ROOT GROWTH AND CROP YIELD
OF TWO VARIETIES OF WHEAT
GROWN UNDER DIFFERING IRRIGATION REGIMES.

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ABSTRACT

Root growth and crop yield of Gamenya, a standard height variety, and Karamu, a semi-dwarf, spring wheat were compared under 3 irrigation regimes: daily watering; infrequent (fortnightly) watering; and sub-irrigation, where water was introduced into the soil profile at 40cm, the plots being protected from rainfall.

Root growth and development were similar between varieties apart from an indication that the Karamu root system was more extensive at depth. The three irrigation treatments grew distinctly different root systems which was probably due partly to soil compaction differences between the treatments rather than the spatial distribution of the soil water supply.

Karamu outyielded Gamenya because of a higher grain weight per ear due to higher floret viability and greater grain weight. Yield differences between irrigation treatments, where the infrequently irrigated treatment was superior, was due to ear population differences related to the differing root systems.

With daily irrigation Gamenya used more water, due possibly to the lower leaf water potentials developed in the crop. An inverted water potential difference between the ear and the flag leaf was observed during the middle of the day.

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CHAPTER ONE. LITERATURE REVIEW.

1.1 INTRODUCTION

This literature review is presented in three distinct parts. Firstly, methods of studying root systems will be discussed. Then, present knowledge regarding root growth and the relationships between the root system and the shoot will be reviewed. This will also include a section on aspects of the physiology of shoot growth with some discussion of the effects of moisture stress on plant growth; and because a short statured wheat variety has been used in this experiment, this part of the review will conclude with a section on the properties of semi-dwarf wheats. The third part of the review will consider briefly some aspects of water relations of plants - the movement of water from soil through the plant to the atmosphere, and the role of the root system.

All references cited will be understood to refer to wheat, barley and oats unless otherwise stated.

1.2 TECHNIQUES FOR STUDYING ROOT SYSTEMS IN THE FIELD

1.2A Sampling of Root Systems

Characterisation of root systems in the field has involved four approaches.

1. Excavation alongside the plant or crop row and direct observation of the rooting patterns of the plant or crop root system. This method was used extensively by early workers interested in the growth of roots under natural conditions. Weaver and co-workers (Weaver 1926) employed this method almost exclusively. The method is extremely laborious but it is the only sure way of determining rooting depth and hence is used occasionally nowadays for this reason.

2. Removal of Monoliths - the pin-board method (Schuurman & Goedewaagen 1965). With this method a hole is dug alongside the plant or crop row and a vertical wall is shaped beside the root system of interest. A pin-board is placed on this wall and either hammered or 'jacked' into the soil so that the pins are completely buried into the soil face. The pin-board and soil can then be cut away from the bulk soil and the soil particles washed from

the pin-board.

This method has a number of advantages over "excavation and observation". The vertical distribution remains essentially the same as in the natural situation and because a fixed volume of soil is removed, quantitative measurements of root mass and length can be made. Nevertheless because the depth of sampling is restricted by the dimensions of the pin-board it is difficult (although not impossible) to characterise the total root system down to the maximum rooting depth. As with the excavation method, use of pin-boards is an extremely laborious procedure.

3. Core Sampling - The majority of work involving field sampling of root systems in recent years has utilised various types of core sampling methods. There are two approaches to coring:

(i) short cores less than 15 cm are removed in succession down to the required depth (Schuurman & Goedewaagen 1965).

(ii) an "undisturbed" core is taken, the depth being determined by the design of the corer and the method by which it is inserted into the soil (Baker 1964). The soil core can then be sectioned into desirable lengths. The coring action can be effected either by rotary means (augering), or by driving the corer into the soil. 'Auger' type corers need machine power which is generally provided by a tractor, e.g. the auger corer of Kelley et. al. (1947). 'Driven' type corers can be hammered into relatively heavy soils with a suitable hand rammer or a small motorised vibrator as used by Welbank and Williams (1968). Thus 'driven' type corers being less cumbersome can be used in a standing crop or on small experimental plots.

Removing a "driven" corer from the soil requires the use of tractor hydraulics or some form of hoist. Ease of removal from the soil is similarly determined by the design of the corer (Baker 1964).

4. Tracer Techniques - Use of radioactive tracers for estimating root distribution has been investigated by a number of workers particularly Ellis (Russell & Ellis 1968, Ellis & Barnes 1973). This method has two advantages which other field methods cannot provide. Firstly, the contribution to the root system of the finer root members is included for these are generally lost when roots are washed from soil samples. Secondly, the dead roots and roots from morphologically similar weed species do not take up tracer, hence only living roots are estimated. Rubidium-86, an energetic gamma ray emitter, is the most suitable isotope (Ellis & Barnes 1973).

1.2B Washing Out Roots from Soil Cores

Most workers use streams of water often at high pressure to dislodge soil and remove it from the roots by washing through a screen. With this method fine root members are generally lost by being broken off the larger roots and washed through the screen.

More gentle methods are available e.g. the shaker-type washer of Fehrenbacher and Alexander (1955) or the soil elution method of Upchurch (1951).

Nevertheless in field samplings where only proportions of root systems can be removed and many samples are taken, no practical method can effectively separate all roots from the soil even if the experimenter had patience sufficient to attempt it; the finer roots which are lost in the washing out process are only a small proportion of the total mass although they would contribute a higher proportion to both total root length and total root tips or apices.

1.2C Root Length Measurement

The most common method for estimating the length of root in a sample is Newman's 'line intersection method' (Newman 1966a). An improved modification of this method has been described by Evans (1970) which removes the need to define the area over which the sample is spread.

Another method involves examination of the roots exposed on the surface of a soil block (Melhuish & Lang 1968, Lang & Melhuish 1970). Indirect determinations of length and distribution of roots within the soil block can be made by this method.

1.3 GROWTH OF CEREAL ROOT SYSTEMS

1.3.1 PHYSIOLOGICAL PRINCIPLES OF ROOT GROWTH

1.3.1 A. The Vegetative Stage

The morphological development of the cereal root system is described in Troughton (1962). In monocotyledons the primary root originating from the radicle in the embryo, and other seminal roots belonging initially to the embryo, are generally supplemented with adventitious roots that arise from the basal nodes of the stem. As growth proceeds, primordia develop in the pericycle of the main roots and give rise to first order laterals or primary laterals. The first order laterals give rise to secondary laterals and laterals of a higher order can be produced. In cereals, laterals have not been identified until division of the pericycle has begun, often 15 mm from the root apex (Hackett1972).

The overall growth of the root system or its increase in weight is determined by the availability of assimilate from the shoot in the vegetative stage with growth regulators being of minor importance (Hackett 1969, Street 1969, Hatrick & Bowling 1973, Drew et. al. 1973). The sources of this assimilate are the lower leaves on the stem (Rawson & Hofstra 1969, Ryle & Powell 1972), and, of that assimilate translocated to the root system, possibly no more than one third of the total is utilised for growth; the balance is respired (Hatrick & Bowling 1973) or exuded into the exterior medium (Barber & Gunn 1974).

The spatial development of the root system of graminaceous species is achieved "within a framework of some remarkably constant principles" (Hackett & Rose 1972). The relations between the total number, length, surface area, and volume of the root members remains approximately constant during the vegetative stage of growth. This is a finding of great significance in plant physiology, because it implies that the growth of the root system is controlled by the plant in a systematic way by a sophisticated and as yet unknown coordinating mechanism.

Root Elongation.

The root tip can be differentiated into 4 zones along the axis (Brown & Broadbent 1950, Tanton & Crowdy 1972a). The root cap is restricted to the first 0.4 mm. Within the first 1.5 mm zone the cells are all meristematic except for the cap. Behind this zone for approximately 2 to 3 mm along the axis is the elongation region and this zone also contains the first vascular connections - the protophloem (Heimsch 1951). Depending on the species and the state of development of the individual roots suberisation of the axis begins within 50 to 100 mm from the apex and the zone between the meristematic region and the area which marks the beginning of suberisation of the axis, is the major region of uptake both of ions and water (Tanton & Crowdy 1972a, Lauchli 1972). It is over this region that root hairs commonly develop (Evans 1973).

It is assumed as a first approximation that the rate of volume growth or cell extension in the zone of elongation is equal to the rate of uptake of water into the root in this zone (Greacen & Oh 1972). The resistance to water movement across the root membranes in this zone is very small and only -0.1 bar water potential difference is sufficient to drive water uptake into the cells (Greacen & Oh 1972).

For the cell to elongate the hydrostatic pressure in the vacuole must be greater than that necessary to deform the cell wall; for peas Greacen and Oh calculate that wall pressure will be equivalent to 6.0 bar at maximum elongation rates. The hydrostatic pressure necessary to cause elongation is achieved by osmoregulation; solute concentration, primarily of sugars (Brown & Sutcliffe 1950) increases to lower the osmotic potential which increases water uptake into the vacuole. This increases the hydrostatic pressure and thus extends the cell wall.

Burstrom's (1971) work has shown that active elongation occurs only in the peripheral layers of the root tip, and presumably the stele elongates by passively taking up water, filling the intercellular spaces which develop as the peripheral cells expand.

When the root is in the soil the hydrostatic pressure must also counteract the pressure applied externally from the soil which has two components:-

(i) The water potential of the soil water.

(ii) The mechanical resistance of the soil particles.

Using a penetrometer this resistance can be compared directly with the hydrostatic pressure within the cells.

A number of workers (Barley <u>et. al</u>. 1965, Taylor & Ratliff 1969, Lawlor 1973) have found that root growth is unaffected by decreasing soil water potential down to low values (e.g. -10bar in wheat, Lawlor 1973); but root growth is much more sensitive to mechanical impedance (Barley <u>et. al</u>. 1965). Greacen and Oh (1972) have shown that this is due to the action of osmoregulation in the cells themselves. They found that peas could osmoregulate with 100% efficiency down to -15bar soil matric potential i.e. decrements in soil matric potential were matched by equivalent drops in vacuolar osmotic potential. Against mechanical stress the plant's osmoregulation works at only 70% efficiency. This explains the sensitivity of root growth to mechanical impedance (Barley et. al. 1965) and the relative insensitivity of root growth to changes in soil water potential.

Thus roots proliferate in wetter zones because the mechanical resistance is low rather than because the soil water potential is high, and so at moderate levels of bulk soil water potential root growth will be determined by mechanical resistance primarily. Nevertheless roots of cereals will not penetrate soil layers where the moisture content is very low i.e. at or below permanent wilting point (Salim et. al. 1965).

Root Branching

As mentioned previously there is an apparently fixed relationship between root dimensions (Hackett 1969, 1971, 1972) implying that the extension and branching of root systems is a highly coordinated process.

In concentrations of minerals in the soil there is a localised growth response and the number of laterals and the rate of extension is markedly increased (Barley 1970). The physiological basis of this response has been investigated by Hackett (1972) and Drew et. al. (1973) - work which also sheds light on the mechanisms by which root growth is coordinated.

Concentrations of nutrients and their subsequent uptake induces a localised response on the root axis which is either a stimulation of metabolic activity (i.e. increases "sink strength") or else acts to stimulate the localised synthesis of growth regulators. In both alternatives growth regulators are involved either by being attracted to the site of lateral initiation or being synthesised locally (Drew et. al. 1973).

At present, while it is agreed that growth regulators are involved in the control of root growth the mechanisms are a subject of speculation although there is mounting information on the mechanisms of hormonal control of root growth (Street 1969).

Under conditions of mineral deficiency, metabolites appear to be conserved by minimal production of lateral roots (Drew et. al. 1973); e.g. deficiency of potassium completely inhibits the formation of secondary laterals (Hackett 1968).

1.3.1 B. The Reproductive Stage

Many workers have noted a reduction in root weight following the initiation of reproductive development (Troughton 1962). The cause is primarily due to a reduction in assimilate translocation to the root system due to increased competition for assimilates from the meristems of the shoot, particularly those in the stem internodes (Ryle & Powell 1972). During the vegetative phase root meristems receive approximately 30% of the available pool of assimilate, but in Lolium temulentum this reduces to less than 10% when the main shoot has developed an inflorescence and stem elongation begins (Ryle 1972). Assuming that two thirds of assimilate translocated to the stem before reproductive development occurs is utilised for respiration (Hatrick & Bowling 1973) it follows that maintenance of the total root system cannot be sustained on changing to reproductive growth and death of part of the root system must occur. How this senescence is distributed within the root system and whether laterals preferentially die is unknown at present.

1.3.2 DEVELOPMENT OF THE ROOT SYSTEM IN THE FIELD

The root system of cereal plants grown under favourable temperate conditions consists of two distinct systems. Of these the seminal (or primary) develops from primordia present in the embryo. The second system, the nodal (or adventitious, coronal or crown) develops from the lower nodes of the shoot and from the lower nodes of the tillers. Adventitious root formation from each tiller occurs immediately following initiation of growth of the axillary bud (Soper & Mitchell 1956, Pinthus 1969) suggesting a direct physiological connection between the two initiation processes which is probably hormonal in character (see following discussion). In most cases nodal root production is restricted to primary and secondary tillers (Rawson & Donald 1969).

During the first stages of growth the plant is entirely dependent upon the seminal roots for the absorption of water and minerals. Within 2 to 3 weeks the nodal roots begin appearing (Pinthus 1969, Schuurman & de Boer 1970). Depending on the height of the crown node, if the surface soil is dry they may fail to penetrate below the topsoil and cease growth (Boatwright & Ferguson 1967, Ferguson & Boatwright 1968, Passiora 1972), but subsequent rainfall or irrigation re-stimulates nodal root development.

Under favourable conditions both systems develop concurrently during the vegetative stage. There is no evidence to suggest that the seminal root system has any distinct physiological significance and studies by Williams (1962) and Boatwright and Ferguson (1967) show that once the plant has established a sufficient number of adventitious roots these are quite capable of supporting it and the seminal roots are then simply a part of the general root system with no specific role.

Because of this it is unnecessary to consider the separate development of the two systems particularly since interpretation of experimental results is complicated by most workers not considering adventitious root development on a per tiller basis; neither have they accounted for the effect of sequential tiller initiation and, later on, tiller death. Nevertheless in general the adventitious system increases in importance and within 5 to 7 weeks it will be the greater proportion of the total weight of the root system (Schuurman & de Boer 1970). Thus because minerals taken up in any part of the root system can be translocated throughout the plant (Williams 1962), the adventitious system assumes increasing importance to the plant for water and mineral supply as plant development progresses.

With the cessation of tillering following floral initiation and the start of the reproductive stage, root initiation stops (Pinthus 1969), although it may resume if late, post-flowering tiller production occurs (Boatwright & Ferguson 1967).

Root weight reaches a maximum prior to heading and then declines until harvest, although some workers have not observed a decline (Troughton 1962, Pinthus 1969, Schuurman & de Boer 1970).

The maximum depth is reached relatively early in the life of the plant - Schuurman and de Boer (1970) found their maximum depth of 70cm was reached by the seminal system within 4 weeks. As expected from the previous discussion concerning extension of roots the soil type is a very important determinant of the depth of rooting. In deep light soils, roots of spring cereals penetrate below 100 cm (Kirby & Rackham 1971, Troughton 1962), but in heavier soils 60 to 70 cm may be the maximum (Troughton 1962, Welbank & Williams 1968).

1.3.3 DISTRIBUTION OF THE ROOT SYSTEM

Regardless of the rooting depth the major part of the root system occurs in the upper layers of the soil (Troughton 1962). Both root weight and number decrease markedly with depth although the number does not decrease as rapidly as weight (Bloodworth <u>et</u>. <u>al</u>. 1958). Generally under favourable conditions the top 30 cm contains over half the root system while even in light soils over 90% of the root system will be within the top 100 cm (Kirby & Rackham 1971).

Lateral distribution of plant roots has not been well characterised. Weaver (1926) stated that wheat, oats and barley have a lateral spread of less than 30 cm although more recent work has shown that varietal differences are quite marked (Matheson 1971, **Subbiah** <u>et</u>. <u>al</u>. 1968, Pinthus & Eshel 1962).

The distribution of crop root systems has been shown to be affected by a number of soil characteristics. The principal ones are:-

Aeration - Very low oxygen levels (less than 1%) can cause death of root tips (Huck 1970) and it is likely that in soils of low oxygen concentration (2 - 5%) distribution of the root system may be determined by oxygen gradients particularly in conditions where soil moisture is high (Gingrich & Russell 1956).

Soil Nutrients - As noted previously roots proliferate in concentrations of nutrients and studies on fertiliser banding also show this effect (Duncan & Ohlrogge 1958). Root proliferation in topsoil is also explained by the effect of nutrients on lateral root initiation and the dense root system in the surface layers vastly improves the uptake of low mobility ions such as phosphorous (Andrews & Newman 1970).

Soil Compaction - The effect of soil mechanical resistance was noted in a previous section to be an important factor in determining root extension and hence distribution of the root system (Barley et. al. 1965). In unusually compacted soils roots may be unable to penetrate beneath the cultivation depth because they are unable to overcome the mechanical obstruction offered by the cohesion of the soil particles (Schuurman 1965). Also compaction reduces pore space and hence gaseous exchange (Gradwell 1965).

Moisture Status - Root growth is relatively insensitive to decreasing levels of soil water potential in the range down to -4 to -7 bar but below this point there is a marked reduction in most species of plants including cereals (Gingrich & Russell 1956, Newman 1966b, Taylor & Ratliff 1969). Lawlor (1973) found that growth of wheat roots stopped at -10bar. Nevertheless in some grass species roots can grow into soil below permanent wilting point provided another part of the root system is growing at a lower soil moisture tension (Salim et al. 1965); annual cereals do not demonstrate this effect, for as with flax (Newman 1966b), root growth does not appear to be influenced by water potential elsewhere in the plant.

1.3.4 VARIETAL DIFFERENCES IN ROOT GROWTH

Varietal differences within species in root dimensions occur and can be quite significant (Weaver 1926, Pinthus & Eshel 1962, Troughton & Whittington 1969), e.g. the two barley varieties Maris Badger and Procter studied by Hackett (1968), or Thatcher wheat compared to other lines grown on the Canadian Prairies (Hurd 1969); although the effect of different tiller numbers and hence adventitious root number can often account for some varietal differences (Pinthus & Eshel 1962, Monyo & Whittington 1970).

A number of workers have investigated the relationship between genotypic differences in root growth and genotypic differences in drought tolerance. Earliness of maturity is probably the most important variable affecting drought tolerance because early maturing varieties e.g. Stewart (Derera _et al_. 1968) have fewer tillers; but factors such as the rate of elongation into the moist subsoil and the ability to increase the density of rooting at lower depths are components of the process of root system development which also have a marked effect on the ability of the plant to explore the soil for water, and hence on drought tolerance (Hurd 1968, Derera _et al_. 1969).

With the recent introduction of semi-dwarf wheat genotypes into arable farming systems some comparisons with standard tall varieties have been made. Matheson (1971) considered that the semi-dwarfs had shallower root systems which explained their disappointing yields under arid conditions and their ability to respond to applied nitrogen, but Subbiah _et al_. (1969) found that 2 gene dwarf Sonora had a more vertically penetrating system than the tall varieties they grew. Also thorough studies by Lupton _et_. _al_. (1974) comparing semi-dwarf selections from crosses TL363 and TL365a with standard varieties Cappelle-Desprez, Maris Ranger and Maris Nimrod, found that semi-dwarf root systems were more extensive although the differences were small. Thus it appears that as a rule semi-dwarfs do not have a distinctly different root system to standard height varieties.

