** $p \leq 0.01$
*** $p \leq 0.001$

Table 4.3.3

Significant inter-genotypic differences in number of pods shown by least significant differences.

		Genotypes					
Mean	Genotype	A	AIVS	F	G	IVSC	Maris Bead
11.300	A						
6.500	AIVS						
13.200	F		*				
16.500	G		**				
5.700	IVSC			*	**		
17.400	Maris Bead		**			***	

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.3.4

Significant inter-genotypic differences in number of seeds shown by least significant differences.

		Genotypes					
Mean	Genotype	A	AIVS	F	G	IVSC	Maris Bead
29.70	A						
14.00	AIVS						
36.80	F		*				
42.30	G		**				
11.50	IVSC	*		**	**		
55.90	Maris Bead	**	***	*		***	

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.3.5

Significant inter-genotypic differences in weight of seeds shown by least significant differences.

		Genotypes					
Mean	Genotype	A	AIVS	F	G	IVSC	Maris Bead
8.184	A						
5.194	AIVS						
12.687	F		*				
14.718	G	*	**				
2.942	IVSC			**	***		
16.143	Maris Bead	*	**			***	

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Genotypes G, F and Maris Bead gave mean values significantly greater than the highly inbred lines A, AIVS and IVSC.

4.4 Irrigation and density trial

4.4.1 Analysis of data from sampled plants

Vegetative characteristics

Analysis of variance showed that vegetative characteristics such as plant height, total stem length, number of leaves and dry weight of straw were markedly effected by genotypic and environmental differences (tables 4.4.1.1, 4.4.1.3, 4.4.1.5, 4.4.1.7) The two genotypes differed significantly for all the vegetative characteristics measured, in each case genotype Maris Bead gave a higher value than genotype G (tables 4.4.1.2(a), 4.4.1.4(a), 4.4.1.6(a) and 4.4.1.8(a)). Added irrigation also had a highly significant effect on the vegetative growth of the plants (tables 4.4.1.1, 4.4.1.3, 4.4.1.5, 4.4.1.7) In each case irrigation produced increased vegetative growth (tables 4.4.1.2(b), 4.4.1.4(b), 4.4.1.6(b), 4.4.1.8(b)). The differing planting densities used had no significant effect on plant height but did produce a highly significant increase in total stem length (table 4.4.1.4(c)), number of leaves (table 4.4.1.6(c)), and dry weight of straw (table 4.4.1.8(c)). There was strong evidence of a difference in plant height between plots (table 4.4.1.1), this was due to the higher value for plot W (table 4.4.1.2(c)). The difference between plots for total stem length (table 4.4.1.3) was also due to a higher value for plot W (table 4.4.1.4(d)).

For all the vegetative characteristics there was a significant genotype x irrigation interaction (tables 4.4.1.1, 4.4.1.3, 4.4.1.5, 4.4.1.7). Examination of means showed this to be due to a greater response to added irrigation in Maris Bead than in G (tables 4.4.1.2(d), 4.4.1.4(e), 4.4.1.6(d), 4.4.1.8(e)).

Table 4.4.1.1

Analysis of variance for plant height in the irrigation and density trial.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	76077.188	76077.188	566.063	***
Irrigation	1	113057.000	113057.000	841.216	***
Density	1	40.837	40.837	0.304	n.s.
Plot	2	1661.358	830.679	6.181	**
Genotype x irrigation	1	10547.004	10547.004	78.476	***
Genotype x density	1	507.504	507.504	3.776	n.s.
Genotype x plot	2	150.905	75.453	0.561	n.s.
Irrigation x density	1	33.004	33.004	0.246	n.s.
Irrigation x plot	2	5665.508	2832.799	21.078	***
Density x plot	2	39.024	19.512	0.145	n.s.
Genotype x irrigation x density	1	45.937	45.937	0.342	n.s.
Genotype x irrigation x plot	2	315.571	157.786	1.174	n.s.
Genotype x density x plot	2	813.790	406.895	3.028	*
Irrigation x density x plot	2	76.801	38.400	0.286	n.s.
Error	218	29298.563	131.397		
Corrected Total	239	238330.063	997.197		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.4.1.2

Cell mean values of significantly differing sources of variation found in table 4.4.1.1 - maximum plant height.

(a) Genotype

G	Maris Bead
107.32	142.93

(b) Irrigation

Non-irrigated	Irrigated
103.42	146.83

(c) Plot

V	W	X
123.95	128.77	122.66

(d) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	92.25	122.40
Genotype Maris Bead	114.60	171.27

(e) Irrigation x plot

	Plot V	Plot W	Plot X
Non-irrigated	98.40	113.92	97.95
Irrigated	149.50	143.63	147.38

(f) Genotype x density x plot

	Density					
Genotype	40 plants/m²			80 plants/m²		
	Plot V	Plot W	Plot X	Plot V	Plot W	Plot X
G	101.50	111.55	105.80	108.55	111.45	105.10
Maris Bead	147.25	147.80	139.35	138.50	144.30	140.40

Table 4.4.1.3

Analysis of variance for total stem length in the irrigation and density trial.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F probability
Genotype	1	48792.016	48792.016	37.514	***
Irrigation	1	106597.313	106597.313	81.959	***
Density	1	18797.398	18797.398	14.453	***
Plot	2	10684.105	5342.051	4.107	*
Genotype x irrigation	1	26797.066	26797.066	20.603	***
Genotype x density	1	1033.350	1033.350	0.795	n.s.
Genotype x plot	2	2519.378	1259.689	0.969	n.s.
Irrigation x density	1	3666.017	3666.017	2.819	n.s.
Irrigation x plot	2	13657.613	6828.805	5.250	**
Density x plot	2	4651.645	2325.822	1.788	n.s.
Genotype x irrigation x density	1	106.667	106.667	0.082	n.s.
Genotype x irrigation x plot	2	1116.904	558.452	0.429	n.s.
Genotype x density x plot	2	2191.497	1095.749	0.842	n.s.
Irrigation x density x plot	2	1608.336	804.168	0.618	n.s.
Error	218	283535.188	1300.620		
Corrected Total	239	525754.500	2199.810		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

** $p \leq 0.001$

Table 4.4.1.4

Cell mean values of significantly differing sources of variation found in table 4.4.1.3 - total stem length.

(a) Genotype

G	Maris Bead
123.47	151.99

(b) Irrigation

Non-irrigated	Irrigated
116.66	158.81

(c) Density

40 plants/m^2	80 plants/m^2
146.58	128.88

(d) Plot

V	W	X
132.71	147.16	133.32

(e) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	112.97	133.98
Genotype Maris Bead	120.35	183.63

(f) Irrigation x plot

	Plot		
Irrigation	V	W	X
Non-irrigated	104.60	136.55	108.82
Irrigated	160.82	157.77	157.82

Table 4.4.1.5

Analysis of variance for number of leaves for the irrigation and density trial.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	135.000	135.000	5.992	*
Irrigation	1	1306.667	1306.667	58.000	***
Density	1	700.417	700.417	31.090	***
Plot	2	25.833	12.917	0.573	n.s.
Genotype x irrigation	1	410.817	410.817	18.235	***
Genotype x density	1	17.067	17.067	0.758	n.s.
Genotype x plot	2	161.200	80.600	3.578	*
Irrigation x density	1	64.067	64.067	2.844	n.s.
Irrigation x plot	2	149.433	74.716	3.316	*
Density x plot	2	44.434	22.217	0.986	n.s.
Genotype x irrigation x density	1	0.150	0.150	0.007	n.s.
Genotype x irrigation x plot	2	11.434	5.717	0.254	n.s.
Genotype x density x plot	2	75.832	37.916	1.683	n.s.
Irrigation x density x plot	2	8.133	4.067	0.181	n.s.
Error	218	4911.301	22.529		
Corrected Total	239	8021.785	33.564		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

** $p \leq 0.001$

Table 4.4.1.6

Cell mean values of significantly differing sources of variation found in table 4.4.1.5 - number of leaves.

(a) Genotype

G	Maris Bead
20.34	21.84

(b) Irrigation

Non-irrigated	Irrigated
18.76	23.42

(c) Density

40 plants/m^2	80 plants/m^2
22.80	19.38

(d) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	19.32	21.37
Genotype Maris Bead	18.20	25.48

(e) Genotype x plot

	Plot V	Plot W	Plot X
Genotype G	19.02	21.25	20.75
Genotype Maris Bead	22.82	21.85	20.85

(f) Irrigation x plot

	Plot V	Plot W	Plot X
Non-irrigated	18.15	20.32	17.80
Irrigated	23.70	22.77	23.80

Table 4.4.1.7

Analysis of variance for dry weight of straw in the irrigation and density trial.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	2695.460	2695.460	80.004	***
Irrigation	1	2740.552	2740.552	81.343	***
Density	1	771.602	771.602	22.902	***
Plot	2	73.155	36.578	1.086	n.s.
Genotype x irrigation	1	1554.280	1554.280	46.131	***
Genotype x density	1	371.068	371.068	11.014	***
Genotype x plot	2	198.228	99.114	2.942	n.s.
Irrigation x density	1	116.431	116.431	3.456	n.s.
Irrigation x plot	2	124.153	62.076	1.843	n.s.
Density x plot	2	65.573	32.787	0.973	n.s.
Genotype x irrigation x density	1	123.372	123.372	3.662	n.s.
Genotype x irrigation x plot	2	108.160	54.080	1.605	n.s.
Genotype x density x plot	2	289.241	144.621	4.293	*
Irrigation x density x plot	2	10.773	5.386	0.160	n.s.
Error	218	7344.723	33.691		
Corrected Total	239	16586.719	69.400		

n.s. non-significant

* $p \leq 0.05$

*** $p \leq 0.001$

Table 4.4.1.8

Cell mean values of significantly differing sources of variation found in table 4.4.1.7 - dry weight of straw.

(a) Genotypes

G	Maris Bead
8.69	15.39

(b) Irrigation

Non-irrigated	Irrigated
8.66	15.42

(c) Density

40 plants/m^2	80 plants/m^2
13.83	10.24

(d) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	7.85	9.52
Genotype Maris Bead	9.46	21.31

(e) Genotype x density

	40 plants/m^2	80 plants/m^2
G	9.24	8.14
Maris Bead	18.43	12.35

(f) Genotype x density x plot

	Genotype G		Genotype Maris Bead	
	40 plants/m^2	80 plants/m^2	40 plants/m^2	80 plants/m^2
Plot V	7.94	8.48	22.68	12.11
Plot W	10.09	8.08	15.50	12.43
Plot X	9.67	7.85	17.09	12.51

A significant genotype x density interaction was observed in the case of dry weight of straw produced (table 4.4.1.7), this was due to the greater drop in weight of straw with increased planting density in Maris Bead than in G (table 4.4.1.8(f)). The significant difference found in the genotype x plot interaction observed for number of leaves (table 4.4.1.5) was due to a low value for genotype G in plot V (table 4.4.1.6(e)). The irrigation x plot interactions observed for plant height, total stem length and number of leaves (tables 4.4.1.1, 4.4.1.3, 4.4.1.5) were attributed to high values for plot W without applied irrigation (tables 4.4.1.2(e), 4.4.1.4(f), 4.4.1.6(f)).

Three-way genotype x density x plot interactions were found for plant height and dry weight of straw (tables 4.4.1.1, 4.4.1.7). In the case of plant height table 4.4.1.2(f) showed that plot W planted with genotype G produced taller plants than the other plots at density 40 plants per metre^2, Maris Bead plants on plot X were shorter than on the other plots. In the case of dry weight of straw table 4.4.1.8(g) showed that on plot V at 40 plants per metre^2 plants of genotype G were shorter than on the other plots, whilst those of genotype Maris Bead were taller than those grown on other plots.

Total reproductive characteristics

Some significant inter-genotypic differences were found for total reproductive characters (number of flowers, number of pods set, number of pods 'filled', number of seeds and dry weight of seeds), but the major sources of differences were irrigation, density genotype x irrigation and genotype x density. A few other isolated significant differences were found (tables 4.4.1.9, 4.4.1.11, 4.4.1.13, 4.4.1.15, 4.4.1.17).

Table 4.4.1.9

Analysis of variance for number of flowers in the irrigation and density trial.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	355.267	355.267	1.952	n.s.
Irrigation	1	9102.016	9102.016	50.017	***
Density	1	3067.350	3067.350	16.856	***
Plot	2	183.225	91.612	0.503	n.s.
Genotype x irrigation	1	1430.817	1430.817	7.863	**
Genotype x density	1	1760.417	1760.417	9.674	**
Genotype x plot	2	470.560	235.280	1.293	n.s.
Irrigation x density	1	1109.400	1109.400	6.096	*
Irrigation x plot	2	989.760	494.880	2.719	n.s.
Density x plot	2	975.927	487.963	2.681	n.s.
Genotype x irrigation x density	1	123.267	123.267	0.677	n.s.
Genotype x irrigation x plot	2	484.554	242.277	1.331	n.s.
Genotype x density x plot	2	502.564	251.282	1.381	n.s.
Irrigation x density x plot	2	763.515	381.758	2.098	n.s.
Error	218	39671.367	181.979		
Corrected Total	239	60990.000	255.188		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.4.1.10

Cell mean values of significantly differing sources of variation found in table 4.4.1.9 - number of flowers.

(a) Irrigation

Non-irrigated	Irrigated
38.14	50.46

(b) Density

40 plants/m^2	80 plants/m^2
47.88	40.72

(c) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	39.37	46.80
Genotype Maris Bead	36.92	54.12

(d) Genotype x density

	40 plants/m^2	80 plants/m^2
Genotype G	43.95	42.22
Genotype Maris Bead	51.80	39.23

(e) Irrigation x density

	40 plants/m^2	80 plants/m^2
Non-irrigated	39.57	36.72
Irrigated	56.18	44.73

Table 4.4.1.11

Analysis of variance for number of pods set in the irrigation and density trial.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	43.350	43.350	1.639	n.s.
Irrigation	1	2747.267	2747.267	103.889	***
Density	1	470.400	470.400	17.788	***
Plot	2	2.058	1.029	0.039	n.s.
Genotype x irrigation	1	281.667	281.667	10.651	***
Genotype x density	1	264.600	264.600	10.006	**
Genotype x plot	2	50.175	25.088	0.949	n.s.
Irrigation x density	1	84.017	84.017	3.177	n.s.
Irrigation x plot	2	59.158	29.579	1.199	n.s.
Density x plot	2	56.875	28.437	1.075	n.s.
Genotype x irrigation x density	1	74.817	74.817	2.829	n.s.
Genotype x irrigation x plot	2	10.209	5.104	0.193	n.s.
Genotype x density x plot	2	108.325	54.162	2.048	n.s.
Irrigation x density x plot	2	25.608	12.804	0.484	n.s.
Error	218	5764.867	26.444		
Corrected Total	239	10043.391	42.023		

n.s. non-significant

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.4.1.12

Cell mean values of significantly differing sources of variation found in table 4.4.1.11 - number of pods set.

(a) Irrigation

Non-irrigated	Irrigated
7.66	14.42

(b) Density

40 plants/m^2	80 plants/m^2
12.44	9.64

(c) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	8.32	12.92
Genotype Maris Bead	7.00	15.93

(d) Genotype x density

	40 plants/m^2	80 plants/m^2
Genotype G	10.97	10.27
Genotype Maris Bead	13.92	9.02

Table 4.4.1.13

Analysis of variance for number of pods filled in the irrigation and density trial.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	3.504	3.504	0.201	n.s.
Irrigation	1	1575.937	1575.937	90.209	***
Density	1	329.004	329.004	18.833	***
Plot	2	9.033	4.517	0.259	n.s.
Genotype x irrigation	1	82.837	82.837	4.742	*
Genotype x density	1	133.504	133.504	7.642	**
Genotype x plot	2	67.034	33.517	1.919	n.s.
Irrigation x density	1	34.504	34.504	1.975	n.s.
Irrigation x plot	2	18.300	9.150	0.524	n.s.
Density x plot	2	40.533	20.267	1.160	n.s.
Genotype x irrigation x density	1	36.037	36.037	2.063	n.s.
Genotype x irrigation x plot	2	27.101	13.550	0.776	n.s.
Genotype x density x plot	2	140.133	70.067	4.011	*
Irrigation x density x plot	2	19.233	9.617	0.550	n.s.
Error	218	3808.414	17.470		
Corrected Total	239	6325.109	26.465		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

** $p \leq 0.001$

Table 4.4.1.14

Cell mean values of significantly differing sources of variance found in table 4.4.1.13 - number of pods 'filled'.

(a) Irrigation

Non-irrigated	Irrigated
6.59	11.72

(b) Density

40 plants/m^2	80 plants/m^2
10.32	7.98

(c) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	7.30	11.25
Genotype Maris Bead	5.88	12.18

(d) Genotype x density

	40 plants/m^2	80 plants/m^2
Genotype G	9.70	8.85
Genotype Maris Bead	10.95	7.12

(e) Genotype x density x plot

	Genotype G		Genotype Maris Bead	
	40 plants/m^2	80 plants/m^2	40 plants/m^2	80 plants/m^2
Plot V	8.60	8.95	13.45	6.55
Plot W	10.95	8.60	9.85	7.25
Plot X	9.55	9.00	9.55	7.55

Table 4.4.1.15

Analysis of variance for number of seeds filled in the irrigation and density experiment.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	700.417	700.417	4.225	*
Irrigation	1	14883.750	14883.750	89.782	***
Density	1	2884.267	2884.267	17.399	***
Plot	2	29.358	14.679	0.089	n.s.
Genotype x irrigation	1	1938.017	1938.017	11.691	***
Genotype x density	1	1144.067	1144.067	6.901	**
Genotype x plot	2	393.810	196.905	1.188	n.s.
Irrigation x density	1	240.000	240.000	1.448	n.s.
Irrigation x plot	2	282.775	141.387	0.553	n.s.
Density x plot	2	75.658	37.829	0.228	n.s.
Genotype x irrigation x density	1	345.600	345.600	2.085	n.s.
Genotype x irrigation x plot	2	18.260	9.130	0.055	n.s.
Genotype x density x plot	2	1022.801	511.400	3.085	*
Irrigation x density x plot	2	110.777	55.388	0.334	n.s.
Error	218	36139.199	165.776		
Corrected Total	239	60208.746	251.919		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.4.1.16

Cell mean values of significantly differing sources of variation found in table 4.4.1.15 - number of seeds.

(a) Genotype

G	Maris Bead
24.15	27.57

(b) Irrigation

Non-irrigated	Irrigated
17.98	33.73

(c) Density

40 plants/m^2	80 plants/m^2
29.32	22.39

(d) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	19.12	29.18
Genotype Maris Bead	16.85	38.28

(e) Genotype x density

	40 plants/m^2	80 plants/m^2
Genotype G	25.43	22.87
Genotype Maris Bead	33.22	21.92

(f) Genotype x density x plot

	Genotype G		Genotype Maris Bead	
	40 plants/m^2	80 plants/m^2	40 plants/m^2	80 plants/m^2
Plot V	22.15	23.95	38.85	20.40
Plot W	28.70	22.45	29.65	22.10
Plot X	25.45	22.20	31.15	23.25

Table 4.4.1.17

Analysis of variance for dry weight of seeds for the irrigation and density trial.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	130.612	130.612	6.202	*
Irrigation	1	1607.818	1607.818	76.348	***
Density	1	300.758	300.758	14.282	***
Plot	2	2.913	1.456	0.069	n.s.
Genotype x irrigation	1	451.850	451.850	21.456	***
Genotype x density	1	146.488	146.488	6.956	**
Genotype x plot	2	40.498	20.249	0.962	n.s.
Irrigation x density	1	37.326	37.326	1.772	n.s.
Irrigation x plot	2	55.208	27.604	1.311	n.s.
Density x plot	2	8.450	4.225	0.201	n.s.
Genotype x irrigation x density	1	62.025	62.025	2.945	n.s.
Genotype x irrigation x plot	2	8.632	4.225	0.205	n.s.
Genotype x density x plot	2	109.956	54.978	2.611	n.s.
Irrigation x density x plot	2	11.810	5.905	0.280	n.s.
Error	218	4590.902	21.059		
Corrected Total	239	7565.250	31.654		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.4.1.18

Cell mean values of significantly differing sources of variation found in table 4.4.1.17 - dry weight of seeds.

(a) Genotype

G	Maris Bead
8.32	9.80

(b) Irrigation

Non-irrigated	Irrigated
6.47	11.65

(c) Density

40 plants/m^2	80 plants/m^2
10.18	7.94

(d) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	7.10	9.54
Genotype Maris Bead	5.84	13.76

(e) Genotype x density

	40 plants/m^2	80 plants/m^2
Genotype G	8.66	7.98
Genotype Maris Bead	11.70	7.90

Some evidence of a difference between genotypes was detected for number of seeds (table 4.4.1.15) and dry weight of seeds produced (table 4.4.1.17). These differences were attributable to the greater number of seeds produced by Maris Bead (table 4.4.1.16(a)) leading to a greater dry weight of seeds than that of genotype G (table 4.4.1.18(a)). There was very strong evidence of a difference between irrigations for all of the total reproductive characters measured (tables 4.4.1.9, 4.4.1.11, 4.4.1.13, 4.4.1.15, 4.4.1.17). In each case this was due to a substantial increase in the measured character in response to added irrigation (tables 4.4.1.10(a), 4.4.1.12(a), 4.4.1.14(a), 4.4.1.16(b), 4.4.1.18(b)). Increased planting density also resulted in a highly significantly different value for each of the yield components measured (tables 4.4.1.9, 4.4.1.11, 4.4.1.13, 4.4.1.15, 4.4.1.17). This was attributed to a fall in yield component value with increased planting density (tables 4.4.1.10(b), 4.4.1.12(b), 4.4.1.14(b), 4.4.1.16(c), 4.4.1.18(c)).

There was a significant genotype x irrigation interaction for each measured yield component, the level of significance of the interaction differed between components (tables 4.4.1.9, 4.4.1.11, 4.4.1.13, 4.4.1.15, 4.4.1.17). The interaction was, in each case, due to a differential genotypic response to added irrigation. Without irrigation the values of the yield components of Maris Bead were below those of G, when irrigation was applied the increase in value of Maris Bead was greater than that of G for each component (table 4.4.1.10(c), 4.4.1.12(c), 4.4.1.14(c), 4.4.1.16(d), 4.4.1.18(d)). There was strong evidence of a genotype x density interaction for each of the total yield components measured (tables 4.4.1.9, 4.4.1.11, 4.4.1.13, 4.4.1.15, 4.4.1.17). This was because the genotypes responded differentially to increased planting density in yield component values. Genotype G showed either

no change or a slight decrease in value for each component, whilst the values for Maris Bead fell to considerably lower levels (tables 4.4.1.10(d), 4.4.1.12(d), 4.4.1.14(d), 4.4.1.16(e), 4.4.1.18(e)). Some evidence of an interaction between irrigation x density was detected for number of flowers produced (table 4.4.1.9), this was attributed to the lower number of flowers produced on irrigated plots at higher planting density than that of non-irrigated plots (table 4.4.1.10(e)).

The only significant three-way interactions detected were for genotype x density x plot for number of pods 'filled' (those containing one or more seeds) and number of seeds (tables 4.4.1.13, 4.4.1.15), in both cases plot V at planting density 40 plants per metre^2 gave a lower value for genotype G and a higher value for genotype Maris Bead than either of the other plots.

Number of reproductive nodes involved

The effects of genotype, irrigation and density on number of flowering nodes, number of nodes with pods set and number of nodes with 'filled' pods were investigated by analysis of variance. Significant differences were found in each case when irrigation was applied (tables 4.4.1.19, 4.4.1.21, 4.4.1.23), in each case examination of means revelaed an increase in number of nodes involved at each stage of yield production when irrigation was applied (tables 4.4.1.20(a), 4.4.1.22(a), 4.4.1.24(a)). Increased planting density also had a significant effect on the numbers of reproductive nodes (tables 4.4.1.19, 4.4.1.21, 4.4.1.23), this was due to a decrease in number of nodes involved in yield production with increased planting density in each case (tables 4.4.1.20(b), 4.4.1.22(b), 4.4.1.24(b)). There was very strong evidence of a genotype x irrigation interaction for number of flowering nodes (table 4.4.1.19), strong evidence of an interaction for number

Table 4.4.1.19

Analysis of variance for number of flowering nodes in the irrigation and density trial.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	8.817	8.817	1.098	n.s.
Irrigation	1	308.267	308.267	38.396	***
Density	1	264.600	264.600	32.957	***
Plot	2	42.325	21.162	2.636	n.s.
Genotype x irrigation	1	106.667	106.667	13.286	***
Genotype x density	1	24.067	24.067	2.998	n.s.
Genotype x plot	2	41.608	20.804	2.591	n.s.
Irrigation x density	1	12.150	12.150	1.513	n.s.
Irrigation x plot	2	72.758	36.379	4.531	*
Density x plot	2	16.425	8.123	1.023	n.s.
Genotype x irrigation x density	1	1.350	1.350	0.168	n.s.
Genotype x irrigation x plot	2	23.509	11.755	1.464	n.s.
Genotype x density x plot	2	44.408	22.204	2.766	n.s.
Irrigation x density x plot	2	1.425	0.712	0.089	n.s.
Error	218	1750.249	8.029		
Corrected Total	239	2718.623	11.375		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.001$

Table 4.4.1.20

Cell mean values of significantly differing sources of variation found in table 4.4.1.19 - number of flowering nodes.

(a) Irrigation

Non-irrigated	Irrigated
8.29	10.56

(b) Density

40 plants/m^2	80 plants/m^2
10.47	8.38

(c) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	9.15	10.08
Genotype Maris Bead	7.43	11.03

(d) Irrigation x plot

	Plot V	Plot W	Plot X
Non-irrigated	7.77	9.52	7.57
Irrigated	11.17	10.30	10.20

Table 4.4.1.21

Analysis of variance for number of nodes with pods set in the irrigation and density trial.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	3.504	3.504	0.713	n.s.
Irrigation	1	877.837	877.837	178.580	***
Density	1	124.704	124.704	25.369	***
Plot	2	21.700	10.850	2.207	n.s.
Genotype x irrigation	1	44.204	44.204	8.993	**
Genotype x density	1	10.004	10.004	2.035	n.s.
Genotype x plot	2	14.233	7.117	1.448	n.s.
Irrigation x density	1	10.004	10.004	2.035	n.s.
Irrigation x plot	2	24.700	12.350	2.512	n.s.
Density x plot	2	4.633	2.317	0.471	n.s.
Genotype x irrigation x density	1	5.704	5.704	0.160	n.s.
Genotype x irrigation x plot	2	7.033	3.517	0.715	n.s.
Genotype x density x plot	2	14.533	7.267	1.478	n.s.
Irrigation x density x plot	2	0.233	0.117	0.024	n.s.
Error	218	1071.610	4.916		
Corrected Total	239	2234.638	9.350		

n.s. non-significant

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.4.1.22

Cell mean values of significantly differing sources of variation found in table 4.4.1.21 - number of nodes with pods set.

(a) Irrigation

Non-irrigated	Irrigated
4.25	8.07

(b) Density

40 plants/m^2	80 plants/m^2
6.88	5.44

(c) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	4.80	7.77
Genotype Maris Bead	3.70	8.38

Table 4.4.1.23

Analysis of variance for number of nodes with pods 'filled' in the irrigation and density trial.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	10.004	10.004	2.232	n.s.
Irrigation	1	683.438	683.438	152.452	***
Density	1	95.004	95.004	21.192	***
Plot	2	22.658	11.329	2.527	n.s.
Genotype x irrigation	1	26.004	26.004	5.801	*
Genotype x density	1	22.204	22.204	4.953	*
Genotype x plot	2	5.658	2.829	0.631	n.s.
Irrigation x density	1	9.204	9.204	2.053	n.s.
Irrigation x plot	2	14.475	7.237	1.614	n.s.
Density x plot	2	7.258	3.629	0.810	n.s.
Genotype x irrigation x density	1	5.704	5.704	1.272	n.s.
Genotype x irrigation x plot	2	2.908	1.454	0.324	n.s.
Genotype x density x plot	2	18.858	9.429	2.103	n.s.
Irrigation x density x plot	2	1.308	0.654	0.146	n.s.
Error	218	977.284	4.483		
Corrected Total	239	1901.971	7.958		

n.s. non-significant

* $p \leq 0.05$

*** $p \leq 0.001$

Table 4.4.1.24

Cell mean values of significantly differing sources of variation found in table 4.4.1.23 - number of nodes with pods 'filled'.

(a) Irrigation

Non-irrigated	Irrigated
4.02	7.39

(b) Density

40 plants/m^2	80 plants/m^2
6.33	5.07

(c) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	4.55	7.27
Genotype Maris Bead	3.48	7.52

(d) Genotype x density

	40 plants/m^2	80 plants/m^2
Genotype G	6.23	5.58
Genotype Maris Bead	6.43	4.57

of nodes with pods set (table 4.4.1.21) and some evidence of an interaction for number of nodes with pods 'filled' (table 4.4.1.23). This was in each case due to the value for Maris Bead without irrigation being lower than that of G; when, when irrigation was applied, Maris Bead increased to a greater extent than G. The exact extent of the relative increases varied, thus producing the different levels of significance (tables 4.4.1.20(c), 4.4.1.22(c), 4.4.1.24(c)).

There was some evidence of an interaction of genotype x density for number of nodes with 'filled' pods (table 4.4.1.23); this was due to the greater reduction in number of nodes involved in Maris Bead at higher planting densities than in G (table 4.4.1.24(d)). There was also some evidence of an irrigation x plot interaction for number of flowering nodes (table 4.4.1.19); this was due to the high values of plot V when irrigated and plot W when not irrigated, compared with values of the other plots (table 4.4.1.20(d)).

Pattern of variation

In order to observe the overall pattern of significant values for each of the sources of variation in all the measured parameters a summary table (table 4.4.1.25) was compiled. From that table a pattern of significant variations was observed. Different genotypes had a significant effect on all the vegetative characteristices, but of the reproductive characteristics only number of seeds and weight of seeds were effected. Irrigation produced significant changes in all of the characteristics measured, as did density. Some differences between plots were detected for some of the vegetative characteristics, but none for the reproductive characteristics. There was a significant genotype x irrigation response in all characteristics measured. The genotype x density interaction was significant for all the total reproductive characteristics, but for none of the nodal characteristics. There was a significant irrigation x plot interaction for some of the vegetative characteristics. Other significant differences were found, but none of these fell into a recognisable pattern.

Table 4.4.1.25

Summary of the F probabilities of each source of variation of each plant characteristic recorded in the irrigation and density trial.

	Vegetative Characteristics				Total Reproductive Characteristics					Reproductive Nodes		
Source of Variation	Plant Height	Total Stem Length	Number of Leaves	Dry Weight of Straw	Number of Flowers	Number of Pods Set	Number of Pods 'Filled'	Number of Seeds	Dry Weight of Seeds	Number of Flowering Nodes	Number of Nodes with Pods Set	Number of Nodes with Pods 'Filled'
Genotype	0.000 ***	0.000 ***	0.015 *	0.000 ***	0.164	0.202	0.655	0.041 *	0.014 *	0.296	0.399	0.137
Irrigation	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***
Density	0.582	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***
Plot	0.002 **	0.018 *	0.564	0.339	0.605	0.962	0.772	0.915	0.933	0.074	0.112	0.082
Genotype x irrigation	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.006 **	0.001 ***	0.031 *	0.001 ***	0.000 ***	0.000 ***	0.003 **	0.017 *
Genotype x density	0.053	0.374	0.385	0.001 ***	0.002 **	0.002 **	0.006 **	0.009 **	0.009 **	0.085	0.155	0.027 *
Genotype x plot	0.571	0.381	0.030 *	0.055	0.277	0.389	0.149	0.307	0.384	0.077	0.237	0.533
Irrigation x density	0.621	0.095	0.093	0.064	0.014 *	0.076	0.161	0.230	0.184	0.220	0.155	0.153
Irrigation x plot	0.000 ***	0.006 **	0.038 *	0.161	0.068	0.329	0.593	0.428	0.272	0.012 *	0.083	0.201
Density x plot	0.865	0.170	0.375	0.380	0.071	0.343	0.315	0.796	0.818	0.361	0.625	0.446

Table 4.4.1.25 (continued)

Source of Variation	Vegetative Characteristics				Total Reproductive Characteristics					Reproductive Nodes		
	Plant Height	Total Stem Length	Number of Leaves	Dry Weight of Straw	Number of Flowers	Number of Pods Set	Number of Pods 'Filled'	Number of Seeds	Dry Weight of Seeds	Number of Flowering Nodes	Number of Nodes with Pods Set	Number of Nodes with Pods 'Filled'
Genotype x irrigation x density	0.559	0.775	0.935	0.057	0.411	0.094	0.152	0.150	0.088	0.682	0.283	0.261
Genotype x irrigation x plot	0.311	0.651	0.776	0.203	0.266	0.825	0.462	0.946	0.815	0.234	0.490	0.723
Genotype x density x plot	0.050 *	0.432	0.188	0.015 *	0.254	0.131	0.019 *	0.048 *	0.076	0.065	0.230	0.125
Irrigation x density x plot	0.752	0.546	0.835	0.852	0.125	0.617	0.577	0.715	0.756	0.915	0.977	0.864

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Regression analysis

All data and residual distributions were checked for normality and found to satisfy that criterion for analysis. Standardised (Z) data scores were used in the first analysis. That showed the best estimators of plant yield to be the standardised scores for number of seeds, dry weight of straw, number of nodes with pods filled and number of nodes with pods set in the following equation:-

Predicted weight of seeds per plant = (Z no. of seeds x 0.71449) + (Z dry weight of straw x 0.18794) + (Z no. of nodes with pods filled x 0.21713) + (Z no. of nodes with pods set x -0.13326) + (-6.80426 E-15)

The multiple regression value thus obtained was 0.9480.

The use of parameters such as dry weight of straw and number of seeds as predictors of seed yield was seen to be impractical as they could only be evaluated at harvest, when seed yield itself could be obtained. Therefore number of seeds and dry weight of straw were eliminated from the regression analysis and a different set of predictors obtained. Regression analysis showed that, of the plant parameters that were measured in the field whilst the plants were growing, the following were involved in the equation predicting seed yield:-

Z no. of pods filled

Z plant height

Z no. of leaves

The equation was

Predicted weight of seeds per plant = (Z no. of pods filled x 0.75984) + (Z plant height x 0.15956) + (Z no. of leaves x 0.09509) + (-3.75957 E-15) (Equation 1)

The multiple regression value obtained from the equation was 0.9125.

When the analysis was repeated using the raw non-standardised data the same variables were involved in the regression equation. The equation was as follows:-

Predicted weight of seeds per plant = (No. of pods filled x 6.42062) + (Plant height x 3.51748) + (No. of leaves x 3.83388) + (-32.29867)

(Equation 2)

The multiple regression value thus obtained was 0.8576, a lower value. When the plot of actual weight of seeds against predicted weight of seeds resulting from the above equation was examined it was found to be curvilinear (figure 4.4.11). The deviation from a linear relationship accounted for the lower multiple regression value and thus the reduced accuracy of predicted seed yield.

Taking natural logarithms of all the variables involved in the analysis resulted in the following regression equation:-

Predicted weight of seeds per plant = (ln no. of pods filled x 0.85309) + (ln plant height x 0.39914) + (ln no. of leaves x 0.19770) + (-2.19632)

(Equation 3)

The multiple regression value obtained was 0.9208. The relationship between the natural logarithm of the recorded seed weight per plant was linear (figure 4.4.1.2) and the correlation highly significant.

Plant profiles

Plant profiles were plotted to show the mean number of flowers (figure 4.4.1.3), mean number of pods set (figure 4.4.1.4), mean number of pods 'filled' (figure 4.4.1.5), and mean number of seeds at each node of each genotype with each of the treatments applied (figure 4.4.1.6).

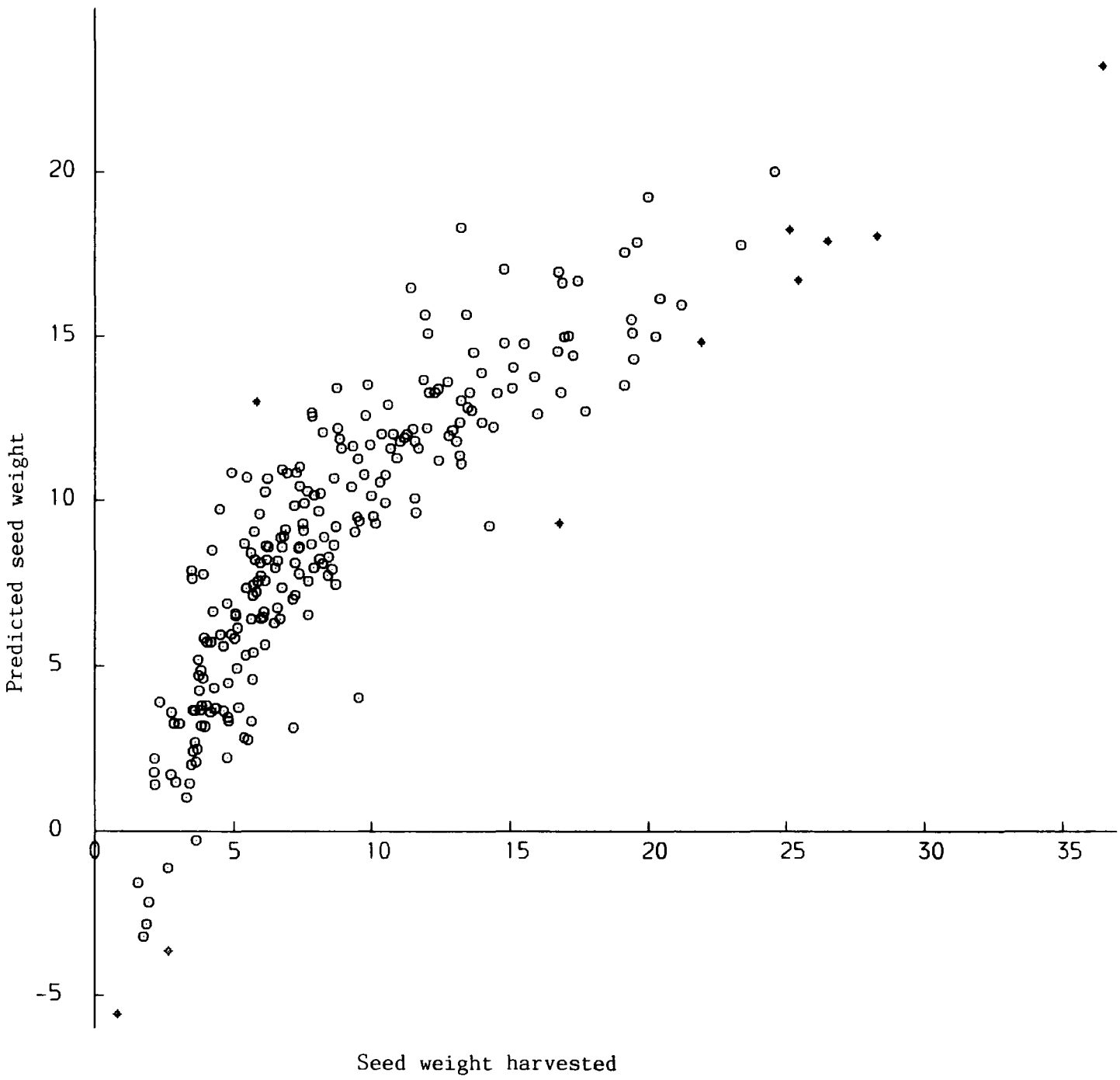


Figure 4.4.1.1 Seed weight harvested plotted against seed weight predicted by equation 2.

o points fitting the line

* outliers

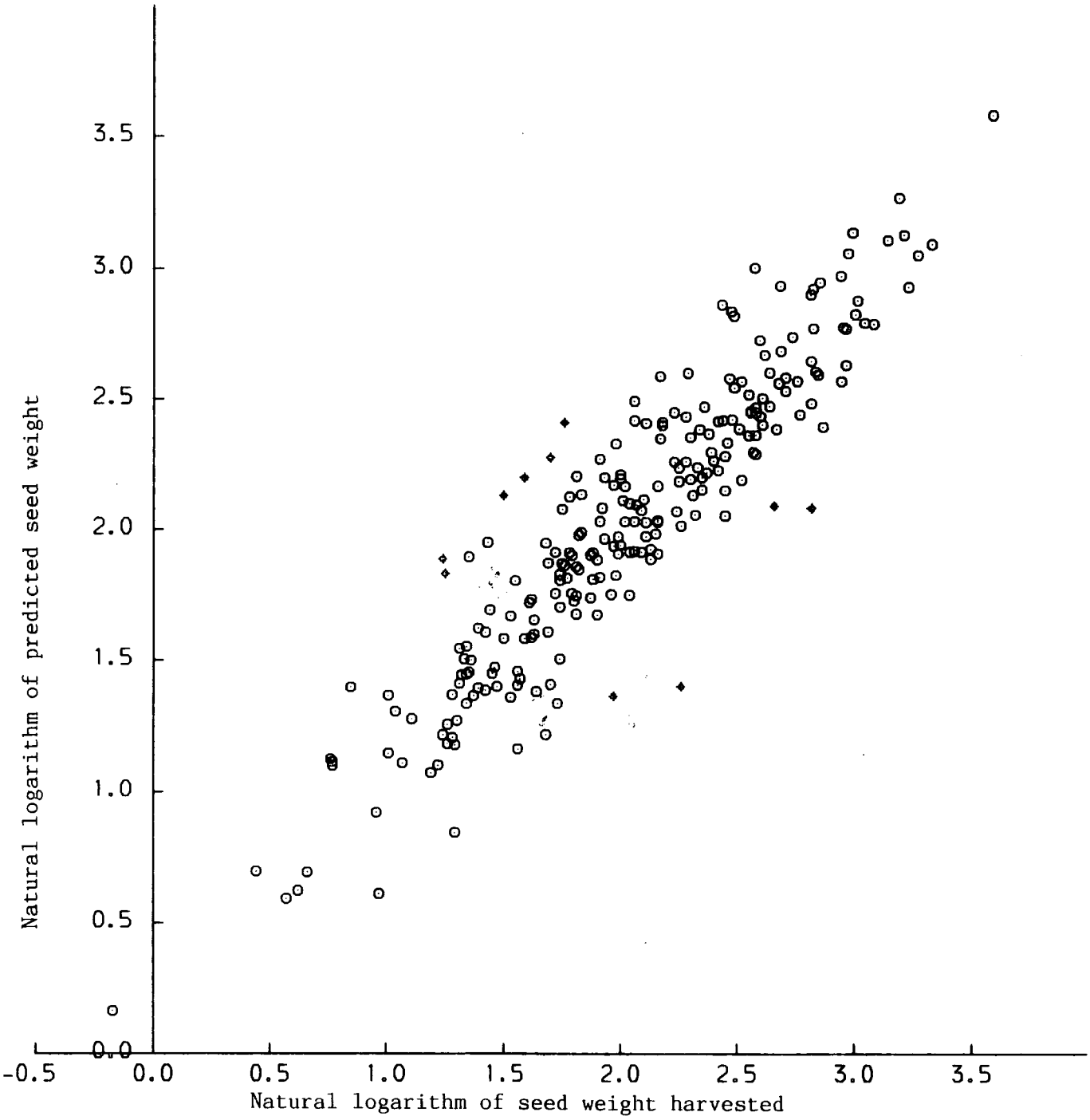


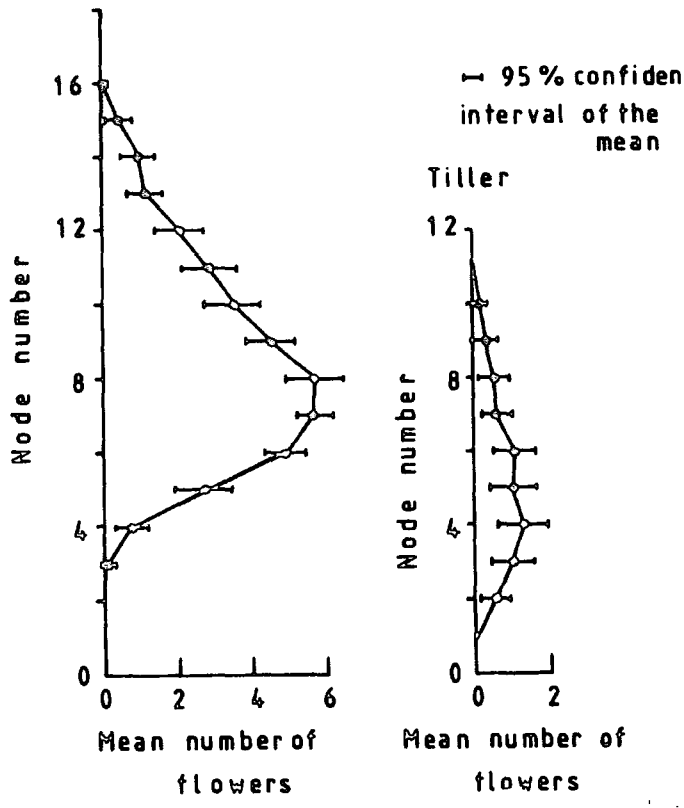
Figure 4.4.1.2 Natural logarithm of seed weight harvested plotted against natural logarithm of seed weight predicted by equation 3.

o points fitting the regression line
* outliers

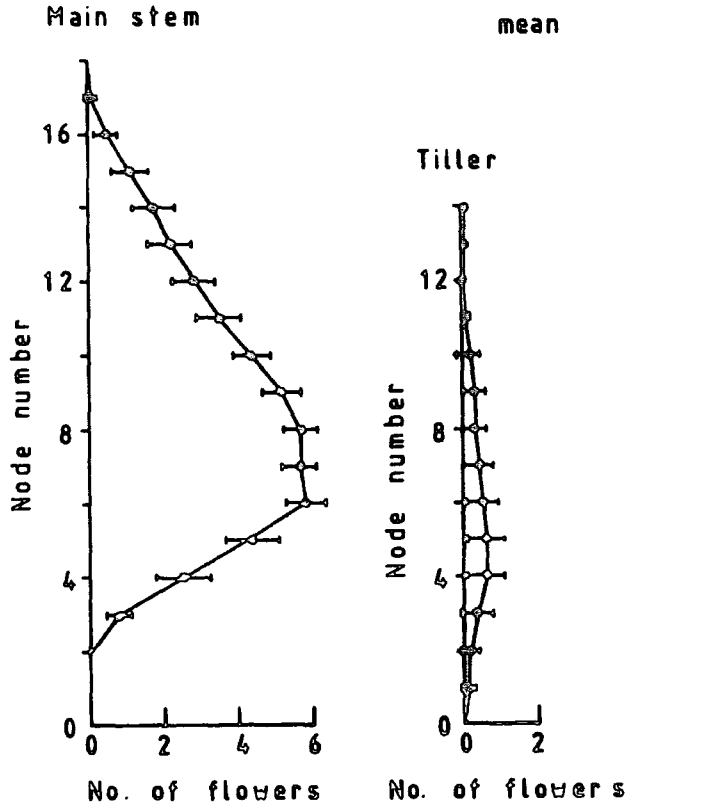
Figure 4.4.1.3 (see overleaf) Plant profiles for number of flowers present at each node of genotypes G and Maris Bead at planting densities of 40 and 80 plants/m^2 both with and without irrigation.

