EFFECTS OF WATER STRESS AT DIFFERENT STAGES OF GROWTH ON SEED YIELD OF SAFFLOWER

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ABSTRACT

Safflower plants were grown from seed in controlled environment rooms. The light and dark period temperatures were 23°C and 18°C respectively. Plant water deficits of -8 to -10 bar were imposed for 20 days during each of the periods floral initiation, inflorescence development, flowering, the post flowering period, and for 12 days during secondary head flowering. Water stress during floral initiation or inflorescence development significantly reduced yield over water stress at any other stage of growth. Seed yield was reduced 46% and 57% by water stress during floral initiation and inflorescence development respectively, compared with well watered plants.

Of the sequentially developing traits of seed yield, number of seeds per head accounted for most variation in seed yield, followed by number of heads per plant. Seed weight had relatively little effect on variation in seed yield.

Water stress at floral initiation reduced seed yield due to a 32% reduction in head number per plant at final harvest. Fewer florets developed in each head, contributing to a 53% reduction in the potential seed number per plant. Water stress during inflorescence development reduced the number of heads per plant by 30% and the number of seeds per head by 34%. Water stress during the flowering period reduced seed weight by 23%. This was attributed to a 38% reduction in seed hull weight. Water stress after flowering reduced seed hull content by up to 15% and was associated with a higher seed oil content of 26.5% compared with 22.3% for well watered plants.

It was concluded that safflower should be planted early to minimise the risk of water stress during inflorescence development, and that seed quality may be improved by dry conditions after flowering. From the results it was suggested that safflower may not necessarily be dependant on an extensive root system for its independence of late season rainfall.

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TABLE OF CONTENTS PAGE NUMBER

LIST OF TABLES: PAGE NUMBER

LIST OF FIGURES

APPENDICES:

BIBLIOGRAPHY:

INTRODUCTION

Safflower (Carthamus Tinctorius L) is an oilseed crop traditionally adapted to fairly low altitude, semi-arid regions. Introductions to America from the old centres of culture were initially grown in California and Mexico where they were best adapted. Successful development was attributable largely to the efforts of plant breeders through increased seed oil content and resistance to disease. Success from improvements of this nature may have been to the detriment of production research, since poor adaptation of varieties to the environment continues to limit seed yields in new areas of production (Cutting 1974). Better information is needed about how safflower responds under environmental stress in order to improve production practices and increase seed yields.

Crop yield has been limited by lack of water in most areas, although safflower is particularly responsive to irrigation. Much of the information relating to drought effects on safflower has in general, been of limited value as it has been almost entirely location and season specific. This experiment was designed to quantitatively determine the effects of water stress on seed yield of safflower under controlled environmental conditions.

CHAPTER 1 - LITERATURE REVIEW

This review is in two main parts. The first part briefly discusses certain problems associated with measuring plant water deficit, and interpretation of plant responses in terms of yield. It then discusses the relative sensitivity of some key physiological processes involved in yield formation, and in the light of this, goes on to discuss the significance of drought at different stages of growth to yield formation. The second part discusses the significance of some major environmental factors to safflower growth and yield, and implications of this for safflower production.

1.1.1 Uncertainty in Water Deficit Quantification

How to measure plant water stress suitably in terms of dehydration level and plant response, has long been a fundamental task in the development of plant water relations research. Water flow through plants is driven by water potential gradients (Slatyer 1967, Weatherley 1970). As the rate of transpiration increases, a movement of water from tissues into the mainstream results in absorption being less than transpiration, and the lowering of water content in the tissues represents a water deficit in the plant. Water potential is now widely used as a measure of plant water status. It relates to the energy associated with the water in the plant, and is closely related to plant growth.

The relationship however, is not always the same. The use of water potential alone, does not account for adjustment of its components (largely turgor, solute and matric potentials), in response to

stress (Brown 1972). It implicitly assumes absence of osmotic adjustment in response to water deficit, therefore limiting the interpretation applicable to the responses observed (Wieve 1972). From the view point of plant responses for example, turgor potential is perhaps a better indicator of water stress when concerned with turgor-dependant processes such as growth (Hsiao 1973, Hsiao et al 1976). In some cases, where resistance of roots and leaves to water movement can be functions of the transpiration rate (Weatherley 1976), the flow of water is not proportional to the gradient of water potential, and the relationship between flux, and potential gradients may become non-linear (Hansen 1974). With these factors acknowledged however, total water potential is at present probably one of the parameters most accurately measured, and most easily correlated with plant processes or yield. It is therefore commonly used.

1.1.2 Problems in Plant Responses Interpretation for Yield

Almost all aspects of yield formation in plants can be affected by plant water deficits that are severe and long enough, however water stress at certain stages of growth may cause more yield reduction than at other stages (Salter and Goode 1967). An approach to interpreting stress-yield relations must therefore consider responses to water stress in terms of stress severity, duration, and stage of growth. To determine what 'aspects of yield formation' and how they are affected within these criteria, it is necessary to establish the time sequence of events that occur as water deficit develops. This provides an insight into their nature. Some can be distinguished as causes, others as effects. These can be further characterised as

being direct or indirect. In practice, this is a difficult task, because changes at the molecular level are rapid relative to changes in tissue water status. Therefore, despite reviews from time to time of physiological responses to water stress (Crafts 1968, Slatyer 1969, Kozlowski 1972, Hsiao 1973), the physiochemical mechanisms involved in these alterations to metabolism, remain largely obscure.

Nevertheless, some useful deductions can be made from considering the relative sensitivity to level of deficit, of major physiological processes, since most sensitive processes are normally altered first (Hsiao 1973, Hsiao and Acevedo 1974). Over a period of time, such alterations, in turn, may lead to other changes. As the period of water deficit is extended therefore, the interpretation of stress effects for long term growth and yield is complicated as the result of indirect as well as secondary alterations occurring. Such complexity of casual connections between cellular events and the integrative effects on yield makes quantification very difficult, and so in practical terms, little is known of how desiccation of plant tissues during drought is transformed into reductions in seed yield.

1.2.1 Water Stress and Leaf Growth

The effects of water stress on the growth of leaves is important as they represent the major photosynthetic surface of most plants. In some cases as for example in lupin (Gates 1968), barley (Husain and Aspinall 1970) and sunflower (Marc and Palmer 1976), the rate of leaf initiation may be reduced or even stopped. Generally it seems cell division is less affected by water deficit than cell enlargement

(Meyer and Boyer, 1972), although the relative effects on cell division and cell enlargement may depend on the degree of water deficit imposed (Slatyer 1969, Hsiao 1973, Kleinendorst 1975).

The supply of water to growing tissue depends on the water potential gradient (Slatyer 1967, Weatherley 1970). However cell enlargement requires turgor for cell wall extension (Hsiao 1973). In many types of plant tissue, much of the initial reduction of water potential from cells at nearly full turgor is attributable to a reduction in turgor potential (Hsiao and Acevedo 1974). Growth therefore reflects a balance between enlargement on the one hand, and the gradient in water potential supplying water for expansion on the other (Boyer 1968).

With decreasing water potential, leaf growth is generally inhibited sooner and more severely than photosynthesis (see for example, Wardlaw 1969, Boyer 1970a, Hsiao 1973). Boyer (1970a) found high sensitivity of leaf growth to small levels of desiccation in soyabean, sunflower and corn. Leaf enlargement was maximised at about -1.5 to -2.5 bar but was reduced to 25% this rate or less when leaf water potential fell to -4 bar. Considering the high sensitivity of leaf enlargement to low water potential, normal diurnal changes in water status may often be enough to limit leaf growth largely to the night. In sunflower, leaf growth during the dark period of a controlled environment was more than five times that during the light period (Boyer 1968). Leaf water potential in the dark and light periods were -1.9 and -3.5 bar respectively.

In some situations however, growing leaves never reach water potentials as high as -4 to -6 bar, e.g. the leaves of plants adapted to saline soils (Boyer 1976). There is some evidence for field grown maize that turgor can be maintained in the face of changing leaf water potential by osmo-regulation (Hsiao et al 1976), and may be an important mechanism for adaptation to dry conditions.

1.2.2. Water Stress and Photosynthesis

The photosynthetic activity of leaves at reduced water potentials is important since it is responsible for accumulation of the bulk of plant drymatter, and the reduced drymatter yield due to water stress can limit seed yield. The response of photosynthesis to declining leaf water potential appears to differ between species. Boyer (1970a, 1970b) found rates of photosynthesis for corn was limited at leaf water potentials below -3.5 bar, whereas sunflower was unaffected by desiccation until below -8 bar, and soybean below -11 bar. More tentative data suggest CO_2 assimilation starts to decline within a range of about -5 to -15 bar, depending on species (Hsiao 1973).

When stomata close in response to leaf desiccation, there is often a reduction in net photosynthesis concurrent with the reduction in transpiration (Brix 1962). Photorespiration appears to decrease as leaf water potential decreases (Boyer 1971b), as does dark respiration in many species (Boyer 1976). In cases where dark respiration increased (Brix 1962), the rise was small and ultimately the rate declined. Thus decreases in net photosynthesis are unlikely to involve increases in respiration. Much of the effect on photosynthesis has been

attributed to stomatal closure impeding the inward passage of CO_2 and thus reducing CO_2 assimilation (Hsiao 1973). Other studies however, have indicated the presence of non-stomatal inhibition of photosynthesis (Slatyer 1969, Hsiao 1973) for water deficits lasting days (Boyer 1971b) or longer term (Jones 1973). At the subcellular level, Boyer and Bowen (1970) found oxygen evolution by isolated chloroplasts was inhibited by moderate stress when leaf water potentials fell below -12 bar in pea and -8 in sunflower, and inhibition was proportional to leaf water potential below these limits. It appears then that inhibition of photosynthesis by water stress involves both stomatal and chloroplast responses, and the net effect on CO_2 assimilation may depend on the species involved, which of the responses is most limiting and the degree of stress. In water stressed cotton, there was also some evidence that the photosynthetic system adjusted over a period of time (Jones 1973).

After a period of low water potential, recovery of photosynthesis for stressed sunflower was incomplete, despite recovery of leaf water potential and photochemical activity (Boyer 1971a). The effect was associated with partial stomatal closure lasting several days. There was some evidence that for whole plants, the photosynthetic rate of older leaves never fully recovered, and that regrowth of the plant was required for a return to high photosynthetic activity (Boyer and McPherson 1975).

1.2.3. Water Stress and Translocation

Under moderate to severe stress, movement of assimilates in plants

may be reduced (Crafts 1968, Slatyer 1969, Hsiao 1973). During water stress assimilates may accumulate at sites of photosynthesis, if expansion growth is restricted sooner, and to a greater degree than photosynthesis. Wardlaw (1969) found that in water stressed ryegrass movement of photosynthate out of a mature leaf was no longer suppressed, if the other mature leaves were removed to eliminate sources competing for the diminished sink brought about by reduced growth. These results suggest that stress may lower source strength due to diminished sink demand or by reducing photosynthesis, and lower sink strength by inhibiting growth, thus reduce assimilate movement. The conducting mechanism itself was considered to be relatively resistant to desiccation. Changes in translocation due to this effect, may be important in that the translocation pattern determines partition of assimilates among different parts of the plant. In studies with wheat (Wardlaw 1971) and maize (McPherson and Boyer 1974) translocation was apparently not prevented at levels of water stress that inhibited photosynthesis. The effects of desiccation on source and sink that alter translocation patterns may therefore vary between species, and could be an adaptive mechanism for some species under dry conditions.

1.3 Significance of Water Stress at Different Stages of Growth to Yield Formation

There are many important facets of stress-yield relations and their interactions are particularly complex where yield of seed is concerned. Seed formation depends on progressive initiation and differentiation of tissue and organ primordia, and contributions by the major physiological processes photosynthesis and translocation of assimilate, nutrient

supply, cell division and enlargement, during the appropriate stages of plant growth. In turn, these events depend on the appropriate environmental inputs for completion of each stage of growth. When water is limited, tissues and organs growing most rapidly, suffer the greatest check to growth (Williams and Shapter 1955, Aspinall et al 1964, Claassen and Shaw 1970). The extent to which this response influences seed yield, will depend on the severity and duration of water deficit in relation to the stage of growth at which the stress occurs.

1.3.1. Water Stress at Floral Initiation

A potentially important plant response to water deficit is that affecting growth and development at the shoot apex at the time of floral initiation, due to the central role of the apex in subsequent plant development. Floral initiation is the stage of plant growth in which the potential number of inflorescences and potential number of seeds to be set in each is first determined. It is also the stage where in determinate crops, the number of leaves to develop and support yield formation is fixed. The initiation of reproductive development exerts an influence on the timing of subsequent ontonogenetic stages of growth.

The initiation of vegetative primordia can be very sensitive to small water deficits. In lupin, initiation of foliar primordia was inhibited early in the drying cycle (Gates 1968) and in sunflower, the rate of leaf initiation was decreased at a shoot water potential of -5 bar (Marc and Palmer 1976). In these cases however the capacity for

subsequent resumption of initiation after stress relief was apparently unimpaired, and similar numbers of leaves to well watered plants eventually developed. In sunflower, at levels of water stress greater than -5 bar, a reduction in total leaf number resulted from the decreased rate of leaf initiation before the transition to floral initiation (Marc and Palmer 1976). An extended stress period had no additional effects, possibly because water stress could no longer affect leaf formation after the transition of vegetative apex to the flowering state.

Perhaps the more immediate consequence of water stress on seed yield around floral initiation is that of reducing the number of floral primordia produced and thus the number of yield sites available for subsequent development. Floral initiation appears to be affected similarly to foliar initiation by relatively mild and brief periods of water deficits. In barley, primordium formation ceased completely when the soil water potential reached -2 to -2.5 bar (Nicolls and May 1963). On stress relief, the rate of primordial appearance increased, causing little effect on the total number of primordia finally developing. Reversible development of retarded ear initiation on stress relief may occur to a greater degree for crops with indeterminate inflorescence development, than in determinate species where inflorescences are terminal, thus restricting the number of compensatory yield sites available. However a prolonged stress at this stage could limit the potential number of seeds per plant, as development in primordia already initiated on the apex may continue at stress levels that inhibit further primordium formation (Nicolls and May 1963, Hussain and Aspinall 1970). It appears that just as leaf initiation may be limited by the onset of the

flowering state during water stress, the initiation of floral primordia may be influenced by the attainment of differentiation into the next stage of ontogeny - that of floral development.

The effect of severe water stress at floral initiation appears to vary between species. In sunflower, stress levels of -10 to -30 bar for ten days had relatively little effect on time of floral initiation but reduced flower size by reducing the number of involucral bracts and florets contained in each (Marc and Palmer 1976). In contrast, sorghum that suffered wilting for more than a week had a correspondingly later flowering date, but with flower heads that developed not unlike those of well watered plants (Whiteman and Wilson 1965).

How plant responses to water stress at floral initiation are mediated is still largely a matter of conjecture. A limited supply of photosynthate to the shoot apex may occur at moderate stress levels due to inhibition of photosynthesis, however in sunflower, primordial initiation is reduced at levels of stress (-5 bar) that do not restrict photosynthesis (Boyer 1970a). As leaf expansion is likely to be inhibited even for mild stress, the demand for assimilates at meristems may outstrip that provided by the restricted photosynthesising surface. Husain and Aspinall (1970) suggest that sensitivity of primordium production to water stress is not necessarily by direct effects on apical water potential nor on assimilates. They speculated that the response may develop due to the less mature apical meristem with a limited supply of essential factors, being monopolised by the existing primordia, during periods of stress.

In the sorghum study (Whiteman and Wilson 1965) it was apparent that the floral apex might develop at a water stress sufficient to prevent leaf expansion. In sunflower also, the developmental processes leading to inflorescence formation were relatively unaffected (Marc and Palmer 1976), and in barley differentiation of initiated primordia continued at levels of stress inhibiting further initiation (Nicolls and May 1963). It appears therefore, that vegetative growth may be more sensitive to stress than reproductive growth and development of initiated floral primordia less sensitive than the initiation process.

1.3.2. Water Stress During Floral Development

Yield reductions in many annuals are the most severe due to water stress between floral initiation and flowering. (Salter and Goode 1967). At this stage of growth competition for assimilate within the developing plant is severe, and floral development is very dependant on the photosynthetic activity of the developing leaves. In barley, a delay between initiation and extension of a tiller bud prevents further development of the bud (Gallagher et al 1976). Thus the potential number of inflorescences per plant may be limited at an early stage if water stress prevents elongation of stems subtending buds.

Often the most severe and direct influence on seed yield is reported to be a lowering of seed set. An increase in floret sterility has contributed directly to a yield reduction in barley (Aspinall et al 1964), wheat (Langer and Ampong 1970) and maize (Moss and Downey 1971, Damptey and Aspinall 1976). The stress levels imposed were drying cycles to wilting point in barley, 25% soil water holding capacity

in wheat, less than 84% relative turgidity for maize (Moss and Downey 1971), and down to about -13 bar for maize (Damptey and Aspinall 1976). The physiological reasons for the effect however are little understood. Changes in the availability of carbohydrate and nutrients may be an important way by which the effects are mediated, since a reduction in either can lead to a lower seed number (Slatyer 1969).

In maize, growth of the uppermost auxillary inflorescence was inhibited during any period of water deficit coinciding with rapid growth, but this inhibition was compensated by rapid growth after stress relief (Damptey and Aspinall 1976). Similarly, brief inhibition of leaf enlargement can be reversed on stress relief, as the tissues appear to enter a rejuvenating phase (Gates 1968). Compared with the complete suspension during stress of primordial initiation, cell division may continue at stress levels that inhibit cell expansion, and provide the opportunity for 'compensation' by resumption of expansive grwoth when stress is relieved (Slatyer 1969). Hsiao and Acevedo (1974) consider that generally, a brief and mild water deficit at this stage tends to postpone plant growth and development, and that the longer term effect on yield will be influenced by the length of the growing season, and amount of flexibility in harvest timing.

In contrast, water stress that limits leaf enlargement for an extended period can cause a reduction of leaf area development that is only partially recoverable (Fisher and Hagan 1965, Boyer 1970a). As cell enlargement is closely associated with the laying down of fairly rigid cell wall materials, slower rates of cell enlargement are generally

associated with smaller final size (Slatyer 1969). There is also the possibility that reduced rates of cell division due to a prolonged mild stress may be an indirect result of reduced cell expansion (Hsiao 1973). Thus the opportunity for 'compensatory growth' is restricted and maximum leaf area attainable is reduced.

The reduction in yield resulting from floret sterility were associated with moderate or greater stress levels (see for example, Moss and Downey 1971, Damptey and Aspinall 1976) which probably also affected the rate of photosynthesis. However in view of the finding that leaf enlargement is usually more sensitive to stress than CO_2 assimilation, it cannot be assumed that yield will be unaffected by stress levels that do not directly reduce photosynthesis. When water stress occurs in field situations, fluctuations in crop growth rate are often largely attributable to variations in leaf area development at this stage of growth, (Fischer and Hagan 1965, Dougherty 1973), as dry matter yield is a function of crop growth rate over the entire growth period (Yoshida 1972), and a reduction in dry matter yield often reflects on seed yield.

The known relation between leaf area and seed yield as a result of water stress, often remains only a correlation (see for example, Langer and Ampong 1970) because mechanisms are involved over a period of time and our knowledge of their manifestation is largely obscure. During the stage of floral development when leaf area is rapidly expanding but still relatively low, the extent of yield reduction due to prolonged, mild stress may depend on two important factors : whether leaf area

index is limiting assimilation by restricting light interception, or potential assimilatory surface; and whether assimilates can accumulate in existing leaves without their actual rate of photosynthesis being reduced. If Photosynthetic activity is not inhibited by accumulation of photosynthate in the non-expanding leaves, then the rate of crop growth will be limited by the leaf area index. By this reasoning, drymatter yield is likely to be more sensitive to mild levels of water stress during this stage of growth, than during the filling of seed after most of the leaves have developed. In the seed filling stage, assimilate supply is more dependant on current photosynthetic activity and on translocation of previously stored material, than on the more stress susceptible turgor-dependant processes involved in leave development.

In maize subjected to pre-treatment desiccation, grain yield was dependant on the total drymatter accumulated during the growing season, rather than just that which occurred during grain fill (Boyer and McPherson 1975). This suggests that limitation of drymatter production by either reduced leaf area development or reduced photosynthetic activity during the pre-flowering stage could reduce seed yield since plants can mobilise the photosynthate produced at this stage, and use it to fill the grain. Langer and Ampong (1970) found that low grain weight in wheat was associated with water stress expressed as 25% of the soil water holding capacity for three weeks prior to anthesis. The treatment was associated with a large reduction in leaf area which, because of the lateness of the treatment, was not recoverable.

Toward the end of floral development when leaf growth is near maturity, a prolonged water-stress may cause loss of photosynthetic tissue by leaf senescence (Boyer 1976). If the stress has been severe enough to cause breaks in the columns of water transport to leaves, desiccation may continue despite rewatering of the soil (Hsiao 1973), and in determinate crops, represents an irreversible loss of photosynthetic capability by the crop. The metabolic conditions that lead to senescence are unknown (Boyer 1976). An early change is the movement of nitrogen from the senescing leaf toward meristematic regions (Slatyer 1969) indicating disruption of normal cell metabolism and degredation of proteins in the senescing leaves. This may be part of a more general plant response, since in many annuals, the rate of reproductive processes are accelerated at the expense of vegetative growth (Dougherty 1973) and earlier flowering can result (Salter and Goode 1967).

1.3.3. Water Stress at Anthesis

Anthesis is a very critical stage for the development of seed yield since it is a relatively brief but essential period of the life cycle. The effect of water stress on seed yield at anthesis therefore does not provide opportunity for 'compensation' in the same way that stress at an earlier stage of growth may do. The physiological factors responsible for stress effects at anthesis, along with those during floral development are the least understood although they frequently result in large reductions in seed yield.

In cereal crops, a reduction in fertilization and seed set usually occurs (Aspinall et al 1964, Claassen and Shaw 1970, Langer and Ampong 1970). Such effects have been attributed to possible dehydration of pollen grains, or the possibility of impaired growth of the pollen tube, stamens and styles necessary for fertilization (Slatyer 1969). In addition to the effect of dehydration on fertilization, interference with deposition of carbohydrates at sites available for seed formation may reduce seed numbers (Langer and Ampong 1970). In cotton, water stress resulting in severe leaf wilting during the early part of flowering caused shedding of new flower buds, but had no effect on current flowering (Grimes et al 1970).

In some cases, water stress at anthesis increases seed set. Campbell et al, (1969) found that seed set of two wheat varieties increased with water stress at anthesis, although the stress levels appear severe (soil water potential - 1.4 bar and -15 bar). Poor soil aeration in well watered plants caused damage to anthers and pollen resulting in a lower seed set (Campbell et al 1969). For pepper plants, a reduction in plant water potential from -2.9 to -6.2 bar during the first week of flowering increased fruit set to about four times that of control plants (Kaufmann 1972).

Most of the leaves are mature organs by anthesis, thus any senescence due to water stress at this stage represents an irreversible loss of vegetative tissue. Drought-induced senescence of leaves may possibly represent a mechanism by which plants sacrifice carbohydrates and nitrogen compounds in the senescing leaves for the maintenance of

growing points (Boyer and McPherson 1975). This is a possible way in which assimilate flow to sites of fertilization could be increased at stress levels severe enough to restrict photosynthesis. Often hastened senescence due to stress at anthesis is associated with lower seed set (see for example, Claassen and Shaw 1970) and evidence of survival-orientated mechanisms is obscured.

1.3.4. Water Stress and Seed Filling

During the seed filling stage most of the increase in dry matter yield is due to increase in seed weight. It is also a terminal process so that any reduction in yield due to water stress at this stage has virtually no opportunity for compensation. In view of the finding that photosynthate may be translocated to the seed from plant parts other than leaves, and that the process can operate at relatively 'severe' stress levels, it might be argued that a reduction in leaf photosynthesis early in the seed fill stage may be compensated for by translocation of stem reserves. In stress treated maize, the crops' ability to mobilise reserves for grain filling indicates that under good moisture conditions a considerable amount of potential grain dry weight is present but never reaches the grain (Boyer and McPherson 1975). With wheat there is evidence that water stress occurring late in seed development may have little influence on final seed weight (Wardlaw 1967, Langer and Ampong 1970).

Seed weight is usually depressed most by water stress during early development starting from anthesis (Aspinall *et al* 1964, Claassen and Shaw 1970), and is associated with an earlier cessation of seed maturation (Aspinall 1965). Water stress at this stage also results

in an acceleration of senescence from the lower leaves (least active in supplying photosynthate to the seed) to the upper leaves, and this loss of photosynthetic tissue probably limits the increase in seed weight. To what extent seed weight may have fallen had senescence not accelerated, is unclear however. In wheat, water stress that limited photosynthesis, retarded the movement of assimilate out of wilting leaves although the velocity of translocation itself was not affected (Wardlaw 1967). As stress causes earlier cessation of seed maturation, this response may also contribute to a lower seed weight.

In further studies with wheat, Wardlaw (1971) found that although senescence was accelerated and photosynthesis reduced by water deficit, the supply of assimilates for the upper most parts of the plant were always in excess of grain requirements. In this case, the effect on seed weight appeared indirect. Although not affecting seed weight until near maturity, it is possible that in barley, water stress may reduce yield by suppressing cell division during endosperm development, thus limiting future development (Aspinall et al 1964, Aspinall 1965). It is also possible that premature cessation of seed filling may be mediated by the effect of enhanced leaf senescence on changes in type and quantity of metabolites reaching the inflorescences (Wardlaw 1971).

Water stress causing leaf senescence and inhibition of photosynthesis during seed filling can reduce assimilate supply and therefore seed weight. In contrast, events which alter the distribution pattern of

assimilates, solutes and other substances may have less obvious effects on seed development, and it is not clear which are unavoidable consequences of desiccation, and which are survival mechanisms. When wheat was placed under stress conditions during seed development, the leaves and stem lost water to a greater degree than did the ear. This was reflected in lower rates of photosynthesis in the stem and leaf (Wardlaw 1971). Vertical profiles of water potential and solute potential within a maize canopy presented by Hsiao et al (1976) indicate that turgor maintenance through osmotic adjustment may enable leaves on top to withstand lower water potentials without closing their stomata. Soluble sugars in leaves had a vertical trend similar to solute potential, although this was not sufficient to account for the vertical gradient in solute potential (Hsiao et al 1976). Similar responses have been observed in wheat (Simmelsgaard 1976, Millar and Denmead 1976), maize, sorghum and tobacco (Turner 1974). There is also the possibility that photosynthetic activity becomes less sensitive to desiccation with age. In vegetative maize, photosynthesis was reduced to 70% of that in well watered plants for leaf water potentials of -12 bar. In comparison, the same degree of inhibition during grainfill did not occur until leaf water potentials of -16 bar (Boyer and McPherson 1975).

An important consideration emerging from the foregoing is that changes in metabolism elicited by water stress may represent plant regulatory responses rather than unavoidable damage as a result of desiccation. These responses may be a form of adaptation that operate to minimise inhibiting effects of water stress on the seed formation process.