1.3.5. HORMONAL RELATIONSHIPS BETWEEN ROOT AND SHOOT

The root system is a site of synthesis for all the main classes of growth regulators except IAA (Street 1969, Atkin _et_. _al_. 1973). While substances which are active in conventional auxin bioassays are present in the root system (Luckwill & Whyte 1968), authorities in this field e.g. Street (1969) are satisfied that IAA is not produced in the root system - either from root tips, or the root cap (Kundu & Audus 1974).

There appear to be two growth inhibitors produced and the evidence is strongly suggestive that they are in fact xanthoxin and abscisic acid, ABA (Wilkins et. al. 1974, Kundu & Audus 1974).

Root production of growth regulators during the vegetative phase appears to determine the mechanisms of morphogenesis and the distribution of assimilate to meristems. Some of the processes which are controlled hormonally are:-

(i) Root elongation and branching (Street 1969).

(ii) Axillary bud growth or tiller initiation appears to be controlled by some mechanism involving shoot auxin and root cytokinins (Jewiss 1972, Langer et al. 1973).

(iii) The root system in conjunction with leaves appears to be involved in GA production for stem elongation (Nicholls & May 1964, Railton & Wareing 1973).

The significance of the root system for hormone production and export to reproductive structures is unknown. Hormonal effects appear to occur within the wheat ear (Evans et. al. 1972) and it is likely that the hormone requirements are satisfied by localised production rather than root production (Wheeler 1972, Sheldrake 1973, Hann et al. 1974).

At this point it should be mentioned that the GA metabolism of dwarf types is altered in comparison with standard tall varieties and the increased tillering which dwarfs display (Gale & Marshall 1973) is apparently related to this, as are other processes under GA regulation e.g. resistance to sprouting (Gale 1974).

1.4 ASPECTS OF SHOOT GROWTH

The past five years have seen a sudden improvement in the quality of research into cereal plant and crop physiology. The most active and important area of research has been the study of the relationship between morphogenesis and growth of the plant and the availability of assimilate and growth regulators. The aim of this work has been to elucidate the factors limiting grain yield. Knowledge of this relationship is particularly relevant to understanding the effects of water stress on growth stages and grain yield.

Two stages of development are receiving most attention because of their obvious importance. They are

1. Tiller development.
2. Processes of grain development.

These will now be discussed separately. Discussion of another important area, that being the interactions of temperature and photoperiod with vernalisation and photomorphogenesis will be omitted because of its limited relevance.

1.4.1. TILLER DEVELOPMENT

(A) Early Tiller Growth - Kirby and Faris (1972) have separated early tiller development into two phases.

(i) Initiation of growth of the axillary bud or tiller bud initiation.

(ii) Growth of the bud and emergence from the subtending leaf sheath.

The evidence suggests that given an adequate availability of assimilate both processes are hormonally mediated. As mentioned previously the initiation of tiller bud growth is apparently controlled by the endogenous balance of auxin to cytokinin (Jewiss 1972, Langer *et al*. 1973).

Kirby and Faris (1972) found that while a bud could be initiated, further growth in the second phase did not necessarily follow as a direct consequence and they suggested that a GA mediated system controls this second phase. In this early tiller growth stage, tiller growth rates were unaffected by effects of plant density or tiller position also suggesting hormonal mediation rather than direct internal competition for assimilates or mineral nutrients. The higher tillering rates of dwarf wheats (Gale 1974) also supports this proposal.

(B) Stem Elongation - The involvement of GA in stem elongation has been recognised for many years (Nicholls & May 1964, Kirby & Faris 1970). GA both promotes the uptake of water into the internode and also promotes the transport of endogenous substrate into the growing region (Adams *et. al.* 1973).

Nevertheless a number of pieces of evidence complicate the understanding of this process. Firstly, the genuine dwarf wheats appear to be insensitive to GA for stem elongation (Gale & Marshall 1973, Gale 1974). Secondly, phytochrome has been shown to participate in stem elongation in chrysanthemum (Cathey 1974) suggesting a role for phytochrome in cereal stem elongation. Also, it appears unlikely that the leaves can solely produce the massive concentration of GA recorded in the stem during elongation (Nicholls & May 1964, Railton & Wareing 1973) and the root system is probably involved (Atkin *et al.* 1973). But an unknown factor from the leaf other than GA is required by the intercalary meristem in the internode to express full stem elongation (Adams *et. al.* 1973). Elucidation of the role of phytochrome in stem elongation may clarify the real action of GA in this process.

(C) Tiller Death - A substantial proportion of tillers in a normal crop do not survive to produce an ear. The great majority of these tillers begin to senesce during the stem elongation phase of the main stem (Puckridge & Donald 1967, Puckridge 1968, Riveros-Rodriguez 1968, Rawson & Donald 1969).

Study of this tiller death has shown that the prime cause of this senescence is the demand for assimilate by stem intercalary meristems i.e. it is a result of competition for assimilate by elongating stems (Ryle & Powell 1972, Kirby & Faris 1972). Senescence is more likely to occur in the youngest tillers as the pool of assimilate and minerals is preferentially utilised by the main stem and primary tillers. (Riveros-Rodriguez 1968, Rawson & Donald 1969). Thus tiller senescence is determined by the production of assimilate, or in other words competition for light. Hence an improvement in light relations of the canopy at this stage appears to be a necessary prerequisite for greater tiller survival. This can be achieved by selecting for smaller more erect leaves - the productive possibilities of this approach have been shown by Berdahl *et al.* (1972) who compared small and large leafed barley varieties and increased crop fertile tiller numbers even though the leaf area index was 25% less in the small leafed crop.

Tiller senescence provides a small source of carbohydrate (Lupton & Pinthus 1969) and mineral nutrient (Rawson & Donald 1969) to the rest of the plant.

1.4.2. PROCESSES OF GRAIN DEVELOPMENT

Study of the factors determining grain yield of the reproductive plant is at present an area of concentrated research effort.

With wheat and barley plants grown under favourable conditions it has been convincingly shown that the wheat plant has a sink limitation to yield i.e. the photosynthetic area is in excess of grain requirements. This is a very important discovery which has only recently been established by a number of workers using various techniques:-

(i) Calculation of net photosynthesis (Wardlaw 1971).
(ii) Sterilisation of florets (Rawson & Evans 1970).
(iii) Growth rate of grains (Bremner & Rawson 1972).
(iv) Changing the effective photosynthetic area by defoliation (Bremner 1972).
(v) Comparison of different varieties (Bremner 1972, Rawson & Evans 1970).
(vi) Sterilisation of ears in the field (Evans _et. al._ 1972).
(vii) Endogenous sucrose levels (Jenner & Rathjen 1972 a & b).
(viii) Shading of leaves of barley in the field (Willey & Holliday 1971 a).

Nevertheless a number of field experiments strongly suggest that in the field there are source factors which limit grain yield (Willey & Holliday 1971 b, Thorne, Ford & Watson 1968). Grain yield interactions with grain number and grain position are at present poorly understood (Evans _et al._ 1972) and may in the future be shown to influence assimilate utilisation by grains. Certainly experiments which have attempted to prove that the crop is source limited by correlating leaf area and grain yield (Simpson 1968, Spiertz _et al._ 1971) need to be re-examined in the light of more recent findings on source-sink relationships in the wheat plant.

Also work by Evans and Rawson (1970) has shown that in awned varieties, all the carbohydrate requirements of the ear can be synthesised from the photosynthetic area above the flag leaf node, thus reducing the importance of the lower leaves for production of carbohydrate for the grain. The importance of awns for increasing the proportion of carbohydrate produced within the ear has been noted by Teare _et. al._

(1972) and Holmes (1974) although McKenzie's (1972) work suggests that very long awns may be detrimental in terms of grain yield.

Characterisation of the sink limitations has involved investigation of two distinct aspects of grain development:-

(i) study of the transport pathways from the leaf into the endosperm.

(ii) consideration of the interactions within the ear which determine floret and spikelet survival and floret grain growth.

Evans et. al. (1970) investigated the phloem connections to the ear from the stem and although their results were essentially inconclusive it appears that the phloem is probably adequately large enough although phloem diameters may need to be increased if plant breeders continue to increase the proportion of grain carbohydrate which is derived from below the ear. The primary limitation in the transport pathway is linked with the rate of sucrose transport into the grain; through the rachilla and the vascular bundle running along the fused margin of the pericarp (i.e. beneath the 'crease') in each grain and then through the pigment strand into the endosperm (Zee & O'Brien 1970, Jenner & Rathjen 1972 a & b). The development of the pigment strand between day 12 to day 40 from anthesis gradually seals the endosperm off and halts physiological development of the grain (Zee & O'Brien 1970 b).

With regard to point (ii) above it appears that there are mechanisms operating within the ear which inhibit grain setting in distal florets and spikelets unrelated to the supply of assimilates and it is suggested that they are hormonal in character (Evans et. al. 1972). Also there are unexplained differences in growth rates of grains within and between spikelets which suggests the hormones could be involved in determining relative sink strengths between grains (Bremner 1972, Bremner & Rawson 1972). Cytokinins, auxins and gibberellins have been shown to be present in grains (Wheeler 1972) but their interacting effects on floret and spikelet survival and grain growth are unknown.

1.4.3. THE EFFECTS OF MOISTURE STRESS

The underlying principle concerning the effects of moisture stress on cereal plant growth and development was first stated by Williams and Shapter (1955) as:-

Plant parts which are growing most actively during the period of water stress are those which suffer the greatest check to their growth.

From this it follows that there are periods of growth when there is greater or lesser sensitivity to water stress measured in terms of grain yield. As mentioned previously a cereal crop generally initiates a surplus of tillers, hence suppression of tillering by moisture stress has been shown to have little effect on grain yield (Aspinall 1964). The most pronounced effects of water stress occur in the reproductive stage.

For the sake of this discussion the reproductive phase can be split into two:-

1. the phase from initiation of floral primordia up to and including anthesis and grain set. In this period the spikelet number and fertility of spikelets (and florets) is decided i.e. grain number is decided.

2. the period of laying down of starch in the endosperm i.e. grain filling. It is during this period that most of the carbohydrate for the wheat grain is synthesised (Rawson & Evans 1970) - the contribution from carbon assimilated before ear emergence is almost insignificant (Rawson & Hofstra 1969).

The first phase during which grain number is decided contains steps which have been shown to be sensitive to water stress. Water stress will reduce the number of spikelet primordia initiated in the early stages of reproductive development (Aspinall <u>et. al</u>. 1964, Slatyer 1969, Langer and Ampong 1970). Floret primordia development is likewise affected (Slatyer 1969) but since so few floret primordia finally set a grain (Langer & Hanif 1973) this effect is unimportant.

The most sensitive phase in the whole life of the crop plant is the period between ear emergence and initial grain filling (Nix & Fitzpatrick 1969, Salter & Goode 1967). Anytime during this period spikelet death can occur under even acute, or very short term, environmental stress (Morgan 1971, Wright 1972). But more importantly this is the stage of development of the floral organs and of the process of flowering itself. The flowering process requires high internal water status because the mechanism of flowering operates by osmotic swelling of lodicules, styles and stamen filaments (Zee & O'Brien 1971, Evans 1964). Also pollen viability and the early stages of grain development are sensitive to water stress (Slatyer 1969, Wardlaw 1971).

The second phase or the period of grain filling is less sensitive (Aspinall et al. 1964) primarily because of the excess of assimilate which is available (Wardlaw 1971) due to the sink limitations and the relative insensitivity of photosynthesis and translocation to moisture stress (Wardlaw 1971, Frank et al. 1973, Brevedan & Hodges 1973).

1.4.4. SEMI-DWARF WHEATS

The use of short statured cereal varieties with their superior yielding ability has been the basis of the so-called "green revolution" of the 1960s; for wheat the semi-dwarf varieties were derived from a Japanese dwarf strain Norin 10 (Vogel et al. 1956, Bourlag 1965, Reitz 1970). Other unrelated dwarf varieties such as Minister Dwarf from Belgium and Tom Thumb from Tibet are also being introduced into breeding programmes (Gale 1974).

The higher yielding potential of short statured wheats results from a fortuitous combination of a number of contributory factors rather than to any single dominant factor (Matheson 1971).

Some of the factors are:-

(i) Resistance to lodging; thus the crop can accept and respond to heavier applications of water and fertilisers (Syme 1967, Beech & Norman 1968).

(ii) Relative insensitivity to photoperiod (Wall & Cartwright 1974) leading to earlier flowering and a longer duration of grain growth (Syme 1967, Matheson 1971) as long as the plants remain unvernalised (Wall & Cartwright 1974).

(iii) If unvernalised there is a larger ear with more spikelets (Syme 1967, Wall & Cartwright 1974).

(iv) Higher ear photosynthesis due mainly to the presence of awns (Evans &Rawson 1970). The lower degree of mutual plant interference in the canopy contributes to a greater contribution of photosynthate by the foliage (Matheson 1971, Thorne et al. 1969).

(v) Resistance to disease, particularly rusts (Bourlag 1965).

Nevertheless there are a number of disadvantages of particular relevance in more temperate regimes which have contributed to disappointing responses.

(i) Marked sensitivity to vernalisation of Norin 10 derivatives. Wall and Cartwright (1974) have shown that Norin 10 derivatives can be vernalised by temperatures as high as 18/13°C. This effect is the major reason why semi-dwarfs perform relatively poorly in temperate regimes. The characteristic large spikelet numbers (up to 25 under favourable conditions Rawson 1970) and relative insensitivity to photoperiod of most wheats derived from Norin 10, which leads to a longer duration of the reproductive phase, holds only if the plants remain unvernalised. Temperate agronomists e.g. Thorne _et al_. (1969), Gandar (1970), and Dougherty _et al_. (1974) report maximum spikelet numbers of only 15 to 17.

(ii) Shallow rooting pattern which is unsuitable for subsoil moisture extraction. (Matheson 1971).

(iii) Rate of seedling emergence has been quoted often as a problem in the use of semi-dwarf types (Allan _et al_. 1965) but it appears that improvements due to plant breeding have almost eliminated this problem (Dougherty _et al_. 1974).

1.5 ASPECTS OF THE DYNAMICS OF WATER RELATIONS OF CEREALS

1.5.1 GENERAL PRINCIPLES

Water flow through the plant occurs predominantly for transpiration. Movement through the soil plant atmosphere system constitutes a thermodynamic continuum and the recent universal adoption of the thermodynamic term, the water potential, has occured in recognition of the fact that water moves along water potential gradients. Thus the field of plant water relations now has a unified terminology (Slatyer & Gardner 1965). Discussions of the water potential concept occur in any text on plant water relations (e.g. Kramer 1969) and will not be mentioned here.

The absolute value of water potential is at present used as a quantitative indicator of physiological water stress. With the present state of knowledge the ~~use~~ absolute value of water potential has been shown to affect most physiological processes and thus measurements of water potential enable comparison of results and experiments. Nevertheless as Hsiao (1973) notes reliance on absolute values of water potential as an indicator of physiological water stress needs to be tempered with caution since evolutionary and physiological adaptation to environment markedly influences the level of water potential at which water stress sets in.

Water movement in the transpiration stream is treated as a catenary process analogous to Ohm's Law, first described by the model of van den Honert (1948) - the rate of water flow between two points in the transpiration stream is determined by the water potential difference divided by the impedance or resistance to flow. Although the theory of movement along potential gradients has become more complex (Cowan 1965, 1972) the Ohm's Law analogy still forms the basis for understanding the processes of plant water relations even though it cannot be strictly adhered to in all aspects (Barrs & Klepper 1968).

1.5.2 DRIVING FORCE TO TRANSPIRATION

The transpiration stream flows through the leaf mesophyll and across the root tissues largely along the cell walls, by-passing the cell protoplasts (Weatherley 1970, Tanton & Crowdy 1972 a & b). The point at which the water leaves the leaf is at present a subject of controversy. The traditional view was that water loss occurred through the stomatal pores although there were a number of workers early this century who questioned this interpretation (see Knight 1917).

Tanton and Crowdy (1972 b) now have suggested that transpirational water loss occurs solely through the cuticle; the transpiration stream moves up the anticlinal walls of the epidermal cells and evaporates from the cuticle and the cuticle/cell wall interface though Tanton and Crowdy suggest that the walls of the guard cells provide the major pathway. This theory can still explain the observation that the rate of water loss from leaves is proportional to the size of the stomatal aperture (see Tanton & Crowdy 1972 b) and hence the importance of the stomata in controlling the rate of transpirational water loss is unchanged.

Liquid water movement through the plant is driven by the difference in water potential from the soil to the evaporating surfaces of the shoot, and movement as vapour from the plant is driven by the difference in vapour pressure. Since transpiration is controlled in most plants by the stomatal aperture and the gradient in vapour pressure from leaf to air, the rate of water movement through plants is controlled chiefly in the vapour phase (Kramer 1969).

The rate of transpiration is determined by two factors -

1. Environmental components such as light intensity, vapour pressure and temperature.
2. Ability of the plant to supply the evaporative demand of the atmosphere which is affected by resistances within the plant to water flow primarily the stomata and also the water supply to the root system.

By interaction of these factors within the micro-environment of each leaf in the canopy the leaf water potential LWP is established, and because the factors influencing the LWP can change so LWP is a dynamic characteristic of a leaf reflecting the fluctuating effects of the atmospheric environment and soil water availability.

The effects of reduced soil moisture supply on LWP have been elucidated by a number of workers e.g. Millar et al. (1968), Yang and de Jong (1972) and Turner (1974). Atmospheric relationships with LWP and transpiration rate have been characterised by many workers although field responses are not well represented. Examples are Yang and de Jong (1971 a), Cary and Fisher (1971), Ehlig and Gardner (1964), Turner and Begg (1973) and Frank et al. (1973). In the field it appears that stomatal closure does not occur until the leaf reaches much lower LWP than many glasshouse studies would suggest (Turner & Begg 1973), and hence the importance of stomatal resistance may often have been over-rated in considering the field situation. Also there is an unfortunate lack of information concerning diurnal transpiration relationships in cereals. It is therefore assumed that cereal crops are similar to other crops studied (Ehlig & Gardner 1964, Kramer 1969, Weatherley 1970), where transpiration is approximately linearly related to environmental evaporative demand measured as net radiation or vapour pressure deficit.

As a final point the water relations of the ear of the cereal plant have only been infrequently mentioned in the literature e.g. Dougherty (1972) and very little is known. It appears likely that on the basis of green area exposed to the environment, their transpiration rates will be lower than leaves because stomatal density per unit area is 80 to 90% lower than leaves (Teare et al. 1972) and the water supply possibly has a higher resistance pathway because the xylem has "discontinuities" (Zee and O'Brien 1970 a).

1.5.3 ROOTS AND WATER SUPPLY TO THE SHOOT

Dynamic Aspects - Although the bulk of water moving from soil to plant does so along potential gradients it is important to note that there is some metabolically-related (or active) uptake of water primarily in the root hair region (Cailloux 1972) which possibly contributes to root pressure (Barrs 1966, Downey & Mitchell 1971).