MB = Maris Bead

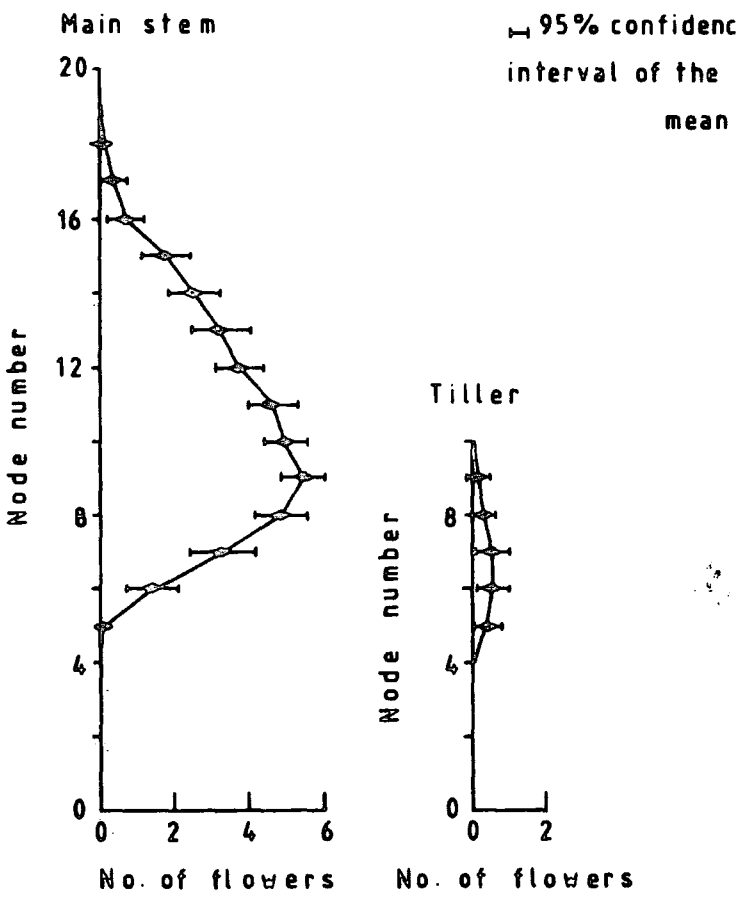
Genotype G 40 plants / m² No irrigation



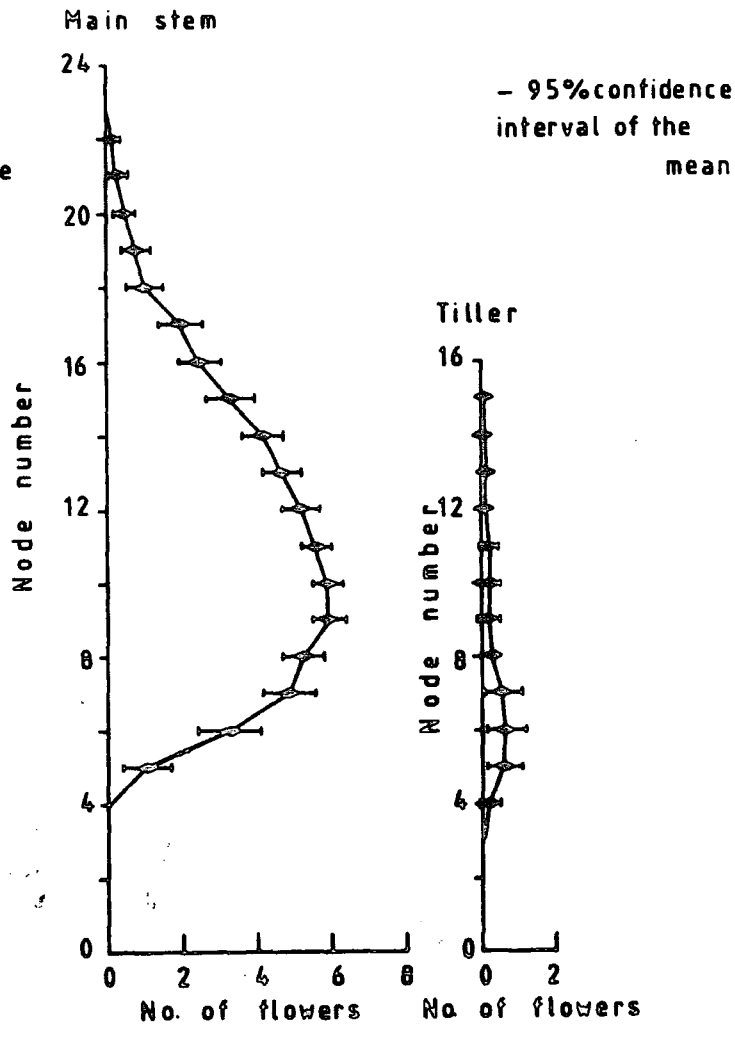
Genotype G 40 plants / m² With irrigation



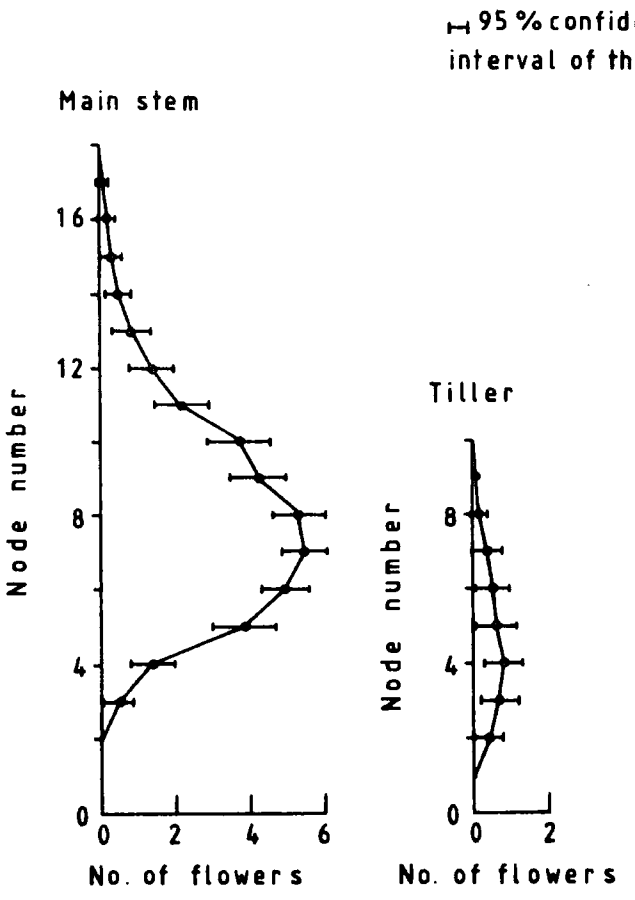
Genotype MB 40 plants / m² No irrigation



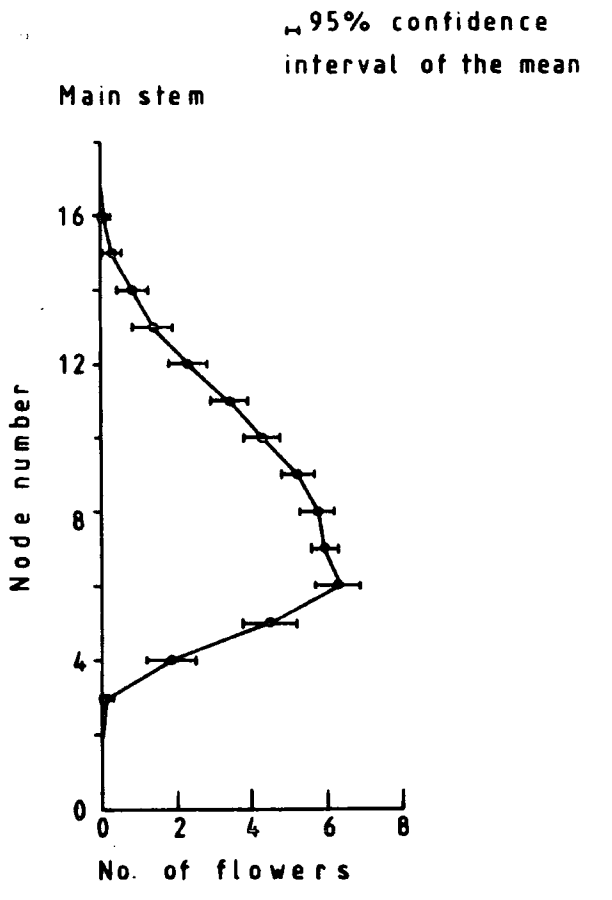
Genotype MB 40 plants / m² With irrigation



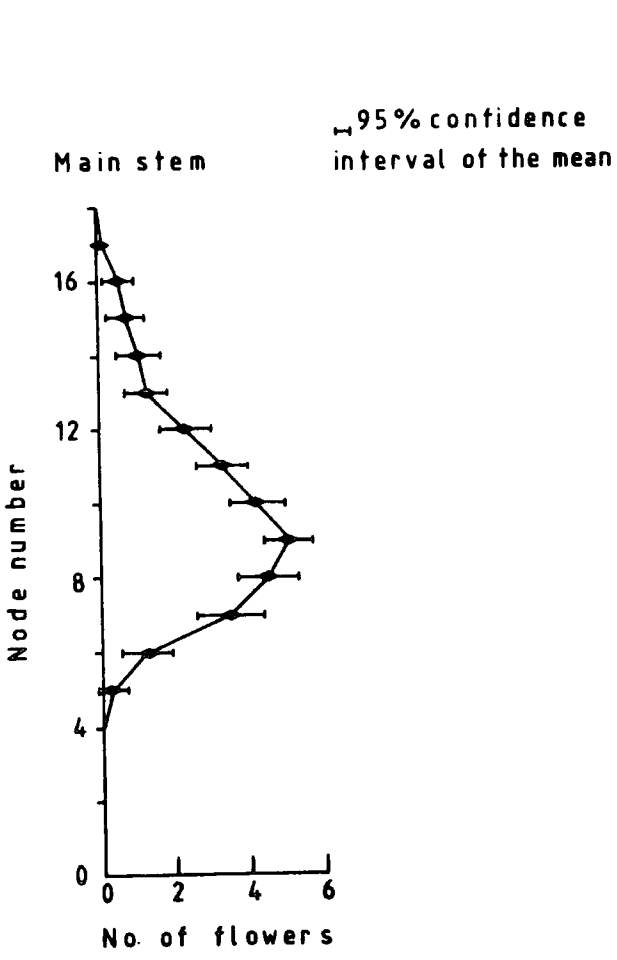
Genotype G 80 plants/m^2 No irrigation



Genotype G 80 plants/m^2 With irrigation



Genotype MB 80 plants/m^2 No irrigation



Genotype MB 80 plants/m^2 With irrigation

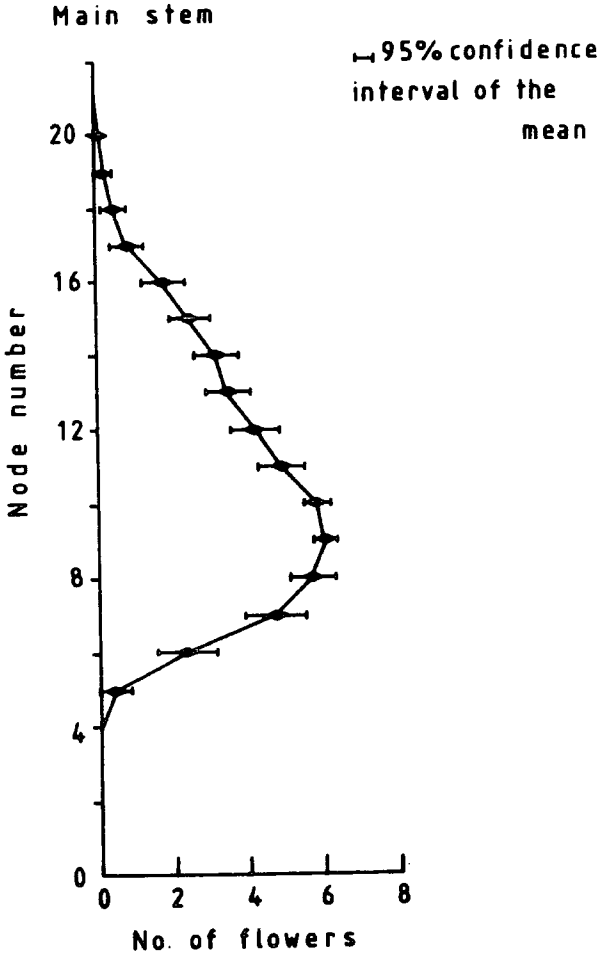
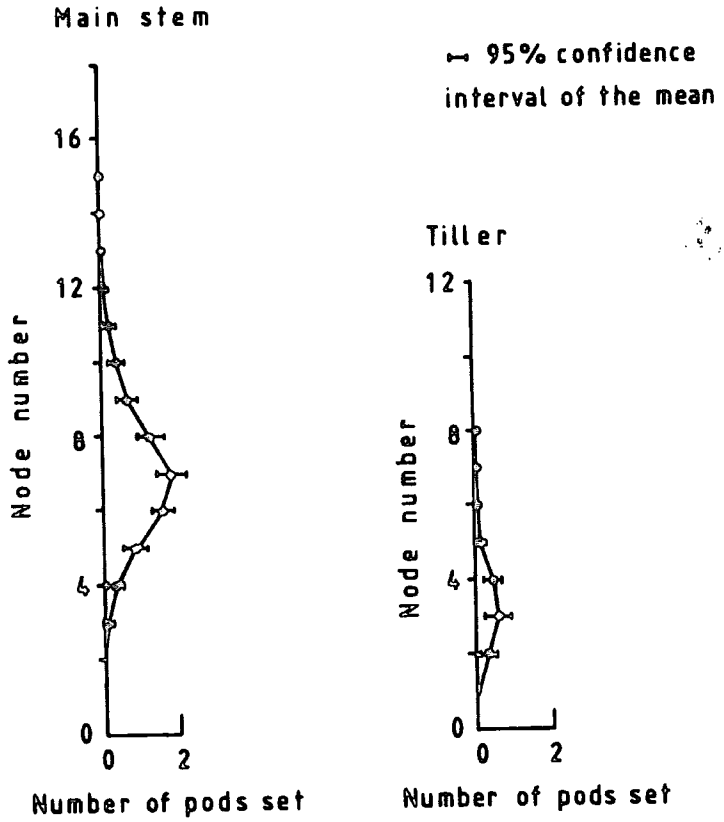


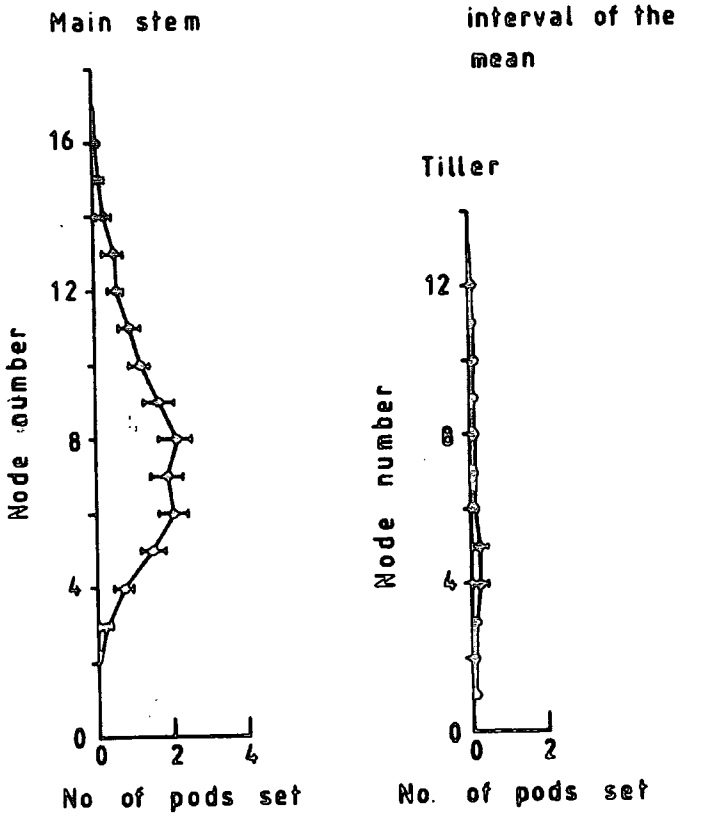
Figure 4.4.1.4 (see overleaf) Plant profiles for number of pods set at each node of genotypes G and Maris Bead at planting densities of 40 and 80 plants/m^2 both with and without irrigation.

MB = Maris Bead

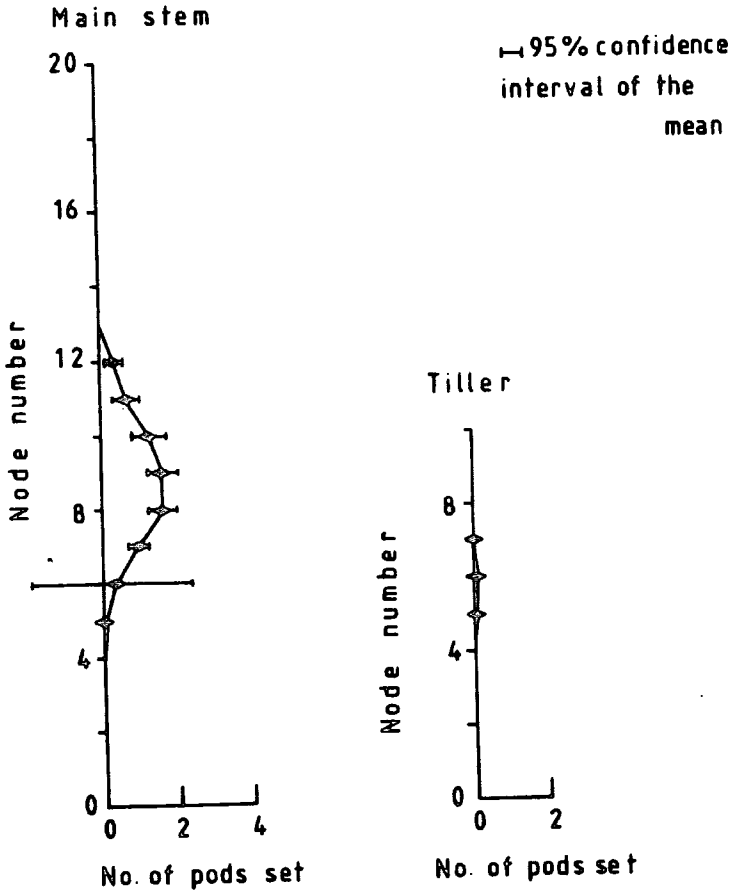
Genotype G 40 plants /m² No irrigation



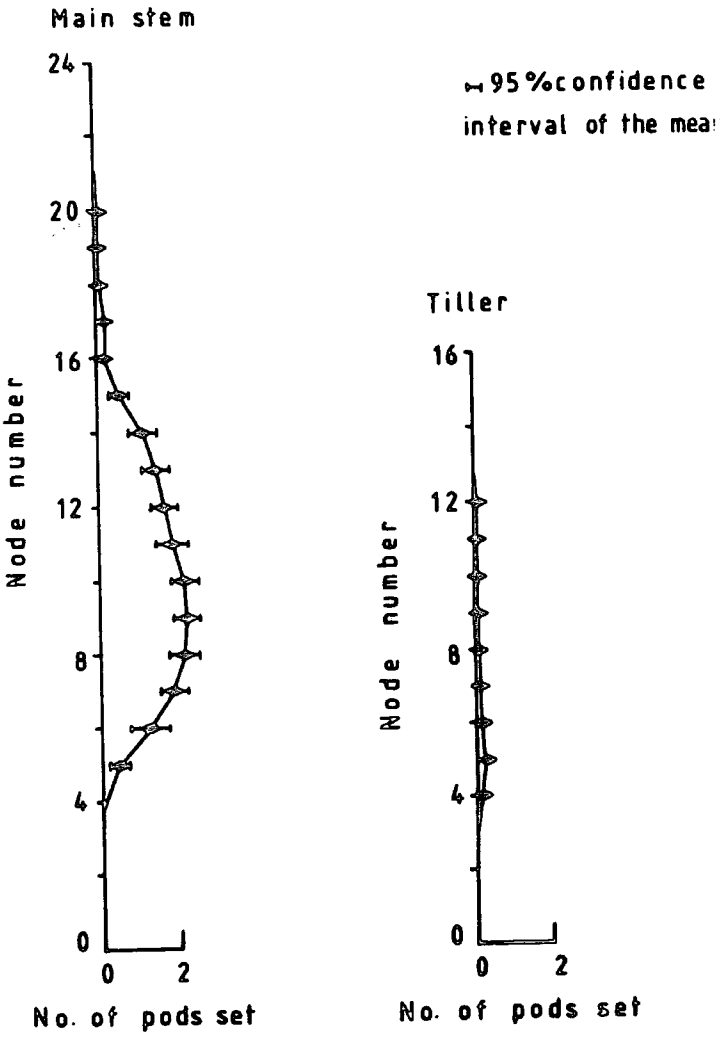
Genotype G 40 plants /m² With irrigation



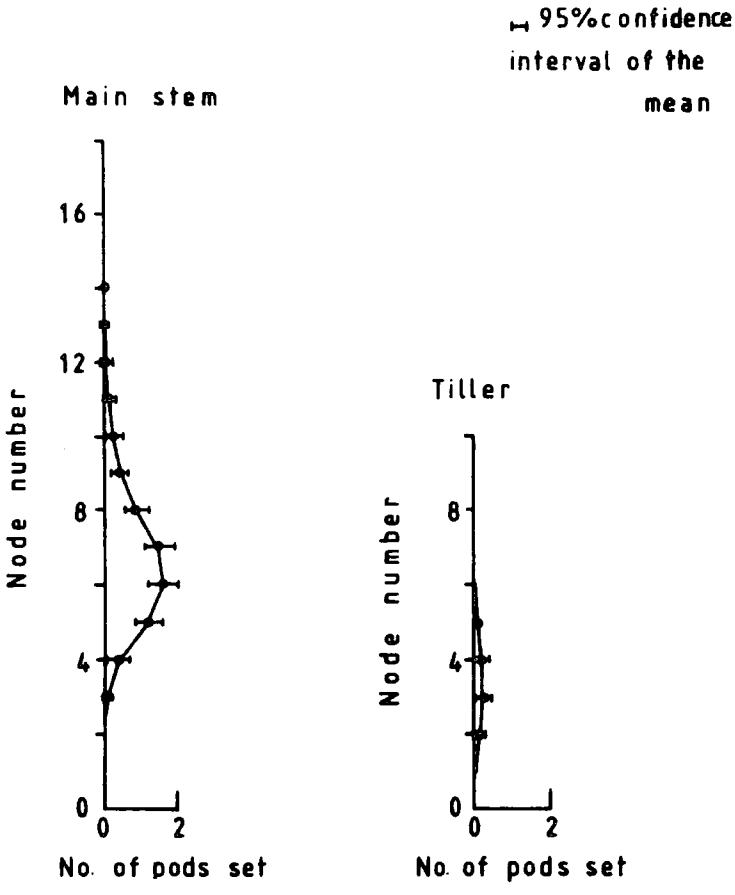
Genotype MB 40 plants/m² No irrigation



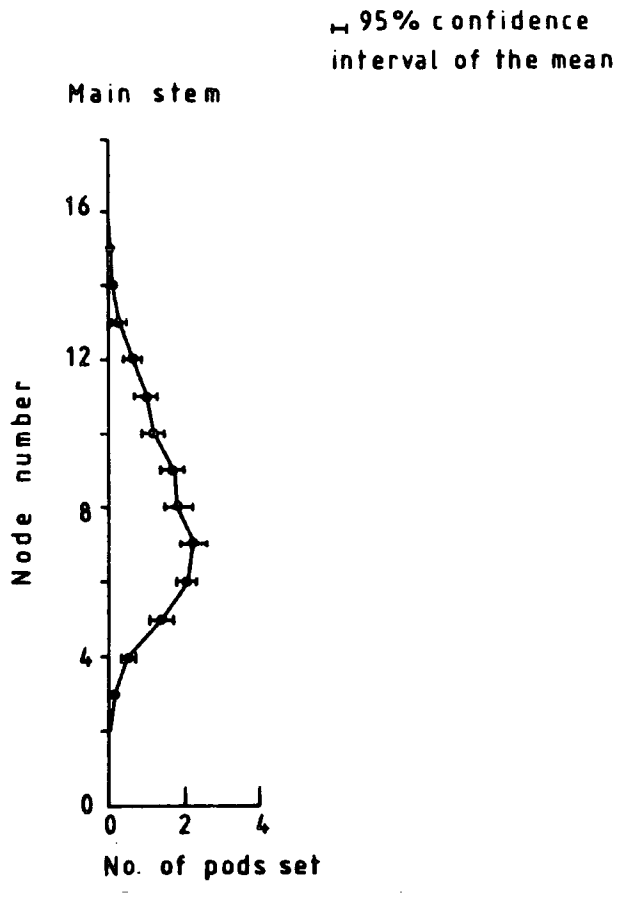
Genotype MB 40 plants /m With irrigation



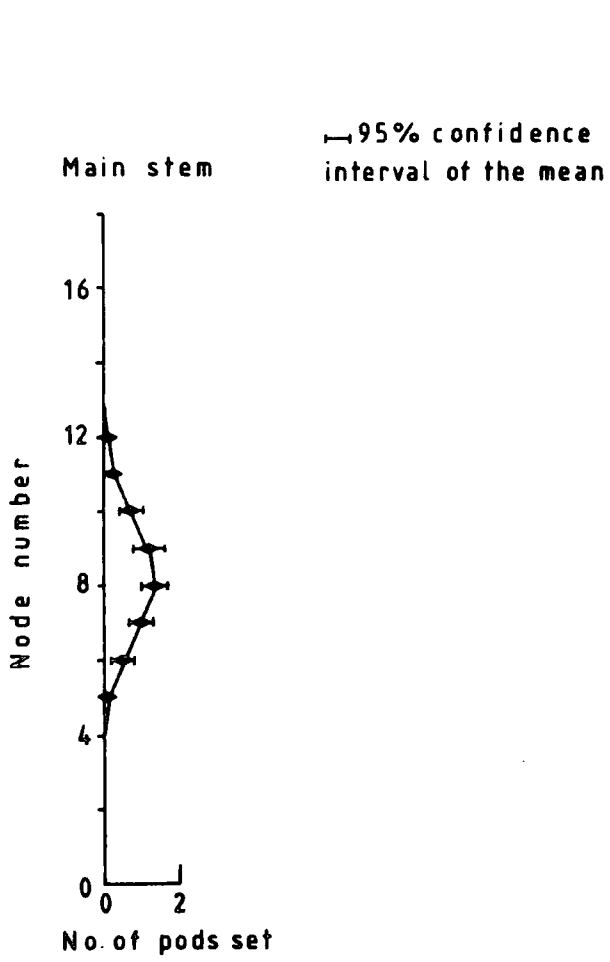
Genotype G 80 plants/m^2 No irrigation



Genotype G 80 plants/m^2 With irrigation



Genotype MB 80 plants/m^2 No irrigation



Genotype MB 80 plants/m^2 With irrigation

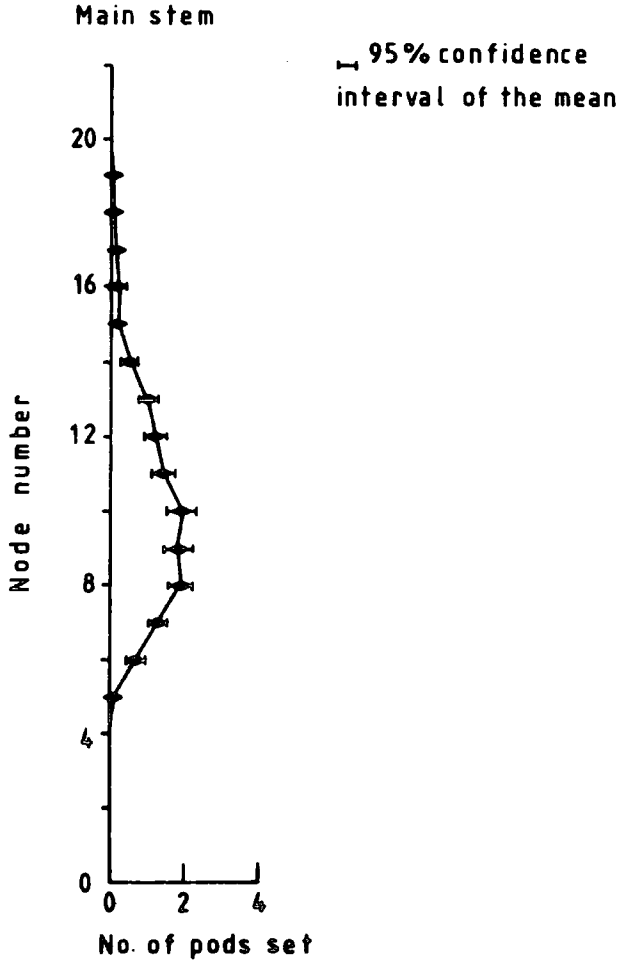
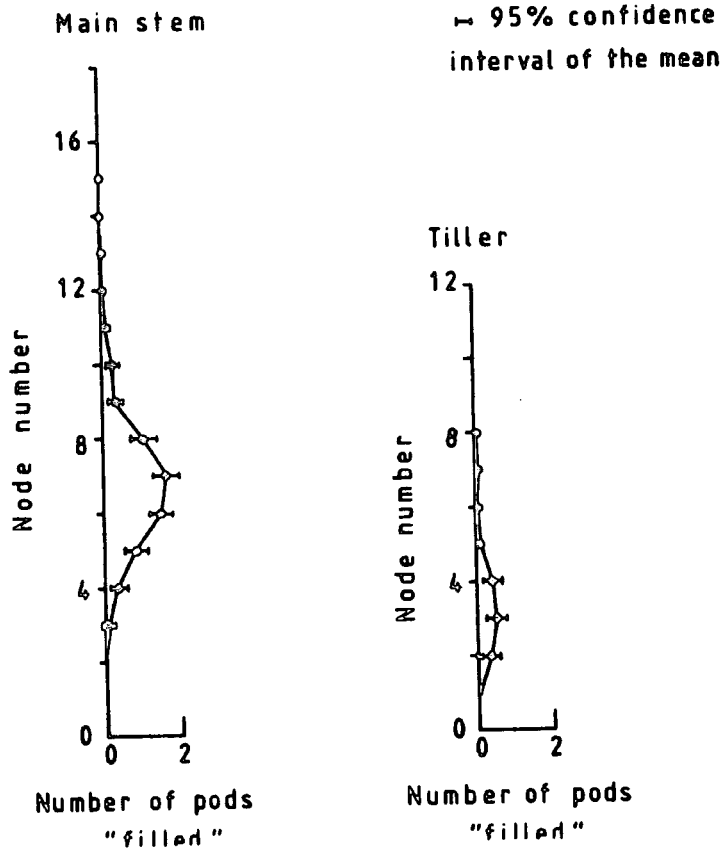


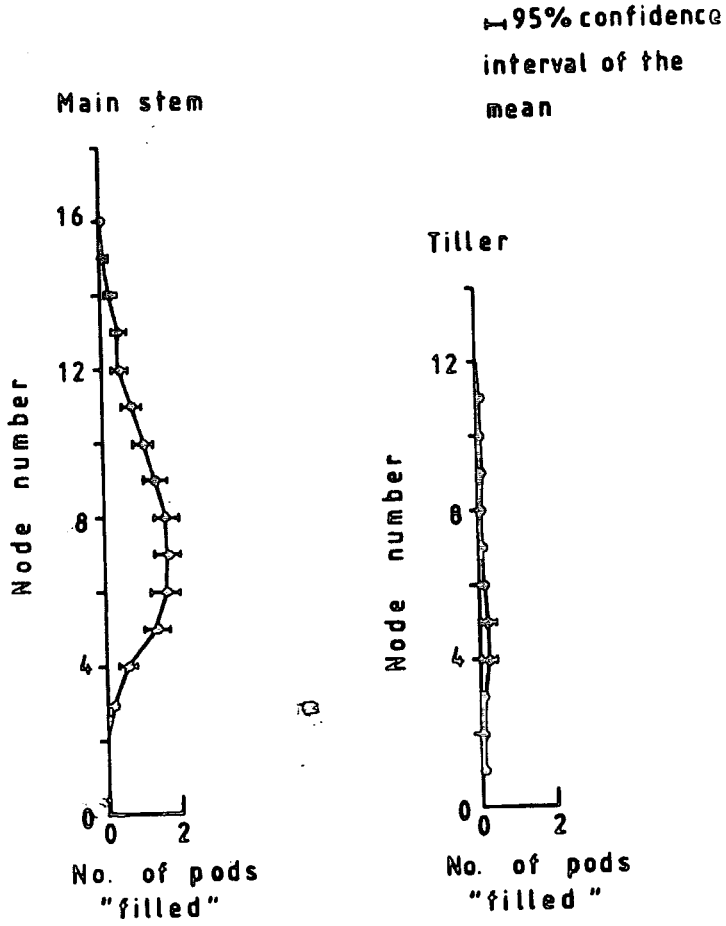
Figure 4.4.1.5 (see overleaf) Plant profiles for number of pods 'filled' at each node of genotypes G and Maris Bead at planting densities of 40 and 80 plants/ m^2 both with and without irrigation.

MB = Maris Bead

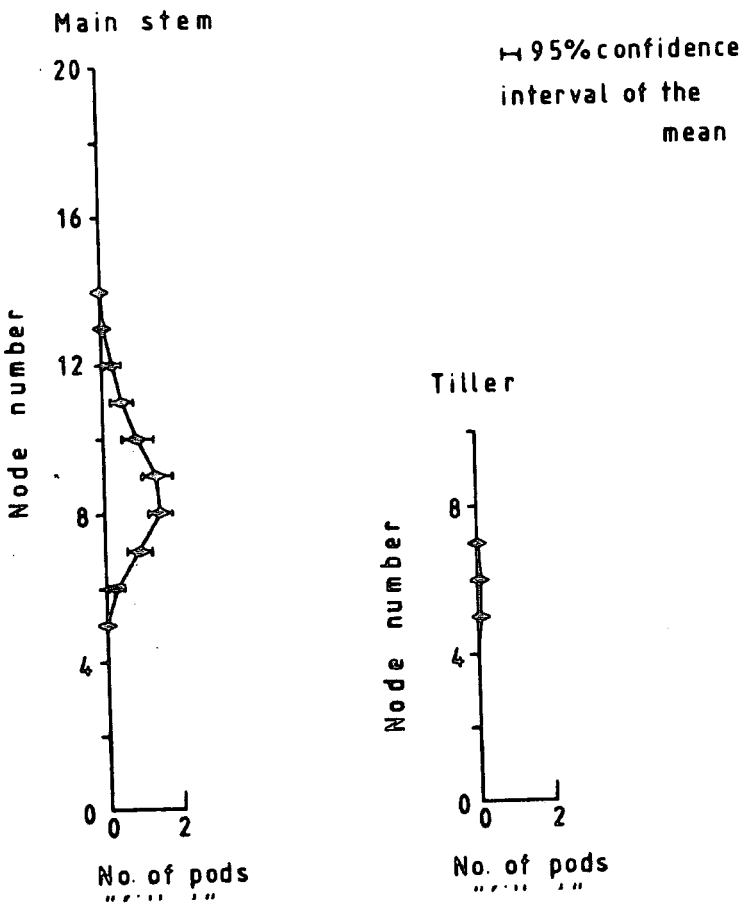
Genotype G 40 plants/m² No irrigation



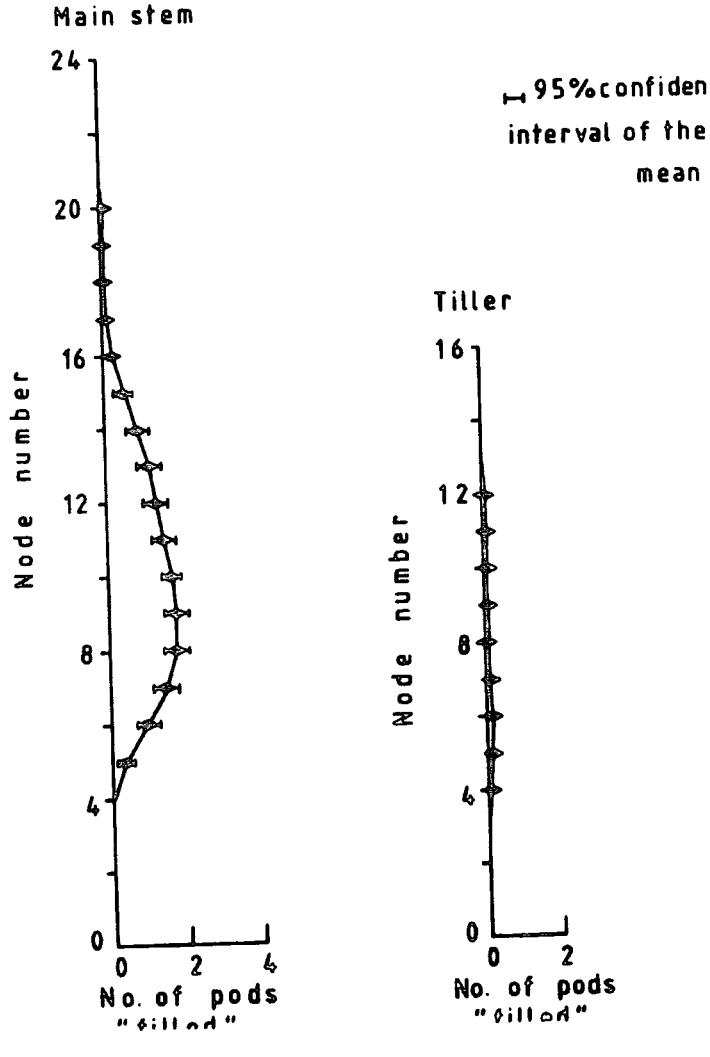
Genotype G 40 plants/m² With irrigation



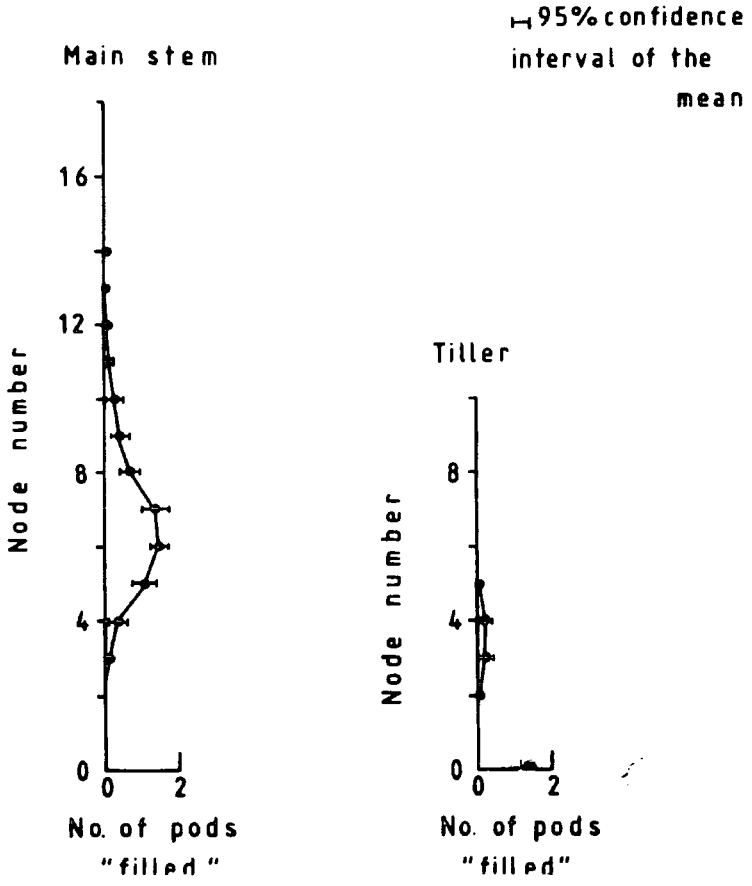
Genotype MB 40 plants/m² No irrigation



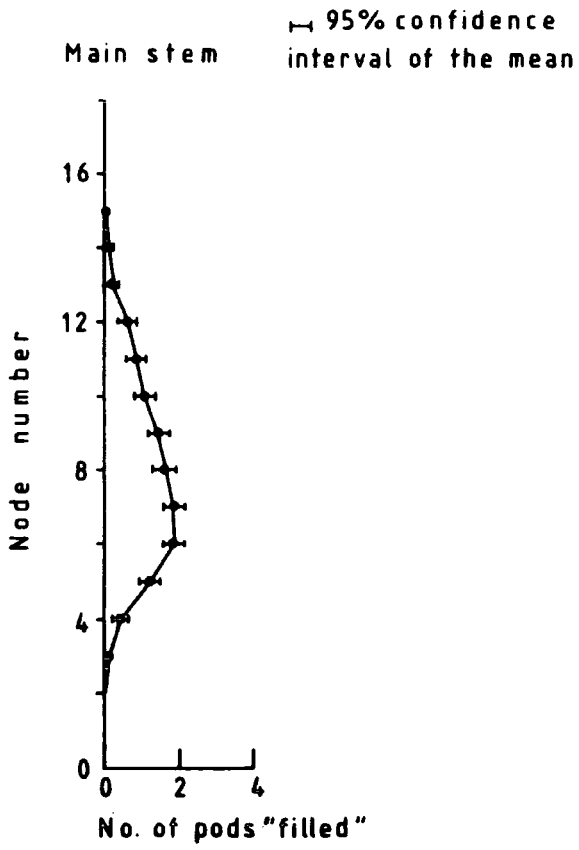
Genotype MB 40 plants/m² With irrigation



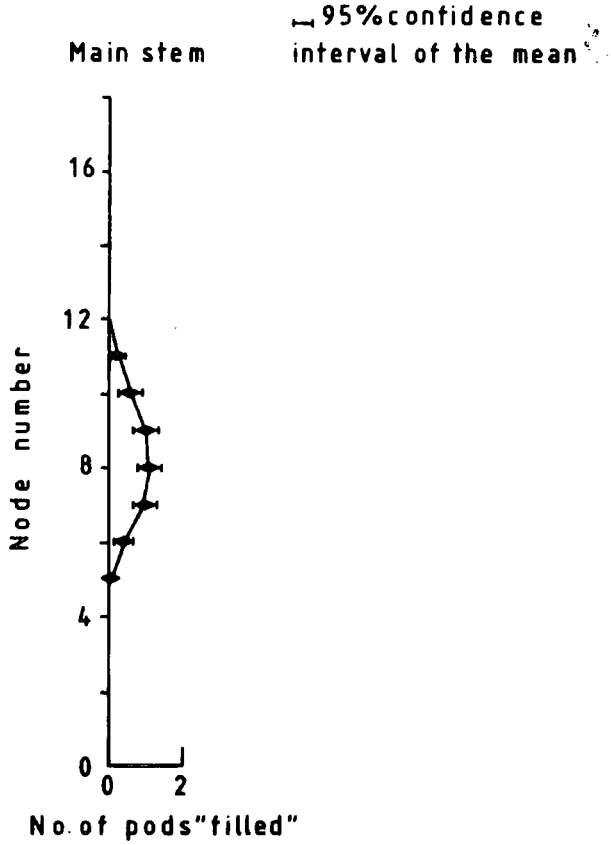
Genotype G 80 plants/m² No irrigation



Genotype G 80 plants/m² With irrigation



Genotype MB 80 plants/m² No irrigation



Genotype MB 80 plants/m² With irrigation

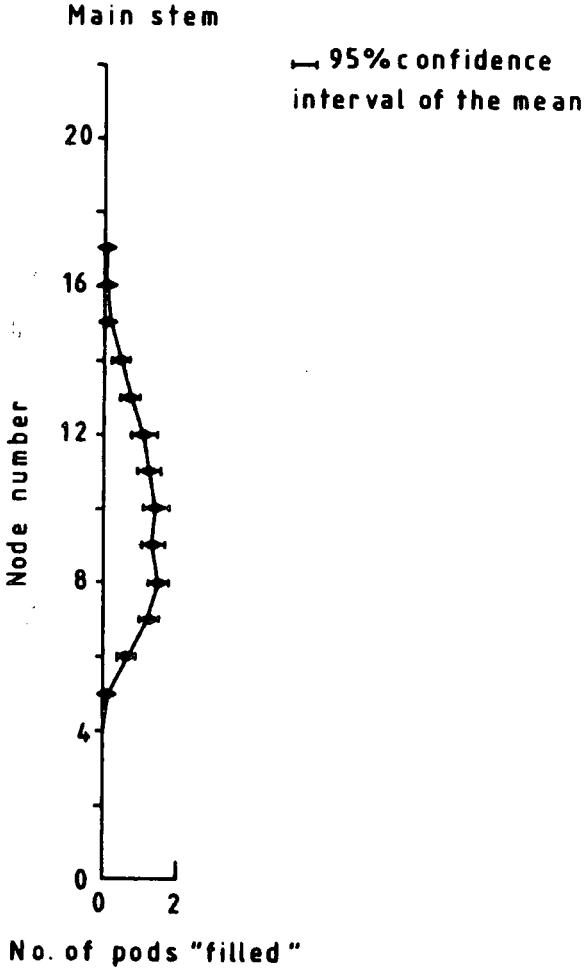
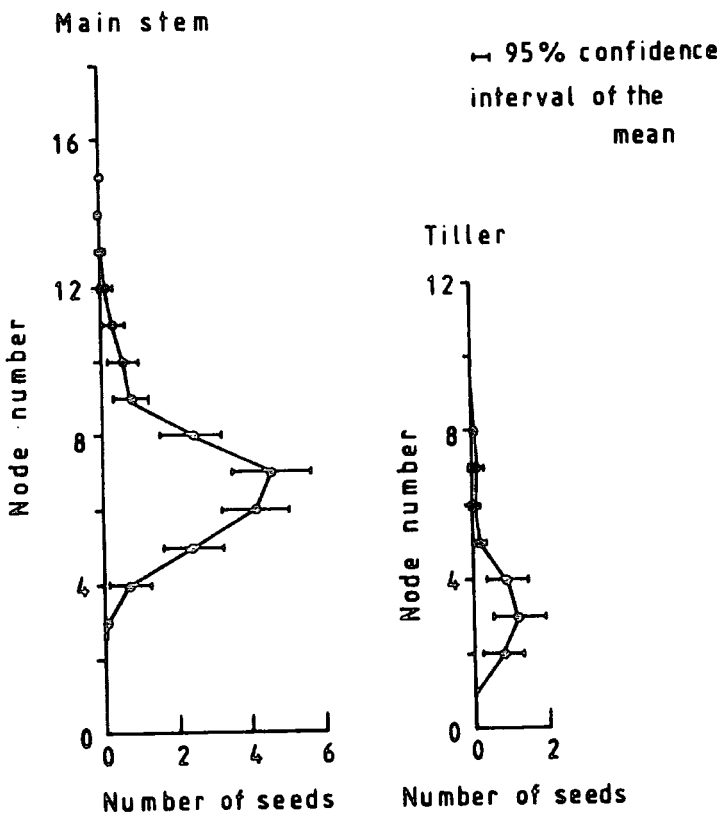


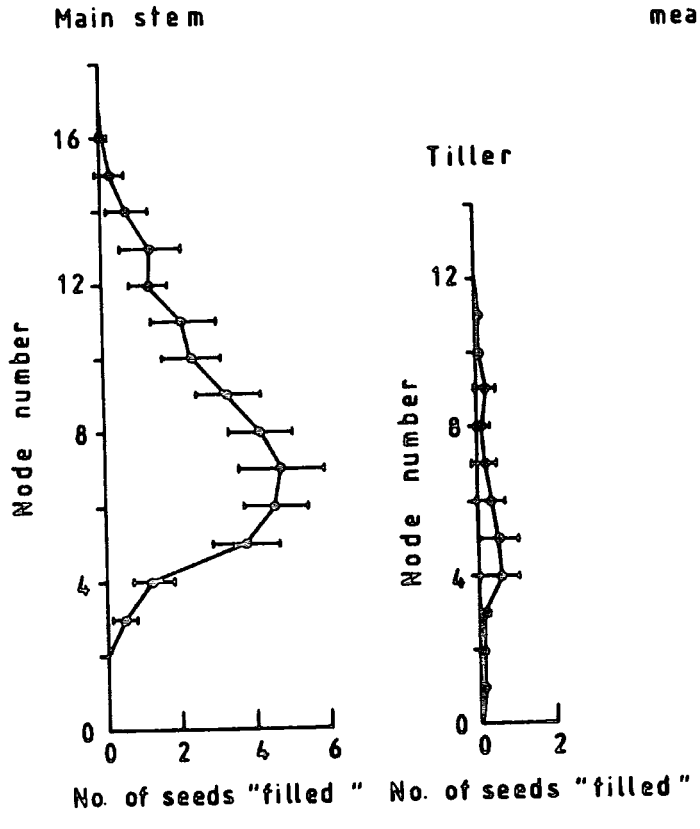
Figure 4.4.1.6 (see overleaf) Plant profiles for number of seeds at each node of genotypes G and Maris Bead at planting densities of 40 and 80 plants/m^2 both with and without irrigation.

MB = Maris Bead

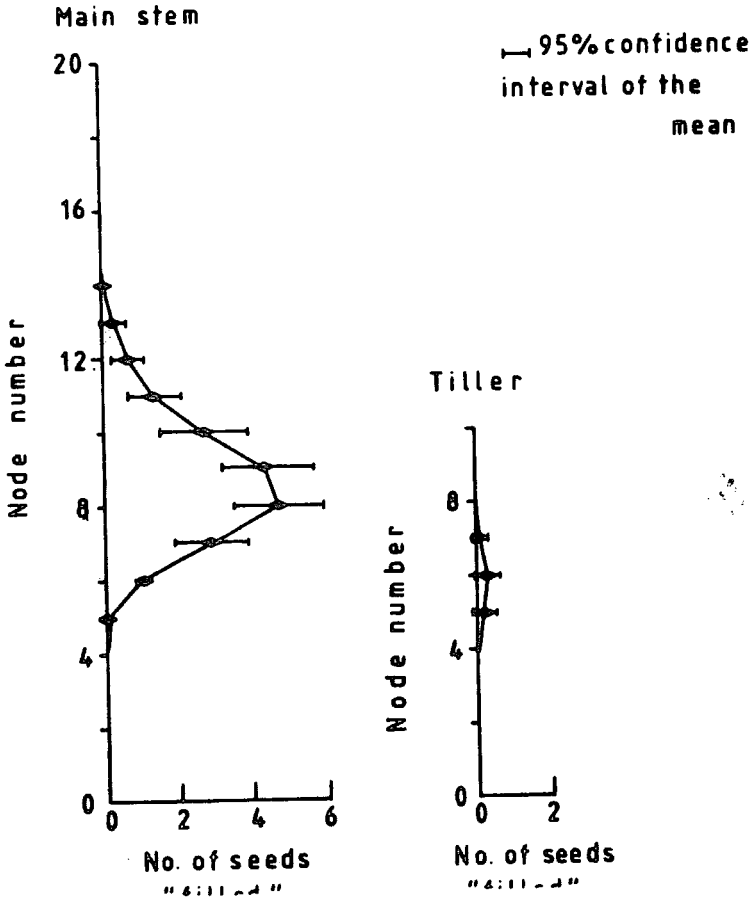
Genotype G 40 plants/m² No irrigation



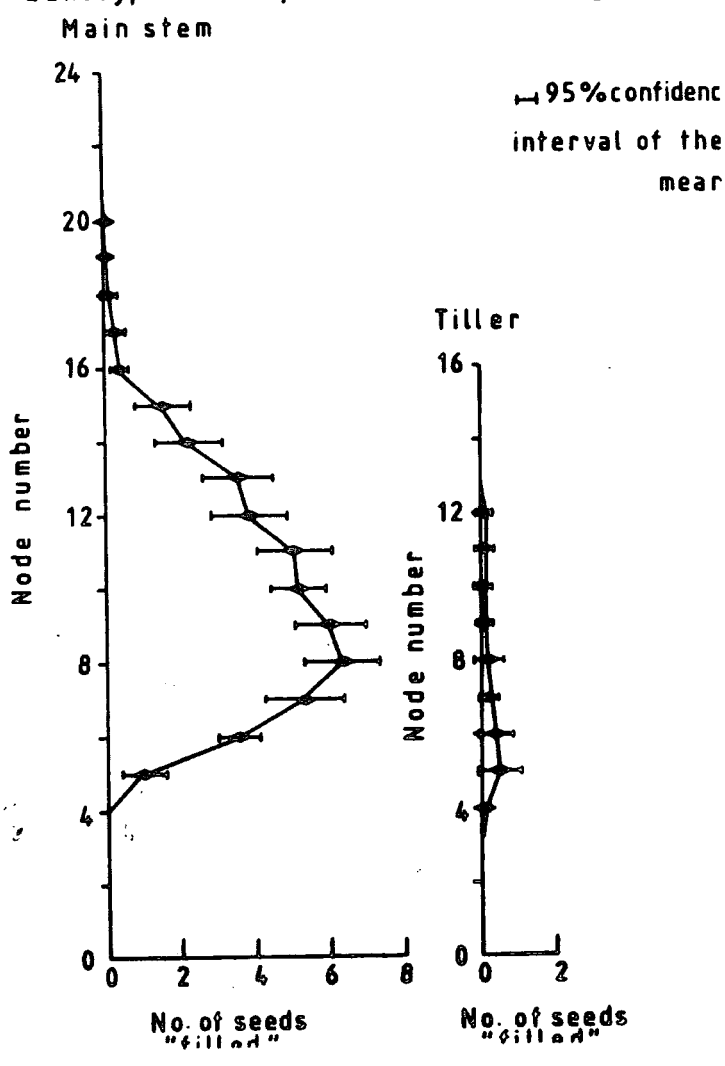
Genotype G 40 plants/m² With irrigation



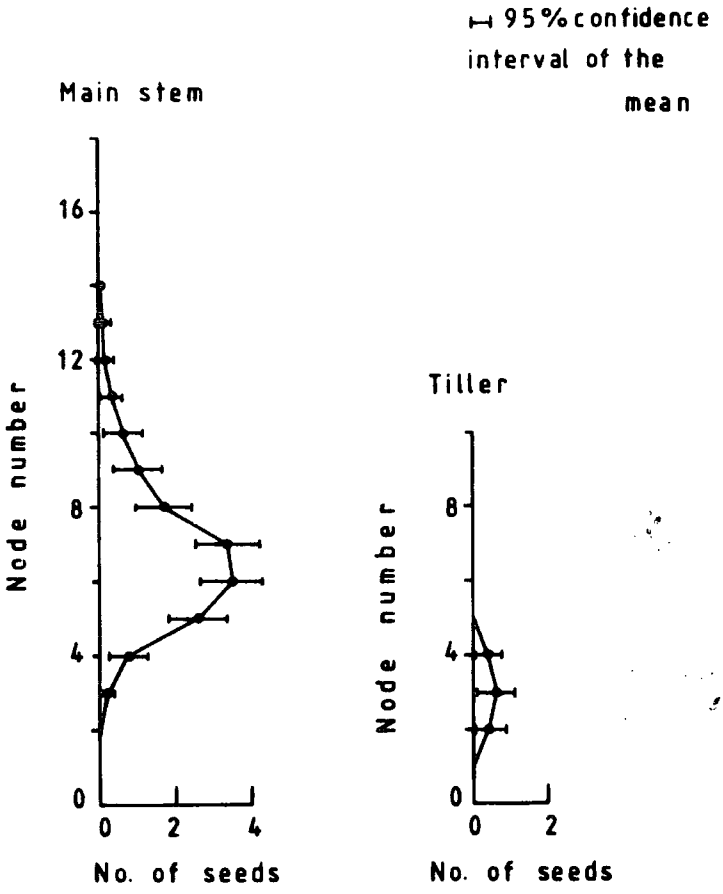
Genotype MB 40 plants/m² No irrigation



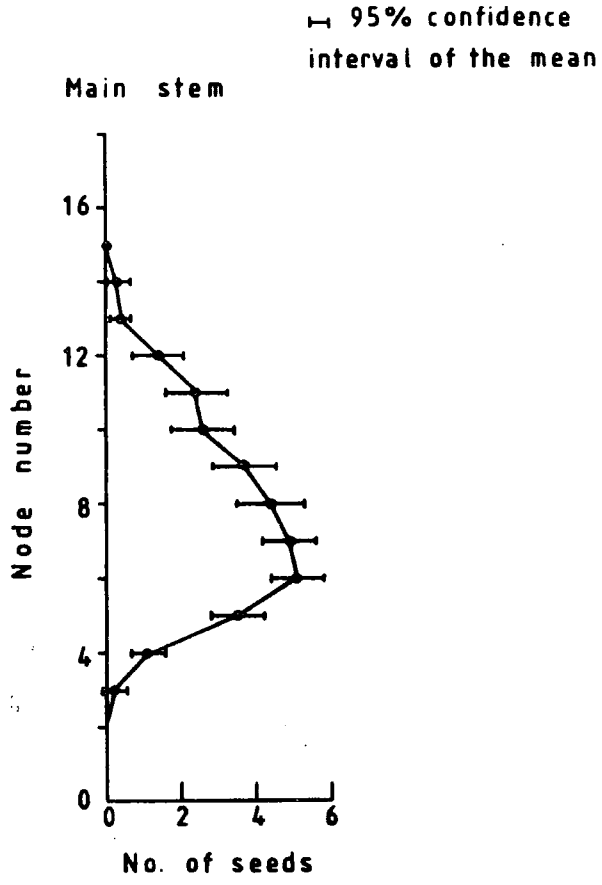
Genotype MB 40 plants/m² With irrigation



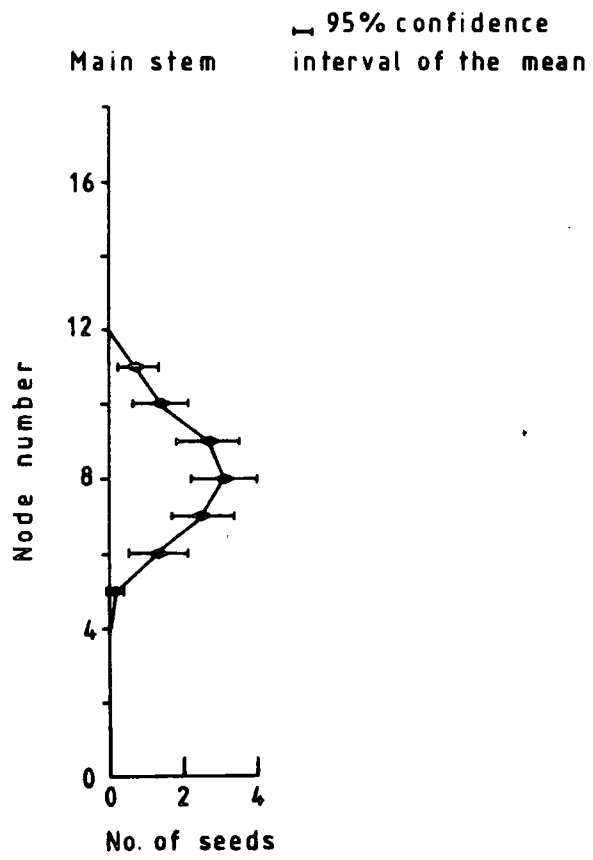
Genotype G 80 plants/m² No irrigation



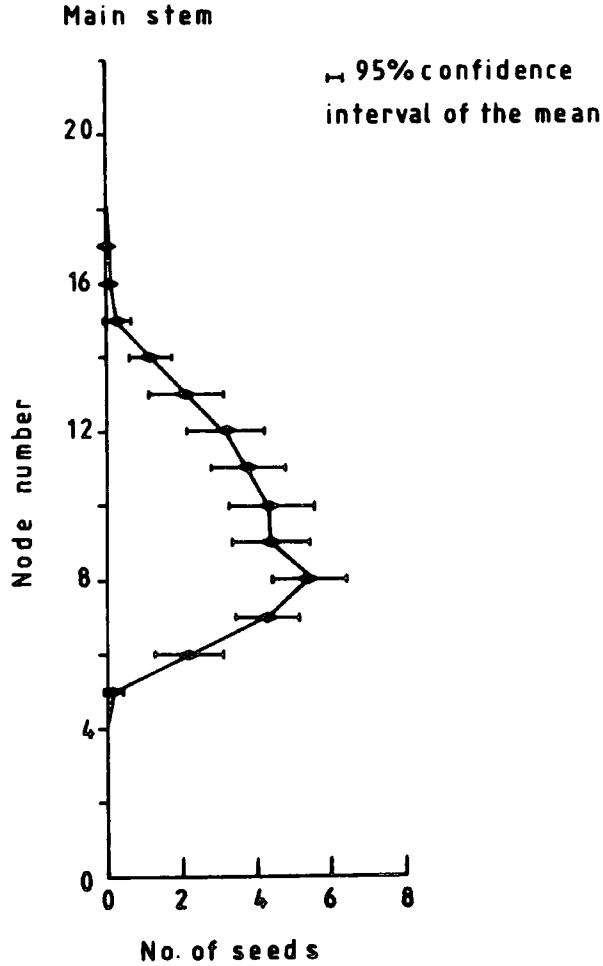
Genotype G 80 plants/m² With irrigation



Genotype MB 80 plants/m² No irrigation



Genotype MB 80 plants/m² With irrigation



4.4.2 Plot yield analysis

Each plot was harvested as indicated in figure 2.3, the resultant yield corrected to dryness and the yields analysed. Mean yields of each treatment were plotted (figure 4.4.2.1). The crossing over of the plotted lines gave some indication of a genotype x environment interaction. Analysis of variance (table 4.4.2.1) showed that, although the different genotypes gave non-significantly differing yields, the different planting densities and irrigations applied gave highly significantly differing yields. High planting density and high irrigation each gave large yield increases (table 4.4.2.2(a)(b)). There was some evidence of a genotype x irrigation interaction, this was due to the greater increase in yield of Maris Bead, when irrigated, compared with that of G (table 4.4.2.2(c)). There was also some evidence of an irrigation x density interaction, this was attributable to the greater yield response to irrigation at high planting density than at low planting density (table 4.4.2.2(d)).