The differing sensitivity of the key physiological processes contributing to seed yield is found to be important when the effects of stress at different stages of growth is considered against their role in seed formation. Whereas cell expansion is inhibited by a very mild water deficit, net photosynthesis is less sensitive and translocation appears relatively unaffected at levels of stress that limit photosynthesis. Thus plant growth is most likely to be limited through inhibition of cell expansion by a water deficit during leaf area development provided the stress it not severe. During flowering lack of both turgor and photosynthetic activity may be major contributors to a reduction in yield. For the seed filling period however, photosynthetic activity is likely to affect seed development most since leaf area is changing only by senescence and translocation is realtively less susceptible to moderate stress levels.

In providing a better insight for stress-yield relations in seed crops, it is important then, to place emphasis on the relations between the sequence of physiological events developing as water stress sets in (Hsiao et al 1976) and the timing of events during the development of seed yield (Boyer and McPherson 1975).

1.4 SAFFLOWER

1.4.1 Origins and Uses

Safflower is an ancient crop which has undergone considerable selection in the process of regional domestication (Ashri 1975a). For centuries it was grown for dye extracted from the flowers and as a minor oilseed crop (Weiss 1971). Fragmentation of the gene pool and subsequent isolation and selection operated with the traditional mode of cultivation, where safflower was grown in small plots, the farmers often planting their own seeds. A number of regional gene pools or centres of culture are recognised; 1) Far East; 2) Indian subcontinent; 3) Iran, Afghanistan; 4) Israel, Jordan, Iraq, Syria; 5) Turkey; 6) Egypt; 7) Sudan; 8) Kenya; 9) Ethiopia; and 10) Morocoo, Spain, Portugal, France (Knowles 1969a, Ashri 1975a).

Only in the last thirty years has safflower developed as an oilseed crop of importance, largely due to the breeding of varieties with higher oil content and resistance to disease (Beech 1969). It is now grown on a commercial basis in western parts of the U.S.A. Mexico and Australia, as well as in its traditional areas of cultivation. In India it is almost entirely consumed locally. The U.S.A. and Mexico are the main exporters (Weiss 1971, Knowles 1975). As safflower oil is highly unsaturated and quick and evenly drying, it is used for both edible and industrial purposes. Initially its commercial uses were mainly industrial, in the field of protective coatings and at present is highly valued in the manufacture of alkyl resins. Edible uses have developed due to the superior level of stability and flavour retention at low temperatures of the oil and its possible medical benefits in reducing blood cholestrol levels of consumers.

1.4.2 Varietal Resources

Safflower (Carthamus Tinctorius L.), is a thistle-like annual belonging to the compositae family of plants (Beech 1969). Most modern varieties have been developed in the U.S.A. since the 1940's. They were bred from germplasm collected in old centres of cultivation, and have recently been introduced into other countries of the old World replacing the older varieties (Knowles 1969a). Fortunately, an extensive germplasm collection of safflower and wild species has been established with the U.S.D.A. It is designed to prevent the disappearance of local types, as agriculture improves in traditional centres of culture and to provide a source of material with which to help overcome problems of culture in the new areas (Knowles 1971). The process of divergence in safflower has provided the germplasm collection with as much variability for morphological traits (Ashri 1975a, Ashri et al 1976) as it has for yield compoents (Ashri et al 1974), oil content (Ashri 1975a), and disease reaction (Ashri 1971).

The collection has provided sources of disease resistance (Knowles 1975, Knowles 1971) and altered quality and quantity of the oil (Knowles 1969b). India was the source of the ol gene which produces a new oil type with high oleic acid content (Knowles 1972). Unlike regular safflower oil with high Linoleic acid content and stability at low temperatures, high oleic types are stable at high temperatures, making them excellent cooking oils (Knowles 1969b). In order to increase seed oil content, efforts have involved a reduction in the hull content. The Rubis thin hull type has up to 46% oil (Knowles 1975), but is weak-stemmed and low in yield due to the effect of reduced secondary

thickening in the stem and in the anthers (Knowles 1969b). More recently an extreme reduced hull type with an oil content of 50% has been developed with normal pollen production and good quality oil. Correlations between yield and yield components and various other traits have shown the collection contains considerable genetic variability for these characters (Ashri et al 1974) which can be used for yield improvement. It should thus be possible to breed earlier, higher yielding varieties with higher oil content (Ashri 1975b).

1.4.3. The General Pattern of Growth and Yield Formation

Growth and development of the safflower plant has been recorded for a number of varieties and a range of climatic conditions, however as these were not always clearly specified, correlation of different results is difficult. The various phases of safflower development have been carefully recorded under irrigation in Western Australia (Stern and Beech 1965). After emergence, the stem apex of the seedling produces a number of leaves which form a rosette. There is no true rosette stage in cultivated safflower, although some Carthumus species require a definite cold period to initiate stem elongation (Weiss 1971). The vegetative state lasted six to seven weeks, and the transition from 'rosetting' to rapid elongation of the stem was between 48 and 55 days from sowing (Stern and Beech 1965).

As the days become longer and temperatures rise, the stem will elongate more quickly and subsequent branching occurs from leaf axils on the main stem beginning at the top of the plant (Jackson and Harbison 1973a). The main stem terminates with the primary head, whereas the

terminal heads of first-order branches are called secondary heads. Heads flower about 28 days after they appear as buds. During bud development the leaf area rose to a maximum after 62 days and declined to almost nil by the final harvest. As flowering approached rapid development of bracts surrounding the heads occurred (Stern and Beech 1965). By flowering the plants have reached their maximum height (Jackson and Harbison 1973a). In a similar sequence to that of bud development, flowering beings in the primary head, followed by the most mature of the secondary heads. Florets of an individual head open over a period of 3 to 5 days, beginning at the margin of the head and proceeding centripetally (Weiss 1971). The flowering period usually lasts about 21 days (Peterson 1965). In the study by Stern and Beech (1965) seed formation commenced between 104 and 111 days, and the crop matured between 125 and 132 days. The seeds are physiologically mature about 20 days after 95% of the flowers have faded (Leininger and Urie 1964, Jackson and Harbison 1973a, Abel and Driscoll 1976).

The regular order in which each of the reproductive organs develops and matures in safflower can be considered more generally in terms of sequential trait development in which each trait is a link in the process of yield formation, differing from the proceeding one only in the amount of environmental resources it uses (Abel and Driscoll 1976). The traits of seed yield (heads/area, seeds/head and seed weight) develop sequentially, their final number and weight depending on interactions between genotypes, the environment, and the critical

stage of development. Although they can be independent of one another in their development they are closely associated with one another physiologically (Khidir 1974, Abel 1976a). Abel and Driscoll (1976) found that genotype had a large effect on seed weight, which was generally inflexible in different environments, but a smaller effect on heads/unit area and seeds/head which were more flexible. Increases in seed weight will therefore have little compensatory effect on reductions in seed number due to environmental stress when seed number is being determined (Abel 1975, 1976a). However together the traits account for 97% of the variation in seed yield (Abel and Driscoll 1976). The influence of environmental stresses on the general growth pattern and yield of safflower will therefore be largely dependent on how successfully each trait in turn, can exploit the available environmental resources necessary for the successive stages of development.

A defoliation study has shown that the critical period for yield due to leaf removal is from the beginning of branching until the start of flowering (Urie et al 1968). Seed weight was reduced most by leaf defoliation at the late bud and early flowering stages. Leaf removal between the late bud and late flowering stages increased oil percentage by about the same amount seed weight was reduced. The increase was directly related to a decrease in hull percentage. In particular, the experiments showed that removal of lower leaves did not influence yield, and that severe defoliation (removal of all leaves except bracts), reduced yield by only 23% (Urie et al 1968). It appears the bracts may play a particularly important role in contributing to seed development.

Aslamy (1972) found that the floral bracts of safflower have a higher stomatal density and chlorophyll content than the true leaves, and that during the flowering stage of growth, floral bracts showed a higher rate of CO_2 assimilation than did the true leaves. Both organs showed a decline of photosynthetic activity with advancing age.

1.5 Environmental and Agronomic Aspects of Safflower Production

Although safflower shows a fairly wide adaptability to climatic conditions, large scale production has been concentrated mainly in fairly low-altitude, semi-arid areas where it is best adapted (Weiss 1971). Initial introductions from the traditional centres of India and Southern Europe competed unsuccessfully with established crops in the new areas such as U.S.A. because of poor adaptation, lack of agronomic information on growing the crop, high hull percentage and low oil content of the seed (Peterson 1965). The successful development of safflower in the U.S.A. is largely the result of improvements in disease resistance, and increased oil content of the seed, through plant breeding (Beech 1969). Major improvements through plant breeding however, may have contributed to some neglect of production research (Knowles 1958). Certainly safflower production in Australia, with the benefit of improved varieties from the U.S.A., has been characterised by the unpredictability, and lack of upward trend in seed yields since the industry began about 20 years ago (Basinski and Beech 1972). The yields obtained have been restricted by poor adaptation to the environment, and by disease (Cutting 1974). This indicates that more information is required on crop growth and phenology in relation to environmental conditions, particularly so with the development of new varieties.

Much of the information concerning environmental limitations to safflower production has been originally derived from initial adaptation trials, designed to provide initial, rough agronomic recipes. It has indicated that the effects of the main environmental factors on safflower depend largely on the stage of its growth. This has important practical implications, because safflower is primarily grown for oil obtained from the seed and agronomic considerations must encompass those factors likely to influence the development of seed yield.

1.5.1. Water

In safflower, crop water relations are particularly important, as reductions in seed yield can result from both a water deficit and a water excess. Reductions in yield due to excess moisture are often the result of disease infection due to greater susceptibility under such conditions. Root-rots are encouraged by excessively high levels of soil moisture, while head-rot and foliar diseases occur where rainfall is frequent or humidity high (Knowles 1955, Jackson and Harbison 1973a). To minimise their incidence, a deep pre-plant irrigation may be applied (Peterson 1965), as safflower can obtain much of its water requirement from the subsoil (Jackson and Harbison 1973b). Frequent irrigations often necessary for other crops are harmful to safflower as this encourages microclimates suitable for disease. Sub-irrigation from ditches has proved profitable (Knowles 1958) as water can be maintained in them at a level related to growth of the crop and permeability of the soil (Weiss 1971).

High rainfall and high humidity may lead to yield reductions in safflower apart from disease infection. Prolonged rainfall at flowering has adversely affected pollination (Rabak 1935, Knowles 1955). For safflower plants grown on high water table land and surrounded by flooded rice fields, greater sterility in heads of those grown in-field, has been attributed to higher humidity within the field than near the perimeter (Zimmerman 1972b). Using a controlled environment, Zimmerman (1972b) found that high humidity for 24 hours at anthesis was sufficient to reduce seed set. The anthesis stage and that prior to anthesis were the most sensitive. The reduction in seed set for plants subjected to high humidity (60/55%) at medium (23/38°c) and high (29/43°c) temperature was 20 and 42% more respectively, than that of plants subjected to comparable temperatures and low humidity (40/45%). In the same study (Zimmerman 1972b) there was a 9% increase in seed weight of plants subjected to high humidity over those subjected to low humidity, at the medium temperatures. In Russia, 1000 seed weight and the hull weight increased under high rainfall conditions, while the oil content of the seed decreased (Weiss 1971) and in South Africa, excessive rain after flowering prevented the seed from filling (Sellschop 1951). In early Canadian experiments, the oil content of seeds was reported to have dropped from 26.5% to 17.5% for C.V. N-6 when grown under irrigation compared to dryland plantings (McGregor and Hay 1952). These results suggest that an increase in seed weight under conditions of high moisture availability does not necessarily increase oil content, and may be due to relatively greater increases in hull weight. This is supported by studies on seed composition which have shown that larger seeds have a lower kernel percentage due to a higher proportion of hull (Yermanos and Francois 1963, El Saeed

1966). A further problem associated with prolonged rain or high humidity near harvest is the hazard of seed germination in the head (Knowles 1955) although wild selections with short term dormancy which readily interbreed with domestic safflower, have been found in a selection programme for pre-harvest dormancy (Zimmerman 1972a).

Rain grown crops are usually more healthy since they are often planted in drier areas, but average yields tend to be low (Weiss 1971). Commercial production is hazardous where water requirements of the plant are dependent only on rainfall during the growing season, and in Australia, water stress is considered to be the main factor limiting yields (Basinski and Beech 1972).

Both wild species (Carthamus oxyacantha Bieb) (Deshpande 1952) and cultivated safflower (Carthamus tinctorius L.)(CSIRO 1955) have gained the reputation of being drought resistant plants. This has been attributed to the deeply penetrating tap-root system safflower develops (Knowles 1955, Peterson 1965) which presumably can enable the crop to withstand extended dry periods during the later stages of growth. However, in the early stages of growth, before the root system is fully established, the crop is sensitive to drought (CSIRO 1955). For suitable deep soils, with no compacted subsoil layers, it has been reported that safflower roots can draw moisture from depths greater than three metres (Henderson 1962, Fischer et al 1967) and provided subsoil moisture is available, there is no response to irrigation. This is important as it reduced the need for frequent irrigations and associated incidence of disease. Compared with wheat, the root system of safflower appears to

penetrate deeper (Knowles 1958, Weiss 1971), develops a smaller proportion of roots near the soil surface (ICRISAT 1974) and draws more water (Harbison 1968, Basinski and Beech 1972, Naughtin 1973). Suitable conditions for extensive root development are often not met however, and either dense subsoils that retard root development (Weiss 1971) or shallow soils, may limit yields due to an insufficient moisture supply (Knowles 1958).

With adequate drainage, safflower has shown considerable response to irrigation (Claassen and Hoffman 1950, Peterson 1965, Basinski and Beech 1972) although the amount of water required to produce a crop varies considerably with seasonal climatic conditions (Weiss 1971). The consumptive use of water by safflower under irrigation, as recorded by various workers, ranges from less than 500 mm (Stern 1965) to well over 1000 mm (see, for example, Erie and French 1969). In some studies however, equivocal results suggest that timing is as important as quantity (Abel 1976b).

From early times in U.S.A. the importance of adequate soil moisture, along with warm soil temperature for germination, has been recognised (Rabak 1935). On dry land, sowings often result in poor stands, apparently due to the hard seed coat and fast drying out of the upper soil layer after sowing (Singh and Wilson 1974). In practice therefore, it is often the coming of rains that determine planting date under rainfed conditions (Jackson and Harbison 1973b). Under various amounts of simulated rainfall, seed germination has been shown to decrease to 33% for 3 mm of water and 13% for 15 mm of water compared with 70

to 87% for 6 to 12 mm applied to soil in pots with a water holding capacity of 18 mm (Bassiri and Sionit 1975). During the first 25 days of early establishment, 15 mm of water at 3 day intervals was required to prevent wilting. On the other hand, continued wet weather at this stage of growth may retard crop development (Rabak 1935), possibly due to soil saturation at a time when oxygen demands by the plant are high. Germination percentage of three safflower varieties in a non-electrolyte osmotic agent was reduced 90% at -13.5 bar osmotic potential in one variety and 35% in another compared with non-stressed seeds (Sionit et al 1973). The most rapid decline occurred below about -5 bar. These studies confirm the need for adequate although not excessive soil moisture for good germination and early establishment of safflower. The only systematic research on the effects of water stress at different growth stages was carried out in pots under glass-house conditions (Seydlitz 1962). The stress level imposed was expressed as 30% of the soil moisture capillary potential, compared with controls maintained at 70%. Water stress during the normal period of maximum growth, between formation of the rosette and flowering, reduced seed yield by 25%, whereas water stress at flowering or after flowering reduced yield by about 40%. However in contrast to the work of Bassiri and Sionit (1973), stress during the first seventeen days, from emergence to forming of the basal rosette, did not adversely reduce growth or yield. The timing of water deficit was reflected in yield components. Number of heads per plant were reduced most by water stress between bud initiation and the start of flowering. Seeds per head were unaffected by stress before bud initiation, but were reduced by 20% or more at other stages of growth. One thousand seed weight and oil content was reduced most

by water stress after flowering. In contrast to the work of Seydlitz (1962), Dastane et al (1971) reported that no irrigation during the leaf stage reduced yield by 30% compared with a reduction in yield of 20% during branching. No irrigation during flowering or seed maturation reduced yield even less compared with irrigation at all stages. This study suggests a declining sensitivity to stress, rather than an increasing one, assuming the stress levels were even at each growth stage.

In the U.S.A. detrimental effects of irrigation cut-off dates ranging from three weeks before first flower, until harvest, increased in severity for each increase in the time without irrigation (Erie and French 1969). Seed yield was reduced over half for the earliest cut-off date, and was reflected in fewer heads, fewer seeds per head, a lower seed weight and oil content of the seed. It is often considered that the last irrigation should be at least one week after full bloom, to ensure the seeds are well filled (Weiss 1971). However Abel (1976b) found that terminating irrigation five days before 95% flower, had no adverse effect on yield or yield components, and that oil content of the seed was not affected. Similarly, other experiments have shown that irrigation after the last flowers have opened, or when seeds are maturing does not necessarily improve yields (Stern and Beech 1965, Erie and French 1969).

Drought occurring in two spells, frequently has a greater effect on yield and its components than only one, and the period of floral development and flowering appear particularly susceptible (Seydlitz

1962, Erie and French 1969, Dastane et al 1971). Fischer et al (1967) found that a pre-irrigation followed by one at the bud stage and one at first flower gave highest yields. These findings indicating the sensitivity of safflower to water stress at this stage, are generally endorsed by earlier experience with the crop. Rabak (1935) noted considerable moisture is necessary until the flowering period, after which less moisture is required. Generally it is stated that when irrigating for maximum yield, it is important irrigation be given early after bud initiation, and then at flowering (Claassen and Hoffman 1950, Knowles 1955, Peterson 1965, Weiss 1971).

Apart from the commonly acknowledged sensitivity of safflower during floral development, contrasting reports of sensitivity for other stages of growth may have arisen in part due to differences in experimental conditions, and in part due to the techniques employed. The value of much information is limited because the magnitude of stresses imposed cannot be accurately extrapolated. A critical period after floral initiation may reasonably be expected when water availability is low, because direction of growth processes towards the formation of reproductive organs results in a higher plant requirement for water (Henckel 1964). Safflower shows particularly rapid growth during this stage throughout which the crop is a very heavy user of water (Erie and French 1969).

1.5.2. Diseases and Water relations

The majority of diseases that have been recorded on safflower are of

minor importance (Weiss 1971), however there are several often fatal diseases associated with excess moisture in the soil or atmosphere (Knowles 1955). Susceptibility to such diseases has resulted in commercial plantings being located in generally dry areas, and has limited the successful adaptation to new areas for commercial production (Peterson 1965). Phytophthora root-rot presents a major problem in some areas, as safflower is often grown on soils of heavy texture. Slow drainage of these soils after irrigation or rainfall, increases the risk of attack by the disease organisms, and rapid death of plants may result particularly when soil temperatures are high (Jackson and Harbison 1973a, Cutting 1974). The wilting induced by Phytophthora root-rot is due to the development of an internal plant water deficit (Duniway 1975).

Infection by Botrytis head-rot is encouraged by warm temperature combined with high humidity caused by irrigation, showers of rain, or frequent dews (Knowles 1955). It is a major factor limiting yields of experimental trials in New Zealand (Massey University Agronomy Department, unpublished data) as currently available varieties do not have complete Botrytis resistance. Spores of the fungus are windborne (Weiss 1971) and infect seed heads in regions where there are prolonged periods of high atmospheric moisture prior to and during flowering. Yield reductions result from under developed seed, and with bad infections detatchment of seed heads from stems results due to the bract area tissue being destroyed (Weiss 1971 , Peterson 1965).

Humid, wet conditions also predispose the plant to several leaf diseases the most important of which are rust, caused by Puccinia carthami cda., and Alternaria leaf spot (Jackson and Harbison 1973a). Rust is present in all the safflower producing areas although its occurrence is less prevalent under dryland conditions than under irrigation (Peterson 1965, Ashri 1971). In most years damage to dryland safflower is not considered important, although under conditions of high humidity rust could become serious as it can be fairly destructive if it attacks the hypocotyl of the young plants (Knowles 1955).

The practical importance of these diseases conducive to humid conditions is that susceptible varieties cannot be grown successfully in humid regions where water is often more available. When grown in dry areas, the crop is more healthy, but yields are low due to lack of water (Weiss 1971). In many cases, irrigation in these warm dry areas results in disease organism infection (Peterson 1965). Of greatest economic value in overcoming the disease problem with safflower has been the evaluation for manipulation of genetic sources of disease resistance (Knowles 1971). Possibly as a result of varying selection pressures, there has been a geographical divergence in disease reaction throughout the years (Ashri 1971,Ashri 1975), which should provide valuable material for genetic recombination in an effort to develop variaties resistant to disease.

1.5.3. Temperature and Photoperiod

Safflower will in general, tolerate a wide range of temperature (Peterson 1965) and much of the information relating to temperature effects on

safflower, concerns the damage caused by extreme temperatures. Although there are varietal differences in tolerance (Knowles 1955) the effects depend largely on the stage of growth. Soil temperature at sowing, together with adequate soil moisture, are the main factors influencing emergence in Safflower. Low seed bed temperatures has an inhibiting effect on germination, and practically no germination occurs at 2.5°c, but almost complete germination at 5°c (Weiss 1971). However at this temperature germination is very slow (several weeks) (Harbison 1968) and temperatures of 13°c to 18°c are required for quick (less than a week) even emergence (Peterson 1965, Weiss 1971). In the seedling stage, most varieties will tolerate temperatures down to -7°c (Claassen and Hoffman 1950, Weiss 1971). However once the stems have begun to develop the plant becomes more susceptible to frost damage and temperatures down to -4°c will damage most varieties (Jackson and Harbison 1973a). During flower bud development and flowering any temperature below 0°c may cause damage in the form of sterile heads without apparent damage to the foliage (Peterson 1965, Harbison 1968, Weiss 1971). Frosts after flowering and during seed maturation can reduce the quality and yield of seeds (Claassen and Hoffman 1950, Knowles 1955, Weiss 1971).

It has been claimed that, given plentiful water, safflower does not suffer undue damage from temperatures well over 40°c although yields are generally higher when day time temperatures at flowering are in a more moderate range of 24-32°c (Knowles and Miller 1965). However experiments under irrigation in Australia showed harmful effects of daily temperatures above 27°c during flowering and ripening on yield,

and to a lesser extent, on oil content (Basinski et al 1961, Beech and Norman 1963). The effects of high temperature on safflower appear most severe at flowering as sterility and poor seed set can result (Phillis 1961, Peterson 1965). Beech and Norman (1963) found that the pollen of plants with reduced seed set was morphologically normal. As fertilization of florets occurs early in the day, it appeared that successful fertilization was dependent on duration of the early morning cool period for growth of the pollen tube. Usually all florets that open during a given day have begun to elongate by sunrise, and another dehiscence occurs soon after (Claassen 1950). Pollination and fertilization, are dependent on an actual increase in length of the style by cell elongation, and on elongation of the embryosac before entry of the pollen tube respectively (Banerji 1940). Some of the reduction in seed set attributed to high temperatures may therefore be confounded with possible water stress effects, since water deficit can excerbate the deleterious effects of high temperatures at flowering in safflower (Weiss 1971).

In comparison, Zimmerman (1972b) found that seed yields of plants subjected to high humidity (60/55%) in low (17/31°c), medium (23/38°c) and high (29/43°c) temperature, were 10, 19 and 86% less, respectively, than those subjected to comparable temperatures with low humidity (40/35%). In these experiments then, the adverse effect of increasing temperature was worsened by raising the relative humidity. Yield reductions were due to fewer seeds. In the high temperature/humidity regime it appeared some impairment of processes involved in seed development occurred, as it lasted throughout seed development and

resulted in lower seed weight. Temperatures up to 26.5°c throughout seed development, have shown no influence on seed oil content or fatty acid composition (Canvin 1965). However in Australia, Basinski and Beech (1972), have stated that effects of high temperatures on seed development can be even more serious than on pollination.

Research on the effects of moderate temperatures on phasic development and yield of safflower appears to have been relatively neglected. Usually, a decline in yield occurs with delayed planting where temperature is considered a major influencing factor. Beech and Norman (1963) found there was a general reduction in leaf number, plant height and yield due to later sowing. This was associated with the later phases of development being progressively curtailed as temperature increased, with the later sowings. In contrast, Naughtin (1975) found that yield reductions from later sowings resulted from reductions mostly in the period to stem extension and to flowering, but did not influence final maturity date. Higher yield with earlier sowing was considered largely due to the advancement of flowering in the season allowing maturation under less severe moisture stress. In the U.S.A., by sowing up to three months earlier, lower temperatures lengthened the rosette period, and higher yields resulted from more heads and seeds per head developing (Abel 1975). When planted at optimum times in different altitude locations, the cool location (10/22°c winter/summer mean), had the highest yield because of increased heads per plant, seeds per head and seed weight. Early planting in the warm temperature regime (14/25°c winter/summer) was associated with some seed abortion and decrease in oil percentage of the remaining seeds due to an increase in their hull

content. This was attributed to the short rosette stage, and the internodes elongating when temperatures were apparently too low for normal floral development. As these were irrigated experiments, it is apparent that a sufficiency of water does not compensate for suboptimal planting dates. Late planting increases the risk of harvesting difficulties and seed quality deterioration from rain at harvest, whereas if sown too early, there is the risk that the crop may be frost damaged (Jackson and Harbison 1973b, Cutting 1974). However in Australia, May or July sowings sometimes yielded as well as June (optimal) (Naughtin 1975). In the U.S.A. the mean yield was not always related to the reduced growth of later sown plants, and oil percentage of the seed was not affected by days to flower or duration of flowering (Abel 1976b). Safflower germplasm evaluation showed that yield per plant was not correlated with the length of the season, or oil content, although the most important yield component was number of heads per plant (Ashri 1975b), followed by seeds per head (Ashri et al 1974). These relations are important, because they suggest that a telescoping of the early phases of development can be engineered without necessarily reducing yield, but that at the same time, the environment must be suitable for normal reproductive development since yield components formed at these stages of growth affect yield so markedly.

Reviews by Beech (1969) and Weiss (1971) have indicated safflower is a day neutral plant, however stages in development of the apex at floral initiations have been shown to be strongly influenced by photoperiod and variety (Horowitz and Beech 1974). As floral development was slower

with longer days, varieties which are non-photosensitive may be required to prevent late flowering and the risk of drought during the seed development stage of rainfed crops. At Leeton, Australia, later sowing reduced the day degrees required for crop development, largely due to a reduction in those required for the period of stem elongation, indicating both temperature and photoperiod influence phasic development (Basinski and Beech 1972). Photoperiod also influences duration of the rosette habit (Zimmerman 1973). Under high temperature (10/20°c min/max) in controlled environment rooms, rosette habit persisted longer in short photoperiod (10 hours) than in long (14 hours). In some entries, there was a longer duration of rosette habit at low temperature (5/15°c) and long photoperiod, than at the high temperature and short photoperiod.

This data, along with that for the time of planting experiments, suggest that phasic development of safflower is dependent on temperature, photoperiod, and genotype. Temperature may be more important until stem extension (or probably floral initiation) whereas day length is also important for floral development from initiation until flowering. The lengths of growth stages from flowering to maturity are less affected by time of sowing. Safflower may require relatively cool, short days for development of the rosette habit and establishment of its root system, but longer and warmer days for reproductive development and crop maturation.