Recent work by Newman (1969 a & b) and Hansen (1974) has shown that the resistance to water movement in the pathway from the soil to the root i.e. across the rhizosphere, is small and does not limit movement into the plant until soil water potential approaches the permanent wilting point. The resistance to water movement across the root system is negligible in the zone within 6cm of the root tip but steadily increases towards the base of the root. Thus while only a very small potential gradient is required to move water from the soil into the xylem near the tip, progressively greater gradients are needed to move water across the root further from the apex (Hansen 1974). This possibly explains the observed diurnal pattern in root resistance (Weatherley 1970) which could be due to an increased uptake by older root, as LWP, which determines the size of the potential gradient within the plant (Cary & Fisher 1971), decreases towards midday and then increases towards evening.

The Effect of Root Distribution and Density - As mentioned previously root elongation and hence root distribution follows gradients of soil moisture, provided no other soil factors prevent this e.g. compaction, and hence the root system will orient itself to the water supply. A number of workers (e.g. Yang & de Jong 1971 b, Taylor & Klepper 1973, Durrant *et al.* 1973) have shown that the root system can extract water from soil at its maximum rooting depth although this will occur only as the more surface layers lose their available water. Thus by adjustment of the potential gradients within the plant, soil moisture can be removed from drying soil down to the point where leaves wilt; the potential gradient between soil and plant then cannot be further increased as LWP has reached its minimum value; and the soil is then considered to be at the permanent wilting point for the soil type and the particular crop (Yang & de Jong 1972).

As a final point, studies of rooting density of cereals has often lead to the questioning of the need for such an intense and extensive root system for irrigated conditions. Work by Downey and Mitchell (1971) with maize suggests that even under very dry soil conditions the plant can supply its transpirative demands with much less root system but during days of very high evaporative demand (high vapour pressure deficit) there are advantages in having a large root system as a plant with a small root system "cannot supply water as fast as it is transpired".

CHAPTER TWO. MATERIALS AND METHODS

2.1 INTRODUCTION

The experiment was conducted in two parts:-

1. A field experiment.
2. A supplementary glasshouse simulation of some features of the field experiment.

2.2 THE EXPERIMENTAL TREATMENTS

Two wheat varieties were chosen; Karamu, a representative of the semi-dwarf type, and Gamenya, a standard height variety. These two varieties were chosen because a previous experiment in the Agronomy Department had shown each to be the highest yielding variety of each plant type. (Clements et al. 1974).

There were three irrigation treatments. All soil water potential measurements were made by tensiometers (Irrometers), which were permanently situated in at least two plots from each treatment.

The treatments were:-

1. Frequent, generally daily applications, the aim being to keep soil water potential, measured at 15 cm depth, above -0.5 bar. Applications were made by watering can. Henceforth this treatment is designated by T (for Top soil layer irrigated).
2. Infrequent, heavy applications; applied during the early stages of growth when soil water potential at 15 cm dropped below -1bar, and later on when soil water potential at 45 cm dropped below -0.5 to -0.7 bar. Applications were likewise made by watering can. This treatment is henceforth designated by F (for Fully irrigated).
3. Sub-surface irrigation. Water was introduced into the plot at a soil depth of approximately 45 cm using "Viaflow" porous tubing, a porous plastic tubing developed by Du Pont. An alkathene pipe was placed at 40 cm depth around the perimeter of each sub-irrigated plot. Along the pipe at the correct intervals holes had been punched and plastic adapters were fitted into each of these holes. Sections of "Viaflow" were buried in hand-dug trenches at 45° to the direction of the crop rows, placed over the adaptors and wired into place. The spacing between each parallel section of "Viaflow" tubing was 25 cm. Thus when water was introduced into this system it was ideally water-tight at all the joins and water entered the soil by "sweating" or seeping from the porous piping. To provide the low water pressure

required for operation of the system a reducing valve was introduced into the water supply, provided by piping water from a stock water trough supply. The system was arranged so that each individual sub-irrigated plot could be irrigated separately using ½ inch alkathene piping to feed each system from the main supply.

The effectiveness of this means of irrigation is outlined in **Appendix** I but it should be mentioned at this point that the system was not completely water tight and tended to leak at the plastic adaptors to which the 'Viaflow' tubing was connected. Thus the system used more water than ideally it should have, and hence no estimate could be made of crop water usage under this irrigation treatment.

Water was applied from the system to maintain the soil water potential, at 45 cm, above -0.3 bar. Henceforth this treatment is designated as S (for Sub-surface irrigation). The S plots were covered from rain using plastic covers, from 2 weeks after emergence (see section on Crop Water Budget).

2.3 THE FIELD EXPERIMENT

The experimental site, $\frac{1}{6}$ ha, was situated behind a stopbank adjacent to the Tiritea Stream on an area managed jointly by the Massey University Sheep and Dairy Husbandry Departments. During the previous three years the area had a cropping history of summer maize for silage and winter Tama ryegrass for grazing. (See App. 1. for map of site)

The soil over the experimental area was Rangitikei silt loam (pers. comm. J. Pollok), an alluvial soil with a silty topsoil of 40-50cm overlying a sandy subsoil. There was sharp definition between these two layers. The area was chosen primarily because the soil, being relatively light in texture, enabled easy removal of roots from the soil and also the absence of stones in the profile facilitated the use of a hand driven soil corer for root sampling.

2.3.A Experimental Design and Layout.

The plots were laid out in randomised blocks with 5 replicates (see appendix 1 for map of site and layout of plots). Thus with 2 varieties and 3 irrigation treatments there were 6 plots per replicate. Each plot was randomised within each block subject to the constraint of a "checkerboard" pattern where one variety was always adjacent to plots of the other variety (see section on Crop Water Budget for explanation). Guard rows of Gamenya were sown at either end of each plot. 2m by 1.5m plots were initially laid out although subsequent excavation (see following section on Crop Water Budget) changed the area of each plot slightly. This was allowed for when fertilising.

2.3.B Cultural Aspects.

A schedule of operations is presented in appendix 2. The site was fenced off by 30.8.73 and the Tama sward was sprayed with 'Paraquat'. The site was subsequently rotary hoed, and the following month until 27.9.73 was spent excavating the plots for placement of the plastic sheeting and the 'Viaflow' porous tubing (see section on Crop Water Budget). On this date the plots were fertilised and rotary hoed with a small garden-type rotary hoe. The seed was sown on the same date using a Planet Junior hand-sower, row width being approximately 12-16 cm giving 7 rows per metre and the seeding rate was approximately 250 kg/ha. Fertiliser was applied to all the plots at a rate equivalent to 628kg 30% potassic super per hectare (5cwt/ac) and 126 kg urea per hectare (1 cwt/ac). The seed of the semi-dwarf wheat Karamu, and standard height Gamenya, was provided by Dr. MacEwan of Crop Research Division, D.S.I.R.

Emergence occurred from 2.10.73 (day 6) and 6 days later (from day 12-14) transplanting and thinning was undertaken. The plots were mended to an approximate between-plant spacing of 1 cm in the rows and watered following transplanting. The operation proved a success with little seedling death. A population count was taken on 26.10.73. Weeding was done by hand throughout.

Because the crop was observed daily pests were a minor problem. The first appearance of aphids occurred on 27.10.73 and the crop was immediately sprayed with Metasystox. Argentine stem weevil began invading the plots by 12.11.73 and on the first following fine day (14.11.73) the crop was sprayed with Lannate. This was repeated on 17.11.73 and on 3.12.73. The last two sprays also included Benlate fungicide to prevent fungal infection of the emerging ear. Birds were a serious hazard and began damaging ears during harvest 2. Therefore as each replicate was harvested (17.12.73 to 22.12.73) it was protected with plastic netting.

On 17.11.73 a further application of nitrogen as urea, was made to all the plots at a rate equivalent to 63 kg/ha ($\frac{1}{2}$cwt/ac). This was dissolved in the water irrigated to each plot.

2.3.C Crop Water Budget

The following variables were accounted for in attempting to describe crop water usage.

Firstly, to estimate crop transpiration as a function of total evapo-transpiration, 2 replicates of the 3 irrigation treatments were laid out and kept bare of vegetation. These sub-plots were irrigated using the same criteria as the experimental plots and hence an estimate of soil evaporation was obtained. These evaporation sub-plots were surrounded by guard rows of Gamenya in an attempt to prevent micro-environmental differences between evaporation sub-plots and the experimental plots.

Secondly, in order to estimate crop water use within the plots, it was essential to prevent movement of water into, or out of, each plot. The plots were therefore isolated from the exterior soil by burying plastic film around each to a depth of approximately 70cm. This also allowed placement of plots beside each other making the layout more compact. The evaporation sub-plots were likewise surrounded to 70cm depth by plastic sheeting. The plastic used for this purpose was almost exclusively thick clear film (0.02mm thick) although some thinner plastic was used to complete the evaporation sub-plots.

Plastic film of this thickness did not rip on placement in the soil nor were roots able to penetrate from either side. Excavation of this sheeting altered the individual plot areas somewhat but for practical convenience this could not be allowed for when irrigating. Nevertheless results were adjusted to allow for differing plot areas.

Thirdly, precautions were taken to prevent rain falling onto the S treatment plots. A system was built which could be erected to cover the plots when it rained and removed during fine weather. For this purpose plastic covers were constructed using wooden frames and UV-inhibited plastic film (0.02mm thick). These were erected using metal standards and wire as a framework to support the covers. Covers were also placed over T plots on replicates 2 and 5 to insure against the possibility of prolonged heavy rain. As noted in the rainfall records (appendix 3) this situation did not arise and all T plots have been regrouped in the results since it is unlikely that the covered T plots differed from the uncovered in crop water supply. As a rule, the covers were erected every night and taken down the following morning unless rain threatened. With regular maintenance the covers gave no further problems.

Fourthly, spare tensiometers were used for purposes other than as indicators of irrigation requirements. Two 15cm tensiometers were placed in S plots to determine the time of the first harvest (see next section). Three long (120 cm) tensiometers were buried to 90 cm in three plots (a KF, KS, and an S evaporation plot) to determine water status at the bottom of the rooting zone.

Finally, to prevent microclimate differences between plots due to the differences in height between Karamu and Gamenya and hence differing evapotranspiration losses within treatments, the plots were laid out on a 'checkerboard' pattern.

2.3.D. Experimental Methods.

Evaluation of the growth and development of the two varieties under the three irrigation treatments involved three main harvests. Because of the time involved in sampling root systems and washing out the cores harvesting took a minimum of 8 days. The first harvest was taken when the soil water potential in the S treatments reached -1bar at 15 cm soil depth. This first harvest period was further lengthened by rain which spread harvest 1 over two weeks from 7.11.73 to 22.11.73. The interpretation of the results must therefore allow for this.

In subsequent harvests, the harvesting spread was unimportant. The second harvest was taken one week following the appearance of anthers on at least 80% of ears in each plot (flowering). The spread in flowering permitted a spread in harvesting dates. Harvest 3 was taken as soon as the flag leaves showed obvious signs of senescence.

(i) Root Sampling

A soil corer was developed for the purposes of this experiment (see appendix 4 for details). Cores were taken between the rows. In harvest 1, 4 cores were removed from each plot, while 3 were taken at harvests 2 and 3. The corer was hand-rammed using a large post rammer to a depth between 75 cm and 100 cm.

The corer was then extracted from the soil using a front end loader attached to a Ford 5000 tractor or a mechanical hoist. The core was removed from the corer and was sectioned into 15 cm sections down to 45 cm, and 30 cm sections below this. The length of the final section was recorded so that the volume of all core sections was known. Thus there were 5 sections from each core:-

Section 1	0 - 15 cm
Section 2	15 - 30 cm
Section 3	30 - 45 cm
Section 4	45 - 75 cm
Section 5	below 75 cm.

At harvests 1 and 2, a small sample of soil was placed in an air-tight plastic vial for subsequent gravimetric moisture content measurement.

A 16 mesh grid had been prepared (see appendix 5) which enabled each section to be grouped with the other sections of the same depth from the common plot. This system was free of the problem of designating the origin of each core section and enabled 5 plots to be cored concurrently. The cores were then washed out in this mesh grid, using a hose spray of moderate pressure. The roots remaining were placed in small metal trays and each sample was cleaned of other plant material, dead roots, non-wheat roots and other rubbish. The cleaned root samples were then preserved in 70% ethanol to await measurement of root weight and length.

(ii) Root Measurements

Depending on the size of the sample, the preserved roots were sub-sampled and root length of the sub-sample was estimated using Evan's (1970) method, which involves counts of intersections of roots on a grid of parallel lines unit distance (1 cm) apart. The sub-sample was teased out evenly over the area of a large Petri dish in which the counts were made. The sub-sample intersections were meaned from 3 counts obtained by rotating the Petri dish slightly with each count. The sub-sample was then blotted dry and weighed, as was the balance from the initial root sample. Thus an estimate of the total root length in each sample could be obtained. The samples from 2 plots of each treatment chosen at random were oven dried at 80°C for 24 hours; the mean was used to evaluate the root dry weight of each sample. From the diameter of the soil core (6.2 cm) and the measurement of the length of each sample the dry weight and the length of root could be calculated per unit soil volume.

The samples from the S treatment at Harvest 2 contained a marked proportion of dead root which could not practically be removed at the time they were preserved. Measurements were made as usual and the samples from one plot of each variety were carefully "cleaned" of dead root and the proportion of both weight and length which was dead was found and the results of all the samples in the S treatments were reduced by the relevant proportion.

(iii) Shoot Sampling

At each harvest plant "tops" were sampled prior to soil coring. Plants were harvested from 10 cm of 6 adjacent rows. The measurements made on the sampled plants differed at each harvest and therefore each harvest will now be considered separately.

Harvest 1 The number of plants sampled in each 10cm of 6 rows was recorded as the plants were being harvested. There was no problem in differentiating between individual plants at this stage. The sample was then taken to the laboratory and weighed. A sub-sample was then taken for determination of dry weight percentage. 10 plants were sub-sampled and their leaf area measured using an Hayashi Denko AAM-5 automatic area meter. A further 15 plants were sub-sampled and on each, the number of tillers was counted. Then the leaves were stripped off and the number of "initiated" axillary buds were counted. An axillary bud was considered "initiated" if it was longer than 3 to 5 mm. From this sub-sample the youngest leaf was removed from each tiller and these were dried and stored for a nitrogen percentage determination by the Kjeldahl method of Clements (1970). This method had been slightly modified by Thom (1974) and the same technique and apparatus were used for the nitrogen determinations in this experiment.

From the 10 plants sub-sampled for leaf area measurement, each stem of all tillers was preserved by freezing for subsequent dissection of the reproductive primordial apex. Because of the large number of dissections (more than 800) the stem was sliced in half along the axis and spikelet primordia counted on one side of the apex only. This was then doubled to give the total number of spikelet primordia. Also noted during dissection was the relative stages of plant development. To enable analysis of these results this information was then transformed numerically using the following code:

	Numerical Code
No spikelet development	1
Double ridges	2
Primordial development but no stem elongation	3
Primordial development, stem elongation no nodes developed	4
1 node developed	5
2 nodes developed	5
3 nodes developed	7

Harvest 2 The second harvest was taken 1 week following anthesis and hence the days from sowing to harvest 2 were noted to provide an indication of the effect of treatment on the rate of plant development. Plants were sampled as in harvest 1 but it was impossible to distinguish accurately between individual plants at this stage and hence the term is merely used for convenience. The total dry weight was calculated as for harvest 1. A sub-sample of 16 'plants' was taken and the number of ear bearing tillers and dying or vegetative tillers was counted for each 'plant'. From this sub-sample flag leaves were collected for a nitrogen percentage determination. 10 'plants' were sub-sampled for measurement of leaf area per tiller; this included all leaves including those which were senescent. All ears were collected from this sub-sample for subsequent analysis. They were preserved by freezing. The following data were taken on each ear:-

1. Total number of spikelet sites.
2. The number of spikelets which showed full floret development of at least one floret i.e. the number of potentially fertile spikelets.
3. The position of the first 'fertile' spikelet from the base.
4. The number of 'fertile' florets in the 2 central spikelets.
5. The number of 'fertile' florets in the top 3 spikelets.

The latter three measurements were taken to be compared with similar data from harvest 3 so that the viability of spikelets and florets could be examined in relation to the experimental treatments.

Harvest 3. The 'plants' were harvested in 6, 10cm, row lengths as before and the number of ears were counted. A sample of 15 ears was taken and frozen; also an estimate of crop height was taken. At this harvest the crop was not quite mature and hence a further sample of ears was taken a fortnight later from which grain weight was calculated from the weight of 100 grains. The analysis of the preserved ears included the following measurements:-

1. Total spikelet sites.
2. The number of grain bearing or fertile spikelets.
3. The position of the first and last spikelet which contained at least one grain, and the grain number within each of these spikelets.
4. The number of grains in the central two spikelets.
5. The total grain number per ear.

The grain yield per m^2 could then be calculated by multiplying the ear number by the grain number per ear by the weight of each grain.

(iv) Water Potential Measurements.

These were taken using the pressure bomb technique (Schollander et al. 1964, 1965; Boyer 1969). The pressure bomb was fully portable and was constructed by Rodar Precision Ltd. in Palmerston North. Using two different rubber seals - one with a slit and the other with a hole - three measurements could be taken:-

1. Leaf Water Potential (LWP) - by placing the excised leaf through the 'slit' seal.
2. Ear Water Potential (EWP) - by excising the stem just below the ear and placing this piece of stem through the 'hole' seal.
3. Root Water Potential (RWP) - by lifting the crown and roots that remain with the crown, cutting the stem to leave a short length of stem and placing this piece of stem through the 'hole' seal so

that only the crown and roots are inside the bomb. This measurement is called RWP for convenience. The physiological meaning of this method of measuring RWP and EWP is explored in the Discussion of Methods (section 4.2).

Three determinations were made to determine the specific water potential being measured although if these results showed very wide variation further determinations were made. Three aspects of crop water status were examined during typical hot summer days following anthesis. Water status during the vegetative stages could not be examined because the pressure bomb was not available. The aspects of crop water status examined were:-

1. A comparison between Gamenya and Karamu on all three treatments measuring both flag leaf LWP and RWP. This experiment was conducted at two times - (i) early morning 2.1.74 from 5.45 a.m. in rep 2. (ii) midday 31.12.73 from 1 p.m. in rep 5, temperature 27°C. The determinations were made on each treatment in turn measuring LWP first and RWP second but alternating between varieties. These results were amenable to statistical analysis.

2. Diurnal change in LWP and RWP for the three treatments of Karamu. This was conducted during 1.1.74, on rep 1. Flag leaf LWP was measured every hour in S - F - T treatment sequence from 5 a.m. to 8 p.m. RWP was recorded every 2 hours from 7 a.m. Temperature was recorded hourly to give an indirect indication of evaporative demand. The values are plotted on Figure 2.

3. Diurnal change in EWP, LWP and RWP of Karamu T treatment. An initial survey was conducted on 4.1.74 measuring EWP, LWP and RWP at 7 a.m. and 1 p.m. A more complete characterisation of the diurnal change was made 5.1.74 on KT plot rep 4. Measurements were taken from 6.45 a.m. to 7 p.m. with a break from 11 a.m. to 3 p.m. because the gas bottle pressure was less than 250 lb/in^2. Measurements were taken on different plants in the order LWP, EWP and RWP and plotted (Fig. 3).