4.5 Waterstress trial

4.5.1 Whole plant analysis

Analysis of variance showed many significant differences between genotypes, treatments and the various interactions in both vegetative and reproductive parameters measured. Analysis of plant height (table 4.5.1) showed that, except for replicates as a main effect, all other sources of variation gave significant F ratios. Genotype Maris Bead was taller than G (table 4.5.2(a)). Waterstress at flowering/pod set and at pod fill produced taller plants than in the control (table 4.5.2(b)). The genotype x treatment interaction (table 4.5.2(c)) showed that there was an increase in height in genotype G when waterstress was applied at flowering/pod set, whereas in Maris Bead waterstress at pod fill brought about an increase in plant height. The significant genotype x replicate interaction (table 4.5.2(d)) was due to the low value of G in replicate 1 and the high value of Maris Bead in replicate 4. The treatment x replicate interaction (table 4.5.2(e)) was due to the considerable

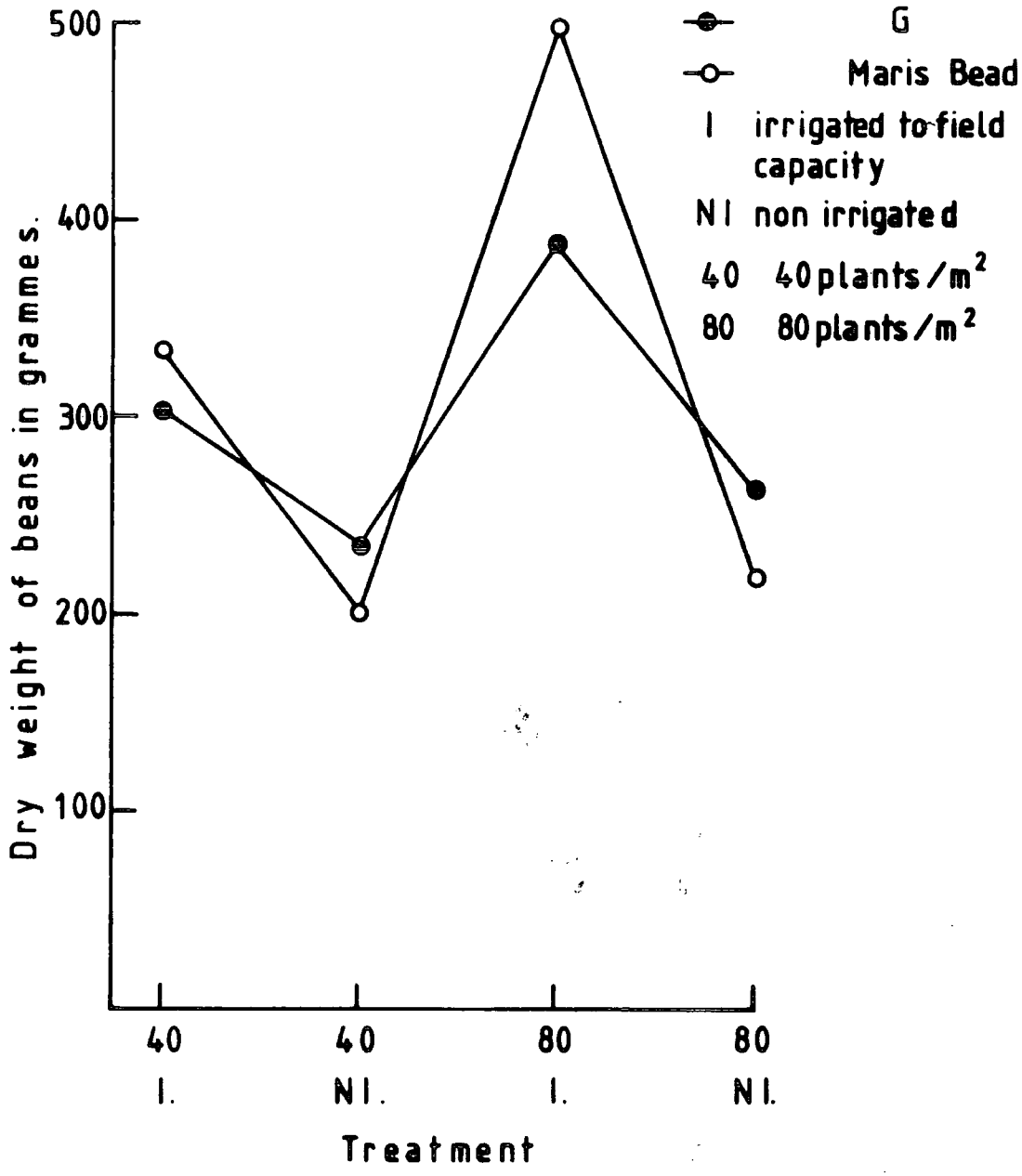


Figure 4.4.2.1 Mean seed yield of each genotype at each irrigation level and planting density tested.

Table 4.4.2.1

Analysis of variance of seed yield per plot corrected to dry weight.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	3599.761	3599.761	1.203	n.s.
Density	1	38295.281	38295.281	12.794	***
Irrigation	1	192076.020	192076.020	64.172	***
Genotype x density	1	3304.845	3304.845	1.104	n.s.
Genotype x irrigation	1	21166.531	21166.531	7.072	*
Density x irrigation	1	21725.701	21725.701	7.259	*
Residual	25	74828.055	2993.122		
Corrected Total	31	354996.195	11451.490		

n.s. non-significant

* $p \leq 0.05$

*** $p \leq 0.001$

Table 4.4.2.2

Cell mean values of significantly differing sources of variation found by analysis of variance for yield (table 4.4.2.1).

(a) Density

40 plants/m^2	80 plants/m^2
269.69	338.88

(b) Irrigation

Non-irrigated	Irrigated
226.81	381.76

(c) Genotype x irrigation

	Non-irrigated	Irrigated
Genotype G	241.92	345.44
Genotype Maris Bead	211.70	418.09

(d) Density x irrigation

	Non-irrigated	Irrigated
40 plants/m^2	218.27	321.11
80 plants/m^2	235.35	442.41

Table 4.5.1

Waterstress trial - analysis of variance of maximum plant height.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	76734.031	76734.031	524.472	***
Treatment	3	1761.906	587.302	4.014	**
Replicate	3	853.594	284.531	1.945	n.s.
Genotype x treatment	3	3277.781	1092.594	7.468	***
Genotype x replicate	3	1689.844	563.281	3.850	*
Treatment x replicate	9	2849.219	316.580	2.164	*
Genotype x treatment x replicate	9	5656.594	628.510	4.296	***
Residual	96	14045.500	146.307		
Corrected Total	127	106868.469	841.484		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.5.2

Cell mean values of significantly differing sources of variation found in analysis of variance of maximum plant height.

(a) Genotype

G	Maris Bead
100.91	149.88

(b) Treatment

Waterstress pre-flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
121.28	126.59	130.88	122.81

(c) Genotype x treatment

	Waterstress pre-flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
Genotype G	93.81	110.50	101.63	97.69
Genotype Maris Bead	148.75	142.69	160.13	147.94

(d) Genotype x replicate

	1	2	3	4
Genotype G	92.50	103.56	107.75	99.81
Genotype Maris Bead	149.56	148.25	147.06	154.63

(e) Treatment x replicate

	1	2	3	4
Waterstress pre flowering	111.50	128.25	120.75	124.63
Waterstress at flowering/ pod set	120.63	129.75	126.13	129.88
Waterstress at pod fill	134.63	129.13	127.63	132.13
Control - no waterstress	117.38	116.50	135.13	122.25

Table 4.5.2 continued

(f) Genotype x treatment x replicate

	Genotype G				Genotype Maris Bead			
	1	2	3	4	1	2	3	4
Waterstress pre flowering	80.50	105.50	93.25	96.00	142.50	151.00	148.25	153.25
Waterstress at flowering/ pod set	84.75	125.50	117.00	114.75	156.50	134.00	135.25	145.00
Waterstress at pod fill	113.75	91.00	103.25	98.50	155.50	167.25	152.00	165.75
Control - no waterstress	91.00	92.25	117.50	90.00	143.75	140.75	152.75	154.50

variation between replicates in each of the treatments. The genotype x treatment x replicate interaction (table 4.5.2(f)) could similarly be attributed to wide variations between replicates, that variation following no particular pattern.

Analysis of variance of number of stems gave significant F ratios for genotype and genotype x treatment x replications only (table 4.5.3). Mean values for each of the genotypes (table 4.5.4(a)) showed that G had a greater mean number of branches than did Maris Bead. The three-way interaction (table 4.5.4(b)) was attributable to substantial random variations between replicates for mean number of stems.

When total stem length was analysed (table 4.5.5) many sources of variation were found to have significant F ratios. Examination of means showed that Maris Bead had a greater total stem length than did G (table 4.5.6(a)). The significant difference between treatments was attributed to the low value of plants that were stressed in the pre-flowering stage and the high value of plants stressed at pod fill (table 4.5.6(b)). The genotype X treatment interaction was due to differential genotypic responses to waterstress at the developmental stages tested (table 4.5.6(c)). In genotype G waterstress pre-flowering produced a smaller total stem length than the control, waterstress at flowering/pod set yielded a greater total stem length than the control. In Maris Bead waterstress pre-flowering and at flowering/pod set produced shorter total stem length than the control, but stress at pod fill yielded plants of greater total stem length than the control. The treatment x replicate interaction (table 4.5.6(d)) and genotype x treatment x replicate interaction (table 4.5.6(e)) were both due to wide random variation between replicates.

Analysis of variance of total number of leaves showed no highly significant differences, but some significant differences of lower order (table 4.5.7). The difference

Table 4.5.3

Waterstress trial - analysis of variance for number of stems per plant.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	15.820	15.820	11.796	***
Treatment	3	1.336	0.445	0.332	n.s.
Replicate	3	1.336	0.445	0.332	n.s.
Genotype x treatment	3	8.211	2.737	2.041	n.s.
Genotype x replicate	3	3.461	1.154	0.860	n.s.
Treatment x replicate	9	19.883	2.209	1.647	n.s.
Genotype x treatment x replicate	9	26.633	2.959	2.206	*
Residual	96	128.750	1.341		
Corrected Total	127	205.430	1.681		

n.s. non-significant

* $p \leq 0.05$

*** $p \leq 0.001$

Table 4.5.4

Cell mean values of significantly differing sources of variation found in analysis of variance of number of stems.

(a) Genotype

G	Maris Bead
4.08	3.38

(b) Genotype x treatment x replicate

	Genotype G				Genotype Maris Bead			
	Replicate				Replicate			
	1	2	3	4	1	2	3	4
Waterstress pre flowering	4.25	2.50	3.50	4.50	3.50	3.50	4.25	3.00
Waterstress at flowering/ pod set	3.50	5.75	3.50	4.50	3.25	3.50	2.25	2.75
Waterstress at pod fill	5.25	3.75	3.50	3.50	3.25	3.50	4.50	3.50
Control - no waterstress	3.50	4.50	4.75	4.50	4.00	3.75	2.75	2.75

Table 4.5.5

Waterstress trial - analysis of variance of total stem length per plant.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	215578.195	215578.195	34.525	***
Treatment	3	170802.148	56934.049	9.118	***
Replicate	3	24659.523	8219.841	1.316	n.s.
Genotype x treatment	3	158562.023	52854.008	8.465	***
Genotype x replicate	3	22025.148	7341.716	1.176	n.s.
Treatment x replicate	9	146019.508	16224.390	2.598	**
Genotype x treatment x replicate	9	223519.008	24835.445	3.977	***
Residual	96	599434.750	6244.112		
Corrected Total	127	1560600.305	12288.191		

n.s. non-significant

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.5.6

Cell mean values of significantly differing sources of variation found in analysis of variance of total stem length.

(a) Genotype

G	Maris Bead
289.67	371.75

(b) Treatment

Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
274.47	335.50	376.78	336.09

(c) Genotype x treatment

	Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
Genotype G	216.44	346.81	292.56	302.88
Genotype Maris Bead	332.50	324.19	461.00	369.31

(d) Treatment x replicate

	1	2	3	4
Waterstress pre flowering	258.63	254.75	315.88	268.63
Waterstress at flowering/ pod set	297.00	428.13	280.38	336.50
Waterstress at pod fill	395.38	352.50	406.38	352.88
Control - no waterstress	316.13	332.88	385.00	310.38

Table 4.5.6 continued

(e) Genotype x treatment x replicate

	Genotype G				Genotype Maris Bead			
	1	2	3	4	1	2	3	4
Waterstress pre flowering	199.00	197.75	202.50	266.50	318.25	311.75	429.25	270.75
Waterstress at flowering/ pod set	215.25	478.25	321.00	372.75	378.75	378.00	239.75	300.25
Waterstress at pod fill	389.00	239.50	299.50	242.25	401.75	465.50	513.25	463.50
Control - no waterstress	228.00	297.75	388.00	297.75	404.25	368.00	382.00	323.00

Table 4.5.7

Waterstress trial - analysis of variance of total number of leaves per plant.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	845.633	845.633	3.661	n.s.
Treatment	3	2695.023	898.341	3.889	*
Replicate	3	620.961	206.987	0.896	n.s.
Genotype x treatment	3	3745.773	1248.591	5.405	**
Genotype x replicate	3	1579.211	526.404	2.279	n.s.
Treatment x replicate	9	5277.758	586.418	2.539	*
Genotype x treatment x replicate	9	6399.258	711.029	3.078	**
Residual	96	22175.750	230.997		
Corrected Total	127	43339.367	341.255		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

between treatments was due to the very low value of plants stressed pre-flowering, the low value of plants stressed at flowering/pod set and the higher value of plants stressed at pod fill compared with the value of the control (table 4.5.8(a)). The genotype x treatment interaction was due to a differential genotypic response to the treatments applied (table 4.5.8(b)). Values for genotype G stressed pre-flowering and at pod fill were lower than that of the control. Maris Bead gave a lower value than the control when stressed at flowering/pod set and a higher value when stressed at pod fill. The treatment x replicate interaction (table 4.5.8(c)) and genotype x treatment x replicate interaction (table 4.5.8(e)) were both attributed to random variation betwen replicates.

Analysis of variance of dry weight of straw showed highly significant F ratios for genotypes, treatments, genotypes x treatments and genotypes x treatments x replicates (table 4.5.9). Cell mean values showed genotype G to have a lower dry weight of straw than Maris Bead (table 4.5.10(a)). The difference between treatments was due to the lower weight of straw produced by plants stressed pre-flowering and the increased weight of straw produced by plants stressed at pod fill compared with the weight produced by the control plants (table 4.5.10(b)). The genotype x treatment interaction was again due to different responses of the genotypes tested to the stresses applied (table 4.5.10(c)). Genotype G gave less weight of straw when stressed pre-flowering and a greater weight of straw when stressed at flowering/pod set than the weight of straw of the control. In Maris Bead stress pre-flowering and at flowering/pod set resulted in a lower weight of straw than in the control. Stress at pod fill produced a greater weight of straw than in the control. The genotype x treatment x replicate interaction (table 4.5.10(d)) was due to random variation between the replicates.

Table 4.5.8

Cell mean values of significantly differing sources of variation found in analysis of variance of total number of leaves.

(a) Treatment

Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no Waterstress
60.78	65.63	72.38	70.94

(b) Genotype x treatment

	Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no Waterstress
Genotype G	53.94	70.56	63.88	71.06
Genotype Maris Bead	67.63	60.69	80.88	70.81

(c) Treatment x replicate

	1	2	3	4
Waterstress pre flowering	60.50	54.00	68.88	59.75
Waterstress at flowering/ pod set	59.63	79.00	56.38	67.50
Waterstress at pod fill	81.13	65.25	76.88	66.25
Control - no waterstress	69.75	74.13	77.75	62.13

Table 4.5.8 continued

(d) Genotype x treatment x replicate

	Genotype G				Genotype Maris Bead			
	1	2	3	4	1	2	3	4
Waterstress pre flowering	55.00	44.75	48.25	67.75	66.00	63.25	89.50	51.75
Waterstress at flowering/ pod set	54.25	89.50	62.50	76.00	65.00	68.50	50.25	59.00
Waterstress at pod fill	84.75	56.25	59.75	54.75	77.50	74.25	94.00	77.75
Control - no waterstress	59.50	71.75	83.75	69.25	80.00	76.50	71.75	55.00

Table 4.5.9

Waterstress experiment - analysis of variance of dry weight of straw per plant.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	4671.215	4671.215	51.167	***
Treatment	3	2047.396	682.465	7.475	***
Replicate	3	175.189	58.396	0.640	n.s.
Genotype x treatment	3	1767.518	589.173	6.454	***
Genotype x replicate	3	129.940	43.313	0.474	n.s.
Treatment x replicate	9	1488.033	165.337	1.811	n.s.
Genotype x treatment x replicate	9	3690.135	410.015	4.491	***
Residual	96	8764.215	91.294		
Corrected Total	127	22733.642	179.005		

n.s. non-significant

*** $p \leq 0.001$

Table 4.5.10

Cell mean values of significantly differing sources of variation found in analysis of variance of dry weight of straw.

(a) Genotype

G	Maris Bead
28.57	40.65

(b) Treatment

Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
29.39	33.79	40.62	34.65

(c) Genotype x treatment

	Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
Genotype G	23.03	32.83	29.20	29.21
Genotype Maris Bead	35.75	34.74	52.03	40.08

(d) Genotype x treatment x replicate

	Genotype G				Genotype Maris Bead			
	Replicate				Replicate			
Treatment	1	2	3	4	1	2	3	4
Waterstress pre flowering	22.85	21.05	19.97	28.26	31.48	31.31	45.40	34.81
Waterstress at flowering/ pod set	18.96	41.24	34.58	36.54	44.77	37.07	26.11	31.01
Waterstress at pod fill	45.06	24.68	25.84	21.21	47.04	52.06	60.66	48.37
Control - no waterstress	20.55	28.83	39.54	27.94	42.55	32.63	40.74	44.40

Significant differences in number of flowering stems were found for genotypes, treatments, genotype x treatments, treatments x replicates and genotypes x treatments x replicates (table 4.5.11). Examination of means revealed that genotype G had more flowering stems per plant than did Maris Bead (table 4.5.12(a)). The difference between treatments was due to the number of flowering stems of plants stressed pre-flowering being lower than in the control and that of those stressed during pod fill being higher than the control (table 4.5.12(b)). The genotype x treatment interaction was due to different responses to stress applied at different developmental stages in each genotype (table 4.5.12(c)). In G plants stressed pre-flowering gave lower values than the control, whilst plants stressed at flowering/pod set gave higher values, Maris Bead stressed pre-flowering and at flowering/pod set gave lower values than the control, but stress at pod fill resulted in a higher number of flowering stems. The treatment x replicates interaction (table 4.5.12(d)) and genotype x treatment x replicate interaction (table 4.5.12(e)) were due to wide random variations betwen treatments.

Significant differences in total number of flowering nodes per plant were found for treatment, genotype x treatment and genotype x treatment x replicate by analysis of variance (table 4.5.13). Mean values showed the difference between treatments to be due to waterstress pre-flowering giving a lower value and waterstress at pod fill giving a higher value than the control (table 4.5.14(a)). The genotype x treatment interaction was due to differential genotypic responses to the stresses applied (table 4.5.14(b)). Genotype G gave a low value compared with that of the control when stressed at the pre-flowering stage and a high value when stressed at the flowering/pod set stage. Maris Bead gave a lower number of flowering nodes when stressed at pre-flowering or flowering/pod set stages compared with the control. Maris Bead stressed at

Table 4.5.11

Waterstress trial - analysis of variance for number of flowering stems per plant.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	7.031	7.031	6.750	*
Treatment	3	20.687	6.896	6.620	***
Replicate	3	1.750	0.583	0.560	n.s.
Genotype x treatment	3	8.906	2.969	2.850	*
Genotype x replicate	3	0.594	0.198	0.190	n.s.
Treatment x replicate	9	18.937	2.104	2.020	*
Genotype x treatment x replicate	9	23.969	2.663	2.557	*
Residual	96	100.000	1.042		
Corrected Total	127	181.875	1.432		

n.s. non-significant

* $p \leq 0.05$

*** $p \leq 0.001$

Table 4.5.12

Cell mean values of significantly differing sources of variation found in analysis of variance of number of flowering stems.

(a) Genotype

G	Maris Bead
3.45	2.98

(b) Treatment

Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
2.56	3.34	3.66	3.31

(c) Genotype x treatment

	Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
Genotype G	2.63	4.00	3.63	3.56
Genotype Maris Bead	2.50	2.69	3.69	3.06

(d) Treatment x replicate

	1	2	3	4
Waterstress pre flowering	2.63	2.13	3.13	2.38
Waterstress at flowering/ pod set	3.13	4.00	2.75	3.50
Waterstress at pod fill	4.25	3.13	4.00	3.25
Control - no waterstress	3.13	3.63	3.50	3.00

Table 4.5.12 continued

(e) Genotype x treatment x replicate

	Genotype G				Genotype Maris Bead			
	Replicate				Replicate			
	1	2	3	4	1	2	3	4
Waterstress pre flowering	2.75	2.00	2.75	3.00	2.50	2.25	3.50	1.75
Waterstress at flowering/ pod set	3.25	5.00	3.50	4.25	3.00	3.00	2.00	2.75
Waterstress at pod fill	5.25	2.75	3.50	3.00	3.25	3.50	4.50	3.50
Control - no waterstress	2.75	4.00	4.25	3.25	3.50	3.25	2.75	2.75

Table 4.5.13

Waterstress trial - analysis of variance of total number of flowering nodes per plant.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	12.500	12.500	0.282	n.s.
Treatment	3	3284.594	1094.865	24.725	***
Replicate	3	334.156	111.385	2.515	n.s.
Genotype x treatment	3	698.625	232.875	5.259	**
Genotype x replicate	3	74.312	24.771	0.559	n.s.
Treatment x replicate	9	751.969	83.552	1.887	n.s.
Genotype x treatment x replicate	9	870.562	96.729	2.184	*
Residual	96	4251.000	44.281		
Corrected Total	127	10277.719	80.927		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

** $p \leq 0.001$

Table 4.5.14

Cell mean values of significantly differing sources of variation found in analysis of variance of total number of flowering nodes.

(a) Treatment

Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
17.16	26.22	30.41	28.41

(b) Genotype x treatment

	Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
Genotype G	17.38	30.06	27.69	28.31
Genotype Maris Bead	16.94	22.38	33.13	28.50

(c) Genotype x treatment x replicate

	Genotype G				Genotype Maris Bead			
	1	2	3	4	1	2	3	4
Waterstress pre flowering	20.00	17.25	16.75	15.50	15.50	16.00	22.50	13.75
Waterstress at flowering/ pod set	18.75	33.25	33.75	34.50	22.25	25.50	19.00	22.75
Waterstress at pod fill	34.25	26.75	28.00	21.75	33.00	29.50	38.25	31.75
Control - no waterstress	22.25	31.75	35.50	23.75	31.00	27.50	30.00	25.50

pod fill produced a greater number of flowering nodes than the control. The genotype x treatment x replicates interaction (table 4.5.14(c)) was attributed to wide random variation between the replicates.

Analysis of variance of the number of flowers formed showed significant differences between genotypes, treatments and replicates and a significant genotype x treatment interaction (table 4.5.15). Examination of mean values showed Maris Bead to form more flowers than G (table 4.5.16(a)). The difference between treatments resulted from all the treatments having different values (table 4.5.16(b)). The difference between replicates was due to replicate 3 having a higher value than the others (table 4.5.16(c)). The genotype x treatment interaction (table 4.5.16(d)) was due to differential genotypic responses to the stresses applied. Genotype G had a lower number of flowers when stressed at the pre-flowering stage than the number of flowers in the control. In Maris Bead each treatment yielded a different number of flowers.

Analysis of variance of the number of pods set showed significant F ratios for treatments, genotype x treatment interactions, treatment x replicates interactions and genotype x treatment x replicates interactions (table 4.5.17). Examination of treatment means (table 4.5.18(a)) showed all the treatments to have differing mean numbers of pods set. The genotype x treatment interaction also showed a variation of means, the increased and decreased values being in different treatments for the different genotypes (table 4.5.18(b)). The significant treatment x replicates interaction (table 4.5.18(c)) and genotype x treatment x replicates interaction (table 4.5.18(d)) were attributable to wide random variation between replicates.

When analysis of variance was carried out for the number of ovules present in pods set the significant sources of variation were found to be treatment, genotype x treatment, treatment x replicate and genotype x treatment x replicate (table 4.5.19). Examination of the treatment means revealed that all the treatments applied produced differing

Table 4.5.15

Waterstress trial - analysis of variance of number of flowers per plant.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	34387.531	34387.531	29.398	***
Treatment	3	102496.094	34165.365	29.208	***
Replicate	3	10390.156	3463.385	2.961	*
Genotype x treatment	3	23564.344	7854.781	6.715	**
Genotype x replicate	3	2688.781	896.260	0.766	n.s.
Treatment x replicate	9	15893.469	1765.941	1.510	n.s.
Genotype x treatment x replicate	9	20475.094	2275.010	1.945	n.s.
Residual	96	112294.500	1169.734		
Corrected Total	127	322189.969	2536.929		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.5.16

Cell mean values of significantly differing sources of variation found in analysis of variance of number of flowers.

(a) Genotype

G	Maris Bead
121.63	154.41

(b) Treatment

Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no Waterstress
92.13	139.75	167.81	152.38

(c) Replicate

1	2	3	4
128.84	138.66	152.38	132.19

(d) Genotype x treatment

	Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
Genotype G	82.75	139.44	130.88	133.44
Genotype Maris Bead	101.50	140.06	204.75	171.31

Table 4.5.17

Waterstress trial - analysis of variance of number of pods set per plant.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	508.008	508.008	1.662	n.s.
Treatment	3	3033.398	1011.133	3.189	*
Replicate	3	853.523	284.508	0.897	n.s.
Genotype x treatment	3	5133.648	1711.216	5.397	**
Genotype x replicate	3	1825.023	608.341	1.919	n.s.
Treatment x replicate	9	9112.695	1012.522	3.193	**
Genotype x treatment x replicate	9	12249.445	1361.049	4.293	***
Residual	96	30438.250	317.065		
Corrected Total	127	63153.992	497.276		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.01$

Table 4.5.18

Cell mean values of significantly differing sources of variation found in analysis of variance of number of pods set.

(a) Treatment

Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no Waterstress
48.47	55.69	61.69	52.19

(b) Genotype x treatment

	Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
Genotype G	43.88	67.75	59.75	54.63
Genotype Maris Bead	53.06	43.63	63.63	49.75

(c) Treatment x replicate

	1	2	3	4
Waterstress pre flowering	49.63	42.63	57.25	44.38
Waterstress at flowering/ pod set	43.25	75.00	43.38	61.13
Waterstress at pod fill	71.13	61.00	64.13	50.50
Control - no waterstress	46.50	49.13	63.88	49.25

Table 4.5.18 continued

(d) Genotype x treatment x replicate

	Genotype G				Genotype Maris Bead			
	Replicate				Replicate			
	1	2	3	4	1	2	3	4
Waterstress pre flowering	50.25	36.25	48.25	40.75	49.00	49.00	66.25	48.00
Waterstress at flowering/ pod set	35.25	105.00	54.56	76.25	51.25	45.00	32.25	46.00
Waterstress at pod fill	91.00	57.50	46.00	44.50	51.25	64.50	82.25	56.50
Control - no waterstress	42.25	61.00	71.25	44.00	50.75	37.25	56.50	54.50

Table 4.5.19

Waterstress trial - analysis of variance of number of ovules in pods set per plant.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	6258.008	6258.008	1.337	n.s.
Treatment	3	64453.398	21484.466	4.590	**
Replicate	3	7119.023	2373.008	0.507	n.s.
Genotype x treatment	3	101957.648	33985.883	7.261	***
Genotype x replicate	3	27259.773	9086.591	1.941	n.s.
Treatment x replicate	9	141262.820	15695.869	3.353	***
Genotype x treatment x replicate	9	205109.195	22789.911	4.869	***
Residual	96	449337.750	4680.602		
Corrected Total	127	1002757.617	7895.729		

n.s. non-significant

** $p \leq 0.01$

*** $p \leq 0.001$

numbers of ovules present in the pods set (table 4.5.20(a)). The genotype x treatment interaction showed differential genotypic response to the treatments applied (table 4.5.20(b)). In G waterstress applied pre-flowering resulted in a reduced number of ovules being present, whereas waterstress at flowering/pod set resulted in an increase in number of ovules in pods set, waterstress at flowering/pod set reduced the number of ovules present in Maris Bead, whereas stress at pre-flowering or pod fill stages resulted in an increased number of ovules present. The treatment x replicate interaction (table 4.5.20(c)) was partially due to the values for replicate 4 tending to be lower than those of the other replicates for equivalent treatments. The interaction was also partially attributable to variation in response patterns to imposed stress within replicates. The genotype x treatment x replicate interactions (table 4.5.20(d)) was attributed to wide random variations between replicates.

Analysis of variance of number of seeds revealed genotype, treatment, genotype x treatment, treatment x replicate, and genotype x treatment x replicate to be significant sources of variation (table 4.5.21). From mean values Maris Bead was seen to produce more seeds than G (table 4.5.22(a)). Treatment means showed that waterstress pre-flowering or at flowering/pod set resulted in a reduced number of seeds being produced, whereas stress at pod fill produced an increased number of seeds (table 4.5.22(b)). The genotype x treatment interaction (table 4.5.22(c)) showed that in genotype G waterstress pre-flowering resulted in a decreased number of seeds being produced, stress at flowering/pod set produced a small decrease in number of seeds produced compared with the control. In Maris Bead the response pattern was different, waterstress or flowering/pod set reduced the number of seeds produced, stress pre-flowering or at pod fill resulted in an increased number of seeds compared with the control. The treatment x replicate interaction (table 4.5.22(d)) was due to different response patterns to stress

Table 4.5.20

Cell mean values of significantly differing sources of variation found in analysis of variance of number of ovules in pods set.

(a) Treatment

Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
182.56	222.44	241.72	199.50

(b) Genotype x treatment

	Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
Genotype G	161.31	273.25	227.75	211.88
Genotype Maris Bead	203.81	171.63	255.69	187.13

(c) Treatment x replicate

	1	2	3	4
Waterstress pre flowering	188.75	148.00	216.75	176.75
Waterstress at flowering/ pod set	180.13	282.50	168.50	258.63
Waterstress at pod fill	275.50	237.75	250.38	203.25
Control - no waterstress	184.38	192.75	250.88	170.00

Table 4.5.20 continued

(d) Genotype x treatment x replicate

	Genotype G				Genotype Maris Bead			
	Replicate				Replicate			
	1	2	3	4	1	2	3	4
Waterstress pre flowering	185.50	127.75	174.00	158.00	192.00	168.25	259.50	195.50
Waterstress at flowering/ pod set	129.25	386.00	209.00	368.75	231.00	179.00	128.00	148.50
Waterstress at pod fill	338.75	220.00	180.50	171.75	212.25	255.50	320.25	234.75
Control - no waterstress	166.00	232.75	278.75	170.00	202.75	152.75	223.00	170.00

Table 4.5.21

Waterstress trial - analysis of variance of total number of seeds per plant.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	34485.945	34485.945	25.254	***
Treatment	3	32138.711	10712.904	7.845	***
Replicate	3	4484.273	1494.758	1.095	n.s.
Genotype x treatment	3	27404.523	9134.841	6.689	***
Genotype x replicate	3	7224.211	2408.070	1.763	n.s.
Treatment x replicate	9	24574.383	2730.487	1.999	*
Genotype x treatment x replicate	9	43453.193	4828.133	3.536	***
Residual	96	131096.250	1365.586		
Corrected Total	127	304861.492	2400.484		

n.s. non-significant

* $p \leq 0.05$

*** $p \leq 0.001$

Table 4.5.22

Cell mean values of significantly differing sources of variation found in analysis of variance of number of seeds.

(a) Genotype

G	Maris Bead
108.83	141.66

(b) Treatment

Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
115.47	110.41	151.44	123.66

(c) Genotype x treatment

	Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
Genotype G	85.81	110.88	119.25	119.38
Genotype Maris Bead	145.13	109.94	183.63	127.94

(d) Treatment x replicate

	1	2	3	4
Waterstress pre flowering	106.88	98.88	138.88	117.25
Waterstress at flowering pod set	91.63	128.00	93.63	128.38
Waterstress at pod fill	163.63	154.25	158.38	129.50
Control - no waterstress	111.13	120.63	147.13	115.75

Table 4.5.22 continued

(e) Genotype x treatment x replicate

	Genotype G				Genotype Maris Bead			
	Replicate				Replicate			
	1	2	3	4	1	2	3	4
Waterstress pre flowering	92.25	70.75	84.00	96.25	121.50	127.00	193.75	138.25
Waterstress at flowering/ pod set	70.00	134.00	99.50	140.00	113.25	122.00	87.75	116.75
Waterstress at pod fill	180.00	124.50	89.50	83.00	147.25	184.00	227.25	176.00
Control - no waterstress	88.75	134.50	151.50	102.75	133.50	106.75	142.75	128.75

among the replicates. The genotype x treatment x replicate interaction (table 4.5.22(e)) was attributed to a wide random variation between replicates.

When weight of seeds produced was analysed by analysis of variance genotype, treatment, genotype x treatment and genotype x treatment x replicate were revealed to be significant sources of variation (table 4.5.23). Examination of means showed Maris Bead to produce a greater seed yield than G (table 4.5.24(a)). The treatment means showed that stress pre-flowering or at flowering/pod set reduced seed yield, whereas waterstress at pod fill increased the yield (table 4.5.24(b)). The genotype x treatment interaction (table 4.5.24(c)) was due to differential yield responses of the genotypes tested to the stresses imposed. In G any imposed stress resulted in a decreased seed yield, stress pre-flowering resulted in the greatest yield decrease. Stress at flowering/pod set reduced yield in Maris Bead, but stress at pod fill resulted in a yield increase. The genotype x treatment x replicate interaction (table 4.5.24(d)) was attributed to the wide variation between replicates in responses to stress.

4.5.2 Main stem yield component profiles

Plant profiles of the mean number of flowers (figure 4.5.1), mean number of pods set (figure 4.5.2), mean number of ovules present in pods set (figure 4.5.3), mean number of seeds 'filled' (figure 4.5.4) and mean weight of seeds (figure 4.5.5) at each node on the main stem facilitated examination of treatment differences at the nodal level.

Table 4.5.23

Waterstress trial - analysis of variance of seed weight per plant.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotype	1	6352.477	6352.477	27.175	***
Treatment	3	3736.369	1245.456	5.328	**
Replicate	3	1324.750	441.583	1.889	n.s.
Genotype x treatment	3	3984.957	1328.319	5.682	***
Genotype x replicate	3	262.519	87.506	0.374	n.s.
Treatment x replicate	9	2554.864	283.874	1.214	n.s.
Genotype x treatment x replicate	9	5207.995	578.666	2.475	*
Residual	96	22440.781	233.758		
Corrected Total	127	45864.711	361.139		

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 4.5.24

Cell mean values of significantly differing sources of variation found in analysis of variance of seed weight.

(a) Genotype

G	Maris Bead
40.79	54.88

(b) Treatment

Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
43.36	42.32	55.70	49.95

(c) Genotype x treatment

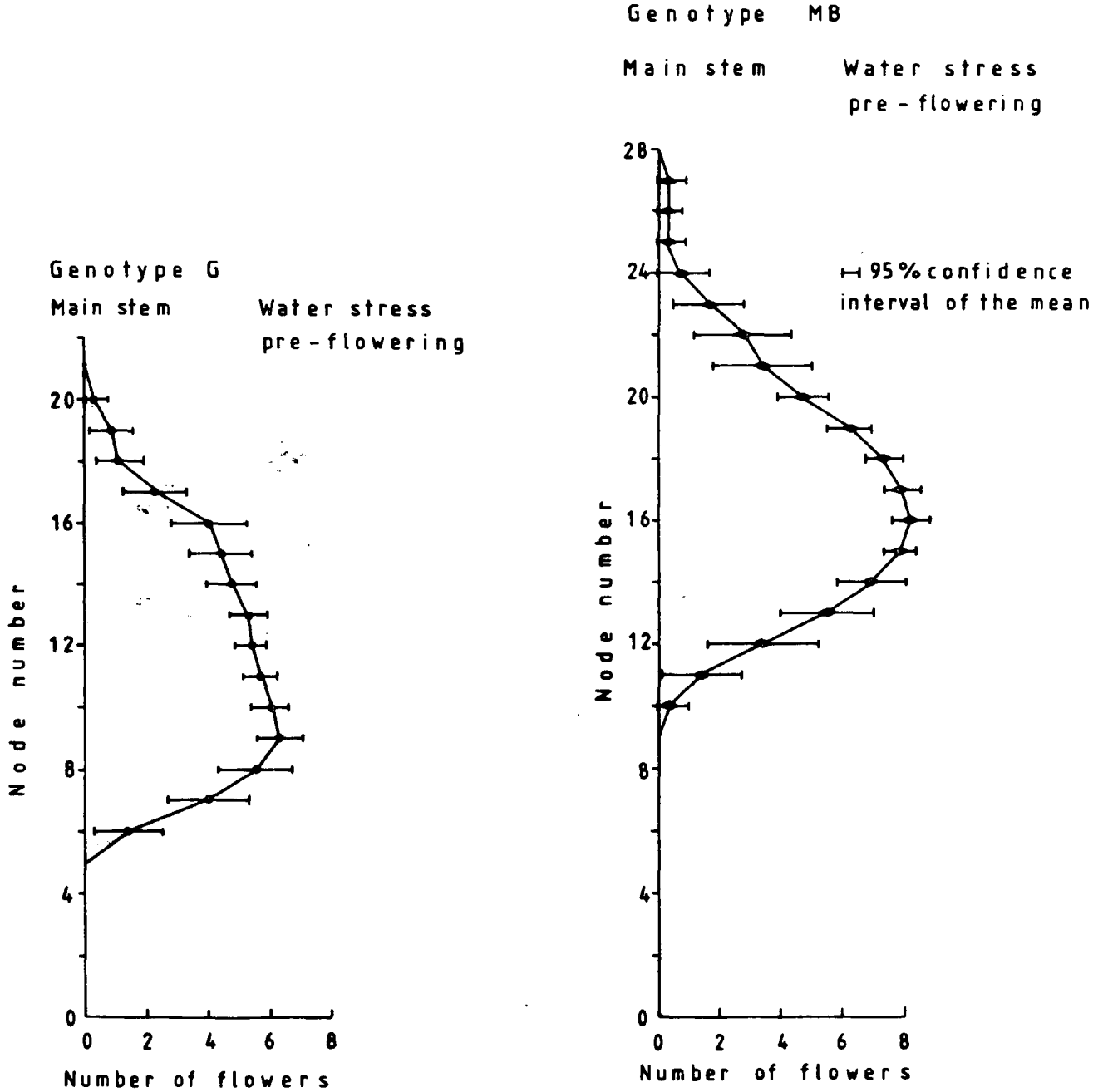
	Waterstress pre flowering	Waterstress at flowering/ pod set	Waterstress at pod fill	Control - no waterstress
Genotype G	33.47	42.82	41.38	45.49
Genotype Maris Bead	53.25	41.83	70.02	54.42

(d) Genotype x treatment x replicate

	Genotype G				Genotype Maris Bead			
	Replicate				Replicate			
	1	2	3	4	1	2	3	4
Waterstress pre flowering	29.61	33.31	27.49	43.46	41.10	50.09	67.70	54.20
Waterstress at flowering/ pod set	22.99	54.96	49.56	43.77	42.62	44.67	36.89	43.12
Waterstress at pod fill	59.17	41.35	33.82	31.18	61.67	71.60	78.78	68.02
Control - no waterstress	30.14	47.03	61.77	43.00	56.22	48.35	58.98	54.13

Figure 4.5.1 (see overleaf) Main stem profiles for number of flowers present at each node of genotypes G and Maris Bead with each of 4 waterstress treatments applied: waterstress pre-flowering, waterstress at flowering/ pod set, waterstress at pod fill, control - no waterstress.