1.5.4 Soils and Nutrition

It is usually stated that safflower requires deep, well-drained fertile soils of neutral reaction (Knowles 1955, Peterson 1965, Harbison 1968,

Beech 1969, Weiss 1971). Despite the importance of soil physical factors influencing water holding capacity, drainage, and root development, only general reference to the suitability of different soils for safflower is found. The preferred soils have ranged from open sandy soils, to sandy loams, clay loams and clay (Rabak 1935, Knowles 1955, Peterson 1965, Weiss 1971).

Responses to fertilizer depend on soil type (ICRISAT 1974), soil moisture level (Harbison 1968, Jones and Tucker 1968), cultural practices, (Weiss 1971, Abel 1976b) and the inherent fertility of the soil. However there is little evidence to suggest that safflower nutritional requirements differ greatly from those of other crops. As safflower is a deep rooted crop, it can draw on a relatively large volume of soil for its nutrients, and phosphate requirements in terms of added fertilizer are seldom great. Phosphate requirements of safflower are generally moderate (Weiss 1971) and if cereal grains produce satisfactorily without fertilizer, safflower is expected to respond the same (Peterson 1965). The minimum recommended rates for other crops in an area are applicable to safflower, although on soils deficient in phosphorus, good yield responses can be obtained even in rain grown crops (Harbison 1968). Small amounts at planting usually give a more rapid initial growth, allowing the young plants to compete more effectively with weeds.

Nitrogen is generally the nutrient most often required by safflower in any quantity. Field observations in California indicate at least as much nitrogen as that for small grains is required, and often more

(Knowles 1955). In Australia, when moisture is adequate, nitrogen can become the next factor in limiting yields (Harbison 1968). However variable responses have been recorded under irrigation (Weiss 1971) and rainfed conditions (Peterson 1965). Nitrogen can influence total seed yields, but does not generally affect oil content (Abel 1976b) or iodine value of the oil, except at very high levels of application (Werkhoven et al 1968). Largest yield responses from nitrogen appear mainly through its effect on head number per plant (Gilbert and Tucker 1967, Hoag et al 1968), the greatest increase being with lower order heads (Yermanos and Hall 1964). Jones and Tucker (1968) found that nitrogen increased seed yield through development of more tertiary heads and increased weight per head in secondary and tertiary positions. Increased head weight was due to heavier seeds in secondary heads, and larger numbers of seeds in tertiary heads. It appeared the increased supply of metabolites due to added nitrogen were first utilized in the initiation of more tertiary heads with larger numbers of florets and increasing seed size in secondary heads. Primary heads were little affected, possibly since these normally have more access to initially available metabolites in the plant than the later developing heads.

Yields have increased with each 50 kg increment of nitrogen up to 150 kg/ha applied at planting, although further increases result from splitting total nitrogen into two applications (Gilbert and Tucker 1967). High levels of nitrogen at planting damages seedlings, especially when moisture is low. Stern and Beech (1965) found split applications at planting and budding most favourably improved head number and weight,

although nitrogen applied at flowering had little effect on final seed yield. However, Jones and Tucker (1968) have indicated that nearly half of the nitrogen uptake occurs between flowering and maturity. In experiments by Abel (1976) it appeared residual nitrogen was adequate to produce maximum oil % at all levels of applied nitrogen. Possibly greater yield responses are realised from an increase in heads per plant because yield is so markedly affected by this component, whereas late applications may alter the pattern of water usage, and retention of green leaves or a prolonged growth period may render harvesting more difficult, thus limiting any desirable effects. It is apparent that with safflower, nitrogen response is particularly dependent on timing of application (Stern and Beech 1965), however amount (Gilbert and Tucker 1968) available moisture (Jones and Tucker 1968) planting date (Abel 1976b) and other factors are also important to the way nitrogen can influence safflower development and yield.

Compared with many arable crops, safflower is relatively tolerant to salinity, although its tolerance levels appear to vary with moisture conditions (Weiss 1971) stage of growth (Yermanos et al 1964) and variety (Francois et al 1964 , Ghorashy et al 1972). It has similar tolerance to barley when rain grown (Knowles 1958) but is slightly more sensitive than barley and cotton when irrigated (Harbison 1968). Safflower is especially tolerant of sodium salts, and will accumulate high concentrations in semi-arid regions to which the plant is relatively well adapted (Weiss 1971). Sodium applied at 4 meg/litre to safflower grown in nutrient solutions of PH5.5 has increased growth by 40 to 50% (Aslam 1975). This beneficial effect suggests that sodium accumulation may be essential for safflower under certain conditions.

Very high levels of salinity result in plant responses similar to those occurring with water stress, although safflower is only half as tolerant during germination as during later stages of growth (Yermanos et al 1964). Salinity delays initial emergence which subsequently tends to be irregular, while very high levels of salinity also reduce the germination percentage. At later growth stages, plants grown in saline water become thicker and darker green in appearance. Plant height is reduced and the reduction in vegetative growth closely parallels reduction in seed yield (Weiss 1971). Francois et al (1964) found that salinity accelerated flowering and maturation. This effect on development resulted in fewer flowering heads and lower seed yield per head, due to lighter seed. Seed number per head remained fairly constant. Oil percentage of the seed was also reduced, along with an increased hull content. Under high salinity, decrease in oil content is most pronounced in tertiary and least in primary heads, whereas normally, the primary heads have highest hull content, seed weight and lowest oil content. Oil composition however, is not changed (Yermanos et al 1964).

An important factor emerging from the foregoing is that crop development and yield in safflower is particularly dependent on availability of the necessary environmental inputs at the appropriate stages of development. Many of the reported differences in response of safflower to environmental limitations, may be resolved when studied on a quantative basis, not limited largely to yield data alone, and the interactions between each taken into account. Poor adaptation of varieties to environment have therefore resulted in low yields (Cutting 1974). However safflower shows considerable potential for overcoming these limitations through

agronomic and varietal manipulations, provided further research develops the necessary information.

CHAPTER 2 - METHODS

2.1 Environmental Conditions

Safflower plants (var 022) were grown from seed in controlled environment rooms of the Climate Laboratories, DSIR, Palmerston North. The environment consisted of 12-hour photoperiods of 160-180 Wm^{-2} light intensity, with day/night temperatures of $23^{\circ}c/18^{\circ}c \pm 0.5^{\circ}c$. The corresponding relative humidities were 75% and 85% $\pm$ 5% respectively. Carbon dioxide was maintained at ambient levels. The seeds were sown in 1.5 litre containers equally filled with a sterilized soil mix of 1:1 Manawatu fine sandy loam and Opiki loam. The containers were supported by drainage trays on trolleys. Soil moisture content was made even by saturating the soil in each container with water and allowing to drain. Seeds of 50-60 mg were selected and sown just under the soil surface. Four were sown in each container, and after 20 days plants were evenly thinned to one per container. Half-strength Hoaglands nutrient solution was added, and thereafter at two-weekly intervals.

2.2. Treatments

2.2.1 Definition of Growth Stages

Plant water deficits were induced at five different growth stages, and were defined as follows:

Treatment		Mean period of stress in days after sowing	Mean duration of period in days
T_1	Water stress during floral initiation	34-53	19
T_2	Water stress during inflorescence development	53-75	22
T_3	Water stress during flowering	75-95	20
T_4	Water stress during secondary head flowering	83-95	12
T_5	Water during the post flowering period	95-114	19

Preliminary studies under glasshouse conditions had indicated that these growth stages could be specifically determined by observing morphological changes in development. The approach of floral initiation was determined by dissecting excised apices and noting changes in the shape of the stem apex under a dissecting microscope. The stage of development taken as floral initiation was the same as that illustrated by Horowitz and Beech (1974). At this stage the meristem is surrounded by the developing inner involucral bracts, and the first floral initials are just visible at the base of the apex. The appearance of the tertiary buds in leaf axils signified that floral initiation was complete in all developing heads as very few tertiary buds developed. The first growth stage was therefore defined as from the pre-floral initiation state of the apex until the appearance of tertiary buds. As plants treated at floral initiation did not initiate tertiary buds, the treatment was terminated when tertiary buds became visible in well watered plants.

The stage of inflorescence development was defined as that from the appearance of tertiary buds, until the morning the first florets of the primary head elongated, signifying the start of anthesis. The appearance of tertiary buds coincided with the stage at which the initials of the earliest buds had formed florets. These then developed, and leaves expanded until flowering began.

Once fertilization has occurred, the florets wilt and fade. At 95% flower fade, all but very late heads have flowered, signifying the end of flowering for heads that will develop mature seed. The flowering stage was therefore defined as from and including bud burst in the primary head, until 95% of the flowers had faded. The primary head flowers first, followed by the secondary heads in order of development. The stage of secondary head flowering was from and including bud burst in the first flowering secondary head until 95% of the flowers had faded. Both flowering treatments therefore finished at 95% flower fade. The first started at primary bud burst, whereas the second did not start until secondary head bud burst, after the primary head had flowered. The final stage of development was from 95% flower fade until physiological maturity when most leaves and bracts had turned brown, 20 days after 95% flower fade. To overcome plant to plant variations in rate of development, the start and end for each of these stages were determined on a per plant basis to ensure each plant was treated according to the correct stage of development.

2.2.2 Treatment Implementation

The daily watering system needed to be efficient to minimise the time plants were out of the controlled environment, accurate to ensure all

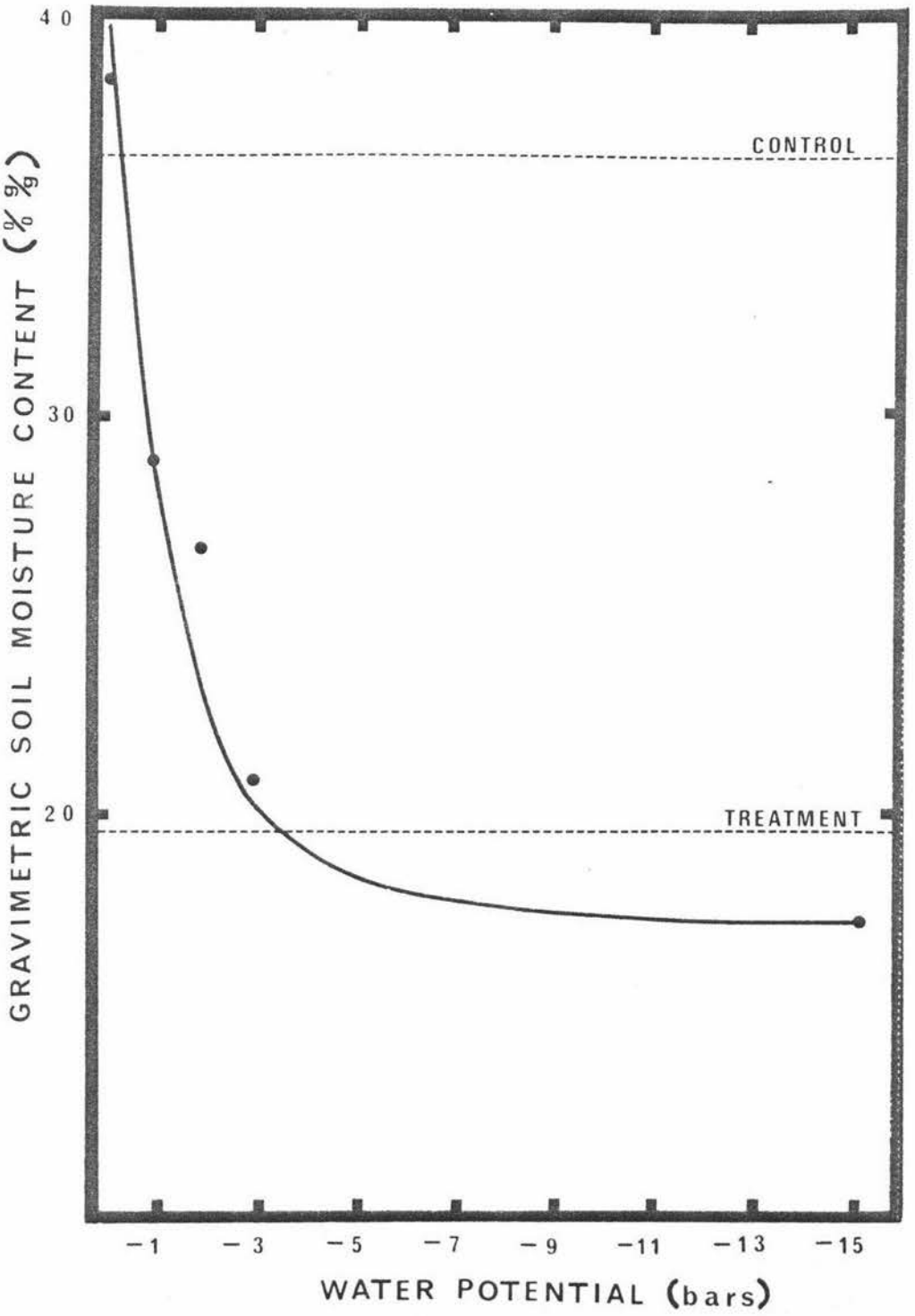
plants were treated similarly, and able to water to a predetermined soil moisture content. These requirements were met with an electro-mechanical device (DSIR internal report) which was used to rewater the soil in each container to a preset weight accurate to ± 2 g. Control plants were watered every second day, while treatment plants were watered daily. With 200 plants involved, the watering operation required less than one hour for well watered containers, and about $\frac{1}{2}$ hr for treatment containers. Treatments were initiated by withholding water until a predetermined soil moisture content had been reached. Drying down usually required about 2 days. A plastic cover was placed over the top of the soil to reduce water loss from the surface. In the same way as for well watered plants, the soil was cycled between an upper and lower soil moisture content, except water was added with a large plastic syringe through a small hole in the plastic cover. The watering nozzle of the electromechanical device dispersed water over the soil surface, therefore using a syringe prevented water loss at the container sides, and the covers could be left in place. Nutrient solution was not added to containers during treatments.

2.2.3 Measurement of Treatments

Soil water potential

The relationship between soil water potential and soil moisture content (SMC) was found from the soil moisture retention curve (Fig 1), which was determined using a pressure plate membrane apparatus. Soil moisture content was related to the water holding capacity of the soil to establish container weights of various corresponding soil moisture contents. Initially, a few grams of soil were lost from the container, due to fine

Figure 1 Soil moisture retention curve



material washing out. Once settled the water holding capacity was just over 500 g. Well watered containers were cycled above approximately -0.3 bar soil. This corresponded to 36-46% SMC, or initially, 1450 to 1550 g container weight. As the experiment progressed, these weights were increased to account for increases in plant weight. Treatment containers were cycled between 20% and 24% SMC which corresponded to a rewatering minimum of about -3.5 bar soil and initially, 1300 g container weight. The watering regimes were checked at the end of each treatment by determining the gravimetric moisture content of the weighed soil from containers of harvested plants.

Plant water potential

Leaf and flower head water potential were measured using the pressure chamber method (Boyer, 1969). Pressure seals were made from silicon rubber polymerised *in situ* to accomodate the crescent-shaped petiole of the leaf, and the circular shape of flower head stems. Gas entering the pressure chamber was humidified by bubbling it through water at the base of the cylinder. Measurements of water potential were taken half an hour before the photoperiod began. This also represented the minimum soil moisture content in the cycle as containers were rewatered after the measurements were taken. A torch was used to locate plants, and excised leaves and flower heads were immediately placed in the pressure chamber for measurement. A low heat dissecting lamp was used to illuminate the cut end of the petiole, and the end point was observed using a 10 x microscope lens. Young, rapidly expanding leaves were used for measurement until flowering began. Thereafter young flower heads were selected as most leaves by this time had fully

expanded. Three measurements were made from well watered plants, and three from treatment plants every second day throughout, from the beginning of T_1.

2.3 Measurement of Plant Response

Plants were harvested at the beginning and end of each treatment, except the beginning of T_4. Five plants per treatment were used at each harvest except the final one in which ten plants per treatment were used. The number and dry weight of plant components (stem, leaf, bract, heads) were measured where applicable. As all buds that formed in the leaf axils did not develop the number of visible buds were recorded separately from the number of developing buds. Plant material was dried in a vacuum oven at 40°c for 24 hours, then equilibrated at 22°c and 55% RH for a few hours before weighing. Plant height was measured from the stem base at the soil surface, to the uppermost part of the plant. Leaf and bract area were measured with an AAM-5 type automatic area meter.

At 95% flower fade and at final harvest, additional components of seed yield measured were potential and actual seed number per head, and 1000 seed weight. As each floret and associated embryosac in the head is capable of producing a seed, their total number were termed the potential number of seed per head. The embryosacs and seeds were counted after clipping off the florets with scissors and removing the bracts with tweezers to expose the capitulum. The proportion of seeds was therefore a measure of seed set. One thousand seed weight was determined for each plant by dividing the weight of seed per plant by the number

of seeds per plant and multiplying by 1000. Flowering dates were recorded on tags tied to each inflorescence the morning they began flowering.

Seed quality was measured by determining the proportions of hull and kernal in the seed at 95% flower fade and at final harvest. Seeds were split open with a sharp scalpel blade and the kernel removed from the hull for weighing. At final harvest, oil content and quality was determined by gas liquid chromatography (Slack, 1976). Protein content of the seed was estimated from determinations of percentage nitrogen in the seed using a modified micro Kjeldahl method as described by Haslemore and Roughan (1976).

2.4. Statistical analysis

A completely randomised experimental design was used due to the flexibility in physical arrangement of experimental units (plants) available in the controlled environment rooms. In the process of routine watering, trolleys were moved to new positions within the room, and plants were moved to new positions on the trolleys. As there were no identificable sources of variation among the experimental units other than treatment effects, this design was initially most useful, and preferred for its relative simplicity. The recorded data was analysed by one way analysis of variance, using a Social Science Stastical program available for use on the B6700 computer unit at Massey University. Least Significant Difference was applied for mean separation in cases where mean inequality was statistically significant at the 5% level or less. Relationships between yield and yield

components were determined by multiple regression. A preliminary analysis of the data indicated that the variances from different treatments were approximately proportional to the means therefore a log transformation was applied to the data before the analyses. The higher means were largely associated with plants well watered throughout, and plants not treated until later stages of maturity. The larger variances of these means may have been associated with greater expression of variability in the later treated plants.

CHAPTER 3 - RESULTS

3.1 Soil Water Status

The minimum soil moisture contents for harvested plants are shown in Table 1. The overall means correspond to approximately -3.5 bar and -0.3 bar soil water potential for treatment and control plants respectively (see Fig 1). There was little variation in soil moisture content for plants harvested at different stages of growth. Differences between containers within treatments at each harvest were also small, although well watered ones were slightly more variable. Some of this variation was attributable to some plants having a higher fresh weight than others. The results indicate that adjustment in container rewatering weights for changes in mean plant fresh weight minimised differences between treatments, and the rewatering system based on container weights was effective in maintaining the difference between treatment and control soil moisture contents.

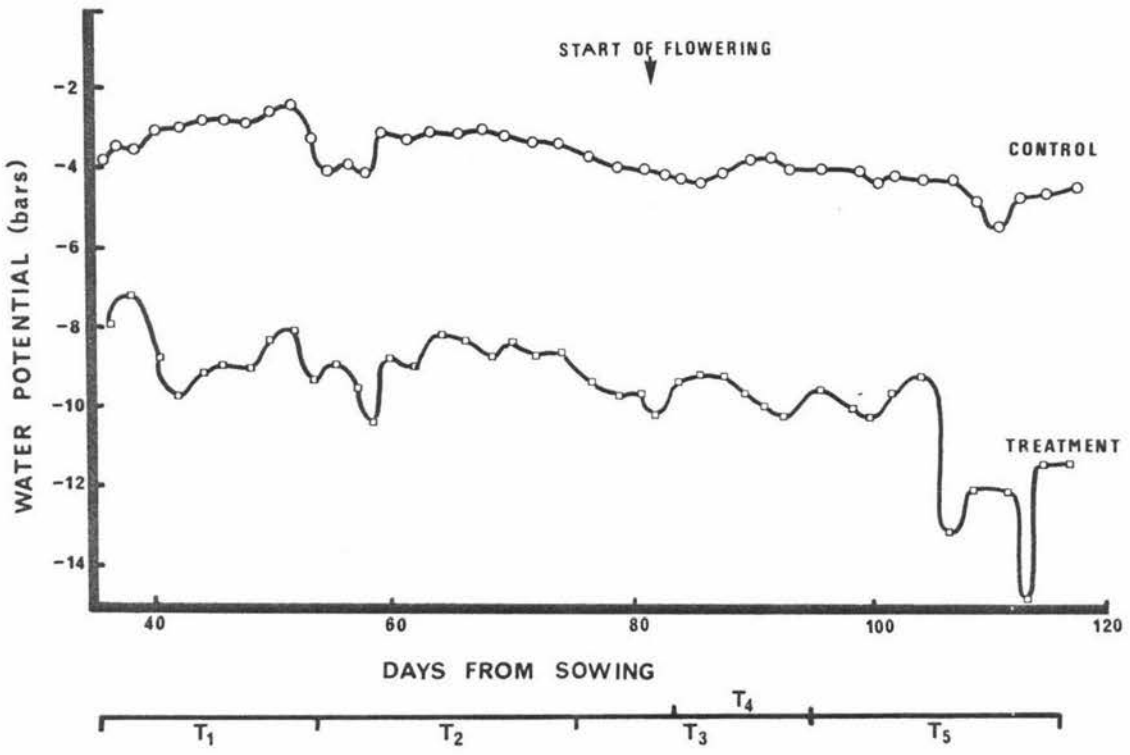
TABLE 1 Mean Gravimetric Soil Moisture Content (% g/g) at Harvests

Harvest Number	Days from Sowing	Treatment	Control
1	34	-	34.3
2	53	20.1 (T_1)	35.1
3	75	21.1 (T_2)	41.1
4	95	19.4 (T_3)	
		18.8 (T_4)	36.6
5	114	19.7 (T_5)	34.8
	Overall Mean	19.8	36.4

3.2 Plant Water Status

Leaf and head water potential, corresponding to the rewatering soil moisture content, gradually declined throughout plant growth and development (Fig 2). There was more day to day variability in the water potential of water stressed plants, possibly because small differences

Figure 2. Changes in leaf and head water potential



in soil moisture content had a relatively greater effect on plant water potential at treatment levels than at control levels (see Fig 1). Differences in head water potential were greatest toward the end of the final treatment when flower heads were drying down and nearing maturity. As most readings were within a 2 bar range, a reasonably even difference in water potential was maintained between 'well watered' and 'water stressed' plants throughout.

3.3 Plant dry weight

Well watered plants increased in dry weight most rapidly once floral initiation began, and during the flowering stage of growth (Fig 3). Plant dry weight was reduced most by water deficit during floral initiation (T_1), and was 30% less than control at final harvest. Water stress during floral development (T_2) reduced dry weight 18% by the stage of 95% flower fade and 19% by final harvest. Stress during secondary head flowering (T_4) resulted in a significant reduction in dry weight of 11% after flowering. Treatments T_3 and T_5 followed the same trend, but were not significantly different from well watered plants at final harvest.

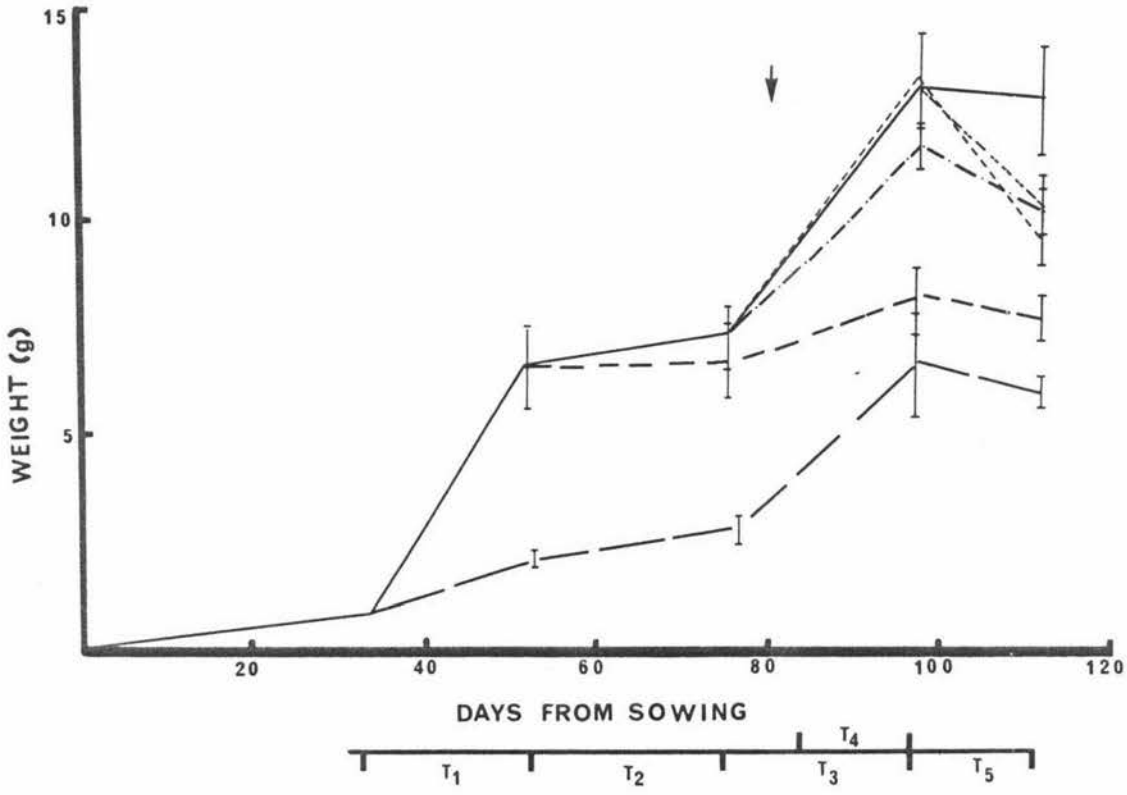
3.4 Components of plant dry weight

The cumulative changes in dry weight are shown for each treatment in Figs 4 to 9.

3.4.1 Stem

Total stem dry weight accounts for a large proportion of the plant, and changes due to water stress at the different growth stages resulted in similar trends to those for plant dry weight. Primary stem dry weight was almost halved by T_1 and was significantly less than that

Figure 3 Mean dry weight per plant



Treatment duration

for other treatments at all stages of growth (Fig 10). The reduction due to T_2 was 22% by the stage of 95% flower fade and significantly less than later treatments, but at final harvest was 15% and not significantly less than that of the later treatments (T_3, T_4, T_5).

The dry weights of secondary head stems increased most markedly between 53 and 95 days from sowing, after much of the primary stem had developed (Fig 11). It was severely restricted by T_1, being only 13% of that of well watered plants at the end of the stress period, and 25% of that of well watered plants by final harvest. Treatment T_2 reduced dry weight of secondary head stems 53% by the end of flowering. There was no significant reduction due to T_3 or T_4 at the stage of 95% flower fade, but thereafter T_3, T_4 and T_5 resulted in a decline toward final harvest which was most severe for T_5.

3.4.2 Leaf

Leaf dry weight increased most between 34 and 53 days from sowing (Fig 9) and was considerably reduced by water stress at any stage after this (Figs 5-8). Treatment T_1 reduced leaf dry weight 56%, however by the stage of 95% flower fade it was not significantly less than that of well watered plants. By final harvest the leaf dry weight of T_1 and control was 72% greater than that of other treatments.