2.4. THE GLASSHOUSE EXPERIMENT

This experiment was conducted to clarify aspects of the vegetative growth of the wheat crop which had shown up in the field experiment. Also since the pressure bomb had not been available during the vegetative growth stages of the field experiment it was necessary to know the water status of the plant during the period of floral primordial development.

Four large boxes (1.5m by 0.6m by 0.6m) were constructed and filled with soil taken from the experimental site (see appendix 6 for photos). The three irrigation treatments were imposed using 3 boxes with Karamu and the fourth box contained treatment GT allowing one varietal comparison. Fertiliser was watered on to the plots in solution at the following rates:-

GT and KT	60g potassic super - equiv. to field experiment.
	12g urea - equiv. to field experiment.
KF	65g pot. super
	14g urea
KS	70g pot. super
	20g urea

This differential fertilisation was intended to improve the nutrient supply to the more water stressed treatments in an attempt to eliminate the lowered plant mineral levels which were indicated from the nitrogen determinations from the field experiment. One 15cm tensiometer and one 60cm tensiometer (at 45cm depth in the soil) were placed in each half of the box such that they would be undisturbed by the first sampling (see app. 6).

The crops were sown in 7cm rows across the boxes, with approximately 1cm between plant spacing within the rows, on 27.2.74. Emergence occurred on 3.3.74.

By the use of a time clock and 2 fluorescent light banks plus two incandescent bulbs per bank (giving 7000 lux per light bank), on both sides of the glasshouse, daylength was increased to approximate the daylength during the corresponding period in the field experiment. Also the glasshouse used had a degree of temperature control (see appendix 7 for details of daylength and temperature control). The plants were regularly sprayed with Malathion to control aphids, mites etc.

The irrigation treatments began on 10.3.74 and by 22.3.74 the 15cm tensiometers in the S treatment had reached -1bar. All boxes were sampled from this date (harvest 1), sampling from both ends of the box to give 2 results for each treatment. Unfortunately too much soil was removed from the box containing the S treatment at harvest 1 and hence only 2 harvests could be made in this treatment. The second harvest was made from 4.4.74 after spot dissections showed that primordial development was almost complete. A final harvest of only one row per box was made at complete emergence of 90% of the ears remaining in the box.

In all three harvests the root system was sampled after harvesting the 'tops'. The soil under 5 rows was removed and a vertical wall was shaped beneath the 5th row. A metal box of known volume (15cm by 3.5cm by 3.5cm) was then pressed into the soil between the 5th and 6th row and in this way a block of soil was removed at 15cm depths from the surface to the bottom of the box. These soil blocks were then wrapped in black muslin and soaked for 24 hours. The samples were gently washed out and preserved in 70% alcohol for subsequent measurements. Root weight and length measurements were made as in the field experiment. Also after counting for root length the number of lateral branches on all roots in the sub-sample were also counted.

Leaf area measurement in harvest 1 and 2 was made by measuring length and width of each, obtaining the product, and multiplying by a conversion factor. Because wheat leaves in the vegetative phase are very oblong the conversion factor for maize of 0.75 (McKee 1964) was used.

Harvests 1 and 2 were made in the following order. Plant number per 40cm of row was counted in one row with at least 5 rows between this row and the end of the box. 10 plants were then harvested and the leaf area of green leaves was measured. They were then dried and weighed and preserved for determination of nitrogen percentage. A further sample of plants was taken for apical dissections and preserved by freezing. In harvest 1, 8 plants were sampled and dissections were made to determine the stage of development of the apex. In harvest 2, 16 plants were preserved and dissected for counting of total spikelets on each primordial ear.

At harvest 1 and 2 just prior to shaping the vertical wall for removing the soil blocks, at the tensiometer depths of 15cm and

45 cm, samples of soil were removed for gravimetric analysis of water content. Also at harvest 1 at these depths samples of root were dissected from the soil for measurement of water potential by the dye method. (Knipling 1967). Small samples of root system approximately 0.1g were prewashed for 15 min in a range of mannitol solutions at 0.5 bar intervals from -0.5 bar to -3 bar. Each sample was then placed in a small vial with the same solution as it's prewash solution and left for 24 hrs before water potential was estimated (see Knipling 1967 for detailed description of this method).

2.5 STATISTICAL METHODS

Statistical analysis of results from the field experiment was approached using analysis of variance derived from application of regression theory and the use of linear models to describe the data (see appendix 8 for discussion of the statistical theory underlying this method of analysis). The analysis of variance was done in two parts:-

1. All variables measured in all harvests were analysed between treatments within harvests; this involved analysis of variance of 116 measured variables i.e. 41 shoot variables, and 25 root variables measured at each of the three harvests.
2. Root variables were analysed between harvests within treatments. This involved 150 analyses of variance i.e. 25 root variables by 6 treatments. With regard to this second analysis, caution is needed in interpretation of the results of statistical analysis since sampling positions on the plots could not be completely randomised.

Of the water status experiments analysis was made on experiment 1; that being the comparison between varieties experiment. It was difficult to randomise the Diurnal experiments properly with respect to the time of taking measurements and hence these results were not analysed. Regression analyses of the results were done on an I.B.M. 1620 computer using the regression programme BAR 3 (Burr 1968).

Analysis of results in part 1 above i.e. between treatments, was made initially to test whether there were significant treatment effects i.e. this included variety, irrigation and interactions. A second computer run was then taken on results which showed significant treatment effects. The variety sum of squares, irrigation sum of squares and the variety by irrigation (VI) interaction sum of squares were separated as components of the Treatment sum of squares and for each an F value was calculated. Least Significant Differences between irrigation treatment means were then calculated for means which showed significance below the 5% level.

CHAPTER THREE RESULTS

The results are presented predominantly in the form of tables of means with the statistical analysis and Least Significant Difference between means of irrigation treatments, being included with each table. Both root and shoot results are presented for each harvest and it must be emphasised that results from harvest 1 need to be interpreted with **caution,** since because of the spread in harvest dates there are significant differences in the stage of plant development. Table 7 contains an estimate of the physiological stage of development at the first harvest. These differences are:-

1. Karamu was more advanced than Gamenya.
2. Gamenya F and S treatments (GF and GS) were markedly more advanced than GT.
3. **Karamu** T and S treatments (KT and KS) were slightly more advanced than KF.

3.1 CROP ROOT SYSTEM

3.1. A Total Root System at each Harvest

The total weight and length of root system per square metre is presented in Table 1. There are no varietal differences in total weight or length. The significant differences occur between irrigation treatments. At the first harvest the S treatment had significantly less root length than the other treatments particularly with Karamu which shows very large irrigation differences. At the second harvest the F treatment had highest root weight and length but by the third harvest there were no treatment differences although the results suggest that Karamu retains more of its root system to final harvest than Gamenya.

3.1. B Root Distribution at each Harvest.

The distribution of the crop root system is tabulated. Tables 2A, 3A and 4A contain the meaned results of dry weight distribution and Tables 2B, 3B and 4B contain the meaned results of root length distribution. At the first harvest (tables 2A and 2B) varietal differences show up. Karamu produced more root at the lowest depths i.e. below 45 cm although this may be due to Gamenya's earlier harvesting. Nevertheless Gamenya had a greater weight of roots in the 30-45cm zone and had a higher proportion of its total root mass in this zone and above.

TABLE 1. Total Dry Weight (D.W.) and Length of Root System to 1m soil depth.

Trt.	Harvest 1		Harvest 2		Harvest 3	
	D.W. g/m^2	Length m/m^2	D.W. g/m^2	Length m/m^2	D.W. g/m^2	Length m/m^2
GT	70.8	15498	40.6	8138	29.0	5670
GF	74.8	14676	46.6	11180	27.2	5626
GS	89.6	11462	45.4	9018	27.6	5416
KT	58.4	13814	40.0	10864	31.8	6222
KF	115.6	19846	47.4	11868	32.6	6908
KS	65.8	8900	41.8	7468	36.6	7276

Statistical Analysis

	Dry Weight			Length		
Harvest	1	2	3	1	2	3
Variety						
Irrign.	xx	x		xx		
LSD	135	72		3496		
VI intactn	xx					

LSD calculated at 5% level of significance
xxx significant at 0.1% level
xx significant at 1% level
x significant at 5% level

VI denotes the Variety by Irrigation Treatment interaction.

The method of irrigation likewise affected root distribution. The F treatment had more weight of root in the surface layer and in Karamu had greater length in this zone. The S treatment resulted in a greater distribution of root system to lower depths in the soil although there was little difference between S and the other two in actual length at lower depths; the effect wasprimarily due to reduced root length in the surface zones.

By the second harvest (tables 3A and 3B) differences were less apparent. Once again S had significantly more of its root system at depths below 30cm. At the third harvest (tables 4A and 4B) crop root systems between irrigation treatments were distributed almost identically. Karamu had slightly more of its root system at this stage although the effect is significant only at the 10% level.

Table 5 presents the root distribution data from the glasshouse experiment. No marked treatment differences are apparent although it appears that in the S treatment root branching could have been reduced in the surface layers in favour of branching at lower depths.

TABLE 2A. First Harvest. Root Dry Weight (D.W.) in each section of soil core.

Variety		Gamenya		Karamu	
Irrig. Trt.	Sect. of core	D.W. mg/cm^3	D.W./cm^3 as % of total	D.W. mg/cm^3	D.W./cm^3 as % of total
T	1	192	54.2	165	56.4
	2	99	28.0	64	21.4
	3	38	10.7	31	10.6
	4	19	5.4	25	8.5
	5	5	1.4	8	2.7
			100%		100%
F	1	205	54.8	376	65.1
	2	77	20.6	108	18.7
	3	59	15.8	47	8.1
	4	22	5.9	34	5.9
	5	12	3.2	13	2.2
S	1	167	37.3	138	42.0
	2	133	29.7	73	22.0
	3	89	19.9	63	19.2
	4	43	9.6	36	11.0
	5	15	3.3	19	5.8

Statistical Analysis

Sectn. of core	Variety		Irrigation		VI interaction	
	DW/cm^3	As %	DW /cm^3 with LSD	As % with LSD	DW/cm^3	As %
1			xxx 45.7	xx 8.6		
2		x			x	
3	x		xxx 14.5	xxx 3.1		
4			x 10.4			
5			xx 4.2	x 1.4		

TABLE 2B First Harvest. Root Length in each section of soil core.

Variety		Gamenya		Karamu	
Irrig. Trt.	Sect. of core	Length cm/cm^3 (10^{-3})	Length/cm^3 as % of total	Length cm/cm^3 (10^{-3})	Length/cm^3 as % of total
T	1	5231	67.5	5145	74.5
	2	1943	25.1	997	14.4
	3	376	4.9	461	6.7
	4	139	1.8	227	3.3
	5	60	0.7	77	1.1
			100%		100%
F	1	4998	68.1	7274	73.3
	2	1369	18.7	1535	15.5
	3	627	8.5	589	5.9
	4	274	3.7	389	3.9
	5	70	1.0	135	1.4
S	1	2729	47.6	1937	43.5
	2	1731	30.2	1010	22.7
	3	624	10.9	848	19.1
	4	549	9.6	468	10.5
	5	99	1.7	187	4.2

Statistical Analysis

Sectn. of core	Variety		Irrigation		VI interaction	
	Length per cm^3	As %	Length per cm^3 with LSD	As % with LSD	Length per cm^3	As %
1			xxx 1320	xxx 8.9		
2			x 753			
3				xxx 3.2		x
4			xx 420	xxx 2.2		
5	xx	xx	xx 35	xxx 0.8		x

TABLE 3A Second Harvest Root Dry Weight in each section of soil core.

Variety		Gamenya		Karamu	
Irrig. Trt.	Sect. of core	D.W. mg/cm^3	D.W./cm^3 as % of total.	D.W. mg/cm^3	D.W./cm^3 as % of total
T	1	98	48.4	111	55.5
	2	54	26.7	43	21.5
	3	24	11.8	25	12.5
	4	15	7.4	13	6.5
	5	11	5.4	8	4.0
			100%		100%
F	1	128	54.9	138	58.2
	2	44	18.9	44	18.6
	3	29	12.4	32	13.5
	4	21	9.0	15	6.3
	5	11	4.7	8	3.4
S	1	106	46.8	87	41.6
	2	52	22.9	48	23.0
	3	34	15.0	35	16.7
	4	20	8.8	17	8.1
	5	14	6.2	22	10.5

Statistical Analysis

Sect. of core	Variety		Irrigation		VI interaction	
	DW/cm^3	As %	DW/cm^3 with LSD	As % with LSD	DW/cm^3	As %
1						
2			x 8.4			
3			xxx 8.8			
4			x 7.0			
5			xxx 5.0	xx 1.8		

TABLE 3B Second Harvest. Root Length in each section of soil core.

Variety		Gamenya		Karamu	
Irrig. Trg.	Sect. of core	Length cm/cm^3 (10^{-3})	Length/cm^3 as % of total	Length cm/cm^3 (10^{-3})	Length/cm^3 as % of total
T	1	2291	56.3	3640	67.0
	2	988	24.3	944	17.4
	3	485	11.9	505	9.3
	4	140	3.4	182	3.4
	5	165	4.1	161	3.0
			100%		100%
F	1	3760	67.3	4020	67.7
	2	860	15.4	840	14.2
	3	472	8.4	675	11.4
	4	320	5.7	242	4.1
	5	178	3.2	157	2.6
S	1	2708	60.1	2079	55.7
	2	831	18.4	600	16.1
	3	437	9.7	487	13.0
	4	286	6.3	238	6.4
	5	247	5.5	330	8.8

Statistical Analysis

Sect. of core	Variety		Irrigation		VI interaction	
	Length per cm^3	As %	Length per cm^3 with LSD	As % with LSD	Length per cm^3	As %
1						
2						
3						
4			xx 83	xx 1.8		
5			xx 88	xx 2.0		

TABLE 4A Third Harvest. Root Dry Weight in each section of soil core.

Variety		Gamenya		Karamu	
Irrig. Trt.	Sect. of core	D.W. mg/cm^3	D.W./cm^3 as % of total	D.W. mg/cm^3	D.W./cm^3 as % of total
T	1	78	53.8	81	50.9
	2	32	22.1	35	22.0
	3	18	12.4	24	15.1
	4	9	6.2	14	8.8
	5	8	5.5	5	3.1
			100%		100%
F	1	71	52.2	87	53.4
	2	32	23.5	38	23.3
	3	17	12.5	23	14.1
	4	9	6.6	11	6.7
	5	7	5.1	4	2.5
S	1	59	42.8	85	46.4
	2	33	23.9	44	24.0
	3	23	16.7	21	11.5
	4	14	10.1	19	10.4
	5	9	6.5	14	7.7

No statistically significant differences exist.

TABLE 4B Third Harvest. Root Length in each section of soil core.

Variety		Gamenya		Karamu	
Irrig. Trt.	Sect. of core	Length cm/cm^3 10^{-3})	Length/cm^3 as % of total.	Length cm/cm^3 (10^{-3})	Length/cm^3 as % of total
T	1	1548	54.6	1557	50.0
	2	543	19.2	633	20.3
	3	460	16.2	484	15.5
	4	169	6.0	316	10.2
	5	115	4.1	121	3.9
			100%		100%
F	1	1614	57.4	2126	60.0
	2	589	20.9	688	19.4
	3	308	10.9	437	12.3
	4	182	6.5	207	5.8
	5	120	4.3	83	2.3
S	1	1310	48.4	1999	54.9
	2	546	20.2	789	21.7
	3	451	16.7	402	11.1
	4	237	8.8	261	7.2
	5	164	6.1	187	5.1

No statistically significant differences exist

TABLE 5. Glasshouse experiment Root data. Dry Weight (DW), Length (L) and Branches (B) per cm^3 in each section as %age of the total.

Trt. & Sect.	Harvest 1			Harvest 2			Harvest 3		
	DW	L	B	DW	L	B	DW	L	B
KT 1	40.2	57.6	70.6	32.0	34.9	66.0	43.0	45.2	61.6
2	23.3	18.3	13.5	19.1	31.5	7.4	21.8	17.7	12.9
3	19.1	19.4	12.9	22.0	16.8	9.2	13.4	11.9	8.3
4	17.3	4.7	3.1	27.0	16.8	17.4	21.8	25.1	17.3
	100%	100%	100%	100%	100%	100%	100%	100%	100%
KF 1	54.3	64.5	73.4	51.5	53.5	72.8	51.5	58.1	82.6
2	20.5	17.4	11.0	15.2	16.4	12.0	14.9	15.1	9.1
3	10.3	9.8	8.0	15.2	12.0	8.3	14.3	11.8	4.0
4	14.9	9.1	7.6	18.3	18.1	6.9	19.3	15.0	4.3
KS 1	48.1	51.3	56.9	47.0	40.6	62.4			
2	21.3	17.0	15.7	17.5	17.8	14.4			
3	18.7	15.9	14.6	16.9	16.7	12.6			
4	12.0	15.8	12.8	18.7	24.9	10.6			
GT 1	51.2	63.5	81.9	40.8	49.8	71.6	49.3	63.9	84.0
2	21.0	14.2	8.2	14.1	10.9	9.5	16.3	7.1	2.1
3	14.8	13.9	5.3	18.7	18.7	9.2	16.3	15.7	8.3
4	13.0	8.5	4.7	26.3	20.5	9.6	18.2	13.4	5.6

3.1.C. Crop Root Development.

The analysis of root data between harvests for the field experiment is presented on table 6. There is a significant reduction in both total weight and length for all treatments at each harvest but the drop from harvest 1 to 2 is in most cases the greatest. This reduction in root system is predominantly due to decreases in weight and length in the surface layers down to 30cm.

Examination of Figure 2 from the glasshouse experiment shows that this reduction in the root system begins approximately at the time of stem elongation in the crop.

TABLE 6. Statistical analysis of Root data between harvests within treatments, with Least Significant Differences.

