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

A thesis presented in partial
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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 GROWTH1.3.1 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 (Hackett 1972).

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 & Gumm 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 *et. al.* 1965, Taylor & Ratliff 1969, Lawlor 1973) have found that root growth is unaffected by decreasing soil water potential down to low values (e.g. -10 bar in wheat, Lawlor 1973); but root growth is much more sensitive to mechanical impedance (Barley *et. al.* 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 -15 bar 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 (Hatrack & 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 *et. al.* 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 *et. al.* 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 (Salin *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 Cappello-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 *et. al.* 1964, Slatyer 1969, Langer and Among 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 un-vernalsised (Wall & Cartwright 1974).

(iii) If unvernalsised 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 unvernalsed. 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 occurred 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 ^{absolute value} use 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".