3.4.3 Head

The total dry weight of flower heads per plant increased to a maximum at the stage of 95% flower fade (Fig 9). Head dry weight was reduced 74% by T_1, although this was only 30% by the start of flowering. By final harvest it was significantly lower in all treatments, compared with well watered plants, with T_4 having the smallest reduction of 11%.

Primary head dry weight of T_1 and T_2 was not significantly less than control at the start of flowering but by the end of flowering were 29% and 22% less respectively than control, while that of T_3 and T_4 was not. By final harvest, the primary head dry weight for all treatments was less than that of well watered plants (see appendix). As with total head dry weight, the later the stage in development at which stress occurred, the less was the effect on final secondary head dry weight.

3.4.4 Bracts

Bract dry weight increased most rapidly between 53 and 75 days after sowing, reaching a maximum at 95% flower fade, after 95 days. The pre-flowering treatments T_1 and T_2 highly significantly reduced bract dry weight (65 and 44% respectively at flowering) whereas for the flowering and post-flowering treatments T_3, T_4 and T_5, it was not significantly reduced compared with well watered controls. Primary head bract dry weight was reduced 59% by T_1 and 8% by T_2, whereas for secondary heads, T_2 was more severe than T_1.

3.4.5 Dead Matter

The dead matter was leaf material which had turned brown as a result of leaf senescence. None appeared in well watered plants until the flowering stage and most senescence occured after flowering (Fig 9). Treatment T_1 caused a significant amount of dead matter to develop by day 53, and persisted with little change until the final harvest when there was significantly less for T_1 than for well watered plants (see Appendix). Treatment 2 resulted in accumulation of dead matter more severe than T_1 by the start of flowering but not significantly different from well watered plants at final harvest. Treatments T_3 and T_4 had most dead matter at 95% flower fade, with T_5 causing the more severe increase.

Figure 4 Cumulative changes in mean dry weight per plant. (T1)

Key ---------- = Treatment duration

arrow = Start of flowering

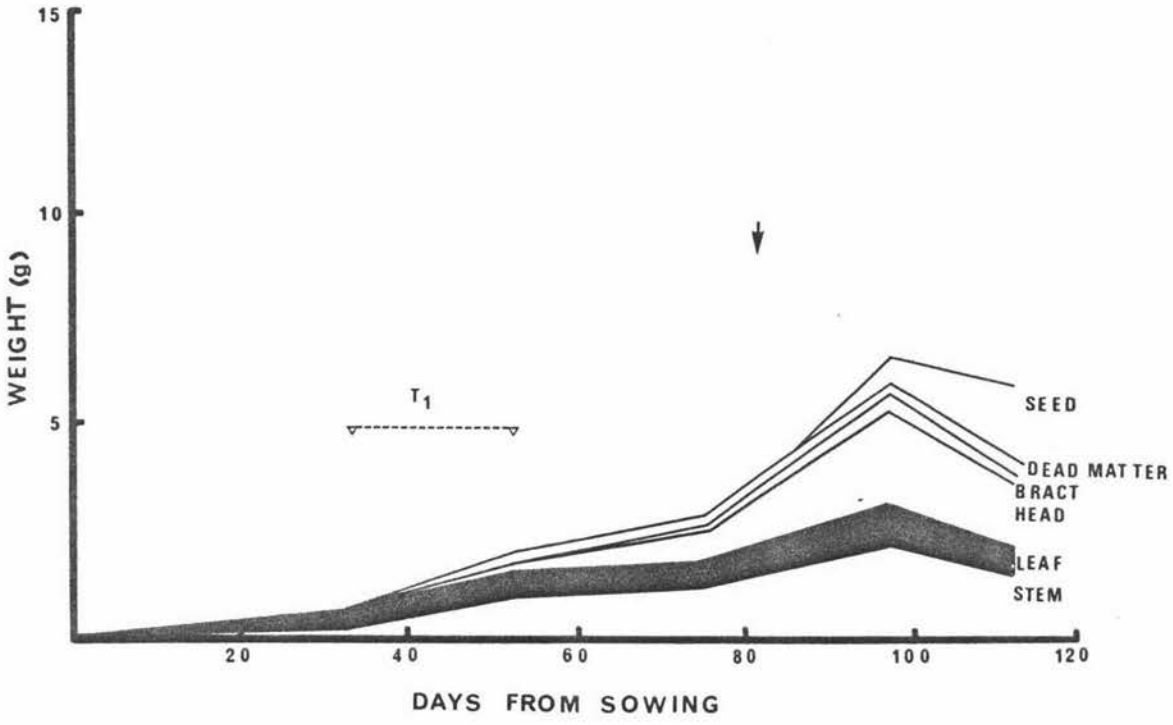


Figure 5 Cumulative changes in mean dry weight per plant. (T2)

Key ---------- = Treatment duration

arrow = Start of flowering

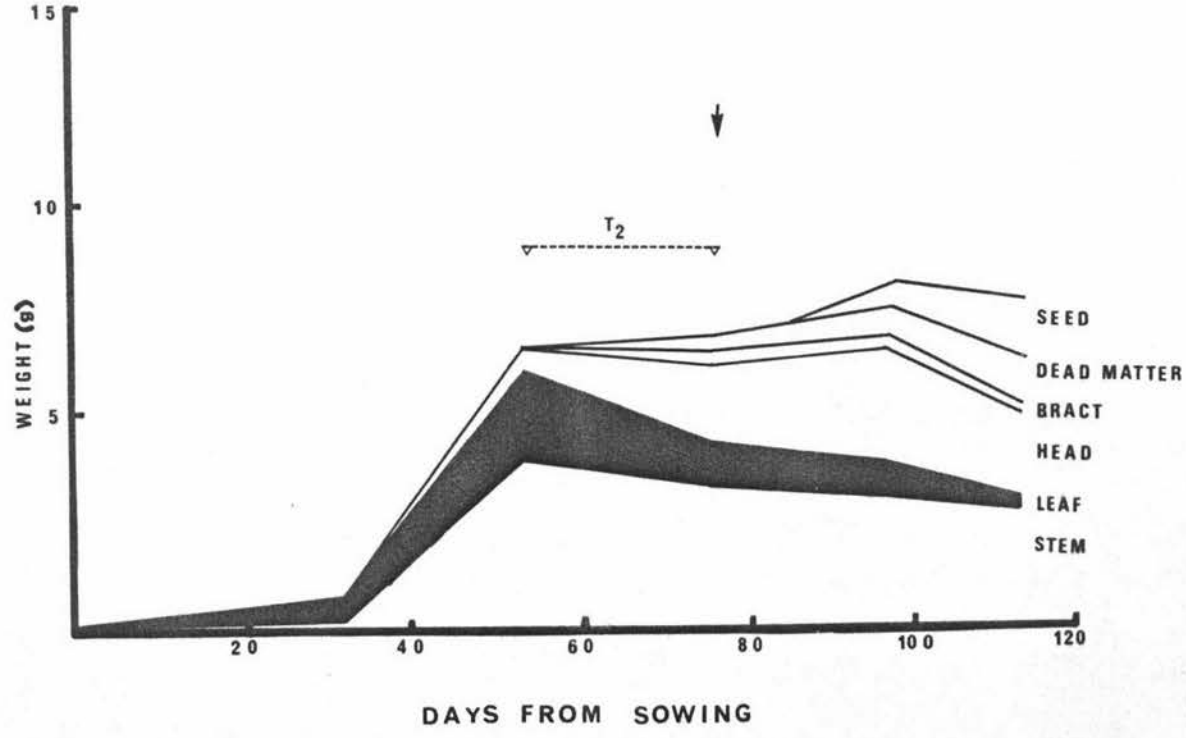


Figure 6 Cumulative changes in mean dry weight per plant (T3)

Key ---------- = Treatment duration

arrow = Start of flowering

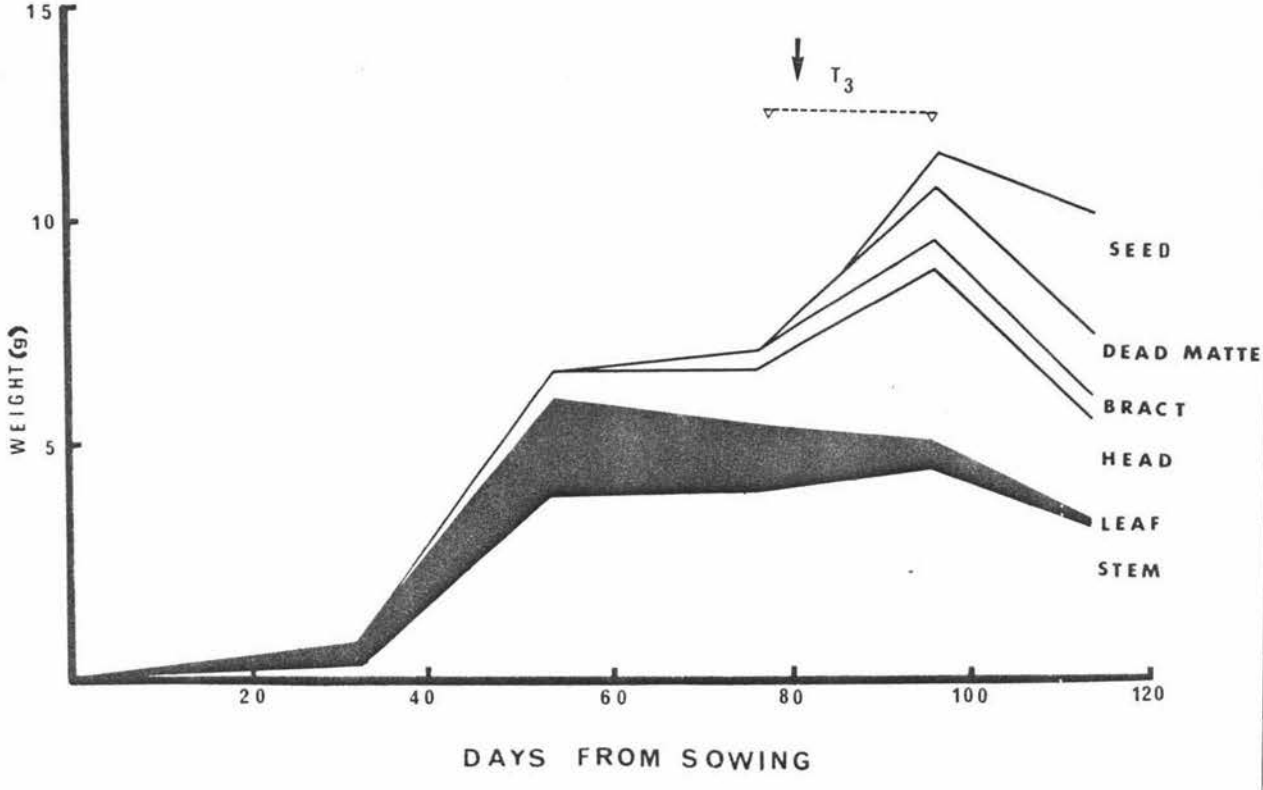


Figure 7 Cumulative changes in mean dry weight per plant (T4)

Key ---------- = Treatment duration

arrow = Start of flowering

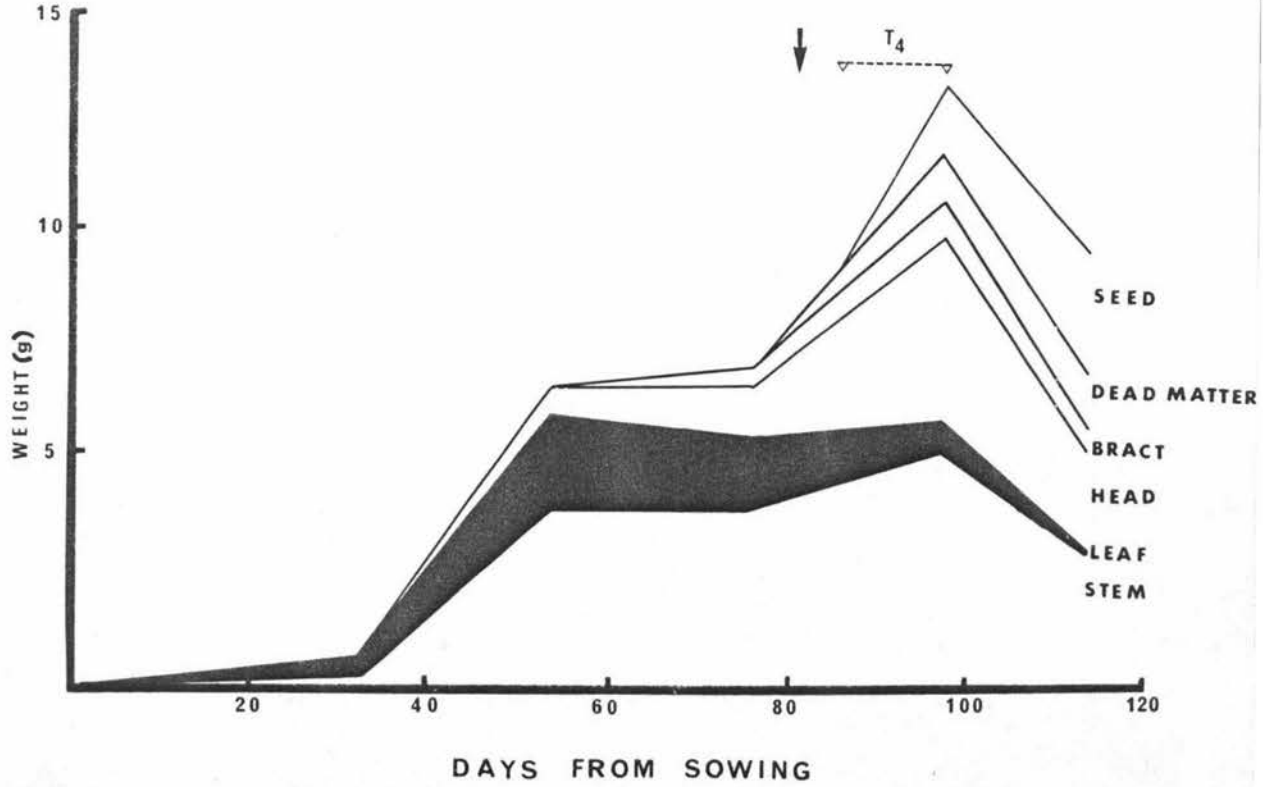


Figure 8 Cumulative changes in mean dry weight per plant (T5)

Key ———— = Treatment duration

arrow = Start of flowering

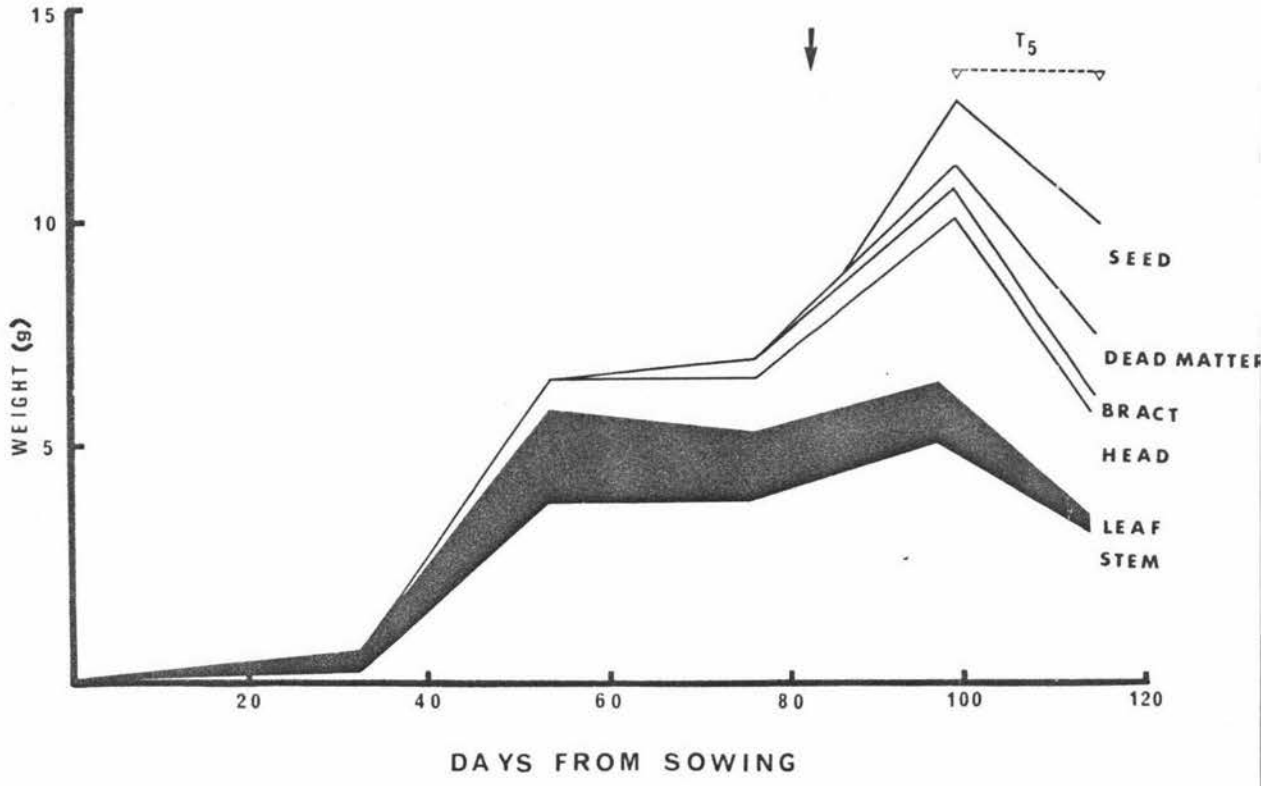


Figure 9 Cumulative changes in mean dry weight per plant (C)

Key ———— = Treatment duration

arrow = Start of flowering

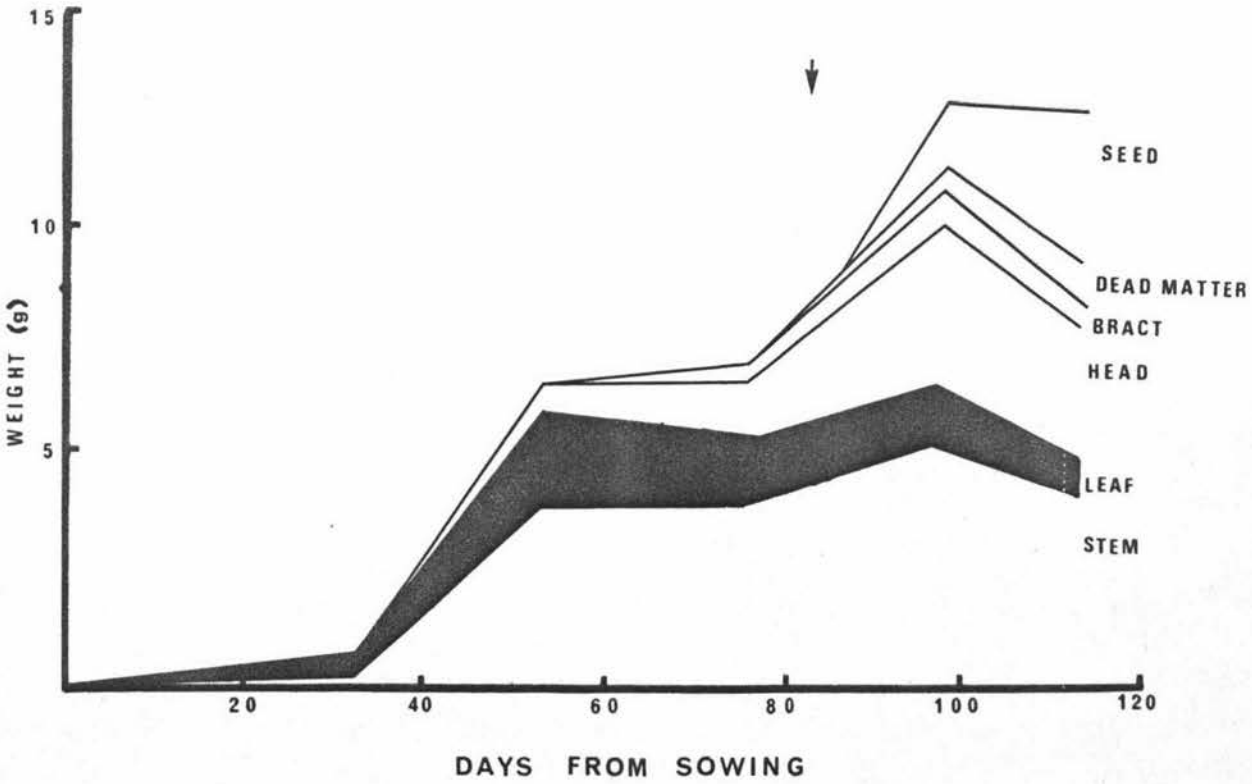


Figure 10 Mean primary stem dry weight per plant

Key T1 ——— ——— ———

T2 — — — — — — — —

T3 ——— · ——— · ———

T4 .....

T5 ——— ·· ——— ·· ———

C ———————————

arrow = start of flowering

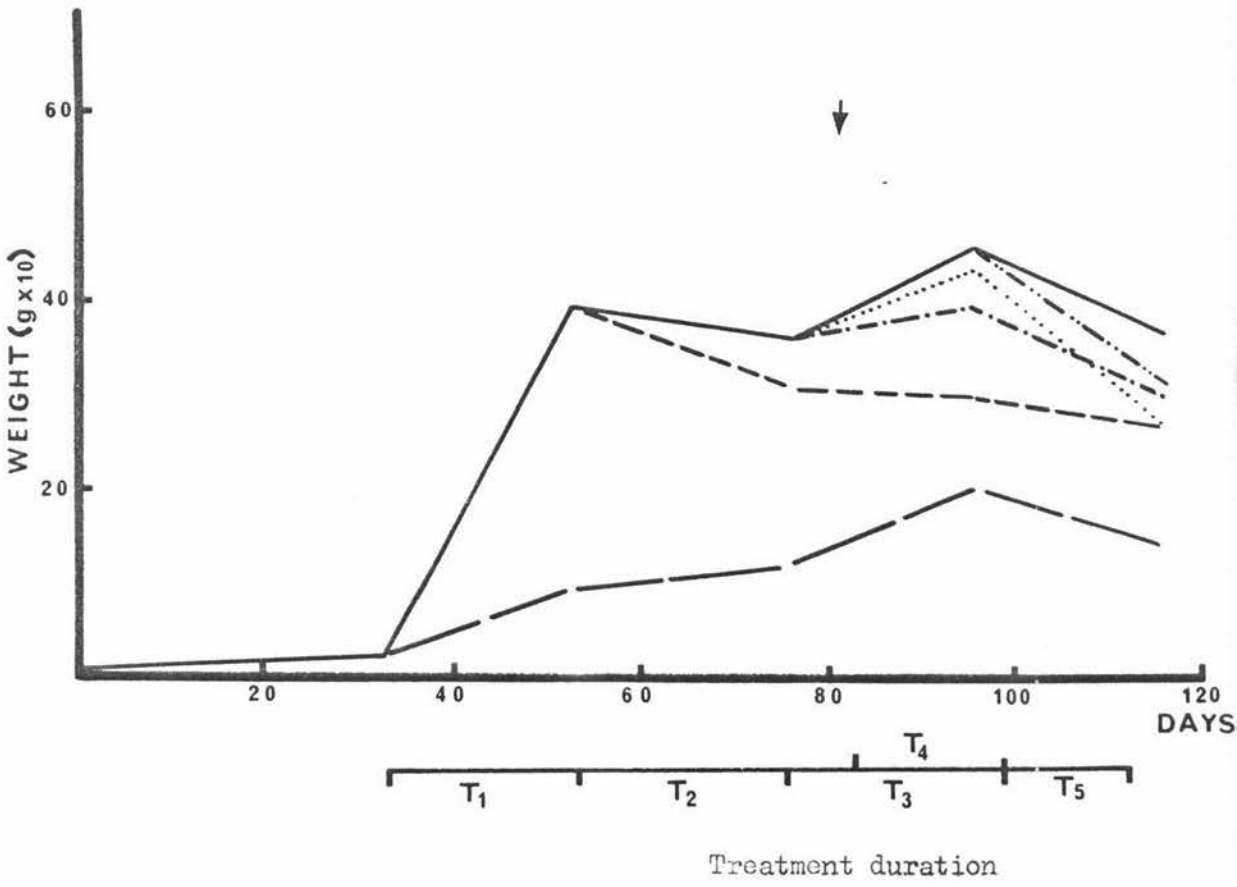
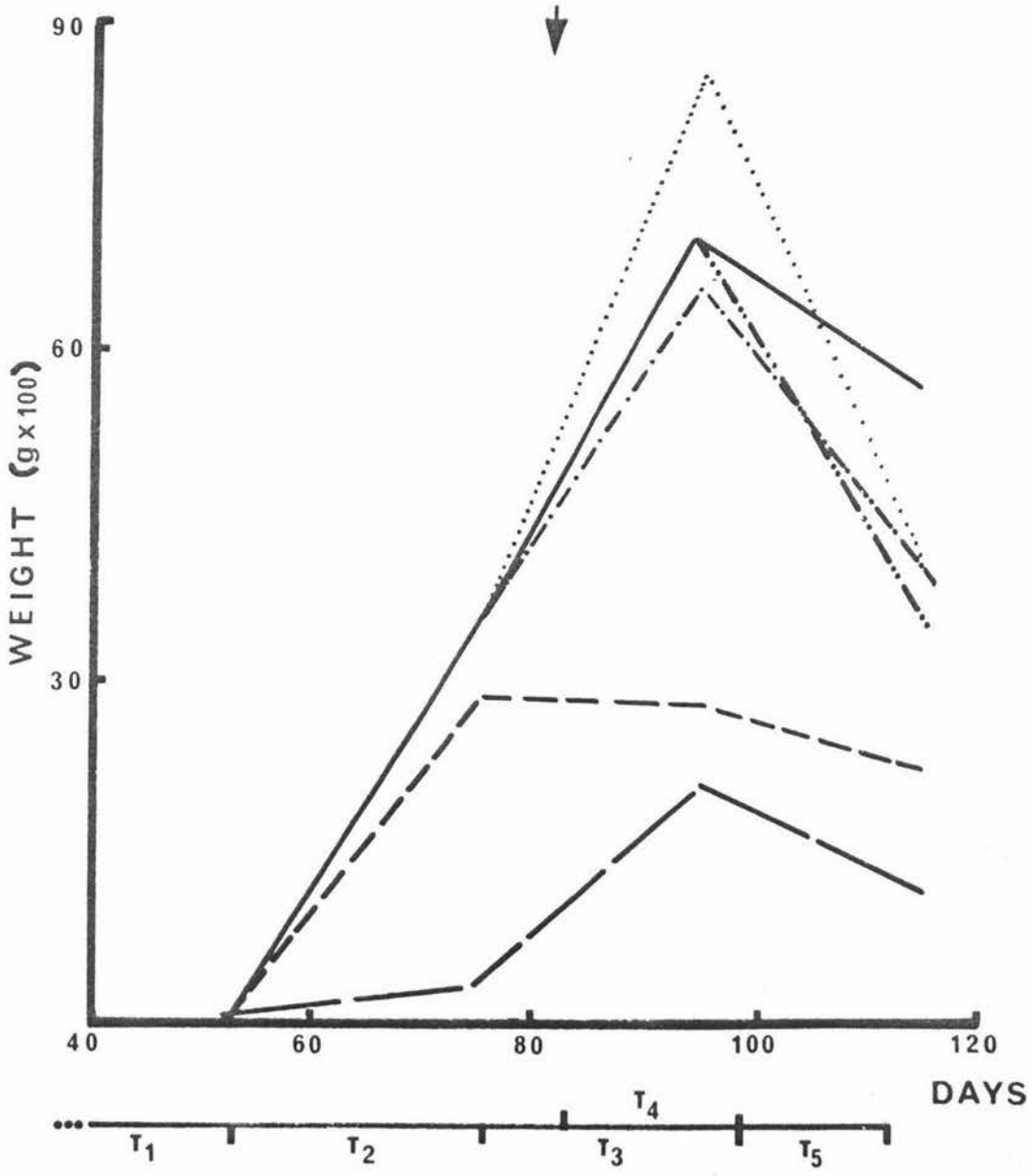


Figure 11 Mean secondary stem dry weight per plant

Key T1 ——— ——— ———
T2 – – – – – – – – –
T3 ——·——·——
T4 ·····
T5 ——··——··——
C ———————

arrow = start of flowering



Treatment duration

At final harvest, T_5 had the highest amount of dead matter, although it was not significantly greater than that of treatments T_2, T_3 and T_4.