MB = Maris Bead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Main stem
Water stress
pre-flowering
Node number
Number of flowers
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12
16
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0
2
4
6
8
Genotype MB
Main stem
Water stress
pre-flowering
95% confidence
interval of the mean
Node number
Number of flowers
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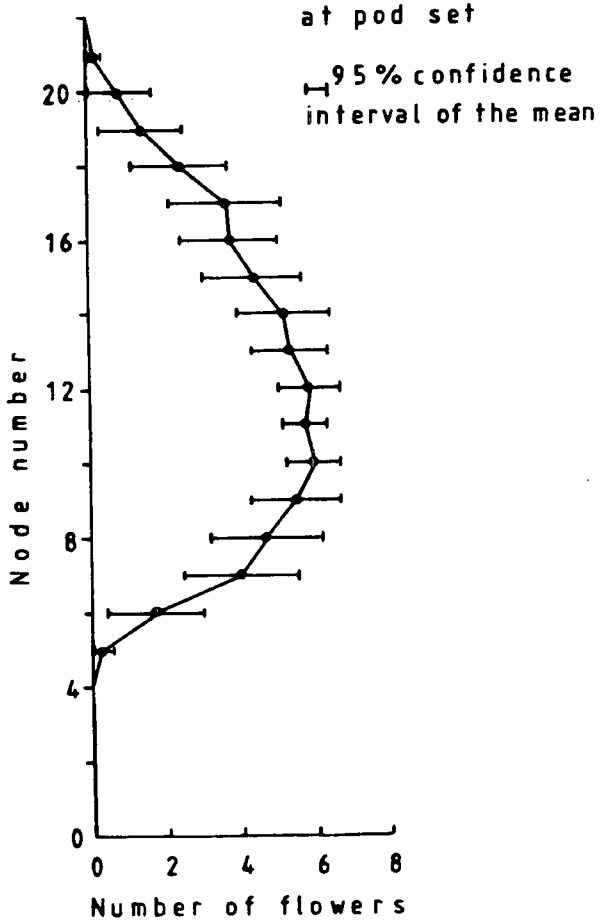
20
24
28
0
2
4
6
8


Genotype G
Main stem
Water stress
at pod set
95% confidence
interval of the mean
Node number
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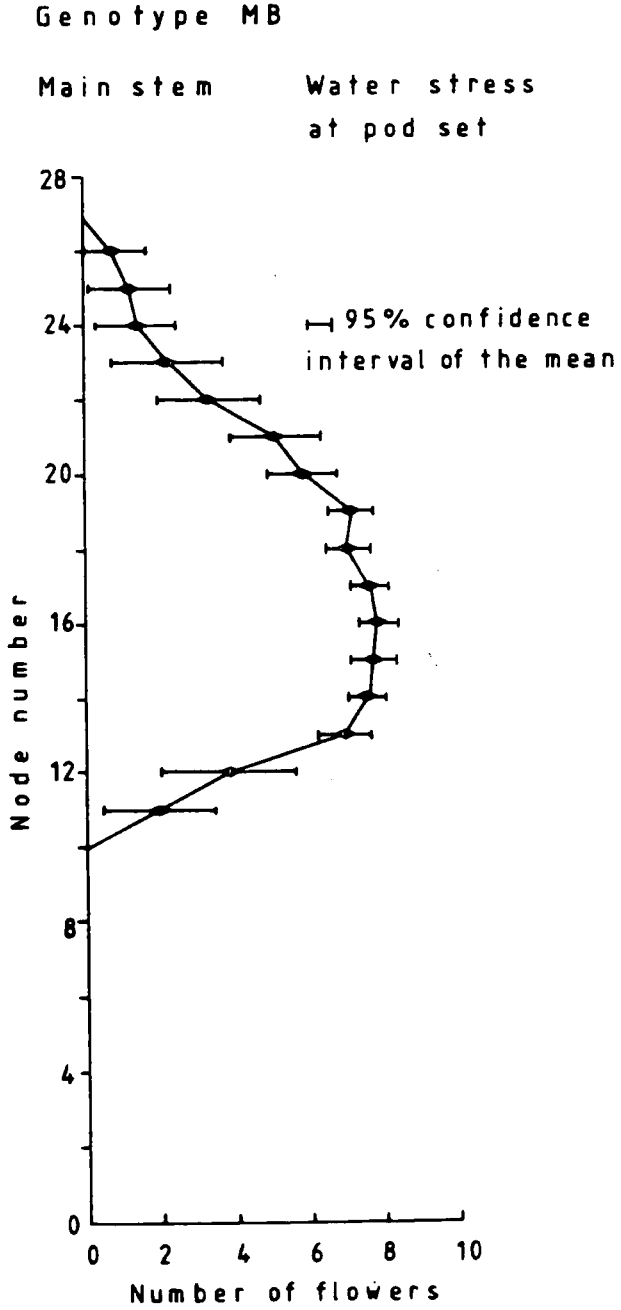
4
8
12
16
20
0
2
4
6
8
Number of flowers


Genotype MB
Main stem
Water stress
at pod set
95% confidence
interval of the mean
Node number
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8
12
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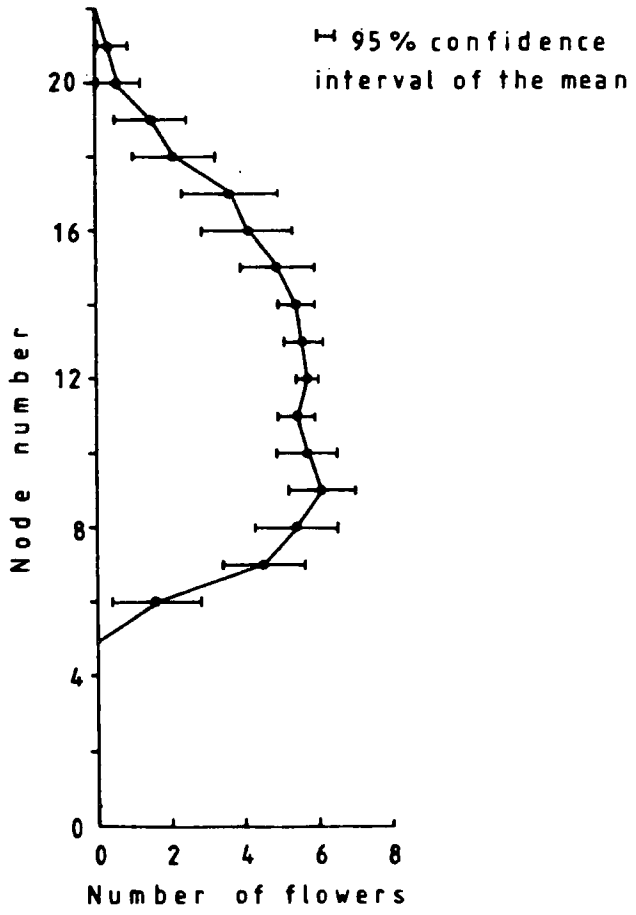
20
24
28
0
2
4
6
8
10
Number of flowers


Genotype G
Main stem
Water stress
at pod fill
95% confidence
interval of the mean
Node number
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8
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16
20
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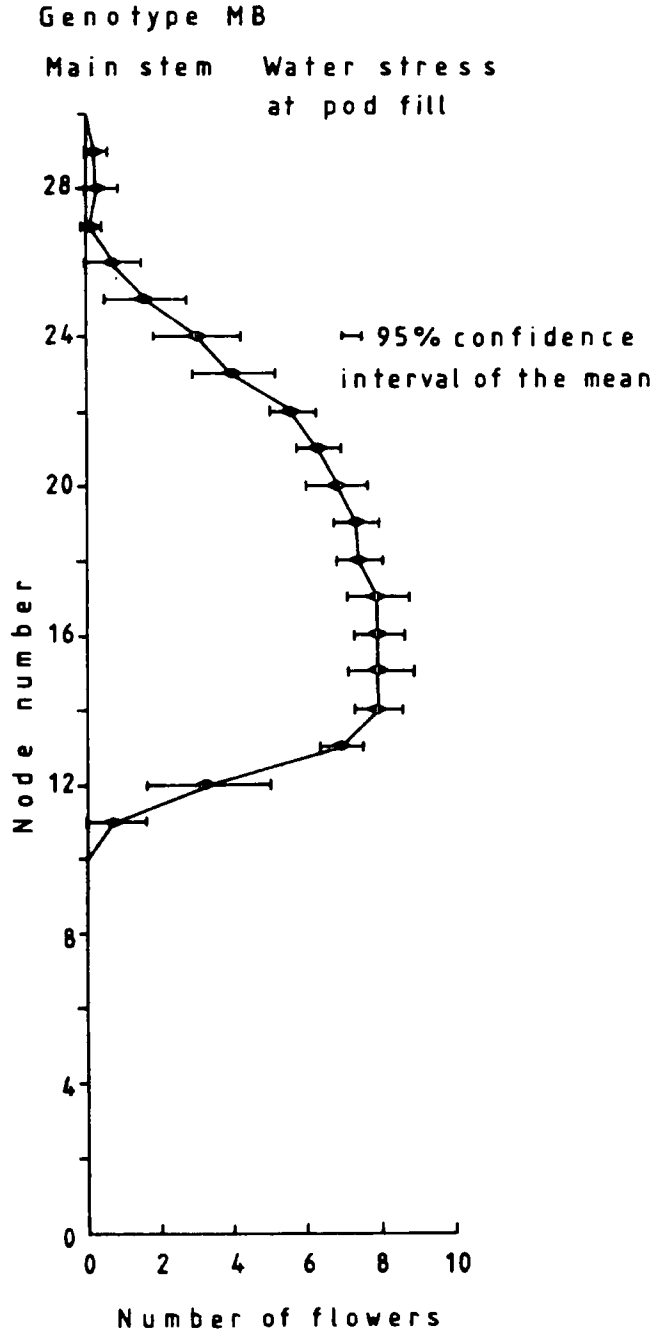
2
4
6
8
Number of flowers


Genotype MB
Main stem
Water stress
at pod fill
95% confidence
interval of the mean
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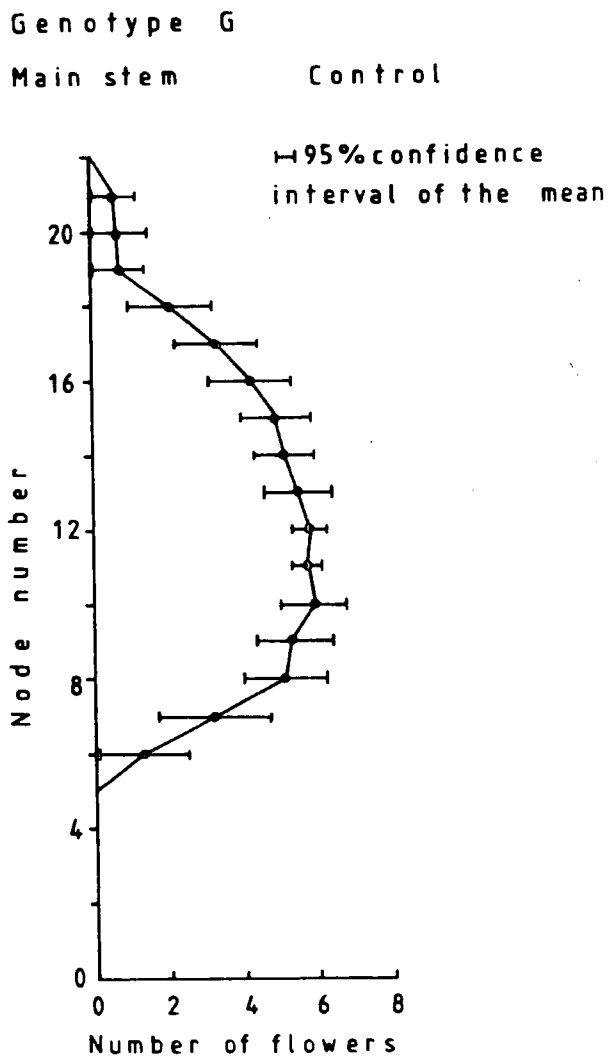
2
4
6
8
10
Number of flowers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Main stem Control
⊢⊣95% confidence interval of the mean
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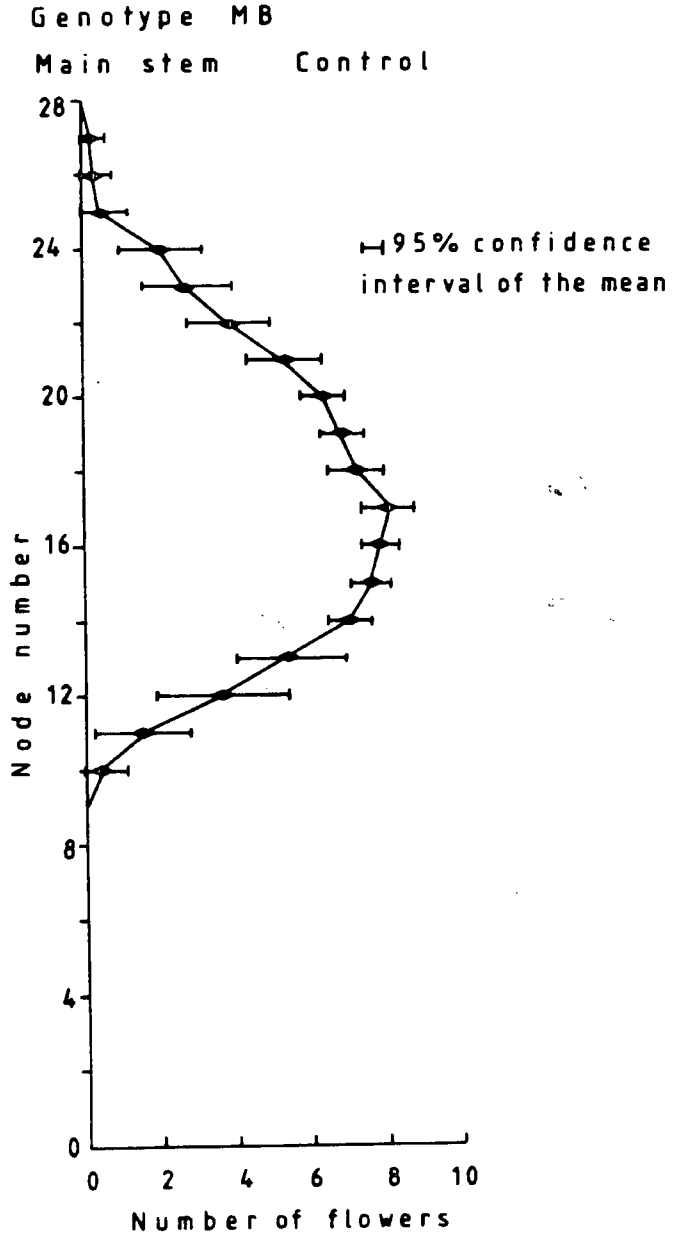
20
0 2 4 6 8
Number of flowers


Genotype MB
Main stem Control
⊢⊣95% confidence interval of the mean
Node number
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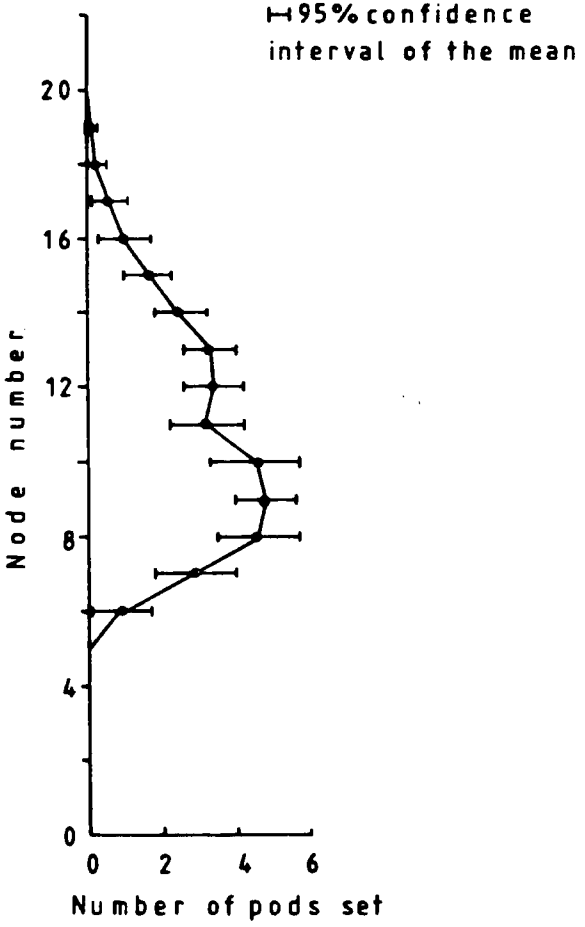
4
8
12
16
20
24
28
0 2 4 6 8 10
Number of flowers

Figure 4.5.2 (see overleaf) Main stem profiles for number of pods set at each node of genotypes G and Maris Bead with each of 4 waterstress treatments applied: waterstress pre-flowering, waterstress at flowering/ pod set, waterstress at pod fill, control - no waterstress.

MB = Maris Bead


Genotype G
Main stem
Water stress
pre-flowering
95% confidence
interval of the mean
Node number
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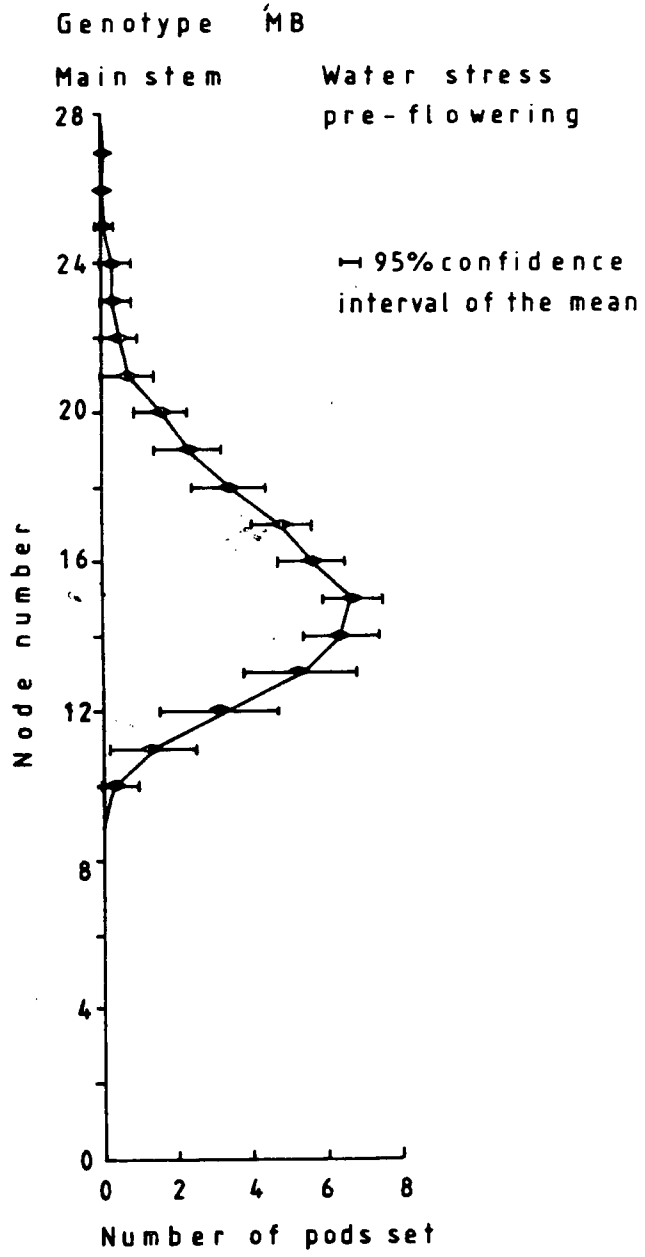
4
8
12
16
20
0
2
4
6
Number of pods set


Genotype MB
Main stem
Water stress
pre-flowering
95% confidence
interval of the mean
Node number
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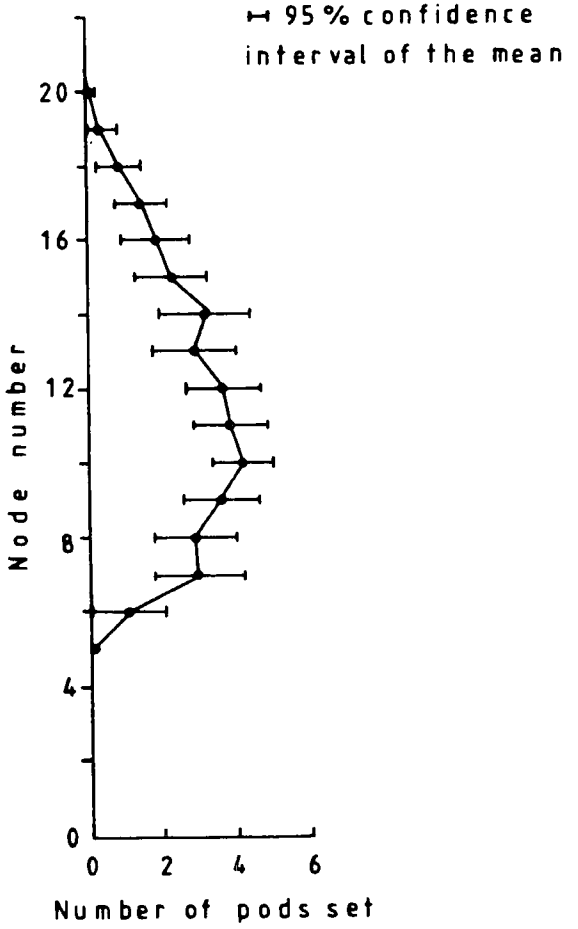
8
12
16
20
24
28
0
2
4
6
8
Number of pods set


Genotype G
Main stem
Water stress
at pod set
95% confidence
interval of the mean
Node number
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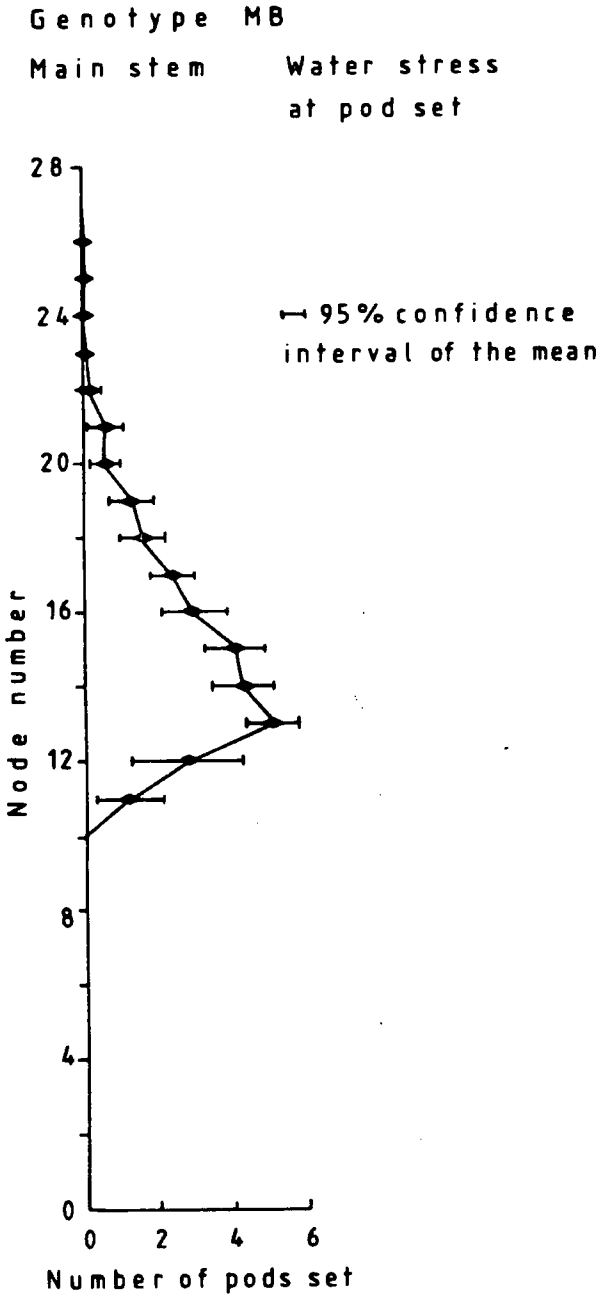
4
8
12
16
20
0
2
4
6
Number of pods set


Genotype MB
Main stem
Water stress
at pod set
95% confidence
interval of the mean
Node number
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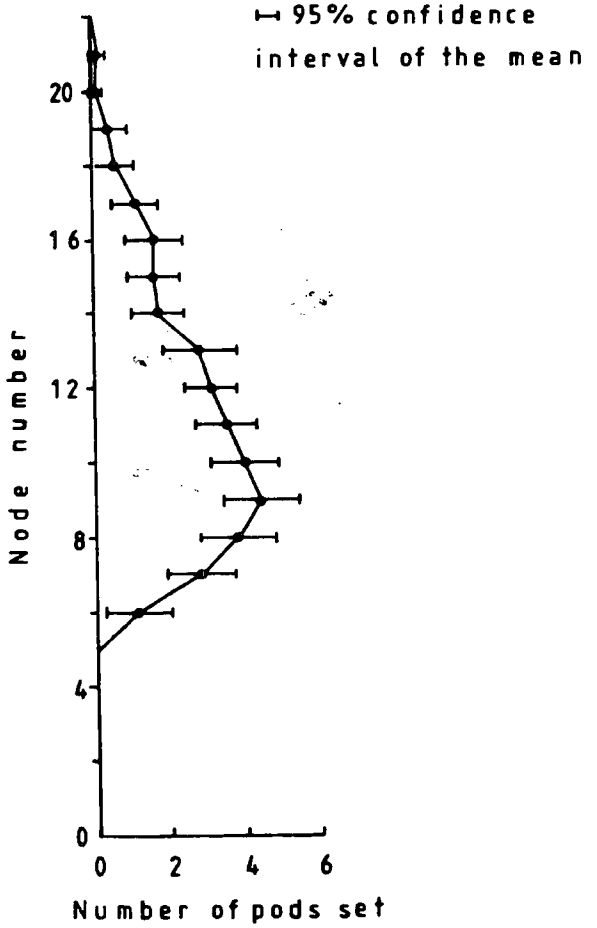
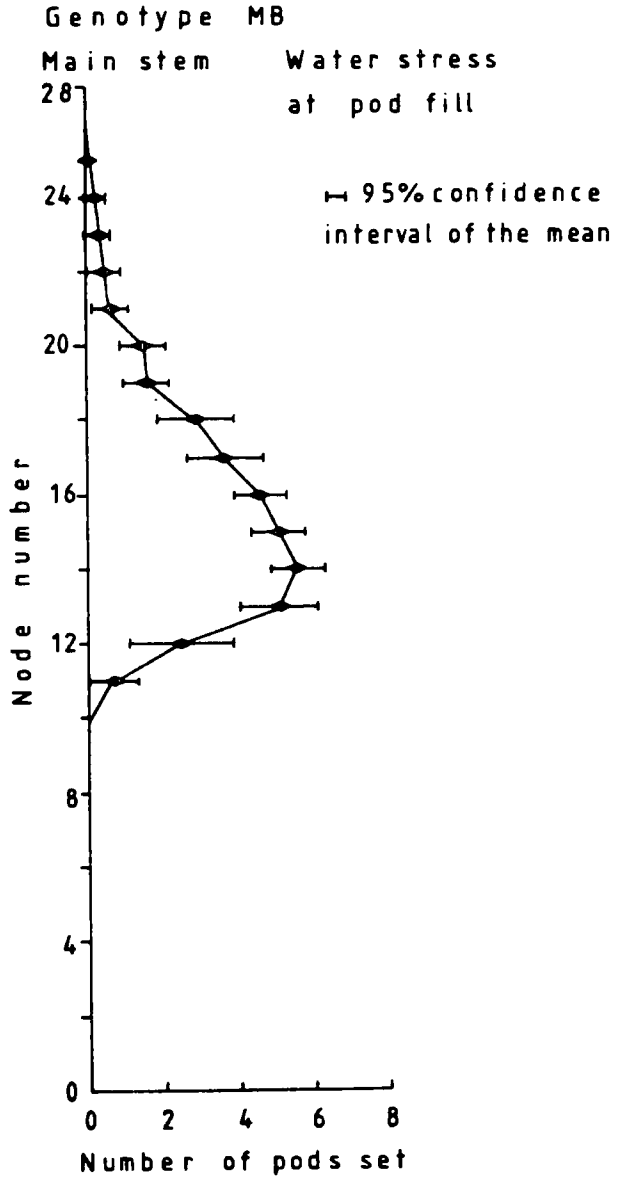
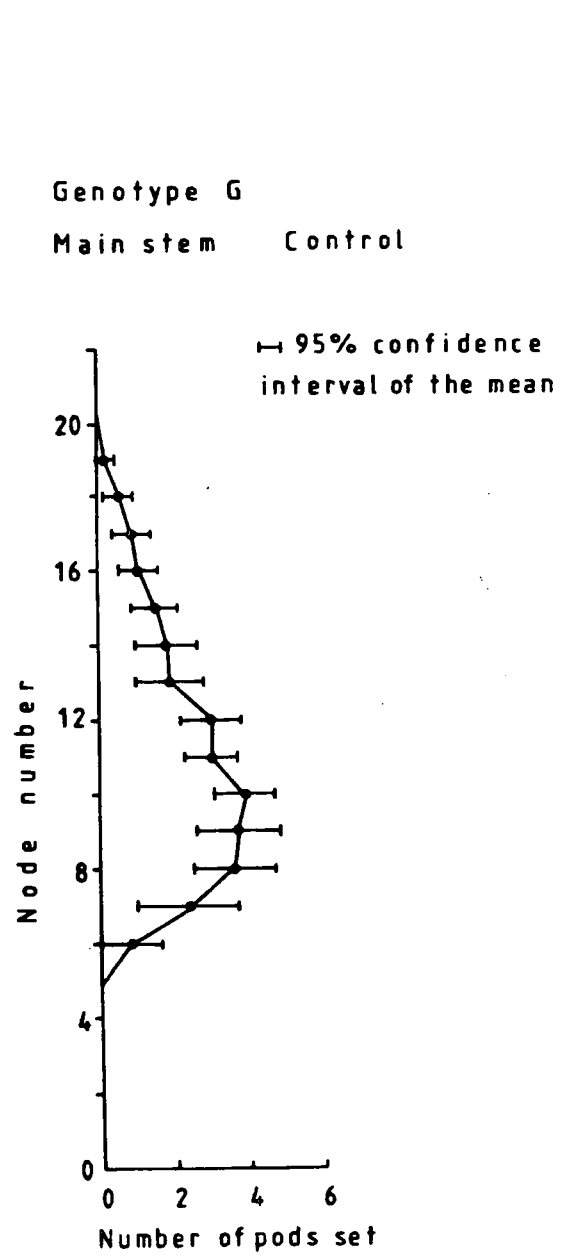
4
8
12
16
20
24
28
0
2
4
6
Number of pods set


Genotype G
Main stem
Water stress
at pod fill
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
0
2
4
6
Number of pods set


Genotype MB
Main stem
Water stress
at pod fill
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
24
28
0
2
4
6
8
Number of pods set


Genotype G
Main stem Control
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
0 2 4 6
Number of pods set

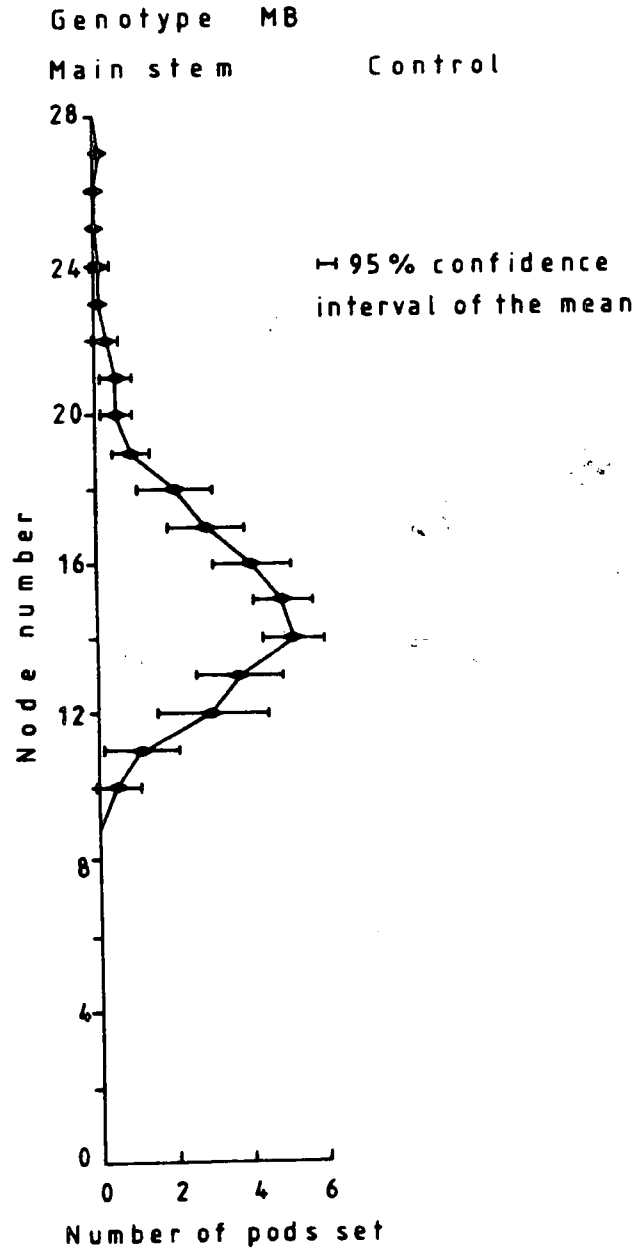
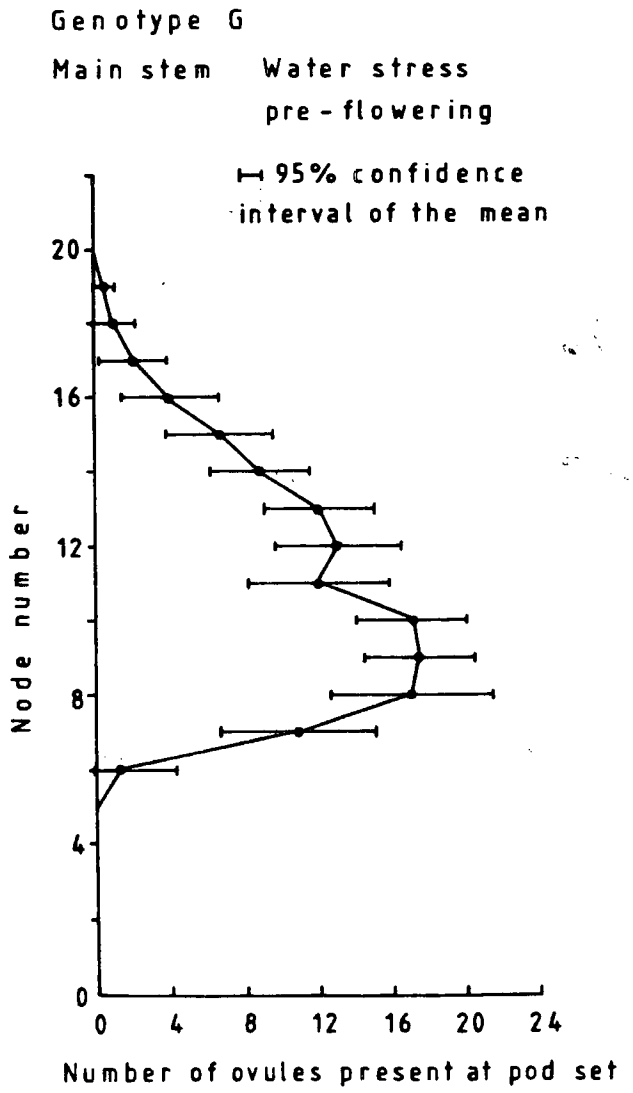
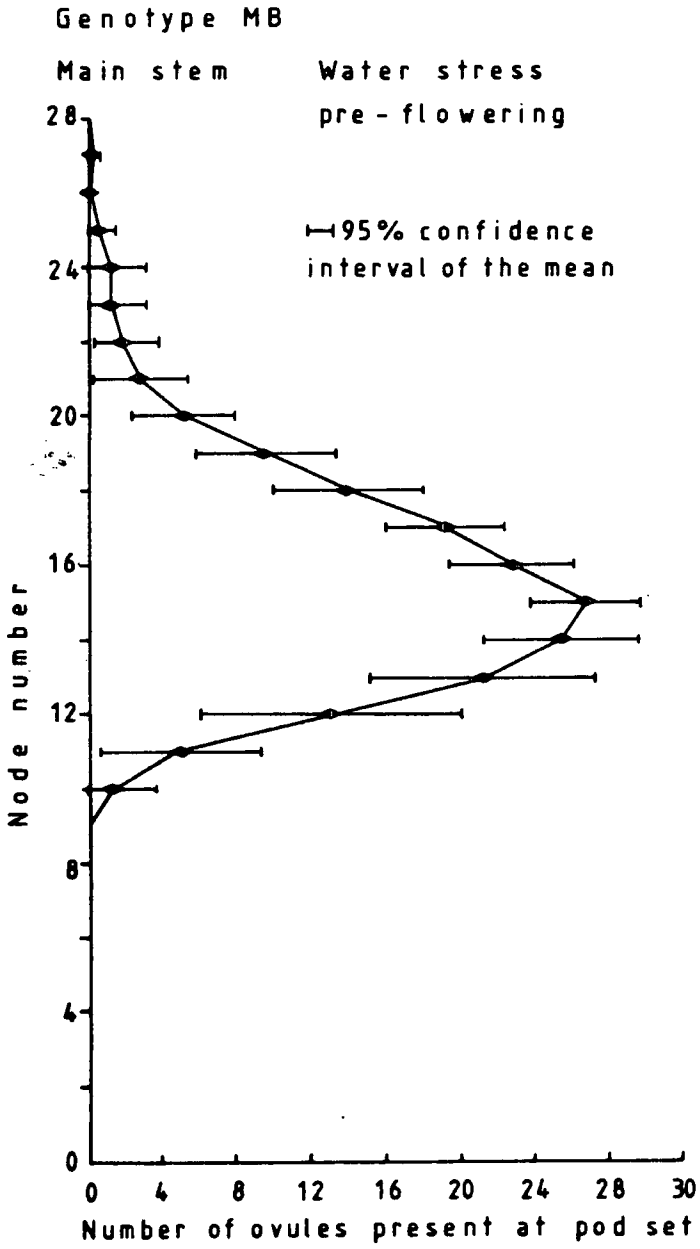
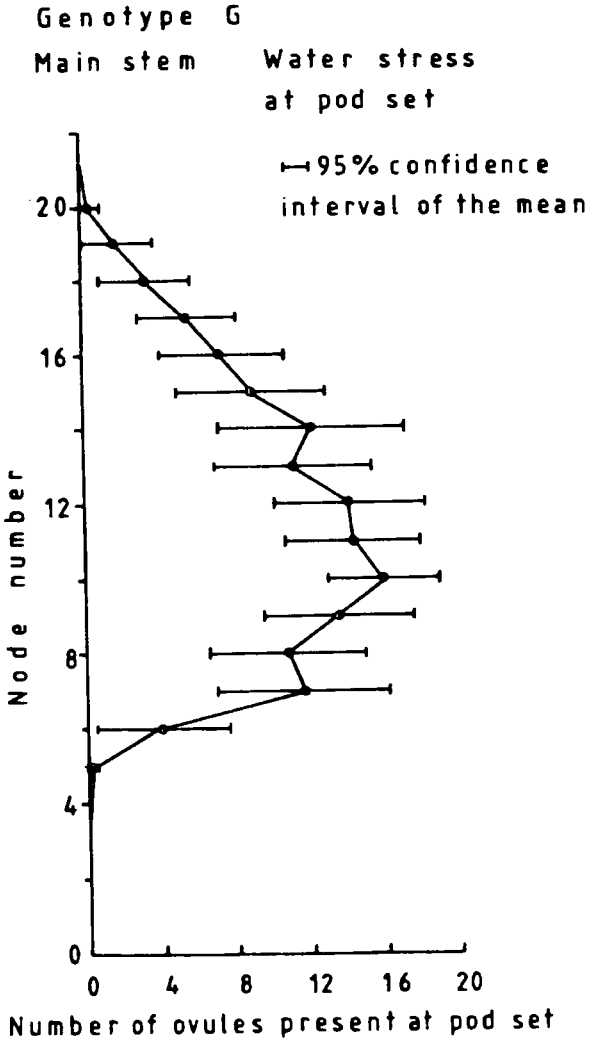

Genotype MB
Main stem Control
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
24
28
0 2 4 6
Number of pods set

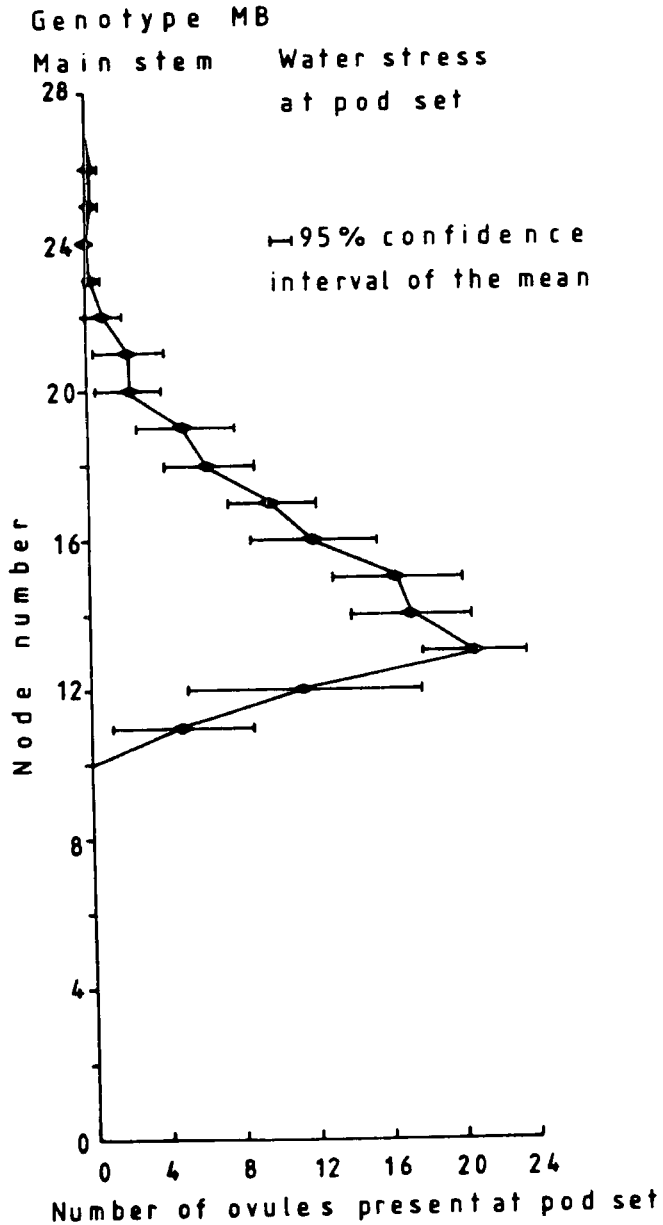
Figure 4.5.3 (see overleaf) Main stem profiles for number of ovules present in pods set at each node of genotypes G and Maris Bead with each of 4 treatments applied: waterstress pre-flowering, waterstress at flowering/pod set, waterstress at pod fill, control - no waterstress.

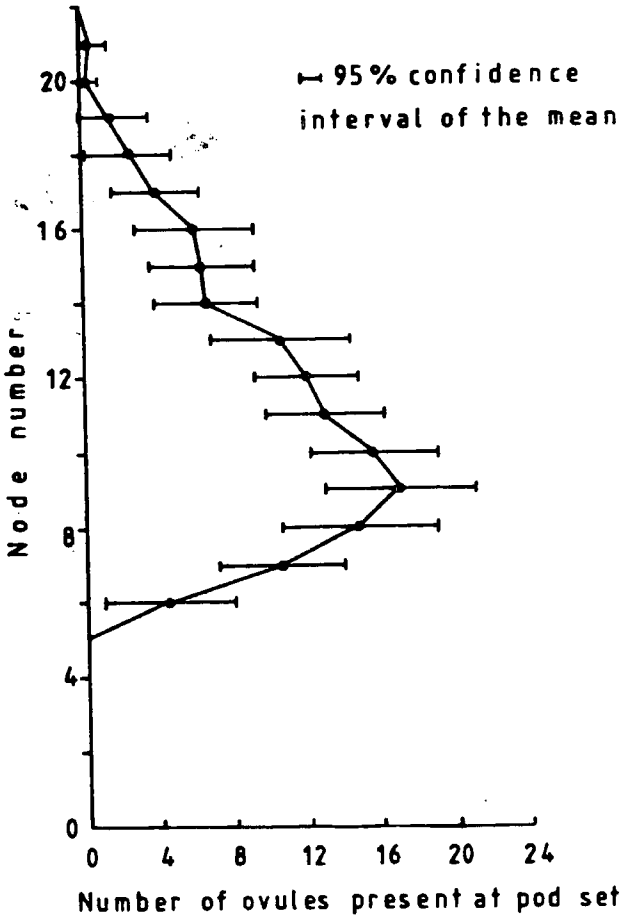
MB = Maris Bead

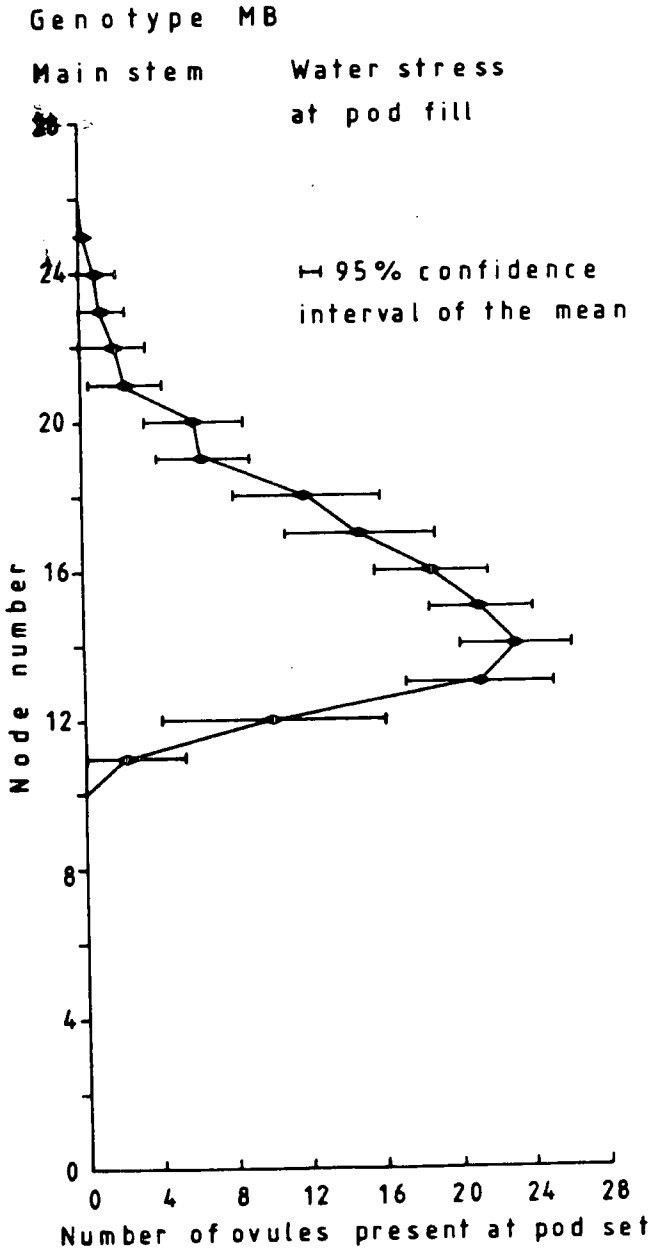

Genotype G
Main stem Water stress
pre-flowering
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
24
Number of ovules present at pod set

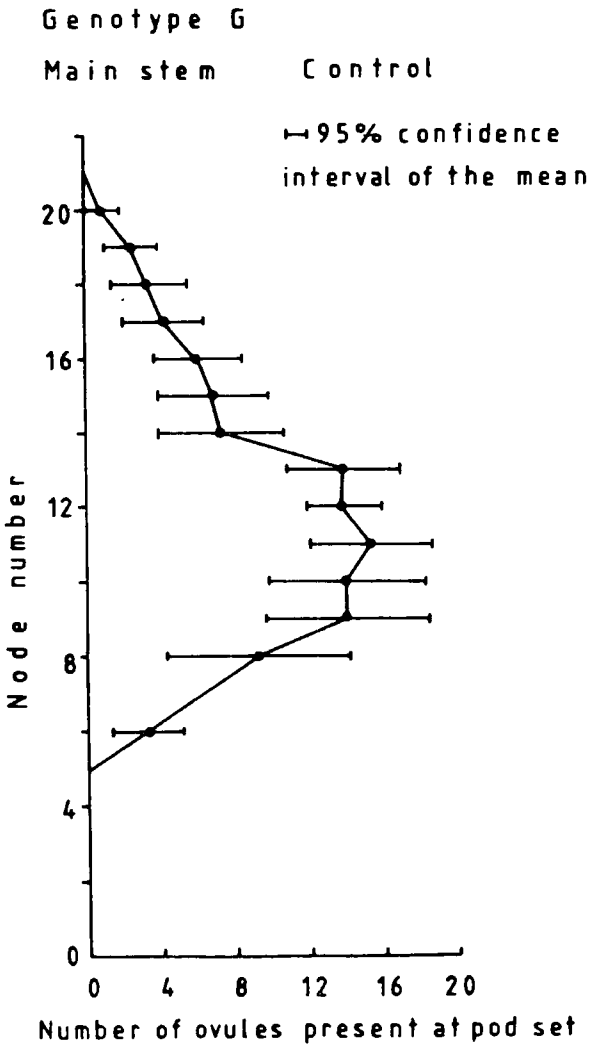

Genotype MB
Main stem Water stress
pre-flowering
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
24
28
30
Number of ovules present at pod set


Genotype G
Main stem
Water stress
at pod set
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
Number of ovules present at pod set


Genotype MB
Main stem
Water stress
at pod set
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
24
28
Number of ovules present at pod set


Genotype G
Main stem
Water stress
at pod fill
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
24
Number of ovules present at pod set


Genotype MB
Main stem
Water stress
at pod fill
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
24
28
Number of ovules present at pod set


Genotype G
Main stem Control
95% confidence interval of the mean
Node number
Number of ovules present at pod set
0
4
8
12
16
20

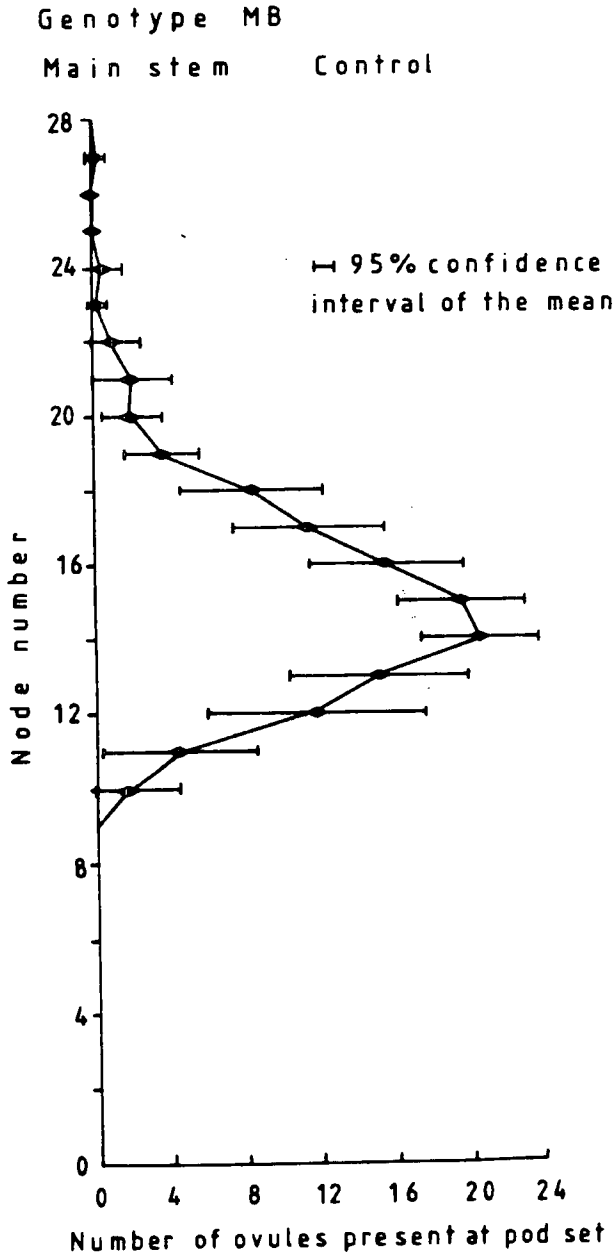
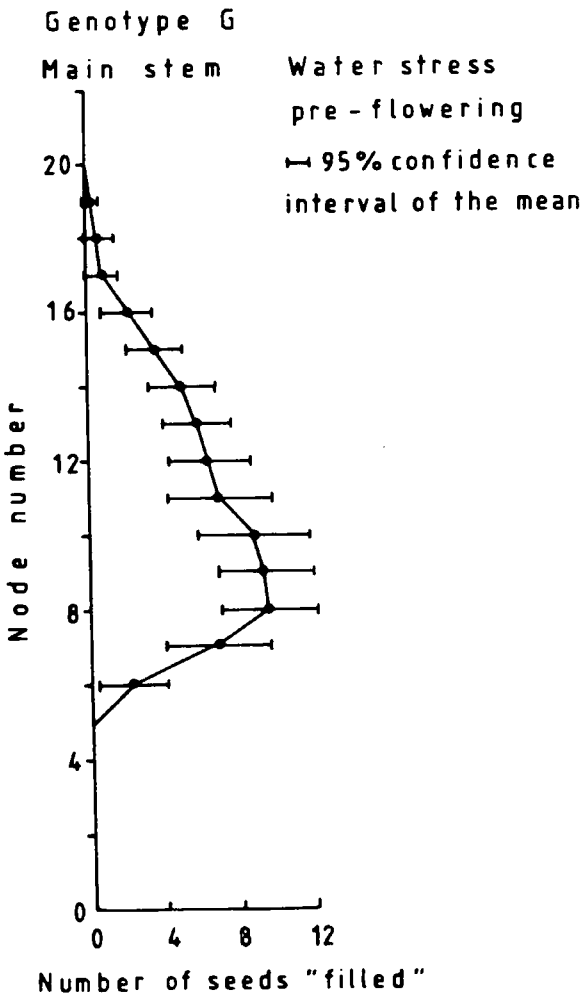
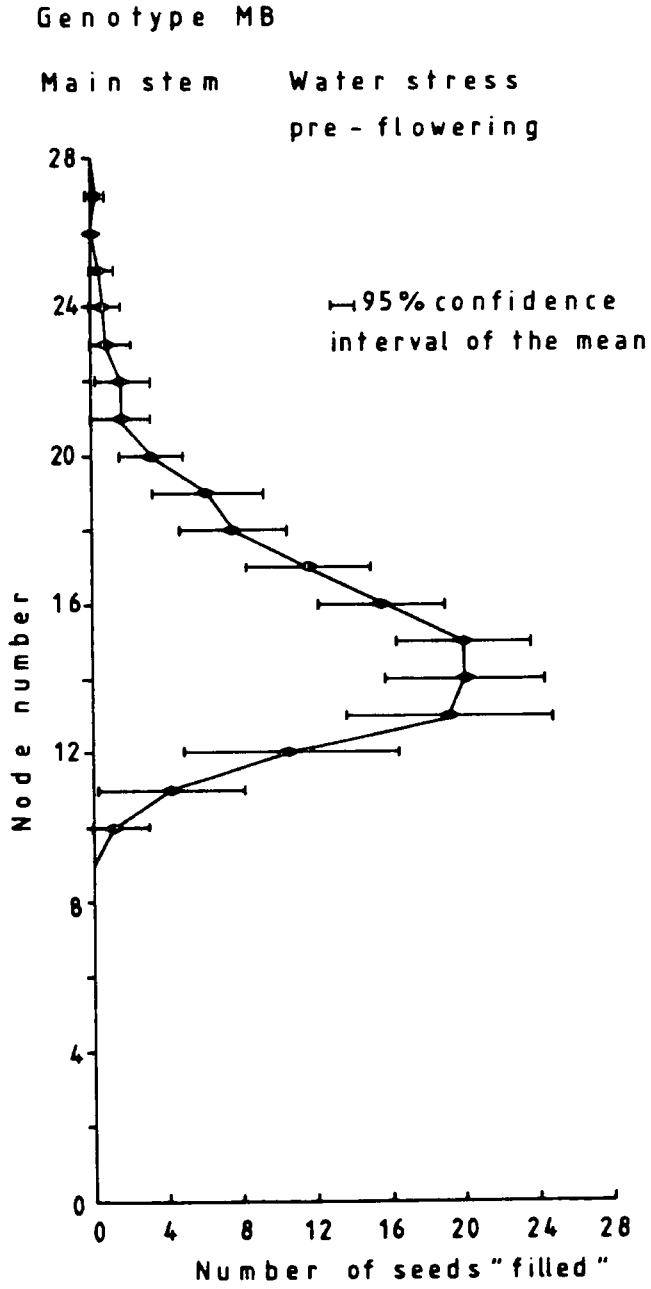
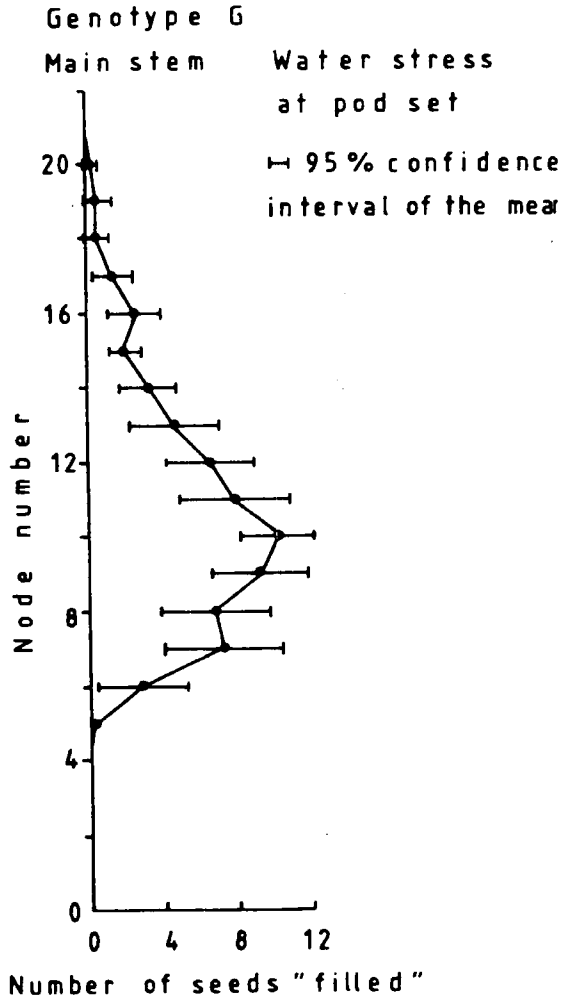

Genotype MB
Main stem Control
95% confidence interval of the mean
Node number
Number of ovules present at pod set
0
4
8
12
16
20
24
28

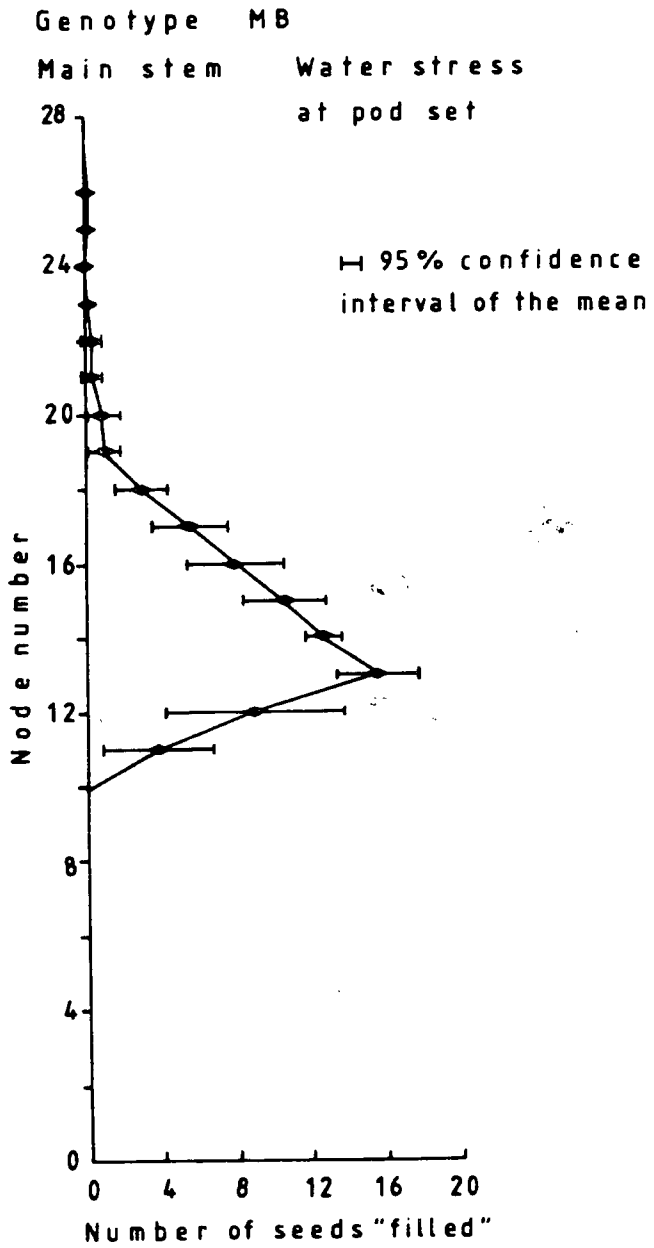
Figure 4.5.4 (see overleaf) Main stem profiles for number of seeds 'filled' at each node of genotypes G and Maris Bead with each of 4 treatments applied: waterstress pre-flowering, waterstress at flowering/pod set, waterstress at pod fill, control - no waterstress.