Treatment	GT	GF	GS	KT	KF	KS
Total DW	x 162	xxx 88	xxx 72	x 90	xxx 114	xx 64
Total L	x 4062	x 2752	xx 1508	x 2264	xxx2028	
DW by sect						
1	x 47	x 41	x 34	x 29	xxx 37	
2		xxx 8	xxx 14	x 11	xxx 15	x 9
3		xx 9	xxx 11		x 7	xx 11
4		x 5	x 9		xx 6	
5			x 4		x 3	
DW as %						
1					x 4.5	
2					x 2.3	
3					x 2.5	
4			x 1.9			
5	x 1.7					
L by sect						
1	x 1191	x 1338	x 754	x 1161	xxx 961	
2		xxx137	xx245	x 112	x 319	
3		x 117				
4						
5	x 30	x 36	x 55			
L as %						
1				x 7.9		
2						
3				x 3.5	x 2.8	
4	x 1.8			xx2.1		
5	x 1.0	xx 0.9	x 1.5			

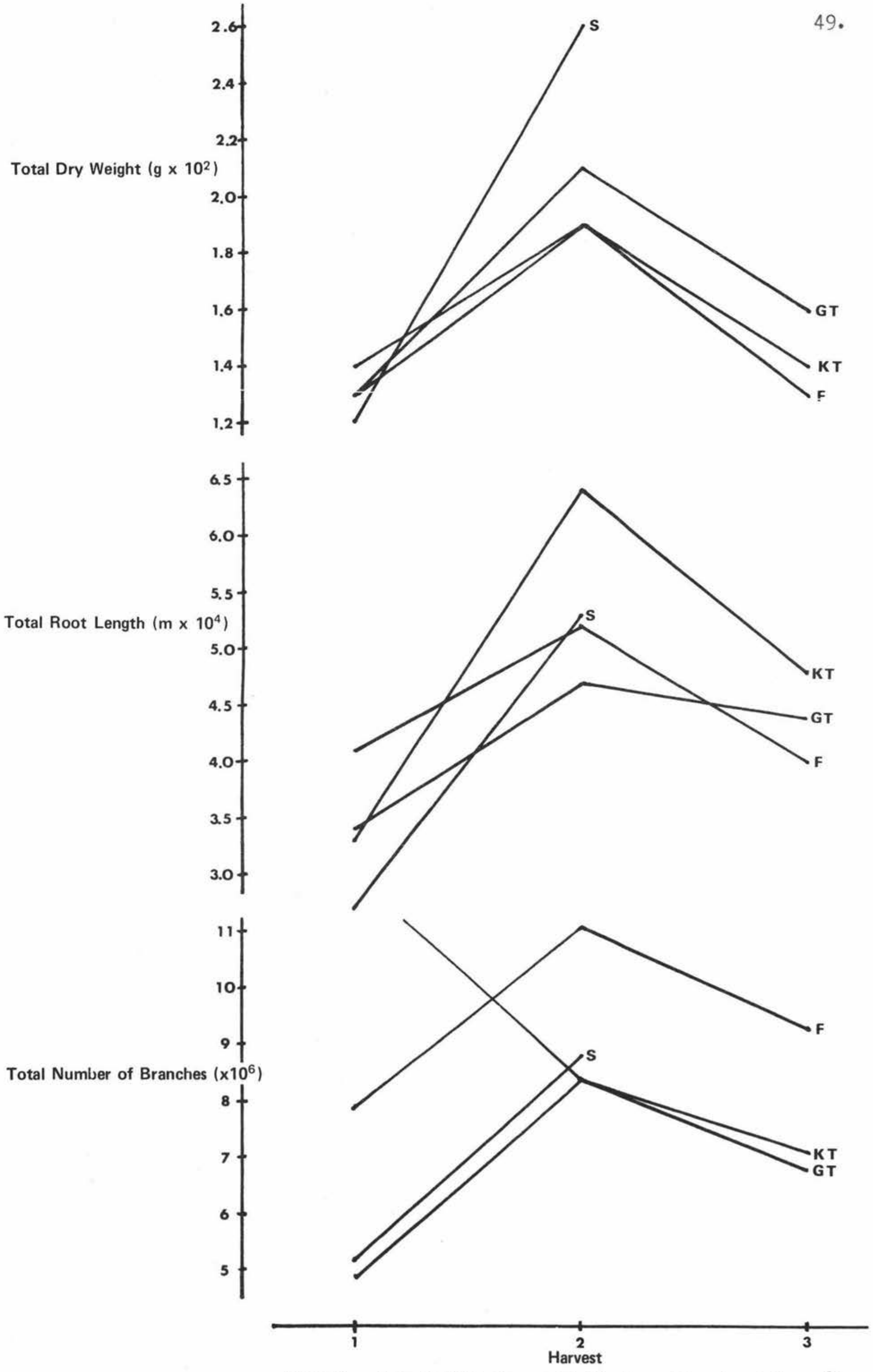

Figure 1 Crop Root Development in Glasshouse Experiment (per m^2)

Note: Only two harvests for treatment S.

3.2 SHOOT RESULTS

Results of shoot measurements are presented for each harvest on tables 7, 8 and 9. It is clear from the first harvest results (Table 7) that the irrigation treatments have distinct effects on shoot development.

Although the initial plant populations did not differ, by the first harvest the F treatments had significantly less plants per unit area. This reduction in plant population is not reflected in the tiller population because the F treatment had significantly more tillers per plant than the other treatments. Nevertheless from a "t test" on the regression coefficients provided for in the statistical analysis the T treatment had significantly more tillers per area (P of<3.1%) than the other treatments. It must also be noted that Karamu initiated more axillary bud development than Gamenya, and F more than T and S although this was not translated into increased tiller numbers per area.

The dry weight productivity was also affected by irrigation treatment allowing for GT having an earlier physiological 'age' than the other treatments. This was due directly to the production of foliage as seen from plant leaf area and LAI results.

The most important result from harvest 1 is the data from apical dissections which showed a significant gradation of decreasing spikelet number from T to F to S. The significant varietal effect can be explained by the earlier harvesting of Gamenya particular GT.

Finally, leaf nitrogen percentage was slightly lower in the S treatment at harvest 1 and from a "t test" on regression coefficients this effect is statistically significant (P of<3.9%).

TABLE 7. First Harvest. Shoot Data

Treatment	GT	GF	GS	KT	KF	KS	Signif. & LSD
Variable							
Initial plant Popn/m^2	795	778	784	745	697	700	NS
Harvest 1.							
Plant Pop/m^2	651	572	656	670	476	602	I xx 54
Tillers/plnt	2.5	2.6	2.2	2.5	2.9	2.1	I x 0.3
Axillary buds/plant	2.2	2.3	1.9	2.9	3.6	2.5	V xxx I x 0.4
Tillers/m^2	1628	1487	1443	1675	1380	1264	NS
DW/m^2	379	485	359	575	436	414	V x I x 62 VI x
Plant Leaf Area (cm^2)	84.3	83.5	74.1	156.4	124.3	76.8	V xxx I xxx 16.3 VI xx
L.A.I.	5.5	4.7	4.8	10.2	6.0	4.6	V xxx I xxx 1.0 VI xx
Stage of Develpmt	3.2	4.3	4.2	4.8	4.6	4.9	V xxx I xx 0.3 VI xx
Spikelet primordia per tiller	15.1	15.5	13.7	17.6	15.4	14.1	V x I xxx 0.8 VI x
Nitrogen % age	4.3	4.0	4.1	4.5	4.0	3.8	NS

Data from the second and third harvests (Tables 8 and 9) continue to show significant treatment effects. The S treatment significantly increased the rate of crop development and this treatment reached flowering approximately 4 days before F which was 2 days before T. Death of tillers occurred from harvest 1 to 2 and after harvest 2 there was only a small decrease to the final ear population which showed no significant treatment differences apart from a suggestion that F had higher ear numbers.

Crop dry weight showed the same treatment gradation as in harvest 1. The difference between T and F was due primarily to their differing tiller populations as the leaf area per tiller was similar; while S was lowest because of a significantly lower leaf area per tiller. Irrigation effects also showed up in the length of the top internode and final crop height.

Ear Data. Ear data from harvest 2 and 3 show a number of important treatment effects. The total number of spikelet sites showed a treatment gradation from T to S as expected from results of apical dissections at harvest 1. The increase in spikelet site number from harvest 2 to 3 indicates that tiller death over this period eliminated tillers with fewer spikelets than average (for the specific crop). Also the number of fertile spikelets showed a decrease from T to F to S. Comparing the count of the number of sterile spikelets at the base of the ear between harvest 2 and 3 it is also apparent that death of tillers eliminated those with more than average sterile spikelets. There was still significantly more sterile spikelets in Karamu than Gamenya which accounts for the lack of difference between varieties in the number of fertile spikelets even though Karamu had more total spikelet sites.

While Gamenya had more florets developed in spikelets at harvest 2, Karamu with a lower total abortion of florets set more grains per spikelet than Gamenya. Finally, the grain number per ear at harvest 3 reflected the effect of irrigation treatment on fertile spikelet number and showed the T to F to S treatment gradation decrease.

TABLE 8. Second Harvest. Shoot Data.

Treatment	GT	GF	GS	KT	KF	KS	Signif & LSD
Variable							
Days to H2	76.8	74.4	70.2	75.6	73.4	69.4	I xxx 1.4 VI x
Ears/m^2	1011	849	924	1028	1084	852	I x 98
Total tillers per m^2	1288	1150	1443	1269	1084	1344	I x 142
D.W./m^2	1651	1493	1342	1657	1437	1167	Ixxx 108
Leaf No/eared tillers	3.3	3.6	3.6	3.3	3.4	3.5	NS
Leaf Area/ eared tiller (cm^2)	58.7	61.9	29.8	63.1	59.6	25.2	I xxx 7.2
L.A.I.	6.1	5.2	2.7	6.4	5.4	2.2	V x I xxx 0.9
Top internode length (cm)	33.6	35.4	31.7	30.4	32.7	31.5	V x I x 1.5
Flag leaf N % age.	3.7	3.7	3.7	3.8	3.4	3.6	NS
Ear Data							
Spklt. sites per ear	17.2	16.0	14.5	18.3	17.4	14.0	V x I xxx 0.6 VI x
Fertile spklts/ear	14.8	14.0	12.6	14.6	14.2	11.0	I xxx 0.7
1st fertile spklt.	3.7	2.9	2.9	4.7	4.2	4.0	V xxx I x 0.4
Fert. florets in central spklt.	3.0	3.3	3.1	2.8	2.9	2.6	V xxx
Fert. florets per spklt at top of ear	1.6	2.1	2.1	1.5	1.7	1.7	V xx I x 0.2

TABLE 9. Third Harvest. Shoot Data

Treatment	GT	GF	GS	KT	KF	KS	Signif. & LSD
Variable.							
Ears/m^2	845	994	945	898	922	882	NS
Crop Height (cm)	100	101	91	78	74	68	V xxx I xxx 3.6
Ear Data							
Spklt sites per ear	18.0	16.3	14.5	18.4	17.7	14.8	V xx I xxx 0.5
Fertile spklts/ear	16.4	14.5	12.6	15.4	14.9	11.9	I xxx 0.6
Spklt positn of 1st grain	2.4	2.7	2.8	3.7	3.7	4.0	V xxx
Grains in 1st fert. spklt	1.9	1.7	1.6	1.7	1.7	1.7	NS
Positn of last grain (from top)	1.2	1.2	1.1	1.3	1.1	1.0	I xx 0.2
Grains in last spklt	1.2	1.4	1.3	1.4	1.5	1.5	V x
Grains in central spklt	2.5	2.4	2.6	2.8	2.9	2.6	V xxx
Grain no. per ear	35.0	29.8	27.1	36.0	34.8	25.9	I xxx 2.1
Yield Data							
Weight per grain * (mg)	36.2	37.3	38.6	39.7	40.8	44.0	V xxx I xx 1.4
Grain Yield per ear (g)	1.27	1.11	1.05	1.43	1.42	1.14	V xxx I xxx 0.09
Grain Yield (g/m^2)	1055	1100	991	1290	1309	995	V x I x 148

* At 13.2% moisture content.

Yield Data Karamu showed significantly heavier weight per grain than Gamenya and a treatment gradation decrease from T to F to S opposite to most other variables. This increased weight per grain of the S treatment nevertheless did not equalise the lowered grain number per ear and the S treatment had significantly lower grain weight per ear than the two other treatments. Karamu had heavier ear than Gamenya because of a higher grain weight.

In total grain yield Karamu outyielded Gamenya. The S treatment had a significantly lower grain yield than the others and F had a slight yield advantage over T due to its slightly higher ear number.

The results from the glasshouse experiment (Table 10) largely support the results obtained in the field, although there was considerably higher initial plant population, almost no tillering and a higher ear number than in the field. Most importantly, apical dissections substantiated the effect found in the field experiment with a treatment gradation decrease from T to F to S in spikelet primordia.

TABLE 10. Harvest data from Glasshouse Experiment.

Treatment	KT	KF	KS	GT
Variable				
Harvest 1.				
Plants/m^2	1357	1411	1321	1339
DW/m^2	197	154	126	216
Leaf Area/plant (cm^2)	40.8	30.9	23.4	39.5
L.A.I.	5.5	4.4	3.1	5.3
Leaf No./plant	4	5	4	5
Plant Development	3.0	2.6	1.9	1.4
Leaf N %age	5.1	5.3	4.4	4.1
Root Water Potential				
at 15cm	0.3	0.4	0.7	0.5
at 45cm	0.4	0.5	0.4	0.4
Harvest 2.				
Plants/m^2	1286	1411	1321	1339
Tillers/m^2	1286	1446	1321	1464
DW/m^2	292	361	233	366
Leaf Area/tiller (cm)	51.5	53.2	36.1	53.7
L.A.I.	7.2	7.5	4.8	6.6
Leaf No./tiller	4	4	5	3
Spiklt Primordia per tiller	16.7	15.0	12.2	16.9
Flag leaf N %age	3.4	4.1	3.6	3.1
Harvest 3.				
Ears/m^2	1179	1179		1250
Flag leaf N %age	4.2	3.3		4.1

3.3 CROP WATER STATUS

3.3.A. Crop Water Budget

The total water irrigated on to T and F treatments is presented below.

TABLE 11. Amount of water irrigated to T and F between 16.10.73 and 4.1.74.

Treatment	GT	GF	KT	KF
Total water irrigated (L/m^2 ormm)	186	140	148	143
Extra water added to covered T plots	24		20	

During this time 136 L/m^2 was added to the T evaporation sub-plots and 34 L/m^2 was added to the F evaporation sub-plot. Rainfall over this period was 130 mm (or L/m^2; see appendix 3). Following normal hydrological practice (pers. comm. D.G. Bowler) 4-5 mm was subtracted from each daily rainfall to allow for interception, suspension in the crop and re-evaporation. This reduces the rainfall to approximately 30 mm which was only slightly more than the amount added to the covered T plots.

From table 11 it is apparent that irrigation treatment T used more water and that GT used more than KT, an effect which was also shown in the glasshouse. (Table 12 below).

TABLE 12. Water usage in glasshouse experiment, 1.3.74 to 31.4.74.

Treatment	GT	KT	KF
Water added per box (L)	93	86	59

3.3.B Plant Water Status

1. **Comparison** between Gamenya and Karamu. The results of this comparison are presented in table 13. In all treatments Gamenya had lower LWP than Karamu. RWP differences were less marked. In most treatments Gamenya had lower RWP

TABLE 13. Varietal Differences in Flag Leaf Water Potential and Root Water Potential (bar)

Associated with each pair of means is the level of significance of the varietal difference.

			Approximate Time of WP Determination			
Irrig. Trt.	Var.	WP	6 A.M. (sunrise)		1 P.M.	
T	G	LWP	-4.1	x	-17.3	NS
	K		-2.8		-15.9	
	G	RWP	-1.1	NS	- 2.4	NS
	K		-1.1		- 2.0	
F	G	LWP	-6.1	x	-17.5	x
	K		-4.0		-14.0	
	G	RWP	-1.5	NS	- 2.7	xx
	K		-1.3		- 3.4	
S	G	LWP	-7.6	x	-17.4	x
	K		-5.9		-18.5	
	G	RWP	-2.6	x	- 5.8	x
	K		-2.2		- 2.8	

than Karamu except for the F treatment at midday where the difference was reversed.

2. Diurnal changes in LWP and RWP of irrigation treatments. From Figure 2 there appear to be three distinct phases in the diurnal cycle in LWP.

(i) A rapid decrease in LWP to 10 a.m.
(ii) A reduced rate of decrease to a midday minimum.
(iii) A rapid rate of LWP increase after 3 pm.

RWP mirrored these changes but not so dramatically. There were treatment differences but they were relatively unimportant in absolute terms.

3, Diurnal changes in EWP, LWP and RWP. The important feature of this comparison depicted in Figure 3 was the 'cross-over' effect when LWP decreased at a more rapid rate and reached a lower minimum than EWP at midday.

4. Glasshouse results during vegetative growth. The results of the determinations taken at harvest 1 and 2 in the glasshouse experiment are presented in Table 14. Apart from low LWP of the lowest leaves which could be due to senescence, there was the expected gradation of decreasing LWP up the stem. Once again LWP of Gamenya was lower than Karamu. Also of importance was the gradation of decreasing RWP from T to F to S. These values gave some indication as to the water potential in the apex at the time of floral primordial development during the field experiment.

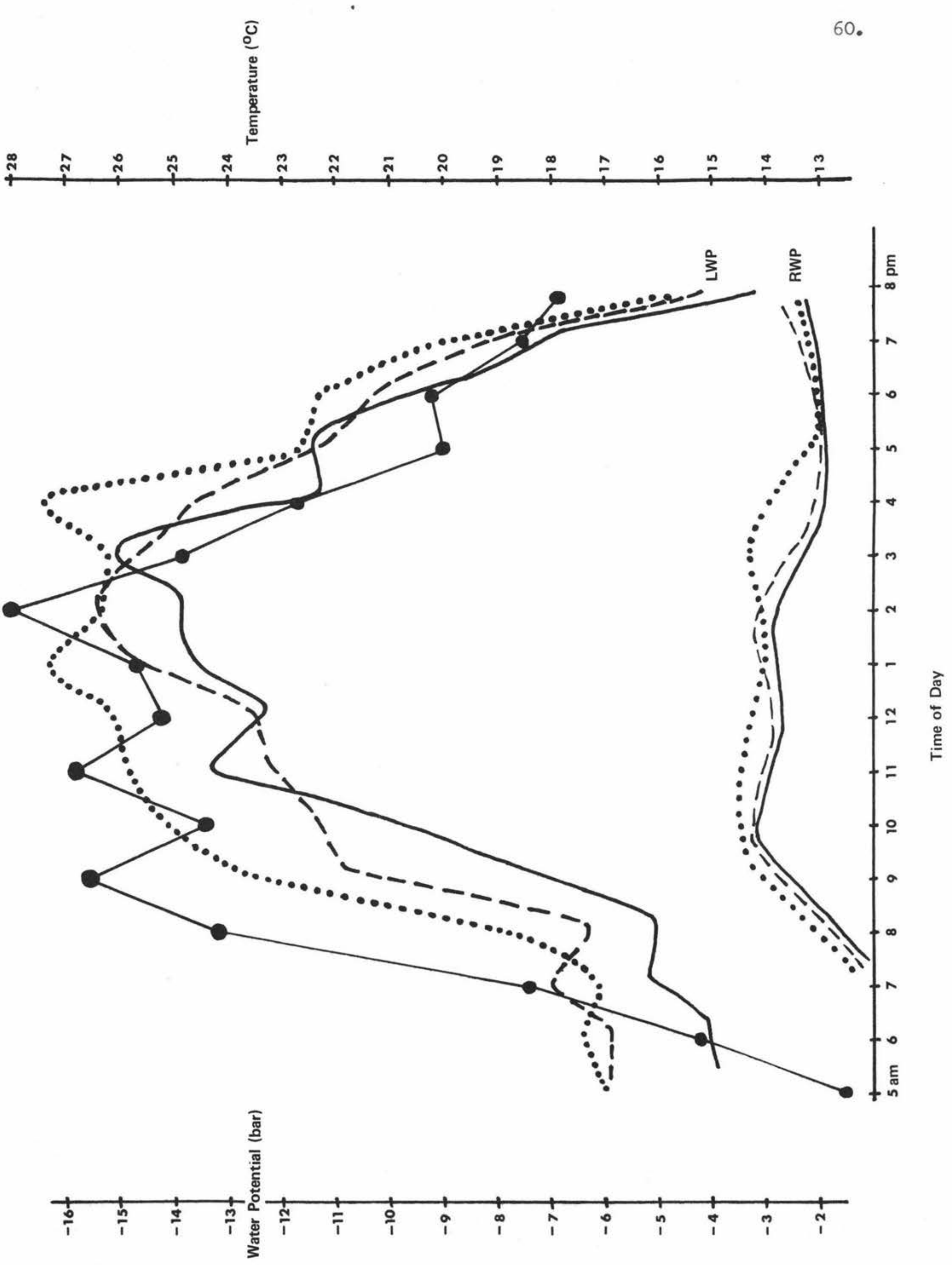

Figure 2. Diurnal Change in Flag Leaf Water Potential (LWP) and Root Water Potential (RWP) of T, F, and S Irrigation Treatments obtained during the Grain Filling Stage of the Wheat Crop.