3.5 Plant Height

Plant height increased very rapidly once floral initiation had started (Fig 12). In well watered plants, plant height had essentially reached a maximum by the start of flowering. Treatments during and after flowering had no significant effect on plant height. However T_1 and T_2 which were applied during the period of rapid height increase, resulted in plants significantly lower than those of later treatments and well watered ones. Treatment T_1 had the most severe effect with plants of significantly lower height than in T_2 except at 95% flower fade.

3.6 Green Leaf Number

The number of green leaves developing reached a maximum by the end of the floral initiation stage. Thereafter in well watered plants, leaf number gradually declined until final harvest (Fig 13). Changes in green leaf number were similar to the changes in leaf dry weight already described. Treatment 1 significantly reduced the number of green leaves developing by the end of the stress period. Green leaf number was reduced during and after the stress period by T_2, T_3, T_4 and during T_5.

3.7 Green Leaf Area

As with green leaf number, T_1 highly significantly reduced green leaf area during and following the period of water stress (Fig 14). Non-reversible reductions in green leaf area resulted from later treatments which were imposed after maximum leaf area had been reached in well watered plants. By the stage of 95% flower fade plants in all treatments

Figure 12 Mean plant height

Key T1 —— —— ——

T2 – – – – – – – –

T3 —·—·—

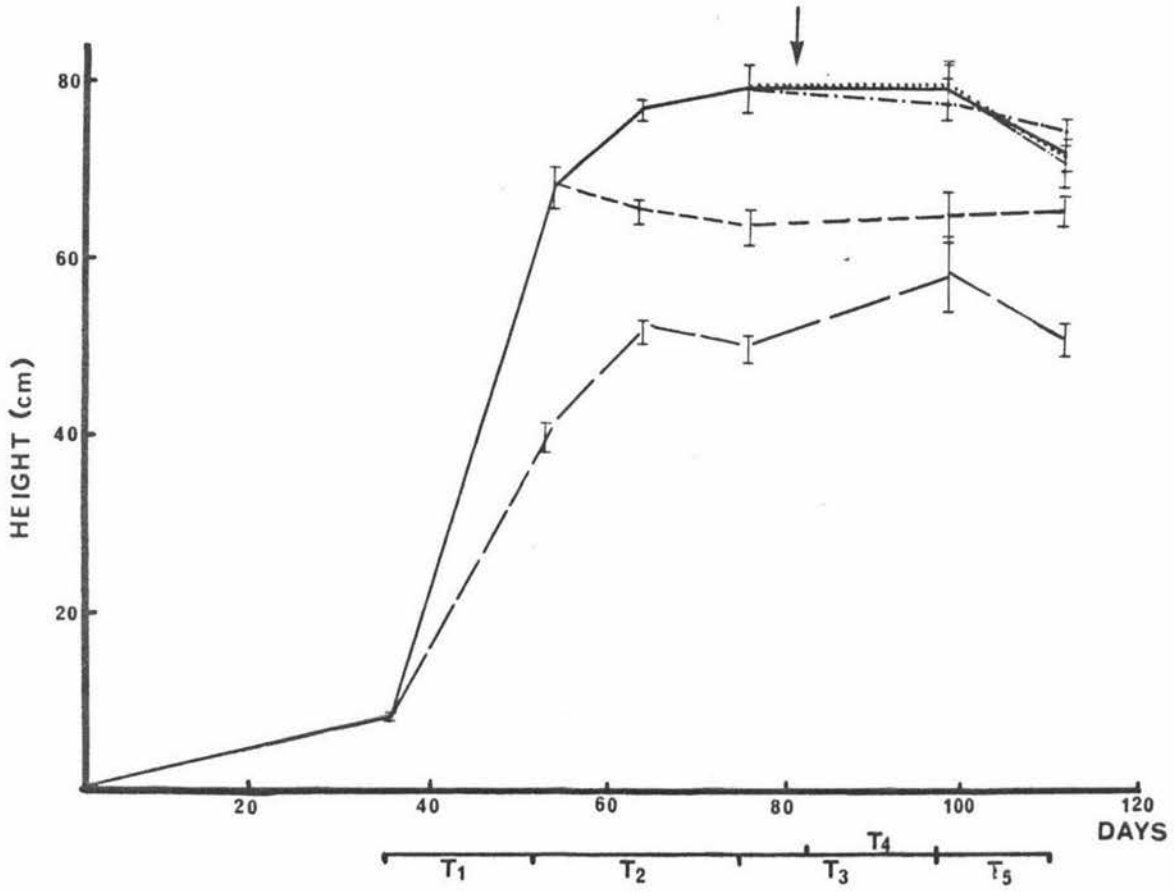
T4 .....

T5 ——··——··——

C ————————

Verticals = 2 x $S_{\bar{x}}$

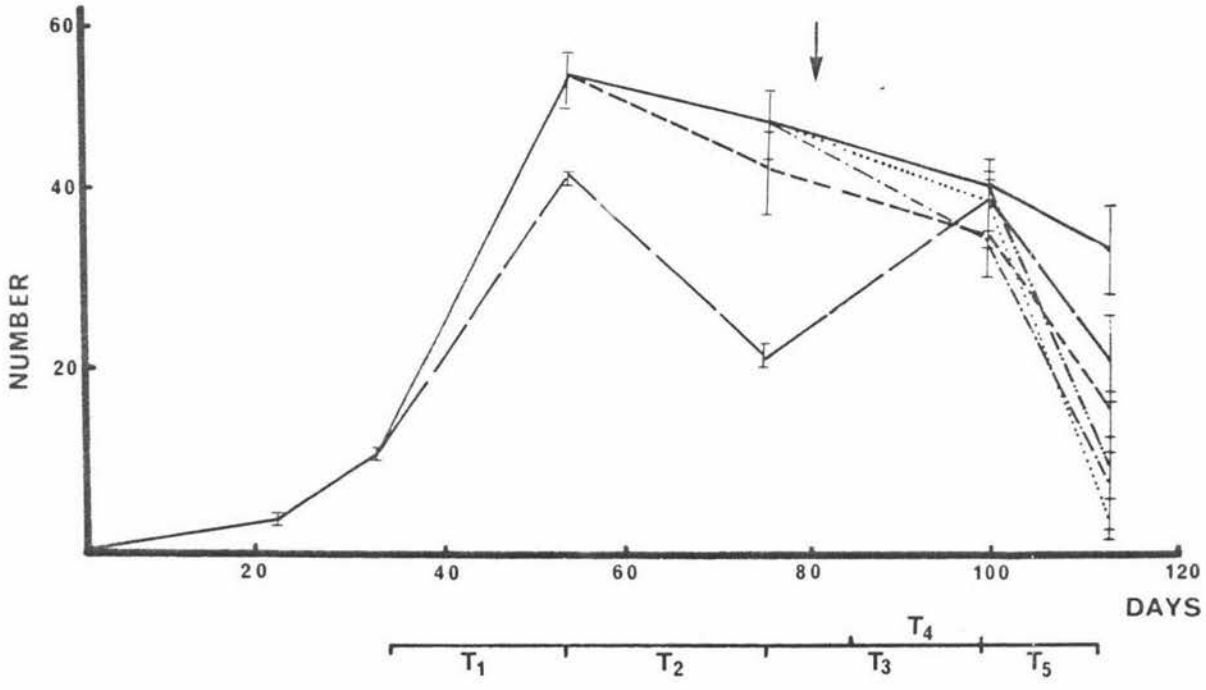
arrow = start of flowering



Treatment duration

Figure 13 Mean green leaf number per plant

Key T1 ——— ——— ———
T2 - - - - - - -
T3 —•—•—•—•—
T4 ••••••••••••
T5 —••—••—••—••
C ———————



Treatment duration

Figure 14 Mean leaf area per plant. Treatment duration

Key: T1 ——— ——— ———

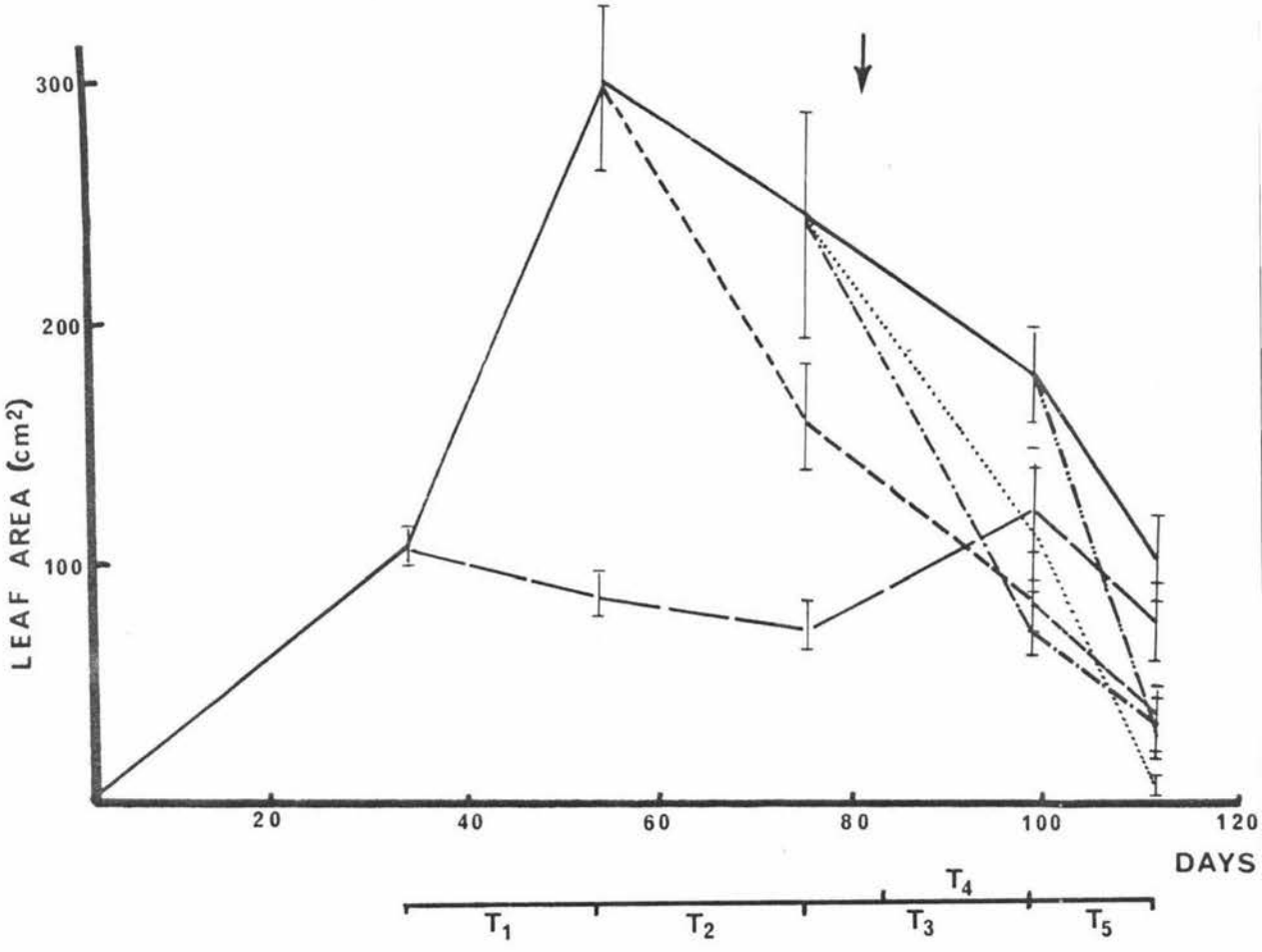
T2 – – – – – – –

T3 –·–·–·–·–

T4 ··········

T5 –··–··–··–··

C ———————



Treatment duration

except T_1 had a significantly lower green leaf area than well watered ones. At final harvest plants from T_1 and control had highest green leaf area despite the smaller size of plants from T_1. Treatment T_4 caused a highly significant reduction in green leaf area at final harvest even though this was the shortest period of water stress.

3.8 Bract Area Per Head

Changes in bract area per head were similar to changes in bract dry weight. Most bract area increase occurred between 53 and 75 days from sowing in well watered plants (Fig 15, Fig 16). Bract area per head was reduced by water stress before flowering (T_1, T_2) but not during or after flowering (T_3, T_4, T_5). At final harvest plants from T_1 had a significantly lower bract area per head than those from T_2 which in turn were significantly different from treatments T_3, T_4, T_5 and control.

Bract area per primary head was highly significantly reduced by T_1 and T_2 (Fig 16). During flowering, bract area increased to a greater degree in these treatments than in well watered plants, and by final harvest there was no statistically significant difference between T_2 and later treatments or control. However the bract area per primary head was most severely reduced by T_1 which at final harvest was significantly less than that of all other treatments and control. Changes in bract area per secondary head were similar to those for all heads (see Fig 15). Bract area per secondary head tended to be reduced more by T_2 than T_1 whereas bract area per primary head was more severely reduced by T_1 than T_2.

3.9 Visible Bud Number Per Plant

The number of buds that were visible increased to a maximum over the period of floral initiation (Fig 17). Only Treatment 1 significantly

Figure 15: Mean bract area per head

Key: T1 —— —— ——

T2 - - - - - - -

T3 -.-.-.-.-.-.

T4 .....

T5 -..-..-..-..-..

C ————————

arrow = start of flowering

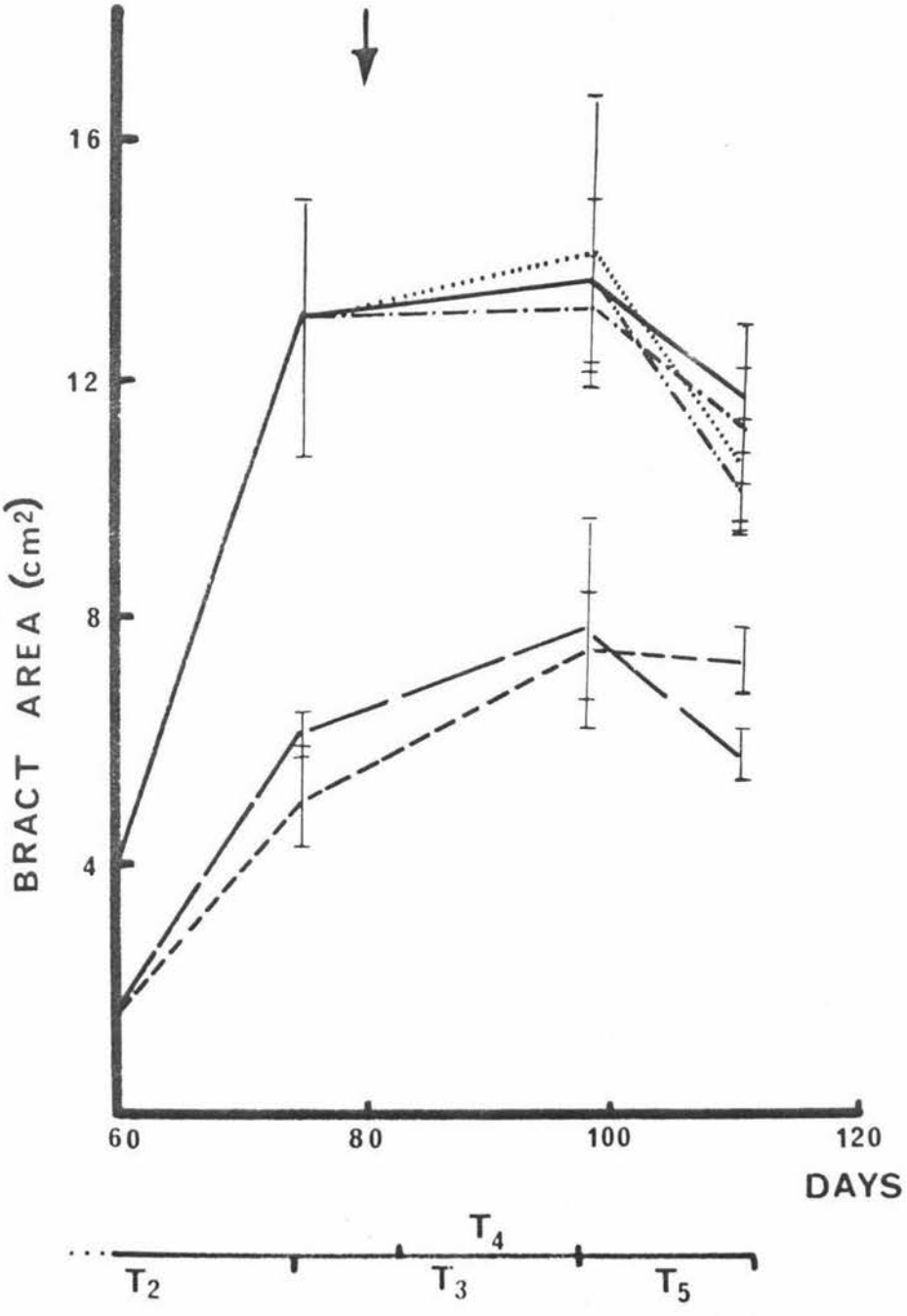


Figure 16 Mean bract area per primary head

Key T1 —— —— ——
T2 - - - - - - - -
T3 —·—·—·—
T4 .....
T5 ——··——··—
C ————————

arrow = start of flowering

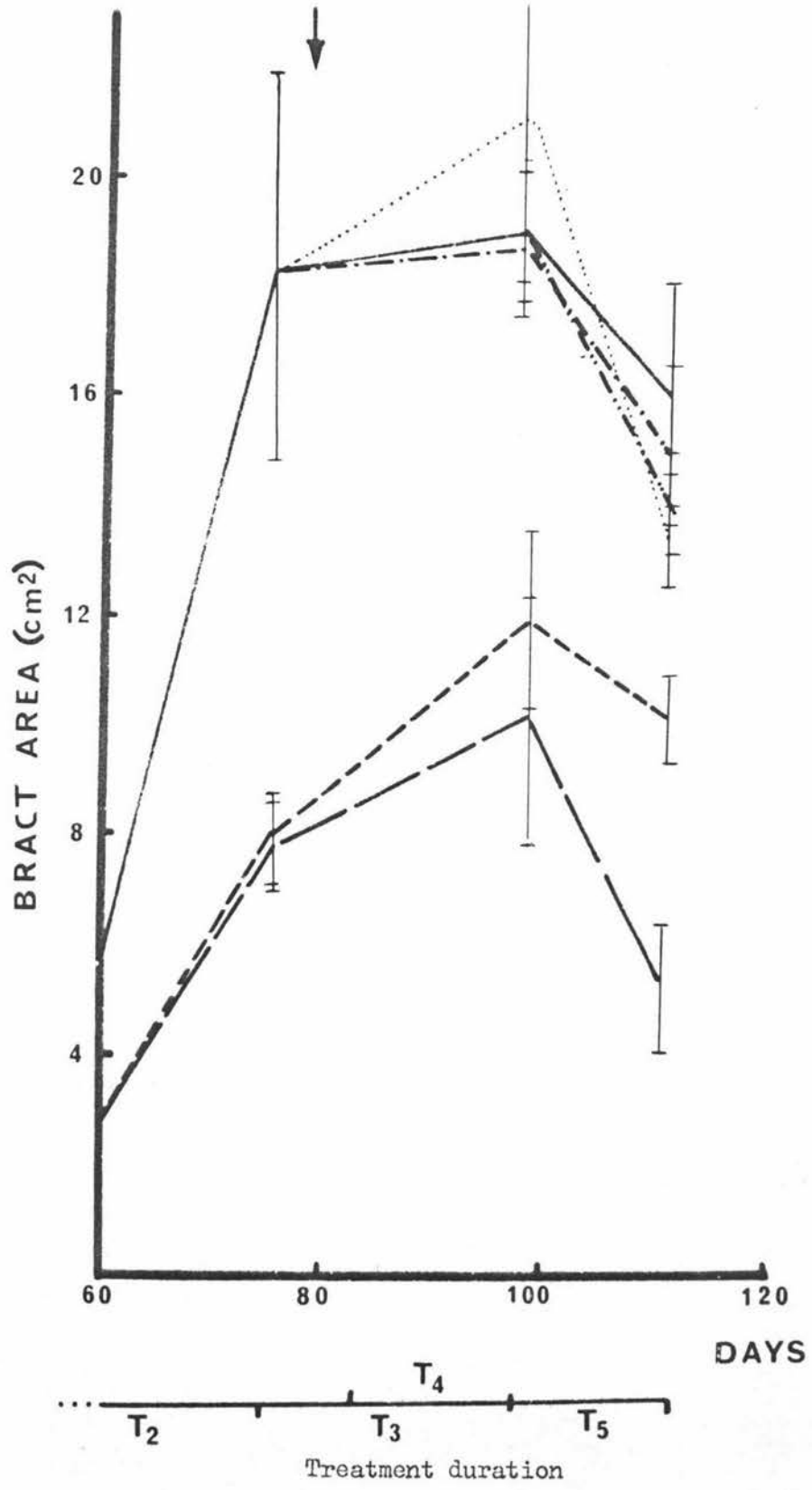
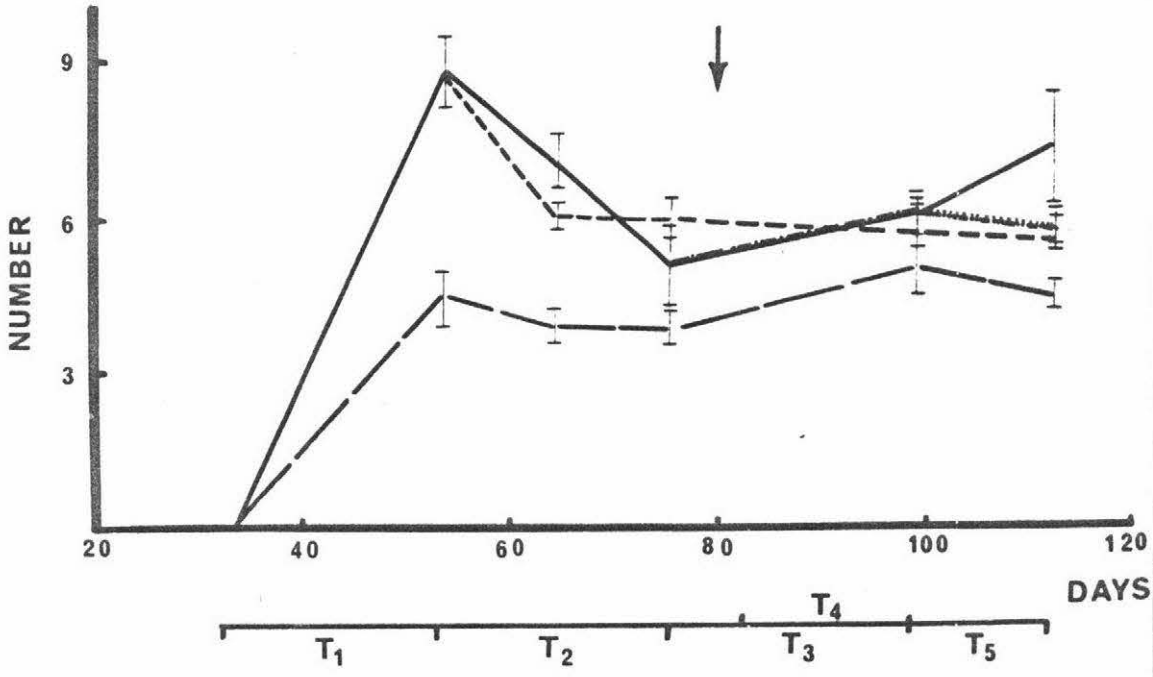


Figure 17 Mean visible bud number per plant

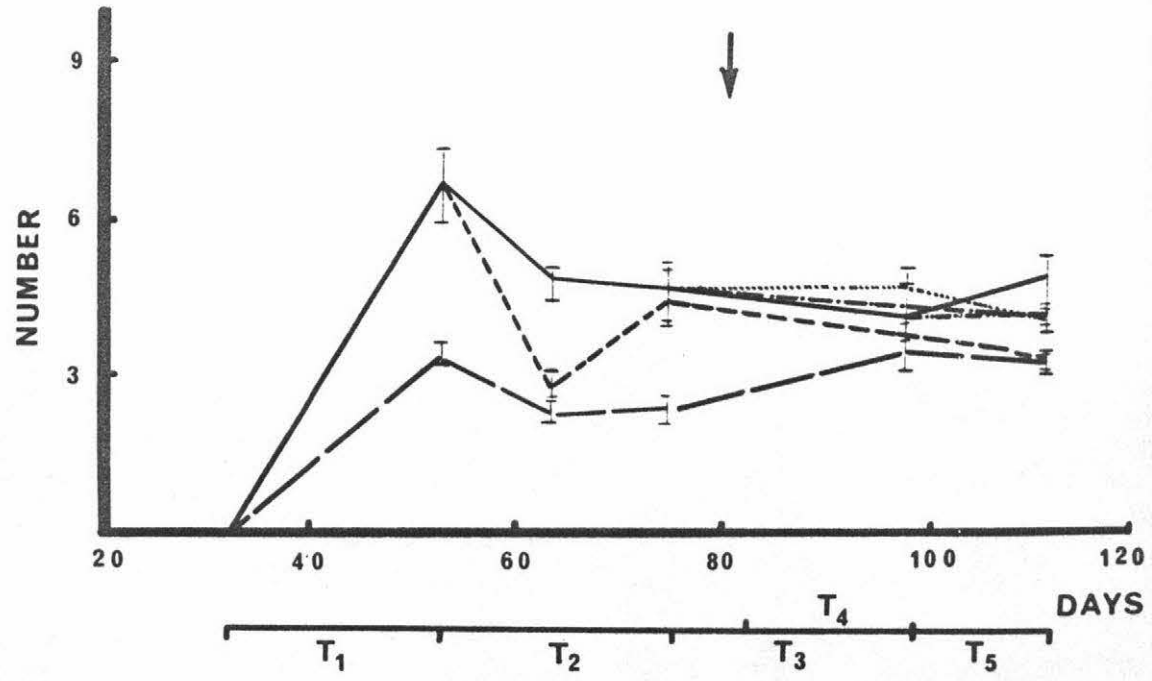
Key T1 — — —
T2 - - - - - - -
T3 — · — · —
T4 .....
T5 —··—··—
C ———————

Verticals = 2 x $S_{\bar{x}}$
arrow = start of flowering



Treatment duration

Figure 18 Mean developing head number per plant



reduced the visible bud number compared with well watered plants.