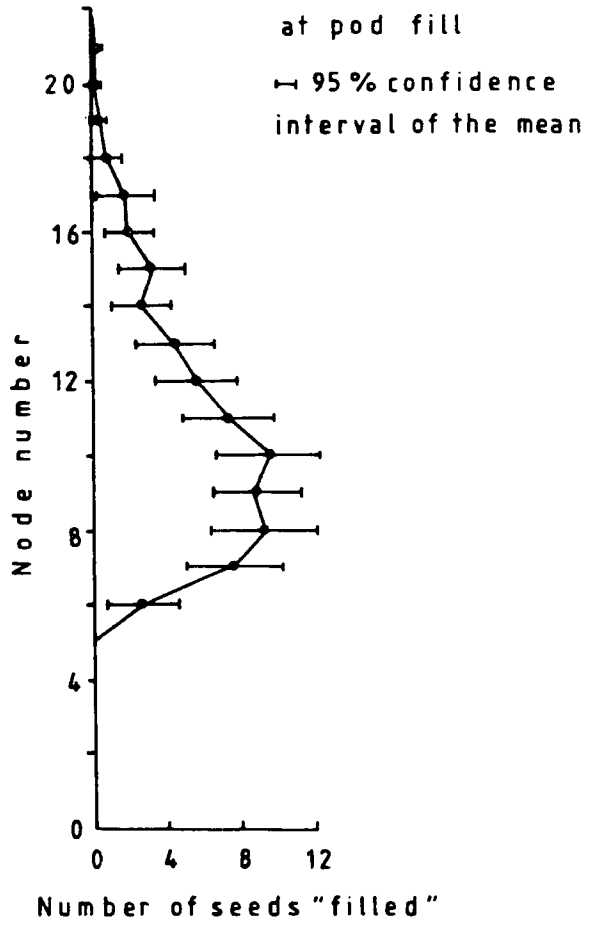
MB = Maris Bead

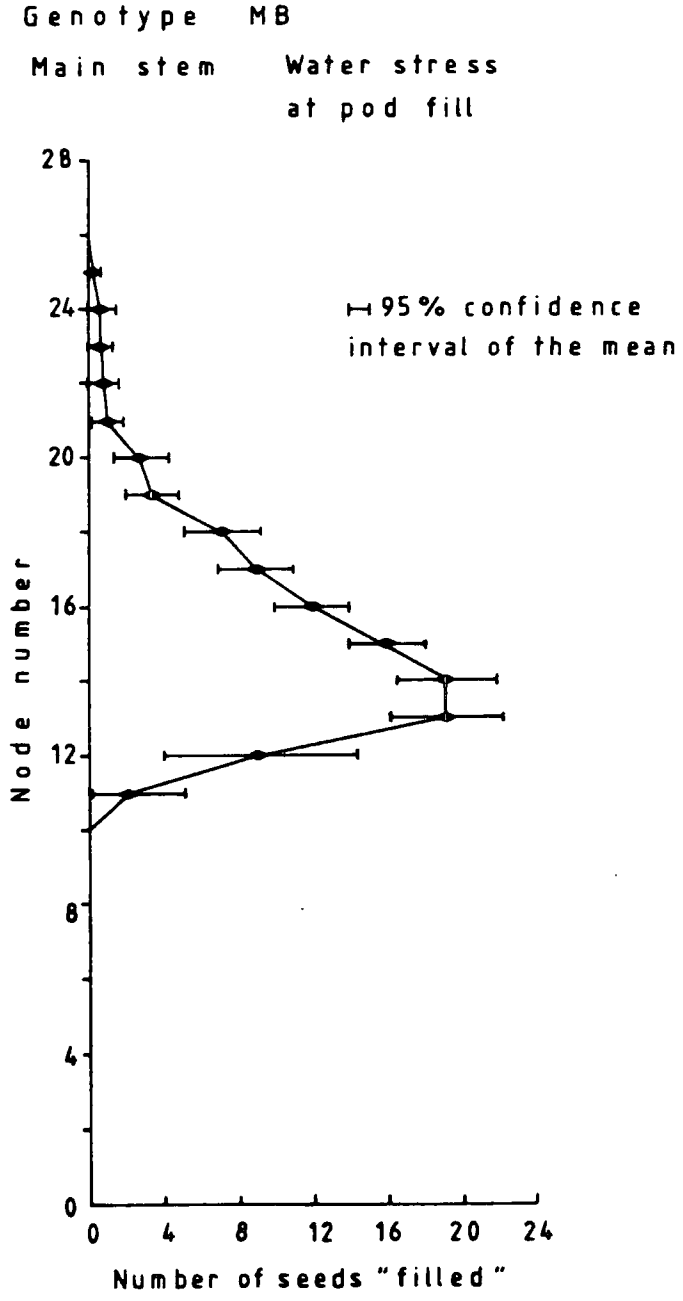

Genotype G
Main stem
Water stress
pre-flowering
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
0
4
8
12
Number of seeds "filled"


Genotype MB
Main stem
Water stress
pre-flowering
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
24
28
0
4
8
12
16
20
24
28
Number of seeds "filled"


Genotype G
Main stem
Water stress
at pod set
95% confidence
interval of the mean
Node number
Number of seeds "filled"
0
4
8
12
16
20


Genotype MB
Main stem
Water stress
at pod set
95% confidence
interval of the mean
Node number
Number of seeds "filled"
0
4
8
12
16
20
24
28


Genotype G
Main stem Water stress at pod fill
95% confidence interval of the mean
Node number
0
4
8
12
16
20
0
4
8
12
Number of seeds "filled"


Genotype MB
Main stem Water stress at pod fill
95% confidence interval of the mean
Node number
0
4
8
12
16
20
24
0
4
8
12
16
20
24
Number of seeds "filled"

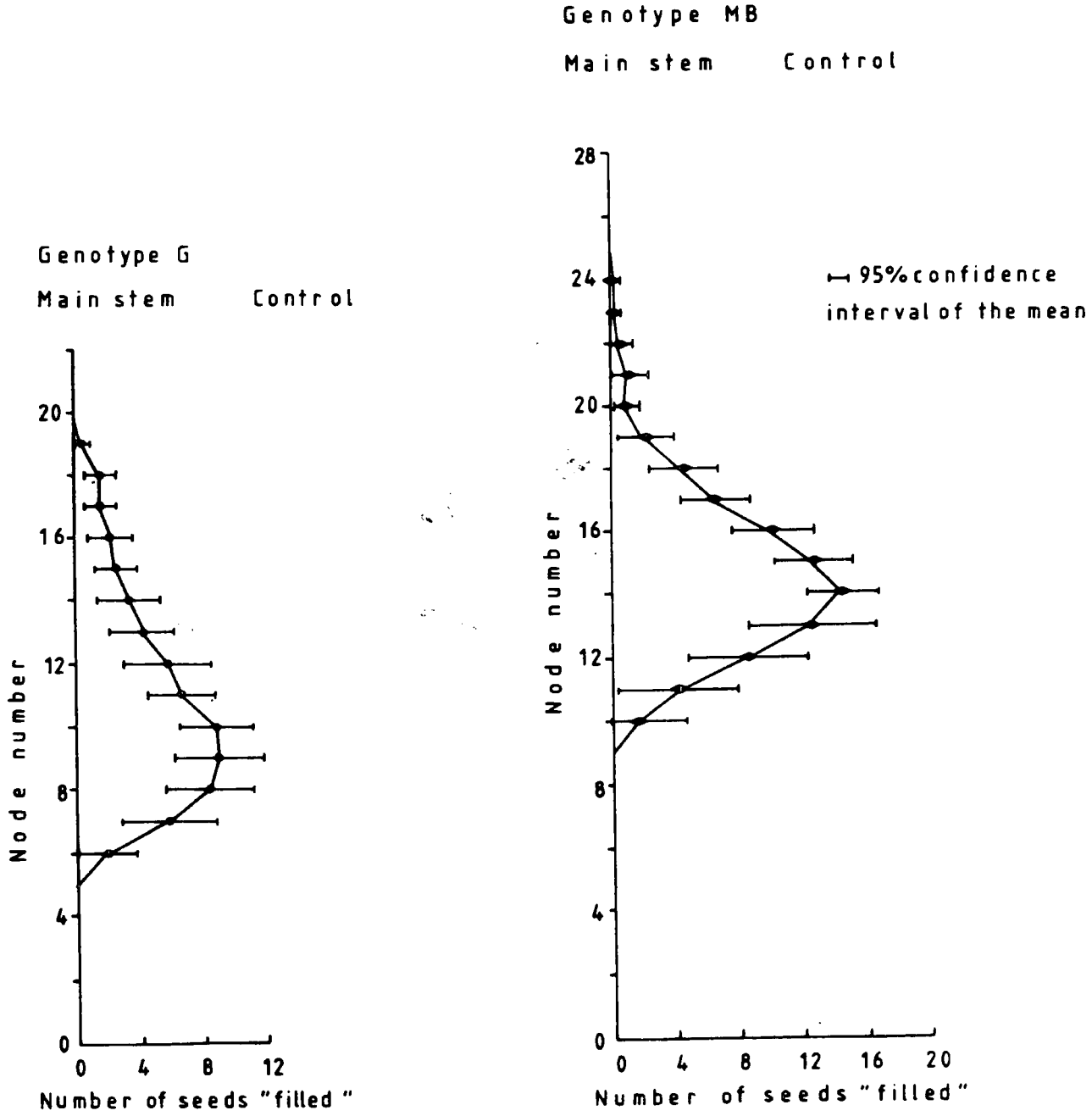
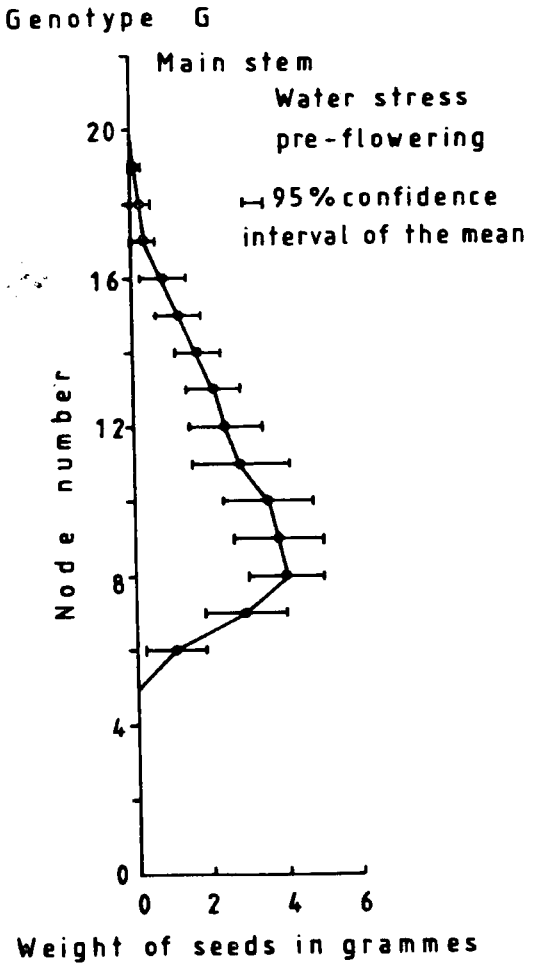
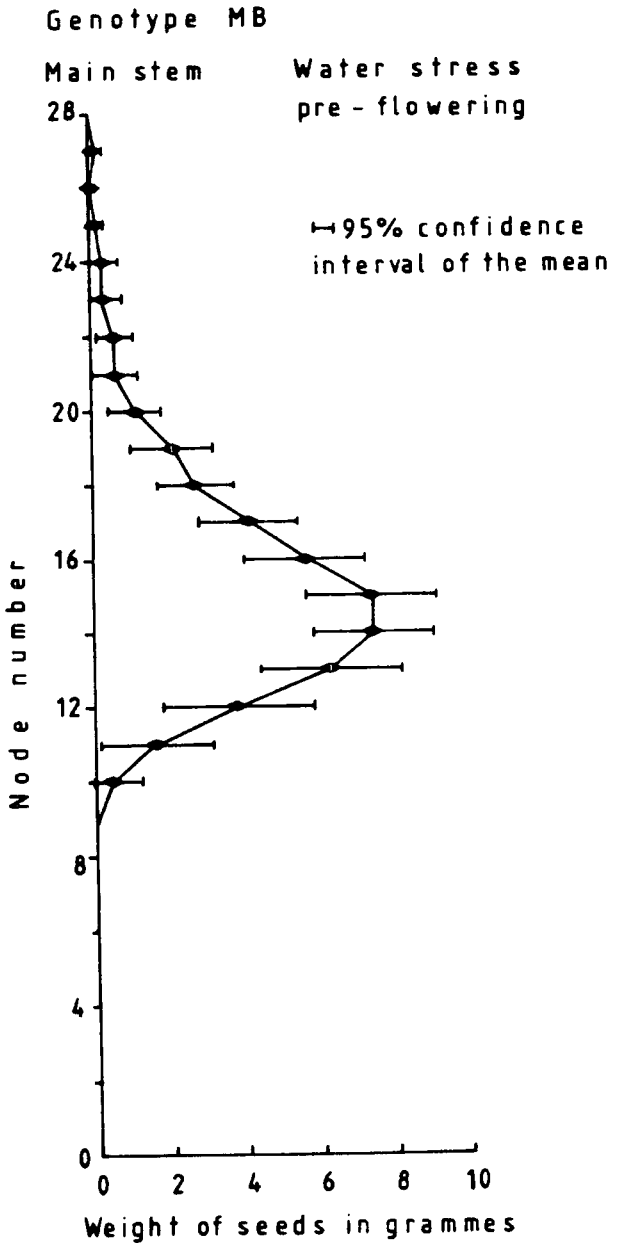
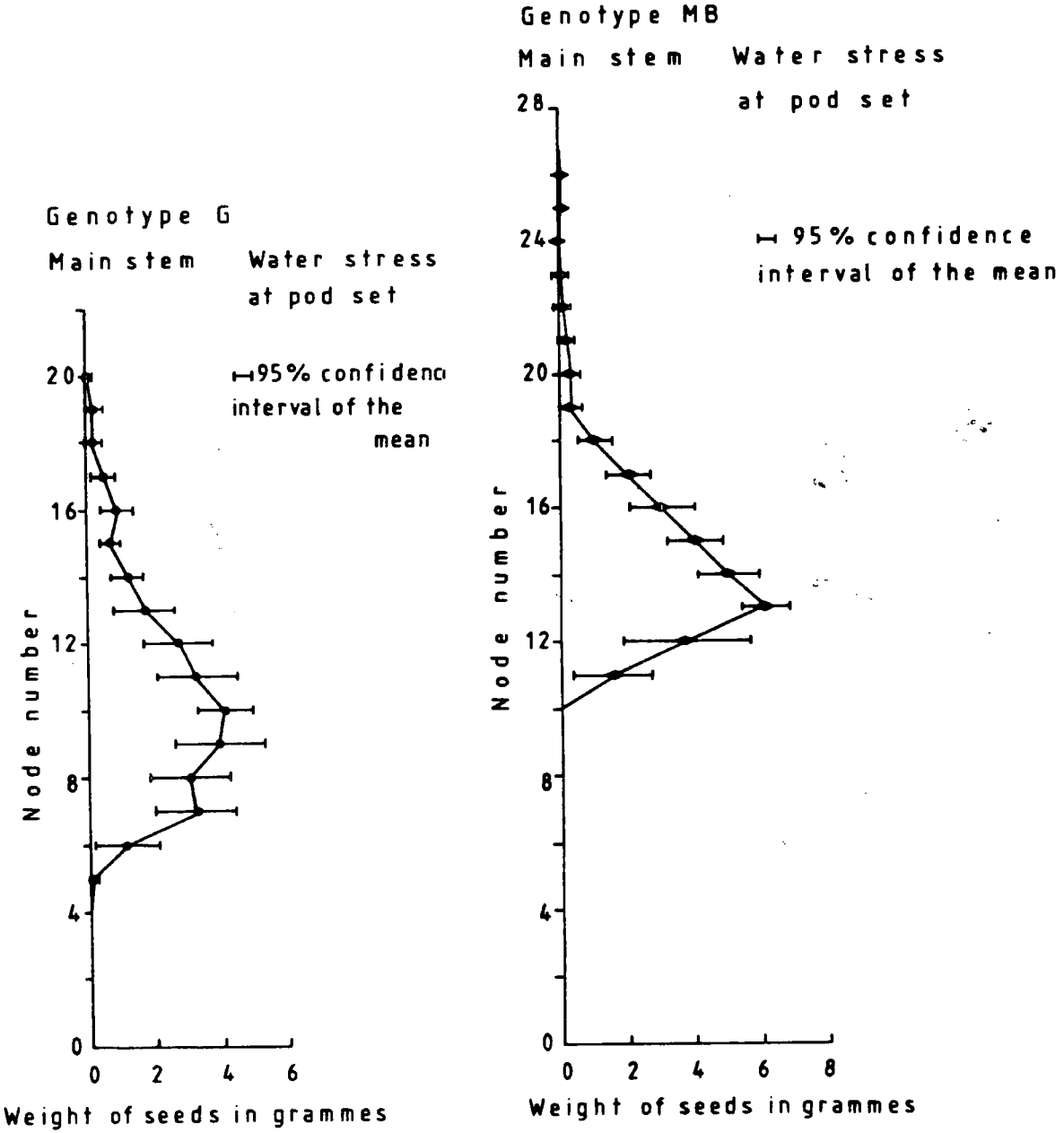

Genotype G
Main stem Control
Node number
Number of seeds "filled"
Genotype MB
Main stem Control
95% confidence interval of the mean
Node number
Number of seeds "filled"

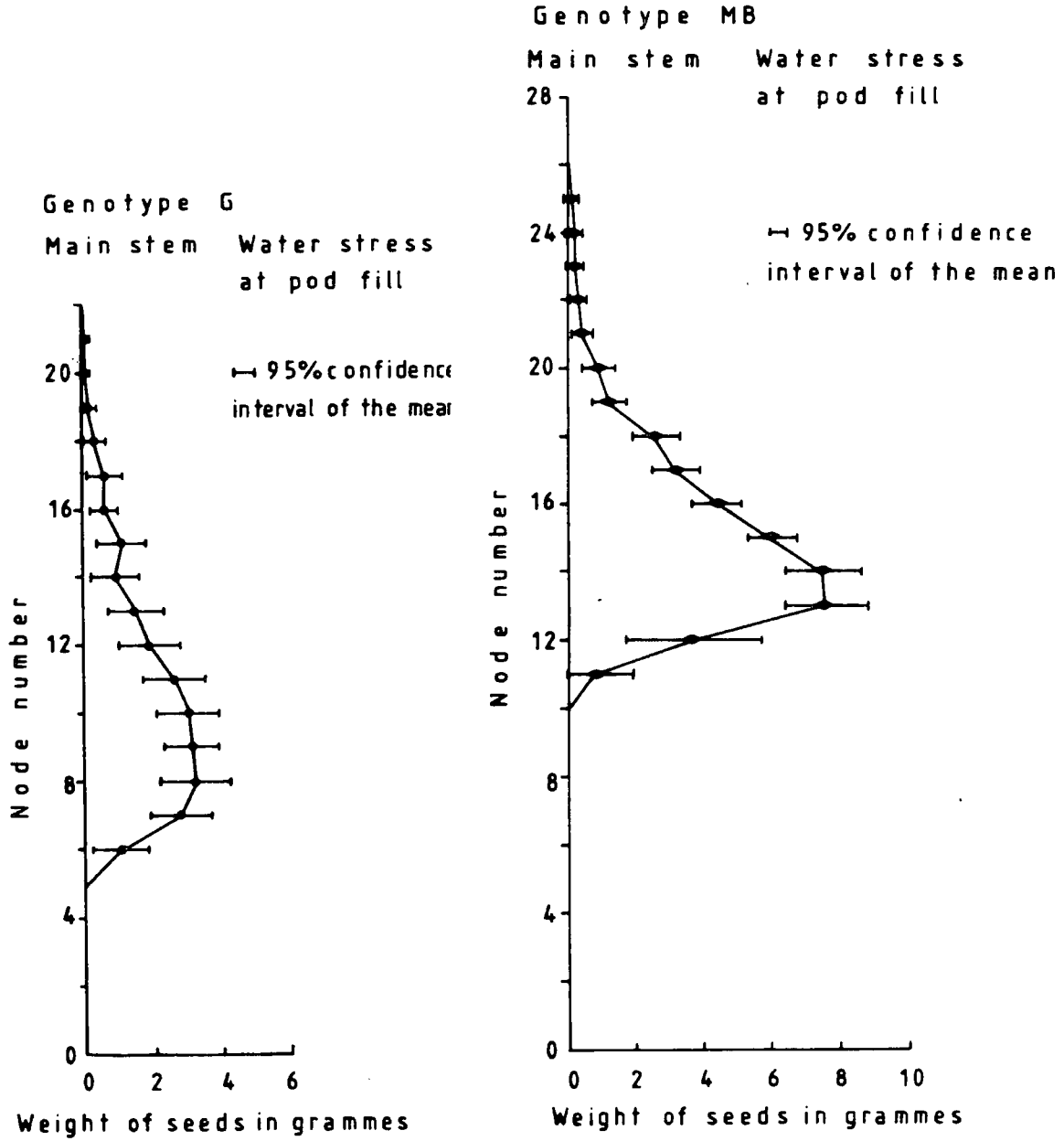
Figure 4.5.5 (see overleaf) Main stem profiles for weight of seeds at each node of genotypes G and Maris Bead with each of 4 treatments applied: waterstress pre-flowering, waterstress at flowering/pod set, waterstress at pod fill, control - no waterstress.

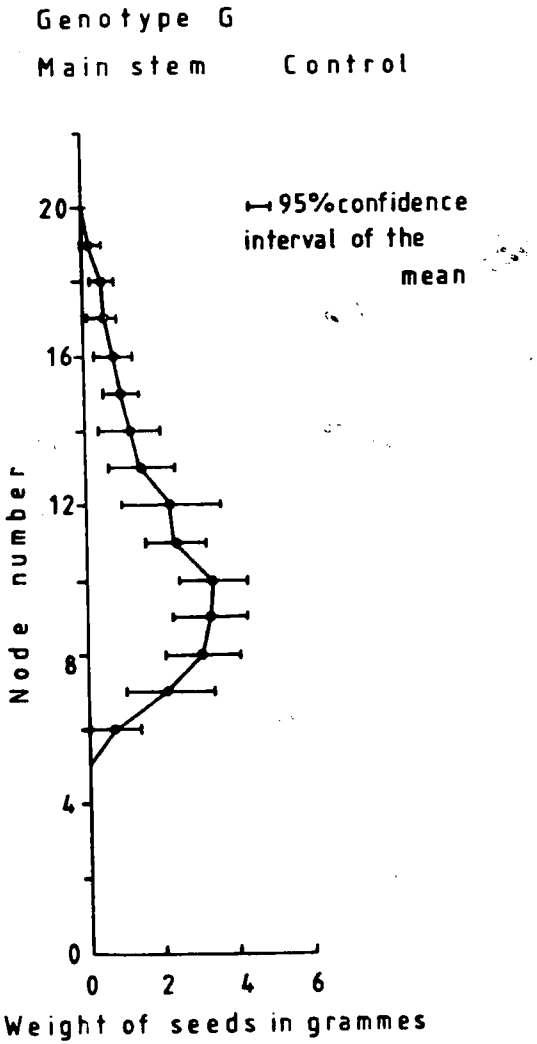
MB = Maris Bead

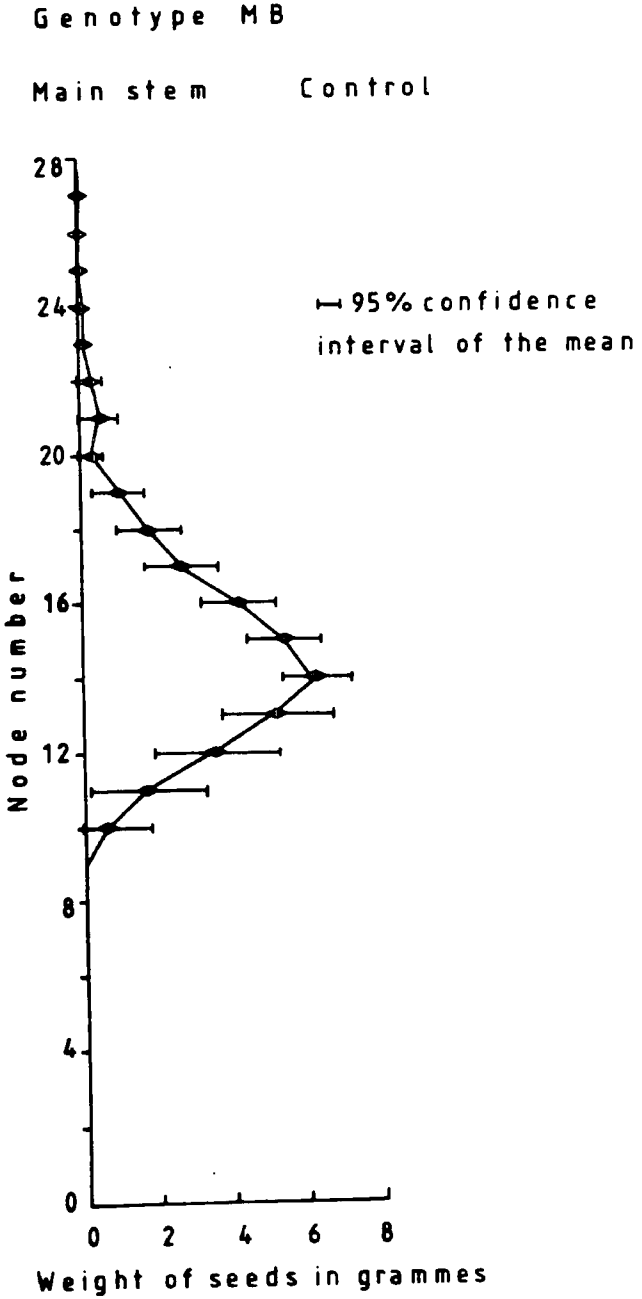

Genotype G
Main stem
Water stress
pre-flowering
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
0
2
4
6
Weight of seeds in grammes


Genotype MB
Main stem
Water stress
pre-flowering
95% confidence
interval of the mean
Node number
0
4
8
12
16
20
24
28
0
2
4
6
8
10
Weight of seeds in grammes


Genotype G
Main stem Water stress at pod set
⊢95% confidence interval of the mean
Node number
Weight of seeds in grammes
Genotype MB
Main stem Water stress at pod set
⊢ 95% confidence interval of the mean
Node number
Weight of seeds in grammes


Genotype G
Main stem Water stress at pod fill
95% confidence interval of the mean
Node number
Weight of seeds in grammes
Genotype MB
Main stem Water stress at pod fill
95% confidence interval of the mean
Node number
Weight of seeds in grammes


Genotype G
Main stem Control
95% confidence interval of the mean
Node number
0
4
8
12
16
20
0
2
4
6
Weight of seeds in grammes


Genotype MB
Main stem Control
95% confidence interval of the mean
Node number
0
4
8
12
16
20
24
28
0
2
4
6
8
Weight of seeds in grammes

CHAPTER 5

RESULTS OF STUDIES IN POD GROWTH AND DEVELOPMENT

5.1 Pod length growth

The mean values for pod length of each of the three genotypes showed that 22 and G followed a similar growth pattern (figure 5.1), G grew slightly more slowly than 22, but both attained a similar final length. Maris Bead grew more slowly than either of the other genotypes, but attained a greater final pod length.

Results of analysis of variance (table 5.1.1) showed that during early pod development, during late pod development, and at pod maturity, significant inter-genotypic differences in pod length were detected. Examination of the differences found by least significant differences showed the differences to be due to genotypic variations in growth pattern (table 5.1.2). Significant differences detected at anthesis (table 5.1.2(a)) were due to the shorter ovary of genotype 22 compared with those of the other genotypes. Differences found in early pod development were due to the rapid growth of pods of 22 to lengths significantly greater than that of at least one other genotype (table 5.1.2(c), (d), (e), (f)). At late pod development and at pod maturity the differences found were due to the greater length of Maris Bead pods compared with those of either 22 or G (table 5.1.2(l), (n)).

5.2 Pod wall structure

Examination of the sections showed clear differences in structure between the genotypes investigated (plate 2). All genotypes showed a lignified 'hinge' structure along the adaxial pod vein (plate 2(a), (c), (e)).

The difference between the genotypes was in the pattern of lignification of the pod wall mesocarp. Genotype 22 showed no thickening at all (plate 2(b)), genotype G showed a discontinuous

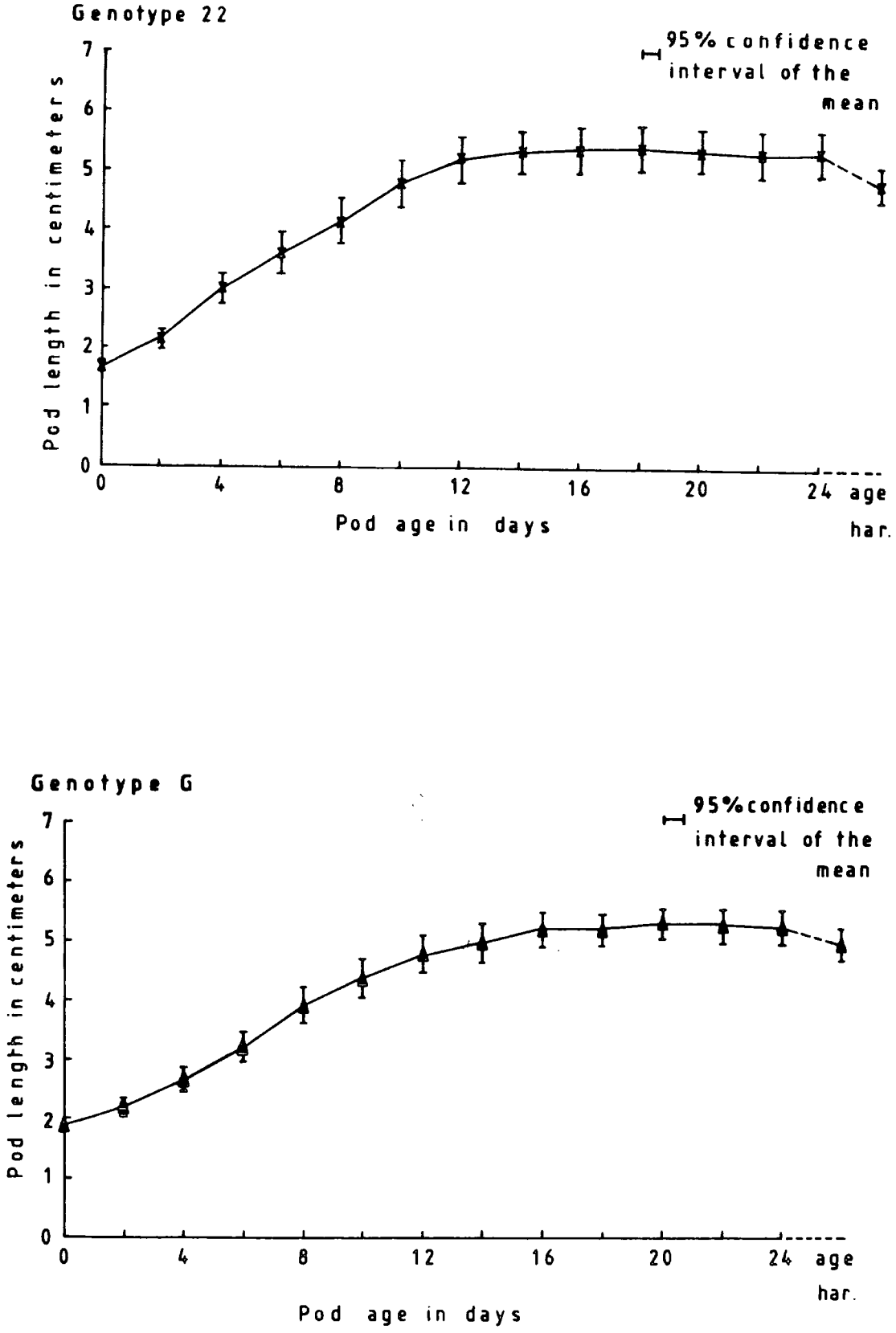


Figure 5.1 Mean pod lengths of genotypes 22, G and Maris Bead during growth and at maturity (age har).

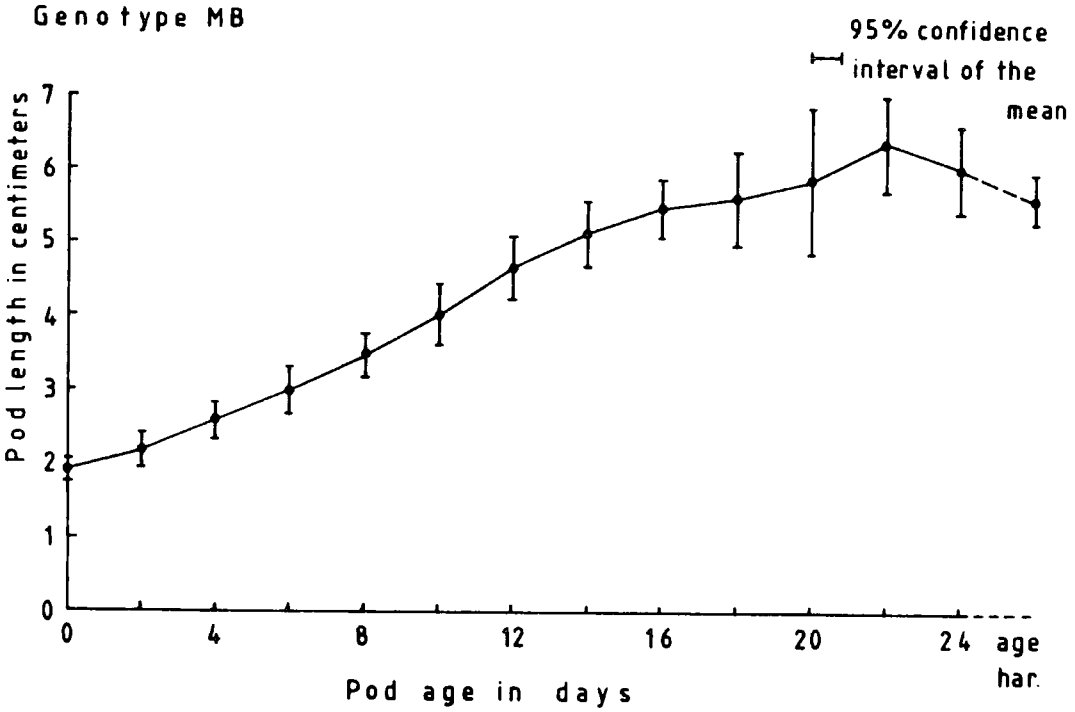


Figure 5.1 (continued)

Table 5.1.1

Summary of analysis of variance performed on measured pod length, at the various ages recorded, in order to discover at which ages differences between genotypes occurred.

Pod age in days	F Ratio	F Probability
0	3.9165	*
2	0.1914	n.s.
4	3.0419	n.s.
6	3.6859	*
8	3.4253	*
10	3.5027	*
12	2.1106	n.s.
14	1.1976	n.s.
16	0.8263	n.s.
18	1.3833	n.s.
20	1.2794	n.s.
22	3.3737	*
24	0.4973	n.s.
Mature pod	6.4794	**

n.s. non-significant

* $p \leq 0.05$

** $p \leq 0.01$

Table 5.1.2

Locations of inter-genotypic differences found by analysis of variance (table 5.1.1).

(a) 0 day old pod

			Genotype	
Mean	Genotype	22	G	Maris Bead
1.6870	22			
1.9231	G	**		
1.9176	Maris Bead	*		

(b) 2 day old pod

No significant differences found

(c) 4 day old pod

			Genotype	
Mean	Genotype	22	G	Maris Bead
3.0043	22			
2.6667	G	*		
2.5765	Maris Bead	*		

(d) 6 day old pod

			Genotype	
Mean	Genotype	22	G	Maris Bead
3.5957	22			
3.2051	G	*		
2.9765	Maris Bead	*		

(e) 8 day old pod

			Genotype	
Mean	Genotype	22	G	Maris Bead
4.1565	22			
3.8821	G			
3.4588	Maris Bead	*		

(f) 10 day old pod

			Genotype	
Mean	Genotype	22	G	Maris Bead
4.7870	22			
4.3487	G			
4.0118	Maris Bead	*		

Table 5.1.2. continued

(g) 12 day old pod

No significant difference detected.

(h) 14 day old pod

No significant difference detected.

(i) 16 day old pod

No significant difference detected.

(j) 18 day old pod

No significant difference detected.

(k) 20 day old pod

No significant difference detected.

(l) 22 day old pod

Mean	Genotype	Genotype 22	G	Maris Bead
5.2957	22			
5.2412	G			
6.3500	Maris Bead	*	*	

(m) 24 day old pod

No significant difference detected.

(n) Mature pod

Mean	Genotype	Genotype 22	G	Maris Bead
4.8130	22			
4.9282	G			
5.6176	Maris Bead	**	**	

* $p \leq 0.05$

** $p \leq 0.01$

Plate 2

Fluorescence micrographs of transverse sections of fully grown pods.

(a) Genotype 22 - adaxial pod vein.

(b) Genotype 22 - pod wall.

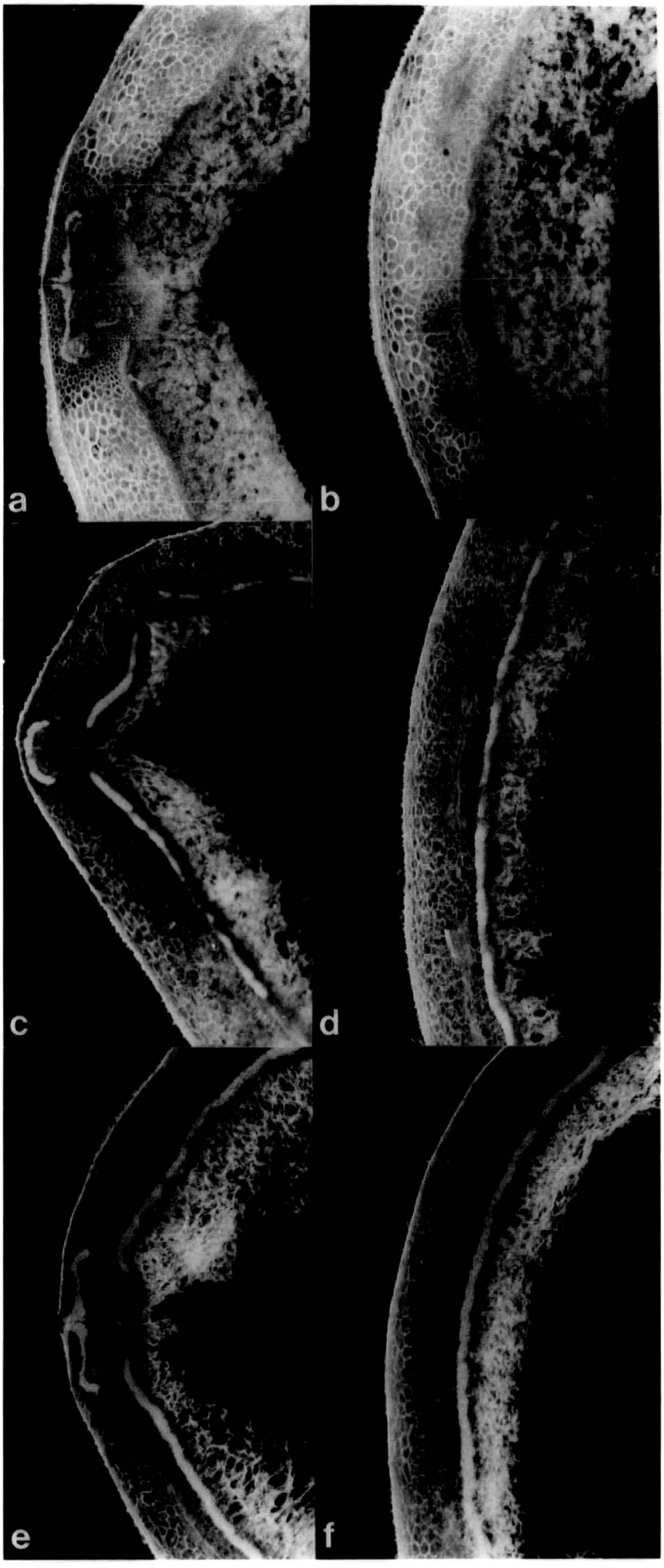
(c) Genotype G - adaxial pod vein.

(d) Genotype G - pod wall.

(e) Genotype Maris Bead - adaxial pod vein.

(f) Genotype Maris Bead - pod wall.

Scale: 1cm. on plate represents 0.364mm. tissue


a
b
c
d
e
f

lignified layer, a 'platy' structure (plate 2(d)). In genotype Maris Bead the lignified tissue formed a continuous layer (plate 2(f)).

The measured thickness of the lignified mesocarp layer varied between genotypes (table 5.2.1), G having a thinner layer than Maris Bead.

Table 5.2.1

Measured thickness of the lignified pod wall layer in the genotypes investigated.

Genotype	Thickness of lignified layer
22	- none present
G	80 µm
Maris Bead	135 µm

5.3 Distribution of hairs and stomate pores on the pod surface

From plate 3 it was seen that there were more hairs found on pods of genotype 22 than on those of G or Maris Bead. No such inter-genotypic difference in density of stomata was immediately apparent. The counts per unit area of stomata and pod wall hairs (table 5.3.1) bore out the evidence seen in the SEM, pods of 22 being hairier than those of G or Maris Bead.

Analysis of variance of number of stomata revealed no significant difference between genotypes (table 5.3.2). Analysis of number of pod hairs did, however, show a highly significant inter-genotypic difference (table 5.3.3). Further examination of this result by least significant differences showed no significant difference between G and Maris Bead, but both those genotypes had mean numbers of hairs per unit area highly significantly less than that of genotype 22 (table 5.3.4).

Plate 3

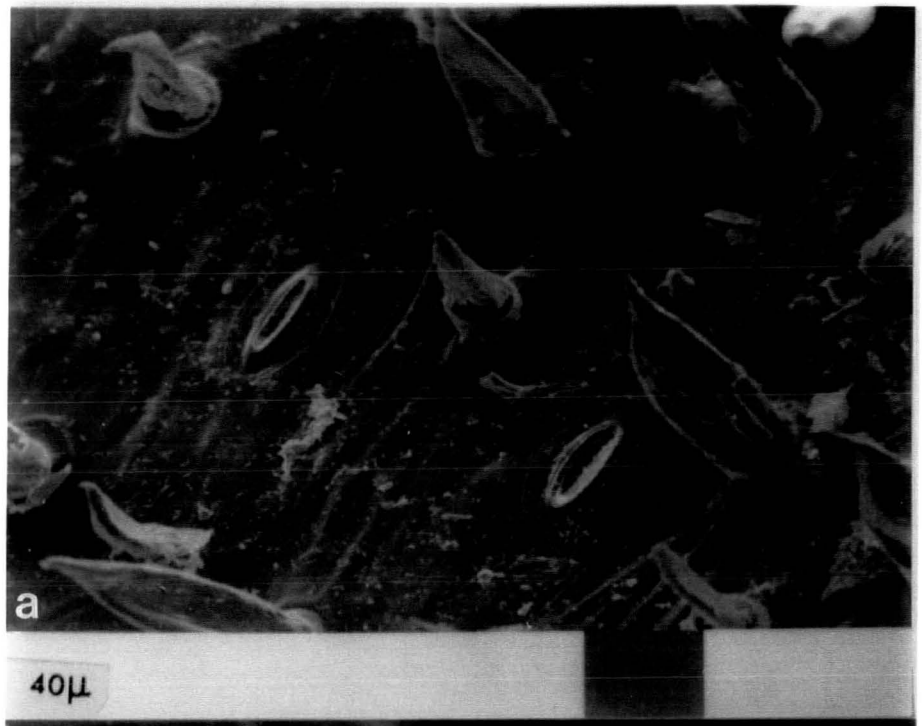
Scanning electron micrographs of external pod wall surfaces.

(a) Genotype 22.

(b) Genotype G.

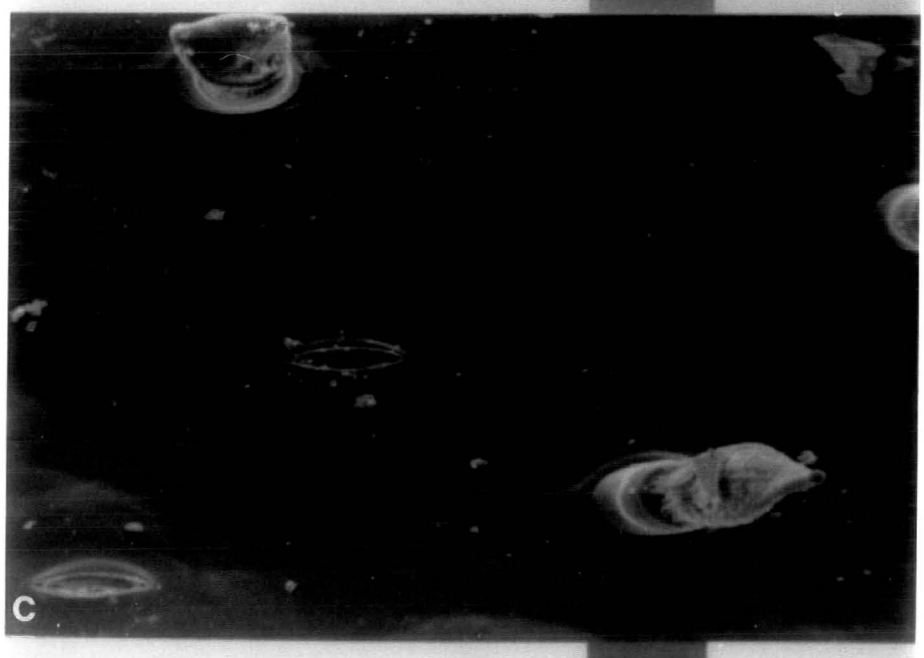
(c) Genotype Maris Bead.

Scale: lcm. on plate represents 0.025mm. tissue



40μ

40μ



40μ

Table 5.3.1

Counts of numbers of stomata and pod wall hairs visible in each of 10 fields of view under the fluorescence microscope at magnification x 100.

Field of View	Genotype 22		Genotype G		Genotype Maris Bead	
	Stomates	Hairs	Stomates	Hairs	Stomates	Hairs
1	5	43	11	17	12	23
2	7	36	9	24	13	21
3	5	34	12	27	12	22
4	9	38	8	27	7	24
5	6	39	8	27	9	17
6	8	49	10	22	7	18
7	8	43	13	22	10	17
8	9	36	8	25	8	22
9	10	49	11	28	6	24
10	13	52	9	35	9	31
Total	80	419	99	254	93	228
Mean	8.0	41.9	9.9	25.4	9.3	22.8

Table 5.3.2

Analysis of variance of number of stomate pores per field of view in genotypes 22, G and Maris Bead.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotypes	2	18.8667	9.4333	1.8867	n.s.
Error	27	135.0000	5.0000		
Corrected Total	29	153.8667			

Table 5.3.3

Analysis of variance of number of pod hairs per field of view in genotypes 22, G and Maris Bead.

Source of Variation	Degrees Freedom	Sum of Squares	Mean Square	F Ratio	F Probability
Genotypes	2	2281.6667	1140.8333	42.7694	***
Error	27	720.2000	26.6741		
Corrected Total	29	3001.8667			

n.s. non-significant

*** $p \leq 0.001$

Table 5.3.4

Results of analysis of the mean numbers of pod wall hairs per field of view by least significant differences.

		Genotype		
Mean	Genotype	22	G	Maris Bead
41.900	22			
25.400	G	***		
21.900	Maris Bead	***		

*** $p \leq 0.001$

CHAPTER 6

RESULTS OF STUDIES OF THE CHANGES IN FRESH AND DRY WEIGHTS OF REPRODUCTIVE TISSUES DURING DEVELOPMENT FROM ANTHESIS TO MATURITY

From plots of fresh weight increases in peduncles (figure 6.1), pedicels (figure 6.2), pods (figure 6.3) and seeds (figure 6.4) a scattered distribution of points was visible, although the graphs were somewhat lacking in definition trends in growth were visible. An early, rapid increase in fresh weight of pedicels (figure 6.2), pods (figure 6.3) and seeds (figure 6.4) of genotype 22, compared with those of G and Maris Bead, was visible. Maris Bead showed the greatest, most rapid increase in fresh weight of peduncles (figure 6.1).

Plots of dry weight increases for each plant part revealed a similar pattern to that shown on fresh weight plots; on these plots, however, the points were less scattered and the trends more clearly visible (figures 6.5, 6.6, 6.7, 6.8). There was a clearly visible trend in developmental sequence, for each genotype the peduncle (figure 6.5) was first to increase in dry weight, then the pedicel (figure 6.6), then the pod (figure 6.7), and finally the seed (figure 6.8).

By plotting the log (fresh weight/initial fresh weight) the scatter of the points was greatly reduced. The various parts increased in relative fresh weight by differing orders of magnitude. In all three genotypes the peduncle increased by around 10^4 during development (figure 6.9), the pedicel by around 10^6 (figure 6.10), the pod by around 10^6 (figure 6.11), and the seed by around 10^{10} (figure 6.12). The rapid weight increase of all parts of genotype 22 was clearly visible.