Key:
●—● Temperature
— — F treatment
—— T treatment
• • • • • • S treatment

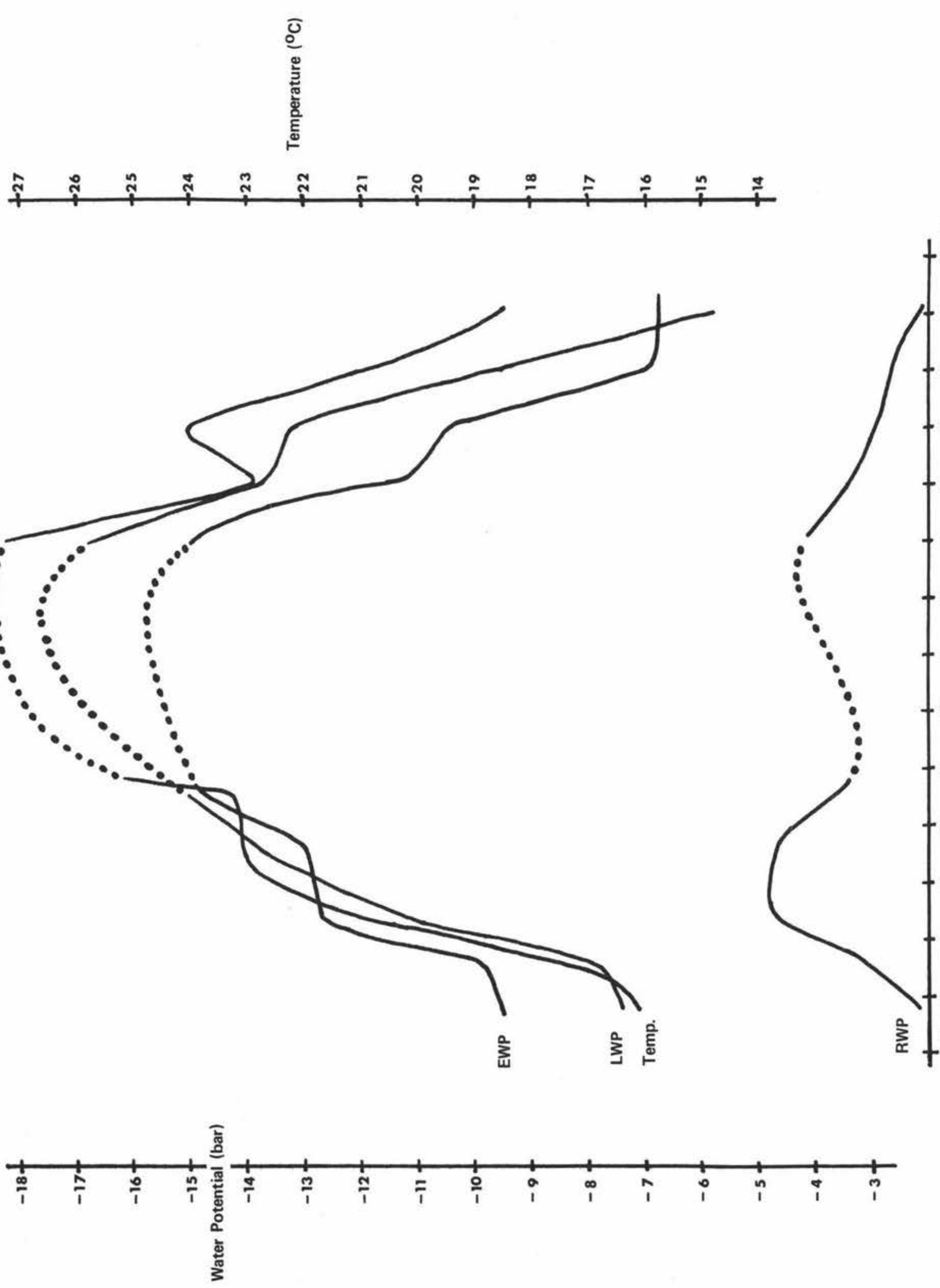

Figure 3. Diurnal Change in Flag Leaf Water Potential (LWP), Ear Water Potential (EWP) and Root Water Potential (RWP) obtained during the Grain Filling Stage of the Wheat Crop (Dotted lines are estimates)

TABLE 14. Water Potential Measurements from Glasshouse Experiment

Treatment	KT	KF	KS	GT
<u>Measurement</u>				
Harvest 1.				
LWP 1*	-3.1	-3.7	-6.1	-4.0
LWP 2	-3.0	-3.5		-3.8
LWP 3	-3.9	-4.7		-5.8
RWP	-1.2	-2.6	-3.7	-1.1
Harvest 2.				
LWP 2		-3.9	-5.0	
LWP 3		-3.6	-3.7	-5.7
LWP 4	-2.8	-4.8	-3.5	-7.5
LWP 5	-5.9	-5.4	-3.6	
LWP 6		-5.7		
RWP	-1.8	-2.2	-3.0	-2.0

* refers to leaf position number i.e. leaf 1.
Blank positions indicate either dead or dying leaves; or immature leaves.

CHAPTER 4 DISCUSSION

4.1 INTRODUCTION

Before formally discussing the results some points relating to the conduct of the experiment and the methods used need clarification and qualification.

4.2 EXPERIMENTAL METHODS

4.2. A Root Sampling

The core sampling of the root systems and the medium-pressure washing out of the cores involved an inevitable loss of fragmented root members and fine lateral roots. Visual inspection of washings suggest that this loss was significant particularly with regard to root length. Thus quantitative comparisons with published results cannot be safely made unless the methods of sampling are identical (Troughton 1962). It is assumed that in this experiment the errors were constant across the experimental treatments.

Secondly, although the corer could not be taken down to the maximum rooting depth, an approximate 1 metre-deep core was taken and it is therefore safe to assume that over 90% of the root system was being sampled (Troughton 1962, Welbank & Williams 1968, Kirby & Rackham 1971).

Finally, compaction of the core was slight, provided coring was stopped when movement through the soil was markedly reduced. Appendix 4 describes the corer and its use. Core compaction was assessed by comparing the length of the core with the depth to which the corer had been driven. Adjustments were made in sectioning the core if noticeable compaction had occurred. This arose only in a few instances during harvest 1.

4.2. B Shoot Results

Rusting of the crop was first noticed in GS plots following the second harvest and by the third harvest all plots were infected although Karamu was markedly less affected than Gamenya. This may partially account for Gamenya's lower grain weights, although the S treatment which was the worst infected of the irrigation treatments had highest grain weights.

4.2.C Crop Water Budget

The measurement of soil water status by tensiometer is now a recognised and respected technique under high soil moisture conditions. The relationship between soil water potential measurements by tensiometer and gravimetric moisture content determination is discussed in appendix 9.

As noted in section 3.3.A water loss by T evaporation sub-plots gives meaningless results probably due to the complete difference in the microenvironment. Nevertheless the evaporative loss from the T treatment plots must have been a considerable proportion of the total evapo-transpirative loss accounting partially for the greater water use by the T treatment crops. For the F treatment not more than 20% of crop water loss was soil evaporation.

4.2.D Plant Water Status

While the pressure bomb technique is widely used for measurement of leaf water potential, use of the technique to measure the water potential of other plant parts is less common (Gee et al. 1974). Pressure bomb measurement of root water potential has in the past produced variable and questionable results (De Roo 1969, Gee et al. 1974).

Measurement of root water potential in this experiment involves important differences with previous work. Firstly, the plants were grown under field conditions. Secondly, because the plant was torn from the soil, only a small proportion of the root system was removed with the plant and damaged root system at that. Thirdly, the plant was not detopped until after removal from the soil.

Cutting the xylem during periods when the plant is transpiring results in the release of tension in the transpiration stream, and presumably water potentials of vacuolar sap in cells surrounding the xylem are able to equilibrate with that in the xylem. By detopping the plant after removal from the soil, the tension in the xylem is released as a function of the transpirative demand from the shoot (i.e. as a function of the water potential gradient which "drives" the transpiration stream). Hence the result obtained (by measuring the water potential by the pressure bomb technique) is an indication of the steepness of the water potential gradient across the shoot and the root system prior to the removal of the plant from the soil. Thus the value is called Root Water Potential (RWP) for this reason, i.e. it is an indication of the potential gradient which leads to water uptake by the root system.

Also because the xylem water partially equilibrates with the surrounding cellular (symplastic) water, an indication of the water potential of the tissue in the crown region is obtained. This can be used to infer the water status of the shoot apex during vegetative growth and early reproductive development before the stem elongates.

4.3 IRRIGATION TREATMENT EFFECTS

As a basis for discussion of the results it is necessary first to define the effects of the irrigation treatments in terms of their relationship to plant development as a whole.

While the spatial distribution of soil water and root system differed between the treatments, the basic difference in whole plant terms was the differing availability of water to the shoot. This is quantified in the water status data of Tables 13 and 14. Plant water potential was higher in the T treatment than the F treatment which was higher than the S treatment. Thus the shoot growth data (Tables 7 to 10) displays patterns of development which are explained by considering the treatments as providing increasing levels of moisture stress from T to F to S (Slatyer 1969, Wardlaw 1971). Slatyer (1969) describes most of the effects of moisture stress on crop characters and these are shown in this case e.g. decreased tiller numbers, reduced D.M. production, reduced crop height, reduced leaf area, decreased reproductive primordia, accelerated rate of development and reduced yield.

These effects are displayed despite the fact that soil water potential in the profile below 15 cm in treatments T and F was not allowed to fall below -1 bar, while in the S treatment the water potential at 15 cm did not reach -1 bar until immediately before the first harvest i.e. the crops were growing in soil of 'high soil water potential' (Turner 1974) in all treatments.

4.4 ROOT SYSTEM GROWTH AND DEVELOPMENT

4.4.A. Root Growth and Distribution

At first sight the results of root growth and distribution particularly Tables 2A, 2B, 3A, and 3B support the widely held conclusion that root growth operates to orientate the root system to the water supply. Thus the T treatment had a more surface rooted crop than the S treatment. The results of the glasshouse experiment however (Table 5), showed no treatment effects on root distribution at all, and recent research findings suggest that this conclusion is erroneous.

Many workers (e.g. Barley et al. 1965, Taylor & Ratliff 1969, Lawlor 1973) have found that root growth is insensitive to very low water potentials possibly because the resistance to movement of water across the rhizosphere is small even when the soil is depleted almost to the permanent wilting point (Newman 1969 a & b, Hansen 1974), and hence water uptake for elongation (Greacen & Oh 1972) will be relatively insensitive to soil water potential. Thus soil water potential gradients which operated in this experiment (not greater than 2 bars, app.9) are highly unlikely to have caused the marked effects noted in Tables 2A & B.

The possibility that the root distribution was determined by the availability of mineral nutrients causing localised branching (Hackett 1972, Drew et al. 1973) must be considered although this probably cannot explain the differences between the field and glasshouse experiment where in both cases fertiliser application was confined to the surface layers of the soil profile.

The results support the conclusion that root distribution is primarily determined by soil compaction, and associated aeration properties of the soil profile (Barley et al. 1965, Greacen & Oh 1972). The crops in the glasshouse grew almost uniformly distributed root systems in soil which was essentially uncompacted because of the way in which the large boxes were filled with soil. Thus the probable reason why the field crops showed a greater concentration of their root systems in zones of high soil water content was because in wetter soil zones root elongation was less limited by mechanical resistance (Greacen & Oh 1972).

Nevertheless the mechanism by which the roots proliferated at lower depths in S is not completely clear. Root development is a function of both extension growth and lateral root production. The greater root length below 45 cm in the S treatment suggests that a higher rate of branching occurred in this zone, a proposal which is supported by the results of the glasshouse experiment (Table 5). Understanding the underlying mechanism causing this response is made difficult because this glasshouse effect, if real, occurred in the probable absence of soil compaction. The effect may have been due to an increased availability of mineral ions in this zone due to the higher water status, although this seems unlikely since the availability of minerals (especially potassium, Hackett 1968) in this zone, even with water, seems unlikely to be greater than in the surface layers which show relatively less root system compared with F and T.

Perhaps the initiation of lateral branches is sensitive to small differences in soil water potential surrounding the root. Water stress may mediate by directly affecting the increased metabolic activity in the root branching zone which precedes lateral initiation (Drew et al. 1973). Thus lateral initiation may have been suppressed in surface layers by the lower soil water potential.

The other interesting effect shown in Tables 1, 2A, 2B, 3A and 3B is the greater development of the F treatment root system particularly in terms of an increased root length in the profile above 45cm. This response was composed of 2 factors:-

(i) an increased nodal root production which resulted from the increased tiller initiation. This is discussed in section 4.5 A which follows.

(ii) an increased root branching in the F treatment (see Figure 1).

An explanation of the increased branching in the F treatment can only be speculative. Perhaps the T treatment resulted in a higher rate of leaching of minerals particularly nitrogen from the surface layers; thus nutrient-stimulated lateral branching was lower when compared with the F treatment. Perhaps there is a water potential optimum for lateral initiation. Studies of the relationship between water status and lateral initiation do not appear to have been conducted, and, in general, literature concerned with the affect of environmental factors on lateral initiation is particularly scarce (see Hackett 1969).

4.4.B Root Development

Consistent with the findings of numerous workers (Troughton 1962), the root system displayed a decrease in weight and length from first to final harvest (Table 6). The major decrease followed the stem elongation phase (Figure 2) and is explained in terms of the decreasing availability of assimilate at this time (see section 1.3.1.B).

More interesting are the results of Tables 1, 4A and 4B which show all treatments for each variety, having a similar root system at harvest 3. The reduction in the root system is mainly a result of a reduction in weight and length in the surface layers down to 30 cm, which strongly suggests that root death is more prevalent in higher order lateral roots rather than death of main roots, which would show a decrease in root system throughout the profile.

4.4.C. Varietal Differences

This study, similar to that of Lupton et al. (1974) showed no outstanding differences between the root system of a semi-dwarf compared with a standard height type. Lupton et al. (1974) suggested that the root system of the semi-dwarf is more extensive at depth, and this was shown in this study (Tables 2A & 2B). However this effect is not marked and may possibly be due to Gamenya distributing a higher proportion of its root system above 45 cm.

Two minor root system characteristics of Karamu are of interest. Firstly, Karamu displayed a more marked response to irrigation treatment than Gamenya (Tables 1, 2A & 2B). Secondly, although the effect is not highly significant, Karamu retained more of its root system to final harvest (Table 1). This is possibly related to the increased availability of assimilate for plant 'sinks' other than the ear in awned varieties (Evans & Rawson 1970) and hence Karamu was able to retain and maintain more root system during the post-anthesis stages.

4.5 SHOOT GROWTH AND INTERRELATIONSHIPS WITH THE ROOT SYSTEM

4.5.A Vegetative Development

As noted in section 4.3, some of the features of plant development compared between the three irrigation treatments can be explained in terms of the effects of moderate levels of water stress (Slatyer 1969). Not all the differences can be explained in this way, for the pattern of tillering displayed treatment effects which were unrelated to the direct effects of moisture stress (see Aspinall et al. 1964).

The reduction in plant population up to harvest 1 was most marked in the F treatment and yet the total tiller populations reflected the increasing moisture stress gradation from T to F to S. A mechanism appears to exist in the F treated crops which favours the survival of primary tillers of certain plants at the expense of main tillers of smaller plants. Competition for light is assumed to be the cause of plant death during this period (Puckridge & Donald 1967) but it cannot explain the response completely since the more profusely tillered plants in the F treatment have a lower plant leaf area than those in the T treatment. Therefore competition for light cannot be the sole mechanism by which larger plants, in terms of leaf area, dominate and suppress their less well endowed neighbours.

The competitive effect is possibly mediated by the root system, as the F treatment had a distinctly better developed root system in terms of root length than the other treatments, particularly with Karamu which displayed a more marked reduction in plant number and a higher per-plant tiller number than Gamenya. It is unlikely that the more extensive root system plants had a decisive advantage in the uptake of minerals since this would have been reflected in an increased leaf area, or an increase in leaf nitrogen percentage, neither of which were displayed. Water uptake may have been improved slightly but this effect is probably not of major significance, particularly when comparing the T and F treatments.

It is suggested therefore that the F treatment root system was responsible for an improved supply of growth regulators to the stem, principally cytokinins and GA, thus increasing tillering and tiller survival. While there is no direct evidence to support this hypothesis forthcoming from this study, it is not mere speculation, because some indirect evidence is available; nor is it a valueless exercise, since understanding the control of both tiller development and survival becomes a necessity if we are to increase yields by increasing ear populations (Dougherty & Langer 1974).

Firstly, the assumption must be made that an increased length of the root system is indicative of an increased number of root apices. This is a reasonable assumption supported by the glasshouse experiment, the work of Evans (1970), and the theory of coordination of root growth proposed by Hackett (1969, 1971, 1972, Hackett & Rose 1972). Root apices are widely agreed to be the main sources of synthesis of growth regulators produced by the root system (Jones & Phillips 1966, Short & Torrey 1972, Atkin et al. 1973, Sheldrake 1973).

Thus presumably an increase in root apices per plant results in an increased output of growth regulators from the root system and a higher concentration in the stem of the plant. Hence the higher tiller numbers and initiated axillary buds of the F treatment plants (Table 7), can be explained by the greater concentration of cytokinin which has been shown to initiate the development of the axillary bud (Langer et al. 1973), although cytokinin does not sustain growth of the tiller. This is presumably the role of GA (Kirby & Faris 1970, 1972, Gale 1974) which acts to mobilise assimilate to meristematic sites (Kirby & Faris 1970, 1972, Adams et al. 1973).

Initiation of each axillary bud results in nodal root production, regardless of whether the initiated bud develops into a tiller (Soper & Mitchell 1956). This has the effect of both increasing the size of the plant root system and increasing the number of root apices. This gives the plant a competitive advantage over less well developed neighbours. Thus the higher per-plant tiller numbers of the F treatment and its lower plant numbers can be explained hypothetically by the combined effect of plant competition and supply of growth regulators.

Further senescence of whole plants and tillers, occur in the reproductive stage.

4.5.B. The Reproductive Phase and Crop Yield.

(i) The Process of Determination of Ear Number.