3.10 Developing Head Number Per Plant

In well watered plants, changes in the number of developing heads were similar to those for the visible bud number although not all visible buds developed into flowering heads (Fig 18). As expected, T_1 reduced the number of developing heads compared with well watered plants. Treatment 2 had a significantly lower number of heads developing after approximately 10 days of water stress. Although the number of developing heads per plant increased in later harvests, there were significantly fewer developed heads per plant at final harvest than on plants from later treatment and control plants. Treatments 3, 4 and 5 had little effect on the number of developing heads and were not significantly different from control.

3.11 Phasic Development

The mean dates for different stages of growth are shown for each treatment in Table 2. There was very little difference between treatments in time taken to reach different stages of development. Plants that were well watered throughout tended to be slightly later than water stressed plants during the later stages of development. There was no significant difference between treatments in the mean period of flowering or duration of flowering per head. However plants from T_2 started flowering significantly earlier than well watered plants. They reached 95% flower fade earlier and were physiologically mature earlier than plants well watered throughout.

TABLE 2

Phasic Development

Stage of Development	Days from sowing T_1	T_2	T_3	T_4	T_5	C	Overall Mean
Start of floral initiation	-	-	-	-	-	34	34
End of floral initiation	53	-	-	-	-	53	53
Primary bud burst	81	75	80	79	81	82	80
95% flower fade	96	93	95	95	95	99	95
Physiological maturity	114	111	114	114	115	118	114

3.12 Seed Yield per Plant

Seed yield was reduced by all treatments, however this was statistically significant only in the pre-flowering treatments T_1 and T_2 (Table 3). The lowest seed yield per plant resulted from T_2. Although seed yield per plant from primary heads followed the same trend, these differences were not statistically significant. Seed yield from secondary heads was the major source of yield per plant. Plants from T_2 had a lower seed yield per plant from secondary heads than other treatments or control.

TABLE 3

Mean Seed Yield Per Plant (g)

Treatment	T_1	T_2	T_3	T_4	T_5	C
	1.80	1.43	2.95	2.64	2.59	3.32
	b	b	a	a	a	a

Mean Seed Yield Per Plant from Primary Heads (g)

Treatment	T_1	T_2	T_3	T_4	T_5	C
	0.46	0.39	0.77	0.71	0.66	0.66
	(N.S.)					

Table 3 cont'd

Mean Seed Yield Per Plant from Secondary Heads (g)						
Treatment	T_1	T_2	T_3	T_4	T_5	C
	1.34	1.04	2.18	1.93	1.93	2.66
	a	b	a	a	a	a

3.13 Components of Seed Yield

The three direct components of seed yield are the number of heads per plant, the number of seeds per head and seed weight. As the potential number of sites available from which seed may set can be variable, the potential number of seeds per head was also considered as a component of seed yield.

3.13.1 Number of Heads per Plant

The mean number of productive heads per plant ranged from 3.4 for T_1 to 5.0 for well watered plants (Table 4). Treatments 1 and 2 resulted in a significantly lower number of heads per plant at final harvest whereas water stress during and after flowering had not significant effect. The number of productive secondary heads per plant were reduced most by T_2. Plants from T_1 also produced significantly fewer secondary heads than well watered plants but not significantly less than treatments 3, 4 and 5.

TABLE 4

Mean Number of Productive Heads per Plant at Final Harvest		
Treatment	Total	Secondary
T_1	3.4 b	2.7 bc
T_2	3.5 b	2.5 c
T_3	4.2 a	3.2 ab
T_4	4.2 a	3.2 ab
T_5	4.3 a	3.2 ab
C	5.0 a	3.6 a

Plants from all treatments produced one primary head per plant except for several in T_1, where the primary head did not develop past a small bud stage. A few late tertiary heads had developed in the whole population by final harvest. These were confined to plants from T_5 and control and made a negligible contribution to seed yield

3.13.2 Potential Number of Seeds per Head

A highly significant reduction in potential number of seeds per head resulted from water stress during floral initiation (T_1) (Table 5). For water stress at all other stages of growth there was no significant change from that of plants well watered throughout. The reduction in potential seed number per head due to T_1 tended to be slightly less severe in the later developing secondary heads than in primary heads.

TABLE 5

Mean Potential seed number per head

Treatment	Total	Per Primary Head	Per Secondary Head
T_1	25 b	22 b	25 c
T_2	36 a	40 a	35 b
T_3	39 a	41 a	38 ab
T_4	37 a	41 a	35 ab
T_5	42 a	44 a	42 ab
C	42 a	45 a	42 a

3.13.3 Number of Seeds per Head

In all cases, the potential number of seeds per head was not realized and actual seed number per head was considerably lower. The total number of seeds per head were highest in T_3 and lowest in T_2 (Table 6).

Treatment 2 had significantly fewer seeds per head than all other treatments except T_1. Although T_1 tended to have fewer seeds per head, this was significantly less than the flowering treatments T_3 and T_4 only. These trends were evident for seed number per primary head, but not statistically significant. For the larger number of secondary heads, number of seeds per head showed the same significant difference as those developed over all heads.

TABLE 6

Mean Seed Number per Head

Treatment	Total	Per Primary Head	Per Secondary Head
T_1	9.2 bc	8.1 (N.S.)	9.7 bc
T_2	8.3 c	6.2	9.2 c
T_3	14.8 a	14.2	15.0 a
T_4	13.2 a	13.5	13.6 a
T_5	11.9 ab	10.4	12.3 ab
C	12.5 ab	9.3	13.4 ab

3.13.4 Potential and Actual seed number per plant

The effect of differences in heads per plant, potential and actual seeds per head on potential and actual seeds per plant are shown in Table 7.

TABLE 7

Mean Potential and Actual seed number per plant, and percentage seed set

Treatment	Mean potential seed number per plant	Mean seed number per plant	Percentage seed set
T_1	93 c	34 b	37 a
T_2	131 b	29 b	22 b
T_3	163 a	62 a	38 a
T_4	155 ab	57 a	37 a
T_5	177 a	50 a	29 ab
C	197 a	58 a	29 ab

The potential seed number per plant was not significantly different for treatments T_3, T_4 and T_5 however the overall trend is an increase in the potential number of seeds per plant from T_1 through to Control. A comparison between treatments at flowering (T_3 and T_4) and other treatments is given in Table 8.

TABLE 8

Comparison of Treatments for mean seed number per head and mean percentage seed set

(i) Mean number of seeds per head

	Total	Primary head	Secondary head
T_1, T_2, T_5, C	10.5 b	8.3 b	11.0 b
T_3, T_4	14.0 a	13.5 a	14.0 a

(ii) Mean percentage seed set

	Total	Primary head	Secondary head
T_1, T_2, T_5, C	29.9 b	22.3 b	31.2 b
T_3, T_4	37.2 a	33.5 a	39.0 a

When grouped together, treatments during the flowering period gave a significantly higher percentage seed set and number of seeds per head than other treatments and well watered plants.

3.13.5 Seed Weight

One thousand seed weight at 95% flower fade was not significantly different for any treatment (Table 9). The weight of seed from secondary heads was about half that from primary heads.

At final harvest 1000 seed weight of plants from T_1 and control was significantly greater than that from treatments 3 and 4 (Table 10). Total 1000 seed weight tended to be lower in plants from T_2 and T_5

however these differences were not statistically significant. There was little difference in 1000 seed weight for primary head seed, although that of well watered plants tended to be higher. The lower mean 1000 seed weight for primary head seed in T_1 is merely due to some plants not developing seed bearing primary heads. Practically all the differences between treatments in seed weight were due to those in the secondary head seed.

TABLE 9

1000 Seed weight (g) at 95% flower fade (Harvest 4)

Treatment	Total	For Primary head seed	For Secondary head seed
T_1	18.8 (N.S.)	39.6 (N.S.)	15.4 (N.S.)
T_2	26.0	30.0	21.8
T_3	26.4	42.4	23.4
T_4	23.4	38.2	20.2
C	18.4	37.4	15.4

TABLE 10

1000 Seed weight (g) at final harvest

Treatment	Total	For Primary head seed	For Secondary head seed
T_1	57.1 a	46.9 (N.S.)	56.4 a
T_2	52.7 abc	64.1	49.5 abc
T_3	44.0 c	59.6	40.7 c
T_4	46.8 bc	58.8	45.5 bc
T_5	54.8 ab	63.3	52.0 ab
C	57.2 a	77.3	54.3 a

3.14 Relationships between yield and components

The relationships between seed yield per plant and its components were determined by multiple regression, and are summarised in Table 11. Over all treatments, 95% of the variation in seed yield could be accounted for by the three components seeds per head, heads per plant and 1000 seed weight. Seed number per head had the highest single correlation coefficient, and the highest standardized partial regression coefficient (Beta). There was a small negative correlation between seed yield per plant and 1000 seed weight.

Treatment three had a slightly lower multiple correlation coefficient between yield and yield components, and relatively less variation in seed yield (74%) was accounted for by these components than in the other treatments. Water stress after flowering (T_5) resulted in the largest negative correlation between seed yield and 1000 seed weight.

TABLE 11

Summary for multiple regression of seed yield on seed yield components

Treatment	Trait	Multiple R	R^2	Simple R	Beta	
T_1	1000 seed weight	0.47	0.22	- 0.47	0.37	
	Seeds/head	0.93	0.86	0.90	1.13	**
	Heads/plant	0.94	0.89	0.40	0.15	
T_2	1000 seed weight	0.26	0.07	- 0.26	0.57	**
	Seeds/head	0.94	0.89	0.85	1.33	**
	Heads/plant	1.00	0.99	0.01	0.33	**
T_3	1000 seed weight	0.32	0.10	0.32	0.17	
	Seeds/head	0.85	0.72	0.83	0.78	**
	Heads/plant	0.86	0.74	0.28	0.13	
T_4	1000 seed weight	0.03	0.00	- 0.03	0.65	**
	Seeds/head	0.78	0.60	0.60	0.75	**
	Heads/plant	0.98	0.97	0.80	0.66	**
T_5	1000 seed weight	0.79	0.63	- 0.79	0.73	**
	Seeds/head	0.86	0.86	0.93	1.70	**
	Heads/plant	0.99	0.99	- 0.00	0.50	**
C	1000 seed weight	0.58	0.34	- 0.58	0.32	**
	Seeds/head	0.69	0.48	0.69	1.24	**
	Heads/plant	1.00	1.00	0.40	0.80	**

3.15.1 Seed hull and kernel weights at final harvest

Differences in seed weight between treatments for the seed sample used in the kernel and hull analysis followed similar trends to those found for all seed. In seed from primary heads, T_4 had the lowest kernel weight whereas T_5 had the highest (Fig 19). Primary head seed from well watered plants had a particularly high hull weight, while that from the flowering period treatments had low hull weight.

Figure 19 Mean primary head seed hull and kernel weight

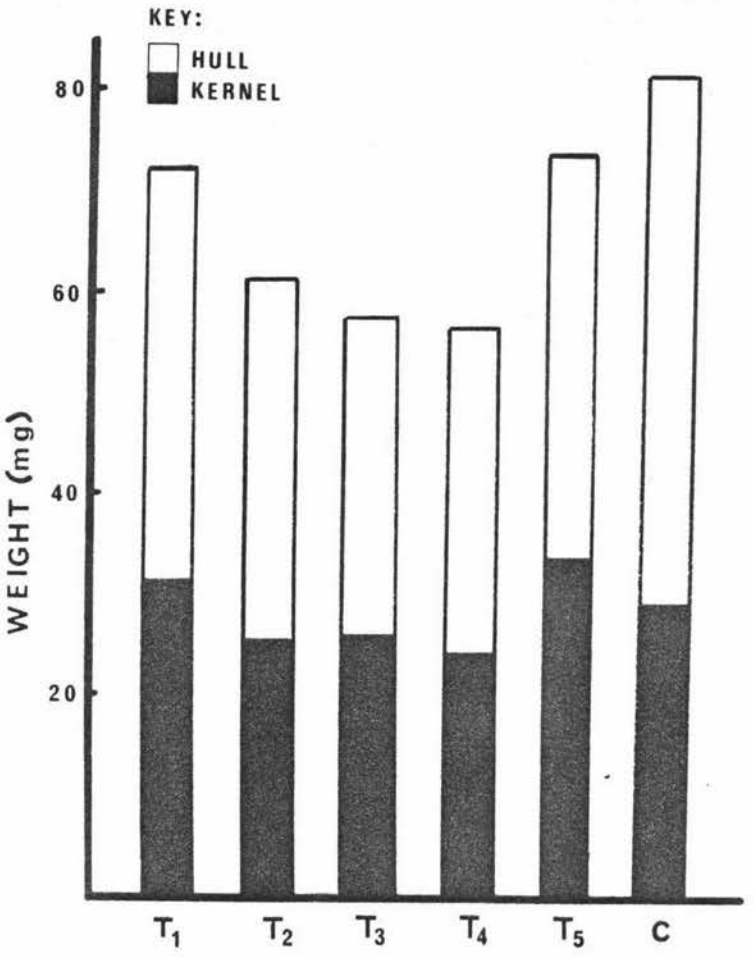
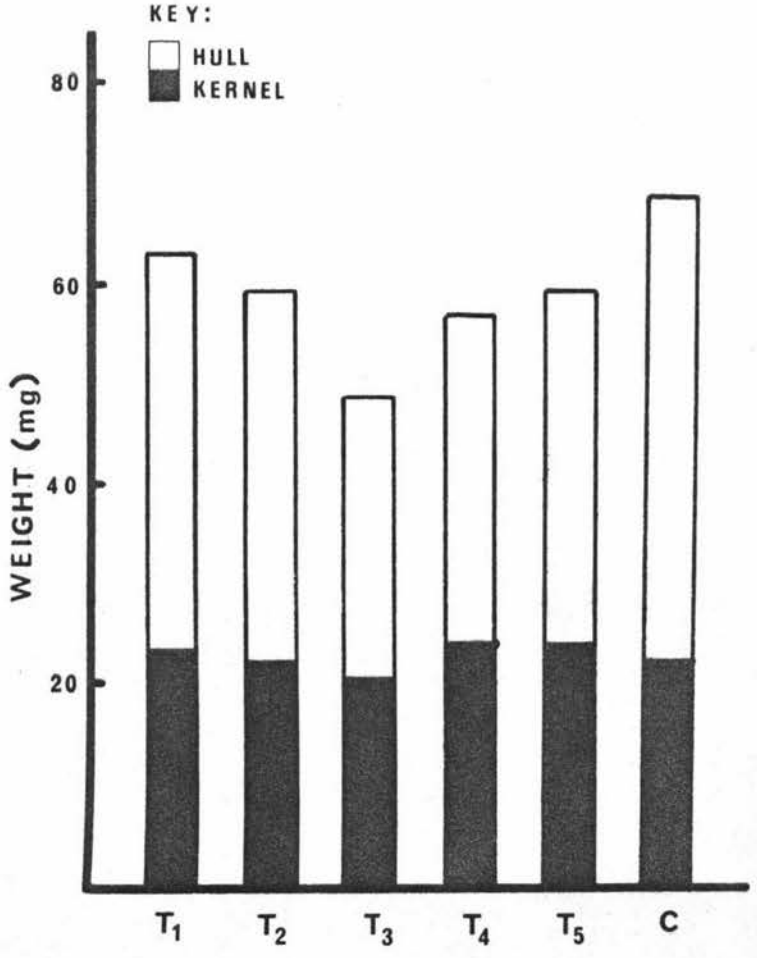


Figure 20 Mean secondary head seed hull and kernel weight



The high percentage kernel in T_5 (Table 12) appears to be due to the high kernel weight, whereas for T_3 and T_4 it appears to be due to the low hull weight.

TABLE 12

Percentage kernel

Treatment	T_1	T_2	T_3	T_4	T_5	C
In Primary head seed	40.4 c	41.7 bc	44.2 ab	43.4 abc	45.1 a	35.3 d
In Secondary head seed	35.1 cd	36.2 bc	42.1 ab	42.7 a	39.4 abc	31.8 d

Differences between treatments in the proportion of hull and kernel for secondary head seed were similar to those for primary head seed (Fig 20). In secondary head seed there was no significant difference in kernel weight between treatments. However the hull weight of seed from well watered plants was significantly greater than that in all treatments except T_1. Treatments 3 and 4 had the lowest hull weight for secondary head seed. As with primary head seed, this resulted in the flowering and post flowering treatments having seed of highest percentage kernel (see Table 12).

3.15.2 Seed and Hull weight at 95% flower fade

As the secondary head seed had just began to develop by this stage, only the primary head seed was sampled for analysis of kernel and hull proportions. There was no significant difference between treatments for 1000 seed weight (Table 13), as found for all seed at 95% flower fade. The 1000 seed hull weight was lowest for T_2, T_3 and T_4, although the difference for T_3 and T_4 was not significant at this stage of growth.

The mean percentage hull in the seed and the mean hull weight as a percentage of the final hull weight was 84% (Table 14). The seed of treatments 3 and 4 developed only 2% more hull after flowering in contrast to a further 37% developed in seeds of well watered plants.

TABLE 13

Sample seed and hull weight of primary head seed at 95% flower fade (Harvest 4) (g)

Treatment	1000 seed weight	1000 seed hull weight
T_1	38.9 (N.S.)	34.4 a
T_2	33.3	26.5 b
T_3	36.4	31.7 ab
T_4	40.3	31.7 ab
C	37.8	33.3 a

3.16 Seed Composition

TABLE 14

Treatment	Mean Proportion of hull in seed (%)	Mean hull weight as % of final hull weight
T_1	88.4	84.5
T_2	79.6	74.2
T_3	87.1	97.5
T_4	78.7	99.1
T_5	-	82.8
C	88.1	63.3
Mean	84.4 %	83.6 %

3.16.1 Seed Hull, Kernel and Percentage Oil Composition

The results from a bulked sample analysis used for the oil quality analysis are given in Table 15. Differences between treatments in seed weight, hull weight and % kernel in these samples are similar to those already described. Percentage oil in the kernel tended to be high in seed from T_5 and well watered plants. Percentage oil in the seed varied little between treatments, except in T_5 where a high percentage kernel and percentage oil in the kernel combined to give a slighter higher percentage oil in the seed. The high percentage oil in the kernel of seed from well watered plants was not associated with a high seed oil content, probably because this seed had a high hull weight and low percentage kernel.

TABLE 15

Sample seed and hull weight, % kernel and % oil

Treatment	Seed weight (mg)	Hull weight (mg)	% Kernel	% Oil in kernel	% Oil in seed
T_1	72	44	38	62	23.6
T_2	59	38	35	65	23.2
T_3	52	32	38	61	23.2
T_4	58	35	41	58	23.7
T_5	69	41	40	67	26.5
C	71	50	30	74	22.3
Mean	64	40	37	65	23.8

3.16.2 Seed Oil Quality

Oil from the seed was of high quality and showed little variation between treatments (Table 16). The mean percentage of linoleic acid was

relatively high (85%). The slightly lower level in T_1 and C was associated with an increase in percentage oleic acid.

TABLE 16

Percentage Oil Composition

Treatment	Palmitic	Stearic	Oleic	Linoleic
T1	6.0	1.9	8.2	84.0
T_2	5.5	1.7	7.1	85.7
T_3	5.9	1.6	6.4	86.1
T_4	5.9	1.7	7.0	85.5
T_5	5.4	1.9	6.6	86.1
C	5.4	2.7	9.5	82.4

3.16.3 Seed Protein Content

Water stress had little effect on seed protein content as estimated from percentage nitrogen in the seed, for any stage of growth (Table 17).

TABLE 17

Seed Protein Content (% N x 6.25)

Treatment	T_1	T_2	T_3	T_4	T_5	C
	15.0	14.0	14.7	15.9	15.6	14.7

Seed from T_2 had the lowest protein content, however the difference between highest and lowest values was only 1.9% and there was little evidence of a specific stress effect.

3.17 Harvest Index

The harvest index or efficiency of seed production in each treatment is shown in Table 18.

TABLE 18

Treatment	T_1	T_2	T_3	T_4	T_5	C
Harvest Index	29.8	19.1	26.3	27.1	25.4	26.4
	a	b	a	a	a	a

The harvest index was not significantly reduced due to water stress at any of the growth stages except floral development (T_2). Following the rapid increase in plant dry weight during floral initiation, the effect of water deficit on development of florets probably contributed to the low harvest index in T_2. Water stress during floral initiation (T_1) reduced plant dry weight (Fig 4) and this resulted in lower seed yield but not a lower efficiency of seed production. The values of harvest index obtained in this study compare favourably with those obtained elsewhere. Stern and Beech (1965) reported a range of 13-20 depending on plant density, while Beech and Norman (1963) gave values of 21 to 25 depending on planting date. The high values in Table 13 probably result from favourable growing conditions obtainable in controlled environment rooms.

CHAPTER 4 - DISCUSSION

From the review of literature it was evident that an approach to interpreting stress-yield relations should consider the plant response according to stage of growth, within reference frames of stress severity and duration. Also it was apparent that due to the sequential development of traits of seed yeild, the effects of stress on seed yield of safflower would be dependent on the stage of plant growth. The results will be discussed in terms of plant responses for the different stages of growth at which water stress was imposed.

4.1 Stress Severity

The role of the watering system was to provide similar levels of stress severity at different stages of growth, and to maintain an even difference in water potential between 'well watered' plants and 'water stressed' plants. The plant water deficit as measured by leaf and head water potential was reasonably even for all treatments, mostly between -8 and -10 bar. To what extent plant water deficit may have increased during the photoperiod is not known, although on these values alone, the treatments represented at least 'moderate' water stress.

Control plant water potentials were mostly between about -2.5 and -4.5 bar. Duniway (1975) has recorded leaf water potentials of about -2 bar in young well watered safflower plants using psychrometric methods. He considered that the resistance to water movement through the stem was small in comparison with resistance to water uptake in the leaves. In safflower the lower leaves of even well watered plants tend to drop at the later stages of growth. In this experiment the control plants

exhibited rapid rates of leaf enlargement indicating that in these plants, turgor-dependent processes such as cell expansion were not inhibited at the water potentials measured. In the absence of information on this aspect of safflower other than that of Duniway (1975), a critical comparison of the absolute values of the water deficits measured is not possible. It is of interest to note that safflower is suited to similar conditions as those for cotton and the two crops are often grown in rotation (Weiss 1971). Cotton plants may never attain water potentials above -3 to -5 bar in well watered soils (Keipper et al 1973, Bielorai and Hopmans (1975).

In quantifying the stress severity, the water potential measurements in this experiment indicate that a stress of similar severity was imposed for each of the growth stages considered. That an even difference in water status between well watered and water stressed plants was maintained is supported by the results in Tabl 1 which indicate the corresponding soil moisture contents determined at each harvest.

4.2 Stress Duration

The treatments were designed to provide periods of water deficit of comparable duration at different stages of growth. As there was little change in phasic development due to water stress at any of the growth stages (Table 2), it was possible to maintain a similar period of stress duration. This was about 20 days in all treatments except T_4 which was 12 days due to the shorter stage of development being considered.

Plants water stressed during floral development (T_2) began flowering before well watered ones, 75 days after sowing. At this stage plants selected for water stress during flowering (T_3) were dried down so that they were at stress levels by primary head bud burst a few days later. Therefore although in well watered plants the stage of floral development was slightly longer than the period of flowering (Table 2), the actual duration of water stress was similar for both and comparable with that for the other stages of growth except secondary head flowering.

The mean duration of water deficit can be considered as at least moderate, in which many indirect and secondary alterations to plant growth and metabolism would be expected to occur. Nevertheless, such period of drought can be reasonably expected under rainfed conditions of safflower production, and it is the resulting changes due to the many physiological responses contributing to seed yield that are being considered in this study.

4.3 Stage of Growth

4.3.1 Water Stress during floral initiation (T_1).

Water stress during floral initiation reduced seed yield by almost half that of well watered plants. The basic source of yield reduction was due to fewer seeds per plant (Table 7) since seed weight was not affected by water deficit at this stage of growth (Table 10). Both fewer heads per plant and fewer potential seeds per head contributed to a reduction in potential number of seeds per plant. Because the lower number of inflorescences was associated with a lower number of visible buds (Figs 17 and 18) water stress at this stage appears to have reduced

head number by limiting flower bud development. The lower potential seed number per head in stressed plants appears to be a direct result of fewer florets being initiated on the apex of each flower bud. This type of response has been reported in sunflower (Marc and Palmer 1976) and barley (Nicolls and May 1963, Hussain and Aspinall 1970). As fewer florets developed in each head, seed number per head tended to be low, however the percentage seed set was relatively high (Table 7) thus the actual seed number per head was not significantly less than that of well watered plants.

The reduction in plant growth resulting from water stress during floral initiation was expressed by lower dry weight of practically all plant organs (Fig 4). This may in part be due to the effects of water stress on cell division and expansion in organ primordia which by restricting early development of the primordia could limit the final organ size. Slatyer (1969) has indicated that slower rates of organ development are generally associated with smaller mature organ size. This response has been found in leaf development due to an extended period of water stress (Fisher and Hagan 1965, Boyer 1970a). Certainly the dry weight of bracts and flower heads which were initiated at the time of stress but developed largely after the period of stress was significantly lower than that of well watered plants. The bract dry weight of secondary heads tended to be less affected than that of primary heads since secondary head bracts are later developing. Green leaf number was reduced during the period of stress, probably due to a reduction in the rate of foliar primordium initiation before transition of apices to a reproductive state. In sunflower stressed at levels greater than

-5 bar (Marc and Palmer 1976) total leaf number was reduced due to a lower rate of leaf initiation at that stage of development. After the period of stress, a further reduction in green leaf number was in part due to the death of several basal leaves. Leaf expansion was severely inhibited during the period of stress and showed little recovery until flowering began (Fig 12). During flowering however, there was some increase in leaf area per plant along with a general increase in the size of other plant organs. At final harvest the plants had a similar leaf area to that of well watered plants despite their smaller size. This was largely due to the relative increase in leaf area of plants from T_1 during flowering when that of other plants was declining (Fig 14). As most leaves on the main stem had reached mature size by flowering, the increase in leaf area was probably due to late secondary stem leaf development.

Post flowering leaf senescence tended to be slower in the T_1 plants so at final harvest they had a higher proportion of green leaf but similar actual leaf area to well watered plants. These responses appear to have had no significant influence on the harvest index (Table 18). The apparent postponement of plant growth therefore has not affected the efficiency of seed production. However the smaller plant size compared with well watered plants limited the yield per plant obtainable.

4.3.2. Water Stress during inflorescence development (T_2).

Plants that were water stressed during the stage of inflorescence development suffered the greatest reduction in seed yield, being less than half that of plants which were well watered throughout.