The plots of log (dry weight/initial dry weight) showed the relative increase in dry weight of peduncles (figure 6.13), pedicels (figure 6.14), and pods (figure 6.15) of genotype 22 to be one or two orders of magnitude greater than those of genotypes G or Maris Bead. The relative increase in dry weight of seeds was, however, of the same order of magnitude in all three genotypes (figure 6.16). An early, extremely repaid increase in relative dry weight of all parts of genotype 22 was clearly visible.

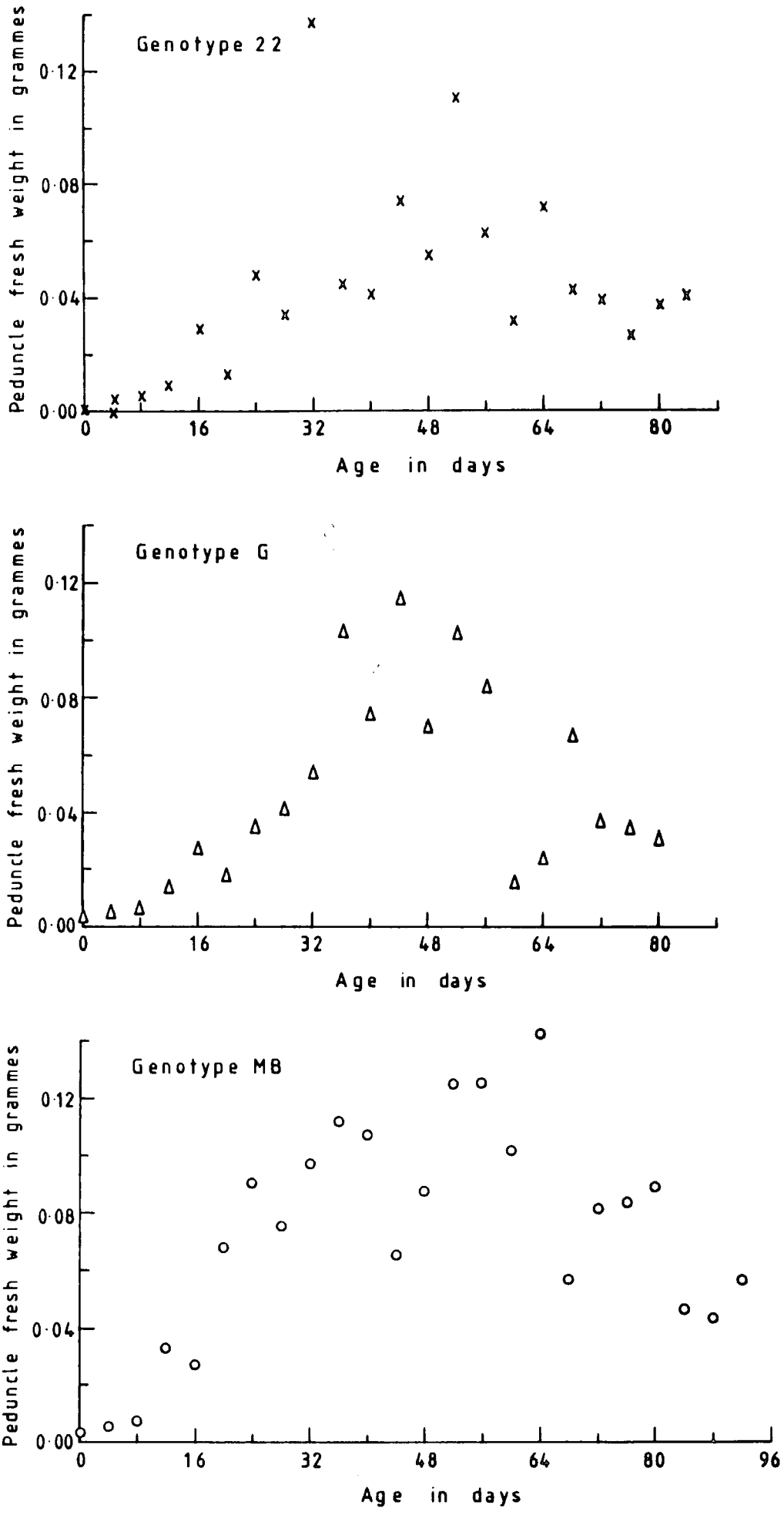


Figure 6.1 Change in peduncle fresh weight from anthesis to maturity.

MB = Maris Bead

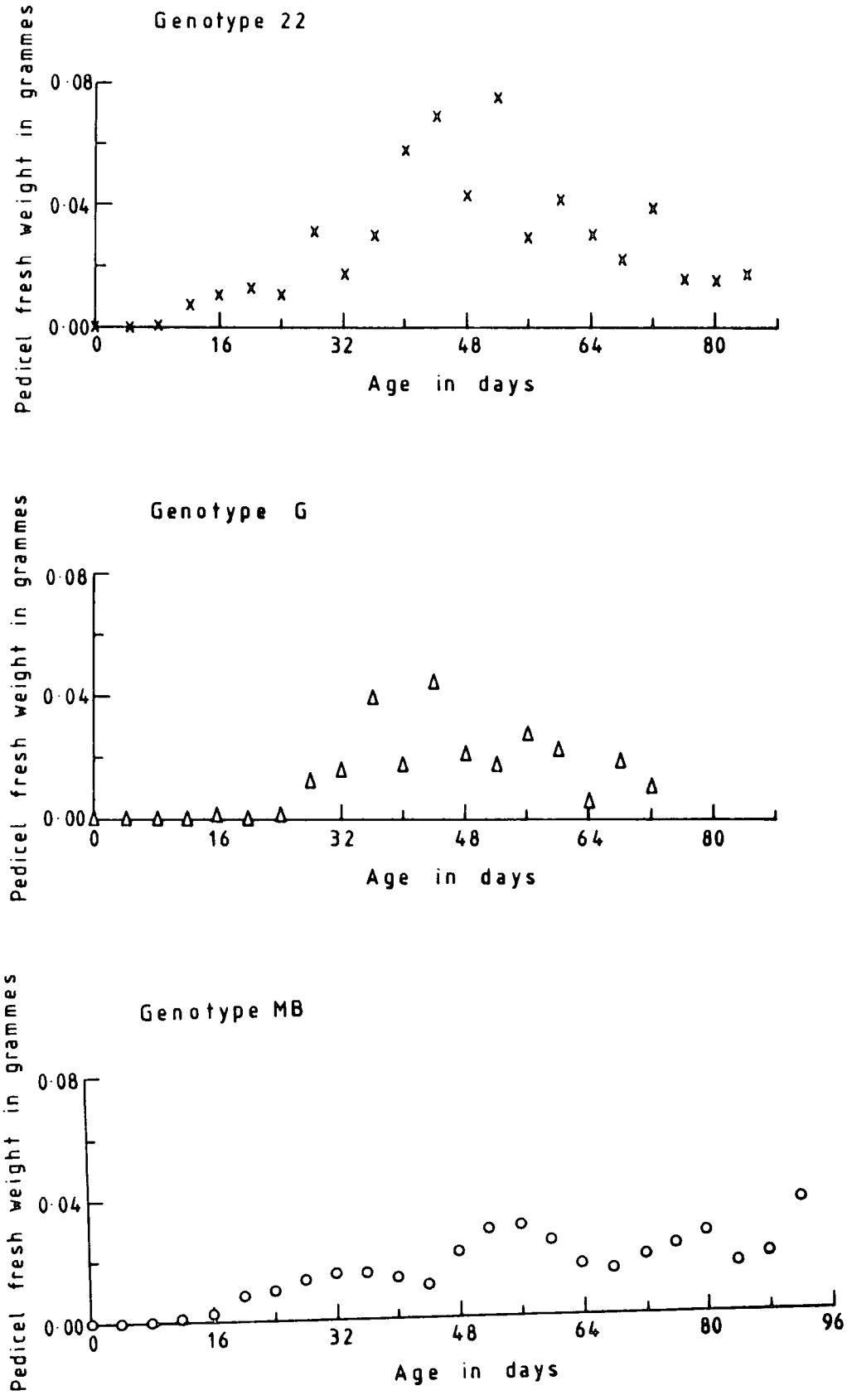
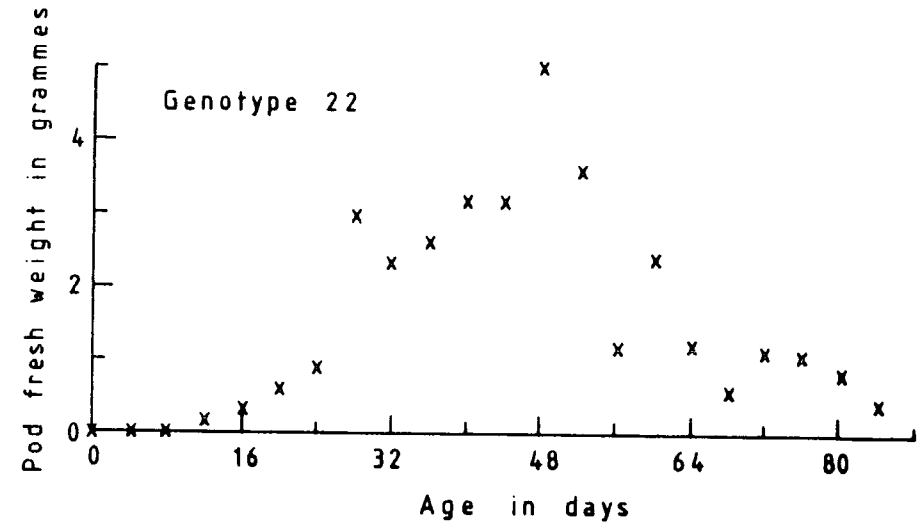
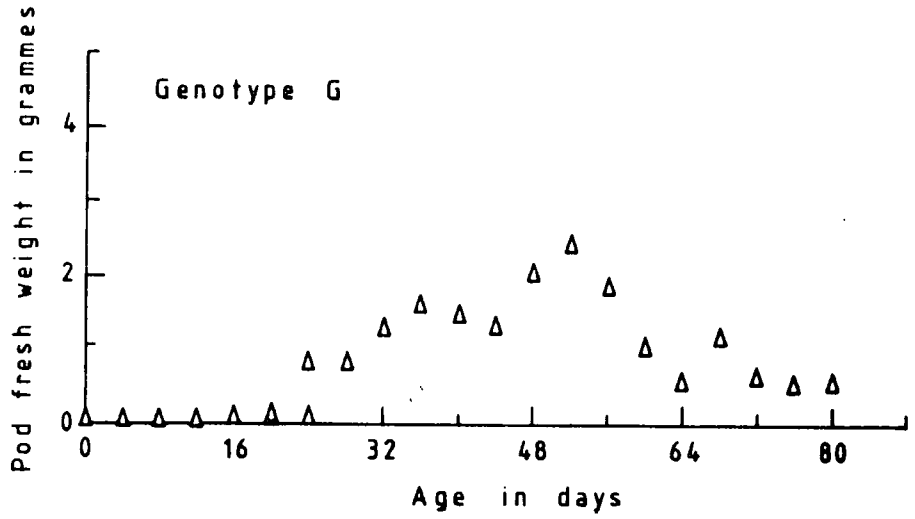


Figure 6.2 Change in pedicel fresh weight from anthesis to maturity.

MB = Maris Bead





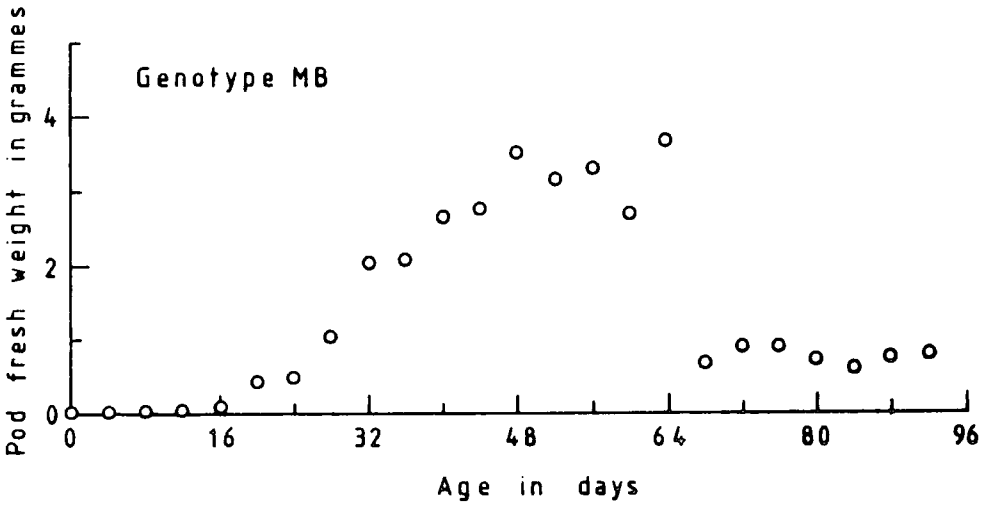
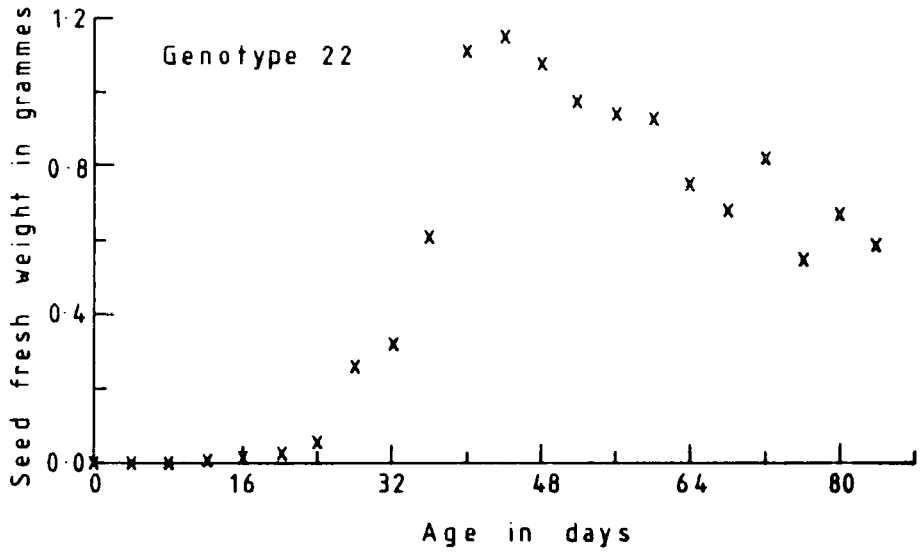
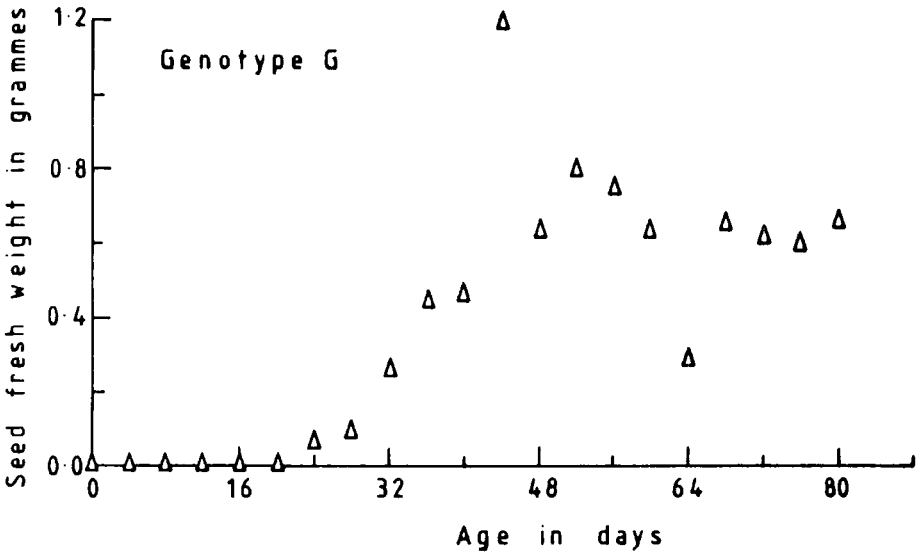


Figure 6.3 Change in pod fresh weight from anthesis to maturity.

MB = Maris Bead





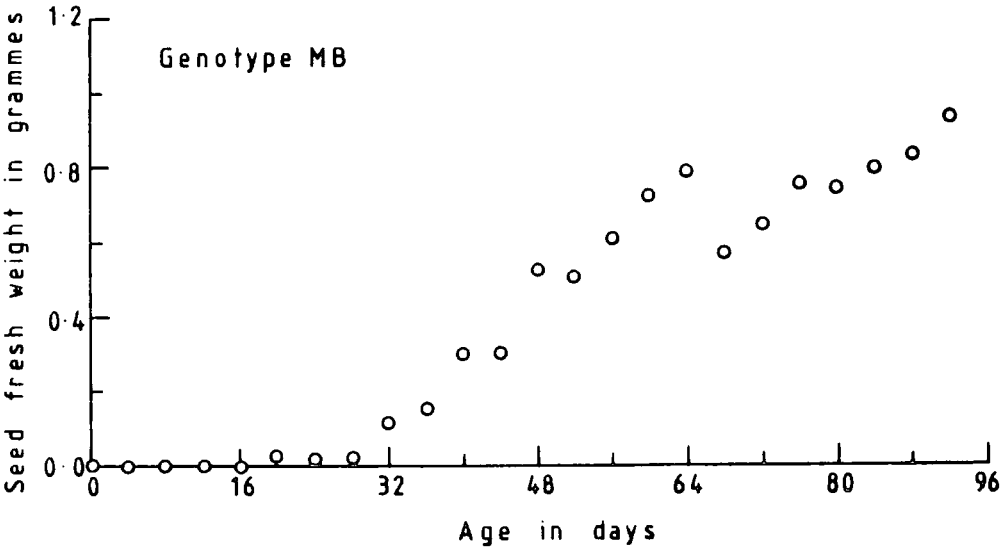
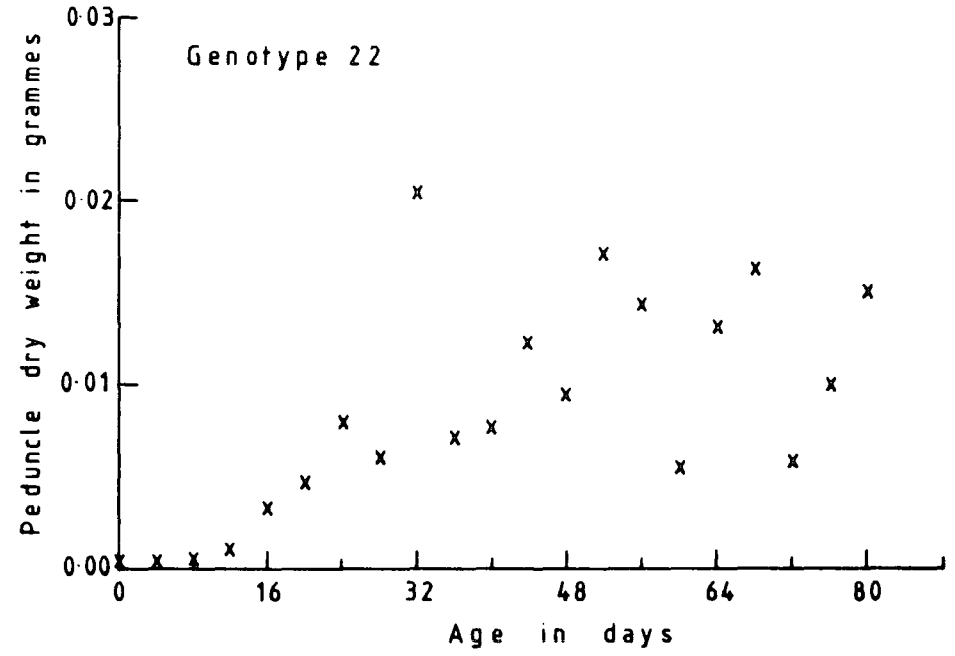
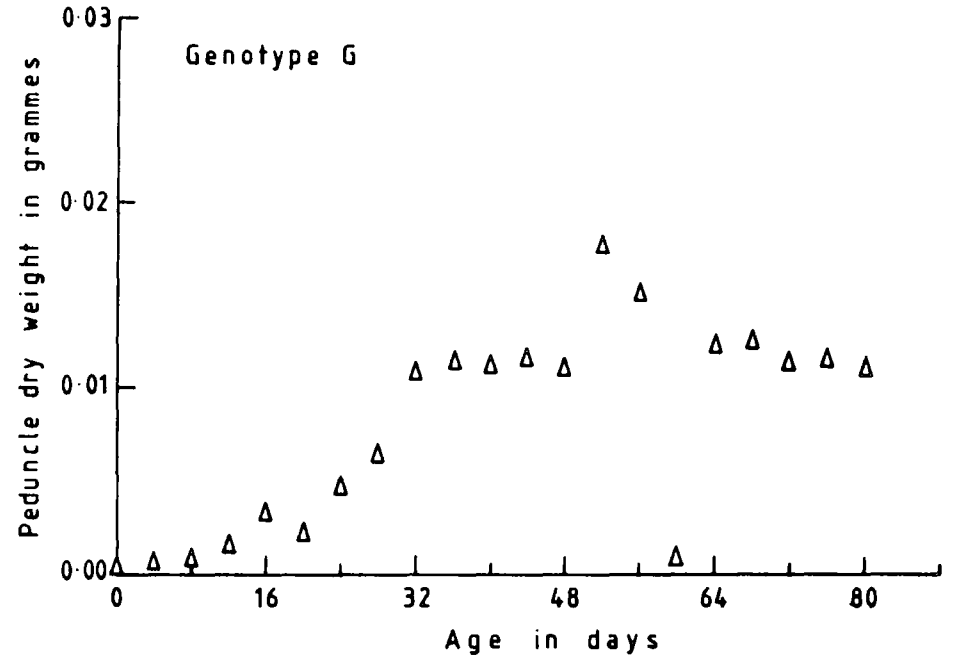


Figure 6.4 Change in seed fresh weight from anthesis to maturity.

MB = Maris Bead





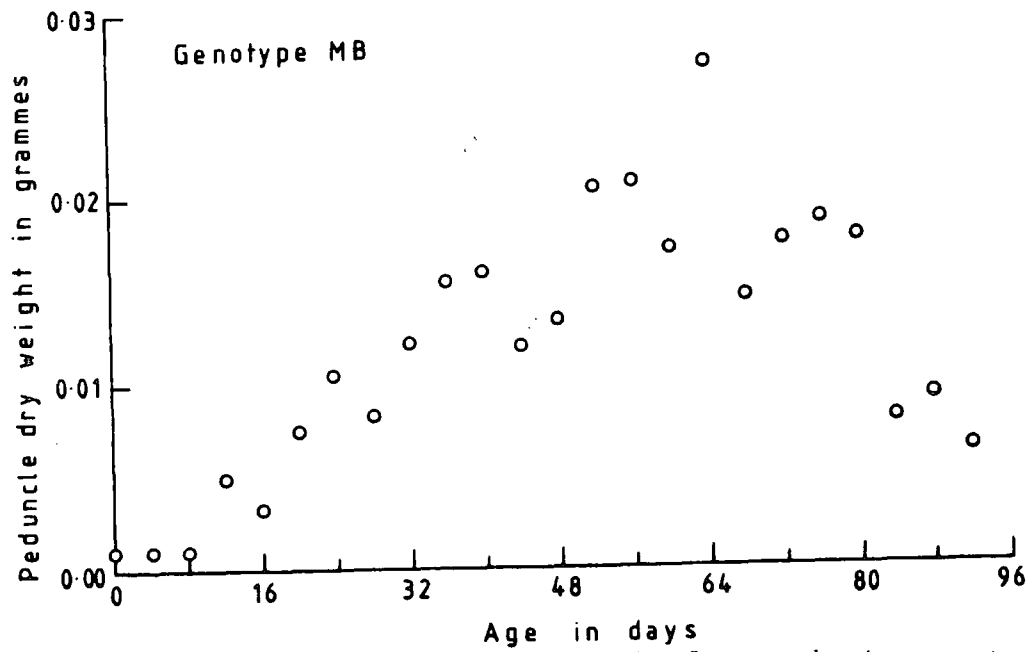


Figure 6.5 Change in peduncle dry weight from anthesis to maturity.
MB = Maris Bead

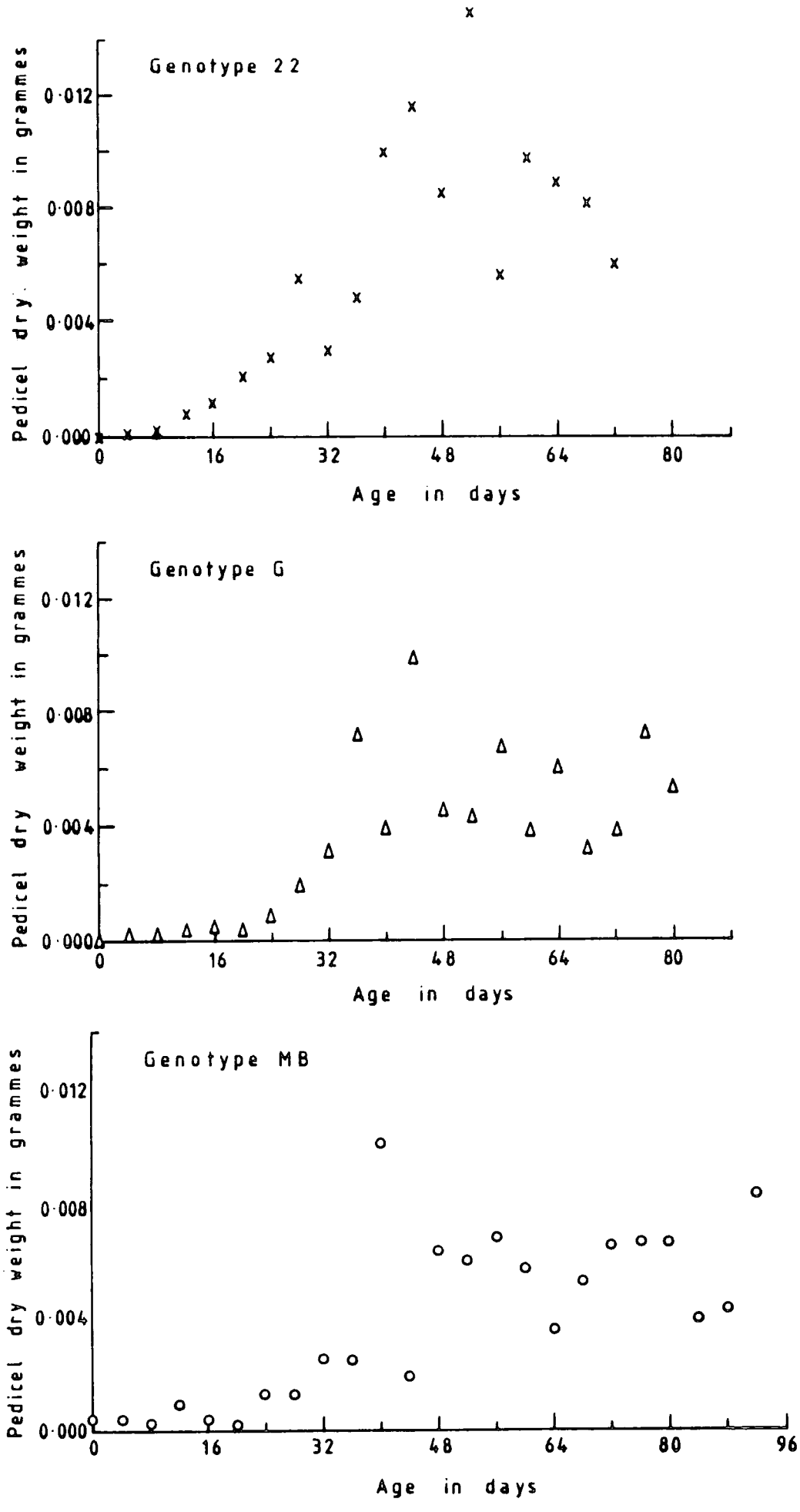
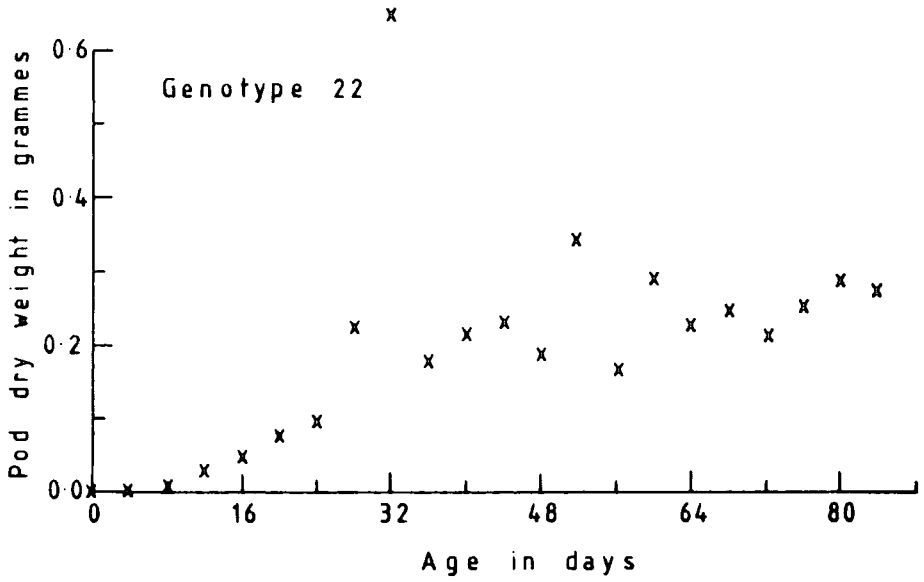
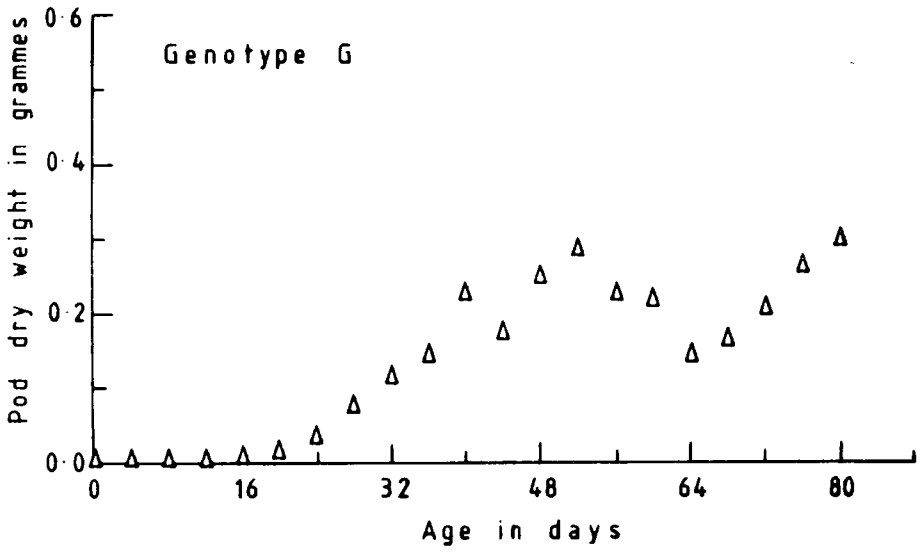


Figure 6.6 Change in pedicel dry weight from anthesis to maturity.
MB = Maris Bead





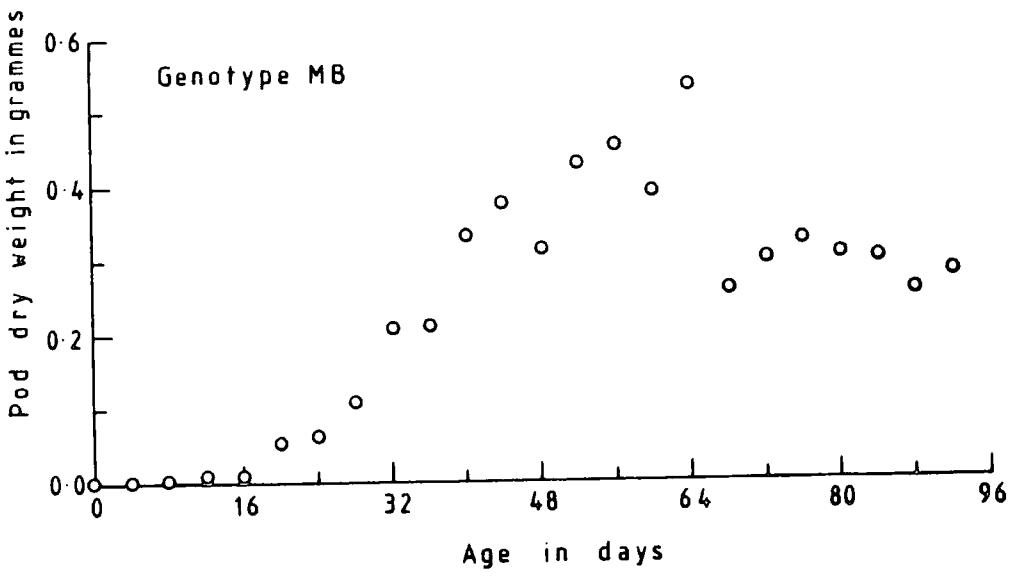


Figure 6.7 Change in pod dry weight from anthesis to maturity.
MB = Maris Bead

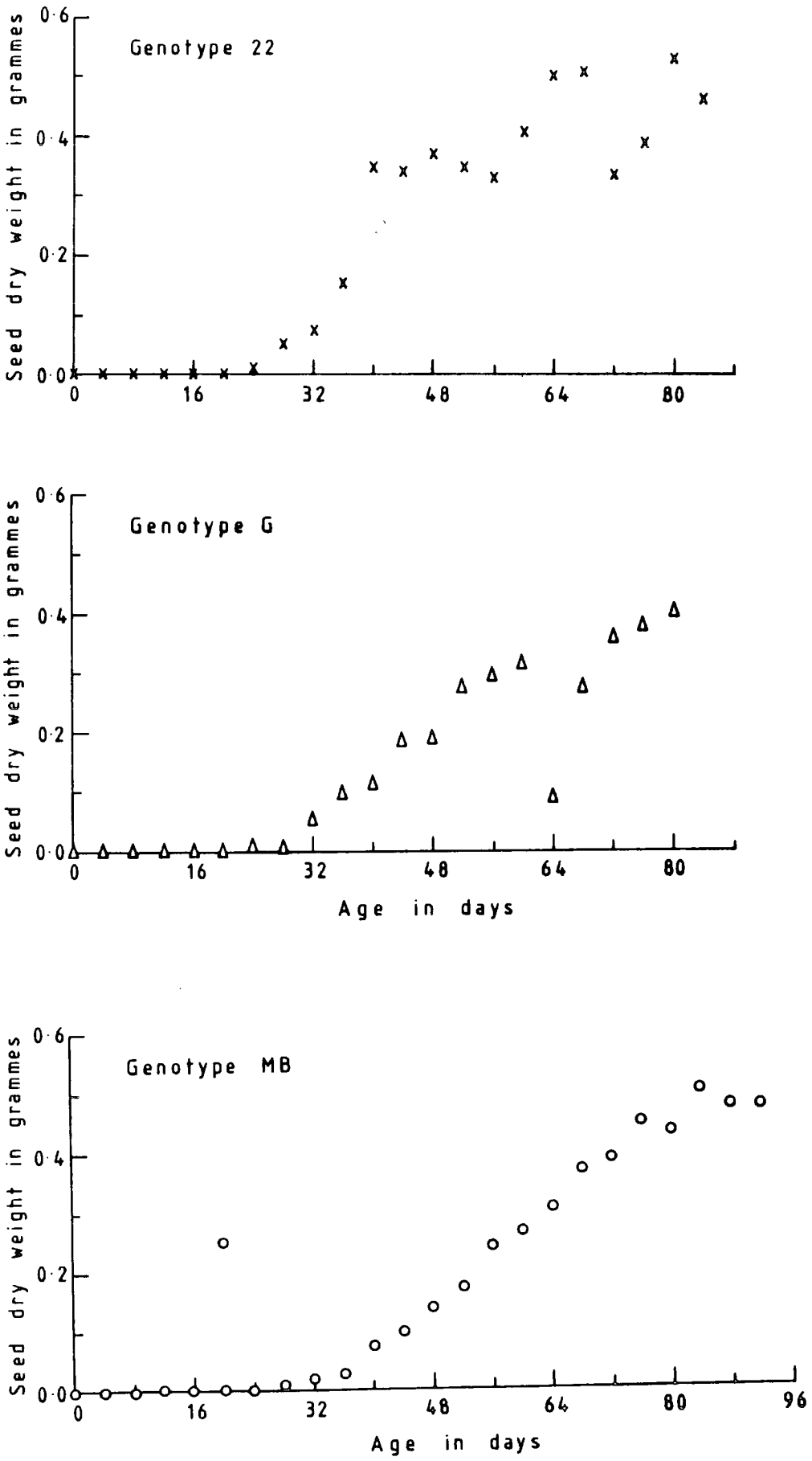
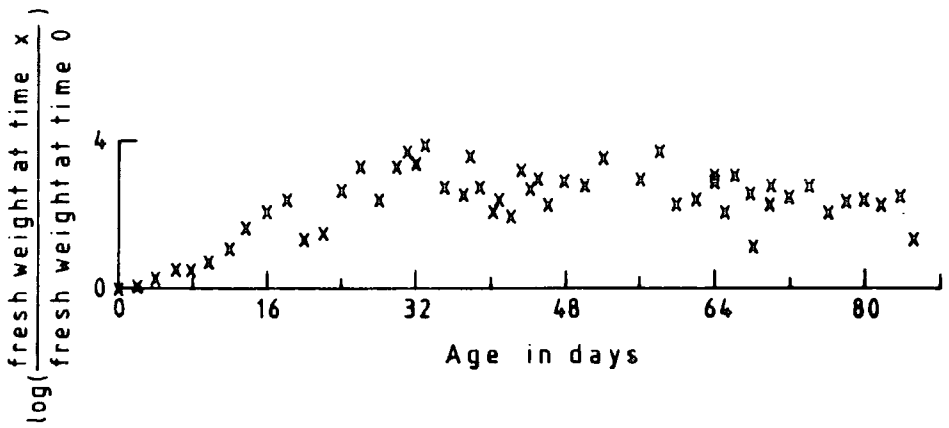
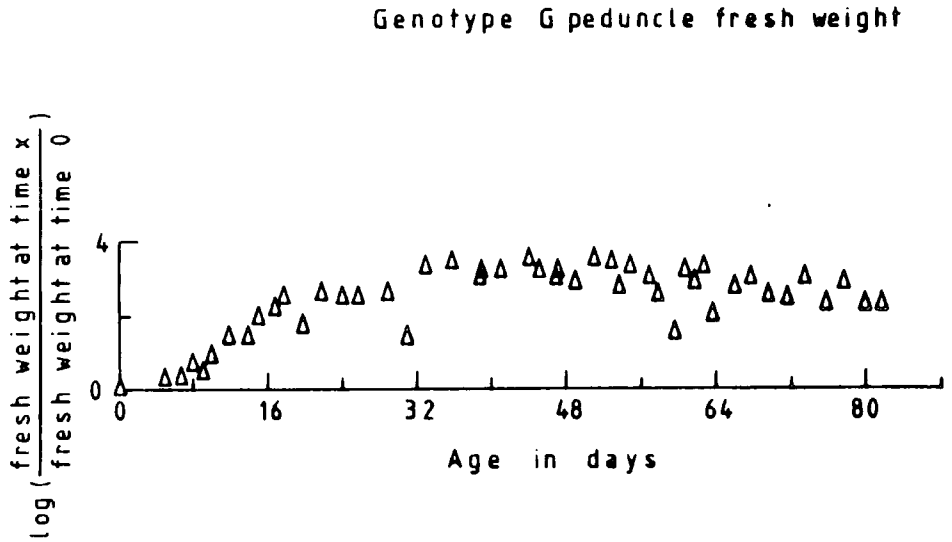


Figure 6.8 Change in seed dry weight from anthesis to maturity.
MB = Maris Bead





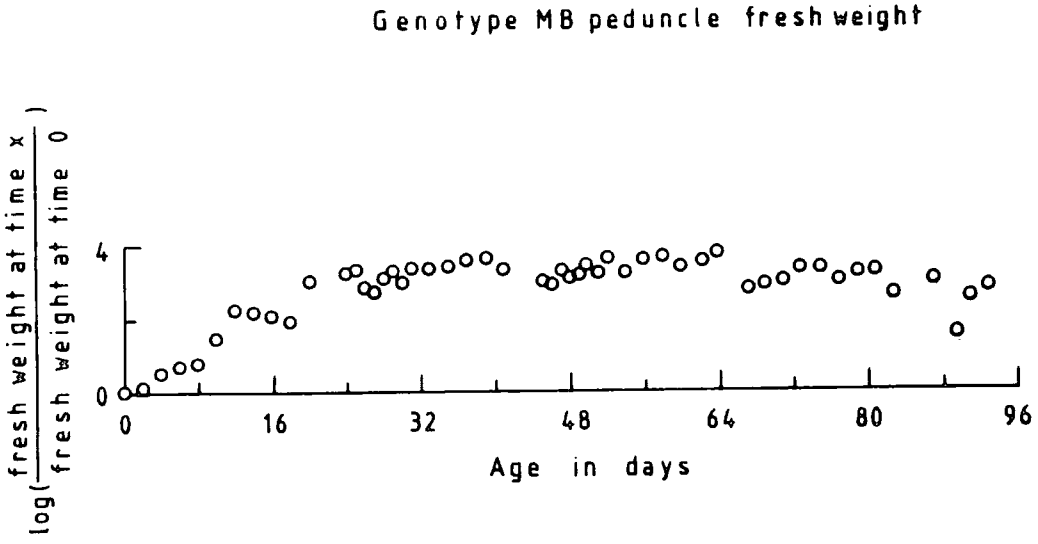
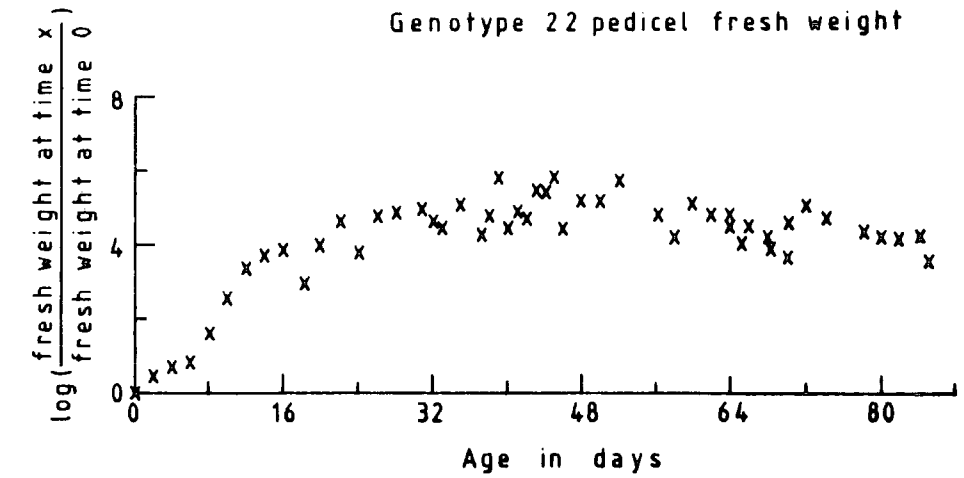
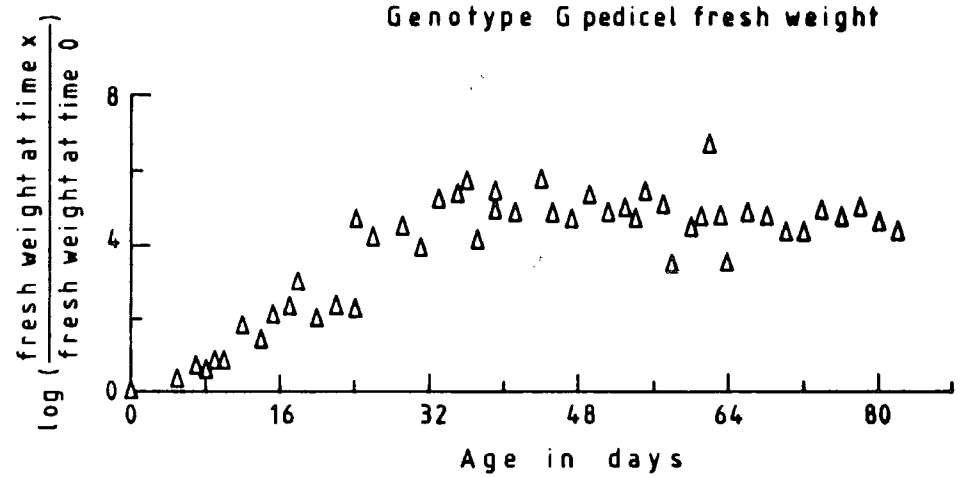


Figure 6.9 Change in log of peduncle fresh weight relative to weight at anthesis.

MB = Maris Bead





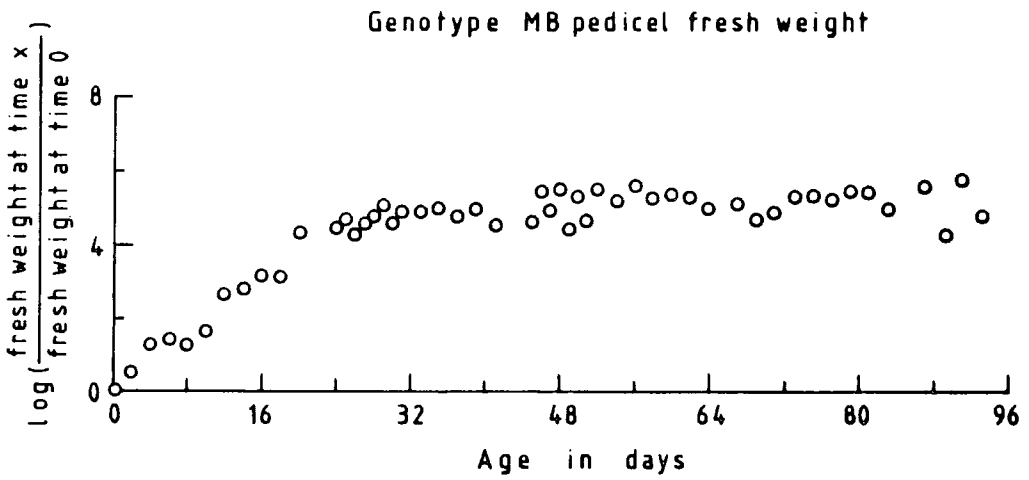
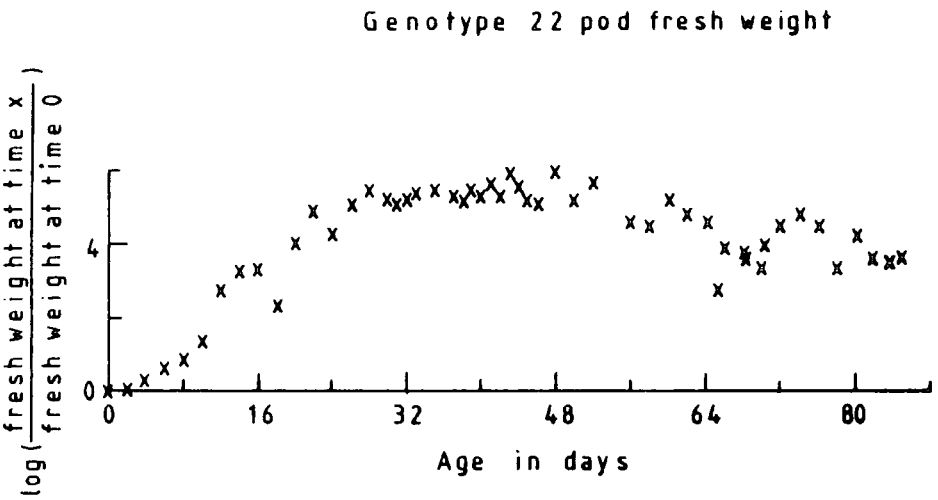
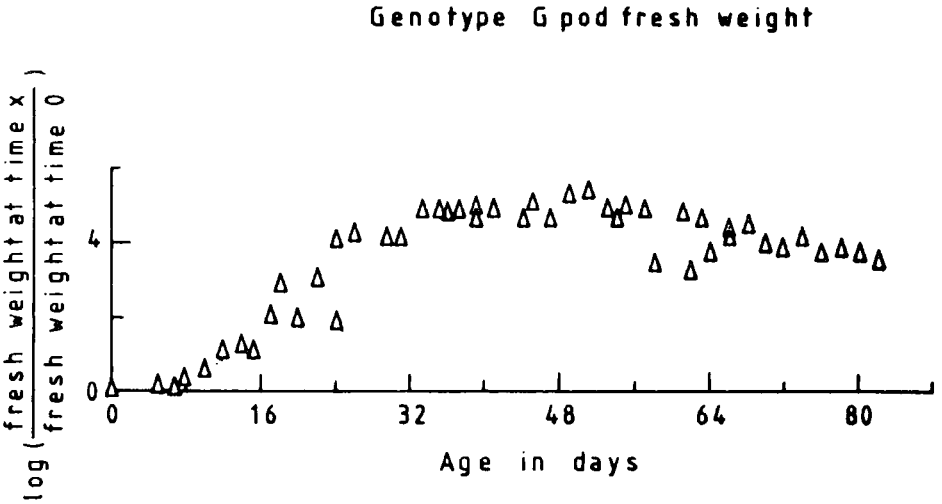


Figure 6.10 Change in log of pedicel fresh weight relative to weight at anthesis.

MB = Maris Bead





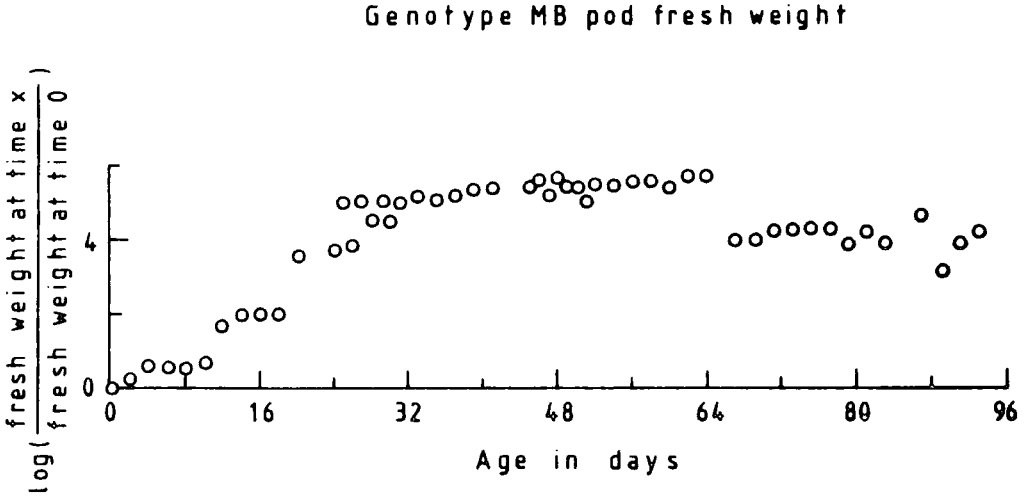


Figure 6.11 Change in log of pod fresh weight relative to weight at anthesis.