Some tiller death occurred during the period after anthesis (i.e. between harvest 2 and 3) but these tillers were showing signs of senescence by harvest 2. The reduction in ear number following flowering was probably significant only in the T treatment although the effect was slight. This study is in agreement with previous work e.g. Riveros-Rodriguez (1968), Rawson and Donald (1969), with tiller senescence occurring predominantly in the stem elongation phase due primarily to competition for assimilate within the plant which is accentuated by competition for light (Puckridge 1968). The death of tillers was not at random, but resulted from competitive suppression, as indicated by data of Tables 7, 8 and 9 where tiller death operated to eliminate tillers with fewer than average spikelets, and, after Harvest 2, with a higher than average number of sterile spikelets.

GA appears to play a central role in assimilate distribution within the plant (Kirby & Faris 1970, 1972) although its action is mediated by phytochrome (Jones 1973) and possibly other unknown factors (Adams et al. 1973) also as noted previously the role of GA in semi-dwarf wheats is confused particularly with respect to stem elongation (Gale & Marshall 1973, Gale 1974).

In spite of possible moisture stress effects the F treatment retained a higher ear number than T (and S). This occurred despite the F treatment's markedly lower LAI when compared with T. Thus presumably growth regulator mediation can determine tiller survival in the face of internal competition for assimilate. Possibly increased GA levels in standard height wheats increased the photosynthetic rate in leaves and thus plants with an improved growth regulator status can compensate for lower leaf area by increasing their photosynthetic rate (Treharne & Stoddard 1968, Wareing et al. 1968). Research into this area of the action of GA during the stem elongation phase could be of great assistance in understanding the control mechanisms determining survival of tillers.

The importance of ear number as a component of yield cannot be overrated, because in general, variation in the density of ears accounts for most of the differences in grain yield between wheat crops (Dougherty & Langer 1974). For example . crop yield in this experiment was roughly three times that of Clements et al.(1974) conducted in the previous year; a difference which can be attributed almost completely to the ear population being three times higher in this experiment.

(ii) Ear Development and Yield of Grain

The initial primordial spikelet number appears to be closely related with the moisture stress of a given treatment (Tables 7 & 10). There were maximum spikelet primordia of 17-18 in the T treatment with a gradation to 13-14 in the S treatment. Assuming that RWP measurements obtained from the glasshouse study (Table 14) are a reliable guide to the water status of the apex during the period of primordia formation in the field, then this decrease of 4 spikelets from T to S occurred in response to a water potential decrease of only 2 bars (i.e. from approx. -1.5 bar to -3.5 bar). Thus as shown by Langer and Ampong (1970) the production of spikelet primordia is quite sensitive to moisture stress.

The further development of the ear is probably influenced by other factors. With an almost constant two infertile basal spikelets in Gamenya ears and three in Karamu for each treatment, the number of fertile spikelets, i.e. grain bearing spikelets, was linearly related to the results of the apical dissections and showed the T to F to S gradation. Thus if inhibitory influences on spikelet fertility are operating in a wheat ear (Evans _et al_. 1972) they are independent of moisture stress in the range studied in this experiment. Likewise, viability of florets from harvest 2 to 3, which was similar in all irrigation treatments, suggest that inhibitory influences on grain set in florets operate independently of moisture stress in the range studied in this experiment; hence grain numbers per ear were related linearly to initial spikelet primordia.

An interesting feature of development is the _increase_ in grain weight from T to F to S. The cause of this effect is not clear. It does not necessarily suggest that there was a "source" limitation in the T and F treatments; considering the evidence for "sink" limitations to yield it is more probable that the capacity of the grain to accept assimilate may have been lower than in the S treatment. The possible causes of this must remain speculative. The evidence of a correlative inhibition between developing grains (Rawson & Evans 1970) suggests that the fewer the number of florets the more enhanced is the development of the remaining florets, presumably by an ability to construct a larger endosperm capacity either in physical or metabolic terms. This effect would be restricted to the period within 10 days following anthesis when the endosperm tissue is completely formed (Percival 1921, Buttrose & May 1959, Frazier & Appalanaidu 1965).

The increased grain weight of the S treatment was insufficient to overcome the lower grain number of this treatment. While T had the highest ear weight, the F treatment had slightly higher yield due directly to its greater ear population.

4.5.C. Varietal Effects

The yield advantage of Karamu over Gamenya (Table 9) is due to the higher grain weight per ear rather than an increased ear number. Similar ear numbers occurred in spite of Karamu's higher LAI, thus further supporting the hypothesis that the period of stem elongation is less a period of direct assimilate competition between tillers due to insufficient leaf area, than a stage where survival of tillers is determined by their ability to stimulate the photosynthetic rate of the present leaf area, similar to the stimulation of flag leaf photosynthetic rate by the ear (Evans & Rawson 1970). Norin 10 derivatives and other lines derived from true genetic dwarfs are insensitive (for some processes) to their high endogenous levels of GA (Gale & Marshall 1973), and possibly GA stimulation of photosynthetic rate (Wareing <u>et al</u>. 1968) may be affected (see previous section 4.5.B (i)). Could it be that by the present universal selection for small stature we are selecting against the possibility of improving ear numbers? The reduction in photosynthetic rate and tiller numbers in the evolution of the modern wheat plant (Evans & Dunstone 1970) could be causally linked by the GA status, although Evans and Dunstone (1970) ascribe this effect to unspecified "apical dominance" being more strongly developed in the modern wheats.

The 9% (S treatment) to 28% (F treatment) advantage in weight of ears which Karamu displayed over Gamenya may not be related to the increased spikelet primordia which Karamu produced, because there was no varietal difference in the number of fertile spikelets, Karamu having more basal spikelets infertile. Karamu's yield advantage was derived primarily from a higher level of floret viability, which gave a higher grain number per ear (except in the S treatment), and an increased grain weight.

The results of this study are typical of those obtained in other temperate situations particularly New Zealand, with the semi-dwarf producing a relatively small ear (Gandar 1970, Dougherty <u>et al</u>. 1973, Clements <u>et al</u>. 1974). Gandar (1970) reports one of the largest eared crops for New Zealand conditions obtained with Pitic 62 grown under very low density. The ear averaged 18 spikelets with 54 grains, although grain weights were extremely low. Compared with spikelet numbers of 25 and grain numbers up to 60 reported overseas (e.g. Rawson 1970) the results obtained in New Zealand seem disappointingly low.

This reduced number of spikelets can probably be attributed directly to the effects of both seed and seedling vernalisation which is almost certain to occur under temperate i.e. New Zealand conditions (Wall & Cartwright 1974, Halse & Weir 1974). Vernalisation of Norin 10 derivatives reduces the length of the reproductive phase and accelerates the entire reproductive process (Wall & Cartwright 1974). The effects of accelerated reproductive development are not completely known but certainly growth of the floral primordia has been shown to be extremely sensitive (Kirby & Faris 1970, Rawson 1970, Single 1964). Floret survival is also affected (Langer & Hamif 1973) as is tiller survival (Kirby & Faris 1970, 1972). Halse and Weir's (1974) experiment is worth further investigation in New Zealand because by using unvernalised seed of semi-dwarf Mexico 120, they increased spikelet numbers by over 30% to a maximum of 26 and increased the number of days to floral initiation by approximately 20% i.e. they reduced the rate of plant development by using unvernalised seed.

Whether florets per spikelet and grain weight would increase if the reproductive phase was lengthened is not clear because of evidence for negative correlations between spikelet number and grain weight (Syme 1970, Rawson 1970) in semi-dwarfs. This may be related to the floret inhibition effect mentioned previously (sect. 4.5.B. (ii)), for plants with high spikelet numbers but low florets per spikelet show higher grain weight. Nevertheless the varietal differences in grain weight in this experiment do not show this effect and until the mechanism of floret inhibition of "sink" capacity is understood an explanation will not be forthcoming.

4.6 WHEAT PLANT WATER STATUS

4.6.A. Varietal Effects

Gamenya used more water than Karamu. Since Karamu generally had a greater LAI, greater leaf area per plant, and a slightly greater root length, the effect would appear to be due to the lower leaf water potential which Gamenya leaves develop (Tables 13 & 14). In this way the water potential gradient is larger in Gamenya and this leads to an increased loss of water from the crop. This conclusion needs further investigation since it contradicts the belief that crop water usage is linearly related to leaf area. The effect could be due to altered micrometeorological conditions and hence altered evaporation of soil moisture although the fact that Gamenya is generally a taller crop during most stages of development would tend to operate against this suggestion.

4.6.B. Dynamic Water Relations of the Crop Plant

Research in the field of plant water relations is at present largely concerned with defining the resistances to water movement in the soil-plant-atmosphere system. It is assumed that the flow of water through the plant conforms to a relation analogous to Ohm's Law where the resistance can be calculated by dividing the water potential gradient across two points in the system by the transpiration rate (Richter 1973). The pathway considered most often is from the soil through the roots to the leaves (Janes 1970).

While measurement of total plant transpiration is not difficult, quantifying the potential gradient through the soil-plant-atmosphere system or the "driving force" to transpiration in practical terms involves numerous difficulties. The most widely used technique is to measure either the LWP of one leaf, generally the youngest mature leaf, or all the leaves and average the result (Janes 1970); the soil water potential is then subtracted from this value to give the potential gradient. But is this valid? There are a number of objections to this approach to determining the water potential gradient.

(i) Under conditions of high transpiration rates the water pathway through the leaves and roots is apoplastic (Boyer 1974). Excision of a leaf breaks this continuous stream of water and presumably the transpiration stream equilibrates with the symplasm in terms of water potential. Hence the water potential measured by a method needing prior excision, is too high and this possibly explains the large changes in internal resistance which Janes (1970) found when potential gradients were altered within the plant. Nevertheless because the apoplasm and symplasm are in diffusional connection this measurement of LWP is probably an indicator of xylem water potential.

(ii) Transmission of water potential changes is assumed to be instantaneous and transmitted by the water in the apoplast (Spomer 1968). One may wonder therefore whether reductions in potential of each leaf on the plant consequent upon its diurnal fluctuation in LWP (Figure 2, 3, Yang & de Jong 1971a) should be averaged as at present, or whether they should be summed to provide a true estimate of the increasing gradient which the shoot transmits to its root system as the day progresses and leaf water potentials decrease.

To cast some light on this point it is worth quoting here some unpublished results of water potential measurements taken in the glasshouse two weeks after seedling emergence. At this stage Karamu had three leaves and Gamenya had two. The mature first leaves of Karamu had a higher water potential than Gamenya as expected (-5.1 bar to -6.2 bar). The RWP showed the reverse pattern with Karamu having a lower root water potential than Gamenya, -2.2 bar to -1.6 bar The inference from this is that the crown and roots of the Karamu plant had a lower water potential because of the transmission to the roots of the LWP of the extra (third) leaf.

Objections to this type of experiment are obvious, e.g. the comparison of different varieties, the RWP differences may not have been significant, etc. Nevertheless if the movement of water is considered in purely physical terms this result, if real, is not easily explained if the potential gradient is calculated by averaging the leaf water potentials of each leaf on the stem.

(iii) A water potential gradient exists up the stem in the absence of transpiration (i.e. at night) effected by osmotic potentials (Turner & Begg 1973) and hence the gradient causing transpiration is probably more influenced by turgor potential changes rather than total LWP. Unfortunately at present the measurement of turgor potential must be inferred from measurements of total LWP (and osmotic potential).

Information on transpiration of individual leaves on a transpiring plant under natural conditions is non-existent at present largely because of the difficulty of measuring transpiration without affecting the water and metabolic status of the leaf in the process (Kramer 1969). Lack of information on this point is holding up real progress towards improving the theory of plant water relations for assistance in considering how to predict and control crop water use.

The inverted potential difference between the flag leaf and ear (Figure 3) is extremely difficult to interpret in the absence of knowledge concerning the transpirative loss from each structure. The water pathways are connected (probably at the node below the flag leaf node O'Brien & Zee 1971) and hence this difference which can range up to 6 bar (unpublished data) is not easily explained. Three questions are raised in understanding this inverted water potential difference.

(i) Does this difference between flag leaf and ear indicate an underlying physiological purpose?

(ii) Is the effect unimportant?

(iii) Does it result ~~from measurements~~ from measurements of water status which are physiologically suspect.

A theoretical case can be made to support the latter two conclusions, but the possibility that there is an undiscovered physiological role involved is not thereby disproved. If the flag leaf is removed from the stem during a period when the leaf is transpiring, a water potential decrease is observed in the ear within 30 minutes (unpublished data). The question which arises from this is, whether the flag leaf can increase the flow rate in the xylem above that needed to satisfy its own transpiration, thus decreasing the water stress in the ear following emergence of the ear during crop development. Answering that is completely beyond the limits of this experiment, and of the present literature.

4.7 CONCLUSION

This study of root and shoot development of the wheat crop plant has pinpointed two areas of research which should receive priority.

1. The action of GA in tiller development and "source-sink" relationships in the vegetative and early reproductive stages.
2. Vernalisation and its interaction with grain yield.

From consideration of the interrelationships between the root and shoot growth it is apparent that not only does the root system function in supplying the plant with water and nutrients, but also it is an important source of growth regulators which mediate in [illegible] development of the shoot.

Finally, in comparing the two varieties Gamenya and Karamu, it is apparent that the semi-dwarf displayed greater sensitivity to the environmental changes, or in other words, its growth was more "plastic" in terms of morphological adaptation to the different water regimes.

APPENDIX 1

LAYOUT OF FIELD EXPERIMENT

The layout of plots on the experimental site is shown in Figure 5 on the following page.

With reference to the sub-irrigated treatment (sect. 2.2) the diagram below (Figure 4) indicates the layout of the system in the plot.

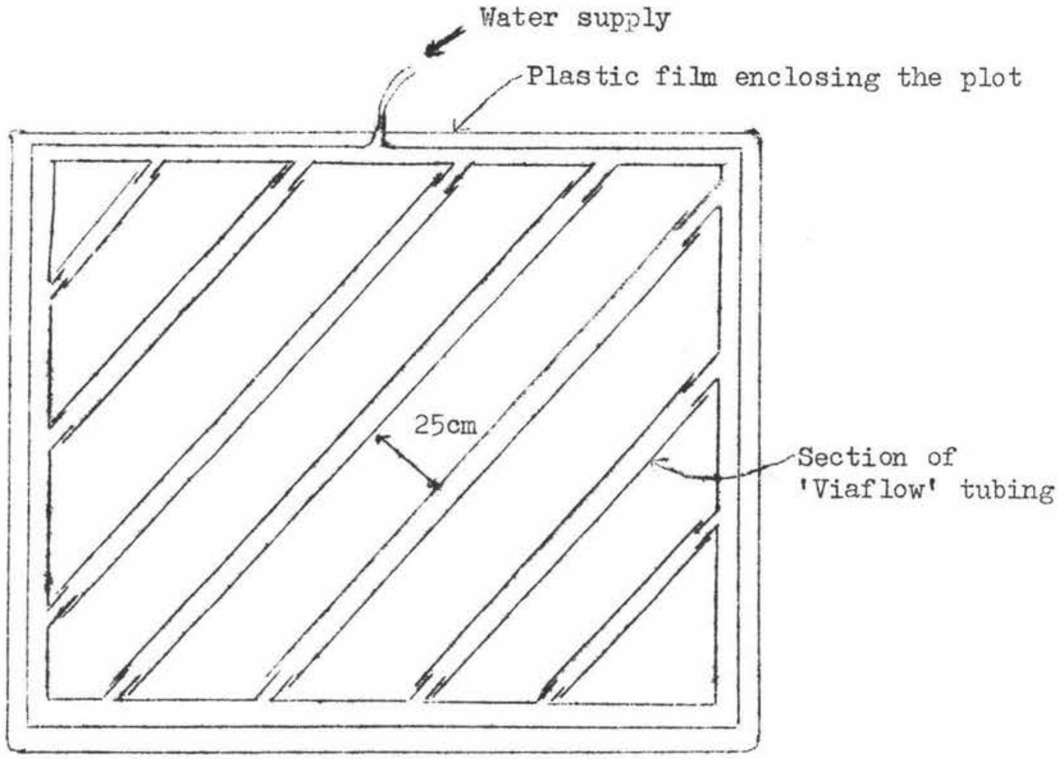

Figure 4. Layout of sub-irrigation system of "Viaflow" tubing buried in each S treatment plot.

The system was not completely effective in distributing water evenly into the soil profile at 40cm. In the process of burying the tubing some sections became crushed and water did not flow in them. Also leaks occurred where the tubing and adaptor was joined to the alkathene feeder pipe. Nevertheless as data from appendix 9 shows the system worked satisfactorily.

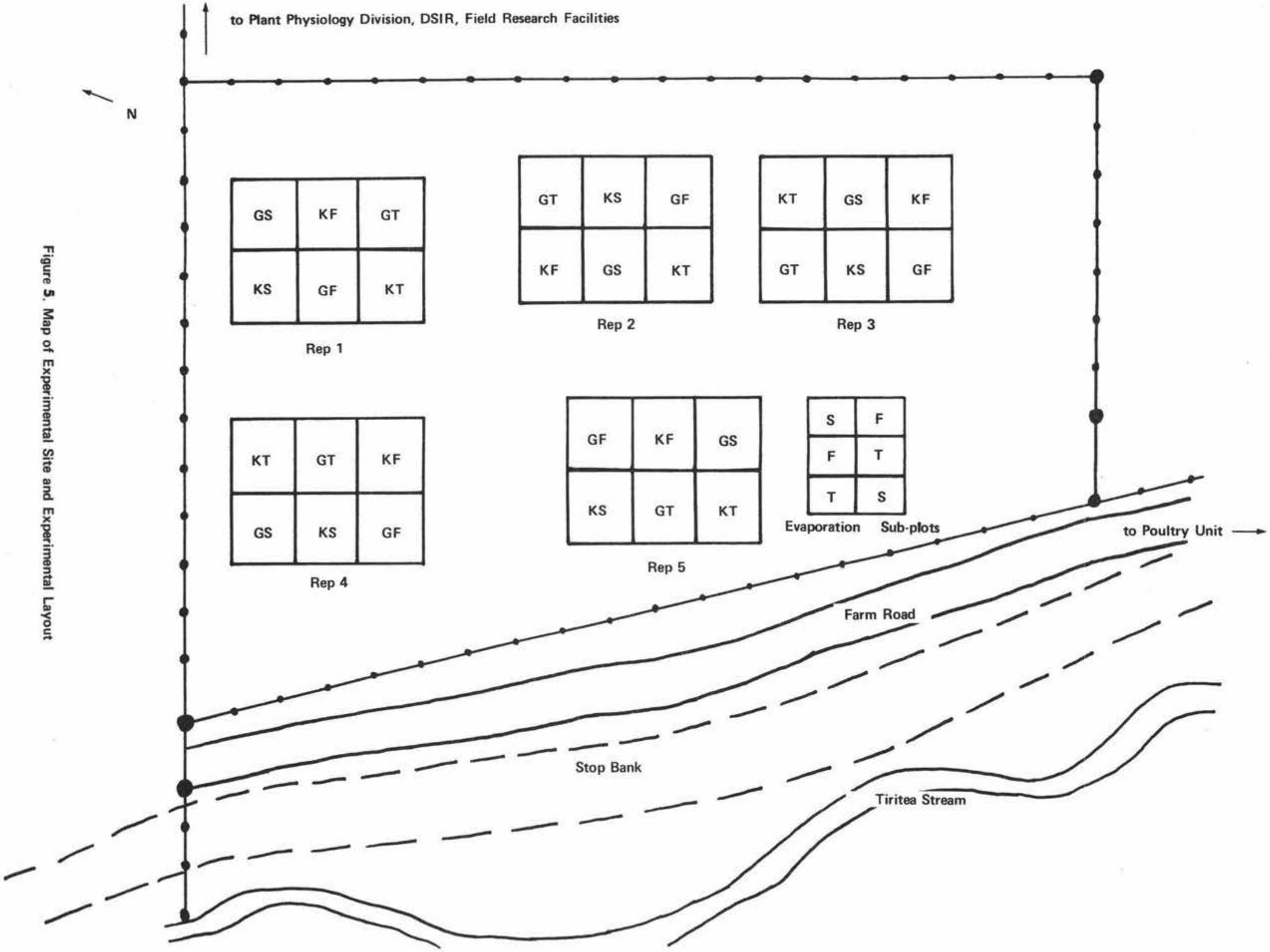

Figure 5. Map of Experimental Site and Experimental Layout

APPENDIX 2

SCHEDULE OF OPERATIONS

Date	
August	
28-30	Fenced off site.
September	
3-5	Paraquated and rotary hoed plots.
5-25	Prepared plots - buried sub-irrigation systems and plastic film surrounding each plot. Prepared water supply system. Constructed plastic covers.
26	Fertilised plots.
27	Rotary hoed plots and sowed seed.
October	
2-4	Emergence of crop.
8-10	Mended plots.
12	Placed tensiometers in plots.
17	Started irrigation treatments.
18	Covers constructed and began covering S and T plots at night.
26	Initial population counts.
27	First appearance of aphids; sprayed with Metasystox.
7-23	First Harvest.
17	Sprayed Lannate to control Argentine stem weevil.
December	
3	Flowering began.
11-23	Second Harvest.
20-23	Erected netting for bird protection.
January	
1-6	Water Status measurements.
14-22	Third Harvest.
February	
1-8	Final Grain sampling from field experiment. Field experiment then dismantled and site cleared.
12-15	Prepared boxes for glasshouse, assembled and filled with soil.