Inflorescence development has been reported as the most sensitive stage to water stress in safflower by numerous workers (Seydlitz 1962, Erie and French 1969, Dastane et al 1971), although the extent of yield reduction varied. In many other annuals also, the stage between floral initiation and flowering results in the greatest reduction in seed yield (Salter and Goode 1967). The large reduction in seed yield resulted from th se plants having the lowest number of seeds per plant. Apart from those of T_3 and T_4, they also had the lowest 1000 seed weight. Langer and Ampong (1970) found that prolonged water stress in wheat prior to flowering was associated with lower grain weight. However in this study the 1000 seed weight was not significantly less than that of control (Table 10). A lower seed number per plant resulted from a reduction in both the potential number of seeds per plant and the percentage seed set, or the proportion of potential sites actually filled (Table 7).

The reduction in potential seed number per plant was due to fewer productive secondary heads developing. Floral initiation had occurred before the period of water stress, thus the potential number of seeds per head was not affected (Table 5). As in this study, Seydlitz (1962) found that the severity of yield reduction at this stage of growth was the result of head number per plant being reduced more than at other stages under stress conditions. Unlike plants stressed during floral initiation, the lower head number was not associated with a lower visible bud number (Figs 17 and 18) therefore the early development of flower buds was not affected by water deficit at this stage. However at final harvest the number of developed heads as a

percentage of the visible bud number was 69.4% for plants stressed during floral development, and 79.4% ± 0.6 for all other plants. The visible buds which had not developed into flower heads on the stressed plants were mostly supported by a short stem, rather than remaining in the axils of leaves on the primary stem. This suggests that water deficit during floral development reduces the productive head number by preventing the development of a porportion of buds that have formed and begun development into a flower head. The stress probably resulted in a delay between bud formation and extension of the stem, which could prevent further development of the bud as described for barley by Gallagher et al (1976).

A lower percentage seed set in heads that did develop resulted in fewer seeds per head. This may have been due to interference with the normal development of florets because at this stage there is intense competition for assimilate within the plant, and a reduction in the availability of carbohydrates or nutrients can result in a lower seed number (Slatyer 1969). A low seed set due to water stress during floral development has also been reported for other seed crops (Aspinal et al 1964, Langer and Ampong 1970, Moss and Downey 1971). As this type of response has a direct influence on the seed yield it can be expected to reduce the efficiency of seed production, and appears to have been the case in this study (Table 18).

The period of water deficit continued to a stage where plant height had reached a maximum in well watered plants, therefore in stressed plants the inhibition of increase in plant height was not reversed

On stress relief (Fig 12). As leaf area was near a maximum at the start of the stress, the reduction in green leaf area was largely the result of leaf senescence rather than an inhibition of leaf enlargement. This is apparent from Figs 13 and 14 which show an irreversible decline in leaf number and area toward maturity. As the largest leaves on the plant are near the stem base, and these senesced first under stress, it is possible that some development of upper leaves occurred while the green leaf area per plant was declining. Yellowing of leaves declined after stress relief as indicated by a fall from 50% to 25% during flowering of the proportion of green leaf yellowing. Nevertheless, leaf senescence was more severe at this stage of growth than during floral initiation and probably contributed to a reduction in assimilate supply resulting in reduced seed yield. This response appears similar to that found by Urie et al (1968) in defoliation studies with safflower, where leaf removal was most critical to yield during this stage of inflorescence development.

The floral bracts which normally grow most rapidly at this stage of growth were severely restricted in size but showed no signs of senescence. Work by Aslamy (1972) suggests that development of floral bracts is particularly important to the safflower plant. They are very active photosynthetically from flowering onwards. The inhibition of bract area expansion during floral development would limit the assimilatory surface available particularly where leaf senescence has also occurred. The smaller bract size of the water stressed plants therefore probably contributed to the reduction in seed yield that resulted.

4.3.3 Water Stress during flowering (T_3)

In contrast to the severe reduction in seed yield due to water stress during floral development, stress sover the flowering period caused no significant reduction in seed yield. The number of heads and potential number of seeds in each had been determined before flowering therefore these components were not a source of yield reduction. A low seed number was not involved, since there were more seeds per head in these plants than in those stressed at other stages of growth (Table 6). The significant stress effect was a lower seed weight. The most severe reduction in seed weight occurred in seed from secondary heads (Table 10).

As the process of flowering in safflower is sequential in nature, the flowering period also includes the phase of rapid seed development immediately after anthesis, and appears to be the main reason for the reduction in final seed weight due to water stress at this stage of growth. Much of the initial increase in seed weight is due to development of the seed hull. By the stage of 95% flower fade, seed from primary heads of all plants consisted of more than 80% hull (Table 14). The lower weight of seed from plants stressed during the flowering period is thus largely due to a low hull weight. By restricting growth of the hull(most rapidly developing seed component) during the period of water deficit, further hull development on stress relief was restricted. In contrast, the kernel weight increased toward maturity and was comparable with that of well watered plants at the final harvest (Fig 19). These responses led to seed of higher percentage kernel and lower hull content.

Water stress over the flowering period had little influence on the increase in dry weight of most plant organs that had reached mature size. This included dry weight of stem, head and bracts. However a large increase in dead matter resulted due to enhanced leaf senescence as evidenced by a rapid decline in green leaf area, and more so after 95% flower fade, leaf number (Figs 13 and 14). This was associated with a decrease in green leaf dry weight (Fig 6). The greater reduction in dry weight of stems and flower heads of these plants than well watered ones may have been partly in response to the loss of green leaf material during the period of stress. Urie et al (1968) has found that seed weight in safflower is reduced most by leaf removal at the late bud and early flowering stages. As T_3 involved the early flowering stage, the enhanced senescence of leaves may have resulted in lower seed weight due to similar mechanisms involved in defoliation at this stage of growth. The defoliation studies also show that decrease in seed weight due to defoliation at flowering is directly related to a decrease in hull content. The results are similar to those found in this study, where leaf senescence was rapid due to water stress at flowering. Although seed weight was depressed, seed yield was little affected since the number of heads per plant and number of seeds per head accounted for most of the variation in yield. As indicated by the findings of Urie et al (1968) and Aslamy (1972) the floral bracts appear to have played an important role in maintaining seed development, compensating for the severe loss of green leaf material.

4.3.4. Water stress during secondary head flowering (T_4)

The primary head tended to be less vulnerable to stress effects than

secondary heads. This may be due to components of the primary head having a lower relative growth rate than those of secondary heads at this stage of growth. In other studies (Williams and Shapter 1955, Aspinall et al 1964) it has been reported that when water is limited, organs growing most rapidly suffer the greatest check to growth. As would be expected from the results of T_3, the significant effect of water stress during secondary head flowering was lower seed weight (Table 10). A similar response pattern in T_4 to that resulting from stress over the whole flowering period (T_3) occurred for the proportions of hull and kernel in the seed (Table 12).

Water stress at this stage of growth (T_4) was designed to affect both seed set in the secondary heads, and seed weight increase in the primary head, since both processes would be occurring at the same stage of growth. The yeild of both primary and secondary heads was influenced by effects on both seed set and seed weight.

A response to water stress common to both treatments 3 and 4 was the tendency for a high number of seeds per head not found in plants water stressed at other stages of growth or in well watered plants. Overall variation in seed number per head is due to differences in the potential number of seed sites and the proportion of these that are filled. In T_1 where the potential number of seeds per head were low and percentage seed set tended to be high, both traits were important in determining seed number per head. Water stress during the flowering period did not influence the potential number of seeds per head, thus the percentage seed set was most important in determining the number of

seeds per head. The close association in T_3 and T_4 of a high seed number per head with a high percentage seed set (Table 8) suggests that under the environmental conditions of this experiment, water stress during the flowering period tended to increase seed set thereby increasing the number of seeds per head. A similar response has been reported in wheat and pepper plants (Campbell et al 1969, Kaufmann 1972).

The fertilization process of safflower is severely impaired by high humidity, and has been affected at levels lower than those used in this study (Zimmerman 1972b). Therefore any changes in plant water relations or the immediate environment around the reproductive parts of the plant that might reduce the effects of high humidity may also allow an increase in seed set. The stress effect on seed set was similar for both T_3 and T_4 (Table 8). If the fertilization process only was impaired, then it would be expected that the primary head from T_4 would not be affected. However the results indicate that the primary head from T_4 was affected similarly to that from T_3 (Tables 6 and 8). There is the possibility that rapid leaf senescence during the period of water deficit may have increased the flow of metabolites to sites of fertilization. Slatyer has reported that an early change associated with leaf senescence is the movement of nitrogen from the senescing leaf toward meristematic regions. An increase in the supply of carbohydrates or nutrients may increase seed set, since a reduction in the availability of either can lead to a reduction in seed number (Slayter 1969).

Apart from the increase in dead matter due to leaf senescence, there were insignificant changes in dry weight of plant organs during this period of stress. Thereafter however significant reductions in the dry weight of stem, heads and green leaf (but not bracts) resulted (Fig 7). This may have been in response to the premature onset of rapid leaf senescence. Despite the shorter period of stress involved, water stress at this stage of development resulted in green leaf area per plant as low as that for T_3 and T_5 by the final harvest.

4.3.5 Water Stress during the post flowering period (T_5)

Water stress during the post flowering period had no significant effect on seed yield per plant, and in contrast to stress at earlier stages of growth, had negligible influence on any of the direct components of seed yield. This is in contrast to the large reduction in yield found by Seydlitz (1962). However others (Stern and Beech 1965, Erie and French 1969, Abel 1976b) have shown that water stress after flowering does not necessarily decrease yields. Nevertheless stress effects on indirect components of yield appear to have influenced seed quality.

The plant response at this stage of growth was characterised by a reduction in the dry weight of plant organs that was greater than in well watered plants. The reduction in dry weight of secondary head stem, flower heads and leaf were particularly severe whereas that of the floral bracts was more moderate (Fig 8). At final harvest plants from T_5 had accumulated a large amount of dead matter as a result of extensive and rapid leaf senescence. Of the green leaf area that

remained, virtually all of it was yellowing whereas for that of well watered plants in the process of natural senescence, about half was yellowing. The rapid rate of senescence may have influenced the amount and type of metabolites reaching the seed, thereby altering seed quality. This type of response to water stress has been suggested by Wardlaw (1971) in studies with wheat.

The hull weight of the T_5 seed was greater than for plants stressed during the flowering period since much of the hull had developed before the treatment was imposed. Increase in hull weight must be restricted to a certain extent by water stress after flowering since well watered plants tended to have a greater seed hull weight than those from T_5. Studies that have associated high hull content with excessive rain or high humitidy after flowering (McGregor and Hay 1952, Weiss 1971) suggest that seed quality could deteriorate if excessive water is present during seed maturation. Water stress during the flowering period increased percentage kernel in the seed largely by restricting an increase in hull weight. A higher kernel weight may have also contributed to the high percentage kernel in the seed of plants stressed in the post flowering period. During the post flowering period it appears that proportionately more hull than kernel accumulated in the seeds of well watered plants. The seed of water stressed plants tended to accumulate relatively more kernel than hull. Therefore by final harvest seeds from the water stressed plants had a greater percentage kernel and a lower hull weight than those from well watered plants. These differences suggest that water deficit at this stage of growth may have resulted in an increased flow of assimilates from other plant parts into the kernel of the seed, since there was a reduction in the

dry weight of plant organs to a greater extent than in well watered plants. As with water stress during the flowering period, the degree of leaf senescence was of such an extent that the bracts enclosing the seeds in the head became a large proportion of the remaining photosynthetically active surface area. As a result of the large loss in green leaf area the bracts may have played an important role in maintaining assimilate supply to the seed, during this stage of seed development.

Seed from plants stressed after flowering had a relatively high percentage oil in the kernel and in combination with a high percentage kernel, resulted in having the highest seed oil content. Well watered plants also had a high percentage oil in the kernel but this was offset by the high seed hull content which limited the percentage oil in the seed.

4.4 Effects of Water Stress on the Sequentially Developing Traits of seed yield

Over all treatments, 95% of the variation in seed yield per plant was determined by the sequentially developing traits heads per plant, seeds per head and seed weight (Table 11). However differences in yield may not be as marked as those for its components because of mutual compensation of the components (Ashrie et al 1974). It may therefore be useful to consider the effects of water stress on trait development when the traits of seed yield are transformed into directly comparable units. The effects of water stress at different stages of growth on the sequential development of traits are compared in Fig 21. The original units of the traits (x_1 = heads/plant, x_2 = seeds/head, x_3 = seed weight) were placed on the same scale by transformation to plus

and minus deviations with a mean of 0 and a variance of 1 by the formula: -

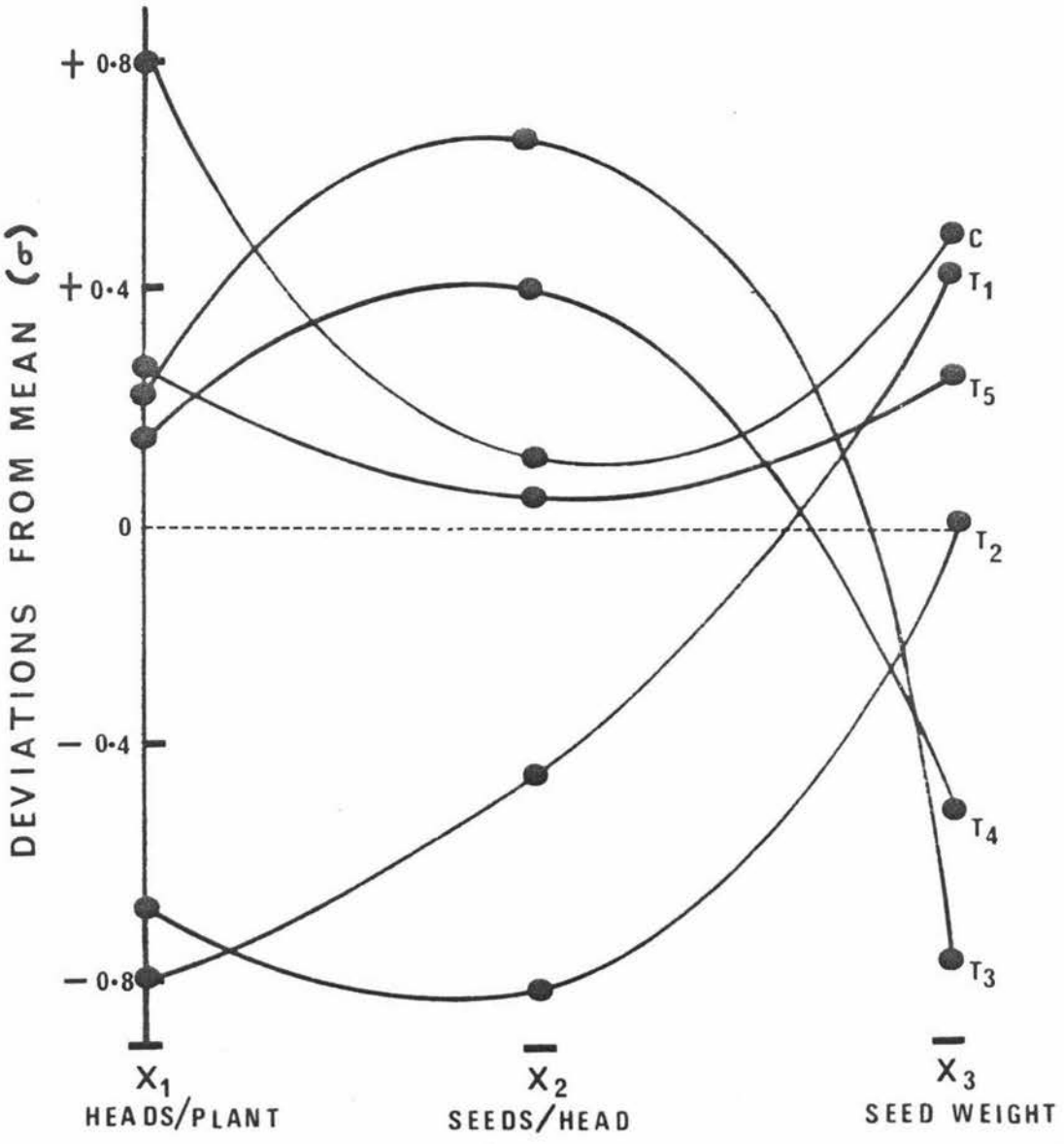
$$x_1 = \frac{(\text{Log } X_1) - P_1}{r_1}$$

Where P_1 and r_1 denote, respectively, the sample mean and standard deviation of log X_1 (Driscoll and Abel 1976).

The negative deviations for each trait are closely associated with water stress at the stage of growth in which each trait was developing. Therefore the trait heads per plant which was determined between floral initiation and flowering suffered the greatest reduction due to stress at this stage of growth (T_1 and T_2). Increase in seed weight was most rapid during the flowering period therefore it was limited to the greatest extent by water stress at that stage (T_3 and T_4). These comparisons emphasise the need for environmental resources to be available at the appropriate stages of development.

The effect of water stress on seed yield was thus dependent on the stage of growth, because this determined which traits would be restricted. Figure 21 shows that plants from T_1 had a high seed weight whereas plants from T_3 had low seed weight. As plants from T_3 had a higher seed yield than those from T_1 is appears that seed weight has relatively little influence on seed yield. On the other hand, plants from treatments with positive deviations for heads per plant (T_3, T_4, T_5, C) had higher seed yield than those with negative deviations for this trait (T_1 and T_2). A close relationship between seed yield per plant and the number of seeds per head indicates that changes in seed

Figure 21 Comparison of sequentially developing traits in standardised form



number per head were also an important determinant of seed yield. This relationship is supported by the multiple regression of yield onto the yield components.

Water stress during and after flowering thus had little effect on seed yield because a reduction in seed weight was relatively unimportant. However the large effect on seed yield due to a change in head number per plant contributes greatly to the greater sensitivity of seed yield to water stress between floral initiation and flowering. A low seed number per head in plants from T_2 on the one hand, and a high value for plants stressed during flowering on the other emphasises the strong effect this trait had on seed yield.

4.5 Implications to Agricultural Production

The traits of seed yield in safflower develop sequentially but differ in the extent to which they can influence total seed yield, therefore the effects of water stress on seed yield of safflower are particularly dependant on the stage of growth. High seed yields are especially dependant on the availability of adequate water between floral initiation and flowering because seed yield is reduced most due to water stress at this stage of growth. Crops which are sown late will have more risk of being affected by drought, therefore provided safflower is planted early, the critical stage of inflorescence development will usually occur under more favourable moisture conditions. If the cropping rotation or a factor of the environment such as low temperature does not permit early planting, then irrigation during this stage of growth should be considered under dry conditions to prevent depression of seed yields.

Water stress after flowering improved seed quality without significantly reducing seed yield, by reducing the seed hull content compared with plants kept well watered. In humid conditions or where the seed is maturing late in the season and subject to autumn rain, the seed may develop a high hull content which is undesirable. Early establishment may therefore improve seed quality by avoiding wet conditions during seed ripening, without risk of large yield reductions due to drought after flowering. Safflower may be suited to areas with dry late summer/autumn periods, provided temperatures are warm enough for early planting and moisture adequate during inflorescence development.

As the plants were grown in containers the root system was restricted. Nevertheless seed yield was resistant to water stress during the later stages of development. This indicates that safflower may not necessarily entirely depend on an extensive root system for its independence of late season rainfall as suggested by Weiss (1971). The floral bracts are probably important organs under stress conditions due to the large loss of green leaf through enhanced senescence. Should a physiological basis for drought resistance be determined in safflower, genetic material from the world collection could be utilized to improve safflower yields under dry conditions.

EFFECTS OF WATER STRESS ON PLANT GROWTH (1)

Plate 1. Treatment 1 compared with control
56 days from sowing

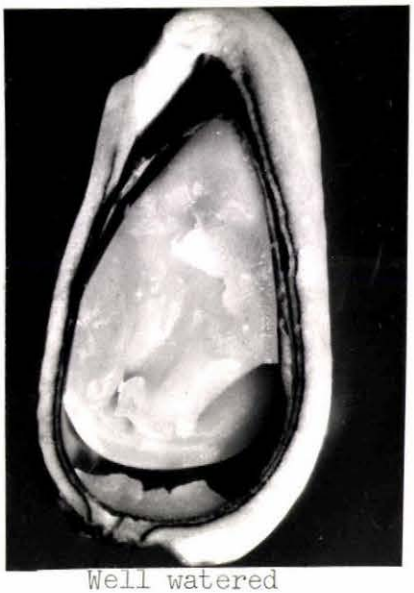
EFFECTS OF WATER STRESS ON PLANT GROWTH (2)

Plate 2. Leaf senescence and earlier flowering in T_2. 78 days from sowing

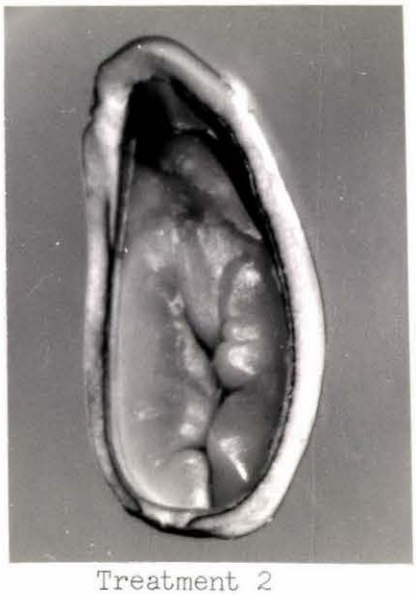
EFFECTS OF WATER STRESS ON PLANT GROWTH (3)

Plate 3. 88 days from sowing. From left to right the plants are, respectively, well watered, T_4, T_3. Lower leaves are green for well watered, yellow for T_4, yellow and brown for T_3 plants.

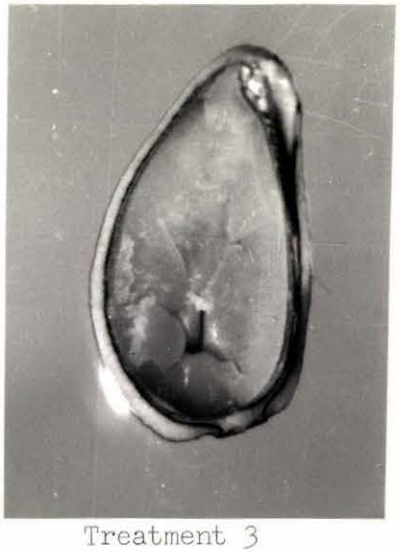
EFFECTS OF WATER STRESS ON SEED DEVELOPMENT



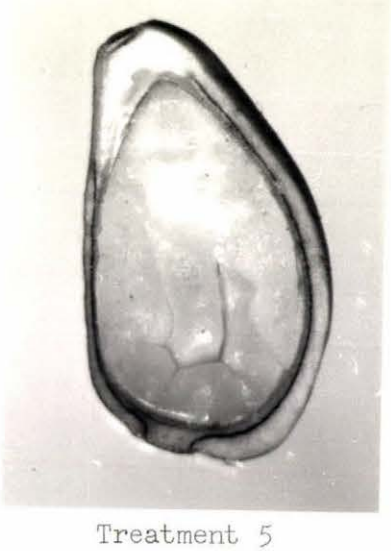
Well watered



Treatment 2

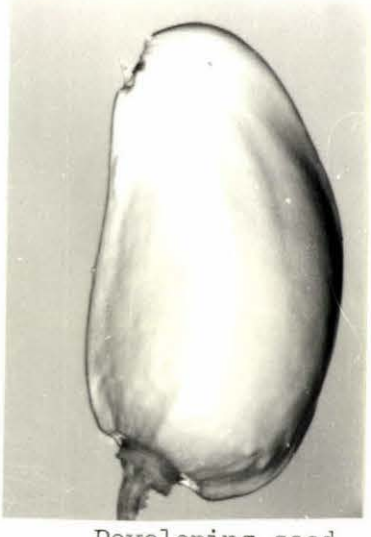


Treatment 3



Treatment 5

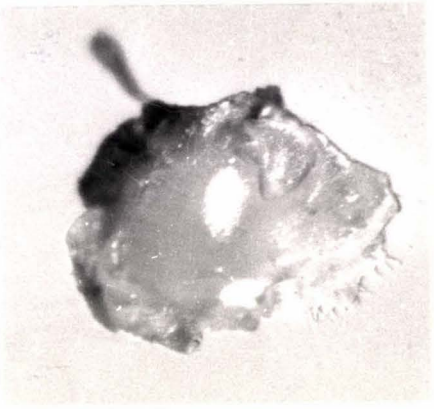
Non-developing seed
Treatment 5



Developing seed
Treatment 5

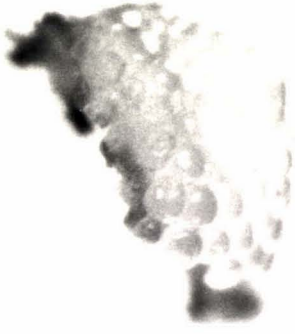
DIFFERENT STAGES OF APICAL DEVELOPMENT IN SAFFLOWER

Vegetative apex. Side view

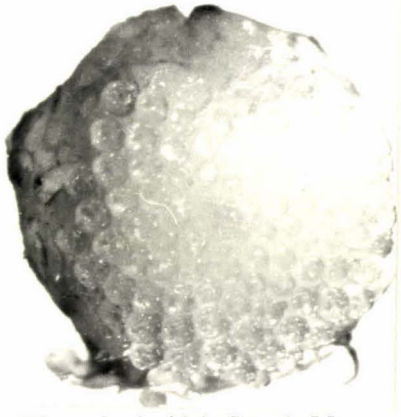


Vegetative apex
Top view

Early stage of floral initiation
Top view. (T_1)



Floral initiation almost
complete. Side view. (T_1)



Floral initials fully
formed. Top view (T_1)

DIFFERENT STAGES OF INFLORESCENCE DEVELOPMENT IN SAFFLOWER

Florets developing within enclosing involucral bracts (T_2)

Flower stage. (T_3, T_4)

Post flowering stage (T5). Non-developing seed at far left, middle and far right

STATISTICAL ANALYSES

Summaries of the statistical analyses are presented for the transformed data. All analyses were made after transforming to logs. The analyses for dry weight and seed yield were made using log (number + 1) to avoid negative logarithms. The time of harvest is shown in brackets after each harvest number, in mean number of days from sowing. For the statistical notation, values having the same letters are not significantly different at the 5% and 1% levels for small and capital letters respectively.