MB = Maris Bead

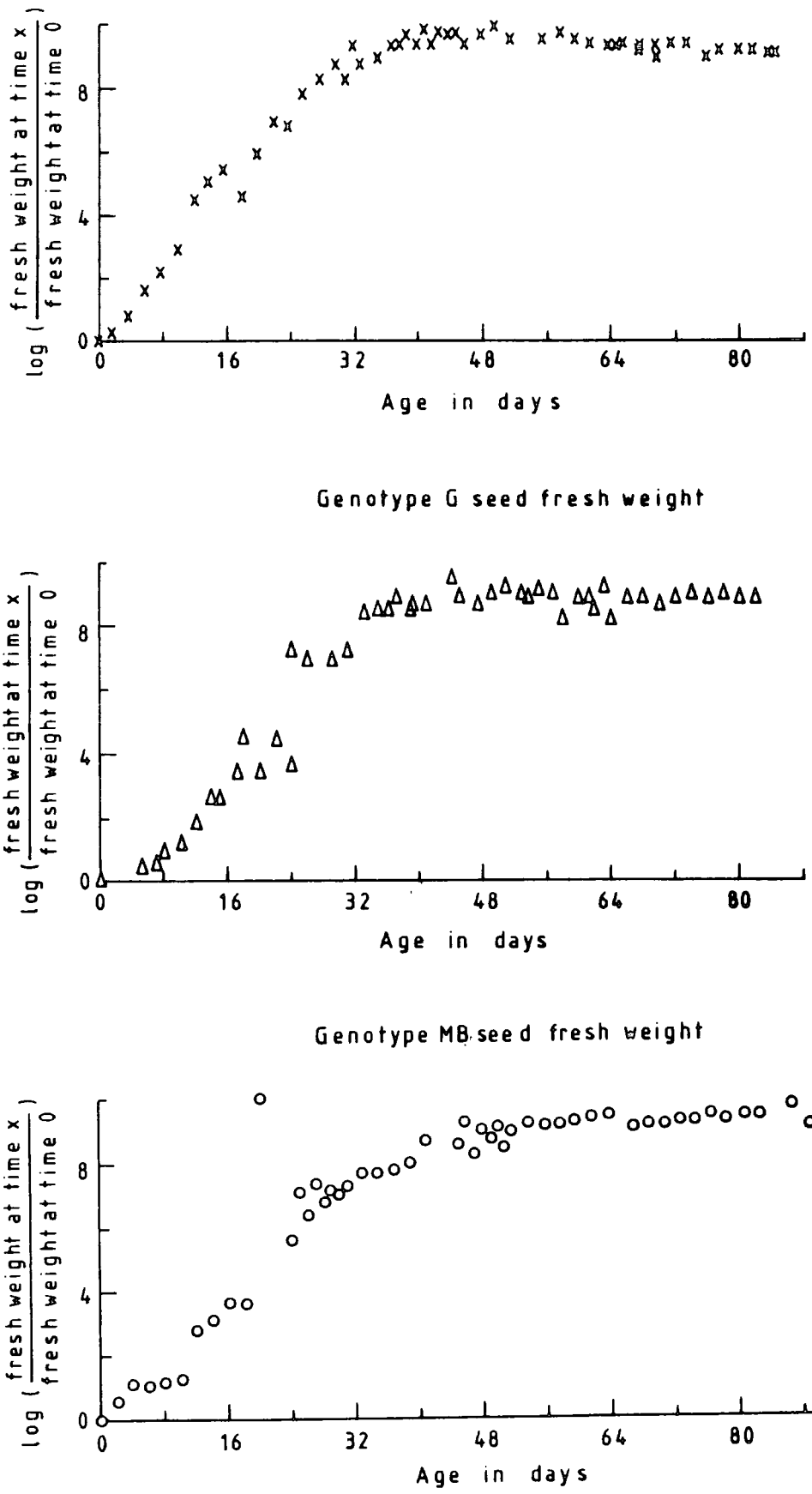


Figure 6.12 Change in log of seed fresh weight relative to weight at anthesis.

MB = Maris Bead

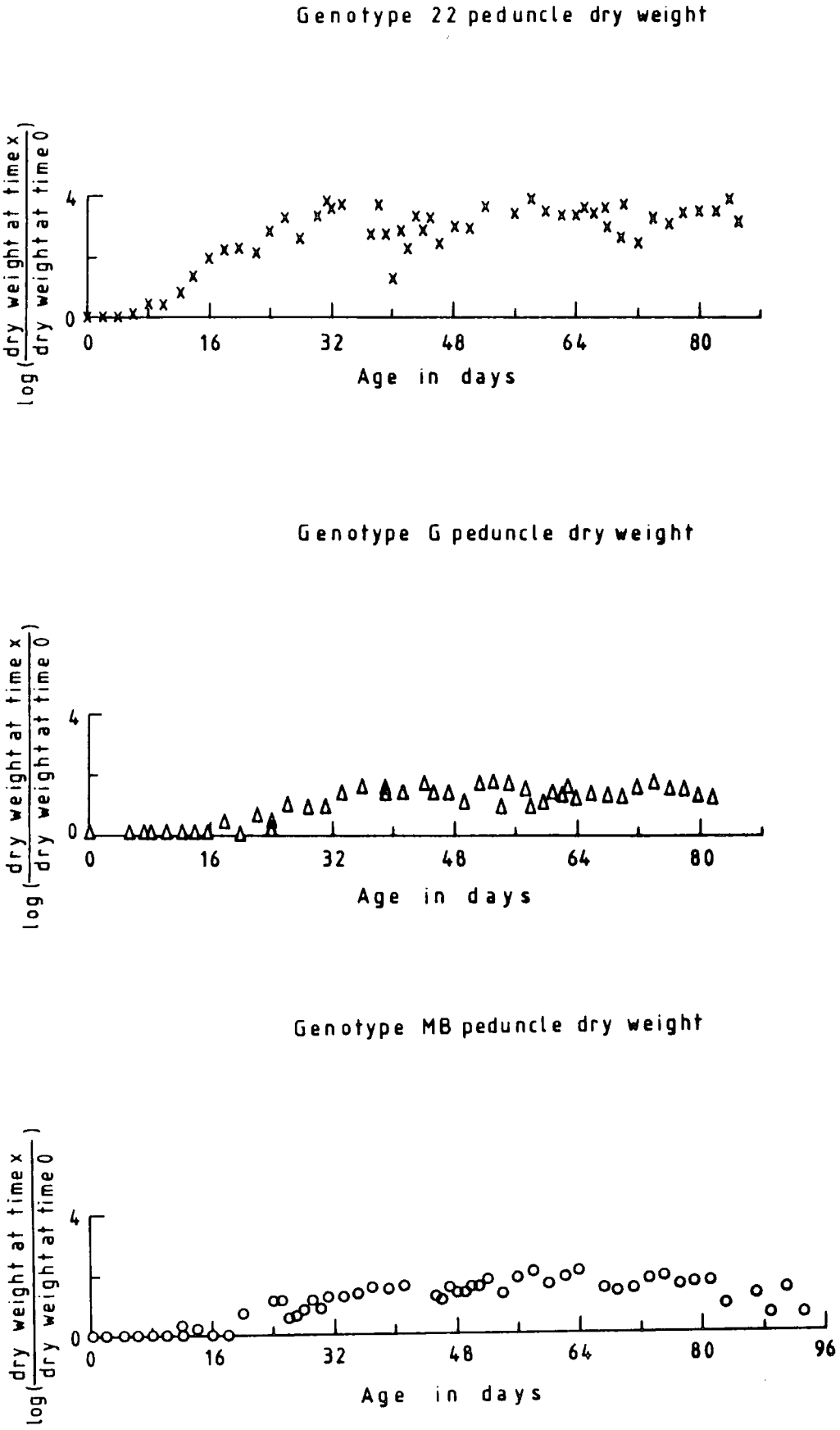
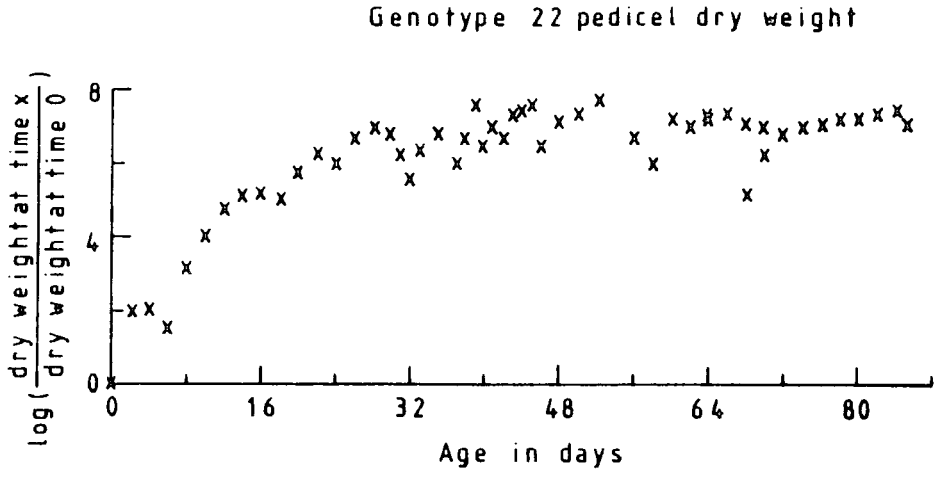
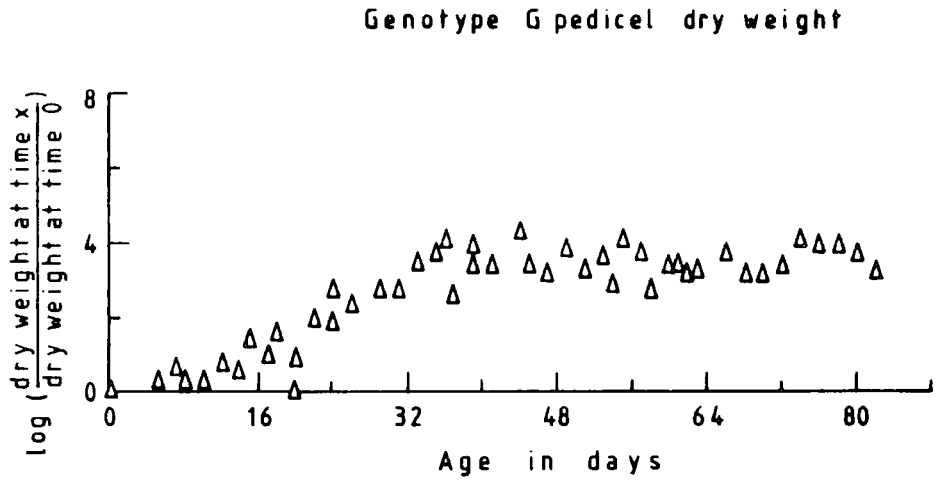


Figure 6.13 Change in log of peduncle dry weight relative to weight at anthesis.

MB = Maris Bead





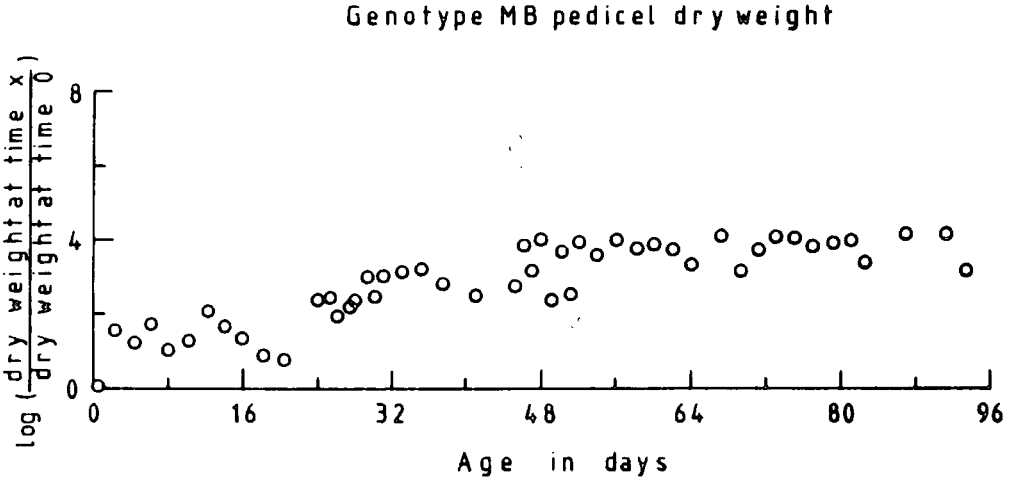


Figure 6.14 Change in log of pedicel dry weight relative to weight at anthesis.

MB = Maris Bead

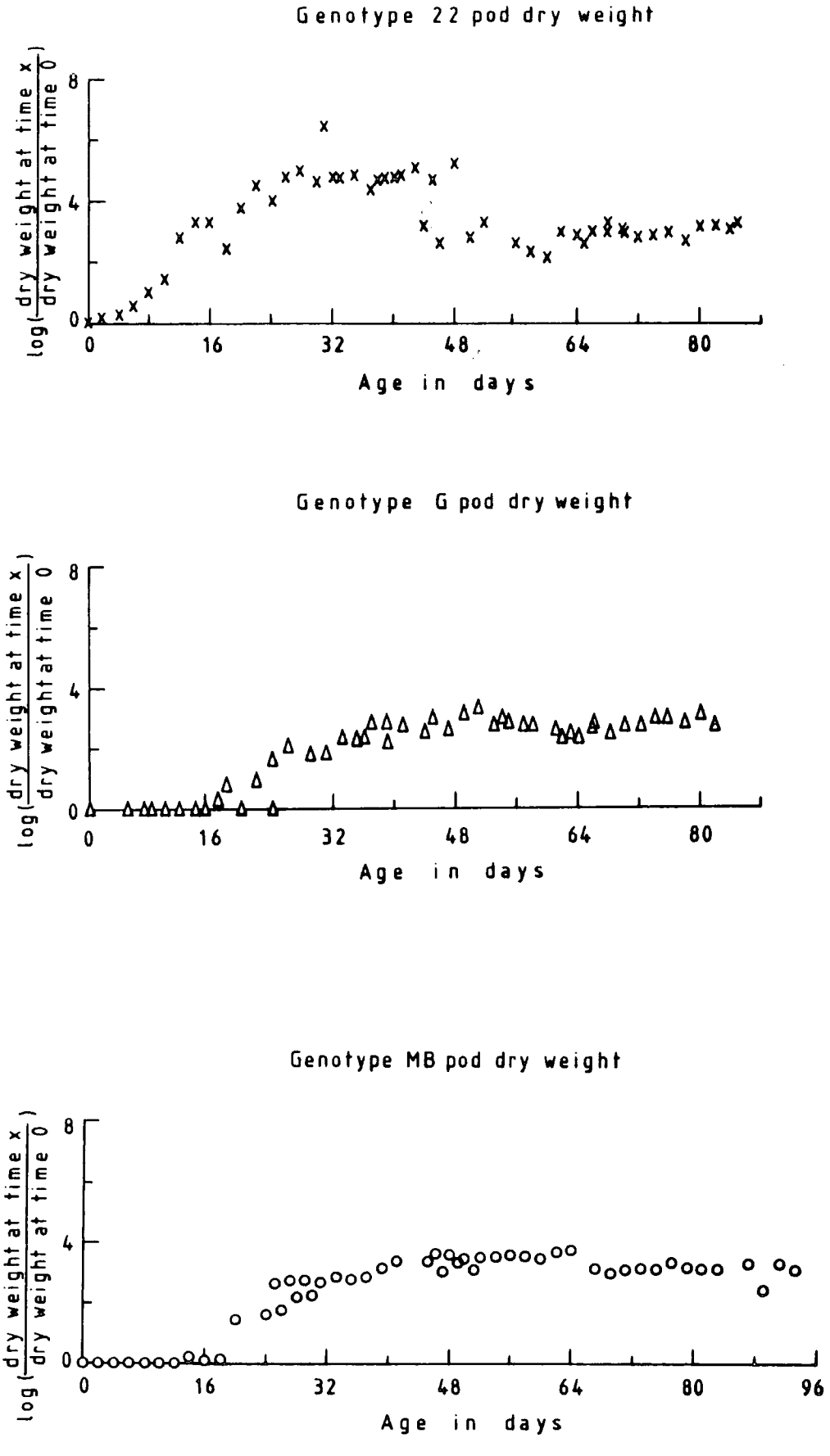
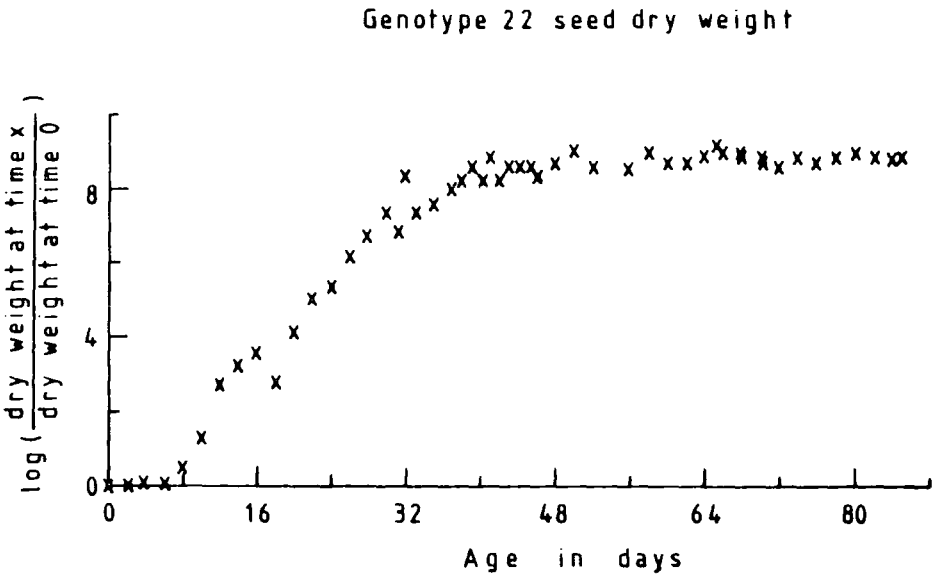
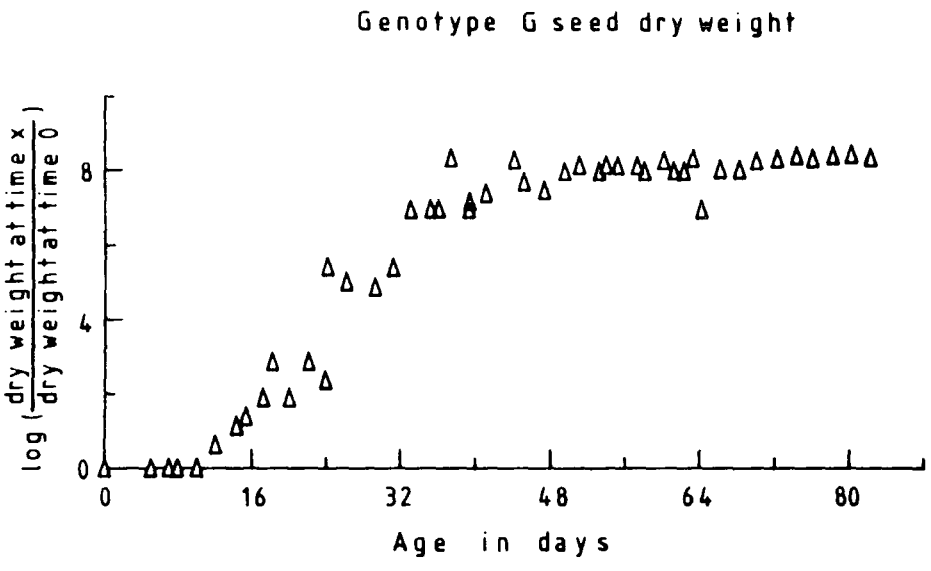


Figure 6.15 Change in log of pod dry weight relative to weight at anthesis.

MB = Maris Bead





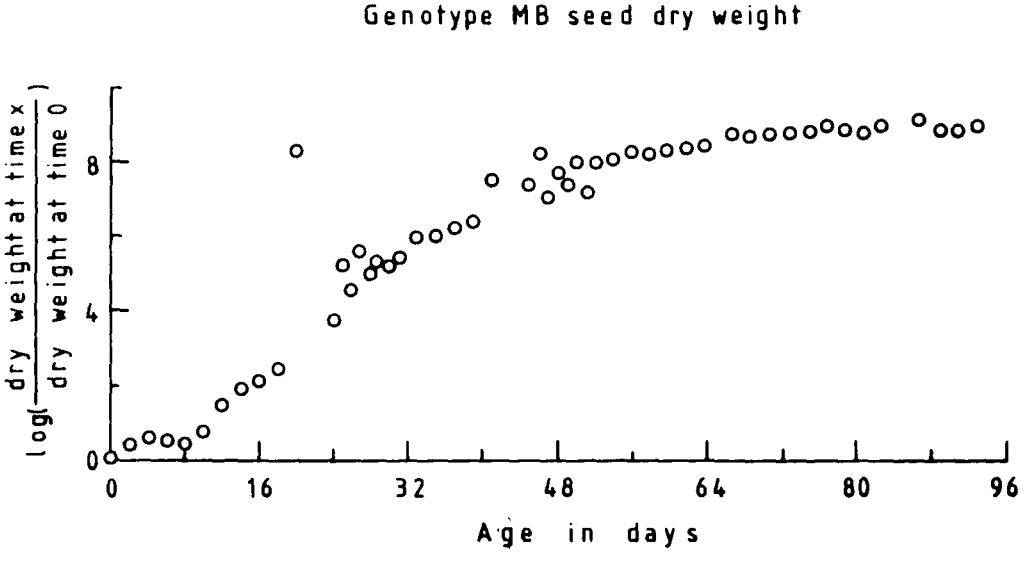


Figure 6.16 Change in log of seed dry weight relative to weight at anthesis.
MB = Maris Bead

CHAPTER 7

RESULTS OF STUDIES IN THE DEVELOPMENT OF THE VASCULAR SUPPLY WITHIN THE RACEME

During development a massive increase in cross-sectional area of the peduncle and pedicel was clearly visible (table 7.1). Examination of the structure of the peduncle at anthesis (plate 4(a)) and at full pod development (plate 6) revealed a massive increase in the area of vascular tissue present, particularly xylem. The vascular structure changed from a series of discreet vascular bundles to a continuous ring of vascular tissue. Considerable areas of sclerenchyma also developed. Similar increases in area of vascular tissue were observed in the pedicel (plate 4(b), plate 7). The increase in area of vasculation in the pod adaxial vein, which supplies the seeds, was also considerable (plate 5, plate 2(e)). At anthesis the funicle was very small and the vascular strand formed a small proportion of the total area of the funicle, only three sieve elements were visible. At full development thirty sieve elements were found. The vascular supply from the funicle to the seed was seen to be continuous across the funicle/hilum junction through the micropyle (plate 8). The vascular supply in the seed ran along the inside of the testa, gradually reducing in area, finishing around 5mm. from the micropyle.

Examination of transverse sections of the main stem (plate 9) showed a change in function of the stem. At anthesis large amounts of stored starch were visible in the cortical parenchyma (plate 9(a)), at full pod development the starch had disappeared (plate 9(b)).

Table 7.1

Cross-sectional areas of pedicels and peduncles at anthesis and at full development.

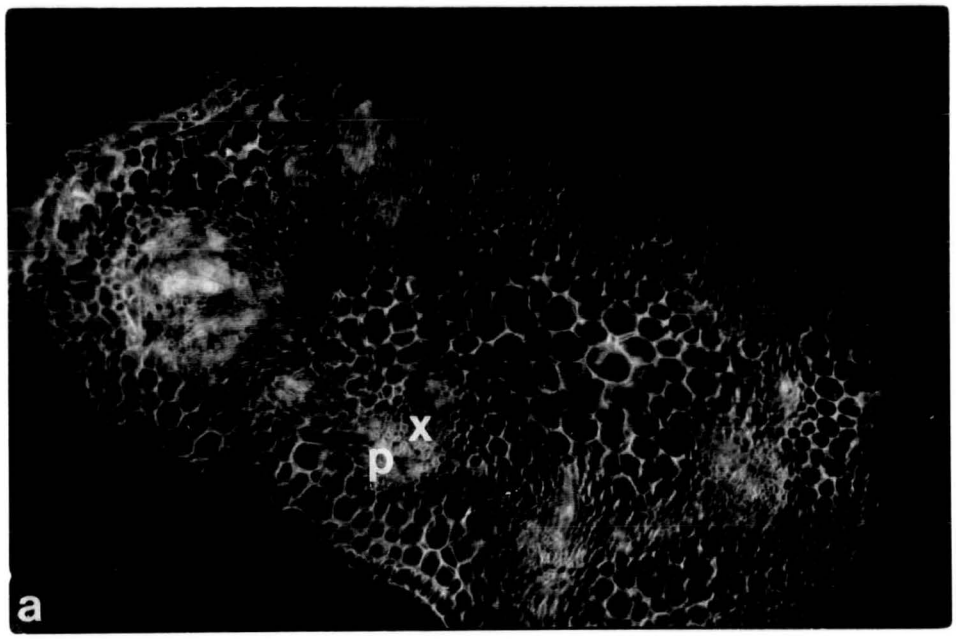
	Anthesis	Full Development	Ratio
Peduncle	5.488 mm^2	27.312 mm^2	5.0
Pedicel	2.932 mm^2	16.547 mm^2	5.6

Plate 4

Transverse sections of
(a) the peduncle and (b)
the pedicel at anthesis.

p = phloem tissue
x = xylem tissue

Scale:
peduncle - 1 cm. on plate
represents 0.256 mm.
tissue
pedicel - 1 cm. on plate
represents 0.168 mm.
tissue


x
p
a

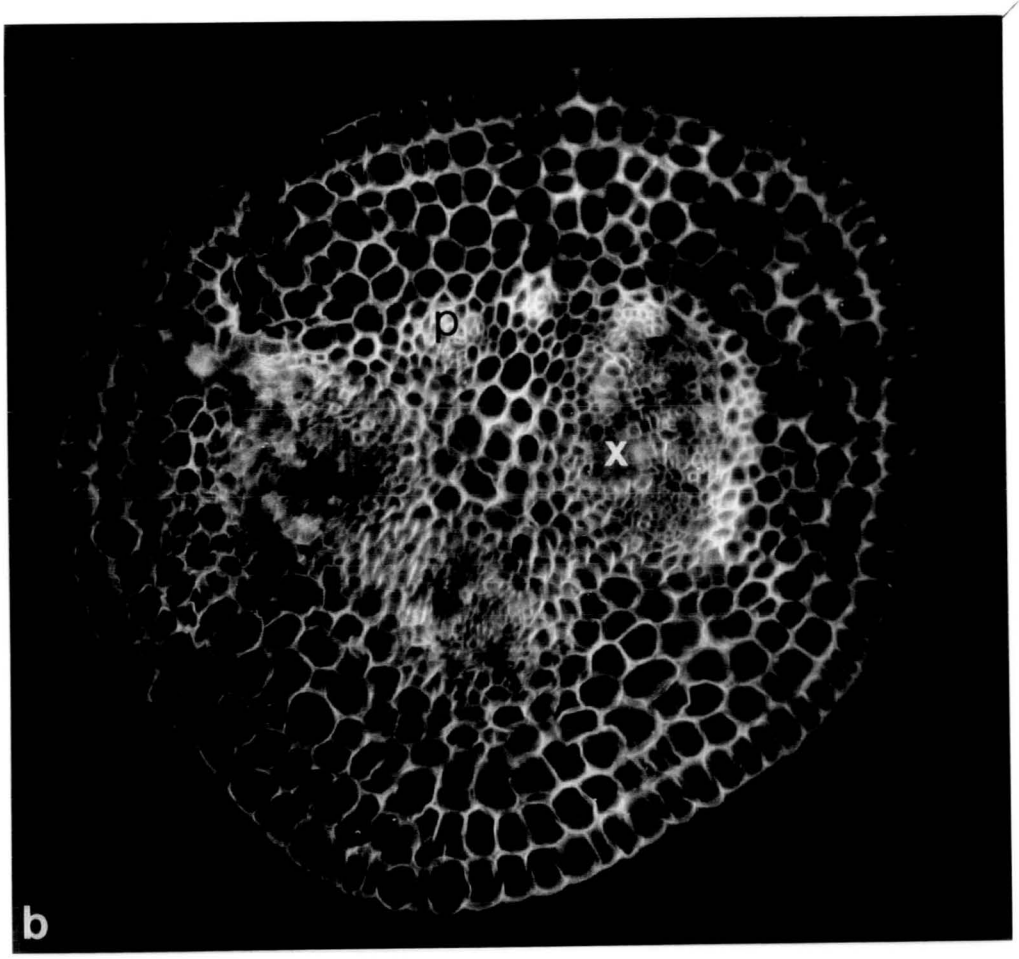
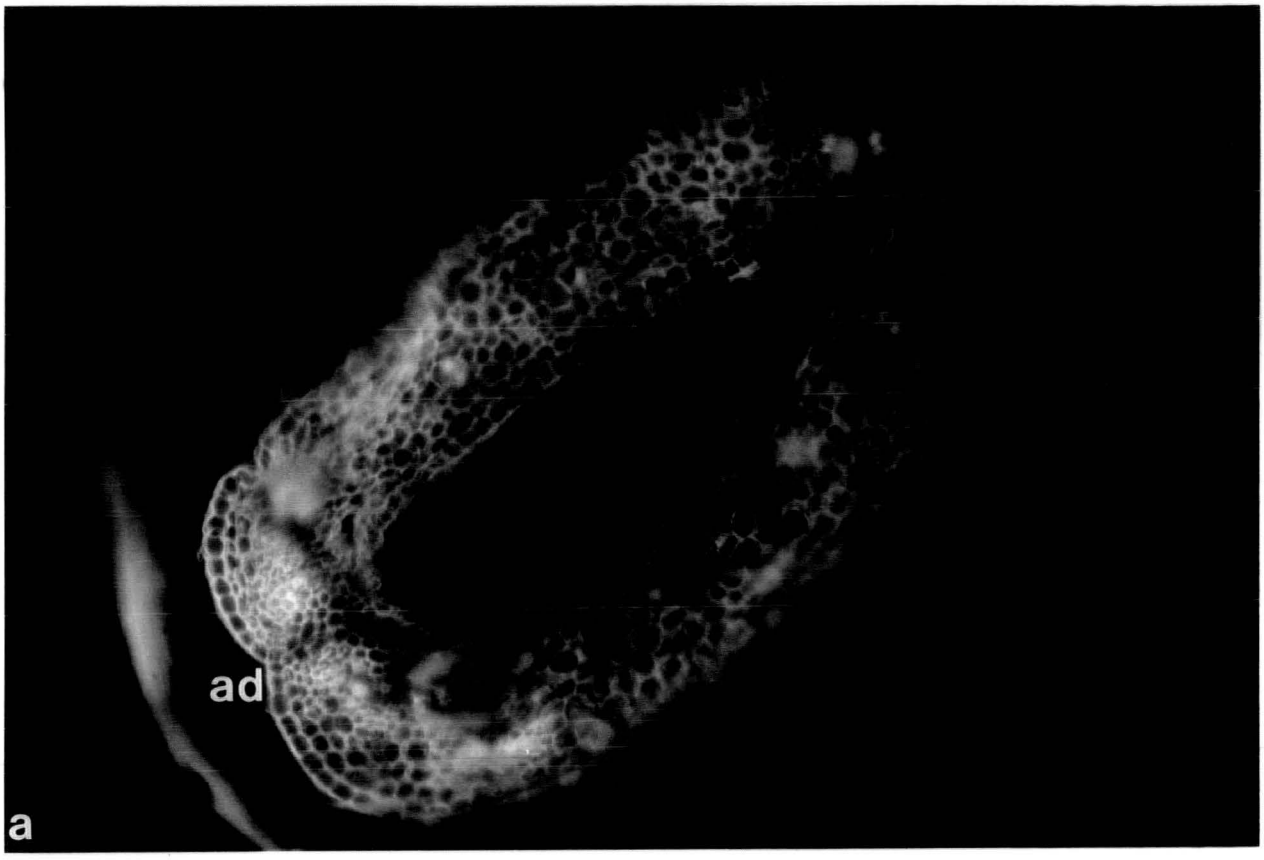

p
x
b

Plate 5

Transverse sections of a pod
at the anthesis stage.
(a) T.S. whole pod x 20
(b) T.S. adaxial pod vein x 50

ad = adaxial vein
l = lignified tissue
p = phloem
x = xylem

Scales:
(a) 1 cm. on plate represents
0.192 mm. tissue
(b) 1 cm. on plate represents
0.084 mm. tissue


ad
a

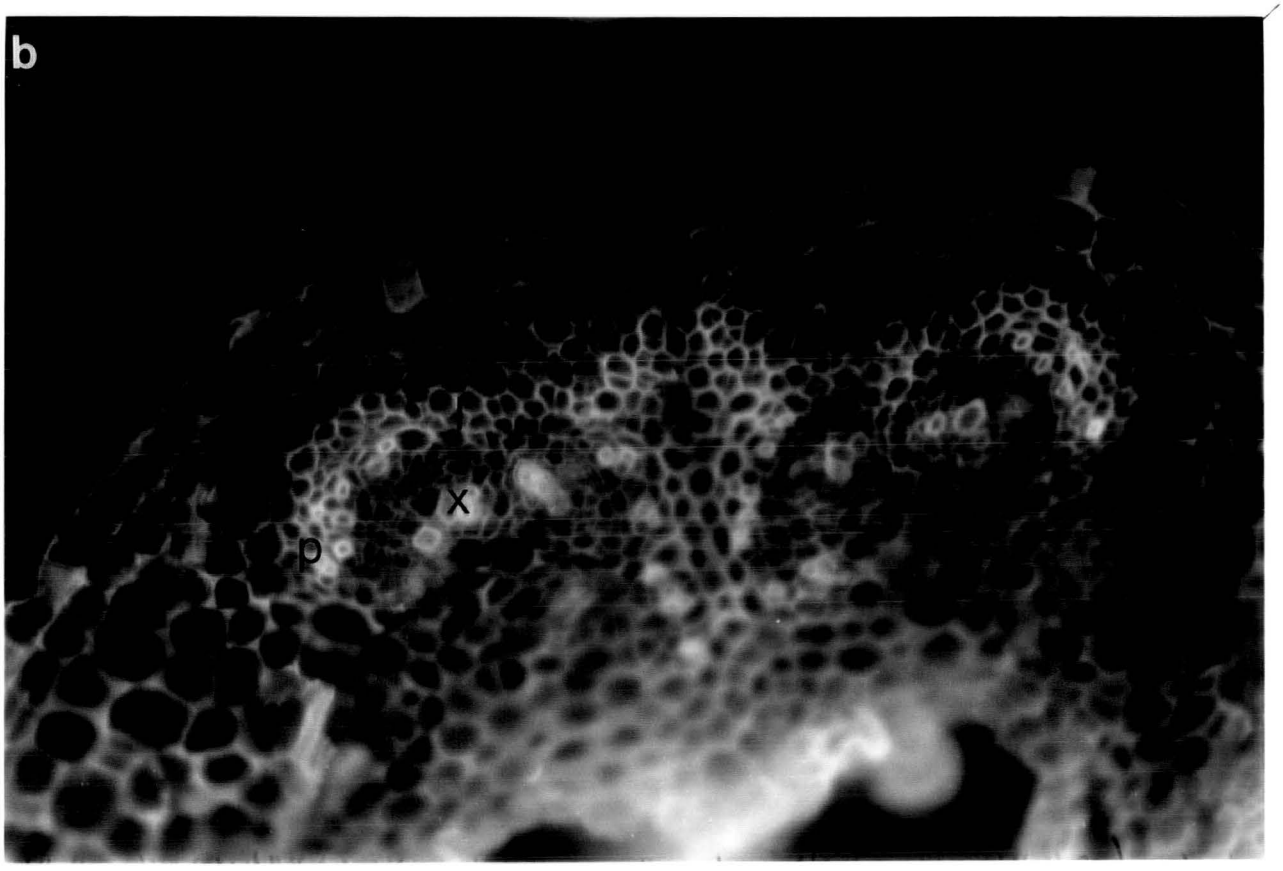

b
x
p

Plate 6

Transverse section of a mature peduncle.

c = cambium
lx = lignified xylem
p = phloem
sc = sclerenchyma

Scale:
1 cm. on plate represents
0.33 mm. tissue

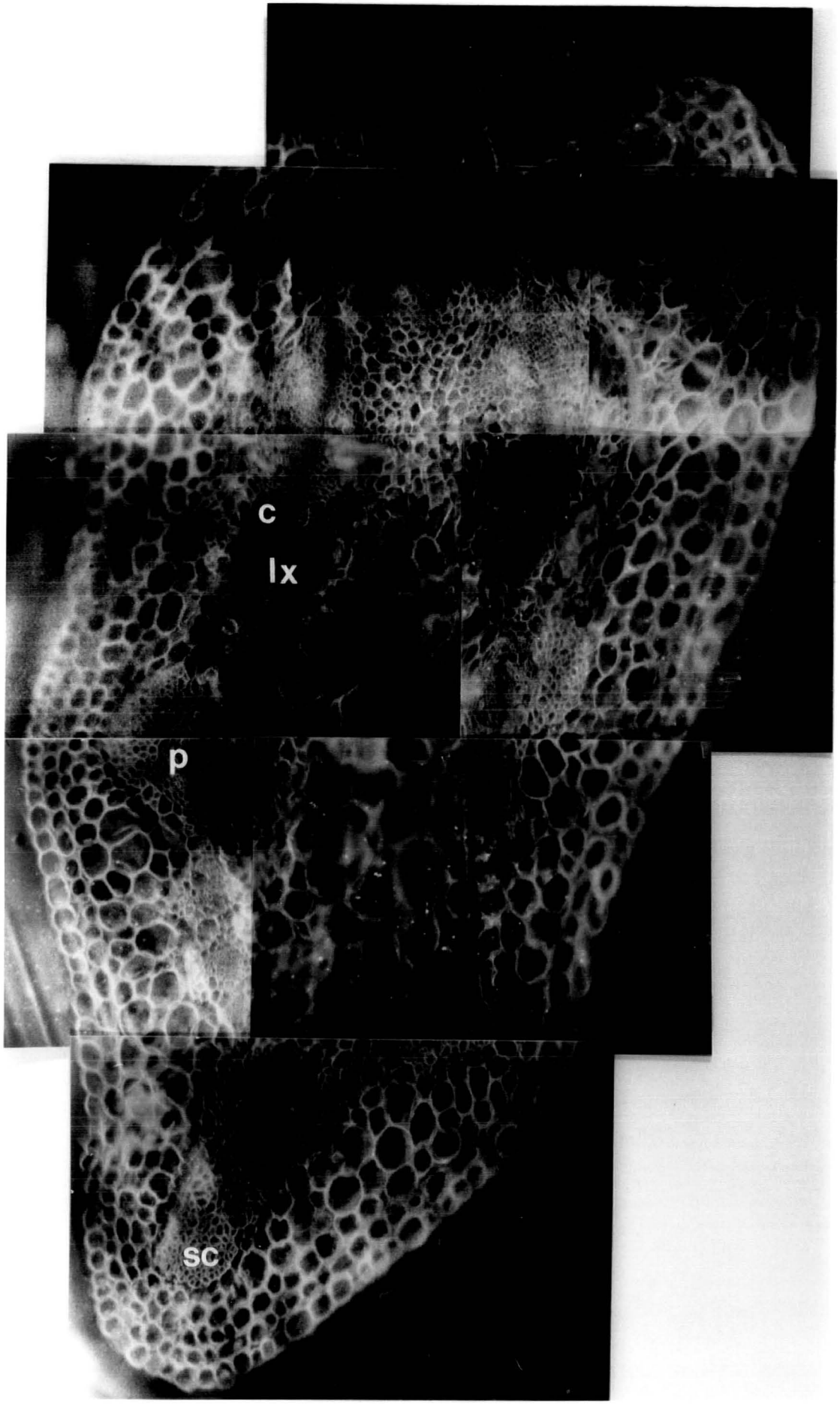

c
lx
p
sc

Plate 7

Transverse section of a pedicel at pod fill.

c = cambium
p = phloem
sc = sclerenchyma
x = xylem

Scale:
1 cm. on plate represents
0.27 mm. tissue

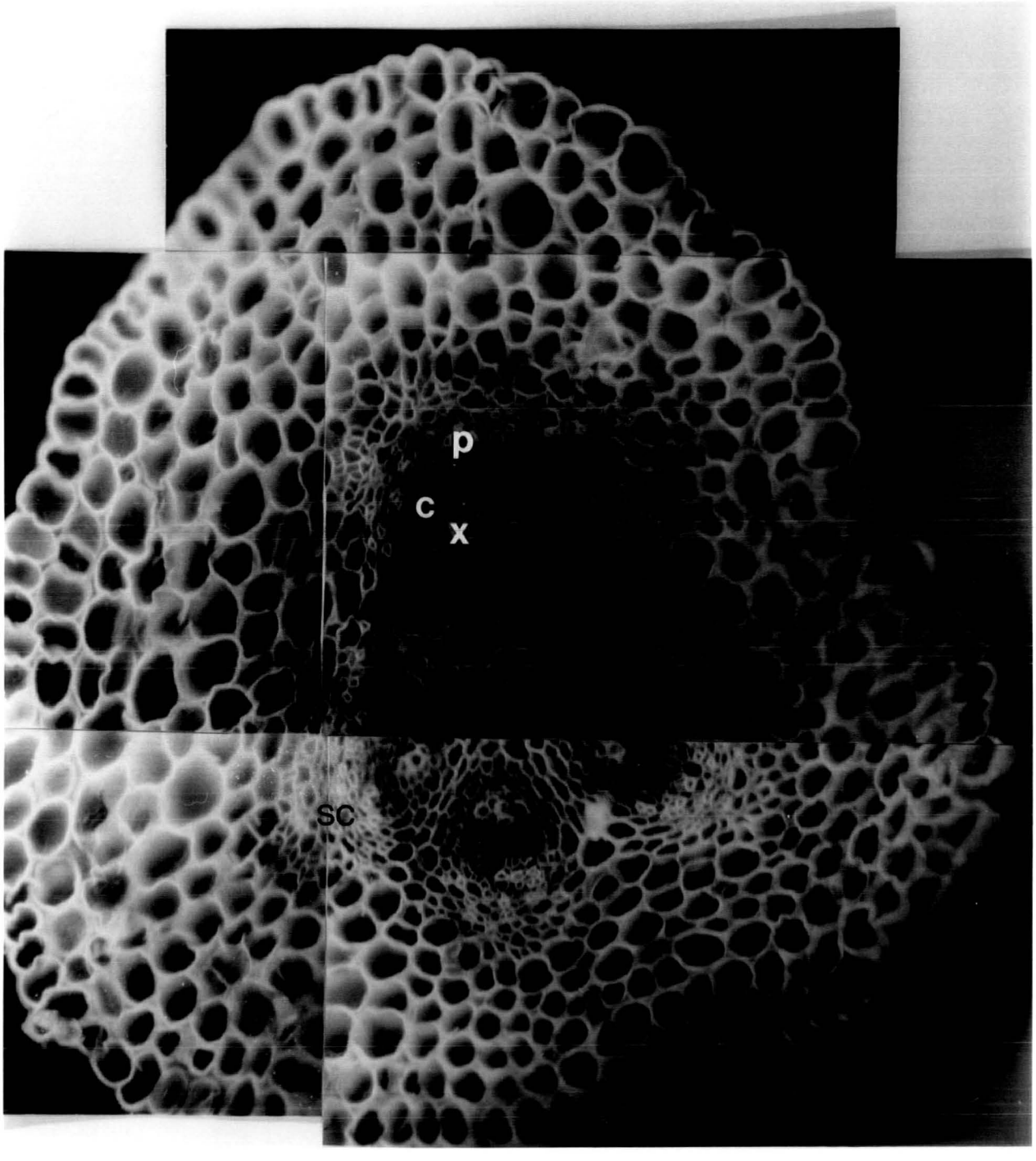
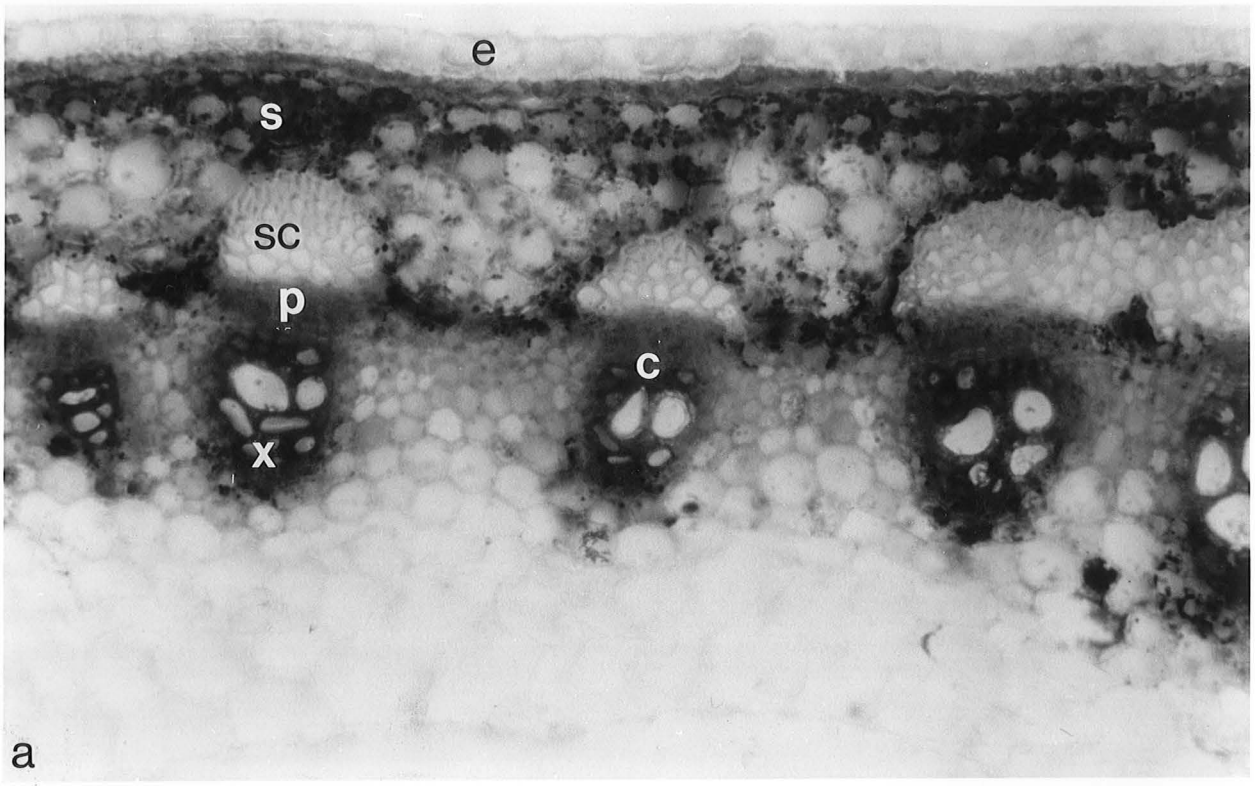

p
c
x
sc

Plate 8

Longitudinal section of the seed vascular supply passing from the funicle into the seed, full sized seed.

c = cotyledon
f = funicle
h = hilum
m = micropyle
t = testa
vs = vascular strand

Scale:
1 cm. on plate represents
0.033 mm. tissue


e
s
sc
p
c
x
a

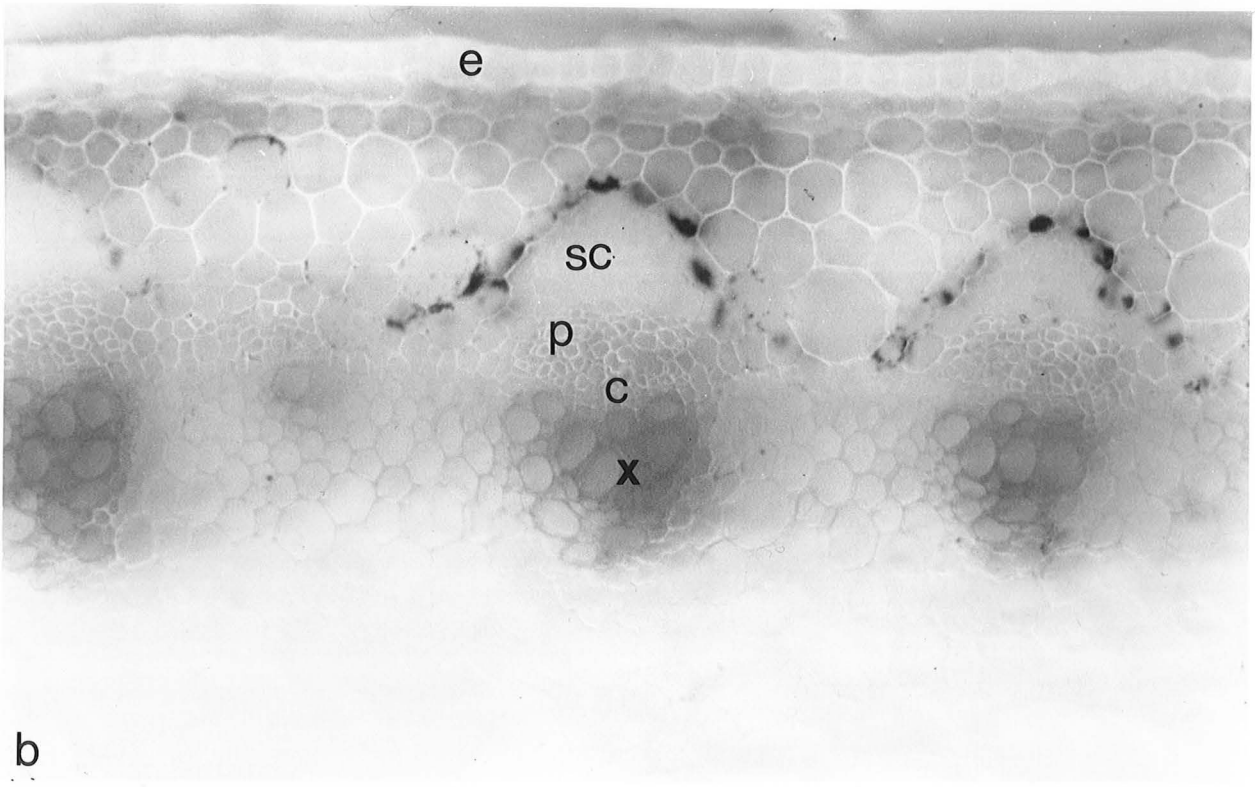
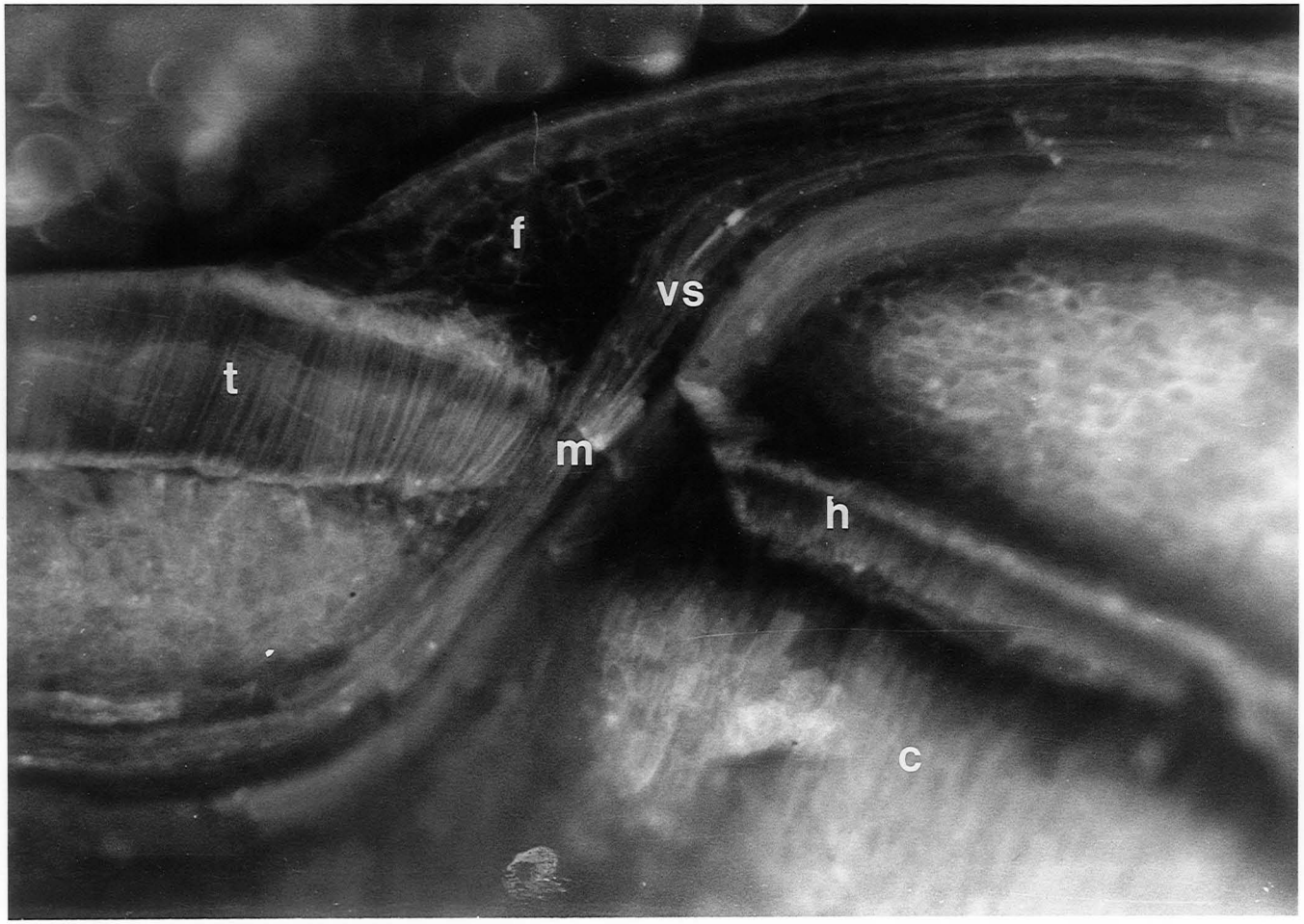

e
sc
p
c
x
b

Plate 9

Transverse sections of the main stem (a) before flowering, and (b) at early pod fill.

c = cambium
e = epidermis
p = phloem
s = stored starch
sc = sclerenchyma
x = xylem

Scale:
1 cm. on plate represents 0.383 mm. tissue


f
vs
t
m
h
c

CHAPTER 8

DISCUSSION

In order to propose a realistic crop ideotype much information about factors involved in the production of yield is needed. In the case of V. faba, yield is known to be directly related to the number of pods filled per unit area. During the course of the Durham plant breeding programme some lines of V. faba that fill a high number of pods on each plant have been selected, and these were found to differ from the normal commercial lines of beans in their peduncle vascular architecture. In the majority of genotypes the vascular traces in the peduncle are branched, the supply to each flower branching off the trace which supplied the flower beneath it. In the high pod set lines an unbranched peduncle vascular architecture was found, each flower having a separate vascular supply. During extensive studies on flower drop in V. faba Smith (1982) found that in the independent vascular supply type plants the incidence of flower drop was considerably lower than in the traditional branched vascular supply type plants.