March	
3	Emergence of glasshouse "crops".
23-26	First Harvest in glasshouse.
April	
4-7	Second harvest in glasshouse.
19-28	Final harvest in glasshouse at emergence of ears.

Appendix 3 Rainfall during Field Experiment

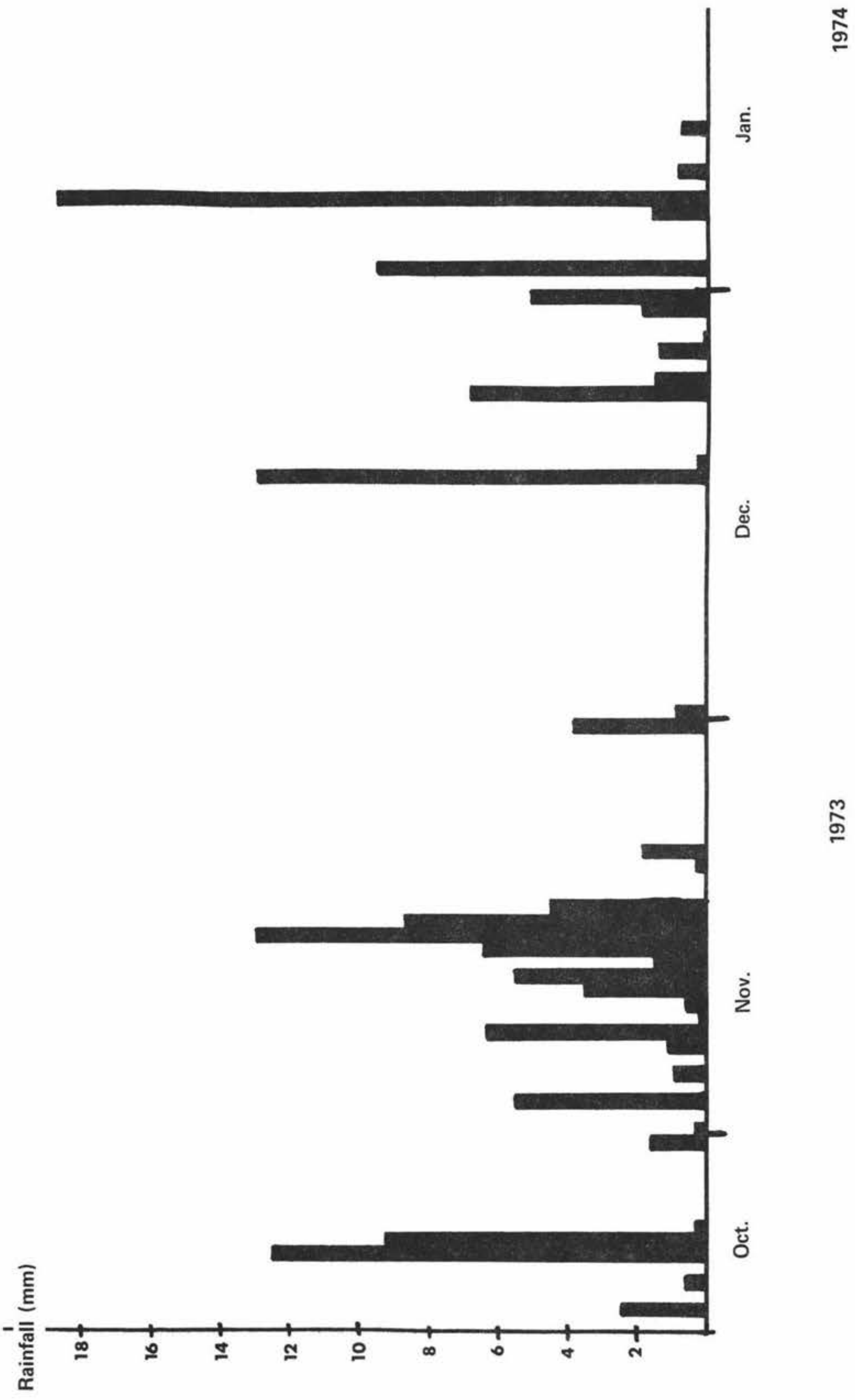

Figure 6. Rainfall Data. Measured at Grasslands Division, DSIR, (approx. 500 m from experimental site).

APPENDIX 4

THE SOIL CORER AND ITS USE

The soil corer was constructed and field tested during February and March 1973; see plates 1 to 5 on following pages. Plate 1 depicts the corer and its associated fittings. The main body of the corer was a section of pipe used previously for well drilling and hence was of sufficient strength. A $2\frac{1}{2}$ inch galvanised down-pipe, of 4 feet in length, was split into two to form the inner liners to the corer. A plunger (at left of the corer in Plate 1) was inserted from the top of the corer and held the liner in place. The plunger was held in place by a pin inserted from the outside of the corer through a hole drilled through the corer at the lugs (see Plates 1, 3 & 4). The two pipe spanners were used to unscrew the cutting head from the corer. The head was removed and the core and inner liners pushed out using the plunger. Plate 2 shows the cutting head and the liners.

Plate 3 shows the corer in position in a plot with the rammer which was used to drive the corer into the soil. The corer was removed from the soil by utilising the front-end-loader hydraulics of a sufficiently powerful tractor (a Ford 5000, plate 4), or if this was not available the corer was winched out (Plate 5).

The corer was hand-rammed into the soil until its progress began slowing down; if the corer was rammed any deeper the core began to compact. The reason for the sudden decrease in movement is unknown, for the soil at the depth where the core began slowing down (75-100cm) was sandy (sect. 2.3). Perhaps the frictional force between soil and the corer markedly increased when more than 80cm of corer was in the soil.

Problems were encountered with the inner liners which were not strong enough and had to be repaired often. For long term use this corer needs some form of shock absorber, or an ample supply of new liners. But in general this corer provided excellent soil cores with minimum compaction or disturbance of the soil.

Plate 1. The soil corer and associated fittings.

Plate 2. Close-up of cutting head and inner liners at base of corer.

Plate 3. The corer in the plot with hand-rammer.

Plate 4. Removal of corer using Ford 5000 front-end-loader hydraulics.

Plate 5. Removal of corer from soil using a winch.

APPENDIX 5

WASHING OUT OF CORES

Plate 6 on the following page shows the grid which was used for orderly collection of the cores and their subsequent washing out, using a medium pressure hose spray. 16 mesh was used in the washing grid which may be considered to be too coarse for root washing. This size of mesh was considered to strike an adequate balance between retaining as much root as possible in the washing process on one hand, and enabling the handling of a large number of cores on the other. The assumption is made that loss of fine roots was common with all treatments.

The soil blocks from the glasshouse study were washed through muslin cloth and through the mesh (on which the muslin was placed), thus loss of fine roots in the washing process in the glasshouse experiment was considerably less than the field experiment.

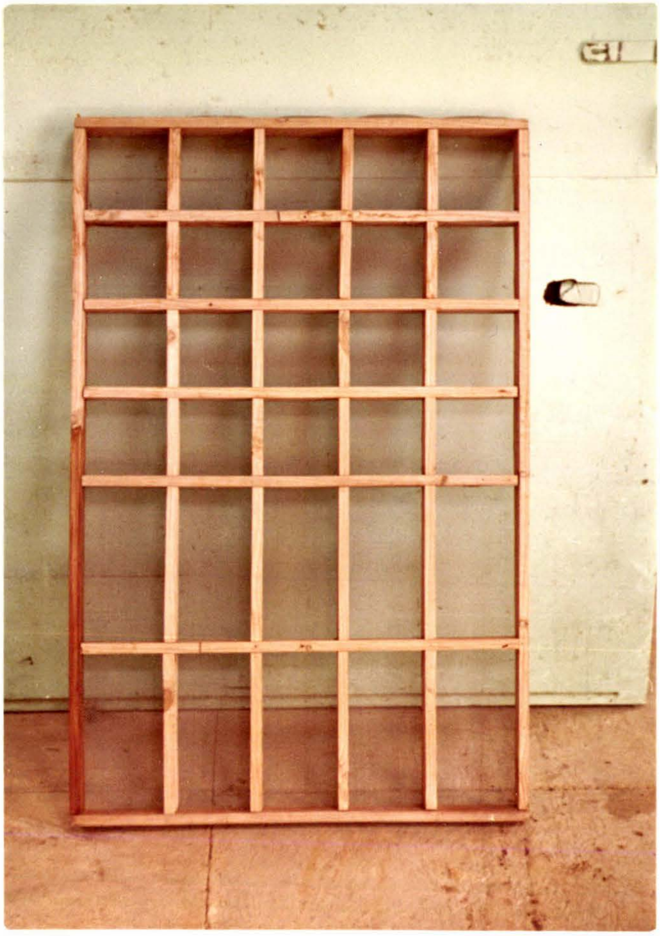

Plate 6. The mesh grid for collection
of cores and washing out.

Plate 7. The mesh root-washing grid mounted on table.

APPENDIX 6

PHOTOGRAPHS OF GLASSHOUSE EXPERIMENT

Plates 8 and 9 on following page show the boxes used in the glasshouse and the placement of the tensiometers in each box. Plate 8 was taken at emergence.

Plate 9 shows the S treatment box with soil removed prior to obtaining the soil blocks for root measurements. Once the soil blocks were taken, the end walls were placed against the exposed soil face and nailed temporarily into place until the next harvest.

Plate 8. The boxes used for the glasshouse experiment showing the positioning of tensiometers.

Plate 9. Soil removed from S treatment box at harvest 1.

APPENDIX 7

GLASSHOUSE ENVIRONMENT CONTROL

Daylength

Increasing daylength was supplied using 2 fluorescent light banks controlled with a time clock. 13 hours 20 minutes was the initial daylength (from 3rd March) and day length was increased by 20 minutes every week until by the end of the experiment (20th April) daylength was 15 hours.

Temperature

The glasshouse had some temperature control in that it could be kept down to ambient temperature by ventilation, and could be heated. Initial temperature regime was 14.5/10.5°C and this was achieved by setting the temperature minimum at night and raising it in the morning. The glasshouse was ventilated above 25°C throughout the experiment. The day/night temperature minimums were increased by 0.5°C every 10 days until at the end of the experiment the (minimum) temperature regime was 16.5/12.5°C.

Records of temperature taken by thermal hydrograph showed that minimum temperatures were maintained; and the glasshouse only rose above 30°C on two occasions during the experiment.

APPENDIX 8

STATISTICAL THEORY

The application of regression theory to data analysis first involves the construction of mathematical models to describe the data. Models applicable to description of the data in this experiment are called classification models; as distinct from functional models where the variables on which the resulting data depend (i.e. the independent variables or the treatment variables) are quantitative levels of a variable. For example a functional model would be used to describe the data from an experiment where crop growth was measured under differing quantitative levels of irrigation application whereas a classification model describes an experiment where crop growth was measured under differing methods of irrigation as in this experiment.

The classification models which are expected to describe the data for the two parts of the analysis of this experiment are:-

1. Analysis between treatments and varieties within harvests.

The classification model for this experiment of randomised block design is:-

$$y_{ij} = u + b_i + t_j + e_{ij} \;\ldots\ldots\; (1)$$

for the plot within each harvest in the ith block receiving the jth treatment where:-

y_{ij} is the yield (or value of a measured variable) for the plot in the ith block receiving the jth treatment.

u is the general mean effect.

b_i is the effect due to the ith block

t_j is the effect due to the jth treatment.

e_{ij} is the error which includes residual effects not incorporated in the block or treatment effects.

For this analysis $i = 1$ to 5 for the five blocks.

$j = 1,2,3 =$ GT, GF, GS

$j = 4,5,6 =$ KT, KF, KS

u, b_i and t_j are termed regression coefficients.

2. Analysis between harvests within treatments.

The classification model applicable here is:-

$$y_{ik} = u + b_i + h_k + e_{ij} \qquad ....(2)$$

for the plot within each treatment group in the ith block at the kth harvest, where:-

y_{ik} is some measurement on a given variable for the plot in the ith block at the kth harvest.

u is the general mean effect.

b_i is the effect due to the ith block.

h_k is the effect due to the kth harvest.

e_{ij} is the error which includes residual effects not incorporated in the block or harvest effects.

For this analysis i = 1 to 5 for the 5 blocks.
k = 1,2,3 for the 3 harvests.

The theory behind the analysis will now be outlined using part 1 (equation 1) as an example; the principles apply equally to part 2 (equation 2). Because we are interested in the effects of the treatments in this particular case we compare equation (1) to the 'null hypothesis' that "there are no treatment effects", i.e.

$$y_{ij} = u + b_i + e_{ij}$$

Analysis of variance is then undertaken to test whether the data differs significantly from that described by the null hypothesis; using the F statistic (which follows the F frequency function under the assumption that the null hypothesis is true) to obtain a test of significance (or measure of uncertainty) for the null hypothesis. The steps in forming an analysis of variance table are as follows:-

1. The regression coefficients in each model are estimated; in this case by the method of Least Squares estimation. Least Squares estimation of the regression coefficients involves the formation of Normal Equations. By writing down the model in the form of a Tableau the Normal Equations can be easily formed. A Normal Equation is formed for each regression coefficient and then these are solved as a set of simultaneous equations using matrix algebra to give the value for each regression coefficient. A discussion on the method of Least Squares estimation of the regression coefficients and the use of the Tableau to obtain regression coefficients is given by Pascoe (1973, app 4).

2. The Total Regression Sum of Squares (TRSS) is then calculated for each model by summing the products of each regression coefficient with the right hand side of the Normal Equation associated with it.

3. The Analysis of Variance table is then constructed.

Source	Sum of Squares	Mean Squares	F
TRSS eqn (1)	Calculated		
TRSS null hypothesis Ho	Calculated		
Difference or Treatments	TRSS (1) - TRSS (Ho)	Treatment M.S.	$\frac{\text{Trt MS}}{\text{Err MS}}$
Error	Total - TRSS (1)	Error M.S.	
Total	Total S.S.		

The analysis of the classification model such as the one above used for this experiment involves a complication, since the Normal Equations have an infinite number of solutions; in matrix algebra terms the Tableau is not full-rank. To overcome this the model is "reparametrized" so that the Normal Equations can be solved to give unique values for the regression coefficients.

Reparametrization of the classification model used here involves the formation of the new model:-

$$y_{ij} = u + \overline{b}_i + \overline{t}_j + e_{ij}$$

where $\overline{b}_i$ and $\overline{t}_j$ are linear functions of the original regression coefficients b_i and t_j respectively. The number of regression coefficients are reduced by one to form $\overline{b}_i$ (and $\overline{t}_j$), the Tableau is now full-rank and the Normal Equations for $\overline{b}_i$ and $\overline{t}_j$ can be easily solved and the values for $\overline{b}_i$ and $\overline{t}_j$ found.

Reparametrization can be made so that the $\overline{t}_j$ is a meaningful function of the original t_j. In this case:-

$\overline{t}_1$ estimates $(t_1 + t_2 + t_3 - t_4 - t_5 - t_6)$ i.e. the average effect of variety.

$\overline{t}_2$ estimates $(-t_1 + t_3 - t_4 + t_6)$ i.e. the linear irrigation effect or the difference between the T and S treatments.

$\overline{t}_3$ estimated $(-t_1 + 2t_2 - t_3 - t_4 + 2t_5 - t_6)$ i.e. the quadratic irrigation effect or the difference between the F treatment and the mean of the T and S treatments.

$\overline{t}_4$ estimates $((-t_1 + t_3) - (-t_4 + t_6))$ i.e. the linear interaction; between varieties and irrigation treatments T and S.

$\overline{t}_5$ estimates $((-t_1 + 2t_2 - t_3) - (-t_4 + 2t_5 - t_6))$ i.e. the quadratic interaction; between varieties and the F irrigation compared with T and S.

These linear functions of the t_j's are orthogonal (i.e. the sum of cross products between regression coefficients equals zero) and hence the variety S.S., irrigation S.S. and VI interaction S.S. sum to the Difference term in the AOV table (Treatment S.S.) and can be taken out for separate testing of significance of each.

APPENDIX 9

SOIL WATER STATUS DURING FIELD EXPERIMENT

Small samples of soil were taken at harvest 1 and 2 from each core section sampled, for gravimetric moisture content (MC) determination (see sect. 2.3 D(i)). The results are not presented in full but the following is a summary of some aspects of soil water status during the experiment.

The field capacity to -1bar water potential range was equivalent to a range in MC of approximately 25% to 18%.

At harvest 1 the MC at 15cm in S plots was 16.7% for Gamenya plots and 18.1% for Karamu. By the second harvest the values were 14.6% and 15.0% respectively. In results for each replicate the **S** treatments showed an increase in MC down to section 4 (45-75cm) suggesting the sub-irrigation systems were effective.

The T and F treatments showed similar soil water status although the irrigation of T treatments had to halt 2-3 days prior to harvesting to allow for soil coring.

The two 120cm tensiometers placed in KS and KF plots generally showed little change following irrigation, but from ear emergence they showed a gradual decrease in water potential suggesting that by this stage the plants were removing water from below 1m in the profile.

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