ANALYSES OF VARIANCE OF MEAN DRY WEIGHT PER PLANT

	HARVEST 2 (53)		HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	1	3.344	2	1.469	4	0.517	5	0.681
WITHIN GROUPS	8	0.089	12	0.109	20	0.058	54	0.056
TOTAL	9		14		24		59	

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

GROUP								
T1	0.691	b B	0.988	b B	1.850	b B	1.761	d C
T2			1.897	a A	2.096	b B	2.021	c BC
T3					2.454	a A	2.309	ab A
T4					2.583	a A	2.238	b AB
T5							2.308	ab A
C	1.848	a A	1.954	a A	2.558	a A	2.502	a A

ANALYSES OF VARIANCE OF MEAN TOTAL STEM DRY WEIGHT PER PLANT

	HARVEST 2 (53)		HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	1	1.958	2	1.167	4	0.438	5	0.579
WITHIN GROUPS	8	0.065	12	0.061	20	0.042	54	0.048
TOTAL	9		14		24		59	

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

GROUP								
T1	0.672	b	B	0.669	b	B	1.142	b C	0.900	c C
T2				1.429	a	A	1.402	b BC	1.324	b B
T3							1.708	a AB	1.454	ab AB
T4							1.808	a A	1.378	b AB
T5									1.458	ab AB
C	1.557	a	A	1.566	a	A	1.822	a A	1.602	a A

ANALYSES OF VARIANCE OF MEAN PRIMARY STEM DRY WEIGHT PER PLANT

	HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	2	1.038	4	0.348	5	0.479
WITHIN GROUPS	12	0.058	20	0.035	54	0.041
TOTAL	14		24		59	

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION					
T1	0.648	b	B	1.077	c	C	0.854	c	B
T2	1.361	a	A	1.331	b	BC	1.262	b	A
T3				1.578	a	AB	1.348	ab	A
T4				1.665	a	AB	1.274	b	A
T5							1.372	ab	A
C	1.495	a	A	1.704	a	A	1.493	a	A

ANALYSES OF VARIANCE OF MEAN SECONDARY HEAD STEM DRY WEIGHT PER PLANT

	HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	2	0.096	4	0.165	5	0.130
WITHIN GROUPS	12	0.010	20	0.022	54	0.019
TOTAL	14		24		59	

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION					
T1	0.037	b	B	0.191	b	C	0.110	d	C
T2	0.252	a	A	0.249	b	BC	0.207	cd	BC
T3				0.513	a	AB	0.360	ab	AB
T4				0.590	a	A	0.334	ab	AB
T5							0.286	bc	AB
C	0.295	a	A	0.532	a	A	0.439	a	A

ANALYSES OF VARIANCE OF MEAN LEAF DRY WEIGHT PER PLANT

	HARVEST 2 (53)		HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m,s.	df	m.s.
BETWEEN GROUPS	1	1.032	2	0.352	4	0.122	5	0.414
WITHIN GROUPS	8	0.025	12	0.041	20	0.036	54	0.055
TOTAL	9		14		24		59	

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

GROUP									
T1	0.480	b	B	0.413	b	B	0.713	ab	
T2				0.747	a	AB	0.549	bc	
T3							0.445	c	
T4							0.552	bc	
T5									
C	1.122	a	A	0.936	a	A	0.840	a	

T1	0.500	a	A						
T2	0.208	b	B						
T3	0.152	b	B						
T4	0.044	b	B						
T5	0.175	b	B						
C	0.547	a	A						

ANALYSES OF VARIANCE OF MEAN TOTAL HEAD DRY WEIGHT PER PLANT

	HARVEST 2 (53)		HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	1	0.270	2	0.285	4	0.246	5	0.273
WITHIN GROUPS	8	0.005	12	0.025	20	0.029	54	0.024
TOTAL	9		14		24		59	

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

GROUP								
T1	0.114	b	B	0.561	c	B	1.076	c	C	0.848	d	C
T2				1.039	a	A	1.263	bc	BC	1.045	c	B
T3							1.561	a	AB	1.169	bc	AB
T4							1.602	a	A	1.141	bc	B
T5										1.197	b	AB
C	0.443	a	A	0.806	b	AB	1.478	ab	AB	1.339	a	A

ANALYSES OF VARIANCE OF MEAN PRIMARY HEAD DRY WEIGHT

	HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	2	0.101	4	0.034	5	0.067
WITHIN GROUPS	12	0.053	20	0.005	54	0.007
TOTAL	14		24		59	

GROUPS	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION					
T1	0.379	n.s.	0.485	c	C	0.264 b B
T2	0.646	[illegible]	0.535	bc	BC	0.434 b B
T3			0.641	a	AB	0.456 b B
T4			0.621	ab	AB	0.452 b B
T5						0.461 b B
C	0.429		0.686	a	A	0.492 a A

ANALYSES OF VARIANCE OF MEAN SECONDARY HEAD DRY WEIGHT PER PLANT

	HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	2	0.340	4	0.276	5	0.199
WITHIN GROUPS	12	0.021	20	0.035	54	0.028
TOTAL	14		24		59	

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

GROUPS						
T1	0.262	c	B	0.834	c	C	0.698	d	C
T2	0.783	a	A	1.041	bc	BC	0.832	cd	BC
T3				1.348	a	AB	0.970	abc	AB
T4				1.407	a	A	0.938	bc	AB
T5							0.991	ab	AB
C	0.533	b	AB	1.224	ab	AB	1.105	a	A

ANALYSES OF VARIANCE OF MEAN TOTAL BRACT DRY WEIGHT PER PLANT

	HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	2	0.083	4	0.080	5	0.101
WITHIN GROUPS	12	0.006	20	0.014	54	0.010
TOTAL	14		24		59	

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION		
T1	0.138 b B	0.290 b BC	0.198 b B
T2	0.219 b B	0.279 b C	0.223 b B
T3		0.493 a AB	0.405 a A
T4		0.556 a A	0.369 a A
T5			0.385 a A
C	0.390 a A	0.477 a ABC	0.437 a A

ANALYSES OF VARIANCE OF MEAN PRIMARY HEAD BRACT DRY WEIGHT

	HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	2	0.013	4	0.007	5	0.014
WITHIN GROUPS	12	0.001	20	0.002	54	0.002
TOTAL	14		24		59	

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION					
T1	0.079	b	B	0.106	c	B	0.062	b	C
T2	0.085	b	B	0.135	bc	AB	0.095	b	BC
T3				0.179	ab	A	0.148	a	A
T4				0.192	a	A	0.133	a	AB
T5							0.149	a	A
C	0.170	a	A	0.191	a	A	0.152	a	A

ANALYSES OF VARIANCE OF MEAN SECONDARY HEAD BRACT DRY WEIGHT PER PLANT

	HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	2	0.045	4	0.059	5	0.057
WITHIN GROUPS	12	0.003	20	0.011	54	0.007
TOTAL	14		24		59	

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION					
T1	0.065	b	B	0.207	bc	BC	0.144	b	B
T2	0.146	b	AB	0.172	c	C	0.140	b	B
T3				0.366	a	AB	0.294	a	A
T4				0.428	a	A	0.267	a	A
T5							0.265	a	A
C	0.253	a	A	0.338	ab	ABC	0.311	a	A

ANALYSES OF VARIANCE OF MEAN DEAD MATTER DRY WEIGHT PER PLANT

	HARVEST 2 (53)		HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	1	0.195	2	0.126	4	0.339	5	0.393
WITHIN GROUPS	8	0.000	12	0.004	20	0.023	54	0.039
TOTAL	9		14		24		59	

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

GROUP								
T1	0.279	a	A	0.166	b	B	0.131 d C	0.302 c B
T2				0.318	a	A	0.556 bc AB	0.744 ab A
T3							0.796 a A	0.788 ab A
T4							0.697 ab A	0.812 ab A
T5								0.819 a A
C	0.000	b	B	0.000	c	C	0.415 c B	0.640 b A

ANALYSES OF VARIANCE OF MEAN PLANT HEIGHT

	HARVEST 2 (53)		HARVEST 2b (64)		HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	1	0.626	2	0.729	2	0.262	4	0.097	5	0.191
WITHIN GROUPS	8	0.007	57	0.009	12	0.005	20	0.013	54	0.009
TOTAL	9		59		14		24		59	

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

GROUP														
T1	3.736	b	B	3.973	c	C	3.927	c	C	4.079	b	C	3.955	c	C
T2				4.194	b	B	4.171	b	B	4.188	b	BC	4.198	b	B
T3										4.355	a	AB	4.327	a	A
T4										4.400	a	A	4.291	ab	A
T5													4.264	ab	AB
C	4.236	a	A	4.353	a	A	4.385	a	A	4.390	a	AB	4.299	ab	A

ANALYSES OF VARIANCE OF MEAN GREEN LEAF NUMBER PER PLANT

	HARVEST 2 (53)		HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	1	1.316	2	0.867	4	0.025	5	10.019
WITHIN GROUPS	8	0.015	12	0.049	20	0.065	54	1.605
TOTAL	9		14		24		59	

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION			
T1	3.232 b B	3.060 b B	3.622 n.s.	2.395 a AB
T2		3.716 a A	3.537	2.402 a AB
T3			3.512	0.980 b BC
T4			3.613	0.842 b C
T5				1.246 b BC
C	3.957 a A	3.833 a A	3.688	3.357 a A

ANALYSES OF VARIANCE OF MEAN GREEN LEAF AREA PER PLANT

	HARVEST 2 (53)		HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	1	3.852	2	1.703	4	0.554	5	19.349
WITHIN GROUPS	8	0.059	12	0.173	20	0.173	54	2.443
TOTAL	9		14		24		59	

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION								
T1	4.429	b	B	4.259	b	B	4.770	ab	N.S	3.622	ab	A
T2				5.011	a	AB	4.493	b		2.835	bc	AB
T3							4.244	b		1.286	d	BC
T4							4.570	b		0.952	d	C
T5										1.641	cd	BC
C	5.670	a	A	5.408	a	A	5.133	a		4.424	a	A

ANALYSES OF VARIANCE OF MEAN BRACT AREA PER HEAD

	HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	2	1.045	4	0.530	5	0.971
WITHIN GROUPS	12	0.106	20	0.129	54	0.101
TOTAL	14		24		59	

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION					
T1	1.818	b	B	1.968	b	1.599 c C
T2	1.608	b	B	1.993	b	1.970 b BC
T3				2.556	a	2.385 a A
T4				2.580	a	2.323 a AB
T5						2.287 a AB
C	2.483	a	A	2.588	a	2.363 a A

ANALYSES OF VARIANCE OF MEAN BRACT AREA PER PRIMARY HEAD

	HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	2	1.063	4	0.624	5	2.567
WITHIN GROUPS	12	0.118	20	0.112	54	0.250
TOTAL	14		24		59	

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION					
T1	2.012	b	B	2.223	b	B	1.376	b	B
T2	2.026	b	B	2.426	b	AB	2.267	a	A
T3				2.923	a	A	2.655	a	A
T4				3.003	a	A	2.583	a	A
T5							2.621	a	A
C	2.818	a	A	2.933	a	A	2.679	a	A

ANALYSES OF VARIANCE OF MEAN BRACT AREA PER SECONDARY HEAD

	HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	2	1.151	4	0.687	5	0.770
WITHIN GROUPS	12	0.121	20	0.096	54	0.086
TOTAL	14		24		59	

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION		
T1	1.625 b B	1.936 b B	1.608 b B
T2	1.427 b B	1.860 b B	1.804 b B
T3		2.546 a A	2.277 a A
T4		2.594 a A	2.224 a A
T5			2.163 a A
C	2.339 a A	2.575 a A	2.235 a A

ANALYSES OF VARIANCE OF MEAN VISIBLE BUD NUMBER PER PLANT

	HARVEST 2 (53)		HARVEST 2b (64)		HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	1	1.257	2	2.007	2	0.255	4	0.040	5	0.193
WITHIN GROUPS	8	0.048	57	0.074	12	0.059	20	0.045	54	0.066
TOTAL	9		59		14		24		59	

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

GROUP										
T1	1.455	b B	1.313	b B	1.329	b N.S.	1.588	n.s.	1.477	b N.S.
T2			1.788	a A	1.781	a	1.726		1.704	a b
T3							1.813		1.705	a b
T4							1.772		1.711	a
T5									1.716	a
C	2.164	a A	1.914	a A	1.553	ab	1.786		1.915	a

ANALYSES OF VARIANCE OF MEAN DEVELOPING HEAD NUMBER PER PLANT

	HARVEST 2 (53)		HARVEST 2b (64)		HARVEST 3 (75)		HARVEST 4 (95)		HARVEST 5 (114)	
SOURCE	df	m.s.	df	m.s.	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	1	1.049	2	2.550	2	0.704	4	0.062	5	0.175
WITHIN GROUPS	8	0.044	57	0.082	12	0.049	20	0.020	54	0.035
TOTAL	9		59		14		24		59	

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

GROUP														
T1	1.214	b	B	0.821	c	B	0.855	b	B	1.258	b	N.S.	1.214	b	C
T2				1.061	b	B	1.512	a	A	1.386	ab		1.243	b	BC
T3										1.476	a		1.431	a	ABC
T4										1.557	a		1.420	a	ABC
T5													1.449	a	AB
C	1.862	a	A	1.523	a	A	1.498	a	A	1.386	ab		1.559	a	A

ANALYSES OF VARIANCE OF MEAN DAYS TO FLOWER, DAYS TO 95% FLOWERFADE, DAYS TO HARVEST, DURATION OF FLOWERING AND DURATION OF FLOWERING PERIOD PER HEAD.

	DAYS TO FLOWERING		DAYS TO 95% FLOWERFADE		DAYS TO HARVEST		DURATION OF FLOWERING		DURATION PER HEAD	
SOURCE	df	m.s.	df	m.s.	df	m.s.	df	m.s.	df	m.s.
BETWEEN GROUPS	5	0.008	5	0.006	5	0.004	5	0.018	5	0.098
WITHIN GROUPS	113	0.002	79	0.002	54	0.001	79	0.051	79	0.049
TOTAL	118		84		59		84		84	

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION									
T1	4.394	ab	A	4.562	b	AB	4.739	bc AB	2.638 n.s.	1.392 n.s.
T2	4.350	c	B	4.528	c	B	4.709	c B	2.674	1.386
T3	4.388	ab	A	4.555	bc	AB	4.739	bc AB	2,674	1.234
T4	4.374	bc	AB	4.551	bc	B	4.732	bc AB	2.715	1.251
T5	4.395	ab	A	4.551	bc	AB	4.743	ab AB	2.637	1.213
C	4.407	a	A	4.591	a	A	4.770	a A	2.721	1.223

ANALYSES OF VARIANCE OF MEAN SEED YIELD PER PLANT AND PER HEAD

SOURCE	df	MEAN SQUARES: SEED YIELD PER PLANT	SEED YIELD PER PRIMARY HEAD	SEED YIELD PER PLANT FROM SECONDARY HEADS
BETWEEN GROUPS	5	0.446	0.101	0.296
WITHIN GROUPS	54	0.057	0.050	0.109
TOTAL	59			

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION							
T1	1.009	b	BC	0.337	N.S.	1.001	a	N.S.
T2	0.866	b	C	0.312		0.687	b	
T3	1.344	a	A	0.559		1.069	a	
T4	1.267	a	AB	0.520		1.041	a	
T5	1.262	a	AB	0.479		1.048	a	
C	1.415	a	A	0.483		1.204	a	

ANALYSES OF VARIANCE OF MEAN POTENTIAL SEED NUMBER PER HEAD

MEAN SQUARES

SOURCE	df	MEAN POTENTIAL SEED NUMBER PER HEAD	POTENTIAL SEED NUMBER PER PRIMARY HEAD	POTENTIAL SEED NUMBER PER SECONDARY HEAD
BETWEEN GROUPS	5	0.372	2.985	0.342
WITHIN GROUPS	54	0.028	0.483	0.042

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

GROUP								
T1	3.204	b	B	2.399	b	B	3.218	c	B
T2	3.576	a	A	3.673	a	A	3.531	b	A
T3	3.643	a	A	3.691	a	A	3.627	ab	A
T4	3.601	a	A	3.715	a	A	3.551	ab	A
T5	3.724	a	A	3.782	a	A	3.702	ab	A
C	3.719	a	A	3.798	a	A	3.730	a	A

ANALYSES OF VARIANCE OF MEAN NUMBER OF HEADS PER PLANT

SOURCE	df	MEAN SQUARES: TOTAL NUMBER OF HEADS PER PLANT	NUMBER OF SECONDARY HEADS PER PLANT
BETWEEN GROUPS	5	0.175	0.168
WITHIN GROUPS	54	0.035	0.043
TOTAL	59		

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

Group					
T1	1.214	b	C	0.977	bc	BC
T2	1.243	b	BC	0.896	c	C
T3	1.431	a	ABC	1.156	ab	ABC
T4	1.420	a	ABC	1.138	ab	ABC
T5	1.449	a	AB	1.156	ab	AB
C	1.559	a	A	1.240	a	A

ANALYSES OF VARIANCE OF MEAN SEED NUMBER PER HEAD

MEAN SQUARES

SOURCE	df	MEAN SEED NUMBER PER HEAD	SEED NUMBER PER PRIMARY HEAD	df	SEED NUMBER PER SECONDARY HEAD
BETWEEN GROUPS	5	0.619	1.678	5	2.316
WITHIN GROUPS	54	0.180	0.906	178	0.617
TOTAL	59			183	

MEANS AND STATISTICAL NOTATIONS FOR MEAN SEPARATION

GROUP						
T1	2.183	bc	AB	1.514 N.S.	2.028	bc AB
T2	2.009	c	B	1.531	1.823	c B
T3	2.686	a	A	2.510	2.557	a A
T4	2.571	a	A	2.353	2.538	a A
T5	2.405	ab	AB	1.999	2.305	ab AB
C	2.428	ab	AB	1.970	2.242	ab AB

ANALYSES OF VARIANCE OF MEAN POTENTIAL SEED NUMBER PER HEAD FOR HARVESTS 4 AND 5 COMBINED

		MEAN POTENTIAL SEED NUMBER PER HEAD	POTENTIAL SEED NUMBER PER PRIMARY HEAD	POTENTIAL SEED NUMBER PER SECONDARY HEAD
SOURCE	df	m.s.	m.s.	m.s.
BETWEEN GROUPS	5	0.416	2.347	0.401
WITHIN GROUPS	79	0.031	0.395	0.043
TOTAL	84			

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION		
T1	3.292 c C	2.789 b B	3.287 c C
T2	3.540 b B	3.658 a A	3.485 b BC
T3	3.643 ab AB	3.720 a A	3.616 ab AB
T4	3.670 a AB	3.756 a A	3.621 ab AB
T5	3.724 a AB	3.782 a A	3.702 a AB
C	3.751 a A	3.845 a A	3.742 a A

ANALYSES OF VARIANCE OF MEAN SEED NUMBER PER HEAD FOR HARVESTS 4 AND 5 COMBINED

		MEAN SEED NUMBER PER HEAD	SEED NUMBER PER PRIMARY HEAD	SEED NUMBER PER SECONDARY HEAD
SOURCE	df	m.s.	m.s.	m.s.
BETWEEN GROUPS	5	1.165	1.639	1.276
WITHIN GROUPS	79	0.265	0.899	0.307
TOTAL	84			

GROUPS	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION		
T1	2.248 a AB	1.593 n.s.	2.237 bc AB
T2	1.861 b B	1.560	1.878 c B
T3	2.435 a A	2.213	2.450 ab A
T4	2.612 a A	2.374	2.610 ab A
T5	2.406 a AB	2.000	2.413 ab AB
C	2.598 a A	2.084	2.686 a A

ANALYSES OF VARIANCE OF MEAN POTENTIAL SEED NUMBER PER PLANT, MEAN SEED NUMBER PER PLANT, AND MEAN PERCENTAGE SEED SET

MEAN SQUARES

SOURCE	df	POTENTIAL SEED NUMBER PER PLANT	SEED NUMBER PER PLANT	PERCENTAGE SEED SET PER PLANT
BETWEEN GROUPS	5	0.696	1.188	0.576
WITHIN GROUPS	54	0.061	0.194	0.174
TOTAL	59			

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

GROUP							
T1	4.512	c	C	3.436	b	BC	3.541	a	N.S.
T2	4.842	b	B	3.230	b	C	2.993	b	
T3	5.074	a	AB	4.099	a	A	3.631	a	
T4	5.023	ab	AB	3.985	a	A	3.567	a	
T5	5.161	a	A	3.833	a	AB	3.276	ab	
C	5.238	a	A	3.951	a	AB	3.319	ab	

ANALYSES OF VARIANCE OF MEAN SEED NUMBER PER HEAD FOR GROUPED DATA, T1 T2 T5 C VRS T3 T4

SOURCE	df	MEAN SQUARES: MEAN SEED NUMBER PER HEAD	SEED NUMBER PER PRIMARY HEAD	SEED NUMBER PER SECONDARY HEAD
BETWEEN GROUPS	1	1.846	6.124	1.635
WITHIN GROUPS	58	0.189	0.882	0.242
TOTAL	59			

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION		
T1, T2, T3, T5, C	2.256 b B	1.754 b N.S.	2.276 a N.S.
T3, T4	2.628 a A	2.431 a	2.626 b

ANALYSES OF VARIANCE OF MEAN PERCENTAGE SEED SET FOR GOUPED DATA, T1 T2 T5 C VRS T3 T4

SOURCE	df	MEAN SQUARES: PERCENTAGE SEED SET PER HEAD	PERCENTAGE SEED SET PRIMARY HEAD	PERCENTAGE SEED SET PER SECONDARY HEAD
BETWEEN GROUPS	1	1.337	7.839	1.463
WITHIN GROUPS	58	0.188	1.256	0.218
TOTAL	59			

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION		
T1,T2, T5, C	3.282 b B	2.566 b N.S.	3.312 b N.S.
T3, T4	3.599 a A	3.333 a	3.643 a

ANALYSES OF VARIANCE OF MEAN SEED NUMBER PER HEAD FOR GROUPED DATA, T1, T2 T5 C VRS T3 T4

		MEAN SQUARES		
SOURCE	df	MEAN SEED NUMBER PER HEAD	SEED NUMBER PER PRIMARY HEAD	SEED NUMBER PER SECONDARY HEAD
BETWEEN GROUPS	1	1.846	6.124	1.635
WITHIN GROUPS	58	0.189	0.882	0.242
TOTAL	59			
GROUP		MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION		
T1, T2, T3, T5, C		2.256 b B	1.754 b N.S.	2.276 a N.S.
T3, T4		2.628 a A	2.431 a	2.626 b

ANALYSES OF VARIANCE OF MEAN PERCENTAGE SEED SET FOR GROUPED DATA, T1 T2 T5 C VRS T3 T4

		MEAN SQUARES		
SOURCE	df	PERCENTAGE SEED SET PER HEAD	PERCENTAGE SEED SET PRIMARY HEAD	PERCENTAGE SEED SET PER SECONDARY HEAD
BETWEEN GROUPS	1	1.337	7.839	1.463
WITHIN GROUPS	58	0.188	1.256	0.218
TOTAL	59			
GROUP		MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION		
T1, T2, T5, C		3.282 b B	2.566 b N.S.	3.312 b N.S.
T3, T4		3.599 a A	3.333 a	3.643 a

ANALYSES OF VARIANCE OF MEAN 1000 SEED WEIGHT AT FINAL HARVEST (HARVEST 5)

SOURCE	df	MEAN SQUARES TOTAL	FOR PRIMARY HEAD SEED	FOR SECONDARY HEAD SEED
BETWEEN GROUPS	5	0.117	2.382	0.146
WITHIN GROUPS	54	0.035	1.327	0.043
TOTAL	59			

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION						
T1	4.029	a	N.S.	2.914	n.s.	4.015	a A
T2	3.935	abc		3.811		3.871	abc AB
T3	3.776	c		4.057		3.696	c B
T4	3.831	ba		4.047		3.794	bc AB
T5	3.991	ab		3.815		3.936	ab AB
C	4.037	a		4.332		3.982	a A

ANALYSES OF VARIANCE OF MEAN 1000 SEED WEIGHT AT 95 % FLOWERFADE (HARVEST 4)

		MEAN SQUARES		
SOURCE	df	TOTAL	FOR PRIMARY HEAD SEED	FOR SECONDARY HEAD SEED
BETWEEN GROUPS	4	0.158	0.624	0.189
WITHIN GROUPS	20	0.081	0.597	0.110
TOTAL	24			

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION		
T1	2.872 n.s.	3.647 n.s.	2.661 n.s.
T2	3.231	2.853	3.031
T3	3.243	3.693	3.104
T4	3.124	3.611	2.974
T5	3.124	3.611	2.974
C	2.902	3.608	2.727

ANALYSES OF VARIANCE OF MEAN 1000 SEED WEIGHT FOR SEED FROM ANALYSES OF HULL & KERNEL PROPORTIONS.

		MEAN SQUARES	
SOURCE	df	PRIMARY HEAD 1000 SEED WEIGHT	SECONDARY HEAD 1000 SEED WEIGHT
BETWEEN GROUPS	5	0.228	0.139
WITHIN GROUPS	54	0.030	0.034
TOTAL	59		

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION					
T1	4.267	a	AB	4.143	ab	A
T2	4.101	b	BC	4.064	ab	AB
T3	4.047	b	C	3.873	c	B
T4	4.014	b	C	4.015	bc	AB
T5	4.283	a	AB	4.076	ab	AB
C	4.391	a	A	4.219	a	A

ANALYSES OF VARIANCE OF MEAN 1000 SEED KERNEL WEIGHT AND MEAN 1000 SEED HULL WEIGHT

		MEAN SQUARES			
SOURCE	df	PRIMARY HEAD SEED KERNEL WEIGHT	SECONDARY HEAD SEED KERNEL WEIGHT	PRIMARY HEAD SEED HULL WEIGHT	SECONDARY HEAD SEED HULL WEIGHT
BETWEEN GROUPS	5	0.140	0.032	0.369	0.320
WITHIN GROUPS	54	0.030	0.061	0.041	0.050
TOTAL	59				

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION							
T1	3.357	ab	3.074	n.s.	3.749	b	AB	3.704 ab AB
T2	3.227	bc	3.040		3.561	cd	BC	3.613 bc AB
T3	3.234	bc	3.025		3.460	d	C	3.325 d C
T4	3.166	c	3.159		3.447	d	C	3.457 cd BC
T5	3.491	a	3.137		3.676	bc	BC	3.626 bc AB
C	3.351	ab	3.037		3.949	a	A	3.829 a A

ANALYSES OF VARIANCE OF MEAN PERCENTAGE KERNEL

SOURCE	df	PRIMARY HEAD SEED	SECONDARY HEAD SEED
BETWEEN GROUPS	5	0.079	0.162
WITHIN GROUPS	54	0.009	0.031
TOTAL	59		

GROUP	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION					
T1	3.694	c	B	3.537	cd	BC
T2	3.726	bc	AB	3.582	bc	ABC
T3	3.793	ab	AB	3.739	ab	AB
T4	3.758	abc	AB	3.750	a	AB
T5	3.813	a	A	3.666	abc	A
C	3.566	d	C	3.421	d	C

ANALYSES OF VARIANCE OF MEAN 1000 SEED WEIGHT, AND MEAN 1000 SEED HULL WEIGHT FROM PRIMARY HEAD SEED AT 95% FLOWERFADE (H_4)

		MEAN SQUARES	
SOURCE	df	1000 SEED WEIGHT	1000 SEED HULL WEIGHT
BETWEEN GROUPS	4	0.212	0.215
WITHIN GROUPS	95	0.129	0.064
TOTAL	99		

GROUPS	MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION			
T1	3.637	n.s.	3.516	a N.S.
T2	3.493		3.259	b
T3	3.424		3.364	ab
T4	3.662		3.428	a
C	3.618		3.492	a

ANALYSES OF VARIANCE OF MEAN HARVEST INDEX PER PLANT

SOURCE	df	MEAN SQUARES
BETWEEN GROUPS	%	0.284
WITHIN GROUPS	54	0.065
TOTAL	59	

MEANS AND STATISTICAL NOTATION FOR MEAN SEPARATION

GROUP			
T1	3.380	a	A
T2	2.888	b	B
T3	3.258	a	A
T4	3.294	a	A
T5	3.217	a	A
C	3.222	a	A

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