In the course of the studies discussed here the potential of an independent vascular supply type line as a commercial cultivar was investigated. In a glasshouse experiment the basic growth pattern and yield development pattern were established and the discussion of these results establishes the basic intra-plant competition characteristics of plants of differing peduncle vascular architecture. In a crop situation yield stability is of great importance and the notoriously unstable yield of field beans (Gates et al, 1981) has been attributed to the effect of environmental stress on flower and pod drop. To test the stability of the independent vascular supply type plants compared with that of the conventional type plants, a series of trials was carried out to evaluate the response of such plants to various environmental stresses. During the course of the field trials the pods of independent vascular supply type plants were seen to dry out more quickly than those of normal type beans, and an investigation of pod

growth and structure was subsequently carried out under glasshouse conditions to investigate this. Earliness is an extremely desirable character in field beans, and if one genotype is ready to be harvested earlier than another then the rates of growth of the reproductive structures may be different. To investigate this a glasshouse experiment was carried out to evaluate the changes in fresh and dry weight of each part of the raceme. The peduncle, pedicel and pod all perform two functions in relation to the seed, that of nutrient and water supply, and that of support. The nature of the growth shown by dry weight increases was studied using the technique of fluorescence microscopy.

From these studies information was gathered about yield structure and stability, earliness, and the growth and development of reproductive structures of plants of different genotypes. The differing peduncle vascular architecture of the independent vascular supply type plants carries with it, in this case, many other morphological and physiological differences. The values of the various characters are considered in relation to the construction of an ideotype.

Reproductive potential and efficiency

The analysis of total yield components shows differing values for different components in the genotypes investigated (table 3.1.1.). The values obtained for G and Maris Bead were, in most cases, similar; the values for 22 being considerably lower than those of either of the other genotypes. The differences observed are a result of the genetic constitutions of the plants being expressed as differences in anatomical and physiological characteristics.

Genotype 22 is of the independent vascular supply type peduncle architecture, is of almost determinate growth habit, and forms fewer floral initials and fewer ovules per ovary than most genotypes. All of these factors are of great importance in the source-sink relationships of the plant. The genotype is expressed as anatomical and physiological characters which operate to reduce intra-raceme competition, resulting

in an even pod fill. Shortly after the commencement of flowering, vegetative growth ceases. Thus the developing pods become the predominant sinks considerably earlier in their development than do pods of indeterminate growth type plants. Bud abortion in 22 is extremely high on the upper flowering nodes, indicating high inter-raceme competition. Once past this stage of development there is very little shedding of reproductive structures. The IVS type peduncle serves to prevent flower and pod shedding by eliminating the movement of hormonal abcission promoters up the raceme to the more distal blooms (Smith, 1982) and by avoiding intra-raceme competition. Assimilate competition within the developing pods is greatly reduced by there being only two or three ovules in each pod, thus the difference in time of fertilization between the ovule most proximal to the stigma and that most distal is reduced. Reduced competition increases the chances of each fertilized ovule forming a mature seed. There is evidence that yield in 22 is source limited in that the senescence and abcission of most of the leaves occurs before pod drying. This is in agreement with the description of source limited plants given by Sinclair and de Wit (1976). This implies that genotype 22 is operating at its maximum reproductive efficiency (table 3.1.3), given its particular genetic constitution. On examination of table 3.1.3 the plants of all three genotypes appear very inefficient when number of seed bearing pods is calculated as a percentage of the number of buds formed. If, however, the number of seed bearing pods is calculated as a percentage of the number of flowers, then 22 fills over 50% of its possible number of pods, a very high ratio.

Genotype G is of a different genetic constitution from that of 22: it is of semi-determinate growth habit, frequently producing tillers. It is of the independent vascular supply type peduncle architecture and produces a high number of racemes, each of which has as many as ten flowers with three or four ovules per ovary. The source-sink relations of plants of this genotype are intermediate between those of 22 and Maris Bead. Vegetative growth continues at the onset of flowering, although it ceases before the end of the flowering period. Therefore the vegetative apex is the primary assimilate sink during the very early

stages of pod development. Immediately the young pods become effective sinks, apical growth ceases. Owing to the strong sink activity of firstly the vegetative apex and then the developing pods on the lower nodes, bud abortion on the upper reproductive nodes is high owing to lack of assimilate supply. Bud abortion on tillers is extremely high and total bud abortion is not uncommon. Flower shedding accounting for the loss of 8% of the total potential yield was evenly distributed throughout the whole plant. Pod shedding accounted for the loss of a further 15% of the reproductive potential. Both flower and pod shedding can be explained in terms of pollination timing, as was the failure of pods to fill. The large number of flowers on each raceme results in increased intra-raceme competition. The lower flowers on a raceme may be fertilized up to six days before the upper ones, and so gain a competitive advantage for assimilates. Inter-raceme competition may also be of importance in these courses of yield loss as the lower flowers on the second inflorescence will be fertilized before the upper ones on the first. On the whole the inter-raceme competition favours the lower reproductive nodes as these are the first to set pods and to develop assimilate pathways and to compete for the assimilates. Failure of ovule development is common in those ovules positioned distal to the stigma. This may be ascribed to intra-pod competition. The ovules proximal to the stigma are likely to be fertilized first as growing pollen tubes reach these ovules first. These proximal ovules start their development before those occupying more distal positions in the pod, and therefore gain an advantage of assimilate flow. Three competition gradients are inter-acting during yield development, inter-raceme, inter-pod and inter-ovule: the interactions of these determine yield structure. Genotype G also exhibits canopy senescence before pod maturity, and indication of source limitation of yield. The percentage of buds forming seed bearing pods (10.8%) is low, and the percentage of flowers forming seed bearing pods is much higher (25%). The actual number of pods bearing seed is 60% higher than that of 22, and the weight of seeds filled by G is 350% greater than that of 22. G appears to be more efficient in yield production than 22; it is source limited and yet produces a much greater seed yield.

Maris Bead is of indeterminate growth habit with peduncles of the branched vascular supply type, and many floral initials are formed, characteristically having four ovules per ovary. Being of indeterminate growth habit, the stem apex of Maris Bead remains the primary assimilate sink for a considerably longer time than those of G and 22. Relatively few reproductive nodes were formed, due to the lack of tillering. Massive bud abortion was found at higher reproductive nodes due to the inability of the buds to compete for assimilates with the apex. Some flower abortion was observed, although less than reported by Smith (1982) for both glasshouse and field trials. A greater source of yield loss was that of young pods, defined here as any stage of development after the collapse of the corolla. Both flower and pod loss are attributed to the nature of the peduncle. The inter-dependent vascular supply allows translocation of abcission promoters to flowers more distal to the stem (see Smith, 1982, for discussion). Failure of pod fill occurs predominately at the higher reproductive nodes. As with G, 25% of the flowers formed give rise to seed bearing pods. Intra-pod competition in Maris Bead did not seem to be as significant a factor as in the other genotypes, and four seeds were frequently harvested from one pod. There is no evidence of source limitation of yield in Maris Bead, pod drying and leaf senescence occurring simultaneously.

Significant inter-genotypic differences in the values of various yield components were found at individual nodes (tables 3.2.1 to 3.2.8). In the case of the genotypes investigated here this is mostly due to the low values recorded for genotype 22. In addition some differences between G and Maris Bead were found (tables 3.2.9 to 3.2.16).

As these plants were observed under glasshouse conditions it should be stressed that results from this study on reproductive development may not be directly comparable to those of trials performed under field conditions, although the basic patterns of development will be similar.

There is much evidence to support the developmental patterns described here, and this is found in work on V. faba and on other leguminous crops. High bud abortion rates in V. faba were observed by Kambal (1968). The competition for assimilates between the vegetative apex and the reproductive structures and that between racemes and within racemes of V. faba has been investigated by Chapman and Sadjadi (1981), Gehriger, Bellucci and Keller (1978), Chapman, Fagg and Peat (1979), Chapman, Guest and Peat (1978), Jacquiéry and Keller (1978a, b), and Kambal (1969), and all of these authors are in agreement over the intra-plant competition in V. faba and its effect on yield development. Similar reports have been published for other crops, e.g. Lupinus angustifolius, the narrow leaved lupin (Pate and Farrington, 1981), Lupinus albus L., the white lupin (Pate, Layzell and Atkins, 1980), Glycine max. (L) Merrill, soya bean (van Schaik and Probst, 1958), and Vigna unguiculata (L) Walp., the cowpea (Ojehomon, 1972). In these studies the cause of pod and flower abortion is generally stated as poor ability to compete for assimilates. Smith (1982) clearly showed the role of abcission promoting hormones produced by the earliest fertilized flowers in a raceme inducing the abcission of flowers higher up the raceme.

The investigations of ovule abortion that have been carried out suggest failure of development of the vascular supply to the aborting ovules (this study; Kambal, 1969). The cause of this has not been investigated in V. faba. The hypothesis has been put forward that the time difference in fertilization of individual ovules gives those most proximal to the stigma a competitive advantage over those more distal (Kambal, 1969). As soon as the ovule proximal to the stigma is fertilized the resultant zygote begins to divide and grow; a time difference of as little as one hour in fertilization can affect the competitive ability of an ovule in Phaseolus. Kambal (1969) proposes that in V. faba the larger seeds, more advanced in development, produce more auxin than the smaller ones and thus the more advanced seeds become much stronger competitors for assimilates. This hypothesis is borne out by the data collected in this study. Other data supporting this

concept was presented by Gabelman and Williams (1962) for green beans. In studies of soybean seed growth Egli et al (1981) proposed that seed growth rate was controlled by the number of cells present in the cotyledons. The earliest fertilized seeds would quickly grow to become those with the most cells in their cotyledons and hence the greatest potential for producing hormones. Such seeds rapidly become the strongest influence on pod development and quickly become the strongest sink in that particular pod. Further support for this hypothesis is given by Lee (1984) who proposed that pollen tube growth is under genetic control and therefore the fastest growing pollen would compete successfully for ovules, leading to very early fertilization of the ovules proximal to the stigma. This pollen fitness criterion would, ultimately, lead to an even greater lag between the fertilization of the proximal and distal ovules. This would lead to the reinforcement of the intra-pod competitive gradient.

From the evidence discussed here it can be seen that the intra-plant competition in V. faba is extensive and complex. The understanding of the basic pattern of yield development in the genotypes to be tested is of importance in interpreting field trial results where imposed stress and environmental variation must be taken into consideration.

Field trials

In a crop situation plants are frequently subjected to environmental stress. These may be divided into two groups; those that may be either imposed by or controlled by man's cultural techniques such as planting density, nutrient availability, weed control, and pest and disease control, and those imposed directly by the environment in which the plants are growing, such as soil type, temperature, light intensity, humidity and water availability. In planning field trials the effects of only those factors that can be reasonably controlled and measured can be tested. Temperature, light intensity and humidity were eliminated on these grounds. As the trials were performed on one site the effects of variation in soil type could not be considered, and on this site weed

and pest and disease control was a routine measure; these factors were therefore not considered. The effects tested were those of water availability and planting density and their interactions. The yield and yield distribution of plants of several genotypes grown under conditions of minimal environmental stress were also recorded. Initially the effects of different planting densities and irrigation on different genotypes of faba bean were tested in separate trials. In order to establish the effects of a range of planting densities on the yield and yield distribution of genotypes of differing peduncle vascular architecture a systematically designed spacing trial was used. In the same season (1982) the yields of several genotypes grown under the measured maximum conditions established by Thompson and Taylor (1979) were evaluated. In 1983, using information from the previous irrigation and density trials, a trial was set up to investigate the effects of both high and low planting density at both high and low irrigation levels on the yield and yield structure of genotypes of V. faba of differing peduncle vascular architecture. A further trial was set up to investigate the effects of water shortage on the yield of different bean genotypes at various stages of plant development. In order to control water availability the plants used were pot grown and hand watered; water was withheld at pre-determined growth stages. These field trials provide important information about yield stability and structure in a range of environments.

In the systematically designed spacing trial the responses of the various yield components to increasing inter-plant competition was similar to those found by other workers (Hodgeson and Blackman, 1956; Ishag, 1973a, b; Abo El-Zahab, Al-Babaway and Abd El-Latif, 1981; Abo El-Zahab, Al-Babaway and Nidawy, 1981; Keller and Burkhard, 1981; Barry and Storey, 1979). Some differential genotypic responses to increased inter-plant competition were detected. The node number of the first flowering node appears to be a remarkably stable characteristic; unaffected by plant population (figure 4.1.1), genotype G commences flowering at an earlier node than do F or Maris Bead. This is of value

in conferring earliness of yield as flowers at lower nodes set pods early and so are at maturity earlier than the pods on higher nodes. The yield of G is located lower down the plant than that of Maris Bead and the plants are ready for harvest approximately four weeks earlier than Maris Bead plants. Keller and Burkhard (1981) reported that at high planting densities flowering started higher up the plant than at low densities, and Hodgeson and Blackman (1956) found that flowering commenced at the same node both at high and low planting densities, but that at higher densities the internodes were longer in response to increased competition for light. From this evidence it can be seen that, although flowering commenced at the same node at all planting densities tested, that node may be higher off the ground at a high density than at a low density, thus rendering these findings in agreement with those of Keller and Burkhard (1981). Having the pods higher off the ground makes mechanical harvesting of the crop easier and fewer pods are left on the stubble than at low densities. The consistent values obtained for the number of the first flowering node implies the existence of a genetically determined juvenile period that must occur before reproductive development can commence.

The number of flowering nodes per plant (figure 4.1.2) and number of flowers per plant (figure 4.1.3) both fell in response to increased plant population; the fall in number of flowers was somewhat greater than that of number of flowering nodes. This suggests a decrease in both number of flowering nodes and number of flowers per flowering node in response to increased inter-plant competition, but the greatest decrease was that of number of flowering nodes. This is in agreement with Hodgeson and Blackman (1956) who stated that the number of flowering nodes formed is a consequence of the duration of the meristematic activity involved in the formation of floral initials. Increased inter-plant competition seems to result in a reduced period of formation of such initials.

The number of podded nodes per plant (figure 4.1.4) fell in response to increased planting density, but the decrease in value of this parameter was, however, less marked than that of number of flowering nodes per

plant, indicating that this is a more stable characteristic than number of flowering nodes. There was a marked decrease in number of pods per podded node (figure 4.1.5) with increasing planting densities, indicating that inter-pod competition was greater at high planting densities.

The number of pods set at each density was greater than the number filled; both of these values fell with increasing plant populations (figure 4.1.6). At higher planting densities genotype G set far more pods than either of the other genotypes, even though the number of pods filled was similar in all genotypes. The implication of a vast number of pods being set and not filled is that, even though in all yield components examined so far the vascular architecture of G has led to reduction in intra-raceme competition and therefore a less marked response to increased plant population, here assimilate supply becomes the limiting factor for pod fill, resulting in the failure of many pods to fill. The intra-plant competition discussed earlier becomes more marked at higher planting densities when less resources are available for each plant. The result of this is that those flowers that are pollinated first, and thereby gain a competitive advantage over flowers pollinated later, maintain that advantage and gain the monopoly of the reduced assimilate supply available. The potential yield, measured in number of pods set, is far higher in G with its IVS type peduncle than that of Maris Bead at high plant populations. At a planting density of 80 plants/m^2, twice the normal commercial planting density, G set 11 pods per plant, whereas Maris Bead sets only 5 pods per plant. Therefore, if more assimilates were available, the yield of G could be twice that of Maris Bead.

All three genotypes produced similar numbers of seeds at corresponding planting densities (figure 4.1.7) as might be expected from the similarity in number of pods filled (figure 4.1.6). The number of seeds per pod was unaffected by plant population (figure 4.1.8), the pods of G containing fewer seeds than those of Maris Bead or F. A

slight increase in individual seed weight with increasing planting density was detected (figure 4.1.9) in agreement with the findings of Hodgeson and Blackman (1956). Yield per plant is therefore a product of number of pods filled x number of seeds per pod x weight per seed. The actual seed yields (figure 4.1.10) of G and Maris Bead, at corresponding planting densities, were very similar; those of F were higher owing to the heavier individual seed weight.

Calculations of potential yield per unit area in terms of number of pods set revealed enormous inter-genotypic differences (figure 4.1.11). The values for genotype G showed an increasing number of pods set as density increased up to over 80 plants/m^2 where 800 pods/m^2 were set. Maris Bead, however, showed increased pod set up to 40 plants/m^2 when 450 pods/m^2 were set, then reaching a plateau when no further increase was observed. In F a somewhat ill-defined plateau in number of pods set/m^2 occurred at 45 plants/m^2 when 600 pods/m^2 were set. This is a consequence of F being a segregating population, not a pure line. Some plants in the stand were of the IVS type peduncle architecture and some were of the non-IVS type. The number of pods set per $metre^2$ is related to the proportion of IVS type plants in the population; this is a possible marker for estimating the extent to which a population is of the IVS type plants. These figures may be regarded as a consequence of the differing peduncle vascular architectures of the genotypes tested having effects on intra-plant competition when inter-plant competition was changed. In Maris Bead the highly polarised assimilate flow leads to higher incidences of abcission than normal when less assimilate is available in each individual plant as is true at high planting densities. Conversely the vascular architecture of the peduncles of G serves to even out the intra-plant competition so that even at high planting densities many pods may set. Source limitation does, however, prevent these pods from all filling. As might be expected from the number of seeds per plant, the number of seeds per m^2 is similar for all genotypes (figure 4.1.12), as is the extrapolated yield in tonnes per hectare (figure 4.1.13).

Even though in this trial no real difference in yield obtained was recorded for G, there is a vast potential yield in the IVS type peduncle plants compared with that of Maris Bead. This trial points to the need to select for plants with prolonged leaf area duration as proposed by Chapman, Guest and Peat (1978). This would result in a prolonged seed fill period and increased total assimilate supply. Suitable planting densities for a replicated trial to investigate the combined effects of planting density and irrigation on yield and yield structure were selected from these results. The densities selected were 40 plants/m^2, the normal commercial planting density, and 80 plants /m^2, the optimal density for pod set in IVS type plants.

The results of the 1982 irrigation trial show that for all of the yield components evaluated, only the effects of genotype and the genotype x irrigation interactions yield significantly different values. Irrigation alone has significant effects only on the vegetative characteristics recorded. Added irrigation increases vegetative growth in all genotypes tested (table 4.2.1.7., figure 4.2.1), as this results in tall plants that are very susceptible to lodging, an undesirable trait in field crops. Genotypic differences in height are highly significant, Maris Bead being taller than either of the other genotypes, both of which are of the IVS type peduncle structure. The pattern seen for numbers or weights of reproductive structures is that Maris Bead has the greatest value in each case, so creating a consistently significant genotypic effect for each parameter recorded. Each genotype responded differently to the irrigations applied, and, in the case of Maris Bead, more irrigation resulted in increased values for each measured parameter. In genotype A irrigation to 75 centibars soil moisture tension, a value greater than that found in the field during a dry season but less than field capacity, no change in number of podded nodes (table 4.2.1.9) or number of pods (table 4.2.1.10), but irrigation to 25 centibars soil moisture tension, a level close to field capacity, resulted in a decrease in both of these yield components. The number of seeds and weight of seeds were increased by the lower level of irrigation and decreased when further

irrigation was applied (tables 4.2.1.11, 4.2.12). In G the lower level of irrigation increased the number of podded nodes and number of pods (tables 4.2.1.9, 4.2.1.10) and yet further irrigation decreased the number of podded nodes to a value equal to that of the non-irrigated plants and the number of pods to a value below that. Irrigation to the lower level had no effect on the number of seeds or weight of seeds harvested, but the higher level of irrigation resulted in decreased values for both of these yield components.

When plot harvests were taken and the resultant yield analysed the effects of genotype and genotype x irrigation were again found to be the only significantly differing sources of variation (table 4.2.2.1). The mean yields of each genotype was significantly different from that of the other two (table 4.2.2.2), and the irrigation x genotype interaction showed similar response patterns for all genotypes. The interaction was due to the low values of A recorded under all conditions and the response of Maris Bead to added irrigation was much greater than that of G, as Maris Bead more than doubled in yield in response to added irrigation.

Reports have been made of a direct relationship between yield and water use (de Wit, 1958; Krogman, McKenzie and Hobbs, 1980; French and Legg, 1979; Myers et al, 1957; Gibali et al, 1968). These findings are interpreted on the basis that carbon dioxide uptake by leaves for photosynthesis is essentially related to water loss by transpiration, and that the energy needed for photosynthesis is correlated with that needed for transpiration. In the trial discussed above water availability, not water use, is measured. It is reasonable to assume that when irrigation is applied to plants during a dry season they will actually use some of that water in evapo-transpiration and therefore enhance photosynthate production. It might therefore be expected that the application of irrigation would result in an increase in yield that was related to the ability of plants of each genotype to make use of the added water. In experiments testing the effects of a water table

maintained at different levels Alvino et al (1984) found that excess water resulted in substantial yield reductions, but wide varietal differences in response to water table levels were recorded. The results obtained in the irrigation trial in this study may be interpreted on the basis of the above findings. All three genotypes tested were able to make some use of the water added in the lower level of irrigation and so produce an increased yield. The extent of the increase in water use was reflected in the yield increases and the increased production of vegetative growth. Further irrigation could only be utilized by Maris Bead, but this high water level was excessive to the requirements of the other genotypes and therefore yield reduction was incurred.

In terms of source-sink relationships, the lower irrigation level results in the raising of the values of all of the reproductive and vegetative characteristics measured, with a slight emphasis on vegetative growth, implying that the vegetative growth period is prolonged before the pods become the primary assimilate sinks. With further irrigation the yield of A drops and no further increase in height is recorded. This may indicate that the roots of the plant are effectively waterlogged and so the plant is unable to make use of the high level of irrigation applied. Although the yield of G falls drastically in response to high irrigation, the vegetative growth increases; this is the result of a change in source-sink relationships, the vegetative apex continuing to grow as fewer pods are set and so their sink activity is effectively reduced and the vegetative apex remains the primary assimilate sink for a longer period of time. The higher levels of irrigation, when applied to Maris Bead, produced a small increase in vegetative growth and yet a slight overall decrease in seed yield as in genotype G.

As water availability is an important environmental variable the plant response to such a growth factor is of primary importance. The combined effects of water availability and plant population are of great

interest as they yield information as to which genotypes are best grown at high or low planting densities in areas of high or low rainfall, and this may, to some extent, be used to determine which soil types within a region will yield best at which specific planting densities. From the present study it would appear that genotype G is best grown in a fairly dry area.

If, in addition to maintaining a high level of available soil water, nutrients are maintained at optimal levels for the crop and a form of support is available for the resultant lush vegetative growth, then the effects of much reduced environmental stress may be tested. These conditions are described by Thompson and Taylor (1979); the plants grown under such conditions are very tall (table 4.3.2) and have little thickening tissue to confer rigidity. Pod set and seed yield per plant were fairly high under these conditions in lines tested that were not suffering from inbreeding depression (Maris Bead, F, G). This growth regime supports increased photosynthetic rates; assimilate partitioning does not, however, favour the production of high seed yield. Other reports on similar trials (Thompson, 1979, 1983; Thompson and Taylor, 1979, 1981) show that the yield achieved is unstable and does not reliably exceed that of control plots. Prolonged leaf area duration is observed in these trials (Thompson, 1983), yet the partitioning of the assimilates produced favours increased vegetative growth. The results of such trials seems to point to the need for some environmental stress to be present in order to maximise reproductive efficiency and yield. This is a pattern commonly observed in weeds and is a reminder that faba beans are themselves weedy in growth habit and development.

In the irrigation and density experiment of 1983 the main effects follow a different pattern to that found in the irrigation experiment in 1982. This apparent discrepancy between years may be due to the seed stock, as the progeny of the 1982 trial were used for the 1983 trial, the outcrossing that occurred between plants of genotype G may have resulted in a more vigorous population. The effect of the different genotypes is

only of significance with regard to vegetative characteristics, but there is no significant difference between the genotypes with regard to any of the yield components recorded. In analysis of individual plants Maris Bead gave higher values for the vegetative characteristics than did G, but the values of reproductive characteristics were similar. In 1983 irrigation as a main effect has a highly significant effect on the values of all yield components and vegetative characteristics measured, but this was not so in 1982. As might be expected, the values of vegetative characteristics all increase in response to added irrigation, and the values of all of the reproductive characteristics also increase in response to irrigation, yet this is the opposite to the effect observed in 1982. A possible explanation for this is that 1983 might have been drier than 1982 and so raising the soil moisture tension in the controls, this would reduce the evapo-transpiration and consequently reduce photosynthesis and therefore the amount of assimilate available for reproductive development. The formation of a greater number of flowering nodes when irrigation was applied suggests that meristematic activity involved in the production of floral initials was prolonged by the favourable conditions. Planting density has a highly significant effect on all the parameters measured except plant height; the increased plant population results in a decrease in the value of any parameter measured for an individual plant, and this is in agreement with the results of the systematically arranged spacing trial. A plot effect was detected for plant height, and consequently for total stem length, the plants in plot W being slightly taller than those in plots V or X.

Of the interactions possible the most important ones here are those of genotype x irrigation and genotype x density, but the irrigation x density interaction was generally non-significant. The interactions that do occur may all be ascribed to the greater sensitivity of Maris Bead to environmental differences, and the application of irrigation results in an increase in a variable in both genotypes but that increase is far more marked in Maris Bead than in G. Increased planting density,

as might be expected, results in a decrease in value of a parameter measured in an individual plant.

This experiment verifies the arguments put forward for the effects of planting density on the basis of source-sink relationships and yield production in the different genotypes. The effects have been found to differ from year to year: the different results seem to arise from a difference in the use that genotype G is able to make of the extra available water for both vegetative and reproductive growth. In 1983 the plants were able to make use of the high levels of available water which was not possible in 1982. The results of the 1983 irrigation and density experiment follow fairly closely the results of the 1982 irrigation trial with the lower level of irrigation applied. This suggests that the arguments put forward for water use and yield response to irrigation in that experiment may apply here.

From the data collected in this trial an attempt was made to produce a general regression equation using variables that could be measured in the field to predict the seed yield of plants before harvest. This would potentially be a useful selection criterion along with other phenotypic selection criteria such as flower colour, peduncle architecture, etc. Using raw data a curvilinear yield prediction plot was produced (figure 4.4.1.1.) and the scatter of points about the regression line was quite wide. By taking natural logarithms of all values a straight line plot was achieved (figure 4.4.1.2) with all the data points lying quite close to the regression line. The use of this regression equation to predict seed yield has yet to be tested. If it does give an accurate indication of yield considerable use could be made of such an equation in selecting for high yielding lines in a segregating population.

The plant profiles plotted give the mean distribution of yield components on plants from each treatment. As might be expected, increased planting density results in little change in the number of flowers produced by G, but a considerable reduction in number of flowers produced

by Maris Bead. Added irrigation results in the production of an increased number of flowers in both genotypes, and again it is Maris Bead that is most effected by the irrigation applied. Irrigation also increases the duration of the flowering period. The same pattern of decreased values due to increased planting density and an increase in value due to the addition of irrigation may be seen for pod set, number of pods filled, and number of seeds. At low planting densities the yield producing zone of the plant involves more nodes. The addition of irrigation also extends the yield producing zone. Planting density and irrigation have no effect on the node number of the first reproductive node in either genotype: this might be expected considering the results of the density trial.

The analysis of plot yields shows effects due to density and irrigation to be highly significant (table 4.4.2.1). The increased planting density resulted in a 25% increase in yield per unit area and the application of irrigation resulted in an overall yield increase of 68% (table 4.4.2.2). The genotype x irrigation interaction shows that the yield of G is more stable than that of Maris Bead under different irrigation regimes. The yield of G increases by 43% in response to irrigation, whereas that of Maris Bead increases by 97%. The influence of irrigation was different at different planting densities; at 40 plants/m^2 irrigation increased yield by 47%, whereas at 80 plants/m^2 it increased yield by 88%. Thus yield of either the traditional type of beans or the IVS type may be enhanced by irrigation if the prevailing conditions are such that the plants can utilise the extra available water. A more careful study of the water use of various genotypes of beans under different environmental conditions needs to be made in order to understand when irrigation may be appropriate to procure an increased yield. This would, however, only be appropriate in situations where a rain gun could be installed when necessary and such measures are only taken when the crop is of high value, and in order to justify these measures in the bean crop a high reliable yield would be necessary. A further important factor to be considered here is the influence of irrigation on harvest date. If water supply is plentiful

then the senescence of the plant is delayed and therefore early harvesting is not possible. If delayed until September the weather often breaks and makes harvesting difficult, the use of heavy harvesting machinery on a wet soil results in soil compaction and loss of structure, and the growth of subsequent crops may be impeded by this. If harvesting is possible directly the cereal harvest is finished these problems should be avoidable.

Another limitation to photosynthesis imposed by water availability is that produced by water shortage. In the field this is difficult to test as rainfall may, at any time, remove any stress due to water shortage, and to avoid this the plants used for this experiment were pot grown (see Materials and Methods). By growing the plants in this way the source-sink relationships are somewhat altered as root growth is restricted and therefore more of the assimilate synthesised is used in stem growth. Also pot grown plants are more prone to tillering and branching than are field grown plants and their plant structures are therefore quite complex. The treatments used were imposed at different stages in the reproductive life of the plants. Water withheld at the pre-flowering stage may have an effect on the meristematic activity forming floral initials. Waterstress at flowering and early pod set was found by Smith (1982) to promote abcission of reproductive organs of plants of non-IVS peduncle architecture, and in this trial the effects of such a stress on IVS and non-IVS lines is compared. Waterstress at pod fill seems to enhance seed production.

The significant sources of variation found by analysis of variance of individual plant yield and yield structure were those of genotype, treatment, genotype x treatment, treatment x replicate and genotype x treatment x replicate. The effects of genotype are much as would be expected from the growth patterns observed in previous trials. Maris Bead is taller than G; this reflects the source-sink relationships discussed earlier. The tendency to produce branches and tillers is greater in G than in Maris Bead and results in the formation of a highly significantly greater number of stems. The total stem length

of G is, however, less than that of Maris Bead as G is a short bushy plant when pot grown. When an active stem apex is present in Maris Bead the activity of that apex continues until the pods formed at the lower flowering nodes become the primary sinks. The period of vegetative growth following flowering in Maris Bead is considerably longer than that of G. A possible hypothesis of this inter-genotypic difference is that the line taken in translocation of hormones from developing seeds to the active sources is longer in Maris Bead owing to the greater distances to be travelled in the taller plant. No significant difference between genotypes were found for the number of leaves formed: this is in agreement with the earlier findings. The number of leaves formed is the same in both genotypes, but, owing to the differences in plant structure, these are differently distributed. The dry weight of straw produced by Maris Bead is greater than that of G; this is due to the longer internodes and increased stiffening tissue found in stems of Maris Bead. The production of much vegetative material is not a desirable characteristic as the assimilates employed in this could have been used for pod filling, but there is, of course, a need for sufficient stem thickening to produce lodging resistant plants as severe lodging may result in considerable yield losses.

Examination of genotypic differences in reproductive development shows differences in number of flowering stems and number of flowers, but not in number of flowering nodes formed: this implies a difference in number of flowers per flowering node. G produces more flowering stems than Maris Bead and an equal number of flowering nodes, but fewer flowers and therefore has fewer flowers per flowering node. The production of more flowers by Maris Bead has no effect on pod set and no significant difference between the genotypes could be detected for the number of pods set. Similarly, no significant difference was detected for the numbers of ovules contained within those pods. This is contrary to predictions based on the fact that ovaries of G usually contain fewer ovules than do those of Maris Bead. A greater number of seeds were filled by Maris Bead and thus a heavier yield produced than that of G, but the extent of the difference in yield of the two

genotypes was somewhat greater than expected when considering the results of earlier trials. This may be due to the greater ovule abortion in G, as in this genotype many pods with only a few seeds per pod are produced, whereas in Maris Bead more seeds are filled in each pod. The reason for the ovule abortion in G is not clear, but high intra-pod competition may be a significant factor.

The treatment effects are somewhat difficult to interpret owing to the frequent low values of the controls. Waterstress pre-flowering effects the vegetative characteristics of the plants by producing shorter plants with fewer leaves and a reduced dry weight of straw than any of the other treatments or the control. Waterstress at flowering/pod set results in plants slightly taller than the control, but of equal total stem length, fewer leaves and a dry weight of straw equal to that of the control plants. This treatment seems to favour internode elongation rather than node formation. Waterstress pre-flowering resulted in less vegetative growth overall. Increased vegetative growth was recorded, compared with control plants, when waterstress was imposed at the pod fill stage, but no satisfactory explanation for this can be offered.

The effect of waterstress on reproductive development is related to the stage at which the stress was imposed. When stressed pre-flowering a reduced number of flowering stems, flowering nodes and flowers was produced. This must be a consequence of the effects of waterstress on the apical meristem during the period of production of reproductive initials. This effect, as might be expected, may be followed right through the reproductive development of the plant to the weight of seeds harvested. The production of fewer reproductive organs at the beginning of the reproductive phase is usually indicative of a low final yield. Waterstress at the flowering/pod set stage results in fewer flowers but no reduction in pod set or the number of ovules present in the pods that are set, but the number of seeds filled and weight of those seeds are, however, reduced compared with the values of the control plants. The decrease in flower number may be due to the timing of the imposed stress to coincide with early pod set on the lower nodes of the main stem interfering with the meristematic activity

forming flowers on the branches of the plants. A reduction in pod set was expected in response to waterstress at this stage of development (Smith, 1982), but no such reduction was recorded. This implies that fertilization, accompanied by the development of one or more seeds prevented abcission even under drought conditions. Fewer seeds per pod were filled, as intra-pod competition seems to be drastically increased by the limitation of assimilate production caused by the water shortage. Waterstress at pod fill resulted in consistently high values for all of the growth parameters recorded, and the only possible explanation of this is a difference in plant vigour, but this does, however, seem unlikely. The higher yield may be produced by the rapid and efficient translocation of non-structural carbohydrate (starch) from other plant parts into the seeds when the water shortage was imposed. This could prevent extensive yield loss, although why this should happen in this treatment and not in the others is not known.

Examination of the genotype x treatment interaction reveals a stable pattern of variation. In genotype G the value of all yield components is reduced by waterstress pre-flowering: otherwise yield component values change very little in response to waterstress. In Maris Bead a far greater response to waterstress is seen; the values recorded vary considerably. The imposition of waterstress at pod fill seems to result in increased values for most yield components. This may be a result of stress enhancing reproductive capacity, or more likely a result in variation in plant vigour. The yield component values for G are consistently low but are more stable than those of Maris Bead. The remaining interactions, those involving replicates, are attributed to the low replication levels used. There were only four plants per replicate of each genotype with each treatment, but higher replication was not possible owing to the labour involved in maintenance of the experiment.

This experiment reveals that water shortage at the pre-flowering stage has the most drastic effect on both genotypes and the effects of stress imposed at other stages of development depends on the vascular archi-

tecture of the plant. In the IVS type plants the inter-pod competition is altered such that the effects of the environment are buffered and the stress experienced is less strongly reflected in final yield and to a minimal extent in pod set.

From all of the field trials several consistent genotypic differences arise. The yield of G is consistently lower than that of Maris Bead but is relatively stable when tested in a range of environments. Plants of G are, without exception, ready for harvest at least four weeks earlier than those of Maris Bead. The reason for this has been investigated in an anatomical study. Irrigation may be of benefit to IVS type beans only if the prevailing conditions are such that use may be made of the applied water. Owing to the yield stability of G a higher pod set may be obtained at high planting densities, but as yet no IVS type plant has been tested in the field that is able to fulfill its potential sink capacity. If the leaf area duration of G could be genetically improved without undue delay in harvesting, then the procurement of a high reliable yield might be possible. Further selection and testing is necessary to find an IVS type line that yields as well as present commercial lines. If this were found the stability conferred by the peduncle architecture could make the bean crop a more attractive proposition than the present commercial varieties with their inherent yield instability.

Pod growth and development

When considerable differences between the genotypes with regard to pod maturity times was observed there were considered to be two possible sources of this variation. The first was a purely genotypic control with the source-sink relationships of the plant governing the development and senescence of the pods. The second was that there may be genotypic differences in pod growth and structure. Contrasting genotypes were selected for a study of pod growth and a survey of pod anatomy. Earlier in this discussion the source-sink relationships of these three genotypes were discussed in detail. It should be remembered that plants of genotype 22 flower two weeks before those of

Maris Bead, and, at the end of the growth period, yield is source limited. The rapid senescence of such a plant releases stored assimilates: these are then translocated to the growing seeds. Genotype G flowers a week later than 22 and is also source limited; Maris Bead flowers last and gives no indication of source limitation. The differences in flowering dates do not account for the vast differences in pod maturity date: the rapidity of senescence may play a considerable part in bringing about the genotypic differences in maturity. There still remains a strong possibility that the rates of reproductive development and the structure of the pod may be involved in bringing about the differences observed. Growth in pod length, the structure of the pod wall, and the surface of the pod were studied in search of genotypic differences.

The rates of pod length growth were found to differ only at the outset of growth and at the later stages of growth (figure 5.1). At the outset of growth pods of genotype 22 were slightly longer than those of other genotypes and grew most rapidly and attained lengths greater than those of G or Maris Bead (table 5.1.2), but after ten days no significant difference between genotypes was detected as the pods of G and Maris Bead rapidly reached lengths similar to those of 22. At later stages of development the pods of Maris Bead were significantly longer than those of 22 or G. This is likely to be associated with a higher number of seeds per pod in Maris Bead. The rate of reproductive growth with respect to pod length growth varied between genotypes, but not enough for this alone to have an effect on pod maturity dates.

The examination of the structure of the pod wall in cross section revealed an interesting and important anatomical variation between genotypes. In the rapidly maturing pods of 22 there was no "parchment" layer; in the pods of G this was present but as a discontinuous structure; in Maris Bead a thick, continuous layer of lignified tissue was present in the mesocarp. This layer, where present, may serve two functions. Firstly it creates internal tensions enabling the pod to dehisce, flinging the seeds out as the valves of the pod separate and twist in opposite directions: secondly it may serve to inhibit water loss from the endocarp. The presence of a layer of water-proofed

lignified tissue would prevent free passage of water from the endocarp to the surrounding atmosphere. This would control and effectively slow down pod drying. If no such layer is present the evaporation of water from the endocarp would be much faster and so pod maturity arrived at more quickly.

In an arid environment the free evaporation of water from the pods of genotypes with no lignified layer present in their walls could be a problem as the pods would easily dessicate before seeds had been ~~produced~~ matured. Examination of the pod surface revealed the presence of an anatomical difference between genotypes that would help to control water loss from pods with no lignified mesocarp. The density of pod wall hairs was much higher ~~of~~ for genotype 22 than for the other genotypes, and the difference was highly statistically significant, but no such difference in the number of stomata was recorded. The high density of pod wall hairs would result in the formation of a deep boundary layer of humid air close to the pod and prevent the removal of that layer by air currents and thereby reduce the rate of evapo-transpiration. This result suggests an integrated control over pod maturity: the source limitation means that pod senescence commences earlier in 22 than in G or Maris Bead and earlier in G than in Maris Bead. The pod wall structure enables the pods to dry out more rapidly when appropriate and so together these characters control pod maturity dates. Further investigations into the mechanisms of pod senescence and drying could be valuable in determining selection criteria for use by breeders.

Reproductive growth - fresh and dry weight increases

If the period of time available for seed growth varies from genotype to genotype it would seem logical that the rates of seed growth may differ. If the seeds grow at different rates in terms of fresh and dry weights then, by implication, so must the pods. If the pods are growing along with the seeds then the supporting tissues, that is the pedicel and peduncle, must also grow in order to retain their supportive role. The fresh and dry weights recorded (figures 6.1 to 6.16) support both of these concepts. The increase in dry weight of

the seeds is dependent on the development of the other tissues involved. At the outset of raceme development the peduncle becomes the primary sink, followed by the pedicel, the pod, and finally the seed (figures 6.13 to 6.16). The fertilization of an ovule is rapidly followed by cell division, and these cells produce plant hormones which may be of significance in the growth of the peduncle, pedicel and pod wall (Egli et al, 1981).

Genotypic differences in reproductive growth rates are detectable: genotype 22 is the first to increase in dry weights in all parts and grows most rapidly; this is followed by genotype G, and then Maris Bead. The duration of growth also differs between genotypes, and from figure 6.16 it can be seen that maximum seed dry weight is attained for 22 after only 40 days. In G the seed development period is 48 days, and in Maris Bead over 64 days.

This data, together with information on pod wall structure and source-sink relationships of the plants of the different genotypes studied, provides a pattern of the reproductive development of the plants. The maturity date of the pods of any genotype is the result of the source-sink relationships of the plant together with the growth rate of the reproductive tissues. The pod drying is controlled by plant senescence together with the pod wall structure.

Vascular development

Two further questions remain to be answered: what is the nature of the increase in weight of the peduncle and pedicel? Is it purely an increase in supportive tissue, or is it due to an increase in vascular tissue supplying the growing seed, or, indeed, a combination of the two? The second question concerns the origins of the assimilate supplied to the seed during the period of very rapid seed dry weight increase at the beginning of seed growth. Is this assimilate a product of rapid photosynthesis, or is this a supply of assimilate that has been temporarily stored elsewhere in the plant? A study of the pedicel and peduncle at anthesis and maturity was made in order to answer the first question, and the vegetative parts of the plants were screened for sources of non-

structural carbohydrate that could be seen to disappear shortly after the beginning of pod fill in order to answer the second question (Gates et al, 1981).

Examination of cross sections of the peduncle and pedicel at anthesis and at maturity revealed a massive increase in area of xylem and phloem, the tissues involved in transport of water and translocation of assimilates into the seeds. This development would make rapid, efficient translocation into the seeds possible. The vascular tissue in the adaxial vein of the pod also increased considerably in area. This is the continuation of the pathway into the seed: also a ten-fold increase in the number of phloem sieve tubes crossing the hilum into the seed was observed, and thus vascular development increases to allow efficient assimilate transport right into the seeds. It was noted that failure of ovule development was accompanied by failure of the development of the vascular supply to that ovule. As fertilization is unlikely to be a limitation on seed development (Stoddardand Lockwood, 1984) intra-pod competition seems to be the most likely reason for such failure of development, the seed and hormonal output of seeds proximal to the stigma controlling the development of the seeds more distal to the stigma.

The source of the assimilate supplied to the seed during rapid reproductive tissue growth is the stem. Large reserves of starch are visible in the outer cortex of the stem at the commencement of flowering: during rapid pod fill the starch disappears (plate 9). This suggests that the stem is acting as a temporary assimilate sink before pod fill starts. This finding renders the relative importance of the vegetative apex as the primary assimilate sink open to question: just how strong a sink the stem can be is not known. This is clearly of importance and justifies further investigation in order to incorporate the location and capacity of temporary sinks of non-structural carbohydrate into a future faba bean plant ideotype.

Conclusion - a possible crop ideotype

In conclusion, the independent vascular supply type faba bean plants may be regarded as a step forward in the domestication of the crop. The

non-IVS genotypes in common agricultural use show many weedy characteristics, such as a prolonged flowering period, high floral wastage, sink limitation of yield, indeterminate growth habit, and dehiscent pods. The change in peduncle vascular architecture and the accompanying switch from sink to source limitation confers a shorter flowering period, is of semi-determinate growth habit, and fills its pods rapidly.

During the course of these studies the IVS type plants of genotype G were tested in field trials in which various environmental stresses were imposed on the plants. The yields of G were more stable than were those of Maris Bead. Under dry conditions the yield of G was equal to that of Maris Bead. At high planting densities G set far more pods than did Maris Bead, but not all of those pods were filled. This is due to source limitation of yield. The evaluation of the growth pattern and rate of the various reproductive parts showed that the seed fill period is shorter in G than in Maris Bead, and that this, coupled with the earlier flowering of G, results in the plants being ready for harvest earlier than those of Maris Bead. A ten-fold increase in the number of phloem sieve elements was noted; such an increase is prerequisite for the period of rapid seed growth. At the outset of raceme development the peduncle, pedicel and pod function as assimilate sinks. The sink activity of the seed does not commence until the xylem transport and phloem translocation pathways are established. During rapid pod fill assimilates located in stem tissue serving as a temporary sink are mobilised and rapidly translocated into the growing reproductive structures.

The information from this study, together with that found in the literature, may be used to construct a crop model or ideotype for the faba bean crop. Such an ideotype is proposed using the existing knowledge of the crop; this should not be left unchanged as the state of knowledge of the crop advances, but should be flexible; the ideotype should be updated as more facts emerge about desirable plant types for various field situations. As the crop may be grown in a variety of climatic conditions several ideotypes are necessary. By this means a plant breeder may select for plants that would produce a good yield in a

particular geographical region as the climate and the cultural techniques used in that region and taken account of in the selection programme. In Britain an ideotype must result in plants that grow reliably well in spite of our extremely variable climate. When considering desirable crop characteristics it is necessary to examine the characters not in isolation but as parts of an integrated genetic system, taking into account genetic linkages and the results of environmental modification of gene expression.

Using the available information the following crop ideotype is proposed:-

Independent vascular supply type peduncles

As seen in the results of field trials in this study and those of Smith (1982), this character results in a more even raceme development as there is no direct hormonal influence passing from one flower to another, and so abcission is prevented and more pods are set. The inter-pod competition at any one raceme is less polarised; the result of this is that more seed bearing pods are harvested at each podded node. The IVS plants, because of their reduced abcission rates, gave a more stable yield under conditions of environmental stress.

Synchronous anthesis at each node

By this means the flowers at any node may be pollinated and fertilized at the same time, and so no gradient of competition within the raceme is established, and even pod development at the lower flowering nodes is observed. Such a system tends to produce earlier maturing pods as the available assimilates are rapidly utilised by pods at lower nodes, and so those at the upper nodes do not develop due to assimilate shortage.

Auto-fertility

Lee (1984) states that the growth rates of pollen tubes are genetically determined. If this is so then auto-fertility is of significance in reducing the intra-pod competition and so bringing about more even ovule development within a pod. The pollen of an auto-fertile flower

is of uniform genetic background and so the pollen tubes will grow at the same rate: by this means the advantage of the ovules proximal to the stigma over those more distal is minimised so enhancing the chances of several seeds filling.

White flowers

The production of white flowers is strongly linked to the production of tannin free seeds. Such seeds are more digestable than those of most commercial lines which contain large amounts of tannins. This character could increase the cash value of the crop.

Four or more seeds per pod

The number of seeds filled per pod appears to be a stable character (see density experiment). Thus if this were increased along with the characters discussed above, a higher yield would be procured. These characters together would produce a plant with a high stable yield.

Short plants

This is partially linked with the source-sink relations of the plant and the general state of intra-plant competition. By producing short plants vast amounts of assimilate are not used in the production of vegetative plant parts. Most of the short plants examined have the same number of leaves produced, but shorter internodes. This means that the photosynthetic area is not greatly reduced. Such plants are more resistant to lodging than tall plants, and so mechanical harvesting is easier.

Source limitation of yield

If a plant is source limited then the sources present must be functioning efficiently, and the end of the life of such a plant occurs sooner than in a sink limited plant. A consequence of this is that the plants mature early so facilitating early harvesting when the prevailing conditions are favourable.

Thick stems

By possessing thick stems the non-structural carbohydrate reserves of a plant may be greater so the rapid early pod fill of many pods would be possible. An additional function of such stems would be that of support for the heavy clusters of filled pods.

Improved leaf area duration

A plant with a genetically determined prolonged leaf area duration would have a longer seed fill period and so more, heavier seeds could develop. This could be achieved by the plant having a thicker pallisade mesophyll layer, or by there being more layers of pallisade cells, so increasing the rate of photosynthesis and supplying more assimilate to the seeds. Chapman (1981b) lists some genotypes of Vicia faba with a three cell thick pallisade mesophyll. The leaf area duration should not be prolonged at the expense of early maturity.

Absence of or reduction in the parchment layer in the pod wall

If this were possible then the pods would senesce very quickly once maturity was reached. By this means a longer seed fill would not necessarily result in a late harvest as the pods would dry much more quickly than in the traditional genotypes and so still mature early.

Flowering at low nodes

This results in flowering commencing sooner after planting and so the pods start to develop earlier. This is yet another factor contributing to an early harvest.

The following characters are also considered desirable in the crop but are not directly related to the findings of this study:- Good root development to enable the plant to use available water and to extract water from soil some distance from the soil surface. Nodulation is of importance to seed yield as most of the nitrogen in the seed protein is derived from Rhizobial activity. Nodulation of a leguminous crop also results in the enriching of soil nitrogen for subsequent crops, a form of free fertilizer. Pest and disease resistance also aids yield

production as less crop loss is incurred due to these factors. A further consequence of pest and disease resistance is a reduction in man hours required to tend the crop and therefore a more profitable crop.

A plant with all of the above characteristics would produce a high, reliable yield under a range of environmental stresses. Regional modification of the ideotype could be made to suit a particular environment. Such a variety would increase the popularity of the crop as many of the risks of growing faba beans would be minimised or eliminated. Selection of possible commercial varieties that have many of these characteristics is continuing at Durham (plate 10).

Suggestions for further work

During the course of this study several areas of possible further study have emerged. The most important is concerned with non-structural carbohydrate reserves stored in the stem. The origins of this, its patterns and sites of accumulation would yield information about the intra-plant competition before pod fill, and the amount of carbohydrate that is translocated to the developing racemes. Tracer experiments could be performed to trace assimilates from their source to their final site of deposition. This work would be of value in determining photosynthetic rates of plants at various stages of their development. Root growth of and water use by different genotypes vary: the inheritance and mechanisms of these variations should be studied in order to establish a better ideotype and more selection criteria for breeders.

Plate 10

Independent vascular supply type plants from a field grown segregating population.

(a) main zone of yield production

(b) close up of one podded node


a


b

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